

A LABORATORY APPROACH TO ECOLOGICAL STUDIES
OF THE GRASSES: ARRHENATHERUM ELATIUS (L.)
BEAUV. EX J. AND C. PRESL AGROSTIS TENUIS
SIBTH. AND FESTUCA OVINA L.

by

ABDEL SALAM MAHMOUD

Department of Botany, University of Sheffield

Thesis for the degree of Doctor of Philosophy

November 1973



IMAGING SERVICES NORTH

Boston Spa, Wetherby

West Yorkshire, LS23 7BQ

www.bl.uk

BEST COPY AVAILABLE.

**TEXT IN ORIGINAL IS
CLOSE TO THE EDGE OF
THE PAGE**



IMAGING SERVICES NORTH

Boston Spa, Wetherby
West Yorkshire, LS23 7BQ
www.bl.uk

**CONTAINS
PULLOUTS**

For my wife.

ACKNOWLEDGEMENTS

I am grateful to Professor A.J. Willis for the use of his departmental research facilities at Sheffield and for his guidance and advice in supervision of this work. To Dr. J.P. Grime, my supervisor, I am particularly indebted for his continual encouragement, helpful criticism and advice.

I am also grateful to Dr. R. Hunt for helping in computation of the data, and for useful discussions, and to Mr. G. Wood for photography.

I would like to express my warmest thanks to Mrs. Jean Grime who generously offered her service and help at all times.

I also wish to thank Mrs. J. Czerny for her patience in typing the thesis.

ABSTRACT

Abdel Salam Mahmoud (1973). A Laboratory approach to ecological studies of the grasses: Arrhenatherum elatius (L.) Beauv. ex J. and C. Presl Agrostis tenuis Sibth. and Festuca ovina L.

Ph.D. thesis

University of Sheffield.

An attempt has been made to recognise laboratory characteristics which allow features of the ecology of three common British grasses, Arrhenatherum elatius (L.) Beauv. ex J. and C. Presl, Agrostis tenuis Sibth. and Festuca ovina L. to be predicted.

Experimental work was carried out in controlled and semi-controlled environments and involved a consideration of plant morphology, measurements of responses in germination and growth to light and temperature, and measurement of responses to nutrient stress, metal toxicity, and defoliation. In some experiments, additional species, Deschampsia flexuosa and Zerna erecta, were included in order to provide a wider basis for comparison.

Predictions of the field ecology, were evaluated by reference to published accounts of the ecology of the species and predictions of competitive ability were tested by carrying out competition experiments.

Attributes which when used singly or in combination appear to have a predictive value include seed weight, seed dormancy, response of germination and vegetative growth to temperature, relative growth rate under productive conditions, dry matter production in seedlings subjected to mineral nutrient stress or manganese toxicity, root growth of plants exposed to soluble aluminium, leaf extension growth in shade, light intensity compensation point and tiller production under continuous clipping.

The ecological significance of the differences between the species with respect to these attributes is explored in the Discussion.

The data on which predictions have been based were derived from investigations carried out on a single field population of

each species. Evidence of the need to account of intra-specific variation was obtained in the present study; it was necessary to carry out additional experiments to take account of morphological variation in Arrhenatherum elatius. It is concluded, however, that whilst genetic variation within the species may have an important influence, the laboratory characteristics of plants drawn from a single field population frequently reveal attributes which control the broad ecology of the species.

CONTENTS

	<u>Page</u>
CHAPTER 1. INTRODUCTION.	1.
PART 1. GENERAL ECOLOGY OF THE SPECIES UNDER INVESTIGATION.	11.
CHAPTER 2. ECOLOGICAL SYNOPSIS OF THE SPECIES UNDER INVESTIGATION.	12.
a) Geographical distribution.	12.
b) Habitats.	16.
c) Distribution in relation to slope and aspect.	17.
d) Distribution in relation to geological strata and soil-surface pH.	20.
e) Distribution in relation to management.	23.
PART 2. COMPARATIVE STUDIES UNDER CONTROLLED CONDITIONS.	25.
CHAPTER 3. SEED WEIGHT, SIZE OF SEEDLING AND MORPHOLOGY OF MATURE PLANT.	26.
CHAPTER 4. GERMINATION CHARACTERISTICS.	30.
CHAPTER 5. EFFECT OF TEMPERATURE ON THE GROWTH OF <u>ARRHENATHERUM ELATIUS</u> , <u>AGROSTIS TENUIS</u> , <u>FESTUCA OVINA</u> , <u>DESCHAMPSIA FLEXUOSA</u> , AND <u>ZERNA ERECTA</u> .	50.
CHAPTER 6. RESPONSE OF <u>ARRHENATHERUM ELATIUS</u> , <u>AGROSTIS TENUIS</u> , <u>FESTUCA OVINA</u> AND <u>DESCHAMPSIA FLEXUOSA</u> TO SHADE.	76.
CHAPTER 7. SUSCEPTIBILITY OF <u>ARRHENATHERUM ELATIUS</u> , <u>AGROSTIS TENUIS</u> , <u>FESTUCA OVINA</u> AND <u>DESCHAMPSIA FLEXUOSA</u> TO ALUMINIUM AND MANGANESE.	90.
Response to aluminium.	93.
Response to manganese.	101.
CHAPTER 8. INVESTIGATION INTO THE MINERAL NUTRITION OF <u>ARRHENATHERUM ELATIUS</u> , <u>AGROSTIS TENUIS</u> AND <u>FESTUCA OVINA</u> .	107.
Response to potassium supply.	108.
Response to nitrogen.	114.

	<u>Page</u>
CHAPTER 9. <u>RESPONSE OF ARRHENATHERUM ELATIUS,</u> <u>AGROSTIS TENUIS, AND FESTUCA OVINA</u> <u>TO CLIPPING.</u>	124.
PART 3. COMPETITION EXPERIMENTS.	142.
CHAPTER 10. <u>COMPETITION BETWEEN ARRHENATHERUM</u> <u>ELATIUS, AGROSTIS TENUIS AND FESTUCA</u> <u>OVINA AT TWO LEVELS OF FERTILITY.</u>	143.
CHAPTER 11. <u>THE INFLUENCE OF COMPETITION ON LATERAL</u> <u>VEGETATIVE SPREAD OF ARRHENATHERUM</u> <u>ELATIUS, AGROSTIS TENUIS AND FESTUCA</u> <u>OVINA.</u>	150.
CHAPTER 12. <u>COMPETITION BETWEEN AGROSTIS TENUIS</u> <u>AND PROSTRATE FORM OF ARRHENATHERUM</u> <u>ELATIUS IN A CLIPPED TURF.</u>	162.
CHAPTER 13. <u>EFFECT OF CUTTING AND SOIL FERTILITY</u> <u>ON THE STATUS OF ARRHENATHERUM</u> <u>ELATIUS, AGROSTIS TENUIS AND FESTUCA</u> <u>OVINA IN A GRASS MIXTURE.</u>	166.
CHAPTER 14. DISCUSSION.	173.
CHAPTER 15. SUMMARY.	202.
REFERENCES.	209.
APPENDIX 1. <u>SHOOT HEIGHT, AT FOUR TEMPERATURE</u> <u>TREATMENTS, OF ARRHENATHERUM ELATIUS,</u> <u>AGROSTIS TENUIS, FESTUCA OVINA,</u> <u>DESCHAMPSIA FLEXUOSA AND ZERNA ERECTA.</u>	223.
APPENDIX 2. <u>FITTED LEAF AREA RATIOS AND FITTED</u> <u>LEAF RATES FOR ARRHENATHERUM ELATIUS,</u> <u>AGROSTIS TENUIS, FESTUCA OVINA,</u> <u>DESCHAMPSIA FLEXUOSA AND ZERNA ERECTA.</u>	224.
APPENDIX 3. <u>INVESTIGATION OF THE FREQUENCY OF</u> <u>DISTRIBUTION OF DIFFERENT GROWTH FORMS</u> <u>OF ARRHENATHERUM ELATIUS IN THE FIELD.</u>	225.

CHAPTER 1.

INTRODUCTION

Various approaches have been adopted by ecologists in their attempts to understand the mechanisms controlling the ecology of plant species. However, almost without exception, such ecological investigations have begun with field work. Where experiments under controlled conditions have been undertaken, these have been usually in the latter stages of the investigation. However, with the widespread development of plant growth-room facilities an alternative approach is possible. This is to measure the responses of the plant to environmental variables and to use the results to predict the field ecology of the species.

In fact it is not merely responses to laboratory treatments that are useful in making predictions. Genetic attributes which are relatively insensitive to environment e.g. flower colour, are also worthy of examination.

This approach involves important advantages. One is that data from growth-room investigations may be collected in such a way that they are comparable with those collected for other species by other workers (Grime 1968). Another is that predictions can be tested against actual descriptions of the field ecology.

A main objective of the present research is to attempt to recognise those measurements which when carried out under

standardised laboratory conditions allow predictions to be made of the features of the ecology of the plant species concerned. In order that any predictions could be effectively tested the species chosen for the study - Arrhenatherum elatius (L.) Beauv. ex J. and C. Presl, Agrostis tenuis Sibth. and Festuca ovina L. - are common plants about which a great deal is already known. The three species provide many sharp contrasts with respect to their ecology. The selection was restricted to grasses in order to simplify the problems of quantifying morphological features and morphogenetic responses to treatment. In certain parts of this investigation additional grass species have been included in order to give a wider scope for comparison.

The thesis is written in three parts. Part 1. is a brief review of existing knowledge of the field ecology of the three species and deals with their geographical distribution, the range of habitats exploited in the Sheffield region, their distribution in relation to geological strata, soil pH and grassland management. Part 2. consists of an account of the results of experimental work carried out in controlled and semicontrolled environments with the object of investigating the responses of the three species in monoculture to selected environmental factors. These studies involved considerations of plant morphology, measurements of seed weight, of responses in germination and growth to light

and temperature, and of responses to nutrient stress, to aluminium and manganese toxicities and to defoliation.

We are far from a complete knowledge of which plant attributes determine specific responses. It follows therefore that what was required of these laboratory studies was, in some cases, merely the design of a convenient procedure for quantifying responses which were already known to be of critical importance (e.g. stunting of roots by Al^{+++}) whereas in others (e.g. responses to grazing) preliminary work was needed to characterise the critical responses before attempting to quantify them.

The work included in Part 3. describes experiments which deal with measurements of responses of the plants to competition under different fertility levels and clipping treatments and the results are used, in addition to published accounts of the ecology of the species and field observations (given in Part 1.) to evaluate predictions based on the results of the laboratory experiments in Part 2.

The usefulness of measurements on a range of plant characteristics obtained under laboratory conditions in predicting the field ecology of plants is particularly evident in the work of Myerscough and Whitehead (1967) in their comparative study of the biology of Tussilago farfara L., Chamaenerion angustifolium (L.) Scop., Epilobium montanum L., and Epilobium adenocaulon Hausskn.

In the present investigation an attempt has been made to concentrate attention on plant characteristics likely to exercise a major influence on the field ecology of the species.

Selection of these plant characteristics has been based on a large volume of published work. The remainder of this introductory chapter is devoted to a brief summary of the more important published work which guided the selection of plant characteristics for investigation and the choice of methods.

Information on the seed biology of a species is of great importance in predicting the field ecology of the species concerned.

The ecological significance of seed size and weight in relation to the survival of the seedlings in different environmental conditions was first pointed out by Salisbury (1942). He suggested that the capacity of a species to invade and colonize areas where competition may be intensive appears to be associated with the amount of food reserve which the seeds contain and that the possession of a large seed confers an additional advantage in competitive situations. More precise work on the ecological significance of this plant attribute was performed by Harper et al. (1963, 1965, 1967) and Black (1958). Harper and Clatworthy (1963) suggested that the possession of a large seed gives the species two important characteristics which could be of

competitive advantage: (1) large seeds have large embryos which produce large seedlings with an initially large photosynthetic area (2) large seeds are normally provided with a greater embryonic capital and food reserve which may increase the actual (as compared to relative) growth rate of the growing plant.

The ecological significance of data on the dormancy of the seeds has been recognized by many workers. The ^dDelayed germination is of value to the plant, especially in the temperate zone where winters are apt to be severe and the seeds must be protected from germination when they fall to the ground in autumn. "Seedlings produced at that time would be killed by cold weather" (Crocker and Barton, 1957) Ratcliff (1961) discussed the importance of delayed germination in determining the time of germination suitable for the germination and survival of a number of annuals in Derbyshire Limestone.

The use of data obtained under laboratory conditions, on germination responses to temperature in understanding germination behaviour in the field has been recognized by many workers. Wagner (1967), for example, used a thermo-gradient bar to investigate the germination temperature optima (G.T.O.) for four species of Plantago; P. major and P. rugelli were found to have a G.T.O. of about 28°C whereas

P. aristata and P. virginica showed a G.T.O. of about 16° C. These optima were correlated with germination pattern in the field. The first pair normally germinates in early summer at relatively high mean surface temperature, and the second pair germinates in autumn when the mean surface soil temperature is lower.

The extensive work of Thompson (1968, 1970 a,b) provides a good example of the usefulness of using data on germination temperature responses in understanding the ecological or geographical range of a species. He showed that the distribution of certain species was reflected in their germination responses. The temperature responses of species distributed predominantly in deciduous woodland zones of Europe (mean limits of germination range 12 - 30°C) could be distinguished from those of species around the Mediterranean (4 - 24°C) and in turn from those for species in Steppe areas of Central and Eastern Europe (6 - 30°C).

Responses of vegetative growth to temperature have been studied extensively in the laboratory for many years. Attempts to relate these studies to natural conditions have been reviewed by Hiesey and Milner (1965). Eagle (1967) showed that responses of growth to temperature can throw light on the geographical range of Dactylis glomerata. Mitchell (1956) comparing the growth, at a range of constant temperatures, of perennial ryegrass (Lolium perenne L.),

short rotation ryegrass (Lolium perenne X L. multiflora Lam.) browntop (Agrostis tenuis Sibth.), Yorkshire fog (Holcus lanatus L.), paspalum (Paspalum dilatatum Poir), white clover (Trifolium repens L.), subterranean clover var. Mount Barker (Trifolium subterraneum L.) and Lotus major (Lotus uliginosus Schkuhr) came to the same conclusion.

Artificial shading experiments on seedlings can provide a more critical and more widely applicable analysis of the effects of solar radiation on the vegetative growth of plants, than field experiments with natural shade. Studies of shade tolerance in plants have considered different aspects of plants: (1) their carbohydrate economy at low light intensity (Böhning and Burnside, 1956; Bourdeau and Laverick, 1958; Grime, 1965; Loach, 1967; Okali, 1972), (2) morphological responses to shade (Blackman and Wilson, 1951; Blackman and Black, 1959; Evans and Hughes, 1961; Grime and Jeffrey, 1965), (3) shade tolerance for longer periods of darkness (Hutchinson, 1967) and (4) susceptibility of shaded plants to fungal attack (Vaartaja, 1962).

The ecological significance of aluminium and manganese have been demonstrated by many workers. Several have provided experimental evidence which indicates that the depression of plant growth on acidic soil is associated with release of aluminium (Hartwell and Pember, 1918; Clymo, 1962; Hodgson, 1972) and manganese (Jacobson and Swanback, 1932, Bortner, 1935).

Bradshaw, Lodge, Jowett, (1958, 1960 a), Bradshaw, Chadwick, Jowett, Lodge and Snaydon (1960b), Snaydon and Bradshaw (1961), Clymo (1962), Bradshaw, Chadwick, Jowett and Snaydon (1964) and Jefferies and Willis (1964) have shown that measurements of responses of a species to a variation in the rate of supply of an individual major nutrient in sand or water culture can assist our understanding of edaphic tolerance of a species.

Manual or mechanical clipping has been extensively used in field plots to simulate grazing. (Aldous, 1930; Graber, 1931; Stoddart, 1946; Albertson, Riegel and Launchbaugh, 1953; Baker, 1957 b; Neiland and Curtis, 1959; Heinrichs and Clark, 1961) and appears to be a useful technique in that it provides an insight into the response of the plant to defoliation whether by clipping or grazing.

Despite the extensive use of clipping techniques to simulate grazing in field plots, there is hardly any literature on the use of clipping technique to study response of plants in monoculture to controlled defoliation in the laboratory, in an attempt to measure sensitivity to mowing and grazing. In planning experiments in this field note has been taken of the objections of Culley, Campbell and Canfield (1933) who list the following respects in which clipping fails to simulate grazing in the field:- (1) livestock pull and break off forage at random heights instead of at uniform

heights, (2) species preference of animals is not taken into consideration, (3) there is no trampling, and (4) litter accumulation follows a different pattern from that which occurs under grazing.

Certain attributes measured in the present investigation were selected primarily because there was evidence that they might be useful in predicting the outcome of interspecific competition under particular conditions.

The significance of shoot height and litter production, as competitive attributes had been noted by Salisbury (1929), Monsi and Sacki (1953), Watt (1955), and Black (1960). Grime (1973), in an attempt to assess the competitive ability of species under productive conditions, devised a "competitive index" which is derived from scores for each of four "competitive" attributes: (a) tall stature, (b) a growth form (usually large densely branched rhizome or tussock structure) which allows extensive exploration of the environment above and below the ground, (c) a high maximum relative growth rate, (d) a tendency to deposit a dense layer of litter at the ground surface.

An additional purpose behind the selection for study of attributes such as responses to mineral nutrients and clipping was the attempt to predict the extent to which factors such as mineral nutrient stress and defoliation would affect the outcome of competition.

The data on which predictions are based in the present investigation are derived from experiments involving a single field population for each of the three species. It is acknowledged that this approach involves a major difficulty in the need to take account of intraspecific variation. The three species selected for this work are peculiarly suitable for an appraisal of this problem. Each is wide-ranging in its field ecology and ecotypes have been recognised for Agrostis tenuis and Festuca ovina (Snaydon and Bradshaw, 1961; Gregory and Bradshaw, 1965). Nevertheless each of the species has distinct and consistent characteristics at the species level and there is reason therefore to suspect that certain attributes which control the ecology of the species will be evident in all populations.

However, it is fully recognised that both within and between populations there is likely to be considerable genetic variation and that this variation may influence the detailed ecology of the species and may be vital to its survival in the long term.

PART 1.

GENERAL ECOLOGY OF THE SPECIES
UNDER INVESTIGATION.

CHAPTER 2.

ECOLOGICAL SYNOPSIS OF THE SPECIES

UNDER INVESTIGATION.

(a) Geographical distribution

Arrhenatherum elatius.

Arrhenatherum elatius is a native species in most of Western Asia, Europe and North Africa. It is a common species in all parts of the British Isles and is reported by Clapham, Tutin and Warburg (1957) to occur in every vice-county (Plate 1). The plant was introduced as a herbage crop and is now naturalized in Japan (Matsumura 1905) and in Australia since 1878 (Ewart 1930) and in North America, Chile, Tasmania and New Zealand (Hultén 1964). The map in Plate 4 shows the World distribution of the species.

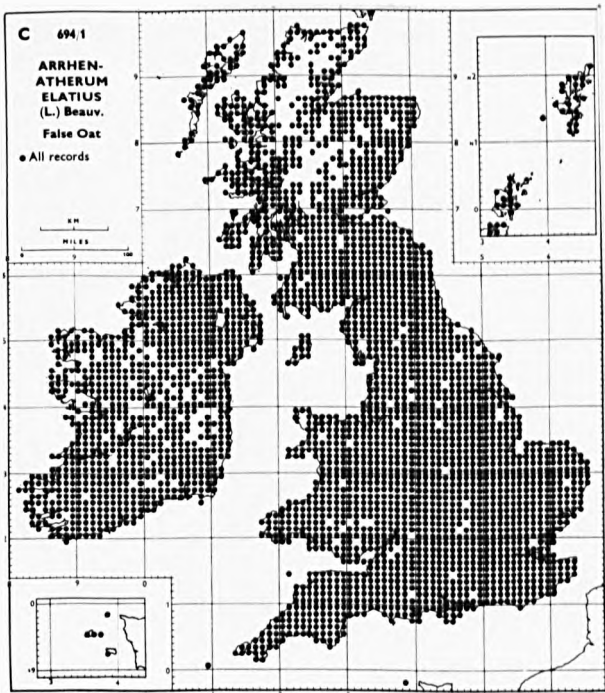
Climatic factors which are mainly influenced by altitude and latitude seem to be very important factors in governing the limits of the extension of the species.

The distribution of Arrhenatherum elatius in Europe and North Africa shows a considerable range in latitude. The species extends from about 70°N in Norway (Tromsø district) to about 30°N in Morocco. Hultén (1950) gives the northern limit of the species in Europe as a line which extends along the Norwegian coast from about Tromsø to Bergen, omitting the Scandinavian Alps; it follows a north-easterly direction

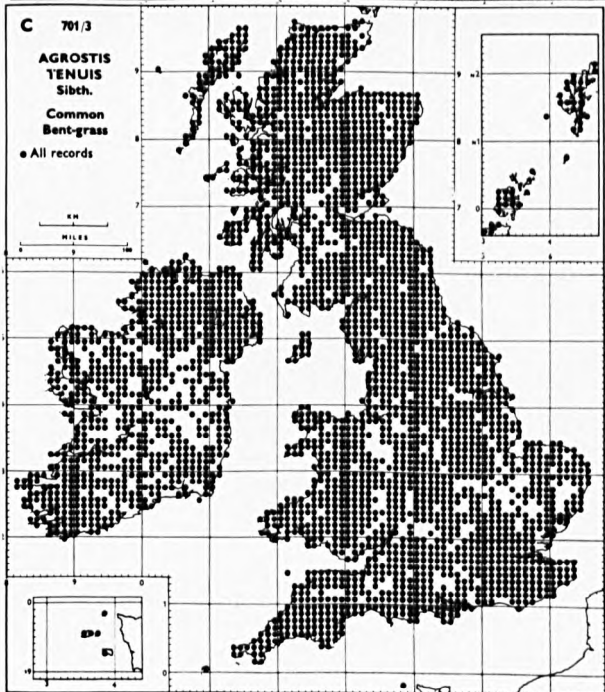
Plates 1 - 3.

Distribution maps of the three species
in the British Isles.

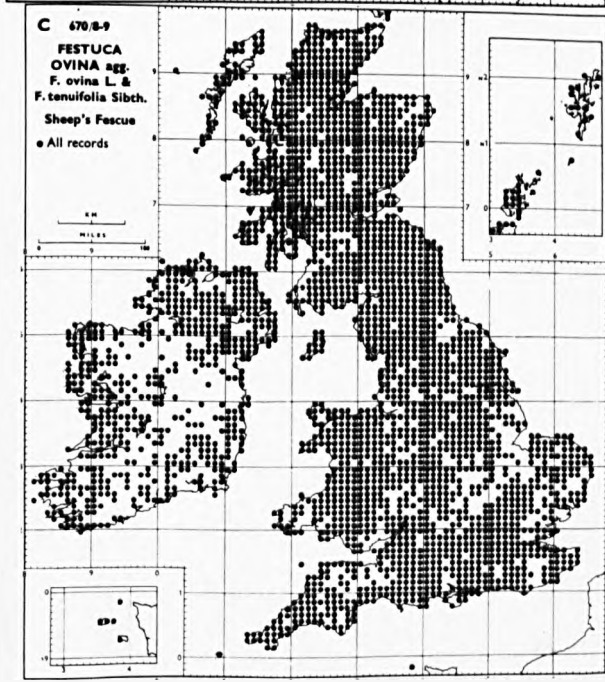
1. Arrhenatherum elatius
2. Agrostis tenuis
3. Festuca ovina



1



2

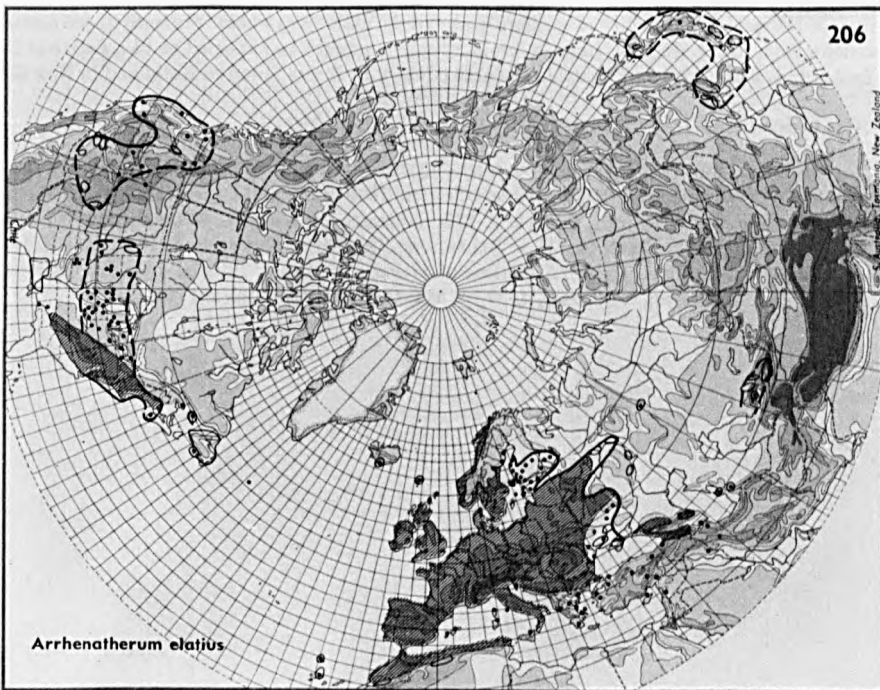


3

Plates 4 - 6.

World distribution maps of the three species.

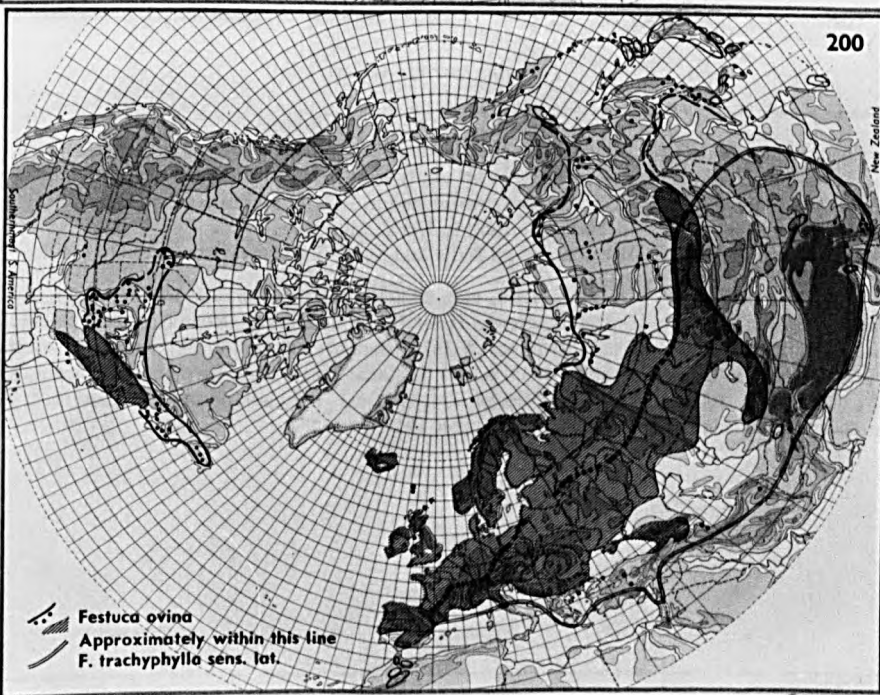
4. Arrhenatherum elatius
5. Agrostis tenuis
6. Festuca ovina



4



5



6

passing through central Sweden, reaching approximately 65°N on the western coast of the Gulf of Bothnia. In Finland it occurs only in the extreme south-western and south-eastern part of the country.

According to Maire (1953) the southern most territory of Arrhenatherum elatius is the Anti-Atlas range in south Morocco (30°N) at the northern edge of the Sahara. It seems that the hot dry climate of the desert restricts the spread of the species further south.

The extension of Arrhenatherum elatius in altitude seems to be dependent on latitude. In northern Europe, the species is completely absent from the Scandinavian Alps (Hultén 1964); Arrhenatherum elatius is confined to the coastal lowland of Norway. The altitudinal limit of the species in Britain is 430 m. The upper limit of the altitudinal spread of the species becomes progressively higher as the species approaches its southern boundary.

Under the dry and warm climatic conditions of southern Europe, Arrhenatherum elatius is reported to grow at high altitudes. According to Boissier (1884) the limit of the distribution of Arrhenatherum elatius in the Caucasus is 3000 m. at Mount Talysh. In southern Italy, Sicily and North Africa, the distribution of the species was shown by Parlatoire (1848) and Maire (1953) to be confined to high altitudes.

Agrostis tenuis

Agrostis tenuis is abundant and widely distributed in the British Isles (Plate 2). Agrostis tenuis is distributed throughout Europe and Temperate Asia; introduced and established in North and South America, Australia and New Zealand (Hubbard 1968). Hultén (1964) provided the distribution map in Plate 5 and gave the following description for the distribution of the species. "Its area is very incompletely known and is only tentatively given on the map. Outside the area of the map it occurs introduced in Australia, Tasmania and New Zealand. In America it is introduced as probably also in Greenland. Doubtless it occurs introduced in many places outside the range given in the map.

In southern Norway Agrostis tenuis extends to about 1100 m. and in the Alps to about 2450 m."

In the British Isles its distribution ranges from sea-level to about 1213 m. (Hubbard 1968).

Festuca ovina

Festuca ovina is widely distributed in the British Isles and is reported in every county (Plate 3) and is widespread in the northern temperate zone (Hubbard 1968).

Hultén (1964) provided a distribution map of Festuca ovina (Plate 6) and the following description for its geographical distribution. "An extremely complicated and

variable complex with more than 70 variations described, for the present impossible to clear up geographically."

The present map (Plate 6) and discussion must be regarded as very preliminary.

Possibly the complex consists of two major groups, one European very variable lowland plant and another series of Arctic-montane type, just as in the case of F. rubra, but the situation is too confused to allow of details. One arctic-montane type with glabrous leaves has been called F. supina Schur. and is believed to occur from the Scandinavian mountains and along the arctic coast of Europe going south-wards in the mountains to Japan, Korea, Pamir, the Caucasus and the central European mountains. Along the southern and eastern edge of the range as given on the present map (Plate 6) very numerous species have been proposed by Kretchetovics and Borrov in Fl. SSSR. It is a difficult task to try to find some order in this mixture. Festuca ovina s. str. is considered to occur in western Europe and in northern Russia, the Caucasus and western Siberia only.

Several somewhat better known closely related taxa occur and probably integrate with Festuca ovina viz. F. trachyphylla (Hack) Krecz. (F. duriuscula auct.) in northern and north-western Europe and the Caucasus, F. capillata Lam. (= Festuca ovina ssp Capillata Sch. and Kell.) in central western Europe, also introduced in eastern

(and western?) America, F. palesica in northern and central Russia, south-eastern Scandinavia and Poland and lastly the variable F. vallesiaca Grand. (taken in a wide sense including F. pseudovina Hack. and F. sulcata Hack.), the approximate northern limit of which is given in the map.

The Caucasian and Asiatic subdivisions are involved taxonomically.

Festuca ovina coll. is introduced in New Zealand and southern most South America.

In southern Norway Festuca ovina coll. (excluding F. vivipara) extends to about 1900 m., in the Alps, to about 2750 m. and in Colorado to about 3700 m.

In the British Isles its distribution ranges from near sea-level to over 1213 m. (Hubbard 1968).

(b) Habitats

Within their geographical (climatic) range the three grasses occur on a wide spectrum of habitats. Arrhenatherum elatius is common in rough grassland hedgerows, road-sides, shingle, gravel banks, and waste ground (Hubbard 1968). Grime and Hodgson carried out a survey of an area of 900 square miles in the Sheffield area traversing the boundary between upland and lowland Britain. Thirty-four major types of habitat were recognized and in each of these samples of the herbaceous vegetation were described. The data abstracted for Arrhenatherum elatius (Fig.1) confirm that

Fig.1. Range of habitats of Arrhenatherum elatius in Derbyshire.

The frequency of Arrhenatherum elatius in each of the major habitats of the Sheffield region.

Values in the terminal categories refer to the % of the samples containing the species. The values at higher levels of the hierarchy are means to which the immediate sub-units contribute equally.

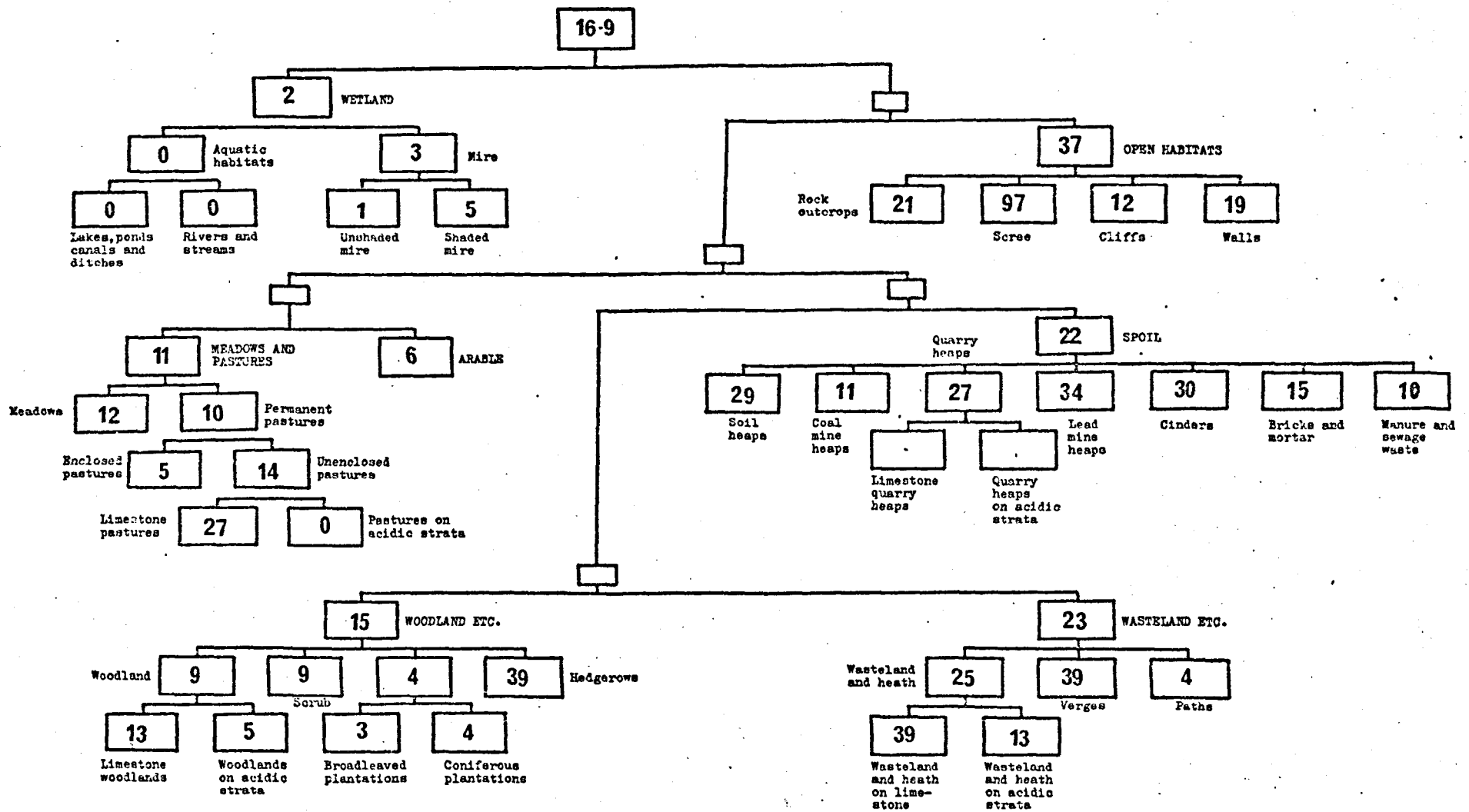


Fig. 1

Fig.2. Range of habitats of Agrostis tenuis in Derbyshire.

The frequency of Agrostis tenuis in each of the major habitats of the Sheffield region.

Values in the terminal categories refer to the % of the samples containing the species. The values at higher levels of the hierarchy are means to which the immediate sub-units contribute equally.

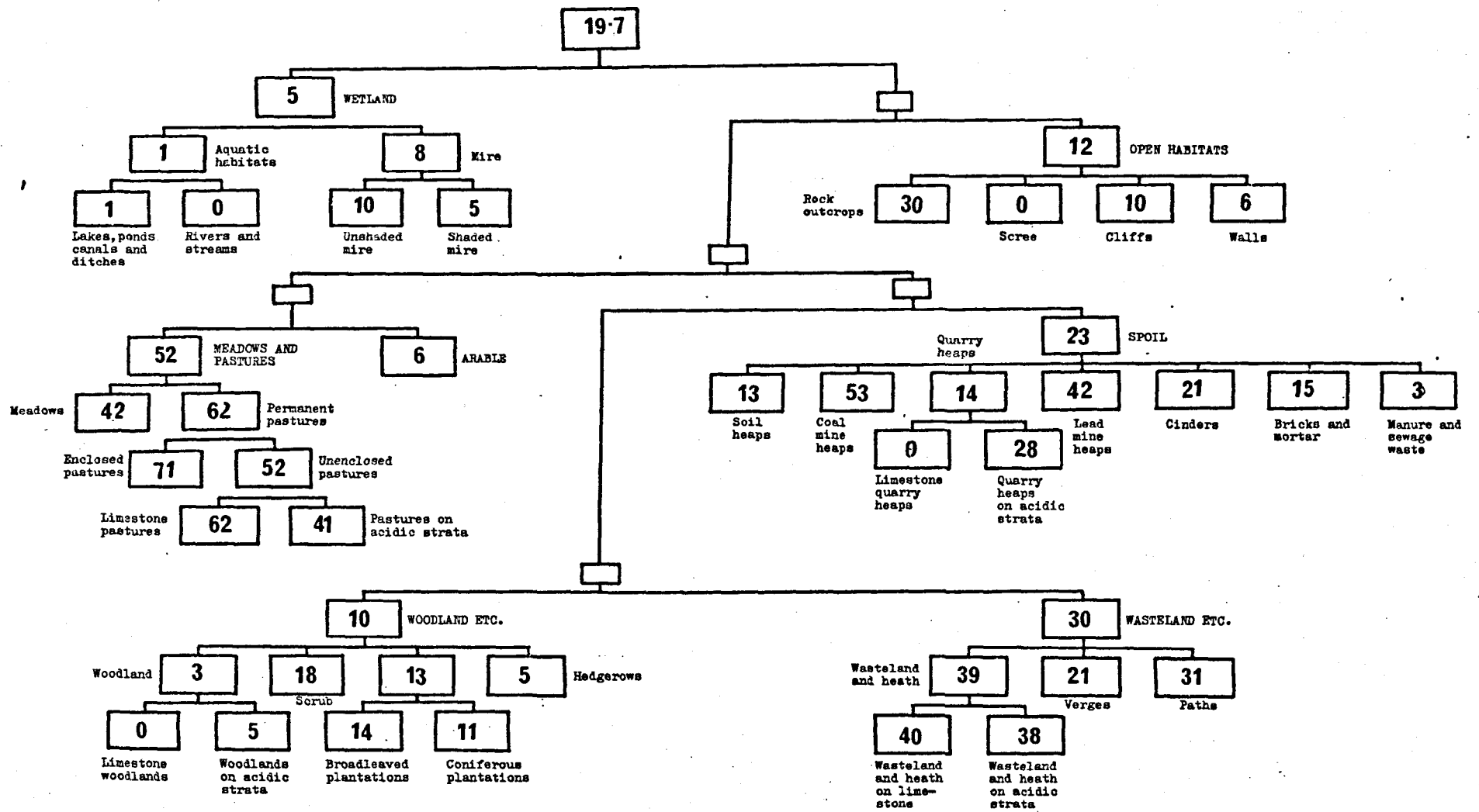


Fig. 2

Fig.3. Range of habitats of Festuca ovina in Derbyshire.

The frequency of Festuca ovina in each of the major habitats of the Sheffield region.

Values in the terminal categories refer to the % of the samples containing the species. The values at higher levels of the hierarchy are means to which the immediate sub-units contribute equally.

