THE AGRICULTURAL ECOLOGY OF HAY MEADOWS WITHIN THE SOMERSET LEVELS AND MOORS ENVIRONMENTALLY SENSITIVE AREA

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THE AGRICULTURAL ECOLOGY OF HAY MEADOWS WITHIN THE SOMERSET LEVELS AND MOORS ENVIRONMENTALLY SENSITIVE AREA

by

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ABSTRACT

The Agricultural Ecology of Hay Meadows within the Somerset Levels and Moors Environmentally Sensitive Area.

Francis William Kirkham

Ecological and productivity responses to agricultural management were studied over eight years in species-rich hay meadows within a Site of Special Scientific Interest on a Somerset peat moor. The vegetation typified that of many wet meadows on the Somerset Levels and elsewhere, definable as MG5 (*Cynosurus cristatus-Centaurea nigra* meadow) and MG8 (*Cynosurus cristatus-Caltha palustris* flood pasture) within the National Vegetation Classification.

The effects of inorganic fertilizers on species diversity, soil nitrogen loss and agricultural productivity (hay yield and beef production during aftermath grazing), were investigated during 1986-90. These data were subsequently analyzed for the effects of variations in water table depth on productivity and soil N losses. Further studies in 1991-93 covered: (a) soil seed bank composition in relation to above ground vegetation; (b) the effect of different cutting dates on seed rain, vegetation composition and herbage yield and quality; and (c) seed shedding as influenced by hay making operations.

The vegetation was sensitive to even small fertilizer inputs, particularly of P and K, both in terms of increased productivity and reduced botanical diversity. Species diversity also declined on unfertilized plots in one experiment, after a change from aftermath grazing to cutting only. Leaching and denitrification of soil N following N application were both high compared with soils elsewhere, due to the high water table. Fertilizers caused a four-fold shift in soil seed bank composition towards nitrophilous species and increased the ratio of short-term to long-term persistent species. Cutting in May or September affected both the total seed rain and the balance of species represented and significantly reduced vegetation diversity, compared with cutting in July or August.

The thesis includes an extensive literature review and the results are discussed in the context of (a) current theories on the relationships between species diversity, soil fertility, disturbance and productivity, and (b) hay meadow management within Environmentally Sensitive Areas. It is concluded that production response to fertilizers is not constrained by the species richness of the vegetation, but there is no scope for increasing soil fertility without reducing species diversity. Nitrate leaching risk is increased with N rates above about 75 kg ha^{-1} $year^{-1}$ at ambient water table levels, but no N should be applied where high water tables are maintained. Occasional cutting after July is necessary to allow most species to set seed and to maintain a persistent soil seed bank.

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ACKNOWLEDGEMENT

The work described in this thesis was undertaken in two phases. During the first phase (1986-1990) the author was employed by the Institute of Grassland and Environmental Research (IGER - formerly called the Institute for Grassland and Animal Production) who were contracted by the Ministry for Agriculture, Fisheries and Food (MAFF), the Department of the Environment (DoE), and English Nature (formerly the Nature Conservancy Council) to undertake the research in collaboration with the Institute of Terrestrial Ecology, Monk's Wood (ITE). The funding provided by these three bodies is gratefully acknowledged.

A large number of people assisted in the setting up and running of the project during this first phase and I am very grateful to the various members of the North Wyke farm staff for initial fencing and site maintenance work, to Trevor Hole for hay making, and particularly to Ian Hael for hay making, stock minding and assistance in numerous other ways. The following students each worked on the project during six-month placements from college or during the summer vacation and I am very grateful for their assistance: Richard Ellerton and Linda Gavin (1986); Steven Jones and Sarah Newman (1987); Christine Venus and Sarah Redstone (1988); Anna Smyth and Simon Thorpe (1989). I would also like to express my thanks to Linda Atkinson, Jean Smyth, Siobhan Brookman, Morag Webb and Sue Wilson for their technical assistance at various times during this period. Valuable guidance was provided by the project Management Group which was composed of representatives from the three funding bodies and the two research institutes. Membership changed frequently between 1986 and 1990, and only the author, Professor R.J. Wilkins (Head of the the Ecology and Land Use Division at IGER), and Dr B. Johnson (English Nature) remained members for the whole of this period. The Management Group was chaired in turn by H. Harland (MAFF), M.J. Finnigan (MAFF), D.A. Brown (DoE) and J. Hopkins (English Nature). Extra funding was provided in 1990-91 by MAFF and the National Rivers Authority (NRA), to analyse existing data from the project for the influence of variations in water table depth.

The studies carried out during 1991-93 were financed mainly by me witnout assistance from a funding body, and I am very grateful for office, computing and laboratory facilities provided without charge by IGER. I am also very grateful to Professor Roger Wilkins for guidance during both phases of the work, firstly as Department Head, and

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Finally, I wish to give very special thanks to my wife Angela, who has had to bear the brunt of my absence in the evenings and on very many week-end days over a number of years, and without whose support and understanding I would not have been able to complete this thesis. Also, a special mention for our three boys, Jonathan, Tim and Daniel. I greatly regret not having been able to spend as much time with them as I would have liked in recent years and I hope they will understand and forgive me.

AUTHOR'S DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

During 1986-1990, as Project Officer for the first phase of the Tadham Moor Project, I was personally responsible for conducting and reporting on the research work involved, including the studies reported in Chapters 3-5 of this thesis. I ceased to be employed by IGER In August 1990 and registered to study for MPhil/PhD with the University in the following October. The work on the effects of cutting date on productivity and botanical composition, carried out in 1991-93 and described in Chapter 7 and part of Chapter 8 of this thesis, represented an expansion of work already proposed (originally by me) as part of the second phase of the Tadham Moor Project. Some of this work I carried out in collaboration with J.R.B. Tallowin of IGER and with assistance from his staff (see Acknowledgements above). I am also grateful to J.R.B. Tallowin for the use of 1990 hay yield data from the Tadham Moor site, which were collected by his staff and which I included in studies on the effects of variation in water table depth on productivity reported in Chapter 3. Some botanical data collected by ITE staff in 1986 and 1990 from one of the two experiments (Experiment 1) are included in Chapter 5 for comparison with data collected by me from Experiment 2. I am grateful to Caroline Sargent and Owen Mountford of ITE for the use of these data. With the exception of the 1990 hay yield data and the ITE botanical data, all the data reported in this thesis were collected by me or under my supervision.

I undertook a programme of study in 1990-91. This included second year BSc courses in Vegetation Patterns and Plant Processes, Soil Processes and Management, and Geographical Analysis and Computer Processing, and a post-graduate course in Hydrologic Modelling.

During the time in which the research studies reported in this thesis were carried out, I regularly attended relevant scientific seminars and conferences at which I often presented work, and I prepared several papers for publication (see below).

Publications

Refereed journal papers:

KIRKHAM, F.W. and TALLOWIN, J.R.B. (in press) The influence of cutting date and previous fertilizer treatment on the productivity and botanical composition of species-rich hay meadows on the Somerset Levels. *Grass and Forage Science.*

KIRKHAM, F.W. MOUNTFORD, J.O. and WILKINS, R.J. (in press) The effects of nitrogen, potassium and phosphorus addition on the vegetation of a Somerset peat moor under cutting management. *Journal of Applied Ecology.*

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Technical Reports:

TALLOWIN J.R.B., KIRKHAM F.W., WILKINS R.J., SMITH R.E.N., THOMAS G.H., MOUNTFORD J.O. and LAKHANI K.H. (1994) *The effects of inorganic fertilizers in flower-rich hay meadows on the Somerset Levels. Executive Summary and summary of results and conclusions of the MAFF/DoE/English Nature TADHAM MOOR PROJECT 1986-1993.* Okehampton: Institute of Grassland and Environmental Research.

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Review articles and reports:

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Contract reports:

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KIRKHAM F.W. (1988) *The effects of nitrogen on species diversity and agricultural production on the Somerset Moors.* Second annual report to the Management Group of the MAFF/DoE/NCC Tadham Moor Project, February 1988, pp. 60.

KIRKHAM F.W. (1987) *The effects of nitrogen on species diversity and agricultural production on the Somerset Moors.* First annual report to the Management Group of the MAFF/DoE/NCC Tadham Moor Project, February 1987, pp. 36.

Presentations and Conferences/Symposia attended:

(*PR* = gave theatre presentation of paper; *PO* = poster presentation of paper; *JA* = joint author of paper presented by co-author)

British Grassland Society Research Meeting, Welsh Agricultural College, September 1988. (*PO*)

British Grassland Society Winter Meeting, December 1988. (*PO*)

Tadham Moor Project Demonstration Days, 6 and 7 June 1989 (gave oral presentations and organized the events)

Practical Conservation and Profitable Farming. Event sponsored by Wilmot Conservation, July 1990. (*PO*)

Floristic Diversity in European Grasslands. EC-sponsored International Workshop, IGER, September 1993

Grassland Management and Nature Conservation. British Grassland Society Occasional Symposium No. 28, held in conjunction with the British Ecological Society, Leeds University, September 1993. (*JA*)

European Lowland Wet Grasslands: their Ecology, Management and Restoration. Proceedings of a conference held at ICOLE, Loughborough University, December, 1994. (*PR*)

Occasional attendance at winter and/or summer meetings of the South West of England Soils Discussion Group

External contracts:

MAFF/DoE/English Nature funded Tadham Moor Project: The effects of nitrogen on species diversity and agricultural production on the Somerset Moors. 1986-1990 Project Officer as employee of IGER.

MAFF/NRA contract: The effect of variations in water table depth on productivity and losses of soil nitrogen in hay meadows on the Somerset moors. Sub-contracted by IGER through Polytechnic Enterprises Plymouth Ltd.

Signature: ....

Date: 9 March 1996

CHAPTER 1

INTRODUCTION TO THE THESIS

1.1. INTRODUCTION

The low-lying peat moors of the Somerset Levels represent one of the few remaining extensive wetland habitats in Britain (Nature Conservancy Council, 1977). They consist mainly of pastures and meadows with high water-tables, lying within a close network of ditches and watercourses. The hay meadows, in particular, are of great ecological interest, both for the diversity of flowering plants they support and because they provide valuable breeding and overwintering sites for wading birds (Smith, 1983; Storer, 1985; Johnson, 1988).

The work described in this thesis examines the interactions between various agricultural practices and the plant ecology, soil chemistry and productivity of these hay meadows. This introductory chapter describes the aims and contents of the thesis and explains the background to the work. The character of the Somerset peat moors is described within a geological and historical framework, including a brief account of the history of the draining of the moors and of how this has influenced the present agricultural and wildlife value of the hay meadows in particular.

Statutory schemes aimed at preserving and enhancing the wildlife value of the moors by controlling agricultural management are then described and the manner in which the introduction of these schemes led to the work described in the thesis is explained. The last two sections describe the location, design and broad experimental approach of the work and explain how the studies are organized into chapters in the thesis.

1.2. TRADITIONAL MANAGEMENT OF HAY MEADOWS - IMPORTANCE FOR WILDLIFE

The water levels on the Somerset moors are controlled to a large extent by pumps and sluices at the mouths of the rivers and main drains, and ditch levels are kept high throughout the summer to provide effective field boundaries and drinking water for stock. Maintaining a high water table, cutting late for hay (July onwards) and excluding grazing cattle until mid-summer, or allowing spring grazing only at very low stocking densities, are all important factors in allowing wading birds such as Snipe (*Gallinago gallinago*) and

Redshank (*Tringa totanus*) to breed successfully (Green, 1986). These practices are characteristic of traditional farming in the area and, coupled with the customary use of little or no inorganic fertilizer, are thought to be responsible for the great diversity of flowering plants in the meadows and ditches (Nature Conservancy Council, 1977).

Aftermath growth in hay meadows is normally grazed at low stocking rates until October or November, either intermittently with dairy cows or continuously with beef cattle and young stock. Grazing with sheep is much less common. Low intensity grazing at this time of year leaves a patchy vegetation structure in the autumn which is beneficial to overwintering birds (Green, 1986). Grazing also influences the cycling of plant nutrients (Gillingham, 1987; Jarvis *et al.,* 1989a) and helps to maintain species diversity by creating niches for seedling establishment and vegetative regeneration (Grubb, 1977; Grime *et al.*, 1988; Watt and Gibson, 1988).

1.3. AIMS OF THE PROJECT

The primary aims of this thesis are twofold:-

(a) to investigate the effects of certain key agricultural practices on the plant ecology and soil chemistry of species-rich hay meadows of the Somerset peat moors and to define the scientific principles involved

(b) to define the implications for farmers of restricting these practices in terms of production foregone.

Three management practices were examined in detail:-

(I) inorganic fertilizer use
(II) variations in water table depth
(III) variations in cutting date

The experimental designs and techniques used within each of these three subject areas are summarized later in Section 1.8 and are described in detail in the relevant chapters of the thesis.

In order to fully appreciate the significance of the work reported in this thesis it is necessary to understand the specific geological, ecological and human influences operating within the Somerset Levels, both past and present. This section and Sections 1.5 and 1.6 describe how these influences have combined to affect the ecological and agricultural development of the area, leading to the need for the statutory controls as described in Section 1.7.

1.4. THE SOMERSET LEVELS AND MOORS

The Somerset Levels and Moors, usually known collectively as the Somerset Levels, cover about 56,650 hectares of flood plains of the Rivers Axe, Brue, Huntspill, Tone and Parrett and their tributaries (Figure 1.1). The area is bounded by the Mendip Hills to the North and the Quantock and Blackdown Hills to the south and is divided by the Polden Hills running roughly east-west across the centre. An 8-10 km wide belt of clay land (the Levels) borders the Bristol Channel to the east, with several lower-lying areas containing thick peat deposits further inland, known collectively as the Moors (Barnett, 1981). In some places, peat is overlain with clay, but on most moors peat lies at the surface to a depth of 1-6 m, (Figure 1.2) with deposits over 8 m deep in some parts of Queen's Sedge Moor and West Sedge Moor (Cope, 1988). Small 'islands' of sandy loam soil overlying shelly marine sands or gravels, known as Burtle Beds, exist in some areas (Figure 1.2).

1.3 THE LANDSCAPE AND SOILS OF THE SOMERSET LEVELS

The formation of the characteristic soils and vegetation of the peat moors has been greatly influenced by the topography and lithology of the surrounding limestone escarpments through the effect these features have on the volume and chemistry of the water passing through the river basins. Agricultural development in these low-lying areas has been intimately related to the progress of improvements in drainage, the pace of which has, in turn, been dictated as much by human factors as by the physique of the landscape (see Section 1.6).

THE FORMATION OF THE LEVELS

The original glacial valley floors between the Mendips and the Quantocks lie buried to a depth of 35 m or more below present Ordnance Datum (OD). These valley floors roughly coincide with the sea level of about 9000 years ago (9000 B.P.). The sea began to rise at

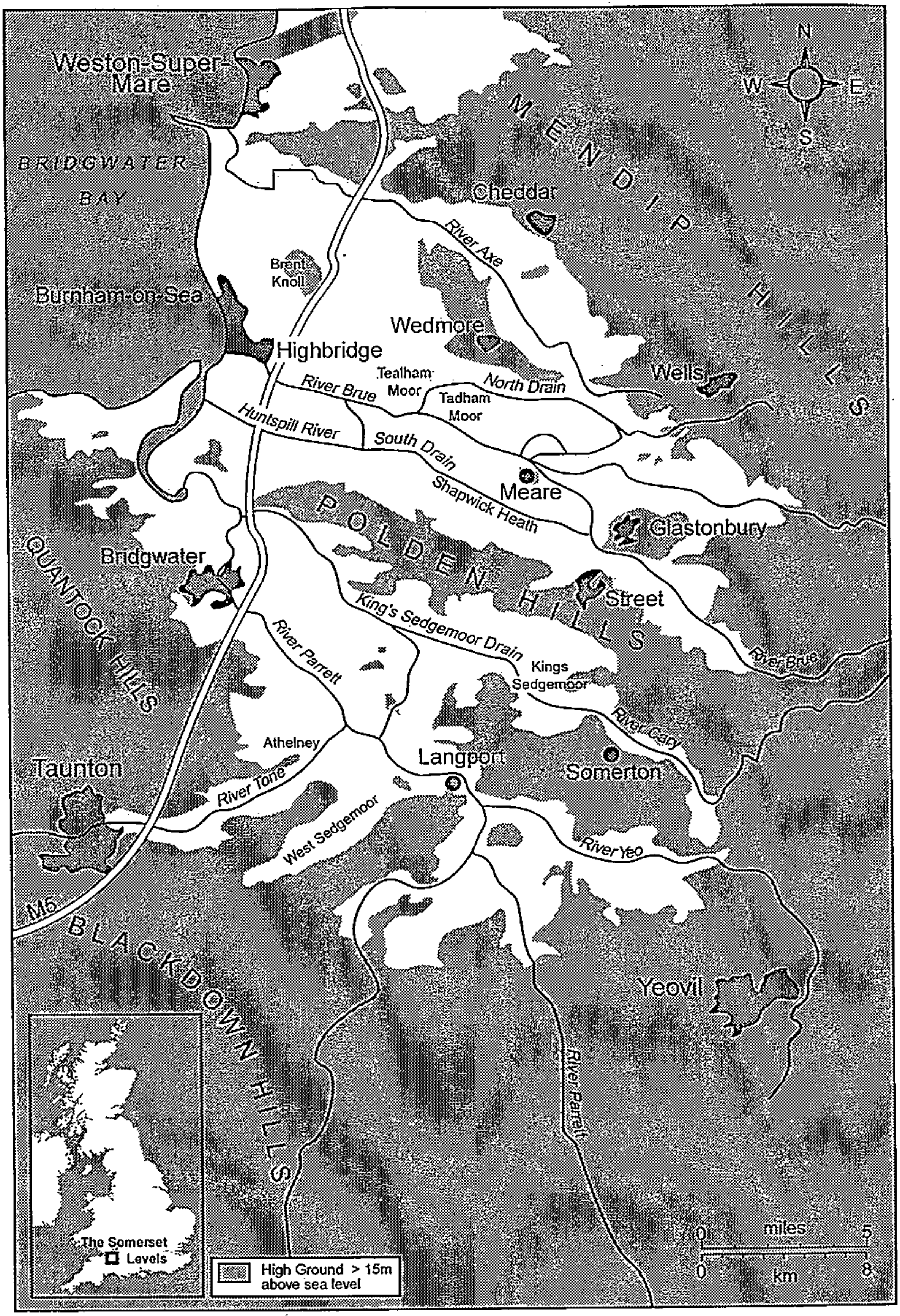


Figure 1.1. The Somerset Levels

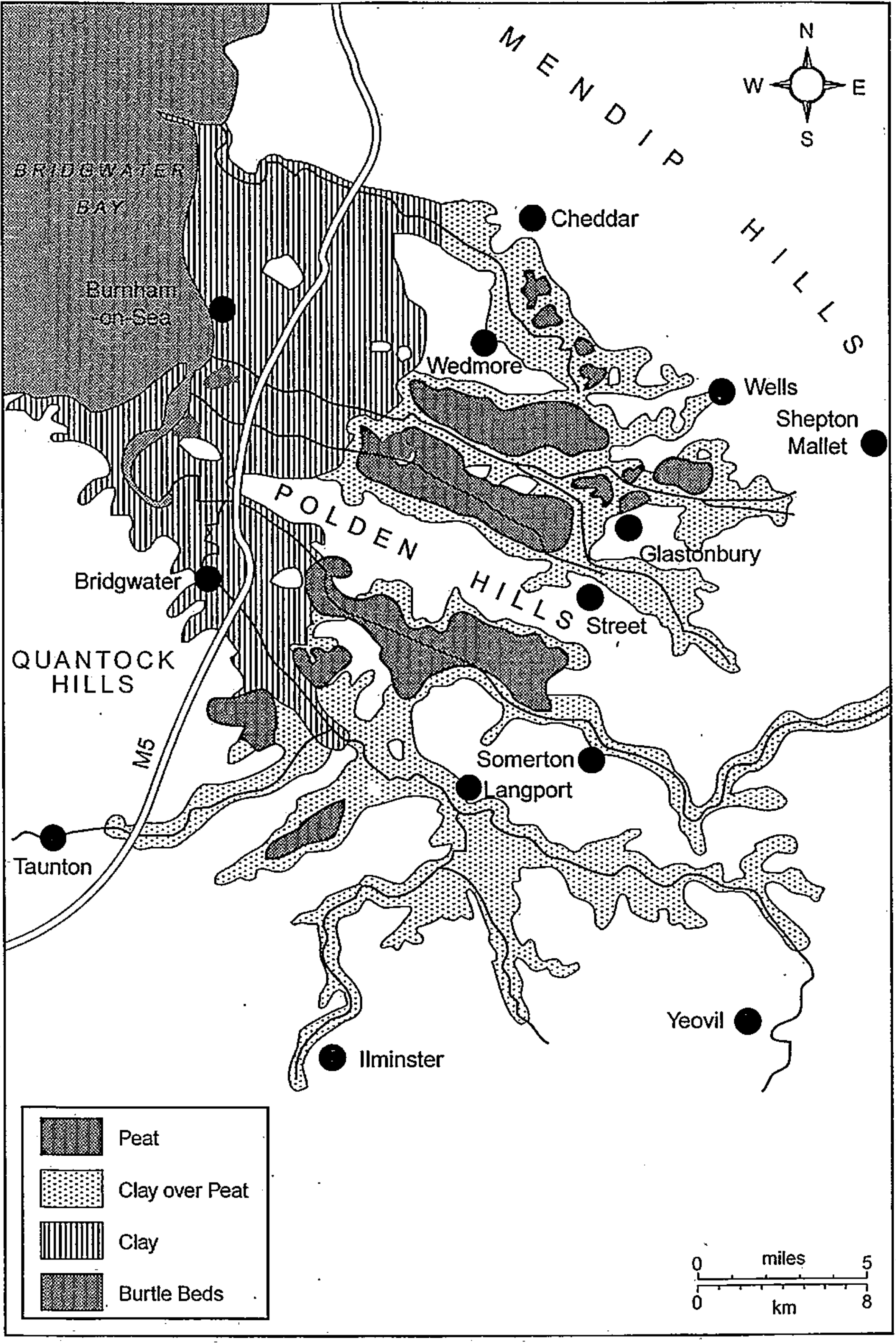


Figure 1.2. A simplified soils map of the Somerset Levels [reproduced from Barnett (1981)].

This would have led to leaching of minerals and an increase in acidity, causing the bog to grow at its centre by the increased deposition of plant remains. The acidity and oligotrophic nature of such soils persisted even after the bogs cease to grow, since their raised topography allowed them to escape the effects of dissolved salts in the ground water (Etherington, 1983).

The coastal clay belt is, on average, about 3m higher than the valleys converging onto it (Barnett, 1981). This belt probably formed during a rise in sea level in Romano-British times which caused the deposits of brown clay which now overlie the blue clay. A natural sea wall was built up gradually when fresh water carrying suspended mud particles met sea water, causing the particles to flocculate and settle out (Storer, 1985). As this process continued, the area of deposition extended inland. Deposition continued until a fairly stable sea wall had formed, at which stage local inhabitants reinforced it artificially. These reinforcements were not always successful until comparatively recent times. In 1607, and again in 1811, hundreds of square km of the Somerset Levels were under water, with the floods reaching Glastonbury (Storer, 1985).

THE INFLUENCE OF LOCAL TOPOGRAPHY ON PEAT CHEMISTRY

Annual rainfall on the Somerset Levels is low at about 750 mm, but is much higher on the surrounding upland areas at up to 1300 mm (Barnett, 1981). Since the area of upland which drains through the Levels is approximately four times that of the Levels themselves, the soils and lithology of these upland areas have a profound effect on the chemistry of the peat in the lowland basins (Ross, 1988). Water running off the Lias limestone of the Polden Hills and the carboniferous limestone of the Mendips is rich in dissolved salts, particularly calcium (Ca) and magnesium (Mg). The valley floor of the river Brue is also Lias limestone, whilst the valley floors of the Axe and the Parrett are lined by Triassic Keuper Marl with a high gypsum content, itself a source of Ca and sulphur. As a result, the Ca content of the peat in some of the moors is 100-200 times that of comparable peats elsewhere, whilst Mg contents are up to 10 times higher (Ross, 1988).

Estuarine peats are usually high in sodium (Na) and those of the Somerset Levels are typical in this respect, although some values fall near the top of the expected range (Ross, 1988). Since the upland areas are farmed more intensively than the moors, water originating from them probably contains higher amounts of nitrate than that originating from the moors themselves. Furthermore, some transference of dissolved nitrate may occur between drained and undrained peats, since drainage, through increased aeration, can increase the amount of nitrate N released from the soil (Ross, 1988).

1.6. AGRICULTURAL DEVELOPMENT

CONFLICT AND CONFRONTATION - THE HISTORY OF THE DRAINING OF THE SOMERSET LEVELS

The history of drainage and agricultural development on the Somerset Levels is a story peppered with examples of confrontation and conflict of interest, mainly between the drainers and the local inhabitants (Williams, 1970; Sutherland and Nicolson, 1986; Purseglove, 1988). It has been largely due to these conflicts, rather than to the engineering difficulties encountered, that the Levels were never developed to the extent seen in the East Anglian Fens (Purseglove, 1988).

The early inhabitants

Until the 13th century, the whole of the Somerset Levels were covered in marsh and swamp. The first recorded settlements were Iron Age villages on the edge of a large lake which stretched from Glastonbury to Meare, a distance of about three km (Storer, 1985). The Meare lake village was abandoned sometime in the second century BC when annual rainfall increased and the lake level rose. Sea levels rose again in about 250 AD and the whole area was flooded with sea water, coinciding approximately with the cessation of peat formation and the beginning of the formation of the coastal clay belt.

The Romans showed little interest in the Levels, so the Celtic Christian monks sought the solitude of the 'islands' of higher ground. The first monastery was established at Glastonbury in about 500 AD. This was perhaps the most significant development in the history of the area since, as in many parts of the country (Purseglove, 1988), it was the monks who first started drainage work. The first known drainage expert lived on the Somerset Levels and appeared in the Domesday Book. He was called Girard Fossarius, 'Gerard of the Drain' (Purseglove, 1988).

The establishment of an arterial drainage system

The first activities were minor attempts at reclamation by digging ditches and drainage channels, still known today as rhynes (pronounced 'reens'). Many land ownership disputes arose between the various ecclesiastical estates, particularly between the Abbott of Glastonbury and the Bishop of Bath and Wells, although a fairly stable agreement was reached between these estates in 1327 (Williams, 1970). Sometime between 1234 and 1252 the monks of Glastonbury straightened the River Brue between Street and Meare pool and then westwards to Highbridge, where they put in the first sluice. They also created a six mile cut, running to the west of Wedmore to join the rivers Brue and Axe. This system forms the basis of that operating in the area today. Apart from providing arterial drainage, these cuts were used for navigation, servicing Glastonbury via the Axe and Brue. South of the Poldens, the Parrett was navigable as far as Langport and by Richard I's time the banks had been built up to reduce flooding and aid navigation.

Minor improvements continued until the dissolution of the monasteries, when all work stopped and much that had been done already fell into disrepair. The disastrous flood of 1607 revived the incentive to drain, although this was not a sentiment shared by the commoners. Their resistance prevented any real progress despite the enthusiasm first of James I, who now owned King's Sedgemoor, and then of Charles I. In 1625, Charles I sold his share to Sir Cornelius Vermuyden, the famous fenland drainer, but even he was unable to overcome the resistance of the commoners, as had been done in the fens of East Anglia (Purseglove, 1988).

In the Somerset Levels, as in most large wetland areas subjected to reclamation, drainage was seldom in the interest of the majority of the commoners who used the land (Purseglove, 1988). The usual purpose of drainage was to upgrade the land from marsh grazing to hay meadow or, more rarely, to use it for arable cropping. This invariably involved the loss or diminution of communal grazing rights. Furthermore, from early medieval times, taxes were levied to pay for the costs of drainage, with land graded into marsh, mow, pasture and meadow and charged accordingly (Storer, 1985). This inevitably caused resentment among those who had previously enjoyed unfettered communal grazing on the land. There were also clashes of interest between those who saw the waterways as a transport system and those who wanted to install weirs to enhance the fishing or to operate mills.

Later, after a reasonably effective arterial drainage system had been established in the Brue valley, conflicts arose between the farmers of the coastal clay belt and those in the lower moors inland. The level which suited the clay belt farmers, filling their ditches and providing drinking water for stock, was too high for the moorland farmers whose land was frequently flooded as a result. The Somerset Drainage Commission, who were responsible for the maintenance of the river systems until 1929, were predominately composed of representatives from the clay belt, and the interests of those inland were seldom taken into account. This conflict went largely unresolved until major improvements were made to the system in the 1940s.

Modern developments

The first major era of drainage activity since medieval times began in 1770 with the introduction of the Enclosure Acts. By 1830, all the peat moors had been drained to some extent. This was reflected in a large increase in the number of settlements on the moors between 1782 and 1822 (Williams, 1970), by which time the North and South Drains had been completed in the Brue valley and King's Sedgemoor Drain south of the Poldens. There were some attempts at arable farming. Some good crops of wheat were grown initially, mainly on King's Sedgemoor, but the soils soon became exhausted and repeated ploughing and burning reduced the land levels. The existing drainage was unable to cope with the increased risk of flooding which was exacerbated by the recently developed practice of pipe drainage in the adjacent higher grounds. These difficulties, combined with national trends from arable to pastoral farming, encouraged a reversion to grassland farming throughout the Levels by 1873 (Darby, 1873). However, the growing of willows or 'withies' for basket and furniture making, which was introduced on West Sedgemoor in 1825, still flourishes today (Barnett, 1981).

The maintenance of existing drains improved after the Somerset Drainage Act in 1877, which identified 19 separate Internal Drainage Districts, each with its own Drainage Board. However, no structural improvements were made to the arterial systems until after the Land Drainage Act 1930. The disastrous floods which covered most of the area between November 1929 and February 1930 no doubt increased the incentive to pass the bill. The act led to the establishment of the Somerset Catchment Board, but it was only after an engineer was appointed in 1939 that progress was finally made. King's Sedgemoor Drain was greatly improved and the Huntspill River was excavated in 1940. The South Drain was joined to the Huntspill by a pump, but drainage was not improved in the north Brue valley until 1959, when a pump was installed at the junction of the North Drain and the Brue. By this time all the old steam pumps had been replaced by diesel, which further increased the efficiency of the system as a whole.

The current status of drainage

Only minor improvements to the existing system were made in recent decades. Large-scale and co-ordinated drainage works would still be necessary if the Somerset Levels were to be converted to a predominately cereal and root crop growing area like the East Anglian Fens (Williams, 1970). That this was never accomplished has been mainly due to the resistance of local inhabitants. However, two major environmental factors have also been significant. First, the tidal range in the Bristol Channel, which at 12 m is the second highest in the world, creates the need to store large amounts of water in the rivers to be let out as the tide falls. Secondly, the total area of land which drains through the Somerset Levels is four times that of the Levels themselves, compared with a ratio of only two to one in the East Anglian Fens (Purseglove, 1988). This difference is made more significant by the fact that average annual rainfall is greater in Somerset than in East Anglia.

Nevertheless, when a party of Internal Drainage Board chairmen from the Levels visited the Lincolnshire Fens in 1976, they were impressed by the potential it represented for their own area. In an article in the *Somerset Farmer*, land owner and IDB chairman Ralph Baker wrote

> *'We came back feeling hopeful...that Somerset will be drained and also aware of our responsibilities for this as members of the Internal Drainage Boards in Somerset...the fuller utilization of the Somerset Lowlands could become a project of prime importance, with massive capital injection from national resources.'* (quoted from Purseglove, 1988)

The following year, farmers were offered a proposal by the Wessex Water Authority to spend up to £1 million on a drainage improvement scheme on West Sedgemoor. After much deliberation they turned it down, fearing an increase in rates due to the anticipated dependence upon piped water for cattle troughs. They also realised that the disappearance of water from the ditches would result in heavy fencing costs. At least, these are the reasons given by Purseglove (1988). Sutherland and Nicolson (1986) maintain that the scheme presented conflicts of interest between farmers in different parts of the moor which they were unable to resolve and also that doubts were raised as to the long-term effects of the scheme on soil stability.

Whatever the case, it is clear that the renewed appreciation amongst the farmers of what they already owned disappeared very rapidly upon the Nature Conservancy Council's notification of the whole of West Sedgemoor as a Site of Special Scientific Interest in 1982. The prospect of any further drainage improvement on the moor had now gone, to be replaced by a wide range of management restrictions aimed at preserving the wildlife value of the moor. A large group of protesting farmers congregated outside the Black Smock pub to burn effigies of the local conservationists. History, in repeating itself, had taken a strange twist: two centuries before, the ancestors of these farmers had stoned the local drainage agent, Richard Locke, and his effigy had been burned by 'these owners of geese', as Locke described them (Williams, 1970). There is a certain irony in the fact that the greatest consensus of opinion ever achieved amongst the farming community should have been expressed in their opposition to the conservationists who, amongst other things, were seeking to prevent drainage improvements (Purseglove, 1988).

However, it would be wrong to interpret the farming community's attitude towards drainage as inconsistent on the basis of the foregoing historical perspective. Resistance to drainage in the past was mainly stimulated by the loss of communal rights which accompanied it, rather than by a lack of appreciation of the improving effects on agriculture of drainage *per se.* While the area was wet and boggy and only accessible during the dry summer months, rough grazing with cattle or geese was the only practicable use for the land. Subsequent control of the water levels gave much more flexibility, allowing hay making and extending the grazing season. Further improvements allowed access to the land earlier in the spring and increased its value for grazing, introducing the possibility of more intensive farming.

THE RESULTS OF IMPROVED DRAINAGE ON THE SOMERSET LEVELS

The effects on modern agriculture

The main effect of the drainage improvements carried out since 1930 has been to improve pastoral farming. Extension of the grazing season has brought about a decline in mowing and an increase in the use of fertilizers (Barnett, 1981). In recent years, the national trend away from hay making and towards conserving grass as silage has been reflected on the Somerset Levels, although probably to a lesser extent than elsewhere. Silage making usually involves applying inorganic fertilizers to stimulate spring growth which is then harvested in May, compared with traditional hay making in late June or July. However, a high water table offers farmers at least one advantage in that it gives more grass growth in mid-summer. This was very noticeable during the dry summers of 1984, 1990 and 1995.

Mixed cropping is still difficult since the ideal water table depth differs between crops, from about 45 cm for grassland to greater than 105 cm for cereals (Barnett, 1981). In practice, this means that to grow cereals, the water table in individual fields or blocks of land must be lowered by deepening the surrounding ditches, isolating them from the main system and pumping water out into adjacent rhynes. This process invariably involves the installation of tile drains (under-drains).

The effects on wildlife

Lowering the water table has a direct effect upon the ability of wading birds such as snipe and redshank to feed. These species probe the damp soil for invertebrates which are concentrated in the surface layers by a high water table (Barnett, 1981; Green and Robins, 1993). Nesting is also badly affected by spring grazing and by cutting before July (Green, 1988; 1990), these operations being more common on drier land. Wader populations have declined sharply on the moors in recent years and this seems to have been correlated with a progressive reduction over time in the water level at which the IDBs have started pumping (Green and Robins, 1993). The Somerset Levels are an important staging area for migrating waders such as whimbrel (*Numenius phaeopus*) (Ferns *et al.*, 1979) and for overwintering swans, ducks and waders which are attracted by the winter floods (Salmon *et al.*, 1989).

The vegetation of the unfertilized and undrained meadows (i.e. those without piped under-drainage) contains a wide diversity of plants, many of which are typical wetland species (Nature Conservancy Council, 1977; Mountford *et al.*, 1993a). Moreover, the distribution of these species within a particular meadow indicates their sensitivity to small variations in soil moisture regime (Mountford and Chapman, 1993). Improved drainage is usually accompanied by other operations which also reduce species diversity; including the use of inorganic fertilizers (many examples are cited in Chapter 2). However, work in the Netherlands has shown that drainage on its own reduces botanical richness on peat soils (Strien and Melman, 1987).

The rhynes and ditches of the Somerset Levels (Plate 1.1) are estimated to cover a total area of 600 ha (Barnett, 1981) and are nationally important for the rare and endangered species of flora and fauna they support (Wolseley *et al.*, 1984). Much of this habitat is destroyed by too frequent maintenance, particularly when watercourses are widened and deepened (Barnett, 1981; Somerset County Council, 1992). In parts of West Sedgemoor, deepening of the ditches to allow under-drainage can cause contamination of the water by sulphur leached out of adjacent land (Barnett, 1981). This water is not only unpalatable to stock but also does not support aquatic flora and fauna. Drainage can also cause increased oxidation and wastage of peat, and the same processes can lead to an increase in the nitrate content of water in the rhynes and ditches (Purseglove, 1988; Ross, 1988).

1.7. AGRICULTURE AND WILDLIFE CONSERVATION

THE SSSI AND ESA SCHEMES

Sites of Special Scientific Interest - SSSIs

The Wildlife and Countryside Act 1981 gave the Nature Conservancy Council (now called English Nature) statutory powers to notify areas as SSSIs and to control their management. The SSSI regulations contain a list of 'Potentially Damaging Operations' (PDOs) which cannot be carried out without agreement with English Nature. English Nature's policy has been to establish the farmer's current farming practice and to give consent for it to continue, unless it contains operations likely to lead to deterioration in quality of the site (M.J. Edgington, personal communication). Farmers who wish to 'improve' the land are

Plate 1.1. A typical example of the large number of ditches which intersect the moors, adding to the great diversity of flora and fauna in the area.

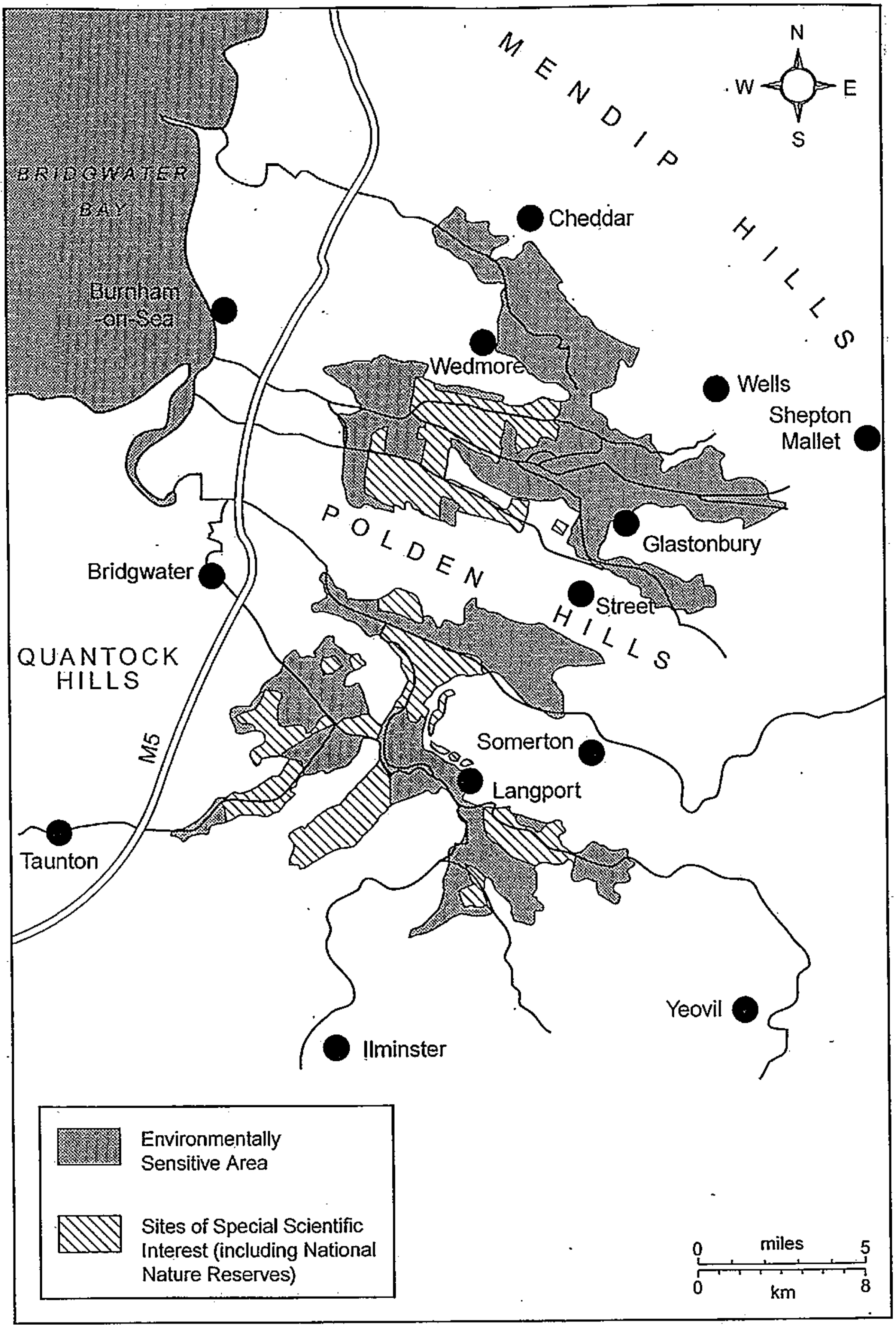


Figure 1.3. The Somerset Moors and Levels. Simplified map of the Environmentally Sensitive Area (shaded) and Sites of Special Scientific Interest (hatched), the latter including National Nature Reserves.

persuaded to enter into a management agreement whereby, in exchange for financial compensation on the basis of profit foregone, they agree not to carry out the proscribed operations. Before English Nature will accept a proposal as the basis for a compensation agreement, they must be satisfied that it would be both financially and technically feasible on that particular farm .

The list of PDOs is long, but those most relevant to species-rich hay meadows are: ploughing and reseeding; installing under-drainage; using herbicides (spot-treatment of certain weeds is sometimes allowed); applying inorganic fertilizers; cutting before July; and rolling or harrowing in spring. In addition, there are regulations about the regularity and severity of ditch maintenance.

The total area of SSSIs on the Somerset Levels in November 1993 was 7,272 ha (Figure 1.3). Some of these sites have been purchased by English Nature in recent years and are known as the Somerset Levels and Moors National Nature Reserve. Together with the previously established 335 ha Shapwick Heath National Nature Reserve they occupy a total of about 640 hectares.

The Somerset Levels and Moors Environmentally Sensitive Area - ESA

In 1987, a total area of 27,657 ha on the Somerset Levels was designated an ESA under the Agriculture Act 1986 (Figure 1.3). This established a voluntary scheme in which farmers were initially offered a choice of two 'Tiers' of management, each with a specific set of rules and a fixed payment. The scheme was extended in 1992 to include a third Tier, which contained a more stringent set of rules and attracted the highest payment (£350, compared with £120 per ha for Tier 1 and £180 for Tier 2).

All the rules applying within Tier 1 apply also to Tiers 2 and 3, but with some additions and refinements in each of the latter. The regulations are laid out in detail in Schedules 1-5 of the 1992 Designation Order (Her Majesty's Stationary Office, 1992). The following is a brief summary, with the main emphasis on rules relating to water table management, fertilizer use and hay cutting date.

Tier 1 rules specify that the water level in ditches must be maintained at no lower than that provided in the main system by the relevant Internal Drainage Board (IDB), and that there must be at least 15 cm of water in the bottom of the ditches throughout the summer. A similar rule applies within Tier 2, except that ditches must contain at least 30 cm of water in summer. To qualify for Tier 3 payments, water levels must be at or above ground level ('surface splashing') between 1 December and 30 April and the level in ditches must not be more than 30 cm below mean field level between 1 May and 30 November.

These Tier 3 water table provisions were introduced in 1992 with the aim of reversing the sharp decline in wading bird populations recorded on the Levels in recent years (Green and Robins, 1993). The ditch levels required are higher than those in the IDB maintained rhynes and in order to achieve them, the ditches surrounding a particular field or block of land have to be isolated from the main system with water pumped into them in the summer. Farmers operating within Tiers 1 or 2 may opt to maintain the Tier 3 water levels in exchange for a supplement of £70 per ha in addition to the basic Tier 1 or Tier 2 payment.

Spot herbicide treatment of certain weeds is allowed within all Tiers. Some inorganic fertilizers are permitted within Tiers 1 and 2, although in no case can farmers increase fertilizer usage above their current levels upon entering the scheme. Maximum permitted amounts are 75 kg N ha^{-1}, 37.5 each of phosphate and potash (16.4 kg P and 31.3 kg K) for Tier 1, and 25 kg N ha^{-1}, 5.5 kg P and 10.4 kg K in Tier 2. No inorganic fertilizers are permitted in Tier 3.

There are no restrictions on hay or silage cutting dates within Tier 1, but meadows must not be cut before 1 July in Tier 2 and 8 July in Tier 3. In all three Tiers, aftermath growth must be grazed to provide an uneven sward structure which is particularly beneficial to overwintering birds (Green, 1986).

The ESA scheme is administered by the Ministry of Agriculture, Fisheries and Food (MAFF). Unlike that operating within SSSIs, the scheme is entirely voluntary, although legally binding once a farmer has entered it. English Nature will normally allow farmers with SSSI land to opt for the ESA scheme in preference to an SSSI agreement, provided that they enter a Tier containing all the restrictions appropriate to the particular site.

1.8. THE MAFF/DOE/ENGLISH NATURE TADHAM MOOR PROJECT

REASONS FOR THE TADHAM MOOR PROJECT

As a result of the debate which followed SSSI notification on West Sedgemoor, it became clear that too little was known about the exact relationships between farming and wildlife on the Moor. A joint MAFF/Nature Conservancy Council (NCC) working group was set up in 1983 to identify the areas of total conflict of interest and highlight areas where scope for reconciliation existed. The group would also make recommendations for research in remaining areas of uncertainty.

Whilst much was known about the response of grasslands in general to inorganic fertilizers, it was recognized that there was scant knowledge about the effects of fertilizers in the plant communities growing on the specific soils and under the specific hydrological conditions existing on the moors. In particular, it was uncertain whether any fertilizers should be allowed in the SSSI hay meadows and there was too little information to identify the production foregone by restricting or preventing fertilizer use. Consequently, MAFF, NCC and the Department of the Environment, jointly agreed to fund a research project to address these problems. MAFF and DoE also funded further work to investigate the influence of fertilizer N application on fluctuations in soil mineral N and denitrification. The project, known as the Tadham Moor Project, was started in 1986, after a preliminary survey was carried out in 1985 to provide information on variations in vegetation composition and productivity across the proposed study area.

THE STUDY AREA

The Tadham Moor Project was carried out within 21 hectares of the Tadham and Tealham Moors SSSI near Wedmore, grid reference 51° 12'N, 2° 49'W. The elevation of the moors averages 2-3 m above Ordnance Datum. A soil survey of the experimental area, carried out in 1990 by members of the Wetland Evaluation Research Project at Exeter University (D. Hogan, unpublished), showed that soils belonged to the Altcar, Adventurer's and Blackland series, with some oligo-fibrous Turbary Moor peat (Avery, 1980). The pH of these soils is 5.5-6.0 in the top 10 cm, with a total depth of peat of 1.5-2.0 m over marine clay.

The meadows have a long history of hay cutting followed by aftermath grazing and no inorganic fertilizer use. The resulting vegetation contains a mosaic of communities falling within the MG5 (*Cynosurus cristatus-Centaurea nigra* meadow) and MG8 (*Cynosurus cristatus-Caltha palustris* flood pasture) categories of the National Vegetation Classification (Rodwell, 1992).

MANAGEMENT OF THE TADHAM MOOR PROJECT

Phase 1 (1986-90)

The Agricultural and Food Research Council (AFRC) Institute of Grassland and Animal Production (IGAP, now the Biotechnology and Biological Sciences Research Council (BBSRC) Institute of Grassland and Environmental Research - IGER) was contracted to conduct the research, initially for a period of four years. The Institute of Terrestrial Ecology (ITE) at Monk's Wood were sub-contracted to carry out botanical surveying on one of the two field experiments established in April 1986 (Experiment 1 - see below). During this period, the author was Project Officer for the project as an employee of IGAP/IGER.

The first phase of the work was completed in May 1990. By this time the project had provided sound data on the effects of inorganic fertilizers on botanical composition, increases in agricultural output, and losses of nitrogen from the soil. Throughout this phase, weekly measurements of water table depth had been taken in a series of dipwells installed across the site in 1986. In November 1990, MAFF and the National Rivers Authority (NRA) funded a study using these data to investigate the effects of variations in water table depth on agricultural output and losses of soil nitrogen. This information was needed to assess the likely effects of the changes in water table management which were subsequently introduced into the ESA scheme.

Phase 2 (1990-93)

Phase 1 of the Tadham Moor Project had provided no information on the composition of the seed bank in these meadows, nor on the extent to which this had been affected by changes in the vegetation brought about by repeated fertilizer use. Furthermore, during the years since the initiation of the project, in addition to water table management, debate had focused upon hay cutting date. SSSI and ESA rules prevent cutting before early July, not only to allow ground nesting wading birds to rear their young undisturbed, but also to allow plants to set seed. However, many plants are still flowering during July and work in the Pennine Dales showed that hay cutting there needed to be delayed at least until August for most species to set seed (Smith and Jones, 1991). This led to a rule within the Pennine Dales ESA that hay must be cut in August or later in at least one year in five (Younger and Smith, 1993). Information was needed to see if a similar rule was necessary on the Somerset Levels, and also to see how variation in cutting date might influence the regeneration of species diversity following cessation of fertilizer use.

THE PHD PROJECT

The purpose of the PhD project and of this thesis was to define clearly the ecological and agronomic implications of variations in the three main agricultural practices affecting species-rich hay meadows on the Somerset Levels - inorganic fertilizer use, water table management and hay cutting date. The thesis incorporates data from three experiments covering these topics which were carried out at the site, Experiments 1, 2 and 3. However, each topic was not addressed separately by each experiment. The effects of inorganic fertilizer use on vegetation composition and productivity were studied largely during Phase 1 of the project (1986-90) in Experiments 1 and 2. Data collected from Experiment 1 during this period were also used to investigate the influence of variations in water table depth on productivity and losses of soil N. The effects of variations in cutting date were studied during Phase 2 (1990-93), mainly within Experiment 3, whilst soil seed bank measurements were also made in March 1991 on these same plots. The location and layout of each experiment, and the broad approach to each of the studies carried out, are summarized below, whilst detailed descriptions of the methods and forms of data analysis used in each study are given in the relevant chapters of the thesis.

Figure 1.4. shows the layout of the three replicate blocks of the large-scale experiment, Experiment 1, with labels N0 to N200 indicating the levels of fertilizer N applied (see below). Experiments 2 and 3 were carried out within this same area, with plots of Experiment 2 laid out in a single area within replicate block 1 of Experiment 1. PLots of Experiment 3 were located in six separate groups with two within each replicate of Experiment 1, so that three of these groups were on previously fertilized vegetation and

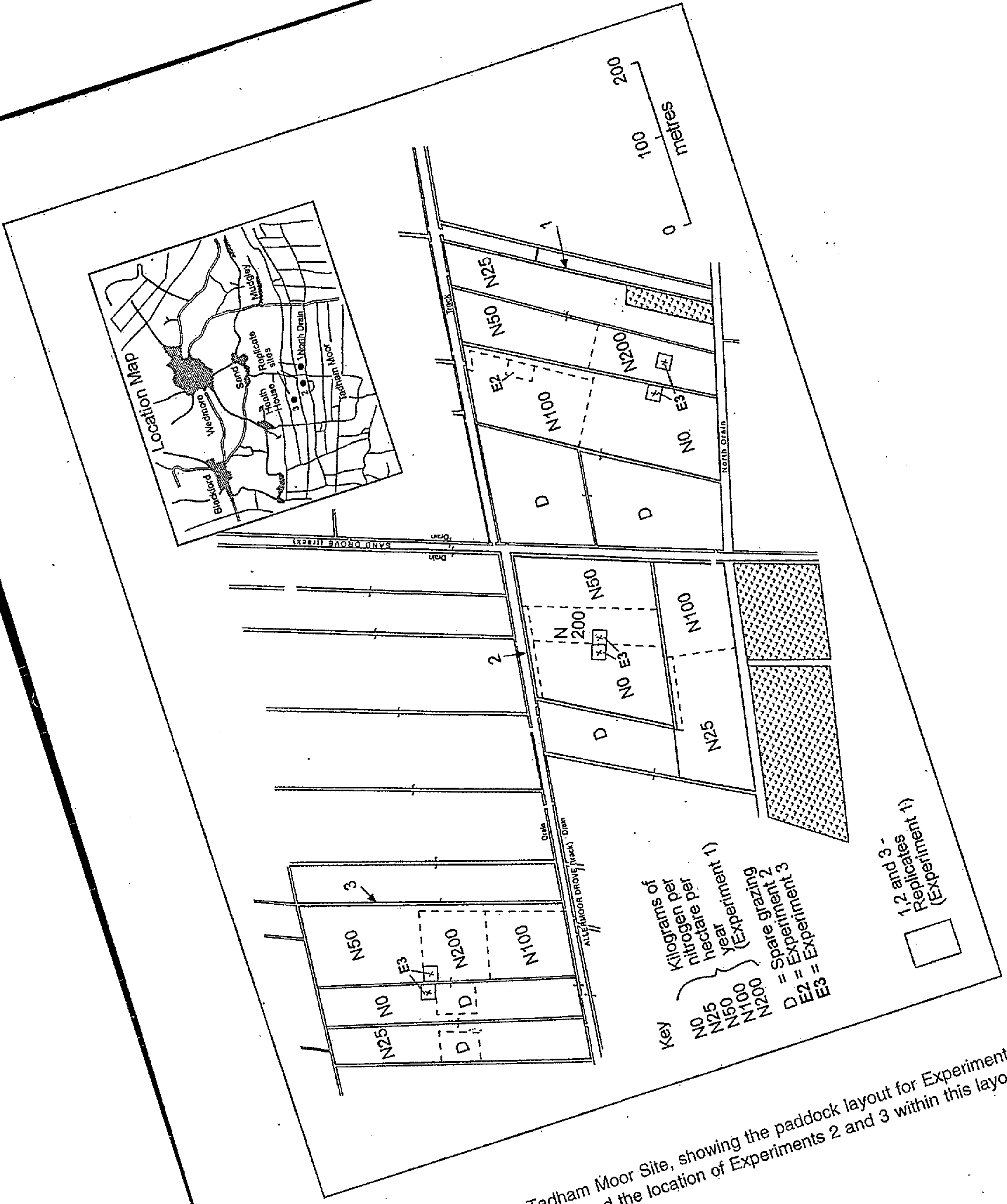


Figure 1.4. Plan of the Tadham Moor Site, showing the paddock layout for Experiment 1 (N0-N200, blocks 1, 2 and 3) and the location of Experiments 2 and 3 within this layout.

three on unfertilized area (see Figure 1.4). Experiments 1 and 2 were run concurrently from 1986 to 1990 (Phase 1), whereas Experiment 3 was carried out between 1991 and 1993 (i.e. in Phase 2). The plot layout of Experiment 2 is described in Chapter 3 and that of Experiment 3 in Chapters 6 and 8.

The use of inorganic fertilizers

In Experiment 1, various rates of fertilizer nitrogen (N) were applied to large scale plots laid out in a randomized block design (Figure 1.4). Plots were cut for hay as soon as possible after 1 July each year and then grazed by cattle into the autumn. Phosphorus (P) and potassium (K) were applied at rates sufficient to replace the amounts harvested in hay, but not to unfertilized control plots. The effects of these treatments on botanical composition, agricultural production (from hay + grazing) and on fluctuations in soil mineral N and denitrification were measured over a period of four years. The relationships between above ground vegetation composition and composition of the soil seed bank in unfertilized meadows and after five years of fertilizer application were also investigated within Experiment 3.

The effects of a wider range of fertilizer treatments, including variations in P and K, on botanical composition and on herbage production and nutritive value were investigated in the smaller-scale experiment, Experiment 2, where plots were cut instead of grazed in the second half of the growing season .

Variations in water table depth

The effects on agricultural production and losses of soil mineral N of variations in water table depth (measured weekly) were investigated using correlation and regression analyses of data collected over five years in Experiment 1. No attempt was made to relate botanical composition to water table depth since this aspect was covered by other studies at the site (Mountford and Chapman, 1993).

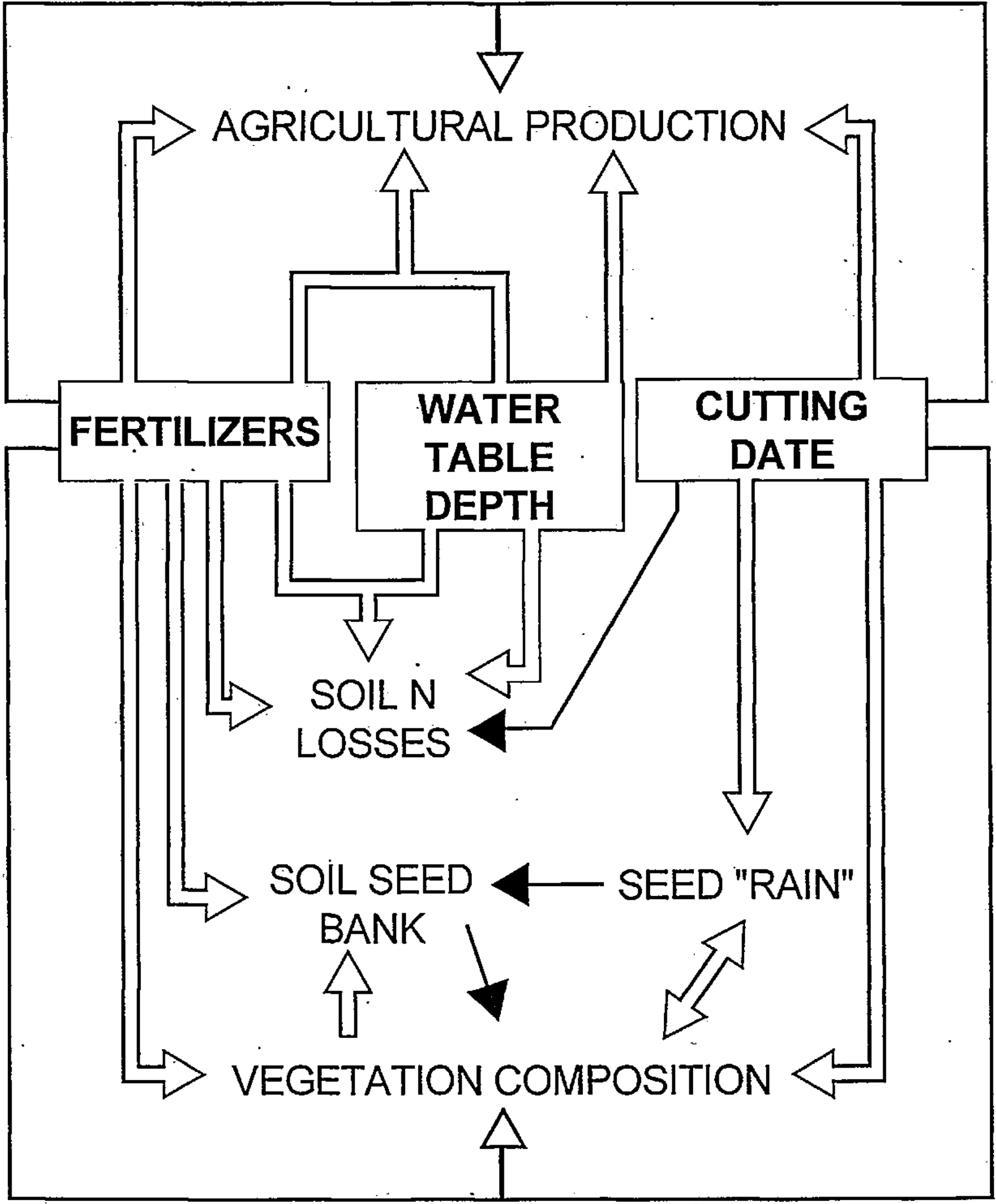


Figure 1.5. Schematic representation of the relationships investigated between three management inputs - (a) use of inorganic fertilizers; (b) variations in water table depth; (c) variation in cutting date - and (i) vegetation composition, (ii) seed 'rain' (iii) the composition of the soil seed bank, and (iv) losses of soil nitrogen. Hollow arrows represent measured effects, solid arrows represent relationships partially defined or implied by the data. The outermost lines, joining CUTTING DATE and FERTILIZERS, represent relationships between variations in cutting date and *previous* fertilizer application, i.e. after cessation of fertilizer use.

Variations in cutting date

A third experiment (Experiment 3) was established to investigate the effects of cutting primary growth in May, July, August or September in two consecutive years on herbage yield and nutritive value, seed rain and botanical composition. The importance of the various stages of hay making in stimulating seed shedding was also investigated, and the individual phenologies of seed production, seed shedding and viablity of three selected dicotyledonous species were defined in a separate study.

A schematic representation of the relationships investigated between these three management variables and the variables measured (i.e. vegetation composition; the composition of seed rain and of the soil seed bank; and losses of soil N by leaching and denitrification) is given in Figure 1.5.

1.9. STRUCTURE OF THE THESIS

The following is a summary of the subject areas covered by each chapter:

Chapter 1 (this chapter) - Introduction to the thesis.

Chapter 2 - Review of the scientific literature relevant to the subject areas covered by Chapters 3-8.

Chapter 3 - The effect of fertilizer application and variations in water table depth on agricultural production.

Chapter 4 - The effect of fertilizer N application and variations in water table depth on losses of mineral N from the soil.

Chapter 5 - The effect of inorganic fertilizers on vegetation composition and the influence of aftermath grazing.

Chapter 6 - Composition of the soil seed bank in relation to the above ground vegetation in fertilized and unfertilized meadows.

Chapter 7 - The effect of variations in cutting date on productivity.

Chapter 8 - The effect of hay cutting date and previous fertilizer use on seed 'rain' and vegetation composition.

Chapter 9 - Implications of the results described in Chapters 3-8 for the management of species-rich hay meadows.

The final chapter, Chapter 9, brings together the results of the thesis as a whole. The implications of these results for the management of species-rich hay meadows within the Somerset Levels and elsewhere are discussed, both from the agricultural and the plant ecological/environmental viewpoint. The need for modifications to the existing rules applying within SSSIs and the ESA is discussed, and subjects needing further research are highlighted. A bibliography of all the literature cited is given at the end of the thesis.

CHAPTER 2

THE AGRICULTURAL ECOLOGY OF SPECIES-RICH GRASSLAND - AN OVERVIEW

2.1. SUMMARY

A dramatic decline in the wildlife value of British grassland has occurred over the last 60 years due to agricultural intensification and this has been typified by a near eradication of herb-rich hay meadows. This chapter begins with a review of prevalent theories, concepts and methodologies surrounding plant communities, vegetation analysis and classification (Section 2.3.). This is followed by a review of a large body of literature on the effects of agricultural practices on both the ecology and productivity of species-rich grassland, falling within three main topic areas: the effects of changes in soil fertility and the use of inorganic fertilizers (Sections 2.4 to 2.6); the impacts of changes in water table depth (Section 2.7); the consequences of variations in fertilizer use, cutting and grazing management for seed rain/seed bank dynamics (Sections 2.8 and 2.9). Ecological implications are reviewed mainly in terms of vegetation structure and composition, but the effects of fertilizer application and water table manipulation on soil nitrogen processes and their implications for environmental pollution are also covered (in Sections 2.6 and 2.7).

Section 2.10 discusses evidence for the agronomic significance and implications for faunal wildlife of species richness in agricultural grasslands. The final section, Section 2.11, provides a synthesis of the major conclusions to be drawn from the literature, under six main headings: the effects of fertilizers on yield and botanical composition; fertilizers and pollution; water table depth and drainage; seed banks, seed rain and cutting date; the agronomic implications of cutting date; the significance of species-rich vegetation.

2.2. INTRODUCTION

The Nature Conservancy Council (1984) estimated that only 3% of lowland neutral grassland in the UK had been left undamaged by agricultural intensification since the 1930s, and that the greatest change had been in the number of herb-rich hay meadows. A survey completed in 1981 showed that only 4.9% of surviving hay meadows could be regarded as species-rich and only 1.6% were worthy of protected area status (Nature Conservancy

Council, 1984). In a more detailed review of grassland surveys carried out between 1930 and 1984, Fuller (1987) concluded that the Nature Conservancy Council's assessment of the conservation interest of lowland grassland was, if anything, optimistic. These surveys paint a very different picture to that described by Tansley (1939), who showed that until the late 1930s most hay meadows contained a wide variety of grasses and herbs. Moreover, a recent survey has shown that loss of species diversity in UK grassland is continuing, and that the species which are declining include those which are already nationally scarce and associated with unimproved meadows (Barr *et al.*, 1993).

Initially, most of these losses were due to ploughing and drainage, but fertilizer use has increased over the same time scale, improving even old and undrained grassland (Fuller, 1987). Whilst there is a greater proportion of grassland of conservation interest in upland areas of England and Wales, the uplands have also shown a progressive decline in species-rich grassland in conjunction with an increase in fertilizer usage (Hopkins and Wainwright, 1989). Few extensive surveys have been carried out on the continent of Europe, but it is recognized that a widespread decline in species-rich grassland has also occurred there (van Duuren *et al.*, 1981; Ellenberg, 1988; Losvik, 1988; Bakker, 1989; Willems, 1990; Berendse *et al.*, 1992; Garcia, 1992).

In reviewing the factors which control productivity and affect the ecology of species-rich grassland, this chapter focuses on three main topics: -

(a) the influence of changes in soil fertility (e.g by fertilizer application)

(b) changes in water table depth (by drainage or 'penning up' - see Chapter 1)

(c) seed rain/seed bank dynamics (the influence of grazing, cutting date etc.)

Within each topic, the effects of the relevant agronomic practices, both on vegetation structure and composition and on agricultural productivity, are covered.

However, much of the content of this review, and of the remainder of this thesis (Chapters 5, 6 and 8), involves studies on vegetation composition and dynamics. An appreciation of the prevalent theories and methodology surrounding vegetation analysis is an important prerequisite to such studies, and this review begins with a brief summary of these concepts and methods.

2.3. CONCEPTS OF PLANT COMMUNITY AND INDIVIDUAL PLANT STRATEGY IN AGRICULTURAL GRASSLANDS

The research presented in this thesis is concerned with hay-meadow plant communities and the factors affecting their composition. A large number of experiments have been carried out on grassland composition, although most have concentrated on the performance of individual species. The longest-running of these experiments, and probably the most well-known study of the effects of agricultural practice on vegetation composition, is the Park Grass Experiment at Rothamsted Experimental Station (Williams, 1978). This experiment, which studies the effect of fertilizers on yield and botanical composition in plots cut for hay, was started in 1856 and is still running. A vast amount of data has been collected and many reports have been published (e.g. Lawes and Gilbert, 1858, 1859a,b,c, 1880; Lawes *et al.*, 1882; Brenchley, 1924; Brenchley and Warington, 1958; Thurston *et al.*, 1976; Williams, 1978,1989). Most of these reports are very long and give detailed information on the proportions of individual species and species groups, i.e. grasses, legumes and 'others', resulting from different fertilizer treatments. Some broad generalizations about the nutrient preferences of individual species are possible on the basis of this kind of data and Grime *et al.* (1988) make frequent references to the results of the Park Grass Experiment in their book *Comparative Plant Ecology.*

However, much of the data reviewed in this chapter make it clear that, in mixed vegetation, the response of a particular species to a specific nutrient input can vary widely according to a number of other, interacting external factors. To attempt to study in detail the interactions of even a few species in a variety of environmental conditions is an extremely arduous task. Such methods, favoured by some ecologists (e.g. Harper, 1982) have been likened by Grime (1985) to 'putting from the tee'. An alternative approach is to look for generalities in vegetation science and to identify criteria by which species can be grouped and related to external factors. The most broad-based examples of this kind of approach stem from the concept of a plant community.

PHYTOSOCIOLOGY AND THE PLANT COMMUNITY

The organismic versus the individualistic approach

The dichotomy between ecologists in their basic approach to vegetation science has a long history (White, 1985; Goldsmith *et al.*, 1986). It was typified by the organismic concepts of Clements (1916), who saw vegetation in terms of closely integrated, well-defined and repeatable communities, compared with the individualistic approach of Gleason (1917), who saw vegetation as a continuum, with a unique combination of species at any point on the earth's surface. The Clementsian approach has led to techniques of classifying and naming vegetation types (Braun-Blanquet, 1932; Rodwell, 1991a,b, 1992, 1995). These techniques have been largely rejected by those who prefer a more reductionist approach based upon individual species (Harper, 1977, 1982). Some ecologists are sceptical about the extent to which multivariate techniques based upon the analysis of vegetation as a whole have furthered the understanding of vegetation processes (Crawley, 1986a), although these techniques are intended to be largely descriptive rather than explanatory (Kent and Coker, 1992). A similar dichotomy exists between those who look for behavioural similarities by which species can be grouped and classified (Rabotnov, 1975,1985; Grime, 1979,1985; Grime *et al.*, 1988) and those who believe that an understanding of vegetation can only be reached by detailed studies of the biology of individual components and their interactions (Harper, 1977,1982).

Differences are still prevalent therefore, and several pleas have been made for a more integrated approach (Grime, 1985; White, 1985; Wilmanns, 1985; Kent and Coker, 1992). However, most modern ecologists agree about the existence of identifiable plant communities that are repeatable over space. The study of phytosociology is based upon this concept and upon the need to define and name such communities.

Methods of vegetation classification and description

Stapledon (1914) recognized explicitly the concept of a plant community as a particular aggregation of species by which a particular grassland 'type' could be identified, although his scheme was developed within the relatively narrow context of fertilizer use in agricultural grasslands. Each type was identified by the normal abundances of its 'fundamental' species, each species having a maximum, minimum and optimum value within each grassland type. The fundamental species could be expected to fluctuate within their 'cardinal' values according to seasonal and environmental variation or with small alterations in fertility or management. Large changes in either the weather or in management could

force the fundamental species outside their cardinal limits and thus change the grassland from one type to another. Stapledon recognized that prevailing husbandry, including fertilizer use, grazing or hay cutting, could be classed as an environmental factor.

Stapledon's ideas of classification have some similarities with the more complex nomenclature schemes later developed by the Zurich-Montpelier School (Braun-Blanquet, 1932) and with the more recent National Vegetation Classification (NVC) scheme (Rodwell, 1991a,b, 1992, 1995). Of these, the Braun-Blanquet method and nomenclature scheme is still the most widely used in Europe. This method has been described in detail by various authors (e.g. Westhoff and van der Maarel, 1980; Goldsmith *et al.*, 1986; Kent and Coker, 1992). The NVC scheme, which uses a broadly similar approach, but with a unique nomenclature system (Rodwell, 1991a,b, 1992, 1995), is growing in use in the UK. The methodology used in the original NVC survey led to the development by Hill (1979) of the computer program TWINSPAN (Two Way Indicator Species Analysis) for vegetation classification and description (Rodwell, 1991a).

Traczyk and Kotowska (1976) used Braun-Blanquet classification to describe different plant community types resulting from contrasting fertilizer treatments. Both TWINSPAN and another computer program - TABLEFIT (Hill, 1991) have been used to relate quadrat data from the Tadham Moor Experiment to NVC vegetation types (Mountford and Smyth, unpublished; Mountford *et al.*, 1993a). This showed that nitrogen application had changed the vegetation from that of a typical species-rich wet grassland into more species-poor mesophytic types, a process referred to by Rabotnov (1977) as 'biological drying'.

Direct and indirect gradient analysis or ordination

Gradient analysis allows variation in data to be examined in relation to environmental gradients. With its emphasis on vegetation as a continuum, gradient analysis is more acceptable to those who object to vegetation classification and to a generalizing approach to vegetation science (Grubb, 1985). However, ordination is primarily a means of data reduction and hypothesis generation (Kent and Coker, 1992), and Crawley (1986a) has complained that these techniques too often become an end in themselves. Gradient analysis can either proceed independently of the environmental data, ordering species or quadrats simply on the basis of their floristic content and similarity (indirect gradient analysis), or by plotting species directly against environmental gradients or gradients of factor complexes (direct gradient analysis). The influence of environmental factors can also be explored with indirect methods by fitting environmental variables after ordination, but the most valuable use of indirect gradient analysis is where environmental data are not available or their underlying importance is unclear. The most commonly used indirect method is Detrended Correspondence Analysis (DCA) (Hill and Gauch, 1980). Canonical Correspondence Analysis (CCA) is a more sophisticated technique and is, strictly speaking, a hybrid between direct and indirect methods, since the ordination axes are constrained by multiple regression with environmental factors (ter Braak, 1988). Both methods produce two-or three-dimensional ordination diagrams which allow conclusions to be drawn about the relationship of each species and/or quadrat to the environmental factors tested, and indicate the relative strengths of each of these factors in determining the ordination (ter Braak, 1988). Both DCA and CCA are used fairly extensively in Chapter 5 to relate botanical composition to differences in available nitrogen (N), phosphorus (P) and potassium (K), where the different amounts of each element applied in various treatments are treated as environmental variables.

THE PERFORMANCE OF INDIVIDUAL SPECIES WITHIN A PLANT COMMUNITY

Classification of individual species

It is axiomatic that the ability of a species to co-exist with others must be a function not only of the environment and the performance of its neighbours but also of its own attributes. It is therefore generally accepted that the study of individual species is important in understanding how plant communities are constituted and how they change (Grubb, 1977; Grime, 1979; Crawley, 1986a,b). However, it is not clear to what extent the performance of a particular species can determine the properties of a community as a whole, as some writers believe. Rabotnov (1975) called such species 'edificator' species (citing Braun-Blanquet and Pavillard's *edificateurs*) although he preferred the term 'determinants', while zoologists refer to 'keystone' species (Paine, 1980). Several authors have pointed out that a particular species can behave quite differently in different situations, and that generalizations are sometimes hard to sustain (Rabotnov, 1977,1985; Tilman 1982,1986;

Grubb, 1985; Wilmanns,1985). The performance of species in even quite simple mixtures cannot be easily predicted from their performance in pure stands (Harper, 1977) and there is a general discordance between the physiological and ecological tolerance of individual species. The ecological amplitude of a species along an environmental gradient is usually much more restricted than its physiological amplitude (Rorison, 1969; Austin and Austin, 1980). Pigott (1982) gave several other examples of how the response of a plant to changes in its environment are determined by the context of the community in which the plant exists. Some of these are discussed later in the context of the influence of nutrient addition on the species richness of vegetation.

The terms 'edificator' and 'determinant' imply a positive role in determining the composition and species richness of vegetation. Experimental data presented later provide some justification for this concept. In describing the ecology of a wide range of species in the UK, Grime *et al.* (1988) classified each species according to the level of species diversity with which it is associated, with occasional reference to the ability of a particular species to exert dominance over the vegetation.

Plant strategies

Several workers have attempted to classify species according to ecological characteristics in order to explain their existence and performance within particular plant communities (Pianka, 1970; Ramensky, cited in Rabotnov,1975,1985; MacLeod, cited in Grime *et al.*, 1988). However, the most recent and probably the most comprehensive scheme was devised by Grime (1974, 1979). Grime's scheme is very similar to that proposed by Ramensky in the late 1930s, although Ramensky's writings seem to have escaped notice outside Russia until highlighted by Rabotnov (Rabotnov, 1975,1985).

Grime's 'established' strategies

Grime suggested that there were three main determinants of vegetation - competition, stress and disturbance - and that each has invoked a distinct strategy on the part of the flowering plant. This concept led to the C-S-R model which classified species as 'competitors', 'stress-tolerators' or 'ruderals' (Grime, 1977; Grime et al., 1988). Competitors exploit conditions of low stress and low disturbance, stress-tolerators are associated with high stress and low disturbance, whereas ruderals are characteristic of low stress and high disturbance. Each type is located within a triangular ordination where the left-hand, right-hand and bottom sides of the triangle represent axes for the relative importance of competition, stress and disturbance respectively. Each axis runs from 0-100 in a clockwise direction, so that competitors (C) fall within the apex of the triangle, stress tolerators (S) in the right hand corner and ruderals (R) in the left-hand corner. The model allows for intermediate positions i.e. C-R, C-S, S-R and C-S-R. Grime termed these *established* strategies. He defined a separate group of strategies operating in the juvenile stages - the *regenerative* strategies (Grime, 1979; Grime *et al.*, 1988).

Grime's 'regenerative' strategies

This scheme described five strategies by which a species may regenerate:

(i) by vegetative expansion

(ii) by seasonal regeneration involving the production of seeds or vegetative propagules in a single cohort

(iii) by a persistent seed or spore bank, viable seeds or spores present throughout the year, some persisting more than 12 months

(iv) by numerous widely dispersed seeds or spores

(v) by persistent juveniles - seedlings are capable of long-term persistence in a juvenile state

A species may be capable of regenerating in two or more different ways and the degree of flexibility it shows in this context will help to determine the ecological amplitude of the species (Grime, 1979).

Objections to Grime's 'strategies'

The term *strategy* is disliked by some theorists, notably by Harper (1982), who objected to its teleological and anthropomorphic connotations. Other objections have been raised about the C-S-R categories themselves, both on semantic and theoretical grounds (Harper, 1982; Grubb, 1985; Rabotnov, 1985). Both Grubb (1985) and Rabotnov (1985) objected to the generalizations involved in identifying a particular strategy to each species, pointing out that the same species can behave quite differently in different habitats. These objections resonate with Wilmann's (1985) warning that:

> *' a demographic statement is valid only for a specific environment...The scope of its generalization is amplified only if it is checked in other stands (a) of the same syntaxon and (b) of syntaxa of graded similarity'.*

Since Grime is extremely influential in ecological circles and his ideas are very widely quoted, it is worth listing some of Grubb's (1985) objections to the C-S-R model:

- There is no generally applicable concept of stress in plant ecology, so it is not possible to identify stress tolerators.
- Competition is the relationship between two plants that have potential to occupy a given landscape unit (considered over their whole life cycles); the ability of one plant to reduce the performance of another is best called 'interference'.
- It is misleading to describe a single type of plant as a 'competitor', such definitions should be habitat-specific.
- The performance of many plants are facultative according to disturbance.
- The best way of differentiating species in relation to environmental conditions is to order them along gradients of factor complexes by direct gradient analysis, or to order them on a two-dimensional framework of environment *v.* disturbance.
- The concept of plant strategies is unsustainable in the context of the whole world's vegetation.

Harper (1982) shared Grubb's objections to the term 'stress'. He quoted extensively the objections raised against use of the term in medicine by Pickering (1961), who preferred to view biological behaviour simply in terms of stimulus and response. However, these terms suggest a positive reaction to some input, force or perhaps deprivation, and are therefore inadequate to explain the behaviour implied by the word 'tolerator'. This is a passive term, suggesting either: (a) a lower physiological requirement than most species for one or more resources such as light, water, nutrients or energy; or (b) a higher resilience or resistance against trampling, extreme temperature or toxic metals, for example; or (c) any combination of (a) and (b). The description 'tolerator' is probably adequate on its own, without the prefix *stress.*

Ellenberg numbers

In an appendix to his *Vegetation Ecology of Central Europe,* Heinz Ellenberg (1988) assigned seven 'ecological indicator' values to each of a large number of species found throughout Central and Eastern Europe. These values were based on the habitat characteristics within which the species are commonly found and indicate the species' relative preference or tolerance of each of the following seven ecological factors: light intensity, temperature, continentality (occurrence on a gradient from the Atlantic coast to the inner parts of Eurasia), water, reaction (pH), available nitrogen, salt, and heavy metals tolerance. Each value fell within a 9-point scale, except for water (12-point), salt (4-point) and heavy metals tolerance (resistant/not resistant). Note that these indicated the mean ecological tolerance of each species, based upon a vast amount of survey and phytosociological data, and not the physiological tolerance. The codes allowed for indifference or a wide amplitude of tolerance to a particular factor (x) or unclear behaviour (y).

In theory, the 'Ellenberg numbers' should allow some prediction of the effect of a change in environment or vegetation management on the abundance of individual species within a plant community. However, these codes are generalizations made from a wide variety of habitats. In common with Grime's established and regenerative plant strategies, it may be over-optimistic to expect the Ellenberg codes to be reliable predictors of performance in specific situations.

2.4 SOIL FERTILITY AND THE USE OF FERTILIZERS

Much of this thesis is concerned with the effects of inorganic fertilizers on both the productivity and vegetation composition of species-rich meadows at Tadham Moor (see Chapters 3 and 5). A wide range of papers and reports covering both these aspects of fertilizer use is therefore reviewed in this Section. Most of these publications give detailed data on the effects of different fertilizer rates and/or elements (i.e. N, P and K), and production response and vegetational response results are reviewed under separate sub-sections. This is followed by sub-sections reviewing models and theories which seek to relate species-richness, soil fertility, disturbance and above-ground biomass, and which help to explain how these factors interact to influence the potential for species coexistence in grassland communities.

First, however, there follows a brief description of the main sources and functions within the plant of the major plant nutrients, with special emphasis on N, P and K.

ESSENTIAL MINERAL ELEMENTS

Macro- and micronutrients

Essential plant nutrients are usually divided into macronutrients and micronutrients on the basis of the amounts required by plants. Macronutrients are: nitrogen (N), phosphorus (P), potassium (K), sulphur (S), calcium (Ca), magnesium (Mg) and iron (Fe) (Sutcliffe and Baker, 1981), although Fe is often classed as a micronutrient (e.g. Fitzpatrick, 1986). The remaining micronutrients are: copper (Cu), manganese (Mn), zinc (Zn), sodium (Na), boron (B), molybdenum (Mo) and chlorine (Cl).

Deficiency of any one of the macro- or micronutrients can limit plant growth and plants may compete for any or all of them in any given situation. Nevertheless, the supply of most of these elements is usually adequate and only N, P, K or Ca are normally applied to agricultural grasslands, although other macro- or micronutrients may be present as impurities in agricultural fertilizers (Sutcliffe and Baker, 1981). Ca, in the form of lime, is most often applied as a means of raising soil pH, rather than to rectify plant deficiencies in Ca. This affects the availability of the other macronutrients, most of which become less available to plants as pH falls below about 6.0-6.5 (Sutcliffe and Baker, 1981; Brady, 1990).

Nitrogen

N occurs in the soil solution as nitrate, nitrite, ammonium and free ammonia. However, most N in the grassland soils is in the form of organic matter, partly in plant remains (humus), partly in microorganisms and partly as organic acids (e.g amino acids, amides). Gaseous N in soil air spaces can be fixed by microorganisms, some of which are symbiotic with legumes which obtain N from this association. N is an essential component of nucleic acids, proteins, chlorophyll and various co-enzymes (Sutcliffe and Baker, 1981).

Phosphorus

P is also found in humus and in microbial biomass, from which it is released mainly in the form of phosphates. In acid soils, P occurs as relatively insoluble iron and aluminium phosphates and as phosphate ions adsorbed onto clay particles (Brady, 1990). P is an essential component of nucleic acids and of cytoplasmic membranes in the form of phospholipids. Organic phosphates such as adenosine di- and triphosphate perform an essential role in metabolic processes within the plant (Sutcliffe and Baker, 1981).

Potassium

Unlike N and P, most of the K in soils is in inorganic form, although significant amounts are also associated with organic materials and humus (Sutcliffe and Baker, 1981; Brady, 1990). Most exchangeable K in mineral soils is associated with clay particles. K forms loose associations with proteins and is a cofactor for numerous enzymes. Surprisingly high concentrations are required for these processes and this is thought to be due to the low affinity for protein molecules shown by K (Sutcliffe and Baker, 1981). K also performs an important role in osmotic regulation within the plant tissues, including an involvement in the control of turgor within the stomata guard cells, thereby influencing water regulation within plant leaves (Suttcliffe, 1979; Sutcliffe and Baker, 1981).

PRODUCTION RESPONSE TO FERTILIZERS

In the context of fertilizer response in species-rich grassland, three questions arise;-

(a) how does the potential to increase production by inorganic fertilizer application in these grasslands differ from that of species-poor grassland?

(b) do these two broad categories of grassland differ in the factors limiting production?

(c) is it possible to generalise on these questions?

Unfortunately, few if any studies specifically aimed at addressing these problems have been carried out, and the kind of fertilizer response data which have been obtained from species-poor to moderately species-poor swards are not available in any detail for species-rich vegetation. On the other hand, a large number of experiments have been carried out, many in species-rich vegetation, where a more limited range of treatments have been used, often aimed at finding out which elements limit growth, rather than defining growth responses. Many of these have been conducted under single cut management, or with hay cutting followed by a second cut, whereas the more detailed fertilizer response trials in species-poor vegetation have been carried out with 4-6 cuts per season. As will be seen below, cutting frequency can significantly affect dry matter production and fertilizer response.

The following account summarises the results of a number of experiments where fertilizers have been used in a range of grassland types and attempts to explore the range of responses both between and within different soil and vegetation types. Since the studies presented in later chapters of this thesis were carried out on peat, some emphasis is placed on these soils. However, it is not possible to see the extent to which these soils differ from others without a reasonably comprehensive review of vegetation response in a range of soils.

N, P and K response trials

Two multi-site trials, conducted across the UK by Morrison *et al.* (1980) (21 sites) and Hopkins *et al.* (1990) (16 sites), measured the response of grassland to fertilizer nitrogen. These trials differed from each other in that the first was carried out on perennial ryegrass (*Lolium perenne*) swards which, with the exception of one permanent pasture site, had all recently been established within an arable rotation or after cereals. The second trial compared the response of existing permanent pastures with that of pastures reseeded with *L.perenne*. In both trials, phosphorus (P) and potassium (K) were applied to all plots at rates sufficient to ensure that these elements were non-limiting. Herbage production was measured under 4-weekly cutting (6 cuts per year) in both trials, whilst Hopkins *et al.* also measured production under 8-weekly cutting (3 cuts), and both trials studied a wide range of N levels (0-750 kg N ha^{-1} by Morrison *et al.* and 0-900 by Hopkins *et al.*).

In terms of the number of sites encompassed and the range of N rates used, the above trials are by far the most extensive N-response studies that have been carried out in the UK. However, a number of earlier experiments studying the effect of varying P and K applications on the N response of sown, mixed species grassland cut five times per season were carried out in Scotland (Holmes, 1951; Castle and Holmes, 1960; Reith *et al.*, 1961; Heddle, 1967).

Response to N in fertilizer response trials

Both Morrison *et al.* (1980) and Hopkins *et al.* (1990) showed a more or less linear dry matter (DM) response to N rates up to 300 kg N ha^{-1}. The average response achieved by Morrison *et al.* within this range was 23.0 kg DM per kg of N applied. This was greater than any response recorded in the other trials so far mentioned, which ranged from 7.2 kg DM per kg N between 0 and 291 kg N ha^{-1} (Holmes, 1951) to 19.9 kg DM per kg N between 0 and 300 kg N ha^{-1} for re-seeded permanent pasture (Hopkins *et al.*, 1990). Garstang (1981) showed a similar average response of 20.7 kg DM per kg N between 0 and 272 kg N ha^{-1} in a long term (15 year) experiment in the North of England on permanent pasture initially containing 15% *L. perenne* and cut 6 times per year.

By contrast, Nielsen and Debosz (1994) showed only a small response of 7.2 kg DM per kg of N applied between 0 and 200 kg N ha^{-1} in swards aged between 2 and 14 years on organic soil in Denmark. These swards received 50 kg P and 250 kg K ha^{-1} and were cut three times per year. Control plot yield was high at an average of 9.2 t DM ha^{-1} and the consequently low response to applied N was attributed to a high rate of N mineralization of N from the organic soil.

The magnitude of the response shown by Morrison *et al.* (1980) was mainly attributable to low production without N, averaging 2.69 t DM ha^{-1} (range 0.6 to 5.7), compared with a range of 3.69 to 5.07 for the other trials so far mentioned. Average maximum yields differed far less between the two multi-site trials, at 11.9 t DM ha^{-1} (at 624 kg N ha^{-1}) in that of Morrison *et al.* and 12.3 t DM ha^{-1} (at 669 kg N ha^{-1}) in re-seeded permanent pasture (Hopkins *et al.*, 1990).

In both multi-site trials, production and N response varied greatly between sites. Morrison *et al.* (1980) showed that N response was significantly correlated with spring rainfall and soil available water capacity. Their data also showed that yield without applied N was significantly correlated with initial soil mineral N status, but not with soil K or pH (soil P values were not given).

Response to P and K in fertilizer response trials

Holmes (1951) showed no response to either P or K applied alone, and little improvement in N response by applying P. However, DM production declined over the three years of the experiment without K application, particularly where N was applied, and overall the N response was significantly greater when K was applied. The decline in yield in the absence of K was immediately reversed when K was applied during a further six year continuation of the experiment (Castle and Holmes, 1960). The N response between 0 and 291 kg N ha^{-1} in this second phase was increased from 4.3 kg DM per kg N applied (a 24% increase in DM production) to 12.7 kg DM per kg N (a 73% increase compared with no K), or 9.5 kg DM (40%) compared with plots receiving P and K without N.

Reith *et al.* (1961) showed a very similar dependence upon K application for N response, and a similar lack of response to P at six sites in Scotland. DM production was increased on average by 16% by applying K alone at 156 kg ha^{-1} . Applying N without K gave a curvilinear response of 15.9, 14.3 and 10.4 kg DM per kg N for 98, 195 and 390 kg N ha^{-1} respectively, but with K the response to N was linear throughout the 0-390 kg N range at 14.5 kg DM per kg N. Heddle (1967) continued the experiment at one of the sites (a loam to clay-loam soil) and had still found no response to P after a further 11 years, although the response to K and the N x K interaction had increased as production declined progressively on plots not receiving K.

By contrast, Norman (1956) showed significant increases in DM production by applying P to chalk grassland. Averaged over 3 years, the largest response was obtained by applying 84 kg P ha^{-1} in the first year only, compared with the same total amount applied either in annual or tri-annual instalments. The single application increased DM production by 33% when averaged over three years, giving an increase of 11.5 kg DM per kg P applied. However, the advantage of this one-off application over more frequent instalments was entirely due to the magnitude of response in the first year, and by the third year, yield was significantly greater on plots receiving more frequent instalments. Base productivity was low on this site, with plots receiving no P or K averaging only 2.63 t DM ha^{-1} from 4-5 cuts per year, and 2.82 t ha^{-1} when 46 kg K ha^{-1} were applied, despite the fact that all plots received 69 kg ha^{-1} N $year^{-1}$. The experiment differed from the others so far mentioned in that (a) plots were grazed with sheep (with herbage cut just before the start of each bout of grazing), (b) the sward appears to have been fairly species-rich with herbs and legumes occupying 38% of the vegetation, although it had been re-seeded 9 years before the start of the experiment, following two years of arable cropping, and (c) the experiment was conducted on calcareous soil. In contrast, only one of the sites in the Morrison *et al.* (1980) trial was on chalk grassland. The implications for productivity and fertilizer response of these three factors - soil type, defoliation frequency/grazing, and botanical composition - will be recurrent themes in the following discussion.

Soil type and P and K availability

The experiments conducted by Holmes (1951), Castle and Holmes (1960), Reith *et al.* (1961) and Heddle (1967) were all carried out on loam soils, ranging from light sandy loams to clay- and silty clay-loam. These soils were evidently capable of supplying sufficient P from natural resources or from P persisting from applications to previous crops. However, the response to P shown by Norman (1956) is typical of calcareous soils. A high proportion of the P contained in these soils is in the form of insoluble calcium compounds and unavailable to plants (Olsen, 1953; Brady, 1990). Furthermore, inorganic P can be precipitated out of solution by combination with calcium (Ca) and P applied to calcareous soils is often made unavailable to plants by this process (Olsen, 1953; Boyer and Wheeler, 1989). The same process can immobilize P in other soils fed by calcareous flood water or ground water, including lowland peats (Verhoeven and Schmitz, 1991; Reddy *et al.*, 1993).

Peat soils usually contain little inorganic P, mainly because they are formed from plant material in which P concentration is low, and because they are seldom in close contact with an igneous source of mineral P (Brady, 1990). Moreover, since the bulk density of peat is low and the moisture content high, this has a 'diluting' effect on the amount of P available per unit area compared to its concentration in dry soil (Munro *et al.*, 1973; Brady, 1990). Immobilization of P by soil micro-organisms usually exceeds P mineralization in organic soils, due to a high C:P ratio (Stevenson, 1982). Several experiments on the reclamation of blanket peat have shown complete failures in crop establishment without P application (Ogg and Robertson, 1940; O'Toole, 1968; Reith and Robertson, 1971). However, since lowland peats are usually associated with a high water table, they often receive nutrients brought in from elsewhere by seepage and flood water and P supply can be high where this water is polluted by urban or agricultural effluents (Newbold, 1977; Etherington, 1983; Verhoevan and Schmitz, 1991).

The amount of K also tends to be low relative to plant needs in organic soils compared to mineral soils (Brady, 1990; Munro *et al.*, 1973), partly due to low bulk density and high moisture content as for P, but also because it is relatively easily leached, forming an easily exchangeable cation loosely adsorbed onto the surface of organic colloids (Brady, 1990; Cole, 1970). Both O'Toole (1968) and Cole (1970) remarked that plant uptake and utilization of applied P and K were high during the establishment and growth of grass on blanket peat. Both authors attributed this to low fixation rates. Immobilization of P by soil micro-organisms may have been low in these soils, since the low pH (4.0-4.6) would tend to inhibit microbial activity, although the formation of insoluble ferrous compounds might also be expected at these low pH levels (Brady, 1990).

The influence of botanical composition on fertilizer response

Hopkins *et al.* (1990) found no advantage after the first year of re-seeding permanent swards with *Lolium perenne* when N rates of 0-150 kg ha^{-1} were applied, although output was increased significantly in the first year after ploughing and re-seeding. The authors attribute this initial increase to enhanced mineralization of soil N, which gave a yield response equivalent to 150-200 kg of applied N ha^{-1}. However, re-seeded swards were more responsive to N rates above 300 kg N ha^{-1} than were permanent pastures. This is consistent with data provided by Frame (1981) who showed that, when rates of 240 kg N ha^{-1} or more were applied under 4-weekly cutting, *L. perenne* out-yielded the remaining 10 grass species and varieties with which it was compared. However, *L. perenne* ranked 5th at 120 kg N ha^{-1} and 7th without N, P or K. Under 8-weekly cutting *L. perenne* ranked 2nd to *Holcus lanatus* at the highest N rate used (480 kg ha^{-1}), 3rd at 360 kg N ha^{-1}, when it was out-yielded by *H. lanatus* and by one of two varieties of *Festuca rubra* tested, and only 6th, 9th and 10th at 240, 0 and 120 kg N ha^{-1} respectively. Due to its low productivity at low and zero N rates, *L. perenne* ranked more highly in terms of DM response per kg N applied than in terms of absolute yield, both under 4-weekly and 8-weekly cutting. Responses ranged from 31.2 kg DM per kg N at 0-120 kg N ha^{-1} to 10.5 kg per kg N at 360-480 kg N ha^{-1} under 4 weekly cutting, and between 40.4 and 9.4 kg DM per kg N at 120-240 and 360-480 kg N ha^{-1} respectively under 8 weekly cutting. These results also fit well with the low productivity of *L. perenne* swards without N application shown by Morrison *et al.* (1980) and the consequently greater response in terms of DM produced per kg of N

applied in that trial, compared with that of Hopkins *et al.* (1990) in swards where species such as *H. lanatus*, *F. rubra* and *Agrostis spp.* were prominent. However, Frame (1981) applied N as a compound fertilizer with P and K at ratios of 20N:2.6P:10K, with no P or K applied to zero N plots. It may therefore have been wrong to attribute all the yield responses solely to N (as the author did).

N response within different grassland communities

Hopkins (1993) grouped sites from the multi-site trial of Hopkins *et al.* (1990) according to NVC classifications (Rodwell, 1992) in order to compare the productivity and response to N of these communities. He also expressed their productivity at 150 kg N ha^{-1} as a ratio of the productivity of re-seeded swards at the same N rate. The sites fell within 5 different communities: MG5 (*Cynosurus cristatus-Centaurea nigra* grassland); MG6 (*Lolium perenne-Cynosurus cristatus*); MG7 (*Lolium perenne* leys and related grasslands); MG8 (*Cynosurus cristatus-Caltha palustris*); and MG10 (*Holcus lanatus-Juncus effusus* rush pasture). Average DM production without N (but with P and K) ranged from 3.87 to 5.32 t DM ha^{-1} in the order MG6<MG7<MG8<MG10<MG5. Response to N (0-150 kg N ha^{-1}) differed little between the communities, ranging from 14 to 16 kg DM per kg N applied in the order MG6=MG8=MG10<MG7<MG5. Furthermore, MG5 grassland, which along with MG8 is generally the most species-rich of the five communities (both are characteristic of the vegetation at Tadham Moor), ranked highest both in terms of productivity without N and in terms of N response. However, it should be borne in mind that all swards received substantial amounts of P and K, and that high species-richness in grassland is associated particularly with low soil P status (Adam *et al.*, 1989; Gough and Marrs, 1990a,b; Marrs, 1993; Peeters *et al.*, 1994). One might therefore expect significant response to P in those grasslands where both low productivity and high species-richness are related to low P availability, rather than to some other limiting factor. It is also worth noting that the three sites which Hopkins classed as MG5 were relatively species-poor examples of this grassland type (A. Hopkins, personal communication). In terms of DM yield at 150 kg N ha^{-1} compared with re-seeded swards, the MG5 communities ranked lowest (original : re-seeded sward ratio = 0.86). The MG8 community ranked next (0.92), with MG6 and MG7 communities predictably differing little from re-seeds (both 0.95). The yield of MG10

grassland marginally exceeded that of the re-seed (1.03).

The effect of harvest interval on yield and fertilizer response

The amount of DM produced from grassland is significantly affected by harvest interval. Anslow (1967) showed that grass cut every 6 weeks produced significantly more than that harvested at three-week intervals, whilst Hopkins *et al.* (1990) showed that unfertilized permanent pastures produced 69% more DM per ha with 8-weekly cutting than when cut 4-weekly. The difference was somewhat smaller for re-seeded swards (45%). The shape of the N response curve for 4-weekly cutting was similar to that for 8-weekly cutting, both in permanent and re-seeded swards.

These results contrast with those of Wesolowski (1978), who applied N at 110, 220 and 440 kg ha^{-1} (N110, N220 and N440) to mixed species meadows at three sites on peat soil in Western Pomerania. There were no plots where N, P and K were not applied. There was no response to increasing N when swards were cut twice a year, in mid June and early September, but with 3 cuts per year (late May, late July and late September) treatments yielded in the order N110<N440<N220. With 4 cuts per year (mid May, early July, mid August and mid October), the order was N110<N220<N440. This last cutting frequency gave the greatest annual DM production at the two higher N levels, whilst 2 cuts per year gave the highest production at N110. Clearly, comparisons between experiments must take into account any difference in cutting interval.

In intensively managed grass swards, maximum annual yield is achieved by allowing an extended period of growth in spring, followed by several shorter periods of regrowth (Leafe *et al.*, 1974). This equates with cutting for hay or silage followed by further cuts or by rotational grazing. However, the length of the spring growth period required to give maximum yield may be shorter at higher levels of fertility (see Chapter 3), whilst the stage of maturity at harvest will in turn influence the nutritive value of the herbage produced (Green *et al.*, 1971; NIAB, 1987; see also Chapter 7).

Long-term experiments

A number of the experiments already mentioned provided data on the long-term effects of inorganic fertilizers on both the productivity and the botanical composition of species-rich grassland. Five of these shared several features which together distinguished them from other experiments: they lasted for at least 20 years; they were carried out on old, species-rich meadows; they provided data on the effects of inorganic fertilizers on both botanical change and productivity; and they included both hay making and grazing, either as separate treatments or with grazing following hay making - or, in the case of the Park Grass Experiment, with a change from grazing to cutting in the aftermath phase after 20 years. At least two of these experiments are old enough to be of historical as well as ecological interest: the Park Grass Experiment, which started in 1856 (Lawes and Gilbert, 1858; Williams, 1978); and the Palace Leas Plots at Cockle Park, which started in 1897 (Gilchrist, 1906; Elliott and Thomas, 1934; Pawson, 1960; Arnold *et al.*, 1976; Shiel and Batten, 1988). Both these experiments are still running.

Many reports have been published giving hay yield and botanical data from the Park Grass Experiment (e.g. Lawes and Gilbert, 1858, 1859a,b, 1880; Lawes *et al.*, 1882; Brenchley, 1924; Brenchley and Warington, 1958; Thurston *et al.*, 1976) and the report written by Williams (1978) summarised botanical data covering the whole 120 year period between 1856 and 1976. The field had been in grass for at least 100 years before the experiment started, receiving occasional dressings of farm yard manure (FYM) and sometimes guano, a manure derived from bird droppings and particularly high in phosphorus. The field was normally cut for hay in late June, followed by aftermath grazing by sheep. This management continued for most of the first 20 years of the experiment with each plot grazed separately after hay making, but after 1877 aftermath growth was cut and removed from the plots each year.

The fertilizer treatments applied to the Park Grass plots have been revised frequently and only four plots have remained unchanged throughout - two unmanured controls, one plot receiving ammonium sulphate and superphosphate equivalent to 96 kg ha^{-1} N and 35 kg ha^{-1} P, and one receiving the same with 225 kg ha^{-1} K, 15 kg ha^{-1} Na and 11 kg ha^{-1} Mg (Williams, 1978). The amounts of P, K, Na and Mg have been fixed at these rates wherever they have been applied. Several other treatments applied during the first three years were either replaced or later modified, with three new plots added in 1858 all receiving N as sodium nitrate - one with N alone at 48 kg ha^{-1}, one with the same N treatment plus P, K, Na and Mg, and the third with P, K, Na and Mg plus N at 96 kg ha^{-1}.

In 1859, two sawdust treatments were replaced by a P alone and an NP treatment with ammonium sulphate at 96 kg N ha^{-1} .

As the experiment progressed, the acidifying effects of the ammonium sulphate treatments became increasingly significant (Thurston *et al.*,1976). Some plots received a small amount of lime between 1881 and 1887 and a comprehensive liming scheme was introduced in 1903, with all plots split for ± lime by 1920. A new, more systematic scheme was introduced in 1965 aimed at producing sub-plots of pH 4, 5, 6 and 7 on each main plot (Thurston *et al.*, 1976).

An experiment similar to the Park Grass Experiment was established at the Royal Agricultural College at Cirencester in 1889. Kinch and Stapledon (1911,1912) reported data collected when the experiment had already been running for over 20 years. As with the Park Grass Experiment, most of the treatments were not replicated. This limitation was particularly severe at Cirencester, where soil depth varied between 20 and 46 cm over limestone, with corresponding variations in soil calcium carbonate content of between 20.0% and 1.4%. This had an overriding effect on the results. Shallow soils were dominated by *Bromus erectus*, while deeper soils supported a more even mixture of this species with *Festuca longifolia* (q.v.), *Dactylis glomerata, Lolium perenne* and *Trisetum flavescens*, with a range of more minor grasses, legumes and herbs distributed throughout most plots.

The Palace Leas Experiment is situated on a poorly drained clay loam over Boulder clay, described as naturally infertile though well supplied with potassium in the form of illitic clay (Arnold *et al.*, 1976). The previous history of these plots was similar to that of the Park Grass Experiment, and in common with those at Cirencester, plots were grazed by sheep and cattle after cutting for hay in late June. However, in contrast to the Park Grass Experiment, at Palace Leas and at Cirencester, the experimental area as a whole was released to unrestricted grazing of aftermath growth each year. At Palace Leas this was shown to have caused a regular net transference of nutrients from fertilized to unfertilized plots, which may have influenced the composition and productivity of all the plots (Shiel and Batten, 1988).

The experiment reported by van den Bergh (1979) and Elberse *et al.* (1983) was carried out in a species-rich meadow in a river valley on fairly acidic clay soil near Wageningen in the Netherlands. It was started in 1958 and lasted 20 years. This experiment differed from those described above in that a range of fertilizer treatments were compared either under cutting management alone (hay and aftermath cutting) or on plots grazed individually 3 or 4 times per year with young cattle without cutting. Previously, the meadow had been cut for hay and grazed by cattle in alternate years, with no fertilizers used. Unfertilized control plots were maintained under each defoliation regime, with individual treatments of P, K, PK, NPK and Ca applied to hay cut plots but only PK, NPK and Ca tested on grazed plots. Higher rates of N, P and K were applied under hay cutting than grazing, at 160, 52 and 332 kg N, P and K ha^{-1} respectively for hay, and 60, 18 and 50 kg ha^{-1} respectively on grazed plots. Lime was applied at 1.0 t ha^{-1} (0.7 t Ca ha^{-1}) to both sets of plots.

The experiment carried out by Elliott *et al.* (1974) and continued by Williams (1985) was conducted in the UK on alluvial soil overlying gravel at Begbroke in the Thames valley between 1965 and 1984. Here also, the effects of inorganic fertilizers were studied both under hay making and rotational grazing, following a long history of alternate hay making and grazing without fertilizer use. In this experiment, only two fertilizer treatments were tested under each defoliation regime, a complete nitrogen+phosphorus+potassium (NPK) treatment and a no-fertilizer control. The authors state that "known deficiencies of lime, P and K were made good early in 1965" on fertilized plots, but do not give the amounts applied in that year. Between 1966 and 1971, average N rates of 126 and 183 kg N ha^{-1} year^{-1} were applied to hay and grazed plots respectively. P and K were applied annually to hay plots at average rates of 19 and 73 kg ha^{-1} respectively between 1986 and 1971, and to grazed plots at 22 and 62 kg ha^{-1} in 1966 and 1967 only (Elliott *et al.*, 1974). Initially, aftermath growth on hay plots was grazed by cattle with no free movement between individual plots. However, hay making was abandoned after 10 years and all plots were grazed rotationally during the remaining years. No record of fertilizer rates is available for the years 1972-1975, but N, P and K were applied to all fertilized plots at 170, 17 and 33 kg ha^{-1} year^{-1} from 1976-1984 (Williams, 1985).

Response to fertilizers under hay cutting

Tables 2.1-3 list various sources of data on the response of species-rich meadows to fertilizer application. Where possible, the table gives the response to the individual elements N, P and K achieved, both in terms of DM yield increase per kg of the element applied and with the absolute increase expressed as a percentage of the control plot yield. Where more than one rate of a particular element is applied, the rates to which the response figure relates are noted. Where the data allow both comparisons, N response is quoted both in relation to plots receiving no P or K and compared to those receiving P and K without N. The data in Table 2.1 and 2.2 are from single cuts, taken in late June-July unless stated otherwise, with Table 2.2 including only experiments on calcareous soil. Table 2.3 contains data derived from the total of two cuts in each case (hay + aftermath), since many publications have not presented data for individual cuts separately. The decision to include a particular source in these tables (i.e. to classify the relevant site as 'species-rich') was often an arbitrary one, as most sources do not give the total number of species present. In these cases, the decision was made on the basis of the proportion of dicotyledonous species (forbs) present (e.g >35%) and the low abundance of species like *Lolium perenne, Holcus lanatus, Dactylis glomerata* etc.. Table 2.4 gives information similar to that in Table 2.3 but for vegetation of low-moderate species richness.

All the experiments included in Tables 2.1-2.4 were carried out on mineral soils (including calcareous soils). Table 2.5 includes sources from lowland peat soils for comparison.

All the values quoted in Table 2.1 and those for Somerville (1911) and Kinch and Stapledon (1911,1912) in Table 2.2. are given in terms of made hay. These values would tend to be slightly lower than corresponding yields calculated as DM at cutting, since DM losses during hay making (about 20-25%, see Chapter 3) will exceed the moisture content of made hay (about 12-17%).