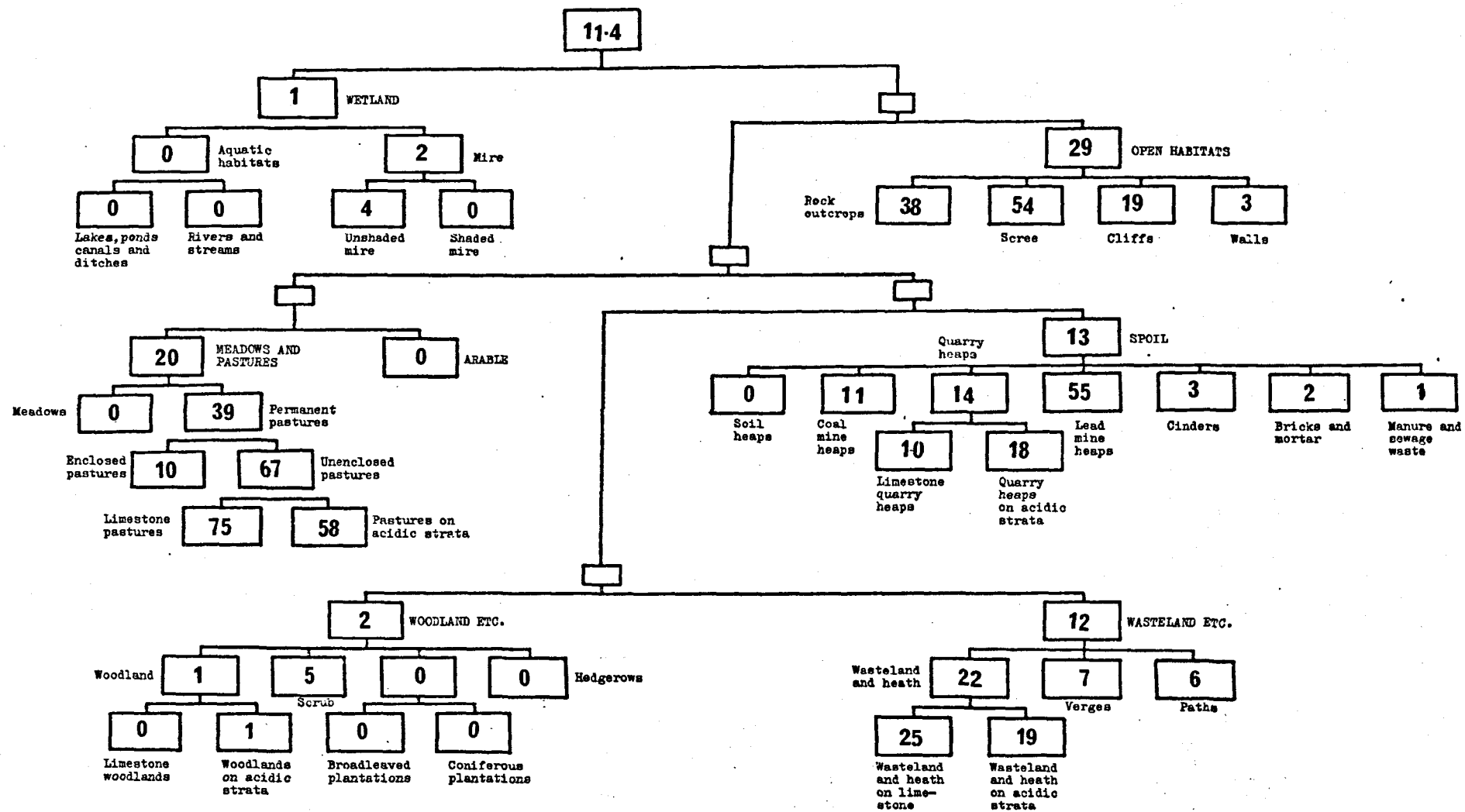


Fig. 3

the species is associated with a wide range of habitat, The plant occurs in open habitats, very common in open limestone scree, and rock outcrops. Arrhenatherum elatius is common in wasteland and occurs in hedgerows, and woodlands. The species is less common in pastures and notably less frequent in wetlands.

Agrostis tenuis is reported by Hubbard (1968) to be common on poor soils on hills and mountains. The data in Fig.2. show that it is abundant in meadows and pastures, in grassland heath and wasteland, spoil (notably on lead mine heaps and coal mine heaps) and rock outcrops. The species is much less frequent in wetlands and woodlands.

Festuca ovina seems to be common in open habitats, notably on limestone scree and rock outcrops. The species is also common in wasteland and heath, in pastures and spoil (again notably on lead mine heaps). Festuca ovina is very scarce in wetlands and woodlands. (Fig.3.)

(c) Distribution in relation to slope and aspect.

The Nature Conservancy Research Unit (Sheffield University) carried out a survey of the vegetation and soils of the semi-natural grasslands of the Sheffield region (Lloyd, Grime and Rorison 1971; Lloyd, 1972). The surveyed area (900 square miles) included six main geological strata i.e. Carboniferous Limestone, (CL) Millstone Grit (MG), Coal Measures (CM), Magnesian Limestone (ML), Toadstone (TS) and Bunter Sandstone (BS).

Data were collected from random one metre quadrats on each of the strata and included rooted frequency estimates of the plant species (i.e. the number of 10 cm² subdivisions of the metre quadrats in which rooted individuals are encountered). In addition, pH determinations were carried out in the laboratory on soil moistened to field capacity. The samples were taken at two soil depths (0-3 cm and 9-12 cm). Other environmental records included, the slope and aspect of the site, geological strata and the incidence and nature of grazing and burning.

It was possible from these data to examine the range in slope and aspect for each of the species. The polar-graphs illustrating the distribution of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina in relation to slope (concentric axes) and aspect (radial axes) in the grasslands of the Sheffield region are shown in Plates 7, 8 and 9 respectively. The range in slope extends from 0° at the centre to 50° at the circumference. Thus a 50° east-facing slope is represented at the extreme right-hand end of the radial axis at the three o'clock position. Radial axes representing the four cardinal points have been drawn, and concentric axes are indicated only by their intersection on the radial axes. Each site of occurrence of the species is marked by a circle, the size of which indicates

Plates 7 - 9.

Polargraphs showing the distribution of the three species in relation to slope and aspect.

7. Arrhenatherum elatius
8. Agrostis tenuis
9. Festuca ovina

Presence
29 28

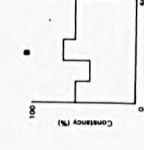
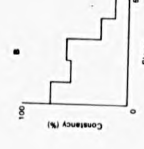
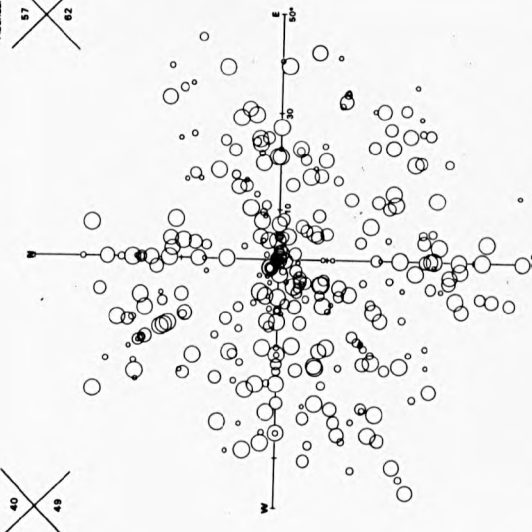
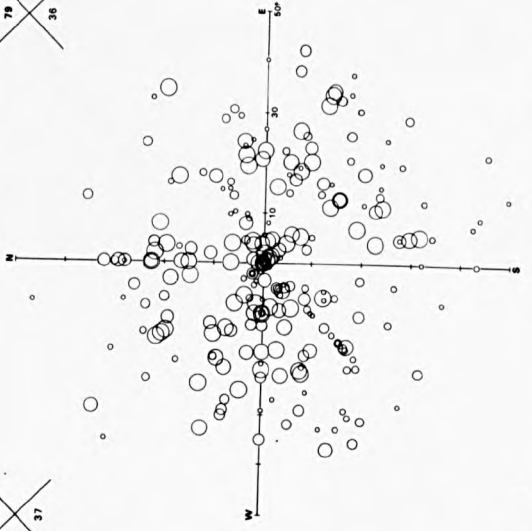
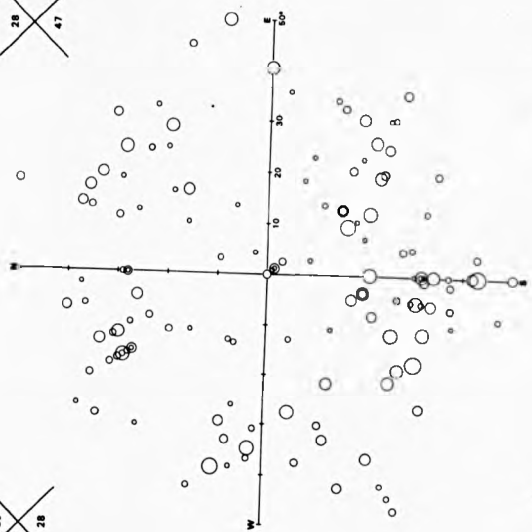
Abundance
28 47

Presence
27 37

Abundance
78 36

Presence
40 49

Abundance
57 62



7

8

9

the recorded frequency. The smallest circle represents a rooted frequency of 1-10 per cent, and the largest 91-100 per cent. Hence a slope or aspect preference may be apparent from the distribution of the sites and the size of the circles. The distribution of the species with respect to aspect is further analysed in the diagrams above the polarograph and with respect to slope in the histograms below the polarograph.

To aid recognition of the aspect preference, the occurrence and abundance of the species are summarized for north-facing and south-facing quadrants of the polarograph. All the records of the species in aspect ranges 315-360-45° and 133-225° on slopes equal to or greater than 5° are given in the left-hand diagram (presence) as a percentage of all the sites sampled in those quadrants. The right-hand diagram (abundance), shows the percentage of those records of presence in which the frequency value of the species exceeded 40%.

To assist recognition of slope preferences, histograms, at the foot of the polarograph illustrate the percentage occurrence of the species in five 10° classes of slope, on acidic formations. (Millstone Grit, Coal Measures and Bunter Sandstone) to the left "A" and on basic formations (Toadstone, Carboniferous Limestone, and Magnesian Limestone) to the right "B" (Grime and Lloyd 1973).

From these data it appears that Arrhenatherum elatius is frequent on steep slopes of all aspects. This finding is consistent with its pioneer role in open screes in the Derbyshire Dales. Higher frequency values are rather more common on south-facing slopes, probably due to the higher frequency of open screes on south-facing slopes.

Agrostis tenuis is common on flat ground and on gentle slopes. The species has a tendency to have lower frequency values on south-facing slopes. Agrostis tenuis was distinguished by Moss (1913) and Balme (1953) as a species characteristic of leached soils of plateau edges on Carboniferous Limestone.

Festuca ovina occurs with wide variations in frequency on all slopes and aspects.

(d) Distribution in relation to geological strata and soil-surface pH.

The 630 sites sampled by (Lloyd, Grime and Rorison (1971) provided a wide range of surface soil pH. The Millstone Grit, the Bunter Sandstone, and Coal Measures contribute the most acidic part of the range, most samples falling below pH 4.0. The samples from the Toadstone fall in an intermediate range of pH (5.0 - 6.5). Most of the samples from the Carboniferous Limestone and Magnesian Limestone have soils of rather higher pH (5.0 - 7.6), although some acidic soils were encountered on both

strata especially from the former. From these data it is possible to calculate the percentage of sites occupied by each species on each geological stratum and also the frequency of occurrence of each species in categories of soil pH range.

Table (1) shows the percentage of sites occupied by Arrhenatherum elatius, Agrostis tenuis and Festuca ovina on each geological stratum and Table (2) shows the percentages of sites occupied by the same grassland species over the pH 3-8.

Table 1.

% occurrence of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina in samples from six geological strata. % values are corrected to the nearest whole number (Data from Grime and Lloyd, 1973).

Species	Geological Strata					
	MG	BS	CM	TS	ML	CL
<u>Arrhenatherum elatius</u>	0	0	7	37	21	51
<u>Agrostis tenuis</u>	30	33	53	87	18	46
<u>Festuca ovina</u>	62	92	33	71	21	76

Table 2.

% occurrence of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina in categories of surface-soil pH. (Data from Grime and Lloyd, 1973)

Species	pH range				
	3 - 4	4.1 - 5	5.1 - 6	6.1 - 7	7.1 - 8
<u>Arrhenatherum elatius</u>	1	13	33	53	52
<u>Agrostis tenuis</u>	34	87	76	32	9
<u>Festuca ovina</u>	55	68	56	68	51

It is possible from the data in the two tables to characterise the ecology of these grassland species in relation to pH. It is clear that the calcicolous species Arrhenatherum elatius is associated with sites of intermediate or high pH (5.1 - 8.0) and is more abundant on the Toadstone, the Carboniferous Limestone and the Magnesian Limestone.

Festuca ovina is a common species over the whole range of soil types and has very high percentages of occurrence in samples from both highly acidic (pH 3 - 4.0) and more calcareous strata (pH 7 - 8).

Agrostis tenuis displays a similar trend with respect to its wide range of distribution, the species is common on strata which have surface soil pH values ranging between 3 - 7, but it is specially frequent in strata (notably the Toadstone) associated with intermediate pH (pH 4.1 - 6.0). The occurrence of Agrostis tenuis and Festuca ovina over a wide

range of soil pH could be related to the occurrence of edaphic ecotypes which are known to occur in both species (Snaydon and Bradshaw 1961; Gregory and Bradshaw 1965).

(e) Distribution in relation to management.

It was possible to assign each of the 630 sites examined during the grassland survey (Lloyd, Grime and Rorison, 1971) to one of the four categories: ungrazed and unburned, grazed burned, ungrazed burned and grazed unburned. Table 3 shows for the separate geological strata, the frequency of occurrence of each species in relation to the preponderance of grazing and burning.

Table 3.

Distribution of Arrhenatherum elatius, Agrostis tenuis, and Festuca ovina on the different geological strata, in relation to four categories of Management. (-) indicates insufficient number of samples for reliable estimate.

(Data from Grime and Lloyd, 1973)

Species	Category of management	Geological Strata					
		TS	CL	MG	CM	ML	BS
		Frequency of occurrence %					
<u>Arrhenatherum elatius</u>	Ungrazed, Unburned	-	77	0	12	-	0
	Grazed, Unburned	0	34	0	0	30	-
	Ungrazed, burned	75	57	-	5	18	-
	Grazed, burned	-	90	-	-	-	-
<u>Agrostis tenuis</u>	Ungrazed, Unburned	-	29	3	56	-	33
	Grazed, unburned	100	54	36	43	0	-
	Ungrazed, burned	69	41	-	67	22	-
	Grazed, burned	-	33	-	-	-	-
<u>Festuca ovina</u>	Ungrazed, Unburned	-	65	21	25	-	92
	Grazed, Unburned	93	80	70	65	50	-
	Ungrazed, burned	38	73	-	5	16	-
	Grazed, burned	-	81	-	-	-	-

These data indicate that Arrhenatherum elatius is common in ungrazed sites, whether burned or unburned. A high proportion of the grazed sites at which the species was recorded were from semi-derelict sheep pastures on the Carboniferous Limestone.

Agrostis tenuis is very abundant in grazed and in ungrazed sites.

Festuca ovina shows highest frequency values in grazed sites. The low frequency of the species in Coal Measures and Magnesian Limestone is associated with the preponderance of ungrazed often burned sites on these strata (Grime and Lloyd, 1973). Festuca ovina is adversely affected by burning (Lloyd, 1968). It is interesting to note, however, that in the Bunter Sandstone, where the sites are ungrazed, the species is abundant. It is perhaps significant that on this stratum the abundance of Festuca ovina in ungrazed turf coincides with conditions leading to a high incidence of droughting i.e. sandy soils in an area of low rainfall.

PART 2.

COMPARATIVE STUDIES UNDER CONTROLLED CONDITIONS

CHAPTER 3.

SEED WEIGHT, SIZE OF SEEDLING AND MORPHOLOGY
OF MATURE PLANT.

The three species - Arrhenatherum elatius, Agrostis tenuis and Festuca ovina show marked differences in the seed size and weight, morphology of seedlings and the mature plant.

a) The seed.

The average weights of the naked cary^oz^opses (for convenience later referred to as seeds) of each species shown in Table 4. (means of 100 naked seeds selected at random and weighed individually by a microbalance) indicate that Arrhenatherum elatius has the largest seed and Agrostis tenuis the smallest seed.

Table 4.

Average seed weights of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina. 95% confidence limits are included.

Species	Mean seed weight
Arrhenatherum elatius	4.5 ± 0.23 mg
Festuca ovina	1.2 ± 0.020 mg
Agrostis tenuis	0.1 ± 0.001 mg

b) The seedlings.

Experiments which were started by seedlings in their early stage of growth, (7 days after germination) allowed

a comparison with respect to size of the seedlings of the three species. It was clear that Arrhenatherum elatius had the largest seedlings and Agrostis tenuis the smallest seedlings.

c) The mature plant.

In experiments in which the three species were allowed to grow under productive conditions, for a year to allow full growth of the plants, (Chapter 10, page 146 Arrhenatherum elatius formed large, loosely tufted plants about 150 cm high.

Plants raised from one seed collection and grown in sand culture in a green house (page 125) and in a growth-room (page 137) and also populations raised from seeds collected from contrasting habitats (a recently derelict pasture, ungrazed wasteland, roadside habitats which were ungrazed, but clipped once every season) and grown in sand culture in the green-house (Appendix 3) showed that a wide range of growth forms could be distinguished.

- (a) A form in which all the shoots are erect.
- (b) A prostrate growth form in which all the shoots approached the horizontal.
- (c) Forms between (a) and (b). In this group are included plants in which most of the shoots are upright, but with some oblique and plants in which most of the shoots were subtended at an angle between 30° and 60°.

The differences in growth form are evident at an early stage of seedling development, i.e. in the first vegetative shoots (Plate 72), and are pronounced throughout the vegetative stage of development. However, with the onset of ^{the} flowering stage, the more prostrate plants form upright culms despite the fact that the vegetative shoots remain in a more or less horizontal position, (Plate 59.). When the distribution of dry matter in unclipped plants (page 135) was analysed by ^{the} stratified clipping technique in which the shoot canopy was separated into 2 cm horizontal strata and the plant material within each stratum oven-dried and weighted, the distribution of dry matter in individual plants of Arrhenatherum elatius confirmed the presence of distinct growth forms. The stratified clip profiles in Fig. 32 show the distribution of dry matter in plants representing each of the three growth forms.

The two extreme forms not only differ in growth habit, but show marked differences in tillering capacity. The plants with prostrate and intermediate growth forms show a greater capacity for producing tillers than plants of the erect growth habit; plants with very prostrate growth form display a greater capacity for producing tillers than plants of the other growth forms (page 138, Plates 73 and 74).

It is important to note that during this work prostrate plants have been recognized under widely different environmental conditions, e.g. in an experimental garden in

Sheffield, in populations raised from seeds and grown in sand culture in a green house and in a growth room. It seems reasonable to conclude (a) that these differences in growth form are genetically determined and (b) that they are not induced by unusual external conditions.

Agrostis tenuis

Agrostis tenuis is a comparatively short grass about 50 cm high, which spreads by short rhizome and stolons (Chapter 10, page 147).

Festuca ovina

Festuca ovina is a tufted non-rhizomatous grass about 20 cm high (Chapter 10, page 147). The stratified clip profiles Fig.32, show that both Agrostis tenuis and Festuca ovina are comparatively short in stature. In the material examined, no evidence of major morphological variation was seen in Agrostis tenuis and Festuca ovina.

CHAPTER 4.

GERMINATION CHARACTERISTICS

The work described below investigates some of the basic biological characteristics of the seeds of the three grassland species: Arrhenatherum elatius, Agrostis tenuis and Festuca ovina. The seeds were collected from three localities in Derbyshire (England). Arrhenatherum elatius and Agrostis tenuis were collected from derelict sheep pasture at Lathkilldale (SK 176656). The former species was collected from a north facing slope and the latter species from a plateau. Festuca ovina was collected from a sheep pasture near Fox-House (SK 272807). This investigation included experiments which examined the course of after-ripening, compared the longevity of seeds and measured the responses of germination to temperature and light.

Experiment A.

After-ripening

In order to test whether the seeds of the three grassland species: Arrhenatherum elatius, Agrostis tenuis, and Festuca ovina require a period of after-ripening, tests of germination capacity were carried out, one day, 30 days, and one year after collection of the seeds. The seeds were stored at room temperature in glass jars while the germination tests were in progress.

Material and methods

The seeds were cleaned by gently rubbing between the fingers, and removing the husk by means of a simple aspirator. This apparatus was first described by Hergert et al. (1966) and modified by Rorison and Sutton (N.C. Sheffield University) by fitting a variable speed rheostat to the motor the more easily to regulate air flow according to the weight of debris to be removed. This cleaning of the seeds allowed selection of fully developed seeds for the test. In addition, removal of the glumes made it possible to detect the radicles at an early stage of emergence. Seeds were sorted out under a dissecting lens to reject broken or insect-damaged ones. There was no discrimination between large and small seeds.

The seeds were germinated on moist filter paper in plastic petri-dishes. Ten replicates (each of 25 seeds) were used for each species. Germination took place in a growth cabinet which provided the following environment: a fluctuating temperature of 20° C day and 15°C by night, alternating periods of 18 hours of light (intensity of 3.3 cal cm⁻² h⁻¹ visible radiation) and 6 hours of darkness. In this experiment and in subsequent work which was carried out in the growth-rooms, light was provided by "warm-white" fluorescent tubes. A seed was considered to have

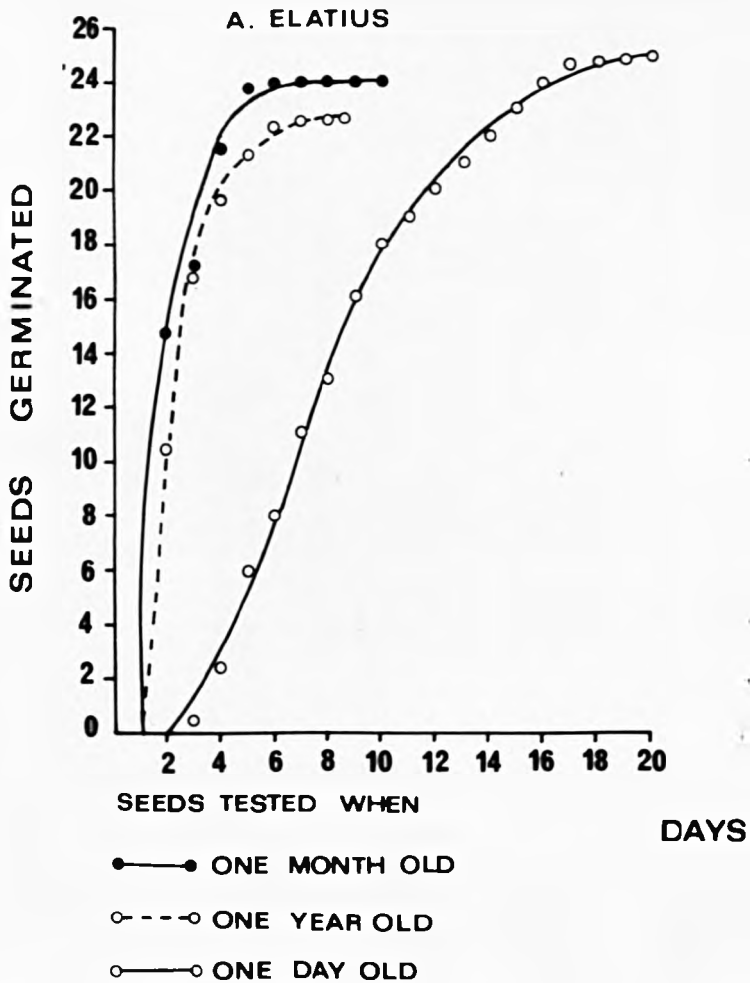
germinated when the radicle emerged. The germinated seeds were discarded immediately and seed counts were made daily until no seeds germinated for seven successive days.

From these data, curves representing the progress of germination during the incubation period were drawn (Fig.4). The mean percentages of germination were calculated using an Olivetti programme which gives the means and standard errors of these means. All the significance tests here and in subsequent experiments were conducted at the 5% level. Coefficients of velocity of germination (Kotowski 1926) were also calculated, using the formula:

$$CVG = \frac{\sum n}{\sum (dn)} \times 100 \quad \text{where } n = \text{the number of}$$

seeds germinating on any given day and d = the number of that day (day of sowing = 0). For convenience the whole is multiplied by 100. In this calculation the early germinating seeds are weighted more than the late germinating ones; hence the higher the figure obtained, the higher the rate of germination. The data representing the mean percentage germination and mean coefficients of germination are shown in Table 5.

Fig.4. Progress of germination of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina, one day, 30 days, and a year after collection. The periods stated refer to the age of the seed when the test started.



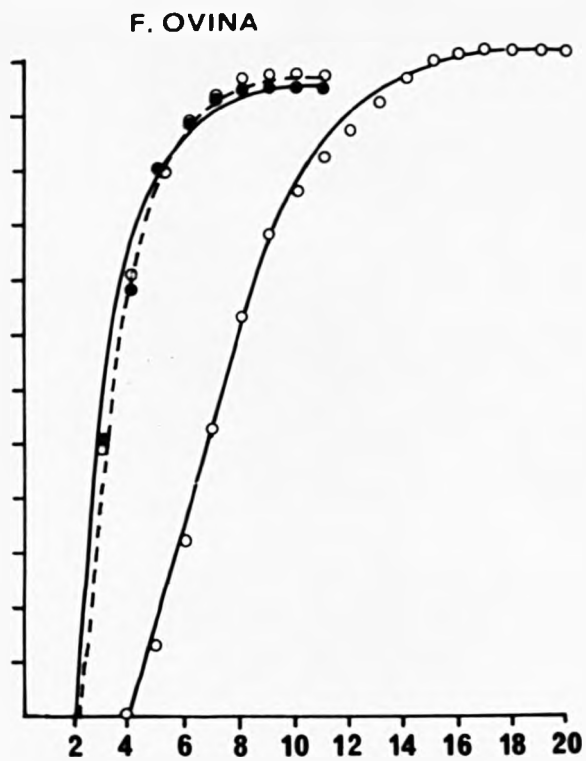
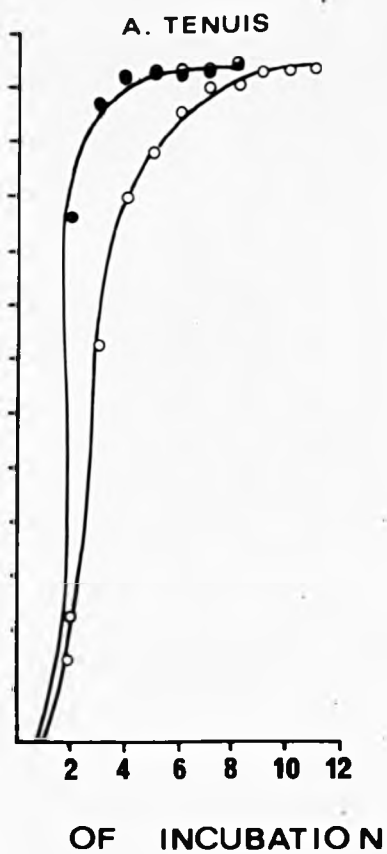


FIG. 4

Table 5.

Mean percentage germination and coefficients of velocity of germination of seeds of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina which were germinated after varying periods of storage after harvest. 95% confidence limits are given.

Species	Age of seed when germinated	Mean coefficients of velocity of germination	Mean percentage germination
<u>Arrhenatherum elatius</u>	One day	11.48 \pm 1.25	99.2 \pm 1.4
	One month	36.40 \pm 2.05	96.0 \pm 1.8
	One year	33.29 \pm 1.47	90.4 \pm 1.4
<u>Agrostis tenuis</u>	One day	26.08 \pm 1.54	98.4 \pm 1.34
	One month	43.74 \pm 1.43	98.4 \pm 1.94
	One year	34.22 \pm 1.34	98.4 \pm 1.1
<u>Festuca ovina</u>	One day	11.68 \pm 0.37	97.4 \pm 0.6
	One month	24.97 \pm 2.01	92.0 \pm 3.0
	One year	23.90 \pm 0.49	93.6 \pm 1.6

Although the freshly harvested seeds of the three species attained very high germination percentages (Table 5) the course of germination in Fig.4 and the mean coefficients of velocity of germination (Table 5) showed that the seeds germinated at a slower rate than the seeds stored for a month or a year

Experiment B.

Germination of Arrhenatherum elatius, Agrostis tenuis, and Festuca ovina at different temperatures in dark and in continuous white light.

In this experiment comparisons were made between the three species with respect to the response of germination to temperature and light.

Materials and methods:

The seeds which were used in this experiment were taken from the same stock of seeds which was used in experiment (A) and the experiment was commenced two months after collection. By this time it was considered that after-ripening had been completed. Replicates of 25 seeds for each species were counted and placed into small sample tubes. To avoid any bias, in allocating seeds to treatments, the sample tubes were taken at random from a box.

The seeds were germinated both in the dark and under continuous white light at the following constant temperatures: 5°C, 10°C, 15°C, 20°C, 25°C, 30°C and 35°C. The temperatures were maintained by means of a series of water-baths, each of which was provided with a stirrer and a thermostat. The seven water-baths were placed inside a growth cabinet with an ambient temperature of 10°C. It was possible to maintain the 5°C and 10°C treatments by circulating the water in the respective water-baths through a supplementary cooling system placed outside the growth-room.

Continuous illumination was provided by banks of "warm-white" fluorescent tubes which gave a light intensity of $3.3 \text{ cal cm}^{-2} \text{ h}^{-1}$ visible radiation. Four replicates

(25 seeds each) for each treatment, for each species, were germinated on moist filter paper discs placed in shallow depressions $\frac{1}{8}$ th inch in diameter which were incised in thick perspex discs. Each perspex disc was placed inside a plastic container which was fitted with a lid. In each container there were thus 25 seeds of each species. Half of the containers in the experiment were used to provide the dark treatment and were painted on the outside with black bituminous paint. The remaining transparent boxes provided the light treatment. In each water-bath 8 containers (four replicates for the dark treatment and four for the light treatment) were floated. The seeds were below the level of the water in the baths. Measurements showed that the air temperatures in the containers were the same as that of the water in the bath and were unaffected by the bituminous paint. To maintain a continuously moist surface for the seeds at the higher temperature treatments (25-35°C) narrow filter paper strips were placed so that one end was underneath the filter paper discs on which the seeds rested and the other was bathed in a reservoir of distilled water at the bottom of the container. In all treatments 2 ml of distilled water were added every day to each of the containers. Plate 10 shows part of the experiment in progress.

Plate 10. The arrangement of floating containers in water baths which was used for the germination tests.



The seeds were considered to have germinated when the radicles emerged; seeds were discarded immediately after germination. A seed count was made daily until no seeds germinated for seven successive days. In the 5°C treatments the start of germination was delayed for seven days or more and tended to continue for a protracted period. The seed count involved the removal of the lid which allowed a change of air and probably prevented accumulation of carbon dioxide from germinating seeds. The count also allowed light to interrupt the dark treatment for a short time.

Results.

The curves in Fig.5 describe the influence of temperature on germination in the three species in the dark treatment and under continuous illumination. It appears from these curves that each of the three species has one or more features to distinguish its germination pattern from that of the other two. Arrhenatherum elatius germinated to a high percentage over a wide range of temperature (5°C - 25°C). Percentage germination declined as the temperature rose above 25°C and fell steeply when the temperature approached 35°C. (Fig.5). The percentage germination of Agrostis tenuis was markedly low at the two

Fig.5. Germination percentages attained by the seeds of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina at different temperatures, in light and in darkness.

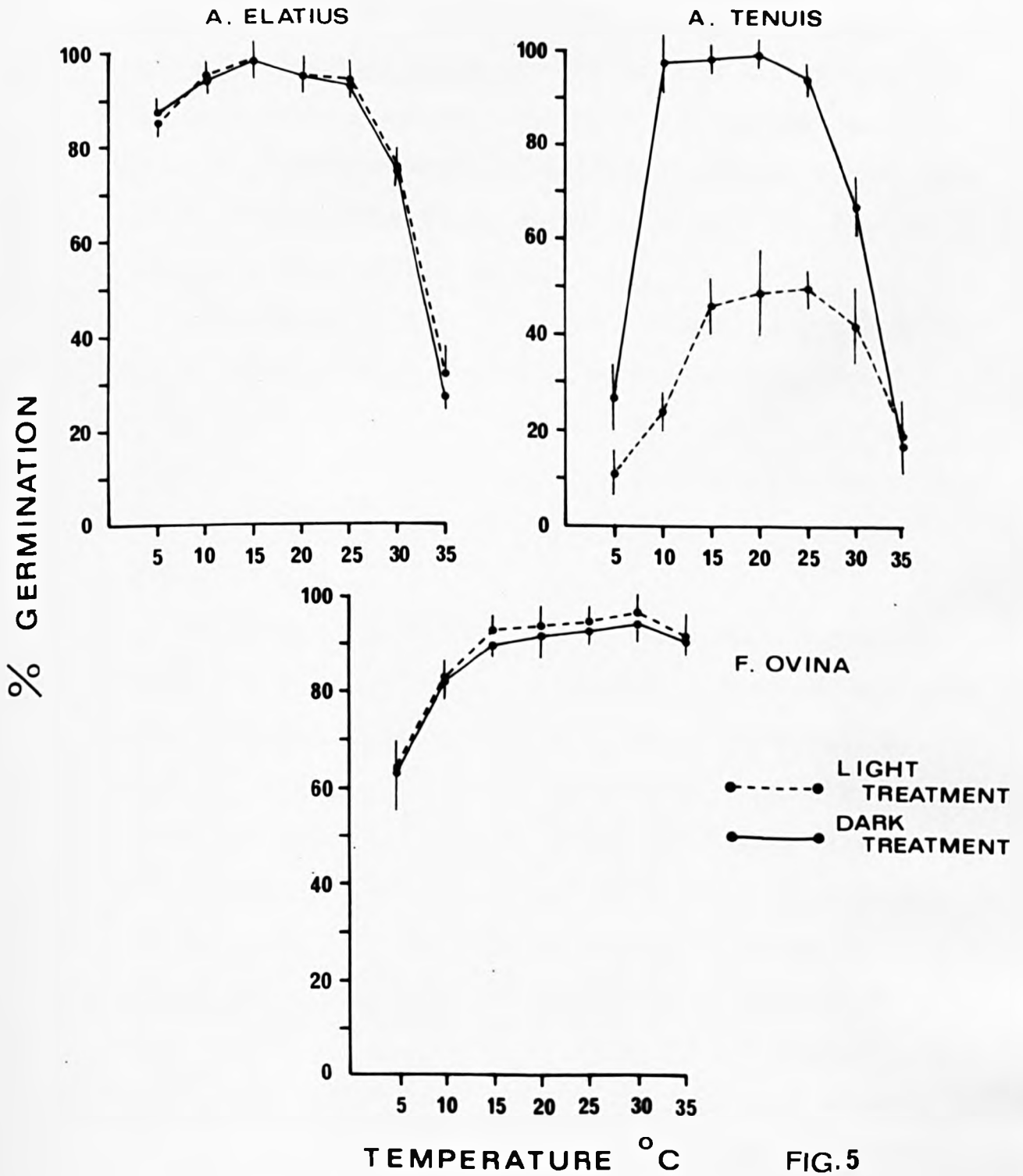


FIG. 5

extreme temperatures (5°C and 35°C), both in the dark and light, but the germination responses to the other temperatures were similar to those of Arrhenatherum elatius. Festuca ovina germinated to a high percentage over the whole range of temperatures investigated. The species germinated more rapidly and to higher percentages at the higher temperature range (15°C to 35°C) than at the lower range (5°C - 10°C).

The curves in Fig. 6 show the course of germination in the three species at the different temperatures (5°C - 35°C) both in the dark and in light. In Fig. 7 further curves are drawn for the three species describing the time required to achieve 50% germination at each temperature.

Although the values for the final total percentage germination of Arrhenatherum elatius (Fig. 5) did not show any difference between dark and light treatments, the curves in Figs. 6 and 7 show that seeds germinated at a faster rate in the dark than under continuous illumination. A comparison of the rate of germination at three temperatures (10°C, 15°C and 20°C) at which the seeds of Arrhenatherum elatius germinated to high percentages both in the dark and in continuous white light illustrate this phenomenon. In the dark, after two days from sowing, the germination percentages were 24.2 ± 5.0 , 56.4 ± 3.2 and

Fig.6. Course of germination of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina over the temperature range 5 to 35°C, in light and in darkness. The numbers on the graphs refer to the time in days after incubation.

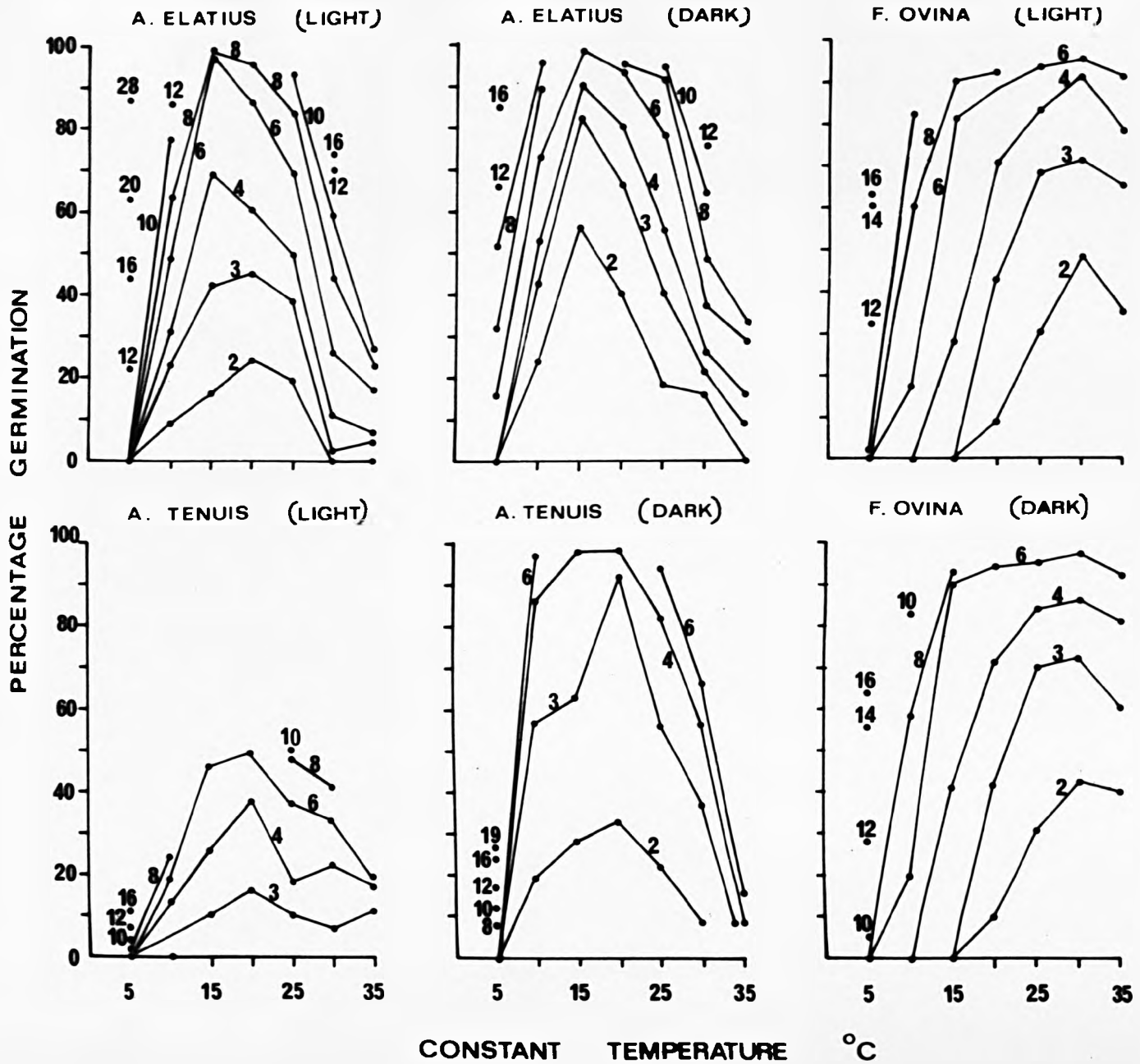


FIG. 6

Fig.7. Length of incubation (days) required
for 50% germination of seeds of
Arrhenatherum elatius, Agrostis tenuis
and Festuca ovina.