Decline in soil fertility without P and K application

P and K were not applied separately in the early years of the Park Grass Experiment (Lawes and Gilbert, 1858), but N alone caused a substantial increase in hay yield. P and K applied without N increased yield by about 38% during the first three years and this may have been due at least in part to the increase in legume content which resulted from this treatment (Lawes and Gilbert, 1858, 1859a,b - see also later discussion under the botanical effects of fertilizer application). However, the yield response to P and K increased

Table 2.1. Experiments giving data on fertilizer response in species-rich hay meadows - hay yields and response at a single cut. Bracketed figures are increases in yield as a percentage of control plot yield. Yield and response figures in this table refer to made hay, except for those of Younger and Smith (1993), which are in dry matter (DM).

Source	Soil type	Treatments (e.g. N48 = 48 kg N ha^{-1}) and miscellaneous notes	Control plot yield (t hay ha^{-1})	Response (kg hay per kg element applied)				
				N	P	K	N +PK$^{(1)}$	N+PK$^{(2)}$
Lawes and Gilbert (1858) - *first 3 years of the Park Grass Experiment (PGE)*	clay loam over chalk	N48 (N_1), N96 (N_2), P35, K225, applied as N_1, N_1PK, N_2PK, PK and control (N0P0K0). Na and Mg also applied with PK. Mean of years 1-3.	3.02	23.5 (44) N0 - 48	-	-	75.4 (142) N0-48	55.2 (75)
				-	-	-	41.5 (156) N0-96	31.4 (86)
Brenchley (1924) (*Further data from PGE)*	"	Same as above, plus N192 (N_3) PK. Mean of years 1-10 (3-10 for N_3).	2.84	30.6 (52)	-	-	66.7 (113) N0-48	37.1 (42)
			-	-	-	-	40.2 (136) N0-96	25.4 (57)
			-	-	-	-	27.1 (183) N0-192	19.7 (89)
Elliott and Thomas (1934)	clay loam over boulder clay	N0P0K0, N35, P26 and K56 in all combinations. Mean of years 1-5	2.60	27.1 (37)	24.2 (24)	nil	38.0 (51)	18.0 (19)
Elliott *et al.* (1974)	alluvial loam over gravel	N126+P19+K73 *vs* unfertilized control	1.76	-	-	-	39.8 (285)	-
Kinch and Stapledon (1911,1912)	calcareous loam	Mean of two years data. Experiment 20 years old. N53, P72, K63 in all combinations *vs* control	1.93	20.7 (56)	15.4 (58)	10.5 (34)	52.1 (142)	35.3 (36)
Younger and Smith (1993)	calcareous loam	N80+P17+K33 v unfertlilized control. Mean of 3 cutting dates (June, July, Sept.) and three grazing treatments (none, autumn, aut. + spring)	4.20 (DM)	-	-	-	18.8 (36)	-

(1) Denotes response to N when applied with P and K compared to nil fertilizer control; (2) denotes response to N (appled with PK) compared to N0 +PK

Table 2.2. Experiments giving data on fertilizer response in species-rich grassland - yields and response at a single cut. Bracketed figures are increases in yield as a percentage of control plot yield. All yield and response figures in this table refer to dry matter (DM) production unless otherwise stated.

Source	Soil type	Treatments (e.g. N111 = 111 kg N ha^{-1}) and miscellaneous notes	Control plot yield (t DM ha^{-1})	Response (kg DM per kg element applied)				
				N	P	K	N +PK(1)	N+PK(2)
Willems (1980)	calcareous	Mean of 6 years yield, cut taken in August or October (mean of 8 years). Plots either previously de-turfed to 5cm (D) or not (O). N111+P355+K115 or N170+P50+K50 compared with no fertilizer	(D) 2.70	-	-	-	36.9 (152) N0-111	-
				-	-	-	24.7 (156) N0-170	-
			(O) 2.90	-	-	-	17.1 (66) N0-111	-
				-	-	-	15.3 (90) N0-170	-
Willems *et al.* (1993)	calcareous	N100, P42, K42+range of micronutrients, applied as K, NK, PK, NPK and no fertilizer. Cut in July	3.02	15.9 (53)	51.9 (72)	nil	28.8 (95)	7.0 (13)
Bobbink (1991)	calcareous	N100, P30, K100 applied singly and as NPK. Cut in October-November	1.99	13.1 (66)	18.3 (27)	nil	61.9 (311)	56.4 (222)
Somerville (1911)	calcareous	(a) P97 applied 9 years previously; (b) P48 and (c) P61, both applied 9 and 6 years previously. (a) and (b) applied as basic slag, (c) as Superphosphate. Plots were grazed by sheep until the current year. Yield and response as hay.	1.76 hay	-	20.7 (114)	-	-	-
				-	15.6 (85)	-	-	-
				-	7.2 (50) (a - c)	-	-	-

(1) Denotes response to N when applied with P and K compared to nil fertilizer control; (2) denotes response to N (appled with PK) compared to N0 +PK

Table 2.3. Experiments giving data on fertilizer response in species-rich hay meadows - hay yields and response from a total of two cuts per year. Bracketed figures are increases in yield as a percentage of control plot yield. All yield and response figures in this table refer to dry matter (DM) production.

Source	Soil type	Treatments (e.g. N48 = 48 kg N ha^{-1}) and miscellaneous notes	Control plot yield (t DM ha^{-1})	Response (kg DM per kg element applied)				
				N	P	K	N +PK(1)	N+PK(2)
Klesnil and Turek (1974)	(i) Podsol	(i) Mesophytic meadow, mean water table depth (WT) 70 cm. 54% legumes and forbs.	(i) 5.14	15.0 (24) N0-100	-	-	30.0 (58)	-
	(ii) Gley	(ii) meso-hydrophytic meadow, WT depth 35 cm (10-70). 81% legumes, forbs, sedges and rushes.		10.9 (42) N0-200	-	-	17.9 (70)	-
				7.8 (46) N0-300	-	-	14.4 (84)	-
		N100, 200,300 ± P22 and K33, compared with no fertilizer control, at both sites	(ii) 4.83	10.6 (22)	-	-	21.6 (42)	-
				8.3 (35)	-	-	15.3 (63)	-
				4.3 (27)	-	-	11.1 (69)	-
Rabotnov (1966)	Alluvial silt loam 3 sites (i-iii)	N60, P25 and K50 applied as: (i) P, K, PK, NPK; (ii) PK, NPK; (iii) N, P, PK,NK,NP,NPK; each site with nil fertilizer control.	(i) 3.72	-	9.7 (7)	23.1 (31)	54.4 (88)	31.9 (38)
			(ii) 5.43	-	-	-	60.2 (66)	46.7 (45)
		Sites i-iii progressively more susceptible to flooding	(iii) 2.19	12.2 (33)	3.0 (3)	2.7 (6)	18.0 (49)	15.3 (42)
Vermeer (1986)	Peat	N450, P50,K160, applied separately, compared with unfertilized control	7.4	4.0 (24)	nil	9.4 (20)	-	-
Elberse *et al.* (1983)	Heavy acid clay	N160, P52, K332, Ca715 applied as P, K, PK, NPK, Ca, compared with unfertilized control	4.8	_	13.5 (15)	nil	25.6 (85)	20.0 (56)

(1) Denotes response to N when applied with P and K compared to nil fertilizer control; (2) denotes response to N (appled with PK) compared to N0 +PK

Table 2.4. Experiments giving data on fertilizer response in species-poor and moderately poor pastures - yield and response totalled over two cuts. Bracketed figures are increases in yield as a percentage of control plot yield. All yield and response figures in this table refer to dry matter (DM) production.

Source	Soil type	Treatments (e.g. N27 = 27 kg N ha^{-1}) and miscellaneous notes	Control plot yield (t DM ha^{-1}	Response (kg DM per kg element applied)				
				N	P	K	N +PK(1)	N+PK(2)
Milton (1934)	Two acid upland sites in Wales	Site (i) Fescue dominated; (ii) *Molinia* dominated. At both sites a no fertilizer control was compared withCaPKN, i.e. Ca3590 every 5th year, P57,K50 and N27 every year. Response values refer to 1st year (1931)	(i) 1.09 (ii) 0.44	- -	- -	- -	18.9 (47) 1.1 (7)	- -
Milton and Davies (1947)	"	The above experiment continued until 1944. Yield and response figures refer to 1944. Other data from the sites suggest that response was mainly to Ca and P rather than N	(i) 2.24 (ii) 1.52	- -	- -	- -	232.2 (280) 144.8 (257)	- -
Jones (1934)	Not given (Welsh lowland)	Unfertilized v CaPKN, with Ca3600, P35, K70, N68. Swards previously grazed, described as 'highly fertile'.	11.2	-	-	-	7.5 (5)	-
Johnson and Meadowcroft (1968)	Heavy clay loam	Factorial design with confounding of treatments within blocks. P31, K125, N78, FYM. Control plot yield = ±P, response to N is mean of ±P and ±K	3.91	-	nil	3.2 (7)	-	22.0 (49)
Smith *et al.* (1971)	Calcareous	N106, K252, control factorial. All plots received P19. N response = (i) -K, (ii) +K. K response =(iii) -N, (iv) +N	0.73	(i) 11.7 (169)	-	(iii) 1.1 (39) (iv) 3.3 (42)	(iv) 19.6 (283)	(ii) 16.8 (176)

(1) Denotes response to N when applied with P and K compared to nil fertilizer control; (2) denotes response to N (appled with PK) compared to N0 +PK. FYM = Farmyard manure (dung)

Table 2.5. Experiments giving data on fertilizer response in vegetation on peat soils. Bracketed figures are increases in yield as a percentage of control plot yield. All yield and response figures in this table refer to dry matter (DM) production.

Source	Soil type	Treatments (e.g. N450 = 450 kg N ha^{-1}) and miscellaneous notes	Control plot yield (t DM ha^{-1})	Response (kg DM per kg element applied)				
				N	P	K	N +PK$^{(1)}$	N+PK$^{(2)}$
Data from one cut /year								
1.) Species-rich:-								
Vermeer (1986)	Peat - 3 sites	Site (i) floating fen; (ii) wet grassland; (iii) Hay meadow. (i) and (ii) cut in July, (iii) in June. N450, P50, K160 applied separately compared with unfertilized control	(i) 3.2	4.0 (78)	12.0 (19)	nil	-	-
			(ii) 4.1	8.8 (63)	16.0 (20)	nil	-	-
			(iii) 4.5	4.4 (44)	nil	4.4 (16)	-	-
2.) Species-poor:-								
Korkman (1976)	Carex peat	P17, K83 applied separately and as PK, compared with unfertilized control. Site previously received some P and K. Control yield declined 1.02 - 0.13 in 7 years	0.99	-	185.9 (320)	nil	-	-
van Vuuren and Verhoeven (1985)	Mesotrophic fen	N292, P71, K92, control. Transplanted sods. Vegetation cut July	4.99	3.0 (18)	nil	nil	-	-
Verhoeven and Schmitz (1991)	3 fen sites	Fens (i) and (ii) fed by Ca-rich groundwater. Fen (iii) frequently flooded by polluted river water. N200, P50, K160 applied as N, P, K, NPK, control	(i) 3.35	6.4 (38)	12.8 (19)	nil	12.3 (73)	9.1 (46)
			(ii) 1.90	nil	26.0 (68)	1.9 (5)	17.4 (183)	10.9 (68)
			(iii) 3.80	3.8 (20)	nil	nil	1.5 (8)	3.4 (20)
Data from 2 cuts / year *(species-poor):-*								
Gotkiewicz (1988)	Well-decomposed alder peat	N60, P22, K83 applied as K, PK, NPK and unfertilized control. (a) = mean years 1-5; (b) = mean years 21-28; (c) = mean years 1-28. P response is relaive to K83 treatment.	(a) 3.06	-	101.8 (29)	55.7 (151)	120.0 (235)	5.7 (3)
			(b) 0.94	-	223.6 (109)	39.3 (380)	150.0 (996)	14.3 (9)
			(c) 1.50	-	209.1 (96)	39.8 (220)	141.7 (567)	10.0 (6)

(1) Denotes response to N when applied with P and K compared to nil fertilizer control; (2) denotes response to N (appled with PK) compared to N0 +PK.

progressively from 50% averaged over years 1-10 to 84% for years 11-20, reaching 173% for years 50-60 (Brenchley, 1924). This effect was mainly due to declining yields on control plots, whereas yield declined little where P and K were applied. When K was omitted from one of the PK plots after the first five years, there was little effect averaged over years 1-10, but thereafter yield declined on the plots without K, the difference increasing from 28% averaged over years 11-20 to 41% for 1896-1905 (years 40-50)(Brenchley, 1924).

P : N and N : K ratios in herbage

The figures in Table 2.1 indicate a curved N response through the range N0-48-96 (Lawes and Gilbert, 1858) which was even more marked when a higher N rate of 192 kg N ha^{-1} was added (Brenchley, 1924). The response to N may have been limited by P and K availability, despite the high rate of K used. Data provided by Knauer (1966) and by Prins *et al.*, (1986) allow an assessment of the adequacy of P and K supply based upon the P:N and N:K ratios in herbage at different levels of herbage N concentration. The values of Knauer were based upon a wide range of experiments in mixed species old meadows in central Europe, most of which were probably species-rich, whilst those given by Prins *et al.* were derived from more intensively managed pastures. Nevertheless, there is fairly good agreement between these two sources in the values presented, although those of Prins *et al.* tend to be more demanding of P and K at high herbage N concentrations. Both sets of criteria show that both P and K appeared to limit N response during the first years of the experiment, but data from Thurston *et al.* (1976) show that by 1920 P was not limiting on plots receiving P, except where it had been applied with the higher N rates. K was limiting on all plots except those receiving K application.

N x P x K interactions

Elliott and Thomas (1934) show substantial increases in hay yield averaged over the first 5 years of the Palace Leas experiment by applying N and P alone, despite the low rates used. This experiment is unusual among the older studies in that all combinations of N, P and K were tested. Multiple regression analysis on these data shows a significant N x P interaction (R^2=0.886), although there was no overall effect of P addition. K had no effect on yield. Similar analyses on subsequent data given by Pawson (1960) and Arnold *et al.*

(1976) show significant overall effects of P and an increasing N x P interaction: $R^2=0.94$ for years 6-10 and 0.97 for years 11-20.

By contrast with the Park Grass Experiment, yield increased significantly over time between 1897 and 1980 on all plots except those where P was omitted ($P<0.001$ for FYM, PK and NPK, $P<0.05$ for P and NP, by linear regression). Hay yield on control plots and those receiving N or NK declined significantly until 1975 ($P<0.05$, 0.05 and 0.001 respectively), but increased again between 1975 and 1980 (Elliott and Thomas, 1934; Pawson, 1960; Arnold *et al.*, 1976; Shiel and Batten, 1988).

Data provided by Elliott *et al.* (1974) in the Thames Valley showed a response per kg N applied similar to that shown by Elliott and Thomas (1934), although the proportionate increase compared with control was nearly six times as great. However, the control plot yield shown by Elliott *et al.* (1974) was low compared with the remainder in Table 2.1. By contrast, the base productivity of meadows in Teesdale, reported by Younger and Smith (1993), was somewhat higher than the remainder. This may have been due to an interaction between fertilizer application, cutting date and/or grazing management, although the authors do not remark on this.

Fertilizer response on calcareous soils

The sites on calcareous soil showed substantial responses to both N and P, but K appears to have been much less important (Table 2.2). The responses to N shown by Kinch and Stapledon (1911,1912) with or without P and K, were close to those shown by Brenchley (1924), although control plot yields were considerably lower. N appeared to be a more important determinant of yield in the chalk grassland reported by Willems (1980), both following de-turfing and in undisturbed turf, since in both cases yield was increased more by the high-N-low-P-and-K treatment compared with the treatment which included a lower N rate and substantially higher rates of P and K. Both N and P, particularly the latter, were limiting at the chalk grassland site studied by Willems *et al.* (1993), although the response to N with P and K was lower than either that shown by Willems (1980) or in the Park Grass Experiment (Lawes and Gilbert, 1858; Brenchley, 1924). Bobbink (1991) showed a greater response to N than to P, which the author attributed to the dominance of the nitrophilous grass *Brachypodium pinnatum* (the botanical results from this experiment are discussed

later). However, herbage P:N ratios (Knauer, 1966; Prins *et al.*, 1986), derived from the data presented, suggest that P supply was insufficient for maximum N response even where P was applied. Note that the vegetation was harvested later in the year in this experiment than others recorded in the Tables.

The marked persistence of the response to P shown by Somerville (1911) was at variance with the later results of Norman (1956) quoted above and with the known behaviour of P in calcareous soils (Olsen, 1953). Somerville attributed this effect to the large and persistent increases in the legume content recorded on P plots, combined with the effects of continuous grazing which would maintain the cycling of available P (Gillingham, 1987; Shiel and Batten, 1988). Norman (1956) recorded small increases in clover content with P application, but these were probably insufficient to account for much of the yield increase. Swards were grazed discontinuously between April and October in Norman's experiment, and nutrient cycling was probably less intensive than in Somerville's experiment.

Yield response of species-rich meadows under a two-cut system

In the experiments of both Klesnil and Turek (1974) and Rabotnov (1966) N response was lowest at wetter sites (Table 2.3). These tended to be the more species-rich sites, particularly in the second of Klesnil and Turek's experiments where grasses occupied only 20% of the vegetation and sedges and rushes were major components. Yields on unfertilized plots were highest on the site where flooding frequency and duration were intermediate in Rabotnov's studies. There was little response to P and K at the wettest site and P had little effect on its own at the driest site where K appeared to be significantly limiting. The yield without fertilizers and response to N recorded by Elberse *et al.* (1983) in an acidic riverine clay soil was consistent with those of the other species-rich meadows shown in Table 2.3, although the response to P was greater than at any of the three sites studied by Rabotnov (1966).

The base productivity of the peatland hay meadow reported by Vermeer (1986) was notably higher than that of any of the other experiments listed in Table 2.3, and it showed no response to P, a moderate response to K and comparatively little response to N. This site is compared with others on peat soil in Table 2.5.

Productivity and fertilizer response in species-poor vegetation

The productivity of species poor sites listed in Table 2.4 is very variable, at least partly reflecting the reasons for the paucity of species. The Welsh upland swards studied by Milton (1934) and Milton and Davies (1947) had previously been subjected to very lax and infrequent grazing and were dominated by fine-leaved *Festuca spp.* and *Agrostis capillaris* or by *Molinia caerulea*. The interaction of fertilizer application and controlled grazing in changing the composition of these swards is discussed later. However, some plots were fenced and allowed to grow hay at two cuts per year without grazing and data from these plots are included in Table 2.4.

Only two treatments were tested on these plots, an unfertilized control and a Ca+P+K+N treatment. Yield increases are expressed in terms of response to N in the Table, but other data from these sites shows that Ca and P were more important on the acid soils. Yield increased with time on all plots, but whereas these increases continued throughout the whole 1931-1944 period on fertilized plots, the main increase on control plots occurred during the first three years. The response to CaPKN was modest initially compared to some of those shown in Table 2.3 for a similar defoliation frequency, but there was a very large increase in response with time. Nevertheless, the productivity even of the fertilized plots was low compared with that of lowland Welsh pastures studied by Jones (1934), which he described as 'highly fertile' and dominated by *L. perenne* and *Trifolium repens*. These swards were previously grazed fairly intensively by sheep and fertilizer application did not improve their productivity significantly.

Despite the comparatively modest productivity of the unfertilized permanent pastures studied in the north of England by Johnson and Meadowcroft (1968), they recorded no response to P and a comparatively modest overall response to K. The response to N with P and K was substantially smaller per kg N applied than those recorded in two of the three species-rich sites by Rabotnov (1966), although in absolute terms the increase was comparable to all three of Rabotnov's experiments (Tables 2.3 and 2.4).

The site of the experiment carried out on chalk downland by Smith *et al.* (1971) is in some ways analagous to those of Milton, although in other ways very different. This sward had not been grazed in recent years by domestic animals and the only defoliation it had received was by rabbits. The vegetation was dominated by *Festuca rubra* and was

of very low productivity, but unlike Milton's swards the soil pH was high. P was applied to all plots and there was a significant N x K interaction.

As noted previously, the hay meadow included in the series of three experiments on peat soil by Vermeer (1986) was fairly productive without N, P or K. This site showed no response to P in contrast with the fen site and the wet grassland, although K appeared to be slightly limiting compared with these other sites. Nevertheless, substantial increases in hay DM were achieved by applying N alone (44-78%), although the high rate used (450 kg N ha^{-1}) means that the response per kg N applied is not comparable with other experiments in Table 2.5.

P and K depletion in organic soils

The experiments of both Korkman (1976) and Gotkiewicz (1988) showed the effects of P depletion by continual removal of hay without replacement of P. The site studied by Korkman had received quite high rates of P and K 37 years beforehand and levels had been regularly topped up since then during the growth of various arable crops. Control plot yield declined dramatically over the first 7 of the 9 years of the experiment, and a very large differential developed between these plots and those receiving a quite modest rate of P. There was no response to K, possibly because of the overriding limitation of P depletion. At the site studied by Gotkiewicz (1988) which had also been cropped previously, DM yield declined rapidly on control plots from 7.6 t ha^{-1} to 1.5 t ha^{-1} over the first five years, and even over this period substantial responses to both P and K were obtained. Differences attributable to the application of both these elements were very large by the last 5 of the 28 years of the trial, but the additional effect of applying N was small throughout, by contrast with the undrained sites of Vermeer (1986). The sites used by Gotkiewicz (1988) and by Korkman (1976) were both well drained and both authors estimate that large amounts of N were mineralized during the experiments. It appears that without inputs of P and K from fertilizers, from flooding or from groundwater, the P status of these lowland peats may have been reduced to levels approaching those limiting crop growth in blanket peat, whilst mineralization of organic N was sufficient to allow large increases in yield when P and K were applied.

N delivery capacity

t'Mannetje (1994) classified grassland soils in the Netherlands into four groups based on 'N delivery capacity' (NDC). Groups 1 and 2, those capable of delivering the highest levels of N, were well-drained and poorly-drained peats respectively, group 3 included mineral soils rich in humus and group 4 comprised other mineral soils. NDC values were 300, 230, 200 and 140 kg N ha^{-1} for groups 1-4 respectively. These differences in NDC were mirrored by corresponding differences in N rates needed to give optimum DM response and utilization of applied N, reported by Wouters and Vellinga (1994). These averaged 190 and 294 kg N ha^{-1} for well-drained and poorly drained peats respectively, compared with 308-356 kg ha^{-1} for mineral soils.

Productivity and fertilizer response in relation to soil type and vegetation composition - some conclusions

Existing data do not suggest a clear-cut relationship between the species composition of vegetation and its productivity and potential response to fertilizers. Swards dominated by *L. perenne* are more responsive to high N rates than mixed species vegetation with frequent defoliation, but other indigenous species are more productive at lower rates and with infrequent defoliation. Data on the response of grassland to high rates of N (>200 kg N ha^{-1}) under hay making are very sparse, particularly from species-rich vegetation.

The response of vegetation to P and K application depends greatly on previous inputs, but P availability is often low in calcareous and organic soils compared with clay soils and loams. However, increases in yield can be obtained in most soil types by applying P and/or K and this is often due to increases in the legume content of vegetation resulting from a more favourable (for legumes) P:N balance in the soil (see later discussion). Therefore, differences in DM response between N and P applied separately do not always reflect accurately differences in N and P availability in unfertilized soil relative to requirements for grass growth, since the response to P may be attributable to an increased supply of legume-fixed N. On the other hand, P and K applications are normally required to obtain maximum response to high rates of N.

The response of lowland peat soils to applied N often depends upon drainage status and pH, both of which influence the rate of N mineralization from organic matter. Drainage status may also be significant for P and K availability if potential flood or seapage water contains significant concentrations of these elements.

FERTILIZERS AND BOTANICAL COMPOSITION

A large number of experiments have been reported giving information about the effects of inorganic fertilizers on the botanical composition of species-rich and moderately species-rich temperate vegetation and many of these have been reviewed previously (e.g. de Vries and Krujne, 1960; Rorison, 1971; Rabotnov, 1977; Snaydon, 1987b; Marrs, 1993). Pigott (1982) noted that in the Park Grass Experiment (Williams, 1978), different treatments have produced distinct, separately identifiable and recognizable vegetation types. Stapledon (1914) had earlier made a similar observation with reference to several of the fertilizer experiments current at the time, including the Park Grass Experiment (Lawes *et al.*, 1882), the Palace Leas Plots at Cockle Park (Gilchrist, 1906) and the Chapel Close Experiment at Cirencester (Kinch and Stapledon, 1911,1912). His fairly rudimentary scheme for classifying grassland 'types' according to their species composition and in relation to fertilizer use was described in Section 2.3.

A more general conclusion from fertilizer experiments is that fertilizer N, applied either alone or with P and K, can rapidly increase the contribution of grasses to biomass or vegetation cover at the expense of legumes and other dicotyledonous (forb) species. The greatest impact has usually been observed when N and P or all three elements have been applied together. These effects have been shown on a variety of soil types in a variety of locations throughout Europe: on calcareous soils in the UK (Kinch and Stapledon, 1911,1912; Kydd, 1965) and in the Netherlands (Willems, 1980; Bobbink *et al.*, 1988; Willems *et al.*, 1993); on a flinty loam overlying flinty clay over chalk in the UK (Lawes *et al.*, 1859a,b; Williams, 1978); on clay loam over boulder clay in the UK (Gilchrist, 1906; Arnold *et al.*, 1976; Garstang, 1981); on sandy loam in Poland (Traczyk and Kotowska, 1976; Traczyk *et al.*, 1976) and in Belgium (Hecke *et al.*, 1981); in sand dunes in the UK (Willis, 1963); on podsol and gley soils in Czechoslovakia (Klesnil and Turek, 1974); on alluvial and river clay soils in the USSR (Rabotnov, 1966,1977), in the Netherlands (Elberse *et al.*, 1983) and in Poland (Petal, 1983; Pasternak-Kusmierska, 1984); and on lowland peat in the Netherlands (Vermeer, 1986), in Poland (Benedycki *et al.*, 1989) and in the UK at

Tadham Moor (Mountford *et al.*, 1993a).

Why do N fertilizers increase grasses at the expense of other species?

Grasses show a number of characteristics which can account for their superiority over forbs and legumes with N application, including more rapid accumulation of biomass in spring (Grime, 1980), more efficient utilization of absorbed N, a larger proportion of roots in the upper soil layer, better water economy, which is improved by N application, and tall growth giving more efficient light interception (Rabotnov, 1966,1977). Pigott (1982) gives several examples of the competitive advantages given by tall stature in plants. He cites work by Monsi and Saeki which shows that a raised canopy can reduce irradiance by a factor of 20 compared with lower canopies where the leaf area index (i.e. the total area of leaf in relation to the area of ground covered) is only slightly lower. Prostrate forb species in particular tend to be eliminated in tall vegetation produced by NPK fertilizer treatments (Williams, 1978; Pigott, 1982). Pigott (1982) quotes the example of *Leontodon hispidus*. This species can respond significantly to N and P in terms of vegetative growth and capitula production under favourable conditions (Lloyd and Pigott, 1967), but since *L. hispidus* cannot raise its leaves above about 15 cm, it is particularly susceptible to shading in tall vegetation. By contrast, *Centaurea nigra* can persist in these situations by producing leafy stems of up to 50 cm in height (Pigott, 1982), although even *C. nigra* can be reduced by NPK application (Williams, 1978; Willems, 1980; Elberse *et al.*, 1983).

Legume content in response to N, P and K

Applying P alone or with K usually increases the contribution of legumes (Lawes and Gilbert, 1859a,b; Middleton, 1905; Gilchrist 1906; Somerville, 1911; Kinch and Stapledon, 1911,1912; Norman, 1956; Kydd, 1965; Rabotnov 1966,1977; Arnold *et al.*, 1976; Williams, 1978; Hecke et *al.*, 1981; Bobbink *et al.*, 1988; Willems *et al.*, 1993). As with the positive effect of N on grass content, several factors can affect the response of legumes to fertilizers. Legumes have a less ramified root system than grasses (Kydd, 1965; Jackman and Mouat, 1972) and are therefore less able to compete for P and K when N is applied. Furthermore, the cation exchange ability of grass roots is superior to that of legumes, so that grasses absorb available K more efficiently (Gray *et al.*, 1953; Mouat and Walker,

1959).

Since legumes have the ability to fix atmospheric N, applying P and K without N tends to alter the nutrient balance in their favour, but when N is applied, grasses respond more rapidly than legumes. The increased shading resulting from the denser vegetation produced by N application has been shown to reduce clover growth (Stern and Donald, 1962), although the mechanisms involved are not straightforward (Thompson, 1993b). Dennis and Woledge (1985) showed that the photosynthetic potential of young *Trifolium repens* leaves was not reduced when N was applied to a *Lolium perenne/T. repens* sward. Although N had reduced the proportion of *T. repens* in the vegetation, the authors concluded that shading by grass was not the cause, since clover was able to elevate most of its leaves to the top of the canopy, with mean petiole lengths reaching 26-28 cm by late June. However, in work by Stern and Donald (1962), clover growth rates were significantly suppressed by shading from grasses when leaf area indices increased above those recorded by Dennis and Woledge (1985). Furthermore, recent work shows that shading at the basal node reduces *T. repens* stolon branching and the number of leaves produced per branch, and that these effects appear to be due to changes in both the quantity and quality (wavelength) of light reaching the nodes (Thompson, 1993b). The same study showed that shading by *Holcus lanatus* reduced *T. repens* leaf production more than shading by *L. perenne* or *Agrostis stolonifera,* whilst stolon branching was reduced to a greater extent by shading from either *Holcus* or *Agrostis* compared with *Lolium.* These results suggest that the confident generalization made by Robson *et al.* (1989), on the basis of work in *L. perenne/T. repens* swards, that grasses do not "shade out clovers under UK conditions and with UK forage species" when N is applied is unjustified, particularly as *L. perenne* (at 10-90 cm) is much shorter in stature than most other 'forage' grasses, e.g. *Lolium multiflorum* (30-100 cm), *Festuca pratensis* (30-120 cm), *Dactylis glomerata* (15-140 cm) and *Phleum pratense* (40-150 cm), as well as other indigenous grasses such as *H. lanatus* (20-100 cm), *Alopecurus pratensis* (30-120) and *Arrhenatherum elatius* (50-150 cm)(Hubbard, 1984). Not only are these taller species more likely than *L. perenne* to overtop clover if undefoliated, but, as noted above, the degree of light attenuation at the base of the sward is likely to be greater than that caused by shorter vegetation at equivalent leaf area indices (Pigott, 1982).

Fertilizer effects in grazed swards

The differences in stature between grasses are particularly relevant when vegetation is harvested infrequently or not at all. Most fertilizer experiments have been conducted under cutting management, presumably for logistical reasons, and in most of those quoted above the first cut was taken for hay in June or July each year. However, several experiments have shown significant fertilizer-induced botanical changes under continuous or rotational grazing (Kydd, 1965; Elliott *et al.*, 1974; Elberse *et al.*, 1983; Williams, 1985; Tallowin *et al.*, 1990). Early studies by Armstrong (1907) showed that the most fertile and productive grazed permanent pastures were those dominated by *L. perenne* and *T. repens*, whilst poorer pastures usually contained a high proportion of *Agrostis* spp. and a wider variety of forbs. In experiments where grazing was compared with hay making, fertilizer application caused botanical changes of similar overall magnitude under each defoliation regime, although the responses of individual species differed significantly between cutting and grazing (Elliott *et al.*, 1974; Elberse *et al.*, 1983).

Variation in individual species dominance

The effect of fertilizers on botanical composition can be very rapid, and significant changes often occur within 1-3 years with repeated application. Species such as *Dactylis glomerata* and *Arrhenatherum elatius* often become dominant within this time-scale with NPK application, particularly in the absence of grazing (Traczyk and Kotowska, 1976; Traczyk *et al.*, 1976; Williams, 1978; Willems, 1980; Petal, 1983; Pasternak-Kusmierska, 1984). In grazed chalk downland in the UK, *D. glomerata* was increased by PK and by NPK treatment compared with K alone, and by resting from grazing from August to November or from August to April compared with resting in April or no rest at all (Kydd, 1965). *Alopecurus pratensis* often increases rapidly with N application (Klesnil and Turek, 1974; Williams, 1978; Elberse *et al.*, 1983) and was favoured by hay cutting as opposed to grazing in work by Elberse *et al.* (1983). However, in two experiments in ungrazed vegetation on peat soils in Poland, *A. pratensis* increased markedly at one site, mainly at the expense of *Phalaris arundinacea*, but declined significantly at the second site where it was apparently replaced by *Poa pratensis* (Benedycki *et al.*, 1989). In the Park Grass Experiment, *A. pratensis* was increased initially only when N was given as sodium nitrate, as opposed to the acidifying ammonium sulphate, although it later increased with the latter treatment when plots were limed (Williams, 1978). *Poa pratensis* can increase rapidly with NPK fertilization (Traczyk and Kotowska, 1976; Williams, 1978; Elberse *et al.*, 1983; Petal, 1984; Benedycki *et al.*, 1989). In work by Elberse *et al.* (1983), *P. pratensis* was increased by NPK and by lime under hay cutting but not under grazing, whilst the opposite was true for *P. trivialis*. Tallowin *et al.* (1990) showed rapid replacement of *P. trivialis* by *L. perenne* during the course of one growing season when N was applied under continuous grazing, whereas elsewhere *P.trivialis* has either increased (Elliott *et al.*, 1974; Traczyk and Kotowska, 1976; Williams, 1978) or declined (Hecke *et al.*, 1981; Tallowin *et al.*, 1990) with NPK application. In the two experiments reported by Benedycki *et al.* (1989), *P. trivialis* was increased in one experiment by moderate fertilizer application (120 kg N, 33 kg P and 99 kg K ha^{-1}) but reduced by higher rates (N180, P44, K132), whereas in the other experiment it was reduced by all rates of NPK (i.e. N60, P22, K66 and above). Elliott *et al.* (1974) recorded rapid ingress of *P. trivialis* under both grazing and hay cutting (with aftermath grazing), particularly the latter, although the species was not recorded in the vegetation at the start of the experiment.

Factors affecting the response of L. perenne *and* H. lanatus

In experiments where *L. perenne* was recorded initially, it soon became a major vegetation component with NPK fertilization, provided plots were grazed, either following hay making or throughout the season (Williams, 1978; Elberse *et al.*, 1983; Mountford *et al.*,1993a). In the absence of grazing the species often declines with fertilizer application (Traczyk and Kotowska, 1976; Traczyk *et al.*, 1976; Elberse *et al.*, 1983). However, *L. perenne* was increased very significantly by NPK under 4-weekly cutting in an experiment carried out on a fertile pasture where it initially comprised 15% of the vegetation, especially where very high rates of N (658-850 kg year^{-1}) were applied (Garstang, 1981). These results are consistent with data provided by Frame (1991) who showed that the yield response to N of *L. perenne* relative to other species was greater under frequent than infrequent defoliation and that it ranked higher at 240-360 kg N ha^{-1} year^{-1} than at 120 kg ha^{-1}. *L. perenne* is also notably resistant to trampling and wear compared with other species (Edmond, 1966; Canaway, 1980) and is associated with relatively frequent disturbance

(Grime *et al.*, 1988). It was very significantly increased by N application to grazed swards where cattle grazing intensity was closely related to fertilizer application (Tallowin *et al.*, 1990).

Holcus lanatus tends to increase with moderate levels of NPK but not at higher rates (Traczyk and Kotowska, 1976; Traczyk *et al.,* 1976; Williams, 1978). In the Park Grass Experiment, *H. lanatus* rapidly became co-dominant with *L. perenne* on plots receiving 96 kg N ha^{-1} as ammonium sulphate with P and K, but not where N was applied as sodium nitrate (Williams, 1978). *H. lanatus* eventually dominated plots receiving ammonium N at a higher rate of 144 kg N ha^{-1}, but not until the pH had been lowered substantially by ammonium sulphate application over several decades. Elliott *et al.* (1974) reported a doubling of the *H. lanatus* content after six years of fertilizer application with rotational grazing (N183, P22, K62), but with no difference due to fertilizer application under hay making and aftermath grazing. Under continuous grazing, *H. lanatus* was reduced by N at 400 kg ha^{-1} compared with no fertilizer or N200 (Tallowin *et al.*, 1990). *Holcus* became dominant with NPK application in the large scale experiment (Experiment 1) at Tadham Moor under hay making and aftermath grazing, although it was displaced somewhat by *L. perenne* in the fourth year (Mountford *et al.*, 1993a). *Holcus* dominance was very marked where high rates of P were applied with N and K to plots cut three times per year in the small scale experiment (Experiment 2, see Chapter 5).

With the exception of *H. lanatus,* all the species noted so far are associated with moderately fertile or fertile environments and have Ellenberg N scores of 6 or 7 (Ellenberg, 1988 - see Section 2.3 above). Ellenberg gives *H. lanatus* an N score of 3, indicating that it is more often found on N deficient soils than under fertile conditions, but Grime *et al.* (1988) describe it as typical of relatively fertile soils in the UK, though usually distributed only sparsely in grazed pastures. It is less tolerant both of trampling and of frequent and severe defoliation than *L. perenne* (Edmond, 1966; Watt and Haggar, 1980). Baker (1937) compared the vegetation of grazed and mown species-rich meadows near Oxford where the management had remained unchanged for at least 100 years. *H. lanatus* was marginally more common with mowing than grazing. *L. perenne* was dominant in all but the wettest areas under grazing and was far less abundant in mown meadows.

Grime *et al.* (1988) classed both *H. lanatus* and *P. pratensis* as having an intermediate established strategy, i.e. competitor-stress tolerator-ruderal (C-S-R), whereas both *L. perenne* and *P. trivialis* were classed as intermediate between C-S-R and C-R, indicating a slightly greater association with disturbance. *Arrhenatherum elatius* was classed as a competitor (C) in recognition of its preference for fertile, undisturbed habitats (Grime *et al.*, 1988), whilst both *D. glomerata* and *A. pratensis* were intermediate in classification between C-S-R and C.

Dominance in chalk grassland

The vegetation of chalk grassland is characterised by the low productivity and high species-richness which are associated with low levels of soil P or N and P (Lloyd and Pigott, 1967; Grime and Curtis, 1976; Willems *et al.*, 1993). In several experiments carried out in the Netherlands, application of inorganic fertilizers led to dominance by *Brachypodium pinnatum* (Bobbink *et al.*, 1988; Bobbink, 1991; Willems *et al.*, 1993). These experiments showed that *B. pinnatum* dominance was greater when N was applied alone than when applied with P or P and K . This response was attributed to greater efficiency of P uptake and translocation in this species compared with its competitors (Bobbink, 1991; Willems *et al.*, 1993). *B. pinnatum* was classed by Grime *et al.* (1988) as a stress tolerant competitor (S-C) and was associated with little-grazed areas. Ellenberg (1988) gave it an N score of 4. *Bromus erectus*, which often grows with *B. pinnatum* in the UK, was given a slightly lower Ellenberg N score of 3. This species, classed as C-S-R/S-C by Grime *et al.* (1988), was the dominant species in a long term experiment carried out in calcareous grassland in the UK, where its dominance was further increased by applying NPK (Kinch and Stapledon, 1911,1912).

Each of the species noted so far has achieved dominance, at least in the short term, in one or more of the experiments quoted in this section. Most are associated with low-intermediate species-richness (Grime *et al.*, 1988). *A. pratensis* is associated with moderately species-rich vegetation, except where it is abundant, when species-richness is usually lower (Grime *et al.*, 1988). *Brachypodium pinnatum* and *Bromus erectus* are associated with intermediate to high and high species richness respectively, although *B. pinnatum* is associated with low diversity where defoliation is infrequent (Grime *et al.*, 1988).

Whilst the classifications and strategies attributed to these species are confirmed in broad terms by their response to fertilizers in grazed and un-grazed vegetation, these responses vary greatly between experiments, even in the short term. The behaviour of individual forb species is somewhat more predictable.

Response of forbs to fertilizers

Most vulnerable among the forbs are prostrate and rosette species such as *Plantago lanceolata, Leontodon hispidus, Pilosella* spp. and *Hypochaeris radicata*, although other more erect species such as *Picris hieracioides, Artemisia vulgaris, Campanula patula, Centaurea nigra* and *Leucanthemum vulgare* are also susceptible (Traczyk and Kotowska, 1976; Williams, 1978; Willems, 1980; Elberse *et al.*, 1983; Pasternak-Kusmierska ,1984). All these species are associated with species-rich vegetation in the UK (Grime *et al.*, 1988). *Rumex acetosa*, which is associated with intermediate levels of species-richness (Ellenberg, 1988; Grime *et al.*, 1988), has shown variable results, either increasing (Traczyk and Kotowska, 1976; Williams, 1978) or declining (Elliott *et al.*, 1974; Traczyk *et al.*, 1976; Elberse *et al.*, 1983; Williams, 1985) with NPK application. The decline of this species on fertilized plots recorded by Elliott *et al.*, (1974) was more pronounced under grazing than under hay making with aftermath grazing. *Anthriscus sylvestris* was greatly encouraged by NPK fertilization under hay making but not in grazed swards (Elberse *et al.*, 1983). This species also became moderately abundant in the Park Grass Experiment on plots receiving sodium nitrate N with P and K (Williams, 1978), although in both experiments it took about 10 years to appear in the plots. This species was classed as a competitive-ruderal (C-R) by Grime *et al.* (1988), who noted that it was susceptible to frequent defoliation and to trampling, and was therefore most often found at the edges of fields. Grime *et al.* (1988) noted that, where it was abundant, *A. sylvestris* was characteristic of species-poor vegetation. Ellenberg (1988) gave it an N score of 8, unusually high for a forb species, indicating a preference for nutrient-rich soils.

The foregoing paragraphs are by no means a comprehensive account of the changes that can be induced in the short term by fertilizer application. The experiments quoted were chosen merely as representative of the large number of studies that have been carried out on a variety of soil types. However, the results illustrate the point noted in Section 2.3 that the response of individual species in mixed vegetation can vary greatly in different situations. Whilst much of this variation could be accounted for by differences in defoliation management, much variation still existed between experiments where cutting/grazing management was similar.

Long-term trends in species composition

Most long-term experiments showed large temporal fluctuations in the relative abundances of the major vegetation components (Lawes and Gilbert, 1859a,b; Lawes *et al.*, 1882; Kinch and Stapledon, 1911,1912; Elliott *et al.*, 1974; Williams, 1978; van den Bergh, 1979; Elberse *et al.*, 1983). These fluctuations were often notable even on unfertilized plots, although usually more marked with fertilizer application. However, of these studies, only the Wageningen experiment included detailed botanical assessments made annually throughout its whole 20 year duration (van den Bergh, 1979; Elberse *et al.*, 1983). Elberse *et al.* (1983) emphasised the need for regular monitoring of the vegetation in long term-studies. They remarked that, because of the wide fluctuations in botanical composition, quite different conclusions would have been reached had the experiment been terminated after say five, ten or fifteen years with assessments made only at the beginning and end of the experiment. Even in the Park Grass Experiment there were large periods when no complete botanical assessment was made. Notable gaps were between 1877 and 1903 and between 1949 and 1973, although hay samples were separated into grasses, legumes and 'others' in each year from 1878 to 1902 (Williams, 1978). At Begbroke, plots were assessed annually from 1965-1969 and in 1971 (Elliott *et al.*, 1974), and finally in 1979 and 1984 (Williams, 1985). Botanical data from the Palace Leas plots at Cockle Park are sparse. Complete assessments were made at the beginning of the experiment in 1897 and in 1984 and some of these data have been summarised in terms of species diversity by Smith, (1987). Gilchrist (1906) made some largely anecdotal references to the reaction of individual species after 8 years and further details of assessments made in 1973 and 1981 have been reported (Arnold *et al.*, 1976; Shiel and Batten, 1988).

At Wageningen, where the vegetation was previously managed by hay cutting and grazing in alternate years, grazed unfertilized plots showed the least interchange between species over the 20 years of the experiment (van den Bergh, 1979). However, even on these plots the abundance of species such as *Poa trivialis, Alopecurus pratensis, Agrostis spp., Ranunculus acris* and *Plantage lanceolata* varied greatly either from year to year (particularly *P. trivialis*) or over longer periods, e.g. *P. lanceolata* and *R. acris.*

Influence of grazing on long-term trends

Some of the differences between experiments in the behaviour of individual species may be attributed to differences in defoliation management, i.e. aftermath grazing compared with cutting only or cutting *versus* grazing, but this is not always clearly the case. For example, *Holcus lanatus* increased sharply at first with NPK fertilizers, both at Rothamsted (Lawes and Gilbert, 1859a,b; Williams, 1978) and at Wageningen (van den Bergh, 1979; Elberse *et al.*, 1983). At Wageningen, it declined equally sharply after 3-4 years under hay cutting, though less so where P was applied alone, whereas higher levels were maintained with grazing. At Rothamsted (where all plots were cut for hay followed by aftermath grazing during the first 20 years), *H. lanatus* declined gradually after the first two years to levels equivalent to unfertilized plots by 1877, then increased again. By the 1920s, *Holcus* dominated those NPK plots that received N as sulphate of ammonia, making up 100% of the herbage on these plots by 1930. After 1948 it declined to only 13% in 1973, by which time it appeared to have been replaced largely by *Anthoxanthum odoratum.* The ascendancy of both these species from 1905 onwards was attributed to the acidifying effect of ammonium sulphate, since neither reached anything like such prominence on similar areas which received lime from 1914 onwards (Williams, 1978).

In contrast with results from Wageningen, at Begbroke *Holcus* was more abundant with hay making followed by grazing than with grazing only during the period that both defoliation managements were in operation (Elliott *et al.,* 1974). And in contrast to results from both Rothamsted and Wageningen, *H. lanatus* showed little effect of fertilizer application in the first six years of the Begbroke experiment (Elliott *et al.,* 1974), although by 1979, 4 years after the abandonment of hay making, it had been significantly increased by fertilizer application (Williams, 1985). At Cockle Park, this species had been increased by farm yard manure (FYM) and mineral fertilizers after eight years (Gilchrist, 1906), but 67 years later (in 1973) it was abundant only on plots receiving mineral NPK or NK (Arnold *et* *al.*, 1976). After a further eight years it was most abundant on all plots receiving NPK, either alone or alternating with FYM, but was *least* abundant on plots receiving NK, and only slightly more abundant where P was applied alone (Shiel and Batten, 1988).

At Wageningen, *L. perenne* almost disappeared from the hay plots but became dominant on grazed areas where lime, P and K or N, P and K were applied (van den Bergh, 1979; Elberse *et al.*, 1983). In the Park Grass Experiment, this species was increased initially by N and by NPK, but declined to trace levels between 1877 and 1903, coinciding with the change from grazing to cutting of aftermath growth (Williams, 1978). In the long-term experiment at Begbroke (Elliott *et al.*, 1974; Williams, 1985), *L. perenne* increased steadily from nil to 16% ground cover on fertilized plots by 1984, but reached only 1% cover without fertilizer. However, there was no discernible difference between plots cut for hay followed by aftermath grazing compared with those grazed only (Elliott *et al.*, 1974). It appears that this species, though primarily associated with grazing, will remain competitive in mown meadows provided a moderate to high level of fertility is maintained and the aftermath is grazed.

The contribution of *A. elatius* increased dramatically on NPK plots in the Park Grass Experiment after the cessation of aftermath grazing in 1877, coinciding with declines in *L. perenne, P. trivialis* and *Bromus hordeaceus* where N was applied as sodium nitrate, whilst *L. perenne* and *H. lanatus* declined on sulphate of ammonia plots (Williams, 1978). However, both *A. elatius* and *A. odoratum* declined on the latter plots as *H. lanatus* returned from 1925 onwards. *Alopecurus pratensis* came to dominate limed and NPK hay plots at Wageningen, but was partially replaced by *A. elatius* from about the 10th year onwards (Elberse *et al.*, 1983). In the Park Grass Experiment, *A. pratensis* shared dominance of the sodium nitrate N NPK plots from 1914 onwards, but remained at low levels throughout the experiment where N was applied as ammonium N (Williams, 1978).

Botanical equilibrium

In view of the complex interchanges between species which occurred in these experiments and the variation in behaviour of the same species in different situations, the grouping of components into the three main taxonomic classifications - grasses, legumes and others (herbs or forbs) is attractive and, as noted previously, has some physiological and ecological justification. Silvertown (1980a) showed that the botanical composition of fertilized plots in the Park Grass Experiment soon reached equilibrium with respect to these three groupings, although noting that interchange of species within each group continued throughout the life of the experiment. In the same study, species richness (i.e species number per plot, species density) and Shannon-Wiener diversity indices both showed significant, negative linear relationships with biomass and with soil pH and these relationships were constant over time. The effects of biomass and pH were additive on both species density and species diversity.

Temporal changes in species richness and diversity

Species richness and diversity are useful criteria by which the impact of management on vegetation can be gauged (Grime, 1979; Bakker, 1989; Losvik, 1993). In reviewing changes in species density in a number of studies, both Bakker (1989) and Losvik (1993) differentiated between species indicating 'traditional' hay meadow vegetation and those of lesser ecological significance.

The number of species per plot declined progressively in all plots in the Park Grass Experiment, including control plots. However, whilst the decline in species-richness occurred from the outset on most fertilized plots, a similar trend was noticeable on control plots only after a change was made from grazing in the second half of the season to taking a second cut (Lawes *et al.,* 1882; Williams, 1978). A similar trend was noticed on hay cut plots during the 20 years of the Wageningen experiment (Elberse *et al.*, 1983). The data show a significant declining trend for all treatments except P, implying that the decline in species richness was related to P depletion. However, there was no discernible decline in soil mineral P during the course of the experiment, and species richness also declined significantly on all the grazed plots. It would seem that both on grazed and on cut plots, the decline may have been at least partly related to a change from previous management. The authors also noted a progressive lowering of the water table due to improved land drainage in adjacent areas, to which they attribute the loss of several species typical of wet grasslands (Elberse *et al.*, 1983). No decline in species density occurred on unfertilized plots at Palace Leas, and Smith (1987) attributes this difference compared with the Park Grass Experiment to the maintenance of aftermath grazing on the Palace Leas plots.

As with data reviewed in following sections of this chapter, a summary of the main conclusions to be drawn from the foregoing review of the effects of inorganic fertilizers on the yield and botanical composition of grassland is provided in Section 2.11.

2.5. SOIL FERTILITY, DISTURBANCE, SPECIES DENSITY AND ABOVE-GROUND BIOMASS

Fertilizer treatments, particularly those including N, frequently lead both to an increase in biomass and to a reduction in species density (Lawes *et al.*, 1882; Brenchley, 1924; Willems, 1980; Elberse *et al.*, 1983). This can lead to the assumption that the second of these factors is a direct consequence of the first, and that loss of species density can be averted or minimised by preventing the accumulation of biomass by frequent defoliation or grazing (Marrs, 1993). In reality the interactions between soil fertility, species density, defoliation and biomass accumulation are fairly complex. The relationship between productivity and species density is, however, highly important in relation to a fundamental question: can significant increases in productivity be achieved without loss of species richness?

GRIME'S 'HUMP-BACK' MODEL

Grime (1979) proposed a 'hump-back' model relating species density to above-ground biomass plus litter in herbaceous vegetation. The model was developed by combining the principles of competitive exclusion with the effects of stress (Grime, 1973a,b,1979) and was supported by the data of Al- Mufti *et al.* (1977). In the model, high species density occured within a corridor of moderate biomass, with low species densities at both high and low levels of biomass. Grime's final theoretical model (Grime, 1979) was a series of symmetrical, bell-shaped curves (Figure 2.1) incorporating the influence of soil pH upon the relationship (Lloyd *et al.*, 1971; Grime, 1973b).

Application of Grime's model

The 'hump', or bi-tonic response, is integral to Grime's model, yet there are few clear-cut examples of it in practice, despite the apparent enthusiasm of several authors in trying to fit data to the model (van den Bergh, 1979; Willems, 1980; Vermeer and Berendse, 1983;

Day *et al.*, 1988; Bakker, 1989; Moore and Keddy, 1989; Oomes, 1992; Marrs, 1993; Smith,

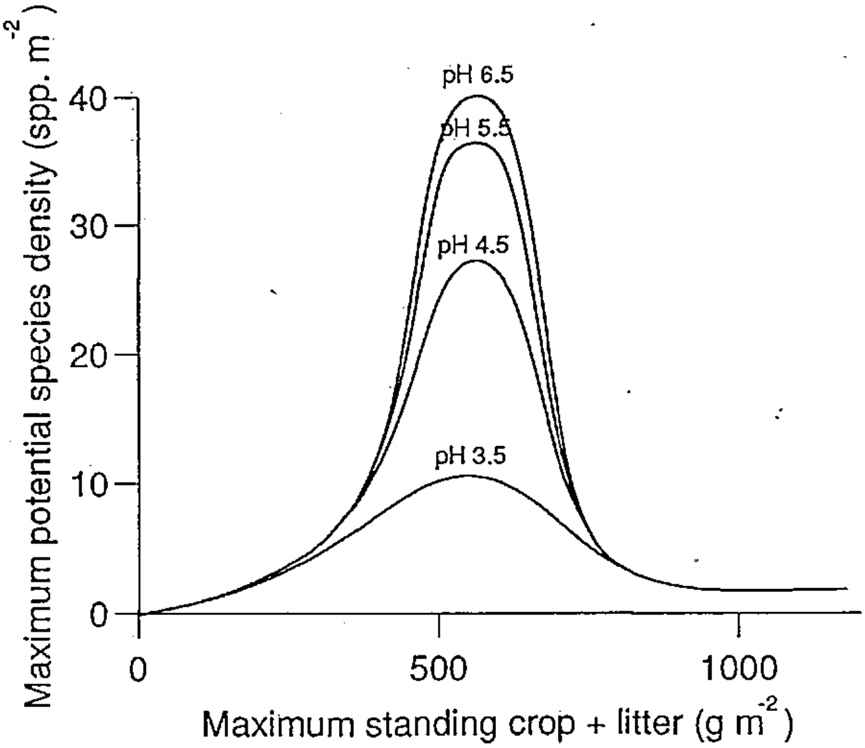


Figure 2.1. Diagram summarizing the relationship between soil pH, seasonal maximum standing crop + litter, and maximum potential species density in herbaceous vegetation of the British Isles (redrawn from Grime, 1979).

1993; Smith and Rushton, 1994). Marrs (1993) cited six examples of temperate vegetation as conforming to the model, but half of these showed only a monotonic decline in species density with increasing biomass, i.e. the right-hand side of Grimes 'hump' (Willems, 1980; Vermeer and Verhoeven, 1987 and Wheeler and Giller, 1982). Indeed, Vermeer and Verhoeven (1987) drew specific attention to the fact that their data did not conform to the Grime model. Where a bi-tonic response has been shown, the curve has almost always been very asymmetrical, with the 'hump' skewed well to the left of the x axis. Data from a range of wetland sites in Canada are typical (Moore and Keddy, 1989). However, even with this study, the relationship was very variable with species density beneath the apex of the curve varying from 3 to more than 20 per 0.25 m^2. A clearer relationship was obtained by dividing the data into 15 approximately equal groups on the basis of biomass and plotting the mean values of biomass and species density (Figure 2.2). Grime (1979) presented unpublished data from Grime, Sydes and Rodman which showed an equally variable pattern. These data were collected from road verges subject to occasional mowing and from semi-derelict limestone pastures and Grime attributed the 'noise' in the relationship to

variation in management. Species density in the current year may be related to

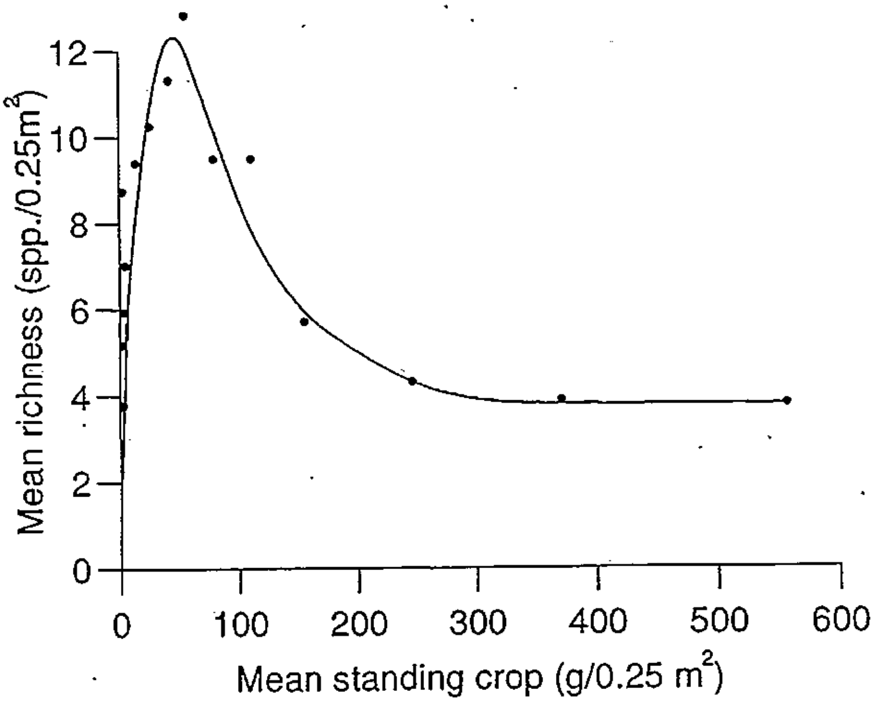


Figure 2.2. Mean species richness in relation to mean standing crop for 15 equivalent standing crop classes as calculated on a logarithmic scale (redrawn from Moore and Keddy, 1989).

management in previous years, and this management may have been different from that resulting in the level of biomass observed in the current year. Bakker (1989) suggested a slightly different reason for his lack of success in fitting data from hay fields in the Anlo valley in the Netherlands to the Grime model. He attributed noise in the data to sites where an equilibrium between the prevailing habitat conditions and the reservoir of species had not yet been reached following a reduction in fertilizer use or a change in defoliation regime sometime previously.

Oomes (1992) showed a bitonic relationship overall between species density and annual dry matter production in 27 hay meadows in the Netherlands (Figure 2.3). Seventeen of these meadows had been fertilized annually for at least 5 years at rates of between 25 and 200 kg N ha^{-1} and these showed a significant, negative relationship between yield and species density (i.e. the right-hand side of Figure 2.3). The ten points grouped to the left-hand side of Figure 2.3 all represented fields which had not been fertilized for at least 15 years. The author claimed, erroneously,* that these ten points

[see overleaf]

*** Addendum/correction**

These comments apply to confidence levels for a two-tailed hypothesis, i e. with no assumption as to whether the relationship might be positive or negative. An *r* value of 0.58 would represent a significant correlation at a probability level of greater than 95% for a directional hypothesis, i e. that the correlation is positive for unfertilized sites represented a significant ($P<0.05$) positive relationship and quoted a correlation coefficient (*r*) of 0.58. An *r* value of 0.576 would represent a statistically significant correlation ($P=0.05$) for 10 degrees of freedom in a regression analysis, i.e. for 12 pairs of values (Fisher and Yates, 1963).* For eight degrees of freedom, an *r* value of >0.632 would be required to indicate a significant relationship at $P<0.05$. Nevertheless, the mean values for DM yield and species number of these ten sites were 4.1 t DM ha^{-1} and 21.4 species per 150 per m^2 respectively, representing a datum point somewhat lower on both axes than the apex of the regression line derived from the 17 fertilized sites.

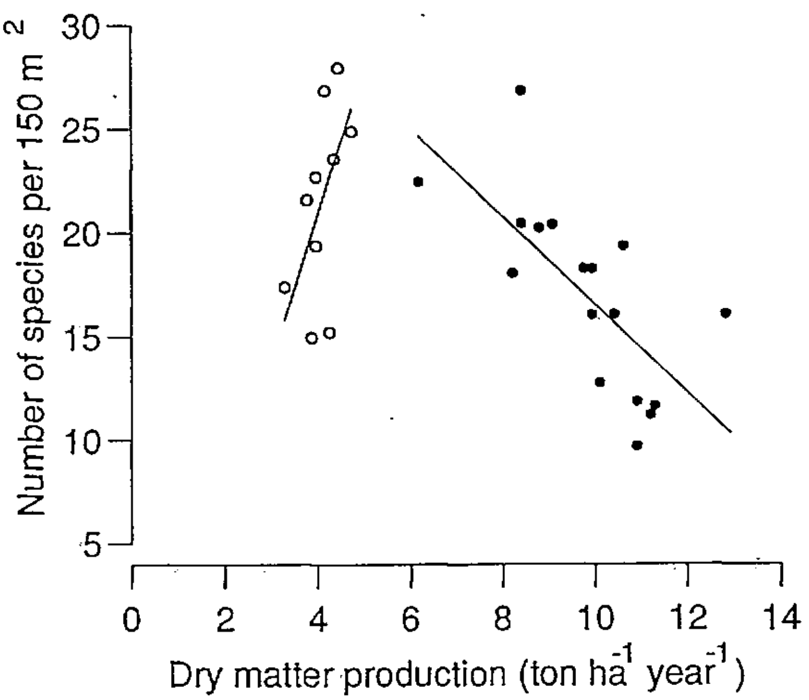


Figure 2.3. Relationship between species richness and annual dry matter production in hay meadows receiving either 25-200 kg N ha^{-1} (solid circles) or which had received no fertilizer for at least 15 years (open circles). Lines are fitted from linear regression equations for each group - see comments in text (redrawn from Oomes, 1992).

The main objective of Oomes' study was to identify an indicator level of DM production to which annual yield should be reduced during the restoration of species diversity in hay meadows. The author did not give a description of the vegetation type at each of the ten unfertilized sites, but stated that three were of the *Cirsio-Molinetum* type. Of the 17 fertilized fields, nine were of *Poo-Lolietum* and the other eight were *Lolio-Cynosuretum*.

The ten unfertilized fields showed a wide range of species richness (about 15-28 species per 150 m^2) within a narrow band of productivity (about 3.3-4.7 t DM ha-1) and differences in species density between these sites were probably related, directly or indirectly, to differences in vegetation type, althought the author did not discuss this aspect. He concluded, however, that a high species density could be expected when annual yield was between 4 and 6 t DM ha^{-1}, based upon the relative distributions of the two sets of data on the graph (Figure 2.3). This conclusion seems safe only if it is assumed that the range of vegetation types in the unfertilized meadows were representative of the range of types to which the fertilized meadows would eventually revert after cessation of fertilizer use, but the author presented no evidence to tie the two data sets together in this way.

Smith (1993) showed no clear relationship between species richness and hay yield across a range of hay meadows in Britain, including data from the Tadham Moor experiments and from a range of sites in the Pennine Dales. However, Smith and Rushton (1994) showed a close approximation to the hump-back model in an experiment studying the effects of variations in grazing management on the vegetation of hay meadows in the Pennine Dales. The overall relationship between hay yield and species richness in the final (4th) year was negative, but when these data were combined with control plot data for each of the four years, the relationship became bi-tonic. The positive relationship between species density and biomass in the left-hand portion of the curve was attributable to climatic differences between years, i.e. those factors which reduced biomass (e.g. moisture stress) also reduced the population of some of the sparsely distributed species. The perception of this effect may have been enhanced by the small quadrat size used (0.0625 m^2)(Crawley, 1986a).

The importance of 'stress' in Grime's model

Much of the discussion surrounding the Grime model has been based upon the assumption, specifically stated by Marrs (1993), that Grime's x axis (maximum biomass + litter) is synonymous with a fertility gradient. Yet, in his original model, Grime clearly attributed values near the origin of the x axis (i.e. low values of both biomass and species density) to the influence of stress, i.e. conditions to which relatively few species are adapted (Grime, 1979). Whilst stress can take the form of nutrient deprivation, this was not the only form taken into account. Of the 14 sites chosen for the study by Al-Mufti *et al.* (1977), the first four points on the x axis (see Figure 2.4a) were all represented by data from woodland understorey vegetation where light attenuation ranged from 11% to 92%. Here, both low species densities and low biomass can be attributed to the 'stress' of light attenuation.

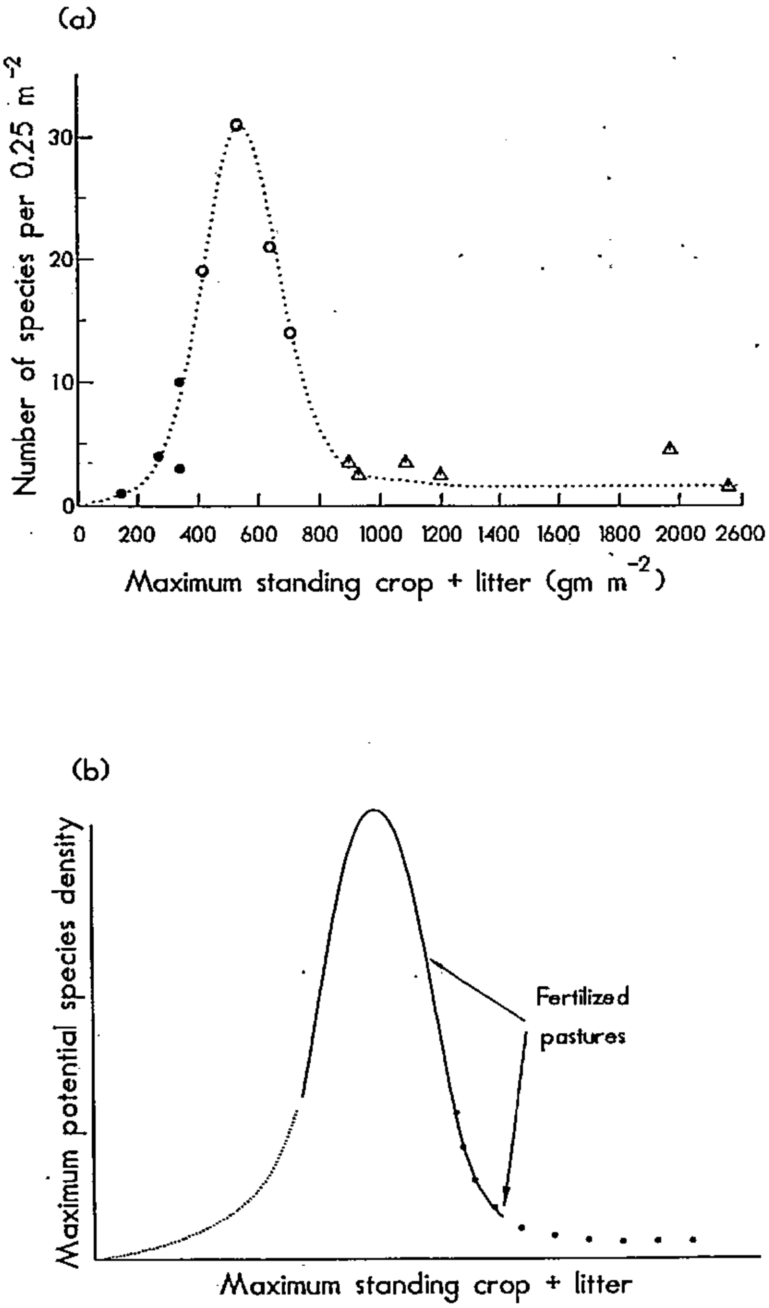


Figure 2.4. The relationship between maximum standing crop + litter and species density in herbaceous vegetation: (a) from 14 sites in northern England (redrawn from Al-Mufti *et al.*, 1977) - filled circles = woodland understorey, open cicles = grassland, triangles = tall herb communities; and (b) a general model relating maximum potential species density to maximum stading crop, simplified from Grime (1979) - solid line = agricultural grasslands, wide spaced dots = derelict fertile pastures.

In presenting a generalized model for herbaceous vegetation, Grime allocated different overlapping portions of the x axis to different habitat types. Moving from left to right on this axis these were: paths (where trampling would be severe); grazed rock outcrops with discontinuous soil cover; infertile and fertilized pastures; and derelict fertile pastures (Grime, 1979). A simplified version of this model (Figure 2.4b) shows that the portion of the curve attributable to infertile and fertilized pastures is relatively narrow. It should also be noted that low species density in derelict fertile pastures can be attributed in part to the negative influence of accumulated litter on seed germination and seedling survival (Grubb, 1977) and Grime's model took account of this (Figure 2.4b). Moreover, in the data presented by Al-Mufti *et al.*, the single point at the apex of the curve (see Figure 2.4a) represented unpublished data provided by S.B. Furness and J.P. Grime from a site on ancient species-rich grassland which was not included in the original study, although sampled at the same time (Al-Mufti *et al.*, 1977). Few details were given about this site, but, whereas the remaining thirteen habitats had remained undisturbed over a long period, the additional site was subjected to grazing by sheep and cattle. This would not only reduce the standing crop but also increase species density compared with undisturbed grassland (see discussion below). It is tempting to conclude that this point was plotted as an afterthought, specifically to accentuate the shape of the curve.

A study relating various types of riverine marsh vegetation to fertility and disturbance gradients showed a bi-tonic relationship between species density and standing crop + litter approximating to the Grime model (Day *et al.*, 1988). However, with the exception of one vegetation type, all the communities followed a pattern of monotonic decline in species richness with increasing biomass which was largely attributable to increasing fertility. Extremely low biomass and species richness at the remaining site was attributed to a combination of low fertility and the stress associated with wave action during prolonged flooding (Day *et al.*, 1988).

Across-community and within-community relationships

The possibility that the relationship between biomass and species density may not always be a clearly negative one has important implications for the application of fertilizers to species-rich grassland. Will small increases in fertility, sufficient to give a worthwhile yield response, always lead to a reduction in species diversity? Even if the data point at the

peak of the Al-Mufti *et al.* model is ignored (see Figure 2.4a), the remaining data still suggest a hump similar to that shown by Moore and Keddy (Figure 2.2) and Oomes (Figure 2.3). Against this it should be borne in mind that of the three remaining grassland sites on the Al-Mufti curve, the one with the lowest biomass was located on a sparse turf growing on thin soil on a steep slope, ie. conditions suggesting significant nutrient and water stress compared with the other sites (Al-Mufti *et al*, 1977). Both Day *et al.* (1988) and Moore and Keddy (1989) noted that their data showed bi-tonic relationships across a range of plant communities, but not within any particular community. These authors warned of the danger of 'sterile debate' if no clear distinction is made between across-community and within-community relationships.

However, Vermeer and Berendse (1983) did show a bi-tonic relationship for one of the 16 plant communities they studied - a wet grassland where *Succisa pratensis, Carex panicea, Cirsium dissectum, Cirsium palustre* and *Molinea caerulea* were the most common species. Here the relationship between species density and biomass was positive below 4.25 t DM ha^{-1} and negative above this level. Across the whole data set for this community, biomass was positively correlated with soil nitrate, phosphate, potassium and pH and negatively correlated with water content. Above 4.25 t DM ha^{-1} biomass was positively correlated with soil conductivity, phosphate and potassium, but in less productive vegetation it was positively related only to pH and negatively correlated with water content. The spread of pH values within the community as a whole was wide at between 3.8 and 6.6, i.e. ranging from values optimum for species diversity down to levels at which low species densities are the norm (Lloyd *et al.*, 1971; Grime, 1973b, 1979). Hewitt (1952) outlined the stresses limiting productivity on acid soils. These include direct injury by hydrogen ions; physiological impairment of the absorbtion of P, Ca and Mg as well as reduced P availability; impairment of the nitrogen cycle and N fixation; the accumulation of soil organic acids and other toxic compounds; and impairment of mycorrhizal activity. Thus low pH, rather than poor nutrient supply, was probably the factor limiting both biomass production and species richness in these parts of the community. The wide range of pH values might be expected to cause variation in vegetation composition accross the site (Grime, 1979). However, the authors gave no indication of any such variation, so that it is not possible to judge the validity of treating the site as a single plant community.

Species density and dominance in relation to qualitative and quantitative changes in vegetation

Evidence from an experiment in chalk grassland (Willems *et al.*, 1993) suggested that qualitative changes in biomass could be as significant as quantitative changes in influencing species density. Applying P without N more than doubled biomass production compared with control plots, with yield almost equalling that on plots receiving N + P and over 50% higher than on plots receiving N without P. Yet species density was significantly reduced both by NP and by N treatments but not by P alone. Light attenuation was much greater on P than N plots, also contrary to the difference in species density. The authors attributed these effects to high spatial variation in light penetration on the P plots, which were dominated by legumes, compared with N plots dominated by *Brachypodium pinnatum.* In another experiment on chalk grassland (Bobbink, 1991), *B. pinnatum* dominance was increased to a greater extent by N alone than by P, K or NPK. This led to a correspondingly greater reduction in species density with N applied alone, although the NPK treatment caused a much greater increase in total biomass.

Comparable results were shown in the Wageningen experiment (van den Bergh, 1979; Elberse *et al*, 1983). Under hay cutting, plots receiving P alone were the only ones where species density did not decline significantly over 20 years, despite a mean increase in annual dry matter (DM) production (from two cuts) of 15% with P application compared to control (5.5 t DM ha^{-1} compared with 4.8 t DM ha^{-1}). Species density declined very significantly on plots receiving P + K and on limed plots, although mean annual biomass production was only marginally greater than with P alone, at 5.7 and 6.0 t DM ha^{-1} respectively. Plots receiving NPK showed both the greatest level of DM production (8.9 t ha^{-1}) and the most rapid decline in species density.

At Wageningen, as in the experiments of Willems *et al.* (1993) and Bobbink (1991), the rate of loss of species appears to have been more closely related to the particular species attaining dominance than to increases in total biomass production. This tends to support the concept of 'edificator' or 'determinant' species noted above (Rabotnov, 1975). The increased biomass on Ca plots was attributed to increased mineralization of organic N, estimated at 33 kg ha^{-1} compared with that on control plots. The results for the Ca treatment in this experiment were therefore comparable with those for N reported by Willems *et al.* (1993) and Bobbink (1991). There, the greater reduction in species density caused by N compared with P was attributed to the structure of the vegetation resulting from the dominance of a particular species (in that case, *B. pinnatum*). At Wageningen, the dominance of *A. pratensis* and *A. elatius*, both notably tall growing species (Hubbard, 1984) appeared to have had a similar effect. *Poa pratensis*, which was also increased by Ca, is rarely dominant in vegetation, but is frequent in tall vegetation dominated by species such as *A. elatius* and *Elymus repens*, where it can produce very long leaves (Grime *et al.*, 1988).

VARIATION IN SPACE AND TIME

Optimal foraging theory and resource ratios

As the foregoing paragraphs suggest, the outcome of inter-species competition is likely to be influenced by the interaction of at least two of a number of potentially limiting resources. These include light, water and a range of macro-nutrients and trace elements, and it has been suggested that each species differs in its preference for a particular ratio of these resources (Tilman, 1982, 1986). Thus, if a plant is limited by N for example, the increase of another resource such as light or P will not increase its growth, unless or until the added resource leads indirectly to an increased supply of N. This is consistent with optimal foraging theory, developed by Tilman (1982) from a model by Rapport (1971), which states that a plant should consume essential resources in the proportion in which it is limited by them. Tilman (1982) used this approach to explain differences in species abundance between treatments in the Park Grass Experiment on the basis of differences in soil N:P ratios. The implication of this theory, seen in conjunction with the principles of competitive exclusion (Grime, 1973a; Crawley, 1986a,b), is that the number of species which can coexist cannot exceed the number of limiting resources, which rarely exceeds four or five in any particular habitat (Tilman, 1986). However, large numbers of species plainly do coexist, often when few resources are limiting, and this can be at least partly attributed to spatial and/or temporal heterogeneity of resource supply (Grubb, 1977; Silvertown, 1981a; Gay *et al.*, 1982; Crawley, 1986b; Tilman, 1986).

Niche differentiation and niche separation

The term *niche* has been defined as:

> *the limits for all important environmental features within which individuals of a species can survive, grow and reproduce* (Begon *et al.*, 1986).

Bazazz (1987) provided another, more behavioural, definition:

> *the pattern of response of an individual, a population or a species to the physical and biological gradients of its environment.*

Bazazz presented strong evidence that niche differentiation is a co-evolutionary process, and also notes the possibility that niche separation between two or more species in a particular location can be the result of pre-adaptation in a previous location. Bazazz noted that niche separation occurs along resource gradients and the continuous nature of resource supply provides constraints on niche differentiation. This gives added significance to the pattern of spatial and temporal heterogeneity in resource supply in plant communities.

Spatial heterogeneity

Crawley (1986a) reviewed a number of models outlining specific mechanisms relating species richness to spatial heterogeneity within habitats. The implication common to most of these is that spatial heterogeneity affords a variety of refuges for inferior competitors in which their numbers can be maintained. Each refuge acts as a source of propagules for dispersal to other parts of the habitat where, in equilibrium, the species would be excluded. Grubb (1977,1984,1985) emphasized the dynamic nature of plant communities and the importance of the creation and partitioning of regeneration niches.

The example from chalk grassland quoted above (Willems *et al.*, 1993) illustrated the influence on species richness of spatial heterogeneity in light attenuation. The persistence of a high species density on plots receiving P was attributed to the greater heterogeneity of the vegetation on these plots compared with those receiving N, despite similar increases in both mean light attenuation and biomass. Spatial heterogeneity in nutrient supply is common, particularly in grazed swards, where nutrient returns from animal excreta are very uneven, particularly with cattle (Petersen *et al.*, 1956; Richards and Wolton, 1976; Tallowin and Brookman, 1988). Dung is rich in P with appreciable amounts of N, Ca, and Mg, whereas urine is rich in N and K but contains little P (Sears, 1956; During

and McNaught, 1961; During *et al.*, 1973). Norman and Green (1958) showed that grazing animals reject herbage growing around dung patches for periods of up to 18 months, whilst urine patches were rejected initially but grazed preferentially later. Animal excretion therefore leads to heterogeneity not only in the balance of nutrients in the soil but also in the frequency and severity of defoliation in grazed swards. Significant changes in botanical composition occurred in the vicinity of dung patches, whilst the effects of urine were smaller and more transitory (Norman and Green, 1958). These effects differed little between grazed swards and those which were defoliated uniformly by cutting to eliminate the effects of selective grazing, except that dung increased *Trifolium repens* to a greater extent on cut swards compared with grazing.

Temporal variation and phenology

Temporal variations in factors such as water and nutrient supply and defoliation afford opportunities for adaptation which can also contribute to the coexistence of a large number of species, provided that there is a regular pattern to such variation. Where the availability of N and P is low, for example in chalk grasslands (Lloyd and Pigott, 1967; Grime and Curtis, 1976; Brady, 1990), these nutrients have shown strong seasonal variation (Gupta and Rorison, 1975; Taylor *et al.*, 1982). Gay *et al.* (1982) showed that the nutrient economy of several species was related to spring peaks in N and P. Grasses tend to peak in growth earlier than forbs such as *Poterium sanguisorba*, *Centaurea nigra* and *Leontodon hispidus* which have a long tap root and are therefore better able to exploit reserves of nutrients and moisture during the dry summer months (Grime, 1979). Many other examples exist of complementary growth pattern (phenologies) among species which share the same habitat (Al-Mufti *et al.*, 1977; Grime, 1979; Gay *et al.*, 1982; Pigott, 1982). Tilman (1982) was puzzled by the evident ability of *A. elatius* and *A. pratensis* to exist as co-dominants in the plot receiving nitrate N plus P and K in the Park Grass Experiment. The most likely explanation lies in the complementary growth patterns of these two species, with *A. pratensis* flowering from April to June and *A. elatius* from June to September (Hubbard, 1984).

DISTURBANCE AND FERTILITY INTERACTIONS

Maximal species density generally occurs in moderately resource-poor habitats (eg. Grime, 1979; Tilman, 1982,1986; Marrs, 1993), although, as Tilman (1986) recognized, few habitats are so nutrient poor as to allow an increase in species richness with an increase in nutrients. Other resources being equal, maximal species richness occurs at intermediate levels of disturbance, since this both prevents dominance and provides some spatial heterogeneity in the habitat without imposing undue stress on the vegetation (Grime, 1973a, 1979; Crawley, 1986a; Marrs, 1993). A three-dimensional model proposed by Huston (1979) allowed these two concepts to be combined in a form applicable to all communities of competing organisms, i.e. not just to plants.

Huston's general hypothesis of species diversity

Like Grubb (1977,1984), Huston was emphatic that all communities exist in a state of dynamic, rather than competitive, equilibrium. This equilibrium results from a balance between the rate of competitive displacement and the frequency of population reduction. In formulating his model, Huston used formulae which had already been applied exhaustively by others (the Lotka-Volterra equations - see Begon *et al.*, 1986). However, he notes that his approach differed from previous theorists in that he investigated non-equilibrium solutions to these equations, in contrast with the assumptions of competitive equilibrium made by others (Huston, 1979).

Huston argued that where the growth rates of all species are high, dominance will be expressed more quickly than where all species are growing more slowly, so conditions leading to high growth rates will tend to reduce species density. High species density is maintained by keeping the population as far as possible away from competitive equilibrium and this is achieved by matching population (or biomass) reduction, e.g. by predation or herbivory, to the rate of competitive displacement. At a given mean growth rate, species density will be low at high rates of population or biomass reduction, since many species will be unable to recover fast enough. At low rates of reduction (disturbance), species density will be kept low by competitive exclusion. Species density will therefore be greatest at intermediate levels of disturbance (Figure 2.5a). When rates of population reduction are low to moderate, all populations have time to recover, so that low growth rates allow a

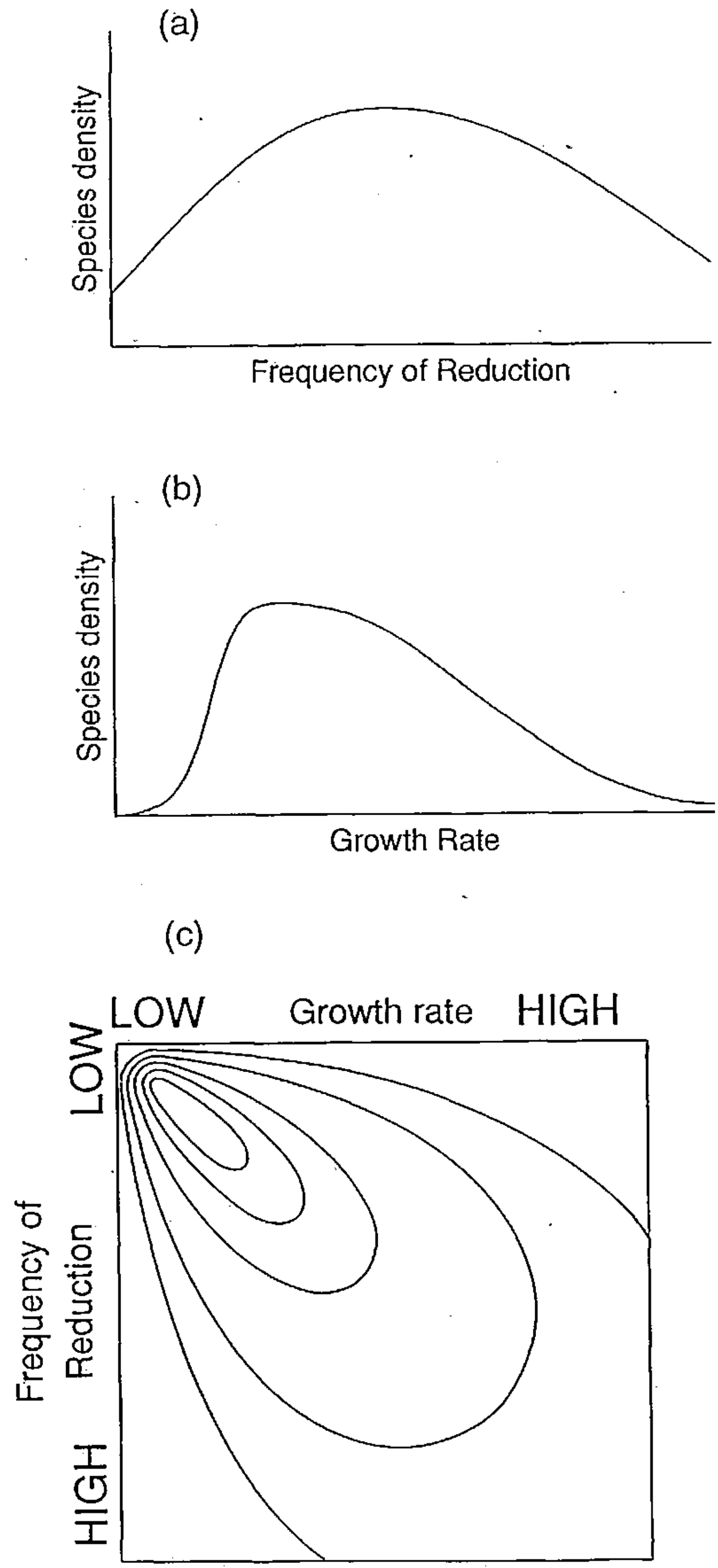


Figure 2.5. Predicted relationships between species diversity (= density) and (a) frequency of population reduction (e.g. by herbivory, predation etc.) and (b) growth rates in non equilibrium systems with low-intermediate frequency of population reduction. (c) Trend surface of dynamic equilibria between the rate of competitive displacement and the frequency or magnitude of population reduction. The inner elipsoid represents the area of highest diversity (redrawn from Huston, 1979).

longer period of survival for species that would be extinct at equilibrium than do high growth rates. An increase in growth rates, either generally or with some species growing faster than others, results in reduced species density. This implies that density will be highest at low growth rates and will decrease monotonically as growth rate increases. Here, growth rate is directly correlated with rate of displacement. Species density will obviously be low where most organisms cannot grow and the model incorporates a 'break point' at very low growth rates. At this point a slight increase in growth rate will be accompanied by a rapid increase in species density (Figure 2.5b). The x axis in Figure 2.5b is labelled 'growth rate'. This may approximate to Grime's 'maximum standing crop + litter', but, as with Grime's model, this axis should not be interpreted simply as a fertility gradient. Note also that the shape of the curve is quite similar to that of Al-Mufti *et al.* (1977) (see Figure 2.4a), particularly if the point at the apex of the Al-Mufti curve is omitted.

Figure 2.5c shows the final three-dimensional response surface for the level of diversity at dynamic equilibrium given by the Huston model. The overall relationship will be affected by the variance between species either in growth rate and response to disturbance or both. Variance between individuals or species will be greatest at extremes. Few species will tolerate either high levels of disturbance or low resource availability. Conversely, since rapidly growing plants show a greater response to added nutrients than slow-growing ones, the decline in species density at high nutrient levels will be more rapid the greater the variance in growth rate between species.

The common ground between the models of Grime and Huston is obvious and it is not difficult to see how these models are complemented and augmented by the concept of optimal foraging combined with the opportunities afforded for coexistence by niche separation along spatial and temporal gradients.

An example of increased species richness caused by fertility-disturbance interactions

It is well established that the disturbance associated with grazing can increase or maintain species diversity in grassland (Harper, 1971; Grime, 1973b,1979; Huston, 1979; Grubb, 1985; Petraitis *et al.,* 1989; Marrs, 1993). This effect is attributable both to the creation of niches for seedling establishment and survival (Grubb, 1977; Watt and Gibson, 1988) and to the prevention of dominance by tall species (Grime, 1973a; Huston, 1979; Bakker, 1989).

In Milton's experiments in the Welsh uplands (Milton,1934,1935,1938,1940; Milton and Davies, 1947), a number of species invaded the plots receiving fertilizer and lime, but only under controlled grazing. The ingress of new species was negligible where sheep were allowed free access to all plots along with the remainder of the hill side or where plots were cut for hay, although fertilizers did bring about a change in the balance of existing species on these plots. However, the pastures studied by Milton were initially very species-poor and dominated by *Agrostis spp., Festuca ovina* and *Molinea caerulea.* Their composition reflected not only the nutrient-poor and acid soil conditions, but also the low level of utilization and management they had received following their virtual abandonment when human occupation of the uplands declined in the late 19th and early 20th centuries (Jones, 1967). Lime on its own, and to a lesser extent P alone, resulted in the most diverse swards when applied in conjunction with controlled grazing. Applying N, P and K with or without lime caused a similar invasion of new species, but also reduced the minor sward components, most of which were forbs and sedges. Since these minor components were not listed separately for each treatment, the effects on total species number are not entirely clear. However, all fertilizers brought about a more even distribution of species, provided they were applied in conjunction with controlled grazing.

Milton's work still represents one of the few examples of increased species diversity with fertilizer use in agricultural grassland and the effect was intimately related to low initial species richness and the subsequent increase in grazing intensity. The species that invaded with fertilizers (particularly lime) and controlled grazing were described by Milton as 'lowland' species - *Holcus lanatus, Poa spp., Lolium perenne, Phleum pratense, Dactylis glomerata, Cynosurus cristatus, Alopecurus geniculatus* and *Alopecurus pratensis.* The source of these invading species is not clear, since of this group only *H. lanatus, Poa spp.* and possibly *A. geniculatus* form a persistent seed bank (Grime *et al.*, 1988). Moreover, Chippendale and Milton (1934) found that the seed bank beneath these pastures was very species-poor, and of the species listed above only *Poa trivialis* was represented.

2.6. FERTILIZERS AND POLLUTION

As noted in Chapter 1, a high water table and the abundance of ditches and watercourses are an integral part the characteristic nature and wildlife value of the peat moors of the

Somerset Levels. Data presented in Chapter 4 of this thesis show that these areas are particularly susceptible to loss of a fertilizer N, both by leaching and by denitrification. A fairly comprehensive review of factors affecting the cycling of N in agricutural grasslands and the wider environmental implications of inorganic fertilizer use are therefore particularly relevant in this context.

Agriculture is a major source of water pollution and the use of inorganic fertilizers is implicated in the contamination of lakes and waterways, both by nitrogen and phosphorus (Cooke, 1976). Whilst organic N can constitute up to 40% of the N in a waterway (Johnes and Burt, cited in Burt and Haycock, 1992), the majority of N in water is in nitrate (NO_3^-) form (Cooke, 1976; Burt and Haycock, 1992). Denitrification, the microbial conversion of nitrate N to nitrous oxide (N_2O) and gaseous nitrogen (N_2)(Firestone, 1982), is also enhanced by fertilizer N application (Ryden, 1983). This effect has potentially wide environmental significance, since N_2O is damaging to the atmosphere both by ozone depletion and as a potent 'greenhouse' gas (Bouwman, 1990) and is also implicated in the formation of acid rain (Badr and Probert, 1993).

Phosphorus compounds are much less mobile than those of nitrogen, and P from fertilizers usually remains near the soil surface, although it is held less tightly within organic soils than within mineral soils (Larsen *et al.*, 1958; Henkens, 1972; Kolenbrander, 1972; Cooke, 1976). The majority of fertilizer P finding its way into waterways does so in the form of suspended solid material resulting from run-off (Ryden *et al.*, 1973). The phosphate in anaerobic muds formed from eroded soil is more soluble and available to plants than phosphate in field soil (Thomas, 1970; Cooke, 1976).

Both nitrate and phosphate are implicated in the unwelcome eutrophication of lakes and waterways (Cooke, 1976; Stewart *et al.*, 1982). The attention paid to problems caused by phosphates from inorganic fertilizers and from animal manures has recently increased (van der Meer, 1994; Pain, 1994), but until now concern has focused largely on problems associated with inorganic N fertilizers. This is partly because of the potential risk to human health resulting from the pollution of drinking water by nitrates (Cooke, 1976).

IMPLICATIONS OF THE POLLUTION OF LAKES AND WATERWAYS

Nitrates and human health

Nitrate in drinking water is thought to increase risk of infantile methaemoglobinaemia ('blue baby syndrome') and can, in theory, increase the risk of stomach cancer in adults (Cooke, 1976). The EC has set limits on nitrate concentrations (11.3 mg nitrate N l^{-1}) and EC legislation is currently being introduced to control nitrate leaching in drinking water (CEC, 1991). However, the incidence of methaemoglobinaemia is very rare in the UK, with only 14 cases attributable to nitrate in the 35 years up to 1985 (Acheson, 1986). Acheson (1986) also reported that although the risk of nitrate-induced stomach cancer existed through possible increases in the body of N-nitroso compounds, epidemiological evidence did not support the suggestion that nitrate causes any form of cancer.

Eutrophication in lakes and waterways

Nutrient enrichment (eutrophication) can severely disrupt the ecology of aquatic ecosystems, particularly in oligotrophic lakes (Lund, 1971; Holden and Caines, 1974). A common and very visible symptom of eutrophication is the developement of algal blooms. These can cause taints in drinking water and filtration problems at water works and also cause serious problems to aquatic life by increasing the biological oxygen demand (BOD) when blooms die and decompose (Cooke, 1976; Department of the Environment, 1986). These problems are most acute when qualitative changes occur in algal populations, often a switch from diatoms to blue-green algae, caused by an alteration in the nitrate:phosphate ratio (Department of the Environment, 1986). Nitrate is seldom the limiting factor in this relationship, but elevated nitrate levels do cause increased growth of aquatic rooted plants: this can affect navigation and flood control, as well as increasing BOD when dead plants decompose (Cooke, 1976; Department of the Environment, 1986). Nitrate introduction can also cause the dominance of individual macrophyte species in an aquatic habitat (Department of the Environment, 1986). As with fertilizer application to terrestrial vegetation, eutrophication ultimately leads to a reduction in the diversity of both flora and fauna in aquatic habitats (Lund, 1971). This therefore poses a serious threat to the characteristic flora and fauna of the ditches and drainage channels in areas such as the Halvergate Marshes and Wicken Fen in East Anglia and on the Somerset Levels (Barnett, 1981; Wolseley *et al.*, 1984; Purseglove, 1988).

Eutrophication in coastal waters

The occurrence of plankton and algal blooms in coastal waters is increasing, due to the cumulative effect of nutrients transported down rivers and running directly off the land (Department of the Environment, 1986). In contrast to freshwaters, nitrate rather than phosphate is normally the growth-limiting nutrient in marine waters, so that nitrates are particularly implicated in causing algal blooms in coastal waters. Such blooms are most marked in shallow waters on the continent, such as Norwegian fiords, the German Bight and Danish coastal waters, which are particularly affected by land run-off (Department of the Environment, 1986).

LOSSES OF FERTILIZER NITROGEN FROM GRASSLAND

The effect of management - cutting vs. grazing

Losses of N from grassland are much greater in grazed grassland than where herbage is cut and removed, since grazing animals return a large proportion of the N they consume, in the form of urine and faeces (Ryden *et al.*, 1984; Steele, 1987; Barraclough and Jarvis, 1989; Jarvis and Pain, 1990; Jarvis, 1992; Lord, 1993).

Sheep and cattle excrete a relatively constant amount of N in faeces, at about 8 g N per kg DM consumed (Barrow and Lambourne, 1962; Barrow, 1967), but the proportion of excreted N passed in urine varies between about 20% and 80% of the total, according to the N content of herbage (Steele, 1987; Jarvis and Pain, 1990). At high cattle stocking rates, the amount of N deposited in urine can be equivalent to 1000 kg N ha^{-1} $year^{-1}$ on those areas wetted by urine (Steele, 1982, cited in Steele, 1987). Even under extensive sheep grazing with no fertilizer application, large amounts of N are deposited at drinking points and night resting areas (Milimonka *et al.*, 1994). In these areas, the soil can contain up to 1000 kg more nitrate N ha^{-1} in the autumn compared with grazed areas, with differences in the amount of N lost by the following March of up to 600 kg N ha^{-1} (Milimonka *et al.*, 1994). When fertilizer N is applied to grazed grassland, the increased amount of N returned to the area as a whole can be equivalent to over 80% of that applied (Jarvis *et al.*, 1989a).

Apparent uptake of applied N in recently sown *L. perenne* swards cut 4-weekly throughout the growing season averaged 64%, 70% and 66% at 150, 300 and 450 kg N applied ha^{-1} in the multi-site trial carried out by Morrison *et al.*(1980). Hopkins *et al.* (1990) showed slightly lower levels of apparent uptake in permanent pastures of 55%, 55% and 49%, and in reseeded permanent pastures of 53%, 63% and 58%, at the same three levels of N. Titchen *et al.* (1989) showed that the amount of mineral N remaining in the soil under permanent pastures in the autumn could be reduced substantially by ceasing cattle grazing in late autumn and removing subsequent grass growth by cutting.

However, even in cut swards, uptake varies markedly between sites. Morrison *et al.* (1980) showed values of apparent N uptake varying between 45% and 87% at 300 kg N applied ha^{-1} accross 21 sites. This variation was most closely related to variation in DM yield, but was also significantly correlated with a composite variable of total rainfall over the growing season combined with soil available water capacity (r = 0.61).

Routes of nitrogen loss from grassland

There are four possible routes of loss for N applied to grassland soils: leaching, denitrification, ammonia volatilization, and run-off in soil particles. Of these, leaching and denitrification are the most important, although ammonia emissions can be high when large amounts of urine are deposited on grassland (Steele, 1987).

Leaching

Leaching losses of over 150 kg N ha^{-1} are not uncommon in highly fertilized swards (Ryden *et al.*, 1984; Macduff *et al.*, 1990a; Tyson *et al.*, 1993). Leaching increases markedly with fertilizer application (Ryden *et al.*, 1984), but the relationship between N application rate and leaching loss varies enormously from site to site (Macduff *et al.*, 1990b), depending upon soil type, past history, current management and drainage status (Jarvis, 1992). At a comparatively modest rate of 200 kg N applied ha^{-1}, Tyson *et al.* (1993) showed 10-year mean leaching losses of 16 kg N ha^{-1} $year^{-1}$ in undrained and 56 kg N ha^{-1} in a drained permanent grassland grazed by cattle at a site in the South West of England. The 7-year mean leaching losses resulting from the application of 400 kg N ha^{-1} were 74 and 194 kg N ha^{-1} $year^{-1}$ for undrained and drained plots repectively. These figures compare with corresponding 6-year mean values of 2 and 5 kg N ha^{-1} year^{-1} in unfertilized grassland, and 5-year means of 27 and 85 kg N ha^{-1} year^{-1} from plots reseeded to *L. perenne* and receiving 400 kg N ha^{-1} year^{-1} (Tyson *et al.*, 1993). The lower losses from reseeded swards compared with permanent swards at the same N application rate can be accounted for by large amounts of N incorporated into the soil as organic matter built up again after ploughing and reseeding (Tyson *et al.*, 1993).

Barraclough and Jarvis (1989) identified 'break points' for nitrate leaching of 150-200 kg and 250-350 applied N ha^{-1} for grazed and cut swards respectively. Above these application rates the rate of N loss by leaching escalated sharply. Work by Watson *et al.* (1992) indicated a break point at 250 kg N ha^{-1} at a grazed site in Northern Ireland. Data presented in Chapter 4 suggests a break point at around 75-100 kg N ha^{-1} at Tadham Moor, showing that these wet peat soils are much more susceptible to N loss than most other soils.

Denitrification

Denitrification rates show high temporal and spatial variation (Ryden, 1983; Scholefield *et al.*, 1990; Jarvis *et al.*, 1991) which makes it hard to estimate accurately the total amount of N denitrified over a given period (Jarvis *et al.*, 1991). Whereas most leaching losses occur in the autumn and winter (Tyson *et al.*, 1993; Jarvis, 1992; Watson *et al.*, 1992), denitrification is normally greatest under warm wet soil conditions (Denmead *et al.*, 1979; Ryden, 1983; Jarvis *et al.*, 1991; Watson *et al.*, 1992). Denitrification is also enhanced by high soil nitrate concentrations (Firestone, 1982; Ryden, 1983) and therefore increases with increasing fertilizer N rate (Ryden, 1983; Jarvis *et al.*, 1991; Barraclough *et al.*, 1992; Watson *et al.*, 1992). Maximum denitrification rates are usually recorded just after fertilizer application or after the next rainfall event (Ryden, 1983) with maximum rates varying from about 170 g denitrified day^{-1} (Scholefield *et al.*, 1990) to 310 g N ha^{-1} day^{-1} (Watson *et al.*, 1992) at application rates of 450-600 kg N ha^{-1} year^{-1}.

In work by Barraclough *et al.* (1992), the proportion of total N losses accounted for by denitrification varied greatly between sites and between years, but decreased with increasing N application rate from 29-99% at 100 kg N ha^{-1} to 14-78% at 450 kg N ha^{-1}. In the experiment reported by Tyson *et al.* (1993), denitrification accounted for 36% of the total N losses (leaching + denitrification + ammonia volatilization) at 200 kg applied N ha^{-1} and 27% at 400 kg ha^{-1}. By contrast, Watson *et al.* (1992) showed an opposite effect, with denitrification increasing as a proportion of total losses from 23% at 100 kg N applied ha^{-1} to 44% at 400 kg N ha^{-1}. The results of Watson *et al.* (1992) also differed from those of others (e.g. Ryden, 1983; Jarvis *et al.*, 1991) in that denitrification during the autumn and winter accounted for up to 58% of the annual total.

Denitrification in organic soils

All the foregoing information for leaching and denitrification refers to mineral soils and there are few corresponding data for organic soils. Koops and Oenema (1994) recorded a peak denitrification rate of 230 g N ha^{-1} day^{-1} in a soil of 34% organic matter (described by the authors as 'peat', although 'humose' would be a more accurate description for a soil of less than 50% organic matter content). This rate was recorded in the top 0-20 cm in March following application of 56 kg N ha^{-1}. From the end of March onwards, denitrification rates were higher in the 20-40 cm horizon than in the surface layer. Denitrification peaked in the 20-40 layer at 194 g N ha^{-1} day^{-1} in June following a fourth fertilizer application (bringing the total to 282 kg N ha^{-1}), but the denitrification rate reached only 93 g day^{-1} in the 0-20 cm layer at the same date. These differences could not be attributed to differences in soil nitrate concentration, since there was more nitrate in the top 0-20 cm layer for most of this period. However, trends in denitrification may have been related to soil moisture and water table depth, the latter varying between 5 cm in winter and 50 cm in summer. The higher organic matter content of the 20-40 cm layer (55%) may also have been significant, since both organic carbon content and soil moisture could be expected to have a positive effect on denitrification rate (Firestone, 1982). The vegetation was managed by regular cutting in this experiment and even higher denitrification rates would have been likely under grazing management (Jarvis, 1992). Much higher denitrification rates of up to 428 g N ha^{-1} were recorded in the top 30 cm at Tadham Moor in October-November after grazing ceased in the autumn, with rates strongly enhanced both by high soil mineral N levels and by high water tables (see Chapter 4).

Further evidence of high denitrification rates in organic soils was given by Dilz and Woldedorp (1960) using transplanted grass sods from a range of soil types. The proportion of N unaccounted for by leaching and plant uptake, and therefore assumed to have been lost by denitrification, was much higher in a wet peat soil than in sandy or clay soils (40%, compared with 16-22%), although denitrification accounted for only 19% of the total lost from dryer peat. Berendse *et al.* (1994), working in a humose clay soil (24% organic matter) overlying deep peat, showed very little difference between 'wet' and 'dry' areas in the total amount of N denitrified per year (16 and 18 kg N ha^{-1}), where the difference in water table was 10-40 cm between the two areas. However, summer denitrification rates were significantly higher in the wet area compared with the dry area, whereas the opposite was true during the winter and spring. No fertilizer was applied during this experiment and herbage was cut and removed at 2-weekly intervals throughout the year. The annual losses from denitrification under both moisture regimes were very high compared with that of 1.6 kg N ha^{-1} $year^{-1}$ recorded on unfertilized plots on a clay loam soil by Ryden (1983). They were also greater than those recorded by Watson *et al.* (1992) on plots receiving 100 kg N ha^{-1} $year^{-1}$ (i.e. 9 kg N denitrified ha^{-1} $year^{-1}$) also on a clay loam soil, and greater than those recorded by Barraclough *et al.* (1992) on a range of mineral soils receiving 250 kg N ha^{-1} $year^{-1}$ (averaging about 11 kg N denitrified ha^{-1} $year^{-1}$).

Ammonia volatilization

Some N can be volatilized directly from fertilizer applied to grassland (Meyer and Jarvis, 1989). However, amounts lost in this way are small unless alkaline fertilizers such as urea or ammonium hydroxide are used, when losses of 18-25% are possible (Steele, 1987; Jarvis and Pain, 1990). Most of the ammonia emitted directly from grassland comes from urine deposited during grazing (Steele, 1987; Jarvis and Pain, 1990). Losses by this route are very variable, depending upon a variety of environmental factors including wind speed, temperature, and vegetation cover (Steele, 1987; Jarvis and Pain, 1990), as well as the N concentration in urine (Jarvis *et al.*, 1989a). Daily losses can be high and Jarvis and Pain (1990) cite values of up to 2.8 kg N ha^{-1} day^{-1} for dairy cows, compared with up to 0.4 kg ha^{-1} day^{-1} for sheep.

Fertilizer N application increases the N concentration in herbage (Morrison *et al.*, 1980; Jarvis *et al.*, 1989b; Tallowin *et al.*, 1990), which in turn influences both the total excretal N returns and the distribution between dung and urine (Steele, 1987; Jarvis *et al.*, 1989a,b; Jarvis and Pain, 1990). In addition, stocking rates are increased with increasing fertilizer application (Jarvis *et al.*, 1989b; Tallowin *et al.*, 1990), so that total ammonia volatilization losses per unit area are increased by a combination of these factors (Jarvis and Pain, 1990). Jarvis and Pain (1990) report losses of up to 41 kg N ha^{-1} $year^{-1}$ by ammonia volatilization with dairy cows grazing swards receiving 550 kg fertilizer N ha^{-1} $year^{-1}$. Nevertheless, such losses represent only a small proportion of inputs, seldom exceeding 8% of the fertilizer N applied (Jarvis and Pain, 1990). Furthermore, much less ammonia is volatilized from swards grazed by sheep compared with cattle, for example 9 kg N ha^{-1} $year^{-1}$ for sheep compared with 16-25 kg N ha^{-1} $year^{-1}$ for beef cattle, both at 420 kg N applied ha^{-1} (Jarvis and Pain, 1990).

Ammonia volatilization shows seasonal variation related to the effect of grass growth patterns on stocking rate (Jarvis *et al.*, 1989b; Tallowin *et al.*, 1990), with generally lower losses in spring and autumn than in summer (Jarvis *et al.*, 1989b). Data also suggest that losses are greater under rotational grazing than under continuous stocking, probably as a result of a greater rate of excretal return over a shorter period (Jarvis and Pain, 1990).

Ammonia from housed cattle

It has been estimated that 81-96% of the total ammonia emission from Europe (including England and Wales) is derived from livestock production (ApSimon *et al.*, 1987; Buijsman *et al.*, 1987). Much of this originates from winter housing of cattle, pigs and poultry and from slurry spreading, and together these losses are large compared with those incurred during grazing. For example, data from the Netherlands shows that dairy cows housed between October and May emit an average of 8.8 kg NH_3-N per cow, whilst a heifer emits 3.9 kg over the same period (Klarenbeek and Bruins, 1988). Presumably, the same principles which relate the amount of excretal ammonia emitted during grazing to fertilizer N application rate can also be applied to the total amount of ammonia emitted from cattle buildings: the number of cattle carried by the farm will be related to fertilizer N use (Forbes *et al.*, 1980), as will the concentration of N in conserved forage (Morrison *et al.*, 1980; Jarvis *et al.*, 1989b; Hopkins *et al.*, 1990). This, therefore, implies that the amount of ammonia emitted from housed cattle during the winter per hectare of grassland on the farm will be positively correlated with the amount of N applied to grass during the growing season.