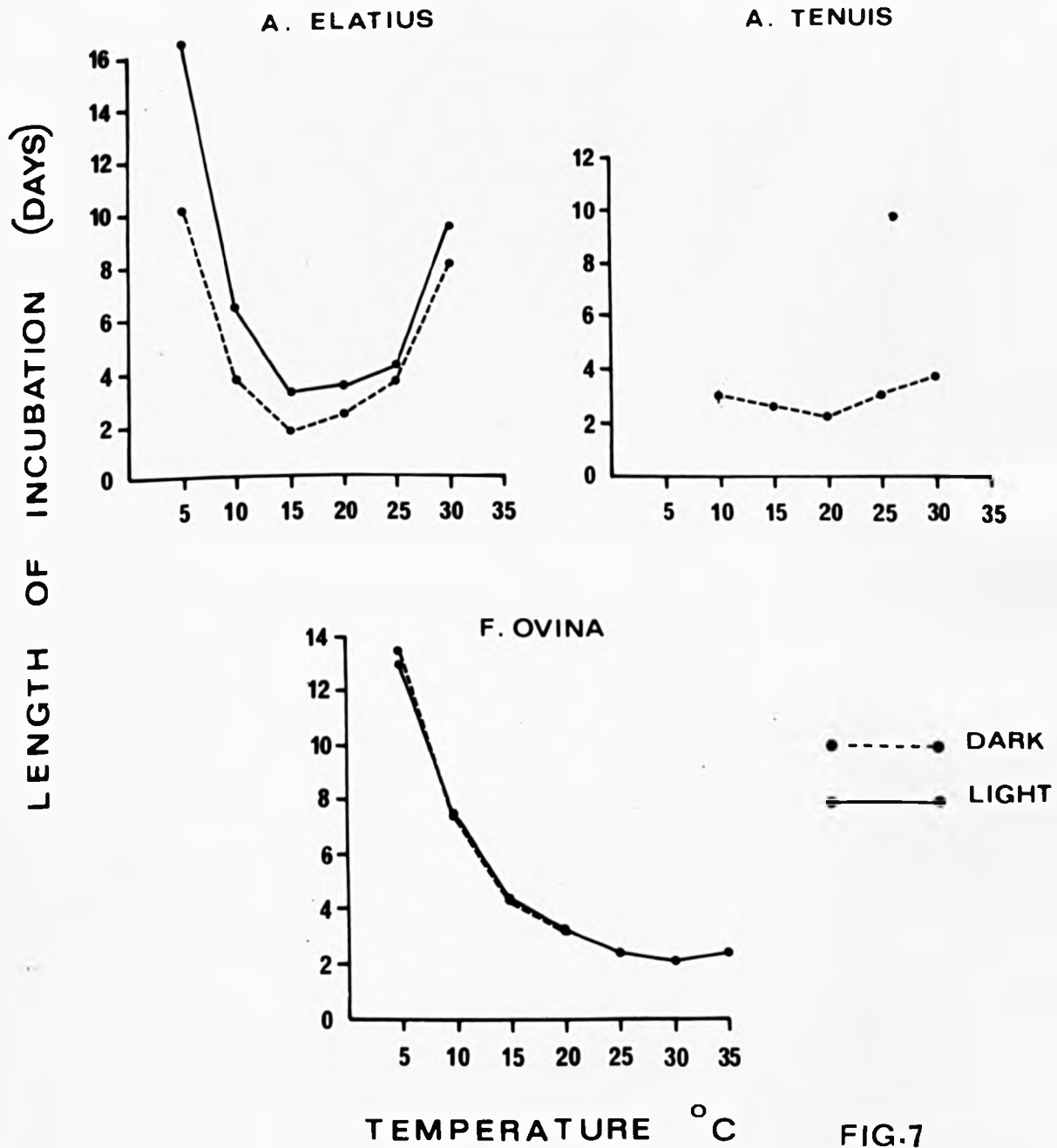


FIG.7

40.2 \pm 3.6 at 10°C, 15°C and 20°C respectively while they were, for seeds germinated in continuous light, 9.2 \pm 3.2, 16.3 \pm 5.1 and 24.3 \pm 5.1 at 10°C, 15°C and 20°C respectively. (Fig.6). The differences were even more obvious when the germination percentages were considered after three days from sowing. The percentages germinated in the dark, at 10°C, 15°C and 20°C were 43.2 \pm 3.5, 82.2 \pm 3.6 and 66.11 \pm 3.65 respectively while, in continuous white light at 10°C, 15°C and 20°C, they were 23.3 \pm 3.2, 42.3 \pm 3.6 and 45.1 \pm 3.2 respectively. The curves in Fig. 7, also showed that the time required for the seeds to reach 50% germination was reduced by darkness.

The data in Figs. 6 and 7 also showed that seeds of Arrhenatherum elatius reached almost 100% germination at 15°C and 20°C more rapidly than at other temperatures; this indicated that the optimum temperature range for the germination of the seeds of this species was between 10°C and 20°C; and that 15°C was probably the treatment closest to the optimum. It is evident that the seeds of Agrostis tenuis are highly light-sensitive. Both germination capacity and speed of germination were favoured by darkness and inhibited by continuous light. This inhibitory effect of continuous white light on the germination of Agrostis tenuis seeds becomes more obvious

when the curves in Figs. 6 and 7 are considered.

Two days after sowing, none of the seeds incubated at 10°C, 15°C, 20°C and 25°C in continuous white light had germinated, but the germination percentages of similar seeds incubated in the dark at 10, 15, 20 and 25°C were 19.2 ± 6.0 , 28.1 ± 5.1 , 33.3 ± 3.2 and 22.2 ± 3.6 respectively (Fig.6). The differences are even more dramatic when the germination percentages of the seeds after three days from sowing are considered.

In continuous white light the germination percentages were 0.00, 10.1 ± 3.6 , 16.1 ± 5.1 and 10.3 ± 3.5 at 10°C, 15°C, 20°C and 25°C respectively, while the germination percentages of seeds incubated in the dark at 10°C, 15°C, 20°C and 25°C were 57.4 ± 6.0 , 63.1 ± 3.1 , 92.1 ± 5.1 and 56.2 ± 5.1 at 10°C, 15°C, 20°C and 25°C respectively. A comparison of the lengths of incubation periods needed for the seeds to attain 50% germination (Fig.7) confirms the inhibitory effects of continuous white light on the germination of the seeds of Agrostis tenuis. Seeds incubated in the dark attained 50% germination, though at varying times depending on the temperature treatment, at most of the temperatures investigated. In contrast 50% germination was attained at only one temperature (25°C) in continuous light.

The data in Figs. 5 and 6, also indicated that Agrostis tenuis seeds had an optimum temperature range for germination between 10°C and 25°C, and that 20°C was probably the best temperature for germination.

That the germination of Festuca ovina was not influenced by light, was very clearly indicated by the almost identical curves for light and dark treatments in Fig.6 and by the overlapping curves in Fig.7.

The curves in Figs. 5 and 6, also showed that for Festuca ovina the optimum temperature range for germination was between 15°C and 35°C and that the most favourable temperature occurred at the higher end of the range (between 25 - 30°C).

Experiment C.

Germination of Agrostis tenuis in complete darkness.

Since the results of experiment "B" indicated that the seeds of Agrostis tenuis were sensitive to light and since the short periods of exposure to light of the seeds germinated in the dark, during the daily seed count might have enhanced germination, a supplementary experiment was set up in which the seeds of Agrostis tenuis were germinated at 20°C in complete uninterrupted darkness for seven days. The procedure adopted was the same as that adopted in experiment "B".

Result

The seeds attained a high percentage germination
(98.2 \pm 2.3)

Experiment D.

Longevity of seeds.

Old seed collections of Arrhenatherum elatius,
Agrostis tenuis and Festuca ovina which had been stored
dry at room temperature, were subjected to germination
tests. The procedure and conditions for the test were
the same as in experiment "A". It is to be noted that
these comparisons were made between different collections
and sources. However, an extensive effort was made to
use comparable sound seeds.

Results.

The curves in Fig.8 show the progress of germination
during the incubation periods. The data in Table 6 show
the mean final percentage germination of the seeds of
each species as well as mean coefficients of velocity of
germination.

In all three species rate of germination as well
as viability of seeds decreased with age.

Seeds of the three grassland species showed marked
differences in longevity.

Fig.8. Course of germination of seeds of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina which had been stored at room temperature. The periods stated refer to the age of the seeds at the start of the test.

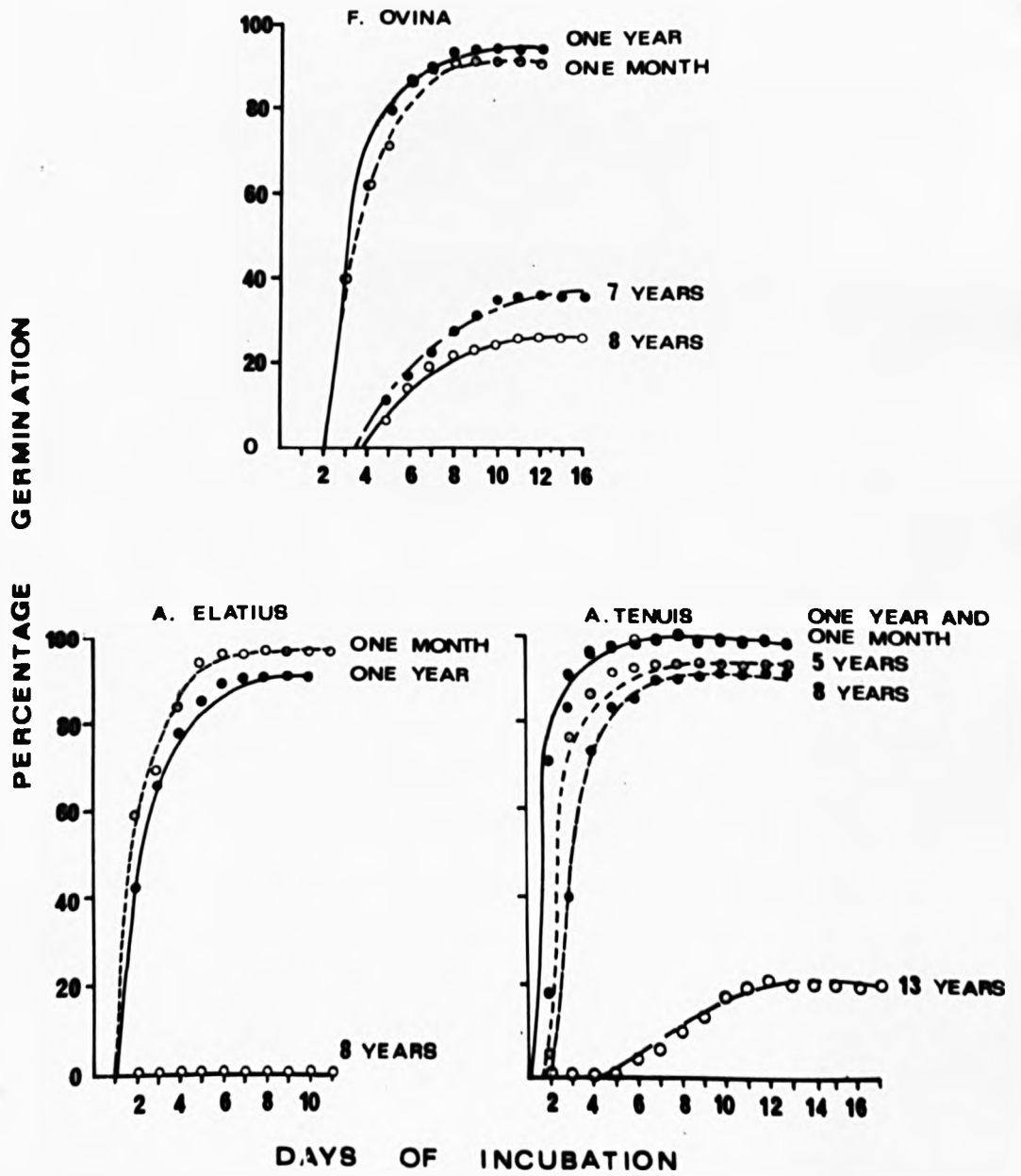


FIG. 8

Table 6.

Mean final percentage germination and mean coefficients of velocity of germination of seeds of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina which were germinated after varying periods of dry storage after harvest. 95% confidence limits are included.

Species	Age of seed when tested	Mean percentage germination	Mean coefficient of velocity of germination
<u>Arrhenatherum elatius</u>	One month	96.0 \pm 1.8	36.4 \pm 2.0
	One year	90.4 \pm 1.4	33.2 \pm 1.4
	8 years	0.00	0.00
<u>Agrostis tenuis</u>	One month	98.4 \pm 1.9	43.7 \pm 1.4
	One year	98.4 \pm 1.2	32.2 \pm 1.3
	5 years	93.6 \pm 1.4	31.1 \pm 1.2
	8 years	91.6 \pm 1.5	25.7 \pm 0.6
	13 years	22.6 \pm 1.5	11.38 \pm 1.6
<u>Festuca ovina</u>	One month	92.0 \pm 3.0	24.97 \pm 2.01
	One year	93.6 \pm 1.6	23.90 \pm 0.4
	7 years	36.6 \pm 1.4	14.0 \pm 1.2
	8 years	25.6 \pm 1.4	13.9 \pm 1.2

Under the conditions of storage used in this experiment, Arrhenatherum elatius appeared to have lost viability much more readily than the seeds of the other species. Storage of Arrhenatherum elatius seeds for one year reduced their germination capacity by 6%; seeds stored for 8 years did not germinate at all.

The seeds of Agrostis tenuis remained viable for much longer periods than the seeds of the other two species. Seeds of Agrostis tenuis stored dry for 8 years had a high germination capacity ($91.6 \pm 1.5\%$) and 22% of the seeds stored for 13 years germinated. Seeds of Festuca ovina which were stored for 8 years had fewer viable seeds than those of Agrostis tenuis, stored for a similar period of time. The germination percentage of seeds of Festuca ovina stored at 7 and 8 years were $36.6 \pm 1.4\%$ and $25.6 \pm 1.4\%$ respectively.

General conclusions and discussion.

The freshly harvested seeds of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina did not seem to exhibit any dormancy, but they germinated at a slower rate than seeds stored for a month or a year (Experiment A). Seeds of these species appear to require a short period of after-ripening treatment in the soil or in storage before rapid germination of high percentage is possible. After ripening effects of this nature were reported by many workers (Toole and Toole, 1939; Borriss, 1941; Lawer, 1953; and Borriss and Arndt, 1967). Tests similar to those carried out in experiment A are in progress in N.C. Unit, Sheffield University and they have produced similar results to those reported above for a majority of the common native grasses examined.

The results of experiment B indicate that the three species differ in their germination responses to light and temperature. Agrostis tenuis seeds are highly sensitive to light. Seeds which were incubated at suitable temperature treatments in the dark germinated very rapidly and almost attained 100% germination; but continuous illumination by white light strongly inhibited both rate and reduced final percentage germination.

The germination of Agrostis tenuis presents an interesting case of interaction between light and temperature. Though the germination percentages fell below the level of the dark treatment, continuous white light illumination became comparatively less inhibitory within the temperature range of 15°C to 25°C; its inhibitory effect was more marked at the two extreme temperatures (5°C and 35°C) (Fig.6).

Seeds of Arrhenatherum elatius germinated in the dark and in continuous light attained similar germination percentages, but the seeds which were incubated in the dark germinated at a faster rate than those germinated in continuous light.

The germination of seeds of Festuca ovina did not seem to be influenced by light or dark; seeds germinated to equally high percentages and at similar speed, when other suitable conditions for germination prevailed.

Effects comparable to the inhibitory effect of continuous white light on the germination of Agrostis tenuis and to a lesser extent on the germination of Arrhenatherum elatius, are very well documented. Soriano (1953) found that the germination of Eschscholzia californica and Amaranthus fimbriatus was strongly inhibited by continuous white light. Isikawa (1957) studied the germination responses of Nigella damascena seeds and found that when they were exposed to a short (1 minute) period of irradiation their germination rates were promoted, but when the same seeds were subjected to longer exposures, the germination rates were inhibited progressively. Koller (1957) found that when the fruits of Atriplex dimorphotegia were during germination exposed to continuous light, germination percentage fell below that of seeds in the dark, although again it was found that a short period of illumination greatly promoted germination.

In view of the reports that a short period of illumination may greatly promote germination in some species (Soriano, 1953; Isikawa, 1957; Koller, 1957, and Koller and Negbi, 1959), and since the seeds which were germinated in the dark in this work were exposed to light for a short time during the daily seed counts, it seems reasonable to suggest that these short periods of illumination may have promoted germination in the dark treatments. However, in

a supplementary experiment, Agrostis tenuis seeds germinated at 20°C in continuous darkness for seven days attained a high percentage germination (98.2 ± 2.3).

The species also showed differences in their germination temperature responses. Festuca ovina and Arrhenatherum elatius differ from Agrostis tenuis in their ability to germinate to high percentages at 5° C. This capacity to germinate readily at this low temperature is consistent with the germination of these two species in the field in autumn, a phenomenon which has been noticed by field ecologists (P.J. Grime, per. comm.).

The capacity of the three species to attain more than 60% germination at very high temperatures (25 - 35°C) which occur only for short periods in their natural habitat in the United Kingdom, may perhaps suggest that their seed physiology retains characteristics evolved in a climate distinct from that experienced in Derbyshire today. It is also possible to suggest that the spread of these species into southern Europe and the Mediterranean countries, where high temperatures are encountered, could not possibly be limited by the failure of these species to germinate at such high temperatures. Festuca ovina is certainly well equipped in this respect. However, the Mediterranean members of the Caryophyllaceae (Thompson, 1970) germinate over the temperature range 4.5 - 24.2°C.

The three species also showed major differences in the longevity of the seeds. Under the storage conditions specified in experiment "C", Agrostis tenuis seeds seemed to have a longer life span than those of the other two species. Festuca ovina was second to Agrostis tenuis in this respect. Arrhenatherum elatius seeds lost their viability very readily.

Although it is difficult to extrapolate from dry storage at room temperature to field conditions in which presumably factors other than moisture (e.g. CO₂ etc.) prevent germination, these differences in viability of seeds may be in part responsible for the abundance of buried viable seeds of Agrostis tenuis and Festuca ovina in the soil and the scarcity of buried viable seeds of Arrhenatherum elatius. Investigations conducted by Milton (1935, 1939) of the content of the buried viable seed in the soils from numerous habitats at various elevations above sea-level, showed that viable seeds of Agrostis tenuis and Festuca ovina occur in great abundance in soil samples. Samples collected from the Derbyshire Dales (Spray in preparation) contained viable seeds of Agrostis tenuis and Festuca ovina, but none of Arrhenatherum elatius. When these soils were put in pots, watered regularly and kept in a heated green-house, seedlings

of Agrostis tenuis and Festuca ovina were always there among the flora. When these seedlings were removed, and the soil disturbed, another population of these seedlings appeared.

Poor seed production cannot be the reason for the failure to find buried viable seeds of Arrhenatherum elatius, since this species produces abundant seeds every year. It is most likely that the mass germination of Arrhenatherum elatius seeds which is observed in the field in late summer and autumn leaves comparatively few ungerminated seeds available for entry into the soil. Furthermore the larger size of the seed as compared with that of Agrostis tenuis and Festuca ovina, probably restricts penetration of seeds into the soil; the shorter potential life span of the seed of Arrhenatherum elatius as compared to those of the other species may contribute further to the scarcity of buried viable seeds. The time at which the seed is shed may also be a factor in determining the availability of buried viable seeds in the soil. Arrhenatherum elatius seeds ripen before the seeds of the other species and are shed very quickly, while the other two species, especially Agrostis tenuis, retain their seeds in the inflorescence; in fact seeds of Agrostis tenuis may be collected in winter. It is possible that a majority of the seeds of Agrostis tenuis are released

at a time when soil temperature does not favour germination and that seeds are washed into the soil during the winter.

The presence of stocks of buried viable seeds in the soil, of Agrostis tenuis and Festuca ovina furnishes these two species with a bank of propagules which will enable the species to regenerate or colonize new areas whenever the opportunity arises. While most grasses depend on vegetative reproduction in maintaining their occupation of the ground, Agrostis tenuis and Festuca ovina appear to possess an additional mechanism involving high densities of buried viable seeds.

CHAPTER 5.

EFFECT OF TEMPERATURE ON THE GROWTH
OF ARRHENATHERUM ELATIUS, AGROSTIS TENUIS,
FESTUCA OVINA, DESCHAMPSIA FLEXUOSA AND
ZERNA ERECTA

Introduction

Temperature is one of the most important of the environmental factors which control the individual processes and reactions of living plants. At every stage in the life cycle of the plant temperature can be a controlling factor. The rate of growth and the form it takes, is the resultant effect of temperature on all such processes as photosynthesis, respiration translocation, mineral nutrient absorption and flower initiation.

In any attempt to understand how a plant species may be adapted to the environment in which it occurs naturally or to which it is to be introduced, it is important to measure the effect of temperature upon both the rate of growth and the allocation of dry matter to various parts of the plant.

Under field conditions, study of the environmental effects on plant growth is hampered by parallel variation in temperature, light intensity and photoperiod. A more precise study of the effects of temperature can be made by use of a controlled environment.

In the experiment described in this chapter an attempt was made to investigate the effect of four constant temperature regimes (15°C, 20°C, 25°C and 30°C on the growth of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa (L.) Trin. and Zerna erecta Huds. The latter two grasses were included in order to place the other species in a wider perspective. Deschampsia flexuosa occurs on damp or wet habitat, often abundant on moors and heaths and also in open woodlands. Zerna erecta occurs on well drained calcareous soils, abundant and often dominant on chalk and limestone downs, on road-side bank and verges (Hubbard, 1968).

Materials and methods.

The experiment was conducted in a controlled environment cabinet. The light intensity at plant height was 0.06 cal. visible radiation $\text{cm}^{-2} \text{min}^{-1}$, with variation less than 10% between the centre and the far corners of the growth-room. Rorison (1964) showed, that this light intensity was sufficient for rapid growth of a range of native species. Relative humidity was c. 70% at 15°C, 20°C and 90% at 25°C and 30°C. A day length of 18 hours was chosen to encourage growth.

Rooting medium

Sand was used as the rooting medium. White washed sand obtained from Messrs. Arnolds Quarries Ltd., Leighton Buzzard, Bedfordshire was purified by acid washing using a procedure similar to that described by Hewitt (1966). Large polyethylene bins, each containing approximately 102 Kg. of sand,

were used for washing the sand. The bottom of the bin was perforated with a number of 2 cm drainage holes which were covered by glass fibre cloth. The following procedure was used to wash each bin-full of sand. Tap water was run onto the sand for two hours; water was allowed to overflow so as to remove any suspended material. This was followed by the addition of 80 litres of 5% hydrochloric acid; the acid was added 20 litres at a time. The sand was then washed by deionised* water until the pH of the washings emerging from the bottom of the bin rose above 4.0. Finally 80 litres of full nutrient solution, pH 5.0, were added to the sand. During all the stages of this acid-washing process, the sand was mixed by stirring. After each experiment, the sand was washed, following the same procedure, and used again.

The 'Long Ashton' complete nutrient solution which was used for rinsing the sand was later used for watering the plants. Table 7. shows the concentrations of the mineral nutrient elements together with their chemical sources (A.R. Grade).

*from a Permutit portable "deminrolit" Mark 6A de-ionising unit.

TABLE 7.

Concentrations of the mineral nutrient elements of a standard Hewitt solution together with their chemical sources (A.R. Grade).

Element	Chemical source	ppm element
Nitrogen	$\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}; \text{KNO}_3$	170
Phosphorus	$\text{Na H}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$	41
Calcium	$\text{Ca} (\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$	160
Magnesium	$\text{Mg SO}_4 \cdot 7 \text{H}_2\text{O}$	36
Manganese	$\text{Mn SO}_4 \cdot 4\text{H}_2\text{O}$	0.55
Copper	$\text{Cu SO}_4 \cdot 5\text{H}_2\text{O}$	0.064
Zinc	$\text{Zn SO}_4 \cdot 7\text{H}_2\text{O}$	0.065
Boron	$\text{H}_3 \text{BO}_3$	0.54
Molybdenum	$(\text{NH}_4)_6 \text{Mo}_6 \text{O}_{24} \cdot 4\text{H}_2\text{O}$	0.048

The volume of sand used as a rooting medium for each individual seedling, was decided in the light of the results obtained by Hunt (1970) in an experiment in which he compared the yields of Helianthus annuus after four weeks of growth, when individual seedlings were grown in a controlled environment in a range of different-sized pots. Hunt concluded that a volume of 500 cm³ of sand was adequate for the range of native plants included in his comparative experiments. However, it was decided in the present work to make allowance for the possibility of very large plants of Arrhenatherum elatius and, accordingly, a slightly larger volume of sand

was used. Transparent polyethylene tubes of diameter 6.5 cm and depth 22.5 cm were used to hold the sand. It was found that the tube could hold 640 cm^3 sand in a vertical cylindrical bag which had a height of 20 cm and a diameter of 6.5 cm. A short upward continuation of the tube (2 cm high) above the level of the sand, retained solution during watering but did not hinder the later emergence and spreading of shoots of the larger species. Four 5 mm diameter drainage holes were made at the bottom of the polyethylene tubes and were covered by pieces of glassfibre cloth.

Preparation of plant material for the experiment.

In order to obtain young seedlings of comparable age, seeds of the different species were imbibed at times so arranged to give simultaneous peaks of germination. A large number of seeds of each species was germinated on a moist nylon cloth in transparent polystyrene boxes, which were placed in a controlled environment cabinet providing the following conditions: Temperature: 20°C (day) 15°C (night). Light intensity: $0.06 \text{ cal cm}^{-2} \text{ min}^{-1}$ radiation. Relative humidity 60%. Day length: 18 hrs.

*Transatlantic Plastics, Garden Estate, Ventnor, I.O.W.

Procedure

Uniformly-sized seedlings were planted singly in individual containers. The age of the seedlings at the time of planting varied between 2 days for species which have larger seeds - Arrhenatherum elatius, Festuca ovina, Deschampsia flexuosa and Zerna erecta and four days for Agrostis tenuis which has a smaller seed. This was to ensure the survival of the seedlings in the experiment.

The experiment was designed to last for five weeks; harvests of 7 replicates at each temperature treatment were made at 2, 3, 4 and 5 weeks.

For all temperature treatments, it was found that the sand in each tube could be kept moist by watering daily with 50 ml of nutrient solution. When watering at this rate, solution emerged from the bottom of the tube and it seems likely that any accumulated nutrients were flushed from the sand. Watering was carried out by means of a 50 ml tilt-measure connected to 1 litre reservoir of solution. The solution used for watering the plants was kept in the growth room. It was feared that under this watering system, the young seedlings especially those of Agrostis tenuis in their early stage of growth, might suffer damage from desiccation because the water content of the top few mm. of sand might be too low for their survival. Therefore during the first week of growth, all the

polyethylene containers were placed in tanks containing solution for a depth of 8 cm. This kept the surface of the sand moist. To avoid displacement of young seedlings by the flow of solution over the surface of sand, watering was carried out by gentle sprinkling using a plastic rose. Excess solution was siphoned off from the tanks after each watering.

After the first week, the tubes were taken out of the tanks and were arranged in rows on a plastic-coated heavy-gauge-steel grille. The latter was supported by rows of inverted 12.5 cm plastic flower pots. This arrangement facilitated completely free drainage from each tube. The plant growth containers were arranged in two randomised blocks, one on each side of the growth-room. This was a precaution to minimize the possible effect of differences between replicates with respect to maintenance. Rorison (1964) has shown that difference in position of plants in the growth-room does not exert a major effect upon yield.

Towards the end of the experiment, the more productive species, Arrhenatherum elatius and Agrostis tenuis, produced shoot material which extended beyond the limit of the aerial enclosure of the containers. However, interspecific shading effect was eliminated by the fact that of the 140 containers present at the beginning of the experiment 70

were removed by the third week. Hence, by the time that the larger species had reached a fairly large size, the early harvests allowed a spacing which eliminated the possibility of shading of the smaller species.

At each harvest, the plants were carefully removed from the sand by submerging the container in tap-water and gradually releasing the plant from the sand. The roots were carefully washed with tap-water.

Measurements

After harvesting, a number of measurements were made on each plant used in the experiment.

These included:-

Shoot height

When the plants were freed from sand, the distance from the sand surface to the furthest point of the shoot was measured.

Tiller production

At each harvest the number of tillers per seedling was counted.

Leaf area

Silhouettes of the leaves, which were removed from each seedling, were made on UNAX 3M3 semi-dry diazo black-line paper*. The leaves were placed on the paper and

*G.A.F. (Great Britain) Ltd., P.O. Box 98, Valmar Road, S.E.5.

flattened beneath a glass sheet. The paper was bleached by exposing it to the lights in a growth-room. The areas under the leaves were developed by wiping with UNAX developer. The paper was air-dried; the images of the leaves were cut out, oven-dried at 100°C and weighed. The leaf areas were determined from lines of areas versus weight drawn from successive known areas of UNAX paper. The limitations of this method of estimating leaf area are discussed by Hunt (1970).

Whole plant silhouettes.

At each harvest a silhouette of a whole representative plant was made on UNAX paper. Photographs of these silhouettes (Plates 11 to 30) provided a visual record of the appearance of the plants at different stages of growth.

Dry weight.

The roots were carefully washed free of sand and were dried between filter paper. The root and shoot on each plant were separated, placed in a paper envelope, oven-dried at 100°C for 48 hours and weighed.

From these data the following growth attributes were determined (unless mentioned otherwise) using the computer programme for plant growth analysis of Hunt and Parsons (1974). The programme involves the fitting of appropriate regressions to logarithmically transformed raw data to derive:--

- (i) Fitted whole plant dry weight (mg).
- (ii) Fitted whole leaf area (cm²).
- (iii) Relative growth rate, rate of increase in dry weight of the whole plant per unit dry weight (g.g.⁻¹ week).
- (iv) Unit leaf rate; rate of increase in dry weight of the whole plant per unit total leaf area (g m⁻² week⁻¹).
- (v) Leaf area ratio, total leaf area per unit plant dry weight (m⁻² g⁻¹ x 10²).

Results

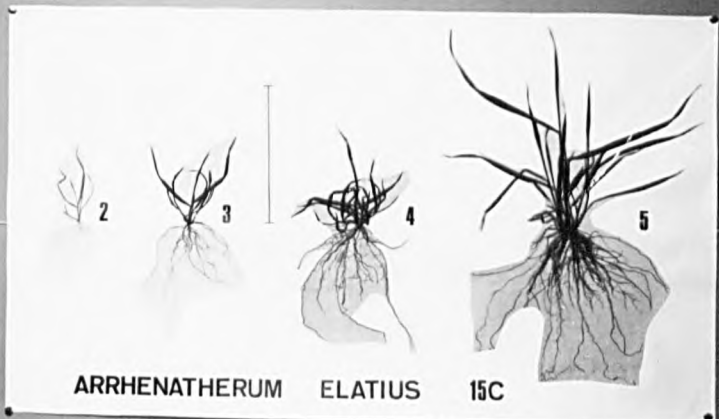
Morphological responses.

Photographs of silhouettes of representative plants of the five species at each harvest at the different treatments are shown in Plates 11 to 30. The graphs in Fig.9 illustrate the mean height (cm) of the five species at final harvest. The data are presented in full in "Appendix 1".

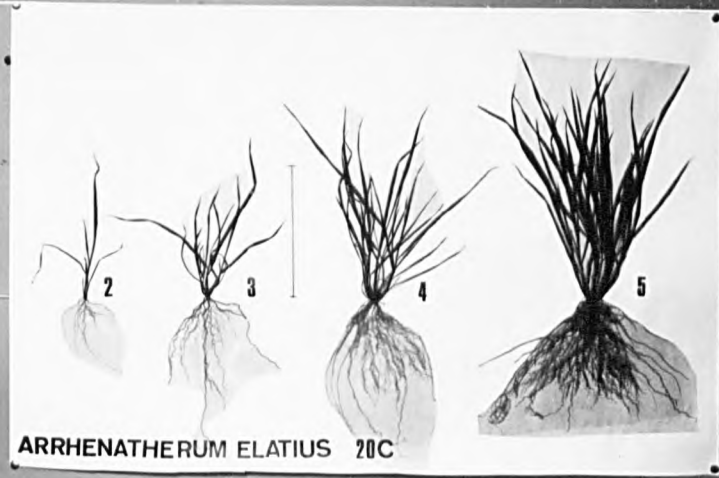
Noticeable differences in morphological responses to temperature were observed in all the species. Plants of all the species were "dwarfed" at 15°C. It was noticed that the foliage of all the species grown at 30°C appeared to have xeromorphic features (i.e. narrower more fibrous laminae). In Arrhenatherum elatius the tallest plants were those grown at a temperature of 25°C. Zerna erecta

Plates 11 - 14

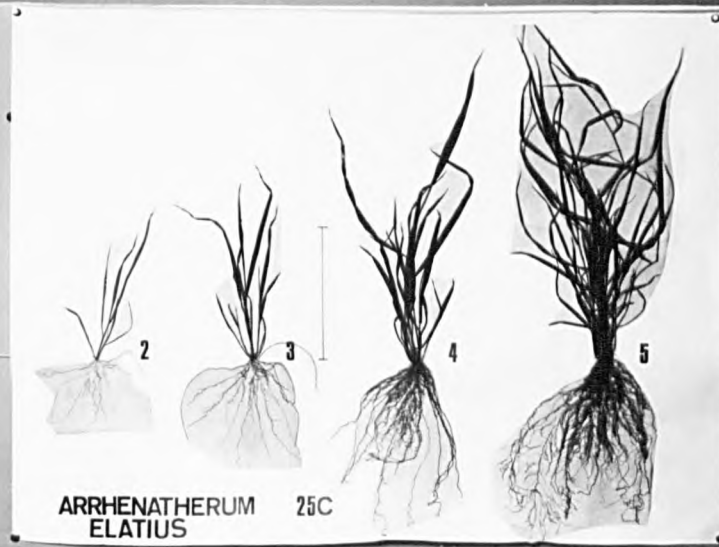
Silhouettes of representative plants of Arrhenatherum elatius, grown at four constant temperatures (15, 20, 25 and 30°C). The figure on the right-hand side of each plant indicates the duration of growth (weeks) at the time of harvest. The vertical scale is 20 cm. in length.



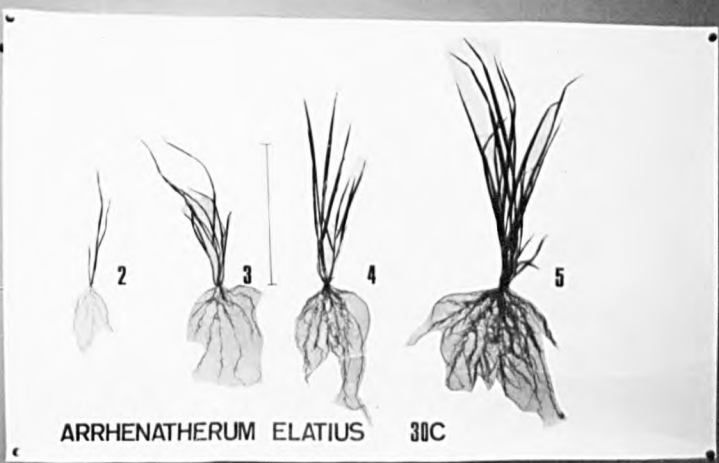
11



12



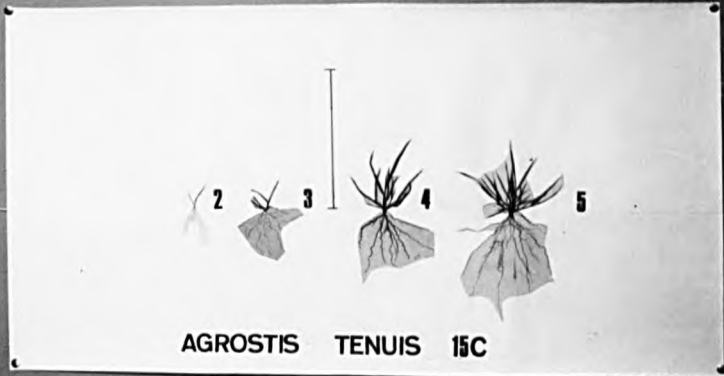
13



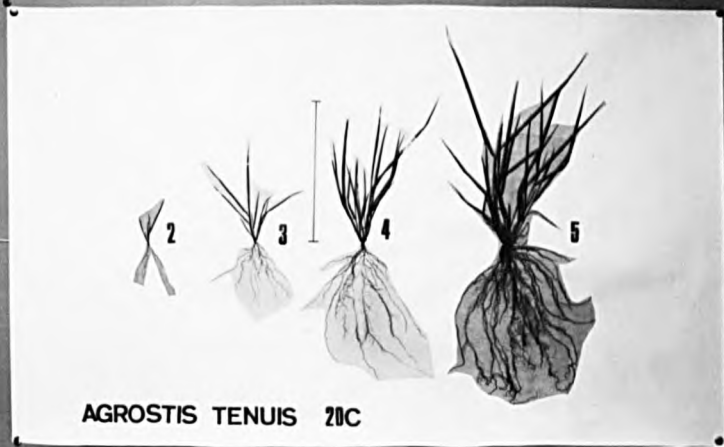
14

Plates 15 - 18

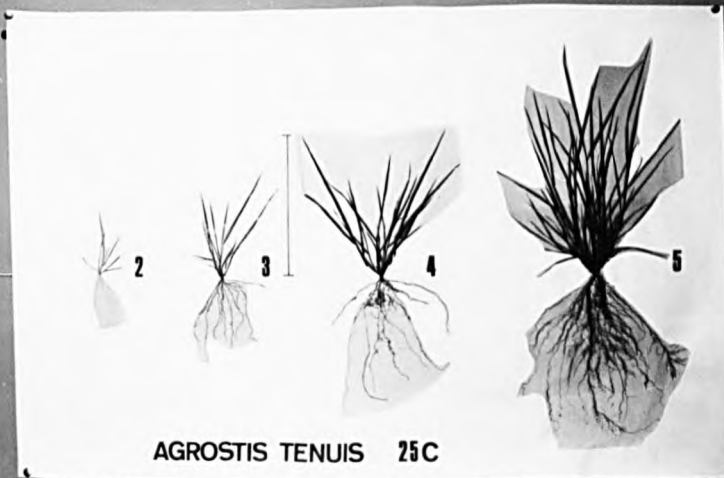
Silhouettes of representative plants of Agrostis tenuis, grown at four constant temperatures (15, 20, 25 30°C). The figure on the right-hand side of each plant indicates duration of growth (weeks) at the time of harvest. The vertical scale is 20 cm. in length.



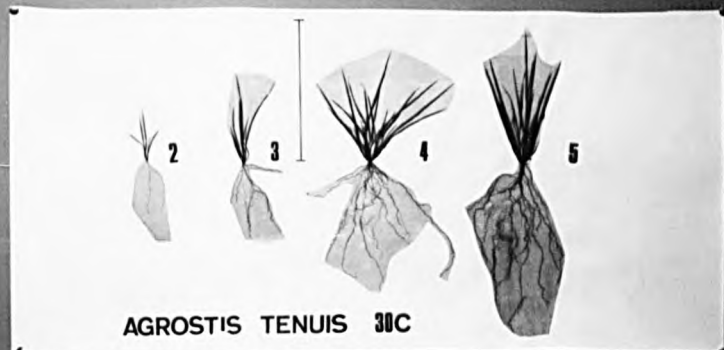
15



16



17



18

Plates 19 - 22

Silhouettes of representative plants of Festuca ovina grown at four constant temperatures (15, 20, 25 and 30°C). The figure on the right-hand side of each plant indicates the duration of growth at the time of harvest. The vertical scale is 20 cm in length.

19



FESTUCA OVINA 15C

20



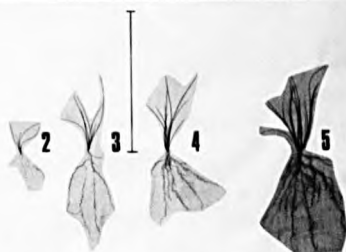
FESTUCA OVINA 20C

21



FESTUCA OVINA 25C

22



FESTUCA OVINA 30C

Plates 23 - 26.

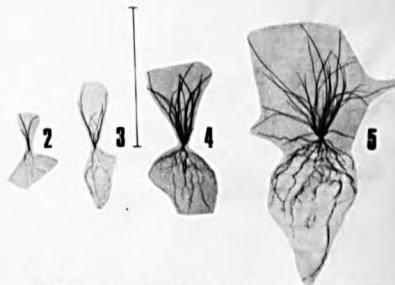
Silhouettes of representative plants of Deschampsia flexuosa grown at four constant temperatures (15, 20, 25 and 30°C). The figure on the right-hand side of each plant indicates the duration of growth at the time of harvest.