Environmental implications of ammonia volatilization

It is thought that the current export of ammonia to the atmosphere has the capacity to neutralise up to 70% of the acid originally present in 'acid rain' over Europe (EMEP/CEC, cited in Jarvis and Pain, 1990). However, this benefit is at least partly offset by the resultant deposition of N in the form of ammonium sulphate and nitrate, which could be detrimental to sensitive ecosystems (Wilson and Pitcairn, 1988). Such deposits are thought to be responsible for the changes in composition and loss of species diversity in chalk grasslands in the Netherlands which have prompted some of the work referred to in the previous section of this Chapter (e.g. Bobbink, 1991).

2.7. THE EFFECTS OF VARIATIONS IN WATER TABLE DEPTH IN GRASSLAND

The historical and geographical accounts given in Chapter 1 make it clear how the development of agriculture in the Somerset Levels has been intimately related to progress in land drainage. These accounts also show how such developments have lead to conflicts of interest in the area, most recently between agriculturalists and wildlife conservationists, and how these conflicts lead indirectly to the initiation of much of the work reported in this thesis. Studies described in Chapters 3 and 4 explored the relationship between variations in water table depth at the experimental site and both agricultural productivity (Chapter 3) and losses of soil N (Chapter 4). This section therefore reviews information on the agricultural benefits or otherwise of land drainage and on the influence of hydrology on the cycling of plant nutrients within the soil. The interaction between hydrology and botanical composition is an important factor in these meadows and work studying this relationship has been reported elsewhere (Mountford and Chapman, 1993). This aspect was not studied for this thesis but a review of relevant literature is included in this section.

WATER TABLE DEPTH AND AGRICULTURAL PRODUCTIVITY

In the UK, most attempts at manipulating water table depth are aimed at lowering it with a view to increasing the usability and/or productivity of the land, i.e. land drainage. Two notable exceptions are

(a) In traditional 'flood meadows', where land is deliberately flooded in late winter-early spring to warm the soil and introduce nutrients (Purseglove, 1988).

(b) Where water levels are 'penned up' in ditches to provide field barriers and drinking water for stock (Barnett, 1981; see also Chapter 1).

As noted in Chapter 1, regulations within the Somerset Levels ESA recognise the ecological benefits of a high water table (see later), and stipulate certain minimum depths of water to be maintained in ditches, with additional incentives available to raise water levels further (Her Majesty's Stationery Office, 1992). There is very little direct information which can be used to calculate the financial implications of raising water tables in this context, and such information as there is relates to drainage of grassland. It may be dangerous to assume that the financial losses incurred by raising water tables will be the same as the gains achieved by draining land, even if the hydrological conditions prevailing before drainage are similar to those aimed at by raising the water table. This is particularly true on peat soils where some of the physical and chemical changes caused to the soil by drainage, e.g. shrinkage and oxidation, can be spectacularly irreversible (Barnett, 1981; Purseglove, 1988; Ross, 1988). Nevertheless, in view of the controversy which has surrounded agricultural drainage, particularly on the Somerset Levels (Williams, 1970; Purseglove, 1988; see also Chapter 1), it is very relevant to review the evidence for increases in productivity of grassland attributable to drainage.

Scenarios for drainage of agricultural land

Trafford (1972) listed four scenarios for land drainage, each with a specific aim for the operation:

(i) To 'reclaim' land, where no 'meaningful farming' (see below) is possible without drainage but where intensive agriculture may be possible afterwards.

(ii) To change the farming system, e.g. from grassland to cereal cropping.

(iii) To rectify a 'breakdown' situation, where the options are either to abandon the current farming system or to drain.

(iv) To improve yields. This is most likely to be worthwhile when the situation is near to a 'breakdown'.

The term 'reclamation' has been used to describe the establishment of major arterial drainage schemes in areas such as the Fens and the Somerset Levels referred to in Chapter 1. However, similar principles can apply on a much smaller, field scale. Trafford

(1972) did not define the term 'meaningful farming', but it presumably means making a worthwhile profit. From the financial standpoint, it can be taken that, unless some form of payment is available either to encourage or to discourage the farmer from draining, the benefit of reclaiming such areas will simply be equivalent to the returns from subsequent cropping or grazing minus the cost of the drainage operations and the subsequent maintenance costs, i.e. assuming that no profit was made before drainage.

In the other categories listed above, calculations need to take into account the initial level of productivity. For example, compensation payments made to farmers who are prevented from under-draining the Halvergate Marshes have been based on the assumption that drainage would allow a change from grazing store cattle to growing continuous winter wheat (Sturgess and Murphy, 1982). Such calculations do not need experimental data, whereas improvements in yield within existing systems (category 4 above) are difficult to assess without such data. Trafford (1972), reviewing evidence for increases in yield due to drainage in a range of crops, remarked that such information was very scanty, particularly for grassland for which he quoted only one source of data (Trafford, 1971). Further evidence has since become available (Berryman, 1975; Temple and Parker, 1987; Baker *et al.*, 1988; Brereton, 1989; Tyson *et al.*, 1993), but the shortage of evidence for the benefits of drainage in general is surprising in view of the huge areas of land which have been drained in the UK since the 1940's. Furthermore, Hill (1976) noted that although there was a wealth of information and advice available about the engineering aspects of land drainage, little attention had been given to the environmental implications and that many of these aspects were imperfectly understood.

The extent of agricultural drainage in the UK

Following the introduction of grants for drainage in 1940, the area of land drained annually under grant aid in the UK rose from about 5,440 ha in 1941 to 59, 090 ha in 1968 (Trafford, 1970). The rate of drainage increased further after 1970 due to encouragement from MAFF following a drainage survey of England and Wales in 1968/69 (Belding, 1971), peaking at about 100,000 ha year^{-1} by the mid-1970's (Robinson and Armstrong, 1988). Over three quarters of a million ha were drained during the 1970s, equivalent to the total area drained in the previous 30 years, before dropping to about 60,000 ha year^{-1} by the late 1980s

(Robinson and Armstrong, 1988). A survey carried out in the late 1970s showed that Britain was one of the most extensively drained countries in Europe (Green, 1979). Up to 60% of the drainage carried out between 1971 and 1980 was renewing or replacing old drains (Robinson and Armstrong, 1988), many of which were originally installed during the agricultural boom in the second half of the 19th century (Trafford, 1970; Robinson and Armstrong, 1988).

Drainage activity was greatest in the east and south of the UK and was primarily associated with cereal growing (Robinson and Armstrong, 1988). In these crops, the main benefit of drainage was in the improved access to land in the autumn, since the economic differential between autumn-sown and spring-sown cereals is high (Robinson and Armstrong, 1988). Most of the grassland drainage in these areas was carried out with the aim of converting wholly to arable agriculture, whereas in Wales and the South West of England, both predominantly grass-growing areas, most of the land remained in grassland after drainage (Armstrong, 1981). Of the total area of agricultural land drained nationally under grant aid between 1971 and 1980, 27% was previously extensively managed grassland, of which nearly half was classed as rough grazing (Armstrong, 1981). The purpose of most of this drainage was to upgrade rough grazing land, or to intensify production from existing extensively managed pastures. Nearly 40% of the drainage of extensively managed pastures was done with the intention of introducing some arable cropping (Armstrong, 1981).

Evidence for the agricultural benefits of draining grassland

Temple and Parker (1987) found that out of the five grassland sites from which they examined data (i.e. sites which remained in grassland after drainage), drainage gave an economic return at only two. However, livestock production was measured at only two of the five sites, and at both of these profits were greater when calculated in terms of liveweight gain than in terms of herbage yield (Trafford, 1971; Tyson *et al.*, 1992). Several experiments have shown substantial increases in grass growth in the spring with drainage, but growth during the summer months is often depressed (Trafford, 1971; Parker, 1983; Tyson *et al.*, 1992, 1993). Tyson *et al.* (1992) noted that the annual increases in herbage DM yield caused by drainage in their experiment were smaller than those achieved by irrigation at an adjacent undrained site , implying that, over the season as a whole, greater benefits were to be gained by adding water than by removing it. This conclusion is supported by several studies of hay production data obtained over long time scales, all of which showed positive correlations between hay yield and the amount of rain falling during spring and early summer (Cashen, 1947; Smith, 1960; Coleman *et al.*, 1987).

However, drainage increases the trafficability of land to both machinery and cattle, particularly in the spring and autumn, and soil strength is linearly related to water table depth (Rycroft, 1974; Steinhardt and Trafford, 1974). The benefits of draining grazed grassland are therefore largely attributable to increased stock carrying capacity in spring and autumn, coupled with the capacity to start grazing earlier and finish later in the season (Berryman, 1975; Armstrong, 1986; Brereton, 1989; Armstrong *et al.*, 1992). Furthermore, data from County Leitrim in Ireland showed that the effects of drainage need to be assessed on a farm scale, rather than simply in terms of the productivity of the drained fields themselves (Brereton, 1989). Herbage yields at a first cut of silage were 50% lower on undrained than on drained soil, placing a higher dependence upon subsequent cuts to produce the required amount of forage and leaving a smaller area of grass for summer grazing. Nevertheless, these considerations do not apply where the first cut is normally delayed until hay making in late June and July, as implied by the positive correlations between hay yield and rainfall noted above (Cashen, 1947; Coleman *et al.*, 1987; Smith, 1960). Neither is increased trafficability and earliness of access to land a significant advantage in unfertilized hay crops where access is not required until late June or July. Data from Tadham Moor, presented in Chapter 3, show no evidence that hay yield on unfertilized plots was depressed in a year when water tables remained high in May and June.

Drainage grants and their influence on the economics of grassland drainage

Until 1979, grants were available to cover 50% of the cost of lowland drainage and 70% in hill areas under the National Scheme (a grant of 60% was available for lowlands under the EEC Development Scheme) (Temple and Parker, 1987). Grants for lowland drainage had been reduced by 1981, and by 1987 the National Scheme had been abolished altogether, although the EEC Development Scheme still provided 15% and 30% grants in lowland and hill areas respectively (Temple and Parker, 1987).

The economic appraisals made by Temple and Parker (1987) and Armstrong *et al.* (1992) showed that where the purpose of drainage was simply to increase the productivity of grassland, drainage would seldom have been an economic proposition for the individual farmer without grant aid. Whether these grants were a worthwhile investment for the nation is difficult to ascertain. They were introduced at a time when it was perceived to be in the national interest to increase home food production (Trafford, 1970), including a need to become more independent of meat supplies from Argentina (Stewart and Lance, 1983). However, it seems unlikely that an accurate economic appraisal can have been made of the benefits on a national scale of paying grants for such work, since data on the production response to grassland drainage did not become available until later (Temple and Parker, 1987).

Flooding and waterlogging

In many low-lying areas, the primary purpose of field drainage is to prevent flooding. A review of data from Hungary showed grass to be less susceptible to waterlogging than arable crops, with production unaffected by periods of up to 3 days flooding at any time of year (Guyon, 1970). For longer periods, the extent of damage depends upon the time of year. For example, 7 days flooding caused an average of 20% reduction in grass growth if the flooding occured in June or July, but only a 10% reduction if it occurred in April or August. Fifteen days flooding in June or July reduced grass production by 50%, but caused only a 10% reduction when it occurred in March (this length of flood period occurring at any time between March and August would completely destroy a potato crop) (Guyon, 1970).

Berryman (1975) reviewed estimates of optimum water table depth for grass growth during the summer which varied between 40 and 125 cm. Kessler *et al.* (cited by Berryman, 1975) showed that grass growing on coarse textured soils could tolerate higher water tables (optimum 40-60) than on medium and fine textured soils (optimum 60-90 cm). However, grassland plants differ greatly in their water requirements and tolerances (Jones and Etherington, 1971; Grime *et al.*, 1988). Those growing in areas regularly flooded and waterlogged have evolved physiological mechanisms and tolerances to suit the conditions (Etherington, 1983) and distinct plant communities develop in response to different hydrological conditions (Grootjans *et al.*, 1988; Rodwell, 1991a,b, 1992, 1995). Studies in the meadows of the Ob' floodplain in Russia showed sharp reductions in biomass when prevailing hydrologic conditions differed significantly from the requirements of the dominant species (Shepeleva, 1986). With smaller changes in hydrology, vegetational changes had a buffering effect on productivity, with changes in the growth of certain species groups resulting in little change in overall productivity.

Several examples are given later of changes in botanical composition caused by variations in water table depth. Many of these changes can be related to differences between species in their tolerance of waterlogging (Jones and Etherington, 1971). However, some are indirect effects, caused by the influence of variations in hydrology on soil nitrogen cycle processes, which in turn influence productivity and losses of N from the soil.

The effects of drainage on soil nitrogen cycling

Several authors have concluded that drainage allows a better uptake of applied N on the evidence that dry matter (DM) and herbage N yields were greater on drained than undrained plots (Trafford, 1971; Parker, 1983; Baker *et al.*, 1988). However, other data have shown that lowering the water table can cause large increases in N-mineralization in grassland soils (Grootjans *et al.*, 1985,1986; Scholefield and Blantern, 1989; Tyson *et al.*, 1992,1993). The greater uptake of N observed on drained plots will therefore be at least partly due to a greater N availability, rather than to greater efficiency of uptake by plants. Tyson *et al.* (1992) noted that this effect would be more pronounced where low fertilizer N rates are used (e.g. Trafford, 1971) or where vegetation was cut and removed (Baker *et al.*, 1988) thereby reducing the rate of N cycling that would have occurred under grazing.

Grootjans *et al.* (1985, 1986) showed that lowering the water table in unfertilized *Calthion palustris* and *Cirsio-Molinetum* stands on fen peat increased N-mineralization by 5-10 fold and 2-3 fold respectively. In *Calthion palustris* stands, drainage increased both the yield of grass cut in June and the proportion of 'nitrophilous' species in the vegetation, but in the *Cirsio-Molinetum* stands herbage production was reduced by drainage, with no increase in nitrophilous species. The authors attributed the differences in response between sites to a low availability of phosphorus at the *Cirsio-Molinetum* site, which was exacerbated by lowering the water table. The large increases in N-mineralization due to lowering the water table, particularly at the *Calthion palustris* site (Grootjans *et al.*, 1985), were much greater than those of 80-130% recorded on clay soil in Devon (Scholefield and Blantern, 1989; Tyson *et al.*, 1993). This much greater potential N supply from peat soils (t'Mannetje, 1994) suggests that much greater production responses to drainage are possible in peat compared with mineral soils, although there are few experimental data available to test this hypothesis.

Drainage of peat soils - hydrology and production response

As already noted, the highest grants have been available for draining hill land. About 20% of hill land in England and Wales is covered by peat of varying wetness and thickness and most hill drainage is carried out on blanket peat and raised bogs (Stewart and Lance, 1983). Drainage of blanket peat is usually very ineffective from the hydrological point of view and there is very little evidence of any production benefit to be gained (Stewart and Lance, 1983). The well humified sub-surface layers in blanket peat are of very low hydraulic conductivity, although peat near the surface is of looser structure and more permeable (Rycroft *et al.*, 1975; Ingram, 1978). Installing surface drains in blanket peat hastens the removal of rainwater but has no effect on the water table depth at distances greater than 2-3 m from each drain (Stewart and Lance, 1983). Since such drains are normally installed at 15-35 m spacings, any effect on the hydrology of these areas is negligible (Stewart and Lance, 1983).

Lowland raised bogs and *Carex* fen peats, such as those on the Somerset peat moors, are more permeable than blanket peat, with hydraulic conductivities of 10^{-2} - 10^{-5} cm sec^{-1} compared with 10^{-4} - 10^{-8} (Stewart and Lance, 1983; Rycroft *et al.*, 1975). Thus, although the degree of humification of fen peats has a significant effect on their permeability (Rycroft *et al.*, 1975), drainage is generally much more effective in these soils than in blanket peat. The hydraulic conductivity values for blanket and fen peats given above encompass those of 10^{-4} - 10^{-5} cm sec^{-1} quoted for saturated clay soils (White, 1979). However, drainage of clay soils is facilitated by the use of mole drains, typically at 2m spacing (Parker, 1983; Tyson *et al.*, 1992). Moreover, when clay soils dry out, they become very fissured and hydraulic conductivity can increase greatly to 0.1 - 1.0 cm sec^{-1}.

There are few sources of data available on the production response to drainage of grassland on lowland peat, and none giving animal production data of the kind provided by Trafford (1971) and Tyson *et al.* (1992) for mineral soils. Most of the data that are available originate from the Netherlands.

In classifying soils in the Netherlands according to N delivery capacity, t'Mannetje recognised that peat soils have a higher capacity to supply N than mineral soils, and that this capacity is greatest in peats where a low water table is maintained (t'Mannetje, 1994). The work by Grootjans *et al.* already referred to above (Grootjans *et al.*, 1985; 1986), showed different effects on 'peak standing crop' in June in the two plant communities studied, both on peat soil. The authors attributed the observed effects largely to the influence of drainage on soil chemistry, rather than to direct plant physiological responses to variations in hydrology. Oomes (1991) found no effect of water table depth on DM yield when vegetation was cut and removed in June and September on a peaty clay soil overlying peat. Water table depths were maintained at 30-50 cm (wet), 40-70 cm (intermediate) and 50-70 cm (dry) during the growing season, with some winter flooding on 'wet' plots during the winter. Uptake of N tended to be higher on the 'dry' and 'intermediate' plots, particularly where nutrient recycling was enhanced by chopping the harvested vegetation and returning it to the plots as mulch.

THE EFFECTS OF DRAINAGE ON BOTANICAL COMPOSITION AND WILDLIFE VALUE

Perceived agricultural benefits of increases in 'superior' species

A National Farm Study carried out in 1974-76 showed that 31% of permanent grassland in England and Wales was poorly or badly drained, with half of the fields on clay soils falling into this category (Forbes *et al.*, 1980). However, the same survey showed that, although there was a very significant negative correlation between poor drainage and the proportion of 'preferred' (i.e. commonly cultivated) species in the swards, there was no relationship between utilized metabolizable energy (UME) output and the proportion of badly drained fields on a farm.

The full economic benefits of drainage are difficult to assess by the individual farmer whereas changes in botanical composition are usually marked (Trafford, 1971; Parker, 1983; Tyson *et al.*, 1992). Pasture grasses differ in their tolerance of water logging, with 'preferred' grasses such as *Lolium perenne, Dactylis glomerata,* and *Phleum pratense* less suited to wet soil conditions than *Agrostis spp., Deschampsia caespitosa, Holcus lanatus* and *Poa spp.*, whilst clovers can only tolerate water logging in the winter (Berryman, 1975). The advantage conferred on species such as *L.perenne* and *D. glomerata* by drier soil conditions may also be compounded by increased N availability due to enhanced N-mineralization. Furthermore, the installation of drainage is usually accompanied by increased fertilizer use. This has certainly been the case in most drainage experiments, where constraints on experimental design have seldom allowed any interaction between the effects of drainage and N application to be properly investigated (Trafford, 1971; Parker, 1983; Tyson *et al.*, 1992).

An increase in the proportion of species such as *L. perenne* in vegetation has often been taken to constitute an improvement in its productive potential, and increasing the *L. perenne* content of pastures has often been put forward as a legitimate objective in itself for draining land (Trafford, 1971; Ministry of Agriculture, Fisheries and Food, 1976; Parker, 1983). Data reviewed in Sections 2.4 and 2.10 show that, in most situations, *L. perenne* is at best only marginally superior to other grasses. Studies have confirmed that *L. perenne* swards are no more productive than those dominated by other grasses unless high rates of N are used (Hopkins *et al.*, 1990; Frame, 1991). It is clear that the proportion of *L. perenne* in a pasture is more often a reflection of its productivity than the cause of it (see comments in Section 2.8).

The influence of drainage on individual species and plant communities

Mountford (1994) carried out an extensive archive search to identify the extent and causes of floristic change since 1840 in three English grazing marshes, including the Somerset Levels and Moors. Of 526 species he studied, over half had declined, and 123 had declined severely. Only 34 species had increased. Drainage was identified as the main causative factor.

Vegetation classification shows that distinct plant communities develop in response to particular hydrological conditions (Rodwell, 1991a,b, 1992, 1995) and this can be related to differences between species in their tolerance of waterlogging and flooding (Jones and Etherington, 1971; Sjoberg and Danell, 1983; Kozlowski, 1984; Ellenberg, 1988; Grime *et* *al.*, 1988). As noted by Ellenberg (1988), most of the conclusions drawn about the hydrological preferences of individual species are based on extensive observations of their distribution and data describing their physiological responses to changes in water regime are sparser.

Some species are adapted to permanent waterlogging by the development of aerenchymatous tissue which allows them to transport oxygen to the roots. These plants can maintain a higher oxygen content in the roots than in the surrounding water (Conway, 1936; Etherington, 1983) and can therefore survive in conditions which exclude others. Several *Carex* species, particularly those commonly occurring on wet, peaty soil (e.g. *C. nigra*), have a high proportion of aerenchymatous tissue in their roots (Jermy *et al.*, 1982). In work by Jones and Etherington (1971), waterlogging reduced tillering and root growth in grasses (*Agrostis stolonifera* and *Festuca rubra*), but had no effect on shoot growth of *Carex flacca* and *C. nigra*, and little effect on root growth in these *Carex* species. Of the two sedges, *C. nigra* was the more tolerant of waterlogging.

Waterlogging tends to increase the availability of P to plants (Patrick and Mahapatra, 1968). Grootjans *et al.* (1986) showed lower levels of available P in drained than undrained soils, despite higher levels of total P. They suggested that P fixation by hydrous oxides of iron (Fe^{+++}) within the soil was responsible, whereas undrained soils contained less iron, most of which they thought would be in the reduced (Fe^{++}) form. However, Jones (1975) showed that P uptake by *F. rubra* and *A. stolonifera* was reduced by waterlogging, although it was increased in *C. flacca* and *C. nigra* under the same conditions. Jones tentatively concluded that the reduced growth observed under wet conditions, particularly in *F. rubra*, was due to P immobilization within the roots by iron.

Differences in tolerance of wet conditions between those grasses which are normally cultivated and several 'non-preferred' species have been noted above. Etherington and Rutter (1964) found that *Alopecurus pratensis* was only marginally more sensitive to water shortage than *Agrostis capillaris*, although the authors suggest that the difference would have been greater had the two species been growing together in competition. Under high water table conditions, root growth in both species was restricted to soil above the saturated zone.

Londo and Ellenberg classification

Londo (1988) classified species in the Dutch flora as 'phreatophytes', i.e. those obtaining their water supply through contact with the saturated zone, or 'aphreatophytes' - those independent of the sphere of influence of the water table. Phreatophytes were sub-divided into obligate phreatophytes (species which only grow within the area of influence of the water table) and non-obligate phreatophytes (those which will grow outside the sphere of influence of the water table if other factors such as pH, soil texture or climate allow). Ellenberg (1988) assigned indicator values for moisture requirement to about 2000 species of vascular plant growing in central Europe. The values, on a 12-point scale, indicated the optimum water availability for each species, from those surviving in arid conditions to those growing permanently or almost constantly under water. The ecological amplitudes and the consistency of classification within the Ellenberg system were tested by ter Braak and Gremmen (1987), and Ellenberg values were incorporated as the botanical data in a model to predict the effects of lowered water tables on vegetation in the Netherlands (Gremmen *et al.*, 1990).

Mountford and Chapman (1993) used Ellenberg and Londo classification and canonical correspondence analysis (CCA) (ter Braak, 1988) to interpret field data from three wetland and wet grassland sites, includingTadham Moor (Mountford *et al.*, 1993a). Of the 122 species recorded in the meadows at Tadham Moor, 26 were obligate phreatophytes, 35 were non-obligate phreatophytes, and the remaining 60 species were aphreatophytes. The mean Ellenberg values for the obligate and non-obligate phreatophytes present were 8.64 and 7.07 respectively, whilst the mean for aphreatophytes (4.83) was typical of species indicating 'moist' sites (Ellenberg, 1988). The CCA ordination showed marked separation not only between species associated with shallow or deeper water tables at the site, but also between species associated with relatively constant or widely fluctuating water tables. Species associated with consistently high water tables included *Equisetum fluviatile, Lychnis flos-cuculi, Carex panicea, Juncus effusus* and *Myosotis laxa*. Those associated with high but fluctuating water tables included *Carex rostrata, Oenanthe fistulosa, Rumex crispus, Ranunculus flammula* and *Glyceria maxima*. Other studies reported in the same paper showed that the vertical distribution of species on ditch banks could be related to their Londo and Ellenberg classifications.

Observed changes in vegetation due to changes in hydrology

In an analysis of data from several studies on peat grassland in the Netherlands, Strien and Melmann (1987) showed that drainage was very detrimental to botanical richness in extensively managed meadows. However, it had little influence on the composition of intensively managed pastures due to the overshadowing effects of fertilizer N.

Several studies have shown that changes in hydrology can affect species composition indirectly, by altering soil chemistry. Studies in fen vegetation by Grootjans *et al.* (1988) showed that lowering the water table influenced vegetation composition by reducing the supply of Ca^{++} and HCO_3^- ions from groundwater and increasing seasonal fluctuations in ground water quality. Rare phreatophytes such as *Dactylorhiza incarnata, D. maculata, Carex appropinquata* and *Valeriana dioica* were absent from areas affected by drainage and were restricted to areas with a more constant supply of Ca^{++}-rich groundwater. Harding (1994) noted that spring-fed valley fens in Suffolk contained a higher proportion of bryophytes among the rare fen species present than did topogenous (rain fed) fens. Smittenberg *et al.* (1984) reported very similar results to those of Grootjans *et al.* (1988), also in fen vegetation, and remarked that any study on the sensitivity of vegetation to changes in hydrology is incomplete if aspects of water quality are neglected.

As already noted, lowering the water table usually results in an increase in the net mineralization of N in the soil (Grootjans *et al.*, 1985,1986; Scholefield and Blantern, 1989; Tyson *et al.*, 1992,1993). Grootjans *et al.* (1985) showed that, at one site, this led to major changes in vegetation, characterised by an increase in the proportion of nitrophilous species. However, where P availability was limited by drainage at another site, vegetation changes appeared to be related to soil moisture and possibly P availability, rather than to the increased N availability which occurred (Grootjans *et al.*, 1986). Smeets *et al.* (1980) recorded temporal changes in vegetation growing on alluvial clay over sand along a gradient away from a river in the De Kampina Nature Reserve in the Netherlands. These changes were caused by a reduction in flooding frequency and a lowering of the water table, but most were attributable to changes in soil fertility. Vegetation was affected both close to the river where land had previously been supplied with nutrient rich water and at a distance where the lowered water table led to eutrophication by increased N-mineralization. The overall result was an expansion of the existing, intermediately located

mesotrophic *Molinetalia* community at the expense of both the eutrophic *Phragmititea* community close to the river and the oligotrophic *Cirsio-molinetum* furthest away from it.

2.8. SEED BANKS AND SEED RAIN IN GRASSLAND

Two of the agricultural practices upon which this thesis concentrates, inorganic fertilizer use and variations in cutting date, have the potential to influence the composition of the soil seed bank, either indirectly through changes in vegetation composition or directly by their effects upon seed return and/or germination behaviour. These aspects are studied in Chapters 6 and 8. This section reviews studies on the composition of grassland seed banks and on the ecological principles governing seed production and seed bank dynamics, and the effect of variations in cutting and/or grazing management on seedling dynamics and vegetation composition.

GRASSLAND SEED BANKS

Significance of sampling methodology

Numerical comparisons between different seed bank studies are sometimes difficult to make because a variety of assessment techniques are used (Roberts, 1981; Warr *et al.* 1993). The depth to which samples are taken is significant, since most seeds are found near the soil surface in undisturbed soil (van Altena and Minderhoud, 1972; Roberts, 1981). Furthermore, a distinction has to be made between viable and total seed numbers, since some counts are based upon the number of seedlings emerging over a period of time from thinly spread soil samples, whilst other studies involve the counting of all seeds present in a given volume of soil (Roberts, 1981). When the former method is used, the time over which counts are made is important. Vega and Sierra (1970) continued counts on samples taken from tropical soils for three years. Of the total numbers of seedlings they recorded, 83% emerged in the first year, 16% in the second and 1% in the third year.

Probabaly the most extensive surveys of grassland seed banks carried out in Britain were those of Chippendale and Milton (1934) and Champness and Morris (1948). Both used the seedling emergence technique. However, whilst Chippendale and Milton took samples to a depth of 30 cm and recorded seedling emergence over three years, the data reported by Champness and Morris were from counts made over one season only, from samples taken to a depth of 17 cm. Champness and Morris retained a few samples for another year to check for further emergence. They concluded that the data they had collected during the first year were substantially reliable for most species, but for a few, notably *Juncus bufonius* and *Coronopus squamatus*, results based on only one year's data were incomplete and possibly misleading.

The numbers quoted in the following paragraphs all refer to viable seeds per m^2.

Size and composition of grassland seed banks

Large numbers of seeds are normally present in soil beneath grasslands, although Warr *et al.* (1993) observed that numbers are usually smaller than in arable soils, undoubtedly due to greater disturbance in the latter (Thompson, 1978 - see later discussion of seed persistence in relation to disturbance). The largest numbers recorded by Chippendale and Milton (1934) were from from lowland pastures formerly in arable rotation (21,259 - 69,903 seeds.m^{-2} at 0-30 cm), although fairly high numbers were recorded in hay meadows (28,310 seeds m^{-2}) and a fertile marsh (31,345 seeds m^{-2}). Although upland pastures generally support lower seedbanks than lowland grassland (Thompson, 1978), occasionally high numbers were recorded in uplands, both by Chippendale and Milton (1934) and by Champness and Morris (1948). These higher than usual numbers were almost invariably due to *Calluna vulgaris* or *Juncus spp.*, both of which produce large numbers of very small seeds (Grime *et al.*, 1988).

Dicotyledonous species are often the most abundant plant group in seed banks (Roberts, 1981). Dicots constituted 97% of the total seed bank in a study on meadow-steppes in Russia, of which legumes were 7% (Golubeva, cited in Roberts, 1981), and 60% in grassland on peat soil in Southern Bohemia (Mika, 1978). Between 24% and 62% of the species recorded by Jalloq (1975) were dicots, of which 3-7% were legumes. *Trifolium repens* is the commonest legume component of seed banks in Britain and Europe (Champness and Morris, 1948; Foerster, 1956; van Altena and Minderhoud, 1972), although *Ulex spp.* can be abundant where seeding has been allowed over a long period (Jalloq, 1975; Ivens, 1978; Zabkiewicz and Gaskin, 1978).

Agrostis spp., Poa spp. and *Holcus lanatus* are the most common grass components of seed banks, but these are seldom as numerous as sedges and rushes where the latter occur in the vegetation. Champness and Morris (1948) recorded few *Juncus spp.* in the 'better' pastures, but where sedges and rushes were present in the vegetation they found up to 11,000 seeds m^{-2} of these species, mainly *Juncus effusus.* More than 50,000 viable seeds m^{-2} of *Juncus spp.* were recorded on the top 23 cm in a marshy area of Wales (Anon, 1967), whilst 8000 - 9000 seeds m^{-2} were recorded in the top 10 cm in Romania (Simtea, cited in Roberts, 1981). Lower numbers of *Juncus spp.* seeds were recorded by Williams (1985) beneath an old meadow near Oxford, at 2780 - 5180 seeds m^{-2} compared with 3300 - 7339 grass seeds m^{-2}. However, no *Juncus spp.* were present in the meadow vegetation, although the area was low-lying and suceptible to a high water table (Elliott *et al.*, 1974). *Agrostis capillaris* was the most abundant grass both in the vegetation (19-24% cover) and in the seed bank (833 - 3270 seeds m^{-2}). Dicots occupied between1.5% and 28% of ground cover but were always major components of the seed bank at 1350 - 1680 seeds m^{-2}.

The seed bank in relation to above ground vegetation

The composition of the seed bank beneath grassland almost invariably differs from that of the vegetation (Chippendale and Milton, 1934; Champness and Morris, 1948; Major and Pyott, 1966; Thompson and Grime, 1979; Williams, 1984,1985; Thompson, 1986; 1987; Bakker, 1989) and a similar phenomenon has been shown in wetlands (van der Valk and Davis, 1976; Wilson *et al.*, 1993). Certain species which are common in grassland vegetation, for example *Dactylis glomerata, Festuca ovina, F. rubra, F. pratensis, Lolium perenne* and *Phleum pratense*, seldom show more than a small presence in the seed bank and are often absent altogether, whilst others, e.g. *Agrostis spp., Poa spp.* and *Juncus spp.* are often much more common in the seed bank than in the vegetation (Chippendale and Milton, 1934; Champness and Morris, 1948). Other species have shown a closer correspondence, eg. *Alopecurus pratensis, Anthoxanthum odoratum* and *Cynosurus cristatus* (Champness and Morris, 1948).

Stress, disturbance, seed bank size and persistence

The frequently observed lack of correspondence between vegetation and seed bank is mainly due to large differences between species in the longevity of their seed in the soil

(Lewis, 1961,1973; Thompson and Grime, 1979; Kivilaan and Bandurski, 1981). Thompson (1978) suggested that species associated with high levels of disturbance are likely to have evolved the ability to produce a persistent seed bank, since selection for buried seeds will be intense under these conditions. Accumulation of a large seed bank is also favoured by low stress conditions, i.e. a low predominance of constraints on DM production (*sensu* Grime, 1979), since an adequate level of DM production is required to support seed production. Thompson quoted data from Chippendale and Milton (1934), Champness and Morris (1948) and Milton (1939) which showed that the size of the seed bank was negatively correlated with altitude. Milton's (1939) work in the Welsh uplands showed this most clearly, with a total of 5,017 seeds m^{-2} at 499 feet on Plynlymon and only 1877 seeds m^{-2} at 733 feet, and 4315 seeds m^{-2} at 366 feet on Cader Idris compared with 1526 seeds m^{-2} at 794 feet. Milton also showed very small numbers of viable seeds (877 seeds m^{-2}) in a salt marsh in the Dovey estuary, where low nutrient (i.e. high stress) conditions prevailed and disturbance was low.

Seed bank 'types'

The composition of the seed bank reflects the strategies of the components of past and present vegetation (Grime, 1979; Roberts, 1981). Thompson and Grime (1979) categorized species into four types according to the longevity of their seed in the soil. The main distinction these authors made was between Types I and II on the one hand, of which seed lasts no longer than one year, compared with Types III and IV which form a persistent seed bank. Types I and II species are adapted to exploit seasonally predictable disturbance, whereas Type IV species have the potential for regeneration when disturbance is temporally or spatially unpredictable.

Type III species are intermediate between Types I and IV, with some seeds germinating soon after release by the plant whilst others contribute to a long term seed bank. Species in this group are associated with the capacity for both rapid population increase and persistence and include some of the most widespread species in temperate grasslands, e.g. *Agrostis spp., Poa trivialis* and *Holcus lanatus* (Grime *et al.*, 1988). Type I species almost always germinate soon after shedding, whereas Type II species germinate in the spring of the following season.

Bakker (1983) used a different set of criteria for identifying species as 'transient' or 'persistent' in the seed bank. He counted seedling emergence from soil collected from beneath fields cut for hay in which the species richness had increased following cessation of fertilizer use. Species were classed as persistent seed bank species if:

(i) more seeds were found in the 2-4 cm and 4-6 cm layers than in the 0-2 cm layer

(ii) they were present in the seed bank but not in the vegetation

(iii) the number of seeds was not related to the above ground abundancy

(iv) no decline was found in the number of seeds under prevention of seed rain.

Species showing the opposite characteristics were classed as transient. These criteria drew a striking distinction between species of what Bakker called 'pioneer communities (treading and/or periodically dry and wet soils) *[sic]* which were invariably classed as persistent according to the above criteria, and 'hayfield' species which fell within the transient group.

All the species quoted by Bakker as 'persistent' were also classified as seed bank Type III or IV species *sensu* Thompson and Grime (1979) by Grime *et al.* (1988), except for *Polygonum mite* (= *P. laxiflora*, Stace, 1991), which was not listed by Grime *et al.* (1988). However, it is interesting to note that almost all the species Bakker classed as 'transient' hayfield species are also Type III or IV species according to Thompson and Grime criteria. These include *H. lanatus, Cerastium fontanum, Ranunculus repens, R. flammula, Anthoxanthum odoratum, Plantago lanceolata* and *Lychnis flos-cuculi.* With the exception of *H. lanatus* and *A. odoratum*, all the species in this list were classed by Grime *et al.* (1988) as relying principally on vegetative reproduction for regeneration (Grime, 1979).

It may be dangerous to try to define the seed bank strategy of a particular species even partly on the basis of the depth of its distribution in the soil in situations where vegetation composition is changing progressively. This point will be particularly pertinent if the management of the vegetation has also changed to one allowing larger numbers of seed to be shed than before (e.g. a change to later cutting or from intensive grazing to hay making). On the other hand, there is also a danger in applying generalizations about preferred regeneration strategy to specific situations. With the exception of *L. flos-cuculi*, which is not included in their detailed autelogical accounts, each of the species in the above list of Bakker's 'hayfield' species is acknowledged by Grime *et al.* (1988) as often reproducing by seed. Regeneration from seed is much more likely to occur where ample opportunity for seed shedding is followed by at least moderate levels of disturbance, as in hay making followed by aftermath grazing. Evidence for the influence of vegetation management on seed bank composition is reviewed later.

Seed burial and dormancy

Almost all of the Type II species listed by Grime *et al.* (1988) require exposure to a period of low temperatures (chilling), which ensures dormancy until the spring. A few species, such as *Valeriana officinalis* and *Succisa pratensis,* do not require chilling but are relatively late flowering and have minimum temperature requirements for germination which are not normally satisfied at the time of shedding; this effect may be amplified by after-ripening requirements such as a period of dry storage (Grime, 1979; Grime *et al.*, 1981; Grime *et al.*, 1988).

Species which form a long-term seed bank usually have a combination of characteristics that ensure both the opportunity for burial and the prevention of subsequent germination until favourable conditions prevail. Most species require an external source of moisture for germination and remain ungerminated at the soil surface under dry conditions. During this period they are available for ingestion and burial by soil microfauna (McRill and Sagar, 1973; Sagar and Mortimer, 1976). Small, hairless and round seeds are an advantage in this context, and many species with long-term seed banks have these characteristics (Thompson, 1987). Grime (1979) listed several mechanisms which delay germination, including:

(i) The need for an extended period of incubation in warm, moist conditions for maturation of the embryo, e.g. *Ranunculus repens, R. acris , Potentilla erecta*

(ii) Inhibition of germination by light, e.g. *Poa pratensis, Cirsium arvense, Anisantha sterilis*;

(iii) Chilling requirements, e.g. *Polygonum aviculare, Galium palustre, Rhinanthus minor*

(iv) Impermeable testa e.g most legumes (often referred to as 'hard' seed).

Breaking dormancy

Once buried, most components of the long term seed bank have exacting germination requirements that ensure their persistence (Grime, 1979; Williams, 1983; Thompson, 1987). Probably the most common safeguard is a partial or total inhibition by darkness (Grime, 1979; Grime *et al.*, 1981; Grime *et al.*, 1988). Grime (1979) noted that seedlings produced from buried small seed would have difficulty in penetrating to the surface and that very small-seeded species all appeared to have an obligate light requirement. Diurnal temperature fluctuation acts as a trigger for germination in some species and ensures that germination occurs both near the surface and in vegetation gaps, since the amplitude of temperature fluctuation is greatest there (Thompson *et al.*, 1977; Thompson and Grime, 1983; Williams, 1983). Williams (1983) notes that nitrate increased the germination of all five grasses he tested, and that the order of response was similar to that to light and temperature. Response to nitrate may well enhance gap detection, since nitrate levels are likely to be higher in soil unoccupied by growing plants (Pons, 1989).

In some species, e.g. *Deschampsia caespitosa, H. lanatus, P. pratensis, P. trivialis* and *Rumex obtusifolius*, a requirement for fluctuating temperatures appears to be interchangeable with a light requirement (Thompson *et al.*, 1977). On the other hand, *Elymus repens* requires both light and fluctuating temperatures, whilst *L. perenne* can give almost complete germination in both light and dark and both with fluctuating or constant temperature (Thompson *et al.*, 1977; Williams, 1983).

Shading and light quality

Light filtering through a vegetation canopy undergoes spectral modification and the ratio of far-red to red light increases with increasing density of shading (Smith, 1973). In several studies, germination of the majority of species tested was inhibited by irradiance with far-red light and stimulated by red or green light (Grime and Jarvis, unpublished data cited in Grime, 1979; Williams, 1983) or germination was inhibited by far-red light but was equally good in red light or daylight (Maas, 1989). Williams (1983) found that short exposure to far-red light followed by transference to favourable conditions had a persistent inhibitory effect on germination three out of the five grasses he tested (*A. capillaris, H. lanatus* and *F. rubra*) , i.e. dormancy had been induced, rather than being enforced by continuing

adverse conditions. Germination of *Cynosurus cristatus* was not inhibited by far-red irradiance and there appeared to be no inhibition in *P. trivialis*, although results were inconclusive for the latter due to poor germinability of the seed used. Hilton *et al.* (1984) showed only enforced dormancy in *P. trivialis* by a high far-red : red ratio. Maximal germination occurred once seeds were transferred to full light. The same study also showed that seeds collected from plants growing in an enclosed grassland habitat were less sensitive to differences in light quality than those collected from arable fields.

Silvertown (1980b) showed leaf-canopy-induced dormancy in 17 of the 27 chalk grassland species he tested which normally germinate equally well in light or dark. All 27 species were additional to those tested by Williams (1983). In Silvertown's work, the phenomenon was particularly prevalent among annuals and biennials, six out of seven of which showed between 27% (*Daucus carota*) and 92% (*Cerastium fontanum*) foliar-induced dormancy. Among the 11 perennials showing some induced dormancy, values ranged from 20% (*Origanum vulgare*) to 78% (*Prunella vulgaris*).

Phytochrome

Responses to spectrally-modified light are related to the behaviour of the pigment phytochrome which exists in two inter-convertible forms in plant tissue, *Pr* anf *Pfr* (Attridge, 1990). *Pr*, the inactive form, is converted to the active *Pfr* form by the action of light within the red spectrum, whereas the reaction is reversed by far-red light. The form in which the pigment exists therefore depends upon the ratio of red : far-red in the light to which the plant tissues (including seeds) are exposed. However, the conversion process is inhibited by dehydration. During ripening on the parent plant, a moisture content will be reached at which the *Pr*/*Pfr* ratio becomes fixed, dependent upon the dominating light regime (Attridge, 1990). Cresswell and Grime (1981) showed that the extent to which chlorophyll was lost from the maternal tissues enclosing the seed during seed ripening was important in influencing subsequent seed germination. They concluded that the effect was dependent upon the rate of change in the filtering property of these tissues in relation to the rate of dehydration of the maturing seeds. The presence of a light requirement for germination in a range of species was strongly correlated with the retention of chlorophyll in the investing tissues.

Cresswell and Grime (1981) noted that many of the species which retain chlorophyll in the investing structures throughout maturation are small-seeded species known to develop persistent seed banks. The light requirement conferred on these species by their maturation environment probably enables them to remain dormant when buried. In larger-seeded species which retain chlorophyll in the seed-enclosing tissues but which are not normally part of persistent seed reserves, the induced requirement for unfiltered light may ensure that germination occurrs only in gaps in the vegetation. Dormancy prolonged by light filtering through a closed canopy will also help to increase the chances of small seeds becoming buried. Cresswell and Grime (1981) also noted that differential rates of chlorophyll loss and/or seed drying within the same inflorescence may explain the germination polymorphism recorded for some species.

Polymorphism of germination requirements

Grime (1979) noted that polymorphism of germination requirements, both within plant populations and between seeds from the same plant, is a feature of many herbaceous species with persistent seed banks. This is particularly significant for ruderals, where synchronous germination could cause large-scale mortality. Van der Vegte (1978) reported two genotypes of *Stellaria media* growing side by side, one of which produced seeds which all germinated in the autumn following shedding, while the other produced a persistent and phenotypically diverse seed reserve.

The effects of vegetation management on seed bank composition

In one of the long-term fertilizer experiments of which the botanical results are described in section 2.4 of this Chapter, Williams (1985) also recorded the effect of fertilizer treatments on seed bank composition. These data showed the usual lack of correspondence between seed bank and vegetation composition in general, but also showed differences in seed bank composition for several individual grasses which corresponded with vegetational differences caused by fertilizer treatment. After nearly 20 years of treatment, differences in seed bank were generally much greater than those in the vegetation. A 26% reduction in ground cover of *Agrostis spp.* was reflected in a more than four-fold reduction in the number of viable seeds, whilst a five-fold increase in ground cover of *Poa spp.* had resulted in a 23-fold increase in the *Poa* seed bank. The picture was quite different for dicotyledonous species which showed an 11-fold reduction in ground cover by fertilizer application, although this effect was not statistically significant.

In work in fen vegetation in Germany, Pfadenauer and Maas (1987) noted that several typical litter fen species had disappeared from the seed bank after 15 years of fertilizer application. Bakker (1989) also reported an absence of 'typical hay field' species in seed banks beneath previously fertilized meadows in the Netherlands, where management techniques aimed at restoring species rich hay meadows were being tested.

In other work by Williams (1984), prevention of seed setting by frequent cutting led to a loss from the seed bank of 27% per year in the number of grass seeds, but only a 16% loss in dicots. When plots were not cut until late June, a large shed of seed, mainly of *Cerastium fontanum*, doubled the seed bank although only transiently. However, 20% of the seed of *Agrostis capillaris* shed in late summer following cutting in early June, became incorporated more permanently into the seed bank.

Seed banks tend to be smaller under intensive managed grazing pastures than under laxer grazing (Champness and Morris, 1948; Douglas, 1965). This is firstly because more frequent defoliation prevents flowering and seed setting (Williams, 1984), and secondly because *L. perenne*, which does not form a long-term seed bank (Grime *et al.*, 1988), is often abundant under intensive grazing (Forbes *et al.*, 1980). Roberts (1981) cited several examples of work in Russia where the effect of cutting and grazing management on meadow seed banks were investigated. Zelenchuk found higher seed numbers in total under mown meadows than under grazing. Grasses were the major component beneath grazed swards but there were few grasses or legumes in seed banks under mown meadows. The same author found that grass seeds were less numerous in peat soil beneath mown meadows compared with unmown, whilst *Carex spp.* and *Juncus spp.* were more numerous. On the other hand, Golubeva found no difference between mown and unmown meadow steppe seed banks in Russia. Roberts (1981) pointed out that the extent to which seed bank composition reflects the management of the vegetation depends greatly on the particular species present in the vegetation and the extent to which their growth and seed production has been affected.

SEED PRODUCTION AND THE EFFECTS OF CUTTING AND GRAZING ON SEED RAIN AND VEGETATION COMPOSITION

Plant species differ greatly in the timing and abundance of their seed production (Salisbury, 1942; Primack, 1985; Smith and Jones, 1991). These factors, combined with the extent to which each species within a community relies on regeneration from seed (Grime, 1979; Grime *et al.*, 1988), are important in determining the effect of changes in cutting/and or grazing management on vegetation composition. Short-lived species which have no seed dormancy are obviously more dependent upon continual seed return and seedling establishment than long-lived perennials which form a long-term seed bank and/or are capable of vegetative reproduction. On the other hand, many species are flexible in their regenerative strategies (Grime, 1979; Grime *et al.*, 1988). Many produce seeds of which some germinate straight away, whilst others become incorporated into the seed bank, i.e. Type III species (Thompson and Grime, 1979). The population dynamics of those meadows where the majority of species are allowed to set seed will therefore be complex. There appears to have been no study relating the components of seed rain in hay meadows directly to seedling survival and subsequent botanical change, although Peart (1989a,b,c) carried out work of this kind in abandoned grassland in California. Studies by Bakker *et al.* (1980), reviewed later, related seedling emergence and botanical change in meadows to differences in harvest dates, but did not include measurements of seed rain.

Even in grazed pastures, some plants are able to set seed, although grazing, especially at high stocking rates, usually reduces reproductive development in vegetation (Rabotnov, 1969; Korte and Harris, 1987; Orr *et al.*, 1988). Differences between species in their capacity for seed production are therefore relevant in both grazed and mown pastures, whilst, in hay meadows, the relationship between time of cutting and the fruiting phenology of the component species is of prime importance (Smith and Jones, 1991; Younger and Smith, 1993).

Reproductive allocation in relation to life history and regeneration strategy

The proportion of its total resources which a particular plant species allocates to seed production varies greatly (Salisbury, 1942; Rabotnov, 1969; Sarukhan, 1974; Sobey, 1981; Hutchinson and Seymour, 1982; Wilson and Thompson, 1989) and usually reflects both its

regenerative strategy and its life history (Grime, 1979; Grime *et al.*, 1988). In an extensive review of literature on seed regeneration in meadows and meadow steppes in the USSR, Rabotnov (1969) reported that 49-68% of the species present produced between 10-20 and 250 seeds per plant, but a few produced more than 1000 seeds per plant.

Wilson and Thompson (1989) showed that reproductive allocation (RA), defined as the proportion of total biomass of mature plants which was allocated to sexually reproductive parts, ranged from 0 to 66% within the 40 grasses they tested. RA was lowest in perennial species with a stoloniferous growth habit, e.g. *Agrostis spp.*, *Festuca rubra*, *Holcus mollis* and *Poa pratensis* (all <10%), and highest in annuals, at between 41% (*Anisantha sterilis*) and 66% (*Catapodium rigida*). Tufted perennials occupied the mid range. RA was relatively high in several perennial grasses common in hay meadows, e.g *C. cristatus* (30.5%), *P. trivialis* (28%), *Trisetum flavescens* (25.3%) and *A.odoratum* (14.1%), but relatively low in some others, e.g *Phleum pratense* (8.7%) and *H. lanatus* (6.4%).

Within each group of species tested by Wilson and Thompson (1989) (i.e. annuals or perennials), there was a broad negative correlation between RA and plant height. There appears to be a trade-off between (a) maximizing the competitiveness of the adult plant by allocating resources to vegetative growth, or (b) producing many and/or heavy seeds in order to increase the chances of successful reproduction. Wilson and Thompson's data illustrated a similar dichotomy within perennial grasses in the allocation of resources between vegetative and sexual reproduction. This point is further illustrated by studies of three closely related buttercup species, *Ranunculus repens*, *R. acris* and *R. bulbosus* in a grazed pasture in Wales (Sarukhan, 1974). *R. repens* regenerated largely by vegetative reproduction, whilst *R. bulbosus* depended wholly on regeneration from seed and *R. acris* mainly did so (Sarukhan, 1974; Harper, 1977; Grime *et al.*, 1988). The latter two species produced on average 6-10 times as many seeds per plant as *R. repens*. The maximum number recorded for *R. repens* was 77 seeds per plant, whereas a large number of *R. acris* and *R. bulbosus* plants produced 40-140 seeds, with maxima of 281 and 287 respectively. Moreover, a smaller proportion of *R. repens* plants flowered (20%) compared with the other two species (60%), with further differences in the number of flowering plants which set seed (25% for *R. repens*, 70% for *R. bulbosus* and 40% for *R. acris*).

Seed size/number

Another trade-off exists between the number and the size of the seed a plant produces. Within perennial grasses, seed weights typically range from 0.05 mg for *Agrostis canina*, 0.06 mg for *A. capillaris* and 0.09 mg for *Poa trivialis*, to 1.53 mg for *Festuca pratensis* and 1.79 mg for *L. perenne* (Grime *et al.*, 1981,1988). Common annual grasses also show a wide range, e.g from 0.26 mg for *P. annua* to 2.9 mg for *Bromus hordeaceus*. Data provided by Grime *et al.* (1981), Salisbury (1942) and Thompson (1984,1987) show a small but insignificant difference in mean seed weight between annual and perennial dicots in favour of the former, but a very much greater mean seed weight in biennials than either annuals or perennials. By contrast, Silvertown (1981b) showed that, within limestone grassland, annuals produced significantly lighter seeds than biennials and perennials, which did not differ. However, as Thompson (1984) pointed out, most of the annuals considered by Silvertown were winter annuals, a group restricted to bare ground for successful regeneration (Ratcliffe, 1961). Thompson (1984) found it difficult to decide whether Silvertown's (1981b) results showed an association between seed size and life history, or between seed size and regeneration niche (Grubb, 1977).

Thompson (1987) concluded that successful establishment of seedlings in closed vegetation was dependent upon a slow rate of exhaustion of seed reserves and that large seed weight was one way of achieving this, another being low relative growth rate (RGR) in seedlings. He also noted, from an analysis of data provided by Salisbury (1942) and others, that biennials produce on average about four times as many seeds per plant as annuals or perennials (Thomson, 1984, 1987). In short-lived species, very dependent upon regeneration from seed, a biennial life history allows greater allocation of resources to seed production than is possible in annuals, which have only a short period to complete both vegetative and reproductive development. For annuals therefore, the choice is more clear-cut between producing a few, large seeds with little or no dormancy, each of which has a good chance of establishing under adverse conditions (e.g. *Bromus spp.*), or producing a greater number of small seeds.

Nevertheless, large seeds are comparatively rare in annuals (Salisbury, 1942; Grime *et al.*, 1988). Thompson (1984) pointed out that, for annuals, it may not be possible to reconcile the production of a sufficient number of large seeds in a single season with the

need to produce sufficient vegetative growth to compete with tall perennials. However, some ruderal species, e.g. *Poa annua* and *Stellaria media*, are able to flower at any time of year and can thus produce large numbers of seeds per annum, although they may bear few seeds at any one time (Sobey, 1981; Hutchinson and Seymour, 1982). Hutchinson and Seymour (1982) estimated that *P. annua* was capable of producing over 200,000 seeds per year, although the number of seeds present at any one time ranged from 40 to 400 seeds per plant, increasing with nutrient availability. The number of seeds produced per annum by *S. media* also varies enormously, due to a combination of its ability to flower at any time of year and its very variable plant size, but estimates of up to 14,000 seeds per annum have been recorded (Sobey, 1981). However, although *P. annua* and *S. media* are commonly found in pastures, they are both primarily species of disturbed habitats where they are unlikely to have to compete with established perennial vegetation (Grime *et al.*, 1988).

Effects of grazing on flowering and seed production

Grazing, particularly by sheep, is often associated with high species richness, particularly in chalk grassland (Grubb, 1976; Willems, 1983) and heathland (Bakker *et al.*, 1983). The survival of many short-lived forbs in chalk grassland is dependent upon establishment from seed which is in turn enhanced by the short turf produced by regular grazing (Shenkevald and Verkaar, 1984). Nevertheless, grazing usually reduces flowering and seed production in pastures, particularly in contrast to hay meadows (Rabotnov, 1969; Korte and Harris, 1987). For example, Zelenchuk (cited in Rabotnov, 1969) noted that 31% of the species in a lowland, extensively grazed meadow in the USSR did not produce any seed, whereas only 17% failed to do so in hay meadows. However, such comparisons are influenced by time of cutting on the one hand and stocking rate on the other. In a permanent pasture grazed by sheep and cattle in Wales, the number of flowering plants of *Ranunculus spp.* which set seed in lightly grazed sites was more than three times that in intensely grazed areas, with an 11-fold difference in the number of seeds set per flowering plant (Sarukhan, 1974). Sarukhan (1974) also noted that flower heads of both *R. acris* and *R. bulbosus* were more susceptible to grazing and to damage by livestock than those of *R. repens*, due to their taller flowering stems.

Rosette-forming plants such as *Hypochaeris radicata, Taraxacum spp, Bellis perennis, Leontodon hispidus* and *Plantago lanceolata* are common in species-rich grazed pastures (Elberse *et al.*, 1983; Bakker, 1989). The prostrate growth habit of these species allows much of their leaf material to escape grazing, and the production of a wiry flower stem, e.g. in *H. radicata*, allows seed heads to ripen undamaged (Grime *et al.*, 1988).

Seed rain in undisturbed meadows

Rabotnov (1969) reported a wide range of values for the total number of seed shed in undisturbed meadows in the USSR, from 7,500 - 8,000 seeds m^{-2} in sub-alpine meadows in the Caucasus to 26,000 - 67,200 seeds m^{-2} in *Nardus stricta* associations in the Carpathians. Peart (1989a) recorded very large numbers of seeds in unmanaged California grassland undergoing successional changes following cessation of fertilizer use. Seed rain was lowest in vegetation patches containing a mixture of annual and perennial species characteristic of the previously managed vegetation, and highest, at about 172,000 seeds m^{-2}, in patches dominated by *Deschampsia holciformis.* Although *Deschampsia* occupied 86% of the vegetation cover in these patches, with *Holcus lanatus* and *Anthoxanthum odoratum* occupying only about 5% each, seed rain was composed of all three species in approximately equal amounts. In patches dominated by *Holcus* or *Anthoxanthum,* seed rain was composed almost entirely of the dominant species at 64,285 and 62,000 seeds m^{-2} respectively, although *Anthoxanthum* produced a mean of 6000 seeds m^{-2} from only 1.8% of the vegetation cover in *Holcus* patches. *Holcus* was absent from patches dominated by *Anthoxanthum.*

Peart (1989a) found no correlation between seed rain and seedling recruitment in either *H. lanatus* or in *A. odoratum,* despite significant correlations between seed rain and biomass with both species, and concluded that inhibition of seedling establishment by vegetation compensated for increased seed input. By contrast, seedling recruitment of the annual grass *Vulpia bromoides* was very significantly correlated with seed input. Of the species studied, *A. odoratum* appeared to be the one most actively recruited from the seed bank. Further studies (Peart, 1989b,c) showed that colonization by *A. odoratum* and *H. lanatus* was increased 6-2500 fold by canopy gap formation (e.g. by plant death, grazing and disturbance by wild animals). *Vulpia bromoides* colonized gopher mounds more effectively than perennial grasses, but was largely excluded by perennials in the second year.

Variations in flowering and seeding phenology

Primack (1985) noted that flowering phenology varies both between and within plant communities. Plants of disturbed habitats tend to flower throughout the season, whilst herbs beneath forest canopies, for example, bloom early, before the canopy becomes closed. In general, time of flowering can be related fairly precisely to temperature, and lateness of flowering increases with latitude, associated with a decrease in the number of specialised bees.

Within communities, species flower in overlapping sequence throughout most of the growing season (Rabinowitz *et al.*, 1981), even in hay meadows which have been cut in mid summer for a great many years (Smith and Jones, 1991). Primack (1985) reviewed the possible explanations for the evolution of differing flowering phenologies within plant communities, the most popular being that this was caused by competition for pollinators. However, Primack believed that convincing evidence for this was provided only by studies of individual pollinators, e.g hummingbirds (Waser, 1978). The explanation did not take account of the wide variety of pollinating fauna in most communities, e.g. birds, butterflies, bees, flies and other insects. Seasonal limitations on flowering times appear to be caused more by phylogenetic constraints, which may not have changed significantly for millions of years, than by the much smaller differences which exist between life forms (Kochmer and Handel, 1986).

Significance of cutting date

The distribution of flowering time among individual species within plant communities is frequently skewed to the right, i.e. towards lateness (Thomson, 1980; Primack, 1985; Smith and Jones, 1991). Smith and Jones (1991) showed that few of the species present in hay meadows in the Pennine Dales had reached maximal ripe seed production by the hay cutting dates prescribed within the Pennine Dales Environmentally Sensitive Area (ESA) (i.e. 1-15 July according to specific Dales). Of the five grasses studied, only *Poa trivialis* reached its maximum before 15 July (on 12 July) and of the ten herbs studied, only four did so: *Geranium sylvaticum*, *Plantago lanceolata*, *Ranunculus acris* and *Rhinanthus minor*. A further two herbs, *Leontodon hispidus* and *Trifolium pratense*, had reached maxima by the last assessment on 21 August, but *Centaurea nigra* and *Filipendula ulmaria* produced no ripe seed at all by this date. No species had reached a maximum in ripe seed production before 1 July and no species had reached maximal dehiscence by 21 August.

In an unpublished study in meadow vegetation, peak seed shedding occurred in late June in *P. trivialis* but appeared not to have been reached by 30 August in *Festuca rubra* or in *Agrostis stolonifera* (Mortimer, reproduced in Kent and Coker, 1992). *H. lanatus* showed a peak in late July, whereas *Elymus repens* shed all of its seed between the 2-16 of August. The result for *F. rubra* is consistent with that reported by Smith and Jones (1991), but *P. trivialis* shed seed much earlier than expected in Mortimer's study compared with either data from Smith and Jones (1991) or the autecological data provided by Grime *et al.* (1988).

Smith and Jones (1991) stated that the phenologies they observed correlated well with those quoted by Grime *et al.* (1988). This was true in general, although they showed slightly later ripening in seed of *Dactylis glomerata* and *Festuca pratensis* than might be expected from the dates quoted by Grime *et al.* (1988), whilst *R. acris* and *T. pratense* ripened a little earlier. These differences were small, but the lack of any seed ripening up to 21 August found in *C. nigra* and *F. ulmaria* was quite inconsistent with the dates given by Grime *et al.* (1988), who state that *F. ulmaria* normally produces ripe seed from August-September and *C. nigra* from July onwards. These dates agree with seed rain data from Tadham Moor (see Chapter 8), where some viable *C. nigra* seeds were shed before 17 July and both this species and *F. ulmaria* were producing substantial amounts of ripe seed by the beginning of August. On the other hand, phenologies provided by Wells (1980) showed *C. nigra* beginning to fruit in late August, consistent with the results of Smith and Jones (1991).

Wells (1980) did not give the source of his phenological data. However, differences in flowering phenology for the same species could be due to geographical differences, i.e. in altitude and latitude, between the sites from which data were collected. Smith and Jones (1991), working in the Pennine Dales, calculated that, in species which respond to temperature, ripe seed production could have been 10-14 days earlier at altitudes 200 m lower than the dale heads. Nevertheless, data presented by Grime *et al.* (1988) were based on surveys carried out in the Sheffield region and encompassed both upland (200 m) and lowland areas. This area is close in latitude to the Pennine Dales and Smith and Jones quote an altitude of about 244 m for one of the dales they studied (Ravenstonedale). Assuming this altitude is typical of the other dales, the phenologies quoted by Grime *et al.* (1988) should be applicable.

Hay meadows in the Pennine Dales are normally grazed in the spring, sometimes until the end of May (Smith and Jones, 1991; Smith and Rushton, 1994). Grazing can delay or inhibit flowering in susceptible species by interfering with reproductive development (Korte and Harris, 1987). Stewart and Thompson (1982) presented strong evidence to show that initiation of flowering was related to a minimum leaf weight in several herbaceous species, including *C. nigra*. Whilst *C. nigra* can survive grazing in pastures, it is much more abundant in meadows, and both this species and *F. ulmaria* are reported to be susceptible to damage by grazing (Grime *et al.*, 1988). Spring grazing could therefore delay flowering by postponing the attainment of a threshold plant size in these species.

The effect of time of cutting on botanical composition

Smith and Jones (1991) presented historic data to show that finishing dates for hay making in the Pennine Dales were 12-27 days earlier in the 1970s than in the 1950s when September finishing dates were quite common (i.e. 2 years in 5). On the other hand, starting dates varied little around 1 July between 1947 and 1986. These trends reflected improvements in hay making methods and machinery (Smith and Jones, 1991) and would therefore be typical of hay meadows in other areas. The sequence in which dales meadows were cut varied little from year to year (Smith and Jones, 1991). Constrained ordination (ter Braak, 1988) showed that this sequence was often the most important variable in determining botanical composition of dale meadows and also that its effect was often in an opposite direction to the effects of soil P, K and Mg (Smith and Jones, 1991). However, the sequence was correlated with the optimum date for the setting of ripe seed in the species present at only one of the six farms studied.

In view of their results, Smith and Jones (1991) recommended that a later cutting requirement should be included in ESA prescriptions within the Pennine Dales ESA. The rules have since been changed. They now preclude cutting before 8 July and also require that cutting should be delayed until August at least once in 5 years (Ministry of Agriculture, Fisheries and Food, 1992). Younger and Smith (1993) subsequently presented experimental data showing that both species richness and species diversity were higher with cutting in late July, compared with either mid June or early September, in a meadow in Teesdale. Askew (1993) used data collected from 151 meadows within the Pennine Dales ESA to investigate which management factors were most closely associated with vegetation of high conservation value. Lack of drainage was the most important factor, but within undrained meadows, cutting date was the most important influence.

Rabotnov (1969) emphasized the importance of seed setting and seedling survival in the population dynamics of meadows in the USSR, on the basis that most species were present in a variety of growth stages and that many were species which only propagate by seed. He also noted that there was a trend for replacing a single late hay cut with a two-cut system involving an earlier first cut. This system had led to selection for those species able to set seed between the first and second cuts, and the earlier the first cut was taken the higher the seed production at the second. Parr and Way (1988) noted that cutting grass verges in May and August allowed several species to flower between cuts. This treatment appeared to be optimum for species richness, compared with cutting once in either June or July or cutting 5 times between May and September. However, they made no attempt to record seed production or seedling emergence for any treatment.

Bakker *et al.* (1980) studied seedling dynamics and botanical composition under various cutting managements (i.e. hay making in July, September, July and September, or no defoliation) in previously fertilized hay meadows in the Netherlands. Seedling emergence was greatest with September hay making or with hay making in July and September, but hay making only in September gave better seedling survival. July hay making favoured establishment and survival of monocot species compared with dicots, whereas the opposite was true for the remaining treatments, especially abandoning (no defoliation) and September hay making. Abandoning resulted in large amounts of litter (90-95% ground cover), which persisted until May or sometimes June. This led to low seedling emergence and survival and a large dominance of *H. lanatus* in the vegetation (<90% ground cover). Hay making in July with no further defoliation also resulted in up to 90%

ground cover of *H. lanatus*. September hay making or hay making in July and September gave the most equitable mix of species in the vegetation and the lowest dominance of *H. lanatus*.

Cutting and grazing - implications for seedling establishment and survival

As the results of Bakker *et al.* (1980) imply, different cutting dates and defoliation managements influence seedling dynamics and botanical composition in two ways: firstly in the extent to which they allow seed to set, and secondly, in the extent to which they aid subsequent germination and survival of seedlings. However, as Peart (1989a) noted, few if any studies have related seedling survival and vegetation dynamics directly to measurements of seed rain in grassland. Without this level of detail, it is not possible to tell how many of the seedlings which emerge originate from recently shed seed and how many result from germination from the soil seed bank. Furthermore, few studies relating vegetation composition to different defoliation managements have included studies of seedling dynamics. In these cases it is usually not possible to tell to what extent the observed effects are due to seed rain/seedling dynamics or to the physiological effects of defoiliation on the relative vegetative performance of each species. Smith and Jones (1991) and Smith and Rushton (1994) attempted to minimise these limitations by using constrained ordination (ter Braak, 1988) to relate the effects of different management inputs on vegetation to the life histories and regenerative strategies of the component species. Some of these results are discussed later.

Vegetation that is defoliated by grazing is frequently more species-rich than swards that are cut only (Wells, 1971,1980; Willems, 1983). For example, after cessation of fertilizer use in chalk grassland previously grazed by cattle and occasionally cut, species richness increased by 40% over 10 years with annual mowing and by 49% with grazing by sheep. Grazing led particularly to an increase in bryophytes and typical chalk grassland species. By contrast, on plots which were not defoliated at all, species richness declined by 7%, with a significant loss of forbs and an increase in grass dominance.

Creation of gaps

The creation of gaps has been shown to be very important for seedling establishment and survival (Gross and Werner, 1982; Watt and Gibson, 1988; Peart, 1989c; Silvertown and Smith, 1989), and the superiority of grazing over cutting alone in maintaining or restoring species richness can be attributed largely to disturbance and gap creation by grazing animals (Grubb, 1977; Grime, 1979; Huston, 1979). In his classic treatise on pattern and process in vegetation, Watt (1947) attributed the patchy distribution of mature species within grassland largely to seedling establishment within gaps. Watt and Gibson (1988) related the amount of bare ground in limestone grassland in the spring to differences in grazing period during the previous year. Grazing with sheep from April to November (with a short rest in mid summer) produced the most bare ground in spring, followed in descending order by grazing from August to November, grazing for 10 days in Autumn, grazing for 10 days the previous spring, and no grazing. The number of seedlings emerging in the vegetation during the second year of treatment followed an identical order. *Bromus spp. (hordeaceous* and *sterilis*) germinated in smaller gaps than herbs and were able to establish through litter, an ability which the authors attributed to the large seed size of these species (Watt and Gibson, 1988). The authors gave no indication of the extent to which seed shedding occurred with April to November grazing, although presumably most species were able to set seed in the remaining treatments. Furthermore, no indication was given of the relative contributions of seed rain and the persistent seed bank. However, it is safe to assume that *B. hordeaceus* and *B. sterilis* seedlings resulted from seed rain, since these species do not form a persistent seed bank and normally only a very few seeds of each species remain ungerminated until spring (Grime *et al.*, 1988).

Watt and Gibson (1988) found that 66% of seedlings germinated in very small gaps (<1.6 mm diameter), too small to break dormancy in those species that require alternating temperatures (Thompson *et al.*, 1977). Seedling survival was generally low, with 41-55% mortality within a month of emergence, and showed no significant effect of gap size. This was probably because the maximum gap size found was only 12.8 mm diameter. Working with a range of annual species, McConnaughay and Bazzaz (1987) found that the chances of a seedling surviving to reproductive maturity was severely reduced in gaps of below 20 cm diameter. Parish *et al.* (1990) found that removing divots of turf 10 cm in diameter from sown swards had no effect on species richness or diversity, although *D. glomerata* and *T. repens* (which were among the sown species) increased substantially, and the volunteer

Festuca spp. and *Rumex acetosella* increased slightly, with divot removal. Parish *et al.* concluded that a 10 cm gap size allowed vegetative encroachment but was not big enough to allow significant seedling survival. The fertility of the soil was probably significant also. A compound fertilizer was used at establishment of all the plots and the data quoted for the effects of divot removal were averaged over further + and - fertilizer treatments. The data showed small fertilizer x divot removal interactions for the abundance of volunteer species and for species richness and diversity but the authors did not draw attention to this in the text. Encroachment from existing vegetation is likely to be more rapid in fertile conditions than where nutrient availability is low, and this may have implications for the size of gap needed to allow seedling establishment and survival.

The relationship between gap size, seedling germination and seedling survival may also be dependent upon the constituent species in the vegetation and the seed bank. Olff *et al.* (1994) showed that successional changes in vegetation following cessation of fertilizer use in hay meadows were accompanied by changes in the germination characteristics of the component species. Species with a fast germination rate and which germinate best at low temperatures were replaced by species showing the opposite characteristics. These changes corresponded with decreases in soil fertility and sward density and an increase in the number of gaps, particularly on a fine scale. Species in early successional meadows showed less stringent germination requirements, with little evidence of RFR inhibition, and these species would tend to germinate soon after shedding, i.e. in autumn.

Fenner (1978) showed that seedlings of species characteristic of closed turf habitats were more shade tolerant than 'colonizing' species typical of disturbed habitats. However, of the five 'closed-turf' species tested, *Rumex acetosa* was exceptional in that it was very susceptible to shading. *R. acetosa* has no seed dormancy and can germinate rapidly after shedding in both light and dark but with a preference for the former (Grime *et al.*, 1981,1988). This species is typical of hay meadows, particularly those where the aftermath is grazed due to its ability to exploit both the mown and the grazed phases (Grime *et al.*, 1988).

Integration of cutting and grazing

It was noted in Section 2.4 of this Chapter that the change from grazing after hay making in the Park Grass Experiment to taking a second cut was followed by a decline in species richness (Williams, 1978). Integrating grazing and hay making within the same season is a common traditional practice in Great Britain (Barnett, 1981; Hughes and Huntley, 1988; Smith and Jones, 1991; Askew, 1993), although it appears to be less common in central Europe (Ellenberg, 1988) and the Netherlands (Bakker, 1989), where a two cut system is more common. Experimental data directly comparing the effects of these two systems on botanical composition appear to be lacking.

In upland areas of Britain, grazing in both spring and autumn with a hay cut in mid summer appears to be common (Hughes and Huntley, 1988; Smith and Jones, 1991), whereas in wet, low lying areas such as the Somerset Levels, hay meadows are usually grazed only between completion of hay making and autumn-early winter (Barnett, 1981). Smith and Rushton (1994) compared the effect of various grazing periods on the vegetation of a hay meadow in the Pennine Dales: no grazing; grazing in spring only; grazing in autumn only; and grazing in spring and autumn, i.e. continuing current management. All treatments included hay cutting in July-August. Redundancy Analysis, a form of constrained ordination (ter Braak, 1988), showed that autumn grazing rather than spring grazing favoured stress-tolerant ruderals and competitive ruderals (*sensu* Grime, 1979), with the latter also favoured by autumn plus spring grazing. Autumn-germinating species (Type I seed bank *sensu* Thompson and Grime, 1979) were favoured by the autumn grazed and, surprisingly, the ungrazed treatments. Grazing only in spring favoured species that show predominantly vegetative regeneration and 'competitors' (*sensu* Grime, 1979), with the latter also favoured by the ungrazed treatment. Species richness and diversity declined rapidly in the ungrazed treatment. Other treatments varied quite widely from year to year over the four years of the experiment, although species richness was generally lower with spring grazing than with grazing in autumn or in spring and autumn.

Other work, also in the Pennine Dales, combined comparisons of three cutting dates (14 June, 21 July and 1 September) with three grazing treatments (autumn cattle+spring sheep, autumn cattle only, and no grazing), both without fertilizer and with 80 kg N, 17 kg P and 33 kg K ha^{-1} year^{-1} (Smith, 1993). After three years of treatment, species richness and diversity (as measured by Simpson's Index, Simpson, 1949) were generally highest in July-cut plots and generally lower on fertilized than unfertilized plots. Unfertilized late July-cut plots grazed in autumn and spring were the most species rich and diverse of all treatments. Moreover, for this cutting date and grazing treatment, the differences in species richness and diversity due to fertilizer application were marginal. Both species richness and diversity were lowest without any grazing, particularly on fertilized plots where September cutting resulted in the poorest species content of any treatment.

2.9. THE INFLUENCE OF CUTTING DATE ON PRODUCTIVITY

The agronomic consequences of different dates of harvesting primary growth of vegetation are determined mainly by four interrelated factors which change with time of cutting:

- (i) Standing crop yield at the first cut
- (ii) The nutritive value of herbage harvested
- (iii) The rate of recovery of herbage after harvest
- (iv) The length of the growing season remaining after harvest.

PRIMARY GROWTH

Herbage accumulation

When grasses are allowed to grow without defoliation, their herbage accumulates in a more or less linear fashion initially, but net growth eventually levels off to a ceiling yield once light interception by the canopy reaches a maximum (Green *et al.*, 1971; Parsons and Penning, 1988; Robson *et al.*, 1989). At this point, the processes of tissue production, maintenance and death are balanced (Parsons and Penning, 1988). The phase of herbage accumulation is longer in the spring than at other times of year due to a combination of factors, including:

- (i) Increasing light and heat energy receipt (Johnson and Thornley, 1983), which extends the period of herbage accumulation beyond the point where full light interception is reached
- (ii) A high leaf photosynthetic capacity (Parsons and Robson, 1981, 1982)
- (iii) Mobilization of reserve carbohydrates, especially fructans, accumulated during summer, autumn and winter (Pollock and Jones, 1979)
- (iv) Physiological and morphological changes accompanying reproductive development (Parsons and Robson, 1981; Robson *et al.*, 1989).

As reproductive development proceeds, young leaves are elevated to the top of the canopy where they both develop and phosynthesise in full light. Stem and flag leaves are retained longer than those on vegetative tillers, so that their development allows a greater accumulation of tissue (Robson *et al.*, 1989). When grass is continuously grazed to an optimum height for sheep production, reproductive development is greatly reduced (Orr *et al.*, 1988). These swards show a small peak in growth in early spring, but growth throughout the season is much more even than where larger amounts of herbage are allowed to accumulate (Corrall and Fenlon, 1978).

When cultivated grasses are defoliated regularly throughout the season but at an interval sufficient to allow some reproductive development, they show a distinctive pattern of a peak in yield in May-June, sometimes followed by a second, much lower peak in late summer (Anslow and Green, 1967; Corrall and Fenlon, 1978). Although the timing of the spring peak in growth varies somewhat between species and cultivars (Green *et al.*, 1971), the general pattern appears to be similar for most cultivated species (Anslow and Green, 1967). However, Haggar (1976) showed that *L. perenne* (cultivar S23), *P. trivialis, H. lanatus, A. stolonifera* and *F. rubra* all differed significantly in seasonal growth pattern. Both *P. trivialis* and *H. lanatus* showed patterns of increasing growth between April and late May very similar to that of *L. perenne*, but both declined sooner, *P. trivialis* to a notably lower level than *L.perenne* or *H. lanatus*. *H. lanatus* produced a substantially greater second peak in growth during July than any of the other four grasses. Both *A. stolonifera* and *F. rubra* equalled *L. perenne* in productivity from late June onwards, although neither showed as distinct a peak in growth in spring as did the other grasses. Other work has shown that *A. capillaris* produces a higher proportion of its growth in mid-season than other grasses, including *L. perenne* (Henderson *et al.*, 1962).

Timing of maximum yield

Thus, even in mixed grass swards, a maximum yield of primary growth can be expected at some time during the spring or summer, although this is likely to be less pronounced than in vegetation dominated by a single species. After this, standing crop yield can be expected to decline as the rate of tissue senescence and decay overtake the rate of tissue production (Leafe *et al.*, 1974; Parsons and Robson, 1982). This occurs both as a result of a transition back to vegetative growth and also as a result of declining day length (Johnson and Thornley, 1983). Soil water deficit in mid summer may also accentuate this effect (Garwood and Williams, 1967).

The rate of accumulation of yield has been shown to vary within grasses, both between species and between cultivars of the same species (Green *et al.*, 1971; Haggar, 1976). However, these studies did not measure yield of uninterrupted growth beyond late June, and were not therefore able to demonstrate a decline phase in standing crop for any of the species studied. Younger and Smith (1993) showed a large increase in hay yield between 14 June and 21 July in a Teesdale meadow (3.8 and 5.4 t DM ha^{-1}), but only a small further increase by 3 September (to 5.7 t DM ha^{-1}). However, it is not possible to tell from these data whether or not a higher peak in standing crop occurred between 21 July and 3 September. Data from Tadham Moor, presented in Chapter 3, show that DM yield declined between 21 June and 11 August on a plot which had received 100 kg N ha^{-1} in April, but continued to increase between these dates both on the unfertilized plot and where 50 kg N ha^{-1} had been applied. These trends were almost entirely due to the monocot components of the vegetation. Yields of forbs increased more slowly, peaking in early June and, except on unfertilized plots, declining thereafter. Other data from Tadham Moor, presented in Chapter 7, showed large increases in yield between late May and early July and between July and early August, and a further small increase between August and early September. These plots received no fertilizer, although half of them had received 200 kg N ha^{-1} year^{-1} in previous years. These data suggest no penalties in terms of hay DM yield in delaying harvest until September, although changes in herbage quality are likely to be of overriding significance.

Temporal changes in herbage quality

As grass yield accumulates its nutritive value declines, both in terms of crude protein content and digestibility (Green *et al.*, 1971; NIAB, 1987; Veira *et al.*, 1982). Green *et al.* (1971) showed that, whilst DM yield was still increasing on 19 June (their last assessment date) with all grasses, most appeared to be reaching a peak in yield of digestible organic matter, although only *Dactylis glomerata*, two cutivars of *Phleum pratense* and one early growing variety of *Lolium perenne* actually did so. Legumes also show a decline in digestibility with increasing yield, although digestibilities differ greatly between different legume species (NIAB, 1987). *Trifolium repens* consistently shows high values, while *T. pratense, Onobrychis vicifolia* and *Medicago sativa* maintain high values initially, but then decline more rapidly to values equivalent to grasses such as *L. perenne* and *Festuca pratensis* by early June (NIAB, 1987; Gill *et al.*, 1989).

Data from the species-rich vegetation at Tadham Moor (Chapter 7) showed no decline in digestibility or herbage N content between August and September harvests, although both had shown a significant decline up to then. By contrast, Veira *et al.* (1982) showed a progressive decline in crude protein content between 16 June and 16 August in grassland dominated by *Ph. pratense, F. rubra* and *Poa compressa* in northern Ontario. Cattle fed *ad libitum* on silage made on these dates showed marked differences in live weight gain (LWG), decreasing from 0.94 kg LWG day^{-1} for silage made on 16 June to 0.35 kg day^{-1} for silage made on 16 August. Silage quality had no effect on daily intake, so that differences in LWG were entirely due to differences in nutritive value. The pattern of decreasing LWG with time of harvest was linear and gave no indication of levelling off at later dates, in fact the LWG achieved with silage made at the last date was slightly lower than the linear trend described by earlier harvest dates. Nevertheless, it would be dangerous to attempt to draw any conclusions about apparent differences in seasonal effects on herbage quality between data from the Somerset Levels compared with Northern Ontario, since these areas differ in latitude and, presumably, climate.

ANNUAL PRODUCTION

Effect of time of first cut on annual productivity

Data from intensively managed swards have shown that maximum annual yield is obtained by an extended period of growth in the spring followed by a series of more frequent cuts or rotational grazing (Leafe *et al.*, 1974). Logic suggests that, from the agricultural point of view, there can be no advantage in the period of yield accumulation in spring extending beyond the time when a ceiling in yield of digestible organic matter is reached, i.e. late June for most grasses (Green *et al.*, 1971). In fact, much earlier cutting is likely to be preferable, since this combines high herbage quality at the first cut with a greater aftermath period available for further production. The optimum date of first cut will be earlier with high rates of fertilizer N application, since this brings forward the time when complete canopy cover is attained, at the same time accelerating regrowth.

Work in the central high plains in the USA showed that, for a range of grasses tested, maximum annual yield (from 2-4 harvests per year) was obtained when the first harvest was taken at the 'boot heading' stage, i.e. at ear emergence, compared with either earlier cutting or cutting later at anthesis (Fairbourn, 1983). This effect was shown by almost all of the 9 grasses tested in each of three years, despite substantial differences between grass species in the date at which the three growth stages were reached.

2.10. FURTHER IMPLICATIONS OF SPECIES-RICHNESS IN VEGETATION

AGRONOMIC SIGNIFICANCE OF BOTANICAL COMPOSITION AND SPECIES RICHNESS

Assumptions made in agronomic textbooks about growth patterns, plant physiological behaviour and response to management in grassland are based almost exclusively upon data from grasses and legumes, largely cultivated varieties and, in the case of grasses, mainly *L. perenne* (e.g. Robson *et al.*, 1989). Grime *et al.* (1988) predict that *L. perenne* will be less consistently recommended by agronomists once the ecological features of other species are better understood.

The influence of botanical composition on productivity

Much of the commitment to *L. perenne* appears to have been based upon a belief that prevailed until quite recently that grassland productivity could be increased simply by increasing the proportion of certain species. This belief probably originated from studies such as that by Armstrong (1907) which showed that the most productive grazing pastures were those that contained a high proportion of *L. perenne*, often with a significant proportion of *T. repens.* The perception that the proportion of *L. perenne* is more often a reflection of the productivity of a pasture than the cause of it, is comparatively recent (e.g. Dibb and Haggar, 1978). Similarly, a high content of *T. repens* could be seen as much as an indicator of soil fertility (i.e. of high levels of available P and K) as a contributor to it in terms of fixed N.

Marked increases in the proportion of *L. perenne* in mixed grass swards can be induced by selective herbicides without changing any other management input (Haggar and

Elliott, 1978; Kirkham *et al.*, 1982). Such changes have shown no overall benefit in terms of productivity, although Haggar and Elliott (1978) showed a slight shift in animal production towards the earlier part of the season following an increase in the dominance of *L. perenne* at the expense of species such as *H. lanatus, Agrostis spp.* and *Poa spp.*.

Yield and digestibility

In a comparison of growth and digestibility curves of five grass species receiving 400 kg N ha^{-1} $year^{-1}$, Haggar (1976) showed that *L.perenne* would out-yield other species by at least 25% if the primary growth of each were harvested for silage at 65% organic matter digestibility. However, at this level of digestibility, the difference in yield between *L. perenne* and *H. lanatus*, the next most productive species, was due to a more rapid accumulation of dry matter in *L.perenne* during the second half of May. A more recent trend is to harvest grass for silage earlier than before, at higher levels of digestibility than 65% (NIAB, 1987). Re-examination of Haggar's data shows that at a slightly higher digestibility of 67%, the difference in yield between *L. perenne* and *H. lanatus* would be completely reversed, although both species would still out-yield the others tested (*A. stolonifera, F. rubra* and *P. trivialis*).

In contrast to the wealth of knowledge about the normally sown species, little information about temporal changes in yield and nutritive value is available for the wide range of dicots, sedges and rushes common in species-rich meadows. Thus, while the effects of various management practices on botanical composition, particularly of fertilizer application, are well documented, the full agronomic implications of these effects are hard to predict.

Nutritive value of grasses

As Snaydon (1987a) pointed out, there is no consistent difference in digestibility between the grasses that are normally sown and those which are not. The digestibility of *D. glomerata, Festuca rubra* and *F. ovina* is consistently about 5% lower than that of *L. perenne,* whilst *H. lanatus* and *Poa trivialis* are usually more digestible. *Agrostis spp.* are usually slightly less digestible, than *L. perenne* at equivalent stages of growth (Green *et al.*, 1971; Thomas and Morris, 1973; Haggar, 1976; Wilson and Collins, 1980). In work by

Frame (1991), *L. perenne* showed the highest organic matter digestibility (at 79.6%) of the 11 grass varieties and species tested when averaged over 6 cuts per year and two years, with *H. lanatus, Cynosurus cristatus, Ph. pratense* and *Anthoxanthum odoratum* giving marginally lower values at 75.8%, 74.9%, 74.8% and 74.6% respectively. The P content of *L. perenne* was the lowest of all the grasses, whilst its Ca content was the highest at 0.58%. The K content of *L. perenne* was exceeded by all the other grasses except *F. rubra* and *Agrostis castellana*, whilst its Mg content was equalled by *H. lanatus* and *C. cristatus* though not exceeded by any other grass. Grasses indigenous to infertile, upland vegetation, e.g. *Nardus stricta* and *Molinia caerulea*, tend to be of lower digestibility than sown species (Newbould, 1979).

Nutritive value and intake of dicotyledonous species

Barber (1985) reviewed the digestibilities and mineral and crude protein contents of a range of dicot 'weed' species. Digestibility values in May ranged from 67% for *R. acetosa* to 56% for *Tussilago farfara.* However, the digestibility of *R. acetosa* appeared to decline more rapidly than other species and it showed the lowest digestibility in July (43%) of all the 9 species presented except *R. obtusifolius* (41%). Digestibilities in July of the remaining species ranged from 53% for *Chamerion angustifolium* to 62% for *Vicia cracca.* Except for the values shown by the *Rumex spp.*, these July values fell within the range of digestibilities recorded on 19 June for most varieties of perennial and Italian ryegrass, *Festuca pratensis* and *Ph. pratense,* and exceed those of all varieties of *D. glomerata* (Green *et al.*, 1971).

Data given by Barber (1985) also showed *R. acetosa* to be notably high in Mn and Zn in May-June compared with other dicots, but low in Cu. *Cirsium arvense* and *Urtica dioica* were notably high in both Ca and P content whilst *T. farfara, Cirsium vulgare, P. lanceolata* and *Taraxacum officinale* were all above average in Ca, the latter also showing a notably high Mg content. Except for *R. acetosa* which had a Ca content of 0.39% in May-June, all the 'weed' species quoted by Barber (1985) showed a higher Ca content (at 0.72 - 2.76%) than any of the grasses tested by Frame (1991), i.e. 0.41% - 0.58%. Five of the 12 'weeds' exceeded the highest %P value for grasses quoted by Frame (0.43%) and all 12 easily exceeded the highest grass Mg value (range 0.20 - 0.36% for 'weeds', compared with 0.16 - 0.18% for grasses).

R. acetosa and *V. cracca* were both high in crude protein content in May and June at 107-171 and 188-228 g kg^{-1} DM respectively (Barber, 1985). *Lotus corniculatus* and *Chamerion angustifolium* were also high in crude protein in June at 139 and 120 g kg^{-1} respectively, whilst *V. cracca* and *L. corniculatus* retained very high values in July (162 and 135 g kg^{-1} respectively). These values were all much higher than most of the grasses recorded by Green *et al.* (1971), which ranged from about 80 - 112 g kg^{-1} on 9 June. Data provided by Frame (1991) suggested a similar range of crude protein values for the grasses he tested, i.e. between 77 g kg^{-1} for *L. perenne* to 108 g kg^{-1} for *A. capillaris*, averaged over 6 cuts per year and receiving 120 kg fertilizer N ha^{-1} year^{-1}. Green *et al.* (1971) used a higher N rate of 175 kg N ha^{-1}, but whereas they applied all the N in two dressings to primary growth, Frame applied the annual total of 120 kg ha^{-1} in six equal dressings, one for each cut. Differences between these two sources in crude protein content per kg of N applied can be attribiuted to a dilution effect of a greater DM accumulation by 9 June in the grasses reported by Green *et al.* (1971). Crude protein contents recorded by Green *et al.* on 10 May were typically between 150 and 200 g kg^{-1}, equivalent to values recorded by Frame (1991) for grasses receiving 240 kg N ha^{-1} year^{-1}.

Derrick *et al.* (1993) measured the digestibility and rate of voluntary intake by sheep of five herb species - *Stellaria media*, *Taraxacum officinale*, *Rumex obtusifolius*, *Plantago lanceolata* and *Spergula arvensis* - compared with *L. perenne.* The *in vitro* digestibility of *S. media*, *T. officinale*, *R. obtusifolius* and leafy *P. lanceolata* was as high as that of *L. perenne*, but the *in vivo* digestibility of all five herbs was lower. Nevertheless, the voluntary intake of herbs was higher than might have been predicted from their digestibility values. This was particularly noticeable with *S. arvensis* and, to a lesser extent, with *T. officinale.* Sheep fed the latter two species *ad libitum* showed a superior voluntary intake and live weight gain compared with those fed other species which was associated with a lower chewing requirement per g of dry matter consumed. Sheep were able to chew each of the five herb species more rapidly than *L. perenne.*

Contribution of herbs to hay quality

In a comparison of Welsh hays with other British hays, Ashton and Morgan (1952) showed that meadow hays had a higher crude protein content than 'seeds' hay, i.e. hay made from reseeded pastures, and marginally higher Starch Equivalent values (a measure of the energy value). The high crude protein contents were attributed to the high proportion of *P. lanceolata* and *Rhinanthus minor* in most meadows at the time. Several studies have been made on hay and its constituent species from the Palace Leas experiment at Cockle Park. Thomas and Thompson (1948) showed that *Rhinanthus minor* was remarkably high in all minerals and was a particularly good source of Cu, Mn, Na and Mg. However, the authors noted that this species had a reputation for being 'distasteful' to stock. Both *P. lanceolata* and *Ranunculus spp.* were high in Ca and P. *P. lanceolata* was also rich in Na and quite a good source of Cu and Co, though poor in Mn. *Ranunculus spp.* were rich in K, Cu and Co, but poor in both Mn and Na. Among the grasses, *C. cristatus* was a poor source of most minerals, although P levels were moderate. *H. lanatus* was a reasonable source of most minerals, though quite low in Mn and Co. *F. rubra* was quite high in Fe and contained moderate concentrations of Mn, but was very low in all other minerals and trace elements. In another study of plants from the same experiment analysed at different growth stages, Thomas *et al.* (1952) confirmed that herbs and legumes were generally much more mineral efficient than grasses (including *L. perenne*). Herbs were generally richer in total mineral content than legumes, and *Cichorium intybus* and *P. lanceolata* were outstanding. *Festuca pratensis* was more mineral-rich than the other grasses. Most minerals declined with plant maturity, but herbs generally showed no significant decline in Na, with Na increasing with maturity in the four legumes tested. *P. lanceolata* was the only species to show a significant decline in Ca content. In further analyses of hay from the same experiment, unfertilized plots and those receiving P alone (as basic slag) gave the highest nutritive value in terms of digestibility and mineral content (Thomas *et al.* 1955a,b). This was attributed both to a high herb content, e.g. of *Plantago spp.*, and to a lower maturity of plant material.

In earlier trials using material from the the Palace Leas Experiment, hay was fed as a supplement to sheep receiving maintenance rations and their live weight gain (LWG) was measured (Gilchrist, 1906; Pawson, 1960). The best LWGs were achieved using hay from plots receiving farm yard manure (FYM), P (as basic slag) or P and K, the latter giving the highest LWG (0.146 kg day^{-1}). Regression analyses on data given by Pawson (1960), to relate animal LWG to the constituents of the hay, showed a significant correlation between LWG and ash (total mineral) content ($r = 0.606$, $P<0.05$). There was no significant relationship with any other constituent (values for individual minerals were not given separately) or with the grass/legume/herb content. This implies that applying P and K in organic or inorganic form to the plots had an overriding effect both on the mineral content of vegetation and the animal performance achieved, compared with any effect species composition may have had.

SIGNIFICANCE OF BOTANICAL CHANGE FOR WILDLIFE FAUNA

This review has concentrated on the effects of various management practices on vegetation ecology. Most of these practices also have direct effects on wildlife fauna. For example, both late hay cutting and a high water table are important for the breeding success of ground nesting wading birds, as was noted in Chapter 1. Similar principles in relation to cutting date apply to other ground nesting birds (O'Connor and Shrubb, 1986), although for those which do not need to probe the soil for food the direct effects of drainage on soil physical conditions may not be significant.

Relationship between botanical composition and insect populations and diversity

Fertilizer application in the Park Grass Experiment, particularly in relation to the amount of lime and nitrogen applied, had very significant effects on soil fauna (Edwards and Lofty, 1975), but the effects on surface-living fauna were more indirect and less distinct (Edwards *et al.* (1976). The authors of this work were struck by the large number of species and individuals of spider living in the hay meadows at Rothamsted, several of which were scarce or rare species. The number and diversity of spiders appeared to be related to vegetation height and density rather than to the specific fertilizers used. However, in a study in meadow vegetation in Poland, fertilizer application did not change the number or diversity of meadow spiders over 8 years, but it did change the order of dominance in favour of smaller, less mobile spiders (Kajak, 1981). As a consequence, the total biomass of spiders fell with fertilizer application, though the effects on species composition became less distinct with time.

In other work in Polish meadows, populations of *Diptera* were increased by fertilizers and 2-3 times as many dipterans emerged in fertilized vegetation than unfertilized (Olechowicz, 1977). This effect was shown to be directly related to increases in biomass, with both saprophagous and phytophagous dipterans increasing more than zoophagous species.

Many butterflies and moths require specific food plants (i.e. they are monophagous), or, more commonly, they are oligophagous, i.e. restricted to a narrow range of food plants (Novak, 1980). Furthermore, for nectar-loving species a variety of plants flowering at different times in the season is an obvious requirement, since the flowering period of most plants is much shorter than the lifespan of most adult butterflies. Not surprisingly, both the number and diversity of this type of fauna in a habitat and the individual species present are related to the composition of the vegetation. Thomas (1984) recorded 23 species of butterfly in a patchy, unimproved pasture, but only one species in a grass-clover ley.

Ehrlich and Raven (1964) pointed to the relationship between butterflies and plants as strong evidence of coevolution. They argued that reciprocal selective responses had been greatly underestimated as a factor in the origination of organic diversity in the widest context, and that the plant herbivore 'interface' may be the major zone of interaction responsible for generating this diversity. It follows that maintenance of these same reciprocal relationships is essential for the maintenance of organic (bio-) diversity world-wide. It is not hard to recognise the validity of this philosophy within the more specific context of the maintenance of biodiversity within semi-natural grassland.

2.11. SYNTHESIS OF DATA ON THE AGRICULTURAL ECOLOGY OF SPECIES-RICH MEADOWS

THE EFFECTS OF FERTILIZERS ON YIELD AND BOTANICAL COMPOSITION

Botanical composition and fertilizer response

There is no clear-cut evidence that species composition alone has a significant effect on the potential of grassland to respond to moderate rates of inorganic fertilizers. This is probably because fertilizer application, particularly of N, normally causes a rapid increase in the proportion of the more productive grasses. However, the response to high rates of N (>300 kg N ha^{-1}) is greatest in vegetation dominated by *Lolium perenne*, particularly with frequent defoliation. Applying P and K without N usually increases the proportion of legumes in vegetation, which in itself normally leads to increased productivity.

Fertilizer - grazing interaction

With the exception of a few species such as *Anthriscus sylvestris* and *Rumex spp.*, the abundance of dicotyledonous species (forbs) is normally reduced by the application of fertilizer N. Where vegetation is allowed to accumulate, this effect is often attributed to increased shading by tall grasses. But grasses also tend to replace forbs in grazed swards, where efficiency of N uptake and water utilization, and tolerance of trampling and/or frequent defoliation may be of equal or greater significance than shading.

Aftermath grazing following hay making is important for the maintenance of species diversity and has a significant influence on botanical change in response to fertilizers. Fertilized meadows that are managed by infrequent cutting alone are often dominated by *Arrhenatherum elatius*, but this species is far less common in meadows where aftermath grazing is practised. These meadows are more likely to be dominated by species such *Lolium perenne* and *Holcus lanatus.*

Soil type

High species richness and low productivity are relatively common in calcareous soils where these features are associated with low availability of P, or of N and P. Unfertilized organic soils often contain little P or K, unless enriched by polluted flood or seepage water. Peat soils therefore tend to show a large response to application of these elements since they are a rich source of N, particularly where N mineralization is enhanced by drainage. By the same token, peats generally show a lower response to applied N than mineral soils, whereas calcareous soils are normally more responsive to both N and P application than loam or clay soils.

Species richness and biomass

No single fertilizer experiment could be found for this review which showed the bi-tonic or 'humped' curve which is integral to the Grime model relating species richness and standing crop. A progressive decline in species richness and diversity is the usual result of repeated inorganic fertilizer application, particularly when N is included. Many writers have attempted to fit experimental data to Grime's model but very few have shown a 'humped' response when using data from a single plant community and a single year. Species richness has

been increased by fertilizer application, but only in exceptional (in the agricultural context) cases where low species richness and fertility were associated with poor utilization of growth. In these cases inorganic fertilizers increased the number of species in the vegetation only when combined with an increase in grazing intensity. Nevertheless, there have been comparatively few experiments which have tested the response to low fertilizer rates (i.e. <50 kg N ha^{-1}) in species-rich meadows, particularly in organic soils, and data from the Tadham Moor Project presented in this thesis (Chapter 5) and elsewhere (Mountford *et al.*, 1993a) are important in this respect. There may be situations where small increases in fertility could increase productivity without reducing species richness, as the Grime model suggests, but at Tadham Moor even very low rates of fertilizer N (i.e. 25 kg N ha^{-1}) caused a significant decline in species diversity (see Chapter 5).

FERTILIZERS AND POLLUTION

Agriculture is a major source of pollution of waterways, particularly by N and P. Most of the P entering waterways originates from animal wastes and soil run-off, whereas most of the N comes from leached fertilizer N or N mineralized in soil.

Nitrates in water

Nitrates in drinking water pose a threat to human health, but the number of recorded cases of illness related to this are small. Nitrates are more widely implicated in the eutrophication of fresh and coastal waters, particularly in conjunction with high P levels, and can cause significant changes in aquatic vegetation.

N losses from grassland

Fertilizer N is poorly utilized in grassland, particularly in grazed pastures where much is recycled through livestock. In most grazed grassland, the rate of N loss increases with application rates above about 150-200 kg N ha^{-1}, whereas a higher 'threshold' value of 250-350 kg N ha^{-1} applies under cutting management. Data from this thesis (Chapter 4) suggests a much lower threshold value of 75-100 kg N ha^{-1} in the wet peat soils at Tadham Moor.

N is lost mainly by leaching, denitrification and ammonia volatilization. Denitrification is enhanced by warm, wet soil conditions and a high soil nitrate concentration, and therefore increases both with fertilizer N application and with height of water table. Denitrification rates tend to be high in peat soils due to a high organic carbon content and frequently high soil N and moisture levels. Ammonia volatilization from grassland usually represents a small fraction of total N losses, although it is increased by N application rate through the increased herbage N concentrations that lead to high urea concentrations in the urine of grazing animals. Much larger amounts of ammonia are lost to the atmosphere from housed cattle and these can be related to the amount of fertilizer used on the farm by (a) a greater number of cattle housed and (b) a higher N concentration in conserved forage fed to housed cattle.

Environmental implications of volatilization of N compounds

Both denitrification and ammonia volatilization have strong environmental implications. Nitrous oxide, one of the end products of denitrification, is both damaging to the ozone layer and a potent greenhouse gas, and is also implicated in the formation of acid rain. Ammonia has a high capacity to neutralise acid rain, but this results in the deposition of ammonium sulphate and nitrate, and this is implicated in loss of species diversity in sensitive grassland ecosystems.

WATER TABLE DEPTH AND DRAINAGE

Agricultural benefits

Unless land is so wet as to prevent agricultural use, the available evidence suggests that drainage to improve the productivity of grassland is seldom economically worthwhile on a field-by-field basis. The earlier spring growth and prolonged access to grazing in the autumn associated with drained land may be offset by a greater moisture deficit in mid summer, and early spring growth is of little advantage during the accumulation of a hay crop cut in late June-early July. However, the aim of much grassland drainage has been to introduce arable cropping, particularly in the east of the country, and this is more likely to be economical.

Effects on soil chemistry and vegetation composition

Most of the yield increases resulting from drainage and lowering of the water table are a consequence of increased N mineralization. This adds to the loss of species tolerant of wet soil conditions by increasing the proportion of N-demanding species in the sward, leading to an even geater loss in species diversity. These effects are particularly noticeable in peat soils which have a high organic N content. Changes in vegetation composition can also be brought about when drainage changes the balance between Ca-rich groundwater and Ca - poor rainwater.

SEED BANKS, SEED RAIN AND CUTTING DATE

Seed banks, dormancy and germination

Most seed bank studies have shown a strong dissimilarity in composition between the seed bank and the above-ground vegetation. This is the result of large differences not only in the number of seeds produced per plant but also in the length of time they remain dormant in the soil. Plants show various mechanisms for inducing or enforcing dormancy and various dormancy-breaking mechanisms exist, ensuring both the persistence of seed in the seed bank and that germination occurs in favourable situations, e.g. in gaps.

Reproductive allocation and seeding phenology

Plants vary in the proportion of available resources which are allocated to sexual reproduction, and this is intimately related to their life histories and regenerative strategies. Plant species also differ in the timing of their seed production and this has strong implications for the timing of cutting in hay meadows. Since many species do not set seed until late July or August, late cutting, at least occasionally, appears to be necessary.

Grazing and gap formation

Whilst grazing tends to reduce the amount of flowering that occurs in grassland, many species of grazed pastures rely on setting seed. Many subsequently rely on grazing to increase the chances of successful germination and seedling establishment, e.g. by reducing vegetation cover and creating gaps. Moreover, integration of grazing with hay making seems to be essential for maximum species diversity, particularly in the Pennine

Dales, where grazing in both spring and autumn is traditional.

AGRONOMIC IMPLICATIONS OF CUTTING DATE

Delaying hay cutting much beyond the time when complete canopy cover is reached is unlikely to be economical, since yield increases little after this and a delay in cutting reduces the period of aftermath growth. Nutritive value also declines with increasing maturity, although the rate of decline is not linear. Species differ in their seasonal growth pattern, so that the timing of peak yield is likely to be less distinct in species-rich vegetation compared with that dominated by a single species.

SIGNIFICANCE OF SPECIES-RICH VEGETATION

Nutritive value

Dicot species in general are more efficient at accumulating minerals and trace elements than grasses and are therefore better sources of these elements in forage. Moreover, many herbs and wild legumes are superior in crude protein content than grasses receiving substantial amounts of fertilizer N. Nevertheless, the increased content in herbage of minerals applied as organic or inorganic fertilizer may override the benefits of a high herb content in unfertilized vegetation where the two types of herbage are fed to livestock.

Seasonal patterns in herbage digestibility may be less predictable in species-rich vegetation than in fields dominated by a few cultivated grasses. However, the ability to predict temporal changes in herbage quality is likely to be most significant in fields cut for high quality silage, the majority of which receive high rates of fertilizer and are species-poor.

Interaction with fauna

Botanical composition and species richness in vegetation have strong implications for the populations of butterflies and meadow spiders. Dipterans appear to be more sensitive to biomass than to species composition.

CHAPTER 3

THE EFFECTS OF INORGANIC FERTILIZERS AND VARIATIONS IN WATER TABLE DEPTH ON THE PRODUCTIVITY OF HAY MEADOWS AT TADHAM MOOR

3.1. INTRODUCTION

The research described in this thesis was concerned with the impact of various agronomic practices on both the plant ecology and the productivity of the species-rich meadows at Tadham Moor. The agricultural production response of these meadows to inorganic fertilizer nitrogen (N) applications and to variations in water table depth under hay making and aftermath grazing with beef cattle (Experiment 1) are described in this chapter, whilst the impact of these same factors on soil N flux and denitrification rate are described in Chapter 4. This chapter also includes data on the herbage production response to a range of N, phosphorus (P) and potassium (K) fertilizer treatments of vegetation managed by cutting only (Experiment 2). Botanical data from Experiment 2 are described in detail in Chapter 5 and compared with some of the botanical data from Experiment 1 collected by staff of the Institute of Terrestrial Ecology (ITE).

Within both the SSSI and the ESA schemes operating on the Somerset peat moors, compensation payments are made in order to prevent or restrict various agricultural practices, including the use of inorganic fertilizers and drainage (see Chapter 1). Additional payments are also available to encourage farmers to raise water tables in meadows in order to maintain soil conditions favourable for wading birds (Green, 1986). Recent research has quantified the response of some permanent pastures to fertilizer nitrogen (N), both under cutting management (Hopkins *et al.*, 1990) and under continuous grazing (Tallowin *et al.*, 1990), but none of these studies has included sites comparable in soil type, moisture regime or plant species diversity to the hay meadows of the Somerset Moors. It has therefore been difficult to quantify the production foregone when fertilizer application is restricted or prevented. Similarly, as noted in Chapter 2, there is little information available from which to predict the effect of raising water tables on the productivity of these meadows.

Plate 3.1. Hay meadows at Tadham Moor.

3.2. MATERIALS AND METHODS

PRODUCTION AND RESPONSE TO N FROM HAY AND AFTERMATH GRAZING - THE LARGE- SCALE (LS) EXPERIMENT (EXPERIMENT 1)

Production was measured in the first instance by cutting and making hay each year. Plots were then grazed individually during the whole aftermath phase and production per plot for this phase was measured in terms of animal output.

Experimental treatments.

Five levels of fertilizer N, i.e. 0, 25, 50, 100 and 200 kg ha^{-1} $year^{-1}$ (N_0 - N_{200}) were applied to paddocks (plots) laid out in three randomised blocks. The plots were cut for hay on the first occasion after 1 July with suitable weather conditions and the aftermath growth was

grazed by beef cattle. Plots were between 0.6 and 1.1 ha in area, with the size inversely related to N treatment, sufficient to support a minimum of two steers throughout the grazing period. Treatments were applied as granular ammonium nitrate (34.5% N), using a Bamlett tractor-mounted pneumatic distributor. Annual rates were split between two equal dressings, the first applied as soon as ground conditions allowed after mid-April and the second after the removal of the hay crop. Actual application dates were 14 May and 23 July 1986, 24 April and 27 July 1987, 18 April and 23 August 1988 and 3 May and 24 July 1989. On the first occasion each year the tractor was fitted with low ground pressure 'Terra Tires' to accommodate wet ground conditions.

Phosphorus (P) and potassium (K) were applied in mid-season each year on the day following the second N application, using the same distributor. The rates were calculated from the yield and chemical analysis of hay swath samples as sufficient to replace the amounts removed in hay. Calculations were based on samples taken from herbage at cutting, rather than after hay making. This allowed time for processing and chemical analysis of the samples, so that fertilizer could be applied as soon as possible after removal of hay bales. No adjustment was made for any P and K returned to the soil from herbage lost during hay making. In 1986, P and K were applied together to N-treated plots, at flat rates of 14 kg ha^{-1} P and 42 kg ha^{-1} K as a compound fertilizer. These rates were the closest to the mean requirements for each element that could be supplied by a single commercially available compound fertilizer. From 1987 onwards, P and K were applied separately in the form of triple superphosphate and muriate of potash, at rates calculated individually for each paddock. In order to minimise the impact of fertilizer use on the ecology of the area, no P or K was applied to control (N_0) plots.

Harvest of hay.

Hay was made by local contractors using standard equipment. Yield at cutting was measured by weighing 4 m lengths of two adjacent swaths of measured cut width at five randomly chosen sites per plot. At each site, a sub-sample of about 500 g of herbage was removed from the field, weighed fresh and dried overnight at 80°C before weighing again for dry weight determination. Dried samples were ground in a hammer mill and analyzed for *in vitro* digestibility (Tilley and Terry, 1963), for total N content by micro-Kjeldahl

digestion (Association of Official Analytical Chemists, 1965) and, following wet digestion with sulphuric and nitric acids, for K content by atomic absorption spectrometry and for P by colorimetry on a continuous segmented flow analyzer, after Aspila *et al.* (1976).

Hay was baled in conventional rectangular bales and yield of baled hay was measured by counting the number of bales and weighing a sample of 25 per plot, chosen at random. A total of three samples of herbage, each weighing about 350-550 g, were taken from swaths immediately before baling. These were analyzed for dry matter (DM) content, total N and *in vitro* digestibility as described above. Hay making was completed between the following dates each year: 1-16 July 1986; 1-11 July 1987; 1-17 August 1988; and 2-13 July 1989.

The metabolizable energy (ME) value of hay at cutting and at baling was calculated from the *in vitro* digestibility (% digestible organic matter in the dry matter) and the N content of herbage, using the following formula:

$$\text{ME (MJ per kg DM)} = 0.23 + (0.138 \times \%\text{DOMD}) + (0.01 \times \text{CP})$$

where CP is the crude protein content in g per kg DM, with crude protein assumed to be 6.25 x N. This approach has been recommended as a general formula for grasses, legumes and maize (MAFF, 1975). It was used in preference to other formulae specifically recommended by MAFF (1984) for grass hays and dried grass, e.g. %DOMD x 0.155 or (%DOMD x 0.185) - 1.88, in view of the mixed species composition of the vegetation and the significant treatment effects found in the N content of herbage harvested.

Grazing management.

Plots were stocked with Hereford x Friesian steers aged 10-12 months and weighing on average 240-290 kg at the beginning of the grazing period in early-mid August (early September in 1988). Grazing output was measured using a standard procedure of continuous variable stocking (Wilkins *et al.*, 1983; Tallowin *et al.*, 1990). A minimum of two 'core' steers per paddock, selected for uniformity of size, were maintained until mid-late October each year. These animals were used to calculate individual live weight (LW) gain. Stocking rates were adjusted regularly on each paddock by adding or removing spare cattle, maintaining compressed sward heights (Holmes, 1974) between 5.5 - 6.5 cm for most of the period. All cattle were removed from a paddock after the sward height fell below 5.0 cm at the end of the grazing season.

Animal output data from each plot were derived from individual LW gain of core animals, the number of steer grazing days per hectare (animal grazing days), the mean number of steers per hectare per day (mean stocking rate) and the amount of LW produced per ha (i.e. grazing days per hectare x LW gain per core animal). The Utilized Metabolizable Energy (UME) for each paddock was determined by multiplying the grazing day total by the daily growth and maintenance energy requirements of the cattle for specific periods, using standard formulae described by Forbes *et al.* (1980).

Soil Sampling.

Soil was sampled from the 0-10 cm horizon in March each year 1986-1990 and analyzed for available phosphorus by spectrophotometry and for potassium by flame photometry, by the Agricultural Advisory and Development Service at Starcross in Devon. A 25 mm diameter corer was used to take soil from 15-21 randomly chosen sites within each plot. Samples were air dried for at least 3 days and then passed through a 2 mm sieve before analysis.

Dry matter yield development.

The accumulation of herbage dry matter (DM) between 28 April and 11 August was measured on one replicate of the N_0, N_{100} and N_{200} treatments in 1988. Measurements were made on six occasions and on all but the last of these herbage was cut to a height of about 5 cm using hand shears, from within 0.36 m^2 quadrats. On each occasion, plots were divided by eye into three approximately equal portions. Quadrat locations were chosen from within each portion by casting a marker cane at approximately equal intervals in a diagonal direction, taking a total of nine quadrat positions per plot (3 x 3) at the first assessment and six per plot (2 x 3) thereafter. A different starting point was chosen for each diagonal traverse on each occasion. At the final assessment on 11 August, yield was measured at hay cutting by raking up and weighing a 4 m length of two adjacent swaths at each of six sites per plot chosen as above. From 12 May onwards, samples were separated into monocots (grasses, sedges and rushes) and dicots (herbs and legumes), using whole quadrat samples on the first five occasions and a 300-500 g (fresh weight) sub-sample from each swath sample at hay cutting. DM yields were calculated for each quadrat sample as a whole on 28 April, but thereafter DM yields for each of the two vegetation components were recorded separately.

Data analysis - hay and aftermath production data

Data were analyzed by analysis of variance (ANOVA) using a randomised block design, or by regression analysis, using GENSTAT (GENSTAT V Committee, 1987). All data were examined separately for each year and, where appropriate, averaged over four years. Metabolizable energy (ME) data from baled hay and aftermath grazing, averaged over 4 years, were tested for response to N rate using linear and quadratic regression analyses, as well as standard curve fitting procedures available in GENSTAT. However, since P and K were applied to all plots receiving N but none was applied to control plots, data from the latter were excluded from any analysis aimed at describing an N response relationship.

Treatments were not replicated by plot in the yield development study, so that standard errors were derived for each treatment mean on each occasion using between-quadrat variation. Simple *t*-tests were used to compare means, both between assessments within plots and between plots of different treatments. However, due to the lack of replication of treatments by plot, only tentative conclusions could be drawn from between-plot comparisons (Hurlbert, 1984).

THE INFLUENCE OF WATER TABLE DEPTH ON PRODUCTIVITY

This study used correlation and regression analysis on data from the LS experiment to relate variation in productivity variables (see below) to variation in water table (WT) depth measured at times during the season and averaged over key periods. GENSTAT (GENSTAT V Committee, 1987) was used for all statistical analyses.

Production variables

The following productivity variables were included in the analyses:

(i) vegetation height in May each year

(ii) hay yield at cutting in July

(iii) animal live weight produced per ha (LWP) from aftermath grazing

(iv) animal production response to applied N

Data for mean herbage height per plot, calculated from five measurements per 1.0 m^2 quadrat and 24 quadrats per plot, were extracted from botanical data recorded annually at the site in May by staff from the Institute of Terrestrial Ecology at Monks Wood. Vegetation height was taken to be an indicator of herbage biomass, although it is recognized that other factors, e.g. the proportion of rushes in the vegetation, could have an overriding influence. Hay yield data for 1990, provided by J. R. B.Tallowin, were also included in these analyses, although they are not used elsewhere in this thesis. All paddocks were split into two sub-plots in April 1990 and fertilizer treatments discontinued on one of these. Plots where treatments were discontinued are referred to in Figures with the suffix 'x', i.e. 1990x. Animal production from aftermath grazing in 1990 is not included here, since the grazing management of stock following plot splitting was changed in order to accommodate the smaller paddock sizes.

Water table and rainfall measurements

Water table (WT) depth was recorded weekly from April to November in 1986 and from 2 April 1987 onwards, in 33 dipwells laid out in three parallel lines east-west across the experiment site. Each dipwell consisted of a 100 cm perforated plastic pipe 7.5 cm in diameter, set vertically into the ground with its upper rim at ground level. Each dipwell was covered with an aluminium cap. The layout gave between one and three dipwells per plot, depending upon the shape and size of each plot. No new dipwells were installed after plot splitting. However, the mean water table depth of each sub-plot on each occasion in 1990 was calculated by adjustment of the overall paddock mean depth, using data from a ground levels survey of the site carried out in 1985.

Rainfall was measured continuously in a Meteorological Office Mark 2 tilting syphon gauge and weekly accumulated rainfall totals were also recorded using a simple collecting device.

Data manipulation and analysis

The 'key' periods over which WT and rainfall values were averaged and related to vegetation height in May and hay yield in July were between 1 April and the May botanical assessment (13 May each year), the period 13 May up to the hay cut (first week in July), and the overall mean for both periods. These WT and rainfall means were included with the following variables in a multiple correlation analysis:

(i) N applied in spring and P and K applied in the preceding year
(ii) depths averaged over the three periods noted above
(iii) water table depth at the beginning of each period
(iv) weekly rainfall totals averaged over these periods
(v) hay yield in July.

In order to separate the effects of water table depth from those of other variables, various combinations of these variables were tested by multiple linear regression. Only variables which were not inter-correlated were included together as explanatory variables.

Hay yield data for 1988 presented problems due to the delay in hay making until early August, which allowed a whole extra month of growth and yield accumulation in this year compared with others. Curves were fitted by eye to data from the yield development study carried out in 1988 (see later, Figure 3.1) to estimate yield as at 1 July for treatments N_0, N_{100} and N_{200} in block 2. Existing hay yield values for the remaining two replicates were then adjusted correspondingly to provide full data sets for these three treatments in 1988.

Water table depths in April-May and May-July were found to be correlated with the amounts of P and K applied. This occurred because no P or K was applied before the hay cut in 1986 which was, coincidentally, the year when water tables were highest in the spring (see Figure 3.4). Therefore, data for 1986 could be included only when analyses were restricted to data from N_0 plots, which received no P or K in any year.

Separate analyses, based upon replicate block means for each year 1987-1990 (i.e. excluding 1986 data), were used to investigate the relationship between WT depth and DM response to fertilizer N. Regression analysis was used to calculate individual N response coefficients for each replicate block in each year, for both vegetation height in May and hay yield in July. These values were then tested by correlation and regression analysis against corresponding block/year means for the explanatory variables included in the foregoing analyses.

Animal production from aftermath grazing

A similar procedure of correlation analyses followed by multiple regression was used to analyze data for animal output and N loss. However, the delayed harvest in 1988 also affected production in the aftermath phase by halving the period available for grazing compared with other years. To compensate for this, only the second half of the grazing periods in 1986, 1987 and 1989 were examined i.e. from mid-September to mid-October, except when the relationship between water table depth and animal output response to applied N was examined. Data for each year, including 1988, were converted to live weight produced per hectare per day; the number of days for each paddock in 1988 was taken as that between fertilizer application and cessation of grazing. For other years, the actual numbers of days that each paddock was stocked within the second half of the grazing period was used.

The following explanatory variables were included in a multiple correlation analysis with live weight production data:-

(i) N, P and K applied after hay making each year
(ii) rainfall totalled over the whole and over the second half of the grazing period
(iii) WT depth at fertilizer application
(iv) WT depth at the start of the second half of the grazing period (start of grazing in 1988)
(v) WT depth averaged over second period.

In addition, animal production data were used to derive coefficients for N response for each block and these were related to block/year means for the explanatory variables listed above. The procedure was similar to that used for vegetation height and hay yield data, except that data from all five years were included and coefficients were calculated from animal live weight production data for each of the fertilized plots in each block and year expressed as a percentage of the corresponding N_0 value. Percentage data were used in preference to untransformed values so that data for the whole grazing period each year could be used without undue influence on the results from the much shorter grazing period in 1988.

HERBAGE RESPONSE TO N, P AND K - THE SMALL PLOT (SP) EXPERIMENT (EXPERIMENT 2)

Fertilizer and cutting strategies.

Fifty seven 1.5 m x 5 m plots were laid out in March 1986 in three replicate blocks, with 19 treatment plots per block, in a 25m x 35m enclosure located within the area incorporated by the LS experiment (see Figure 1.5).

The two experiments were established to measure both production response to fertilizers and changes in botanical composition and this is reflected in the design. This experiment tested a wider range of treatments than was possible in the LS experiment where plots were large enough to be grazed individually after hay making. Treatments (see Table 3.1) could be divided into five sub-sets or series, with some treatments common to more than one series. The series were as follows: the Main series (treatments T1-6), these corresponded with treatments in the LS experiment except for the inclusion of treatment T2; the Main + P,K series (T1-6, T14-19); the Seasonal series (T5-7, T9-13); the Early v standard cut series (T7,8); and the N x P factorial series (T1, T14-18). The prime purpose of the Seasonal series was to see if deleterious effects on species diversity caused by fertilizer N could be mitigated by applying most or all of the N after hay cutting, subsequent to completion of the reproductive growth phase of most species. The Early v standard cut compared cutting at the silage stage with hay cutting, both at a high N rate (400 kg ha^{-1} $year^{-1}$).

Granular fertilizer was applied by hand, with most treatments split between spring and mid season (dates 1 and 3 in Table 3.1). No single application consisted of more than 100 kg N ha^{-1}. Application dates 1 and 3 each year coincided to within one or two days with application dates within the LS experiment; date 1 representing the earliest occasion after mid April each year when ground conditions allowed tractor access.

Table 3.1. Application of nitrogen (N), phosphorus (P) and potassium (K) at four possible dates each year in the SP experiment. Figures are kg ha^{-1} of elemental N, P or K as indicated.

		Applied before hay cut						Applied to aftermath					
Application date:			1			2			3			4	
Treatment		N	P	K	N	P	K	N	P	K	N	P	K
No.	N-P-K code												
T1	0-0-0	0	0	0	0	0	0	0	0	0	0	0	0
T2	0-R-R	0	R	R	0	0	0	0	R	R	0	0	0
T3	25-R-R	12.5	R	R	0	0	0	12.5	R	R	0	0	0
T4	50-R-R	25	R	R	0	0	0	25	R	R	0	0	0
T5	100-R-R	50	R	R	0	0	0	50	R	R	0	0	0
T6	200-R-R	100	R	R	0	0	0	100	R	R	0	0	0
T7	400-R-R	100	R	R	100	0	0	100	R	R	100	0	0
T8	400-R-R (EC)	100	R	R	100	0	0	100	R	R	100	0	0
T9	0/100-R-R	0	R	R	0	0	0	100	R	R	0	0	0
T10	0/200-R-R	0	R	R	0	0	0	100	R	R	100	0	0
T11	50/100-R-R	50	R	R	0	0	0	100	R	R	0	0	0
T12	50/200-R-R	50	R	R	0	0	0	100	R	R	100	0	0
T13	100/200-R-R	100	R	R	0	0	0	100	R	R	100	0	0
T14	100-0-R	50	0	R	0	0	0	50	R	R	0	0	0
T15	200-0-R	100	0	R	0	0	0	100	R	R	0	0	0
T16	0-75-R	0	37.5	R	0	0	0	0	37.5	R	0	0	0
T17	100-75-R	50	37.5	R	0	0	0	50	37.5	R	0	0	0
T18	200-75-R	100	37.5	R	0	0	0	100	37.5	R	0	0	0
T19	200-75-200	100	37.5	100	0	0	0	100	37.5	100	0	0	0

R denotes an element applied at 'replacement' rates. These were flat rates of 14 kg P and 42 kg K ha^{-1} at date 3 in 1986 (none at preceding dates in 1986), and thereafter amounts equivalent to those removed in herbage (see text).
Treatment T8 had an extra cut immediately prior to the second application date. The remaining treatments received their first cut (hay stage) soon before date 3.
Application date 1 = April-May; date 2 = late May-early June; date 3 = immediately after hay-stage cut (first week in July all years except 1988, first week in August 1988); and date 4 = after first aftermath cut (see text for exact dates).

Actual application dates were:

Date 1	15 May 1986, 25 April 1987, 20 April 1988, 4 May 1989
Date 2	4 June 1986, 29 May 1987, 25 May 1988, 1 June 1989
Date 3	23 July 1986, 28 July 1987, 24 August 1988, 25 July 1989
Date 4	19 August 1986, 26 August 1987, 19 September 1988, 5 September 1989

Fertilizer N was applied as ammonium nitrate. With all treatments except for T1 control (which received no fertilizer), and those where specific rates of P and/or K were applied (T14-19), sufficient P and K were applied to 'replace' the amounts removed in harvested herbage. Amounts removed at the hay-stage cut (or in the first two cuts from T8) were applied soon after this cut, and those from aftermath cuts were replaced at the next spring application date. The same strategy applied with respect to K for treatments receiving specific rates of P (T14-18). Flat rates of 14 kg ha^{-1} P and 42 kg ha^{-1} K were applied in mid summer 1986 as a compound fertilizer. These rates, which were the same as those applied in the LS experiment, were included for the sake of continuity between the two experiments and were somewhat higher than the amounts removed at the first harvest in this experiment (3.0 - 4.8 kg P ha^{-1} and 23.2 - 42.0 kg K ha^{-1}). In subsequent years, the actual amounts harvested were replaced, calculated per treatment, with P applied as triple super-phosphate and K as muriate of potash. No P was applied to any treatment except T16-19 before the first cut in 1986, nor K to any treatment except T19. Amounts of P applied ranged from 4.6 to 6.3 kg P ha^{-1} in spring and 8.0 - 10.9 kg ha^{-1} after hay cutting, with corresponding values for K of 24.1 - 50.3 and 45.8 - 68.4 kg ha^{-1}.

The first (early) cut for treatment T8 was taken at the second application date each year. Hay-stage cuts were taken from all plots (including T8) on 6 July 1986, 3 July 1987, 1 August 1988 and 6 July 1989, these dates falling within the period of hay making in the main experiment. As in the LS experiment, the 1988 hay cut was delayed for a month beyond the intended date by wet weather. All plots were harvested on a further two occasions (aftermath cuts) in each year, except in 1988 when only one aftermath cut was taken. In all years except 1988, the first aftermath cut coincided with fertilizer application date 4, whilst in 1988 the single aftermath cut was taken on 5 October. Final cuts in the remaining three years were taken on 7 October 1986 and 1987, and 10 October 1989.

At each harvest the central 1 m was mown for the length of each plot using an Arun reciprocating blade mower. Thereafter, herbage sampling for dry matter (DM) yield, *in vitro* digestibility and N, P and K content followed standard procedures, as in the LS experiment. The remainder of the herbage within each plot and on discard areas was mown and removed immediately after each cut.

Data for P and K concentration in herbage not only allowed 'replacement' rates to be calculated but also gave a guide to the adequacy or otherwise of supply of these elements with each treatment (Knauer, 1966; Clement and Hopper, 1968; Prins *et al.*, 1986).

The metabolizable energy (ME) value of herbage was calculated from *in vitro* digestibility (% digestible organic matter in the dry matter: DOMD) and crude protein content, as in the LS experiment.

Soil P and K

Soil was sampled from a sub-set of plots in March 1990 and tested by spectrophotometry for available phosphorus and by flame photometry for exchangeable potassium to quantify any residual effect of high application rates of these elements. Soil was collected to a depth of 10 cm from 5-6 randomly-chosen sites within each 7.5 m^2 plot using a 25 mm diameter corer. Samples were air dried for at least 3 days and then passed through a 2 mm sieve before analysis.

Data analysis

All data were analyzed separately for each year and averaged over four years, by analysis of variance (ANOVA) using GENSTAT (GENSTAT V Committee, 1987). In addition to analyses which included all the treatments, the five different treatment series described earlier were analyzed for data averaged over four years.

N x P factorial analyses were of limited value after the hay cutting in 1986 because the amounts of K 'replaced' were usually correlated with both N and P rates. There was therefore a risk of attributing effects to N or P that may have been heavily influenced by K, particularly as DM yield and N recovery were often more closely correlated with the amount of K applied than with either N or P. However, as no K had been applied to any plot within the N x P series until after the 1986 hay cut, DM data from this cut were tested in 3N x 2P factorial ANOVAs.

DM data were also tested by correlation and regression analysis to investigate the individual contributions of N, P and K to dry matter (DM) production. The effects of P and K were consistently correlated when data from all the treatments were included and when variables were composed of data from all four years individually. However, data from the

Main + P, K series produced satisfactory regression equations when treatment means averaged over all four years were used.

3.3. RESULTS

PRODUCTION FROM HAY AND AFTERMATH GRAZING - THE LARGE SCALE (LS) EXPERIMENT (EXPERIMENT 1)

Soil P and K analyses

There was no significant treatment effect in the amount of extractable soil P in March of any year. Differences between plots receiving P and K in mid season each year and control plots were marginal, with overall means of 7.8 mg P l^{-1} of soil on control plots compared with 8.5 mg l^{-1} on treated ones. Treatment effects were significant for soil K only in 1986 when, presumably by chance, the combined mean of all N treatments was significantly lower than that for control plots. In all subsequent years, the order of these two means was reversed, averaging 137.8 mg K l^{-1} on control plots and 154.6 mg l^{-1} on others.

Hay dry matter (DM) production

Dry matter production averaged over the four years showed significant treatment effects, both at cutting and in baled hay ($P<0.01$ after baling)(Table 3.2). All treatments significantly increased DM production at cutting compared with the control, with increases ranging from 0.86 t ha^{-1} for N_{25} ($P<0.05$) to 1.56 t ha^{-1} for N_{200} ($P<0.001$).

DM yields showed no significant response to fertilizer N in either 1986 or 1988, but treatment effects were significant both at cutting and in baled hay in 1987 ($P<0.01$ for baled hay) and in 1989 ($P<0.001$ both at cutting and for baled hay). In both 1987 and 1989, the largest incremental response to fertilizer treatment was between N_0 (control) and N_{25} treatments when measured at cutting, although only treatments N_{50} and above increased DM production significantly compared with control in 1987 ($P<0.001$ for N_{200}).

Losses in DM ha^{-1} during hay making averaged just over 20% overall, ranging from 10.4% for N_{200} in 1988 to 36.2% for N_{100} in 1989. Averaged over four years, treatments N_{50} and above increased production of baled hay significantly compared with control by amounts ranging from 1.27 t ha^{-1} for N_{50} to 1.47 t for N_{200} (both $P<0.001$). Both N_{50} and N_{200} also increased baled hay yields significantly compared with N_{25}, giving an extra

Table 3.2. Weights of herbage dry matter (tonnes DM ha^{-1}) at cutting and after baling as hay in four years 1986-89 in the LS experiment.

Treatment	Yield at cutting					Yield of baled hay				
	1986	1987	1988	1989	Mean 1986-9	1986	1987	1988	1989	Mean 1986-9
N_0	4.52	4.78	6.32	4.61	5.06	3.47	3.88	5.09	3.75	4.05
N_{25}	3.96	5.96	6.95	6.83	5.92	2.76	4.49	4.85	4.85	4.24
N_{50}	4.78	6.25	7.17	7.57	6.44	3.64	5.45	6.18	6.02	5.32
N_{100}	4.17	6.19	6.82	8.24	6.36	3.30	5.44	6.19	5.25	5.05
N_{200}	4.88	7.11	6.87	7.64	6.62	3.73	6.20	6.09	6.05	5.52
s.e.	0.470	0.422 *	0.275	0.331 ***	0.264 *	0.291	0.295 **	0.370	0.260 ***	0.163 ***

Asterisks denote significance of treatment effects in ANOVA: * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$

1.08 t ($P<0.01$) and 1.28 t ha^{-1} ($P<0.001$) respectively. This overall pattern was influenced greatly by data from 1987 and 1989, with the greatest response to N occurring between treatments N_{25} and N_{50}.

Hay quality

The digestibility (digestible organic matter in the dry matter - DOMD) of herbage at cutting and after baling varied from year to year, averaging, at cutting, between 40.7% when hay was cut late in 1988 and 51.0% in 1989, and, after baling, between 39.8% (1988) and 46.9% (1987)(Table 3.3). Herbage digestibility was affected by applied fertilizer only in1986 and only in baled hay, when DOMD was significantly higher for N_{100} than all other treatments ($P<0.01$ when compared with N_0). The digestibility of herbage sampled fell during hay making with all treatments and in all years except 1987 when it appeared to increase slightly on average.

Table 3.3. *In vitro* digestibility (% digestible organic matter in the dry matter - DOMD) and Metabolizable Energy (ME) value (MJ kg^{-1}) of herbage DM at cutting and after baling, averaged over four years 1986-89 in the LS experiment.

Treatment	At cutting		In baled hay	
	DOMD	ME value	DOMD	ME value
N_0	46.9	7.51	44.4	7.13
N_{25}	46.5	7.57	43.9	7.08
N_{50}	46.5	7.56	44.1	7.12
N_{100}	47.6	7.66	45.1	7.27
N_{200}	45.9	7.64	43.9	7.20
s.e.	0.58	0.057	0.71	0.079

The ME value of hay at cutting and at baling was not significantly affected by treatment in any year, nor when averaged over 4 years (Table 3.3). However, values varied considerably from year to year, from an overall mean of 8.2 MJ per kg in 1986 to 6.7 MJ in 1988 in herbage at cutting. Losses of ME value during hay making reflect quite closely

Table 3.4. Nitrogen concentration (%N) in herbage dry matter sampled at cutting and after baling hay in four years 1986-89 in the LS experiment.

Treatment	%N in herbage at cutting				%N in hay at baling			
	1986	1897	1988	1989	1986	1987	1988	1989
N_0	1.54	1.33	1.39	1.32	1.49	1.09	1.34	1.18
N_{25}	1.64	1.26	1.28	1.08	1.58	1.06	1.26	1.27
N_{50}	1.62	1.24	1.24	1.12	1.55	1.03	1.30	1.03
N_{100}	1.69	1.29	1.41	1.21	1.69	1.12	1.26	1.17
N_{200}	2.26	1.61	1.53	1.58	1.77	1.40	1.46	1.35
s.e.	0.202	0.071	0.028	0.033	0.102	0.072	0.045	0.132
		*	***	***		*		

Asterisks denote significance of treatment effects in ANOVA:
* = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$

Table 3.5. Amounts of nitrogen, phosphorus and potassium (kg N, P and K ha^{-1}) recovered in herbage, and amounts of P and K applied, averaged over four years 1986-89 in the LS experiment.

Treatment	Minerals recovered (kg N, P or K ha^{-1})				Amounts applied^{++} (kg ha^{-1} year^{-1})	
	N	N	P	K	P	K
	At cutting	At baling	At cutting	At cutting		
N_0	70.1	51.7	5.54	39.4	-	-
N_{25}	75.9	50.4	6.63	57.6	8.99	58.8
N_{50}	82.3	63.9	7.49	68.2	9.59	65.8
N_{100}	86.4	64.3	6.38	60.6	8.81	59.5
N_{200}	112.9	80.5	7.07	60.1	9.26	59.1
s.e.	4.39	2.33	0.479	4.76	0.369	3.65
	***	***		*		

Asterisks denote level of significance in ANOVA: * = $P<0.05$; *** = $P<0.001$
$^{++}$ See text for explanation of P and K application strategy

the changes in *in vitro* digestibility noted above, with mean values averaged over all treatments and years declining from 7.6 to 7.2 MJ kg^{-1}.

The concentration of N in herbage at cutting was significantly influenced by N application in each year except 1986, with treatment effects reaching a high level of significance ($P<0.001$) in both 1988 and 1989 (Table 3.4). Treatment effects were less evident after hay making, with N concentrations in baled hay 0.1 - 0.3 percentage points lower on average than at cutting. Hay from N_{200} plots showed the highest N content each year, but treatment effects were only significant in 1987.Concentrations of P in herbage DM were low, with no treatment mean exceeding 0.13% in any year and no significant treatment effect.

Potassium levels remained fairly constant on treated plots, averaging between 0.92% and 0.96% each year, but declined progressively from 0.95% to 0.60% on control plots. In both 1988 and 1989, the K concentration in N_0 herbage was significantly lower than that of all other treatments ($P<0.01$).

The mean amounts of N and K harvested at cutting were significantly related to the amount of N applied, but herbage P yield was not significantly affected by treatments (Table 3.5). Losses in herbage N per ha between cutting and baling were much greater than corresponding losses in DM, reflecting the lower N content of baled hay.

Metabolizable energy (ME) production from hay

The amount of ME produced per ha at cutting averaged over four years was significantly affected by treatments ($P<0.05$), although ANOVAs for individual years showed significant ($P<0.001$) treatment effects only in 1989 (Table 3.6). The only significant difference between N-treatments in 1989 was the increase of 10.3 GJ ha^{-1} between N_{25} and N_{100}, whilst averaged over 4 years all treatments significantly increased ME production compared with control ($P<0.05$ for N_{25}, $P<0.01$ the remainder).

The quantity of ME produced at baling averaged over 1986-89 was increased compared to the control by all treatments except N_{25}, with increases ranging from 7.6 MJ ha^{-1} for N_{100} ($P<0.01$) to 11.0 MJ for N_{200} ($P<0.001$). All three treatments receiving 25 kg N ha^{-1} or more in the spring also increased output compared with N_{25} ($P<0.01$, $P<0.001$ for N_{200}), with the increase of 3.4 MJ ha^{-1} between N_{100} and N_{200} also significant at $P<0.05$.

Table 3.6. Metabolizable energy (ME) production per hectare in herbage at cutting and in baled hay in four years 1986-89 in the LS experiment.

Treatment	ME produced at cutting (GJ ha^{-1})					ME produced in baled hay (GJ ha^{-1})				
	1986	1987	1988	1989	Mean 1986-9	1986	1987	1988	1989	Mean 1986-9
N_0	34.4	35.9	43.1	37.3	37.7	23.8	29.5	33.5	28.0	28.8
N_{25}	32.7	43.6	45.5	55.2	44.2	19.8	32.5	31.5	36.1	29.9
N_{50}	39.7	45.1	47.7	60.2	48.2	26.2	39.6	40.6	44.7	37.6
N_{100}	34.9	45.9	46.4	65.5	48.2	25.8	40.9	40.5	38.5	36.4
N_{200}	41.3	51.5	45.7	62.5	50.2	27.5	46.3	40.4	44.1	39.8
s.e.	3.99	2.90	1.91	2.43 ***	2.00 *	1.98	2.36 **	2.79	2.26 **	1.03 ***

Asterisks denote significance of treatment effects in ANOVA: * = P<0.05; ** = P<0.01; *** = P<0.001

Dry matter yield development.

The pattern of yield development differed significantly between the three plots. Herbage DM yield increased significantly between each consecutive assessment on the N_0 plot until 25 May (Figure 3.1).

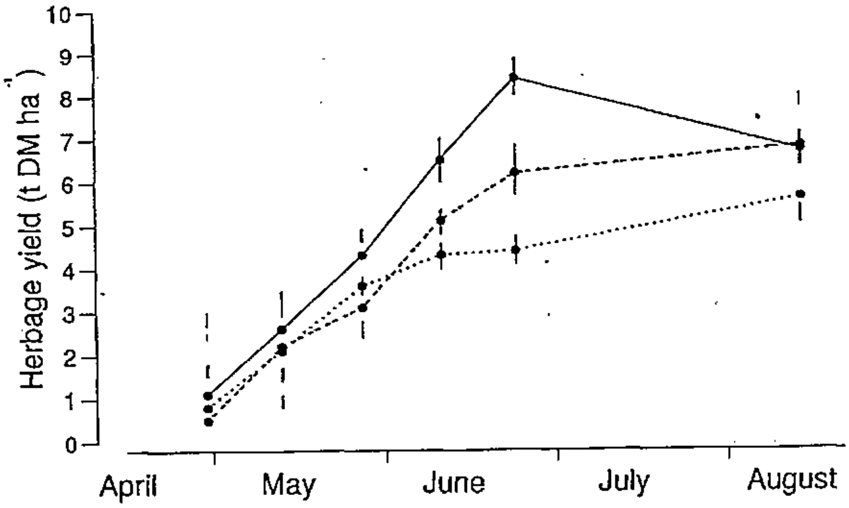


Figure 3.1. Accumulation of herbage dry matter between 28 April and 11 August 1988 on plots which had received 0 (dotted line), 50 (broken line) or 100 (solid line) kg N ha^{-1} on 18 April in the LS experiment. Bars are twice the standard error of the mean in each case.

The rate of DM accumulation slowed after this, with only the difference between 25 May and the final assessment on 11 August significant ($P<0.05$). On the N_{100} plot, yield increased significantly between each assessment until 8 June, with the only significant increment thereafter between this date and 11 August. In contrast with these two plots, yield increased significantly between each assessment on the N_{200} plot until 21 June, but then declined significantly by 11 August. Differences in herbage DM between N_0 and N_{100} plots were small initially, only reaching significance at the last two assessments, but yield was significantly greater on N_{200} than on N_{100} on each occasion except 11 May and 11 August. However, statistical tests of within-plot, between-assessment differences are more reliable than those of between-plot/treatment differences. The latter may have been due to innate differences between plots, rather than to the amount of fertilizer applied (Hurlbert,

1984).

Botanical separation showed that trends in DM production were largely due to the monocot components of the vegetation (Figure 3.2). The yield of both dicots and monocots increased initially until early June, after which the dicot yield remained fairly constant, declining slightly in the N_{100} and N_{200} plots. Monocots continued to increase during June on all plots and closely followed the pattern of total DM production described above.

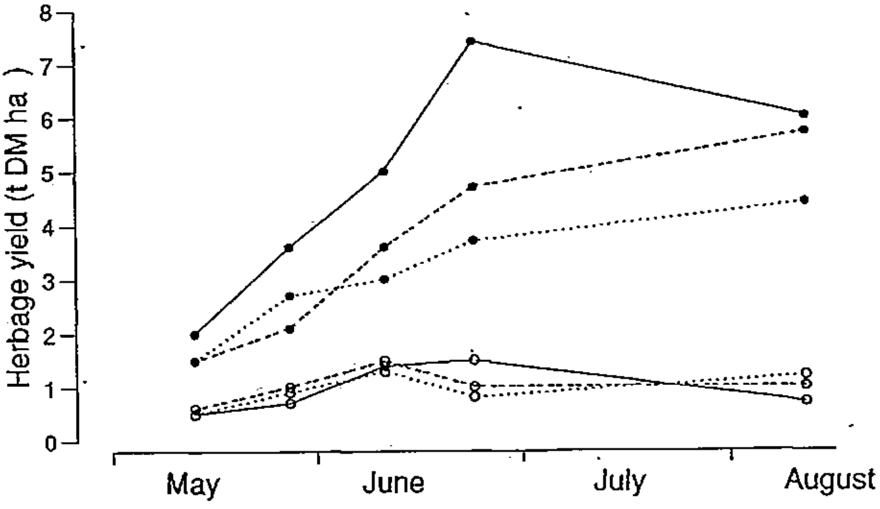


Figure 3.2. Accumulation of herbage DM of monocots (solid symbols) and dicots (open symbols) between 28 April and 11 August 1988 on plots which had received 0 (dotted lines), 50 (broken lines) or 100 (solid lines) kg N ha^{-1} on 18 April in the LS experiment.

Animal production from aftermath grazing

Individual LW gain averaged 1.04 kg day^{-1} overall and showed no significant difference among treatments in any year or averaged over 4 years. The mean growth rate was consistently above 900 g LW per day for all treatments in each year, with the sole exception of animals on N_{100} plots in 1988. A low mean of 760 g day^{-1} for these plots was attributable to poor performance by both core animals on one of the three replicate plots for this

Table 3.7. *Stocking rates, expressed as the number of grazing days per hectare and the mean number of steers per hectare per day, during aftermath grazing in four years in the LS experiment.*

Treatment	Grazing days ha^{-1}					Mean stocking rate (steers ha^{-1})				
	1986	1987	1988	1989	Mean 1986-9	1986	1987	1988	1989	Mean 1986-9
N_0	163.7	219.7	57.1	191.9	158.1	2.9	3.2	2.0	2.8	2.7
N_{25}	194.8	219.3	95.1	271.8	195.2	3.1	3.2	2.8	3.9	3.3
N_{50}	269.0	273.0	144.0	286.5	243.1	4.5	4.0	4.4	4.3	4.3
N_{100}	280.8	249.3	151.5	308.0	247.4	4.9	3.6	4.5	4.4	4.4
N_{200}	317.6	265.0	173.1	300.0	263.9	5.8	4.1	5.3	4.4	4.9
s.e.	14.16	24.80	10.42	27.01	10.67	0.20	0.31	0.36	0.35	0.17
	***		***		***	***		***		***

Asterisks denote the significance of treatment effects in ANOVA: *** = P<0.001

Table 3.8. Live weight (LW) production and utilized metabolizable energy (UME) output from aftermath grazing in four years in the LS experiment.

Treatment	Total LW produced (kg LW ha^{-1})					UME from aftermath grazing (GJ ha^{-1})				
					Mean					Mean
	1986	1987	1988	1989	1986-9	1986	1987	1988	1989	1986-9
N_0	152.9	230.3	49.9	198.0	157.8	11.7	17.3	3.7	14.9	11.9
N_{25}	183.9	229.3	85.1	248.4	186.7	14.3	17.8	6.6	19.4	14.5
N_{50}	266.7	320.0	145.9	325.9	264.6	20.4	24.4	11.0	24.3	20.1
N_{100}	309.7	282.0	116.2	313.8	255.4	23.3	21.0	8.9	24.1	19.3
N_{200}	362.4	277.0	173.7	368.5	295.4	27.5	20.8	13.0	27.1	22.1
s.e.	22.11 ***	28.96	11.14 ***	23.58 **	16.24 **	1.45 ***	2.10	0.72 ***	1.79 **	1.12 ***

Asterisks denote significance of treatment effects in ANOVA: ** = $P<0.01$; *** = $P<0.001$

treatment, but no satisfactory explanation for this was found.

The number of steer grazing days per hectare supported by aftermath growth varied greatly between years and treatments (Table 3.7). Treatment effects were particularly pronounced in 1986 and 1988 ($P<0.001$). In both these years, treatments N_{50} and above increased grazing days ha^{-1} very significantly compared with control ($P<0.001$), but the increase between N_0 and N_{25} was significant only in 1988 ($P<0.05$).

Live weight production per hectare (Table 3.8) followed general trends in grazing day totals, since individual growth rates differed little between treatments. Overall, fertilizer application increased LW production compared with control by between 29 kg ha^{-1} at N_{25} to 137 kg ha^{-1} at N_{200}, although increments were significant only for treatments N_{50} and above ($P<0.01$, $P<0.001$ for N_{200}). Both N_{100} and N_{200} produced significantly more than N_{25} ($P<0.01$). Output from grazing averaged over all 4 years was significantly ($P<0.001$) increased compared to control and N_{25} by N_{50}, N_{100} and N_{200}, but was not increased significantly beyond N_{50}.

Total UME output (baled hay + aftermath grazing).

The total UME produced per year was very significantly affected by N treatment ($P<0.001$), with average output ranging from 40.6 GJ ha^{-1} $year^{-1}$ at N_0 to 61.7 ha^{-1} $year^{-1}$ at N_{200} (s.e.m. = 1.677). Overall, hay UME contributed about two thirds of the total UME output. This proportion declined with increasing N rate, from 71% at N_0 to 65% at N_{200}. Hay, aftermath grazing and total UME data for treatments N_{25} to N_{200} are represented in Figure 3.3. Each data point is the mean of four years for a particular plot.

UME response curves (Figure 3.3).

None of the three UME variables were easy to model for N response, particularly after excluding N_0 values, because of the paucity of data points. The data distribution shows a markedly sigmoidal pattern for all three variables, particularly if the true N_0 mean is taken into account. There was a high degree of confidence about this general pattern, since N_{25} means rarely differed significantly from control, whilst the difference between N_{25} and N_{50} often reached very high levels of significance. Furthermore, because P and K were applied to all treatments except control, intercepts above the N_0 value on the Y axes in Figure 3.3

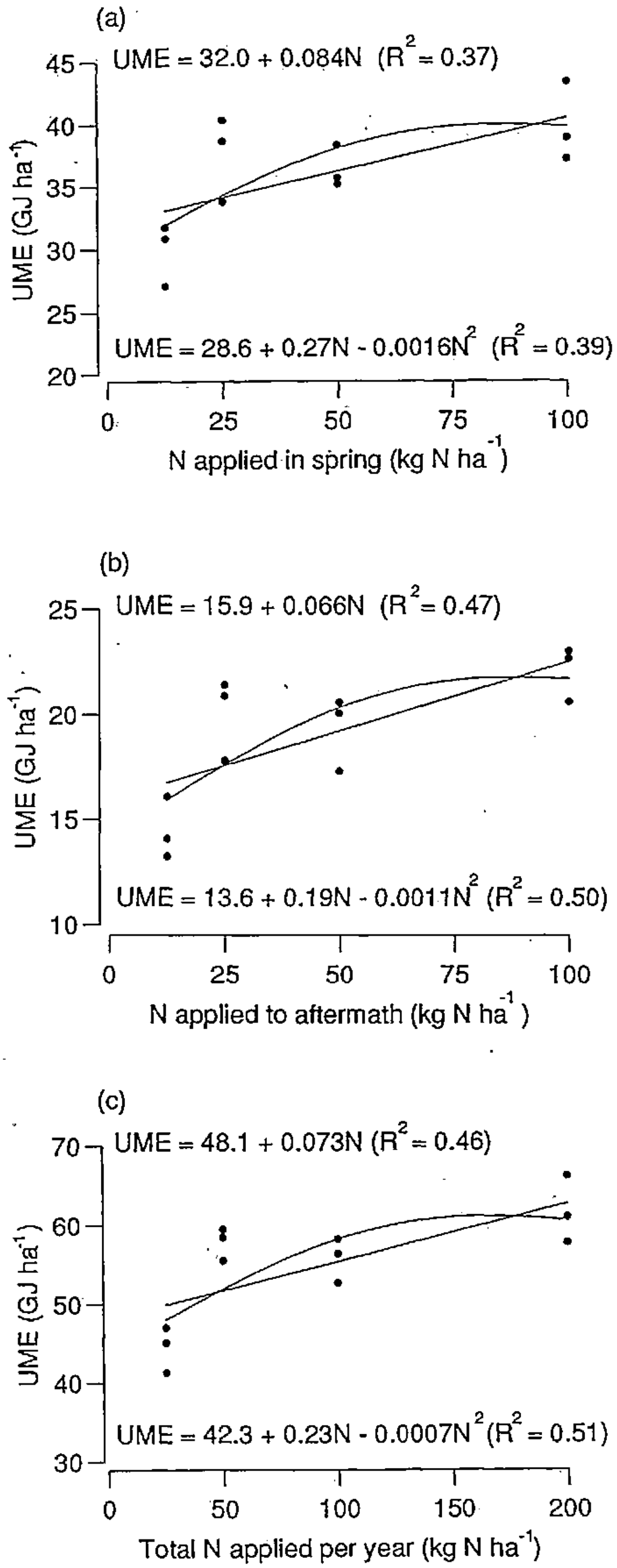


Figure 3.3. Increases in utilized metabolizable energy output (GJ ha^{-1}) from (a) baled hay, (b) aftermath grazing, and (c) hay + grazing in the LS experiment, averaged over four years 1986-89 for each plot, attributable to fertilizer N application. Lines are fitted by linear (straight lines) and quadratic (curves) regression using equations shown.

might be expected. An accurate prediction of these intercept values would give an indication of the underlying contribution of the P and K 'replacement' strategy to increases in output. However, without more data points in the N_0 to N_{50} range it was not possible to model accurately this portion of the curve. Additionally, a curve was sought to smooth the response throughout the range of N rates used. Of the models tested, only the linear and simple quadratic models could account for a significant proportion of the variance in the regression analyses and at the same time satisfy these requirements. Quadratic equations accounted for only slightly (and not significantly) more of the variance than linear models, but since data appeared to be curvilinear, both linear and quadratic models are included in Figure 3.3. In view of the high error estimates about the quadratic coefficients, the equations shown in Figure 3.3 are best seen as illustrative, rather than definitive.

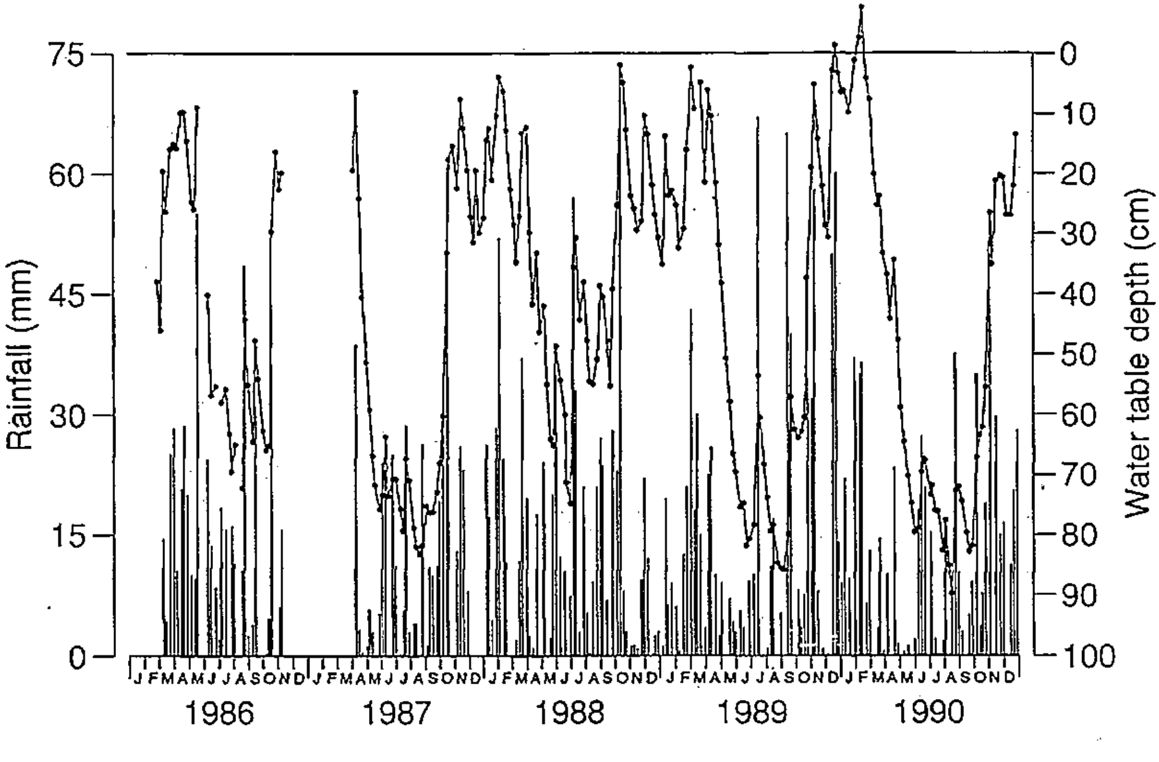


Figure 3.4. Weekly rainfall totals (bars) and water table depth averaged over the experimental area in five years 1986 to 1990. Breaks in the water table line indicate periods when no rainfall or water table reading was taken.

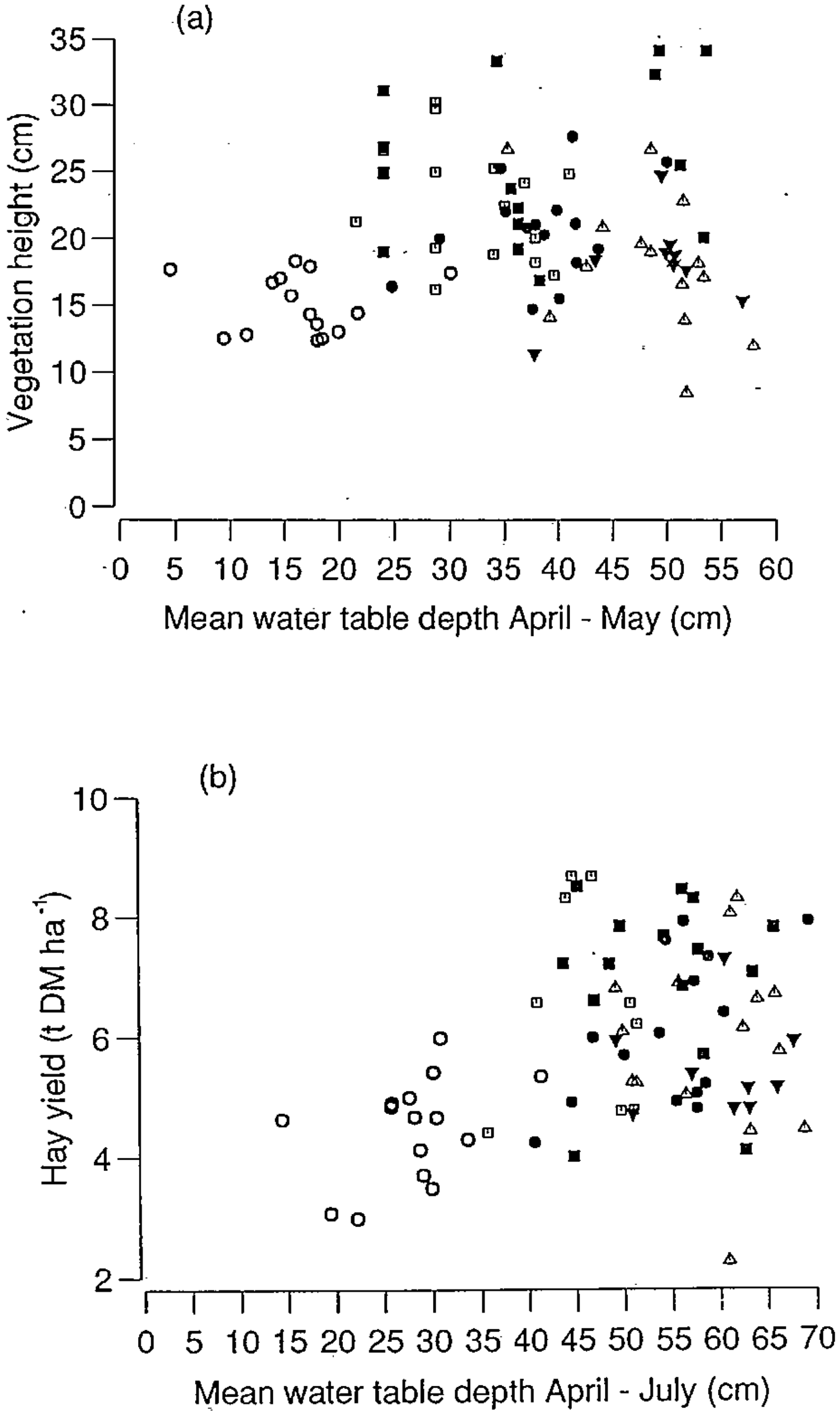


Figure 3.5. Scatter diagrams of (a) vegetation height in May and (b) hay yield in July plotted against mean water table depths, using data from all plots in the LS experiment. Open circles = 1986; solid circles = 1987; open squares = 1988; solid squares = 1989; open triangles = 1990; solid triangles = 1990x, i.e. subplots where treatments discontinued.

THE EFFECT OF VARIATIONS IN WATER TABLE DEPTH ON PRODUCTIVITY

Fluctuations in WT depth averaged over all plots for each occasion, and weekly rainfall data over the same period, are shown in Figure 3.4. Water table depth generally fluctuated between 0 (with occasional flooding) and 30 cm below the soil surface from late autumn until early spring, increasing to 80-90 cm by July-August each year (Figure 3.4).

Influence of WT depth on spring growth and hay DM yield

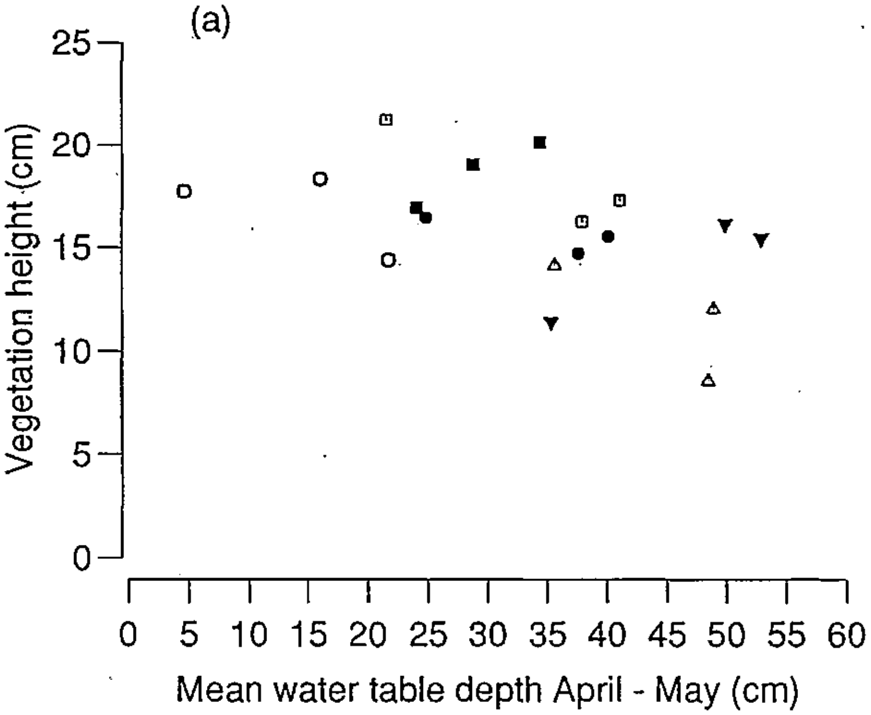
Figure 3.5 shows scatter diagrams for both vegetation height in May and subsequent hay yield plotted against WT depth. These diagrams contain data from all plots and all years. They show no clear overall relationship, although hay yield was positively correlated with WT depth ($r=0.23$, $P<0.05$). However, this weak relationship was strongly influenced by data from 1986, when yield response to N was inhibited by lack of prior P or K application. As noted previously, WT depth was significantly correlated with amounts of both P and K applied ($r=0.47$ and 0.58 respectively for WT mean April-May, $r=0.55$ and 0.59 respectively for April-July, all $P<0.001$). Both vegetation height in May and hay yield were correlated with the amounts of P and K applied ($r=0.55$ and 0.57 respectively for vegetation height; $r=0.50$ and 0.53 for hay yield, all $P<0.001$). When data from all years were used with analyses restricted to N_0 plots only (Figure 3.6), vegetation height in May was negatively correlated with WT depth over the preceding period ($r=0.51$, $P<0.05$), but hay yield was not related to April-July WT depth means ($r= -0.11$).

There was no significant correlation between mean WT depth and N response for 1987-1990, either in terms of vegetation height in May ($r= -0.29$) or hay DM yield ($r= -0.22$).

Influence of WT depth on beef production from aftermath grazing

Production from aftermath grazing was calculated in terms of live weight produced per hectare per day (LWP) for the months of September and October only (i.e. excluding August). This corresponded to the shortened grazing period in 1988 that resulted from the later hay cutting date in that year.

LWP was significantly correlated only with applied N and K ($r= 0.55$, $P<0.001$ and $r=0.31$, $P<0.05$ respectively) when data from all years and treatments were analyzed. No



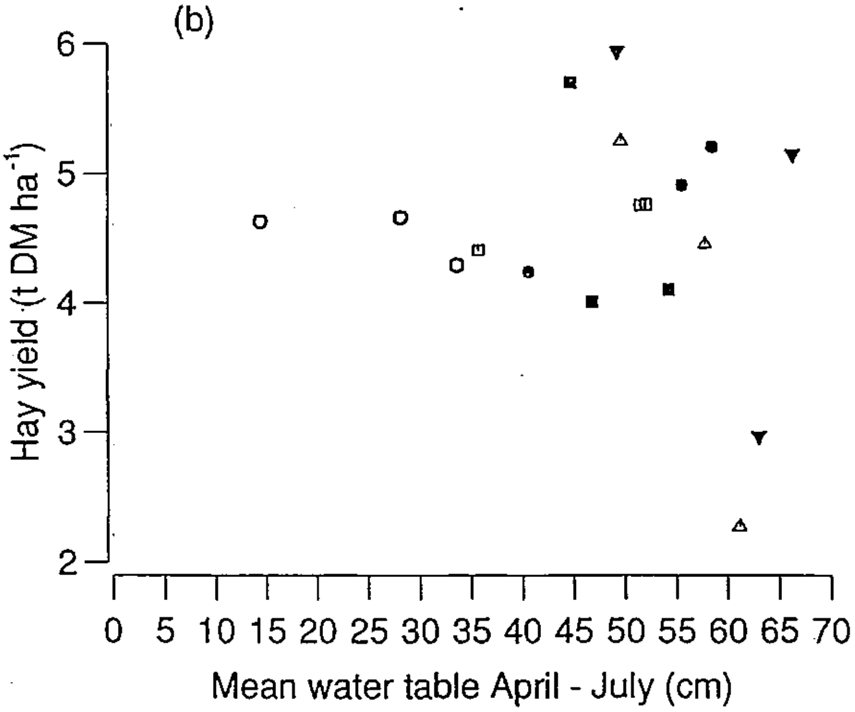


Figure 3.6. Scatter diagrams of (a) vegetation height in May and (b) hay yield in July plotted against mean water table depths, using data from N_0 plots in the LS experiment. Symbols as in Figure 3.5.

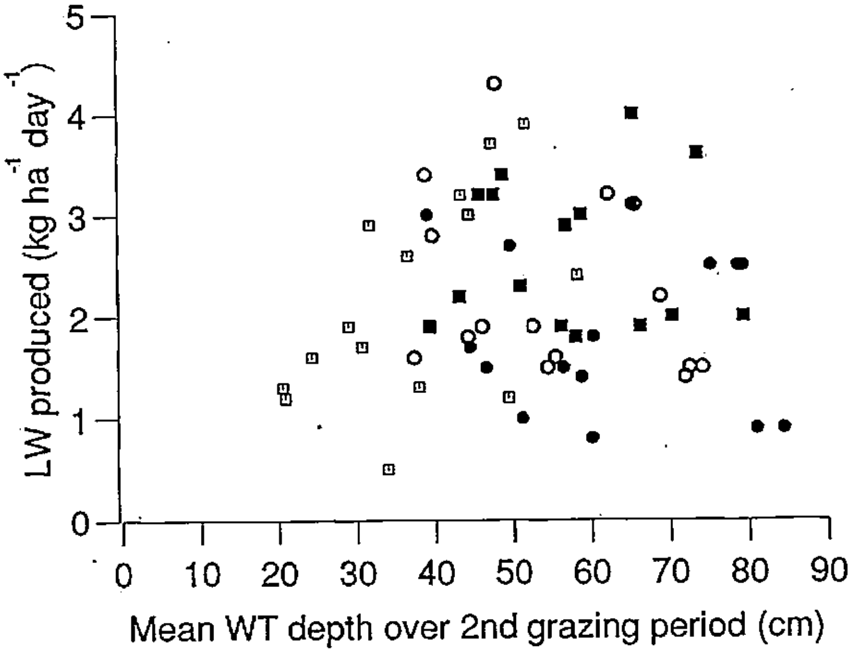


Figure 3.7. Scatter diagram of animal live weight production during the 2nd period of aftermath grazing in the LS experiment, plotted against mean water table depths using data from all plots. Symbols as in Figure 3.5.

multiple regression which included WT depth and/or rainfall with N gave any significant improvement in the regression with N alone, and a scatter diagram of LWP against mean WT depth suggests no overall pattern of response (Figure 3.7).

However, when analyses were restricted to data from the wettest year, 1988, multiple regression showed a significant interaction between applied N and WT depth:

$$LWP = 0.0179\ (\pm 0.0043)N + 0.040\ (\pm 0.0056)WT \qquad R^2=0.67$$

Using data from all four years, LWP response to N was significantly ($P<0.05$) correlated with rainfall over the whole grazing period ($r=0.59$), with WT depth at the time of fertilizer application in mid-season ($r= -0.56$), with the mean WT depth over the whole grazing period ($r= -0.67$), and with the mean WT depth over period 2 ($r= -0.60$). The nature of these correlations was very dependant upon 1988 data. When these were omitted, N response was negatively correlated with rainfall over the whole period ($r= -0.78$, $P<0.05$) and no longer significantly correlated with mean WT depth (r= -0.36).

LWP was particularly low on N_0 plots in 1988 (0.98 kg LW per ha per day, compared with between 1.77 and 2.27 kg per day for other years), whilst response to applied N was correspondingly high. The high N response compared with other years could not be attributed to a greater mean availability of N resulting from a shorter grazing period, because soil mineral N levels in mid September were generally lower in 1988 than in either 1987 or 1989, though not on N_0 plots. These results are discussed again in Chapter 4, in the context of soil N losses in relation to rainfall and WT depth (see Figure 4.1).

HERBAGE RESPONSE TO N, P AND K - THE SMALL PLOT (SP) EXPERIMENT (EXPERIMENT 2)

Herbage DM production

The most consistent effect on hay cut yield within the Main treatment series (T1-6, 0-0-0 to 200-R-R, see Table 3.1), was due to 'replacing' P and K without N (T1, 0-0-0 vs T2, 0-R-R; 'R' indicates a 'replacement' rate). This difference was highly significant for four-year means (P<0.001), whilst only treatment T6 (200-R-R) increased DM output significantly compared with T2 (0-R-R)(Table 3.9).

Among all the fertilizer treatments, i.e T2 to T19, the most pronounced effects on hay yield were caused by P application. Neither treatment receiving N and K without P, i.e. T14 (100-0-R) and T15 (200-0-R) increased DM yields significantly compared with T1 control (0-0-0), whilst all other treatments within the Main + P,K series were significantly higher yielding than T14 and T15. Increasing P from replacement rates to 37.5 kg P ha^{-1} in spring increased hay DM significantly with N at 50 kg N ha^{-1} (T17, 100-75-R compared with T5, 100-R-R), but not with N at 100 kg ha^{-1} (T18, 200-75-R compared with T6, 200-R-R). Increasing K from replacement rates to 100 kg K ha^{-1} with N at 100 kg ha^{-1} in spring increased hay yield significantly by 0.95 t DM ha^{-1}, with the difference compared with replacement rates of both P and K very significant at 1.31 t ha^{-1} (P<0.01). However, the yield response to the higher rates of P and K varied greatly from year to year, being greatest in 1987 and negligible in 1988 when hay was cut late.

There was no significant N x P interaction in the ANOVA for any of the variables tested in 1986, although the overall effects of both elements were significant (P<0.01 for N,

Table 3.9. Dry matter production (t DM ha^{-1}) at hay cutting (including the early cut for treatment T8), from aftermath growth and in total, averaged over four years 1986-89 in the SP experiment.

Treatment No.	N-P-K code		Hay cut	Total of aftermath cuts	Total of all cuts
T1	0-0-0		3.78	0.91	4.69
T2	0-R-R		5.16	1.52	6.69
T3	25-R-R		5.27	1.72	6.99
T4	50-R-R		5.33	1.85	7.17
T5	100-R-R		5.40	1.99	7.39
T6	200-R-R		5.65	2.32	7.96
T7	400-R-R		5.10	2.05	7.15
T8	400-R-R(EC)	1st cut: 2.78 + 2nd cut: 1.85	= 4.63	2.17	6.80
T9	0/100-R-R		4.78	2.22	7.01
T10	0/200-R-R		4.77	2.25	7.02
T11	50/100-R-R		5.48	2.16	7.64
T12	50/200-R-R		5.31	2.09	7.40
T13	100/200-R-R		5.21	2.04	7.25
T14	100-0-R		4.41	1.40	5.81
T15	200-0-R		4.40	1.30	5.71
T16	0-75-R		5.14	1.71	6.85
T17	100-75-R		6.16	2.61	8.76
T18	200-75-R		6.01	2.84	8.84
T19	200-75-200		6.96	3.50	10.46
s.e. T1-6 (10)			0.151 ***	0.058 ***	0.160 ***
s.e. T1-6, 14-19 (22)			0.255 ***	0.071 ***	0.277 ***
s.e. T5-7, 9-13 (14)			0.227	0.067 *	0.241
s.e. T7,8 (2)			0.148	0.087	0.182
s.e. all Trs (36)			0.239 ***	0.068 ***	0.261 ***

See Table 3.1 for description of treatments
Asterisks denote significance of treatment effects in ANOVAs:
* = P<0.05; ** = P<0.01; *** = P<0.001 (degrees of freedom in brackets)

P<0.001 for P). Nevertheless, the following multiple regression for 1986 hay DM accounted for a significantly higher proportion of the variance than each element separately (P<0.001):-

$$DM_{1986} \text{ (t DM ha}^{-1}\text{)} = 2.37\ (\pm 0.200) + 0.012\ (\pm 0.003)\ N + 0.036\ (\pm 0.006)\ P$$

$$R^2 = 0.77$$

Taking an extra cut in late May-early June tended to reduce the early + hay cut total for T8 (400-R-R(EC)) compared with T7 (400-R-R), and this difference was significant in 1987. In 1988, when the hay-stage cut was delayed until August giving an extra months growth between these two cuts, the effect was reversed, though not significantly.

There was no significant treatment effect within the seasonal series (T5-7,9-13), despite large differences in the amount of N applied in spring. This was almost certainly due to the overriding effect of applying P and K in spring to all these treatments. These amounts were higher than those for T2 (0-R-R) for example, because yields were higher in the aftermath phase each year. There was no response to N above 200 kg N ha^{-1} year^{-1}, with DM production from T7 (400-R-R) lower than from T6 (200-R-R), both at hay cutting and in the aftermath phase (Table 3.9 and Figure 3.8). Treatments T9 (0/100-R-R) and T10 (0/200-R-R) were the lowest yielding within the seasonal series at hay cutting, but were exceeded in aftermath production only by T6 (which received considerably more K during this phase). T10 was significantly more productive in the aftermath phase than either T7 (200/200-R-R) or T13 (100/200-R-R), both of which received the same amount of N after hay cutting with no overall difference in the amount of P and K applied.

Aftermath growth produced much less herbage DM than at hay cutting with all treatments, although fertilizer response was proportionately greater. This effect was accentuated by a progressive decline in output from T1 control plots (0-0-0) over the four years, both in absolute terms and relative to other treatments. The difference between T1 and T2 (0-R-R) was marginal in 1986 but highly significant by 1989. These effects were parallelled by a progressive decline in herbage K concentration, described later.

High rates of P and K applied with N greatly increased aftermath output compared

with replacement rates (Table 3.9). Differences were very significant ($P<0.001$) for both treatment T17 (100-75-R) and T18 (200-75-R), with the difference between T19 (200-75-200) and T18 (200-75-R) also highly significant ($P<0.001$).

There was no significant treatment effect for total annual DM production within either the Seasonal (T5-7,9-13)or the Early-v-standard cut (T7,8) series. Overall, all fertilizer treatments within the Main series (T1-6) increased annual DM production very significantly compared with T1 control ($P<0.001$), and treatments T4-6 (50-R-R to 200-R-R) all increased output significantly compared with T2 (0-R-R). Where no P was applied (T14, 100-0-R, and T15, 200-0-R), total annual DM output did not differ significantly from T1 control (Table 3.9). The significant yield increments between T2 (0-R-R) and these two treatments can be attributed to the replacement P applied to T2, since differences in the amount of K applied were negligible. Applying 75 kg P ha^{-1} with N at 200 kg ha^{-1} (T18) increased mean DM yield by 11.1% compared with T6 (200-R-R, $P<0.001$), and increasing K application to 200 kg ha^{-1} increased the difference to 31.4%.

Regression analysis on four-year treatment means showed a significant linear response to N with treatments T2-6 (0-R-R to 200-R-R) for hay DM ($P<0.01$, df=3), aftermath production ($P<0.01$) and total annual DM output ($P<0.001$). When the T7 (400 kg N ha^{-1}) means were included the relationship became curvilinear, with a quadratic model accounting for a high proportion of the variance for all three variables (Figure 3.8).

N response in grass swards usually follows an inverse quadratic model (Morrison *et al.*, 1980; Sparrow, 1979). Such a model fitted these data well, but predicted a very sharp peak in yield between the two highest rates (200 and 400 kg N ha^{-1} year^{-1}). Since there were no intermediate data points to support this portion of the curve, the more conservative quadratic equations shown in Figure 3.8 were used.

Addition of P or K to regression models of DM against N gave no improvement in the model for treatments within the Main series (T1-6), and standard errors for estimates

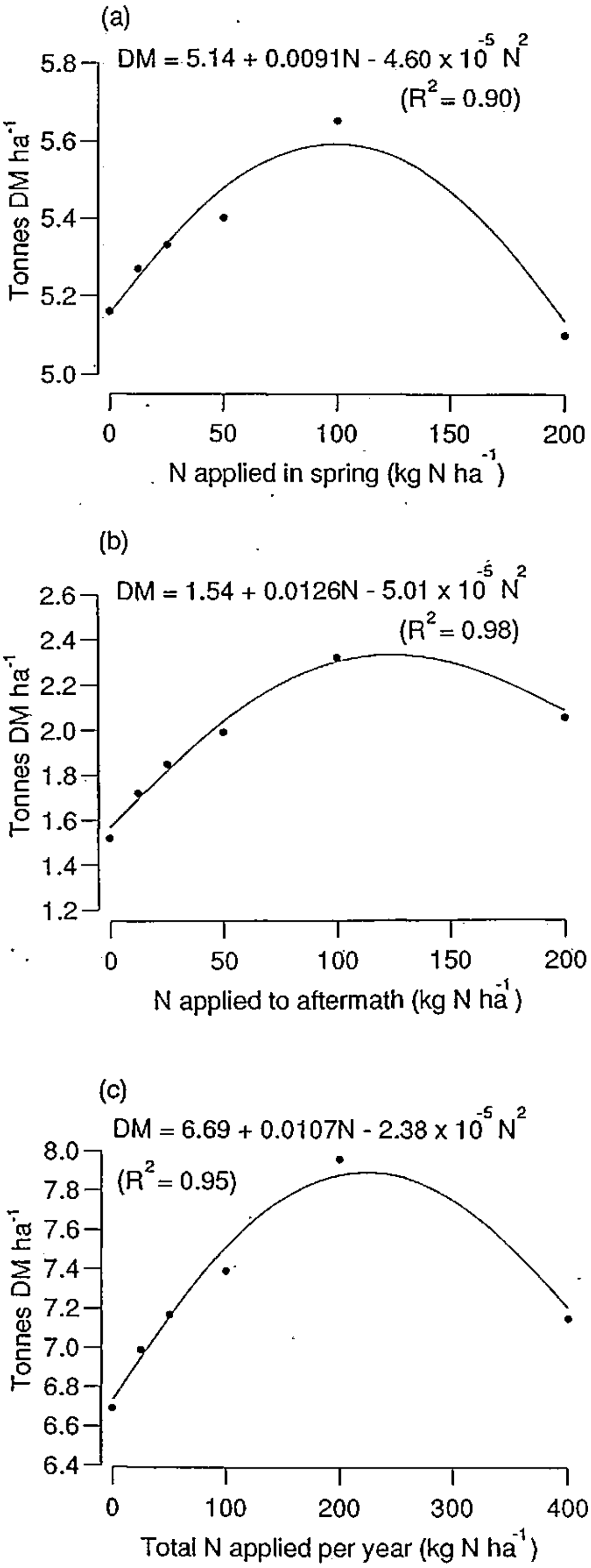


Figure 3.8. Dry matter (DM) response to applied nitrogen at hay cutting, in aftermath growth and total annual DM for treatments receiving replacement rates of P and K (treatments T2-7) in the SP experiment. Curves are fitted to the quadratic equations shown.

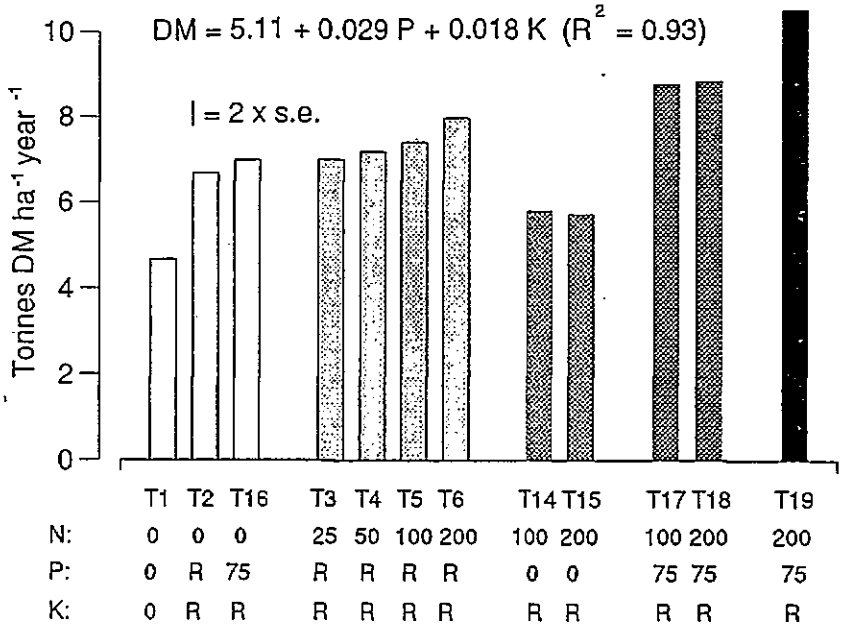


Figure 3.9. Total annual DM yield averaged over 4 years 1986-89 from treatments within the Main + P,K series in the SP experiment.

of the N coefficient were very large for hay, aftermath growth and total annual DM output. P and K together accounted for high proportions of the variance in data from the Main + P,K series (T1-6,14-19) when N was excluded, and addition of N gave no further improvement. A multiple regression equation for the effects of P and K on total annual DM yield for this series is shown with Figure 3.9.

The N, P and K content of herbage.

The N concentration in herbage was consistently highest in plots receiving the highest N rate (400 kg N ha^{-1} year^{-1}), both at the hay stage and in aftermath growth (Table 3.10). Taking an extra, early cut (T8) gave a significantly higher mean N content for cuts 1 and 2 each year compared with hay cutting with all other treatments. Averaged over four years, apparent recovery of applied N (i.e. the difference in herbage N harvested compared with that taken from T2, as a percentage of the amount applied) was increased from 21% for T7 to 34% for T8 (Table 3.11). The N content of hay from other treatments was closely related to the amount of N applied, but was highest for treatment T15 (200-0-R) in all years except 1988. Efficiency of N recovery was significantly increased by applying the high rate of P compared with replacement rates, with T17 (100-75-R) giving the best recovery rate at 39%, followed by T19 (200-75-200) at 35%. These values compare with rates of 23% for T5 (100-R-R) and 21% for T6 (200-R-R), with improvements in uptake attributable to

Table 3.10. Concentration (%) of nitrogen, phosphorus and potassium in herbage (mean 1986-89) in the SP experiment.

Treatment			Hay cut			++Aftermath cuts		
No.	N-P-K code		N	P	K	N	P	K
T1	0-0-0		1.46	0.12	0.66	2.28	0.14	0.76
T2	0-R-R		1.30	0.12	0.85	2.51	0.24	1.26
T3	25-R-R		1.34	0.14	0.89	2.74	0.22	1.44
T4	50-R-R		1.36	0.11	0.88	2.86	0.24	1.41
T5	100-R-R		1.47	0.12	0.78	3.10	0.23	1.32
T6	200-R-R		1.60	0.10	1.17	3.34	0.17	1.86
T7	400-R-R		2.16	0.11	0.99	3.73	0.18	1.39
T8	400-R-R (EC)	1st cut	2.87	0.19	1.38			
		2nd cut	3.25	0.16	1.02			
		mean++=	2.95	0.18	1.27	3.71	0.22	1.48
T9	0/100-R-R		1.31	0.12	0.91	3.37	0.23	1.50
T10	0/200-R-R		1.32	0.11	0.94	3.62	0.18	1.39
T11	50/100-R-R		1.48	0.11	0.86	3.42	0.19	1.35
T12	50/200-R-R		1.47	0.11	0.76	3.68	0.18	1.31
T13	100/200-R-R		1.68	0.10	0.86	3.69	0.18	1.49
T14	100-0-R		1.66	0.10	1.07	2.82	0.12	1.15
T15	200-0-R		1.91	0.12	0.91	3.25	0.16	1.20
T16	0-75-R		1.30	0.32	0.93	2.44	0.41	1.20
T17	100-75-R		1.43	0.30	0.93	3.04	0.39	1.30
T18	200-75-R		1.64	0.30	0.83	3.50	0.40	1.22
T19	200-75-200		1.47	0.27	1.35	3.30	0.40	2.14
s.e.			0.043	0.008	0.043	0.049	0.019	0.080

All treatment effects significant at P<0.001 in ANOVAs
++ Means weighted to take account of differences in DM yield between individual cuts.

differences in DM yield rather than N concentration.

The N concentration of aftermath herbage was generally much higher than at hay cutting and increases with applied N were greater (Table 3.10). Consequently, N recovery rates for some treatments were higher during this period, despite much lower DM yields.

Recovery rates were low for treatments receiving the highest N rate at 18.9% and 20.9% for treatments T7 (400-R-R) and T8 (400-R-R(EC)) respectively, but N recovery within the Main + P,K series ranged from 39.1% for T6 (200-R-R) to 82.0% for T17 (100-75-R)

Table 3.11. Yield of herbage N averaged over four years 1986-89 in the SP experiment.

Treatment			Mean N yield 1986-9 (kg N ha^{1})		
No.	N-P-K code		Hay cut	Aftermath	Total
T1	0-0-0		55.3	21.8	77.1
T2	0-R-R		66.2	38.6	104.8
T3	25-R-R		68.8	47.7	116.5
T4	50-R-R		71.6	52.9	124.5
T5	100-R-R		77.6	61.5	139.2
T6	200-R-R		87.5	77.7	165.3
T7	400-R-R		107.3	76.3	183.5
T8	400-R-R (EC)	1st cut:	78.6		
		2nd cut:	55.4		
		Total:	133.9	80.4	214.3
T9	0/100-R-R		60.9	74.8	135.7
T10	0/200-R-R		62.2	81.0	143.7
T11	50/100-R-R		79.8	73.7	153.4
T12	50/200-R-R		77.3	76.4	153.7
T13	100/200-R-R		86.9	75.3	162.2
T14	100-0-R		73.0	40.5	113.5
T15	200-0-R		84.3	42.1	126.4
T16	0-75-R		65.5	41.9	107.4
T17	100-75-R		85.7	79.6	165.3
T18	200-75-R		97.2	99.3	196.5
T19	200-75-200		101.0	115.1	216.1
s.e.			3.38	2.53	4.46

All treatment effects significant at P<0.001 in ANOVAs.
[++] Means weighted to take account of differences in DM yield between individual cuts.

(Table 3.11). However, since N recovery in hay had been poor, soil N residues will have been high after the hay cut, and these percentages probably overestimate recovery in relation to the amounts available.

Total annual N recovery was very significantly increased (P<0.001) by all treatments receiving the high rate of P compared with replacement P at equivalent N levels (Table 3.11), representing 46% and 61% of that applied for T18 (200-75-R) and T17 (100-75-R) respectively compared with 30% for T6 (200-R-R), and 34% for T5 (100-R-R). N recovery was further increased by addition of high rates of K in T19. By contrast, treatments receiving no P but with replacement K recovered very small proportions of applied N (9-11%). Incorporating an early cut with 400 kg N ha^{-1} $year^{-1}$ and replacement P and K (T7 v T8) significantly increased overall N recovery by 30.8 kg N ha^{-1} (from 19.7% to 27.4%).

Herbage P concentration was generally low at hay cutting but was significantly increased both by applying the high P rate and by taking an extra, early cut, T8 (Table 3.10). As with N, levels of P were higher in aftermath growth, with significant differences between T1 (0-0-0) and T2 (0-R-R) each year (attributable to P replacement), as well as those caused by applying the high rate of P. P concentration in aftermath herbage from treatments T2 (0-R-R) to T13 (100/200-R-R) was generally higher in 1986 than in following years, reflecting the comparatively high flat rate of 14 kg P ha^{-1} applied for replacement in that year.

The K concentration of aftermath herbage was also higher in general in 1986 than other years. However, differences at hay cutting between treatment T19 (200-75-200) and others, attributable to applying the high rate of K, were smaller than those for P caused by high rate P application. K concentration on T1 (0-0-0) declined from 0.83% in 1986 to 0.50% in 1989 for hay and from 1.06% to 0.43% for aftermath growth. There was no corresponding trend in P concentration.

Apparent P recovery rates at hay cutting (calculated relative to T1, 0-0-0), were comparable to those for N (calculated relative to T2, 0-R-R) at 36% for all three treatments T17-19, and ranged from 17% to 65% where P was applied at replacement rates. P recovery rates from aftermath growth were low, ranging from 15% (T16, 0-75-R) to 33% (T19, 200-75-200).

The proportion of applied K apparently recovered at hay cutting was much higher than either N or P (80% to 106% for treatments T2-6, excluding 1986 when these treatments received no P or K in spring). Taking an extra cut in spring significantly increased the amount of K harvested (T8 v T7). K recovery was generally lower in aftermath growth than at hay cutting, ranging from 26% to 52% for treatments T2-6.

Recovery of the high K treatment was high in the aftermath compared to other treatments, and mean annual K recovery was equivalent to 68% of the total applied each year.

Soil P and K residues in March 1990.

Plots of treatments T1, T16, T18 and T19 were sampled for available soil P and K. The mean extractable P concentration of soils from T16, T18 and T19 soils, all of which had received 75 kg P in each of the previous four years, was very significantly ($P<0.001$) higher than that of T1 (0-0-0), and that of T16 soil significantly higher than T19 with T18 intermediate (Table 3.12). These values closely mirror small (and non significant) differences between these three treatments in the amounts of P harvested in 1989, as well as large differences between each of these treatments and T1.

Table 3.12. Concentrations of phosphorus and potassium in dry, sieved soil sampled on 28 March 1990 from plots of a subset of treatments in the SP experiment.

Treatment		Phosphorus	Potassium
No.	N-P-K code	(mg P l^{-1} soil)	(mg K l^{-1} soil)
T1	0-0-0	3.8	103.0
T16	0-75-R	30.7	109.7
T18	200-75-R	24.0	97.5
T19	200-75-200	20.5	95.7
s.e.		2.59 **	7.55
Mean T16,18,19		25.1	100.9
s.e.d. T1 v T16,18,19		1.97 ***	8.57

Asterisks denote significance of treatment effects in ANOVA:
** = $P<0.01$; ** = $P<0.001$ (degrees of freedom = 6)

Converting P concentration to approximate amounts per hectare (from the bulk density of fresh soil, and a measure of the weight to volume ratio of dried sieved soil), gave means of 1.2 kg P ha^{-1} for T1, 9.5 kg ha^{-1} for T16 and 6.3 kg ha^{-1} for T19. The values for treatments T16-19 represent only small fractions of the apparently unrecovered portions of the P applied in 1989, which were 57.6 kg P ha^{-1} for T16 and 53.5 kg ha^{-1} for T19.

Table 3.13. *In vitro* digestibility (DOMD) and ME value (MJ kg^{-1} DM) of herbage harvested, mean of four years 1986-89 in the SP experiment.

Treatment			Hay cut		Mean^{++} of aftermath cuts	
No.	N-P-K code		DOMD	ME value	DOMD	ME value
T1	0-0-0		49.7	8.0	58.0	9.7
T2	0-R-R		48.0	7.7	59.9	10.1
T3	25-R-R		49.7	7.9	60.7	10.3
T4	50-R-R		47.8	7.7	60.7	10.4
T5	100-R-R		46.8	7.6	62.1	10.7
T6	200-R-R		48.6	7.9	61.9	10.9
T7	400-R-R		48.7	8.3	62.8	11.2
T8	400-R-R(EC)	1st cut	61.0	10.4		
		2nd cut	59.8	10.5		
		Mean^{++} =	60.0	10.4	62.7	11.2
T9	0/100-R-R		48.2	7.7	62.9	11.0
T10	0/200-R-R		48.2	7.7	63.7	11.3
T11	50/100-R-R		47.0	7.6	62.2	11.0
T12	50/200-R-R		48.5	7.8	63.1	11.2
T13	100/200-R-R		48.2	7.9	62.4	11.1
T14	100-0-R		50.6	8.2	59.1	10.1
T15	200-0-R		50.5	8.4	60.9	10.7
T16	0-75-R		49.8	7.9	59.2	9.9
T17	100-75-R		48.2	7.8	61.3	10.6
T18	200-75-R		47.1	7.7	62.0	11.0
T19	200-75-200		48.0	7.8	62.9	11.0
s.e.:-						
T1-6 (10)			0.70	0.11	0.36 ***	0.06 ***
T1-6,14-19 (22)			0.65 **	0.10 ***	0.50 ***	0.08 ***
T5-7, 9-13 (14)			0.62	0.09 **	0.30 *	0.04 ***
T7,8 (2)			0.63 **	0.10 **	0.77	0.13
All trs. (36)			0.61 ***	0.09 ***	0.49 ***	0.08 ***

Asterisks denote significance of treatment effects in ANOVA:
* = P<0.05; ** = P<0.01; *** = P<0.001 (degrees of freedom in brackets)
$^{++}$ Means weighted to take account of differences in DM yield between individual cuts.
See Table 3.1 for description of treatments

There was no significant difference in extractable K content between any of the soils, despite the high rate of K applied in previous years to T19 (200-75-200) plots.

Herbage digestibility and ME value

Values for DOMD were much higher in aftermath growth than in herbage cut for hay, except for each of the first two cuts of treatment T8 where DOMDs were comparable with aftermath growth (Table 3.13). The mean digestibility of material from these two cuts was significantly greater than that taken from T7 plots at hay cutting ($P<0.01$), with a mean difference of 11.3 percentage units. With the remaining treatments, digestibility at cutting tended to be inversely related to DM yield. Values at hay cutting were lower overall in 1988 than other years (except for T8), reflecting the greater maturity of vegetation at the delayed harvest in that year.

Digestibility of aftermath growth tended to be inversely related to that at hay cutting, although the mean DOMD value for T8 (400-R-R(EC)) was high at both stages (Table 3.13). Treatment T19 (200-75-200) produced the highest mean aftermath DOMD values within the Main + P,K series, significantly higher than all other treatments except T5 (100-R-R), T6 (200-R-R) and T18 (200-75-R). Within the Main series (T1-6, 0-0-0 to 200-R-R), all treatments significantly increased digestibility compared with T1 control ($P<0.001$ for T5,6, $P<0.01$ for T3,4), with DOMD values for treatments T2-6 (0-R-R to 200-R-R) significantly correlated with applied N ($r=0.84$; df=4).

Because both DOMD and crude protein (6.25 x N) contents were included in the calculation of metabolizable energy (ME) values (Table 3.13), there were some notable differences compared with the trends in DOMD. Treatment T8 (400-R-R(EC)) gave the highest four-year mean ME value at 10.4 MJ kg^{-1} compared with others at hay cutting. Among the other treatments, relatively high mean ME values were given by treatment T7, 400-R-R (8.3 MJ kg^{-1}, attributable to high %N values) and by T14 (100-0-R) and T15 (200-0-R), 8.2 and 8.4 MJ kg^{-1} respectively, each due to both high DOMD values and relatively high N concentration. The T1 control mean ME value was very significantly lower than any other treatment within the Main series ($P<0.001$), and T16 (0-75-R) was the only treatment within the Main + P,K series not significantly higher than T1.

ME production per hectare

Trends in ME output were broadly similar to those in DM yield, but with some important

Table 3.14. Metabolizable energy production (GJ ME ha^{-1}), mean of four years 1986-89 in the SP experiment

Treatment No.	N-P-K code		Hay cut	Total of aftermath cuts	Total of all cuts
T1	0-0-0		30.0	8.8	38.8
T2	0-R-R		39.2	15.3	54.5
T3	25-R-R		41.3	17.7	59.0
T4	50-R-R		40.4	19.1	59.5
T5	100-R-R		40.8	21.3	62.1
T6	200-R-R		44.3	25.1	69.4
T7	400-R-R		42.0	22.9	64.8
T8	400-R-R (EC)	1st cut	28.4		
		+ 2nd cut	19.3		
		Total =	47.6	24.0	71.6
T9	0/100-R-R		36.4	24.3	60.7
T10	0/200-R-R		36.5	25.3	61.8
T11	50/100-R-R		41.5	23.4	64.9
T12	50/200-R-R		41.6	23.3	64.9
T13	100/200-R-R		41.0	22.7	63.7
T14	100-0-R		36.2	14.2	50.4
T15	200-0-R		36.9	13.8	50.7
T16	0-75-R		40.4	16.9	57.2
T17	100-75-R		47.6	27.6	75.2
T18	200-75-R		46.4	31.1	77.5
T19	200-75-200		54.1	38.3	92.5
s.e.:-					
T1-6 (9)			0.89***	0.59***	1.10***
T1-6,14-19 (22)			1.97***	0.75***	2.31***
T5-7,9-13 (14)			1.63*	0.72*	1.81
T7,8 (2)			1.74	1.04	0.70*
All trs (36)			1.85***	0.73***	2.14***

Asterisks denote significance levels for treatment effects in ANOVA:
* = P<0.05, ** = P<0.01, *** = P<0.001 (degrees of freedom in brackets)

See Table 3. 1 for description of treatments

differences related to the differences in ME value noted above. The most striking of these were the contrasts between the T7 (400-R-R) and particularly T8 (400-R-R(EC)) means and other treatments at hay cutting (compare Tables 3.9 and 3.14). Treatment T8 gave one of the lowest values for mean hay DM output (Table 3.9), but in terms of ME output, was exceeded only by T19 (200-75-200), and only by T17-19 (100-75-R to 200-75-200) in terms of annual total ME production (Table 3.14).

The mean increase between T1 (0-0-0) and T2 (0-R-R) in hay output was marginally greater in terms of DM yield than ME production but, for aftermath growth, was much greater in terms of ME output (67.0% for DM, 93.9% for ME). The annual output response to applied N within treatments T2-6 (0-R-R to 200-R-R) was greater in terms of ME than DM production (Tables 3.9 and 3.14).

3.4. DISCUSSION

PRODUCTIVITY AND RESPONSE TO FERTILIZERS

Comparisons with farm study data

The total UME outputs achieved in the LS experiment (40.6 to 61.7 MJ ha$^{-1)}$ compare favourably with a mean of 40.3 GJ ha^{-1} recorded for non-suckler beef farms in a National Farm Study, where the average N use was 66.2 kg N ha^{-1} per year for that category (Forbes *et al.*, 1980). On the other hand, Peel *et al.* (1988) recorded a higher mean output of 72 GJ ha^{-1} on dairy farms in the South West of England, where the average N use was 232 kg N ha^{-1}. The corresponding estimate of 64 GJ ha^{-1} made by Peel *et al.* from data published by the Milk Marketing Board (Poole *et al.*, 1984), where N use averaged 263 kg ha^{-1}, is closer to the mean of 61.7 GJ ha^{-1} recorded for the N_{200} treatment in this experiment.

However, caution is needed in comparing the results of controlled experiments with those from whole farm studies. The put-and-take grazing system used each year during the aftermath phase of the LS experiment is a standard experimental technique for measuring potential animal production from grazed pastures (Wilkins *et al.*, 1983; Tallowin *et al.*, 1990). It involves frequent adjustment of stocking rates in order to maintain an optimum vegetation height (Wilkins *et al.*, 1983). The technique relies on the availability of spare grazing which is not taken into account in calculations of production from the plots, whereas values for UME from farm studies are derived from input and output data taken on a whole farm basis (Forbes *et al.*, 1980; Peel *et al.*, 1988). Doubts have been expressed about the applicability of the results of put-and-take grazing experiments to 'real life' situations (Snaydon,1987b). The difference between the level of control possible under put-and take grazing and that achievable in practice may be particularly great in areas like the Somerset peat moors, where many fields are remote and relatively inaccessible, and ownership of them is very fragmented (see Chapter 1).

Furthermore, values for UME produced from hay were based upon hay as removed from the field. These values therefore over-estimate the ME which livestock would gain from the hay, since no allowance was made for any wastage that might occur during feeding. Hay UME values should therefore be seen as utilizable, rather than utilized, ME. In view of the foregoing reservations, it is safer to compare experimental results with data from other controlled experiments. Unfortunately, few experiments have used both hay making and aftermath grazing, and no data of this kind for peat soils could be found for the review in Chapter 2.

Baseline productivity of meadows at Tadham Moor

Hay yields obtained from unfertilized plots in these experiments indicate a high baseline productivity compared with species-rich vegetation elsewhere. Control plots in the LS experiment averaged 5.1 t DM ha^{-1} at cutting and 4.1 t DM ha^{-1} after hay making, although yields in the SP experiment were somewhat lower at 3.8 t DM ha^{-1}. Yields of hay as made (i.e. probably about 85% DM) in unfertilized species rich meadows typically range from 1.8 t ha^{-1} (Elliott *et al.*, 1974) to 3.0 t ha^{-1} (Lawes and Gilbert, 1858)(see Chapter 2, Table 2.1). Yields at cutting have ranged from 2.0 t DM ha^{-1} (Bobbink, 1991) to 4.2 t DM ha^{-1} (Younger and Smith, 1993). At 5.1 t DM ha^{-1}, the yield at cutting in the LS experiment was closer to the aggregate yields for 2 cuts from a range of species rich meadows on mineral soils (i.e. 2.2 to 5.4 t DM ha^{-1}, see Table 2.3). Hay yields on peat soils covered a wide range of between 1.0 and 4.5 - 5.0 t DM ha^{-1} at cutting, apparently depending mainly upon P availability (Korkman, 1976; van Vuuren and Verhoevan, 1985; Vermeer, 1986).

At 40.6 GJ ha^{-1}, output from nil N control plots in the LS experiment was little lower than the value of 46 GJ ha^{-1} found by Tallowin *et al.* (1990) in a sward of lower species diversity in the same region (south-west of England) and receiving no fertilizer N, despite those swards receiving high levels of P and K. However, the pastures studied by Tallowin *et al.* (1990) were grazed continuously from April to October. As with comparisons between controlled experiments and farm studies, caution is needed in comparing UME data from continuously grazed pastures with data from hay making followed by aftermath grazing, since the latter system is closer to the optimum defoliation strategy for maximum yield (Leafe *et al.,* 1974).

Effects of P and K on productivity and N response

Individual steer growth rates at aftermath grazing were much higher in the LS experiment than those achieved by Tallowin *et al.* (1990) with similar animals on continuously grazed permanent pasture in Devon (e.g 1.12 vs 0.68 day^{-1} at 200 kg N ha^{-1} year^{-1}). However, these high individual growth rates could not compensate for the lower stocking rates achieved at the same level of N input. Although only about 40% of the 74 GJ ha^{-1} quoted by Tallowin *et al.* was produced in the period equivalent to aftermath grazing in this experiment, overall response to N was greater, so that UME output was much higher at 200 kg N ha^{-1} year^{-1} in that experiment than at Tadham Moor. Furthermore, Tallowin *et al.* estimated maximum output occurring at about 500 kg N ha, with UME response increasing approximately linearly up to about 250-300 kg N ha^{-1}. This corresponds broadly with the generalised herbage yield response to N of permanent and resown pastures under regular cutting management (Morrison *et al.*, 1980; Hopkins *et al.*, 1990). By contrast, there was little additional response to N rates above 50 kg ha^{-1} in the LS experiment at Tadham Moor, where P and K were applied at 'replacement' rates only.

In the experiments of Morrison *et al.* (1980), Hopkins *et al.* (1990) and Tallowin *et al.* (1990), care was taken to ensure that P and K did not limit N response on any of the plots. The review of a wide range of fertilizer experiments in Chapter 2 showed that P is seldom limiting in loam or clay soils, particularly if P has been applied in the past, although K deficiency is more common (Holmes, 1951; Castle and Holmes, 1960; Reith *et al.*, 1961, 1964; Widdowson, *et al.*, 1965; Heddle, 1967; Heddle and Crooks, 1967). The Palace Leas experiment showed no overall response to P initially, but regression analysis on data reported by Elliott *et al.* (1934) did show a significant N x P interaction. The magnitude of this interaction increased in later years when data also showed an overall response to P, implying a continual depletion of soil P where P was not applied (Pawson, 1960; Arnold *et al.*, 1976). P deficiency is common on calcareous soils (Olsen, 1953; Norman, 1956; Willems *et al.*, 1993), whilst P availability in lowland peat soils is very variable, usually depending upon the P content of seepage water and the drainage status of the soil (see Chapter 2). K is much more easily leached than P and K availability is often low in organic soils (Brady, 1990; Cole, 1970; Munro *et al.*, 1973).

The DM response to P and K treatments in the SP experiment show clearly that N response at Tadham Moor was limited by the small amounts of P and K applied under the 'replacement' strategy. Increasing P application rates to 75 kg P ha^{-1} and applying K at 200 kg ha^{-1} increased DM yield by 31% at 200 kg N ha^{-1}, compared with replacement P and K only, giving a total of 10.5 t DM ha^{-1} $year^{-1}$. This figure corresponds with a yield of 10.8 t DM ha^{-1} $year^{-1}$ at 200 kg N ha^{-1} $year^{-1}$, estimated from the response curve derived by Hopkins *et al.* (1990) in a multi-site trial on permanent pastures under 8-weekly cutting over four years. Equivalent increases in UME output at N_{200} in the experiment reported here would give an extra 19.1 GJ ha^{-1}, giving a total of 80.8 GJ ha^{-1}, equivalent to the output from 400 kg N ha^{-1} recorded under continuous grazing by Tallowin *et al.* (1990).

However, it was not possible to define optimum levels of P and K for different rates of N in these experiments. Inclusion of a full N x P x K factorial series would have prevented the other objectives of the experiment being met, i.e. comparability between experiments and inclusion of the Seasonal and Early v standard cut series. Some conclusions about the adequacy or otherwise of the P and K rates used in the experiments can be drawn from the herbage concentrations of these elements relative to N (Knauer, 1966; Prins *et al.*, 1986). For example, guidelines presented by Knauer (1966) show that, for mature vegetation with CP at up to 10%, (i.e. 1.6% N, equivalent to the vegetation harvested at hay cutting in these experiments), P and K contents of less than 0.13% and 1.16% respectively indicate pronounced deficiencies, with values below 0.24% P and 1.5% K indicating limiting supplies. As noted in Chapter 2, these guidelines compare closely with those derived later by Prins *et al.* (1986), although the latter are more demanding of P and K at high N concentrations. The P concentrations recorded in the SP experiment therefore suggest severe deficiencies of P in hay for all treatments other than those receiving the high P rate, which provided an adequate supply. At a mean K concentration of 1.35%, even

vegetation receiving 200 kg K ha^{-1} $year^{-1}$ was apparently undersupplied with K during the spring, falling within the 'small deficiency' category described by Knauer. For younger pasture with a CP content of 15-20% (2.4-3.2% N), Knauer suggested that values above 0.37% for P and 2.1% for K indicate sufficiency, whilst values of less than 0.24% and 1.5% respectively suggest very pronounced deficiencies. Clement and Hopper (1968) also defined an indicator value for K of >2% for high yielding ryegrass where about 2.0 t DM were harvested at each cut. Aftermath growth in this experiment therefore appears to have been adequately supplied with P only by treatments incorporating the high P rate, and only the treatment which also included 200 kg K ha^{-1} (T19) supplied both elements adequately.

With adequate P and replacement K, the increase in total annual DM between 0 and 100 kg N ha^{-1} represented a response of 19.1 kg DM per kg N, although applying a further 100 kg N ha^{-1} per year gave no further yield increase unless the high rate of K was used. This response was much greater than that of 6.0 kg DM per kg N achieved with replacement P and K, but was close to that of 20.2 shown by Hopkins *et al.* (1990) between 0 and 150 kg N ha^{-1} in a multi-site trial on permanent pasture under 8-weekly cutting (3 cuts per year) with P and K non-limiting. Mean annual yield was 7.32 t DM ha^{-1} without N but with adequate P and K. This compares with means from this experiment of 6.69 t DM ha^{-1} for nil N plots with replacement P and K and 6.85 t DM ha^{-1} where the high P rate was used. The response curve shown by Hopkins *et al.* shows a yield of about 10.8 t DM ha^{-1} at 200 kg N ha^{-1}, which compares with 10.5 t DM ha^{-1} in this experiment. Thus it seems that up to 200 kg N ha^{-1} at least, the yield potential of these meadows differs little from the average for permanent pasture.

DM yield declined markedly between 200 and 400 kg N ha^{-1} applied with replacement rates of P and K. Although the shape of this response pattern is typical for grassland, maximum DM production is normally reached at much higher rates of about 450-625 kg N ha^{-1} (e.g. Morrison *et al.* 1980; Hopkins *et al.*, 1990; Tallowin *et al.*, 1990). This effect was probably caused by comparatively large amounts of N applied at once combined with a poor ability of plants to assimilate N due to inadequacies of P and K supply. Ammonium N appeared to be rapidly converted to nitrate N (nitrification) in these soils (see Chapter 4) and where comparatively large concentrations of unused N were present this may have resulted in increased acidity in the rooting zone due to the excess H^+ ions released in the oxidation of NH_4^+ ions to NO_3^-.

The high rates of both P and K used in this experiment correspond to recommended rates for grass cut for hay with two subsequent cuts, on soils with an index of 0 for each, i.e. the highest category of deficiency (MAFF, 1980). Recommendations for silage are higher at 100 kg K ha^{-1} (120 kg K_2O) for the first cut and 66 kg K ha^{-1} for each subsequent cut. It seems from these results that equivalent rates are needed for maximum N response under hay cutting in these meadows.

Evidence for mineral depletion without aftermath grazing

Control plot yields declined progressively between 1986 and 1989 in the SP experiment and this decline continued through 1990 and 1991 during a second phase of the experiment (Tallowin and Thomas, unpublished). Differentials in K concentration and K yield between control (0-0-0) plots and all others were maintained in both these later years, despite no fertilizer having been applied to any plot since 1989 This suggests a mineral depletion on control plots due to repeated removal of herbage with no replacement either in the form of mineral fertilizer or by aftermath grazing. However, this hypothesis is only partially supported by data from soil sampling in May 1990. Although very significant differences in soil P resulted from using the high P rate, there was no such difference in soil K, even on plots which had received the highest K rate. Clement and Hopper (1968) have described the difficulties in using soil analyses to predict K availability in mineral soils, where this is very dependent upon the rate at which exchangeable K becomes available to plants from usually large non-exchangeable reserves. A similar situation may have existed in the peat soils at Tadham Moor, although total K reserves will have been lower than in mineral soils (Cole, 1970; Munro *et al.*, 1973; Brady, 1990).

The management of the control plots in the LS experiment was essentially the same as that practised over many years before both experiments started, i.e. hay cutting followed by aftermath grazing by cattle with no fertilizers used. Grazing would allow most of the nutrients taken up by aftermath growth to be returned in animal excreta, with most readily available for continued growth (During *et al.*, 1973; Jarvis *et al.*, 1989a). Levels of P and K available on control plots in the SP experiment in March 1990 were lower than on unfertilised plots in the LS experiment, with P at 3.8 mg l^{-1} compared with 5.7 mg l^{-1}, and

K at 103.0 mg l^{-1} compared with 146.3 mg l^{-1}. However, no soil samples were taken specifically from the SP experiment before the experiments started, so it was not possible to tell if soil in this area contained less P and/or K than the remainder of the experimental site from the outset. This is a possibility since the location for the SP plots was chosen largely on the strength of an even higher species richness than remaining areas, as shown by a preliminary botanical survey carried out in 1985 (Fuller, unpublished). This high species richness could have been a reflection of even lower nutrient availability relative to the rest of the site.

Seasonal variation in N application

DM production was affected little by varying the seasonal pattern of N application in the SP experiment, due to the overriding effect of replacing P and K in both spring and mid season. There were some mitigating effects on botanical change by applying most of the N to aftermath growth, notably with *P. lanceolata*, although all fertilizers reduced this species severely compared with control (see Chapter 5). But this minor ecological benefit would be outweighed by the much poorer recovery of N with these same treatments compared with others.

Fertilizer N recovery

The amounts of N recovered in herbage at hay cutting were low in the LS experiment compared to others (Morrison *et al.*, 1980) attributable partly to the lateness of the cut. Values were lowest in 1988, when harvesting was delayed by a month, at between 4% and 16% of that applied (compared to control plots), compared with 33-49% averaged over four years. These low N recovery rates may have contributed to the high N leaching risk in these meadows reported in Chapter 4. The efficiency of N use (the proportion of applied N apparently recovered in herbage) is obviously important both from environmental point of view and form a financial standpoint. More than 50% apparent recovery of applied N was achieved only by treatments which incorporated the high P rate. Apparent N recovery was low when 400 kg N ha^{-1} was applied; but taking an extra cut in late May greatly increased N efficiency, particularly in 1988, when the delayed hay cut allowed an extra month's accumulation of growth between the two cuts on the early cut treatment. A similar cutting regime, used when high P and K rates were applied, might have given even greater efficiency of uptake of all three macronutrients. Similarly, whilst cutting earlier than July reduces breeding success in ground nesting wading birds (Green, 1986), it may be useful where the aim is to deplete soil fertility in order to restore plant species diversity when fertilizer use has stopped. Further information on the effects of different hay cutting dates on DM yield and N recovery is given in Chapter 7.

Herbage digestibility

The digestibility (DOMD) and N content of aftermath herbage were both much higher than in hay, and both comparable with continuously grazed permanent pasture at the same time of year and receiving the same levels of N (Tallowin *et al.*, 1990). The DOMD value of herbage taken in May-June from the early cut (with 400 kg N ha^{-1}) was somewhat lower at 61% than that of 69% recorded in a silage cut by Tallowin *et al.* in late May with 120 kg N ha^{-1} applied in March, the latter being more typical of grass cut for silage (NIAB, 1987). Primary spring growth in these species-rich meadows may be of lower nutritive value than in agriculturally 'improved' swards dominated by perennial ryegrass, and seasonal changes in digestibility and nutritive value of semi-natural grasslands in general would benefit from further research (see also Chapter 7).

Losses during hay making

Hay making seldom took less than five days on any plot, and drying was undoubtedly hindered by humidity arising from the soil to a greater extent than might be expected in drier areas. However, losses of DM yield and quality during hay making were not excessive in the LS experiment, at about 20% of DM and 27% in terms of ME. ME losses of about 20% can be expected even with good silage-making technology (Wilkins, 1988).

Economic response to fertilizer application

Data from these experiments were used to calculate the economic implications of variations in fertilizer use (Wilkins, unpublished). As noted previously, there is a need for caution when using experimental data to predict output in a farming context, and the calculated margins are very susceptible to relative costs and returns. The following data are more valuable for comparative and illustrative purposes than to define absolute values for increased profit possible from fertilizer application.

Margins calculated over the cost of purchase of beef cattle and fertilizer, contract charges for fertilizer application and hay making and interest on working capital (Nix, 1990), increased from £170 ha^{-1} with no fertilizer to £223 ha^{-1} with 100 kg N ha^{-1} and replacement P and K. The margin was slightly lower at £211 ha^{-1} for 200 kg N ha^{-1} year^{-1}, unless higher P and K rates were used when the margin increased to £256 ha^{-1}. These calculations assumed that 10% and 30% increases in output were possible using higher rates of P and K, as in the SP experiment. These margins compared with a gross margin on farms of £208 ha^{-1} for finishing store cattle for the same period (Nix, 1990). Both absolute margins and differences between treatments are larger when calculations are made in terms of possible utilization of the herbage by dairy cows.

The data provide a useful framework for calculating the implications for farmers of restricting fertilizer use within the ESA and SSSIs in the area. At present up to 75 and 25 and 0 kg N ha^{-1} are allowed within ESA rules in the Somerset Levels for tiers 1, 2 and 3 payments of £120, £180 and £350 ha^{-1} respectively, though these payments cover several other restrictions on management, relating to reseeding, drainage, harrowing etc.. The levels of output response achievable with these N rates can be predicted from the response curves in Figure 3.3, given that these curves increasingly underestimate potential production at N rates above about 50 kg N ha^{-1} when higher rates of P and K are used.