23



DESCHAMPSIA FLEXUOSA 15C

24



DESCHAMPSIA FLEXUOSA 21C

25



DESCHAMPSIA FLEXUOSA 25C

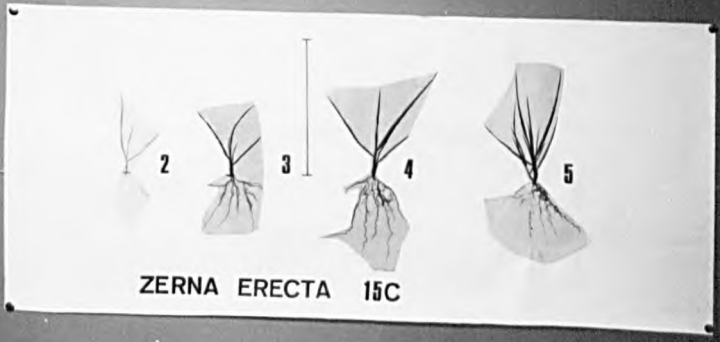
26



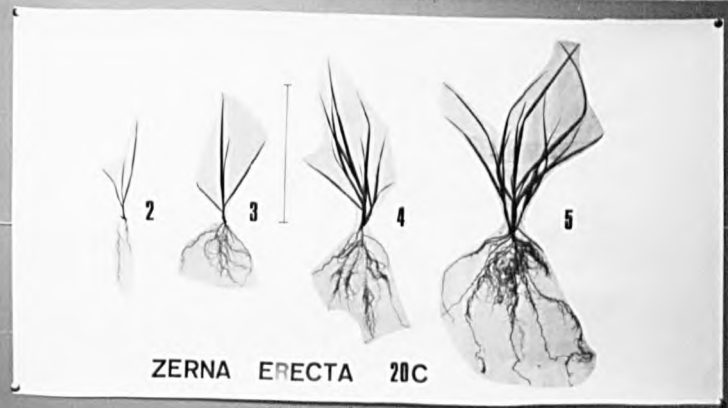
DESCHAMPSIA FLEXUOSA 28C

Plates 27 - 30.

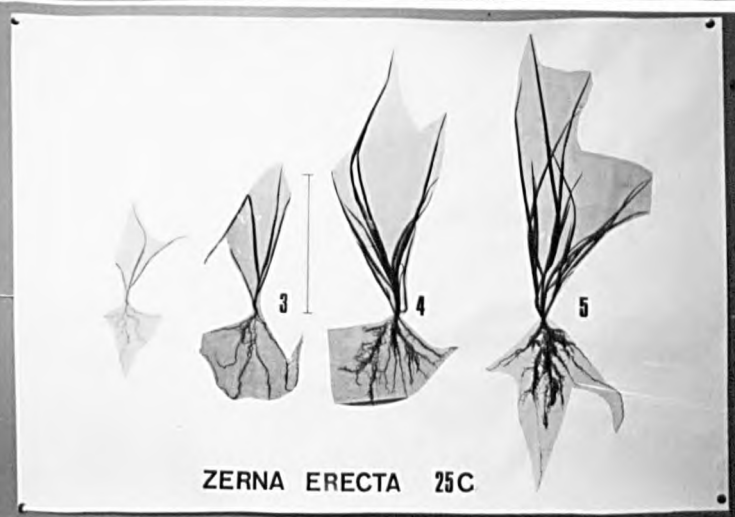
Silhouettes of representative plants of Zerna erecta grown at four constant temperatures (15, 20, 25 and 30°C). The figure on the right side of each plant indicates the duration of growth at the time of harvest. The vertical scale is 20 cm. in length.



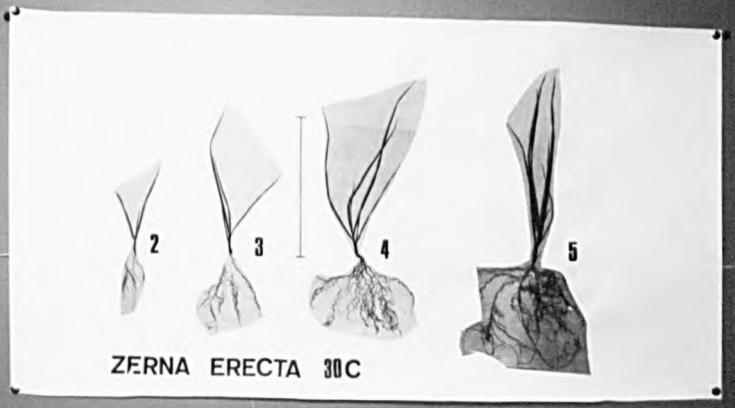
27



28



29



30

Fig.9. Mean shoot height at final harvest (5 weeks) of plants of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa and Zerna erecta grown at four constant temperatures. 95% confidence limits are included. In order to avoid overlap, some confidence limits, here and in subsequent figures, have been deflected from the vertical. In such cases the confidence limit is represented by the length rather than the vertical extent of the line.

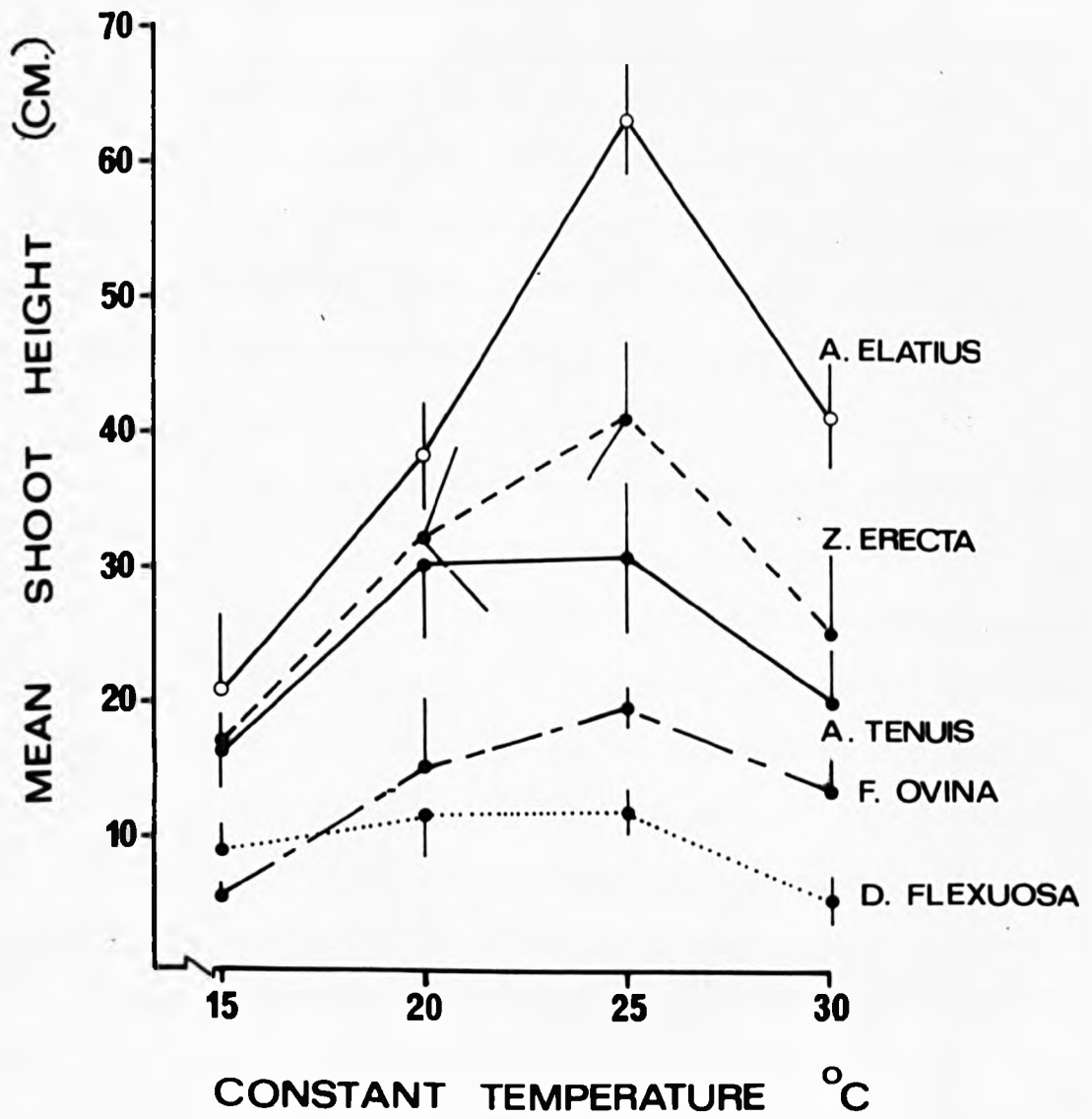


FIG.9

produced tallest plants at 25°C, but a marked decrease in shoot height was noticeable at 30°C. Deschampsia flexuosa showed a marked shoot elongation as the temperature was increased from 15°C to 25°C, but a further increase in temperature to 30°C resulted in a highly significant reduction in height. Festuca ovina and Agrostis tenuis produced tall plants throughout the temperature range 20 - 30°C. The patterns of morphological response to temperature in shoots were evident at the early stages of growth (i.e. by the first harvest) and were maintained until the end of the experiment (Appendix 1).

Tiller number.

The course of tiller production in each species at each temperature is shown in Fig.10 in which the mean log of tillers per plant is plotted against the time of harvest. In Arrhenatherum elatius tiller number seemed to increase as the temperature rose from 15°C, reached an optimum at 20-25°C and was reduced markedly at 30°C. It is interesting to note that although rather dwarfed, the plants of Arrhenatherum elatius produced at a temperature of 15°C maintained a tiller production at a fairly high rate. At 15°C, the tillering capacity of Agrostis tenuis was very much reduced below that of plants grown at 20 to 30°C. In this species the capacity to produce tillers increased

Fig.10. Effect of four constant temperatures on tillering of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa and Zerna erecta. 95% confidence limits are included.

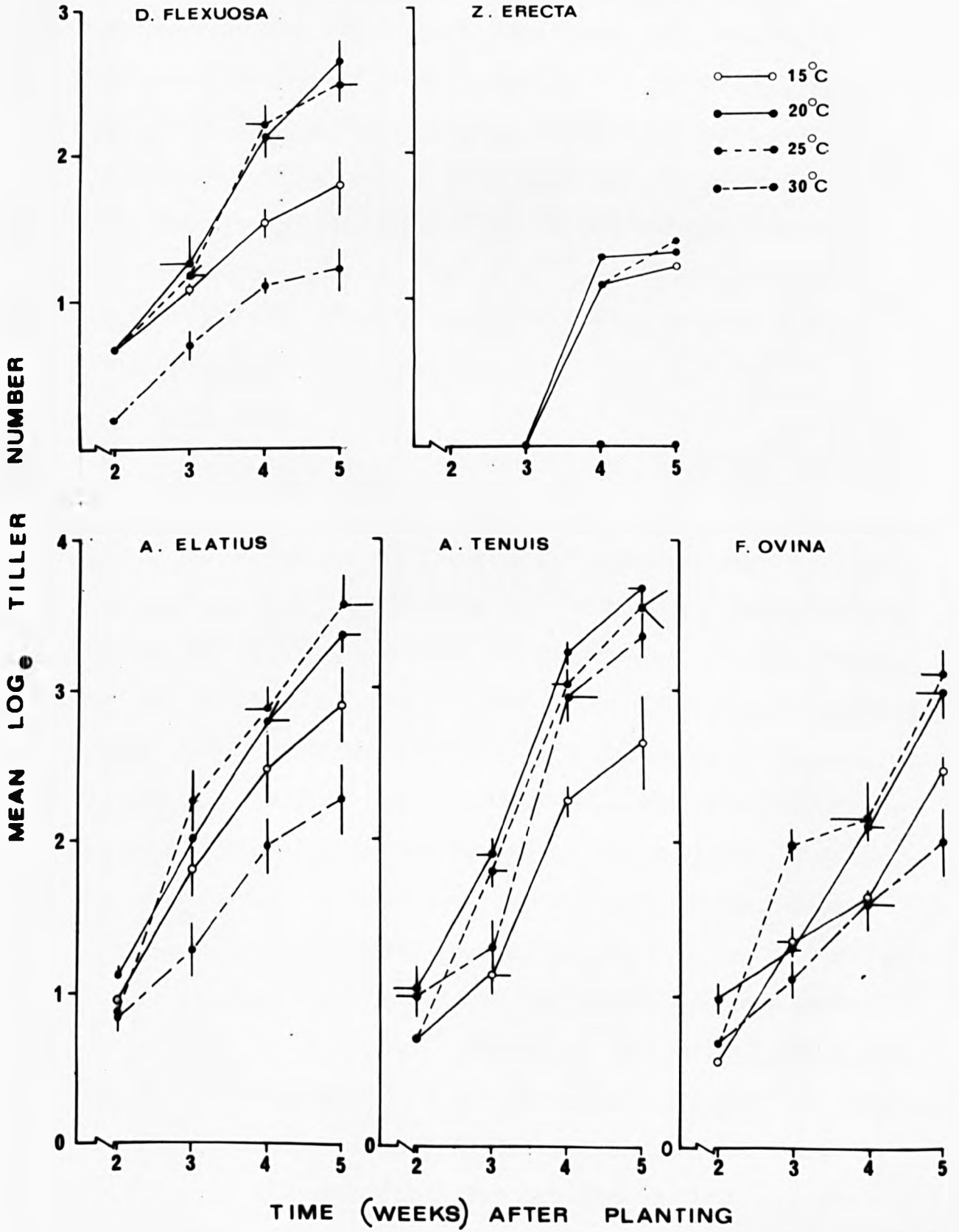


FIG.10

markedly as the temperature rose from 15°C, reached a peak at 25°C and decreased slightly at 30°C. Festuca ovina and Deschampsia flexuosa showed a similar pattern of tiller development in that their number increased as the temperature increased from 15 to 25°C and decreased with a temperature rise to 30°C. At this latter temperature, however, Festuca ovina produced far more tillers than Deschampsia flexuosa.

Leaf area.

Leaf production is one of the most important determinants of yield (Watson 1956). The effect of temperature and light intensity on the rate of growth in leaf surface exposed to incoming radiation determines to a large extent the growth in dry weight of the whole plant. The changes in leaf area, with time, of plants of the different species grown at the different temperatures are shown in Fig.11. In general the leaf area increased exponentially with time at rates dependent on temperature. An increase in temperature from 15°C to 25°C resulted in higher rates of leaf area expansion in all species and a supraoptimal temperature (30°C) resulted in a reduction (of varying degree depending on species) in leaf area expansion. In general the curves for leaf area expansion (Fig.11) resembled those for tiller development, and indicate that temperatures which are optimal for tiller development are also optimal for leaf development.

Fig.11. Effect of four constant temperatures on leaf area expansion of plants of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa and Zerna erecta. 95% confidence limits are included.

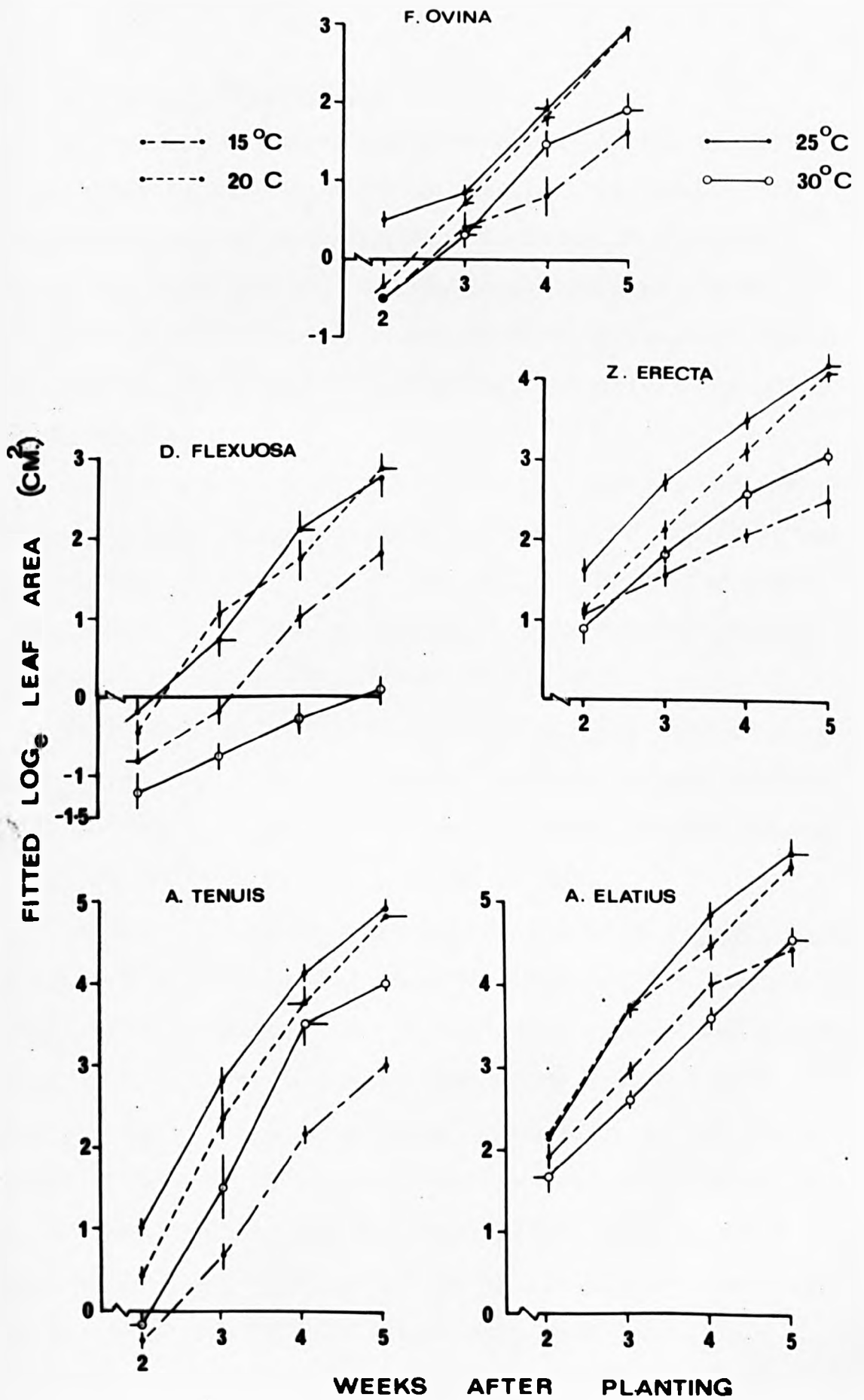


FIG.11

Dry matter production.

The course of dry matter production in each species at each temperature is shown in Fig.12. Generally, all the species showed an exponential increase in dry matter production with time as the temperature increased from 15°C to 25°C. A rise to a supraoptimal temperature caused a reduction in dry matter production, the extent depending on the species.

There was no significant difference between the yields of Arrhenatherum elatius plants grown at 20°C and 25°C, nor between plants grown at 15°C and 30°C. The plants grown at the two former temperatures were significantly greater in yield than plants grown at 15°C and 30°C.

In comparison with Arrhenatherum elatius seedlings of Agrostis tenuis showed a positive response to high temperature in that the yield of the plants grown at 30°C was not far below that of the plants grown at 25°C.

In the first three harvests, seedlings of Festuca ovina grown at 15°C were of significantly lower weight than plants grown at 20°C and 25°C, but in the final harvest the plants grown at 15°C were comparable with those grown at 20°C. Although Festuca ovina responded favourably, in the early stages of growth (see three weeks harvest) to a temperature of 30°C and produced plants comparable in size to those grown at 20°C and 25°C, a decline in yield was evident at the latter stages of growth (see five weeks harvest).

Fig.12. Course of dry matter production in plants of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa and Zerna erecta. 95% confidence limits are included.

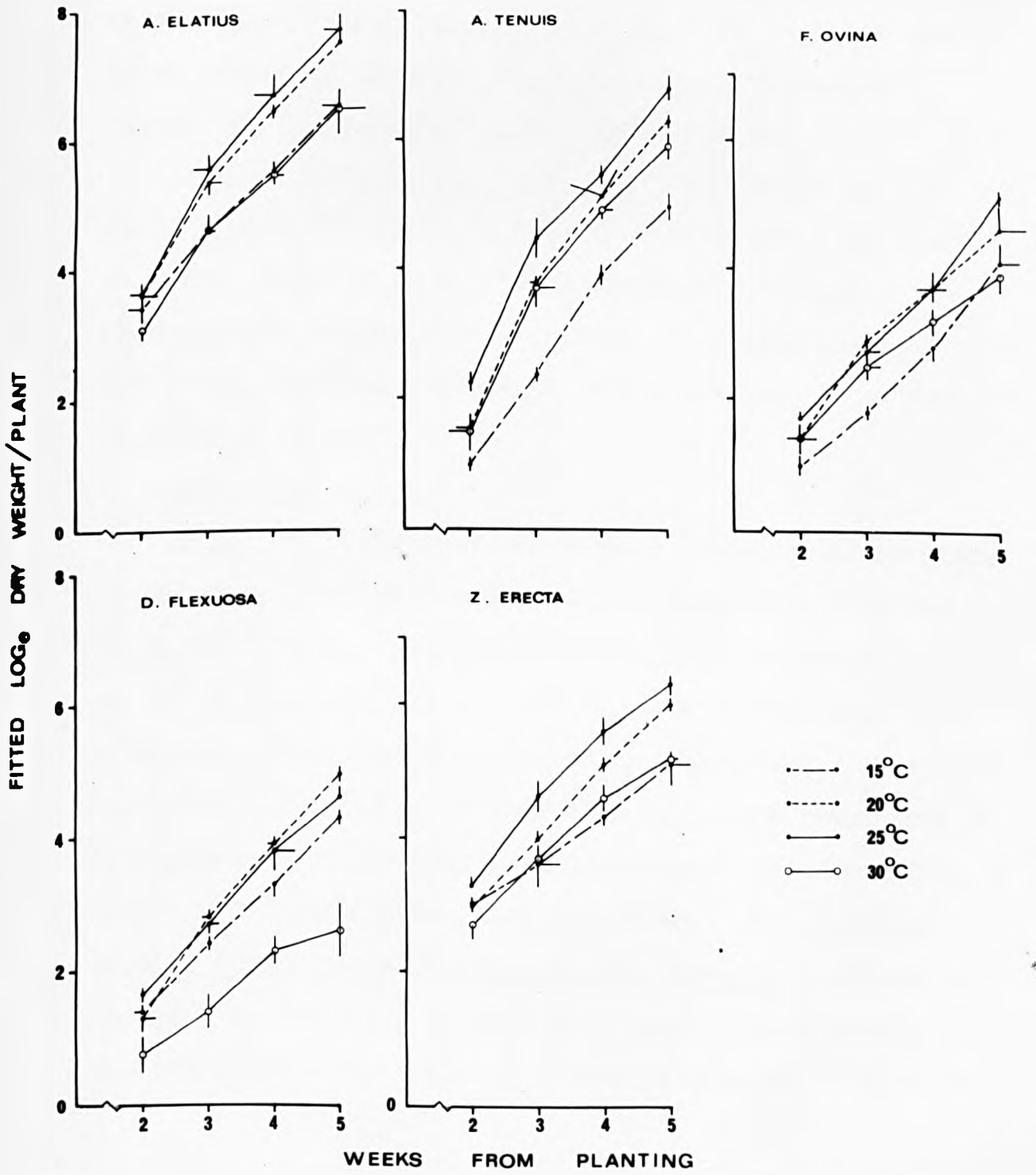


FIG.12

Zerna erecta produced a comparable yield throughout the growing period at 15°C and 30°C, and these yields were, in the latter stages of growth, significantly lower than those of plants grown at 20°C and 25°C. The highest yields were produced by plants grown at 25°C.

Plants of Deschampsia flexuosa grown at 15, 20 and 25°C, produced considerably higher yields than plants grown at 30°C. The yields of plants grown at 20°C were significantly higher than the yields of plants grown at 15°C and 25°C; the plants grown at 25°C significantly outyielded those grown at 15°C.

Leaf area ratio.

Leaf area ratio is of particular interest in any study of the physiology of the whole plant because it provides an estimate of the proportion of the plant potentially active in photosynthesis. The changes in leaf area ratio with time are presented in detail in Appendix 2. The effects of temperature on leaf area ratio are summarised in Fig.13 which is based upon mean values over the five weeks of growth under each temperature treatment. For Agrostis tenuis, Zerna erecta and Deschampsia flexuosa there was an increase in the value of leaf area ratio from 15°C to maximum between 20-25°C, and a decline between 25 and 30°C.

Fig.13. Effect of temperature on unit leaf rate (——) and leaf area ratios (- - - -) of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa and Zerna erecta.

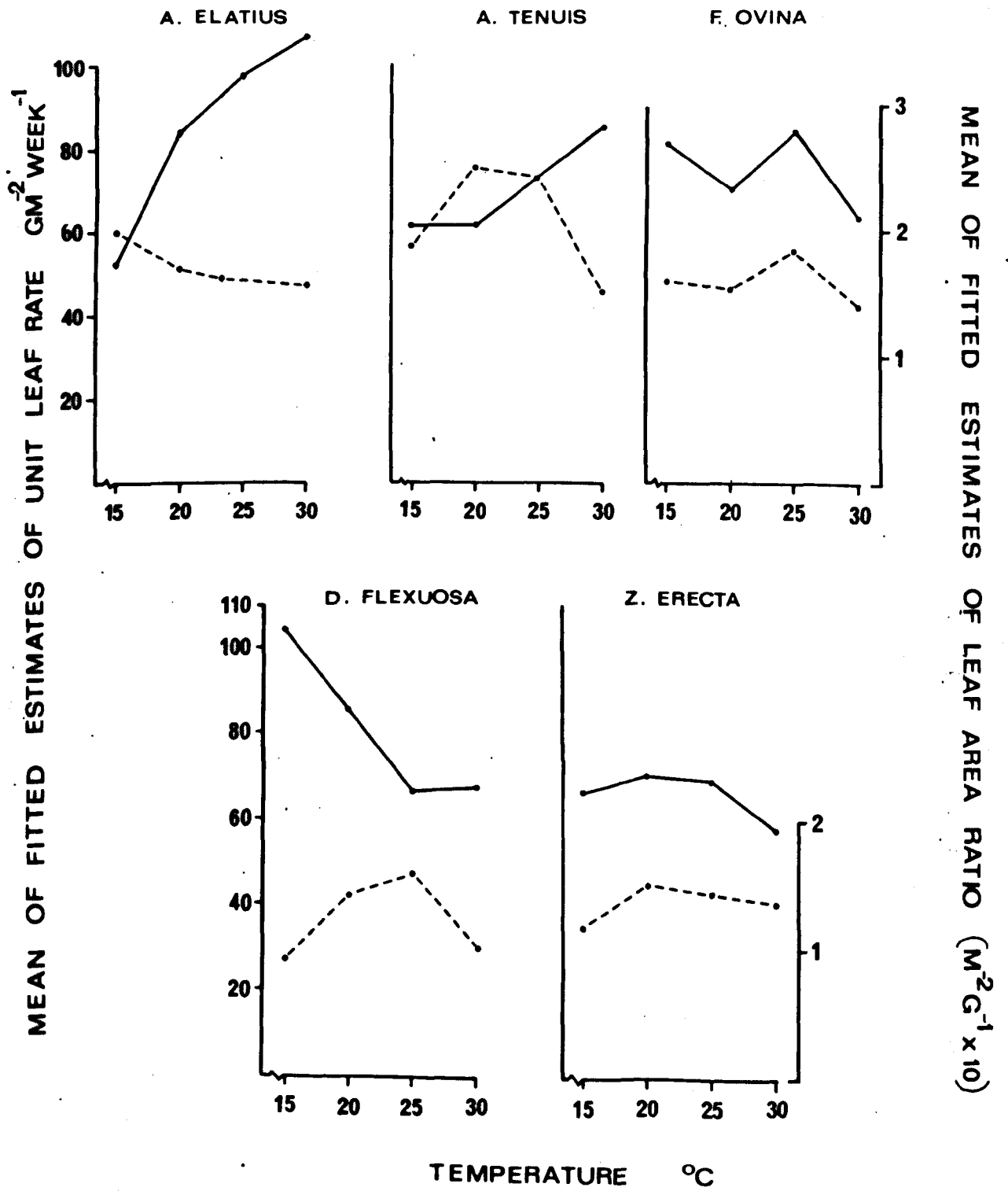


FIG.13

For Arrhenatherum elatius the leaf area ratio decreased as the temperature was raised above 15°C. In Festuca ovina the leaf area ratio declined markedly only at 30°C.

Unit leaf rate.

The changes in unit leaf rates with time are presented in Appendix 2 and mean unit leaf rates are included in Fig. 13. In Arrhenatherum elatius, the unit leaf rate increased as the temperature was raised from 15 C to 30°C. For Agrostis tenuis a temperature rise from 15 to 20°C had no effect on unit leaf rate, but it increased as the temperature increased to 25 and 30°C. Temperature of 25°C produced the highest unit leaf rate in Festuca ovina, but a further rise in temperature to 30°C caused a marked decrease. For Deschampsia flexuosa, an increase in temperature from 15°C to 25°C resulted in a decrease in unit leaf rate, but a further increase to 30°C caused no further decline. The unit leaf rate of plants of Zerna erecta showed relatively little change over the temperature range investigated.

Root/shoot ratios.

The data referring to the effect of temperature on mean root:shoot ratios after five weeks of growth of the five species are presented in Table 8.

Table 8.

Effect of temperature on mean root/shoot ratios after five weeks' growth of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa and Zerna erecta when grown at different temperatures. 95% confidence limits are included.

Species	15°C	20°C	25°C	30°C
<u>Arrhenatherum elatius</u>	0.512 [±] 0.103	0.463 [±] 0.034	0.301 [±] 0.025	0.200 [±] 0.042
<u>Agrostis tenuis</u>	0.447 [±] 0.025	0.356 [±] 0.025	0.335 [±] 0.024	0.272 [±] 0.034
<u>Deschampsia flexuosa</u>	0.365 [±] 0.048	0.247 [±] 0.034	0.235 [±] 0.053	0.234 [±] 1.025
<u>Festuca ovina</u>	0.452 [±] 00	0.313 [±] 0.059	0.313 [±] 0.034	0.365 [±] 0.048
<u>Zerna erecta</u>	0.356 [±] 0.054	0.416 [±] 0.048	0.307 [±] 0.059	0.402 [±] 0.042

For four species: Arrhenatherum elatius, Agrostis tenuis, Festuca ovina and Deschampsia flexuosa the mean root:shoot ratios were highest at 15°C, but decreased at high temperatures. For Zerna erecta the root:shoot ratios did not show statistically significant differences throughout the temperature range used in this experiment. A high root:shoot ratio was maintained at the higher temperature in Festuca ovina and this species showed low plasticity especially in comparison with Arrhenatherum elatius.

Relative growth rate.

The graphs in Fig.14 show dry matter production expressed in terms of relative growth rates.

Fig.14. Relative growth rates attained by plants of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa and Zerna erecta grown at four constant temperatures. 95% confidence limits are included.

RELATIVE GROWTH RATE ($gg^{-1}WEEK^{-1}$)

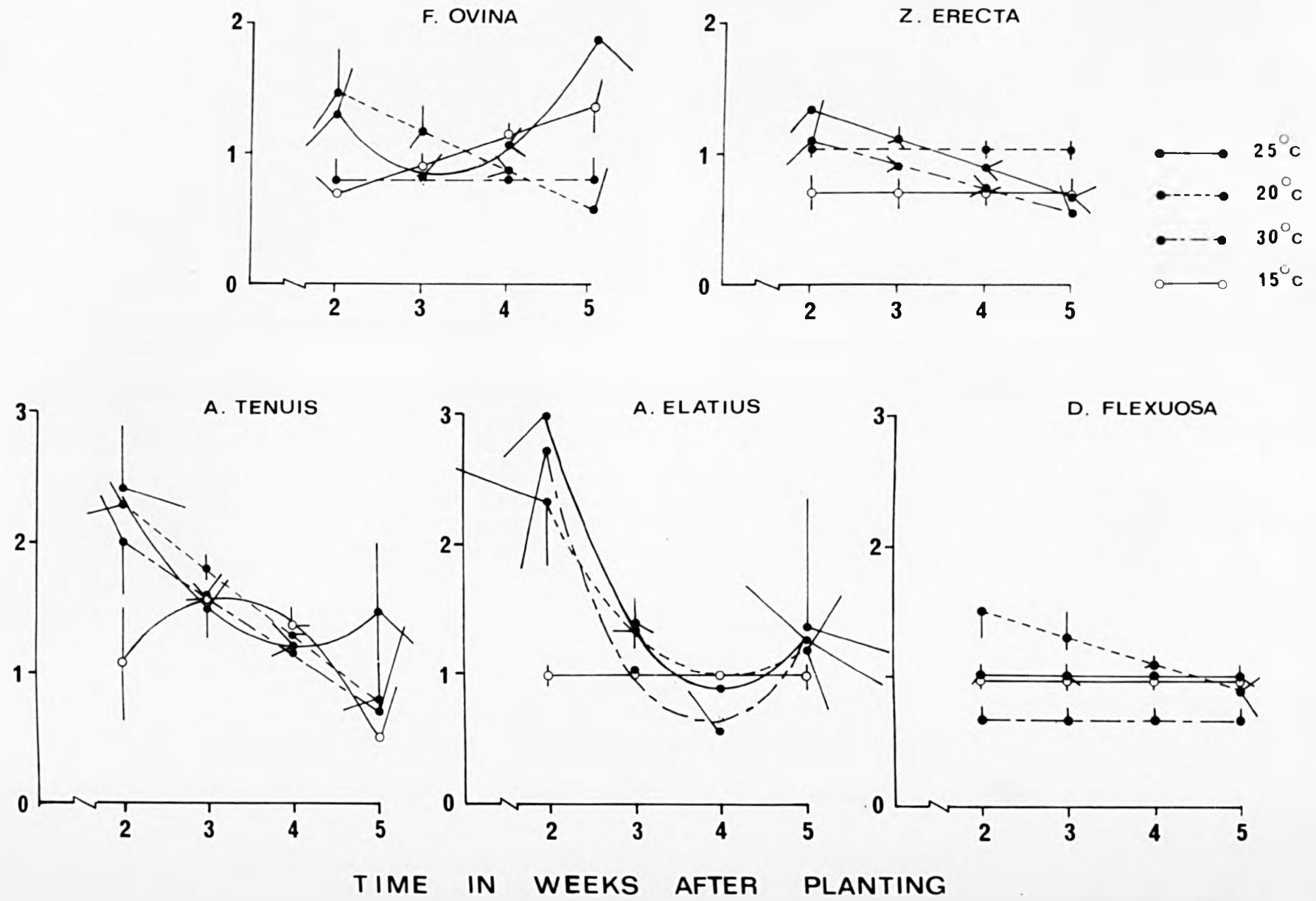


FIG.14

The two potentially fast growing species, Arrhenatherum elatius, and Agrostis tenuis, showed during the early stages of seedling growth, a markedly favourable response to an increase in temperature above 15°C, and attained their maximum relative growth rates at 20°C and 25°C. The relative growth rates of these plants declined steeply with time. Although similar patterns of relative growth rate were shown in the slower-growing species, the curves were much shallower than those of the former two species.

The rise in relative growth rate at final harvest of plants grown at 20, 25 and 30°C in Arrhenatherum elatius, and Agrostis tenuis, a feature which was noticed with plants of Festuca ovina grown at 25°C, is possibly due to the noticeable elongation of the shoot which enabled the seedlings to utilize higher light intensities and/or to an adaptation of the photosynthetic mechanism to these temperatures. These possible explanations were consistent with the fact that the unit leaf rates show a similar upward trend at the end of the experiment.

Plants of Arrhenatherum elatius grown at 15°C had a uniform growth rate which was considerably lower than that attained in the first two weeks by plants grown at 20, 25 and 30°C. The relative growth rates of plants grown at the latter temperatures declined with time, to values comparable to those of plants grown at 15°C, and the rate of fall was faster at 30°C than at 20°C and 25°C.

Plants of Agrostis tenuis grown at 20, 25 and 30°C attained their maximum growth rate after about two weeks of growth. This initial high growth rate was followed by a rapid fall to values comparable with those of plants grown at 15°C. At the latter temperature Agrostis tenuis appeared to grow at a lower rate in the early stages (2 weeks' growth) and attained the maximum growth rates in the third and fourth weeks.

The plants of Festuca ovina grown at 15°C increased their rate of growth steadily with time and attained their maximum growth rate after five weeks of growth. During their early stages of growth, plants grown at 20°C had a higher relative growth rate than plants grown at 15°C. This initially high growth rate declined with time to values lower than those attained by plants grown at 15°C. At 25°C Festuca ovina grew at an initially higher rate than plants grown at 15°C and 30°C. This was followed by a fall in growth rate and then by a rise to a maximum at the end of the experiment. Plants at 30°C grew at a constant relative growth rate which was slower than the initial growth of plants at 20°C, and 25°C and the final growth of plants at 15°C and 25°C.

Plants of Zerna erecta at 15 and 20°C achieved a uniform growth rate, but those grown at 20°C had significantly higher values. At 25 and 30°C, initially high relative growth rates declined with time to values comparable

with those of plants at 15°C. The fall in relative growth rate with time was faster at 30°C than at 25°C.

At 15, 25 and 30°C Deschampsia flexuosa showed no detectable change in relative growth rate over the course of the experiment. Plants at 15°C and 25°C had similar growth rates and these were significantly higher than that of plants grown at 30°C. In the first three weeks, plants grown at 20°C attained a much higher growth rate than that of plants in the other temperature regimes. at 20°C the maximum growth rate was recorded in the first two weeks and was followed by a steady fall to values comparable with those of plants grown at the other temperatures.

General conclusions and discussion.

The data obtained from this experiment show that all the species were greatly affected by the various temperature treatments. Several measures of growth (shoot height, tiller number, yield, relative growth rate) indicate that for all the species the optimum temperature for growth lay between 20 and 25°C.

A marked shoot elongation was observed in plants of all species as the temperature increased from 15 to 25°C. Again in all species a further increase in temperature to 30°C resulted in a decrease in shoot elongation, the extent of which varied with species.

All the species exhibited an optimal temperature for tillering between 20°C and 25°C and warmer temperatures

resulted in a marked reduction in tillering of Arrhenatherum elatius, Festuca ovina, Deschampsia flexuosa and Zerna erecta, but only a slight reduction in Agrostis tenuis.

Tiller production varied between species and in order to understand why, it is necessary to consider what is known about tillering in grasses. In grasses, tiller primordia appear to be initiated at the shoot apex almost as soon as the primordia of the subtending leaves. (Sharman 1942, 1945 Hamilton, 1948). Tiller buds may be found on the axils of the leaves (Evans 1927). Since the tiller primordia are initiated in the axils of leaves, the number of potential tiller sites depends on the rate of leaf appearance. Cooper and Edwards (1961) showed that the upper limit of the rate of tillering is imposed by the rate of leaf expansion and appearance and that a high correlation exists between tiller and leaf appearance rates. The environmental conditions which favour the increase of the rate of production of tiller sites by increasing the rate of production of leaves and which also help the expansion of these buds will increase the number of tillers. Under adverse environmental conditions either the tiller buds do not develop further or they begin to develop but die before the tillers appear. A delay in bud development has been found in Lolium perenne at high

temperatures (Soper and Mitchell 1956) and in barley under conditions of nutrient deficiency (Aspinall 1961). Once tillering starts, tiller numbers frequently increase exponentially with an exponent characteristic of the prevailing environmental conditions until nutrient exhaustion (Troughton 1955) or flower initiation occurs (Aspinall 1961).

Since the plants in this experiment were grown under favourable conditions ensuring adequate mineral nutrients, water and light, and since the plants were harvested before flower initiation, the differences in tiller development presented in Fig.10 were probably due to direct effects of temperature on tiller production.

Throughout the data a close correlation is apparent between tiller number and leaf development expressed in terms of leaf area production. Fig.11 shows an exponential increase in leaf development in plants grown at the different temperatures, the largest increase being observed at 20°C and 25°C.

The general dependence of yield upon leaf area stressed by Watson (1952) is here reflected by the similarity of the curves describing the production of leaf area (Fig.11) and dry matter (Fig.12).

The leaf area ratios and unit leaf rates were also affected by temperature (Fig.13). For Agrostis tenuis, an

increase in temperature from 15°C - 25°C resulted in an increase in leaf area ratio and in a corresponding increase in relative growth rate. Consequently dry matter production increased. The increase in unit leaf rate at 25 and 30°C suggested that, on the basis of leaf area, the species was more efficient in its photosynthetic activity at higher temperatures. In marked contrast the increase in relative growth rate of Arrhenatherum elatius as the temperature increased from 15°C to 25°C could not be explained on the basis of an increasing leaf area ratio, since this did not increase with rising temperature. In this species, increasing relative growth rate with rising temperature is associated with a positive response in unit leaf rate to temperatures above 15°C. In this response, Arrhenatherum elatius appears to resemble Dactylis glomerata. Eagles (1967) showed that the differences in relative growth rates between populations of Dactylis glomerata grown at different temperatures were due to a change in net assimilation rate and not to increased leaf area ratio.

In Festuca ovina, the similarities between the curves describing the responses to temperature in mean leaf area ratio, mean unit leaf rate (Fig.13) indicate that the optimum temperature for the relative growth rate of this species is determined by responses in both leaf area ratio and unit leaf rate.

The increase in relative growth rate of Zerna erecta as the temperature increased from 15 - 25°C, appeared to be associated with an increase in both leaf area ratio and unit leaf rate.