EFFECTS OF VARIATION IN WATER TABLE ON PRODUCTION AND N RESPONSE

Spring growth and hay yield

There was no evidence that high water tables reduced hay yield on unfertilized plots within the range of water table levels encompassed between 1986 and 1990 and vegetation height in May was negatively correlated with water table depth on these plots. However, because the meadows are so level, most of the variation in water table depth was between years rather than between plots. It was therefore unfortunate that the first year of the experiment, when no P or K was applied until after hay making, was also the year when water tables were at their highest in spring. The resultant correlation between water table depth and amounts of P and K applied invalidated any attempts to relate water table depth to hay yield when data from fertilized plots were included.

The spring period is of primary concern because current ESA rules encourage farmers to maintain 'conditions of surface splashing' between 1 December and 30 April, with water levels in ditches kept at not more than 30 cm below mean field level for the rest of the year (Her Majesty's Stationary Office, 1992). The speed with which water tables will drop from May onwards will vary according to rainfall and evapo-transpiration rates. In most years, water tables are likely to be at least as high during May-July as they were in 1986 and July-October levels will probably be similar to those encountered in 1988 (see Figure 3.4).

Summer-autumn water tables

Where mid-summer water levels as high as those now required within the ESA rules have occurred in the recent past, they have usually been directly related to high rainfall, rather than to deliberate 'penning up' of water in ditches. Whilst the hydrology of the area is greatly affected by rainfall in surrounding higher areas, precipitation was also high at the site in the wet year of 1988, so that it was not possible to separate the effects of water table depth from those of rainfall in an overall analysis. This would not be the case where high water tables were maintained artificially, independent of variations in rainfall, in order to qualify for the ESA payment (i.e. by pumping water into as well as out of ditches). Under these conditions, hydrological and chemical processes within the soil could be significantly different from those operating under less controlled conditions.

Need for a purpose designed experiment

Production from aftermath grazing was apparently reduced in a wet year, and this seems to have been related to increased N losses from the soil (see Chapter 4). Some separation of the effects of rainfall and water table depth was possible in the analysis of N loss during aftermath grazing in Chapter 4, but the need to rely on temporal variation in water table depth was a serious weakness in all the water table analyses. This argues strongly for a purpose-designed experiment, where spatial differences in water table depth can be maintained. Such an experiment has already begun at the Tadham Moor site, where two contrasting water table regimes have been established. Regular monitoring of water table depth and botanical and productivity measurements are being carried out. Analyses of soil N, denitrification, P, K and pH measurements would also be very valuable but are, unfortunately, unlikely to be possible within the current budget (J. Tallowin, personal communication).

3.5. CONCLUSIONS

Data from these experiments give a valuable indication of the relative increase in output attainable by using fertilizers in these meadows. Although P and K availability limit response to applied N, the productivity without fertilizers is relatively high compared with similarly species-rich vegetation on other soil types. Hay yields from unfertilized plots were equivalent to some of the best achieved in unfertilized vegetation on lowland peats elsewhere. This suggests that supplies of P and K to the soil, presumably from seepage and occasional flood water and maintained to some extent by aftermath grazing, are adequate to support a moderate level of mineralization and plant utilization of organic N resources. Small additions of inorganic P and K (i.e. replacement rates) allow further utilization of organic N, resulting in a significant yield response. Further inputs of both N and P may be necessary to achieve significant additional increases in yield and the full yield response to applied N cannot be realised unless high rates of of both P and K are applied.

These results also show that fertilizer response is not constrained by the species richness of the vegetation in these meadows, probably because the botanical composition changes rapidly in response to fertilizer application to dominance by grasses responsive to high soil fertility (see Chapter 5).

3.6. SUMMARY

Results from two experiments are reported in this Chapter. In the first, the large scale (LS) experiment, output from hay cut after 1 July each year and from beef production at aftermath grazing was measured over a total of four years. In a supplementary exercise, productivity and nitrogen response data from this experiment were related to temporal and spatial variations in water table depth. The second, small plot (SP) experiment, investigated the effects of fertilizer nitrogen (N), phosphorus (P) and potassium (K) on herbage production. Swards were cut after 1 July each year, followed by one or two aftermath cuts, with no grazing during the course of the experiment. Dry matter (DM) yield at cutting, metabolizable energy (ME) production and recovery of N, P and K were measured over four years.

Total utilized metabolizable energy (UME) output in the LS experiment averaged from 40.6 GJ ha^{-1} year^{-1} without fertilizers to 61.7 GJ ha^{-1} at 200 kg N ha^{-1} (N_{200}), the highest rate used, with about two thirds of this output from hay. When hay cutting was delayed until early August in a wet year, yield response to N was lost because fertilized swards had passed a peak in yield several weeks before harvest. N response was markedly curvilinear above about 50 kg N ha^{-1}, but data from the SP experiment suggested that the comparatively low replacement rates of P and K applied were limiting at higher N rates.

In the SP experiment, total annual DM production increased from 4.7 t ha^{-1} without fertilizers to 10.5 t ha^{-1} with 200 kg N, 75 kg P and 200 kg K ha^{-1} per year, and ME output from 38.8 GJ ha^{-1} to 92.5 GJ ha^{-1}. Applying moderate, replacement rates of P and K without N increased annual DM and N yields by 43% and 36% respectively, but DM response to N was modest unless high rates of P and K were used. Annual ME output and recovery of N, P and K were all significantly increased by taking an additional, earlier cut for silage, even though DM yield was unaffected.

There was no suggestion of any reduction in herbage growth caused by high water tables in the spring in the LS experiment. Indeed, vegetation height in May was negatively correlated with water table depth on unfertilized plots, where the lowest hay yields were recorded at water table depths of below 50 cm averaged over April-July. Neither hay yield nor aftermath cattle production were significantly related to water table depth on these plots, nor could variations in hay yield response to N (across replicates and between years) be related to variations in water table. However, cattle production response to fertilizer N from aftermath grazing showed a significant negative relationship with water table depth, largely due to very low productivity from unfertilized plots in the wet year 1988.

The potential output of these meadows is comparable to a wide range of less species-rich permanent pastures, so that species richness does not appear to constrain output or response to fertilizers. These data will help to estimate the financial implications of fertilizer restrictions within Sites of Special Scientific Interest and the wider Environmentally Sensitive Areas. The data suggest that there is no close relationship between water table depth and hay yield within the range of variation encountered at the site between 1986 and 1990. However, the results of experiments specifically designed to study this aspect must be awaited before firm conclusions can be drawn.

CHAPTER 4

THE EFFECTS OF INORGANIC FERTILIZER APPLICATION AND VARIATIONS IN WATER TABLE DEPTH ON LOSSES OF MINERAL NITROGEN.

4.1. INTRODUCTION

The previous chapter described (i) the increases in agricultural production obtainable by applying inorganic fertilizers to hay meadows on the Somerset Levels and similar areas, and (ii) the influence of variations in water table depth on productivity and nitrogen response. The studies described in this chapter investigated the influence of fertilizer N application and variations in water table depth on losses of mineral N from the soil. The relative sensitivity of the peat moors to losses of soil N by leaching and denitrification is discussed by comparison with data from other soil and grassland types.

The use of inorganic fertilizers is strongly implicated in the contamination of lakes and waterways by nitrate-nitrogen (Cooke, 1976). Nitrate leaching losses of over 150 kg N ha^{-1} are not uncommon in highly fertilized grassland (Ryden *et al.*, 1984; Macduff *et al.*, 1990a; Tyson *et al.*, 1993), but there is little detailed information on fluctuations in soil mineral N in wetland peat soils (see Chapter 2). The behaviour of inorganic fertilizers in the soils on the Somerset peat moors is especially significant in view of the potential damage that nitrate leaching could cause to the ecology of the ditches and watercourses through eutrophication (Lund, 1971; Stewart *et al.*, 1982).

Wet soil conditions and the high organic matter content of these soils would be expected to result in high denitrification rates, particularly where fertilizer N is applied (Firestone, 1982; see also review in Chapter 2, section 2.6). Nitrous oxide (N_2O), one of the end products of denitrification, is known to be damaging to the atmosphere both by ozone depletion and as a potent 'greenhouse' gas (Bouwman, 1990 - see also Chapter 1), so that the influence of fertilizer N application on denitrification rate is also of environmental significance.

In the studies reported in this Chapter, a range of fertilizer N levels was applied to meadows managed by hay cutting and aftermath grazing (i.e. the large scale (LS) experiment - Experiment 1). Soil mineral N status was monitored regularly over a 40 month period and denitrification rates were estimated during the autumn-winter of the latter two years. In a supplementary study, losses of soil mineral N and denitrification rates were related to fluctuations in water table depth.

These studies were not intended to produce a complete balance sheet of N inputs and outputs, nor to characterise in detail the physical and chemical processes involved in the cycling of N in this particular context. Thus, although losses by ammonia volatilization may have been significant while cattle were grazing the plots (Jarvis *et al.*, 1989b), these were not measured, nor were inputs by atmospheric deposition. The main emphasis was placed on fluctuations in soil mineral N and denitrification rate over the autumn-winter period, although an attempt was also made to relate losses of N during aftermath grazing to fluctuations in water table depth and rainfall. Both rainfall and water tables were generally at their highest and soil temperatures at their lowest between October and March, so the potential for N leaching would therefore be greatest during this period. Frequent water-logging and low soil temperatures during the autumn and winter would together have inhibited mineralization and nitrification, so that measuring the cumulative decline in soil mineral N during these months gave reasonable estimates of losses by leaching and denitrification. By estimating denitrification losses over the same period, leaching losses could be estimated by difference.

4.2. MATERIALS AND METHODS

The studies described in this Chapter were carried out in the large scale (LS) experiment (Experiment 1). Full details of fertilizer application and vegetation management were provided in Chapter 3, so only a brief summary is given here.

TREATMENTS, SWARD MANAGEMENT AND MEASUREMENTS MADE

Fertilizer application

Five levels of N, i.e. 0, 25, 50, 100 and 200 kg ha^{-1} year^{-1} (N_0 - N_{200}) were applied each year from 1986 to 1989 to plots of between 0.6 and 1.1 ha, laid out in three randomised blocks, although the N_{25} treatment was not included in any of the soil N assessments (Table 4.1).

Annual rates were split between two equal dressings, the first was applied as soon as ground conditions allowed after mid April and the second after the removal of a hay crop in July each year (August in 1988). Phosphate and potash were applied in mid season each year, at rates sufficient to replace the amounts removed in hay. No P or K was applied to control (N_0) plots.

Sward management

Swards were cut for hay in July each year (August in 1988) and the aftermath growth was grazed with 12-month old beef steers until mid to late October.

Soil sampling

Table 4.1 gives details of the soil sampling programme. On each occasion a 25 mm diameter corer was used and sampling sites were chosen randomly within each plot.

Samples of soil for mineral N content analysis were bulked to give a single sample for each depth on each plot, and these were crumbled by hand and mixed thoroughly before analysis. An incubation method, similar to that developed by Ryden *et al.* (1987),was used to determine denitrification rate. This used acetylene (C_2H_2) to inhibit the reduction of nitrous oxide (N_2O) during denitrification and measuring the amount of N_2O produced in a given time (Ryden *et al.*, 1979). Soil was taken to a total depth of 30 cm at each sampling site, in three separate 10 cm cores. These cores were placed intact in 1000 ml fruit jars, together with the cores from two other sampling sites, to give nine 10 cm cores per jar. Each jar was sealed with a polyacetyl lid fitted with a rubber gasket and incorporating two septum seal stoppers. Fifty cm^3 of acetylene was injected into each jar on the day of sampling, maintaining atmospheric pressure within the jar by venting through a hypodermic needle inserted into the second septum during injection. Each jar was then fitted into a separate hole in the ground and incubated for 22-24 hours. The exact incubation period and mean temperature were recorded for each batch of samples.

Sample analyses

A sub-sample of 99.5 - 100.5 g was taken at each mineral N sampling and analysed for mineral NH_4^+ and NO_3^- nitrogen by extraction in molar KCl solution (Whitehead, 1981). A second sub-sample was weighed fresh, dried overnight at 100°C and reweighed to obtain a measure of the moisture content of the soil. The extractant was passed through a segmented flow autoanalyser, combining a spectrophotometer to measure the ammonium content and a colorimeter to measure nitrate content after reduction of nitrate to nitrite on a cadmium column (Henriksen and Selmer Olsen, 1970). Any nitrite already present in the soil would therefore be included with nitrate in the analysis. However, this is unlikely to cause any significant inaccuracy, since nitrite usually occurs only transitorily and in small amounts in newly flooded soils as a primary breakdown product of nitrate in denitrification (Firestone, 1982).

Table 4.1. Soil sampling details.

	Soil mineral N	Denitrification
Sampling horizons: (cm from soil surface)	0-10, 10-20, 20-30	0-30
Number of field samples per horizon from each plot	15-21 (1)[1]	12 (4)[1]
Sampling frequency:	Monthly July-March 1987-1988 and 1989-90[2], August-March 1988-89, plus addititional assessments on 11 November '86, 19 March '87 and 8 June '89	1988-89 and 1989-90: Weekly mid October-late December, then monthly until March[2]
Treatments sampled:	N_0, N_{100} and N_{200} throughout, plus N_{50} from August 1988, except 8 June '89	N_0, N_{100} and N_{200} throughout

[1] Bracketed figures represent the number of samples per depth from each plot to which field samples were bulked for analysis

[2] No assessment in February 1990 due to flooding

After incubation of the denitrification samples, 2.5 cm^3 of air was removed from each jar and analysed for N_2O content on a Pye Unicam gas chromatograph, using a commercially available gas of known N_2O concentration in nitrogen (N_2) for calibration. The whole soil contents of each jar were then weighed before oven drying for moisture determination.

Water table, rainfall and temperature measurements

A total of 33 dipwells, each consisting of a 100 cm perforated plastic pipe 7.5 cm in diameter, was installed in late February 1986, sited in three parallel lines over the whole experiment area. This gave between one and three dipwells per plot, depending upon the size and shape of each plot. The depth of the water table below ground level was measured at weekly intervals between 1 April and 14 November 1986 and since April 1987. A topographic survey of the position of each of these dipwells in 1988 showed that ground level ranged from 2.13 to 2.49 m above Ordnance Datum.

Rainfall was measured continuously using a Meteorological Office Mk 2 tilting syphon gauge and weekly accumulated rainfall was also recorded in a simple bucket-type recorder.

Temperature recordings were made at 15-minute intervals from April 1987 onwards in air (inside a Stevenson Screen), at the soil surface (under-grass) and at 10 cm depth in the soil using a Grant 'Squirrel' automatic meter/logger. Table 4.2 gives monthly average soil temperatures at 10 cm.

DATA ANALYSIS

Soil mineral N and denitrification

Data for soil water nitrate concentration were analysed for treatment and depth effects by analysis of variance (ANOVA), on the basis of a randomised block split-plot design, with N treatments classed as main plots. A separate ANOVA was performed for each date using GENSTAT (GENSTAT V Committee, 1987). Because the spatial relationship between depths was the same across all plots, and particularly because each depth horizon was sampled at every sample point, little reliance could be placed on depth x treatment interactions, so that error estimates for these are not quoted.

The total amounts per hectare of NH_4^+ and NO_3^- N in the top 30 cm of soil were calculated for each plot on each sampling date and these values, as well as total mineral N (i.e. $NH_4^+ + NO_3^-$), were subjected to ANOVA for treatment effects. Polynominal contrasts (GENSTAT V Committee, 1987) were fitted to the data to investigate linear, quadratic and

Table 4.2. Monthly averages for daily minimum, maximum and mean soil temperatures (^oC) recorded at 10 cm depth between April 1987 and March 1990.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1987	Min	-	-	-	9.6	10.6	15.2	16.4	15.5	11.4	7.4	6.7	6.0
	Max	-	-	-	12.3	14.7	16.9	17.7	17.1	18.9	14.9	9.9	9.1
	Mean	-	-	-	10.8	12.8	15.8	16.8	16.1	14.3	10.3	7.8	8.0
1988	Min	4.7	3.5	5.5	6.8	11.6	13.9	14.0	15.2	13.7	10.1	3.2	5.5
	Max	7.8	8.3	10.4	14.0	17.2	17.9	17.2	16.9	15.0	13.0	8.8	9.2
	Mean	6.2	5.5	7.4	10.0	14.1	15.6	15.5	16.0	14.3	11.5	5.9	7.6
1989	Min	5.6	5.6	6.7	6.8	13.3	14.4	16.8	14.7	13.2	7.6	7.2	5.0
	Max	7.5	7.2	8.7	9.1	16.4	17.0	20.2	19.4	16.7	15.4	8.8	6.3
	Mean	6.7	6.6	7.7	8.1	15.0	16.2	18.8	17.1	15.6	12.1	8.1	5.9
1990	Min	6.1	6.7	7.0	-	-	-	-	-	-	-	-	-
	Max	7.7	8.4	9.3	-	-	-	-	-	-	-	-	-
	Mean	6.9	7.6	9.3	-	-	-	-	-	-	-	-	-

cubic responses to levels of applied N. Data for the amount of N denitrified per hectare per day at each assessment in 1988-9 and 1989-90 were treated similarly.

The total amount of N lost from each plot during the autumn and winter (October-March) was calculated for each of the three years 1987-8, 1988-9 and 1989-90. These figures were arrived at by accumulating the results of subtraction of each months value from that of the previous month, with minimum results constrained at zero. This assumes that any increase in soil N from one month to the next is the result of a net gain in mineralization over leaching and/or denitrification.

Total losses of N per hectare by denitrification between October and March in 1988-9 and 1989-90 were estimated. These were calculated firstly on a week by week basis, using the running mean rate of loss from two assessments, so that the rate for week 1 was taken as the mean of assessment 1 and 2, that for week 2 from assessments 2 and 3, and so on; similarly the amounts denitrified between late December and March each winter were calculated using running means of the monthly assessments during this period. Secondly, losses over the whole period were totalled for each plot and tested for treatment effects by analysis of variance, with fitted polynomial contrasts. In addition, total N losses for the winter 1987-8, 1988-9 and 1989-90 were tested for response to the levels of applied N both by linear and exponential regression, i.e. using the generalised formulae $y = a + bx$ and $y = a + b \times r^x$ respectively, where a, b and r are constants.

The effects of variation in water table (WT) depth

A procedure of correlation analyses followed by multiple regression, similar to that described in Chapter 3, was used to relate data for losses of soil N during aftermath grazing and over the autumn-winter period each year, from mid-summer 1987 to March 1990, to variations in rainfall and water table (WT) depth. Insufficient measurements of soil N were made in 1986 to allow corresponding calculations to be made for that year.

Two WT variables were included in the correlation matrix of data for the grazing period - that at fertilizer application in mid-summer and the WT depth averaged over the whole aftermath period, i.e. from fertilizer application to mid October. Rainfall was also averaged over this latter period. For the autumn-winter period (October-March), N losses were totalled not only over the whole period but also month-by-month, with the correlation matrix also including soil N status at each monthly assessment. WT depth and rainfall variables were included both as averages over the whole period and as monthly values. However, whereas rainfall was averaged over each interval between monthly soil N assessments, for WT, the depth at the beginning of each interval was used. It was hoped that this would reduce the correlation between rainfall and water table depth for each interval.

N losses during the grazing period each year were calculated net of the amount estimated as having been removed in the form of animal tissue; this was calculated by multiplying the total live weight gain per hectare (in kg) by 0.0272, the figure appropriate for steers of the relevant size (about 300 kg) gaining weight at about 1.0 kg day^{-1} (Ørskov, 1982). No account was taken of losses through ammonia volatilization. Where ammonia volatilization was measured during the summer on an experiment at North Wyke Research Station under continuous grazing, a mean rate of loss of 0.23 kg N ha^{-1} day^{-1} was recorded on swards receiving 200 kg N ha^{-1} $year^{-1}$ (Tyson *et al.*, 1993). The average length of time that plots were grazed at Tadham Moor varied between 32 days for 1988 and 68 days for 1989. On the basis of the North Wyke data, losses of N in the form of gaseous ammonia could therefore have totalled between about 7 and 16 kg N ha^{-1} on N_{200} paddocks. However, as will be seen later, these potential losses are small compared with some of the total losses recorded in the experiment. Furthermore, ammonia volatilization would have been lower on plots receiving less or no fertilizer, due to a combination of lower stocking rates and lower N concentrations in the grazed herbage (Jarvis *et al.*, 1989a,b).

The amount of N lost from the soil during grazing on each paddock in each year was calculated by subtracting the amount present in the soil in October from the amount of fertilizer N applied in mid-summer plus the soil mineral N recorded at the preceding assessment. From this was subtracted the amount of N calculated as having been removed in the grazing animal tissue, to arrive at 'net' N loss per hectare. This does not take account of any N mineralized and lost during the grazing period, so that total N losses will be underestimated. Whilst these potential inaccuracies are small compared with some of the total losses recorded, relationships derived in the analysis of these data are best seen as illustrative and comparative rather than definitive. Calculations of N losses during the autumn and winter periods will suffer far less from the limitations noted above, since ammonia volatilization is negligible once cattle are removed from pasture (Jarvis *et al*, 1989a) and N mineralization rates will be much lower at low temperatures and under waterlogged conditions.

Factors affecting denitrification rate

The influences of soil nitrate N, total soil mineral N, water table depth, soil moisture and incubation temperature on denitrification rates, measured weekly from October to December and monthly from January to March in 1988-89 and 1989-90, were investigated by correlation analysis and multiple regression. Soil mineral N analyses and water table depth measurements did not coincide with denitrification assessments, so that values for these parameters as at each denitrification sampling date were estimated by interpolation. Treatment mean values were used in each case, rather than individual plot values, so that variation was largely temporal rather than spatial. There was often significant correlation between the explanatory variables tested, since the decline in soil mineral N occurring on all plots between October and January each year tended to coincide with a general decline in soil temperatures and a rise in water tables and soil moisture. Greater precision in the estimation of the separate effects of these variables and the interaction between them was obtained by restricting the analyses to two month periods, i.e. October and November, December and January, February and March.

In addition, in order to examine influences on denitrification in the absence of fertilizer application, analyses were performed on data from N_0 plots only, both over the whole period and using data from October and November only.

4.3. RESULTS

FLUCTUATIONS IN SOIL N AND DENITRIFICATION RATE

Soil mineral N

Patterns of soil N change in the top 30 cm of soil were broadly similar each year (Figure 4.1). On plots receiving fertilizer, levels peaked soon after the mid season application, returning to low levels by late winter. There were also seasonal fluctuations in nitrate (NO_3^-) N levels on control plots, with highest levels recorded in August or September each year. There was no clear evidence of any progressive build up of extractable N with any of the

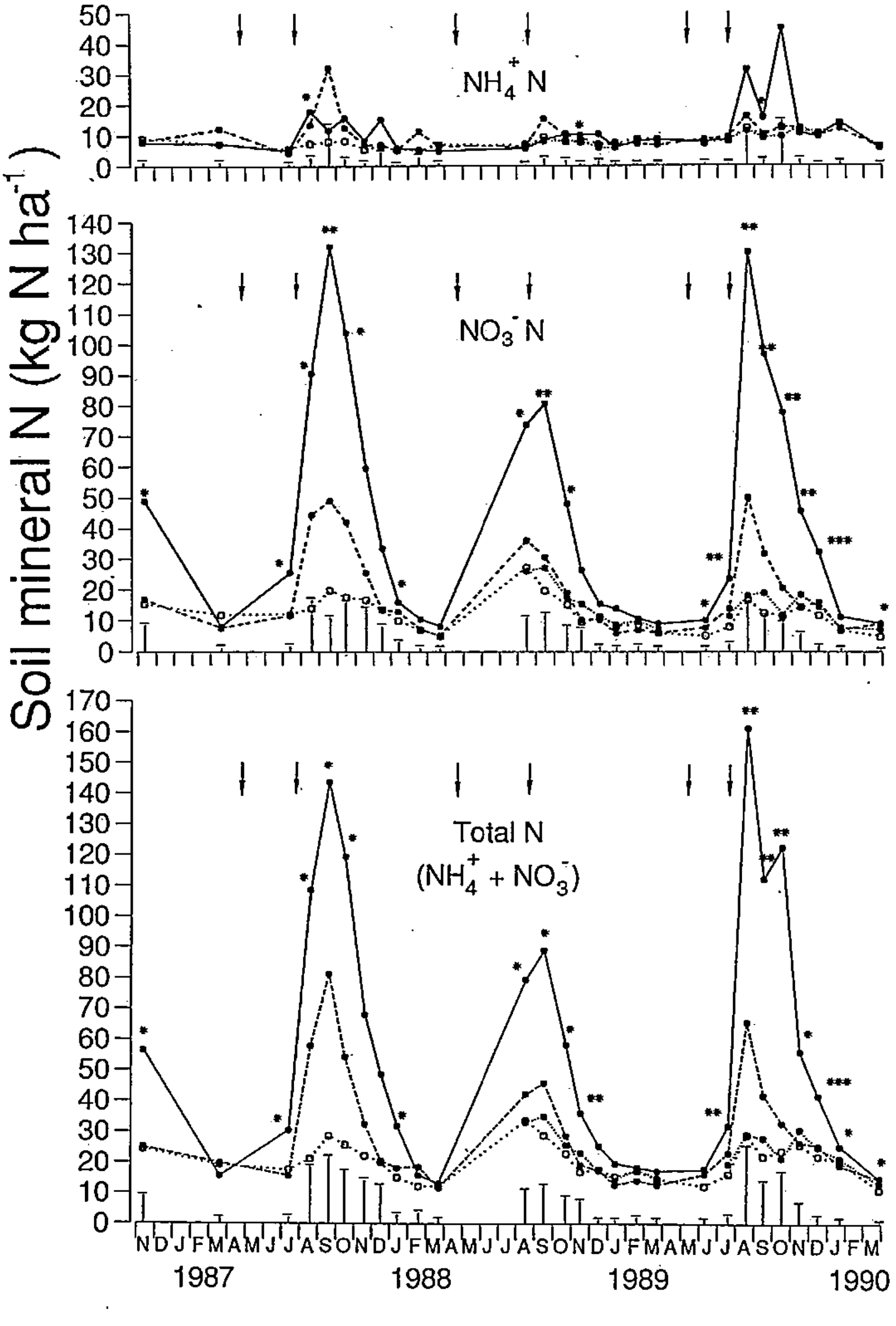


Figure 4.1. Changes in soil mineral nitrogen in the top 30 cm of soil between 11 November 1986 and 27 March, 1990. Solid lines = 200 kg ha^{-1} $year^{-1}$, broken lines = 100 kg N ha^{-1} $year^{-1}$, close-spaced dotted lines = 50 kg N ha^{-1} $year^{-1}$, and wide-spaced dotted lines = no applied N. Vertical bars are effective standard errors for treatment means. Asterisks denote significance levels of linear response to applied N $*P<0.05$, $**P<0.01$ and $***P<0.001$. Arrows indicate timing of fertilizer application.

treatments during the course of the experiment, although NH_4^+ N levels reached higher peaks on N_{200} plots in 1989 than in either of the two preceding years.

For most of each year, soil N was largely in NO_3^- form, so that total mineral N patterns followed those of NO_3^- quite closely. Testing for linear response to applied N rates was generally much more effective in detecting treatment effects than straight analyses of variance, and the probability levels for this response are indicated for each assessment date by star ratings in Figure 4.1. Ammonium N levels were only affected by applied N at the assessments in August 1987, November 1988, and September 1989. By contrast, NO_3^- and total extractable N levels showed significant linear responses at a majority of assessments, particularly when levels were high in summer and autumn. Differences among treatments diminished throughout the winter months and were negligible by March each year, although a significant linear relationship with applied N was still detectable for NO_3^- N on 27 March 1990.

Soil N peaked at lower levels in 1988 than in either 1987 or 1989 (complete data were not available for 1986). Moreover, 1988 results differed from those of other years in that there were notable increases in soil N on all plots - particularly treated ones - between March and the August N application, despite an intervening hay cut.

Nitrate concentrations in soil water

Figure 4.2 shows the nitrate concentrations in soil water in the three separate horizons from mid October to March each year. However, the highest concentrations of NO_3^- N in the soil water fraction were recorded at the first assessment following the mid-season N application each year (data not shown). This reached 167 mg l^{-1} in the upper 10 cm layer of N_{200} soils in August 1987, nearly three times the concentration in the 10-20 cm layer. Once the water table had reached the upper 30 cm horizon in October-November each year, differences between these layers diminished rapidly (Figure 4.2). In both 1987-8 and 1989-90 the NO_3^- N concentration of ground water remained above 10 mg l^{-1} at all three depths beneath N_{200} plots until January, with the sole exception of the 0-10 cm horizon in December 1989 (8.7 mgl $^{-1}$). By contrast, the NO_3^- N concentration beneath N_0 plots did not exceed 5.7 mg l^{-1} nitrate N (the current EC recommended limit for drinking water) in the 20-30 cm horizon after the September assessment in any year, and on N_{100} plots remained at 5.1 mgl^{-1} or less between December and March all three years.

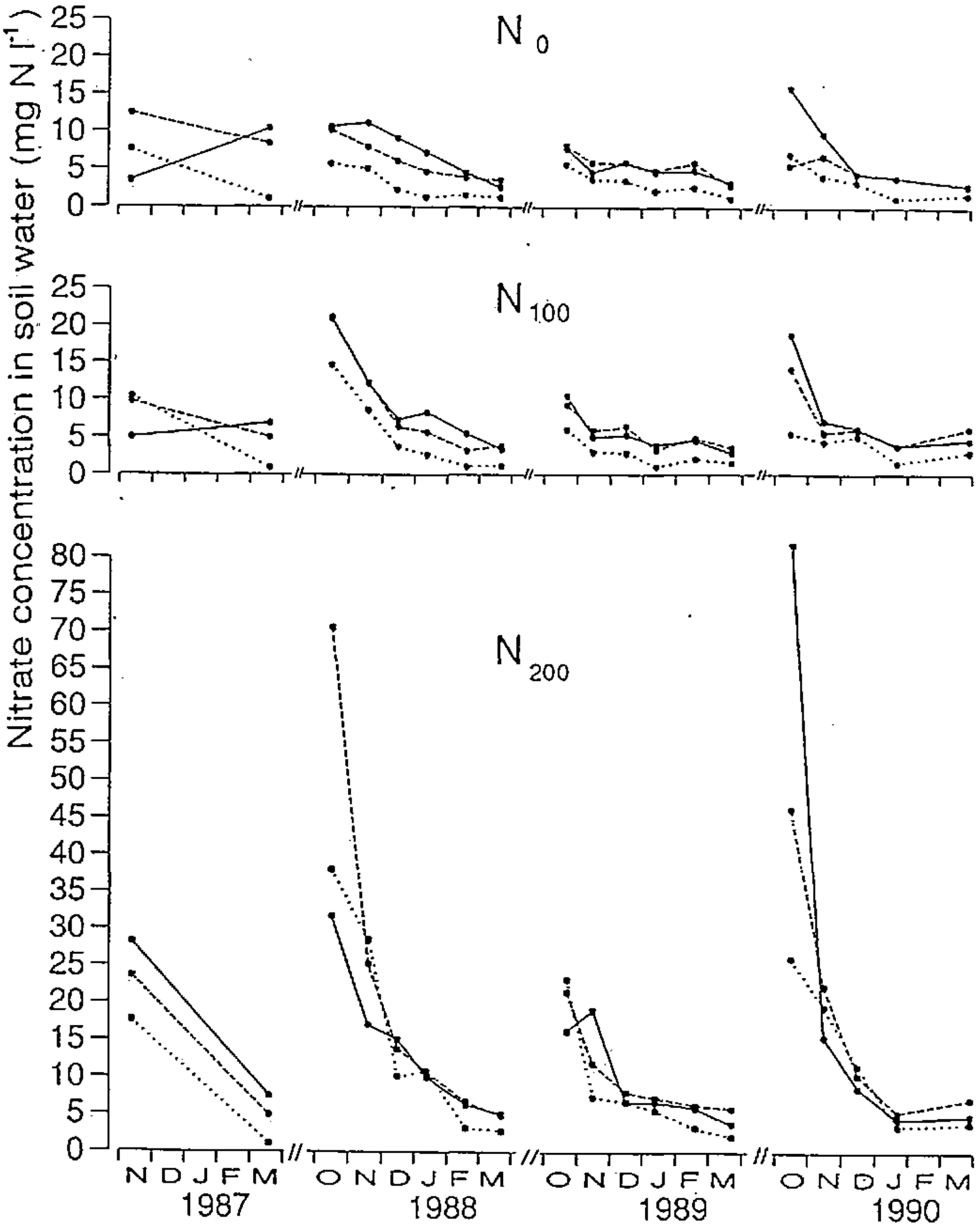


Figure 4.2. Concentration of nitrate (mg l^{-1} NO_3^- N) in soil water at three depth horizons during the autumn and winter following contrasting fertilizer N applications. Solid lines = 0-10 cm, broken lines = 10-20 cm and dotted lines = 20-30 cm.

Denitrification

Denitrification fluctuated considerably from week to week, both in 1988-9 and in 1989-90, although the pattern of these fluctuations differed considerably among years (Figure 4.3).

In 1988-9, rates tended to decline progressively from high levels in October, e.g. 328 g N per day at N_{200}, to less than 35 g per day for all treatments by the following March.

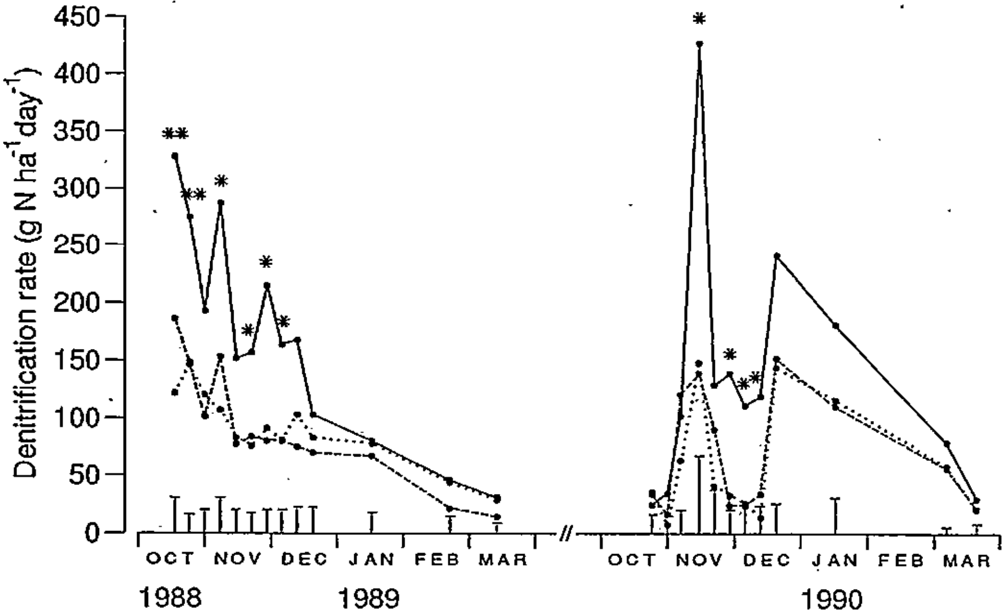


Figure 4.3. Rates of denitrification (g N per day) in the top 30 cm of soil at individual assessments between October and March 1988-89 and 1989-90. Vertical bars are effective standard errors for treatment means. Asterisks denote the probability of a linear response to applied N: * = $P<0.05$, ** = $P<0.01$. Dotted lines = no applied N, broken lines = 100 kg N ha^{-1} year^{-1} and solid lines = 200 kg N ha^{-1} year^{-1}.

By contrast, there was little denitrification occurring during October 1989, initially not exceeding 36 g N per day for any of the treatments assessed. Rates then rose to a peak on 13 November, reaching between 139 g per day (N_{100}) and 428 g per day (N_{200}). An ensuing trough over the next few weeks was followed by a second peak on all plots in mid January, with rates declining progressively thereafter. Differences among treatments were significantly related to the amount of applied N at several of the assessments in both years. However, although there was usually a significant linear response on these occasions, this was invariably because of the influence of the N_{200} treatment, with differences between N_0 and N_{100} usually negligible.

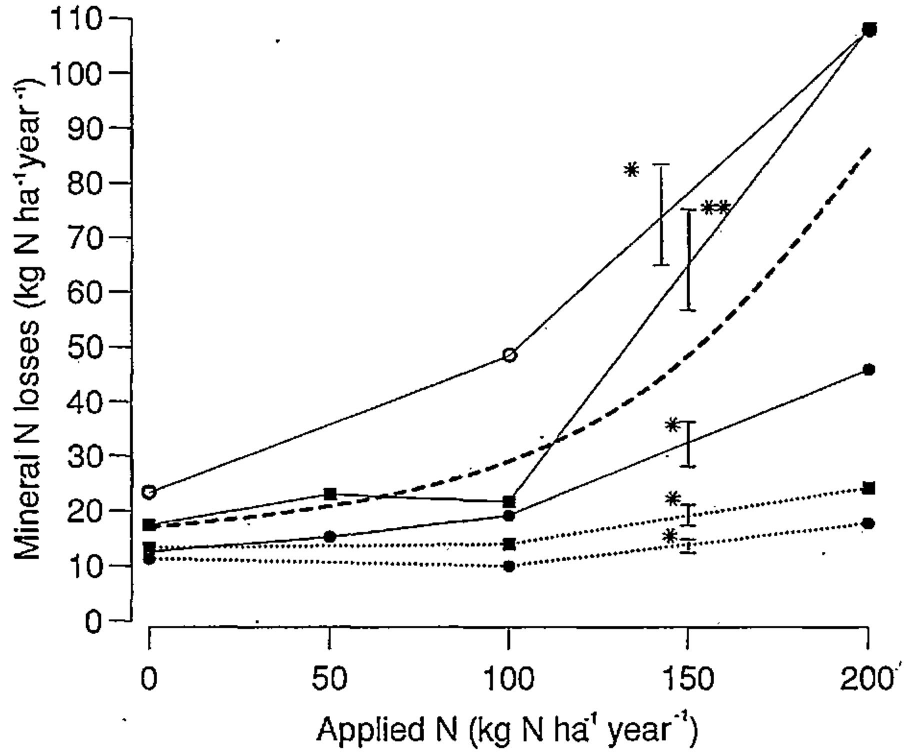


Figure 4.4. Accumulated losses in total (ammonium + nitrate) soil mineral N (kg ha^{-1}) between October and March in 1987-88 (square symbols), 1988-89 (solid circles) and 1989-90 (open circles). Solid lines = total loss, dotted lines = loss by denitrification. Vertical bars are effective standard errors of treatment means; asterisks denote the probability level of a linear response to applied N: * = $P<0.05$, ** = $P<0.01$. The thicker broken line, represents an exponential curve fitted to treatment means for the three years (see text).

Accumulated N losses October-March

Where no N was applied, accumulated losses of mineral N from the soil between October and March totalled 23.3 kg N ha^{-1} in 1987-8, 12.6 kg ha^{-1} in 1988-9 and 17.4 kg ha^{-1} in 1989-90. In the latter two years, denitrification accounted for losses of 11.3 and 13.3 kg N ha^{-1} respectively over the same period. On plots receiving fertilizer N, these losses varied considerably among years (Figure 4.4). Although in 1987-8 more than twice as much N was lost from N_{100} soils compared with N_0, in 1989-90, only the N_{200} treatment stood out as significantly different from other treatments ($P<0.05$). In 1988-9, losses from N_{200} plots were little more than those from N_{100} plots in the previous year. By contrast, accumulated denitrification losses for each treatment differed relatively little between 1988-9 and 1989-90, so that net losses of mineral N from N_{200} plots, i.e. losses not accounted for by denitrification, were much greater in 1989-90 than in 1988-89, (84.0 kg N ha^{-1} compared with 28.2 kg ha^{-1}).

Figure 4.4 shows a fitted curve for total N loss averaged over the three years 1987-8, 1988-9 and 1989-90. This used the treatment means for each year to derive the following formula: N loss (kg N ha^{-1}) = 13.9 + 3.2 (1.0158^N), which explained 68.2% of the variance in the data. This equation implies that applying 100 kg N ha^{-1} $year^{-1}$ might be expected to increase total losses of soil N by an average of 12.2 kg N ha^{-1} over the autumn-winter period, and that applying twice that rate would incur additional losses of 58.2 kg N ha^{-1}. However, the above formula is clearly only valid within the range of N rates used in the model, because for rates above about 290 kg N ha^{-1} it predicts increases in N loss far in excess of the amounts applied.

Denitrification was not measured in 1987-8. However, assuming that denitrification losses in that year were equivalent to the mean of the other two years for each treatment, then apparent leaching losses between October and March (i.e. total loss - denitrification) are estimated as 5 kg N ha^{-1} with no applied N, 17 kg N ha^{-1} $year^{-1}$ at 100 kg applied N ha^{-1} and 67 kg N ha^{-1} at 200 kg N ha^{-1} $year^{-1}$.

THE EFFECTS OF VARIATION IN WATER TABLE DEPTH ON LOSSES OF SOIL MINERAL N AND ON DENITRIFICATION RATE

Water table and rainfall patterns

Water table depth and rainfall patterns differed notably among the three years (see Chapter 3, Figure 3.4.). Summer rainfall was considerably higher in 1988 than in other years. The mean water table depth approached the top 30 cm of soil (the sampling horizon) by mid-July, and much of the area was under water for 2-3 days in early October, although this occurred between dipwell readings and flooding was not therefore recorded. By contrast, the summer of 1989 was very dry and the water table remained low until late October. Soil N levels were correspondingly high, but declined rapidly in response to wet weather from late October onwards. This high rainfall resulted in some flooding of the area in December and again in February 1990 (see Chapter 3, Figure 3.4).

Losses in soil N during grazing

Mean water table depth averaged over the whole aftermath period ranged from 22.9 cm (N_0, block 1 in 1988) to 88.6 cm (N_{50}, block 3 in 1987), whilst changes in soil N losses ranged

from a net gain of 69.1 kg ha^{-1} (N_{200} block 3, 1987) to a net loss of 144.0 kg ha^{-1} (N_{200} block 1 1988). Net losses of mineral N during aftermath grazing are shown in Figure 4.5, summarised by treatment (Figure 4.5a) and by year (Figure 4.5b).

Net losses in soil N (i.e. net of that accounted for by animal liveweight gain) during the period from the mid-season fertilizer application until the end of grazing each year, including amounts of N applied, were inversely and very significantly correlated with mean water table depth over the same period ($r = -0.58$, $P<0.001$). These losses were also negatively correlated with water table depth at the time of fertilizer application, although more weakly so ($r= -0.38$, $P<0.05$).. Net N loss was not significantly correlated with rainfall, but was correlated with the amount of N applied ($r = 0.38$), and even more closely with soil N status prior to fertilizer application ($r = 0.58$, $P<0.001$). Water table depth was not significantly correlated either with applied N or with soil N prior to fertilizer application, although rainfall during grazing was positively correlated with initial N levels ($r = 0.36$, $P<0.05$).

Mean water table depths over the grazing period were significantly correlated with rainfall over the same period ($r = -0.57$, $P<0.001$), but rainfall was not correlated with water table depth at the beginning of the period ($r = 0.09$). A multiple regression with these latter two variables against net N loss accounted for 22% of the variance ($R^2 = 0.22$). This was a small improvement over water table depth on it's own ($R^2 = 0.13$). However, the most successful multiple regression was one which included both total available N and mean water table depth:

$$\text{Net N loss (kg ha}^{-1}) = 67.7 \pm 19.6 - 0.420 \pm 0.102\ (\text{Total N})$$
$$-1.214 \pm 0.283\ (\text{mean WT}) \qquad R^2=0.55$$

R^2 is the r^2 value adjusted for the number of coefficients in the equation.

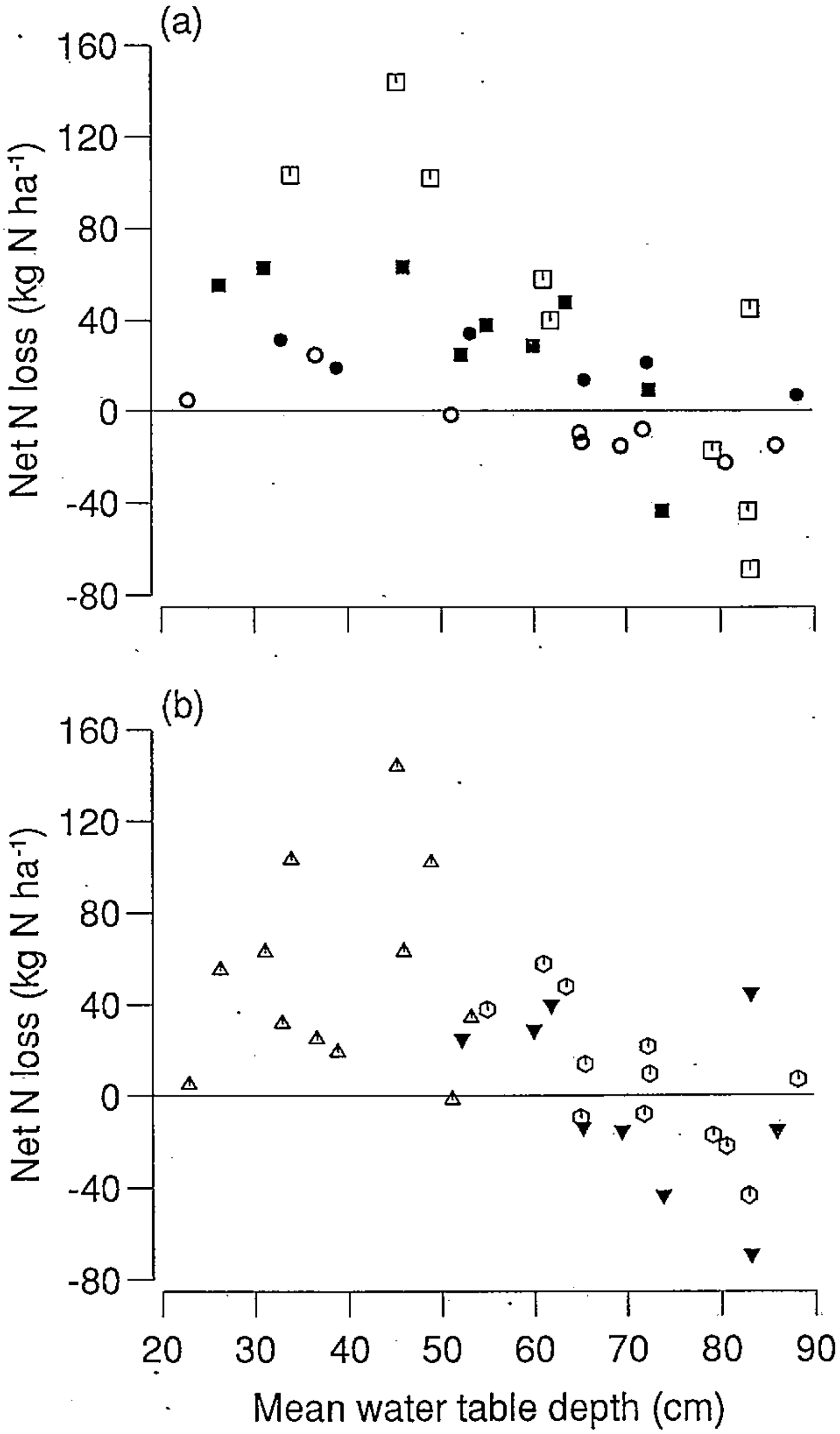


Figure 4.5. Losses of soil mineral nitrogen during aftermath grazing (net of the amounts removed as animal tissue) in relation to mean water table depth. Data summarized (a) by treatment and (b) by year. Open circles = N_0; filled circles = N_{50}; filled squares = N_{100}; open squares = N_{200}. Filled triangles = 1987; open triangles = 1988; open hexagons = 1989.

A similar equation with total available N replaced by initial soil N status accounted for only a slightly lower proportion of the variance (50%).

$$\text{Net N loss (kg ha}^{-1}\text{)} = 56.7\pm22.7 + 0.953 \pm 0.269 \text{ (soil N)} - 1.087\pm 0.308 \text{ (mean WT)} \qquad R^2=0.50$$

These equations are of limited value in helping to predict future losses, since mean water table depth over a given period is a retrospective variable. As already noted, initial water table depth on its own accounted for only 13% of the variance, but when N supply variables were added the variance accounted for rose considerably. The most successful of these equations combined total N available and initial water table depth:

$$\text{Net N loss (kg ha}^{-1}\text{)} = 79.9\pm32.1 + 0.462\pm0.116 \text{ (Total N)} -1.486\pm0.488 \text{ (initial WT depth)} \qquad R^2=0.41$$

with high significance levels associated with estimates of the WT and N components ($P<0.01$ and 0.001 respectively) and lower confidence levels about the constant ($P<0.05$). The variance accounted for was significantly improved when total rainfall was added and the constant omitted from the equation:-

$$\text{Net N loss (kg ha}^{-1}\text{)} = 0.428\pm0.111 \text{ (available N)} + 0.444\pm0.136 \text{ (rainfall (mm))} - 1.479\pm0.381 \text{ (initial WT depth)} \qquad R^2 = 0.47$$

Nevertheless, since total rainfall is also a retrospective variable, this equation too is of limited value for predicting future losses.

Note that all the foregoing equations compute negative 'losses' (i.e. net gains in N), where mineral N levels are relatively low and where values for WT depth are high. Net gains were obtained in all three years, although on only one N_0 plot in 1988, and for all treatments except N_{50} (Figure 4.5). A net gain of mineral N to the system over the grazing period implies that more N was mineralized than was lost by the combined effect of leaching and/or denitrification, animal tissue production and ammonia volatilization and apparent losses due to an increase in the amount of N in standing herbage between the beginning and end of the period under consideration. Net gains were understandably more common on N_0 plots, although some high values (i.e. strongly negative 'losses') were obtained on N_{100} and N_{200} plots, particularly in 1987 when water tables were lower than either 1986 or 1988.

Losses in soil mineral N in autumn and winter

The total amount of N lost from the soil between October and March each year was very strongly correlated over all plots with the amount remaining in the soil when grazing ceased in October ($r = 0.99$, $P<0.001$). Since this was itself significantly correlated with mean water table depth over the aftermath grazing period, October-March N losses were also positively, rather than negatively, correlated with mean water table depths during the earlier period ($r = 0.48$, $P<0.001$). October - March N losses were not significantly correlated with water table depth in October ($r = 0.34$).

N losses tended to be greater in the month October/November than during the following months (see Figure 4.1), so that October-March losses were closely correlated with losses during this month ($r = 0.85$, $P<0.001$), with the strength of the correlation declining for November/December ($r = 0.70$) and December/January ($r = 0.65$, $P<0.001$). Losses from one month to the next were very strongly correlated with soil N status at the beginning of the relevant period ($r = 0.86$ for October-November, $r = 0.89$ November-December and $r = 0.93$ December-January, all $P<0.001$), but not with water table depth at the beginning of each month. Thus any increased risk of N loss when water tables were high from October onwards was masked by differences in the amount of N present in the soil initially, which in turn reflected losses during the preceding period.

Treatment differences in soil N in October had disappeared by March each year, so that applying high rates of N each year had no permanent effect on the base levels of N in the soil (see Figure 4.1). However, there were large differences between years in the water table depth in October, particularly when comparing 1988 with 1989 (see Chapter 3, Figure 3.4). These differences might have been expected to influence the rate at which N was lost during October-November; but there was no indication of this from the relationship between water table depth in October each year and the amount of available N lost over the ensuing month. Rainfall in October-November differed greatly between years (117.6 mm in 1987, 6.5 mm in 1988 and 150.5 mm in 1989), but even so, losses were very poorly correlated with rainfall, both over the whole period and within individual monthly periods. No multiple regression which included WT depth and/or rainfall with soil N status in October could improve on a simple linear regression on October soil N alone in explaining variation in October-March N losses:

$$\text{N loss}_{\text{October-March}}\ (\text{kg ha}^{-1}) = 0.94 \pm 0.022\ (\text{soil N}_{\text{October}}) - 5.5 \pm 1.44 \qquad R^2 = 0.98$$

Denitrification - the influence of water table depth, soil N status and soil temperature

Over all treatments and all assessment dates October-March (df = 73), denitrification rate in g N day^{-1} (DR) was significantly correlated with WT depth ($r = -0.28$, $P<0.05$), but not with temperature or soil water content (although the latter was significantly correlated with WT depth, $r = -0.51$, $P<0.001$). However, of all the explanatory variables tested, DR was most closely correlated with soil nitrate N ($r = 0.46$, $P<0.001$), followed by total soil mineral N ($r = 0.37$, $P<0.001$). Figure 4.6 shows the distribution of DR values recorded at all assessments (using treatment means) plotted against soil nitrate N (Figure 4.6a) and WT depth (Figure 4.6b).

Multiple regression analysis revealed an interaction between soil nitrate N and WT depth, with the following equation increasing the proportion of the variance accounted for significantly ($P<0.001$) to 35% compared with 20% with nitrate N alone:

$$\text{DR} = 110.7 \pm 17.8 + 3.04 \pm 0.536\ \text{N}_{\text{nitrate}} - 3.46 \pm 0.824\ \text{WT} \qquad R^2 = 0.35$$

The correlation between WT depth and DR was stronger when analyses were restricted to data from October and November only ($r = -0.41$, $P<0.01$), whilst the correlation with soil nitrate N levels was weaker ($r = 0.36$, $P<0.05$). The corresponding multiple regression equation was as follows:

$$\text{DR}_{\text{oct-nov}} = 146.9 \pm 29.2 + 2.38 \pm 0.746\ \text{N}_{\text{nitrate}} - 4.07 \pm 1.16\ \text{WT} \qquad R^2 = 0.31$$

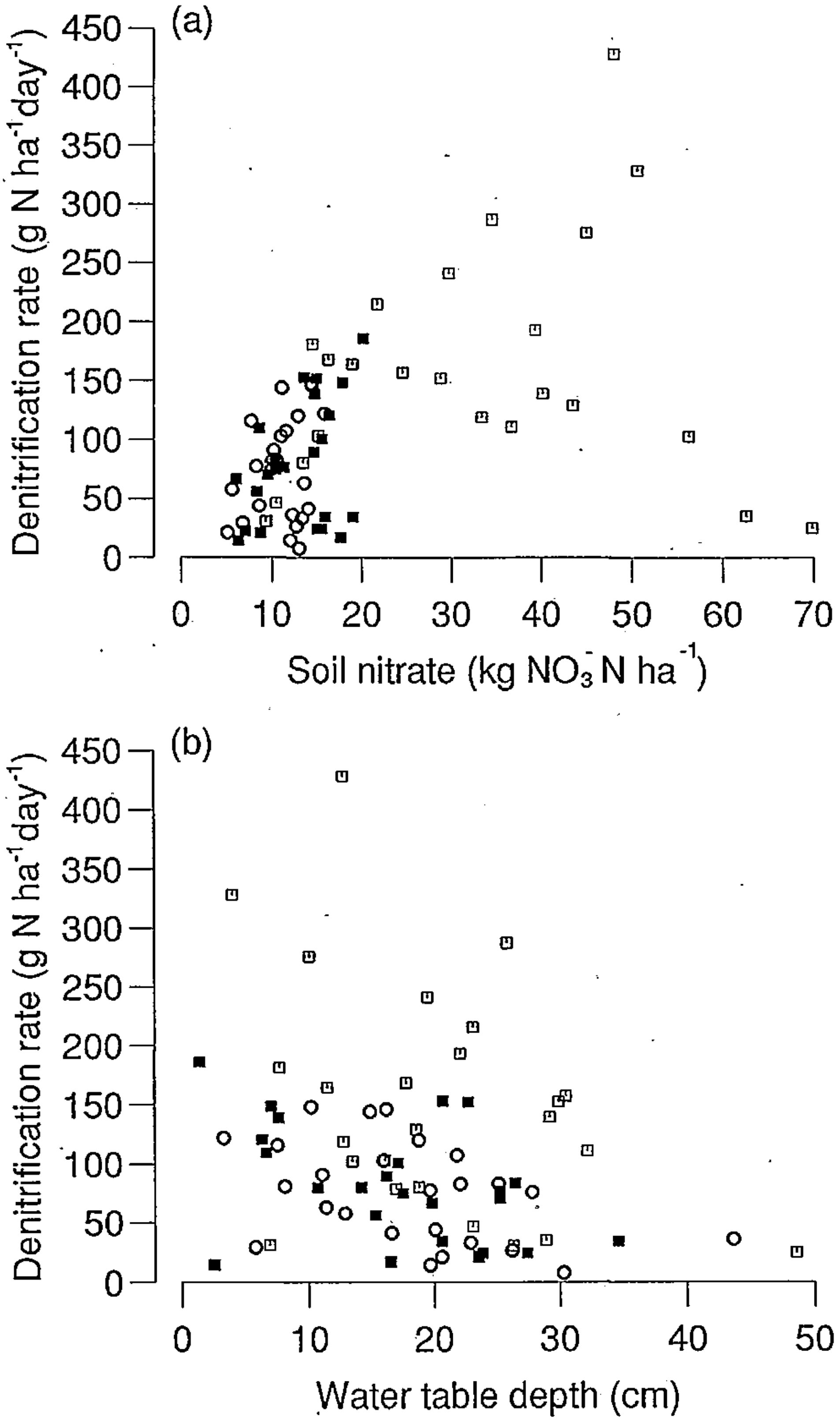


Figure 4.6. Denitrification rate in the top 30 cm of soil at individual assessments between October and March 1988-89 and 1989-90 in relation to (a) the amount of soil nitrate (NO_3^-) N present (kg N ha^{-1}) and (b) water table depth (cm). Data averaged by treatment at each assessment: open circles = N_0; filled squares = N_{100}; open squares = N_{200}.

An equation with WT replaced by soil water content (SWC) accounted for a similar proportion of the variance:

$$DR_{oct\text{-}nov} = 3.19\pm0.781 + 21.1\pm5.39\ SWC - 1497\pm403 \qquad R^2 = 0.35$$

where SWC was expressed as a percentage of wet soil by weight.

The proportion of the variance accounted for by each of the above equations was low and was not improved by addition of any other measured variable to the model. Neither of the latter two equations could explain the high DR values recorded on N_{200} plots in October 1988 (328.0 g N day^{-1}) and November 1989 (428.0 g N day^{-1}). Corresponding DR Values calculated from nitrate N and WT values estimated for each date were 209.0 and 251.0 g N day^{-1} respectively, whilst the equation incorporating nitrate N with SWC produced values of 194.3 and 221.6 g N day^{-1}. The latter equation might have been expected to be the more accurate, since SWC was calculated at each DR assessment, rather than estimated by interpolation as were WT and soil mineral N values.

However, it is clear from Figure 4.6a that the relationship between DR and soil nitrate is not linear. A quadratic equation of the form $DR_{oct\text{-}mar} = k_1(N_{nitrate}) - k_2\,(N^2_{nitrate})$ significantly increased the variance accounted for compared with $N_{nitrate}$ alone (to $R^2 = 0.54$). Nevertheless, this equation also failed to explain the high observed DR values obtained in October 1988 and November 1989, giving estimates of 249.6 and 243.4 g N day^{-1} respectively. The apparent quadratic response to soil nitrate N was strongly influenced by N_{200} data from the two assessments in October 1989 and the first assessment in November 1989, which make up the three points toward the bottom right of Figure 4.6a. Corresponding values for WT depth for these assessment dates were high. Addition of WT depth as a third explanatory variable in the equation did not significantly increase the variance accounted for ($R^2 = 0.53$) compared with nitrate alone, but confidence levels attached to each of the coefficients were large ($P<0.001$).

A non-linear response to nitrate is consistent with the observation that, as nitrate concentration increases, denitrification changes from being nitrate-dependant to being independant of nitrate, although, in laboratory studies, this transition occurred at higher nitrate concentrations than those recorded in October and November in these studies

(Knowles, 1981; Aulakh *et al.*, 1992).

However, the equations derived here still leave about 50% of the variance in the data unexplained, and do not produce values higher than 260 g N day^{-1} for those assessments where values of up to 428 g N day^{-1} were recorded. Analyses of DR at individual assessments, reported above, frequently showed a significant linear relationship between fertilizer N rate and DR (see Figure 4.3). Moreover, the quadratic equations predict zero or minus values for DR at levels of soil nitrate only sightly higher than those observed between October and March, even at zero values for WT depth, which is obviously misleading.

Soil temperature appeared to have no influence on denitrification rate over the whole autumn-winter period or during October and November, but this may have been because of a small but significant positive correlation between soil nitrate N and temperature within the data set ($r = 0.27$, $P<0.05$ for October-March, $r = 0.27$, N.S. for October and November). During December and January, soil nitrate N was negatively correlated with soil temperature ($r = -0.53$, $P<0.01$), but both had a positive influence on DR, although DR was not significantly correlated with temperature alone. The following multiple regression equation accounted for 53% of the variation in the data:

$$DR = 4.44 \pm 0.945\ N_{nitrate} + 11.3 \pm 2.06\ temp - 0.09 \pm 0.032\ WT^2 \qquad R^2 = 0.53$$

where 'temp' is the soil temperature in ^0C.

Denitrification in the absence of fertilizer application

There was no significant correlation between soil mineral N status alone and denitrification on N_0 plots, either over the whole October-March period or during October and November. DR was correlated with WT depth and soil water content over both periods ($r = -0.44$ and 0.45 respectively for October-March, and $r = -0.60$ and 0.58 respectively for October-November). The linear relationships between DR and WT depth for the two periods are given by the following equations:

$$DR = 113.4 \pm 18.80 - 2.13 \pm 0.921\ WT \qquad R^2 = 0.15 \qquad \text{for October-March}$$

and

$$DR = 133.6 \pm 23.3 - 2.56 \pm 1.04\ WT \qquad R^2 = 0.30 \qquad \text{for October-November}$$

Denitrification rates during December and January were not correlated with WT depth on N_0 plots, although they were positively correlated with both soil water content and temperature ($r = 0.78$ and 0.71 respectively, both $P<0.05$). However, since there was a similar, significant correlation between soil water content and temperature ($r = 0.77$, $P<0.05$), it is not possible to say which of these variables was most important in determining DR during the winter period.

4.4. DISCUSSION

Periodic sampling of the soil for mineral N content is not a completely accurate method for measuring N loss, compared with more direct methods (e.g. Dowdell and Webster, 1980; Barraclough *et al.*, 1984; Tyson *et al.*, 1993) and denitrification rates often show wide temporal variation (Scholefield *et al.*, 1990). However, care was taken in the approach to sampling and data analysis to minimise these inaccuracies, and the results give a good indication of the scale of losses that can result from the use of fertilizer N in wetland peat soils.

Total N losses

The main emphasis of this study was on estimating losses over the autumn-winter period. However, the summer peaks in soil N on N_{100} and N_{200} plots were notably lower in 1988 than in either the preceding or the following year, and significant losses occurred between August and mid-October in 1988. Moreover, the mid-season fertilizer application (on 23 August) had relatively little effect on amounts of soil N at the subsequent assessment, in marked contrast with other years. This was almost certainly the result of high summer rainfall and high water table levels throughout the summer in 1988: a total of 57 mm of rain fell in the 22 days between fertilizer application in August and the next soil sampling, compared with 28 mm during the equivalent period in 1989 and only 8 mm in 1987. On the other hand, soil temperatures in August and September 1988 were no lower than usual and intermediate between those of 1987 and 1989. These factors would render soil N particularly vulnerable to both denitrification and leaching in 1988 compared with other years

(Firestone, 1982; Jarvis *et al*; 1989a).

Losses of N measured between October 1988 and March 1989 therefore represent a considerable under-estimate of the total amounts lost during the whole year. This is confirmed by the losses calculated net of animal production in the supplementary study which related these losses to variations in WT depth. Losses were simply estimated by difference, taking account of soil mineral N levels before fertilizer application, the amount applied, the amount remaining in the soil in mid-October and the amount estimated to have been removed in animal tissue. They were taken to represent the sum of losses by leaching, ammonia volatilization and denitrification, although they did not take account of N mineralized and subsequently lost during this period. Further inaccuracies would be caused by differences in the amount of N held in standing vegetation between the beginning and end of this period, but no measure was made of this. The amounts of N lost on N_{200} plots during grazing, estimated in this way, averaged 15.9 kg N ha^{-1} in 1987, 116.3 kg in 1988 and -2.8 kg in 1989.

Thus, although N losses during the autumn and winter were lower in 1988-89 than in either 1987-88 or 1989-90, this was because much more N had been lost during grazing during the wet year 1988, than in the other two years, despite the shorter aftermath period in 1988. Furthermore, if the amount of N estimated as having been lost from N_{200} plots during grazing each year is added to autumn-winter losses for the same plots, the total for 1988 far exceeds those of other years.

NH_4^+ : NO_3^- ratios and their significance

Ammonium (NH_4^+) N levels on all plots tended to be highest during the summer and early autumn, although the majority of the soil N was in nitrate (NO_3^-) form for most of the year. In N_0 soils, the peaks in NH_4^+ N were small and attributable to increased mineralization rates when soil temperatures were high, as well as to the direct supply of NH_4^+ N in the form of animal excreta during grazing (Jarvis *et al.,* 1989a). Although NH_4^+ N peaked on N_{100} and N_{200} plots following fertilizer application, corresponding peaks in NO_3^- N were proportionately much greater. This implies that the NH_4^+ N applied (as ammonium nitrate) was rapidly nitrified to NO_3^- form once in the soil. The ratios of NH_4^+ : NO_3^- N were consequently much lower in these soils than in the silt loam and freely draining calcareous soils assessed by Jarvis *et al.* (1989a) at equivalent rates of N application, and the potential for losses by denitrification and leaching were correspondingly higher.

Denitrification and leaching losses

The peaks in denitrification rate recorded between October and March (328 g N per day in October 1988 and 428 g per day in November 1989) were high compared with rates recorded on mineral soils by Scholefield *et al.* (1990) and Ryden (1983), where equivalent peaks were recorded only immediately after fertilizer application to warm, wet soils. These results suggest high levels of biological activity in the peat soils at Tadham, leading to a high potential for both mobility and transformation of soil N. Nevertheless, denitrification could account for only a small proportion of the observed decline in soil N on N_{200} plots during the autumn and winter, implying considerable leaching losses for this treatment.

Denitrification rates were not measured during the grazing phase of the experiment and the relationship between denitrification and other soil variables may have been quite different then compared with the autumn and winter period. However, using the equations derived from October-November denitrification rates to estimate the total amount of N denitrified on N_{200} plots during grazing gives values of 7.0-20.7 kg N denitrified ha^{-1} in 1987, 10.4-16.2 kg N in 1988 and 6.2-13.6 kg N in 1989; the lower value in each case is that calculated from the equation incorporating water table depth and the higher value that calculated from the soil water content equation. This implies that all or most of the losses incurred during grazing in 1987 and 1989 could be accounted for by denitrification, but denitrification could account for only about 14% of the losses estimated for 1988, adding a further 100 -106 kg N to the total amount lost by leaching from N_{200} plots in the year 1988-89.

It is recognized that multiple regression analysis was only moderately successful in relating measured variables to denitrification rate. Nevertheless, even if a denitrification rate of 428 g N day, the maximum rate recorded at any assessment, was assumed for the grazing period in 1988, this would increase the estimated total N denitrified then to 25.7 kg N ha^{-1}, reducing only slightly the estimate of leaching losses during grazing to 90.6 kg N ha^{-1}.

It was not practicable in this study to measure the concentration of NO_3^- N in water percolating into the ditch system from individual plots, particularly as there were no underground drains present. Whilst dilution and denitrification of NO_3^- ions during their passage through the soil affected the concentration of NO_3^-, the mean concentration from N_{200} plots was almost certainly above 11.4 mg l^{-1} nitrate N, the EC upper limit during most of the October-December period, easily exceeding the EC recommended limit of 5.7 mg l^{-1} for drinking water. These results make an interesting comparison with those from a drainage experiment in a heavy clay soil on sloping ground at North Wyke Research Station (Tyson *et al.*, 1993). The runoff from undrained plots receiving 200 kg N ha^{-1} $year^{-1}$ contained on average less than 10 mg l^{-1} NO_3^- N from late October onwards, with drainage water from equivalent drained plots remaining at above this level until the following January. The mean loss of N (over 10 years) from these soils was 16 and 56 kg N ha^{-1} $year^{-1}$ for undrained and drained plots respectively, compared with an estimate of about 67 kg $ha^{-1}year^{-1}$ for the N_{200} treatment in this experiment.

Much lower leaching losses (1.3-18.1 kg N ha^{-1}) were shown at Letcombe Laboratory by Dowdell and Webster (1980). They measured leaching directly after applying fertilizer at 400 kg N ha^{-1} to monolith lysimeters containing a loamy sand soil sown with perennial ryegrass. However, in their work herbage was cut and removed six times per year and between 118 and 344 kg N ha^{-1} were harvested in herbage in the year of application. In grazed swards, much of this herbage N would have been recycled onto the pasture and become available for leaching or denitrification: Jarvis *et al.* (1989b) found that N equivalent to 81% of that applied could be returned to the soil (at 210 kg N ha^{-1}), and of this proportion less than 5% is lost by ammonia volatilization.

A nitrate leaching 'break point'

Barraclough and Jarvis (1989) introduced the concept of a break point for nitrate leaching, a level of fertilizer N application above which nitrate leaching increased markedly. Based largely on direct measurements of leaching and denitrification, they suggest break points of 150-200 kg N ha^{-1} for grazed swards and between 250 and 350 kg N ha per ha for cut grassland.

The pattern of N loss in response to applied N varied considerably from year to year in the work reported here. Moreover, with a generalized curvilinear response, the identification of a single break point is both arbitrary and subjective. Nevertheless, even if losses during autumn-winter only are taken into account, the risk of substantial nitrate leaching evidently begins at much lower rates of applied N at Tadham Moor than in most agricultural grasslands, i.e. between 50 and 100 kg N ha^{-1} year^{-1}, increasing markedly at rates above 100 kg ha^{-1}. This adds weight to the conclusion that these soils are at particular risk from nitrate leaching, especially as swards were managed by a combination of cutting and aftermath grazing and a break point might have been expected at somewhere between those quoted by Barraclough and Jarvis for grazed and cut swards.

Implications for high water table management prescriptions within the ESA

Current prescriptions within the ESA encourage farmers to maintain ditch levels at no more than 30 cm below mean field level throughout the summer (Her Majesty's Stationary Office, 1992). The mean water table depth at fertilizer application in August 1988 was 55 cm and averaged 39 cm between then and mid October, much higher than in other years due to unusually high rainfall. However, these water table levels are probably close to those that would result from the ESA prescription, allowing for the fact that the water table normally assumes a concave shape during the summer when evapotranspiration exceeds rainfall. The maximum level of fertilizer N allowed within the ESA is 75 kg N ha^{-1} year^{-1}. This rate was not used in the experiment reported here. However, the amount of N estimated as having been lost during grazing in 1988 (net of animal production) averaged between the N_{50} and N_{100} treatments was 44.4 kg N ha^{-1} (note that only half the annual totals of 50 and 100 kg N ha^{-1} were applied in mid-summer). The multiple regression equation incorporating water table depth at fertilizer application, available soil mineral N at this time and total rainfall between then and mid-October, computes a slightly lower figure of 38.4 kg N ha^{-1}. If the 1988 rainfall figure of 209.1 mm (over 9 weeks) is replaced in the equation by the total for the driest year, 1989, i.e. 147.4 mm (over 14 weeks), but the 1988 water table and soil N values are retained, the estimate for N loss falls to 11.0 kg N ha^{-1}. Alternatively, if the 1988 rainfall total is retained and the 1988 water table depth figure (55 cm) is replaced by that for 1987 when water tables were lowest (79.4), the estimate for N loss falls substantially to 2.8 kg N. Using the mean water table depth averaged over 1987 and 1989 gives an estimate of 16.9 kg N ha^{-1} at 1988 rainfall levels.

These calculations imply that where the maximum ESA fertilizer rate was in use, split between spring and mid-summer, total mineral N losses during grazing could be more than doubled by the adoption of the higher water table prescription in a wet year. However, it must be recognized that there are many potential inaccuracies in these calculations, and that the equation used could account for only about half the variance in the data. Nevertheless, the figures illustrate the kind of impact that raised water tables could have on losses of soil N, even where only comparatively modest fertilizer rates are used. In view of this, it is unfortunate that, as noted in the previous Chapter, experiments currently in progress at Tadham Moor to study the agronomic and plant ecological implications of raising water tables do not include any provision for the study of nutrient cycling under different hydrological conditions (J.R.B. Tallowin, personal communication).

Improved uptake and harvest of N

In the SP experiment at Tadham Moor (Experiment 2), where aftermath growth was cut instead of grazed, herbage uptake of N in the aftermath phase was significantly improved by including higher rates of P and K than were used in the LS experiment, reflecting a greater response in herbage production (see Chapter 3). Using these rates on the grazed plots might have resulted in a higher $NH_4^+ : NO_3^-$ ratio in soil mineral N by cycling a greater proportion of the available N through grazed herbage (Jarvis *et al.*, 1989a), but the potential for reducing total soil mineral N is limited. Moreover, work by Campino (1982) suggests that mineralization of organic N might have been increased by additions of high rates of P and K together. Working with incubated silty loam hay meadow soil of 12.4% organic matter, Campino showed a significant P x K interaction for increased N mineralization, with the lowest rates used (equivalent to 87 kg P ha^{-1} and 166 kg K ha^{-1}) causing a significant 21% increase compared with control soils.

Nevertheless, there does seem to be scope for improving N efficiency during the hay phase. Applying 50-100 kg N ha^{-1} in spring (N_{100} and N_{200}) resulted in relatively little extra N being harvested in baled hay compared with the control. Much of the remainder was presumably cycled through plants and returned in leaf material, either as plant tissue turned over during the accumulation of the late hay crop or by leaf shatter during hay making. In the SP experiment, high rates of P and K (75 kg P ha^{-1} and 200 kg K ha^{-1} per year) increased N uptake in the hay crop only marginally compared with taking an extra cut in late May-early June, which doubled the total amount of N harvested (see Chapter 3). A combination of these strategies could give the best utilization of applied N in the hay crop. Unfortunately, cutting dates earlier than 1 July are unlikely to be acceptable in these meadows because of the deleterious effect they would have on the breeding success of wading birds, particularly snipe (Green, 1986).

4.5. CONCLUSIONS

The soils at Tadham Moor are particularly susceptible to N leaching, as a result of a combination of high water tables and apparently rapid conversion of ammonium N to nitrate (nitrification). These same factors, coupled with the high carbon content of the soils, lead to high denitrification rates, and this could lead to substantial losses of N from the soil if high water tables are maintained throughout the summer when soil temperatures are high. Where ambient water table levels are allowed, restricting the fertilizer rate to 75 kg N ha^{-1} appears to be adequate to avoid significant leaching risk, but little or no inorganic fertilizer should be applied if water tables are to be maintained at artificially high levels throughout the summer.

4.5. SUMMARY

Fluctuations in soil mineral nitrogen (N) caused by repeated applications of fertilizer N were investigated over three years in wetland hay meadows in Somerset. Swards were cut for hay after 1 July each year and the aftermath grazed continuously with beef cattle until October. Several N treatments between 0 (N_0) and 200 kg N ha^{-1} year^{-1} (N_{200}) were applied in two equal dressings each year. Denitrification rates were estimated over two consecutive autumn-winter periods, using a soil core incubation method.

A high proportion of soil N was in nitrate form for most of the year and therefore at risk of loss by both leaching and denitrification. Estimated losses of total soil mineral N (ammonium + nitrate) between October and March averaged 17.8 kg N ha^{-1} at N_0, 30.0 kg N ha^{-1} at N_{100} and 88.2 kg N ha^{-1} at N_{200} for the three years 1987-8, 1988-9 and 1989-90. Denitrification losses were significantly related to the amount of applied N in both 1988-9 and 1989-90, but only accounted for a small proportion of the total N loss from N_{200} soils

between October and March. Estimates of leaching losses were based solely upon indirect measurements of N loss, but they do give a good indication of the scale of losses incurred. Leaching losses in autumn-winter were estimated at about 5 kg N ha^{-1} for N_0, 17 kg N at N_{100} and 67 kg N at N_{200}. Further significant losses of up to 116 kg N ha^{-1} in total occurred during the 1988 summer, when prolonged rain following N application resulted in flooding in early October, but losses appeared to be insignificant during the same period in other years.

Adoption of the ESA high water table prescription could result in greatly increased N losses during aftermath grazing where the maximum ESA fertilizer N level (75 kg N ha^{-1} $year^{-1}$) is used, particularly if followed by above average rainfall. Nevertheless, more work is necessary to identify how much of the losses incurred during wet conditions in summer and early autumn can be accounted for by denitrification.

Taking an earlier cut for hay or silage could increase N efficiency and reduce losses of mineral N into the environment, although early cutting might be unacceptable due to its deleterious effect on the breeding success of wading birds.

It is concluded that these soils are particularly susceptible to N leaching, as a result of a combination of high water tables and apparently rapid conversion of ammonium N to nitrate (nitrification). Where ambient water table levels are allowed, restricting the fertilizer rate to 75 kg N ha^{-1} appears to be adequate to avoid significant leaching risk, but little or no inorganic fertilizer should be applied if water tables are to be maintained at artificially high levels throughout the summer.

CHAPTER 5

THE EFFECTS OF NITROGEN, POTASSIUM AND PHOSPHORUS ADDITION ON THE BOTANICAL COMPOSITION OF HAY MEADOWS AT TADHAM MOOR

5.1. INTRODUCTION

MG5 (*Cynosurus cristatus-Centaurea nigra*) and MG8 (*Cynosurus cristatus-Caltha palustris*) plant communities (Rodwell, 1992), such as those at Tadham Moor are found on a range of soil types (Rodwell, 1992), but data on their response to fertilizers on peat soils are sparse. In the absence of inputs from fertilizer application or mineral-rich flood water, peat is commonly deficient in plant-available phosphorus and potassium (Brady 1990; Munro, *et al.*, 1973). Data from Experiment 2 (the small plot experiment), presented in Chapter 3, showed that although the meadows at Tadham Moor are fairly productive compared with species-rich vegetation elsewhere, P and K availability in the peat soils limit response to applied N. Furthermore, significant increases in biomass and herbage N production were achieved by applying base rates of P and K without N, with P and K application apparently stimulating the mineralization and plant uptake of organic nitrogen.

It is well established that inorganic fertilizers, particularly nitrogen (N), can cause significant botanical change when applied to mixed-species grassland, usually increasing the dominance of a few species with an overall loss in species richness (Wells, 1989). This has been widely demonstrated for mineral soils, for example in the classic Park Grass Experiment (Lawes *et al.*, 1882; Brenchley and Warington 1958; Williams, 1978) and others (e.g Reith *et al.*, 1964; Heddle, 1967; Garstang, 1981; Williams 1984). Similar effects have been recorded on chalk grassland (Bobbink 1991), on limestone cliff (Willis, 1989) and in sand dunes (Willis, 1963), but comparable evidence for peat soils is limited (Murphy, 1960; Vermeer and Berendse, 1983; Van Vuuren and Verhoeven 1985; Benedycki *et al.* 1989).

This chapter describes the vegetation response to inorganic fertilizers in Experiment 2 in terms of changes in individual species abundance and species diversity under cutting management. It also contains a comparison with some of the results provided by ITE from the large scale experiment (Experiment 1), where aftermath growth was grazed instead of cut as in Experiment 1.

The main objective of these studies was to identify the extent and nature of botanical change at different levels of N, P and K application. Secondary objectives were:

a) to determine to what extent cutting early at a high N rate (as for silage) influences botanical change compared with cutting for hay at the same N rate

b) to investigate if the effects of fertilizers on species diversity and individual species abundance can be mitigated by applying most or all of the annual N application after hay cutting, i.e. after most species have shed seed

c) by comparing the results of this experiment with those of the large scale experiment (Experiment 1), to assess the effects of replacing aftermath grazing with cutting management, with and without fertilizer application.

Plate 5.1. Species-rich, unfertilized vegetation at Tadham Moor

5.2. MATERIALS AND METHODS

The design and management of Experiments 1 and 2, the large scale (LS) and small plot (SP) experiments, have been described in detail in Chapter 3. A list of treatments in the SP experiment and their identifying codes was given in Table 3.1.

THE SMALL PLOT (SP) EXPERIMENT

Measured botanical variables

Measurements of botanical composition were made in May and October each year from 1986-89, with a final assessment in May 1990. At the first assessment, in May 1986, species cover abundance data were obtained from each plot using a vertical point quadrat to record all hits to ground level at 50 points per plot. These data were supplemented by visual scoring for the relative abundance of each species present within eight 20 x 20 cm quadrats per plot and the two data sets were combined to give relative abundance values (% of total live vegetation cover) for each species on each plot. Percentage cover values for dead vegetation and bare ground were also recorded. Plots were assessed by visual scoring only on subsequent occasions, using two randomly-placed 0.40 x 1.25 m (0.5 m^2) quadrats per plot. The presence of any species found within a plot but not appearing within a quadrat was also recorded and given an arbitrary value of 0.01% so that it could be included in the data analyses described below.

Derived variables

The following were used as measures of community structure:

1. The total number of species recorded per plot.
2. The Simpson Index of diversity (SI) (Simpson, 1949). This is calculated from the formula

$$SI=1-\sum_{i=1}^{s}(p_i)^2$$

where p_i = the fraction of individual species i in the vegetation,

s = the number of species in the vegetation

Data analysis and presentation

As in Chapter 3, treatments in Experiment 2 were grouped into four sub-sets or series for statistical analysis, with some treatments common to more than one series. The series were: the Main series (treatments T1-6), these corresponding with the treatments in the large scale experiment (see below) except for the inclusion of treatment T2; the N,P,K series (T1-6, T14-19); the Seasonal series (T5-7, T9-13); the Early *vs.* standard-cut series (T7,8).

Three forms of data analysis are used -

1. Individual species abundance data, the number of species per plot, Simpson's Index and biomass data were analysed separately for treatment effects within the treatment series described above, by analysis of variance (ANOVA) using GENSTAT (GENSTAT V Committee, 1987).

2. Relative abundance data for each species were used to produce dominance-diversity curves (Whittaker, 1965) for each treatment within the N, P, K series, using the treatment means from the May assessment each year 1986-90. Mean species scores were ranked in descending order of abundance within each treatment and year, and plotted on a logarithmic scale against rank order to illustrate progressive changes in community structure and diversity within each treatment.

3. Two forms of ordination were used to relate community composition to N, P and K applications: Canonical Correspondence Analysis (CCA), and Detrended Correspondence Analysis (DCA) (Hill, 1979; ter Braak, 1987-1992). Both ordinations are normally used to relate plant community composition to measured environmental variables, but in this case fertilizer application rates were used as 'environmental' variables.

CCA was used to produce plot (i.e. site) and species ordination diagrams for 1990 data, treating the amounts of N, P and K applied, averaged over the four years 1986-89, as 'environmental' variables.

DCA was used to show changes in plant communities over time. Two species data sets were constructed, each combining data from May 1986 and 1990. In data used to produce the species ordination, species scores for each year were treated as separate species, enabling them to be plotted separately from the same ordination. Sixty-five species were recorded altogether in 1986 and 60 in 1990 (71 overall), so the data matrix consisted of 57 plots x 125 species. Conversely in the plots (i.e. sites) ordination, plot data from each year were treated as if from separate plots, i.e. from a matrix of 114 plots x 71 species (plots 1-57 = 1986 species data; plots 58-114 = species data from 1990). The corresponding 'environmental' data contained zero values for N, P and K in 1986 (plots 1-57) and the average amounts applied 1986-89 for 1990 (plots 58-114). Using this technique, the change in the plant community on each plot between 1986 and 1990 could be calculated as the distance between its two positions on the ordination diagram. Similarly, the relative sensitivity of each species to fertilizer treatment could be inferred from the distance between its 1986 and 1990 positions on the species diagram in relation to the direction of the fitted fertilizer gradients N, P and K.

In this analysis, DCA was preferred because the environmental data are fitted after the ordination process and so do not influence it. Thus the ordinations for each year are not affected by the use of 'dummy' zero values for 1986, whereas CCA actively uses environmental data to produce ordination axes which are constrained to be linear combinations of the supplied environmental (fertilizer) variables (ter Braak, 1987-1992).

COMPARISON OF DATA FROM THE SMALL PLOT (SP) AND LARGE SCALE (LS) EXPERIMENTS

The percent ground cover of each species found within twenty-four 1 m^2 quadrats per plot in the LS experiment was assessed visually in mid-May each year 1986-90. Statistical comparisons between the LS and the SP experiments were not possible because there was no interspersion of plots between the two experiments (Hurlbert, 1984). Instead, dominance diversity curves and separate DCA ordination diagrams were produced using data from the LS experiment, and using data from the SP experiment restricted to treatments equivalent to those in the LS experiment, i.e. treatments T1 and T3-6. For uniformity between the two experiments, individual species data from the LS experiment were first converted to relative abundance, i.e. % of total live vegetation cover and all analyses used plot or treatment means.

Combined 1986 and 1990 data sets were used in DCA analyses as described above for the NPK series. Mean water table depths (WT) for each plot during April to May, derived from readings taken weekly and averaged over four years, were included with amount of N, P and K applied as 'environmental' variables to relate both to 1986 and 1990 data in DCA species ordinations for the LS experiment.

5.3. RESULTS

SPECIES DIVERSITY AND RICHNESS - THE SMALL PLOT (SP) EXPERIMENT

The effects of N, P and K

In 1987, after only one year, all treatments which included N with both P and K in the Main series (T3-T6, 25-R-R to 200-R-R - see Table 3.1) and treatments T18 and T19 (200-75-R and 200-75-200) in the N, P K series led to significantly ($P<0.05$) reduced Simpson's Index (SI) compared to the control (T1, 0-0-0)(Table 5.1). Moreover, by 1987, vegetation on T19 plots was already significantly less diverse than that of T15 plots, which had received the same amount of N but no P and only 'replacement' K. By 1988, species diversity was significantly lower on plots receiving N with the high rate of P (T17, 100-75-R, T18 and T19) than on those receiving the same amount of N but with replacement P and K only (T5,6) ($P<0.01$ for T17 *vs.* T5 and T19 *vs.* T6, $P<0.001$ T18 *vs.* T6). These differences were even greater in 1989 (all $P<0.001$) but, except for T18 *vs.* T6, differences had contracted slightly by 1990 ($P<0.01$). In 1990, species diversity was significantly lower on T18 plots (200-75-R) than on T19 plots, which had received the same levels of N and P but a higher rate of K (200-75-200).

The mean number of species recorded per plot (species richness) was highest in 1987 for all treatments except T8 (400-R-R (EC)) and declined thereafter. The decline in both SI and species richness on T1 control plots was quite marked, and by 1989 control plot SI was significantly lower than that of T2, that had been receiving replacement P and K without N (0-R-R): although there was a decline in species richness on T2 plots which parallelled that on controls, the SI remained fairly stable from 1988 onwards.

Applying N with P and K only at replacement rates, caused losses in species richness which were only marginally greater than those occurring on T1 controls and T2 plots (Table 5.1), even where 200 kg N ha^{-1} was applied each year (T6). However, including a high rate of P severely increased the rate of loss, where either 100 or 200 kg N ha-1 was applied (T17-19 compared with T5 and T6). Conversely, changes in species richness and diversity were minimal where the high P rate was applied without N (T16).

Table 5.1. Species richness and diversity in May each year 1986-90.

Treatment No.	N-P-K code	Mean number of species per 7.5 m^2 plot 1986	1987	1988	1989	1990	Simpson's Diversity Index 1986	1987	1988	1989	1990
T1	0-0-0	33.3	37.3	35.3	33.0	31.7	0.913	0.932	0.872	0.824	0.846
T2	0-R-R	32.0	36.7	34.7	32.7	30.3	0.930	0.938	0.884	0.899	0.900
T3	25-R-R	29.7	37.0	34.0	29.7	29.7	0.931	0.884	0.861	0.890	0.909
T4	50-R-R	30.7	37.0	32.0	29.7	30.7	0.915	0.872	0.874	0.878	0.913
T5	100-R-R	29.3	33.7	28.3	27.3	27.3	0.904	0.885	0.847	0.794	0.887
T6	200-R-R	30.0	36.0	29.7	28.7	28.3	0.899	0.879	0.864	0.872	0.875
T7	400-R-R	30.3	35.7	29.3	27.7	25.0	0.916	0.884	0.861	0.776	0.819
T8	400-R-R (EC)	32.7	31.3	28.0	26.0	24.5	0.922	0.859	0.844	0.842	0.828
T9	0/100-R-R	31.3	33.7	31.3	30.7	29.0	0.918	0.910	0.868	0.830	0.912
T10	0/200-R-R	33.0	35.7	29.0	28.0	26.0	0.922	0.880	0.879	0.883	0.866
T11	50/100-R-R	30.7	33.0	28.7	29.0	26.3	0.913	0.879	0.865	0.835	0.889
T12	50/200-R-R	30.7	32.7	27.7	27.0	26.0	0.921	0.853	0.868	0.866	0.846
T13	100/200-R-R	30.7	34.7	31.3	28.3	26.7	0.911	0.894	0.843	0.871	0.886
T14	100-0-R	28.3	36.0	33.7	32.3	27.0	0.922	0.924	0.799	0.872	0.853
T15	200-0-R	31.3	35.0	30.0	31.3	26.3	0.917	0.910	0.862	0.892	0.893
T16	0-75-R	31.3	37.0	34.7	32.0	32.7	0.917	0.921	0.889	0.807	0.873
T17	100-75-R	28.7	34.3	27.0	23.3	26.0	0.921	0.901	0.672	0.472	0.708
T18	200-75-R	29.0	31.0	27.0	19.0	18.3	0.924	0.887	0.611	0.542	0.512
T19	200-75-200	29.7	30.0	26.3	22.0	19.7	0.912	0.856	0.685	0.527	0.656
s.e.	T1-6 (10)	2.15	1.91	1.36*	1.39	1.87	0.0132	0.0143*	0.0178	0.0138**	0.0183
s.e.	T1-6, T14-19 (22	1.73	1.94	1.42**	1.74***	1.56***	0.0102	0.0151*	0.0437***	0.0522***	0.0463***
s.e.	T5-7, T9-13 (14)	1.46	2.04	1.92	1.04	1.76	0.0118	0.0134	0.0147	0.0336	0.0225
s.e.	T7,8 (2	1.03	3.52	2.32	0.47	1.93	0.0066	0.0197	0.0225	0.0383	0.0153

Asterisks denote significant treatment effects in ANOVA: * = P<0.05; ** = P<0.01; *** = P<0.001 (degrees of freedom in brackets)

Cutting early compared with hay cutting

Neither species richness nor diversity (Table 5.1) was affected by including an extra cut in late May on plots receiving 400 kg N ha^{-1} year^{-1} (T8 *vs.* T7). However, by 1990, species richness for both these treatments was low compared with plots receiving up to 200 kg N ha^{-1} year^{-1} with replacement P and K, with the number of species recorded marginally lower than T17.

Seasonal variation in fertilizer application

Varying the proportions of the total annual N application between spring and mid-summer (after hay-cutting) had no significant effect on either species richness or species diversity (Table 5.1).

SPECIES DOMINANCE-DIVERSITY

Changes in species dominance and diversity for treatments in the NPK series in the SP experiment are shown in Figure 5.1. These changes are indicated in dominance-diversity curves by: a) changes in convexity or concavity of the curve - the more equitable the mix of species the more convex the curve; b) the height of the curve - the higher the cover of the dominant species the higher the starting point of the curve; and c) the spacing in the upper portion of the curve between the dominant species and the remainder.

In 1986, the vegetation on most plots was 'dominated' by the bryophyte *Brachythecium rutabulum*, reflecting the wetter conditions and slower accumulation of vegetation cover in the spring of that year compared to subsequent years. The wetter conditions not only appeared to favour the spread of bryophytes *per se*, but may also have exaggerated their abundance as a proportion of total cover.

The effects of N, P and K

At nil to low N with replacement P and K, changes in species rank order were generally more noticeable than changes in the pattern of dominance (Figure 5.1). However, control plots (T1) became dominated by *Plantago lanceolata*, with notable shifts in the abundance of other species: *Leontodon hispidus* and *L. autumnalis* both became more prominent, whilst *Rumex acetosa, Anthoxanthum odoratum* and *Cynosurus cristatus* declined. The

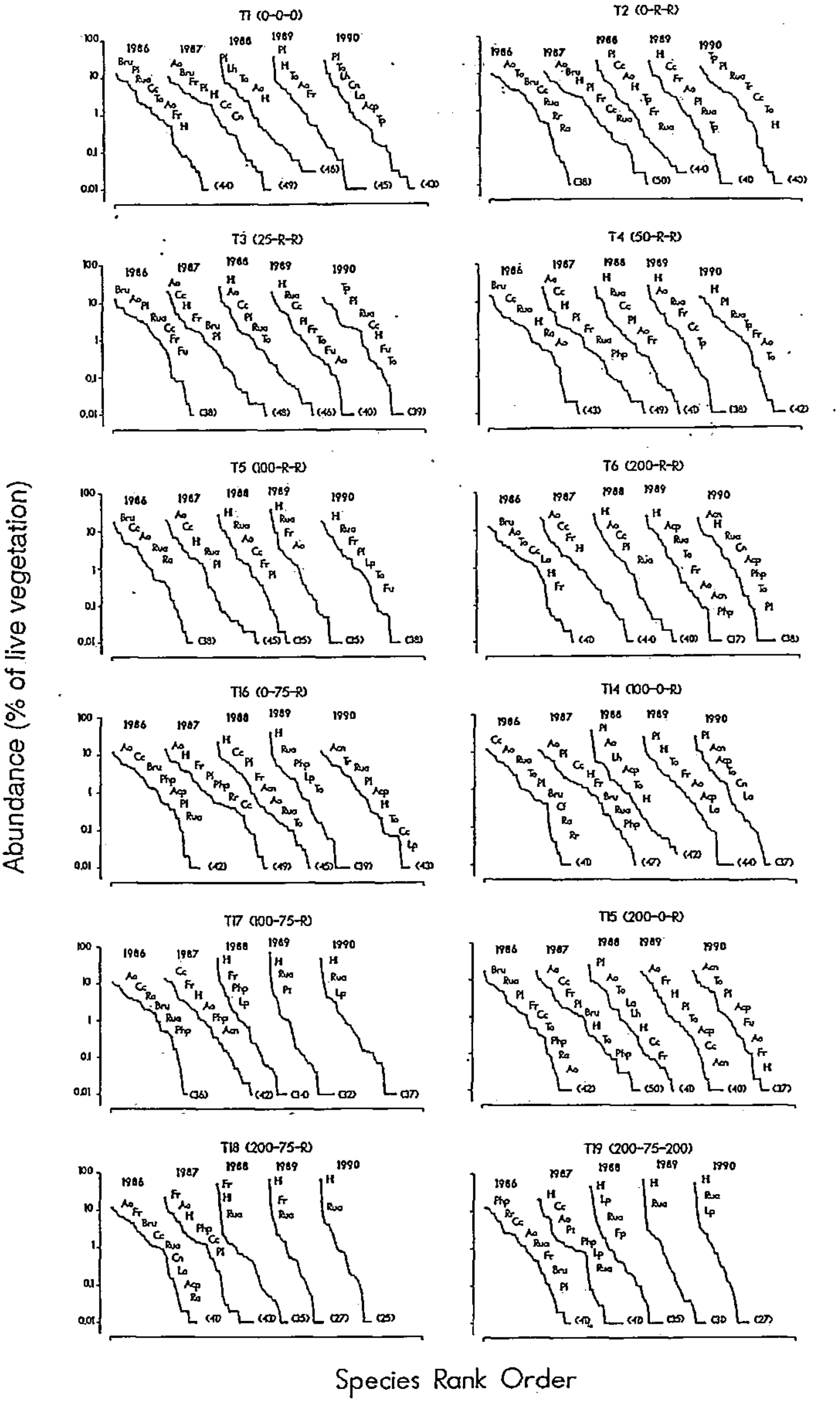


Figure 5.1. Changes between 1986 and 1990 in species dominance-diversity for treatments within the NPK series in the SP experiment. Species of >5% relative abundance are listed in descending order against the appropriate curve (see Table 5.2 for species codes). Species codes are aligned with individual points only where the latter are widely spaced at the top of a curve. Bracketed figures show the number of species for each curve.

Table 5.2. Codes used in Figures for plant species names (taxonomy after Stace, 1991 for higher plants, Smith 1978 for mosses).

Code	Species name	Code	Species name
Acn	*Agrostis canina*	Acp	*Agrostis capillaris*
Ao	*Anthoxanthum odoratum*	Apr	*Alopecurus pratensis*
As	*Agrostis stolonifera*	Bh	*Bromus hordeaceus*
Bp	*Bellis perennis*	Bru	*Brachythecium rutabulum*
Cc	*Cynosurus cristatus*	Ccus	*Calliergon cuspidatum*
Cf	*Cerastium fontanum*	Cn	*Centaurea nigra*
Cpr	*Cardamine pratensis*	Cxd	*Carex disticha*
Cxf	*Carex flacca*	Cxn	*Carex nigra*
Cxp	*Carex panicea*	Dc	*Deschampsia cespitosa*
Dd	*Dactylis glomerata*	Ep	*Eleocharis palustris*
Fp	*Festuca pratensis*	Fr	*Festuca rubra*
Fu	*Filipendula ulmaria*	Gp	*Galium palustre*
Hl	*Holcus lanatus*	Hv	*Hydrocotyle vulgaris*
Je	*Juncus effusus*	La	*Leontodon autumnalis*
Lc	*Luzula campestris*	Lf	*Lychnis flos-cuculi*
Lh	*Leontodon hispidus*	Ln	*Lysimachia nummularia*
Lp	*Lolium perenne*	Lped	*Lotus pedunculatus*
Pa	*Potentilla anserina*	Pam	*Persicaria amphibia*
Php	*Phleum pratense*	Pl	*Plantago lanceolata*
Pp	*Poa pratensis*	Pr	*Potentilla reptans*
Ph	*Poa humilis*	Pt	*Poa trivialis*
Pv	*Prunella vulgaris*	Ra	*Ranunculus acris*
Rr	*Ranunculus repens*	Rua	*Rumex acetosa*
Sa	*Senecio aquaticus*	Sg	*Stellaria graminea*
To	*Taraxacum spp.*	Tp	*Trifolium pratense*
Tr	*Trifolium repens*	Vs	*Veronica serpyllifolia*

extent of *P. lanceolata* dominance that developed on these plots was greater than that of other species on plots receiving 25-200 kg N ha^{-1} with replacement P and K (Figure 5.1). Treatment T14, which received 100 kg N ha^{-1} year^{-1} with no P (100-0-R) was the only other treatment to become dominated by *P. lanceolata* (Figure 5.1). The vegetation on these plots in 1990 differed from that on controls mainly in the greater abundance of *Agrostis canina* and *A. capillaris* (a pattern which developed largely between 1989 and 1990) and the lower proportion of *L. hispidus.* Plots receiving no P but with a higher rate of N (200-0-R), were transitorily dominated by *P. lanceolata* in 1988, but by 1990 were dominated by *A. canina.*

Where all three elements were applied, *Holcus lanatus* tended to dominate (Figure 5.1), particularly with P at the high rate (T17-19 - Figure 5.1), where it comprised 47-66% of the vegetation in 1990. On these plots, *Rumex acetosa* became a secondary dominant, particularly when a high rate of K was applied (T19). By 1988, *Holcus lanatus* had also become dominant where high P was applied without N (T16, 0-75-R); but, as on most other plots, it declined between 1989 and 1990. This left a more even species distribution on T16 plots, with *A. canina, Trifolium repens* and *R. acetosa* the most common species.

By 1990, *Lolium perenne* was also prominent on plots receiving N with high P (Figures 5.1 and 5.2), but remained at very low levels of abundance where only replacement P and K were applied (Figure 5.2). Both this species and *Festuca rubra* changed in abundance on high P plots in apparent interaction with *H. lanatus*, with the main changes occurring during 1988 (Figure 5.2): during 1987 *Festuca rubra* increased progressively in dominance on T18 (200-75-R) plots, reaching a peak in May 1988; but by October 1988 it had declined sharply and remained at a low level thereafter. *Holcus lanatus*, which had also been increasing on these plots, showed a steeper increase between May and October 1988 that matched the decline in *F. rubra*. From 1986 to 1988, *Lolium perenne* had increased on T19 (200-75-200) along with H. lanatus, but declined sharply during 1988, whilst *H. lanatus* increased correspondingly (Figure 5.2). These effects coincided with a later than normal hay harvest in 1988 that may have favoured *H. lanatus* at the expense of other species.

Trifolium pratense increased between 1986 and 1990 on all plots receiving little or no N (Figure 5.1). This was particularly noticeable where P and K were applied at replacement rates, with *T. pratense* dominating T2 (0-R-R) and T3 (25-R-R) plots by 1990, and prominent in T4 plots (50-R-R). *Trifolium repens* became prominent on T16 plots in 1990.

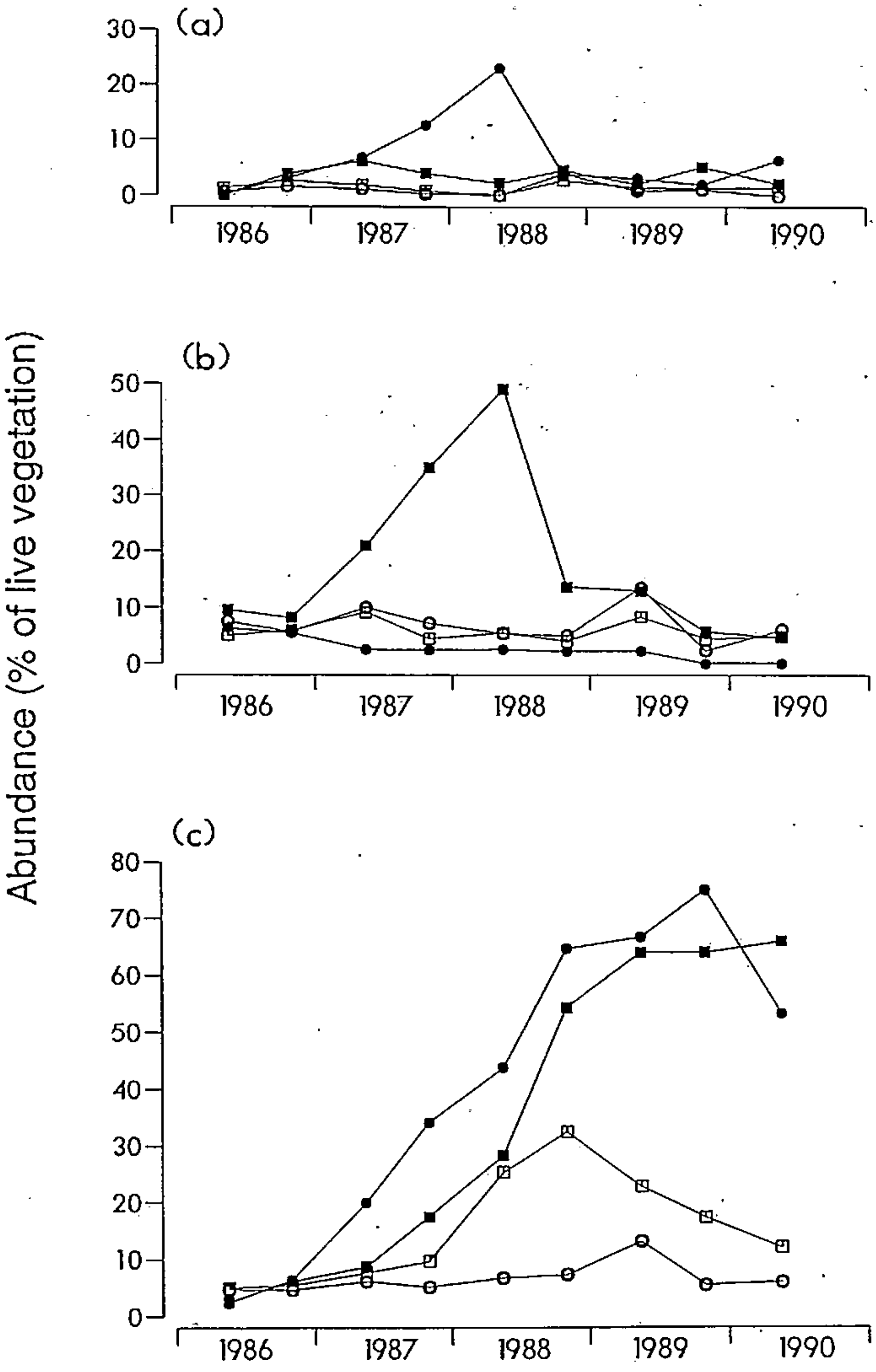


Figure 5.2. Changes between 1986 and 1990 in the relative abundance (% of total live vegetation cover) of three grasses on plots receiving 200 kg N ha^{-1} $year^{-1}$ with differing amounts of P and K in the SP Experiment. (a) = *Lolium perenne*; (b) = *Festuca rubra*; and (c) = *Holcus lanatus*. Open squares = P and K 'replaced' (see Table 3.1); filled squares = 75 kg P ha^{-1} $year^{-1}$ (P75) with K replaced; open circles = nil P, K replaced; filled circles = P75 + 200 kg K ha^{-1} $year^{-1}$.

Early cutting compared with hay-cutting (curves not shown)

There was little difference in the pattern of dominance-diversity between treatments T7 and T8 until 1989, by which time *H. lanatus* had become more abundant on T7 plots (39% of total live cover) than T8 (24%). However, by May 1990, *Agrostis capillaris*, *H. lanatus* and *A. canina* were co-dominant on T7 plots, whilst *H. lanatus* had increased on T8 plots to 32% of vegetation cover.

Seasonal variation in fertilizer application

Differences in species dominance between T5 (100-R-R) and T9 (all the N applied after hay-cutting - 0/100-R-R) were small until 1990 when a more even species distribution had developed on T9 plots (curves for T7-T15 not shown). *Centaurea nigra* increased in general abundance in 1990 and became co-dominant with *R. acetosa* on both T9 and T10 (0/200-R-R) plots. *Agrostis canina* dominated T6 (200-R-R) plots in 1990, but was less abundant on T10 plots, although both this species and *A. capillaris* were amongst those contributing >5% of the vegetation with both treatments.

SPECIES-FERTILIZER ORDINATION (SP EXPERIMENT)

Ordination of 1990 data

Figure 5.3 shows the species/fertilizer biplot given by CCA ordination of 1990 data from the N, P, K treatment series. The heavy arrows indicate the direction of the N, P and K gradients. Their relative lengths show the importance of each in determining the ordination, indicating that P was more influential than either N or K, although there was close correspondence between the P and K gradients.

The ordination (Figure 5.3) suggested that the positive fertilizer responses of *Rumex acetosa, Lolium perenne* and particularly *Poa pratensis* were more closely associated with P and K than N, whereas *Alopecurus pratensis, Holcus lanatus* and *Poa trivialis* were as closely associated with N as with P and K. *Leontodon hispidus, L. autumnalis, Plantago lanceolata* and, to a lesser extent, *Potentilla reptans*, were negatively associated with all three elements, particularly P and K.