The increased relative growth rate of Deschampsia flexuosa as the temperature increased from 15 - 25°C was certainly not attributable to a change in unit leaf rate since this decreased with rising temperature. A more likely explanation derives from the increased leaf area ratio. In a number of previous studies differences in relative growth rate have been associated with differential rates of production of photosynthetic area rather than with the assimilatory efficiency of this area (Shibles and MacDonald 1962; Muramoto et al., 1965; El Shargawy et al., 1965; Hunt and Parsons 1974).

The response to temperature of relative growth rate (Fig.15 a*) and final yield (Fig.15 b) of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina and Zerna erecta

* Relative growth rate was calculated using the formula

$$\frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$
 where W_1 and W_2 are oven dry weights of the whole plants at the time of the first harvest (t_1) and final harvest (t_2).

Fig.15(a) Calculated mean relative growth rates attained by plants of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa and Zerna erecta, grown at four constant temperatures.

Fig.15(b) Dry weights attained by plants of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa and Zerna erecta at final harvest (5 weeks) when grown at four constant temperatures. 95% confidence limits are included.

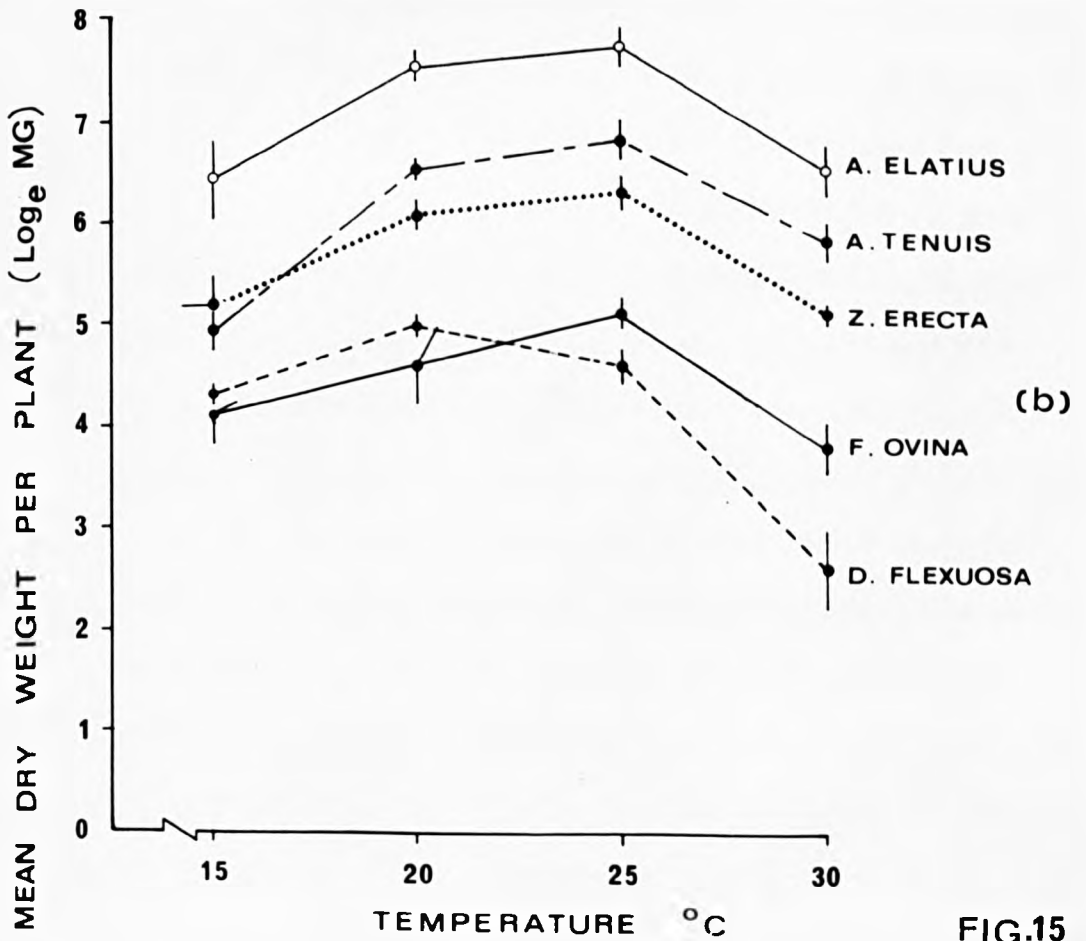
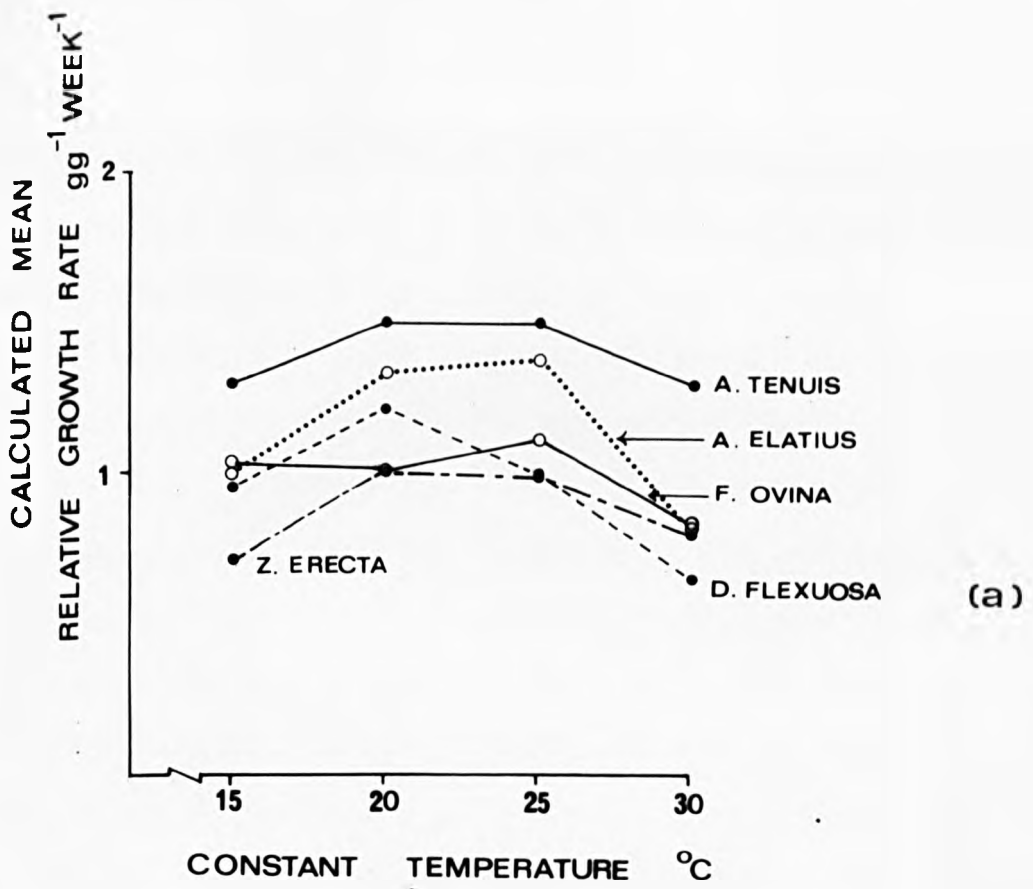


FIG.15

show optima between 20 and 25°C. In Deschampsia flexuosa the optimum was lower than in the remaining species and approximated to 20°C.

Marked effects of temperature on dry-matter distribution within the plant are apparent when the data for root:shoot ratio are examined. In four species, Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, and Deschampsia flexuosa, the root:shoot ratio decreased as the temperature increased from 15 - 30°C. No statistically significant differences in root:shoot ratio were detected in Zerna erecta. Decrease in root:shoot ratio with rising temperature have been reported for many grasses (Harrison, 1934; Barnes, 1936; Brown, 1939; Darrow, 1939; Soper, 1957; Brouwer, 1966; Eagles, 1967). Curtis and Clark (1950) concluded that with few exceptions the root:shoot ratio of plants decreases with temperature rise from 15 to 35°C. Barnes (1936), growing carrot plants at three different moisture levels as well as at three different temperatures, found that at any one temperature the root:shoot ratios were relatively high at low moisture, and at any one moisture they were relatively high at low temperature. In each of the three moisture levels (low, medium, high) which were used, the root:shoot ratios were lower at the higher temperature range (70 - 80°F) than at the lower temperature ranges. Notably low root:shoot ratios were obtained in plants grown in the highest moisture and temperature treatments. Several

workers have concluded that root:shoot ratio is low under favourable edaphic factors and high when these factors are limiting. Davidson (1969 b) showed that soil nutrients and moisture influence the root:shoot ratio. In this study lowest root:shoot ratios occurred when nitrogen phosphorus and water were non-limiting and were highest where there was an imbalance of these factors. Increased nutrient concentration has been associated with a reduction in root:shoot ratio. (Benedict and Brown, 1944; Lovvorn, 1945; Bosemark, 1954; Luckwill, 1960; Neilsen and Cunningham, 1964; Brouwer, 1966; Hunt, 1970).

Since favourable edaphic factors encourage more shoot growth than root growth, it is possible to suggest, from the behaviour of four species, Arrhenatherum elatius, Agrostis tenuis, Festuca ovina and Deschampsia flexuosa, as well as from the data of Barnes (1936), that under favourable edaphic conditions (adequate supply of nutrients and water) and provided that the temperature does not reach a lethal level, some plants will continue to respond to temperatures optimal or supraoptimal for their growth by producing more shoot than root.

The broad similarities between these species in their temperature responses is in agreement with their distribution in Britain; they all seem to occur more or less within similar altitudes. The relatively low optimum temperature

for yield of Deschampsia flexuosa (20°C) and the drastic reduction in yield of the species at 30°C as compared to other species is consistent with the ecology of the species. Deschampsia flexuosa is a species of widespread occurrence in woodlands (see page 51) and the possibility must be considered that the species has evolved in association with woodlands and has expanded into open habitats in relatively recent times.

The favourable response of these species to higher temperatures, which occur only for short periods in their natural habitats in Britain suggests that (provided that other environmental factors are not limiting) these species are adapted to temperature conditions extending beyond the limits of the temperature range commonly experienced in Britain. The ability of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina to grow at comparatively high temperatures, is not surprising in view of the widespread occurrence of these species in Mediterranean countries where as reported by Cooper and Tainton (1965) the mean summer temperature may exceed 30°C and winter daily maxima often exceed 15°C. Arrhenatherum elatius is abundant in Danubian steppes where the climate is relatively hot and dry in summer (annual rainfall (633 mm)(Pfitzenmeyer, 1962).

CHAPTER 6.

RESPONSE OF ARRHENATHERUM ELATIUS, AGROSTIS TENUIS,
FESTUCA OVINA AND DESCHAMPSIA FLEXUOSA TO SHADE.

Introduction.

Plants may react to shade in at least two different ways which may be of ecological interest:- (a) shade avoidance which is effected by rapid initial growth in height which enables the shoot or the individual leaf to penetrate rapidly through the shaded stratum and gain access to higher light intensities and (b) shade tolerance which involves the ability of the plant to survive long periods in which all the foliage is exposed to low light intensities.

Plants which are shade-tolerant must be efficient in carrying photosynthesis at low light intensity and/or able to limit losses through respiration. Went (1957) suggested that the most important adaptation of woodland species was a slow metabolic rate. Grime (1966) and Loach (1967) confirmed this and showed woodland species to have low respiratory rates.

The failure of seedlings of shade-intolerant plants to become established in deep shade has been associated with fungal attack (Vaartaja 1952, 1953, Vaartaja and Cran.1956, Vaartaja 1962). Other workers (Brooks 1908; Foster and Walker 1947; Read 1963; Grime and Jeffrey 1965) suggested that shading increases fungal infection. Grime and Jeffrey (1965) found

that shade-tolerant plants are less susceptible to fungal infection than shade-intolerant species both above and below the compensation point. Many workers (Baker, 1946; Sucharnkov 1956) have established correlations between the falling levels of sugars in shade plants and increased fungal infection. Grime (1966) indeed writes "The carbohydrate economy of the shade-tolerant seedlings is therefore of interest for two reasons. If high levels of sugars are maintained in shade, continued growth may be possible; in addition we may suspect that fungal attack will be restricted".

In the work described below, an attempt was made to determine the lowest light intensities at which each of the four grassland species: Arrhenatherum elatius, Agrostis tenuis, Festuca ovina and Deschampsia flexuosa could maintain a balance between production and consumption of carbohydrate.

Experiment A.

Materials and methods.

The experiment was conducted in a controlled environment room at temperatures of 20°C by day and 15°C by night with an 18 hour day length. Full light intensity was 1100 foot candles and relative humidity was maintained above 60%.

The design of the experiment was 4 species x 4 treatments x 5 replicates. Three shaded treatments were provided by black cloth screens supported on a 62.5 x 57.5 x 40 cm. rectangular 2.5 cm hardwood frame. The screens provided

three light intensities : 25 f.c. 90 f.c. and 330 f.c. Each screen provided one shade treatment and the pots were arranged beneath it in a fully randomised block. At weekly intervals the positions of the blocks within the growth-room were interchanged and the pots were rerandomised within each block. Plants grown in full light provided the control. In order to encourage the circulation of air, the frame of each screen was elevated on four 3 cm thick wooden blocks, one on each corner of the frame.

Seeds were germinated on nylon cloth in transparent polystyrene containers. Uniformly sized seedlings were transferred to the experiment one week after germination. The seedlings were grown in sand-solution culture using 12.5 cm diameter plastic flower pots. Two seedlings were placed in each pot, one in the centre and the other equidistant between the edge and the centre. The pots were watered every other day with excess complete Hewitt solution which was allowed to drain freely.

The plants which had been set marginally in the pots were harvested after one week from the time of their entry into the experiment. The remaining plants were harvested after they had been for four weeks in the experiment. When the first harvest was made, care was taken not to disturb the adjacent seedling.

Because of the difficulties and inaccuracy involved in measuring leaf areas, especially of the two narrow-leaved species, Deschampsia flexuosa, and Festuca ovina, included in this study, estimates of growth involving measurements of leaf area were rejected. The effects of shade were measured in terms of dry matter production. The roots and shoots were measured separately and where necessary a microbalance was used to weigh the small plants. Relative growth rates attained by the species at the different light intensities were calculated by using the formula:

$$R = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \quad \text{where } W_1 \text{ and } W_2$$

are oven-dry weights of the whole plants at first harvest (t_1) and second harvest (t_2). In the calculation of the relative growth rates each pair of plants in a pot was considered as one replicate, thus making it possible to calculate the mean relative growth rates and the standard errors of the means.

Though a complete analysis of morphogenetic responses of these species to shade was not attempted, linear measurements of the shoot were made at the times of the two harvests. The height of the shoot was obtained by measuring the distance from the base of the shoot to the furthest point of the shoot. The increased extension growth, which often accompanies the growth of a plant in the shade, is only

of ecological significance to the plants if it results in the plant gaining access to the less severely shaded aerial environment, i.e. where there is a marked vertical gradient in light intensity close to the ground surface. This experiment provided a uniform shade resembling that which occurs beneath a tree canopy rather than that encountered in grassland. Nevertheless the linear measurements of the shoots are, however, of value in allowing comparison of the abilities of the different species to elongate in shade and assessment of the magnitude of these elongations. In deep uniform shade, the survival of the plant may be dependent, in part, on tolerance of the structural weakening and/or lowering of resistance to fungal infection which are associated with etiolation.

A visual record of the size of representative plants of the different species grown at the different light intensities, was made at the final harvest by making silhouettes of whole plants on UNAX paper. Photographs of these silhouettes were made (Plates 31 to 34).

Results

The measurements of the shoots presented in Table 9 showed that all the species grew in the sense that they increased in linear dimensions with time.

Table 9.

Mean heights (cm) of shoots of plants of four species: Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, and Deschampsia flexuosa, when the plants were grown at different light intensities. 95% confidence limits are shown in brackets.

Light intensity		1100 f.c..		330 f.c..	
Species	Mean shoot height at first harvest	Mean shoot height at final harvest	Mean shoot height at first harvest	Mean shoot height at final harvest	Mean shoot height at final harvest
<u>Arrhenatherum elatius</u>	11.80(±3.07)	47.75(±8.92)	14.80(±2.77)	46.41(±3.87)	
<u>Agrostis tenuis</u>	4.04(±0.113)	23.00(±2.49)	4.34(±0.33)	23.20(±3.74)	
<u>Festuca ovina</u>	3.76(±0.74)	9.46(±2.96)	3.70(±0.74)	15.78(±2.18)	
<u>Deschampsia flexuosa</u>	2.71(±0.50)	8.81(±0.99)	3.40(±0.64)	14.00(±3.15)	

Light intensity		90 f.c.		25 f.c.	
Species	Mean shoot height at first harvest	Mean shoot height at final harvest	Mean shoot height at first harvest	Mean shoot height at final harvest	Mean shoot height at final harvest
<u>Arrhenatherum elatius</u>	14.80(±3.32)	34.60(±3.54)	11.40(±1.40)	21.80(±4.65)	
<u>Agrostis tenuis</u>	2.90(±0.80)	15.80(±2.71)	2.14(±0.26)	2.84(±0.77)	
<u>Festuca ovina</u>	4.28(±0.66)	15.4(±2.82)	4.00(±0.42)	5.64(±0.34)	
<u>Deschampsia flexuosa</u>	3.56(±0.11)	11.28(±0.75)	3.40(±0.49)	4.90(±0.84)	

After the first week of growth, Arrhenatherum elatius produced seedlings in both control and shade treatments which were tall in comparison with the other species, and these differences in height were maintained until the end of the experiment. (Compare plates 31 to 34).

This rapid initial height growth of the seedlings of Arrhenatherum elatius is consistent with the suggestion of Grime and Jeffery (1965), that rapid initial height growth in shade is a characteristic of seedlings of species occurring in dense grassland, and less rapid initial height growth in shade characterises species which are restricted to low turf and bare soil. Since Arrhenatherum elatius commonly occurs in tall ungrazed grassland, it is possible to suggest that this rapid elongation of seedlings permits rapid emergence from the shaded portion of the closed turf and thus makes seedling establishment possible. Professor C.D. Pigott has found that rapid emergence allows colonization of stabilized scree by Arrhenatherum elatius in Derbyshire, England. Seeds are washed down between the rocks and germinate in humid pockets which may be a considerable distance below the scree surface. From this position the first leaf grows upward to the light through a distance up to 10 cm (Grime and Jeffrey 1965).

Fig.16 shows the relationship between light intensity and yields of the four species after four weeks of growth.

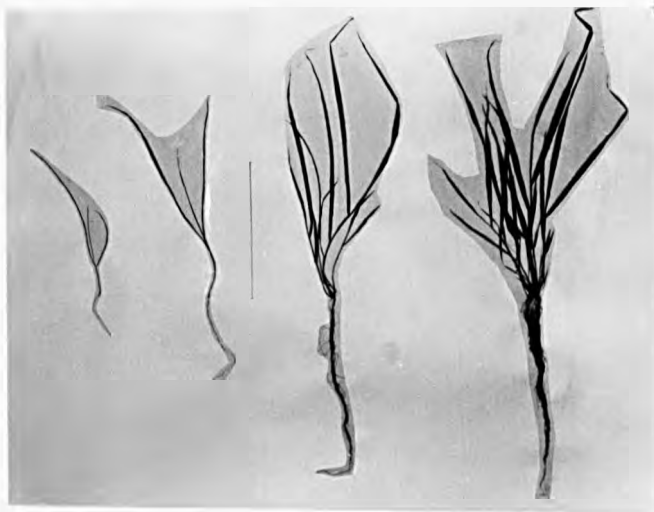
Plates 31 - 34

Silhouettes of representative plants of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa grown for four weeks at four light intensities.

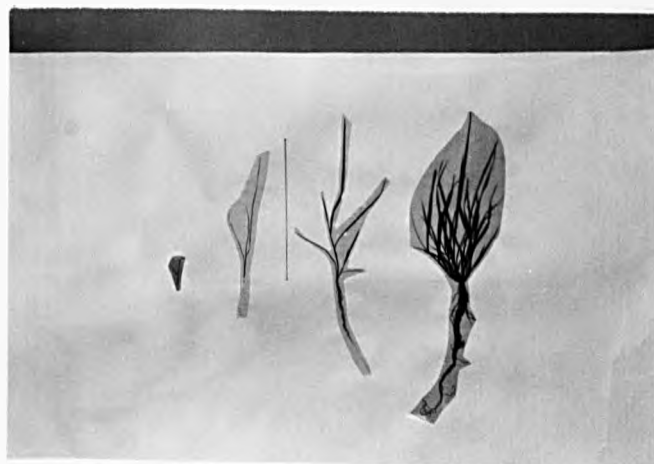
Treatments from right to left are 1100, 330, 90 and 25 f.c.

The vertical scale is 20 cm in length.

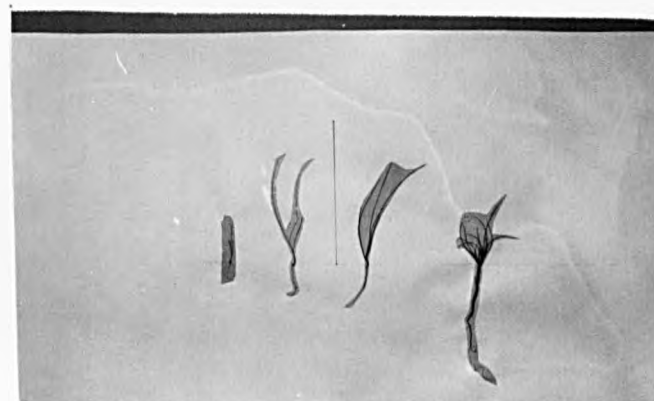
31. Arrhenatherum elatius.
32. Agrostis tenuis.
33. Festuca ovina.
34. Deschampsia flexuosa.



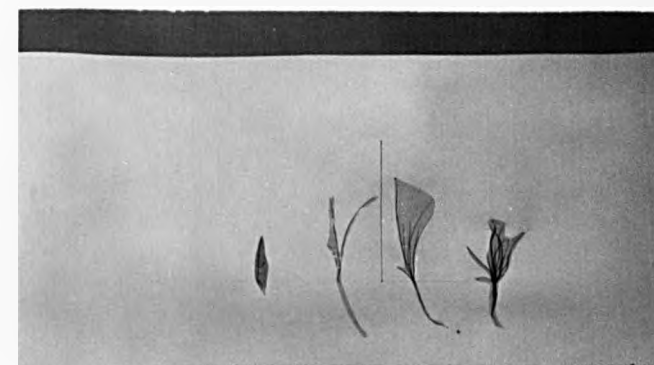
31



32



33



34

Fig.16. Relationship between light intensity and yield of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa, after four weeks of growth.

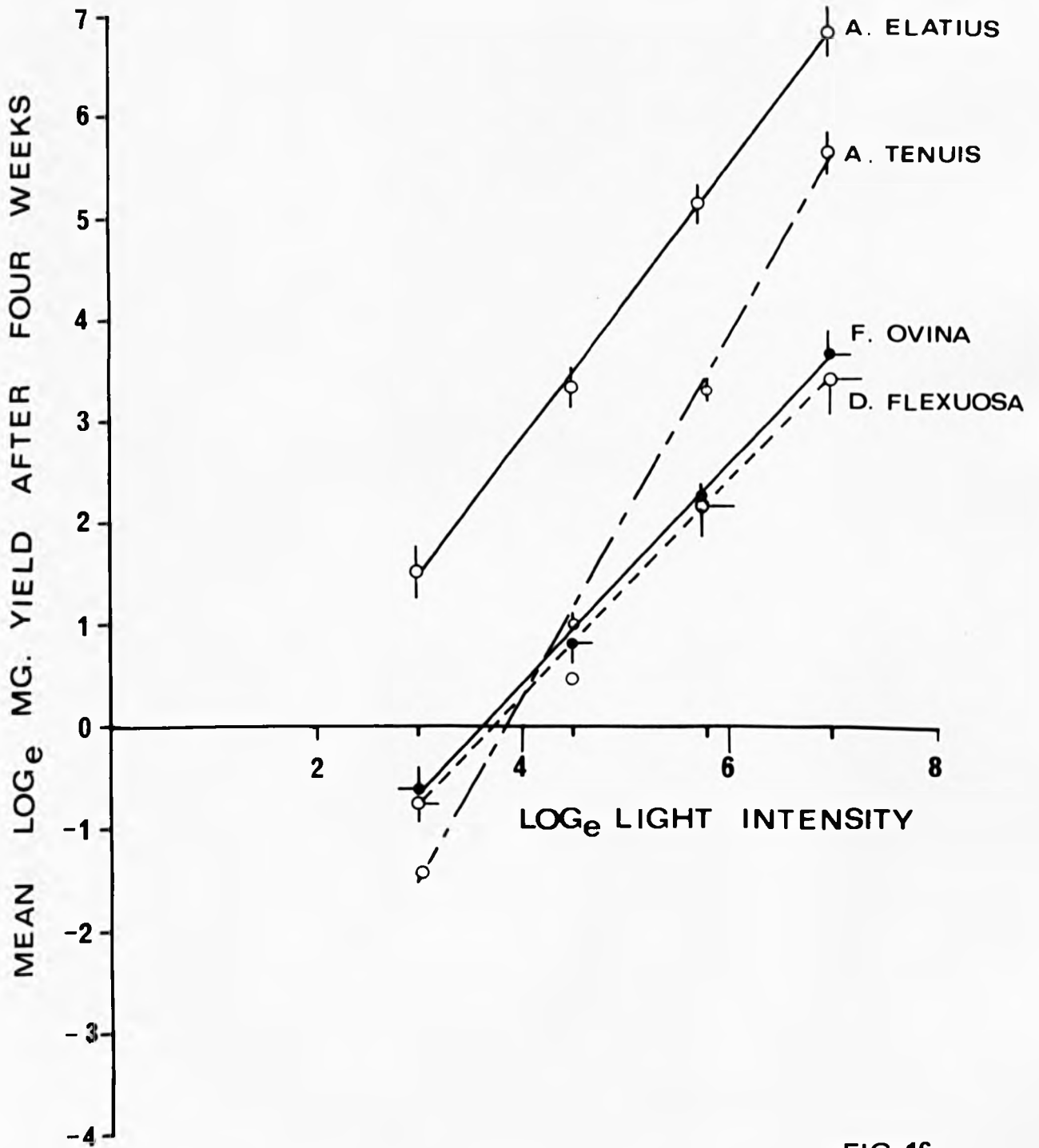


FIG. 16

Fig.17. Relative growth rates attained by seedlings of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, Deschampsia flexuosa grown at different light intensities, over a period of four weeks after sowing.

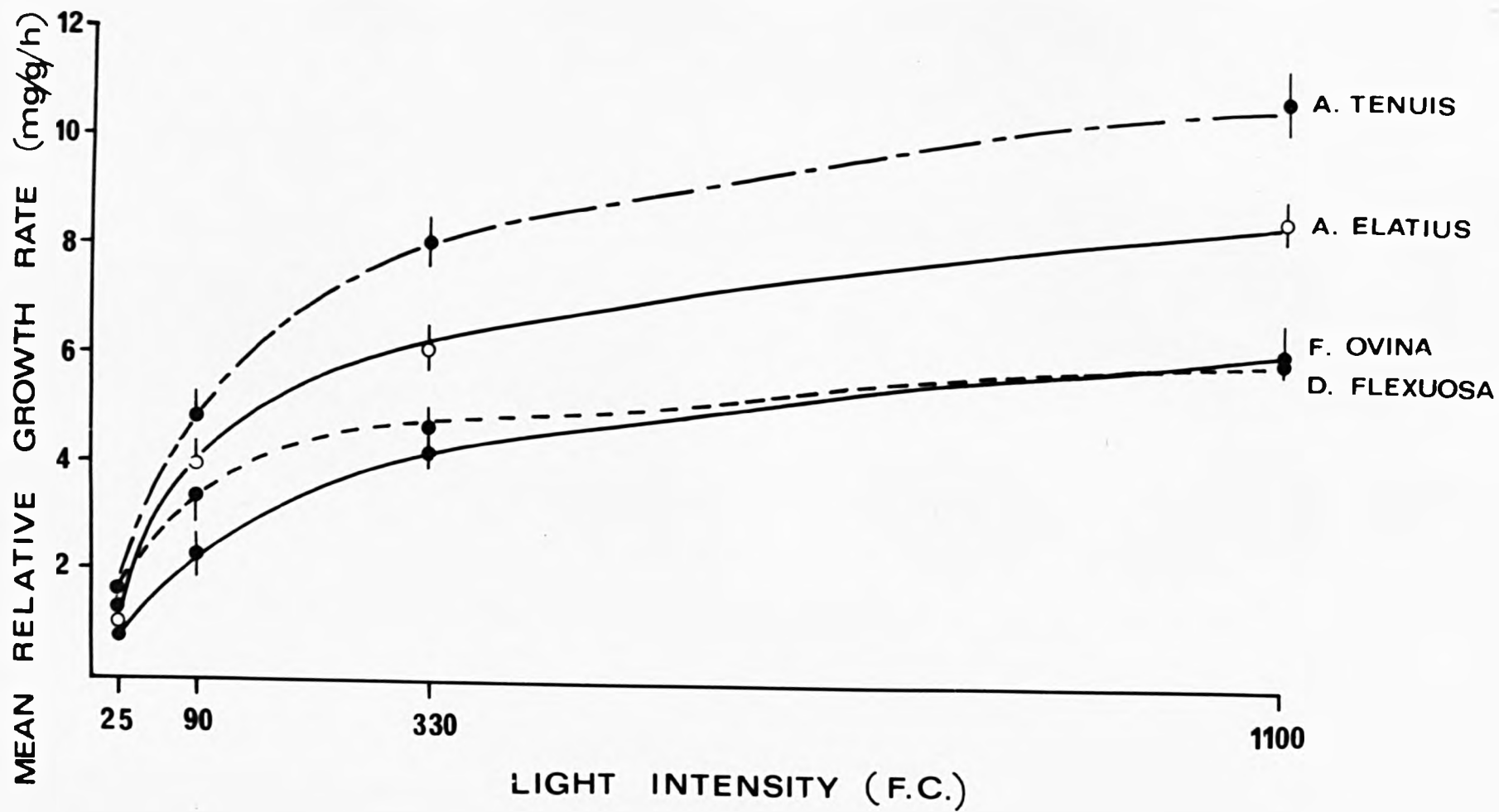


FIG.17

Fig.17 shows the mean relative growth rates attained by the different plant species when they were grown at different light intensities. As expected, Arrhenatherum elatius and Agrostis tenuis, species of known high potential relative growth rate produced the greatest yield and relative growth rates in the control. In both species, growth rates were reduced, at the lowest light intensity (25 f.c.) to values comparable to those of the two slow-growing species - Deschampsia flexuosa and Festuca ovina (Fig.17). At final harvest, the yield of Agrostis tenuis at 25 f.c. was less than that of Deschampsia flexuosa and Festuca ovina. The mean dry weights were 0.236 ± 0.039 , 0.536 ± 0.123 and 0.548 ± 0.123 mg for Agrostis tenuis, Deschampsia flexuosa and Festuca ovina respectively. It is of interest to note that under certain degrees of shading, species of inherently low relative growth rate (Deschampsia flexuosa and Festuca ovina) are able to outyield Agrostis tenuis which under more favourable light environments is far more productive. It is of interest to note that at a very low light intensity (25 f.c.) all the species were able to survive and sustain dry matter production, though at a very low rate.

Root/shoot ratios.

The data on mean R/S in the four species are reported in Table 10.

Table 10.

Mean Root/Shoot ratio in the four grasses: Arrhenatherum elatius, Agrostis tenuis, Festuca ovina and Deschampsia flexuosa grown at four light intensities (1100 f.c., 330 f.c., 90 f.c. and 25 f.c.) 95% confidence limits are included.

Light intensity	1100 f.c.	330 f.c.	90 f.c.	25 f.c.
<u>Species</u>				
<u>Arrhenatherum elatius</u>	0.342 [±] 0.012	0.202 [±] 0.004	0.107 [±] 0.010	0.106 [±] 0.007
<u>Agrostis tenuis</u>	0.310 [±] 0.013	0.203 [±] 0.010	0.120 [±] 0.016	0.266 [±] 0.063
<u>Festuca ovina</u>	0.305 [±] 0.033	0.178 [±] 0.025	0.135 [±] 0.00	0.234 [±] 0.027
<u>Deschampsia flexuosa</u>	0.328 [±] 0.030	0.224 [±] 0.036	0.150 [±] 0.033	0.195 [±] 0.038

At the highest light intensity used the species had comparable values; with increasing shade mean Root/Shoot values fell markedly. This agrees with observations made by Blackman and Wilson (1954), Evans and Hughes (1961) and Hunt (1970).

Experiment B.

Since the light intensities used in the former experiment were not low enough for accurate determination of the compensation points, it was then decided to repeat the experiment using a much lower range of light intensities. Screens were used to provide the following light intensities: 35 f.c., 15 f.c., 8 f.c. and 2 f.c. In order to make it possible to

obtain such low light intensities, some of the fluorescent tubes in the growth room were switched off.

The procedure for the experiment was the same as in experiment (A) except for the following three modifications:

(1) The first harvest was made after two weeks, instead of one week, thus allowing the plants more time to "settle-in" to the experiment before any harvest was made.

(2) Since the size of the plants was expected to be too small to lead to competition between the seedlings, and because it was considered necessary to increase the number of replicates, six seedlings were placed in each pot. Three seedlings were harvested after two weeks: and the remainder

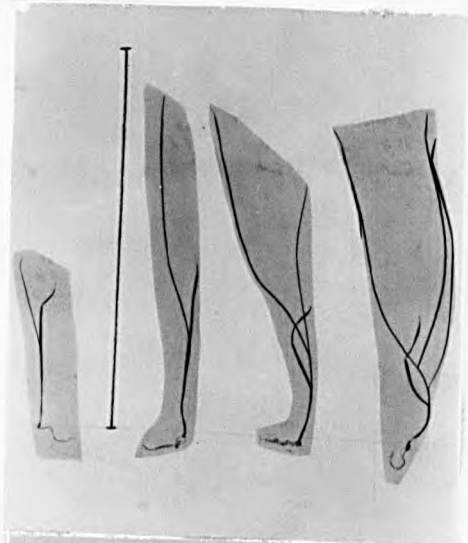
after four weeks. (3) Relative growth rates were calculated using the same formula, $R = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$, but using the mean dry weight of all plants at first harvest (t_1) and at final harvest. (t_2)

Results

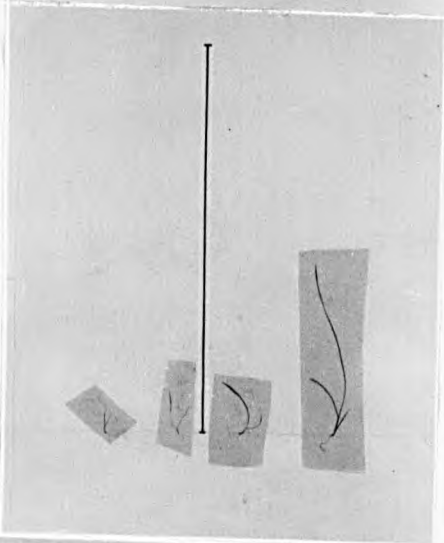
The appearance of the plants (Plates 35 to 38) shows that at 35 f.c. all the species achieved an appreciable amount of growth, in the sense that they increased in size and produced a number of leaves. The size of the plants decreased with reductions in light intensity. Arrhenatherum elatius, as in experiment (A) produced the tallest plants as

Plates 35 to 38. Representative silhouettes of plants of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina and Deschampsia flexuosa grown for four weeks at four light intensities (35, 15, 8 and 2 fc). The vertical scale is 20 cm in length. Treatments in each plante, from right to left - 35, 15, 8 and 2 f.c.

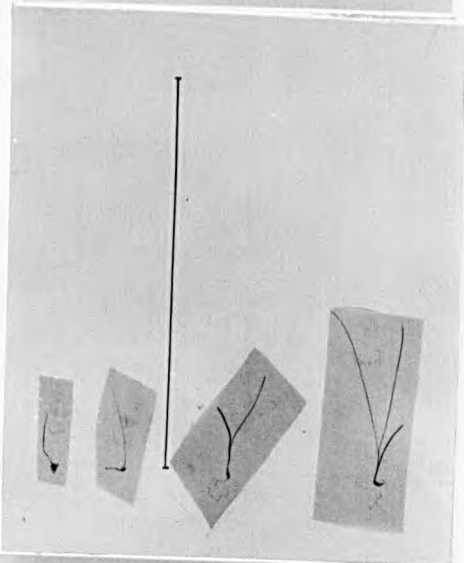
35. Arrhenatherum elatius.
36. Agrostis tenuis.
37. Festuca ovina.
38. Deschampsia flexuosa.



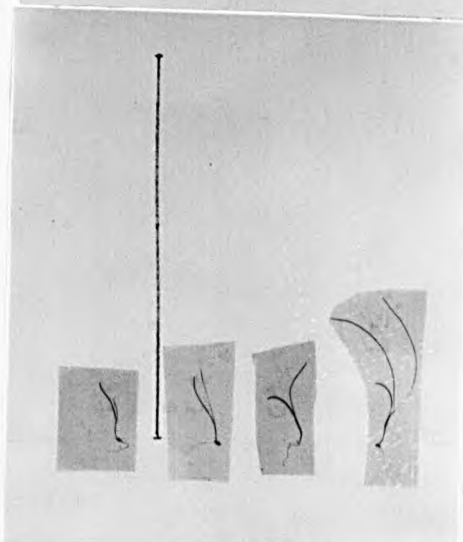
35



36



37



38

compared to the other species. It is worth mentioning that at the three lower light intensities (15 f.c., 8 f.c. and 2 f.c.), the seedlings of Arrhenatherum elatius collapsed and therefore could not have benefited from the slightly higher intensities near the roof of the screens. In deep shade, (2 f.c.) the plants were much shorter in comparison with those grown at the other light intensities, and some of the leaves died during the experiment. Although the plants of Deschampsia flexuosa, grown at the light intensities (15, 8 and 2 f.c.) did not show as much extension growth as those grown at 35 f.c., they were able to survive and did not show any signs of deterioration. The growth of the seedlings of Festuca ovina and Agrostis tenuis deteriorated at 8 and 2 f.c., and dead leaves occurred on most of the seedlings.

Table 11 shows the mean dry weights of whole plants of the four species grown at the four light intensities.

All the species made appreciable growth at 35 f.c. Arrhenatherum elatius seemed to be more efficient than the other three species in utilizing this light environment, in that it produced the largest plants (Plate 35 and Table 11). In this respect it was rivalled only by Deschampsia flexuosa which outyielded Agrostis tenuis and Festuca ovina. The mean dry weights of plants of the four species at final harvest were 4.390 ± 0.382 , 1.014 ± 0.061 , 0.730 ± 0.022 and 0.476 ± 0.074 mg for Arrhenatherum elatius, Deschampsia flexuosa, Festuca ovina and Agrostis tenuis respectively.

As in experiment (A), the two species which have low maximum potential relative growth rates (Deschampsia flexuosa and Festuca ovina) produced larger plants than Agrostis tenuis.

Table 11.

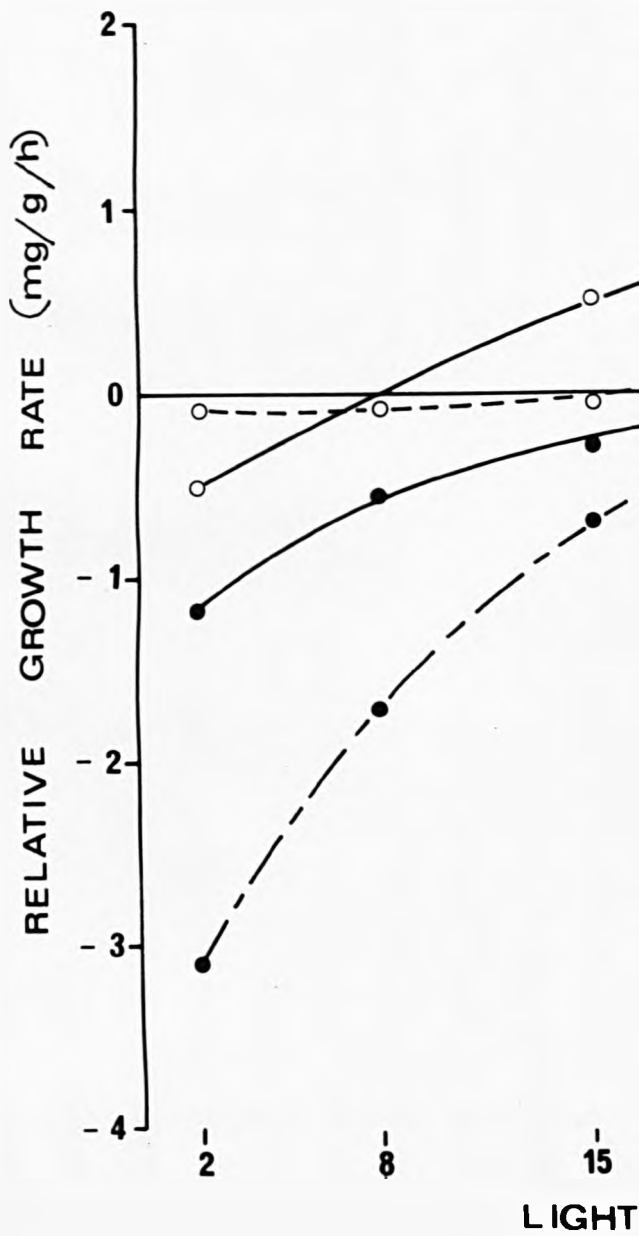
Mean dry weights (mg.) of whole plants of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina and Deschampsia flexuosa grown for four weeks at four light intensities. 95% confidence limits are included.