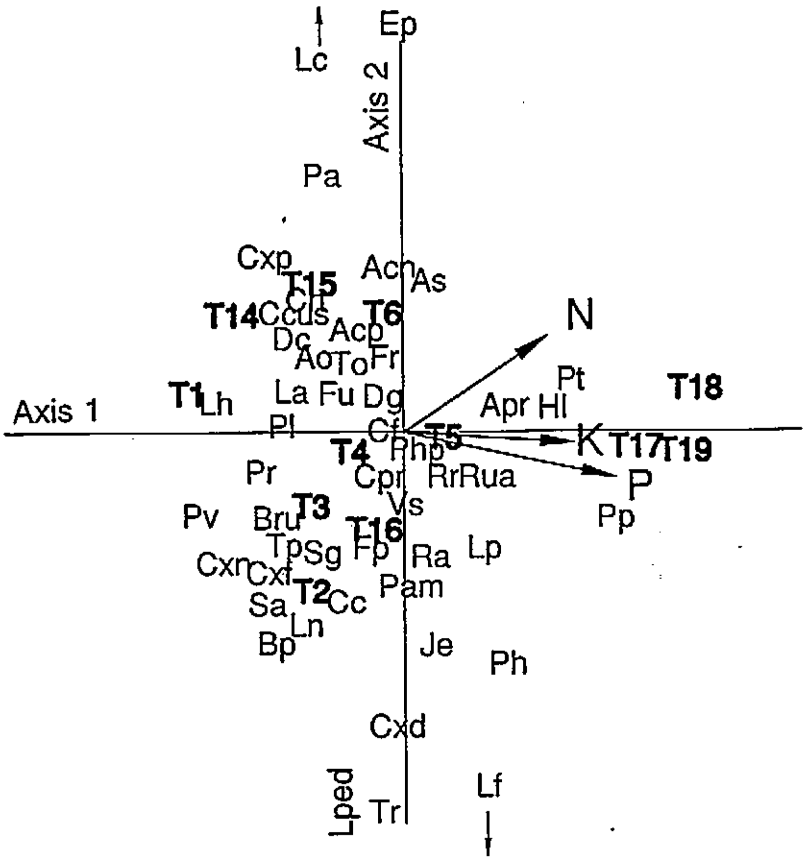


Figure 5.3. Ordination diagram of species and treatments produced from Canonical Correspondence Analysis (CCA) of 1990 species abundance data related to the amounts of N, P and K applied within the NPK treatment series in the SP experiment (see Table 3.1). Symbols in bold type represent the mean ordination position of plots of each treatment. See Table 5.2 for species codes. The positions of the large arrows indicate the direction of the fertilizer gradients, whilst their relative lengths indicate the importance of each in determining the ordination.

In Figure 5.3, the juxtaposition of control plots (T1) with those of treatment T14 (100-0-R) plots, and to a lesser extent T15 (200-0-R), confirmed the similarity between these treatments, which showed a strong negative association with P. Associated species were *Carex panicea, Centaurea nigra, Calliergon cuspidatum* and, to a lesser extent, *Deschampsia cespitosa*. Treatment T6 (200-R-R) plots were positioned in the same quadrant as T1, T14 and T15 with respect to the first two axes, but close to Axis 2, indicating a small positive correlation with N and a slight negative correlation with P (Figure 5.3). However, in contrast with most other treatments and species, treatments T1, T6 and T14 were better separated by their scores on the third ordination axis (scores -0.06, 0.31 and -0.69 respectively). This axis was more closely correlated with K (r=0.43) than either N (r=0.16) or P (r =-0.15). Axis 1 was very closely correlated with P (r=0.81), followed by

K (r=0.65) and then N (r=0.54). Axis 2 was poorly correlated with both P (r=-0.27) and K (r=-0.06), but more closely correlated with N (r=0.57).

Intermediate N treatments were clustered around the centre of the biplot, whilst all those receiving high P with N were positioned to the far right of Axis 1, closely associated with the P gradient.

Change between 1986 and 1990 - DCA ordination

In the DCA diagram for plot ordination (Figure 5.4a), the distance between the 1986 and 1990 orientations for a particular treatment is a measure of the overall change in its botanical composition. These distances were large for all treatments. Control (T1) plots ranked fifth in descending order of magnitude of these distances, only marginally lower than T6 (200-R-R) plots. The rank order for all treatments in descending order was as follows: T18, T19, T17, T6, T1, T15, T14, T3, T2, T4, T16,and T5, with the vector distance for the lowest treatment just under half that of the highest.

Of the total of 71 species recorded on plots of the N, P, K series in 1986 and 1990, 52 were recorded in both years. Vector distances between 1986 and 1990 coordinates (Figure 5.4b) were calculated for each of these species from DCA ordination of all species scores and ranked in descending order of magnitude.

Ter Braak (1987) has noted that, since environmental variables are fitted after ordination in DCA, this can lead to the effects of a particular environmental variable being poorly represented or even missed altogether. Therefore, in interpreting the data more weight is placed upon the magnitude of the vector distance for each treatment or species than upon its direction in relation to the fitted fertilizer variables. Fertilizer gradients are shown only in species/fertilizer biplots where DCA is used. The angle made by particular vectors with each fertilizer gradient is used hereafter as a secondary descriptor of vegetation change between 1986 and 1989. An angle of 45° or less is taken to imply a correlation (+ or -, depending upon the orientation of the 1986 and 1990 species positions relative to the gradient).

The P and K gradients on the DCA species diagram (Figure 5.4b) lie too close to each other to differentiate between them, but the angles between these and the N arrow

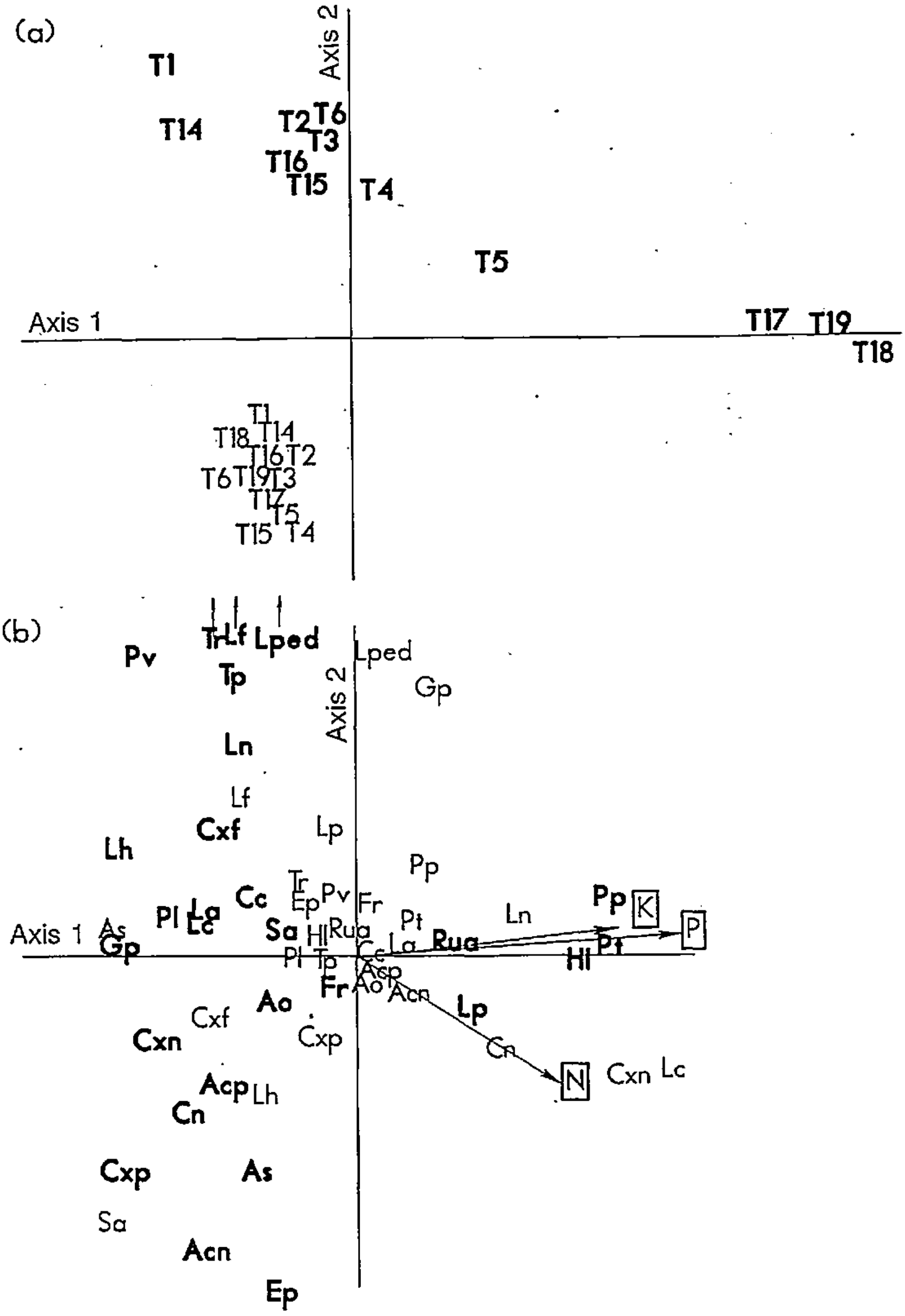


Figure 5.4. Ordination diagram produced by Detrended Correspondence Analysis (DCA) of combined 1986 and 1990 species abundance data from the NPK series in the SP experiment, showing changes between 1986 (normal type) and 1990 (bold type) in: (a) the mean ordination position of plots of each treatment; and (b) the position of each species (see Table 5.2 for species codes). Arrows in (b) show the direction and relative strength of correlation of the fertilizer (N,P and K) gradients fitted to the data after ordination (ter Braak, 1987-1992).

allow some inferences to be made about the independent effects of N *vs* P/K. Most species show an appreciable difference between their 1986 and 1990 positions on the ordination. Of the 21 species showing above average differences in ordination position, 12 showed an apparently negative reaction to N and/or P/K. Of these, *Lychnis flos-cuculi* showed the greatest difference (-N), whilst the vectors for *Trifolium repens* (-N), *Luzula campestris* (-N, -P/K) and *Carex nigra* (-P/K, -N) were twice the average distance or more (Figure 5.4b). Other species showing changes which are >1.5 times the average and apparently related to fertilizer application were: *Lysimachia nummularia* (-N, -P/K), *Centaurea nigra* (-P/K), *Prunella vulgaris* (-N) and *Trifolium pratense (-N)*. Of the remaining species showing above average changes, only three appeared to be positively correlated with fertilizer: *Agrostis stolonifera* (+N), *Holcus lanatus* (+P/K, +N) and *Lolium perenne* (+N). *Lolium perenne* differs in this analysis compared with the CCA in that the latter suggested a closer correlation with P and K than N.

Galium palustre, Eleocharis palustris, Senecio aquaticus and *Agrostis canina* all showed large differences in ordination position between 1986 and 1990 (1.6-2.0 x average) but which were apparently independent of applied N, P or K (Figure 5.4b). These effects may have been related to the change from aftermath grazing to management by cutting only with the commencement of the experiment (see later discussion).

The reactions of *Holcus lanatus* and *Rumex acetosa* (Figure 5.4b) were associated with both N and particularly P/K, in agreement with the CCA (Figure 5.3). Although CCA ordination did not differentiate between N and P/K in influencing *Poa trivialis*, DCA suggests a strong positive correlation with P/K for this species, whilst the influence of N was much less clear. The strong positive influence on *P. pratensis* of both N and P/K shown by CCA was confirmed by DCA. Several species showed little difference in ordination position between 1986 and 1990, notably: *Taraxacum* spp., *Filipendula ulmaria, Cardamine pratensis, Ranunculus acris, R. repens* and *Myosotis discolor*. These species were mostly clustered around the centre of the diagram and have been omitted for clarity.

COMPARISON BETWEEN THE LARGE-SCALE AND SMALL PLOT EXPERIMENTS

Changes in species abundance and diversity in the large-scale (LS) experiment (Experiment 1) have been described in detail elsewhere (Mountford *et al.*, 1993a) and are summarised

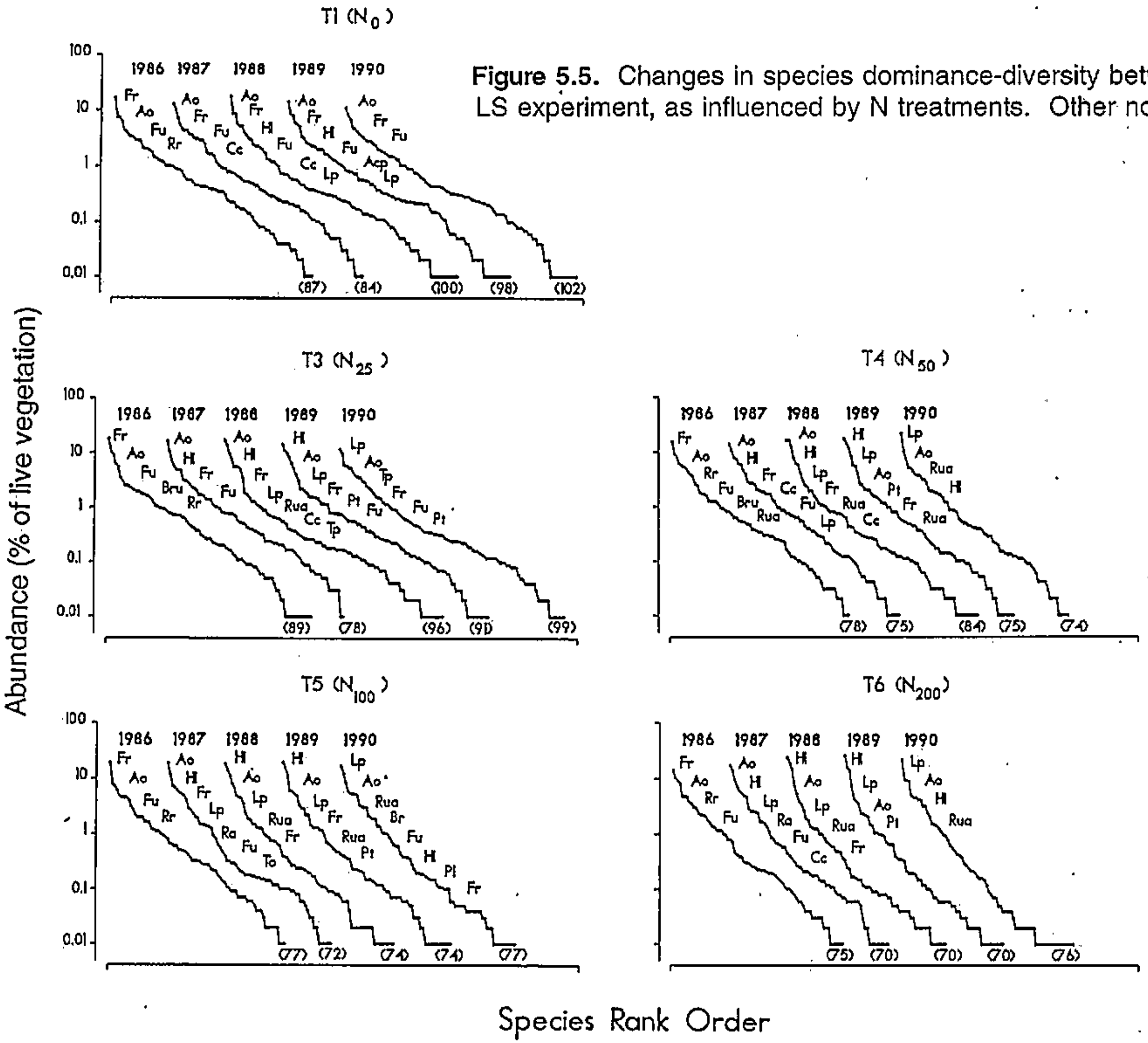


Figure 5.5. Changes in species dominance-diversity between 1986 and 1990 in the LS experiment, as influenced by N treatments. Other notes as in Figure 5.1.

only briefly here in comparison with results from equivalent plots in the SP experiment (Experiment 2).

All treatment plots in the LS experiment were dominated initially by *Festuca rubra* (notably more abundant here than in the SP experiment), with *Anthoxanthum odoratum* and *Filipendula ulmaria* always prominent (Figure 5.5). *Brachythecium rutabulum,* although more prominent in 1986 than subsequent years in both experiments, was less abundant overall in the LS experiment than on the small plots, as were *Cynosurus cristatus, P. lanceolata* and *L. hispidus* (Figures 5.1 and 5.5).

Changes in dominance diversity 1986-1990

The composition of control plots in the LS experiment was notably more stable than in the SP experiment, with the general pattern of dominance-diversity remaining relatively unchanged in the former (Figure 5.5). *Holcus lanatus* increased under the influence of fertilizers in both experiments, but there was a concomitant increase in *Lolium perenne* on LS plots which represented a notable difference between experiments (Figures 5.1 and 5.5). In the LS experiment, *L. perenne* had replaced *H. lanatus* as the dominant species on all fertilized plots by 1990. However, in the SP experiment, the decline of *H. lanatus* which occurred with most treatments between 1989 and 1990 was not associated with an increase in dominance of any other species, except for the increase in *Agrostis canina* on T6 plots (200-R-R, equivalent to N_{200} in LS experiment) and, to a much lesser extent, the increase in *Trifolium pratense* on T2 (0-R-R) plots (Figure 5.1).

Trifolium pratense increased at the lowest N rate (T3) in both experiments (N_{25} and 25-R-R), particularly between 1989 and 1990, but the increase was more marked in the SP experiment (Figures 5.1 and 5.5). This species also became more prominent at 50 kg N ha^{-1} (T4) in the SP experiment than on LS plots, but was reduced by high N rates in both experiments.

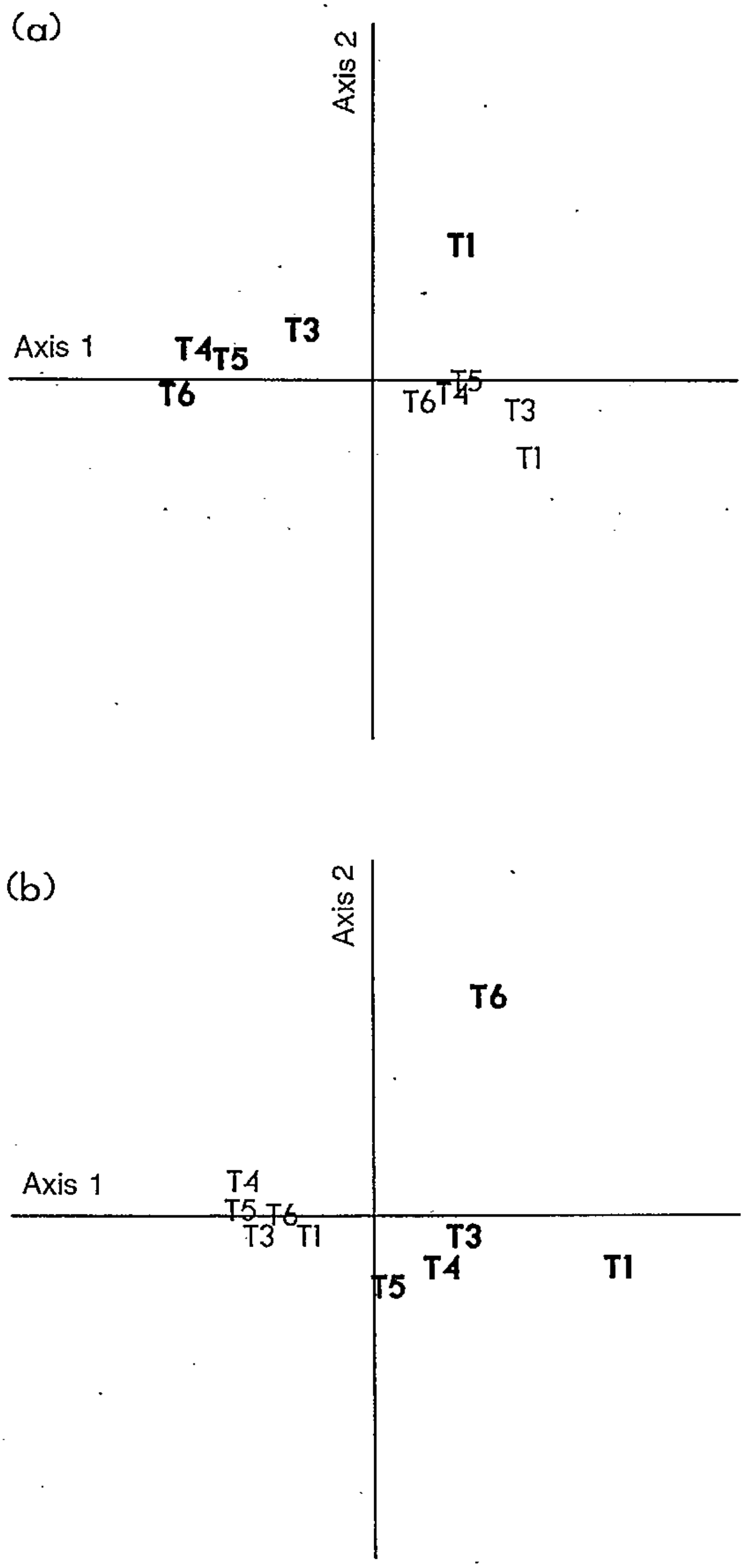


Figure 5.6. Ordination diagrams produced from Detrended Correspondence Analysis (DCA) of combined 1986 and 1990 species abundance data from (a) the LS experiment and (b) the SP experiment, showing changes between 1986 (normal type) and 1990 (bold type) in mean ordination position of plots of each treatment.

Species-fertilizer ordination - change between 1986 and 1990

DCA ordination of species data from the SP experiment was repeated using data only from treatments equivalent to those in the LS experiment. To help compare experiments, the codes T1 and T3-6 are used to refer to these five treatments in both experiments.

In the DCA plot ordination for the LS experiment (Figure 5.6a), the first (horizontal) axis was closely correlated with all four variables N, P, K and WT. The mean ordination positions for most of the treatments in both 1986 and 1990 were distributed mainly around this axis, with the direction of 1986-90 change corresponding with increasing N, P, K and WT depth. However, changes between 1986 and 1990 positions for each treatment showed a marked anti-clockwise rotation with increasing N rate, with a notional line joining these positions for treatment T1 (N_0) making an angle of about 70° to the left of the horizontal axis (Axis 1), but with a corresponding line for treatment T6 (N_{200}) running parallel with this axis.

Changes in the mean ordination positions for each treatment between 1986 and 1990 were generally greater in the SP experiment than in the LS experiment (Figure 5.6b. Moreover, the mean change for T1 was exceeded only by that for T6 in the SP experiment, whilst the corresponding changed in the LS experiment was exceeded by those of all treatments except T5. In the SP experiment, the direction of change in orientation of T1 control plots corresponded with that shown by all the fertilizer treatments except T6. This reflects the fact that, as noted earlier, the N, P and K variables were not involved in the DCA ordination, which merely indicates the magnitude of overall differences in species scores between treatments/years.

In the DCA biplots for species (Figure 5.7a and 5.7b), some species showing little response to fertilizer gradients and clustered around the centre of these diagrams were omitted for clarity. These ordinations showed several marked differences in species reaction between experiments. Whilst changes in ordination position of *Lolium perenne, Holcus lanatus* and *Rumex acetosa* were more positively associated with P and K than N in both experiments (Figures 5.7a and 5.7b), all three species showed much greater changes in the LS experiment (Figure 5.7a) than the SP experiment (Figure 5.7b). This was particularly true of *L. perenne,* which showed a negligible reaction in the SP experiment. *Agrostis capillaris* and particularly *A. canina* showed comparatively large

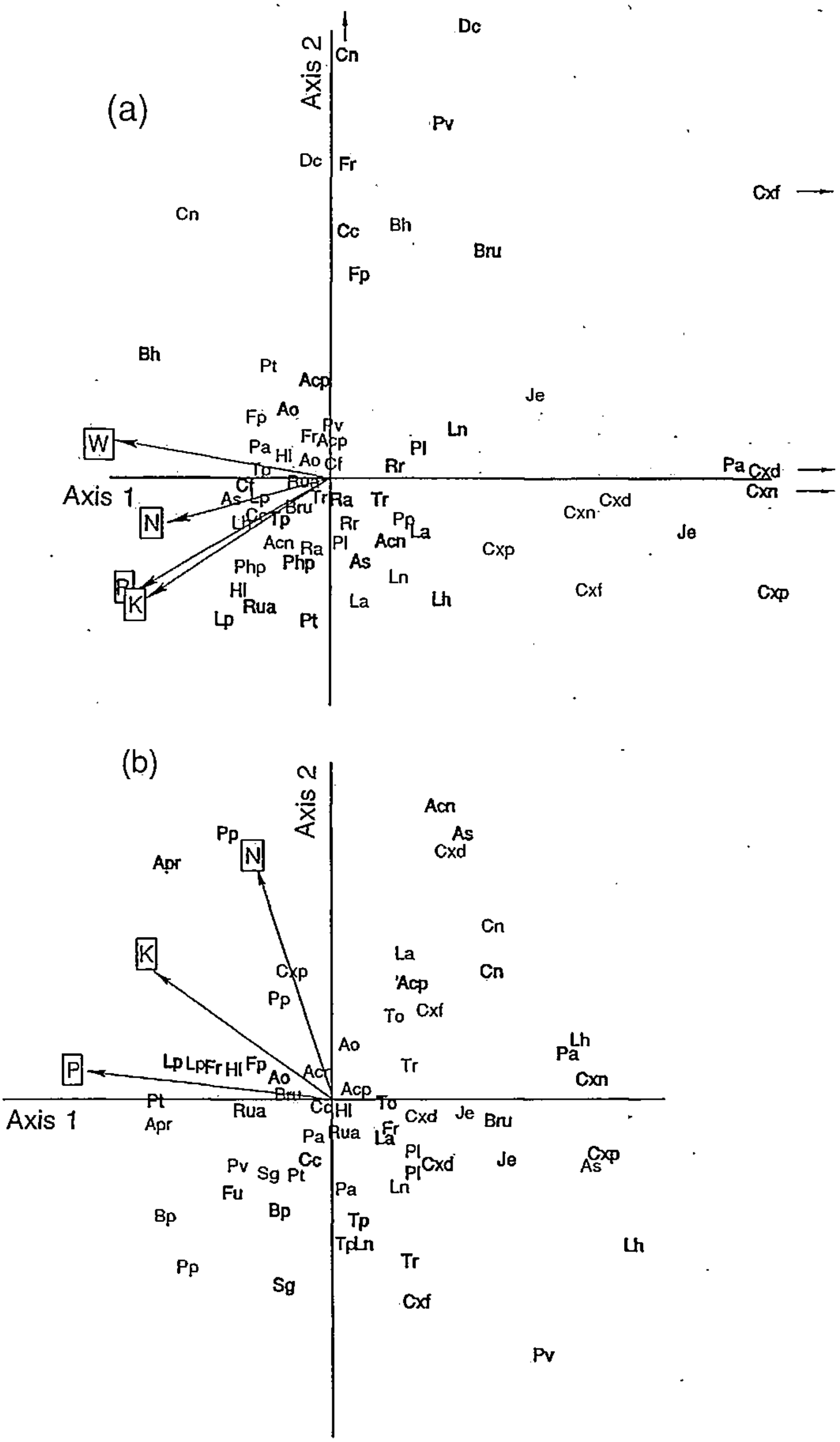


Figure 5.7. Ordination diagrams produced from Detrended Correspondence Analysis (DCA) of combined 1986 and 1990 species abundance data from: (a) the LS experiment; and (b) the SP experiment, showing changes in species orientation between 1986 (normal type) and 1990 (bold type). Other notes as for Figure 5.4 (b).

reactions in the SP experiment, both apparently independent of P and K and at about 45° to the N gradient (Figure 5.7b). These species differed in their reactions in the LS experiment, changes in *A. canina* appearing to be negatively associated with N and those of *A. capillaris* independent of all four gradients (Figure 5.7b).

Several other species, notably *Plantago lanceolata*, *Leontodon hispidus*, *L. autumnalis*, *Cynosurus cristatus*, *Potentilla anserina* and *Festuca rubra*, responded differently between experiments, either in the extent or in the direction of change in their apparent reaction to fertilizer gradients (Figure 5.7). Ordination positions for all the *Carex* spp. changed markedly in both experiments, in a direction away from the N, P and K gradients. The vector distances for *C. flacca* were particularly large in both experiments, although that for *C. panicea* was larger than for *C. flacca* in the SP experiment. However, except for *C. flacca*, changes in ordination position of *Carex* species and of *Juncus effusus* in the LS experiment were more closely associated with WT depth than fertilizer application (Figure 5.7a).

5.4. DISCUSSION

As noted in Chapter 3, the range of objectives set for the SP experiment did not allow a full N x P x K factorial design and in no treatment was P applied without K. Nevertheless, the results consistently showed P to be the most influential of the three elements, both in causing botanical change and in determining herbage production (see Chapter 3).

In much of the previously published work where inorganic fertilizers have been used in mixed species vegetation, botanical change and increased herbage production have been closely correlated (e.g Lawes and Gilbert, 1858, 1859a,b; Brenchley and Warington, 1958; Willis, 1963; Reith *et al.*, 1961, 1964; Heddle, 1967; Williams, 1978, 1984; Garstang, 1981; Bobbink, 1991). In an analysis of data from the Park Grass Experiment, Silvertown (1980a) suggests that there is a generality about this relationship which is independent of the actual species involved.

Experiments in the UK, testing the effects of nitrogen (N), phosphorus (P) and potassium (K) on herbage production, have seldom shown significant yield response to P on mineral soils, although several have shown response to K and significant N x K interactions (Castle and Holmes, 1960; Reith *et al.*, 1961; Widdowson *et al.*, 1965; Heddle, 1967). In these experiments, N was the major element influencing both herbage production and botanical composition. However, peat typically contains about half the P normally found in mineral soils (Brady, 1990). In experiments to determine the minimum fertilizer requirements for improved pasture on deep peat, Floate *et al.* (1981) showed that high rates of both P and K were necessary for pasture establishment and for the maintenance of *Lolium perenne* and *Trifolium repens.* Botanical studies where P has been tested independently of N on peat soils are rare, although Murphy (1960) showed this element to have a strong influence on botanical composition and yield in blanket bog and at a drier site. Korkman (1976) showed that P alone could increase the yield of hay and various root crops on *Carex*-peat soil in Southern Finland, whilst he estimated that the soil had supplied 140 kg N ha^{-1} year^{-1} to hay crops. Phosphorus was the main element limiting biomass production in a 'late'-succession mesotrophic fen in Holland, whilst N was more important in two 'mid'-succession fens (Verhoeven and Schmitz, 1991). The role of P as the major determinant of both productivity and botanical composition in the SP experiment is therefore in line with these findings.

However, it is worth noting that at the last assessment on the SP experiment reported in this study (in May 1990), species diversity (Simpson's Index) was significantly *lower* on plots which had received high rates of both N and P but with only replacement rates of K, compared with those which had received the same rate of N and P with a *high* rate of K (200 kg K ha^{-1}). This effect was contrary to that shown by biomass data, with herbage DM yield significantly higher where the high rate of K was used (Chapter 3). The difference between these plots in the number of species present was minimal in 1990, when treatments were discontinued, but subsequent recovery of species richness was much more marked on plots which had received the high rate of K than where replacement rates had been applied (Tallowin *et al.,* 1995). These results support the suggestion by Tilman (1982) that the ratios in which nutrient resources are available to plants may be as significant as their absolute levels in determining vegetation composition and species diversity.

The comparatively high levels of plant available N recorded in soils at the site (see Chapter 4) allowed a significant DM response to P and K applied without N (Chapter 3). This response was accompanied by changes in individual species abundance, although not by significant differences in the number and diversity of species compared to unfertilized plots. However, there were also changes in vegetation composition on plots receiving no fertilizer in both experiments, particularly in the SP experiment where changes in dominance-diversity were greater than where low to moderate fertilizer rates were used. These changes were most likely to have been due to the change from grazing to cutting in the second half of the season that occurred with the initiation of the SP experiment. Two possible mechanisms were involved. Firstly, grazing is important for the recycling of nutrients in grassland (Jarvis *et al.*, 1989a; Gillingham, 1987). When no fertilizers are applied, a change to repeated removal of herbage by cutting instead of aftermath grazing can be expected to lead to a progressive depletion of soil mineral reserves. Soil analyses carried out in 1990 suggested that depletion of both P and K had occurred on unfertilized plots in the SP experiment (Chapter 3) and this may have led to the observed increase in abundance of the stress-tolerant species *P. lanceolata* and *L. hispidus* (Grime, 1973a,b, 1979; Grime *et al.*, 1988) on these plots. Secondly, disturbance of the soil and vegetation caused by grazing animals provides niches for seedling establishment and this is important in maintaining species diversity (Grubb ,1977; Watt and Gibson, 1988).

A loss of species richness following the cessation of aftermath grazing was evident on all plots in the Park Grass Experiment, including those receiving no fertilizer. For fifteen of the first 21 years, until 1877, plots were grazed after hay-cutting and the number of species recorded on control plots remained remarkably constant at about 50 (Lawes *et al.*, 1882). The plots were not grazed after 1877 and the number of species declined progressively thereafter to an average of 37 (Williams, 1978). This change was accompanied by a decrease in the proportion of grasses and a tendency for *L. hispidus, P. lanceolata* and *Poterium sanguisorba* to dominate. These results are strongly parallelled by those of the SP experiment. Furthermore, in studies on hay meadows in the Yorkshire Dales, preventing autumn and early spring grazing has been shown to have more effect on species diversity than has the application of fertilizers (Younger and Smith, 1993).

Increases in several species, notably *Lolium perenne, Holcus lanatus* and *Rumex acetosa,* appeared to be more closely associated with the application of P and K than N in both experiments. Changes in vegetation caused by the N_{25} treatment in the LS experiment were probably attributable more to the replacement amounts applied of these two elements than to N. Differences between treatments T2 and T3 (0-R-R and 25-R-R) were small in the SP experiment. Both of these treatments, and N_{25} in the LS experiment, caused greater abundance of legumes, particularly *Trifolium pratense,* although increases in this species were more marked in the SP than the LS experiment, possibly reflecting its intolerance of trampling and heavy grazing (Grime *et al.*, 1988). Substantial increases in legumes are undesirable for maintenance of species diversity, since this will lead to a greater availability of N by biological fixation.

One of the main objectives of the work at Tadham Moor was to determine whether there was a level of fertilizer which could be used without significant change in the botanical composition of the meadows. The effect of low fertilizer rates was therefore of primary interest, despite the sparsity of data on the effect of fertilizers in general on this type of vegetation growing on peat soils. Both experiments show that even small increases in fertility in these meadows will lead to significant botanical change. In the LS experiment, differences in species richness as a percentage of control plot values showed a significant downward trend over the 1986-1990 period (measured by regression analysis) for all N treatments, including N_{25} (Tallowin *et al.*, 1995). After a further two years of continued treatment, species richness in plots of all the treatments was significantly lower than that of the control (by analysis of variance - Mountford *et al.*, 1993b). These results are significant in the light of current ESA regulations (Her Majesty's Stationery Office, 1992), which permit 75 kg N, 16 kg P and 31 kg K ha^{-1} $year^{-1}$ in Tier 1, and 25 kg N, 6 kg P and 10 kg ha^{-1} K in Tier 2, with no fertilizer allowed in Tier 3 which attracts the largest payments. Clearly, maximum species diversity will not be maintained or restored unless Tier 3 regulations are adopted. Indeed, continuing studies at Tadham Moor are showing that restoration of species diversity following simple cessation of fertilizer use is a very slow process (Mountford *et al.* 1993b).

The results of both the experiments reported here emphasise the potential instability of species-rich communities. The LS experiment was conducted within the framework of July hay-cutting followed by aftermath grazing, reflecting as far as possible the management previously imposed over a long time scale. There were changes in botanical composition on control plots in the LS experiment, possibly due to an increase in grazing intensity adopted to measure potential beef production (Chapter 3). However, these were small compared with those on equivalent plots in the SP experiment, where aftermath grazing was replaced by cutting and removal of herbage. Aftermath grazing is one of the requirements for hay and silage fields in all three Tiers of the ESA scheme (Her Majesty's Stationery Office, 1992). Although this provision is aimed at ensuring a heterogeneous sward structure for the benefit of overwintering birds, it is clear from these results that both the prevention of fertilizer use and the maintenance of aftermath grazing are essential for preserving species diversity in hay meadows.

5.5. CONCLUSIONS

P was the most influential of the three macronutrients tested in determining both biomass production and botanical change. Applying P and K without N appeared to stimulate mineralization of organic N and increased N uptake by plants, causing both a significant increase in biomass production and significant botanical change.

Comparison of results from the two experiments suggested that marked changes in botanical composition on unfertilized plots in the SP experiment were attributable to the cessation of aftermath grazing, probably due to the combined effects of depletion of soil mineral reserves and a reduction in the amount of disturbance and gap creation.

Even low levels of inorganic fertilizer use will lead to a significant reduction in species diversity after only a few years. The results of the two experiments seen together suggest that only Tier 3 regulations within the ESA scheme, which require both aftermath grazing and preclude fertilizer use, will be effective in maintaining species diversity within these and similar meadows.

5.6. SUMMARY

A range of nitrogen (N), phosphorus (P) and potash (K) fertilizer treatments was applied for four years in a randomized block experiment to a species-rich hay meadow on peat soil within the Somerset Levels Environmentally Sensitive Area. The relative abundance (%) of each species present was recorded in May and October each year on plots cut for hay followed by further cuts of aftermath growth. The effects on species richness, diversity and dominance were analysed, and ordination techniques were used to investigate the effects of fertilizers on plant community composition. The results were also compared with those of a concurrent experiment where aftermath growth was grazed.

P was more important than N in determining botanical change. Changes in botanical composition were small when substantial amounts of N and K were applied without P, but when high rates of P were included species diversity was severely reduced, with *Holcus lanatus, Rumex acetosa* and *Lolium perenne* dominating. *Lolium perenne* was not increased by N and modest rates of P in the absence of aftermath grazing, but dominated all fertilized plots when aftermath grazing was maintained. *Agrostis canina* came to dominate plots receiving 200 kg N ha^{-1}, with modest rates of P and K in the absence of aftermath grazing, but was negatively associated with N where the aftermath was grazed. *Trifolium pratense* became very abundant where P and K were applied with nil or 25 kg N ha^{-1} each year, both with and without aftermath grazing, but all legumes were suppressed at high rates of N, particularly in conjunction with high P.

Substantial changes in botanical composition and reductions in species diversity occurred on unfertilized plots as a result of the cessation of aftermath grazing. These plots became dominated by *Plantago lanceolata*, with significant increases in *Leontodon hispidus* and *L. autumnalis*.

CHAPTER 6

SOIL SEED BANK COMPOSITION IN RELATION TO THE ABOVE GROUND VEGETATION IN FERTILIZED AND UNFERTILIZED HAY MEADOWS

6.1. INTRODUCTION

Grassland seed banks are generally smaller than those of arable soils (Warr *et al.*, 1993), since the high levels of disturbance associated with the latter cause intense selection for species with a persistent seedbank (Thompson, 1978; Grime, 1979). The largest grassland seedbanks recorded by Chippendale and Milton (1934) were in lowland pastures formerly in an arable rotation (21,259-69,903 seeds m^{-2} in the top 30cm), although large numbers were recorded beneath fertile marsh (31,345 seeds m^{-2}) and hay meadows (28,310 seeds m^{-2}).

There is usually a marked dissimilarity between the composition of grassland seed banks and the above ground vegetation (e.g. Chippendale and Milton, 1934; Champness and Morris, 1948; Major and Pyott, 1966; Thompson and Grime, 1979). This dissimilarity is mainly attributable to differences between species in seed bank persistence (Thompson and Grime, 1979), but the effect can be enhanced when the current or recent management of the vegetation differs from that in the past (Chippendale and Milton, 1934; Bakker, 1989). However, changes in vegetation cover of individual species caused by inorganic fertilizers will be reflected in changes in their seed bank abundance (Williams, 1985; Milberg, 1992), so that there can be correspondence between seed bank and vegetation when within-species comparisons are made using data from both fertilized and unfertilized soils. In work by Williams (1985), differences between fertilized and unfertilized plots in the abundance of the dominant species were more marked in the seed bank than in the vegetation after 14 years of fertilizer application, and this effect was enhanced after a further five years.

Extensive vegetation surveys carried out in the experiments at Tadham Moor since 1986 have shown significant effects of fertilizer treatments on species richness and diversity and on the abundance of individual species (Sargent and Smyth, Mountford and Smyth, Mountford, unpublished annual reports; Mountford *et al.*, 1993a; see also Chapter 5). However, prior to the work reported in this chapter, the seed bank had not been recorded in these meadows nor, apparently, in meadows of similar vegetation elsewhere. This in itself represents a significant gap in the understanding of the plant ecology of wet hay meadows. It is also important to know the extent to which the seed bank has been modified by fertilizer use over a comparatively short time (five years) and how any such changes might influence the potential for restoring the above-ground vegetation to its original composition.

This chapter describes measurements of vegetation and seed bank composition made in 1991 on plots marked out within the layout of Experiment I. The areas used were those which had either never received inorganic fertilizers (N_0), or had received 200 kg N ha each year between 1986 and 1990 (N_{200}), with P and K applied at rates sufficient to replace the amounts removed in hay each year. Data were related both to the seed bank behaviour of the component species and to the response to fertilizer application previously shown by individual species during the course of Experiment 1 (Mountford *et al.*, 1993a,b; Chapter 5).

6.2. MATERIALS AND METHODS

PLOT LAYOUT

Seed bank sampling and assessments of vegetation composition were carried out within the plot layout of Experiment 3. This layout consisted of a total of seventy-two 2m x 4m plots in six sets of 12, each set located within each replicate plot of the N_0 and N_{200} treatments in Experiment 1 (see Chapter 1, Figure 1.5). An example layout of one of the six sets of 12 plots is given in Figure 6.1. All sampling was carried out within a notional grid consisting of two rows of eight 50 cm x 50 cm squares running down the central 1m x 4m of each 2m x 4m plot in Experiment 3. The pair of squares at each end of the plot were ignored to give a total of 12 squares and 21 intersections on the grid to be used for quadrat and soil sample location respectively.

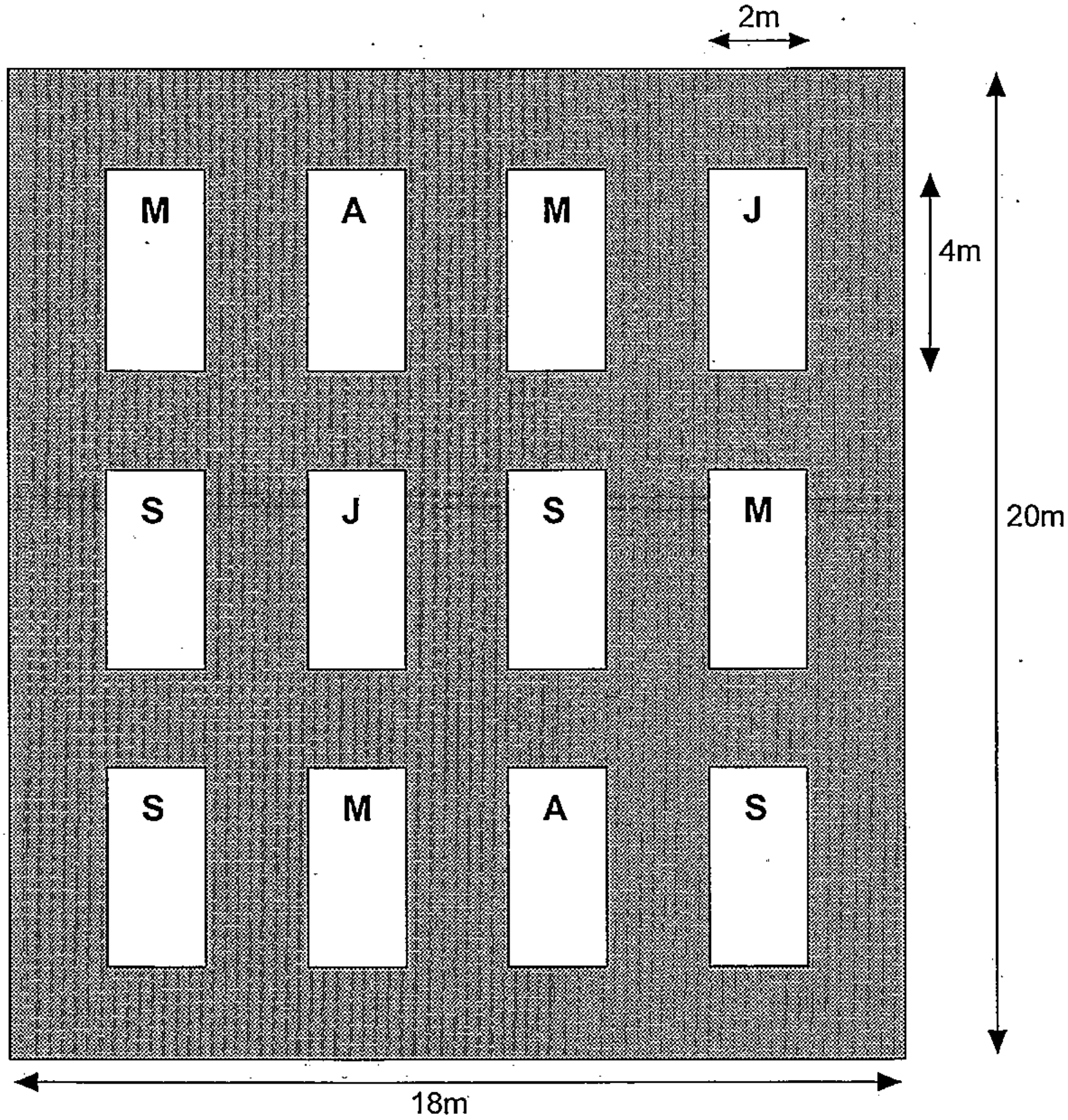


Figure 6.1. Sample layout of one of the six sets of 12 plots used in Experiment 3. One set of plots was located within each of the three N_0 and N_{200} paddocks in Experiment 1 (see Figure 1.5). M, J, A, and S indicate plots harvested in May, July, August and September respectively (see Chapters 7 and 8).

SEED BANK SAMPLING

Soil collection and processing

Twenty 5cm diameter soil cores were removed to a depth of 5cm from each plot on 19 March 1991 using a bulb planter. March was chosen as the optimum month for sampling, being too early to include seed produced during the current year. It was also expected that species producing a transient seed bank would be excluded by sampling in March (Thompson and Grime, 1979; Thompson, 1986).

Cores were taken from each of the intersections of the sampling grid described above, with the final (21st) intersection on each plot being ignored. The 20 samples from each plot were bulked to give a total of 1.963 litres of fresh soil from an area of 392.7 cm^2 per plot. The bulked plot samples were placed in a fan oven for three days at 20 °C until dry enough to process further whilst retaining some moisture. Vegetation and coarse roots were then removed by passing the soil through a 0.5cm sieve and each plot sample was divided into four 20cm x 30cm seed trays, each containing coarse builders sand to a depth of about 1.5cm. This gave a layer of soil of about 0.5-0.7cm in each tray.

Maintenance of seed trays

Trays were laid out in separate blocks of 30 on a bed of sand overlying polythene sheeting in a poly-tunnel (see Plate 6.1). Each of these blocks included six trays filled with peat

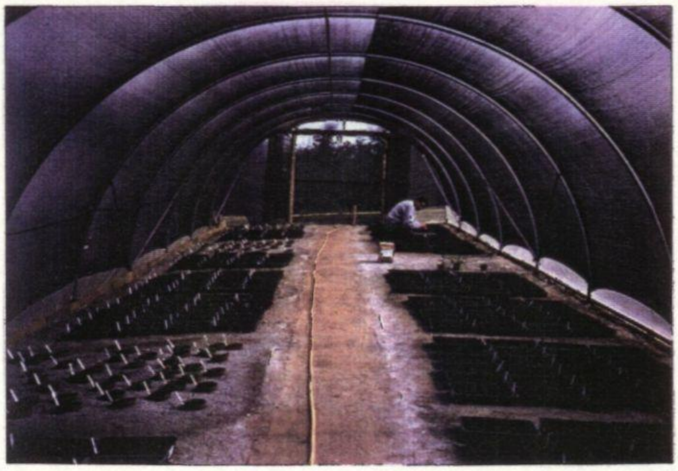


Plate 6.1. Layout of seed trays in the poly-tunnel at Rumleigh Experimental Station.

sterilized in a microwave oven, so that any contamination by airborne seed could be detected. The location of each tray was randomized within each block in the poly-tunnel with two constraints: firstly, trays from plots of the same main replicate block in the field, i.e. replicate 1, 2 or 3 according to the Experiment 1 layout (see Figure 1.5), were allocated to adjacent blocks in the tunnel; and secondly, each of the four trays from a particular 2m x 4m plot in the field was located in a different block in the tunnel.

The poly-tunnel was covered with fine black netting to avoid overheating in hot weather and trays were watered from above, once or twice a day, depending upon weather conditions. Temperature was recorded continuously in the tunnel using a barrel chart thermograph. The highest and lowest temperatures experienced were -4°C and 38°C recorded in January and July 1992 respectively, but temperatures typically ranged from about -1 to +15°C during December-March and from 10 to 30°C during June-August.

Seedling emergence counts

Seedlings were identified, counted and removed at approximately four-week intervals over a period of 19 months until September 1992. At each assessment, any unidentified plants were either left until the next assessment or transferred to pots to grow on for later identification. The soil layer within each tray was disturbed after each count by scratching with forceps in order to help stimulate further germination (Roberts, 1981), taking care to avoid damage to any retained seedlings.

BOTANICAL ASSESSMENTS

The percent ground cover of each species present within four 50cm x 50cm quadrats per plot was recorded in May 1991. The location of each of these quadrats was randomized from within the twelve 50cm x 50cm squares on the sampling grid. The whole of each 2m x 4m plot was then searched for any species not recorded in any of the quadrats. Additional species found in this way were each given an arbitrary score of 0.01% cover for the plot.

It was not possible to differentiate completely between *Bromus racemosus* and *Bromus hordeaceus*, nor with sufficient confidence between *Glyceria fluitans* and *G. declinata*, since only a few *Bromus* plants and no *Glyceria* were flowering at the time of assessment. Combined cover values were therefore given for each of these species pairs (see Table 6.1).

DATA ANALYSIS

Effects of previous fertilizer application

Individual species data for vegetation percent ground cover and for the number of germinable seeds per m^2 in the top 5cm of soil were analyzed separately for the effects of fertilizer treatment by analysis of variance (ANOVA) using GENSTAT (GENSTAT V Committee, 1987). These ANOVAs, and those on species grouped as described below, were carried out on the basis of a randomized block design with three replicates of two fertilizer treatments, using data reduced to the means of each of the six sets of 12 plots in the layout of Experiment 3. Where there was significant skewness in the distribution of these six values for a particular variable, both square root and $\log_{10}$ transformations were tested as a means of normalizing the distribution. Only non-skewed variables, transformed or otherwise, were analysed by ANOVA.

Species aggregation

In addition to analyses on data for individual species, additional analyses were performed on summed species data aggregated according to four different criteria:

- (i) into grasses, dicotyledonous species (forbs), *Cyperaceae* and *Juncaceae*.
- (ii) by seed bank Type I-IV, *sensu* Thompson and Grime (1979) - see below.
- (iii) by previously observed response to fertilizer nitrogen - see below.
- (iv) by a combination of (ii) and (iii) above.

The four seed bank categories (I-IV) used in (ii)-(iv) above describe the degree of persistence or longevity exhibited by seed of a particular species in the soil. Types I and II are species normally appearing only transiently in the seed bank, whilst at least some seed of Types III and IV can persist for at least a year and sometimes much longer (Thompson and Grime, 1979, Grime *et al.*, 1988). Type I species normally germinate in the autumn soon after shedding, whilst in Type II species, germination is normally delayed until the following spring. A high proportion of Type IV seed will enter the long-term seed bank, whilst Type III species normally show behaviour intermediate between that of Types I/II and

Type IV, with a high proportion of seed germinating within 12 months of shedding and a few persisting in the seed bank.

Each species was categorized in this way by reference to the lists given by Grime *et al.* (1988), including those species for which a particular categorization was tentative (prefixed by a ? by Grime *et al.*, 1988 and in Table 6.1 - see page 272).

Criterion (iii) above was based upon the response to fertilizer nitrogen recorded in the large scale experiment (Experiment 1) between 1986 and 1990. Species showing a significant ($P<0.05$) linear trend against fertilizer N rate in ANOVAs of botanical data in one or more year 1987-1990 in Experiment 1 (Mountford *et al.*, 1993a), or for which ordinations of botanical data described in Chapter 5 indicated marked response to N, were classed as either N-positive or N-negative as appropriate. Species which had previously shown no response to N in these studies, or which had not been recorded in the vegetation, were summed and analyzed as a separate, third group. These three groups are identified by the symbols +, -, and x respectively in the second column of Table 6.1 (p. 272).

Correlation between above ground vegetation and the composition of the soil seed bank

Regression analysis was used to test the extent to which variation in the abundance of each species and species group in the seed bank was related to variation in the above ground vegetation. Individual plot values (maximum 72) for each variable were used in these analyses with the number of seed per m^2 in the seed bank treated as the dependent variable in the regressions. Where a species or species group was absent from both the vegetation and the seed bank of a particular plot, that plot was excluded from the analysis for that particular species/species group. In all, three analyses were performed on data for each species/species group: the first including data from plots of both fertilizer treatments (N_0 and N_{200}) together (maximum of 72 plots), and the second and third analyses on data restricted to each treatment separately (maximum of 36 plots for each analysis).

The methodology described above is discussed in some detail later in relation to published data (see section 6.4).

6.3. RESULTS

OVERALL COMPOSITION OF THE SEED BANK AND THE ABOVE GROUND VEGETATION

Contribution of individual species

Ninety one species of vascular plant were germinated from soil sampled in March and 85 species were recorded in the above ground vegetation in May, with 72 species common to both assessments (Table 6.1). Of those species recorded solely in the vegetation, only one exceeded 0.1% ground cover (*Caltha palustris*, <0.4%) and most were present in only trace amounts. Similarly, most of the species that were absent from the vegetation were only small components of the seed bank, typically at densities averaging less than five germinable seeds per m^2. At least one of these species, *Senecio vulgaris*, was seen to be present in the vegetation close to the plots on which it was recorded in the seed bank. *Epilobium hirsutum* was present in slightly larger quantities in the seed bank (average 44 germinating seeds per m^2), although absent from the vegetation on the plots. However, this species, in common with *S. vulgaris*, combines high mobility of seed by wind transportation with the ability to form a persistent seed bank (Grime *et al.*, 1988) and is a fairly common component of the vegetation on ditch banks and field margins at the site.

Contribution of species groups to vegetation and seedbank

Vegetation and seed bank composition differed little in terms of the number of species recorded within the main species groups: 25-28% of all species were grasses, 60% forbs, 7-8% *Cyperaceae* and 5% *Juncaceae*. Above ground vegetation cover was fairly evenly shared between grasses and forbs, at 44% and 48% ground cover respectively averaged over all plots, with *Cyperaceae* and *Juncaceae* averaging 2% and only 0.6% respectively (see Table 6.1). Of the total number of seedlings emerging from seed bank samples, 27% were of grass species, 32% forbs, 2% *Cyperaceae* and 28% *Juncaceae*.

Twelve of the 72 species found in both the above ground vegetation and the soil seed bank were classed by Grime *et al.* (1988) as Type I species, i.e. species normally exhibiting no dormancy (Thompson and Grime, 1979).

Table 6.1. Composition of the soil seed bank (top 5cm) and of the above ground vegetation in March and May 1991 respectively, in unfertilized (N_0) and previously fertilized (N_{200}) meadows. The s.e. values shown are effective standard errors from analysis of variance (ANOVA) on those variables not showing skewness in data. Bracketed figures refer to data transformed $l_nx=\log_{10}(x+1.0)$.

Species name(1), seed bank Type I-IV (2) and N response(3)		% cover in vegetation			Number of germinable seeds m^{-2} in soil		
		N_0	N_{200}	s.e.	N_0	N_{200}	s.e.
Agrostis canina	III/IV -	0.5	1.5	0.28	142	180	45.9
A. capillaris	III/IV -	5.5	5.8	-	1206	685	-
A. stolonifera	III +	1.4	1.5	0.16	7	24	6.5
Alopecurus geniculatus	?II/IV x	-	-	-	5	2	2.8
A. pratensis	I +	0.4	<0.1	-	6	2	-
Anthoxanthum odoratum	III x	4.3	4.7	0.26	1401	968	393.4
Briza media	I x	0.0	tr	-	-	-	-
Bromus hordeaceus	I +		NR		1	4	1.8
B. racemosus	I +		NR		1	1	1.3
B. hord. + racem.	I +	2.7	6.9	0.31*	2	4	1.7
Cynosurus cristatus	I -	2.8	0.6	0.62	282	70	-
Dactylis glomerata	?II x	0.6	0.2	0.17	3	1	1.0
Deschampsia cespitosa	III -	0.1	0.0	-	46	3	-
Festuca arundinacea	I x	0.0	0.1	-	-	-	-
F. pratensis	I x	0.3	0.2	0.16	1	4	-
F. rubra	I -	8.5	3.5	0.60*	35	5	9.3
Festulolium loliaceum	x	tr	0.0	-	-	-	-
Glyceria declinata	?IV x		NR		1	1	1.0
G. fluitans	?IV x		NR		268	55	-
G. decl. + fluitans	?IV x	tr	0.0	-	269	57	-
Holcus lanatus	III +	2.2	7.1	1.26	869	1385	239.4
Hordeum secalinum	? x	tr	0.0	-	1	0	-
Lolium perenne	I +	5.1	17.3	2.86	4	23	4.8
Phleum pratense	I +	1.0	2.3	0.74	4	4	-
Poa annua	III x	-	-	-	0	1	-
P. humilis	? x	tr	tr	-	4	0	-
P. pratensis	?III x	0.1	<0.1	-	7	7	5.6
P. trivialis	III +	0.1	0.3	0.08	794	1813	427.0
Total of all grasses		**35.6**	**51.9**	**3.66**	**5087**	**5237**	**546.1**
Achillea millefolium	?I x	0.0	tr	-	-	-	-
Angelica sylvestris	?II x	-	-	-	0	3	-
Bellis perennis	I -	0.5	<0.1	-	133	57	35.1
Betula pubescens	?III x	-	-	-	0	1	-
Caltha palustris	II x	0.4	0.1	-	-	-	-
Cardamine hirsuta	III x	tr	0.0	-	187	76	72.9

(Table contd.)

Table 6.1. (contd.)

Species		% cover in vegetation			Number of germinable seeds m^{-2} in soil		
		N_0	N_{200}	s.e.	N_0	N_{200}	s.e.
C. pratensis	?III -	1.1	1.0	0.25	156	277	-
Centaurea nigra	? x	4.2	2.7	0.75	35	34	18.4
Cerastium fontanum	III +	0.9	3.6	0.72	1332	2037	353.7
Cirsium arvense	?III x	tr	0.1	-	0	3	-
C. dissectum	? -	0.1	tr	-	0	1	-
C. palustre	?III -	0.1	0.0	-	21	4	-
C. vulgare	I x	tr	0.0	-	-	-	
Crataegus monogyna	? x	0.0	tr	-	1	3	-
Epilobium hirsutum	III x	-	-	-	32	56	-
E. parviflorum	III x	-	-	-	0	1	-
Filipendula ulmaria	?IV x	5.5	7.1	2.63	45	105	32.5
Galium aparine	II x	0.0	tr	-	-	-	-
G. palustre	IV x	0.2	tr	-	6	1	-
Geranium dissectum	?III x	0.1	0.3	0.21	9	5	3.0
Glechoma hederacea	? x	0.1	tr	-	66	2	-
Hydrocotyle vulgaris	? x	-	-	-	1	2	0.5
Hypericum tetrapterum	IV x	-	-	-	2	1	0.5
Hypochaeris radicata	?I x	0.1	<0.1	0.05	4	1	2.0
Lathyrus pratensis	?III x	<0.1	tr	-	-	-	-
Leontodon autumnalis	III -	1	0.5	0.42	200	6	-
L. hispidus	?III -	0.3	0.0	-	14	0	-
Leucanthemum vulgare	III x	0.1	0.0	-	62	1	-
Lotus pedunculatus	?IV -	0.2	0.1	0.12	17	4	-
Lychnis flos-cuculi	?IV -	<0.1	0.0	-	39	4	13.0
Lysimachia nummularia	? -	0.2	0.0	-	3	4	1.3
Mentha aquatica	?IV x	-	-	-	0	1	-
Myosotis discolor	?III -	0.3	0.0	-	332	15	101.7
M. scorpioides	?III x	-	-	-	1	0	-
Oenanthe fistulosa	? x	tr	0.0	-	-	-	-
Persicaria amphibia	?IV x	<0.1	0.0	-	3	1	1.8
Plantago lanceolata	III -	8.2	1.9	3.46	1971	120	780.6
P. major	IV x	-	-	-	3	1	1.8
Potentilla anglica	? x	-	-	-	1	5	-
P. anserina	? -	<0.1	0.3	-	10	0	-
P. reptans	? x	0.1	0.1	0.01	1	1	0.9
Prunella vulgaris	?III -	0.9	<0.1	0.23	120	104	17.9
Ranunculus acris	III -	4.2	2.9	0.23	332	61	36.8*
R. ficaria	II x	tr	0.0	-	0	1	-
R. flammula	?IV x	tr	0.0	-	-	-	-
R. repens	?IV -	2.7	2.0	0.47	1091	405	60.8*
Rhinanthus minor	II x	tr	0.0	-	-	-	-
Rumex acetosa	I +	3.5	9.9	2.28	197	555	98.3
R. crispus	IV +	0.1	<0.1	0.06	1	2	-

(Table contd.)

Table 6.1. (contd.)

Species		% cover in vegetation			Number of germinable seeds m^{-2} in soil		
		N$_0$	N$_{200}$	s.e.	N$_0$	N$_{200}$	s.e.
Sagina procumbens	IV x	0.0	tr	-	141	35	-
Senecio aquaticus	? -	0.3	<0.1	-	27	4	-
S. vulgaris	III x	-	-	-	6	4	2.8
Silaum silaus	? x	tr	tr	-	0	1	-
Sonchus asper	?III x	0.0	tr	-	30	25	-
Stellaria graminea	? -	0.1	0.6	0.28	127	88	33.2
S. media	IV +	<0.1	0.1	0.05	4	70	-
					(0.4	1.3	0.14*)
Taraxacum spp.	I +	7.4	11.7	0.73	151	224	20.8
Trifolium dubium	?III/IV -	<0.1	0.0	-	2	6	2.7
T. pratense	III x	3.3	1.9	0.68	117	49	38.7
T. repens	IV -	0.5	0.7	0.30	74	92	20.8
Urtica dioica	IV x	-	-	-	4	18	2.5
Veronica serpyllifolia	?IV x	0.1	<0.1	0.05	337	137	80.6
Vicia cracca	? -	0.4	0.2	0.10	4	0	-
Total of all dicots		**47.2**	**47.8**	**9.00**	**7444**	**4693**	**874.4**
Carex disticha	? x	1.4	0.1	-	47	22	23.6
C. flacca	?III/IV x	<0.1	0.0	-	10	3	3.6
C. hirta	? x	0.1	<0.1	0.03	6	6	4.3
C. hostiana	? x	-	-	-	11	11	4.0
C. nigra	?IV -	1.1	tr	-	131	4	-
					(1.8	0.5	0.16)*
C. panicea	? -	0.9	0.0	-	175	6	72.0
Eleocharis palustris	?III/IV x	0.1	tr	-	-	-	-
Isolepis setacea	?III/IV x	-	-	-	216	166	42.7
Total of all Cyperaceae		**3.7**	**0.1**	**1.57**	**596**	**216**	**193.9**
Juncus articulatus	IV x	<0.1	tr	-	808	1747	378.5
J. bufonius	?IV x	-	-	-	185	398	67.1
J. effusus	IV -	0.8	<0.1	-	7269	3421	2245.8
J. inflexus	IV -	<0.1	0.1	-	159	513	101.7
Luzula campestris	IV x	0.1	<0.1	-	1	3	1.8
Total of all *Juncaceae*		**1.0**	**0.2**	**0.48**	**8422**	**6082**	**1921.8**

(Table contd.)

Table 6.1. (contd.)

Species		% cover in vegetation			Number of germinable seeds m^{-2} in soil		
		N_0	N_{200}	s.e.	N_0	N_{200}	s.e.
Total bryophyte cover		**0.4**	**<0.1**	**0.16**	-	-	-
Equisetum fluviatile	I x	-	-	-	0	1	-
Grand total		**88.0**	**99.9**	**8.49**	**21553**	**16246**	**2436.6**

(1) Nomenclature after Stace (1991). (2) Seed bank types as defined by Thompson and Grime (1979) and listed by Grime *et al.* (1988). (3) Previously observed N response (see text): + = 'N-positive' species; - = 'N-negative' species; x = species showing no clear N response or which were not recorded previously.
NR = not recorded to species level; tr = trace (<0.01% cover); <0.1 = 0.01-0.05%
Asterisks denote significant treatment effect in ANOVA: * = P<0.05

Type I species together totalled 884 germinating seeds per m^2 averaged over N_0 and N_{200} plots, nearly 5% of the total number recorded (Table 6.2). Most of these were of just three species - *Cynosurus cristatus* (averaging 176 seedlings per m^2), *Rumex acetosa* (376 per m^2) and *Taraxacum spp.* (188 per m^2) - with a significant number also contributed by *Bellis perennis* (95 per m^2). The significance of these results is discussed further in Section 6.4 of this Chapter.

Type I species made a disproportionately high contribution to vegetation cover (average 42% ground cover) relative to the number of species involved (18% of total number) and compared with species of other seed bank types. Type III and IV species accounted for 32% and 28% respectively of all the species recorded in the vegetation and 35% and 18% respectively of the total vegetation cover. Six Type II species were recorded in the vegetation but these were all sparsely distributed, together averaging less than 1% ground cover and contributing only 7-8 seeds per m^2 to the seed bank (Table 6.2).

Compared with other seed bank types, the aggregate contribution of Type I species to the seedbank was understandably low relative to their presence in the vegetation. This group accounted for an average of 21.7 seeds m^{-2} for every 1% of ground cover they occupied in May, compared with equivalent values of 261.1 and 577.3 seeds m^{-2} for Types

Table 6.2. Composition of the soil seed bank (top 5cm) and of the above ground vegetation in March and May 1991 respectively, in unfertilized (N_0) and previously fertilized (N_{200}) meadows. Data are summarized into species groups: (a) by seed bank type (Thompson and Grime, 1979); and (b) by previously observed vegetation cover response to fertilizer N (see text). Numbers in square brackets are the number of species within each category Round bracketed figures refer to data transformed x $\log_{10}$ to correct skewness.

Species group	% cover in vegetation				Number of germinable seeds m^{-2} in soil			
	N_0	N_{200}	s.e.		N_0	N_{200}	s.e.	
Seed bank Type I:								
N-positive	20.1	48.0	2.93*	[7]	364	811	91.0	[7]
N-negative	11.8	4.1	1.08*	[3]	451	132	114.4	[3]
Total	32.3	52.4	1.99*	[15]	819	949	201.4	[13]
Seed bank Type II:								
N-positive	-	-	-	[0]	-	-	-	[0]
N-negative	-	-	-	[0]	-	-	-	[0]
Total	1.0	0.3	0.22	[6]	8	7	0.5	[4]
Seed bank Type III:								
N-positive	4.6	12.4	1.80	[4]	3001	5259	563.3	[4]
N-negative	22.2	13.6	4.04	[12]	4541	1461	606.0	[12]
Total	34.6	33.1	3.33	[27]	9621	8084	146.5*	[32]
Seed bank Type IV:								
N-positive	0.5	0.3	0.28	[2]	5	72	42.3	[2]
					(0.5	1.4	0.14*)	
N-negative	8.7	8.2	1.42	[9]	9039	4908	1939.0	[10]
Total	17.6	17.4	3.58	[24]	12167	8061	2097.6	[30]
Seed bank type ?:								
N-positive	-	-	-	[0]	-	-	-	[0]
N-negative	2.1	1.1	0.70	[7]	347	102	59.8	[7]
Total	8.0	4.0	0.74	[20]	520	187	49.6*	[20]
Total of:								
N-positive species	24.9	60.6	4.15*	[13]	3371	6143	495.3	[13]
N-negative species	41.4	21.7	6.79	[29]	14117	6137	2968.3	[29]
Remaining species	21.3	17.5	-	[43]	4066	3966	562.2	[49]
	(1.3	1.2	0.06)					

Note: several species are included in more than one seed bank category (see Table 6.1)

III and IV respectively (see Table 6.2). Species of unknown seed bank type averaged 55.5

seeds m^{-2} per 1% ground cover.

Of the 13 N-positive species recorded, nine were grasses and the remainder forbs (Table 6.1). In general, N-negative species made a much higher contribution to the seed bank relative to their abundance in the vegetation than did N-positive species, at 311.9 and 118.4 germinating seeds·m^{-2} per 1% ground cover for these two groups respectively. N-positive species contributed 40% of the total vegetation cover overall, 61% on N_{200} plots (Table 6.2). Of this last figure, a large proportion was attributable to seed bank Type I species, with the N-positive/Type I sub-group accounting for nearly half (48%) of the above ground vegetation on N_{200} plots. This sub-group and the N-negative/Type III species were of equal prominence on N_0 plots and together provided 42% ground cover. By contrast, N-negative/Type IV species were the most abundant sub-group in the seed bank at 6974 germinating seeds per m^2 or 37% of the total number of seedlings recorded (Table 6.2). A large proportion of this group was accounted for by *Juncus effusus* which contributed 5345 germinating seeds per m^2 to the seed bank overall, 28% of the grand total (Table 6.1).

THE EFFECTS OF PREVIOUS FERTILIZER TREATMENT

Individual species

The plot layout used in Experiment 3 gave three replicates of two fertilizer treatments and only two residual degrees of freedom in the ANOVAs. Therefore, despite large differences between treatment means for many species in both vegetation and seed bank data, few differences were statistically significant and none reached 99% ($P<0.01$) confidence levels (Table 6.1). Differences quoted as significant hereafter refer to 95% ($P<0.05$) confidence levels unless otherwise stated. However, given the large number of species involved, up to four species in the above ground vegetation and five in the seed bank could be expected to show a significant difference purely by chance at $P<0.05$.

Bromus hordeaceus/racemosus ground cover was significantly greater ($P=0.011$) on N_{200} than N_0 plots, whilst *Festuca rubra* cover was significantly higher on N_0 plots than N_{200}. Treatment effects were close to significant for ground cover of *Prunella vulgaris* ($N_0>N_{200}$, $P=0.053$) and *Taraxacum agg.* ($N_0<N_{200}$, $P=0.054$), and a more than three-fold difference in *Lolium perenne* cover ($N_0<N_{200}$) was significant within 10% confidence limits

(P=0.095)(Table 6.1).

Both *Ranunculus acris* and *R. repens* were significantly less abundant in the seed bank beneath N_{200} plots than N_0, whilst log transformation revealed significant treatment effects for both *Stellaria media* ($N_0<N_{200}$) and *Carex nigra* ($N_0>N_{200}$).

Treatment effects within species groups

Grass species were marginally more abundant in the vegetation on N_{200} plots than N_0, whereas *Cyperaceae* and *Juncaceae* were very scarce on N_{200} plots compared with N_0 (Table 6.1). Nevertheless, none of the treatment differences within these species groups reached significance, either for vegetation cover or for abundance in the seed bank, despite the fact that seed bank density was markedly lower on N_{200} plots compared with N_0 for forbs (-37%), *Juncaceae* (-28%) and particularly for *Cyperaceae* (-64%).

N-positive species were approximately twice as abundant both in the seed bank and in the above ground vegetation of N_{200} plots compared with N_0, whereas the reverse was true of N-negative species (Table 6.2). However, within the N-response groupings only the difference in vegetation cover of N-positive species reached statistical significance. Species cover data aggregated by seed bank type showed significant treatment effects only for Type I species (Table 6.2). Type I/N-positive species were more than doubled, and N-negative species more than halved, by fertilizer application, with a significantly positive response to fertilizer within the group as a whole. Trends in seed bank density within the Type I group corresponded closely with those shown by the above ground vegetation, although none of the treatment effects were significant for seed bank data (Table 6.2). By contrast, the abundance of Type III species in the seed bank was significantly lower on fertilized than on unfertilized plots, largely due to a three-fold difference shown by N-negative species within this group. An even greater apparent reduction by fertilizer of Type IV species failed to reach significance due to a high level of variation between the replicates of both treatments. Fertilizer application increased the abundance of Type IV/N-positive species in the seed bank, reaching significance with log transformed data. However, this effect was almost entirely attributable to the response of *S. media* (noted above). This species and *Rumex crispus* were the only species recorded within this sub-group, and together they accounted for only a small fraction of the total number of germinating seeds of Type IV species present

(Table 6.2).

The abundance in the seed bank beneath fertilized plots of those Type III species which had not been identified previously as either N-positive or N-negative was half that beneath unfertilized plots, despite a less than 10% difference between treatments in the vegetation cover of this group (Table 6.2). In terms of the number of species involved, this was the largest single group, although it occupied only about 8% of the vegetation cover and 8-9% of the total seed bank *in toto*. For most of these species, their sparsity in the vegetation no doubt explains why it was not possible to identify a trend in response to applied N for them.

The 20 species not categorized within any of the seed bank Types I-IV were together twice as abundant in the vegetation of N_0 plots compared with N_{200} and nearly three times as abundant in the seed bank, though only the latter difference reached significance (Table 6.2).

CORRELATION BETWEEN SEED BANK AND ABOVE GROUND VEGETATION

Species groups

There was no significant correlation over all plots between above ground vegetation cover of individual species groups and their seed bank abundance either for grasses or for forbs, but the relationship was significant for grasses on N_0 plots (Figure 6.2). For both *Cyperaceae* and *Juncaceae*, abundance in the seed bank was highly correlated with the contribution each group made to above ground cover (both $P<0.001$). However, both these groups were very sparsely represented in the vegetation of N_{200} plots and in each case the overall relationship was largely attributable to data from N_0 plots (Figure 6.2b and c). Regression equations for grasses and for *Juncaceae* gave large intercept values (4259 and 5610 germinable seeds m^{-2} respectively for data from all plots) with high confidence levels for these estimates ($P<0.001$). The intercept value (regression constant) for *Cyperaceae* did not differ significantly from zero, although *Cyperaceae* were present in the seed bank but absent from the vegetation on several N_{200} plots (Figure 6.2c).

There was a small, positive overall correlation between vegetation cover and seed bank density for seed bank Type I species, with a significant intercept value of 490 germinable seeds per m^{-2} at zero cover of these species (Figure 6.3a). However, this

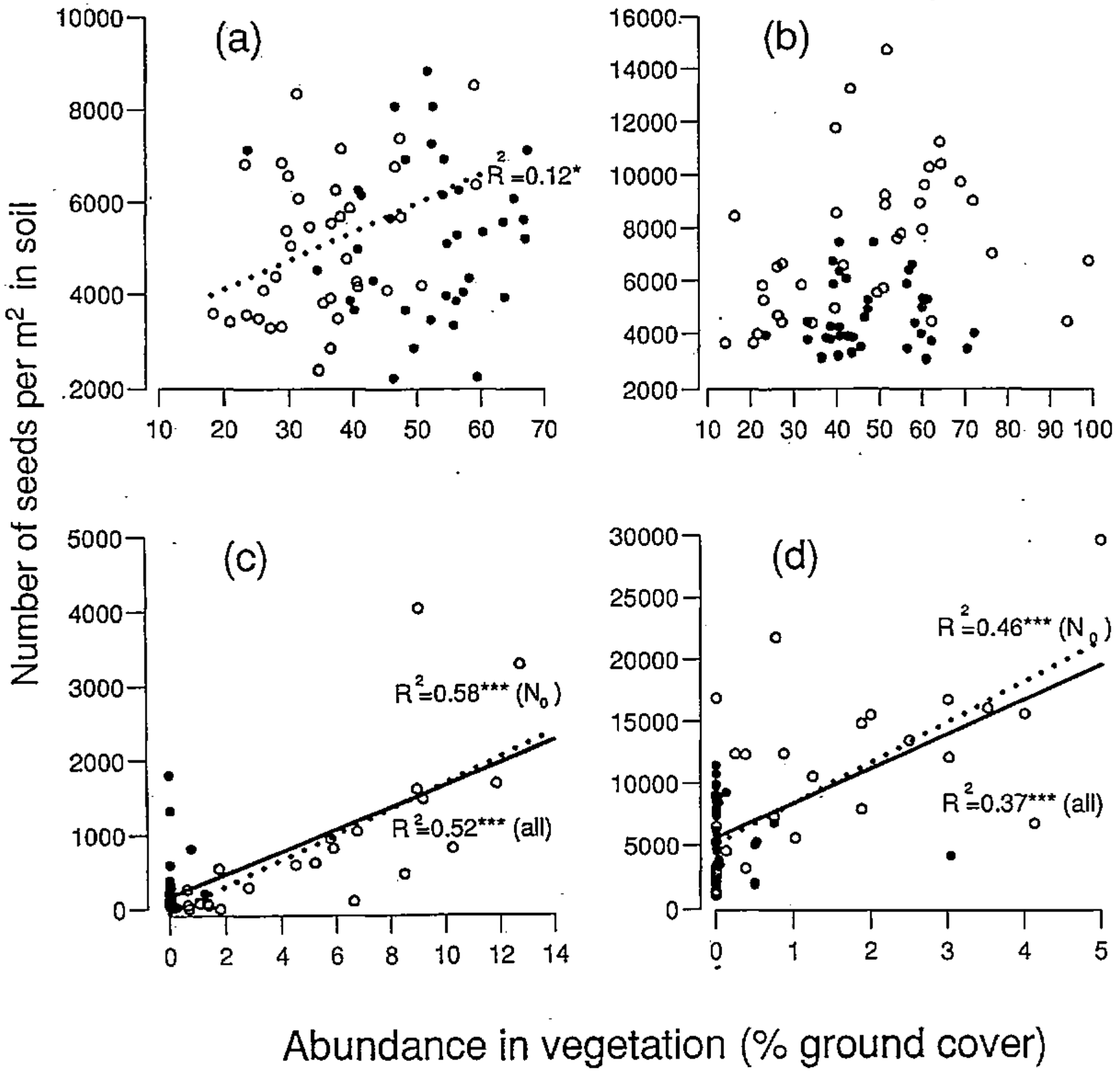


Figure 6.2. The relationship between seed bank abundance and above ground vegetation cover of (a) grasses; (b) dicots; (c) *Cyperaceae*; and (d) *Juncaceae* on N_0 plots (open symbols) and N_{200} plots (filled symbols). Each point represents aggregated data for an individual plot. Lines are fitted by linear regression and only statistically significant regressions are represented: * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$. Solid lines = data from plots of both fertilizer treatments, dotted lines = N_0 plots only. R^2 values are the r^2 value adjusted for the number of coefficients in the equation.

overall relationship masked a large difference in response between plots of the two treatments for this group. The relationship was highly significant ($P<0.001$) on N_0 plots, but was negligible on N_{200} plots (Figure 6.3a). Of the remaining seed bank types, only Type III

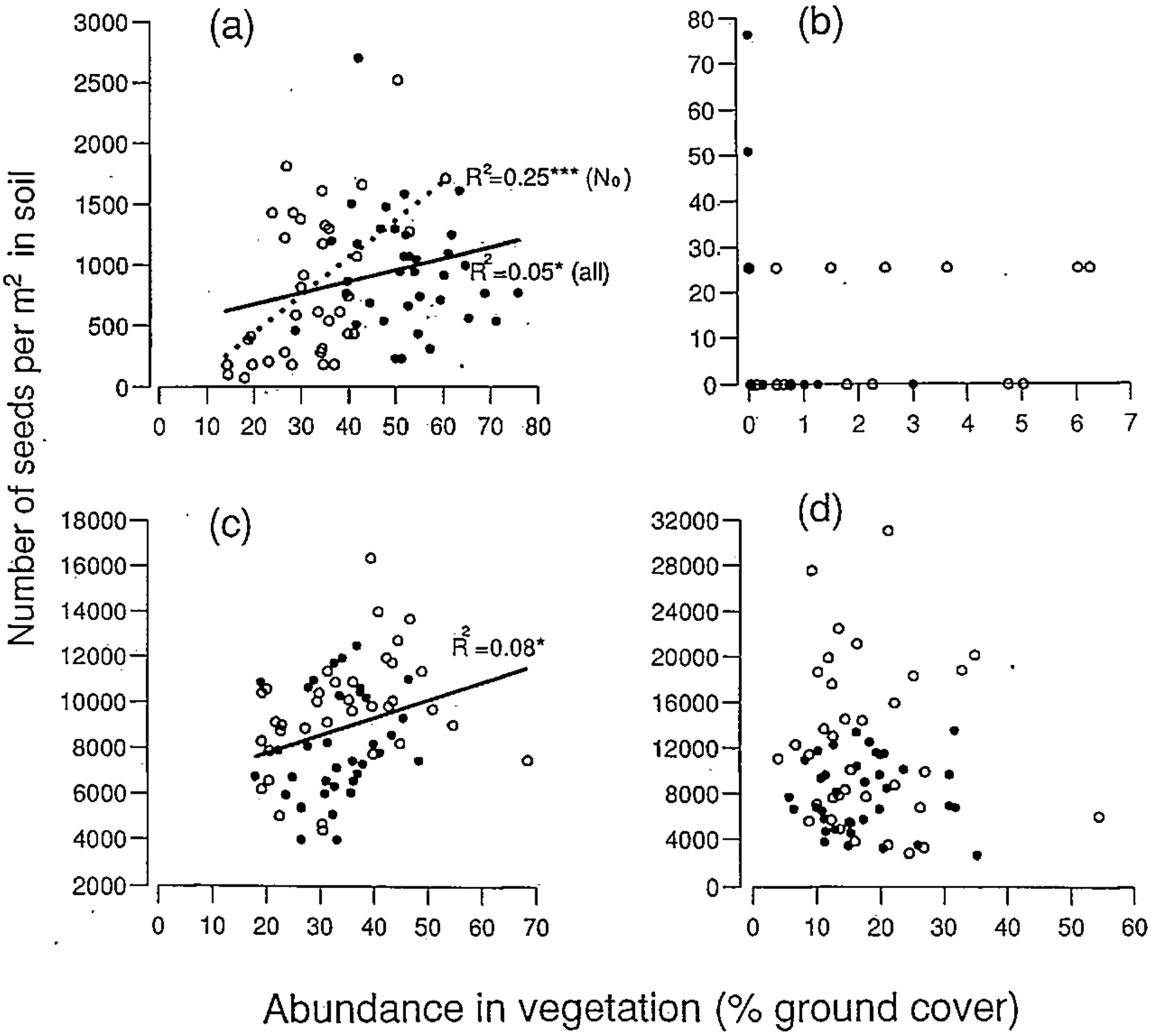


Figure 6.3. The relationship between seed bank abundance and above ground vegetation cover of species data aggregated by seed bank type: (a) = Type I; (b) = Type II; (c) = Type III; and (d) = Type IV; on N_0 plots (open symbols) and N_{200} plots (filled symbols). Other notes as for Figure 6.2.

species showed a significant overall relationship between vegetation cover and seed bank (Figure 6.3c). The relationship was slight, however, and there was no significant correlation when data from each plot were analyzed separately.

Relationships were more clear-cut when analyses were restricted to data for species classified as N-positive or N-negative within each seed bank type (Figure 6.4). Within the Type I group, N-positive species showed a highly significant overall correlation (R^2=0.33, P<0.001, see Figure 6.4a). Data points for N_{200} plots were generally distributed furthest away from the origin of each axis and there was comparatively little overlap between the two data sets (Figure 6.4a). Thus, although seed bank and vegetation cover were significantly correlated on N_0 plots but not N_{200}, the overall relationship was essentially the same as that on N_0 plots alone (regression slopes 12.0 and 14.3 seed m^{-2} per 1% ground cover respectively). N-negative Type I species showed no overall correlation between seed bank density and vegetation cover and, within this sub-group, these variables were correlated only on N_{200} plots where there was a significant (P<0.01) inverse relationship (Figure 6.4b).

In contrast with N-positive Type I species, for N-positive Type III species, the overall relationship between vegetation cover and seed bank density was largely dictated by data from N_{200} plots (Figure 6.4c). Data from N_0 plots within this sub-group were confined to the lower range of values for both variables, whereas those from N_{200} plots were more evenly distributed. The opposite was generally true for N-negative Type III species, although the correlations were not so close within this sub-group (Figure 6.4d) and the slope of the regression both on N_0 and N_{200} plots differed substantially from the overall relationship, at 105.1 and 62.9 seeds m^{-2} per 1% ground cover respectively compared with 125.9 seeds m^{-2}. Furthermore, species within the N-negative Type III sub-group had a smaller seed bank per unit of ground cover than did N-positive species of the same seed bank type, with regression slope coefficients for the latter of 191.6 germinable seeds m^{-2} for N_{200} plots and and 209.2 seeds m^{-2} for the overall regression.

As noted above, only two N-positive Type IV species were recorded on these plots, *S. media* and *R. crispus*. One or both of these species appeared in the seed bank and/or the vegetation on less than half the plots and in only five plots were they recorded in both (Figure 6.4e). N-negative Type IV species were much more numerous and, as with both N-positive and N-negative Type III sub-groups (Figure 6.4c and d), were represented in both the seed bank and the above ground vegetation on all plots (Figure 6.4f). There was no overall relationship between vegetation cover and seed bank density for this group, although the two variables were positively correlated on N_{200} plots (R^2=0.23, P<0.01).

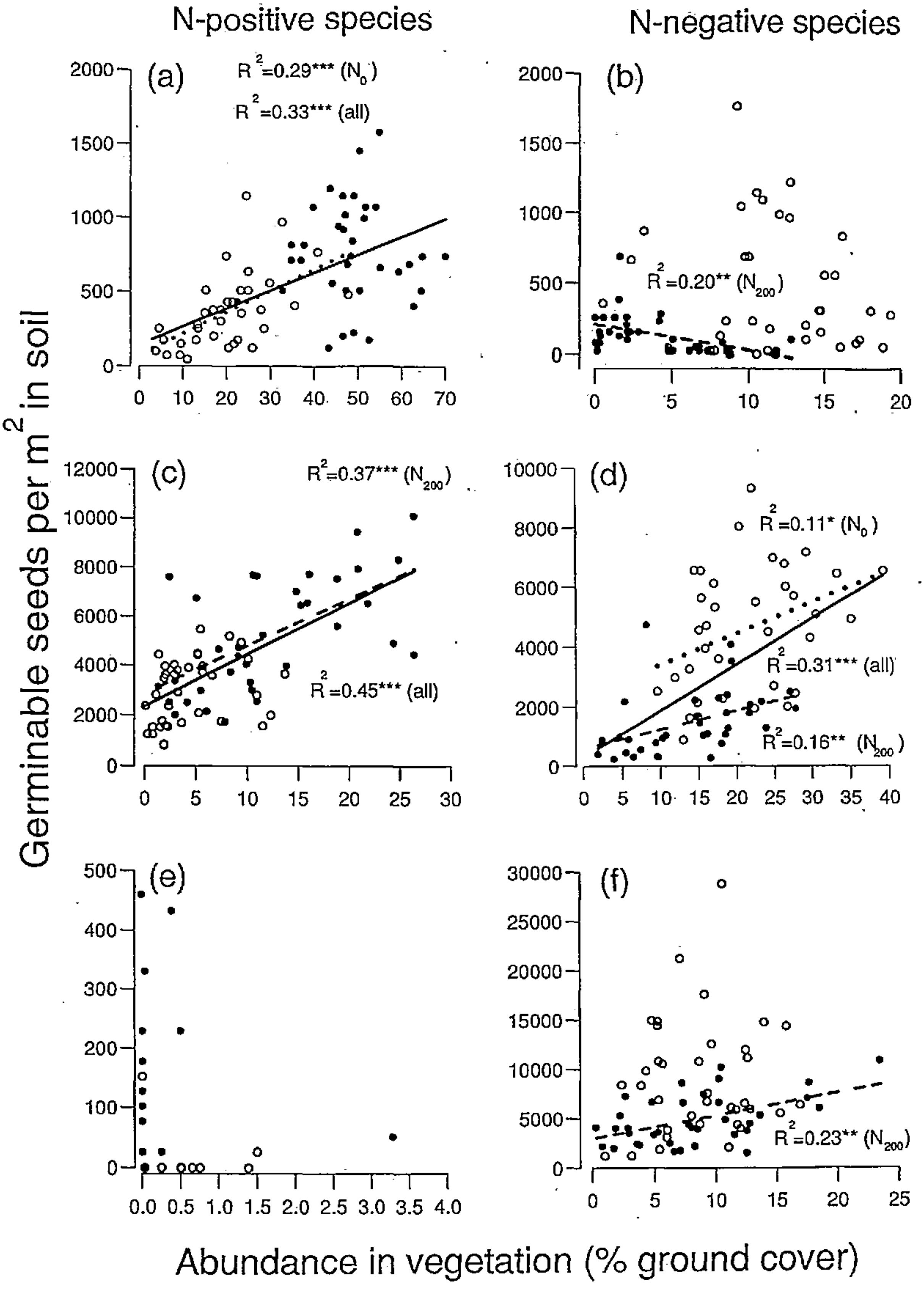


Figure 6.4. The relationship between seed bank abundance and above ground vegetation cover of species data aggregated by seed bank type and further divided by previously observed N response (see text): (a) and (b) = Type I; (c) and (d) = Type III; (e) and (f) = Type IV; on N_0 plots (open symbols) and N_{200} plots (filled symbols). Broken lines represent regressions on data restricted to N_{200} plots; remainder of legend as Figure 6.3.

None of the few Type II species recorded were classifiable as either N-positive or N-negative.

6.4. DISCUSSION

REVIEW OF THE METHODS USED

Sampling density

The four 50cm x 50 cm quadrats used per plot for vegetation cover assessments represented 33% of the surface area of the sampling grid, 12.5% of the total plot area. This compares with the total area sampled for seed bank density measurements of 0.0393 m^2, equivalent to 1.3% of the surface area of the grid and 0.5% of the total plot area. On this basis, much greater confidence can be placed on assessments of vegetation cover than of seed bank composition, although seed bank samples were more evenly distributed. The 20 soil samples taken from each plot were bulked before further processing, so that it was not possible to assess the small-scale heterogeneity of species abundance in the seed bank, nor to obtain estimates of the variance about individual plot means.

Thompson (1986; 1993a) recommends a minimum of 50 samples to give an accurate estimate (i.e. a standard error of <20% of the mean) for the common species in the seed bank, more for the scarcer species. This recommendation was based on a complete assessment of the seed bank beneath a single 112cm x 56cm rectangular area of well grazed acid grassland and was largely confirmed when the same technique was used on an area of neutral grassland maintained by regular mowing (Thompson *et al.*, 1994). In both studies, seeds of most of the species were distinctly clumped. However, Schenkevald and Verkaar (1984) found much less heterogeneity in seed banks beneath chalk grassland, where the distribution of most species did not differ significantly from random. Hayashi and Numata (1971, cited by Thompson, 1986) recommended a minimum soil volume of 500-600 cm^3 to identify the most common species present in grassland soils, although this recommendation was not aimed at identifying species density. This volume of soil is equivalent to 5-6 cores of the size used in this study. Working in an arable soil, Gross (1990) found that the number of species recorded with increasing numbers of 60 cm^3 samples levelled off at 15-18 samples. Her species abundance data show that, using 25 samples (total volume 1500 cm^3), the standard error as a percentage of the mean for the seven most abundant species averaged 21% (range 14-33%) for the most accurate method tested (germination following cold stratification).

The total number of samples taken from each set of 12 plots, i.e. the number contributing to each of the six values (2 treatments x 3 replicates) used in analyses of variance, was 240, giving a total volume of soil of 23.56 litres. This number and volume was almost certainly adequate to assess accurately the mean density of all but the scarcest species present in these areas. On the other hand, on the basis of the work by Thompson (1986), the 20 samples (totalling1963 cm^3) taken from each sampling grid may have been inadequate to account for spatial heterogeneity on an individual plot scale for all but the most abundant species. Nevertheless, the total seed banks recorded by Thompson (1986) and by Thompson *et al.* (1994) were both small at 1325 and 6543 germinable seeds m^{-2} respectively, compared with seed banks ranging from 9070 to 42500 germinable seeds m^{-2} on individual plots in this study. When counts were aggregated into grasses, forbs, *Juncaceae* and *Cyperaceae*, the total number of seeds m^{-2} on every plot for each but the last group far exceeded the grand total per m^2 of all species recorded by Thompson (1986), and the totals for both forbs and *Juncaceae* each exceeded the total total seed bank recorded by Thompson *et al.* (1994). The individual plot totals for seed bank Types III and IV species in this study ranged from 2700 to 31000 seeds m^{-2}, although Types I and II were scarcer at 76-2700 and 0-76 seeds m^{-2} respectively. N-positive species totalled between 1020 and 11300 seeds m^{-2} and N-negative species 2900-37000 seeds m^{-2} on individual plots.

A sampling intensity of 20 cores per plot (at 50cm spacing) is therefore likely to have given reasonably accurate assessments of the major species groups on individual plots, particularly as it seems logical to expect species groups to be distributed more homogeneously than individual species. Some of the N-positive and N-negative sub-groups within the seed bank type main groups were represented more sparsely and individual plot estimates for the sparser of these may be less reliable. Nevertheless, it is also reasonable to expect seed banks beneath hay meadows to be more homogeneous on a small-scale than those of well grazed pastures or grassland maintained by frequent mowing. The vigorous disturbance involved in mechanized hay making would tend to scatter seed to a far greater extent than when seed is shed more passively from standing plants. Data presented in Chapter 8 show that, even when plots were cut as late as September, 40% of the total seed rain occurred during and after cutting. When plots were cut at the usual time in July, seed shed before cutting accounted for only 20% of the total.

Nevertheless, the full causes of small-scale heterogeneity in the seed bank have not been identified and movement of seeds on or in the soil by invertebrates may be at least partly responsible (Thompson, 1986; Thompson *et al.*, 1994). Inaccuracies in the estimates of seed bank density on individual plots of some of the less common species and species groups would tend to increase the variance in regressions of seed bank density against vegetation cover (see later discussion).

Germination and seedling counts

Gross (1990) found that a germination method comparable with the technique used in this study gave a more complete listing of species than other methods she tested, particularly if preceeded by cold stratification (storage of trays in the dark at 5°C for three weeks). Thompson (1986) used a germination method almost identical to that used in this study and found that hardly any seeds germinated after July from soil taken from the field in March. He therefore assumed that the seed bank had been exhausted after five months, although he conceded that some further germination might have occurred had samples been retained until the following spring. On the basis of this experience, Thompson *et al.* (1994) kept samples taken in November in a heated greenhouse for only six months. In the study reported here, 84% of all the seedlings recorded appeared during the first nine months, i.e. before the first winter, although a significant proportion of these emerged after July. However, 44% of all the *Juncus* seedlings recorded over the 19 month period emerged more than 12 months after taking the samples, i.e. during the second calender year (1992), with this proportion ranging from 27% for *J. inflexus* to 62% for *J. bufonius.* For the remaining species, 95% of the total number of emerging seedlings germinated within the first nine months, although *Trifolium pratense* was a notable exception to this, producing only just over half (55%) of its final total in the first year. Most of the remaining *T. pratense* seedlings emerged before the end of May 1992, but germination of *Juncus spp.* was very protracted, with some new seedlings still being recorded at the final assessment in September. These results agree in principle with those of Champness and Morris (1948), who concluded that their counts from the first year were substantially reliable for most species, but incomplete and possibly misleading for a few species. In their work, *Juncus bufonius* and *Coronopus squamatus*, each significant components of the samples in which they appeared, produced 32% and 91% respectively of their final total in the second year.

DISCUSSION OF RESULTS

Size and composition of the seed bank

Dicots were the commonest of the four main species groups identified in this study (grasses, dicots, *Cyperaceae* and *Juncaceae*), both in the vegetation and in the seed bank. There was a marked predominance of seed bank Type III and IV species among the dicots compared with the grasses, so that the abundance of dicots in the seed bank relative to their contribution to above ground vegetation was greater than for grasses. However, the discrepancy between abundance in the seed bank and in the above ground vegetation was extreme for *Juncaceae*. These species contributed about 1% of the total vegetation cover but nearly 40% of the total seed bank on unfertilized plots. These results are consistent with other work showing that *Juncus* species are often far more abundant in the seed bank relative to their above ground abundance than other species present (Chippendale and Milton, 1934; Champness and Morris, 1948; Roberts, 1981; Williams, 1985). Williams (1985) recorded 2780-5180 *Juncus* seeds m^{-2} beneath a low-lying meadow near Oxford, even though no *Juncus* species had been recorded in the vegetation during the 20-year life of the experiment (Elliott *et al.*, 1974; Williams, 1985). The magnitude of the discrepancy that a species shows between its abundance in the seed bank and in the vegetation is widely recognized as an indicator of its seed bank persistency (Chippendale and Milton, 1934; Champness and Morris, 1948; Thompson and Grime, 1979; Roberts, 1981; Bakker, 1983,1989; Williams, 1985; Grime *et al.*, 1988), as is the degree to which its abundance in the soil declines with depth (Chippendale and Milton, 1934; Roberts, 1981; Bakker, 1983,1989; Thompson, 1993).

Seed bank 'types'

It is recognized that the distinction between seed bank Types III and IV is not clear-cut: the two categories represent the opposite ends of a continuum and the same species can often behave as Type III or Type IV at different times and in different situations (Thompson and Grime, 1979; Grime *et al.*, 1988; Thompson, 1993). Thompson (1993) recommended a simpler system, currently in use at the Unit of Comparative Plant Ecology (UCPE) at Sheffield, which recognizes three types of seed bank: 'Transient', which corresponds directly to the Types I and II of Thompson and Grime (1979) system used in this study; 'Short-term persistent', species which persist in the soil for more than one year but less than five years; and 'Long-term persistent', species which persist in the soil for at least five years.

The last two categories correspond with the 'persistent' and 'permanent' types described by Bakker (1989). Bakker was primarily interested in the extent to which seeds were likely to persist beneath plant communities which had been destroyed or degraded at some time in the past. Of the species lost from the original vegetation in such situations, only those which form a 'permanent' seed bank would be present in the soil, and the seed bank could only represent a source of regeneration for these species. In species-rich vegetation, species with a less persistent seed bank (i.e. 'Short-term persistent' species *sensu* Thompson, 1993) could provide a buffer against occasional years when seed set was poor or prevented by cutting too early, and this level of persistence is probably important for the maintenance of species diversity (this aspect is discussed further in Chapter 8). Furthermore, if a change in management brings about an increase in the dominance of a particular species, which is mirrored by an increase in its abundance in the seed bank, recruitment from the seed bank might have the effect of reinforcing the dominance of this species, or of prolonging it after the change in management is reversed. This would apply even if the species shows only short term persistence in the seed bank in situations where seed shedding is followed each year by the disturbance of grazing.

Short- and long-term persistence are therefore likely to be of equal importance in the studies reported in this and following chapters. These studies are concerned both with the maintenance of species diversity in unfertilized meadows and with the potential for reversing fertilizer-induced changes in the vegetation, the latter having occurred over a relatively short time span (five years) compared with those investigated by Bakker (1989). Such changes have been progressive and largely in the form of altered species abundance rather than extinction of individual species (Mountford *et al.*, 1993a).

There is no published text which would allow species to be classified according to the Thompson (1993) and Bakker (1989) criteria as comprehensive as that for the Thompson and Grime (1979) Types I-IV system provided by Grime *et al.* (1988). The data generated by this study show marked differences in performance between species groups aggregated according to the latter system, including differences between Types III and IV. Use of this scheme therefore seems justified as a means of illustrating the influence of seed bank type on the interaction between fertilizer use, vegetation composition and seed bank abundance (see later discussion).

In terms of the numbers of species falling within each category, Types III and IV species were equally numerous, both in the vegetation and in the seed bank. However, the contribution that Type IV species made to vegetation cover was only about half that of Type III species, whereas the two groups differed little in seed bank density. Type IV species were therefore twice as abundant in the seed bank relative to their presence in the above ground vegetation as were Type III species.

The abundance of Type I species in the seed bank in March was surprising, since most or all of the seeds of these species were expected to have germinated during the previous autumn (Thompson and Grime, 1979; Grime *et al.*, 1988). Their presence may have been due to the very dry summer in 1990 when low water tables persisted into early November (see Chapter 3). Spring germination is more common in situations where dry soil conditions in the summer and autumn can delay germination until the following spring, since by the time soil moisture is replenished temperatures may be too low for germination (Grime, 1979). This phenomenon occurs most commonly among species with a relatively high temperature requirement for germination (Grime, 1979; Grime *et al.*, 1988). This explanation may be valid for *Rumex acetosa*, which has a minimum temperature requirement of 16°C, but is very unlikely for *Cynosurus cristatus* which can germinate at temperatures below 5°C (Grime *et al.*, 1981). An alternative, more likely explanation, is that in 1990 dry summer-autumn conditions were rapidly followed by heavy rainfall and a very rapid rise in water tables. Germination of a proportion of the seed present may have been delayed until the spring by anaerobic conditions due to waterlogging, rather than by low temperatures. It was noticeable that for all three of the Type I species most abundant in the seed bank (*C. cristatus, R. acetosa* and *Taraxacum agg.*), seed bank abundance relative to the vegetation was greatest in soil from the wettest areas at the site. Both *C.*

cristatus and *R. acetosa* were recorded in the seed bank in March in a more recent (1994) survey of some of the plots at Tadham Moor (R. Smith, personal communication). No hay crop was taken in the summer preceding this later sampling, and no plots were grazed until the autumn. Some areas were not grazed at all. This would allow a substantial number of *C. cristatus* seeds to remain unshed (see Chapter 8), possibly until the winter. In this case, germination could have been postponed either by waterlogging or by low temperatures, or both.

Comparison of seed bank and vegetation abundance to indicate seed bank persistence of unclassified species

As noted above, the degree of dissimilarity a species shows between its abundance in the vegetation and in in the seed bank is an indicator of its seed bank persistence (Bakker, 1979; Thompson, 1993). Twenty-seven of the 91 species.recorded in the seed bank in this study were not allocated to any seed bank type by Grime *et al.* (1988) and several others present here were identified only tentatively by those authors as belonging to a particular seed bank type. Most of these 27 species were present in too small amounts in this study to allow any firm conclusions to be drawn about their seed bank persistency. Some of these species were recorded only in the seed bank but were known to be present in the vegetation nearby (e.g. *Hydrocotyle vulgaris*) or elsewhere at the site (e.g. *Potentilla anglica*), allowing the possibility of recent, local transference of seeds, or that seeds had originated from isolated plants which had recently died.

However, the results do allow firmer conclusions to be drawn about the seed bank persistency of several other species which were either unclassified or only tentatively classified by Grime *et al.* (1988). Four of the *Carex* species present were unclassified and of these *C. hostiana* provided evidence of a long-term seed bank. Comparatively few *C. hostiana* seeds were found in the seed bank (mean 11 seeds m^{-2}), but the species was absent from the vegetation on the plots and is distributed only very sparsely at the site as a whole. Both *Isolepis setacea* and *Juncus bufonius* contributed substantial numbers to the seed bank (means 191 and 292 seeds m^{-2} respectively) but were absent from the vegetation. *J. bufonius* (Type ?IV) has never been recorded in the vegetation at the site, and *I. setacea* (Type ?III/IV) was only recorded in one quadrat in one of the years between

1986 and 1990 (out of a total of 360 quadrats each year) (Mountford *et al.*, 1993a; Sargent and Smyth, Mountford, Mountford and Smyth - unpublished reports). These results suggest that both the latter species should be classified as Type IV and *C. hostiana* as Type III or IV.

Bellis perennis was classified by Grime *et al.* (1988) as a Type I species, and both Chancellor (1985) and Roberts (1986) state that it is only briefly persistent. *B. perennis* was a very small component of the above ground vegetation in this study (<0.1-0.5% cover), yet a mean of 133 seeds m^{-2} were found beneath unfertilized plots. This was about 2-3 times the number of seeds shed on the same plots during the ensuing six months. If it is assumed that the number shed during the year preceeding the seed bank sampling was of the same order, it would appear that *B. perennis* can produce seed lasting for more than one year in the soil (i.e. Type III), even allowing for the unexpected survival of appreciable numbers of seeds of other Type I species already noted.

The effects of fertilizer application on vegetation and seed bank composition

The influence of previous fertilizer application on vegetation composition was most obvious within the seed bank Type I species group compared with other seed bank types. Type I species made a disproportionately large contribution to ground cover relative to the number of species involved, particularly on fertilized plots. This agrees with the observation of Grime *et al.* (1988) that Type I species tend to be competitive and typical of fertile soil conditions.

Most Type I species rely upon regeneration within predictable seasonally occurring gaps in the vegetation (Grime *et al.*, 1988). They are therefore well suited to hay cutting, management, particularly if followed by grazing which would increase the occurrence of regeneration niches (Grubb, 1977). Two thirds of these species had been identified as either N-positive or N-negative, with the majority falling within the former sub-group. By contrast, a smaller proportion of the Types III and IV species recorded had previously reacted either negatively or positively to N, and of those that did so, more than three times as many were N-negative as N-positive. The Type IV group appeared to be influenced by fertilizer application to a much lesser extent than Type III species, both in terms of vegetation cover and seed bank density.

The majority of the species identified here as N-positive were identified by Ellenberg (1988) as typical components of fertile vegetation in Europe, with 'Nitrogen scores' typically 6-7 on a nine-point scale. An alternative to using data from Experiment 1 to classify species as either N-positive or N-negative would have been to use criteria based upon Ellenberg scores, since most if not all the species could have been classified in this way. However, *Holcus lanatus* and *Bromus hordeaceus* were two notable examples of species whose performance in Experiment 1 did not conform to their Ellenberg scores. Ellenberg gave both a score of 3 - indicating that they are more often found on nitrogen-poor soils than those of average or high N content. The success of *H. lanatus* in fertile conditions under hay cutting and aftermath grazing can be attributed to the flexibility this species shows in both its regeneration and seed bank strategies (Grime *et al.*, 1988), coupled with a high dry matter production response to fertilizer N (Frame, 1991). On the other hand, *H. lanatus* is tolerant of a fairly wide range of growing conditions (Watt, 1978; Grime *et al.*, 1988) but, as noted in Chapter 2, it is generally less abundant in grazed pastures than mown meadows. These last two factors probably combine to give an overall correlation with infertile conditions in a European-wide context. *Bromus hordeaceus,* as an annual Type I species, is a rapidly germinating species very dependent on finding suitable sites for seedling survival soon after shedding (Grime *et al.*, 1988). It is possible that the system of aftermath grazing after hay making allows *B. hordeaceus* to capitalise on fertile conditions, compared with either the two cut hay system without grazing or the traditional litter meadows both of which seem to be more common in central Europe than in Britain (Ellenberg, 1988). Populations of both this species and *B. racemosus* expanded rapidly during the course of Experiment 1 (Mountford *et al.,* 1993a), but only occasional plants of either species have ever been found in the small-scale experiment (Experiment 2), where plots were cut and not grazed in the aftermath phase.