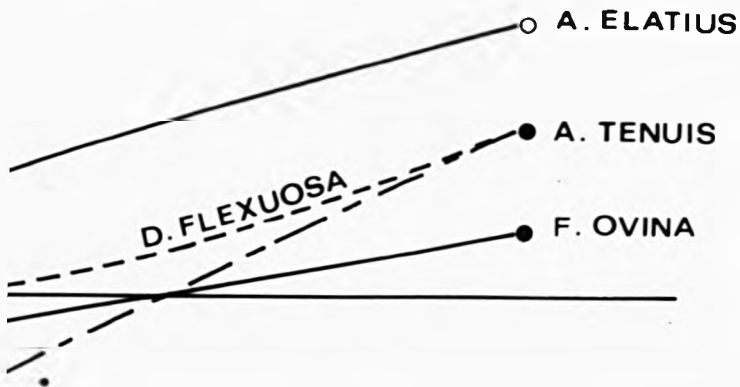
Species	35 f.c.	15 f.c.	8 f.c.	2 f.c.
<u>Arrhenatherum elatius</u>	4.390 [±] 0.382	2.737 [±] 0.210	2.620 [±] 0.256	1.660 [±] 0.078
<u>Agrostis tenuis</u>	0.476 [±] 0.074	0.253 [±] 0.00	0.194 [±] 0.00	0.102 [±] 0.00
<u>Festuca ovina</u>	0.730 [±] 0.022	0.522 [±] 0.00	0.466 [±] 0.026	0.343 [±] 0.010
<u>Deschampsia flexuosa</u>	1.014 [±] 0.061	0.624 [±] 0.00	0.720 [±] 0.071	0.600 [±] 0.022

The response of these species to light intensity is also expressed in terms of relative growth rate.

The two species - Agrostis tenuis and Festuca ovina, which are common and abundant in open or short grassland

Fig.18. Relative growth rates of seedlings of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina, and Deschampsia flexuosa when grown at different light intensities over a period of four weeks.





35

INTENSITY F.C.

FIG.18

communities, lost weight when they were grown at the other three low light intensities (15, 8 and 2 f.c.); i.e. they showed negative growth rates (Fig.18). Of all the species, Agrostis tenuis showed the steepest decline in growth rate with decreased light intensity. It is of interest to note that although Agrostis tenuis and Festuca ovina appear to be similar with respect to the position of the light intensity compensation point, which is apparently higher than that of Arrhenatherum elatius and Deschampsia flexuosa, Agrostis tenuis showed a steeper decline in relative growth rate than Festuca ovina below the compensation point. It is of interest to compare the behaviour of Arrhenatherum elatius and Deschampsia flexuosa which are apparently more shade-tolerant than the other two species and which do in fact occur more frequently in shaded habitats. Arrhenatherum elatius showed a greater gain in weight than Deschampsia flexuosa when both were grown at a light intensity of 15 f.c., maintained a balance between production and consumption of dry matter at 8 f.c. and lost weight rather rapidly at 2 f.c. In contrast, Deschampsia flexuosa although not gaining in weight at 15 f.c., remained close to the compensation point at the three low light intensities (15, 8 and 2 f.c.). In fact, in these three treatments no significant difference could be detected between the mean dry weights of plants at first and final harvests. The failure to detect a significant loss in weight in seedlings apparently below

the compensation point (Fig.18) suggests that this species may be able, in some way, to restrict respiration loss in shade. Although Arrhenatherum elatius and Deschampsia flexuosa were quite similar in respect of the position of the compensation point (Fig.18), (in fact it is lower in Arrhenatherum elatius than in Deschampsia flexuosa), Arrhenatherum elatius has a capacity to respond rapidly to periods above the compensation point, but is more sensitive to weight losses during periods below the compensation point.

CHAPTER 7.

SUSCEPTIBILITY OF ARRHENATHERUM ELATIUS,
AGROSTIS TENUIS, FESTUCA OVINA AND
DESCHAMPSIA FLEXUOSA TO ALUMINIUM
AND MANGANESE

Introduction

Although it is possible to characterise the ecology of plant species in relation to soil pH (Part 1, Table 1), it is probably unwise to attribute the distribution of plant species to one feature of the environment such as soil pH, since plant distribution is a function of the interaction of many environmental factors. A variety of factors may vary in intensity across the pH range and influence the frequency of individual species (soil;-texture, moisture supply, mineral nutrients; prevailing management, etc.). Among the factors which vary in association with soil pH, certain metal toxicities deserve consideration in any attempt to explain the distribution of individual species.

The solubility of aluminium, manganese, and iron depends upon the pH of the soil solution. Magistad (1925) showed that the solubility of aluminium increases with decreasing pH. Pierre, Pohlman and McLlwaine (1932), determining aluminium in soil extracts, reported values which seemed to agree with Magistad. Ligon and Pierre (1932) comparing the levels of aluminium toxic to plants suggested that the upper limit for occurrence of

aluminium toxicity in the field was between pH 4.5 - 5.0.

Several workers have provided experimental evidence which indicates that the depressing action on plant growth associated with soil acidity is linked with the release of aluminium and manganese in soil solution.

That excess manganese in acidic soils is an important factor in limiting plant growth is very well documented. Jacobson and Swanback (1932) showed that tobacco is susceptible to manganese excess which occurred in Connecticut. Bortner (1935) reported the occurrence of similar injury in Kentucky. Hewitt (1946 and 1948), aiming at the resolution of factors in soil acidity by means of sand culture, examined the effect of manganese excess on a number of farm and market and garden crops. Daji (1948) suggested manganese toxicity as a possible cause of the band disease of Areca palm.

There is ample evidence which suggests that the presence of soluble aluminium in the soil may limit plant growth. Hartwell and Pember (1918) obtained evidence that the injurious effects of acidic soils on barley and rye was due to aluminium rather than to hydrogen ions. Conner and Sears (1922), and Blair and Prince (1923) came to the same conclusion that the level of aluminium rather than of hydrogen ions was the most important limiting factor in acidic soils. McLean and Gilbert (1927) showed that aluminium in appreciable amounts in solution is toxic to most plants, causing at first a dwarfing and distortion of the roots and later injury to the entire

plant. Gilbert and Pember (1931) found the yield of lettuce seedlings to be relatively insensitive to the pH of the culture media, but to be depressed by about 30 per cent by 28 mg. aluminium per litre supplied as aluminium sulphate. Most recent research workers (Rorison 1960 a and b; Clymo 1962; Hackett 1965, 1967; Clarkson 1966 a and Sparling 1967) suggested that the failure of certain calcicolous native plant species to establish on acidic soils could be mainly attributed to the presence of aluminium in these soils. Grime and Hodgson (1969) and Hodgson (1972), following the technique of Sparling (1967), measured the aluminium concentration required to induce 50% reduction in root growth in a number of native plants from Derbyshire, England. A close correlation was found to exist between field distribution and sensitivity of the seedlings to aluminium toxicity. Species characteristic of acidic soils, e.g. Deschampsia flexuosa, Nardus stricta and Holcus mollis, were found to be very resistant to aluminium toxicity, while species which occur mainly on calcareous soils, e.g. Briza media, Centaurea nigra and Leontodon hispidus, were very sensitive to aluminium.

In view of the preceding evidence of the ecological significance of aluminium and manganese in acidic soils, experiments were conducted to compare the tolerance of the grasses: Arrhenatherum elatius, Agrostis tenuis and Festuca

ovina to aluminium and manganese toxicity. The tolerance of Agrostis tenuis to aluminium toxicity was not tested and the results obtained by Hodgson (1972) are used to compare its tolerance to aluminium with that of the other two species.

Experiment (A)

Response to aluminium.

Materials and methods.

The technique used by Hodgson (1972) was adopted. The plants were grown in a growth room which provided the following environmental conditions: Light intensity c. $3.3 \text{ cal.cm}^{-2}\text{h}^{-1}$ visible radiation, temperature 20°C by day and 15°C by night, a relative humidity of 70% and a day length of 18 hours.

Root medium.

In order to compare the results of this experiment with those obtained by Hodgson (1972), Rorison nutrient solution was used as a rooting medium. The composition of the standard complete Rorison solution is given in Table 12.

Table 12.

The composition of the standard complete Rorison solution.

Element	Concentration (ppm)	Source
Ca)	80	Ca(NO ₃) ₂ · 4 H ₂ O
N)	56	
Mg	24	Mg SO ₄ · 7 H ₂ O
K	78	K ₂ H PO ₄
Fe	3	Fe-EDTA
Mn	0.5	Mn SO ₄ · 4 H ₂ O
B	0.5	H ₃ BO ₃
Mo	0.1	NH ₄) ₆ MO ₇ O ₂₄ · 4H ₂ O
Zn	0.1	Zn SO ₄ · 7 H ₂ O
Cu	0.1	Cu SO ₄ · 5 H ₂ O

Culture vessels.

Polystyrene boxes 17.1 x 11.5 x 3.1 cm which have a capacity of 500 ml. were used. These were painted black on the outside using bitumastic paint.

Support.

To provide support for the plants in the culture solution a floating raft devised by Hodgson (1972) was used. Plate 39 and Fig.19 illustrate the structure of the raft. A nylon mesh folded to give four thicknesses was sown to a polystyrene framework using white terylene thread. To provide buoyancy, small pieces of polystyrene were placed between the middle two layers of the nylon mesh. The seedlings were placed on the mesh with the shoot in an upright position and the root held horizontally by the surface tension of the nylon mesh (Plate 39 and Fig.19). Plate 40 illustrates a general view of the floating raft technique in operation during the experiment.

The nutrient solution was not aerated, but was changed every two days. Aeration was not considered to be necessary in view of the short duration of the experiment (six days), the small number of seedlings (10) occupying each container and the large surface area to volume ratio of the culture vessels.

By experiment, Hodgson (1972) demonstrated that the illumination of the roots which occurs in this system had no detectable effects upon root growth.

Fig.19. Diagrams illustrating the structure of the floating raft used for supporting young seedlings in the aluminium toxicity experiment.

- F. Polystyrene fragments.
- G. Polystyrene framework.
- H. White nylon mesh sewn on to white terylene thread.

Plate 39. Seedlings of Arrhenatherum elatius in the aluminium toxicity experiment.

Plate 40. A general view of the floating raft technique in operation during the aluminium toxicity experiment.

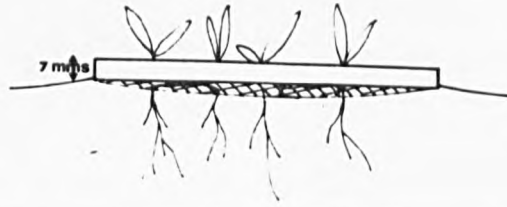
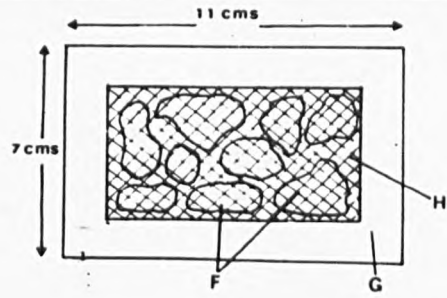
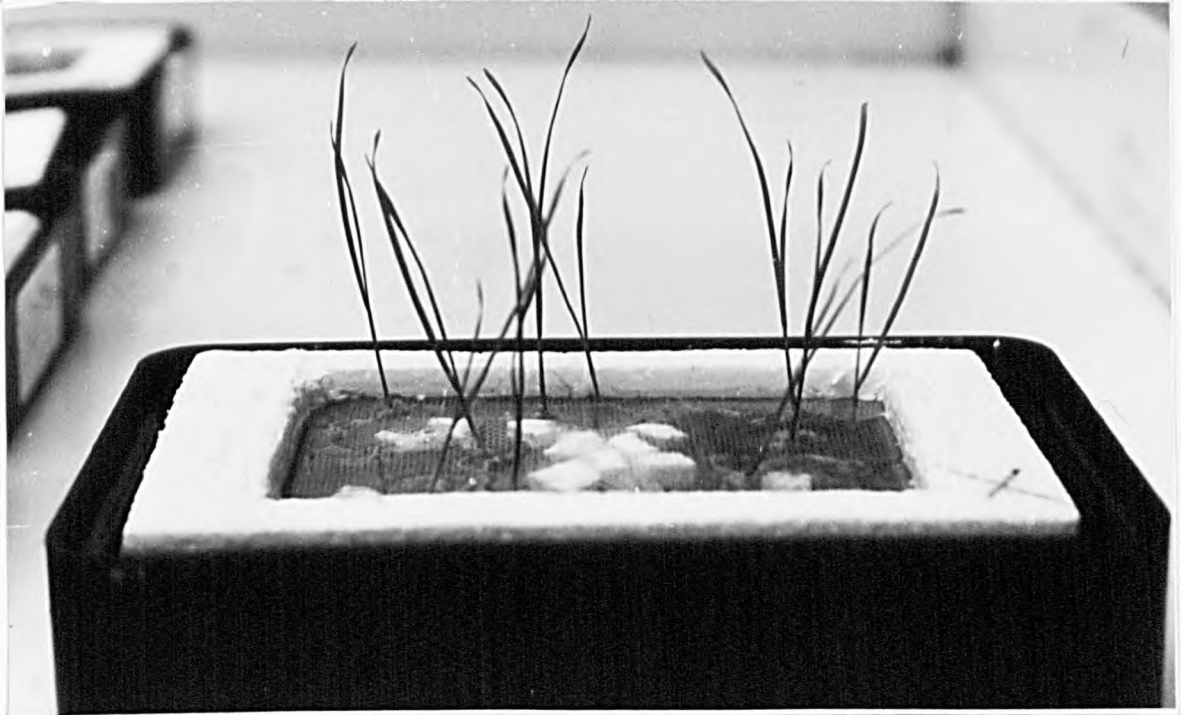
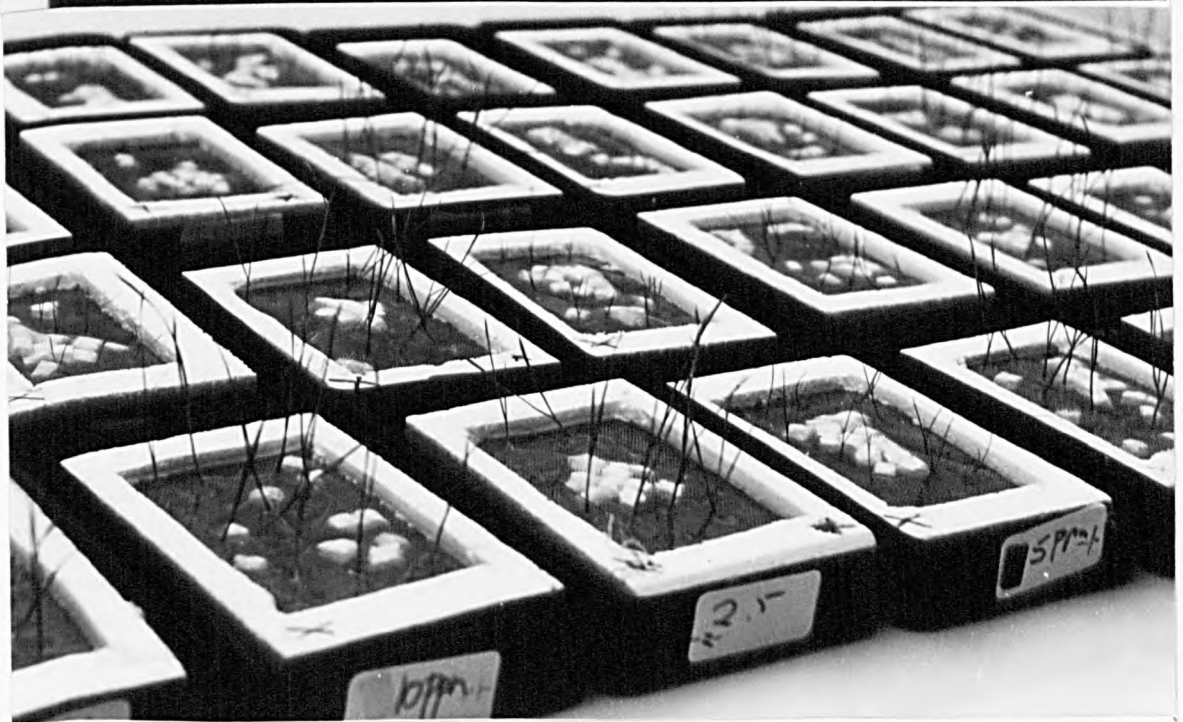


Fig.19



39



40

Preparation of plant material.

A large number of seeds were set to germinate under the controlled environmental conditions on moist nylon cloth in transparent polystyrene boxes. This ensured the availability of a sufficient number of seedlings of comparable age. When the radicles had just emerged, seedlings were selected and transferred to other polystyrene boxes onto nylon cloth moistened with nutrient solution. The seedlings exceeded the number required for the experiment by 100 seedlings. Uniformly-sized seedlings were transferred to the experiment one week after germination by which time they were large enough for easy handling.

Measurements.

Rorison (1958) and Clarkson (1965, 1966 b) reported that the effects of the levels of aluminium in nutrient solution on plant growth can be manifested in (a) root stunting and (b) symptoms of phosphorus deficiency in the shoot.

Under extreme conditions aluminium toxicity is manifested in a large reduction of total yield and eventually by death of the plant. In this experiment, a root feature was used to assess the degree of tolerance of plants to aluminium toxicity because of the following considerations. Many workers have shown that the roots are more susceptible and showed much quicker response to aluminium than the other parts of the plant. Hodgson (1972) showed that, among the conventional measures of growth, root length was

the first to be affected by toxic levels of aluminium. Clarkson (1965) showed that aluminium causes root stunting by inhibiting mitosis, and found that, in culture solutions, the inhibitory effect of aluminium on root growth of Allium cepa could be detected clearly within a period of a few hours.

In view of the preceding considerations total root length was used to determine the degree of tolerance of the seedlings to aluminium toxicity.

Procedure

Aluminium sulphate solution was freshly added to a complete Rorison solution in appropriate volumes to provide solutions which contained the following range of aluminium concentrations: 0, 0.09 mM, 0.18 mM, 0.36 mM, 1.0 mM and 2.0 mM. The pH of the solution was adjusted to pH 4.0. Ten uniformly sized seedlings, which were one week old after germination, were placed on a raft floating on the appropriate solution. Two containers were used for each treatment. The solutions were changed every two days.

After a week the concentration of aluminium causing 50% reduction in root growth was calculated for each species and was taken as an index of tolerance.

It is worth mentioning that the addition of aluminium sulphate to the nutrient solution caused the precipitation of some aluminium as aluminium phosphate. The amount of aluminium precipitated depends on the pH of the solution,

the amount of aluminium added and the concentration of phosphorus (Hodgson 1972).

It should be noted therefore that the amount of aluminium in the concentrated solution which is initially added is not maintained throughout the experiment. The solution may be considered to be supersaturated with aluminium when aluminium sulphate is freshly added to the nutrient solution. Subsequently the level drops to the equilibrium concentration which according to Hodgson (1972) is reached between 6 - 24 hours. It is not certain whether the initial or equilibrium concentration is of greater importance in bringing about the toxic effect on the roots. In view of Clarkson's evidence (1965) suggesting that high concentrations of aluminium may cause root inhibition in a very short time, it is likely that the initial concentration may be more effective in causing the stunting of the roots. In accordance with previous workers and Hodgson (1972), the aluminium levels mentioned in this experiment refer to the initial concentrations.

The addition of aluminium sulphate to the nutrient solution causes changes in the components of the nutrient solution which may be suspected to contribute towards the inhibitory effect of aluminium. These changes are:

- (a) precipitation of aluminium as aluminium phosphate which may result in phosphorus deficiency in the solution,
- (b) increase in the sulphate concentration in solution to a level which may affect plant growth, and (c) additional toxic contaminants may be introduced into the nutrient solution.

These changes were examined by Hodgson (1972) who showed that the inhibition of root growth is unlikely to be due to changes in the components of the nutrient solution. In the present studies no symptoms of phosphorus deficiency were observed in the seedlings. Because of the short duration of the experiment, it seems to be unlikely that phosphorus deficiency would develop in the system. Moreover, it is most unlikely that the rapid and drastic effects on root growth noted in this experiment could be attributed to a nutrient deficiency. The possibility must be considered that toxic factors other than aluminium could be involved. The level of toxic impurities in the "A.R." chemicals used in this experiment rule out this possibility. At the highest levels of aluminium supplied, the concentration of sulphate reached a maximum of just under 4.0 mM. However this appears to fall safely within the range of the sulphate concentrations used in nutrient solutions (Bollard, 1966).

Procedure used in measurements.

Ten uniformly-sized, one week old seedlings were placed on top of the floating raft with all of the root system lying horizontally on the nylon mesh. The new roots grew immediately downwards. By the end of the experiment the total root length of each seedling was divided into two components: (a) the root length which penetrated below the nylon mesh and (b) the original length of root which

remained on top of the nylon mesh. The former was made up of root increments while the latter constituted the initial root length. In order to make it easy to separate the two components at the end of the experiment, all the root material on top of the nylon mesh was painted black with Indian ink. The roots were withdrawn from the mesh and the two components separated using a fine pair of scissors.

Results.

The curves in Fig.20 show the percentage increase in root length of Arrhenatherum elatius and Festuca ovina at different concentration of aluminium. The concentration of aluminium which causes 50% reduction in root growth of these grasses is presented in Table 13. Values obtained by Hodgson (1972) for other grassland species are also included.

Table 13.

The concentration of aluminium which causes a 50% reduction in root growth in a number of grassland species.

Species	Concentration which causes 50% reduction in root growth
<u>Deschampsia flexuosa</u> *	0.48 mM
<u>Nardus stricta</u> *	0.37 mM
<u>Festuca ovina</u>	0.36 mM
<u>Agrostis tenuis</u> *	0.26 mM
<u>Holcus mollis</u> *	0.24 mM
<u>Arrhenatherum elatius</u>	0.09 mM
<u>Plantago lanceolata</u> *	0.08 mM
<u>Leontodon hispidus</u> *	0.07 mM
<u>Centaurea nigra</u> *	0.07 mM
<u>Briza media</u> *	0.06 mM

Festuca ovina and Agrostis tenuis are more tolerant of aluminium toxicity than Arrhenatherum elatius. This is

*data of Hodgson (1972)

Fig.20. Percentage increase in root length of plants of Arrhenatherum elatius, and Festuca ovina grown at five concentrations of aluminium provided in culture solution. 95% confidence limits are included.

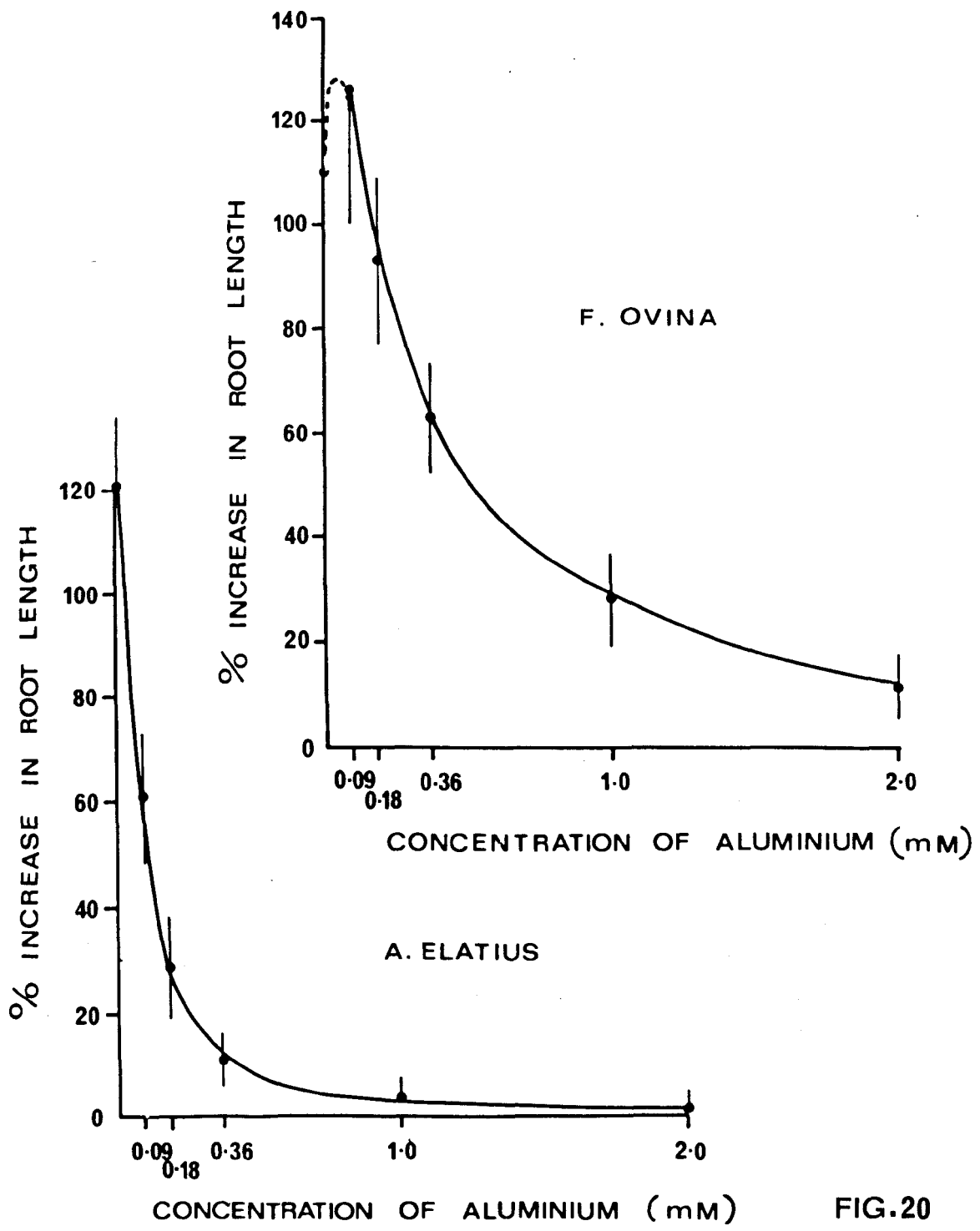


FIG.20

consistent with the findings of Hodgson (1972) which indicate that calcifuges are more tolerant of aluminium than calcicoles. It is clear from Table 13 that Festuca ovina and Agrostis tenuis belong to the former category and Arrhenatherum elatius belongs to the latter group. It is of interest to note that the species which are tolerant of aluminium toxicity (Table 13) have their highest percentages of occurrence on very acidic soils (pH 4.0) and are associated with acidic strata: the Millstone Grit (MG), the Bunter Sandstone (BS) and the Coal Measures (CM), and the species more susceptible to aluminium toxicity are associated with sites of intermediate or high pH (pH 5.1 - 8.0) and are more abundant on the Toadstone, (TS), the Carboniferous Limestone (CL), and the Magnesian Limestone (ML). (Tables 14 and 15).

Table 14.

Percentage occurrence of a number of grassland species in categories of surface soil pH. (Data from Grassland Survey, Lloyd, Grime and Rorison, 1972).

Species	pH Range				
	3-4	4.1-5	5.1-6.0	6.1-7.0	7.1-8.0
<i>Deschampsia flexuosa</i>	96	32	12	3	1
<i>Nardus stricta</i>	40	9	4	-	-
<i>Holcus mollis</i>	14	8	1	2	1
<i>Festuca ovina</i>	55	68	56	68	51
<i>Agrostis tenuis</i>	34	87	76	32	9
<i>Arrhenatherum elatius</i>	1	13	33	53	52
<i>Leontodon hispidus</i>	0	3	19	34	40
<i>Centaurea nigra</i>	0	5	12	9	39
<i>Plantago lanceolata</i>	0	19	58	56	40
<i>Briza media</i>	0	7	31	44	28

Table 15.

% occurrence of selected grassland species in samples from six geological strata. % values are corrected to the nearest whole number.

Species	Geological Strata					
	MG	BS	CM	TS	ML	CL
<i>Deschampsia flexuosa</i>	95	81	88	18	0	16
<i>Nardus stricta</i>	56	11	19	5	0	5
<i>Holcus mollis</i>	4	47	20	5	1	1
<i>Festuca ovina</i>	62	92	33	71	21	76
<i>Agrostis tenuis</i>	30	33	53	87	18	46
<i>Arrhenatherum elatius</i>	0	0	7	37	21	51
<i>Leontodon hispidus</i>	0	0	0	5	47	23
<i>Centaurea nigra</i>	0	0	0	5	47	23
<i>Plantago lanceolata</i>	0	0	4	53	54	38
<i>Briza media</i>	0	0	0	3	38	32

Experiment B.

Response to manganese

Material and methods.

In this experiment the strict calcifuge Deschampsia flexuosa, was included in order to put the results for Arrhenatherum elatius, Agrostis tenuis and Festuca ovina into perspective. The plants were grown under the same environmental conditions as in Experiment "A". Rorison nutrient solution, in 2.5 l (14.5 x 9.5 x 17 cm) polystyrene containers, was used as the rooting medium.

After two weeks of growth five plants from each culture vessel were removed, oven-dried and the roots and shoots were weighed separately. The remaining plants were harvested five weeks after the beginning of the experiment and were similarly treated. These two harvests were used to calculate the growth rates attained by the four species when grown in nutrient

solutions containing different concentrations of manganese. The relative growth rates were calculated using the formula $R = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$ where W_1 and W_2 are mean oven-dry weights of the whole plants at first harvest (t_1) and last harvest (t_2) respectively.

Results.

Manganese toxicity symptoms.

In Arrhenatherum elatius, manganese toxicity symptoms-intervenal brown spots in the leaves accompanied by dieback of leaf tips-appeared in plants which were grown in the solutions containing 25 ppm to 200 ppm. Plate 42 shows these symptoms on a leaf of this species. The plants deteriorated very much as the concentration of manganese in solution reached 100 ppm and most of the foliage was dead on the plants grown at 200 ppm (Plate 41).

Although Agrostis tenuis plants did not show visual symptoms of manganese toxicity, very marked differences in morphology were noticed between the plants grown at high (100 - 200 ppm) and low (5 - 50 ppm) concentrations of manganese. Plants which were grown in the former range of solutions were very much stunted as compared to those from the lower concentrations (Plate 43).

Plants of Festuca ovina and Deschampsia flexuosa did not show any visual symptoms of manganese toxicity nor any morphological differences (Plates 44 and 45 respectively).

Plate 41. Appearance of representative plants of Arrhenatherum elatius grown at different levels of manganese in culture solution. Treatments from left to right, 5, 25, 50, 100 and 200 ppm Mn.

Plate 42. Symptoms of manganese toxicity (interveinal brown spots) in the leaves of Arrhenatherum elatius.

Plate 43. Appearance of plants of Agrostis tenuis grown at different levels of manganese in culture solution. Treatments from left to right 5,25, 50, 100 and 200 ppm. Mn.



41



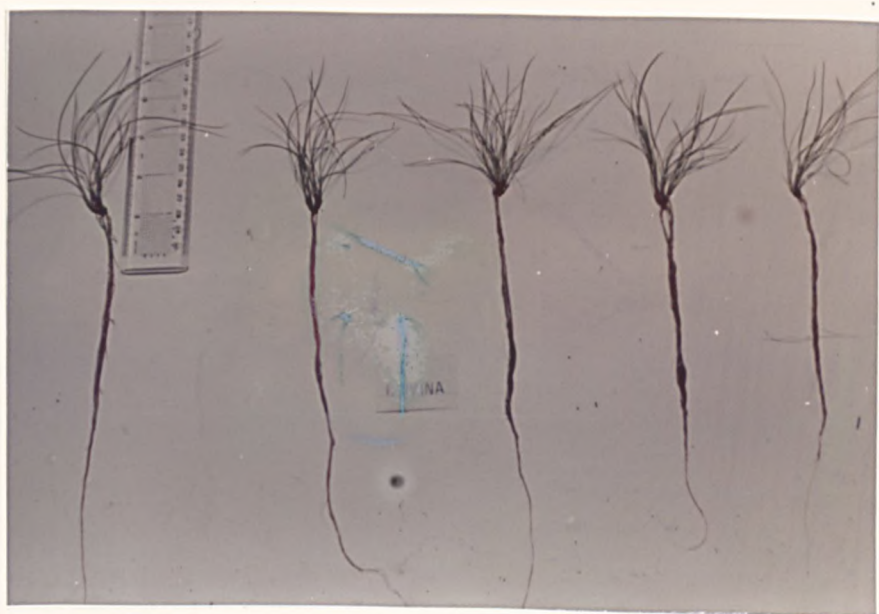
42



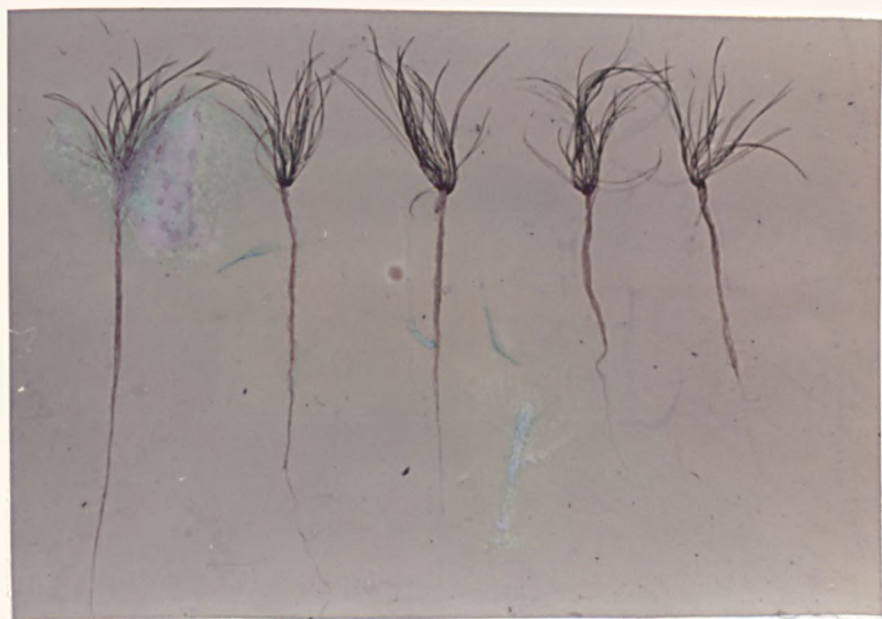
43

Plates 44 - 45.

Appearance of plants of Festuca ovina (Plate 44) and Deschampsia flexuosa (Plate 45) grown at different levels of manganese in culture solution. Treatments from left to right 5, 25, 50, 100 and 200 ppm Mn.



44



45

Effects on yield.

The yields of the four species expressed as a function of manganese in solution, and in terms of mean dry weight per plant at final harvest, are shown in Fig.21.

The four species included in the experiment appear to represent three levels of tolerance of manganese toxicity. Deschampsia flexuosa and Festuca ovina are extremely resistant, Agrostis tenuis is intermediate in sensitivity, while Arrhenatherum elatius is very susceptible. Although the yields of Festuca ovina and Deschampsia flexuosa were not significantly reduced with increasing manganese concentration, the yield of Agrostis tenuis which is less frequent in habitats of very low soil pH, was reduced markedly only when the concentration of manganese reached 100 ppm. The yield of plants grown at 100 ppm and 200 ppm, as compared with that of plants grown at 5 ppm, was reduced by 46.0% and 63.4% respectively. In marked contrast, the yield of Arrhenatherum elatius showed a marked decline at concentrations higher than 5 ppm. The reduction in yield of plants grown at these high concentrations as compared to the yield of plants grown at 5 ppm was 53.8%, 62.8%, 72.3% and 94.0% for plants grown at 25 ppm, 50 ppm, 100 ppm and 200 ppm respectively.

The mean dry weights of shoots and roots of the four species are presented in the histograms in Fig.22. Each of the two resistant species - Festuca ovina and Deschampsia flexuosa - maintained a constant yield and distribution of dry matter between root and shoot. The plants of Agrostis tenuis

Fig.21. Response of plants of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina and Deschampsia flexuosa to five levels of manganese provided in culture solution. 95% confidence limits are included.

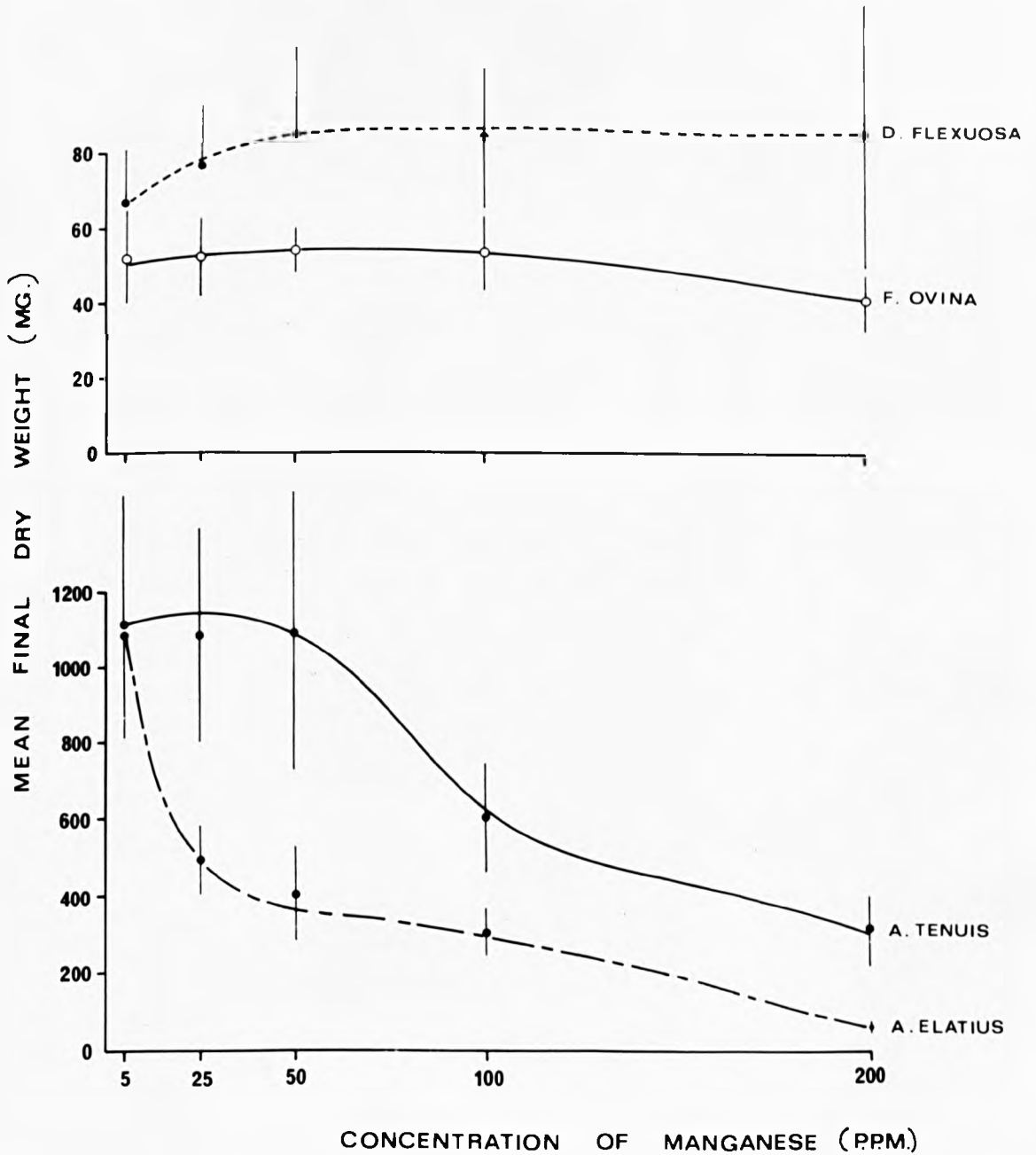


FIG. 21

Fig.22. The effect of five levels of manganese provided in culture solution on shoot and root yields of seedlings of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina and Deschampsia flexuosa. 95% confidence limits are included.

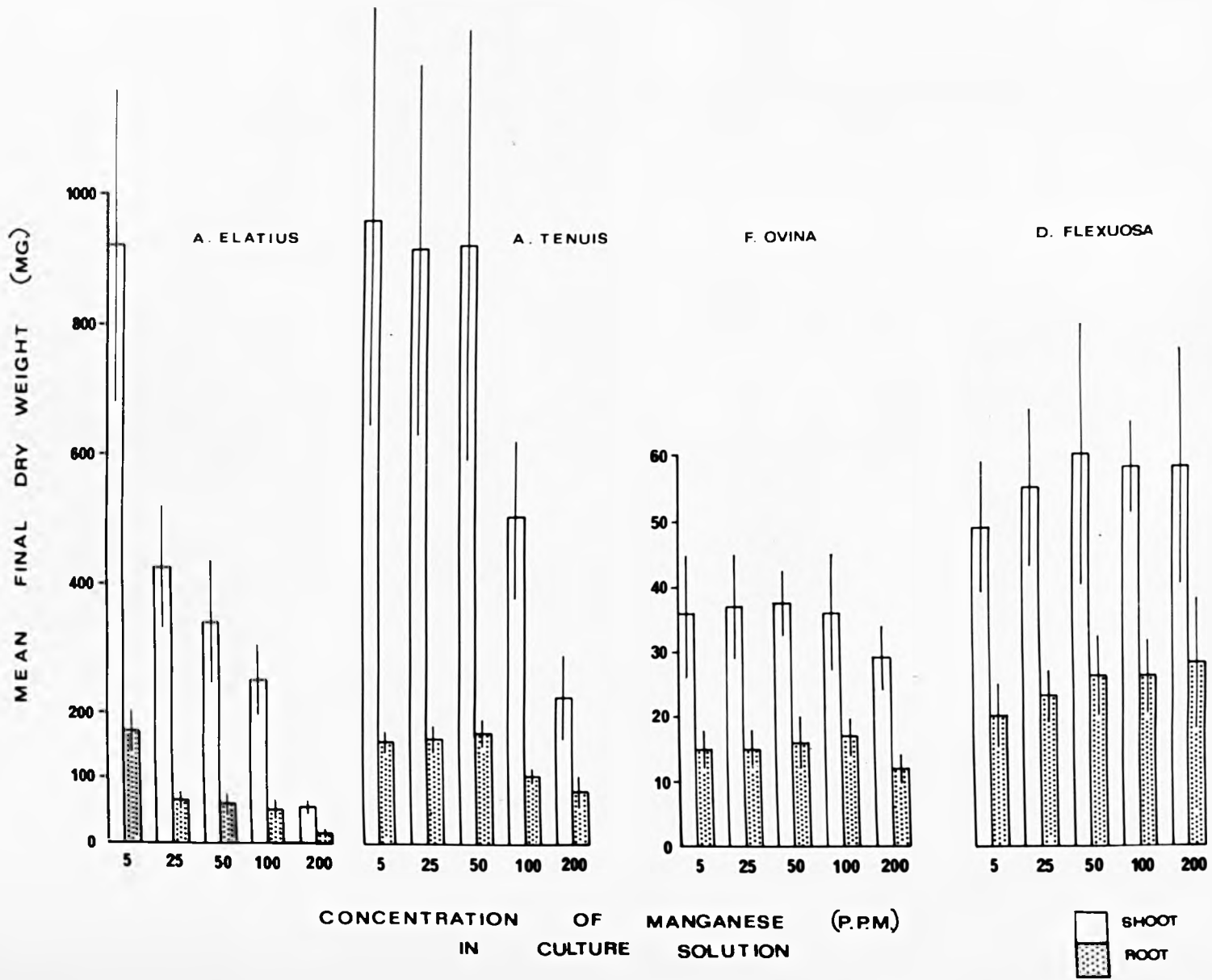


FIG. 22

grown at 100 and 200 ppm manganese showed a significant reduction in yield of both shoot and root from plants grown at 5 ppm. Percentage reduction in yield was greater in shoot than in root. At 100 ppm and 200 ppm, the yield of the shoot was reduced by 47.5% and 76.6% respectively while the yield of the roots was reduced by 32.9% and 48.9% respectively. In Arrhenatherum elatius the percentage reduction in yield of shoot of plants grown at 25 - 200 ppm manganese was comparable to the reduction in yield of roots. The yield of shoot of plants grown at 25, 50, 100 and 200 ppm manganese were reduced by 53.8%, 62.9%, 72.4% and 93.9% respectively while the yield of the root was reduced by 60.5%, 65.4% and 71.2% and 87.7% respectively.

Effect on relative growth rate.

When the response to manganese concentration is expressed in terms of relative growth rate (Fig.23) a tolerance hierarchy is still apparent. However, the calcicole, Arrhenatherum elatius is the only species which showed a marked decrease in relative growth rate with increasing manganese concentration (25 ppm - 200 ppm). The relative growth rate of Agrostis tenuis was reduced markedly only when the concentration of manganese reached 100 ppm. Deschampsia flexuosa and Festuca ovina did not show any significant decrease in growth rate with increasing manganese concentration.

Though Deschampsia flexuosa plants which were grown in the solutions containing the highest concentration of manganese (200 ppm) outyielded the plants of Festuca ovina which were

Fig.23. Relative growth rates attained by seedlings of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina and Deschampsia flexuosa when grown at five levels of manganese in culture solution.

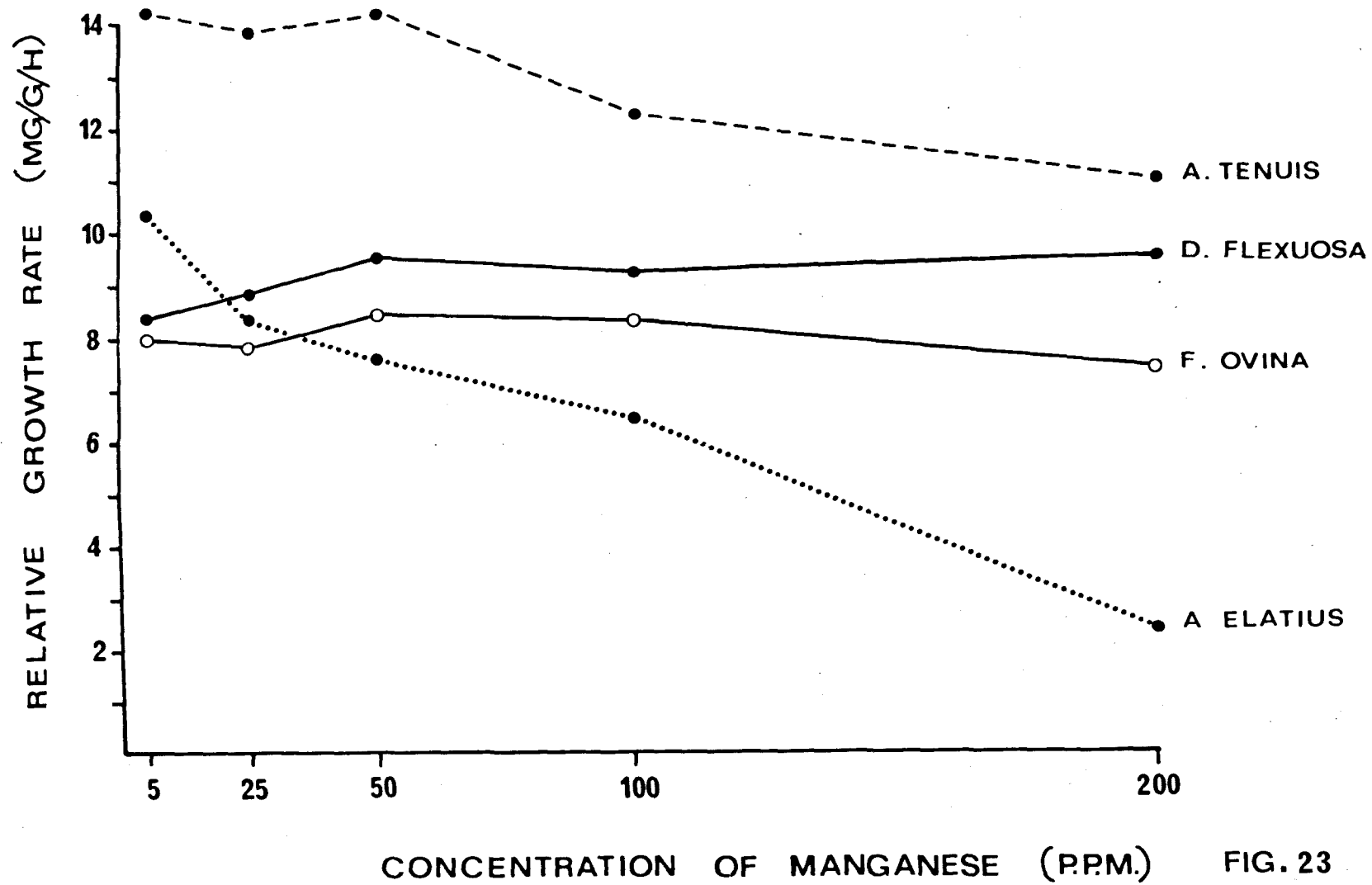


FIG. 23

grown under the same conditions, they were outyielded by plants of Agrostis tenuis. The mean dry weights of the plants at final harvest were 85.9 ± 34.3 mg., 41.2 ± 7.2 mg., and 226.0 ± 69.6 mg. for Deschampsia flexuosa, Festuca ovina and Agrostis tenuis respectively. This seems to conflict in part with the view of Pigott (1970) who suggested that the increased solubility of manganese in very acidic soils probably accounts for the elimination of the majority of pasture plants including Agrostis tenuis and Festuca ovina from swards on leached brown earths invaded by Deschampsia flexuosa. Since the plants of Deschampsia flexuosa, grew at a faster rate and outyielded those of Festuca ovina, it is possible that Deschampsia flexuosa could eliminate Festuca ovina when the two species compete with each other in a sward. But judging by the size of the plants attained by Agrostis tenuis and Deschampsia flexuosa when both species were grown in solutions containing 200 ppm, it is hard to see how through differential responses to manganese alone, Deschampsia flexuosa could eliminate Agrostis tenuis when the two species are in competition in a sward - Agrostis tenuis would be much more likely to exclude Deschampsia flexuosa (compare plates 43 and 45). The dry weights of the shoot presented in the histograms in Fig.22 show the larger size of Agrostis tenuis as compared to Deschampsia flexuosa. It is more likely that in very acidic soils other factors such as decreased availability of major nutrients rather than increased solubility of manganese could shift the balance in favour of Deschampsia flexuosa.

It is also possible that the concentration of manganese in the soils examined by Pigott is higher than the highest concentration used in this experiment.

The species more tolerant of manganese toxicity, Deschampsia flexuosa, Festuca ovina and Agrostis tenuis, are also tolerant of aluminium toxicity, and have a higher frequency of occurrence in sites of low pH (Table 14); Arrhenatherum elatius is very susceptible to both aluminium and manganese, and has low frequency of occurrence in very acidic soils. Since the seeds of both calcicole and calcifuge species used in this experiment germinate to high percentage in very acidic soils (pH 3 - 4) (Grime unpublished data) it seems likely that the low frequency of occurrence of calcicole species such as Arrhenatherum elatius in very acidic soils is due at least in part to failure of seedling establishment in these habitats and that toxicity induced by aluminium and manganese contributes to this effect.

CHAPTER 8.

INVESTIGATION INTO THE MINERAL NUTRITION OF
ARRHENATHERUM ELATIUS, AGROSTIS TENUIS AND FESTUCA OVINA.

Introduction.

The mineral nutrient content of grassland soils may vary widely between soils. Such variation is frequently associated with changes in botanical composition. Some of these changes in botanical composition are likely to be due to differential effects of variation in mineral nutrient supply on the vigour of grassland species. Competition between species for mineral nutrients is likely to be involved in some of these effects.

Previous comparative experiments (e.g., Bradshaw, Lodge, Jowett, and Chadwick, 1958, 1960 a; Bradshaw, Chadwick, Jowett, Lodge and Snaydon, 1960 b; Bradshaw, Chadwick, Jowett and Snaydon 1964) have shown that measurements of the response to the level of supply of an individual nutrient in sand and water culture can throw light on the ecological behaviour of grassland species.

In the experiments described in this chapter an attempt has been made to compare the response of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina to variation in supply of major nutrients. Two experiments have been carried out. The first involves potassium and the second, nitrogen.

Experiment (A)

Response to Potassium supply

Potassium was selected for this experiment because the element had not been used by previous investigators as a variable component in culture experiments involving these grasses.

Materials and methods

The plants were grown under the following environmental conditions: Light intensity $3.3 \text{ cal cm}^{-2} \text{ h}^{-1}$, temperature 20°C by day and 15°C by night, a relative humidity of 70% and a day length of 18 hours.

The plants were provided with Rorison nutrient solution in which potassium was adjusted to four levels. The solution was contained in 2.5 l (14.5 x 9.5 x 17 cm) polystyrene containers which were painted on the outside with bitumastic paint.

Support

The seedlings were supported on floating rafts of 1 cm expanded polystyrene. Each raft had several 2 cm diameter holes. To avoid algal growth in culture solutions the upper surface of the raft was covered with black polyethylene sheet which was sewn to the polystyrene framework with white terylene thread. The polyethylene sheet covering each hole in the raft was cut by a razor blade to form a cruciform slit through which seedlings were inserted. By this means the roots were immersed while the shoots were held clear of the solution and the slots in the polyethylene provided for the expansion of the shoot.

Plate 46. Seedlings of Agrostis tenuis on one of the floating rafts used to support the plants in the potassium experiment.



46

Plate 46 shows the growth of plants of Agrostis tenuis on one of these rafts in a culture vessel.

Aeration.

The plants were not aerated during the first week in order to avoid risk of disturbing the small seedlings. It seemed unlikely that oxygen would be limiting since the seedlings were small and a large volume of solution (2300 ml) was used and was changed every three days. During the four remaining weeks of the experiment continuous aeration was provided.

Preparation of plant material.

A large number of seeds were set to germinate in a controlled environment, on moist nylon cloth in transparent polystyrene boxes. This ensured the availability of a sufficient number of seedlings of comparable age. When the radicles had just emerged, seedlings were selected and transferred to other polystyrene boxes and placed on nylon cloth moistened with equal amounts of the appropriate solution, i.e. that to which they were to be transferred subsequently. The seedlings exceeded the number required for each treatment by a margin of fifty. Seedlings of uniform size were transferred to the experiment one week after germination, by which time they were large enough for easy handling.

Procedure.

The level of potassium in solution was varied by eliminating K_2HPO_4 . The phosphorus level was restored by

adding $\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$ To this basic "minus K" solution varying additions of K_2SO_4 were made. Analytical grade reagents were used. The levels of potassium used in the experiment were 0.13 ppm, 0.78 ppm, 7.8 ppm and 78 ppm. The pH of the solution was adjusted to pH 5.0.

Five, uniformly-sized, one week old, seedlings were placed in each raft. Three replicate containers were used for each treatment for each species. The culture vessels were arranged in three blocks and each block contained one culture vessel for each treatment for each species. Every three days the solution in the culture vessels was replaced by 2300 ml of the appropriate nutrient solution. The seedlings were carefully tended throughout the experiment in order to avoid effects of desiccation or submersion in the solution. After each aeration, the position of the seedlings on the raft was adjusted where necessary and any crystallised salt was washed from the seedlings and raft with distilled water.

The plants were harvested five weeks after the beginning of the experiment at which time measurements of shoot height and root length* were carried out on each plant. The number of tillers was also recorded and photographs of representative plants were taken (Plates 47 to 58). Finally the plants were oven-dried and the shoots and roots were weighed separately.

* Here root length is not total root length, but length of longest straightened root.

Results

Deficiency symptoms and morphological responses.

Deficiency symptoms.

The plants of all species grown at 0.13 ppm potassium showed the classical colour symptoms of potassium deficiency (Wallace 1961). When the species were grown in solutions containing 0.78 and 7.8 ppm potassium, only plants of Arrhenatherum elatius showed symptoms on some of the leaves. Plants of all the species did not show any deficiency symptoms, when they were grown in solutions containing potassium concentrations higher than 7.8 ppm.

Morphological responses.

The curves in Fig.24 show the mean shoot height and mean root length of plants of the different species*. The plants of all species grown at 0.13 ppm potassium survived, but were very stunted in comparison with plants grown at higher concentrations.

Although plants of Arrhenatherum elatius grown at 0.78 ppm potassium grew to a fairly large size, they were still more stunted when compared with plants grown at 7.8 and 78 ppm potassium. Plants grown at these last concentrations were comparable in size. (Plates 47 to 50, and Fig.24).

Although plants of Agrostis tenuis did not show any symptoms of potassium deficiency, marked differences in morphology were noticed between plants grown at different

* Here root length is not total root length, but length of longest straightened root.

Fig.24. Effect of potassium concentration in culture solution on maximum root length and maximum shoot height of plants of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina. 95% confidence limits are included.

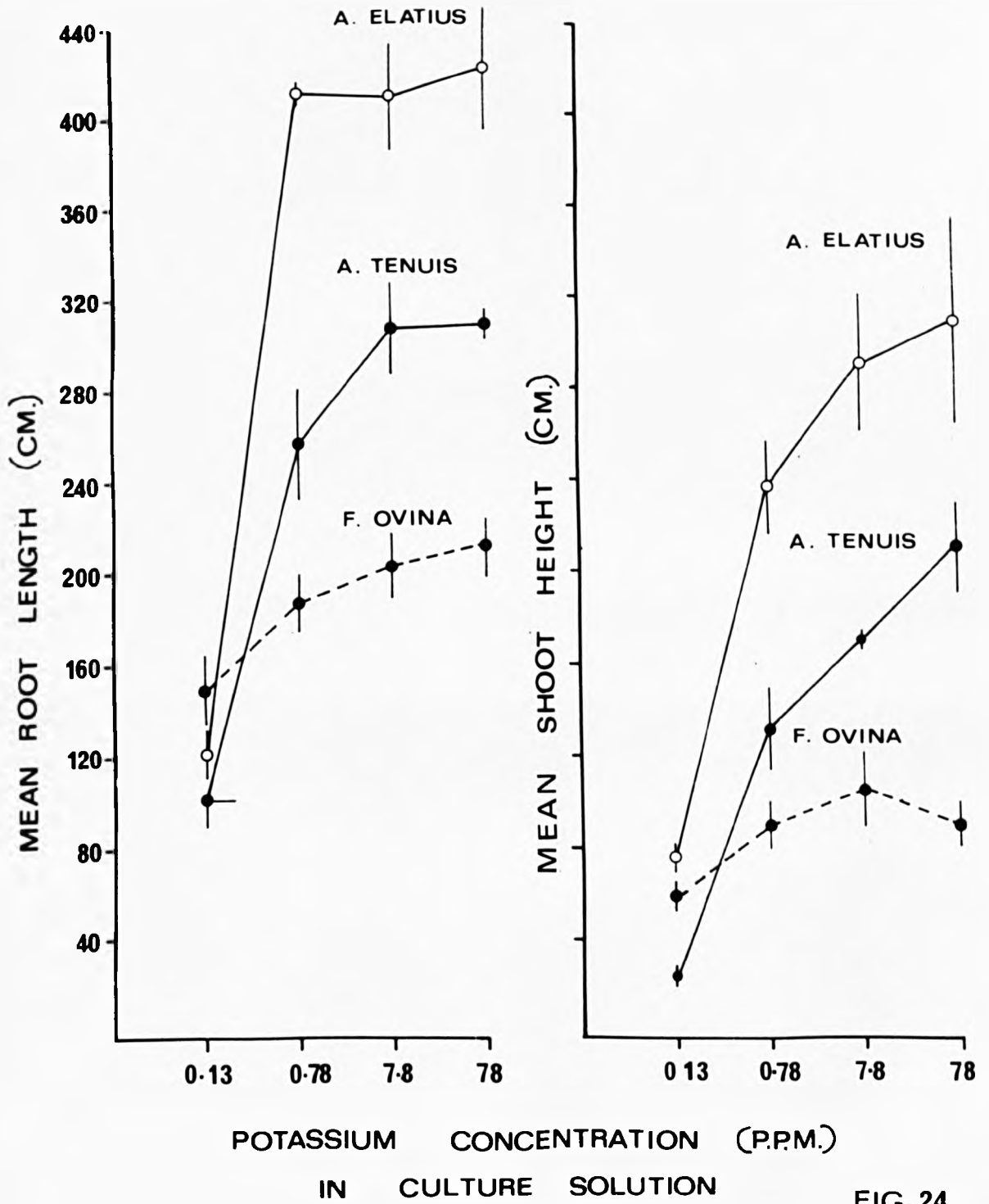


FIG. 24

Plates 47 - 50.

Appearance of representative plants of Arrhenatherum elatius grown at four levels of potassium in culture solution. 0.13 ppm K (Plate 47); 0.78 ppm K (Plate 48); 7.8 ppm K (Plate 49) and 78 ppm K (Plate 50).

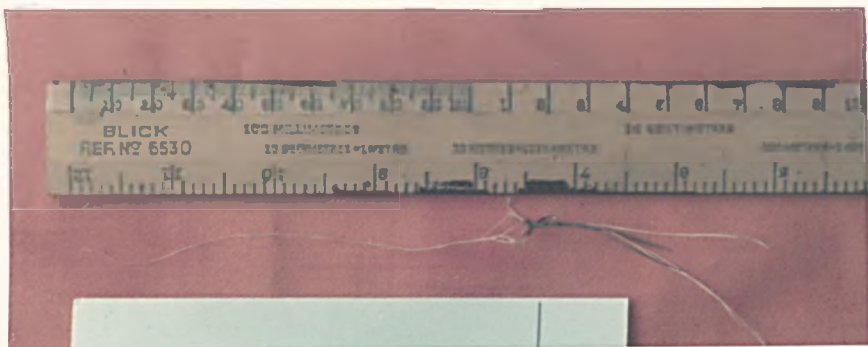
49



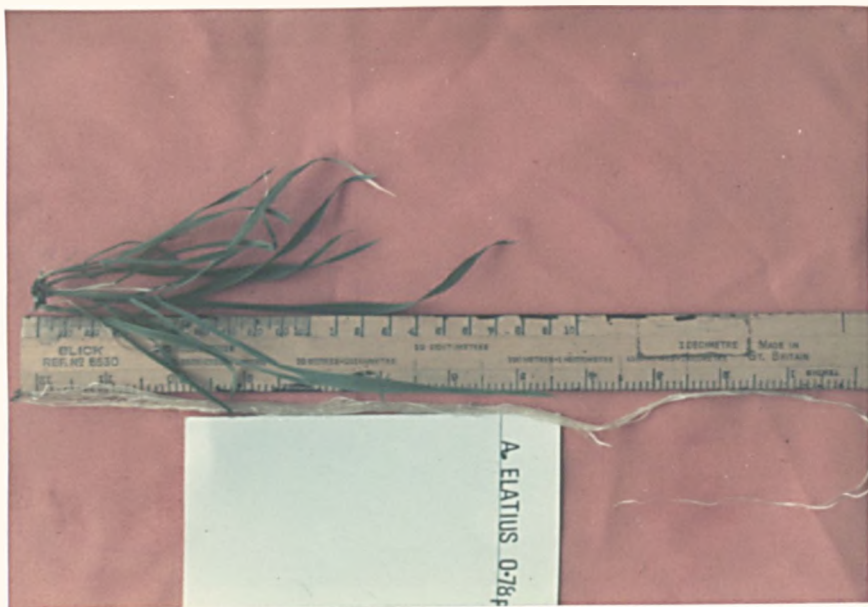
50



47

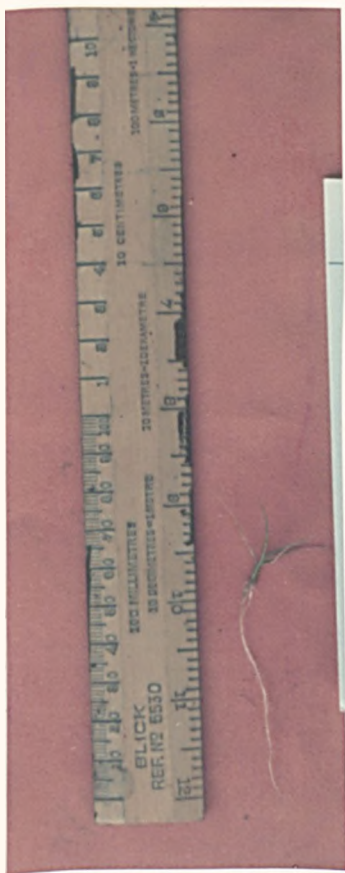


48

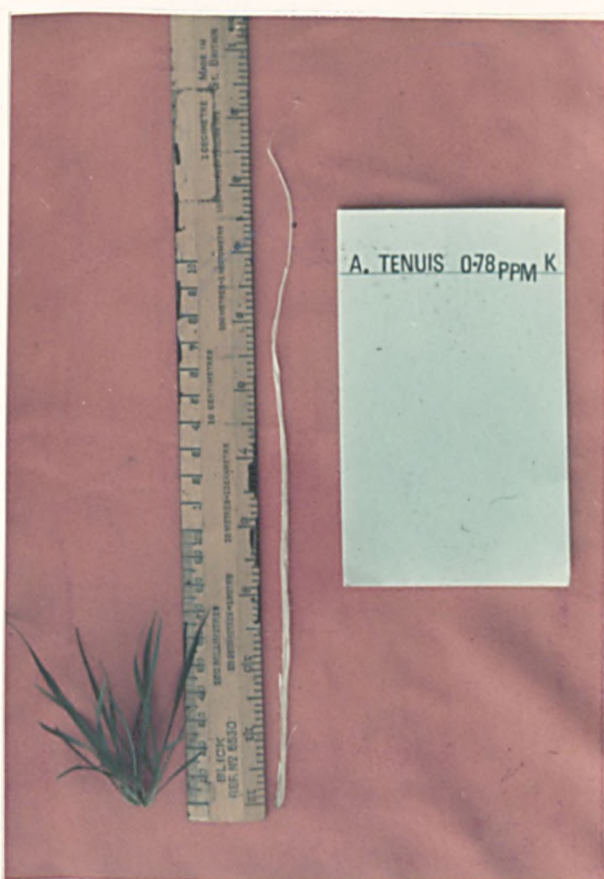


Plates 51 - 54.

Appearance of plants of Agrostis
tenuis grown at four levels of
potassium in culture solution,
0.13 ppm K (Plate 51), 0.78 ppm K
(Plate 52), 7.8 ppm K (Plate 53)
and 78 ppm K (Plate 54).



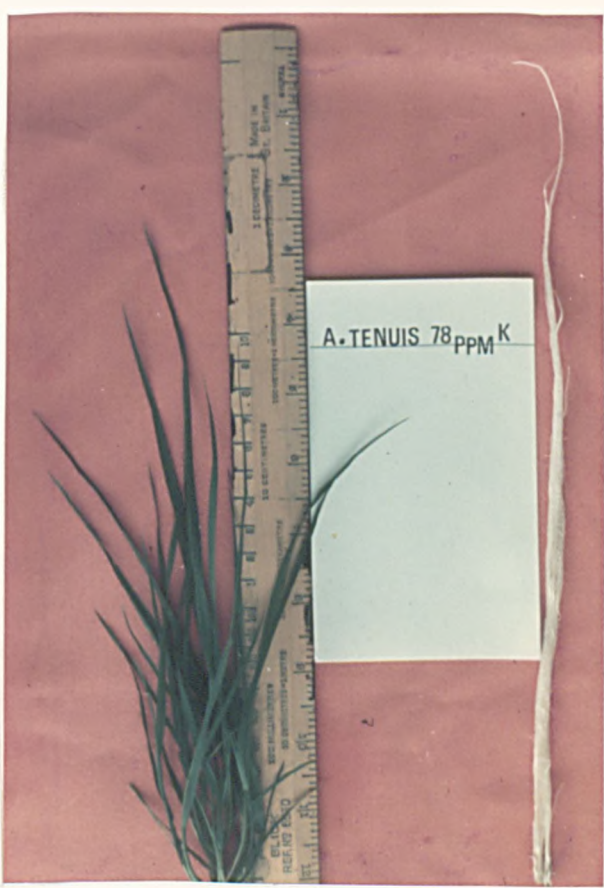
51



52



53



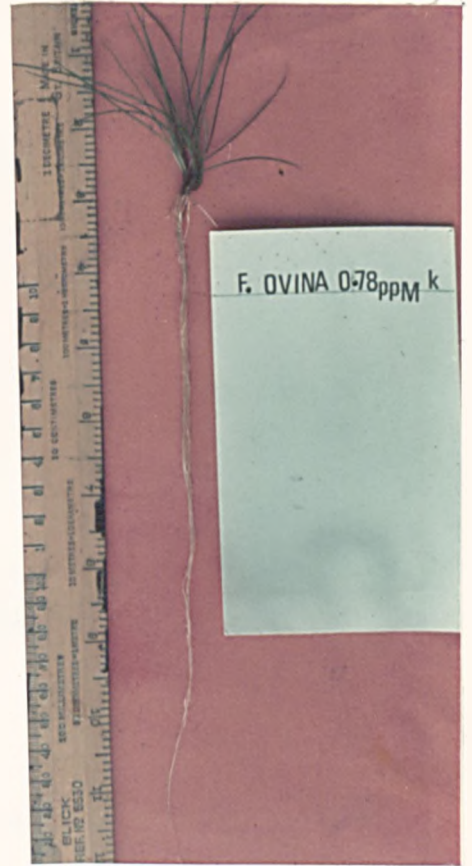
54

Plates 55 - 58.

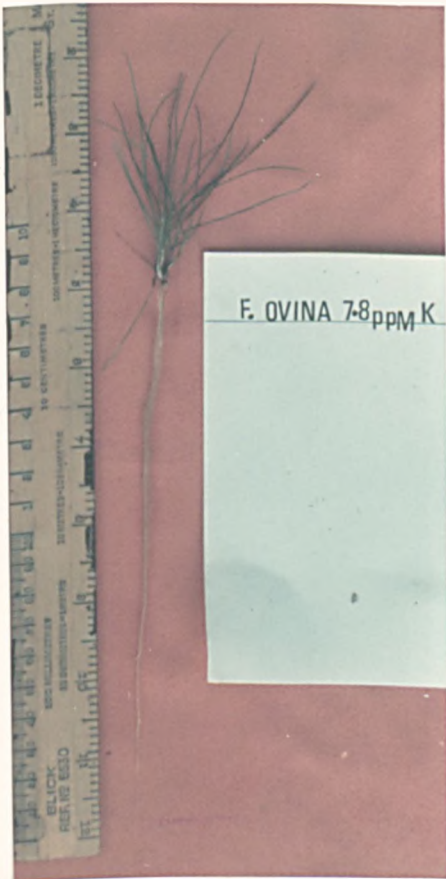
Appearance of plants of Festuca ovina grown at four levels of potassium in culture solution, 0.13 ppm K (Plate 55), 0.78 ppm K (Plate 56), 7.8 ppm K (Plate 57) and 78 ppm K (Plate 58).



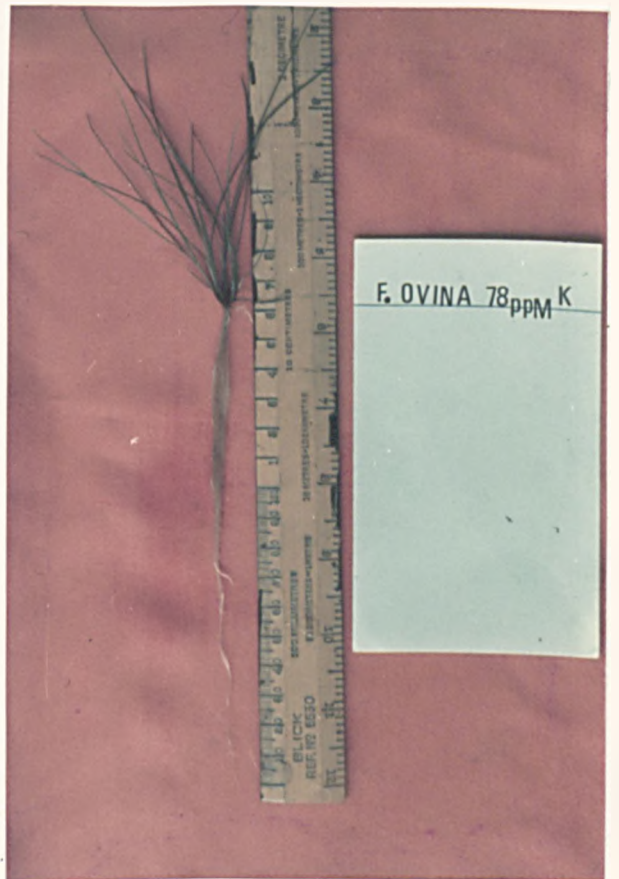
55



56



57



58

concentrations of potassium. At 0.78 ppm potassium, Agrostis tenuis was dwarfed; the size of the plants increased progressively as the potassium concentration in solution increased. (Plates 51 to 54 and Fig.24.) Root length showed similar trends in the species.

Plants of Festuca ovina grown in solutions containing 0.78 to 78 ppm potassium showed no apparent differences in morphology. There were no significant differences in shoot height and root length over the abovementioned concentration range (Plates 55 to 58 and Fig.24).

Tillering.

Data concerning the mean number of tillers of the three species when grown in solutions containing the different concentrations of potassium are presented in Table 16.

Table 16.

Numbers of tillers of plants of Agrostis tenuis, Arrhenatherum elatius, Festuca ovina at four levels of potassium. 95% confidence limits are included.

Species	0.13	0.78	7.8	78 ppm
<u>Arrhenatherum elatius</u>	1.0 [±] 0.0	8.0 [±] 0.6	10.4 [±] 1.2	17.2 [±] 1.5
<u>Agrostis tenuis</u>	1.0 [±] 0.0	7.5 [±] 1.4	15.4 [±] 1.6	14.9 [±] 1.2
<u>Festuca ovina</u>	3.4 [±] 0.5	7.8 [±] 0.7	10.0 [±] 0.4	10.3 [±] 0.6

In Arrhenatherum elatius, the number of tillers increased significantly as the concentration of potassium increased in solution. For Agrostis tenuis, the increase in potassium concentration in solution from 0.78 ppm to 7.8 ppm doubled the

number of tillers, but a further increase to 78 ppm caused no corresponding increase in tiller number. In both species tillering was inhibited when plants were grown in solutions containing 0.13 ppm potassium. Unlike the former two species Festuca ovina grown in solutions containing 0.13 ppm potassium, developed additional tillers. The tiller number was slightly increased as the concentration of potassium in solution was raised from 0.78 to 7.8 ppm, but no further tillering accompanied the increase of potassium to 78 ppm.

Yield.

The yields obtained (mean total dry weight of shoot and root) are given in Fig.25. At 0.13 ppm potassium, each species produced a low yield, but Arrhenatherum elatius and Festuca ovina considerably outyielded Agrostis tenuis. The yield of the three species increased considerably as the concentration of potassium in the solution increased from 0.13 to 0.78 ppm. A further increase in potassium concentration to 7.8 and 78 ppm resulted in corresponding increase in the yield of Arrhenatherum elatius and Agrostis tenuis, but not in the yield of Festuca ovina. In the extent of the response of dry matter production to increasing supply of potassium the three species can be arranged in the order Festuca ovina, < Agrostis tenuis < Arrhenatherum elatius. It is worth mentioning that Arrhenatherum elatius outyielded the other two species at all concentrations and that at 0.78 ppm potassium, Arrhenatherum elatius outyielded Festuca ovina.

Fig.25.

Effects of potassium supply
upon dry weight yields of
Arrhenatherum elatius, Agrostis
tenuis and Festuca ovina. 95%
confidence limits are included.

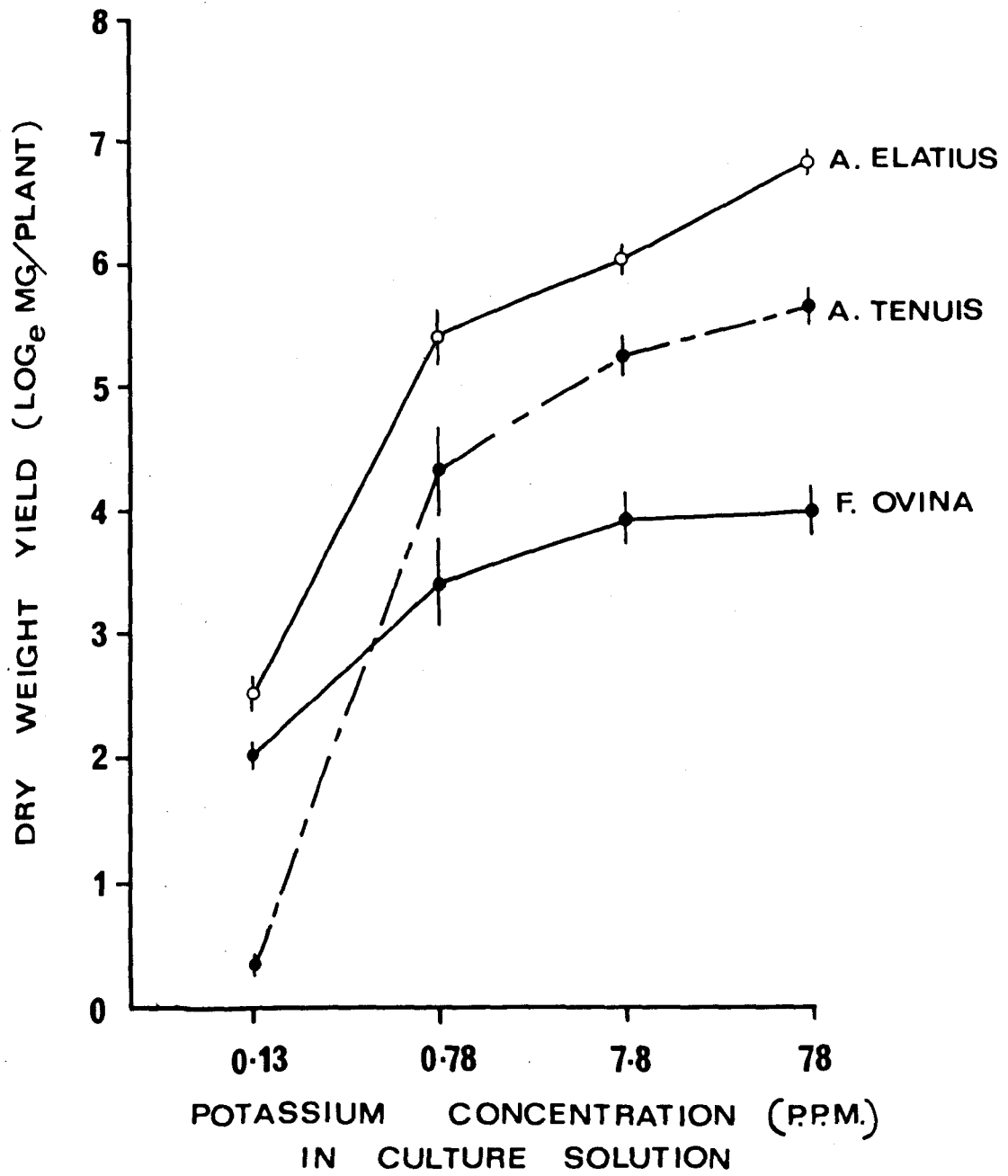


FIG. 25

Root:shoot ratios.

The data referring to the effects of different levels of potassium on root:shoot ratio are shown in Table 17.

Table 17.

Root:shoot ratios of plants of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina grown at four levels of potassium. 95% confidence limits are included.

Species	Concentration of potassium (ppm)			
	0.13	0.78	7.8	78
<u>Arrhenatherum elatius</u>	0.254 [±] 0.094	0.331 [±] 0.036	0.345 [±] 0.021	0.247 [±] 0.021
<u>Agrostis tenuis</u>	0.351 [±] 0.098	0.419 [±] 0.042	0.342 [±] 0.021	0.256 [±] 0.021
<u>Festuca ovina</u>	0.288 [±] 0.052	0.392 [±] 0.064	0.384 [±] 0.021	0.374 [±] 0.021

Festuca ovina showed little response in root:shoot ratio to increasing nutrient concentration and attained comparatively high values in all treatments. In Arrhenatherum elatius and Agrostis tenuis there was a reduction in root:shoot ratio at the highest potassium level as compared to the values at low levels.

Experiment B.

Responses to nitrogen.

Introduction.

The ability of the potentially fast-growing species: Arrhenatherum elatius and Agrostis tenuis to maintain substantial growth at very low concentration of potassium (0.78 ppm) in

Experiment A could possibly be due to (a) either the ability of these plants to absorb this nutrient from solutions of low concentration (b) and/or to an increase in the total absorptive surface of the root*.