In this study, reductions in seed bank density among N-negative species apparently caused by fertilizer application were consistently more marked than increases in N-positive species, particularly when compared with corresponding differences in above-ground vegetation. This led to the observed overall reduction in seed bank density beneath fertilized plots. It also resulted in equal numbers of seeds of N-positive and N-negative species beneath fertilized plots, compared with unfertilized soils where the number of N-negative species was almost four times that of N-positive species. This change in the balance of species in the seed bank represented a significant potential for perpetuating the reduction in botanical diversity in the vegetation which occurred with fertilizer application (Mountford *et al.*, 1993a; Chapter 5), especially in view of the potential for replenishment of and recruitment from the seed bank provided by a combination of cutting and grazing.

The effects of fertilizer on the seed bank shown in this study reflect progressive changes in the vegetation occurring over a relatively short period. As shown elsewhere (Williams, 1985; Milberg,1992), much greater changes could be expected over a longer time period, including exctinction from both vegetation and seed bank of many of the less competitive species (Milberg, 1992). In a fairly species-rich meadow originally dominated by *Agrostis capillaris* and *Festuca rubra* (Williams, 1985), a 19% reduction in *A. capillaris* vegetation cover on fertilized plots compared with unfertilized plots after 14 years was reflected in a 3.5-fold difference in seed bank density. After a further five years, these differences had increased to 26% and 4.4-fold respectively. Over the same total time period, *Poa* species (mainly *P. annua*) had become the most abundant species on fertilized plots, with an 11-fold difference in ground cover reflected in a 23-fold difference in seed bank density. Whereas *Poa* species occupied 20% of the vegetation cover on fertilized plots, they accounted for nearly half the total seed bank.

The results of this study and others (Williams, 1985; Milberg, 1992) clearly demonstrate that fertilizer nitrogen influences seed bank composition indirectly by influencing vegetation composition and this is most clearly expressed by short-term persistent species. However, nitrate has been shown to enhance seed germination directly in both light and dark (Williams, 1983; Pons, 1989), and this could have the effect of depleting reserves of dormant seed in the soil. This in turn might ultimately lead to a decline in the vegetation of certain species, particularly those for which nitrate concentration acts as a gap detection mechanism (Pons, 1989), since this mechanism would normally help to ensure that germination occurs only where the chances of seedling survival are high. There were some examples in this study of species that showed no effect of fertilizer treatment on vegetation cover but a lower seed bank abundance beneath fertilized plots (e.g. *A. capillaris*, *Anthoxanthum odoratum*, *Ranunculus repens*). However, these effects were never clear-cut enough to discount the possibility that they had occurred by chance (and only the treatment difference shown by *R. repens* was statistically significant). The possible influences of applying N, P and/or K on the survival of buried seed of several species is currently under investigation at a range of sites in Europe, including Tadham Moor (Renée Bekker , personal communication)

Correlation between seed bank and above ground vegetation

Previous work has shown little correlation between the abundance in the above ground vegetation and in the seed bank on a small (0.6 m^2) scale for individual species, with heterogeneity in these two variables differing in both pattern and scale. (Thompson, 1986; Thompson *et al.*, 1994). However, this phenomenon will be less pronounced as the spatial scale under investigation increases, since variation in features such as topography and hydrology will become increasingly important. The extent to which patterns in heterogeneity in the seed bank of a particular species on a medium to large scale can be expected to reflect those in the vegetation will depend upon a number of factors. These will include the degree of continuity in vegetation management and other 'environmental factors', both spatially and from year to year, and the life history and seed bank persistence of the species in question.

The regression analyses carried out in this study encompassed variation encountered both within separate 196 m^2 areas and between plots separated by distances of up to 700m. In these circumstances, a strong correlation between seed bank and vegetation implies either that a high proportion of the seeds present have recently entered the seed bank (as with Type I species) or, in the case of species producing a long-term persistent seed bank, a marked heterogeneity of distribution of the relevant species in the vegetation coupled with a reasonable continuity of abundance where the species exists. Of all the different species aggregations investigated, the correlation between seed bank and vegetation was greatest for *Juncaceae* and *Cyperaceae*. This is significant, since the spatial distribution of these species is more closely defined by variations in hydrology accross the site compared with other species (Mountford and Chapman, 1993).

Quite marked year to year fluctuations in the population of individual species are a general rule in field experiments (e.g. Williams, 1978; van den Bergh, 1979; Elberse *et al.*, 1983). This is bound to influence the correlation between seed bank (assessed in the late winter-early spring) and vegetation assessed in the same year, since the seed bank is a reflection of seed shed in previous years. Furthermore, localised disturbance events which stimulate substantial recruitment of a particular species from the seed bank will tend to reduce the correlation between its seed bank and vegetative abundance on a small scale and particularly in the short term, since a portion of the seed bank component will be converted into increased vegetative cover of that species in that particular location. If enough of these events occur close to each other in both space and time, and the number of seeds which germinate represents a substantial proportion of those present in those locations, the result could be a negative correlation between seed bank and vegetative cover over a given area. A negative relationship was shown by Type I N-negative species on N_{200} plots in this study. However, since Type I species are dependent upon disturbance only to enhance seedling survival and not to stimulate germination, this negative correlation was probably a result of heterogeneity in the factors which prevented germination during the previous autumn, i.e. either dry or waterlogged soil. For species which were more abundant in the vegetation, including N-positive Type I species, heterogeneity of vegetative cover would have been an overriding influence, producing a positive correlation.

In terms of the number of species present, the seed bank Type III group was the largest of the four seed bank types present in both the seed bank and the vegetation. The relationship between vegetation cover and seed bank abundance within this group differed greatly between N-positive and N-negative species, particularly on fertilized plots, with the both the intercept and the slope of the regression notably smaller for the latter sub-group. This might suggest that suppression of this group of species in the vegetation has led not only to reduced vegetative abundance but also to a relatively greater suppression of seed production. This would be consistent with the observation that there is a threshold value of vegetative biomass for each species below which seed production cannot be supported (Thompson, 1978; Grime, 1979). However, seed rain data presented in Chapter 8 show that the number of seeds produced in July by N-positive species per unit of ground cover they occupied in May was very similar on both N_0 and N_{200} plots, and that these amounts were 3-4 times greater than those produced by N-negative species on the same plots. This implies that differences between N-positive and N-negative species in seed rain and seed bank abundance were a function of innate differences between species in seed production capacity, rather than a result of competition. The results therefore reflect a positive relationship between seed production potential and competitive success under increased soil fertility conditions (Grime, 1979; Grime *et al.*, 1988).

The results of these studies provide useful insights into the factors which operated in the past to produce the seed bank composition recorded, particularly when seen in conjunction with seed rain data (see Chapter 8 for further discussion). However, detailed studies of seed rain and seedling dynamics carried out during the course of several years of different fertilizer treatments would have been required to explain fully the relationship between vegetation and seed bank composition observed in one particular year. In this Chapter, emphasis has been placed upon seed bank type and aggressiveness under conditions of increased fertility as explanatory variables for the relationships observed, and the results provide some justification for this approach. However, these two properties are themselves integrated expressions of a number of different characteristics operating both within and between species (Harper, 1977; Grime, 1979; Grime *et al.*, 1981,1988). There may be factors of overriding importance operating at the individual species level which are masked by grouping species according to the criteria used in this study.

6.5. CONCLUSIONS

Several clear distinctions emerged between seed bank Type III and IV species, and between these groups and Type I species, which justified the use of the Thompson and Grime (1979) scheme as a means of generalizing the data.

The results showed that, after five years of fertilizer application, the balance of species in the seed bank had been changed in favour of those which are both more competitive under fertile conditions and less persistent in the soil. This could have the effect of prolonging the dominance of these species in the vegetation after fertilizer use has been discontinued. Strategies to restore species diversity in these situations should aim both at reducing fertility and at encouraging species which have declined to set and shed seed. Data presented in the next two chapters suggest that the scope for achieving both these objectives by manipulating cutting date is limited.

6.6. SUMMARY

Assessments were made of the soil seed bank in March, and of the above ground vegetation in the following May, of meadows which had either received repeated applications of inorganic fertilizers during the preceeding five years or were unfertilized. During these preceeding five years, plots had been cut for hay followed by aftermath grazing.

A substantial number of seeds of species which normally germinate soon after shedding (i.e. Type I species *sensu* Thompson and Grime, 1979), had survived in the soil until March. This was thought to have been due to a rapid change from very dry to waterlogged soil in the autumn, with both conditions inhibiting germination. Type I species accounted for a disproportionately large proportion of total ground cover relative to the number of species involved, compared with species of the remaining seed bank types (II-IV).

On the basis of heterogeneity on a between-plot scale, the Type I group showed the closest correspondence between vegetation cover and seed bank abundance, whilst Type IV group showed the least. However, as separate groups, *Juncaceae* and *Cyperaceae* (most of which were Type IV species) showed a close correspondence between vegetation cover and seed bank abundance compared with grasses and dicots. This was thought to be due to marked variation on a between-plot scale in the specific hydrologic conditions for which these species show a stronger preference than others.

Fertilizer application increased the abundance in the vegetation of a few species and reduced the abundance of a larger number, and these effects were mirrored to a large extent by differences in seed bank composition. The effects of fertilizer application were most clearcut within the Type I group, particularly when species were further sub-divided into those which had reacted positively or negatively to applied N in Experiment 1. In general, fertilizers caused a four-fold shift in the balance of species in the seed bank towards those which were previously identified as responding positively to N in terms of vegetation cover, with a smaller concomitant shift from Type IV species to Type III.

It is concluded that management aimed at restoring high species diversity to fertilized meadows should aim at both reducing soil fertility and encouraging those species which have declined to set and shed seed.

CHAPTER 7

THE INFLUENCE OF CUTTING DATE AND PREVIOUS FERTILIZER TREATMENT ON THE PRODUCTIVITY OF SPECIES-RICH HAY MEADOWS

7.1. INTRODUCTION

Data presented in Chapter 5 and elsewhere (Mountford, *et al.,* 1993a) have shown that the plant communities at Tadham Moor are very sensitive to even modest applications of inorganic fertilizers, in broad agreement with findings from previous work in other locations and soil types (e.g. Lawes *et al.*, 1882; Willis, 1963; Heddle, 1967; Williams, 1984; Garstang, 1981). As noted in Chapter 3, the potential productivity of these meadows is very similar to that of a wide variety of less species-rich permanent pastures when inorganic fertilizers are used. However, in addition to restrictions on fertilizer use, both ESA and SSSI schemes include rules on hay cutting date, with no cutting allowed before 1 July in SSSIs and Tier 2 of the ESA, or 8 July for Tier 3 (Her Majesty's Stationery Office, 1992). These dates allow ground-nesting birds such as snipe (*Gallinago gallinago*) to rear their young with a minimum of disturbance (Green, 1986) and are also intended to allow plants to set seed. However, as in the meadows of the Pennine Dales (Smith and Jones, 1991), many species have not set seed by the beginning of July. Whilst the vast majority of these species are perennials, many rely on seed production for regeneration and a significant number germinate rapidly after shedding, exhibiting no seed dormancy (Grime *et al.,* 1988).

In the past, hay cutting has been delayed in some years, usually by wet weather, until August or even later. In these years, late-flowering species will have set seed, many either producing new seedlings or contributing to the soil seed bank (Thompson and Grime, 1979). However, with improvements in technology, hay making is completed increasingly early (Smith and Jones, 1991). In the Pennine Dales ESA, it has been recognized that this may result in a progressive decline in species diversity and the loss of certain characteristic species. There, ESA rules stipulate that hay must be cut after 1 August in at least one year in five (Younger and Smith, 1993). No such prescription is applied at present in the

Somerset Levels ESA.

Where the aim is to increase diversity in species-impoverished meadows, it may be desirable to prevent the dominant species from setting seed. Investigation of the agronomic implications of different cutting dates is needed, both in species-impoverished meadows and in species-rich vegetation. Whilst the relationship between date of cutting, yield and nutritive value is well known for species which are normally sown or encouraged in intensively managed swards (NIAB, 1987), information for species-rich vegetation is limited.

This chapter and Chapter 8 describe the results of Experiment 3, which was begun in 1991 within the framework of the large-scale experiment (Experiment 1) and which also provided the plot layout used for seed bank assessments described in Chapter 6. The effects on productivity of four cutting dates between late May and early September imposed in two consecutive years in paddocks which had received either no inorganic fertilizer previously (N_0) or which had received 200 kg N ha^{-1} $year^{-1}$ between 1986 and 1989 (N_{200}) were investigated. Data on the influence of these treatments on seed rain and vegetation composition are reported in Chapter 8. This chapter describes data on yield and quality of herbage and discusses the agronomic implications of the results for meadow management.

7.2. MATERIALS AND METHODS

EXPERIMENT DESIGN AND TREATMENTS

The location and basic design of the plot layout for this experiment were described in Chapter 1 and Chapter 6 (see Figures 1.5 and 6.1). The experiment had two previous fertilizer treatments: no inorganic fertilizers (N_0); and 200 kg N ha^{-1} with base levels of P and K for the previous five years (N_{200}). There were six randomised sets of twelve 2m x 4m plots laid out in March 1991, one set within each of the three replicate paddocks of the control (N_0) and N_{200} treatments of the existing randomized block lay-out of the large-scale experiment.

No fertilizer was applied to the experimental plots described here after mid-summer 1990. Phosphorus (P) and potassium (K) had been applied to N_{200} plots after hay cutting each year at rates sufficient to replace the amounts removed in hay. These rates averaged 8.7 kg P ha^{-1} and 61.9 kg K ha^{-1} per year. Within each set of plots, four were cut in late May, two in early-mid July, two in early August, and four were cut in early September, with cutting date treatments imposed on the same plots in two consecutive years. Dates of cutting were 22 May, 17 July, 9 August and 4 September in 1991, and 26 May, 6 July, 1 August and 1 September in 1992.

Each plot was cut only once in 1991. All plots were then grazed along with the remainder of the paddock from 11 September to 4 November by 12-month-old steers averaging 297 kg live weight, at mean stocking rates of 1.3 and 2.1 steers per hectare for N_0 and N_{200} paddocks respectively. However, the regrowth on plots cut in May was rejected to some extent by grazing animals in favour of the less mature growth on other areas. This resulted in a significantly greater cover of dead vegetation on these plots by the following spring. Consequently, at the last cutting date in 1992 (1 September), all plots and discard areas were cut to a uniform height and herbage was removed before grazing. Each plot was then grazed along with the remainder of the paddock from 9 September to 20 October at stocking rates of 2.2 (N_0) and 3.6 (N_{200}) steers ha^{-1}. Slightly smaller animals were used in 1992 than 1991, averaging 278 kg live weight.

CUTTING AND HAY MAKING

At each stage of the harvesting process, efforts were made to simulate the action and severity of mechanized hay-making. On each cutting date, a 1m x 4m swath was cut to a height of about 5 cm along the centre of each of the appropriate plots, using a reciprocating blade mower. A sub-sample totalling 300-500 g fresh weight was taken from at least five randomly-chosen sites within each swath for later dry matter (DM) determination and chemical analysis, whilst the remainder was gathered and weighed fresh along with the sub-sample. Herbage was returned to the appropriate plot and distributed along the 1m x 4m cut area before cutting the remainder of the plot, including the surrounding 1m wide guard area. The herbage on May-cut plots was left *in situ* to wilt for 24 hours to simulate silage making, before removal from the plot. At later cutting dates, hay was made manually, turning and tedding at least twice using a hay fork. This process was repeated until herbage was considered dry enough to have been baled. Before clearing each plot, including those cut in May, herbage was transferred by fork from each end of the plot into a wind-row across the centre of the 4m x 4m plot-plus-guard-strip area, but leaving herbage from the 1m guard area at each end of the plot undisturbed. The wind-row was then left for one hour before raking into a tare sheet for removal.

DRY MATTER DETERMINATION AND CHEMICAL ANALYSES

The methods used for dry weight determination and chemical analysis were basically the same as those described in Chapter 3 for Experiment 2. Sub-samples were weighed fresh and dried overnight at 80^0 C before weighing again for dry weight determination. Dried samples were ground in a hammer mill and analyzed for *in vitro* organic matter digestibility (DOMD) by pepsin-cellulase digestion (Jones and Hayward, 1973), for total N content by micro-Kjeldahl digestion (Association of Official Analytical Chemists, 1965) and, following ashing and dissolving in 25% HCl, for K, Ca and Na content by flame photometry, for Mg content by absorption spectrometry and for P concentration by colorimetry on a continuous segmented flow analyser, after Aspila *et al.* (1976). The metabolizable energy (ME) value of herbage at cutting was calculated from the *in vitro* digestibility and the N content of herbage (Ministry of Agriculture, Fisheries and Food, 1975), as in Chapter 3.

In 1992, the yield and composition of regrowth between May and September was measured on May-cut plots. Methods used were as for primary growth, except that all herbage was removed immediately after cutting and weighing.

DATA ANALYSIS

Each year's data were subjected to analysis of variance (ANOVA) using a split plot, randomized block design, with previous fertilizer treatment as main plots, using GENSTAT (GENSTAT V Committee, 1987).

7.3. RESULTS

YIELD AND CHEMICAL COMPOSITION OF PRIMARY GROWTH

Dry matter yield

Dry matter (DM) production, averaged over two years, increased between May and July ($P<0.001$) and again between July and August ($P<0.05$), but not between August and September (Table 7.1). In neither year was there any significant effect of previous fertilizer treatment (N_0 v N_{200}) on DM yield of primary growth nor any significant cutting date x

Table 7.1. The effect of previous fertilizer treatment 1986-90 (N_0 and N_{200} - see text) and different cutting dates on DM production, digestibility (*in vitro* DOMD), ME value and ME output of herbage harvested, averaged over two years 1991 and 1992.

Fertilizer	Cutting date	DM yield (t ha^{-1})	DOMD	ME value (MJ kg^{-1})	ME output (GJ ha^{-1})
N_0	May	1.68	61.7	10.2	16.7
	Jul	4.72	55.4	8.9	41.8
	Aug	5.48	50.9	8.2	44.7
	Sep	5.73	50.2	8.1	46.6
N_0 mean		4.17	55.0	9.0	35.5
N_{200}	May	2.64	63.7	10.5	27.4
	Jul	5.71	52.8	8.3	47.7
	Aug	6.12	47.6	7.7	46.9
	Sep	6.17	48.6	7.9	48.8
N_{200} mean		4.91	54.2	8.8	41.1
Mean N_0/N_{200}	May	2.16	62.7	10.3	22.0
"	Jul	5.22	54.1	8.6	44.8
"	Aug	5.80	49.2	7.9	45.8
"	Sep	5.95	49.4	8.0	47.7
SED fertilizer means:		0.191	0.23	0.06	1.38
SEDs cutting date means:					
May v Sep		0.172	0.50	0.08	1.50
Jul v Aug		0.243	0.71	0.12	2.12
May/Sep v Jul/Aug		0.210	0.61	0.10	1.84
		***	***	***	***
SEDs cutting date x fertilizer:					
(1) Same level N					
May v Sep		0.243	0.71	0.12	2.12
Jul v Aug		0.343	1.00	0.17	3.00
May/Sep v Jul/Aug		0.298	0.86	0.14	2.60
(2) Others:					
May v Sep		0.276	0.62	0.11	2.22
Jul v Aug		0.367	0.94	0.16	3.00
May/Sep v Jul/Aug		0.325	0.80	0.14	2.60
			***	***	*

Asterisks denote significance of treatment effects in ANOVA:
* = $P<0.05$; *** = $P<0.001$

fertilizer treatment interaction.

Herbage digestibility

The overall effect of previous fertilizer treatment on herbage DOMD was not significant but there was a highly significant cutting date x fertilizer treatment interaction ($P<0.001$)(Table 7.1). The DOMD of N_{200} herbage was higher than N_0 when cut in May ($P<0.01$), but the opposite was true for all other cutting dates ($P<0.01$ for July and September, $P<0.001$ for August). Averaged over previous fertilizer treatment, herbage digestibility declined significantly between each cutting date until August ($P<0.001$) with no change between August and September.

Metabolizable energy (ME) output

ME output per hectare increased very significantly between May and July, but showed no further overall change between cutting dates (Table 7.1). There was no significant overall effect of previous fertilizer treatment on ME output but there was a significant cutting date x fertilizer treatment interaction ($P<0.05$). When cut in May, previously fertilized plots produced 10.7 GJ ha^{-1} more ME than N_0 plots, representing a highly significant difference ($P<0.001$). ME output tended to be greater from N_{200} plots than N_0 plots at each cutting date (Table 7.1).

Mineral composition

The concentrations of all the minerals analyzed were significantly affected by cutting date when averaged over the two years, but not by previous fertilizer treatment (Table 7.2). However, there were significant cutting date x fertilizer treatment interactions for concentrations of P ($P<0.05$), K ($P<0.001$) and Na ($P<0.01$). Concentrations of N, P and K were all significantly higher in herbage cut in May than on all other occasions ($P<0.001$). Concentrations of Na were consistently higher in N_0 herbage than N_{200}, though not significantly so, whilst Na concentration declined significantly between August and September on N_{200} plots ($P<0.05$) but not on N_0. Ca concentration was higher in July than at any other cutting date ($P<0.001$) and magnesium concentration declined significantly between July and September ($P<0.05$).

Table 7.2. The effect of previous fertilizer treatment 1986-90 (N_0 and N_{200} - see text) and different cutting dates on the concentration of six minerals in herbage DM, averaged over two years 1991 and 1992.

Fertilizer	Cutting date	Mineral concentration (% of DM)					
		N	P	K	Na	Ca	Mg
N_0	May	2.34	0.13	0.75	0.60	0.69	0.23
	Jul	1.60	0.11	0.68	0.58	0.81	0.23
	Aug	1.46	0.12	0.73	0.60	0.65	0.22
	Sep	1.55	0.12	0.52	0.55	0.69	0.20
N_0 mean		1.81	0.12	0.66	0.58	0.70	0.22
N_{200}	May	2.33	0.14	1.18	0.51	0.59	0.22
	Jul	1.32	0.12	0.70	0.54	0.72	0.21
	Aug	1.38	0.12	0.84	0.46	0.56	0.18
	Sep	1.53	0.13	0.83	0.37	0.56	0.18
N_{200} mean		1.74	0.13	0.93	0.46	0.56	0.20
Mean N_0/N_{200}	May	2.34	0.14	0.96	0.56	0.64	0.22
"	Jul	1.46	0.12	0.69	0.56	0.76	0.22
"	Aug	1.42	0.12	0.79	0.53	0.61	0.20
"	Sep	1.54	0.12	0.67	0.46	0.62	0.19
SED fertilizer means:		0.038	0.004	0.097	0.030	0.031	0.011
SEDs cutting date means:							
May v Sep		0.051	0.003	0.038	0.017	0.025	0.006
Jul v Aug		0.072	0.004	0.053	0.024	0.035	0.009
May/Sep v Jul/Aug		0.063	0.003	0.046	0.020	0.031	0.008
		***	***	***	***	***	***
SEDs cutting date x fertilizer means:							
(1) Same level N							
May v Sep		0.072	0.004	0.053	0.024	0.035	0.009
Jul v Aug		0.103	0.005	0.075	0.033	0.050	0.013
May/Sep v Jul/Aug		0.089	0.005	0.065	0.029	0.043	0.011
(2) Others:							
May v Sep		0.070	0.005	0.107	0.036	0.043	0.013
Jul v Aug		0.101	0.006	0.119	0.043	0.055	0.016
May/Sep v Jul/Aug		0.087	0.006	0.113	0.040	0.049	0.015
			*	***	**		

Asterisks denote significance of treatment effects in ANOVA:
* = P<0.05; ** = P<0.01; *** = P<0.001

YIELD OF MAY-SEPTEMBER REGROWTH (1992)

Yield of May-September regrowth was measured only in 1992. Concentrations of Na in herbage were lower on N_{200} plots than N_0 ($P<0.05$), whilst the opposite was true for K concentration ($P<0.01$) (Table 7.3). None of the other variables measured in May-September regrowth were significantly affected by previous fertilizer treatment (Table 7.3). Dry matter yields were higher in regrowth than in primary growth harvested in May, particularly on N_0 plots, so that, whilst digestibility and ME value were lower, ME yields were higher.

When DM yields from 1992 regrowth were added to those of primary growth in the same year, the resulting totals exceeded those from single cuts in September 1992, both on N_0 and N_{200} plots (6.5 t ha^{-1} compared with 5.4 t and 6.9 t ha^{-1} compared with 5.4 t respectively). Total ME output was also greater, by 39% and 53% on N_0 and N_{200} plots respectively.

Table 7.3. Dry matter yield, *in vitro* digestibility (%DOMD), ME value, ME production and concentration in herbage of N, P, K, Na, Ca and Mg in regrowth between 26 May and 1 September in 1992.

					Concentration of minerals (% of DM)					
Previous fertilizer treatment	t DM ha^{-1}	DOMD	MEvalue (GJ kg^{-1} DM)	ME yield (GJ ha^{-1})	N	P	K	Na	Ca	Mg
N_0	4.09	54.3	9.0	36.3	1.87	0.16	0.64	0.56	0.55	0.27
N_{200}	3.83	54.4	8.9	34.0	1.91	0.17	0.85	0.46	0.46	0.27
SED	0.445	0.52	0.06	3.92	0.041	0.003	0.045 **	0.003 *	0.032	0.011

* = significant treatment effect in ANOVA, $P<0.05$; ** = $P<0.01$

7.4. DISCUSSION

HERBAGE NUTRITIVE VALUE

The decline in digestibility and ME value caused by delaying hay cutting until August is in line with established principles for grass and legume crops (NIAB, 1987). However, even in May, herbage digestibility was lower at 62% than that which would have been typical (67%) for recommended sown grass varieties (NIAB, 1987) and similar to values recorded in a mixed species permanent grass sward by Tallowin *et al.* (1990). Equally low values for DOMD were recorded previously in herbage cut in May from these meadows, on plots receiving 400 kg N ha^{-1} $year^{-1}$ (see Chapter 3).

The concentrations of Ca, Mg and Na recorded in herbage in this experiment would easily meet the dietary requirements of all classes of sheep and cattle, even when cut in September (Agricultural Research Council, 1980). The comparatively high Na concentrations (Whitehead, 1966; Chiy and Phillips, 1993) reflect the marine history of the underlying clay alluvium, which is often connected to the soil surface by a continuous water column due to characteristically high water tables within the peat layers (Ross, 1988). This hydrology also contributes to supplies of Ca which originate from the surrounding limestone hills (Ross, 1988). However, values for crude protein (6.25 x N) in July-September content were low at between 83-100 g kg^{-1} DM compared with 'improved' or intensively managed grass or grass/clover ((Agricultural Research Council, 1980). Even when cut in May, P concentrations were inadequate for ruminant nutrition (Agricultural Research Council, 1980). The low DOMD and ME values of herbage harvested later than July would also make hay made from this herbage unsuitable for highly productive animals, particularly as further losses in ME value could be expected during hay making (see Chapter 3).

AGRONOMIC IMPLICATIONS OF CUTTING DATE

To gain a full appreciation of the agronomic implications of different hay cutting dates aftermath production would have to be taken into account. This aspect was not addressed in the experiment reported here, except to the extent that yield and quality of May-September regrowth were measured in one year. However, in previous work in these meadows (see Chapter 3), aftermath grazing produced 29% of the total annual utilizable ME (UME) from unfertilized swards averaged over three years when hay was cut in early July. In a year when hay making was delayed until the beginning of August, aftermath grazing produced only 8% of the annual UME output, and total annual UME output was reduced by 11% compared with the other three years. These effects can be attributed to declining herbage growth in late summer and autumn (Corrall and Fenlon, 1978) combined with the shorter period available for aftermath grazing. These same factors would almost certainly offset the slight increase in mean hay ME output by cutting in September compared with August recorded in this experiment (i.e. 1.9 GJ ha^{-1}).

The total ME obtained in this experiment in 1992 by cutting in late May followed by a further cut in early September was 64.5 GJ ha^{-1} on previously N_{200} plots and 59.3 GJ on unfertilized plots. These levels of productivity are much higher than those achieved by cutting in September only (46.9 and 44.7 GJ ha^{-1} for N_{200} and N_0 plots respectively). However, they are somewhat lower than might be achieved by cutting in July and harvesting all subsequent regrowth, if it is assumed that the hay ME outputs from cutting in July (47.7 and 41.8 GJ ha^{-1} for N_0 and N_{200} plots) were 65% of those achievable for the whole season as in previous work (see Chapter 3). Any ME obtained after the second cut in September on plots first cut in May would be unlikely to offset these differences.

These calculations are, of course, not definitive. However, they suggest that in unfertilized meadows, or where fertilizer use has been discontinued, there is little or no advantage in terms of ME output of cutting in late May as opposed to early July, unless added weight is given to quality of herbage rather than quantity. Delaying hay cutting from July to August could incur penalties both in terms of reduced hay quality and of reduced total annual production. These particular penalties would not be increased significantly by delaying cutting further until early September, although the practical limitations imposed by the reduced grazing period might be important.

7.5. CONCLUSIONS

Data presented in the next chapter (Chapter 8) confirm the deleterious effects of cutting early (in May) from the plant ecological point of view, and show that there are strong arguments for occasionally delaying cutting from July until August. Data presented here show no significant advantage in terms of metabolizable energy production per hectare of taking a first cut in late May as opposed to July, although the energy value, and therefore the animal production potential, of herbage cut in May is greatly superior to that harvested at later dates. Cutting after July not only produces hay of even poorer quality but also reduces production from aftermath grazing. These factors would have to be taken into account if SSSI or ESA prescriptions were to include a requirement for cutting later than July.

7.6. SUMMARY

The effects on productivity, botanical and chemical composition of cutting species-rich hay meadows in Somerset on four different dates between late May and early September in two consecutive years, were measured. Plots which had received 200 kg N ha^{-1} $year^{-1}$ with low levels of P and K for the previous five years were compared with plots which had previously received no fertilizer.

Previous fertilizer treatment increased metabolizable energy (ME) production only with cutting in May. DM yield increased significantly with date of cutting until August, whilst ME value declined correspondingly. There was no difference in either yield or quality of herbage cut between August and September. ME output per hectare from primary growth increased very significantly between May and July, but showed no further change between cutting dates.

It is concluded that there is an advantage of cutting in late May as opposed to cutting in July in terms of quality of primary growth but not in terms of total metabolizable energy production per hectare if aftermath production is taken into account. The small increase in hay yield by delaying cutting from July to August is unlikely to compensate for the lower quality of hay and the reduced aftermath production which would result.

CHAPTER 8

THE INFLUENCE OF CUTTING DATE AND HAY-MAKING OPERATIONS ON SEED RAIN AND VEGETATION COMPOSITION IN UNFERTILIZED AND PREVIOUSLY FERTILIZED MEADOWS

8.1. INTRODUCTION

Plant species differ greatly in the timing and abundance of their seed production (Salisbury, 1942; Smith and Jones, 1991). The effect of different cutting dates on the botanical composition of a hay meadow will reflect several interacting factors, probably the most important of which will be the seeding phenology of the individual constituent species and the extent to which each relies upon regeneration from seed (Grime, 1979; Smith and Jones, 1991).

Regulations within the Somerset Moors and Levels Environmentally Sensitive Area (ESA) preclude cutting before the 1 July in Tier 2 and before 8 July in Tier 3, and one of the aims of this rule is to allow a wide variety of plants to set seed (Her Majesty's Stationary Office, 1992). Regulations within the Pennine Dales ESA go further, requiring hay to be cut in August at least one year in every five (Ministry of Agriculture, Fisheries and Food, 1992). Evidence supporting this ruling was provided by Smith and Jones (1991) who showed that few of the species present in hay meadows in the Dales has reached maximal ripe seed production by mid July and none had reached maximal dehiscence by late August.

A study of 151 meadows in the Pennine Dales showed that lack of drainage was the most important factor related to high conservation value of the vegetation, but within undrained meadows cutting date was the most important factor (Askew, 1993). Cutting these meadows in late July leads to a higher richness and diversity of species compared with cutting in mid June or early September (Younger and Smith, 1993). Similar information is lacking for the plant communities found on peat moors within the Somerset Levels, and no study appears to have been published which has measured the influence of cutting date on the total number of seeds shed ('seed rain') of the species present in any British meadow community.

The composition of the soil seed bank beneath the meadows at Tadham Moor was described in Chapter 6, and Chapter 7 described the agronomic implications of varying the harvest date of primary growth. This chapter describes studies under three main headings:-

1. 'Seed rain' in relation to cutting date and hay-making operations
   - the number of subsequently germinating seeds shed up to and during harvesting of primary growth between late May and early September.
   - the proportion of these seeds that were shed before cutting and the importance of individual hay-making operations in inducing seed shedding.
2. The influence of cutting date on subsequent botanical composition
3. The phenology of seed production, shedding and viability of three dicotyledonous species and the influence of simulated hay drying.

The studies in 1 and 2 above attempt to explain the results in terms of the regenerative strategies (Grime, 1979) and seed bank behaviour (Thompson and Grime, 1979) of the constituent species.

8.2. METHODS AND MATERIALS

EXPERIMENTAL DESIGN

Most of the work described in this chapter was carried out within the layout of the cutting date experiment (Experiment 3). The location and basic design of this experiment were described in Chapter 1 and Chapter 6 (see Figures 1.5 and 6.1) and the cutting and management of these plots was decribed in detail in Chapter 7. The following is a brief description.

The experiment had two previous fertilizer treatments: no inorganic fertilizers (N_0); and 200 kg N ha^{-1} with base levels of P and K for the previous five years (N_{200}). There were six randomised sets of twelve 2m x 4m plots laid out in March 1991, one set within each of the three replicate paddocks of the control (N_0) and N_{200} treatments of the existing randomized block lay-out of the large-scale experiment (Experiment 1). No fertilizer was applied to the experimental plots described here after mid-summer 1990. Within each set of plots, four were cut in late May, two in early-mid July, two in early August, and four were cut in early September, with cutting date treatments imposed on the same plots in two consecutive years. Dates of cutting were 22 May, 17 July, 9 August and 4 September in 1991, and 26 May, 6 July, 1 August and 1 September in 1992. Each plot was surrounded by a 1m wide guard area cut at the same time as the plot.

Each plot was cut only once in 1991 and all plots were grazed along with the remainder of the paddock from 11 September to 4 November by 12-month-old steers. However, as noted in Chapter 7, differences in maturity of regrowth at the start of aftermath grazing led to selective grazing of the plots, with those cut in May largely rejected. This resulted in a significantly greater cover of dead vegetation on these plots by the following spring. Consequently, at the last cutting date in 1992 (1 September), all plots and discard areas were cut to a uniform height and herbage removed before grazing. Each plot was then grazed along with the remainder of the paddock from 9 September to 20 October.

CUTTING AND HAY MAKING

At each stage of the harvesting process, efforts were made to simulate the action and severity of mechanized hay-making. On each cutting date, the vegetation was cut to a height of about 5 cm using a reciprocating blade mower. The herbage on May-cut plots was left *in situ* to wilt for 24 hours to simulate silage making, before removal from the plot. At later cutting dates, hay was made manually, turning and tedding at least twice using a hay fork. This process was repeated until herbage was considered dry enough to have been baled. Before clearing each plot, including those cut in May, herbage was transferred by fork from each end of the plot into a wind-row across the centre of the 4m x 4m plot-plus-guard-strip area, but leaving herbage from the 1m guard area at each end of the plot undisturbed. The wind-row was then left for one hour before raking into a tare sheet for removal.

LOCATION OF SAMPLING POINTS

All 'seed rain' and vegetation composition measurements were carried out from sampling positions located within the central 1m down the length of each 4m x 2m plot. As described in Chapter 6, this 1m x 4m strip was notionally divided into a grid of sixteen 50cm x 50cm squares (i.e. two rows of eight). Four of these squares were chosen (by random numbers) for botanical assessments, with the restriction that the two squares at each end of the plot (four in total) were not included in any of the studies. Five of the remaining 21 intersections of the grid were then chosen as sampling points for 'seed rain' measurements. Where possible, location of these points was random but, in order to avoid interference between the two sets of measurements, intersections at the corner of each quadrat position were excluded. This meant that the choice of seed rain sampling point was limited, and where insufficient points were available, a position intermediate between grid sections was chosen at random.

'SEED RAIN' IN RELATION TO CUTTING DATE AND HAY-MAKING OPERATIONS

Three studies were made of the timing of seed production, assessed to individual species level:

(i) Measurement of 'seed rain' between early April and completion of harvest of vegetation at one of four cutting dates in 1991 (see below for definition of 'seed rain').

(ii) Assessment of the proportion of seed shed before and after cutting in July, August or September.

(iii) Measurement of seed rain during three phases of mechanized hay making.

In studies (i) and (ii), 'seed rain' was measured indirectly by identifying and counting the number of seedlings which had emerged, or which emerged subsequently, from compost-filled dishes which had been set into the ground in April or May and removed after hay making, or, in study (ii), removed before cutting and replaced with new dishes which were removed after hay making. No attempt was made to count the total number of seeds shed over specific periods in these studies. Instead, the studies measured potential seedling production, as at cutting or completion of harvest, from seed shed up to this date. The number of seedlings recorded of each species was therefore an integration of several separate factors, including:

(a) the total number of seeds shed;

(b) the viability of those seeds;

(c) the proportion of the total number of viable seed produced which was shed

originating from early shed seed becoming so large by the time dishes were removed as to be difficult to differentiate from plants which had invaded the dishes by vegetative growth. It would also minimise the loss of early-shed seeds, or their resultant seedlings, by predation or unsuccessful establishment. However, it became clear that, for later cutting dates, the procedure of locating sampling points and placing the dishes would cause too much disturbance to the vegetation, with the serious risk of some seeds being shed but not captured. Dishes were therefore placed on all the remaining plots on 26 May. In the event, even by the latest cutting date, few seedlings were big enough to cause any problem.

Except for a subset of plots used in study (ii) (see below), dishes remained in place until after harvesting of the vegetation on the relevant date. Dishes were then removed and any seedlings already present were identified, counted and discarded. Ungerminated seeds were covered with a fine sprinkling of potting compost to a depth of 1-3 mm to avoid flotation during subsequent watering. Each dish was then placed in a predetermined, randomised location on a bed of coarse builders sand (Plate 8.1) in a polythene tunnel at Rumleigh Experimental Station and watered once or twice a day thereafter. Emerging seedlings were recorded at approximately monthly intervals until 23 September 1992, i.e. 13 months after the last harvest date. On each occasion, seedlings were counted and removed and the whole surface area of soil was lightly scratched with forceps. Each time dishes were transferred from the field, eight blank dishes were filled with the same compost, placed within the same randomised layout in the polytunnel, and subsequently treated identically to the sample dishes. The final number of seedlings per dish which emerged from all the blank dishes together was subtracted from the final total of the relevant species on each sample dish (with a minimum result of zero). This took account both of any airborne contamination within the poly-tunnel and any seedlings originating from the compost. Very little contamination occurred from either source, although a small number of seedlings of *Juncus effusus* and *Erica spp.* emerged from the compost.

The procedure described above gave data for seed production from late March to 22 May on plots cut on this date and for the period between this date and the relevant cutting date on other plots. In order to produce data relating to the whole period for these later cutting dates, values obtained from May-cut plots were added to the remaining data. Separate means for each replicate block and fertilizer treatment were used for each species, i.e. a total of six values, each a mean of four plots, with the relevant mean added to the remaining eight plots of the same fertilizer treatment on the same block of the experiment.

Measurements of seed rain during May-September regrowth were also made. Dishes removed after cutting in May were replaced after harvesting the vegetation and taken up again at the same time as those on September-cut plots. These dishes were treated in exactly the same way as those from other plots. As already noted, May-cut plots were not cut again before grazing in September in 1991, so that further seed shedding may have occurred during grazing of these plots. Before removing the dishes, an attempt was made to simulate the disturbance caused by grazing animals by beating the standing vegetation with a hay fork. However, the seed shed during this process may not have accurately represented that which would have been shed during grazing, particularly since, as noted previously, these plots were largely rejected by grazing animals. Consequently, the plots probably received less disturbance than that given by hand, with greater opportunity for seed to mature before shedding. No attempt was made to assess any seed rain produced during regrowth of remaining plots and, in the event, very little reproductive development was noticeable on these plots. Occasional flower heads, mainly of *Agrostis capillaris*, had appeared by 4 September on plots cut in July, but very few appeared to be carrying ripe seed by this date. The data collected during regrowth on May-cut plots are presented separately from other data in the results section and, except for some regression analyses relating botanical composition in 1993 and seed rain data (see later), these data were not added to any other data set.

Altogether, seed rain was assessed at 360 sampling points in the field in the main study (5 x 72 plots). However, a subset of the plots was also used in study (ii), where dishes were removed and replaced before cutting, so that, including the 120 used during May-September regrowth on May cut plots, a total of 510 sample dishes were used. On the plots also used in study (ii), the number of seedlings recorded per dish for this (main) study was the sum of that recorded both before cutting and after harvesting vegetation (see below). A total of six dishes used in the main study had to be discarded, three due to disturbance from moles and three because their contents had been largely replaced by vole nests.

The poly-tunnel used was the same as that described in Chapter 6 (seed bank study). Temperatures typically ranged from about 10 to 30°C during June-August and -1 to +15°C during December-March, with highest and lowest temperatures recorded of 38°C and -4°C respectively.

(ii) Seed rain - the proportion shed before cutting

This study was carried out on one replicate block of the N_0 treatment, using those plots cut in July, August and two of the four plots cut in September (total of six plots). On each of these plots, the five sample dishes were removed immediately before cutting and replaced with new ones freshly filled with compost. This second set of dishes was removed after harvesting vegetation. Thereafter all dishes were treated as in the main study.

(iii) Seed rain during three phases of mechanized hay making

Ten sampling locations were chosen within a 19m x 2m strip adjacent to the N_0 plots in block 1 of the cutting date experiment (Experiment 3). These locations were established at 2m intervals down the strip, and at each 2m interval the exact sampling location was selected randomly from a choice of 21 10cm-spaced points accross the 2m width. Only one dish was placed at each 2m interval down the 19m length. A compost-filled dish was placed at each of these 10 locations immediately before cutting with a tractor-mounted drum mower on 9 August 1991. Dishes were replaced at the same locations by freshly filled dishes immediately after cutting, and this second set was in turn replaced four days later by new dishes, immediately prior to rowing the crop up for baling. In the intervening time, the hay was tedded twice, using a standard tractor-powered rotary tedder, to encorage drying. No rain fell during hay making. On 13 August, the hay was drawn into a row approximately 1m wide down the centre of the 19m x 2m strip (all operations were carried out by equipment moving down the length of the strip), using the same tedder reset for rowing, and this was followed within an hour by a standard hay baler producing conventional square bales. The third set of dishes was removed immediately after baling. After removal from the field, each set of dishes was treated in exactly the same way as those in studies (i) and (ii) above.

THE EFFECT OF CUTTING DATE ON SUBSEQUENT BOTANICAL COMPOSITION

Assessments of botanical composition were made within four 50cm x 50cm quadrats per plot during the last three days of April and the first week of May, in 1991 (i.e. prior to imposing different cutting dates), 1992 and 1993. On each occasion, a record was made of the presence of each species within a 50cm x 50cm quadrat placed at each sampling location, along with a subjective score for the percentage ground cover occupied by each species within the quadrat and the ground cover occupied by dead vegetation and bare ground. The remainder of the 2m x 4m plot was then searched for species not recorded within a quadrat and any additional species was given an arbitrary score of 0.01% cover for the plot.

It proved impossible to differentiate between *Bromus hordeaceus* and *Bromus racemosus* before flowering (Hubbard, 1984). As only a small proportion of the total number of plants of these species were flowering before completion of the assessments each year, they were recorded as *Bromus spp.* (no other species of the *Bromus* genus were found on these plots). The relative numbers of flower heads of each species on each plot on 1 June 1993 was used to apportion the data recorded in April-May 1993 between the two species. No other difficulty in species identification was encountered at the earlier assessment.

DATA ANALYSIS

Seed rain main study (study (i)) and botanical data

Data were subjected to analysis of variance (ANOVA) using a split plot, randomized block design, with previous fertilizer treatment as main plots, using GENSTAT (GENSTAT V Committee, 1987). Species scores for ground cover abundance in the vegetation were converted to percentage of total cover of live vegetation to give values for proportional abundance and all data were summarized to plot means before statistical analysis. Both seed rain and vegetation cover data distributions were skewed for a large number of species. Vegetation data were transformed by angular transformation, using the formula: $\text{angular}(\%v) = (180/\pi) \times \text{arcsine}(\sqrt{(\%v/100)})$ (GENSTAT V Committee, 1987) and both seed rain and vegetation data were transformed to logarithms (base 10) and to square roots. Individual ANOVAs were performed for each species using either transformed or untransformed data, whichever showed a normal distribution. In addition, polynomial contrasts were calculated in the ANOVAs of the 1991 seed rain and 1993 species cover data to test for linear and quadratic response to date of cutting, using the number of days after 1 April (meaned between 1991 and 1992 for 1993 botanical data) as the cutting date variable.

Individual species relative abundance data were used to calculate a Shannon-Wiener diversity index (Kent and Coker, 1992) for each plot using the following formula:

$$SWI=-\sum_{i=1}^{s}(p_i)(\log_2 p_i)$$

where

p_i = the proportion of individual species i in the vegetation

s = the number of species in the vegetation

The Shannon-Wiener Index (SWI) combines elements of both species-richness (i.e. the number of species present) and evenness of distribution (Kent and Coker, 1992). It was used in preference to the Simpson's Index (SI - see Chapter 5), since SWI values were more sensitive than SI values to the effects of different cutting date. Of the two indices, the SI, which places more emphasis than SWI on species dominance (Krebs, 1972), was the more sensitive to the effects of fertilizer treatments in the data presented in Chapter 5.

SWI values were analyzed for treatment effects by ANOVA as for the individual species data. Analyses of both seed rain and of vegetation cover data were also performed on species grouped into various different categories, some of which were mutually exclusive (i.e. no species falling within more than one category) and some not exclusive. The categories used for grouping species were as follows:-

1. Grasses, dicots, *Cyperaceae, Juncaceae,* and bryophytes.

2. Seed bank types I - IV (Thompson and Grime, 1979), as described and discussed in Chapters 2 and 6. Species were identified to each group by reference to Grime *et al.* (1988), from which a fifth group was also identified as type '?', i.e. species whose seed bank persistence and behaviour was unknown.

3. Response to fertilizer N observed in previous experiments at the site (Mountford *et al.*, 1993a and Chapter 5); i.e. those responding positively ('N-positive' species), those responding negatively ('N-negative' species) and those which showed no response or for which there were insufficient data ('others')

4. Regenerative strategy (Grime, 1979). Species that regenerate primarily:-
(a) by seedling establishment in seasonally occurring vegetation gaps (mainly in the autumn) = 'S' species;
(b) by lateral vegetative spread, combining three separate groupings differentiated by Grime *et al.* (1988) according to the length of time daughter plants normally remain attached to the parent = 'V' species;
(c) by both strategies (a) and (b); = 'S/V' species.
(d) by means of widely dispersed seed = 'W' species.
(e) by seedling establishment from a persistent seed bank = 'Bs' species.

5. Annuals.

Of the species recorded which fell into category 4(b), only *Ranunculus ficaria* was classified by Grime *et al.* (1988) as regenerating by seasonal vegetative reproduction, i.e. daughter plants attached to the parent for only a short time. Many species regenerating primarily by vegetative spread (group 1(b)) can also regenerate opportunistically from a persistent seed bank or from freshly shed seed (Grime *et al.*, 1988).

Correlation analysis was used to test for association between species diversity (Shannon-Wiener Index) and the abundance of individual species and species groups in 1993, using individual plot values for each variable (df=70). Correlation and regression analyses were also used to investigate the relationship for each species group between seed rain in 1991 and changes in proportional abundance between 1991 and 1993. However, such regressions carried the risk of temporal auto-correlation through the influence of botanical composition in 1991 on both seed rain in 1991 and on botanical composition in 1993, since the more abundant a species the greater the potential change in absolute terms. This effect was avoided by weighting seed rain data for each species group according to its abundance in the vegetation in 1991, i.e. before the imposition of different cutting dates, using the following formula: weighted seed rain = seed rain / (% ground cover + 1.0) for each group on each plot.

As already noted above, seed rain was collected on plots cut in July, August or September during the period after the May cutting date only and data from plots cut in May were added to individual plot data for the later cutting dates to give values for the whole period on each plot. Almost all (94%) of the seedlings recorded from plots cut in May were of *Taraxacum* spp., and very few *Taraxacum* seedlings were produced after later cutting dates. Thus any negative effect of later cutting on the survival of *Taraxacum* seed or seedlings produced before the May cutting date will not have been evident in the data. This may have masked any true correlation between patterns in seed rain and botanical change and also dampened any such effects shown by the remaining species within those groups which included *Taraxacum* (i.e. the 'N-positive' seed bank Type I and the 'W' groups). Two sets of regressions were therefore carried out for each of these groups, one for the group as a whole and the second with data for *Taraxacum* excluded from both the seed rain and the vegetation data.

Data from the six plots used to measure the proportion of seedlings that originated from seed shed before cutting were subjected to ANOVA. A fully randomised combination of two replicates of three cutting date treatments was applied, giving three degrees of freedom in each analysis. These ANOVAs were carried out on the more common species individually and on all species grouped into grasses, dicots, *Juncaceae*, *Cyperaceae* and the overall total. In each case, ANOVAs were performed both on the total number of seedlings recorded and on the number originating from seed shed before cutting as a proportion of this total. These data were tested for both first and second order polynomial contrasts (GENSTAT V Committee, 1987) to give probability estimates of the linearity or non-linearity of response to cutting date, although it was recognized that only three data points (cutting dates) would be insufficient to define a response curve.

THE PHENOLOGY OF SEED PRODUCTION, SHEDDING AND VIABILITY OF THREE SELECTED SPECIES AND THE INFLUENCE OF SIMULATED HAY DRYING

Individual plants of three dicotyledonous species typical of the vegetation of the meadows

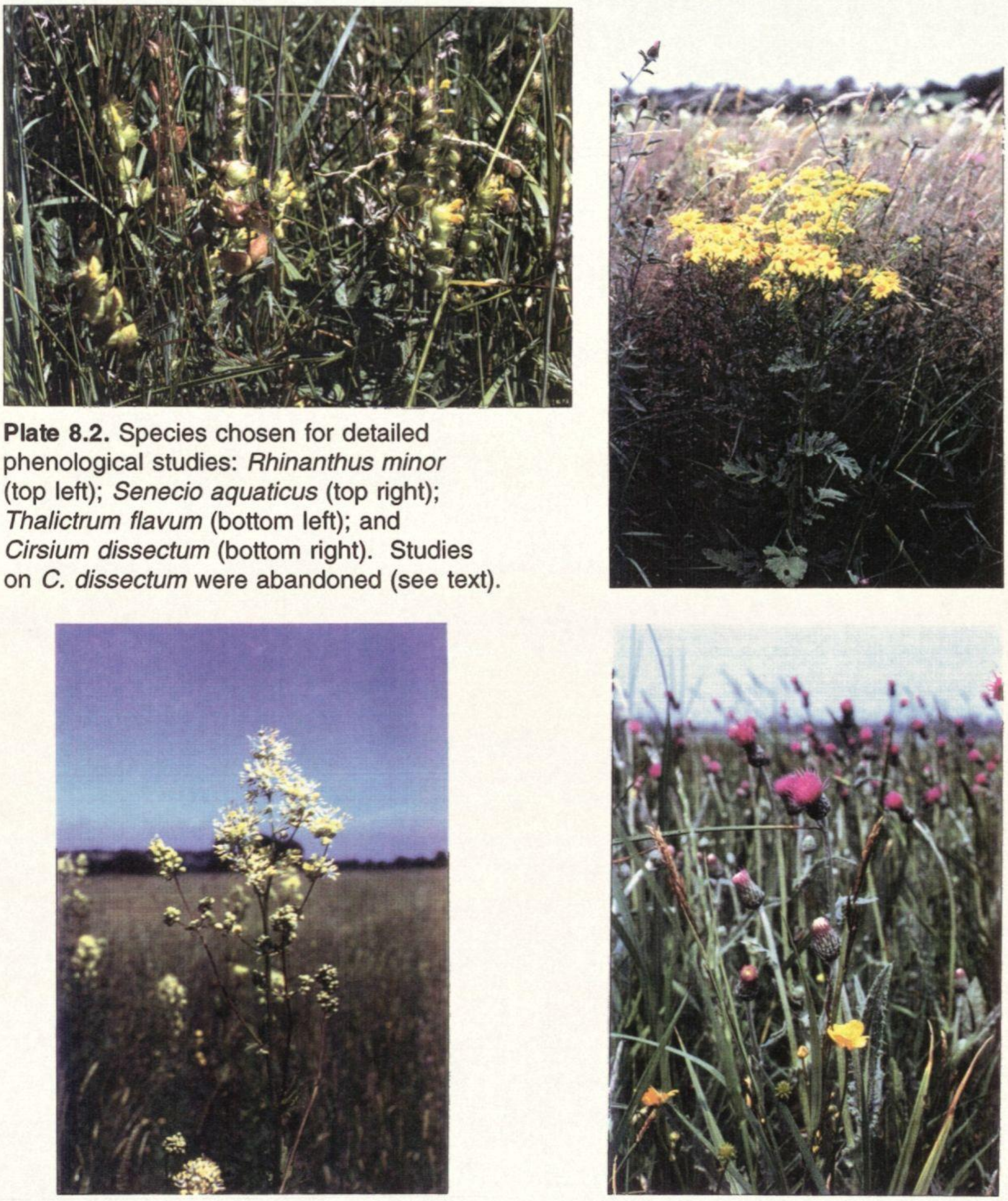


Plate 8.2. Species chosen for detailed phenological studies: *Rhinanthus minor* (top left); *Senecio aquaticus* (top right); *Thalictrum flavum* (bottom left); and *Cirsium dissectum* (bottom right). Studies on *C. dissectum* were abandoned (see text).

but sparsely distributed, *Rhinanthus minor*, *Senecio aquaticus* and *Thalictrum flavum*, were harvested at regular intervals between 15 June and 2 September in 1992. The aim of this study was to assess the impact of harvesting at five different dates on the number and

viability of seeds shed of each of these species, measured directly. A fourth species, *Cirsium dissectum*, was also selected for study, but after assessments were completed it emerged that an unknown proportion of the plants sampled had been *C. dissectum* x *C. palustre* hybrids. Since it was not possible to differentiate between true *C. dissectum* and the hybrid plants, these data are not presented.

Sampling strategy

Plants were taken from several predetermined locations within the 20 ha experimental site as a whole and the same locations were returned to on each occasion. Areas were chosen towards the edge of fields so that they could easily be marked off and avoided by hay making machinery (the site was cut for hay between 25 July and 9 August in 1992). *R. minor* was sampled from a single area about 4m x 7m where the species was abundant, whereas the two remaining species were harvested from two separate sampling areas each. *T. flavum* was most abundant on ditch banks at the site, but for this study, plants were taken from within the meadow vegetation.

The population size of each species within these areas did not allow large numbers to be harvested and it was considered to be important not to deplete these populations excessively by destructive sampling. A total of 20 plants of each species were taken at each assessment on 15, 25 and 30 June, 31 July and 2 September. Plants were selected randomly by moving along five separate transects within each sampling area, taking the first 2 (for *S. aquaticus* and *T. flavum*) or 4 (*R. minor*) plants encountered within a predetermined distance from each transect line. The starting point for each transect was chosen by blind casting of a small marker into each area, with the transect direction predetermined at random. Care was taken not to disturb unselected plants of the relevant species. If too few plants were found at a particular attempt, the procedure was repeated until the required number of plants had been taken from each area. Each plant selected was first covered with a polythene bag, ensuring that all the flowering/seeding parts were enclosed and that the bag was tightly held around the stem. The stem was then cut below the bag with scissors, further ensuring that any shed seed was retained within the bag by first bending the stem over to approximately 90°. Each bag, containing material from a single plant, was sealed and put into a cooled box before further processing in the laboratory. Of the 20 plants harvested of each species, 10 were used to assess stage of reproductive development and the remainder were used to assess the affect of air drying on seed shedding and viability. These procedures are described after the next paragraph.

In addition to the main assessments, estimates were also required of the number of seeds of each species being shed during intervening periods (up to 31 July). A further 10 plants of each species were therefore selected on 13 and 24 July, using a procedure similar to that described above. On these occasions, after enclosing the seed heads of each selected plant within a polythene bag, the bag was lightly flicked against the flower heads to stimulate the release of any dehiscent seed. The bag was then removed from the plant and sealed, taking care to retain any shed seeds. Each plant was then harvested and placed in another bag together with other harvested plants for reproductive stage assessment. The intention during collection of seeds on these occasions was to avoid the severity of disturbance to the plants that would have resulted from mechanical harvesting, whilst procedures adopted on the main harvest dates (see later) were intended to simulate this level of disturbance.

Reproductive development

The stage of development of each species at each assessment date was determined by subjective allocation of each plant to one of several categories, each category easily determined by the naked eye. The three species differed in inflorescence type, so that the developmental categories used, and the means of allocating plants to them, differed between species.

Seeds of *R. minor* develop within pods, becoming detached within the pod while still green and ripening through a straw-yellow colour to mid brown. Eventually, pods split and seeds are then capable of being released. The pods ultimately disintegrate almost completely, by which time very few seeds remain unshed. Pods on standing plants do not normally split until after seeds have reached the final stage of ripening. The number of *R. minor* seeds per plant was recorded within the following four categories: 'developing' (still attached within the pod); 'ripening' (detached within the pod but still green-yellow); 'ripe' (brown); 'dehiscent' (pods splitting and seeds being, or capable of being, released).

S. aquaticus carries several composite inflorescences per plant, each typically producing a large number of individual seeds which are released as individual fruits (achenes) attached to a feathery pappus. Each fruit develops from a white carpel, through a pale green colour to dark brown and achene development and ripening was quite uniform within each inflorescence. The number of inflorescences per plant was recorded within the following five categories: 'pre-flowering' (petals <30% expanded); 'flowering' (petals 30%<fully expanded); 'ripening' (petals beginning to shrivel, seeds pale green-yellow); 'ripe' (seeds brown, still compactly grouped); 'shedding seeds' (achenes absent, or present but detached from inflorescence or easily detached by lightly brushing a finger accross the top of the pappi).

T. flavum carries dense panicles of individual florets, producing seeds in groups of sessile, one-seeded achenes. Development stage was identified either by the number of fruits per plant within defined categories, or as the number of florets per plant bearing seeds predominantly of particular categories. The following categories were used: 'flowering'; 'seeds developing' (seeds green, less than full size); 'ripening' (seeds full size, green-pale yellow); 'ripe' (seeds golden brown); 'dehiscent' (seeds being shed during handling or having been shed).

For each species on each date, the number of seeds or inflorescences per plant within each category was summed for all plants and the sum for each category expressed as a percentage of the overall total.

The influence of air drying on seed shedding

On the day of sampling on 15, 25 and 30 June, 31 July and 2 September, each plant was removed from its polythene bag and transferred individually into a light paper 'Glassine' sample bag. Any seeds shed during this procedure were counted and retained, along with those already in the polythene bag and the total was recorded as the number shed at cutting. 'Glassine' bags were then placed, unsealed, in a wire mesh tray, packed so that each bag stood upright. Trays were placed in a fan oven located in an unheated building, with the oven door left slightly ajar and the heater switched off, in order to simulate field crop drying at ambient temperature. The temperature in the oven typically fluctuated between about 15 and 25 °C, with a maximum temperature of 27°C recorded on 1 August. *S. aquaticus* samples were covered inside the oven with paper towelling to prevent dried seeds becoming airborne, but samples of the other two species were left uncovered.

Except for those taken on 15 and 25 June, samples were removed from the oven after 24 hours in the first instance. Each plant was removed from its bag and lightly 'threshed' against the surface of a laboratory table to simulate the level of disturbance which plants might have experienced during mechanical turning and harvesting. The amount of force used was, of course, arbitrary and not quantified, but an effort was made to treat each sample and each species similarly, both on each occasion and between occasions. The number of seeds shed by each plant during this procedure was recorded and the seeds were retained. Plants were then returned to their bags and to the oven. They were dried for a further 48 hours, after which they were threshed again and the seeds counted as before. At each stage of drying and counting, a note was made of the development stage of all seed shed and numbers allocated appropriately. After three days of drying, the number and development stage of any seed retained on the plants was recorded. Plants of *R. minor* and *S. aquaticus* taken on the 15 and 25 June were removed from the oven and threshed and counted only once, after a total of 3 days of drying. Almost all *S. aquaticus* plants were either still flowering or were only just beginning to flower before 30 June, so no plants of this species were dried before that date. No ripe *S. aquaticus* seed was recorded until 24 July.

Germination tests

Seeds collected at all the harvests and stages of drying described above were tested for viability, both by incubation under contolled conditions and by sowing into peat-filled dishes of the type used in the seed rain assessments described above. Except where the number of seeds available was limited (see below), seeds were tested in two batches of fifty seeds from each of the total amounts shed from all ten plants, bulked for each stage of drying. As for the seed rain samples, the peat-filled dishes were kept in a poly-tunnel at Rumleigh Experimental Station, and watered at least once a day until June 1993. The remaining seeds were placed in petri dishes, on filter paper moistened with de-ionised water. One pair of dishes per sample was then stored for 13 weeks in a fridge at 5°C to satisfy any chilling requirement for germination (Grime *et al.*, 1981). Except for *R. minor*, an equivalent number of petri dishes were placed immediately in an incubator where they were subjected to an alternating regime of 16 hours under full lighting and at 20°C, followed by 8 hours in the dark at 15°C. No attempt was made to germinate *R. minor* without prior chilling, since the chilling requirement of this species is well known (Grime *et al.*, 1977). After the chilling period, petri dishes were transferred to the incubator and stored under the conditions described above.

Dishes were inspected at weekly intervals, both those in the incubator and those in the fridge, and any germinated seeds were counted and removed. Extra deionised water was added as necessary to keep the seeds in an embibed condition. Samples tested in peat were inspected at 7-day intervals initially and any seedlings counted and removed, but from the end of October 1992 until March 1993 counts were made monthly. Dishes were retained in the incubator until no further germination was recorded for eight consecutive weeks. Most samples were then discarded, but following poor germination results for *R. minor* for seeds harvested at each but the last assessment date (2 September), dishes containing seeds of this species were returned to the fridge for a further 13 weeks before again being transferred to the incubator.

On some occasions, the number of seeds available for germination tests was limited. On 2 September, only 56, 37 and 10 *R. minor* seeds were available from those shed at cutting, after 1 day of drying plants and after three days of drying respectively. Of these, 28 each of those shed at cutting were divided between chilling/incubation and sowing in peat, whilst seeds shed after drying were chilled/incubated only. Only 32 *T. flavum* seeds were available in total on 31 July (8, 10, and 14 seeds for each drying stage respectively), and only 10, 10, and 51 seeds were available for each drying stage from plants harvested on 2 September. The numbers of *T. flavum* seed were considered to be too small to divide between chilled and unchilled treatments. No information was to hand as to whether *T. flavum* might require chilling, so the available seeds were sown into compost only, since these samples would receive chilling in the poly-tunnel over winter.

8.3. RESULTS

THE EFFECT OF CUTTING DATE ON 'SEED RAIN'

The total number of seedlings recorded after harvesting at each date ranged from 3012 per m^2 from N_0 plots cut in May to 34629 per m^2 from N_{200} plots cut in August (Table 8.1).

Seventy-three species were recorded altogether. Of these, only 29 species produced germinable seeds up to and including the May harvest date, 51 up to July harvesting, and 63 by the second week in August. Analysis of variance (ANOVA) of data for the mean number of species per plot showed a highly significant cutting date effect ($P<0.001$), whilst analysis for polynomial contrasts showed a highly significant linear trend ($P<0.001$) with an additional significant ($P<0.01$) effect of including a quadratic term in the model (Table 8.1). The number of species recorded per plot increased very significantly ($P<0.001$) between May and July harvests and between July and August on plots of both fertilizer treatments.

Table 8.1. The effects of previous fertilizer treatment (N_0 or N_{200}) and cutting date on (a) the total number of seedlings per m^2, (b) the number of species which produced seedlings, and (c) the mean number of seedlings per m^2 per species, from seeds shed up to and during harvesting vegetation cut on one of four dates in 1991.

Species group		Cutting date 22 May	 17 July	 9 Aug.	 4 Sep.	Significance of treatment effects (1)
Total number of	N_0	3012	9370	18424	21119	C***, L***, Q**, N x C***,
seedlings	N_{200}	3837	24957	34629	27402	N xL*, N x Q***
Mean number of	N_0	4.5	23.0	27.3	28.7	C***, L***, Q***
species per plot	N_{200}	4.0	21.7	27.7	25.8	
Mean number	N_0	950	391	661	755	None
of seedlings per species	N_{200}	1084	1149	1254	1063	

(1) Asterisks denote significance of treatment effects in ANOVAs: * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$. N =effect of previous fertilizer treatment, C = effect of cutting date, L and Q indicate significant overall linear and/or quadratic responses respectively to cutting date, and x = interaction between N and cutting date/cutting date response.

Numbers increased further between August and September on N_0 plots but declined on N_{200} plots, though these differences were not statistically significant. There was no significant effect of previous fertilizer treament. A similar analysis of data for total seed rain (i.e. the total number of seedlings recorded after each harvest) showed a highly significant interaction between fertilizer (N) and cutting date ($P<0.001$) and also detected a significant interaction between N and the curvilinearity of response to cutting date ($P<0.001$). The

difference between May cutting and all other dates was highly significant both for N_0 and N_{200} plots ($P<0.001$), with further significant increases between July and August ($P<0.05$, for N_0, $P<0.01$ for N_{200}). Total seedling numbers increased slightly but not significantly between August and September for N_0 plots, but declined significantly ($P<0.05$) between these dates for N_{200} plots (Table 8.1).

Individual species

Data for most species were not normally distributed and required transformation. ANOVAs of $\log_{10}$ transformed data showed significant treatment effects for only nineteen species (Table 8.2). All of these showed highly significant effects of cutting date ($P<0.001$), with the

Table 8.2. Species showing significant effects of previous fertilizer treatment (N_0 or N_{200}) and/or cutting date on the number of seedlings per m^2 produced from seed shed up to and during harvesting vegetation cut on one of four dates in 1991. All treatment significance ratings (see bottom of table for explanation) refer to $\log_{10}$ transformed data.

		Cutting date				Significance of
Species		22 May	17 Jul.	9 Aug.	4 Sep.	treatment effects (1)
Agrostis canina	N_0	4	82	162	137	C***,L***, N x $L^{0.056}$
	N_{200}	2	21	185	358	
A. capillaris	N_0	2	228	801	5159	C***,L***
	N_{200}	6	964	812	4361	
Anthoxanthum odoratum	N_0	0	1322	908	724	C***,L***,Q***
	N_{200}	1	1878	1213	1274	
Bromus (2)	N_0	0	1376	1120	304	C***, L***, Q***, N x C*,
	N_{200}	0	7512	3112	748	N x L*
Cynosurus cristatus	N_0	0	698	4356	4301	C***, L***, Q***, N x C***,
	N_{200}	4	411	1228	1112	N x L***
Festuca rubra	N_0	0	399	294	335	C***,L***, Q***, N x C**,
	N_{200}	0	1392	269	106	N x Q***
Holcus lanatus	N_0	1	323	906	813	C***,L***, Q***, N x C***,
	N_{200}	3	1847	9696	6492	N x L***
Lolium perenne	N_0	0	65	337	209	C***,L***, Q***, N x C***
	N_{200}	0	329	2683	1379	N x L***
Poa trivialis	N_0	0	30	108	50	C***,L***, Q*
	N_{200}	0	116	311	191	

(Table contd.)

Species		Cutting date				Significance of
		22 May	17 July	9 Aug.	4 Sep.	treatment effects
Cardamine pratensis	N_0	20	22	26	84	C***,L***
	N_{200}	6	36	11	25	
C. hirsuta	N_0	14	49	33	26	C***,L**, Q**
	N_{200}	4	17	6	9	
Centaurea nigra	N_0	0	4	157	590	C***,L***
	N_{200}	1	114	209	309	
Cerastium fontanum	N_0	13	568	1555	1265	C***,L***, Q***
	N_{200}	109	5735	8933	4051	
Filipendula ulmaria	N_0	0	0	69	926	C***,L***, Q***
	N_{200}	0	0	118	928	
Ranunculus acris	N_0	0	198	325	209	C***,L***, Q***, N x C*, N x L*
	N_{200}	1	129	57	112	
R. repens	N_0	3	20	34	41	C***,L***
	N_{200}	0	5	18	34	
Rumex acetosa	N_0	0	50	37	49	C***,L***, Q***, N x C**, N x L***
	N_{200}	3	274	306	564	
Senecio vulgaris	N_0	3	3	7	4	$C^{0.053}$,L**
	N_{200}	6	6	6	8	
Trifolium pratense	N_0	8	68	211	364	C***,L***
	N_{200}	0	53	103	373	

(1) Asterisks denote significance of treatment effects in ANOVAs of log-transformed data: * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$. Superscripted figures are actual probability values. N =effect of previous fertilizer treatment, C = effect of cutting date, L and Q indicate significant overall linear and/or quadratic responses respectively to cutting date, x = significant interaction between fertilizer and cutting date/cutting date response.

(2) Bromus = *Bromus racemosus* + *B. hordeaceus*

exception of *Senecio vulgaris*, for which the overall cutting date effect just failed to reach 95% confidence limits ($P=0.053$). Transformed data for all these species showed a highly significant linear response to cutting date ($P<0.001$ for all except *S. vulgaris* and *Cardamine hirsuta*, for which $P<0.01$), with most species showing a significant response to addition of a quadratic term in the response model. All the significance levels and response trends quoted below for individual species refer to $\log_{10}$ transformed data.

For several species, the quadratic response reflected a maximal number of

seedlings produced by seeds shed in July or August and a lower number at the later assessment(s), with some also showing an interaction with previous fertilizer treatment in the expression of this response. For example, no *Bromus* seedlings were recorded with cutting in May, but the largest numbers were recorded with July cutting, both on N_0 and N_{200} plots, (Table 8.2). Numbers declined progressively between July and the two later dates, both on fertilized and unfertilized plots, but only the difference between July cutting and September cutting on N_{200} plots reached significance ($P<0.01$). The number of *Bromus* seedlings originating from N_{200} plots was significantly greater than that from N_0 plots at each cutting date July-September ($P<0.001$, <0.01 and <0.05 respectively).

Holcus lanatus produced more seedlings after harvesting in August than at other cutting dates, although the only significant differences on N_0 plots were between May cutting and the remaining dates ($P<0.001$) (Table 8.2). On previously fertilized plots, cutting in August significantly increased the number of *H. lanatus* seedlings compared with either July or September cutting (both $P<0.01$). Except with cutting in May, about 6-10 times as many *H. lanatus* seedlings originated from N_{200} plots than N_0, with differences reaching high levels of significance for July cutting ($P<0.001$, $P<0.01$ for August and September). *Lolium perenne* showed similar trends to *H. lanatus,* although the decline in seedling numbers between August and September failed to reach significance with either fertilizer treatment nor averaged over both. Numbers increased significantly between July and August for both fertilizer treatments ($P<0.01$, $P<0.001$ overall).

Cerastium fontanum was the most prolific producer of seedlings amongst the dicots (Table 8.2). There was no significant effect of previous fertilizer treatment, although more seedlings originated from N_{200} than N_0 plots with each cutting date. Both sets of plots showed a similar, non-linear response to cutting date. This trend was highly significant overall ($P<0.001$), with maximal seedling numbers produced by cutting in August, although the ANOVA showed no significant difference between individual cutting dates after July.

For several species, the number of seedlings increased progressively with lateness of cutting on all plots (Table 8.2). ANOVAs (on $\log_{10}$ transformed data) for most of these showed a significant linear response to cutting date, and the actual response therefore tended to increase exponentially throughout the period (in these cases the response would presumably have been sigmoidal had later cutting dates been tested). Notable examples

of this type of response were *Agrostis capillaris* (particularly on N_0 plots), *Centaurea nigra, Trifolium pratense* and *Filipendula ulmaria.* No seedlings of the latter species were recorded until the August harvest.

Of the totals of 3012 and 3837 seedlings per m^2 produced after cutting in May on N_0 and N_{200} plots respectively, the vast majority were of *Taraxacum spp.* (2799 and 3672 seedlings m^{-2} respectively). This species aggregate showed no significant treatment effect, but it must be remembered that data for seedlings produced from seed shed between 27 March and 22 May were added to data for all the remaining plots. Very few *seedlings of Taraxacum* species were recorded after the May cutting date (<43 and <349 on N_0 and N_{200} plots respectively for August cutting). It is likely that a large number of seedlings resulting from *Taraxacum* seeds shed during April or May would have failed to survive until the later cutting dates, since *Taraxacum* has no seed dormancy and could be expected to germinate soon after shedding (Grime *et al.*, 1988). Adding data from plots cut in May to remaining plots may have inflated unduly the July, August and September cutting means for each of the species groups which included *Taraxacum* (i.e. Dicots, N-positive seed bank Type I species, wind-dispersed ('W') species, and the total of all species).

Species groups

Data for all groups except the dicots required either $\log_{10}$ or square root transformation to correct skewness and for other groups all significant treatment effects noted in the text below refer to either $\log_{10}$ or square root transformed data (Table 8.3).

Only the grasses and the annual species group showed a significant overall effect of previous fertilizer treatment, with significantly greater ($P<0.05$) numbers of seedlings originating from N_{200} than N_0 plots (Table 8.3). The 'annuals' group were largely composed of *Bromus spp.* and *C. fontanum.* The inclusion of the latter in this group is somewhat arbitrary, as Grime *et al.* (1988) state that it is more likely to act as a perennial except in highly disturbed conditions. All species groups except the *Cyperaceae* and the 'W' species, were significantly affected by cutting date ($P<0.001$). In addition, dicots, annuals, 'S' species (i.e. those regenerating primarily by seasonal seedling production, usually in the autumn) and 'S/V' species (those commonly regenerating either as 'S' species or by vegetative reproduction) all showed significant fertilizer x cutting date interactions ($P<0.05$ for dicots,

Table 8.3. The effects of previous fertilizer treatment (N_0 or N_{200}) and cutting date on the number of seedlings per m^2 produced from seed of various species groups shed up to and during harvesting vegetation cut on one of four dates in 1991. Treatment significance effect ratings in round and square brackets refer to $\log_{10}$ and square root transformed data respectively. Species groupings 'S', 'V', 'S/V', 'W' and 'Bs' refer to regenerative strategy (Grime *et al.*, 1988 - see text).

Species group		Cutting date				Significance of treatment effects (1)
		22 May	17 July	9 Aug.	4 Sep.	
Grasses	N_0	7	4561	9249	12233	(N*, C***, L***, Q***)
	N_{200}	16	14493	19782	16166	
Dicots	N_0	2997	4753	8989	8806	C***, L***, Q***, N x C*,
	N_{200}	3815	10452	14802	11211	N x Q**
Cyperaceae	N_0	5	13	18	16	None
	N_{200}	1	1	1	3	
Juncaceae	N_0	4	43	168	63	(C***, L***, Q*)
	N_{200}	5	10	44	23	
Annuals	N_0	32	2021	3014	1715	[N*, C***, L***, Q***,
	N_{200}	124	13305	12165	4924	N x C***, N x L, N x Q***]
'S' species	N_0	24	3631	7281	6114	[C***, L***, Q***, N x C***,
	N_{200}	9	10246	8515	5059	N x Q***]
'V' species	N_0	164	1512	3213	8778	(C***, L***)
	N_{200}	26	1423	2289	6792	
'S/V' species	N_0	14	1371	4813	3193	[C***, L***, Q***, N x C***,
	N_{200}	116	9361	19536	11532	N x L***, N x Q***]
'Bs' species	N_0	180	3857	8809	12108	(C***, L***, Q***)
	N_{200}	142	10976	22303	19101	
'W' species	N_0	2804	2859	2974	2981	None
	N_{200}	3672	3903	4031	3847	

(1) Asterisks denote significance of treatment effects in ANOVAs: * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$. N =effect of previous fertilizer treatment, C = effect of cutting date, L and Q indicate significant overall linear and/or quadratic responses respectively to cutting date, and x = significant interaction between N and cutting date/cutting date response.

$P<0.001$ the remainder). Amongst the groups responding significantly to cutting date, all showed a significant quadratic response ($P<0.05$ for *Juncaceae*, $P<0.001$ the rest), with the sole exception of the 'V' group (i.e. species which regenerate primarily by vegetative reproduction) which showed a linear (on log-transformed data) response only ($P<0.001$).

For all the groups except 'V' species, maximal seedling numbers on N_{200} plots were obtained by cutting in July ('S' species) or August (remainder). On N_0 plots, all but the grasses and the 'Bs' group (i.e. species which regenerate from a persistent seed bank) produced peak seedling numbers with August cutting, whilst the number of grass and 'Bs'seedlings increased between each cutting date to September (Table 8.3).

The number of grass seedlings as a proportion of the total number of seedlings recorded increased with lateness of cutting from July onwards on N_0 plots (from 40% to 60%), whilst that of dicots declined (from 51% to 42%)(Table 8.3). The proportions of both these groups remained very constant between the same dates on N_{200} plots, at about 58% and 42% respectively. Since over 90% of all the seedlings recorded after cutting in May were of *Taraxacum spp.*, dicots as a group made a similarly high contribution to the May totals on plots of both fertilizer treatments. The proportion of 'S' species declined with lateness of cutting between July and September, from 40% to 29% and from 41% to 18% on N_0 and N_{200} plots respectively, whilst that of 'V' species increased from 16% to 42% and from 6% to 25% respectively. The contribution of 'S/V' species to the total number of seedlings recorded was greatest with August cutting, at 26% and 56% on N_0 and N_{200} plots respectively. The number of seedlings which were from species commonly regenerating from a persistent seed bank ('Bs' species) increased markedly from July onwards from 41% of the total to 57% in September on N_0 plots, and from 44% to 70% on N_{200} plots. This group represented a very small proportion of the total recorded after cutting in May, 4% on N_{200} plots and 6% on N_0 plots.

Species grouped by seed bank type (Thompson and Grime, 1979) and previously observed response to fertilizer N (Mountford *et al.*, 1993a; Chapter 5) showed markedly different responses to previous fertilizer treatment and cutting date (Figure 8.1 and Table 8.4). A very much greater number of seedlings of N-positive species, both seed bank Type I and Type III, originated from N_{200} than from N_0 plots, although the overall difference between fertilizer treatments reached significance only for Type I species ($P<0.001$ Type I, $P=0.053$ Type III).

The response to cutting date of Type I species differed between N_0 and N_{200} treatments, with a marked peak in seedling numbers with cutting in July on N_{200} plots and a less pronounced peak (compared with later cutting) with August cutting on N_0 plots

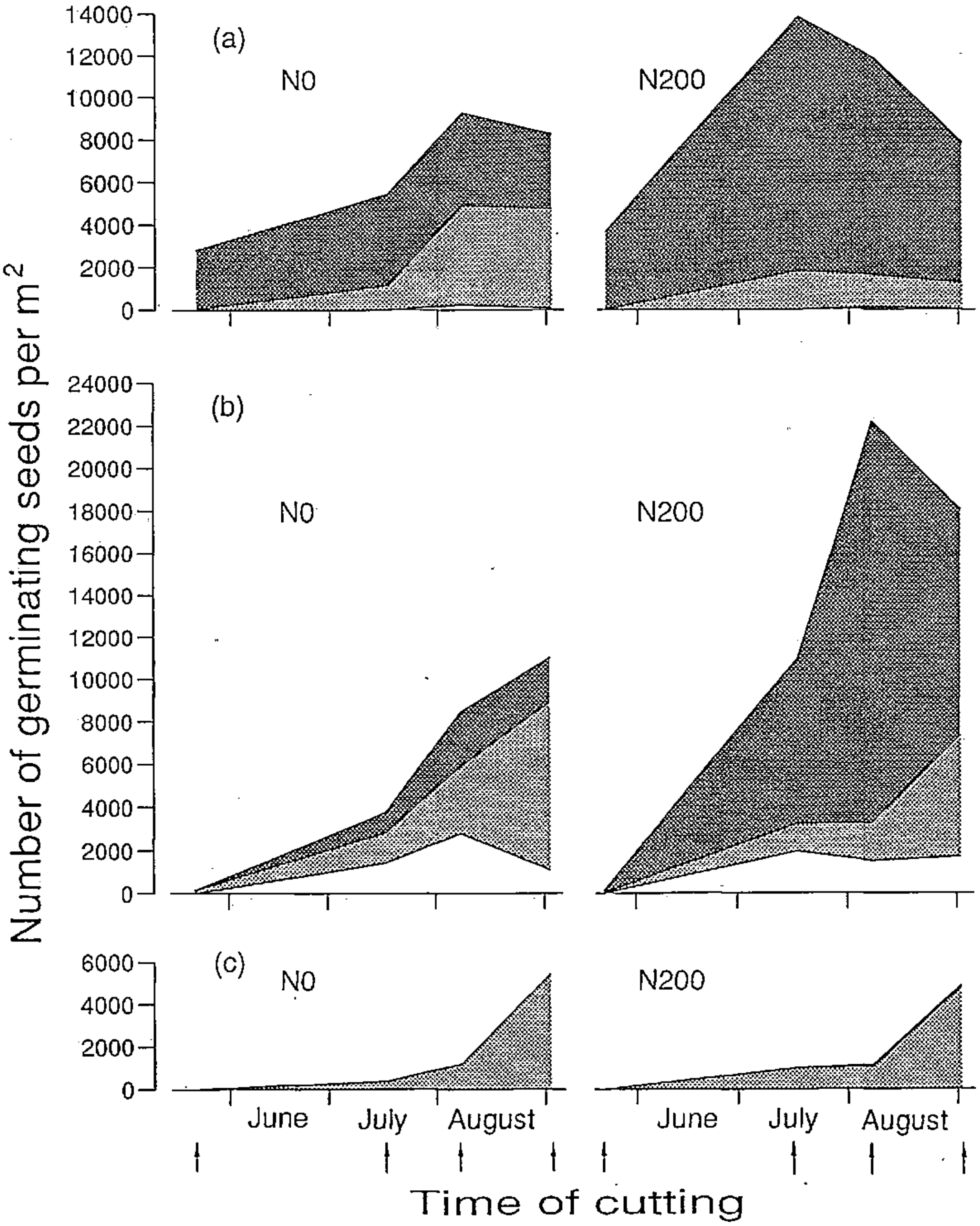


Figure 8.1. The influence of cutting date and previous fertilizer treatment (N_0 and N_{200}) on the number of seedlings produced from seed shed up to and during harvest in 1991. Species grouped according to seed bank type (Thompson and Grime, 1979) and previously observed response to fertilizer N (Mountford *et al.*, 1993a; Chapter 5): **(a)** = Type I species; **(b)** = Type III species; **(c)** = Type IV species. Dark shaded areas = N-positive species; light shaded = N-negative species; unshaded areas = others. Arrows indicate time of cutting. The significance of levels of treatment effects and cutting date response trends shown by ANOVAs of these species groups are given in Table 8.4.

(Figure 8.1a). On N_{200} plots, the decline between August and September was significant (P<0.01), but that between July and August was not, whilst only the differences between May and the remaining cutting dates reached significance on N_0 plots. These differences were reflected in a significant interaction (P<0.001) between N and the curvilinearity of response in the ANOVA (i.e. N x Q) for these species (Table 8.4). The pattern of response to cutting date of N-negative Type I species was somewhat similar to that of N-positive species on N_{200} plots, although N-negative seedlings were much less numerous than N-positive ones. The number of N-negative Type I seedlings originating from N_0 plots did not change significantly between August and September cutting dates (Figure 8.1a).

Within the seed Type III group there was a marked contrast between N-positive and N-negative species in their response to cutting date (Figure 8.1b). Peak seedling numbers

Table 8.4. Significance of treatment effects shown by ANOVAs on data for the number of seedlings produced per m^2 from seed shed up to and during hay making in 1991 of species grouped by seed bank type (Thompson and Grime, 1979) and previously observed N response (Mountford *et al.*, 1993a and Chapter 5 - see text). Figures in square brackets show the number of species within each seed bank type/N-response category.

Seed bank type/ N-response	Significant treatment effects	Seed bank type/ N-response	Significant treatment effects
Type I:		**Type IV:**	
[6] N-positive	N***, C***, L***, Q***, N x C***, N x L*, N x Q***	[2] N-positive	None
[3] N-negative	(C***, L***, Q***)	[10] N-negative	(C***, L***, Q*)
[4] Others	None	[10] Others	(C***, L***, Q*
[13] Type I total	N*, C***, L***, Q***, N x C***, N x Q***	[22] Type IV total	(C***, L***, Q*)
Type 3:		**Type ?:**	
[4] N-positive	($N^{0.051}$, C***, L***, Q***, N x L*)	[0] N-positive	-
[12] N-negative	(C***, L***, Q***)	[5] N-negative	(C***, L***, Q*)
[10] Others	(C***, L***,Q***)	[10] Others	(C***, L***)
[26] Type III total	[C***, L***, Q**, N x C***, N x L***, N x Q*]	[15] Type ? total	(C***, L***, N x Q*)

N and C = significant effect of previous fertilizer treatment and cutting date respectively, L and Q = linear and quadratic responses respectively to cutting date, x = interaction between N and cutting date/cutting date response. Asterisks denote significance of treatment effects: * = P<0.05; ** = P<0.01; *** = P<0.001. Symbols in brackets refer to $\log_{10}$ (round brackets) or square root transformed data [square brackets]. Seed bank Type II species [three species] showed no significant treatment effects.

of N-positive species were recorded with cutting in August on N_0 and N_{200} plots, although differences between July, August and September cutting did not reach significance (log transformed data). N-negative species increased progressively with lateness of cutting until September, with the a significant difference ($P<0.05$) between July and September both on N_0 and N_{200} plots. Type III species unclassified as to N response peaked in August on N_0 plots, but showed no response to cutting date from July onwards on N_{200} plots. Seedlings of this sub-group were much more numerous than unclassified (with respect to N response) species of seed bank Types I and IV together (compare Figure 8.1b with Figures 8.1a and 8.1c), although the the Type III and the Type IV unclassified sub-groups contained the same number of species (10). The pattern of response to cutting date shown by N-negative Type IV species was very similar to that shown by N-negative Type III species (Figure 8.1b and c), although the increase between August and September cutting dates was even more marked, reaching significance ($P<0.05$) for data averaged over both fertilizer treatments.

The group of species whose seed bank behaviour had not been defined (i.e. type '?') showed a somewhat similar pattern to that shown by Types III and IV species, though the numbers involved were smaller. Only five of the 15 species within the Type ? group had previously shown a response to N, all five responding negatively. Seedling numbers of this sub-group peaked in August at 150 and 43 seedlings m^{-2} on N_0 and N_{200} plots respectively. Seedlings of the remaining Type ? species were more numerous, increasing from a mean of 66 seedlings m^{-2} in July to 282 per m^{-2} in August, to 1400 seedlings m^{-2} in September, with each of these increases highly significant in log-transformed data ($P<0.01$ and $P<0.001$ respectively).

Of the total number of seedlings recorded after cutting in May and July, the greatest proportion were of seed bank Type I species, both from previously fertilized and unfertilized plots. However, the contribution of this group declined progressively between July and September, from 58% to 41% on N_0 plots and from 56% to 29% on N_{200} plots. The proportion of Type III species increased correspondingly, from 41% to 54% on N_0 plots and from 43% to 66% on N_{200} plots and this group was the most abundant of the five seed bank types amongst seedlings recorded after harvesting in September. The proportion of Type IV species rose sharply between August and September, from 7% to 36% on N_0 plots and from 3% to 18% on N_{200} plots. Type ? species represented a very small proportion of the total on all plots, increasing with lateness of harvesting to 3% on N_0 plots and 1% on N_{200} plots in September.

Since the vast majority of seedlings recorded after cutting in May were of *Taraxacum spp.*, which are seed bank Type I species (Grime *et al.*, 1988), the Type I group accounted for a correspondingly high proportion of all the seedlings recorded after cutting in May (95%). Moreover, as noted above, the adjustment of data for cutting in July, August and September to include those recorded after cutting in May may have unduly inflated the proportion of seed bank Type I species in data for the last three cutting dates. Therefore, the decline in the proportion of Type I species and the corresponding increases in the proportion of the other seed bank types, were probably even more marked than the data suggest.

Seed rain during May-September regrowth

Only *Cynosurus cristatus* was significantly affected by previous fertilizer treatment in the number of seedlings produced during May-September regrowth on plots cut in May, with

Table 8.5. Species producing a mean of five or more seedlings per m^2 from seed shed during May-September regrowth on plots cut in May 1991. Values in brackets are means and the effective s.e. (±) from an ANOVA of $\log_{10}$ transformed data for *Cynosurus cristatus*. For remaining species, values are overall means.

Species		seedlings per m^2		Species	seedlings per m^2
Agrostis canina		125		*Cardamine pratensis*	6
A. capillaris		1130		*Centaurea nigra*	240
A. stolonifera		9		*Cerastium fontanum*	1826
Anthoxanthum odoratum		138		*Filipendula ulmaria*	104
Bromus$^{(1)}$		364		*Leontodon autumnalis*	22
Cynosurus cristatus	N_0	576		*L. hispidus*	6
	N_{200}	108		*Myosotis discolor*	60
	(N_0	2.62	±0.085*)	*Plantago lanceolata*	832
	(N_{200}	1.70)		*Prunella vulgaris*	44
Festuca rubra		17		*Ranunculus acris*	103
Holcus lanatus		469		*Rumex acetosa*	25
Lolium perenne		249		*Taraxacum spp.*	28
Phleum pratense		27		*Trifolium pratense*	30
Poa trivialis		17		*T. repens*	7
Bellis perennis		115		*Sonchus asper*	28

(1) Bromus = *Bromus hordeaceus* + *B. racemosus*

* = significant effect of previous fertilizer treatment in ANOVA, $P<0.05$

a significantly ($P<0.05$) lower number from N_{200} plots (Table 8.5). Except for *C. pratense* and *Taraxacum* species, seedling numbers from seed shed during this regrowth period were much higher than those recorded for the period up to cutting in May, with a much larger number of species shedding seed, i.e. 57 altogether, averaging 16.8 species per plot overall (Table 8.5). Moreover, for most species, the number of seedlings produced from seed shed during May-September regrowth added to those previously recorded after cutting in May was less than the number recorded after harvesting in July, August or September (averaged over both fertilizer treatments in each case). Notable exceptions to this were: *Lolium perenne*, for which this total exceeded the mean number recorded after July cutting but not after later harvests; *Sonchus asper*, for which the total exceeded both July and September means; *Plantago lanceolata*, which produced a total number equivalent to that recorded after harvesting in August, but less than the September mean; and *Agrostis capillaris*, *Centaurea nigra*, *Filipendula ulmaria* and *Prunella vulgaris*, the total for each of which exceeded the number recorded after harvesting in August, but was less than that recorded after September cutting. The total number of seedlings of all species produced from seed shed during May-September regrowth was lower than the number recorded after harvesting primary growth in July, August or September for both fertilizer treatments (Table 8.6, cf. Table 8.1). This was true even when regrowth totals were added to those for primary growth on May-cut plots, although for N_0 plots the difference was marginal compared with July cutting (8158 seedlings per m^2, compared with 9370). The same held for each of the species groups listed in Table 8.6, with the exceptions of 'V' species (those which regenerate primarily by vegetative reproduction) and seed bank Type IV species. The May + regrowth totals for the 'V' group were nearly twice those for July cutting and about equal to those recorded after harvesting in August, but were equivalent to only about 33% of the number recorded on plots left uncut until September. Regrowth totals for seed bank Type IV species exceeded the numbers originating from primary growth cut in either July or August, but were 27-29% of the primary growth totals for September cutting.

Grasses were much less prominent in seedlings originating from May-September regrowth on N_{200} plots than from primary growth harvested in July, August or September on from plots of the same fertilizer treatment (39% compared with a mean of 58% fro July-September. There was no such difference on N_0 plots (54% compared with 53%). These trends were mirrored by dicots, which accounted for 45% and 61% of the seedlings recorded following regrowth on N_0 and N_{200} plots respectively, compared with corresponding fertilizer treatment mean values of 47% and 42% averaged over July-September harvests.

Table 8.6. The number of seedlings per m^2 produced by various species groups from seed shed during May-September regrowth on plots cut in May 1991, the total number of seedlings produced by all species, the number of species producing seedlings, and the mean number of seedlings m^{-2} produced per species. Standard error (s.e.) values from ANOVAs are quoted only for species for which data were normally distributed. Seed bank types are as defined by Thompson and Grime (1979, see also text). Species groupings 'S', 'V', 'S/V', 'W' and 'Bs' refer to regenerative strategy (Grime *et al.*, 1988 - see also text),. Treatment means did not differ significantly for any group.

Species group		Mean	s.e.	Species group		Mean	s.e.
Grasses	N_0	2789	-	Seed bank Type ?	N_0	324	-
	N_{200}	3015			N_{200}	176	
Dicots	N_0	2302	839.9	'S' species	N_0	1305	336.8
	N_{200}	4712			N_{200}	1143	
Juncaceae	N_0	54	-	'V' species	N_0	2433	-
	N_{200}	0			N_{200}	2651	
Cyperaceae	N_0	2	-	'S/V' species	N_0	1331	-
	N_{200}	4			N_{200}	3833	
Annuals	N_0	908	-	'W' species	N_0	79	-
	N_{200}	3620			N_{200}	43	
Seed bank type I	N_0	1230	227.5	'Bs' species	N_0	3572	728.0
	N_{200}	1115			N_{200}	6388	
" " " II	N_0	5	-	Total all species	N_0	5146	934.2
	N_{200}	2			N_{200}	7731	
" " " III	N_0	3415	749.0	Number of species	N_0	18.3	1.15
	N_{200}	6311			N_{200}	15.2	
" " " IV	N_0	1450	-	Mean number per species	N_0	306	95.9
	N_{200}	1366			N_{200}	526	

Both the seed bank Type I group and the 'S' group accounted for much smaller proportions of the total number of seedlings originating from May-September regrowth compared with primary growth harvested in July-September, whilst the proportions both of 'V' and 'Bs' species were much higher. Seed bank Type I species accounted for 24%

and 14% of the totals form N_0 and N_{200} plots respectively in regrowth, compared with 58%, 50% and 41% on N_0 plots, and 56%, 36% and 29% from N_{200} plots, harvested in July, August and September respectively. Forty-seven percent and 34% respectively of seedlings from regrowth on N_0 and N_{200} plots were of 'V' species, compared with 16-42% and 6-25% of those from primary growth cut in July-September. 'Bs' species accounted for 69% of the regrowth total on N_0 plots and 83% on N_{200} plots, compared with 41-57% and 44-70% for primary growth on remaining N_0 and N_{200} plots respectively cut in July-September.

THE EFFECT OF CUTTING DATE ON BOTANICAL COMPOSITION

Individual species

ANOVAs showed significant treatment effects for only 15 of the 88 species (83 vascular plants and 5 bryophytes) recorded in botanical assessments in April-May 1993 (Table 8.7). Each of these 15 species can be allocated to one of five loose categories on the basis of its response to cutting date: those which generally increased in relative abundance with lateness of cutting; those which declined; those showing a 'humped' response, i.e. which were most abundant following July or August cutting than cutting in May or September; those showing the opposite trend (U-shaped or 'trough-shaped'); and those showing no clear response. The humped response was the most common, shown by *Cynosurus cristatus*, *Lolium perenne*, *Poa trivialis*, *Trifolium pratense* and *Brachythecium rutabulum.* Three species increased in abundance with lateness of cutting date (*Agrostis capillaris*, *Phleum pratense* and *Rumex acetosa*) and two declined (*Ranunculus acris* and *R. repens*). *Taraxacum spp.* were most abundant with cutting in May on N_0 plots with no difference between the remaining cutting dates, but showed a 'trough-shaped' response on N_{200} plots (Table 8.7). *Anthoxanthum odoratum* and *Festuca rubra* were the most abundant species on N_0 plots, but neither showed any clear trend with cutting date. *A. odoratum* was significantly more abundant on N_{200} plots cut in July than at other dates ($P<0.001$ compared with May and September, $P<0.01$ compared with August), but was unaffected by cutting date on N_0 plots.

H. lanatus dominated the vegetation cover on N_{200} plots which had been cut in May or September, occupying 38.1% and 31.4% respectively of the total cover on these

Table 8.7. Species showing significant effects of cutting date in 1981 and 1982 and/or previous fertilizer treatment (N_0 and N_{200}) on their relative abundance (% of total live vegetation cover) in May 1993. Treatment significance ratings and symbols (see bottom of table for explanation) within round, square or curly brackets refer to $\log_{10}$, square root or angular transformed data respectively (see text for formula for the latter).

Species		Mean cutting date 1991-92				Significance of treatment effects (1)
		24 May	11 July	5 Aug.	2 Sep.	
Agrostis capillaris	N_0	4.8	4.7	7.4	7.8	{C*, $L^{0.058}$}
	N_{200}	3.5	3.0	5.4	4.5	
Anthoxanthum odoratum	N_0	17.3	14.3	19.6	13.3	Q*, N x C**
	N_{200}	11.0	23.7	10.8	13.2	
Cynosurus cristatus	N_0	0.7	4.0	4.4	1.4	{N*, C***, Q***, N x C*, N x $Q^{0.052}$}
	N_{200}	0.8	1.3	0.9	0.5	
Festuca rubra	N_0	15.0	17.9	9.1	14.7	N**
	N_{200}	6.8	6.4	6.5	3.7	
Holcus lanatus	N_0	11.7	4.5	3.4	4.1	N*, C***, L***, Q***, N x C**, N x Q***
	N_{200}	38.1	18.5	14.8	31.4	
Lolium perenne	N_0	0.6	0.7	1.2	0.4	(C***, Q***, N x C*, N x Q*)
	N_{200}	2.4	9.2	8.4	2.9	
Phleum pratense	N_0	0.5	0.7	1.4	1.5	(C*)
	N_{200}	1.4	1.5	1.2	2.5	
Poa trivialis	N_0	0.8	0.1	1.7	1.1	(C**, L**, N x C**)
	N_{200}	2.2	2.8	8.4	5.0	
Filipendula ulmaria	N_0	8.9	7.9	6.3	9.9	Q*
	N_{200}	8.7	5.6	6.1	9.2	
Ranunculus acris	N_0	3.4	2.0	2.3	1.9	{L*}
	N_{200}	1.8	2.7	1.2	0.9	
R. repens	N_0	2.2	1.9	2.4	1.8	{L*}
	N_{200}	3.5	2.1	1.9	1.3	
Rumex acetosa	N_0	2.7	2.3	2.9	3.7	C***, L***, N x C***, N x L***
	N_{200}	3.5	6.7	7.5	9.1	
Taraxacum spp.	N_0	4.0	2.3	2.5	2.3	(N x Q*)
	N_{200}	4.0	2.9	2.7	4.5	
Trifolium pratense	N_0	0.9	2.3	1.5	1.0	(N*, C*, Q**)
	N_{200}	0.3	0.4	0.2	0.1	

(Table contd.)

Species		Mean cutting date 1991-92 24 May	 11 July	 5 Aug.	 2 Sep.	Significance of treatment effects (1)
Brachythecium rutabulum	N_0	0.7	0.9	3.9	2.6	[C**, L**, N x C***,
	N_{200}	0.1	0.2	0.3	0.1	N x L***]

(1) Asterisks denote significance of treatment effects in ANOVA: * = P<0.05; ** = P<0.01; *** = P<0.001. N and C indicate significant effects of previous fertilizer treatment and cutting date respectively, L and Q indicate significant overall linear and quadratic responses respectively to cutting date, and x = interaction between N and cutting date/cutting date response.

plots, but was significantly less abundant on plots of the same fertilizer treatment cut in July and August (P<0.001 between May and July and between August and September, P<0.01 between July and September) (Table 8.7). On N_0 plots cut in May, *H. lanatus* was third in abundance (at 11.7% of total cover) *to A. odoratum* (17.3%) and *F.rubra* (15.0%) and was less abundant with later cutting, although it showed no statistically significant difference between cutting dates on these plots.

Further mention is made below of trends shown by some individual species in the context of the regeneration strategy and seed bank type groups within which they are included.

Species groups

Of the primary species groups (i.e. grasses, dicots, *Juncaceae, Cyperaceae* and bryophytes), only data for grasses and dicots were normally distributed and none of the methods of transformation tried were able to correct skewness in the remaining three groups (vegetation abundance data for these five primary groups are not presented in Tables or Figures). Grasses were significantly more abundant on previously fertilized than unfertilized plots (72% and 56% respectively) and declined significantly with lateness of cutting, from 67% with cutting in May to 61% with cutting in September (P<0.05 for linear trend). The abundance of dicots was significantly reduced by previous fertilizer compared with unfertilized plots (at 28% compared with 37% respectively, P<0.01), but showed no response to cutting date.

Figure 8.2 shows the relative abundance in 1993 of species grouped by regeneration strategy i.e. 'S', 'V' and 'S/V' groups. The 'S' and 'S/V' groups showed the greatest

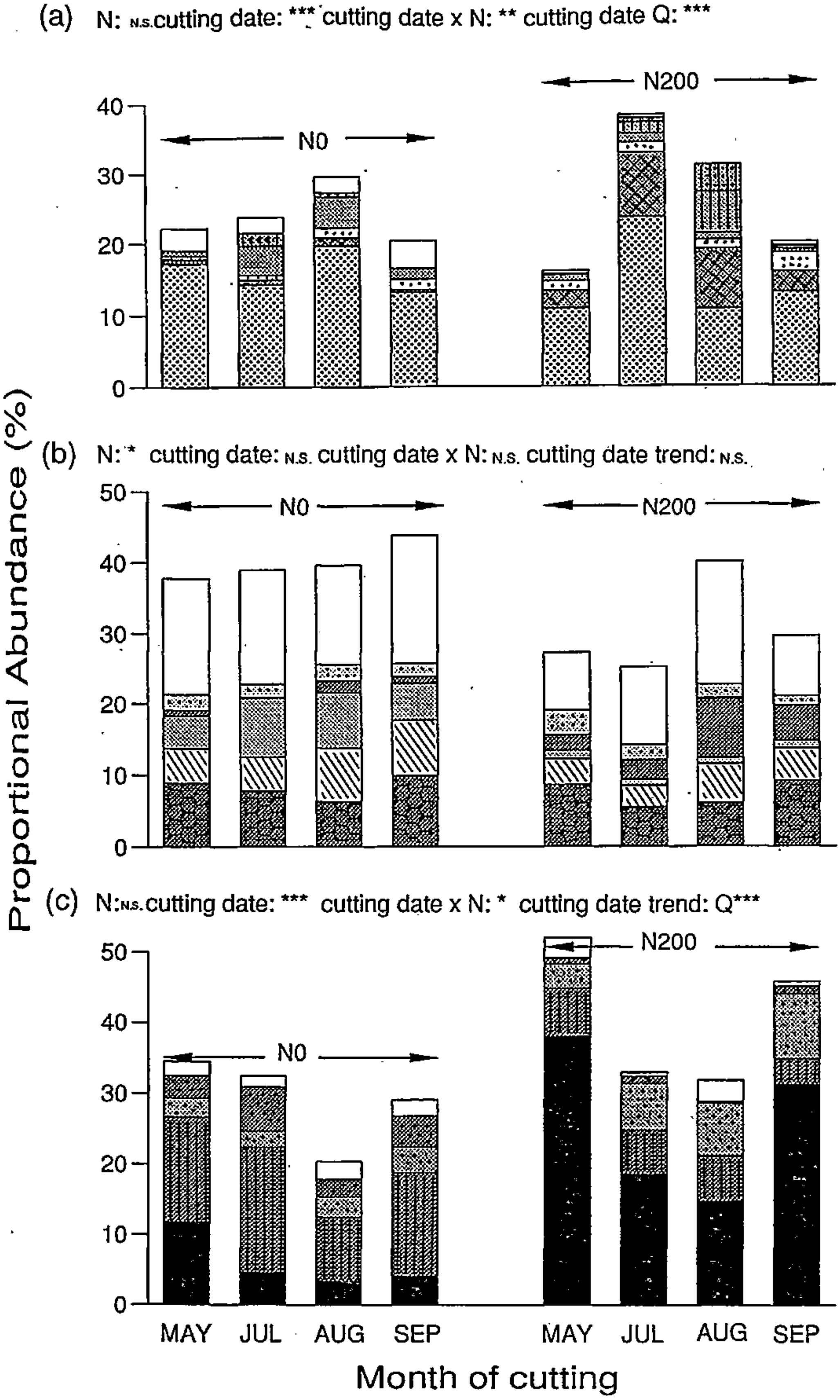


Figure 8.2. The effect of previous fertilizer treatment (N_0 and N_{200}) and of cutting dates in 1991 and 1992 on species abundance in May 1993. Species grouped by regenerative strategy (Grime *et al.*, 1988 - see text): (a) species relying on seasonal seedling regeneration; *A.odoratum* (░), *L. perenne* (▩), *Ph. pratense* (⁙), *C. cristatus* (▒), *B. hordeaceus* (▥), *B. racemosus* (▦); (b) species showing lateral vegetative spread; *F. ulmaria* (▓), *A. capillaris* (▧), *P. lanceolata* (░), *P. trivialis* (▒), *R. repens* (⁙); (c) those that show both strategies; *H. lanatus* (■), *F. rubra* (▥), *R. acetosa* (░), *Cen. nigra* (▓). Other species within each group =(□). Levels of significance relate to whole groups: * = P<0.05; ** = P<0.01; *** = P<0.001. 'Q' = quadratic response to date of cutting.

response to variations in cutting date in preceding years (both $P<0.001$), and both groups showed a significant cutting date x fertilizer treatment interaction ($P<0.05$ for the 'S/V' group, $P<0.01$ for the S group). The patterns shown by these two groups were complementary: both showed significant quadratic responses to date of cutting ($P<0.001$), but, whilst 'S' species were most abundant with cutting in July and August (i.e. a 'humped' response), the 'S/V' group showed an opposite ('trough-shaped') pattern (Figure 8.2b and c). Both groups showed a significant interaction ($P<0.01$) between previous fertilizer treatment and the overall curvilinear response to cutting date, with the 'humped' and 'trough-shaped' responses more prominent on N_{200} plots than N_0 plots. However, the response pattern shown by the 'S/V' group was largely attributable to *H. lanatus*, particularly on N_{200} plots, and without this species the group appeared to show no pattern of response to cutting date (although no statistical analysis was carried out on data for the group with *H. lanatus* excluded). Within the group, however, *Rumex acetosa* showed a highly significant linear response to date of cutting ($P<0.001$) (Table 8.7).

The 'V' group as a whole was significantly ($P<0.05$) more abundant on N_0 plots than on N_{200} plots, but showed no response to cutting date overall (Figure 8.2b). However, within this group, *Agrostis capillaris* abundance tended to increase linearly with date of cutting ($P=0.058$), whilst *Ranunculus repens* showed a significant linear trend of declining abundance ($P<0.05$, angular transformed data)(Table 8.7). Bromus spp. (*B. hordeaceus* + *B. racemosus*) were by far the most common annual species, a group which together exceeded 10% of the vegetation only in N_{200} plots cut in August (Figure 8.3a). However, data both for *Bromus* and for the group as a whole were very skewed and could not be normalized by angular, $\log_{10}$ or square root transformation. *Myosotis discolor* was the only species within this group to show a significant response to cutting date, increasing linearly with date of cutting ($P<0.05$, angular transformed data). However, though widely distributed on N_0 plots, this species accounted for less than 1% of the vegetation cover with any cutting date.

As with the 'S' group, with which it shared several species, the Type I seed bank group showed a highly significant quadratic response to cutting date ($P<0.001$, Figure 3b). The large abundance of this group on N_{200} plots cut in August was mainly due to the contribution of *Bromus* species. The only major component of the Type I group not included elsewhere were the *Taraxacum* species. The significant 'trough-shaped' response shown by this species on N_{200} plots was in the opposite direction to that shown by the group as a whole (Figure 8.3b and Table 8.7).

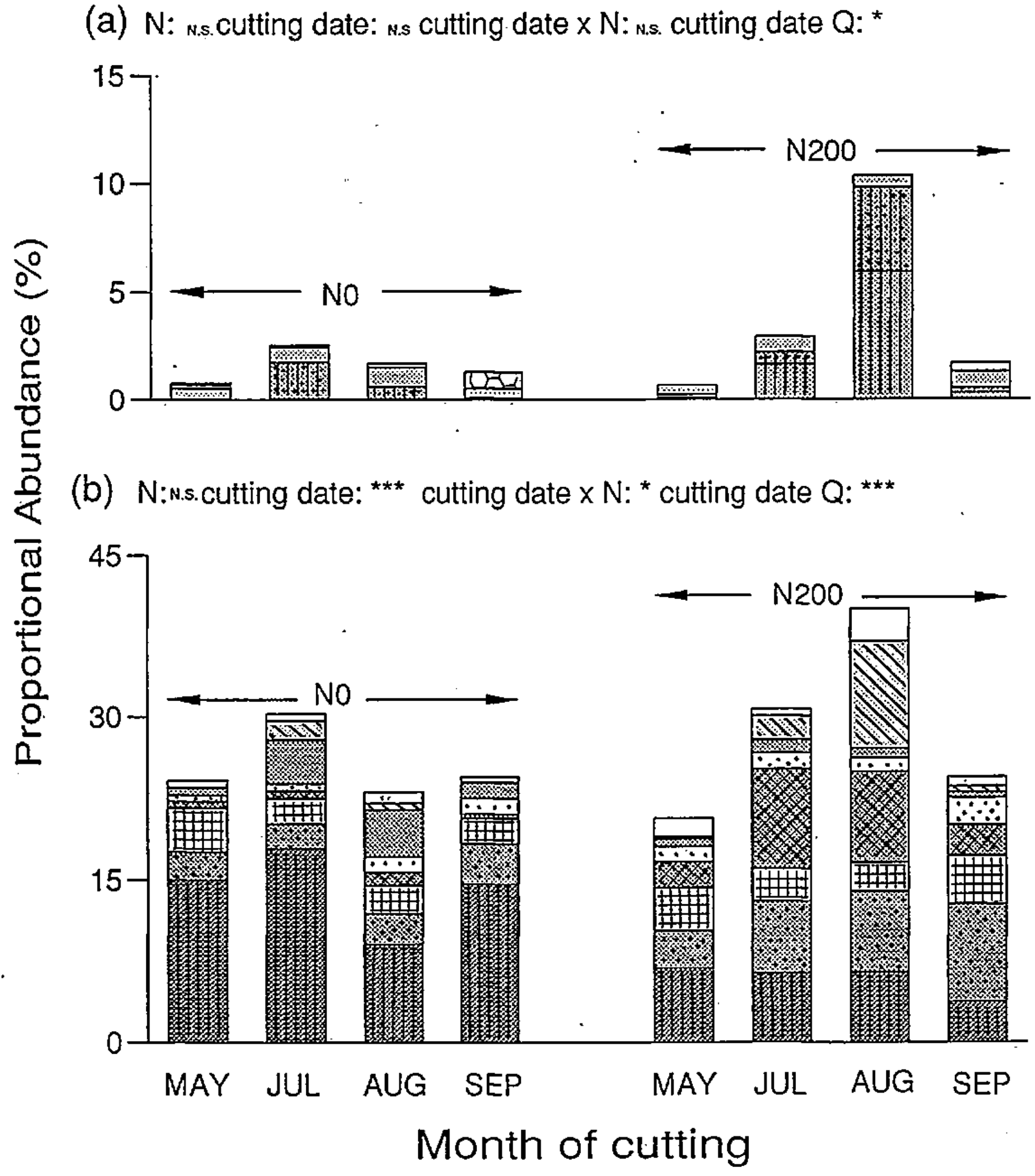


Figure 8.3. The effect of previous fertilizer treatment (N_0 and N_{200}) and of cutting dates in 1991 and 1992 on the abundance in May 1993 of: **(a)** annuals; *B. hordeaceus* (▥), *B. racemosus* (▦), *C. fontanum* (▒), *M. discolor* (⌗); **(b)** species which germinate soon after shedding (Type I, Thompson and Grime, 1979); *F. rubra* (▦), *R. acetosa* (▒), *Taraxacum spp.* (⊞), *L. perenne* (▩), *Ph. pratense* (⁘), *C. cristatus* (▒), *Bromus spp.* (▧). Others within each group = (☐). Levels of significance relate to whole groups: * = P<0.05; ** = P<0.01; *** = P<0.001. 'Q' = quadratic response to date of cutting.

The 'W' group as a whole varied in abundance from 2.3% of live vegetation cover on N_0 plots previoiusly cut in July or September to 4.5% on N_{200} plots cut in September (Table 8.8). The response pattern shown by this group was determined entirely by that of *Taraxacum spp.* The 'W' group was composed of six species in addition to *Taraxacum*: *Cirsium arvense*, *C. dissectum*, *C. palustre*, *Leontodon autumnalis*, *L. hispidus* and *Dactylorhiza praetermissa*. Together these accounted for only 0.2-1.7% of the vegetation, with maximal cover in August on N_0 plots (1.7%) and July on N_{200} plots (0.5%). As with the 'S/V' group, the response to cutting date shown by 'Bs' species was strongly influenced by *H. lanatus* (Table 8.8), although this species accounted for a smaller proportion of this group on N_0 plots than it did of the 'S/V' group (Table 8.8 and Figure 8.2c). Excluding *H. lanatus* from the group left no clearer a pattern of cutting date response on N_0 plots than when it was included. On N_{200} plots, exclusion of *H. lanatus* resulted in a change to a

Table 8.8. The effect of cutting date and previous fertilizer treatment (N_0 or N_{200}) on the relative abundance (% of live vegetation) of (a) species which regenerate by means of widely dispersed seeds ('W' species) and (b) those which commonly regenerate from a persistent seed bank ('Bs' species). Treatment significance ratings and symbols (see bottom of table for explanation) within curly brackets refer to angular transformed data (see text).

Species/group		Mean cutting date 1991-92 24 May	 11 July	 5 Aug.	 2 Sep.	Significance of treatment effects [1]
'W' species:-						
Taraxacum spp.	N_0	4.0	2.3	2.5	2.3	{N x L*}
	N_{200}	4.0	2.9	2.7	4.5	
whole group	N_0	4.3	2.9	4.2	2.6	None
	N_{200}	4.2	3.6	2.9	4.7	
'Bs' species:-						
Holcus lanatus	N_0	11.7	4.5	3.4	4.1	N*, C***, L***,Q***
	N_{200}	38.1	18.5	14.8	31.4	N x C**, N x Q***
whole group	N_0	67.8	59.4	66.8	62.9	C**, Q***, N x C*
	N_{200}	75.9	67.6	57.3	73.3	

[1] Asterisks denote significance of treatment effects in ANOVA: * = P<0.05; ** = P<0.01; *** = P<0.001. N and C indicate significant effects of previous fertilizer treatment and cutting date respectively, L and Q indicate significant overall linear and quadratic responses respectively to cutting date, and x = interaction between N and cutting date/cutting date response.

Table 8.9. The effect of cutting date and previous fertilizer treatment (N_0 and N_{200}) on the relative abundance (% of total live vegetation cover) of species grouped by seed bank type (Thompson and Grime, 1979) and previously observed response to fertilizer N (Mountford *et al.*, 1993a; Chapter 5 - see text)

Species group		Mean cutting date 1991-92				Significance of treatment effects (1)
		24 May	11 July	5 Aug.	2 Sep.	
Type 1:						
N-positive [5]	N_0	8.2	7.7	8.9	8.1	N*, C***, L***, Q***, N x C***, N x L***, N x Q***
	N_{200}	12.9	22.5	30.4	20.0	
N-negative [3]	N_0	15.7	22.1	14.0	16.1	N***, $C^{0.057}$, $Q^{0.059}$
	N_{200}	7.6	7.6	7.4	4.2	
Others [3]	N_0	0.3	0.5	0.2	0.3	None
	N_{200}	0.3	0.6	2.2	0.5	
Type I total [11]	N_0	24.2	30.3	23.1	24.4	C***, Q***, N x C**,N x Q*
	N_{200}	20.7	30.7	40.0	24.5	
Type II:						
N-positive [0]		-	-	-	-	
N-negative [0]		-	-	-	-	
Others [5]	N_0	3.0	0.4	0.7	3.4	None
	N_{200}	0.6	0.1	0.3	0.1	
Type III:						
N-positive [4]	N_0	16.9	6.5	10.1	8.0	N*, C***, L**, Q***, N x Q*
	N_{200}	42.7	26.2	28.8	38.9	
N-negative [12]	N_0	18.2	20.6	21.9	22.4	None
	N_{200}	9.1	8.1	8.5	9.5	
Others [10]	N_0	18.5	16.9	22.0	15.0	Q*, N x C**
	N_{200}	11.5	24.8	11.5	14.0	
Type III total [26]	N_0	53.5	44.1	54.1	45.6	C*, L*, Q*, N x C**
	N_{200}	63.3	59.1	48.7	62.4	
Type IV:						
N-positive [2]	N_0	0.0	0.0	0.0	<0.1	None
	N_{200}	0.0	0.0	0.0	<0.1	
N-negative [10]	N_0	11.5	11.8	11.8	15.6	None
	N_{200}	8.1	6.5	8.2	7.8	
Others [10]	N_0	9.0	8.9	6.5	11.0	Q*
	N_{200}	8.8	5.6	6.1	10.2	
Type IV total [22]	N_0	20.5	20.6	18.3	26.6	Q*
	N_{200}	16.9	12.1	14.3	17.1	

(Table contd.)

Table 8.9 (contd.)

Species group		Mean cutting date 1991-92				Significance of
		24 May	11 July	5 Aug.	2 Sep.	treatment effects (1)
Type ?:						
N-positive [0]		-	-	-	-	
N-negative [6]	N_0	1.7	2.1	1.7	2.2	None
	N_{200}	1.5	0.3	1.0	0.9	
Others [11]	N_0	3.5	6.8	2.6	4.9	None
	N_{200}	1.0	1.0	0.3	1.3	
Type ? total [17]	N_0	5.2	9.0	4.3	7.2	None
	N_{200}	2.5	1.3	1.3	2.2	

Asterisks denote significance of treatment effects in ANOVA: * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$. N and C indicate significant effects of previous fertilizer treatment and cutting date respectively, L and Q indicate significant overall linear and quadratic responses respectively to cutting date, and x = interaction between N and cutting date/cutting date response.

'humped' pattern with the highest mean in July (49.1%) and the lowest value in May (37.8%). Nearly half this July peak was accounted for by *A. odoratum* (23.7%, see Table 8.7), which was also included in the 'S' group (Grime *et al.*, 1988).

When species were grouped by both seed bank type and previously observed N response in ANOVAs (Table 8.9), the N-positive Type I sub-group showed by far the most sensitivity to variations in cutting date, and the most significant interactions between cutting date and previous fertilizer application (all these effects $P<0.001$). On the other hand, N-negative Type I species were the most sensitive to previous fertilizer treatment overall ($P<0.001$). The abundance of N-positive Type I species varied little on N_0 plots, from 7.7% for July cutting to 8.9% on plots cut in August, but were significantly more abundant on N_{200} plots than on N_0 plots with each cutting date ($P<0.05$ for May cutting, $P<0.001$ the rest). On N_{200} plots, these species were significantly more abundant on plots which had been cut in July or August than May or September ($P<0.001$), and August cutting led to a significantly higher ($P<0.01$) abundance of these species than cutting in July (30.4% of total live vegetation cover, compared with 22.5%).

H. lanatus accounted for most of the vegetation cover attributed to N-positive Type

III species on plots cut in May or September, particularly on N_{200} plots where it accounted for 89% and 81% respectively of the vegetation cover attributable to this sub-group (Table 8.9, see Table 8.8 for *H. lanatus* means). The proportions accounted for by *Holcus* on N_{200} plots cut in July and August were lower (70% and 50%), but still high enough for this species to determine the overall pattern of response to cutting date on N_{200} plots. Consequently, the sub-group as a whole showed a marked 'trough-shaped' response on these plots and a highly significant ($P<0.001$) quadratic trend overall in the ANOVA (Table 8.9). *H. lanatus* was also the most abundant single constituent of this same sub-group on N_0 plots, where it accounted for 70% of the contribution to vegetation cover made by the sub-group as a whole on plots cut in May and in July. The remaining species, *Agrostis stolonifera*, *Poa trivialis* and *Cerastium fontanum*, together contributed 50% or more of the cover made by this sub-group on these plots cut in August and September. If *H. lanatus* means are subtracted from those of the N-positive Type III group, the resulting pattern on N_{200} plots is very similar to that shown by N-positive Type I species, though at lower levels of abundance, i.e. 4.6%, 7.7%, 14.0% and 7.5% of live vegetation cover on plots cut in May, July, August and September respectively (Table 8.9, see Table 8.8 for *H. lanatus* means).

N-negative Type III species showed no significant effects of cutting date nor of previous fertilizer treatment, although these species were more than twice as abundant on N_0 plots than on N_{200} (Table 8.9, P for overall difference =0.086). The remaining Type III sub-group, composed of Type III species not classified as to N-response, was most abundant with cutting in August on N_0 plots and with July cutting on N_{200} plots and showed a significant fertilizer x cutting date interaction in the ANOVA ($P<0.01$).

Type IV species showed a significant 'trough-shaped' quadratic response to cutting date overall ($P<0.05$), with this pattern largely attributable to 'other' species within this group, i.e. those not classified as to N response (Table 8.9). Type ? species, those for whom the seed bank behaviour is unknown, accounted for no more than 10% of the vegetation with any treatment, and showed no signficant treatment effect (Table 8.9).

Species richness and diversity

There was no significant effect on species richness (numbers of species per plot) or diversity (Shannon-Wiener Index) of previous fertilizer treatment in 1991 or 1993, nor any cutting date x fertilizer treatment interaction (Table 8.10). By April-May 1993, fewer species were recorded on May-cut plots than any other cutting date, with the difference between

Table 8.10. The influence of previous fertilizer treatment (N_0 and N_{200}) and different cutting dates in 1991 and 1992 on species richness and diversity in May 1991 and 1993.

Fertilizer treatment	Cutting date	Species richness (no. of species per plot)		Species diversity (Shannon-Wiener Index)	
		1991	1993	1991	1993
N_0	May	32.3	31.4	3.93	3.49
	July	28.3	34.7	3.68	3.84
	Aug	33.7	37.2	4.10	3.94
	Sep	31.7	32.9	3.89	3.62
N_0 mean		31.6	33.4	3.90	3.67
N_{200}	May	24.5	23.8	3.54	2.99
	Jul	23.7	27.5	3.65	3.47
	Aug	25.2	25.8	3.62	3.71
	Sep	24.8	26.9	3.63	3.23
N_{200} mean		24.6	25.8	3.60	3.27
Mean N_0/N_{200}	May	28.4	27.6	3.73	3.24
"	Jul	26.0	31.1	3.67	3.65
"	Aug	29.4	31.5	3.86	3.83
"	Sep	28.2	29.9	3.76	3.43
SED N means		2.55	3.06	0.278	0.157
SEDs cutting date means:					
May v Sep		1.15	0.93	0.084	0.091
Jul v Aug		1.62	1.32	0.119	0.128
May/Sep v Jul/Aug		1.40	1.14	0.103	0.111
			C**, L** Q**		C***, L** Q***

C = significant effect of cutting date in ANOVA, L and Q =significant linear and quadratic responses respectively to cutting date. Asterisks denote significance of treatment effects: * = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$
See text for formulae for calculation of Shannon Wiener Index

May and August highly significant ($P<0.001$). Species diversity was lower with May or September cutting compared with both July and August ($P<0.001$), but with no significant difference between the latter two dates. May cutting resulted in significantly lower diversity than September ($P<0.05$). Both species richness and species diversity in 1993 showed significant quadratic responses to cutting date overall ($P<0.001$ and 0.001 respectively), with maximal values for each achieved by cutting in August (Table 8.10). However, as Figure 8.4a shows, a quadratic regression equation (i.e. of the general formula $y=A + Bx - Cx^2$) provided a comparatively poor fit ($R^2 = 0.16$, df=69) to the data for Shannon-Wiener Indices

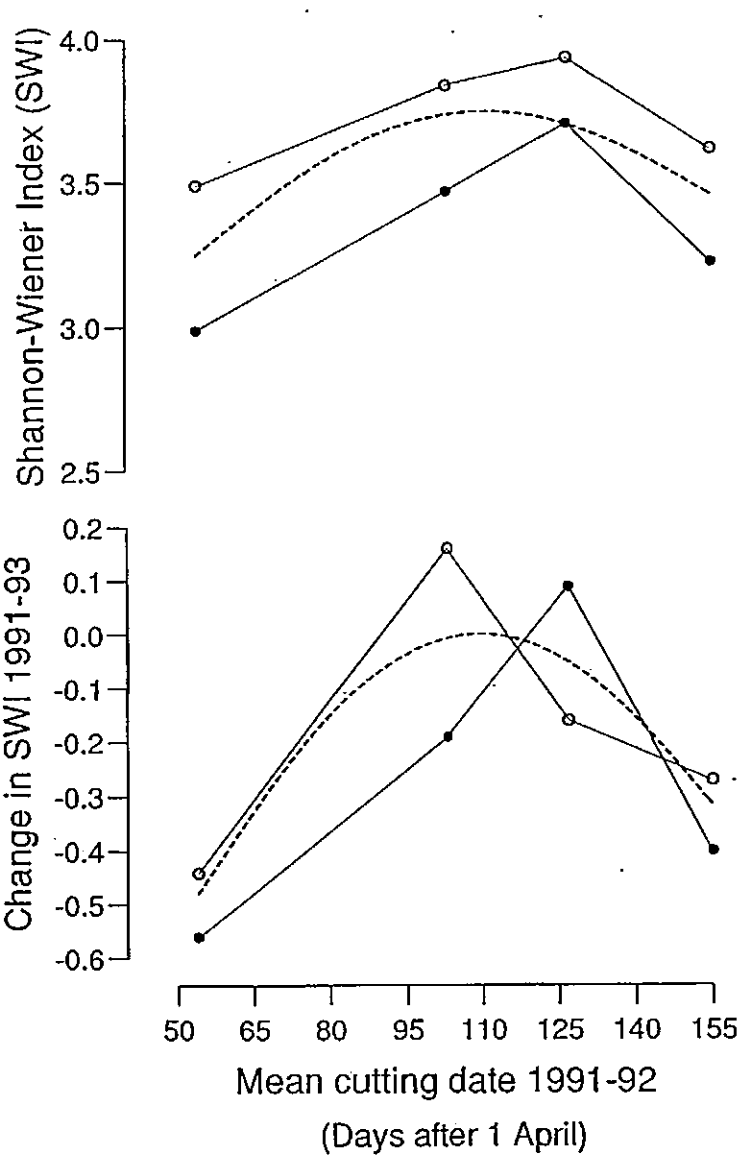


Figure 8.4. The influence of cutting date in 1991 and 1992 on species diversity (Shannon-Wiener Index) in May 1993 (a), and on the difference between 1991 and 1993 in species diversity (b), on previously fertilized (solid circles) and unfertilized (open circles) plots. Dotted lines are curves fitted by quadratic regression equations derived from data from all plots (df=69); $R^2 = 0.16$, $P = 0.001$ (diversity), and $R^2 = 0.14$, $P = 0.002$ (difference in diversity).

(SWIs) for each plot against cutting date, although the F-probability for this equation was high ($P=0.001$) due to the large number of degrees of freedom in the regression. The equation predicted a maximum SWI with cutting 111 days after 1 April, i.e. on 20 July, but it is clear that a more accurate model would predict a maximum value close to the August cutting date (see Figure 8.4a). However, the highest mean SWI value on N_0 plots in 1991 (i.e. before imposition of different cutting dates) also occurred on plots subsequently cut in August. When the difference in SWI between 1991 and 1993 (i.e. 1993-1991) was calculated for each plot, the highest mean value was shown by cutting in July on N_0 plots and in August on N_{200} plots (Figure 8.4b). A quadratic regression equation using these data predicts an overall optimum cutting date on 18 July averaged over both treatments ($R^2=0.14$, $P<0.01$) but it appears from Figure 8.4b that the optimum cutting date is later for N_{200} plots than for N_0. Nevertheless, as noted above, the ANOVA for 1993 data showed no significant N x cutting date interaction, nor did a similar analysis of data expressed as the difference in SWI between 1991 and 1993.

Association between species diversity and individual species/species group abundance

High species diversity (SWI) on unfertilized plots (df=34) was closely associated with the abundance of *Plantago lanceolata* ($r=0.60$, $P<0.001$), *Leontodon autumnalis* ($r=0.55$, $P<0.001$) and *C. cristatus* ($r=0.52$, $P<0.001$). Positive associations between individual species abundance and species diversity tended to be weaker on N_{200} plots, reaching high levels of confidence only for *Dactylis glomerata* ($r=0.55$, $P<0.001$) and *Lolium perenne* ($r=0.44$, $P<0.01$). The abundances of both *P. lanceolata* and *B. hordeaceus* were positively correlated with species diversity on these plots ($r=0.40$ and $r=0.36$ respectively, both $P<0.05$), but that of *B. racemosus* was not ($r=0.23$). *H. lanatus* abundance showed a very strong negative association with species diversity on previously fertilized plots ($r= -0.93$, df=34, $P<0.001$) but not on unfertilized plots ($r = -0.20$).

Species diversity was negatively correlated overall with the abundance of grasses ($r= -0.62$, $P<0.001$, df=70), but less so on N_{200} plots than on unfertilized ones ($r= -0.40$, $P<0.05$, and $r= -0.64$, $P<0.001$ respectively, df=34) (Table 8.11). Of the remaining primary species groups, SWI values were positively correlated with dicots ($r=0.43$, $P<0.01$), *Cyperaceae* ($r=0.51$, $P<0.01$) and *Juncaceae* ($r=0.39$, $P<0.05$) on N_0 plots, but only with

Table 8.11. Association of species diversity (Shannon-Wiener Index) with the proportional abundance of plant species groups in 1993 on unfertilized (N_0) and previously fertilized (N_{200}) plots and overall. Values are correlation coefficients (r).

Species group		N_0 (df=34)	N_{200} (df=34)	All plots (df=70)
Grasses		-0.64***	-0.40*	-0.62***
Dicots		0.43**	0.39*	0.51***
Cyperaceae		0.51**	0.28	0.46***
Juncaceae		0.39*	0.26	0.36**
Bryophytes		0.22	0.31	0.33**
Regenerative strategy(1):-				
'S' species		0.15	0.57***	0.38**
'V' species		0.41*	0.58***	0.60***
'S/V' species		-0.66***	-0.84***	-0.82***
'W' species		0.47**	0.24	0.28*
'Bs' species		0.30	-0.69***	-0.34**
Annuals		0.53*	0.34*	0.22
Seed bank type x N response(2):-				
Type I	N-positive	0.70***	0.67***	0.24*
" "	N-negative	-0.42**	-0.03	0.11
" "	Others	0.23	0.27	0.15
" "	Total	0.08	0.67***	0.39***
Type II	Others/Total	-0.16	>-0.01	0.05
Type III	N-positive	0.17	-0.81***	-0.59***
" "	N-negative	-0.15	0.11	0.26*
" "	Others	-0.08	0.13	0.12
" "	Total	-0.04	-0.74***	-0.56***
Type IV	N-positive	<0.01	0.17	0.08
" "	N-negative	-0.43**	0.02	-0.06
" "	Others	0.12	0.03	0.11
" "	Total	-0.31	0.04	0.02
Type ?	N-negative	0.47**	-0.03	0.33**
" "	Others	-0.57***	-0.06	-0.17
" "	Total	-0.42*	-0.03	-0.04

(1) Species which regenerate primarily by: 'S' =seasonal seedling production; 'V' =vegetative spread ; 'S/V' =both strategies ; 'W' =widely dispersed seeds ; 'Bs' =germination from a persistent seed bank; (Grime *et al.*, 1988 - see text).

(2) Seed bank types as defined by Thompson and Grime (1979); N-response defined with reference to previous work at the site (Mountford *et al.*, 1993 and Chapter 5)

dicots on N_{200} plots ($r=0.39$, $P<0.05$).

There was a strong correlation between the abundance of 'S' species and SWI values on N_{200} plots ($r=0.54$, $P<0.001$), but not on N_0 plots ($r=0.15$) (Table 8.11). 'V' species were significantly correlated with SWI values both on unfertilized and on previously fertilized plots, though more closely on the latter ($r=0.41$, $P<0.05$ and $r=0.58$, $P<0.001$ respectively). 'S/V' species showed a very significant negative association with SWI on all plots, particularly on N_{200} plots ($r= -0.84$, $P<0.001$) where the abundance of this group was highly correlated with that of *H. lanatus* ($r=0.89$, $P<0.001$). The negative association of this group with species diversity was less marked on N_0 plots ($r= -0.66$, $P<0.001$), where the abundance of the group as a whole was associated primarily with *Festuca rubra* ($r=0.77$, $P<0.001$) and *Centaurea nigra* ($r=0.70$, $P<0.001$). 'Bs' species were negatively correlated with SWI on N_{200} plots, and again the influence of *H. lanatus* appeared to be significant ($r=0.69$, $P<0.001$) for correlation between *H. lanatus* abundance and that of the 'Bs' group as a whole).

Species diversity was positively correlated with the abundance of annuals both on N_0 and N_{200} plots ($r=0.53$ and $r=0.34$, both $P<0.05$), but not overall ($r=0.22$, N.S.). This group was very closely associated with both *B. hordeaceus* and *B. racemosus* on N_{200} plots ($r= 0.95$ and 0.99 respectively) but only with *B. hordeaceus* on N_0 plots ($r=0.79$, $P<0.001$, compared with $r=0.13$ for *B. racemosus*).

Within the seed bank type groupings, the strongest correlations with SWI were shown by the N-positive sub-group of the Type I group (both on N_0 and N_{200} plots) and the Type III group (N_{200} plots) (Table 8.11). The association between Type I N-positive species and SWI was much weaker accross all plots ($r=0.24$, $P<0.05$) than on N_0 and N_{200} plots separately ($r=0.70$ and 0.67 respectively, both $P<0.001$)), reflecting the fact that the abundance of this sub-group was associated with different species in each case, i.e. mainly with *Rumex acetosa* and *Taraxacum* on N_0 plots ($r= 0.68$ and 0.77 respectively, both $P<0.001$) and with *B. hordeaceus* ($r=0.58$), *B. racemosus* ($r=0.50$) and *L. perenne* ($r=0.59$) on N_{200} plots (all $P<0.001$).

As with 'S/V' species, the strong inverse relationship on N_{200} plots between species diversity and the abundance of N-positive Type III species ($r= -0.81$, $P<0.001$, Table 8.11) was attributable largely to the inclusion of *H. lanatus* in the group ($r=0.89$ for correlation between *H. lanatus* abundance and that of N-positive Type III group as a whole). Within the seed bank Type IV group, only the N-negative sub-group was significantly correlated with SWI and only on N_0 plots, where the relationship was an inverse one (r= -0.43, P<0.01) (Table 8.11). The abundance of this sub-group was closely associated with that of *Agrostis capillaris* on these plots (r=0.71, P<0.001), with this species negatively correlated with SWI (r= -0.59, P<0.001).

Amongst the species of unknown seed bank behaviour (Type ?), none had been identified as N-positive and neither of the remaining two sub-groups nor the group as a whole showed any significant correlation with SWI on N_{200} plots (Table 8.11). N-negative Type ? species were positively correlated with SWI (r=0.42, P<0.01), whilst the remaining sub-group ('others') showed an even stronger, inverse relationship with SWI (r= -0.57, P<0.001). However, although this sub-group was composed of 11 species, 90% of the ground cover attributed to it was of *Centaurea nigra*, which therefore showed an almost identical correlation with SWI to that of the sub-group as a whole (r= -0.57 for N_0 plots). *C. nigra* abundance was, not surprisingly, very closely correlated with that of the sub-group (r=0.99).

TRENDS IN BOTANICAL COMPOSITION IN 1993 IN RELATION TO SEED RAIN IN 1991

The extent to which variations in seed rain caused by differences in cutting date might have induced changes in vegetation composition between 1991 and 1993 was investigated by regression analysis. Regressions were carried out on seed rain and species abundance data for species grouped by regeneration strategy, N-response and seed bank type as above. However, it should be noted that the presence of a positive correlation between seed rain and vegetation change does not necessarily indicate a causal relationship. Differences in cutting date and length of uninterrupted growth, which might be correlated with the amount of seed shed, could influence the subsequent relative abundance of species by differential effects on vegetative growth (Oomes and Altena, 1987).

Analyses using data from plots of both fertilizer treatments (df=70) showed a significant relationship between seed rain in 1991 and changes in vegetation abundance 1991-1993 for several of the groups, although none of these regressions accounted for more than 30% of the variance in the data. The 'W' group and the 'N-positive' seed bank

Type I group showed the closest correlations ($R^2=0.30$, $P<0.001$ and $R^2=0.18$, $P<0.001$ respectively), but neither group showed a significant relationship when *Taraxacum* data were excluded from the analyses. Changes in abundance of species which rely upon regeneration from seed in the autumn, the 'S' group, were also related to patterns in seed rain ($R^2=0.12$, $P=0.002$). However, species with a persistent seed bank (Type IV) showed a similar level of correlation ($R^2=0.11$, $P=0.003$), with N-negative species within this latter group accounting for most of the relationship shown by the group as a whole ($R^2=0.10$, $P=0.004$). N-positive Type IIII species also showed a small, just significant, relationship ($R^2=0.04$, $P=0.047$).

The species groups mentioned in the previous paragraph showed very similar relationships when analyses were restricted to data from unfertilized (N_0) plots only (df=34), with the exception of the N-positive Type IIII group, which showed no significant correlation on these plots. Species which regenerate vegetatively ('V' species) also showed a significant correlation with patterns in seed rain on these plots ($R^2=0.13$, $P=0.018$). As with analyses which included data from all the plots, exclusion of *Taraxacum* from each group to which it belonged left no significant correlation for the remaining species within the group. N-neutral Type II species were present on only about half the N_0 plots in 1991, but changes in vegetational abundance were more closely correlated with patterns of seed rain on N_0 plots for this group than for any other group ($R^2=0.25$, $P=0.025$, df=15).

The N-neutral Type II group showed a very significant relationship on N_{200} plots ($R^2=0.68$, $P=0.008$, df=6), but this was attributable to its generally low abundance combined with high values on just one of the eight N_0 plots on which it was recorded. Species groups containing *Taraxacum* all showed significant correlations between seed rain and botanical change on N_{200} plots ($R^2=0.20$, $P=0.004$ for N-positive Type I species and $R^2=0.15$ for the Type I group as a whole; $R^2=0.45$, $P<0.001$ for the 'W' group), but none of these relationships reached significance when *Taraxacum* data were excluded.

TIME OF SEED SHEDDING RELATED TO CUTTING AND HAY MAKING OPERATIONS

The proportion of seed rain shed before cutting

For most species and species groups, the number of seedlings recorded which originated from seed shed before cutting, expressed as a proportion of the total (the PBC value),

Table 8.12. The effect of cutting date on the numbers of grass seedlings per m^2 produced from seed shed between late May and completion of hay making on unfertilized plots in replicate block I on three dates in 1991 and on the proportion of each total that was shed before cutting (PBC).

Cutting date	*Anthoxanthum odoratum*		*Bromus racemosus*		*Cynosurus cristatus*		*Holcus lanatus*		*Festuca pratensis*		Total of all grasses	
	No. m^{-2}	PBC	No. m^{-2}	PBC	No. m^{-2}	PBC	No. m^{-2}	PBC	No. m^{-2}	PBC	No. m^{-2}	PBC
17 July	2742	0.16	2849	0.42	1183	0.03	731	0.12	53	0.00	7971	0.22
9 August	1183	0.45	2524	0.49	7662	0.28	1454	0.41	686	0.00	13900	0.24
4 September	1914	0.71	558	0.15	8280	0.69	2238	0.63	377	0.46	14096	0.64
s.e.	768.8	0.052	852.4	0.030	1686.4	0.064	409.0	0.105	383.3	0.024	983.0	0.102
Treatment effect	NS	*	NS	**	NS	*	NS	NS	NS	-	*	NS
Linear trend	NS	**	NS	**	(0.062)	**	(0.080)	*	NS	-	*	(0.060)
Non-linear trend	NS	NS	NS	*	NS	NS	NS	NS	NS	-	NS	NS

Asterisks denote significance of treatment effects and of linear and non-linear trends with cutting date in ANOVA: * = $P<0.05$; ** = $P<0.01$; ** = $P<0.001$; NS = not sigificant. Bracketed figures are F probability values where these fall within $P=0.1<0.05$

Table 8.13. The effect of cutting date on: a) the numbers of seedlings per m^2 of forbs, *Juncaceae*, *Cyperaceae* and total of all species, produced from seed shed between late May and completion of hay making on unfertilized plots on three dates in 1991; b) and on the proportion of each total that was shed before cutting (PBC).

Cutting date	*Cerastium fontanum*		Total of all forbs		Total of *Juncaceae*		Total of *Cyperaceae*		Total of all species	
	No. m^{-2}	PBC	No. m^{-2}	PBC	No. m^{-2}	PBC	No. m^{-2}	PBC	No. m^{-2}	PBC
17 July	490	0.07	1763	0.19	98	0.60	23	0.70	9855	0.22
9 August	3066	0.40	6584	0.24	851	0.12	8	0.00	21344	0.24
4 September	1687	0.81	4566	0.38	294	0.38	8	1.00	18963	0.58
s.e.	1009.6	0.117	1802.9	0.064	143.7	0.117	14.4	-	2444.4	0.073
Treatment effect	NS	(0.092)	NS	NS	(0.069)	NS	NS	-	(0.087)	(0.066)
Linear trend	NS	*	NS	NS	NS	NS	NS	-	(0.085)	*
Non-linear trend	NS	NS	NS	NS	*	(0.076)	NS	-	(0.093)	NS

Asterisks denote significance of treatment effects and of linear and non-linear trends with cutting date in ANOVA, $P<0.05$; NS = not sigificant. Bracketed figures are F probability values where these fall within $P=0.1<0.05$. *Cyperaceae* were unrecorded on too many plots for the group to be included in ANOVAs.

increased progressively with lateness of cutting between July and September (Tables 8.12 and 8.13). For grasses as a whole, the proportion increased from 22% with cutting in July to 64% with September cutting. Although this linear trend just failed to reach significance ($P=0.060$), for both *A. odoratum* and *C. cristatus* the overall increase was highly significant (from 16% to 71% for *A. odoratum*, and from 3% to 69% for *C. cristatus*, both $P<0.01$), with significant differences between each successive cutting date ($P<0.05$). Even with cutting on 9 August, only 45% of *A. odoratum* seedlings and 28% of those of *C. cristatus* originated from seeds shed before cutting, with corresponding values of 49%, 41% and 24% for *Bromus racemosus*, *H. lanatus* and all grasses *in toto* respectively. No seeds of *Festuca pratensis* appeared to have been shed before cutting in July or August, and even with cutting in September, 54% of all *F. pratensis* seedlings came from seed shed at or after cutting (Table 8.12).

In contrast with other species, *Bromus racemosus* showed a significant overall trend of decline in PBC value with lateness of cutting ($P<0.01$), attributable to a more than three-fold difference between August and September (from 49% to 15%, $P<0.01$). This implies a high rate of loss of the viable seed shed before harvesting in September compared with July or August, either by predation or by unsuccessful establishment of germinating seeds.

Amongst the dicots, only *C. fontanum* showed any significant effect of cutting date on PBC values ($P<0.05$ for linear trend, Table 8.13). Overall, 22% of the seedlings of all species recorded on plots cut in July originated from seed shed before cutting, increasing to 24% for cutting in August to 58% for cutting in September. This represented a significant ($P<0.05$) linear trend, although differences between individual cutting dates failed to reach 95% significance levels ($P=0.066$)(Table 8.13.).

The total numbers of seedlings recorded per m^2 from seed rain on plots in this study were comparable with those recorded on all N_0 plots in the main seed rain study, even though the data in this study applied to seeds shed during the relevant periods after 24 May only (Tables 8.1 and Table 8.13). Grasses were more abundant amongst seedlings recorded in this study at 7971-14096 seedlings m^2 compared with 4561-12233 m^2 in the main study, whilst dicots were less abundant (1763-4566 m^2 compared with 4753-8806 m^2). However, differences in the latter group can be largely accounted for by the number of

Taraxacum seedlings from seed shed up to and including cutting in May. Moreover, trends accross cutting dates were fairly representative of those shown in the main study as a whole, except that *H. lanatus* seedling numbers increased progressively between cutting dates in this study (probability of a linear trend: P=0.080), whereas numbers were marginally higher after August cutting than after harvesting in September in the main study (Tables 8.2 and 8.12).

Table 8.14. Numbers of seedlings per m^2 produced from seed shed during three phases of mechanized hay making in early August 1991. Numbers are means ± standard errors derived from seed germinating in ten 132.73 cm^2 compost-filled dishes removed from beneath vegetation after each phase of hay making.

Species/species group	Seedlings per m^2 from seed shed during:-							
	Cutting		Turning/tedding		Rowing/baling		Total	
	Mean	±s.e.	Mean	±s.e.	Mean	±s.e.	Mean	±s.e.
Agrostis canina	136	82.9	912	267.5	166	76.1	1213	352.6
A. capillaris	83	52.0	294	83.6	8	7.5	384	88.1
Anthoxanthum odoratum	452	24.1	1070	226.8	196	147.7	1718	310.4
Bromus racemosus	60	35.4	136	27.1	38	30.1	234	58.0
Cynosurus cristatus	3993	1389.3	3285	699.9	490	390.3	7768	1516.6
Festuca pratensis	279	116.0	753	312.7	23	22.6	1055	409.9
F. rubra	151	64.8	912	320.2	38	23.4	1100	329.2
Holcus lanatus	633	156.0	1288	273.5	68	37.7	1989	324.7
Total of all grasses	6155	639.6	9237	1460.1	1055	650.9	16447	1527.9
Cerastium fontanum	264	168.0	121	59.5	68	52.0	452	170.3
Plantago lanceolata	535	202.7	1755	693.1	158	104.7	2449	710.5
Ranunculus acris	105	37.7	166	42.9	60	35.4	332	67.8
R. repens	15	15.1	23	11.3	0	0.0	38	23.4
Senecio aquaticus	188	101.0	467	110.8	30	23.4	686	144.7
Trifolium pratense	8	7.5	53	22.6	23	11.3	83	26.4
Total of all dicots.	1152	344.3	2878	824.2	452	299.1	4482	771.5
Cyperaceae (total)	0	0.0	60	27.1	8	7.5	68	26.4
Juncaceae (total)	1771	1130.1	595	162.7	889	375.2	3255	1231.1
Total of all species	9079	2682.1	12770	1893.3	2403	1106.8	24252	2447.1

Seed shed during hay making

It is not justifiable on statistical grounds to perform t-tests between mean values for different hay making phases in this study since the location of each sample dish was not re-randomised for each phase (Hurlbert, 1984). However, standard errors are given in Table 8.14. to indicate the level of variation about each mean.

A total of about 24,000 seedlings per m^2 were produced from seed shed during mechanized hay making in early August, with 95% confidence limits around this estimate of ±5140 seedlings m^{-2} (Table 8.14). About half the total of all seedlings recorded originated from seed shed during tedding and turning, with 37% shed at cutting and only 10% during rowing and baling (note that the numbers recorded in this study did not include seed shed before cutting).

About two-thirds of all seedlings recorded were grasses, nearly half of these were *C. cristatus*. Forbs contributed 18% of the total and *Juncaceae* (mostly *Juncus effusus*) 13%. Very few *Cyperaceae* seedlings were produced. For most species or species groups, the number of subsequently germinating seed shed during tedding and turning greatly exceeded that which had been shed at cutting. However, *C. cristatus, C. fontanum, Ranunculus repens* and the *Juncaceae* were exceptions, with seed shed at cutting contributing 50% or more of the total for each of these species. In general, the proportion of seed shed at cutting was slightly lower for forbs than for grasses at 26% and 37% respectively (Table 8.14).

The overall mean for the total number of seedlings recorded from seed shed during hay making in this study of 24,250 seedlings per m^2 was equivalent to that of 21,340 seedlings m^{-2} recorded for the same harvest date (9 August) on adjacent plots in the study described above (Table 8.13.), even though the latter number included those seed shed between late May and just before cutting. Seed shed only during hay making in that study (i.e. from cutting to rowing and carting off inclusively), produced 16,220 seedlings m^{-2} in total, including 10,500 grass seedlings and 5,010 forb seedlings per m^2. The difference between the two studies was therefore in the amount of grass seed shed (compare Tables 8.12 and 8.14).

These comparisons suggest that hay making with tractor-mounted equipment, including a drum mower and a power operated tedder/rower, may have caused a greater seed shed than cutting with a finger bar mower and turning by hand. However, no error estimate was made for individual cutting date means in the previous study, since these means were derived from two separate plots per cutting date. It is not therefore possible to say whether the observed differences were statistically significant. Nor can the possibility be excluded that these differences were related to differences in vegetation density and composition between the two adjacent study areas, since these variables were not recorded in the present study. However, both studies show the importance of hay making operations in stimulating the shedding of viable seed.

THE PHENOLOGY OF SEED PRODUCTION, SHEDDING AND VIABILITY OF THREE SELECTED SPECIES

Rhinanthus minor

Less than 10% of *R. minor* seeds were ripe by mid-June, and only 2% were in dehiscent pods, i.e. were capable of being released (Table 8.15). There was considerable variation in the stage of development of inflorescences on the same plant, with those higher up the plant more advanced than those beneath. However, ripening occurred quite rapidly, so that by 30 June 64% of the seeds on each plant were ripe, and by 13 July all the seeds

Table 8.15. Stage of maturity of seeds of *Rhinanthus minor* on seven dates between 15 June and 2 September 1992. Values are the mean number seeds ± standard error (n=10) per plant falling within each category (see text for definition of categories). Figures in brackets are the means expressed as a percentage of the total number of seeds per plant.

	Development stage			
Date	Developing	Ripening	Ripe	Dehiscent
15 June	65.0 (34) ±29.56	10.8 (57) ±23.18	13.3 (7) ±6.80	3.1 (2) ±2.08
25 June	25.1 (14) ±16.58	69.4 (39) ±34.21	17.0 (10) ±6.16	67.6 (37) ±13.86
30 June	1.1 (3) ±0.38	11.1 (33) ±2.63	21.6 (64) ±5.05	
13,24,24 July and 2 September	-	-	-	- (100)

recorded were contained within dehiscent pods. Eighty-four percent of the seeds shed on 15 June, and 76% of the ripe seeds enclosed within sealed pods, germinated after chilling and incubation (Table 8.16). Viability was lower with unripe seeds at 52%, with no difference between those chill/incubated and those sown into peat and stored at ambient temperature in a poly-tunnel (none of these germinated until the spring following sowing). Surprisingly, 26% of the seeds which were still green and attached within the pods germinated after removal followed by chilling and incubation (none of these were tested in peat). Drying seed at ambient temperature for 3 days appeared to reduce viability at each stage of ripening, with none of the ripe seeds germinating and only 2% of attached ('developing') seeds (Table 8.16). Samples collected on later occasions required a further period of chilling and incubation before substantial germination occurred, and drying appeared to slightly enhance germination of seed collected at these later dates. The final germination percentage of seeds grown in peat was generally much lower than that of those chilled and incubated twice, particularly with seeds collected from 30 June onwards (Table 8.16). Drying for three days tended to increase the proportion of seeds germinating after only one period of chilling and incubation. This effect was most pronounced with seeds shed on 25 and 30 June, whilst the opposite effect was shown by the few seeds not shed until 2 September.

Drying increased the number of seeds shed per plant on both 25 and 30 June. No seed was released at all from undried plants on 25 June, despite the fact that a large number of pods were dehiscent at that date (Table 8.15). Drying these plants for three days increased the total number of seeds shed 6-fold compared with drying for 24 hours only. Drying was less important in stimulating seed shedding on this date than at later assessments, although the number of seeds shed during cutting and 'threshing' on 30 June was still only 79% of the total shed after 24 hours of drying, and 58% of the overall total shed after 72 hours (Table 8.16).

The total number of seeds shed from standing plants on 13 and 24 July was slightly greater than the number extracted by cutting and threshing plants on 30 June (196 seeds per plant compared with 161, Table 8.16). This first total added to the total extracted from 3 days of drying plants on 31 July was 273.1, almost exactly the same as the cumulative total extracted after 3 days drying on 30 June (278.1). The mean of 42.5 seeds per plant

Table 8.16. The effect of air drying at ambient temperature on the number and viability of *Rhinanthus minor* seeds shed at various dates during 1992 and on the viability of seeds at various stages of maturity on 15 and 25 June. Values for seeds shed plant^{-1} are the cumulative means ±s.e. (n=10) for each stage of drying.

Date of harvest	Germination conditions	Drying period (hours)		
		0	24	72
15 June				
Germination (%):-				
Dehiscent seeds	Chill/incubated	84	-	-
Ripe seeds	" "	76	-	0
Ripening seeds	Chill/incubated	51	-	13
	Peat/ambient	52	-	42
Developing seeds	Chill/incubate	26	-	2
	Peat/ambient	-	-	0
25 June				
Seeds shed /plant		0	3.4 ±2.97	20.6 ±13.97
Germination (%):-				
Ripe seeds	Chill/incubate x 1	7	-	28
	Chill/incubate x 2	97	-	95
	Peat/ambient	45	-	44
Ripening seeds	Chill/incubate x 1	12	-	24
	Chill/incubate x 2	55	-	96
	Peat/ambient	50	-	43
30 June				
Seeds shed/plant		161.0 ±14.01	204.5 ±54.17	278.1 ±59.84
remaining unshed		-	-	42.5 ±13.48
Germination (%):-	Chill/incubate x 1	28	17	80
	Chill/incubate x 2	100	98	98
	Peat/ambient	40	44	70
13 July				
Seeds shed/plant(1)		16.4 ±3.82	-	-
Germination (%):-	Chill/incubate x 1	14	-	-
	Chill/incubate x 2	93	-	-
	Peat/ambient	15	-	-
24 July				
Seeds shed/plant(1)		179.7 ±16.34	-	-
Germination (%):-	Chill/incubate x 1	47	-	-
	Chill/incubate x 2	99	-	-
	Peat/ambient	16	-	-
31 July				
Seeds shed/plant		73.5 ±10.43	75.1 ±10.58	77.0 ±11.04
remaining unshed		-	-	0.0

(Table contd.)

Table 8.16 (contd.)

Date of harvest	Germination conditions	Drying period (hours) 0	24	72
31 July (contd.)				
Germination (%):-	Chill/incubate x 1	39	40	45
	Chill/incubate x 2	95	87	90
	Peat/ambient	21	-	-
2 September				
Seeds shed/plant		5.6 ±2.79	9.3 ±4.10	10.2 ±4.36
remaining unshed				0.0
Germination (%):-	Chill/incubate x 1	96	94	30
	Chill/incubate x 2	96	94	80
	Peat/ambient	4	-	-

(1) Seed shed with light flicking/brushing on these dates; for other dates, numbers refer to those shed during cutting and 'threshing' - see text

remaining unshed on 30 June can easily be accounted for by the error limits about each of the means involved. No seeds remained on plants harvested on 31 July after 3 days drying and it seems unlikely that any new seeds were produced between this date and 2 September, since all pods were recorded as dehiscent from 13 July onwards (Table 8.15).

These figures suggest no advantage, in terms of the number and viability of *R. minor* seeds shed, of harvesting after the end of June, as long as the crop is dried and disturbed for at least 3 days, i.e. made into hay. Cutting and removing vegetation on the same day would result in a reduction of about 36%. Wilting for only 24 hours (common practice in silage making) would incur a reduction in potential seed return of more than 25% compared with hay making, and making hay just five days earlier (25 June) would have reduced the potential seed return by over 90%.

Senecio aquaticus

This species flowered much later than *R. minor*, and no plants carrying ripe seeds were found until 24 July (Table 8.17). On 31 July, 12% of potential inflorescences were yet to flower, with less than 25% of flowering sites bearing ripe seeds. Reproductive development progressed quite rapidly during August and 85% of heads had shed or were shedding seed by 2 September. Nevertheless, even at this date 5% of inflorescence sites were either still flowering or were yet to produce flowers (Table 8.17).

Chilling had little effect on germination of *S. aquaticus* seeds, and those shed from 24 July onwards showed high rates of viability when incubated (Table 8.18). Germination was fairly rapid under these conditions, with the time taken to reach 50% of maximal germination (t_{50}) typically 10-16 days. However, germination of seeds sown into peat and stored under ambient conditions was very much more protracted, with t_{50} values ranging between 45 and 247 days, i.e. many seeds did not germinate before the spring. As with *R. minor*, the final germination percentages were generally lower in peat than under incubator conditions (by about 48%).

Table 8.17. Mean stage of reproductive development of *Senecio aquaticus* plants on six dates between 25 June and 2 September 1992. Figures are the total number of inflorescences within each category recorded on ten plants on each occasion, expressed as a percentage of the overall total. See text for definition of categories.

	Stage of development (% of inflorescences)				
Date	Pre-flowering	Flowering	Seeds ripening	Seeds ripe	Shedding seeds
25 June	88	12	<1	0	0
30 June	43	42	15	0	0
13 July	43	36	21	0	0
24 July	24	24	44	8	<1
31 July	12	13	42	24	8
2 September	3	2	5	5	85

Air drying for 72 hours induced some *S. aquaticus* plants harvested on 30 June to shed seed, but very few of these seeds germinated (Table 8.18). No seed was shed without drying for less than 72 hours, either on this date or on 13 July, and only 40% of the seeds shed on the latter date germinated with incubation (17% in peat). Only a small number of seeds were shed from standing plants on 24 July (26.1 ±23.35 per plant), although the viability of these seeds was high (100% when incubated without chilling, 72% in peat).

Drying had a very marked effect on seed shedding on 31 July, with drying for 24 hours increasing the number shed more than four-fold. Drying for 72 hours caused the

Table 8.18. The effect of air drying at ambient temperature on the number and viability of *Senecio aquaticus* seeds shed at various dates during 1992. Values for seeds shed per plant are cumulative means ±s.e. (n=10) for each stage of drying.

	Germination	Drying period (hours)		
Date of harvest	conditions	0	24	72
30 June				
Seeds shed/plant		0	0	269.5 ±125.20
Germination (%):-	Chill/incubated	-	-	10
	Incubated only	-	-	6
	Peat/ambient	-	-	0
13 July				
Seeds shed/plant		0	0	12.1 ±0.18
Germination (%):-	Chill/incubated	-	-	38
	Incubated only	-	-	42
	Peat/ambient	-	-	17
24 July				
Seeds shed/plant(1)		26.1 ±23.35	-	-
Germination (%):-	Chill/incubated	96	-	-
	Incubated only	100	-	-
	Peat/ambient	72	-	-
31 July				
Seeds shed/plant		238.0 ±134.01	1083.0 ±397.00	1733.3 ±416.65
remaining unshed				106.6 ±42.93
Germination (%):-	Chill/incubated	99	93	81
	Incubated only	93	81	83
	Peat/ambient	47	15	17
2 September				
Seeds shed/plant		257.1 ±35.00	349.5 ±53.69	378.0 ±63.43
remaining unshed				14.7 ±7.02
Germination (%):-	Chill/incubated	78	91	59
	Incubated only	71	93	78
	Peat/ambient	45	60	-

(1) Seeds shed with light flicking/brushing on this date; for other dates, numbers refer to those shed during cutting and 'threshing' - see text

release of a further 650 seeds per plant, a 60% increase compared with drying for 24 hours. A comparatively small number of seeds remained on plants harvested on this date after a full three days drying (107 per plant compared with a cumulative total shed of 1733). This was a much smaller proportion than the ratio of inflorescences bearing unripe:ripe seeds (see Table 8.17), yet the viability of the shed seeds was high. Nevertheless, there was some indication that seeds shed after 3 days drying were less viable than those shed at cutting, probably reflecting a higher proportion of immature seeds in the former.

The number of seeds shed at each stage of drying on 2 September was much lower than from plants harvested on 31 July, suggesting that a large number had been shed during the intervening period. The effect of drying was less marked than at the previous assessment, although drying for 24 and for 72 hours still increased the number of seeds shed by 36% and 47% respectively compared with no drying. A few seeds remained unshed after 72 hours of drying (mean = 14.7 per plant). The viability of seeds shed after drying for 24 hours was markedly greater than that of those shed either without drying or after drying for 72 hours (Table 8.18), although the reason for this was not clear.

Thalictrum flavum

This species did no produce ripe seeds until 24 July. Even on this date, only 3% of florets bore ripe or dehiscent fruits with seeds at a very immature stage of development on 90% of florets (Table 8.19). On 2 September, only 50% of florets bore ripe or shedding seeds. Some seeds were shed from plants harvested on 30 June after drying for 72 hours, but these were very immature and only one germinating seed was recorded (Table 8.20). No seed was shed from plants harvested on 13 July, either without drying nor after drying for 72 hours. However, germination tests on seeds forcibly extracted from dried and undried

Table 8.19. Mean stage of reproductive development of *Thalictrum flavum* plants on five dates between 30 June and 2 September 1992. Figures are the total number of florets within each category recorded on ten plants on each occasion, expressed as a percentage of the overall total. See text for definition of categories.

	Stage of development (% of florets)				
Date	Flowering	Seeds developing	Seeds ripening	Seeds ripe	Dehiscent
30 June	49	45	6	0	0
13 July	10	80	10	0	0
24 July	2	90	5	3	<1
31 July	0	26	65	6	3
2 September	0	0	50	11	39

plants showed that about half were viable under incubation conditions, with no consistent effect of chilling on viability. Germination was very poor in peat at 10% and 15% for undried and dried seeds respectively (Table 8.20).

Table 8.20. The effect of air drying at ambient temperature on the number and viability of *Thalictrum flavum* seeds shed on various dates during 1992. Values for seeds shed per plant are cumulative means ±s.e. (n=10) for each stage of drying.

Date of harvest	Germination conditions	Drying period (hours)		
		0	24	72
30 June				
Seeds shed/plant		0	0	20.4 ±8.42
Germination (%)(1) :-	Chill/incubated			0
	Incubated only	-	-	0
	Peat/ambient	-	-	1
13 July				
Seeds shed/plant		0	-	0
Germination (%)(2) :-	Chill/incubated	40	-	67
	Incubated only	70	-	35
	Peat/ambient	10	-	15
24 July				
Seeds shed/plant(3)		7.6 ±3.04	-	-
Germination (%)(1):-	Peat/ambient	24	-	-
31 July				
Seeds shed/plant		0.8 ±0.47	1.8 ±0.93	3.2 ±1.34
remaining unshed		-	-	6.5 ±2.88
Germination (%)(1):-	Peat/ambient	11	0	7
2 September				
Seeds shed/plant		1.1 ±0.72	2.1 ±1.05	7.2 ±2.73
remaining unshed		-	-	3.6 ±2.01
Germination (%)(1):-	Peat/ambient	11	40	61

Germination tests performed on shed seeds(1) or on ripening, unshed seeds(2)
(3) Seeds shed with light flicking/brushing on this date; for other dates, numbers refer to those shed during cutting and 'threshing' - see text

The number of seeds shed and remaining unshed per plant was very small at each assessment and did not allow germination tests under the full range of conditions. Moreover, many whole inflorescences appeared to have fallen from plants between 31 July and 2 September, and it was not possible to tell how many individual seeds had been shed from these, or what the fate of seeds still attached to these detached segments of panicle might have been. As with *R. minor* and *S. aquaticus*, drying increased cumulatively the number of seeds shed, but with *T. flavum* the effect was apparently greater with plants harvested on 2 September than those taken on 31 July (Table 8.20). Error estimates were high about most of the mean values for *T. flavum*, suggesting that, for this species in particular, a sample size at each assessment of greater than 10 plants would have been desirable.

8.4. DISCUSSION

SEED RAIN AND BOTANICAL COMPOSITION

Only 51 (70%) of the total number of species for which 'seed rain' was recorded in this study had produced any seeds by mid-July, i.e. after the date (8 July) when hay making is allowed in the most stringent Tier of the ESA regulations (Her Majesty's Stationary Office, 1992). Ten species (14% of the total) had still produced no seed by the second week in August. On this basis alone, it is clear that cutting in July or even in August will not allow the maximum number of species to set seed in these meadows.

A bi-tonic response to cutting date

The methodology used in these studies did not give a full record of the total number of seeds shed (true 'seed rain'), nor of the survival rate of seedlings originating from seeds shed before cutting. The 'seed rain' data obtained represent the potential number of seedlings generated by harvesting at various dates and no attempt was made to measure germination or seedling survival in the field following harvesting. Most species and species groups showed a 'humped' (bitonic) response to cutting date in the number of seedlings recorded, with maximal numbers after harvesting in July or August and lower numbers after harvesting in September. This response can be explained by an increase in the number of seeds shed before cutting with lateness of harvest date and a corresponding increase in the rate of loss of viable seeds beneath the vegetation canopy prior to cutting. These losses will have occurred by seed predation and/or by seedling mortality. As harvesting is delayed, a maximum in the total number of seedlings ultimately recorded following harvest will occur when the rate of loss of seeds/seedlings before cutting matches the rate of increase with time in the total number of viable seeds shed. In these cases, later cutting will result in fewer seedlings as the rate of loss overtakes the rate of increase in seed shedding. The number of seedlings present at each harvest date and subsequently germinating in sample dishes can therefore be seen as 'net seed rain' and the pattern that a particular species shows will be a function of: (a) the phenology of its seed setting and dehiscence; (b) the ease with which its seeds can germinate beneath a closed canopy; (c) the susceptibility of those seeds to predation either before or after germination; and (d) the ability of seedlings to survive competition and shading beneath a canopy until harvesting.

The bitonic response was most marked with the seed bank Type I group of species collectively, i.e. those which have no seed dormancy (Thompson and Grime, 1979), and with species which regenerate primarily by seedling regeneration in vegetation gaps in the autumn ('S' species) - most of the species in each of these groups were common to both (Grime *et al.*, 1988). Furthermore, there was a clear interaction among species between seed bank type, responsiveness to fertility (as indicated by response to fertilizer N application in prevoius work) and pattern of response to cutting date. The humped response to cutting date was most marked among seed bank Type I species on previously fertilized plots, where it was attributable very largely to the N-positive species within this group. These species occupied both a high proportion of the vegetation and contributed a high proportion of the total net seed rain on these plots (Figure 8.1). Type III species showed a somewhat similar response on previously fertilized plots, although the peak in net seed rain, attributable entirely to the N-positive species, occurred later, i.e. with August cutting, as opposed to Type I species which peaked with cutting in July. N-negative species of each seed bank type tended to produce peak net seed rain with September harvesting.

The influence of germination and dormancy behaviour on patterns of net seed rain

A high proportion of seed bank Type I and 'S' species, particularly N-positive species, were relatively early-flowering and most were grasses. Nevertheless, a monotonic increase in net seed rain (i.e. the absence of a 'hump') did not simply reflect lateness of flowering and seed set. Several of the species for which the maximum net seed rain occurred with September cutting were relatively early-flowering, for example *Ranunculus repens* and, particularly, *Cardamine pratensis.* The species which showed this response most consistently were those which form a persistent seed bank i.e. the seed bank Type IV group (Thompson and Grime, 1979), and the 'Bs' group, those which commonly regenerate from a persistent seed bank (Grime *et al.*, 1988). The latter group was composed of seed bank Types III and IV species, but the Type III group on its own showed a less clear-cut response to cutting date. Many species, particularly those which form a persistent seed bank, display characteristics which increase their chances of burial, including delayed germination (Grime, 1979; Bryant, 1985; Grime *et al.*, 1988). These same characteristics would also tend to prevent inopportune germination of seeds resting at the soil surface beneath a closed canopy prior to cutting. For example, *Ranunculus repens* requires a period of incubation in warm, moist conditions for maturation of the embryo (Grime, 1979) and its germination is also improved by a period of dry storage before imbibition (Grime *et al.*, 1981). Most legumes, including *Trifolium pratense*, have a hard seed coat that inhibits germination. This effect can be alleviated by scarification, but Grime *et al.* (1988) review data which show that this form of dormancy can also be broken by certain combinations of changing water conditions and fluctuating temperature, pointing to it as a mechanism for gap detection (Thompson *et al.*, 1977). *Agrostis capillaris*, *Holcus lanatus* and *Festuca rubra* are examples of species in which dormancy can be *induced* by a period of exposure to far-red wavelength light of an intensity similar to that filtering through an enclosed canopy (Williams, 1983). In these cases, dormancy persists for some time after transference to favourable conditions. Hilton *et al.*, (1984) showed that dormancy in *Poa trivialis* could be *enforced* by exposure to light of a high far-red:red ratio, with maximal germination occurring upon transference to full light. However, the same work showed that *P. trivialis* seeds collected from enclosed grassland habitats were less sensitive to differences in light quality than those from arable fields. Fenner (1978) showed that the germination of a range of dicot species, including *Rumex acetosa*, could be inhibited by shading from *F.rubra*, particularly under tall turf of this species (germination of *R. acetosa* was reduced by 58% in these conditions). Of the species referred to in this paragraph, *A. capillaris*, *R. repens*, *T. pratense* and *R. acetosa* all showed a clearly monotonic increase in net seed rain with lateness of cutting date, although *H. lanatus, F. rubra* and *P. trivialis* did not.

Delayed germination in *T. pratense* was also evident in the high proportion of those seedlings recorded following harvesting in September which did not germinate until the following spring (76%), compared with harvesting in July (41%) or August (40%). *Filipendula ulmaria* showed a similar effect which was accentuated by the lateness of seed set. No 'seed rain' was recorded for this species before the August harvest, and 53% of the seedlings ultimately produced with August cutting did not germinate until spring. Very few (10%) of the *F. ulmaria* seedlings recorded after September harvesting germinated before the following spring-early summer.

Behaviour of Centaurea nigra *and* Filipendula ulmaria

Centaurea nigra, a comparatively late-flowering species of which the seed bank behaviour is uncertain (Grime *et al.* 1988), was one which showed a clearly monotonic increase in net seed rain with lateness of cutting date. Significant numbers of *C. nigra* seedlings were recorded after harvesting in July, although the increase in numbers with cutting date was skewed further towards late cutting on unfertilized plots than on previously fertilized plots. These results and those for *F. ulmaria* contrast significantly with those of Smith and Jones (1991), who found no ripe seed of either species in studies in the Pennine Dales which continued up until 21 August. These anomalies could be due to geographical differences. However, the data reported in this chapter are consistent with dates given by Grime *et al.* (1988) which were based on surveys in the Sheffield region (i.e. not very distant from the Pennine Dales) and which encompassed both upland and lowland areas. As noted in Chapter 2, a delay in flowering in both *C. nigra* and *F. ulmaria* could be caused by the grazing in early spring which is common practice in the Pennine Dales (Smith and Jones, 1991; Smith and Rushton, 1994).

Seed rain during May-September regrowth

The substantial period of regrowth between harvesting in May and the start of grazing in September allowed many species to set seed which had not done so during primary growth. For most species, the total number of seedlings recorded from both periods together did not equal the number produced by primary growth harvested at later cutting dates alone.

However, the balance of species amongst seedlings resulting from this regrowth period was markedly different to that produced during primary growth harvested at later dates. Those favoured were: dicots compared to grasses; species which normally regenerate vegetatively, compared to those which do so by recently shed seeds; and seed bank Type IV species. These three groups shared a substantial number of species in common and it is not clear which particular characteristic was most influential. Rabotnov (1969) noted that a change in Russian meadows from a single hay cut to a two-cut system involving an earlier first cut had led to selection for those species able to set seed between these two cuts. However, Rabotnov gave no indication of the extent to which this change was directly attributable to increased regeneration from freshly shed seeds of these species or to a more indirect process involving changes to the composition of the persistent seed bank. The data presented in this chapter suggest that vegetative reproduction, combined with regeneration from the seed bank, would play a significant role in any long-term trends in vegetation dynamics resulting from a comparable change in management of meadows at Tadham Moor.

Vegetation composition in relation to cutting date

In terms of abundance in the vegetation at the end of the experiment, species with the most persistent seed bank (Type IV species, Thompson and Grime, 1979) and those which rely on vegetative reproduction for regeneration were the least susceptible to variations in cutting date. It was expected that, for species which regenerate exclusively by seed ('S' species), there would be a close correlation between patterns of seed rain and subsequent changes in vegetation composition. This group did show a significant correlation on N_0 plots and overall , though not on N_{200} plots alone. However, the relationship was no closer than that shown by species which regenerate vegetatively ('V' species), nor than that shown by species which form a long-term seed bank (these last two groups shared many species in common). Seed rain of the 'V' species increased linearly with lateness of cutting date, as did the abundance of the group in the vegetation of N_0 plots in 1993, although only the seed rain response was statistically significant. The correlation within this species group may well have been coincidental. A small increase in the abundance of 'V' species with lateness of cutting could be attributed to the greater build up of carbohydrate reserves in above- and below-ground organs allowed by the longer period of primary growth, as noted by Oomes and Altena (1987).

The trend in vegetation abundance in 1993 shown by seed bank Type I species on previously fertilized plots closely mirrored those of *H. lanatus* abundance where this species was co-dominant with *Lolium perenne* at the start of the experiment. By the end of the experiment, *H. lanatus* dominance showed a very strong negative association with species diversity in these plots, where it had increased both with early and with late cutting (May or September), reflecting the flexibility in regenerative strategy of this species (Grime *et al.*, 1988). This trend was also consistent with the species' response to defoliation, in that when *H. lanatus* is cut in late May-early June flowering is severely reduced and cutting is followed by a lush and competitive vegetative growth (Watt and Haggar, 1980). The same authors also concluded that regeneration from seed was much more important than vegetative spread with *H. lanatus* plants that are left uncut, whilst Grime *et al.*, (1988) confirm that regeneration by seed is of prime importance except where seed set is prevented.

Cutting in August resulted in the greatest net seed rain of *H. lanatus* of all four cutting dates but the lowest *H. lanatus* abundance in the vegetation. This implies that with this cutting date, a very large number of *H. lanatus* seeds either germinated but failed to produce surviving seedlings or became incorporated into the seed bank. In the long term, where the aim is to restore diversity to species-impoverished meadows, the influence of cutting date on the contribution to the soil seed bank of competitive species such as *H. lanatus* may be at least as significant as the short term effects on vegetation composition. As noted in Chapter 6, the number of seeds of *H. lanatus* in the top 5 cm of soil in March 1991 was 60% higher beneath previously fertilized plots compared with unfertilized soil. In another experiment at the same site (Mountford *et al.*, 1993b), soil disturbance increased the proportion of *H. lanatus* in the vegetation, presumably through seedling recruitment from the seed bank. In the work reported here, species diversity on previously fertilized plots was highest after two years of harvesting in August. Nevertheless, cutting in August allowed fertility-demanding, transient seed bank species such as *L. perenne, R. acetosa* and *Bromus* spp., to produce a large number of seeds, resulting in the dominance of this group on previously fertilized plots cut on this date. It is therefore difficult to predict whether or not occasional cutting in August would be beneficial during a longer phase of restoration of species diversity. On the other hand, it is clear that cutting in August or later in unfertilzed meadows allows a higher proportion of seed to be shed by those species which contribute to the long-term seed bank, most of which are dicots. By the same token, cutting consistently in July is likely to lead to an increased dominance of grasses and a depletion of the seed bank, both in the total number of seeds and in the diversity of species represented.

TIME OF SHEDDING IN RELATION TO HAY-MAKING OPERATIONS

The high proportion of total net seed rain which occurred at or after cutting, even with cutting in September, reflects both the length of time ripe seeds are held on the plant in most species and the extent of mortality amongst those seeds which are shed before cutting. This second factor was apparently high in *Bromus racemosus* for example, since this species, unlike others, showed a significant decline with lateness of cutting date in the proportion of net seed rain which originated from seed shed before cutting.

No opportunity occurred to measure seed rain during the various phases of mechanized hay- making until the beginning of August in 1991. About half the total viable seeds of all species shed during cutting, tedding and turning, and rowing and baling at this harvest were shed during tedding and turning. Moreover, 37% of the total number of grass seeds that were shed fell during cutting, compared with only 26% of dicots. No seeds of *Cyperaceae* were shed until the crop was tedded and turned, but more than half of the *Juncaceae* seeds were shed during cutting. These results indicate that, even with harvesting as late as August, the combination of crop drying and disturbance which occurs during hay-making is important not only in ensuring maximal shedding of seeds but in determining the balance of species in the seed rain.

The studies carried out on individual plants of *Rhinanthus minor, Senecio aquaticus* and *Thalictrum flavum* illustrated the importance of drying in stimulating seed shedding. No *R. minor* seed was shed on 25 June without drying, and even on 30 June air drying for three days almost doubled the amount of *R. minor* seed shed. As late as 24 July, drying for thee days was required to induce *Senecio aquaticus* to shed its seed, and seeds shed in response to drying before that date were of very low viability. Even by 31 July, drying for three days increased the number of *S. aquaticus* seeds shed more than seven-fold compared with the number shed with the same amount of disturbance but without drying.

ESA PRESCRIPTIONS

It remains debateable whether ESA prescriptions need to include a requirement for cutting in August once in a specified number of years, since, with an 8 July requirement, hay making will sometimes be delayed until August in difficult years. In the seven harvest years that the Tadham Moor Project was run (1986-1992), cutting was delayed until early August in three (1988, 1991,1992). However, the delay in at least one of the last two years was partly due to difficulties with contractors. These operators might have been able to make hay sooner (as was done in the experiment reported here in the same year), although to have done so might have required a higher level of committment in terms of machinery and man-power than is common in these meadows. In the Pennine Dales ESA, where farmers are required to cut in August at least once in five years, it is evidently felt worthwhile to insure against the continuance of the trend towards earlier finish dates for hay-making attributed by Smith and Jones (1991) to improved hay making technology.

8.5 CONCLUSIONS

Even with cutting after 8 July (in accordance with ESA prescriptions) a significant number of species (at least 30% of the potential number) will not shed viable seeds. A high proportion of the species able to shed seeds with harvesting in July will be of species which only form a transient seed bank, compared with those which normally contribute significantly to the long-term seed bank.

In the short term, cutting in either May or September will reduce species richness and diversity compared with cutting in July or August. Cutting later than July in previously fertilized meadows runs the risk of perpetuating the dominance of *H. lanatus*, either rapidly by cutting as late as September, or in the long term by increasing the contribution of this species to the seed bank.

Continual cutting in July in unfertilized meadows, compared with later cutting at least occasionally, is likely to increase the dominance of grasses and reduce species diversity through a loss of species from the seed bank.

Hay-making operations are important in stimulating seed shedding and ensuring an optimum balance of species amongst the seeds shed compared with harvesting without drying and with minimal disturbance, even when hay is made as late as August.

8.6 SUMMARY

A randomized block experiment examined the effects of cutting in late May, early July, early August or early September on 'seed rain' and botanical composition. Treatments were imposed in two consecutive years (1991-92) on meadows which had either received 200 kg fertlizer N ha^{-1} with low rates of P and K each year for the preceeding five years, compared with meadows which had never received inorganic fertilizers. Seed rain was measured indirectly in 1991 by counting the number of seedlings emerging from compost-filled dishes set into the ground in spring and removed after harvest of the vegetation. A similar technique was used to record the number of viable seeds shed during various phases of mechanized hay making in August. Additional studies were carried out on individual plants of *Rhinanthus minor*, *Senecio aquaticus* and *Thalictrum flavum* to record the number and viability of seeds produced on between 15 June and 2 September 1992 and to study the effect of air drying at ambient temperature on seed shedding.

Most species and species groups showed a peak in seedling numbers with harvesting in July or August, followed by lower numbers in September. This 'humped' pattern of response was particularly noticeable with species which form only a transient seed bank, and particularly also among those which had been previously indentified as reacting positively to applied N. Species which form long-term seed banks and/or which regenerate primarily by vegetative means did not show this pattern, with their numbers tending to increase progressively with lateness of cutting. The composition of the vegetation on fertilized plots was strongly influenced by differences in abundance of *H. lanatus* which dominated these plots. *H. lanatus* dominance was increased by harvesting either in May or in September and was lowest with cutting in August.

Species diversity was greatest after two years of cutting in July or August on both previously fertilized and unfertilized plots. However, it was concluded that cutting after July in previously fertilized meadows might hinder the recovery of species diversity in the long term by increasing the contribution of *H. lanatus* to the seed bank. In unfertilized vegetation, later harvesting, at least occasionally, is important to maintain diversity in the seed bank, particularly of dicot species.

Hay-making, as opposed to cutting and harvesting with minimal disturbance, was shown to be important both in stimulating maximal seed shedding and in ensuring an optimal balance of species among the seeds shed, even with cutting as late as August.

CHAPTER 9

THE EFFECTS OF AGRICULTURAL MANAGEMENT ON THE ECOLOGY AND PRODUCTIVITY OF SPECIES-RICH HAY MEADOWS ON THE SOMERSET LEVELS - SYNTHESIS AND CONCLUSIONS

9.1. INTRODUCTION

The research described in this thesis is concerned with the three main agricultural practices affecting the ecology of species-rich hay meadows on the Somerset peat moors and which form the basis of management agreements within Sites of Special Scientific Interest (SSSIs) there and the Environmentally Sensitive Area (ESA) - the use of inorganic fertilizers, water table control, and hay cutting date. It addresses the influence these practices have on the relationship between the plant ecology, soil nitrogen (N) cycling and the productivity of these meadows (see Chapter 1, Figure 1.5). A summary of the regulations concerning management practices, the gaps in knowledge and the areas of doubt which prompted the work described in the thesis, was given in Chapter 1. This final chapter summarises the main conclusions to be drawn from the studies described in the thesis and puts these results into a wider ecological context. The agronomic implications for the management of hay meadows of high wildlife value are also discussed.

A final section outlines the main conclusions to be drawn in relation to the management of these and similar meadows maintained primarily for their wildlife value.

9.2. THE USE OF INORGANIC FERTILIZERS

EFFECTS OF FERTILIZERS ON PLANT ECOLOGY

Above-ground vegetation response

Results presented in Chapters 3 and 5 showed that both P and K, particularly P, were more influential than N in determining both biomass production and botanical change. Dramatic changes in vegetation composition and large increases in biomass production were brought about by applying high rates of all three elements. Applying P and K without N appeared to stimulate mineralization of organic N and increased N uptake by plants, and resulted in both a significant increase in biomass production and significant botanical change.

When high rates of both N and P were applied under cutting management only, ie. with no aftermath grazing, the vegetation became dominated by *Holcus lanatus*, *Rumex acetosa* and, to a lesser extent, *Lolium perenne*. The number of species declined to less than two-thirds of that initially recorded on these plots. On plots where aftermath growth was grazed, fertilizer N with base rates of P and K led to *H. lanatus* dominance at first, but *L. perenne* subsequently superceded *H. lanatus*. Comparison of results from the two experiments (aftermath grazed - the LS experiment, and cut only - the SP experiment) suggested that the marked changes in botanical composition which occurred over time on unfertilized plots in the SP experiment were attributable to the cessation of aftermath grazing, probably due to the combined effects of depletion of soil mineral reserves and a reduction in the amount of disturbance and gap creation.

The results showed that even low levels of inorganic fertilizer use will lead to a significant reduction in species diversity after only a few years. This suggests that only Tier 3 regulations within the ESA scheme, which require both aftermath grazing and abstinence from fertilizer use, will be effective in maintaining species diversity within these and similar meadows.

The seed bank in relation to changes in the above-ground vegetation

After five years of fertilizer application, fertilizers had caused a four-fold shift in the balance of species in the seed bank towards those which were previously identified as responding positively to N in terms of vegetation cover, with a smaller concomitant shift from Type IV species to Type III, i.e. from long-term persistent species to short-term persistent (Thompson and Grime, 1979).

Type I species, i.e. those which normally germinate soon after shedding (Thompson and Grime, 1979) accounted for a disproportionately large proportion of total ground cover relative to the number of species involved, compared with species of the remaining seed bank types (Types II-IV). A substantial number of seeds of this same group had survived in the soil until March. This was probably due to the very rapid rise in water table which had occurred during the previous autumn, resulting in a quick transition from very dry to waterlogged soil, with both conditions inhibiting germination.

The effects of fertilizer application on both vegetation and seed bank composition were most clear-cut within theType I group, particularly when species were further sub-divided by previously observed fertilizer N-response. This group showed the closest correspondence between vegetation cover and seed bank abundance on a between-plot scale, whereas the Type IV group showed the least. However, as separate groups, *Juncaceae* and *Cyperaceae* (most of which were Type IV species) showed a close correspondence between vegetation cover and seed bank abundance compared with grasses and dicots. This was attributable to marked variation on a between-plot scale in the specific hydrologic conditions for which these species show a stronger preference than others.

These results implied that changes in seed bank composition could have the effect of prolonging the dominance of certain species in the vegetation after fertilizer use has been discontinued. Strategies to restore species diversity in these situations should therefore aim both at reducing fertility and at encouraging species which have declined to set and shed seed.

AGRICULTURAL PRODUCTION RESPONSE TO FERTILIZERS

Data presented in Chapter 3 showed that, although P and K availability limited response to applied N, the productivity without fertilizers was relatively high compared with similarly species-rich vegetation on other soil types, although not compared with less species-rich permanent pastures (Hopkins *et al.*, 1990). This suggests that supplies of P and K to the soil, presumably from seepage and occasional flood water and maintained to some extent by aftermath grazing, are adequate to support a moderate level of mineralization and plant utilization of organic N resources. Small additions of inorganic P and K (i.e. replacement rates) appeared to allow further utilization of inorganic N present and may have stimulated further N mineralization, resulting in a significant yield response. However, full yield response to applied N was realised only when high rates of of both P and K were applied.

These results also showed that fertilizer response was not restricted by the species-richness of the vegetation. Provided that adequate rates of P and K were applied, response to fertilizer N application was equivalent to the average recorded in a wide range of less species-rich grassland nationally (Hopkins *et al.*, 1990). This means that existing response data can be used to assess production foregone by farmers in adhering to SSSI and ESA restrictions on fertilizer use in these meadows.

THE EFFECTS OF FERTILIZER N APPLICATION ON LOSSES OF N FROM THE SOIL

Data from Chapter 4 showed that the soils at Tadham Moor were particularly susceptible to leaching of applied N compared with those elsewhere (Barraclough and Jarvis, 1989; Tyson *et al.*, 1993). This can be attributed to a combination of high and widely fluctuatiing water tables and apparently rapid conversion of ammonium N to nitrate (nitrification). These same factors, coupled with the high carbon content of the soils, produced high denitrification rates which could lead to large losses of N from the soil if high water tables are maintained throughout the summer when soil temperatures are high. Where ambient water table levels are allowed, restricting the fertilizer rate to 75 kg N ha^{-1} year^{-1} (the maximum fertilizer N level permitted within the ESA scheme) appears to be adequate to avoid significant leaching risk, but the results suggested that little or no inorganic fertilizer should be applied if water tables are to be maintained at artificially high levels throughout the summer.

Taking an earlier cut for hay or silage could increase N efficiency and reduce losses of mineral N into the environment, but early cutting is unacceptable in these meadows due to it's deleterious effect on the breeding success of wading birds (Green, 1986).

9.3. WATER TABLE MANAGEMENT

EFFECTS OF VARIATIONS IN WATER TABLE DEPTH ON PRODUCTIVITY

Data on the effects of water table management on productivity were less clear-cut than those for fertilizer use and cutting date, since no experiment was designed specifically to study this aspect. Instead, studies relied upon correlation and regression analysis of data from the LS experiment related to water table measurements made weekly on each plot between 1986 and 1990. Within the range of variation encountered at the site during this period, neither hay yield nor aftermath cattle production were significantly correlated with water table depth on unfertilized plots. Nor could variations in hay yield response to N (across replicates and between years) be related to variations in water table. However, cattle production response to fertilizer N from aftermath grazing showed a significant negative relationship with water table depth, largely due to very low productivity from unfertilized plots in the wet year of 1988.

9.4. VARIATIONS IN HAY CUTTING DATE

EFFECTS ON SEED RAIN AND BOTANICAL COMPOSITION

Even with cutting on 17 July (i.e. after the ESA prescribed date), a significant number of species (at least 30% of the potential number) did not shed viable seeds. A high proportion of the seed shed with harvesting in July was of species which only form a transient seed bank, compared with those which normally contribute a large proportion of the long-term seed bank.

Most species and species groups showed a peak in seedling numbers with harvesting in July or August, followed by lower numbers in September. This 'humped' pattern of response was particularly noticeable with species which form only a transient seed bank, and particularly also among those which had been previously indentified as reacting positively to applied N. Species which form long-term seed banks and/or which regenerate primarily by vegetative spread did not show this pattern, with their numbers tending to increase progressively with lateness of cutting.

In the short term, cutting in July or August led to higher species richness and diversity than cutting in either late May or early September. However, cutting later than July in previously fertilized meadows might hinder the recovery of species diversity in the long term by perpetuating or increasing the dominance of *H. lanatus*, either rapidly by cutting as late as September, or in the long term by increasing the contribution of this species to the seed bank.

Hay-making operations are important in stimulating seed shedding and ensuring an optimum balance of species amongst the seeds shed compared with harvesting without drying and with minimal disturbance, even when hay is made as late as August. Furthermore, individual studies of the phenology and germination behaviour of three contrasting species, *Rhinanthus minor*, *Senecio aquaticus* and *Thalictrum flavum*, showed some clear interactions between harvest date and the length of drying period and emphasised the importance of hay drying in stimulating seed shedding.

THE INFLUENCE OF CUTTING DATE ON AGRICULTURAL PRODUCTIVITY

Previous fertilizer treatment increased metabolizable energy (ME) production only with cutting in May. DM yield increased significantly with cutting date until August, whilst ME value declined correspondingly. There was no difference in either yield or quality of herbage cut between August and September. ME output per hectare from primary growth increased very significantly between May and July, but showed no further change between cutting dates.

There was therefore no significant advantage in terms of metabolizable energy production per hectare of taking a first cut in late May as opposed to July. However, cattle fed hay harvested in July would require significant diet supplementation in order to maintain adequate individual growth rates, compared with those fed herbage harvested in May. Cutting after July not only produced even poorer quality hay but would reduce potential output from aftermath grazing. These factors would have to be taken into account if SSSI or ESA prescriptions were to include a requirement for cutting later than July as in the Pennine Dales ESA (Her Majesty's Stationery Office, 1992).

9.5. DISCUSSION

SOIL FERTILITY AND DISTURBANCE

Fertilizer application, species-richness and productivity

Many experiments studying the detrimental effects of inorganic fertilizers on botanical composition and diversity were dicussed in Chapter 2 (e.g. Willis, 1963,1989; Heddle, 1967; Williams, 1978,1984; Garstang, 1981; Vermeer and Berendse, 1983). A general finding of these experiments was that applying inorganic fertilizers, particularly N, caused a monotonic decline in species richness, either with increasing application rate or with time, or both. Nevertheless, ecological models relating species density to productivity predict a humped (sometimes referred to as 'unimodal') response (Grime, 1979; Huston, 1979). These models have been supported by data which show maximal species density within a fairly narrow band of productivity (as represented by maximum standing crop + litter), with lower species density at both higher and lower levels of productivity (Al-Mufti *et al.*, 1977; Moore and Keddy, 1989).

However, evidence for a humped relationship within herbaceous vegetation has been provided almost exclusively by data collected accross several different plant communities. Convincing evidence of the relationship occurring within a single plant community has yet to be produced, despite a claim by Vermeer and Berendse (1983) (see discussion in Chapter 2, section 2.5). It remains uncertain whether there are individual situations where high species-richness can be maintained or even increased in conjunction with inputs of inorganic fertilizers or farm-yard manure (FYM) sufficient to raise productivity, or circumstances where species-richness will drop when nutrient inputs are reduced. Smith (1987) argued that moderate levels of fertility achieved by FYM inputs or small applications of inorganic P are necessary to maintain both species-richness and productivity in Pennine Dales hay meadows. He also re-examined data from the Park Grass Experiment and showed that the rate of decline in species-richness on plots receiving FYM or low rates of P and K was no greater than that on unfertilized control plots. Species diversity, as measured by Shannon-Wiener indices, differed little between unfertilized plots and those receiving P and K without N.

Species-richness and productivity at Tadham Moor data in a wider context

Data from the LS experiment at Tadham Moor showed a continuous and significant decline in species-richness relative to control plots throughout both phases of the experiment (1986-1993), even at 25 kg N ha^{-1} year^{-1}, the lowest N rate applied (Tallowin *et al.*, 1995). No N was applied without P and K in the LS experiment. However, in the SP experiment, applying such low rates of N with 'replacement' rates of P and K had no effect on yield or species richness compared with similar rates of P and K alone. The decline in species-richness under the N_{25} treatment in the LS experiment can probably be attributed to the P and K which were applied with the N, rather than to the N itself.

At 24-28 species per m^2, the unfertilized vegetation at Tadham Moor is very species-rich (Mountford *et al.*, 1993a). However, it is significant that productivity without fertilizer application in these meadows is also high compared with species-rich grassland in general (compare hay yield data presented in Chapter 3 with those in Tables 2.1 and 2.2). The fact that P and K were more important than N, both in limiting biomass production (Chapter 3) and maintaining species richness (Chapter 5), can be attributed at least in part to the high levels of plant available N present during the growing season (Chapter 4). The regular flooding which occurs in winter at Tadham Moor not only maintains a high pH by importing Ca, but probably contributes small amounts of P and K in run-off from neighbouring agricutural land. This may serve to maintain levels of fertility optimum for species-richness and equivalent to small inputs of inorganic fertilizer or FYM in areas such as the Pennine Dales. Although FYM has, traditionally, been applied to meadows on the Somerset peat moors, its use will have been restricted to the less remote areas and those where access is not prevented by high water tables at the time when FYM is usually applied - late autumn or early spring.

No measurement of peak standing crop cut to ground level was made in the studies reported in this thesis, so no direct comparisons are possible with Grime's hump-backed model (Figure 2.1), nor with the data of Moore and Keddy (Figure 2.2) and of Al-Mufti *et al.* (Figure 2.4a). However, in later studies (Tallowin and Donaghy, unpublished), a mean seasonal peak in biomass of 8.5 t DM ha^{-1} was recorded from 10 quadrats cut to ground level on unfertilized areas on 27 August 1993. Oomes (1992) quotes a regression formula for conversion of data for vegetation cut to 5cm to values for ground level standing crop of: $y = 1.10x + 1.896$, where values are expressed in tonnes DM ha^{-1}. Applying this formula to the yield of 5.73 t DM ha^{-1} recorded on unfertilized plots cut in September in Experiment 3 (see Chapter 7, Table 7.1) gives a value of 8.2 t DM ha^{-1}. These values are well to the right of the peaks in species density in the models of Grime, Al-Mufti *et al.* and Moore and Keddy, suggesting that, on the basis of their productivity, the meadows at Tadham Moor should be very species-poor. This assertion is largely supported by data from hay meadows in the Netherlands (Oomes,1992), although the mean annual DM production of from 2-3 cuts per year (not to ground level) in the SP experiment (4.7 t DM ha^{-1}) did correspond with the peak of species-richness in Oomes' data (see Figure 2.3). Nevertheless, the site chosen for the SP experiment was less productive than the Tadham Moor site as a whole. At 4.7 t DM ha^{-1}, mean annual DM production in the SP experiment was no greater than the mean yield of primary growth cut for hay in July on unfertilized plots in Experiment 3 (4.72 t DM ha^{-1}), and only marginally greater than the average hay yield for the three years when hay was cut in July in the LS experiment (4.64 t ha^{-1}). If yield at hay cutting can be assumed to be 62% of the annual potential yield for 2-3 cuts, as Oomes (1992) states, then these values are equivalent to 7.6 and 7.5 t DM ha^{-1} $year^{-1}$

respectively, somewhat to the right of the peak in Oomes graph (Figure 2.3).

The foregoing discussion not only suggests that the meadows at Tadham Moor are exceptional in combining great species-richness with comparatively high productivity, but also explains the negative response in species-richness to only small increases in fertility in the LS experiment. If it is assumed that a narrow hump representing a corridor of productivity exists which allows maximal species-richness to be maintained in such vegetation, the system at Tadham Moor evidently stands at the apex of this hump. An optimum balance appears to be operating between the small nutrient inputs from rainfall, flood water and seepage and the removal of nutrients in hay each year. This balance is easily upset by only small additional inputs of fertility in the form of inorganic fertilizers. Furthermore, significant changes in hydrology which change soil chemistry and nutrient cycling are also likely to affect this balance (see later discussion).

The importance of disturbance by grazing

The management and utilization of aftermath growth by grazing appears to be an essential component of the system at Tadham Moor, not only by helping to maintain the cycling of the main plant nutrients, but also by contributing an important level of disturbance. This may well explain the apparent exceptionality of the relationship between productivity and species richness of the vegetation. Only one of the sites included by Al-Mufti *et al.* (1977) was grazed, that at which the highest species-richness was recorded, and the remaining sites were in undisturbed vegetation. It is unrealistic to expect all types of grassland to conform to this model. Several ecologists have emphasized the importance of interactions between stress, disturbance and fertility in determining species diversity and have highlighted the role of grazing in this relationship (e.g. Grime, 1973b, 1974, 1979; Grubb, 1977; Huston, 1979; Marrs, 1993).

Hay meadows at Tadham Moor and elsewhere on the Somerset Levels remain undisturbed (by human activity) during the accumulation of the hay crop, but aftermath growth is usually well utilized by grazing cattle or sheep. Data presented in Chapter 3 show high levels of animal production even on unfertilized plots. As noted in Chapter 3, the stocking rates achieved in the LS experiment by 'put-and-take' grazing of aftermath growth were probably greater than is normally achieved by continuous stocking in practice.

Plate 9.1. Cattle grazing aftermath growth at Tadham Moor.

Nevertheless, observation of neighbouring fields shows that the vegetation is normally grazed to a similar level, though often by high stocking rates for short periods rather than by continuous grazing. Data presented in Chapter 6 showed that those species which have little or no seed dormancy (seed bank Type I *sensu* Thompson and Grime, 1979) form a high proportion of the vegetation cover. Many of these species rely upon regeneration in gaps in the vegetation in the autumn and grazing is important in providing germination and establishment sites for these species. Gap creation also stimulates the germination of dormant seeds from the seed bank (Thompson *et al.*, 1977; Thompson and Grime, 1983). Furthermore, defoliation by grazing animals helps to restrict the growth of species which would become dominant in undisturbed vegetation (Grime, 1973b,1974). These factors, combined with management which allows most species to set seed at least occasionally, create a dynamic system which can evidently sustain coexistence between a large number of species at a higher plane of productivity than in less disturbed vegetation (see Chapter 2, section 2.5).

Grazing animals themselves contribute to fertility levels by recycling most of the nutrients they consume through dung and urine in a form available to plants (During and Weeda, 1973; Gillingham, 1987; Jarvis *et al.*, 1989a). By contrast, when aftermath grazing is replaced by taking a further one or two harvests, not only can some depletion of soil nutrients be expected, but the level of disturbance to the vegetation and the soil surface will also be reduced. It is therefore difficult to say which factor was most influential in causing the decline in species-richness which occurred on unfertilized plots in the SP experiment, where the previous management of aftermath grazing was replaced by cutting. Results from Chapter 8 also suggest that a third factor may have been involved, namely that

herbage was cut and removed from plots in the SP experiment without drying and hay making, so that the potential for seed shedding will have been reduced. Changes in the vegetation on these plots were characterised by a decline in species such as *Cynosurus cristatus*, *Rumex acetosa* and *Anthoxanthum odoratum* (which normally regenerate from recently shed seed in the autumn) and an increase in species such as *Plantago lanceolata*, *Leontodon hispidus* and *Agrostis capillaris*, species which are not primarily associated with regeneration from freshly shed seeds (Grime *et al.*, 1988). Nevertheless, the prostrate growth habit of the latter species make them best suited to the shorter and less dense growth associated with low soil fertility, so the relative importance of nutrient depletion, reduced disturbance or reduced opportunity for seed shedding in contributing to vegetation change on these plots is still unclear.

Agronomic implications - base-line fertility and production response to fertilizer application
In multi-site trials measuring grassland DM response to fertilizer N (Morrison *et al.*, 1980; Hopkins *et al.*, 1990), the difference between trials in the average maximum yield obtained was much smaller than differences in DM production without N. This is not surprising, since, in addition to climatic and environmental differences between sites, between-site variation in soil fertility will obviously be a major factor accounting for differences in production from plots not receiving N (this point was clearly illustrated by regression analyses relating soil analysis and DM production data presented by Morrison *et al.* (1980) - see Chapter 2, section 2.4). By contrast, where the range of treatments applied at each site encompasses optimal levels of all three macro-nutrients, nutrient supply is eliminated as a source of variation in maximum yield between sites. The slope of a response curve will therefore be very dependant upon the base-line fertility (productivity) of a site and this must be taken into account when calculating the potential yield response to fertilizer application.

The DM response to N obtained in the SP experiment was close to that shown within the same range of application rates by Hopkins *et al.* (1990), provided that high rates of both P and K were applied. The additional cost of these high P and K rates will be a significant component in any calculation of the economic returns achievable by fertilizer application and therefore foregone by farmers complying with fertilizer restrictions in SSSIs and ESAs.

WATER TABLE MANAGEMENT

There was no indication of any reduction in hay yield caused by raised water tables in the study reported in Chapter 3, although there was some evidence of reduced production from aftermath grazing in a wet year. However, without a purpose-designed experiment, analyses relied heavily upon year-to-year variation, so that it was difficult to separate the effects of water table effects from those of several other variables. No attempt was made to relate botanical composition to hydrology in any of the studies in this thesis, although other papers have addressed this aspect to some extent (Mountford and Chapman, 1993; Mountford, 1994).

An experiment was started at Tadham Moor in 1994 to record the effects of raised water tables on both agricutural productivity and on vegetation composition. However, the work suffers from two limitations. Firstly, that the experimental design has been superimposed on the existing plot layout from the original Tadham Moor project, resulting in statistical limitations, and secondly that no provision has been made in the funding of the work for studies on nutrient cycling (Tallowin, personal communication). Several studies reviewed in section 2.7 of Chapter 2 make it clear that changes in botanical composition following changes in hydrology are often caused more by resultant changes in soil chemistry than by changes in soil water content *per se* (e.g. Smeets *et al.*, 1980; Smittenberg *et al.*, 1984; Grootjans *et al.*, 1985, 1988). Smittenberg *et al.* (1984) were emphatic that any study of the sensitivity of vegetation to changes in hydrology is incomplete if aspects of water quality are neglected. The same can be said of studies of agricultural productivity in relation to water table management, where the effects on the cycling and availability from the soil of plant nutrients, particularly N, are likely to be very influential (see Chapter 2, sections 2.6 and 2.7).

SEEDING PHENOLOGY AND CUTTING DATE

The seed rain studies reported in Chapter 8, show that, as in the Pennine Dales (Smith and Jones, 1991), hay making needs to be delayed at least until August if most species are to be allowed to set seed. However, it proved difficult in the two years of the experiment

(Experiment 3) to relate botanical change directly to trends in seed rain. This was presumably because factors other than regeneration from seed are important in determining the vegetation response to different cutting dates, including the length of a period of uninterrupted growth on the ability of certain species to build up carbohydrate reserves in their roots (Oomes and Altena, 1987).

Studies of seed rain and the phenological studies presented by Smith and Jones (1991) show the potential number of seeds or seedlings which could result after different cutting dates, but they give no information on seedling survival in the field, nor of the degree of recruitment of shed seed into the soil seed bank. Results described in Chapter 8 showed that the number of seeds shed before cutting as a proportion of the final total increased with lateness of cutting, but that, even with cutting in September, the hay making process itself was still important in inducing maximal seed shedding. For species which normally germinate soon after shedding, the time of harvest in relation to seasonal climatic factors and the onset of disturbance could have an overriding effect on seedling survival compared with the actual number of seeds shed. For other species whose regeneration strategy is dependant upon a phytochrome response to induce or enforce seed dormancy, an extended period of exposure to spectrally modified light is important (see Chapter 2, section 2.8). The phytochrome reaction, which induces a light requirement for germination, can be brought about in seeds lying at the soil surface by light filtering through a closed vegetation canopy, or, in some species, *in situ* on plants by light passing through chlorophyll-bearing maternal tissues surrounding the seed (Cresswell and Grime, 1981). The reaction is halted either when the moisture content of the embryo declines to a certain level or when the quality (wavelength) of light changes, e.g. through removal of the canopy or through a decline in the chlorophyll content of the enclosing tissues. For these species, the time of harvest may determine not only the number of viable seeds produced but also whether they germinate soon after shedding or become dormant and enter the soil seed bank.

It is clear from the discussion in previous paragraphs and in Chapter 2 that disturbance is a key factor in maintaining species-richness and this emphasises the importance of regeneration. It therefore follows that the management of vegetation for maximal species-richness should accomodate a wide variation of regeneration behaviour, both between and within species, if a dynamic equilibrium is to be maintained. Variations in cutting date, either year to year or within a small number of years, will add to the effects of other forms of environmental and climatic variation in helping to ensure that this range of regeneration strategies is expressed. Experiments such as Experiment 3, where particular cutting date treatments were applied to the same plots in two consecutive years, do not lend themselves to testing this hypothesis. However, the results were valuable in defining the interaction between cutting date, seeding phenology and germination/seed bank type of the component species, as well as providing useful data on the agronomic implications of varying cutting date. They also showed clearly the risk of increasing *Holcus lanatus* dominance and further reducing the species diversity of previously fertilized meadows by cutting either early or very late.

It appears that harvesting later than mid-July occasionally is important in maintaining species diversity, but it is not clear how often this would be necessary. The once-in-five-years rule applied in the Pennine Dales ESA (Her Majesty's Stationery Office, 1992) seems a sensible insurance policy. Most species depending largely on regeneration from the seed bank can survive in the soil for this length of time (Grime *et al.*, 1988; Thompson, 1993). A decision on whether a similar rule needs to be incorporated into the Somerset Moors and Levels ESA regulations should take into account current variations in cutting date as influenced by the weather. Smith and Jones (1991) make the point that, whereas the dates at which hay-making started in the Pennine Dales changed little between the 1950s and the 1980s, average finish dates have become progressively earlier, presumably reflecting improvements in mechanization and methodology. It is safe to assume that hay meadows on the Somerset Levels would show a similar trend. However, hay meadows in the Pennine Dales are normally grazed in the early spring (Smith and Rushton, 1994). This, coupled with differences in both latitude and altitude between the Pennine Dales and the Somerset Levels, might result in later flowering phenologies in the Dales, providing a stronger argument for later cutting there (see discussion in Chapter 2, section 2.8).

The advantage of the one-in-five-years rule is that it sets a maximum interval beween late harvests. This may be much more important than a system where the interval between late cutting averages five years - or where the mean cutting date averaged over five years is 1 August - since there is no guarantee that the detrimental effects of cutting in early July for, say, seven consecutive years can be compensated for by cutting in

September in one of the following three years. It would really only be possible to illustrate accurately the impact of any trend of increasingly shorter hay making period on botanical diversity if reference could be made to botanical data collected over the same time-scale, ie. 30-40 years. Even if such data were available for the Somerset Levels, temporal trends attributable to cutting date would almost certainly be masked by those of changes in hydrology caused by improvements in the arterial drainage system (see Chapter 1) and by changes in the activities of the Internal Drainage Boards (Green and Robins, 1993).

Agronomic implications of cutting date

Any compensation payments made to encourage late hay cutting would have to take into account both of the shortened period available for aftermath grazing and of the poor quality of the hay produced. The nutritional quality of hay made in August or later at Tadham Moor was such that it would not have been adequate for growing animals or productive dairy cows without mineral supplementation (Agricutural Research Council, 1980). However, this probably applies to hay cut as late as this in agricuturally improved grasslands too. The protein and phosphorus content of hay from unfertilized hay meadows at Tadham Moor was low compared with areas receiving inorganic N and P fertilizer (see Chapter 3), but concentrations of Ca, Na and Mg were easily sufficient to meet the dietary requirements of all classes of sheep and cattle, even with Septemember cutting. High levels of availability of these elements in the soil are attributable to the geology of the area and its surrounding hills (see Chapter 1). Nevertheless, the main inadequacy of hay made as late as this is in it's low energy value and such hay is often used for bedding rather than for feed. Compensation payments would probably have to be based upon this assumption, coupled with an estimation of the cost of buying in hay of the quality achievable by cutting in early July.

An assessment of the impact of late cutting on aftermath production would have to take into account not only the shorter period of regrowth but also the fact that mean herbage growth rates and animal production would be substantially lower than when averaged over a period starting earlier in the summer (Corrall and Fenlon, 1978; Tallowin *et al.*, 1990). In years when hay was cut in early July, aftermath DM yield in the SP experiment averaged 32% of total annual yield, but only 13% in a year when cutting was delayed until early August. Corresponding values for the same years based upon utilized metabolizable energy (UME) from aftermath grazing in the LS experiment were 29% and 8% respectively. However, it must be recognized that the delay in hay making was due to very wet conditions. It is apparent from data presented in Chapters 3 and 4 that high water tables were responsible for excessively low productivity, probably due to excessive losses of soil N by leaching and denitrification.

9.6. CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT WITHIN SSSIs AND THE ESA

The traditional management of hay meadows at Tadham Moor, by cutting for hay after the beginning of July, grazing the aftermath, and without external nutrient inputs other than those from flood, seepage and rain water, allows an optimum balance between productivity and species-richness. Even small inputs of inorganic fertilizer upset this balance and reduce species-richness and diversity. Within the ESA regulations, only those of Tier 3, which allow no fertilizer use, are likely to be successful in maintaining species-richness.

Both the disturbance and the nutrient cycling processes associated with grazing are essential components in the dynamic equilibrium which exists within the plant communities and which allows coexistence of a large number of species at a moderate (in agricutural terms) level of productivity.

The production response to N in these meadows (at least up to 200 kg N ha^{-1}) is equivalent to the average recorded for a wide variety of less species-rich agricultural grasslands, provided that high levels of P and K are applied. The extra cost of these high P and K rates would have to be taken into account when using N response data to assess the potential profit foregone by farmers in adhering to low or nil fertilizer N rates.

Occasional late cutting (in August) is important in allowing maximal expression of a variety of regeneration strategies within the plant communities and ensuring that the size and diversity of the seed bank is maintained. A once-in-five-years rule within ESA regulations would be a sensible insurance policy, although access to farm records on cutting dates should be sought to see if such a regulation is necessary. Cutting either earlier than July or later than August should be avoided, particularly in previously fertilized meadows where this will lead to increased *Holcus lanatus* dominance and further reductions in species-richness.

Cutting in August will incur financial penalties for the farmer both in the low nutritive value of the hay produced and in reduced production from aftermath grazing.

Significant changes in hydrology are likely to upset the nutrient balance in the soil with consequent effects on both vegetation composition and productivity. Smaller variations within the range encompassed during 1986-1990 do not appear to affect hay yields, although yields were lowest in a dry year. Aftermath production was reduced in 1988 when water tables were equivalent to those defined in the ESA high water table option, although the results of a current experiment showed an increase in animal production from aftermath grazing under raised water table conditions in the dry year of 1995 .

The soils at Tadham Moor are particularly susceptible to N losses by both leaching and denitrification. Where current water table management is maintained, adhering to the ESA Tier 1 or Tier 2 regulations (i.e. applying no more than 75 kg N ha^{-1} $year^{-1}$) will avoid the risk of significant increases in the loss of N to the environment. Losses in soil N will be enhanced if water tables are raised according to the ESA high water table option and in these cases little or no fertilizer N application should be allowed.

9.7. NEEDS FOR FURTHER RESEARCH

IMPACT OF RAISED WATER TABLES ON SOIL NUTRIENT AVAILABILITY

As already noted, the current experiment measuring the effects of raised water tables on productivity and botanical composition at Tadham moor includes no study of nutrient cycling. In order to understand fully the implications of adopting the high water tables option within the ESA regulations (Her Majesty's Stationery Office, 1992, see also Chapter 1), it is important to define the consequent changes in: (a) the ratios of rainfall : flood water : ground water seepage as sources of minerals such as N, P K and Ca; and (b) the cycling of N, P and K, e.g. N mineralization : denitrification, rates of P and K mineralization and availability. Experimental units for these assessments should be of a number, size and location which would allow correlation with botanical assessments.

THE IMPORTANCE OF AFTERMATH GRAZING FOR THE MAINTENANCE OF SPECIES DIVERSITY IN HAY MEADOWS

Studies reported in Chapter 5 and in the Park Grass Experiment showed a decline in species richness when aftermath grazing was discontinued (Williams, 1978, see also discussion in Chapter 2). Recent studies at a total of 27 sites in Belgium, The Netherlands, Spain and Great Britain showed that the most species-rich grasslands were those managed by a combination of grazing and hay making, i.e. in the Pyrenees and on the Somerset Levels (unpublished data from EC project AIR3-CT 920079). However, this evidence is somewhat circumstantial. Specific studies are required to relate aftermath grazing to the relative contributions made by seed rain, the soil seed bank and vegetative spread to the regeneration dynamics of species-rich hay meadow vegetation, including reference to the regeneration and established strategies (*sensu* Grime, 1979) of the species involved. These studies should include assessments of changes in nutrient availability and heterogeneity following cessation of aftermath grazing, compared with plots where aftermath grazing is maintained, with measurements related to botanical changes occurring on a local e.g. 1 m^2, scale.

VEGETATION DYNAMICS IN SPECIES-RICH GRAZED PASTURES

The mechanisms involved in the maintenance of species-richness in pastures managed by grazing only need definition. Since regeneration from the seed bank is an important component in the mechanisms involved (Grime, 1979; Tallowin and Smith, in press), it follows that grazing intensity should be such as to allow germination and establishment of seedlings from the soil seed bank, at the same time allowing a sufficient number of plants to flower and set seed. Ecological models suggest that maximal species diversity is dependent upon moderate levels of disturbance (Grime, 1973b, 1979; Huston, 1979), but these 'moderate' levels need defining in terms of grazing intensity in specific vegetation types, e.g on the Somerset Levels (Johnson, 1988) and in *Cirsio-Molinetum* communities in culm grassland (Tallowin and Smith, in press).

Management by grazing at low-moderate intensity has at least one advantage over cutting for hay in that it allows very late-flowering plants to set seed. For example, *Succisa pratensis*, a species characteristic of grazed culm grassland, produces ripe seeds from

August-November (Grime *et al.*, 1988), but regenerates almost entirely by seed which germinates in the following spring and has no further dormancy (Grime *et al.*, 1988). Studies on the regeneration dynamics of species-rich *Cirsio-Molinetum* culm grasslands in relation to variations in grazing intensity would be a useful adjunct to recent studies (Tallowin and Smith, in press). Such work should include measurements of reproductive development, seed rain, seedling establishment and survival and overall botanical change, in relation to variations in stocking intensity. Analysis of the results in relation to the regenerative and established strategies of the relevant species (Grime, 1979) would not only allow a more confident definition of optimal grazing management in these pastures, but would, by increasing unserstanding of the ecological principles involved, provide scope for the application of the results to other pasture types.

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