Increases in root:shoot ratio in plants grown in nutrient deficient media are now well documented (Benedict and Brown, 1944; Lovvorn, 1945; Troughton, 1956; Bosenmark, 1954; Luckwill, 1960; Nielsen and Cunningham 1964; Brouwer, 1966; Hunt 1970), but there is a shortage of data with which to compare plant species with respect to the rate and extent of such responses. There are indications however that the level of nutrients supply which promotes a response varies with different species (Hargreaves; unpublished). In addition to modifications in the allocation of dry matter to the roots, changes in root morphology may occur; root length has been reported to increase in low nutrient conditions. May (1965) grew barley seedlings under three nutrient treatments; 100% (standard solution) 50% and 10%, and examined the root growth at weekly intervals during the five weeks following emergence and found that total root length was greatest throughout the experimental period in those plants grown in 10% nutrient concentration despite the fact that this solution was suboptimal with respect to the dry weight yield of shoot and root. Bosenmark (1954) studying the influence of nitrogen supply on

*However, further analysis of material collected from the field (Rorison et al, unpublished) suggest that we can discount the ability of these species to maintain growth at very low internal concentration of potassium.

root development of wheat showed that an increase in root length was induced by nitrogen deficiency and was due to an increase in cell length. He found that at high rates of supply root length was reduced as a result of the combined action of a lowered rate of cell multiplication and cell elongation.

The stimulated root production under conditions of low nutrient supply appears to be a mechanism by which plants "scavenge" the soil environment. Depletion results in local nutrient stress and this appears to stimulate the root to extend into a new and greater volume of soil. We do not know for certain the ecological significance of the "scavenging response". In theory, such a mechanism could be advantageous in severely nutrient deficient soils or, alternatively it may be a characteristic of plants which experience intensive competition for mineral nutrients.

In this experiment an attempt was made to determine and compare the levels of nitrogen which promote and increase total root length in Arrhenatherum elatius, Festuca ovina and Agrostis tenuis. A lead-heap population of Agrostis tenuis (L.H.) which grows in soils which are poor in nutrients, was included in this experiment in order to compare its responses with those of the grassland population of Agrostis tenuis (G). Nitrogen was chosen for this experiment because it is one of the most important, and most generally deficient, soil nutrients limiting the growth of plants (Black 1957). The reports of many workers (e.g. Boyd and Lessels 1954; Voisin 1959,

1960) on increased productivity of natural and semi-natural communities following the application of nitrogen suggest the prevalence of suboptimal levels of nitrogen in these communities.

Materials and methods.

The experiment was carried out in a controlled environment similar to that used in experiment A. Methods of preparation and cultivation of seedlings were similar to those adopted in experiment A.

The plants were grown in solution cultures contained in 500 ml (10 x 10 x 8 cm) plastic pots. These were painted black on the outside with bitumastic paint. Eight nitrogen levels (2.5, 5, 7.5, 10, 20, 40, 80 and 100 ppm) were obtained by reducing the content of calcium nitrate in the Hewitt solution and compensating for the missing calcium by appropriate additions of calcium sulphate. The composition of the complete standard Hewitt nutrient solution is given in Table 7, page 53. The solutions were constantly replenished by means of a system of a gravity flow to the pots from large reservoirs. A rate of 15 litres per 24 hours per treatment (500 ml pots) was maintained. In order to maintain an even pressure distribution between the pots, a small length of capillary tubing was inserted at the entrance to each pot. Mixing of the nutrient solution within each pot was effected by inserting the solution at the bottom of the pot and allowing overflow from a hole near the top. A randomized block design was used, and with the total of three blocks in

the growth room (each of 24 pots) three species were grown at a time*. For each species, each treatment was represented by three pots each containing, initially, six uniformly-sized one week old seedlings. The seedlings were supported in rafts similar to those used in experiment (A).

Since the work of Bosemark (1954), May (1965) and Hargreaves (unpublished) showed that root responses to low nutrient concentration become evident early in the life of the seedlings and because of the difficulties in avoiding nutrient depletion and in obtaining accurate measurements of total root length in large seedlings, the plants were harvested after three weeks. The process of root length measurement is laborious and necessitated a short period of storage of the seedlings. The plants were placed in beakers containing some of the solution in which they were grown in the experiment and were stored in a refrigerator at 0°C.

The total length of root was estimated by the line intersection method (Newman 1966).

Results.

The foliage of plants of all the species grown at the lowest nitrogen concentration (2.5 ppm) did not show the classical colour symptoms of nitrogen deficiency (Wallace 1961).

*The experiment formed part of a series of experiments involving other species (Grime and Hargreaves unpublished).

Dry matter production.

The graphs describing dry matter production are shown in Fig.26(a). The first point of note is the yield attained by each species at the highest nutrient level. The order of dry matter production was Arrhenatherum elatius > Agrostis tenuis (grassland population) > Agrostis tenuis (lead-heap population) > Festuca ovina.

In their response to increasing nitrogen concentration, all the species except Festuca ovina showed an increase in yield followed by a plateau. The minimum concentration of nitrogen at which the maximum dry matter production was attained occurred at 2.5, 5, 7.5 and 20 ppm in Festuca ovina, Agrostis tenuis (L.H.) Agrostis tenuis (G) and Arrhenatherum elatius respectively. Because the range of nitrogen concentration does not go below 2.5 ppm, it is not possible to determine precisely the concentration of nitrogen at which the element becomes limiting on the growth of Festuca ovina.

It is perhaps important to note that this experiment measures responses to a fixed external concentration and is therefore different from the experiments of Bradshaw et al. (1958, 1960 a, 1964). A very large volume of solution was used and therefore the experiment measures the ability of the species to obtain nitrogen from low concentration rather than the ability to survive progressive exhaustion of an aliquot of nitrogen.

The fact that plants of Arrhenatherum elatius did not show nitrogen deficiency symptoms at low levels of nitrogen

Fig.26(a)

Effect of nitrogen concentration in water culture on dry weight yields of plants of Arrhenatherum elatius, Agrostis tenuis (grassland (G) and lead-heap (L.H.) populations), and Festuca ovina.

(b)

Effect of nitrogen concentration in water culture on total root length of Arrhenatherum elatius, Agrostis tenuis (grassland (G) and lead-heap (L.H.) populations) and Festuca ovina. 95% confidence limits are included.

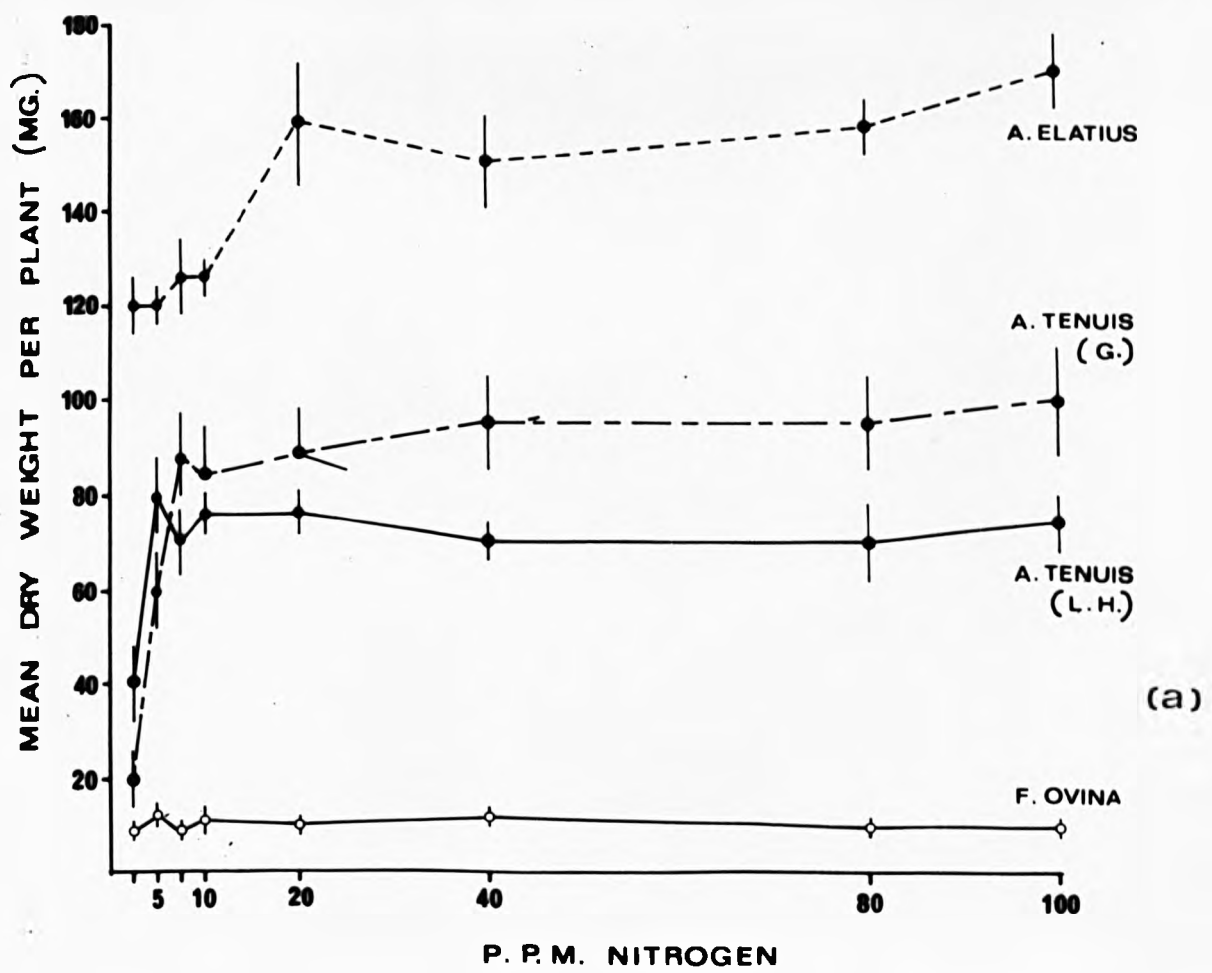
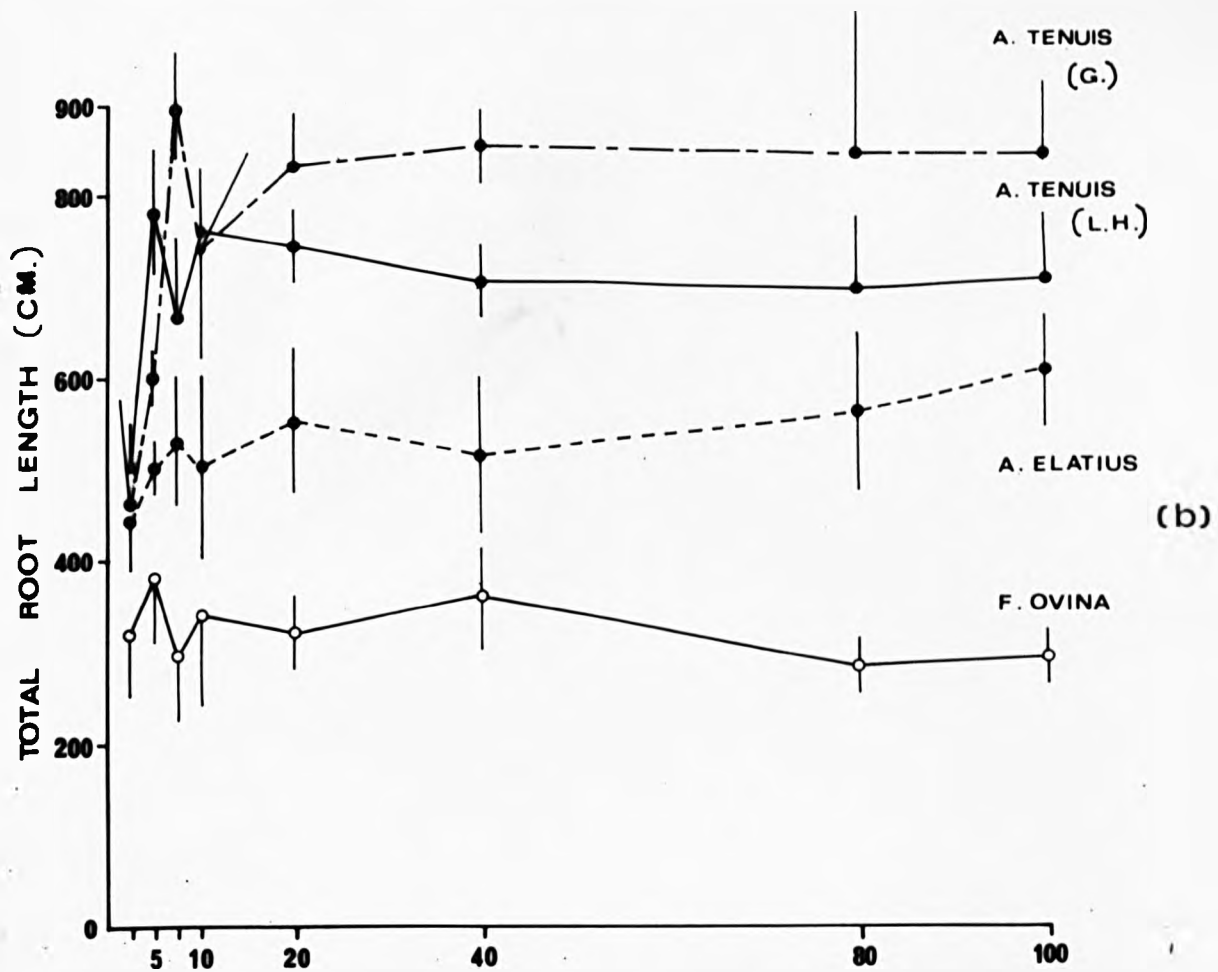


FIG. 26

and outyielded the other two species suggests that the species was efficient in nitrogen uptake. The results indicate, however, that Arrhenatherum elatius requires a higher external concentration than the other species in order to maximize dry matter production. There is no evidence on the basis of this experiment to suggest that the plants from nutrient deficient habitats (Festuca ovina, and Agrostis tenuis (L.H.)) are better able than Arrhenatherum elatius to maintain dry matter production at low external concentrations of nitrogen.

Root:shoot ratios.

The data concerning the effect of the different levels of nitrogen on root:shoot ratios of plants of Arrhenatherum elatius, Agrostis tenuis (G) and (L.H.) populations and Festuca ovina are presented in Table 18.

The root:shoot ratios presented in Table 18. indicate that Festuca ovina resembles the lead-heap population of Agrostis tenuis in showing relatively little response in root:shoot ratio to decreasing nitrogen concentration. Both maintained relatively high values at all concentrations of nitrogen. Arrhenatherum elatius and Agrostis tenuis (G) showed decreased root:shoot ratio with increasing concentrations of nitrogen.

Table 18.

Mean root:shoot ratios of plants of Arrhenatherum elatius, Agrostis tenuis (grassland and lead-heap) and Festuca ovina, grown at different levels of nitrogen. 95% confidence limits are given.

Species	Concentration of nitrogen (ppm)			
	2.5	5	7.5	10
<u>Arrhenatherum elatius</u>	0.367 [±] 0.014	0.341 [±] 0.017	0.313 [±] 0.026	0.313 [±] 0.026
<u>Agrostis tenuis</u> (G)	0.620 [±] 0.055	0.554 [±] 0.062	0.354 [±] 0.012	0.294 [±] 0.012
<u>Agrostis tenuis</u> (L.H.)	0.543 [±] 0.043	0.366 [±] 0.031	0.301 [±] 0.014	0.388 [±] 0.037
<u>Festuca ovina</u>	0.533 [±] 0.090	0.401 [±] 0.073	0.363 [±] 0.043	0.373 [±] 0.043

Species	Concentration of nitrogen (ppm)			
	20	40	80	100
<u>Arrhenatherum elatius</u>	0.261 [±] 0.014	0.251 [±] 0.012	0.247 [±] 0.012	0.248 [±] 0.017
<u>Agrostis tenuis</u> (G)	0.293 [±] 0.018	0.281 [±] 0.014	0.260 [±] 0.017	0.249 [±] 0.012
<u>Agrostis tenuis</u> (L.H.)	0.304 [±] 0.017	0.302 [±] 0.014	0.312 [±] 0.07	0.321 [±] 0.017
<u>Festuca ovina</u>	0.384 [±] 0.099	0.405 [±] 0.067	0.380 [±] 0.053	0.367 [±] 0.066

Total root length.

The graphs describing the total root length are presented in Fig.26(b).

There was no significant difference in total root length in Festuca ovina and Arrhenatherum elatius. Both populations of Agrostis tenuis showed marked and statistically significant responses over the range 2.5 to 10.0 ppm.

General conclusions concerning experiments A and B.

When Arrhenatherum elatius, Agrostis tenuis and Festuca ovina were grown at different concentrations of potassium, the yield of the species increased significantly from 0.13 ppm to 0.78 ppm. An increase in potassium concentration to 7.8 and 78 ppm resulted in corresponding increase in the yield of the two species of potentially rapid growth rate, Arrhenatherum

elatus and Agrostis tenuis, but not in the slow-growing species, Festuca ovina. Arrhenatherum elatus outyielded the other two species at all concentrations and Agrostis tenuis outyielded Festuca ovina at 0.78 ppm.

When Arrhenatherum elatus, Agrostis tenuis (grassland (G) and lead-heap (L.H.) populations) and Festuca ovina were grown at different concentrations of nitrogen (2.5 - 100 ppm) all the species except Festuca ovina showed an increase in yield to a maximum, followed by a plateau. This maximum yield was attained at 2.5, 5, 7.5 and 20 ppm in Festuca ovina, Agrostis tenuis (L.H.), Agrostis tenuis (G) and Arrhenatherum elatus respectively. The order of dry matter production at 2.5 was Arrhenatherum elatus, > Agrostis tenuis (L.H.) > Agrostis tenuis (G) > Festuca ovina.

At high nutrient levels, the species showed differences in overall yields, the order being Arrhenatherum elatus > Agrostis tenuis > Festuca ovina.

Differences with respect to plasticity in root:shoot ratio are apparent between the species. The two species of potentially rapid growth, Arrhenatherum elatus and Agrostis tenuis (G) showed an increase in root:shoot ratio at the lower nutrient levels (both potassium and nitrogen). A high proportion of root relative to shoot under conditions of low nutrient supply might be expected to place a species at an advantage relative to other species of similar dry weight (Hunt 1970). The low root:shoot ratio of these species at high nutrient levels is of special merit in competitive

situations where shoot production is obviously an advantage. That increased nutrient concentration causes a reduction in root:shoot ratio is well documented. (Benedict and Brown, 1944; Lovvorn, 1945; Bosenmark, 1954; Troughton, 1956; Luckwill, 1960; Nielsen and Cunningham, 1964; Hunt 1970).

The more or less generally high and uniform root:shoot ratios of the two species which are associated with soils of low fertility, Festuca ovina and Agrostis tenuis, (L.H.) is in agreement with results reported by Hunt (1970) for species which occur on similar soils.

CHAPTER 9.

RESPONSE OF PLANTS OF ARRHENATHERUM ELATIUS,
AGROSTIS TENUIS, AND FESTUCA OVINA TO CLIPPING.

Arrhenatherum elatius, Agrostis tenuis and Festuca ovina show considerable differences in frequency of occurrence in grazed and ungrazed sites - Arrhenatherum elatius is less frequent in heavily grazed or repeatedly mown turfs while Agrostis tenuis and Festuca ovina are more abundant in heavily grazed or frequently mown turfs. (Lloyd 1972; Grime and Lloyd 1973).

In an attempt to investigate these differential responses, experiments were set up in which Arrhenatherum elatius, Agrostis tenuis and Festuca ovina were grown in monoculture and were subjected to various clipping treatments.

Experiment A.

Materials and methods.

One-week-old seedlings of comparable size were planted individually in sand culture in 18 cm diameter plastic flower pots. The experiment was conducted in a heated green house in which 18 hour days were maintained by mercury vapour lamps. Each pot was watered every week with 100 ml of complete Hewitt solution and twice a week with 100 ml of distilled water. In order to minimize leaching and to prevent desiccation the runoff was allowed to collect in plastic saucers.

After four weeks of growth, each species was subjected to the following treatments:-

1. Unclipped control.
2. Clipped weekly at 6 cm from soil surface (T_2).
3. Clipped at 2 cm from soil surface (T_1).

The experiment was replicated 5 times and the pots were arranged in 5 randomized blocks. Weekly counts of leaf and tiller number were made on all plants on the same day immediately before clipping. The plants were harvested ten weeks after commencement of the experiment.

Results.

The plants of Arrhenatherum elatius and Agrostis tenuis grew to a large size and were probably pot-bound by the end of the experiment. Arrhenatherum elatius showed two distinct growth forms (erect and prostrate). Plate 59 illustrates both forms at the flowering stage. From this photograph it can be seen that although the culms of the prostrate form are erect, the vegetative shoots still maintain an oblique position. Agrostis tenuis and Festuca ovina did not show any signs of flowering.

A comparison of tiller and leaf production by the control plants (Fig.27) showed that Agrostis tenuis plants developed more tillers and leaves than either of the two other species. However, Arrhenatherum elatius developed very much larger leaves than Agrostis tenuis and Festuca ovina. The superiority of Agrostis tenuis in tiller and leaf production in comparison with Arrhenatherum elatius may be attributed to a number of possible factors: (a) most of the Arrhenatherum elatius plants included in this treatment belonged to the erect

Plate 59.

Appearance of two growth forms of Arrhenatherum elatius (prostrate "A" and erect "B") at flowering stage. Observe that although the culms of the prostrate form are erect, the vegetative shoots maintain an oblique position.



A

59

B

Fig.27. Tiller and leaf production in unclipped (control) plants of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina. 95% confidence limits are given.

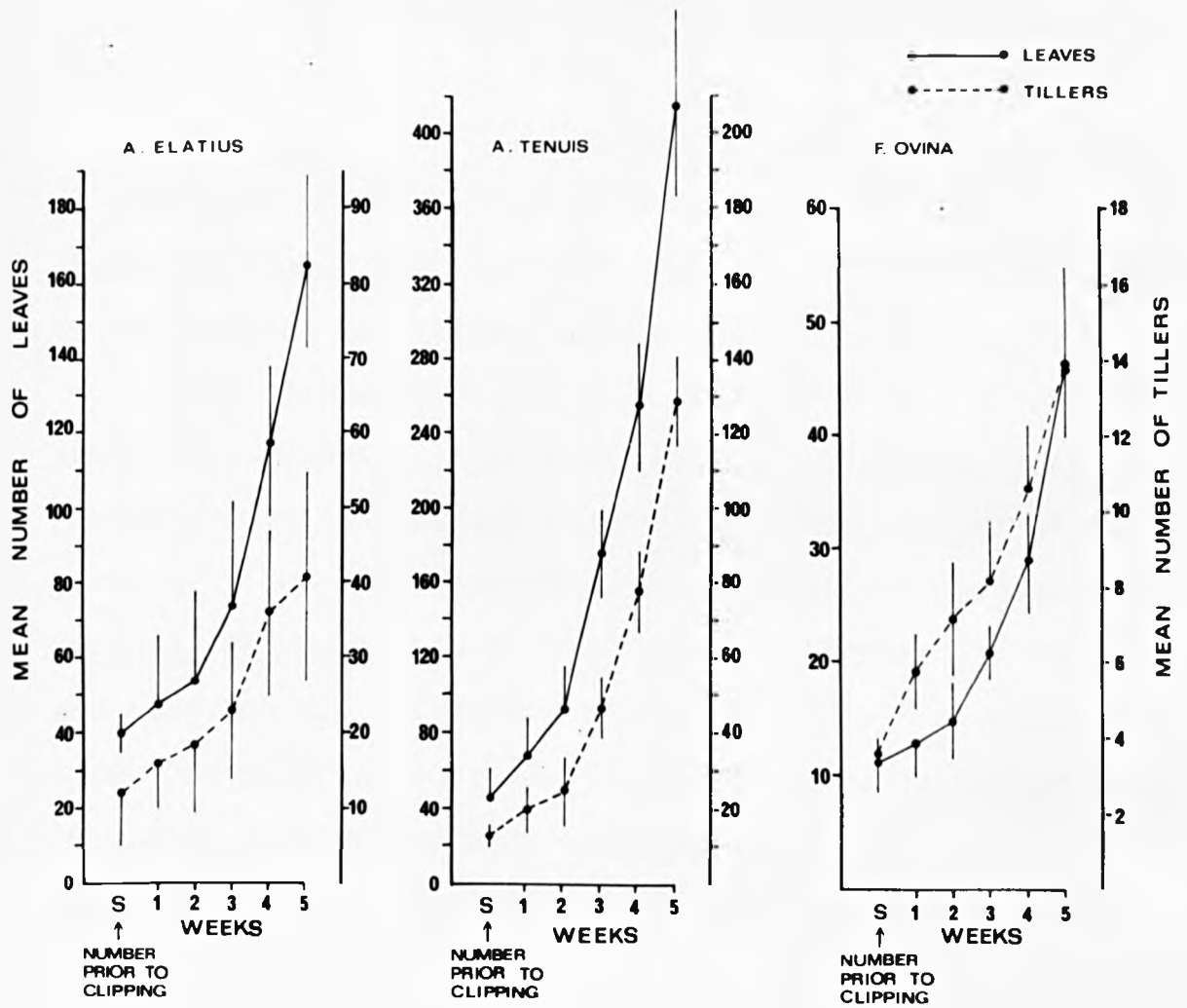


FIG. 27

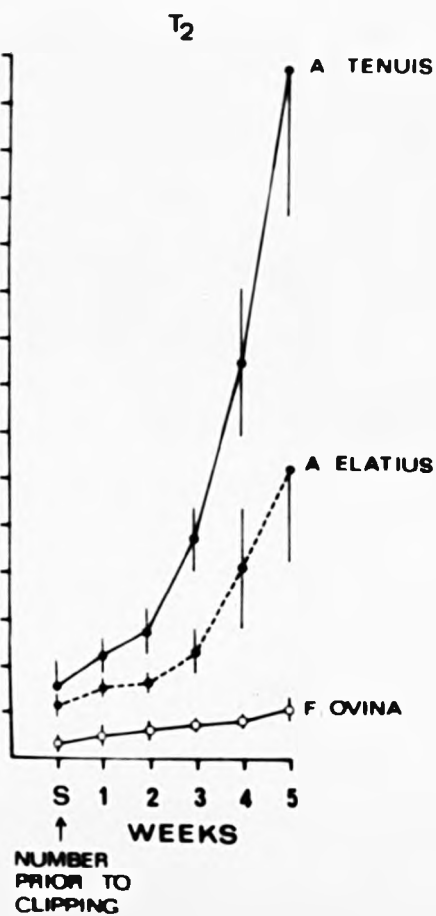
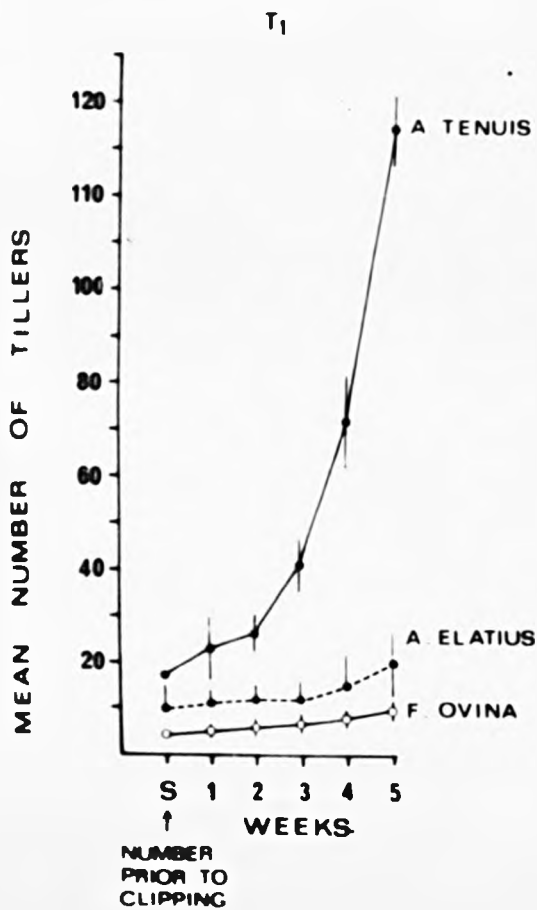
form which seems to have a low tillering capacity as compared to the prostrate form (b) Arrhenatherum elatius produced the largest plants which were likely to be pot bound before the other species and (c) since the plants of Arrhenatherum elatius flowered after seven weeks of growth, it is possible that a considerable amount of its photosynthate was expended on reproductive rather than vegetative shoots.

The graphs in Fig.28 compare tiller and leaf development, in the three species, under both clipping treatments. The graphs in Fig.29 show for each species, the tiller development in the control and clipped plants.

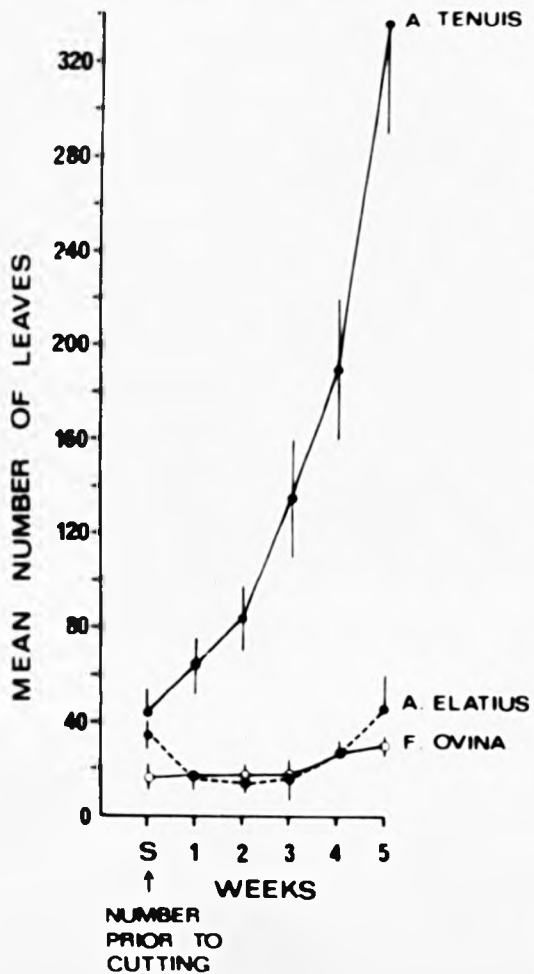
The graphs in Fig.28 show that under both clipping treatments (i.e. cutting at 2 cm and at 6 cm) Agrostis tenuis produced more tillers and leaves than either of the other two species. The tillers produced by the clipped specimens of Agrostis tenuis were very short and the leaves were numerous and very small. Comparison with the controls reveals no effect of clipping on tiller and leaf number in Agrostis tenuis (Fig.29). Clipped plants of Agrostis tenuis had fewer leaves than controls but these differences were not statistically significant.

Data in Fig.28 show that, for Arrhenatherum elatius, the height of clipping is a very crucial factor in determining the abundance of tillers and leaves. Close clipping (2 cm) reduced the number of both leaves and tillers very considerably, while clipping at 6 cm did not reduce significantly tiller and leaf numbers

Fig.28. Tiller and leaf production in plants of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina clipped at 6 cm (T_2) and 2 cm (T_1) from soil surface. 95% confidence limits are included.



T₁



T₂

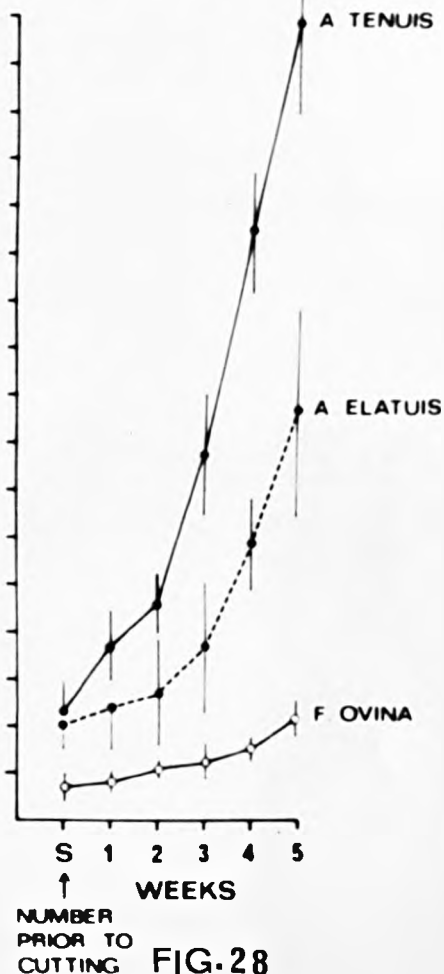


FIG. 28

Fig.29. Leaf and tiller production in control and clipped plants of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina.

T₂ = clipped at 6 cm.

T₁ = clipped at 2 cm.

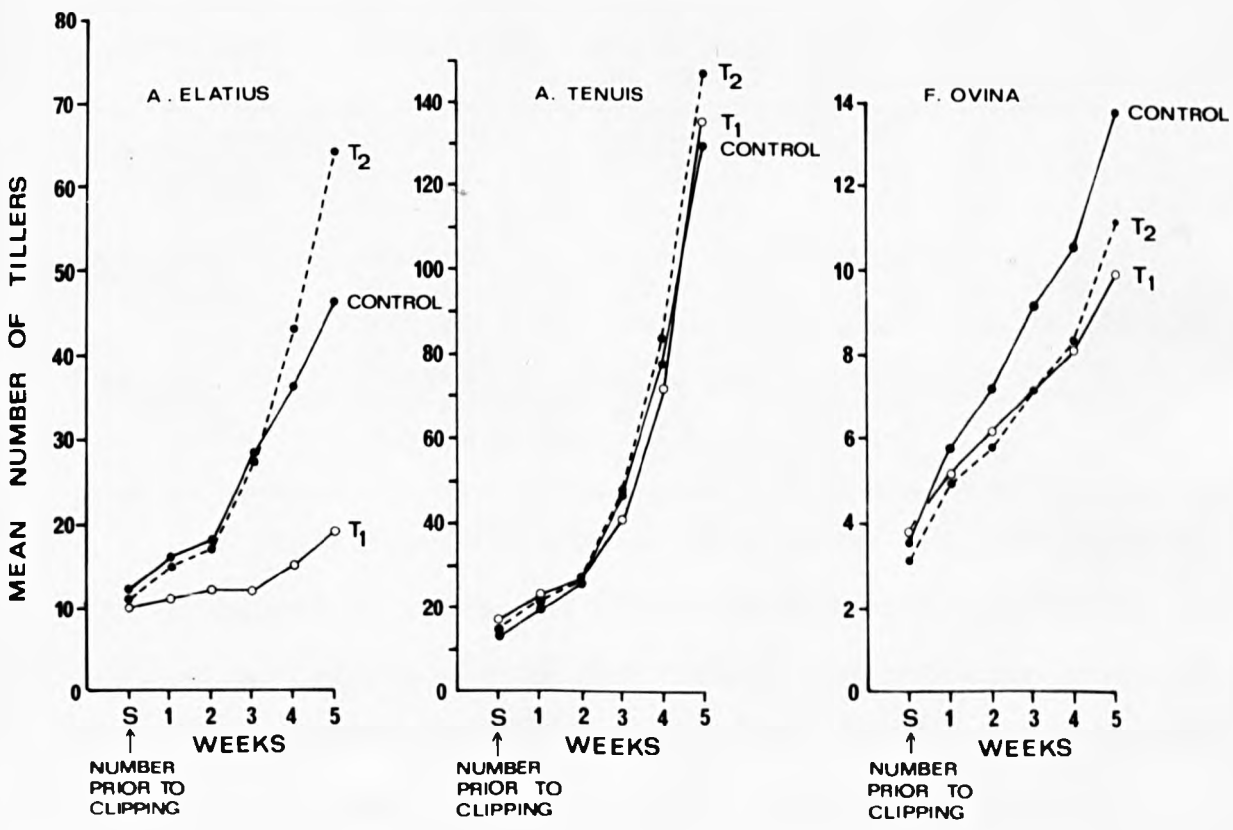
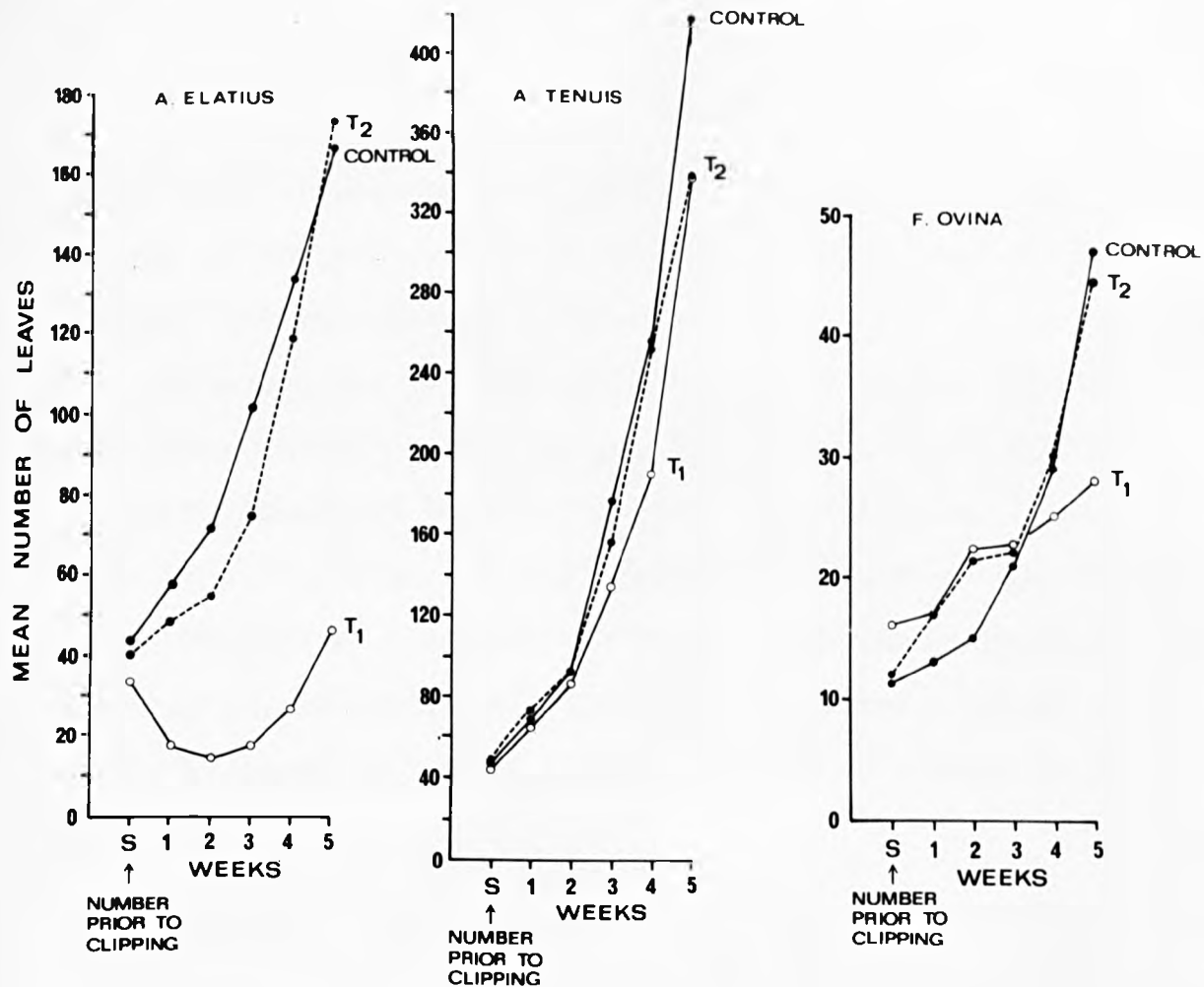


FIG. 29

below that of the control plants. Examination of the plants at the end of the experiment revealed that many tillers had been killed under close clipping.

Although the two clipping treatments did not reduce tillering production in Festuca ovina (Fig.29), a decline in leaf number was associated with close clipping (Fig.29). This is probably due to the more erect nature of the species which results in considerable defoliation (and possibly also destruction of meristems) when the plants were cut at 2 cm. Table 19 shows the mean oven dry weights of plants at final harvest.

Table 19.

Mean dry weight (mg) of plant material at final harvest.
95% confidence limits are included.

Species	Treatment	Mean dry weight(mg) of shoot	Mean dry weight(mg) of shoot	Mean dry weight(mg) of shoot
<u>Arrhenatherum elatius</u>	Control	7203 [±] 949	2693 [±] 333	9896 [±] 333
	Cut at 6 cm	1452 [±] 320	396 [±] 94	1849 [±] 400
	Cut at 2 cm	266 [±] 116	123 [±] 34	390 [±] 151
<u>Agrostis tenuis</u>	Control	4629 [±] 433	1953 [±] 423	6584 [±] 415
	Cut at 6 cm	1300 [±] 303	590 [±] 30	1890 [±] 116
	Cut at 2 cm	640 [±] 73	245 [±] 49	885 [±] 116
<u>Festuca ovina</u>	Control	151 [±] 16	44 [±] 7	196 [±] 22
	Cut at 6 cm	128 [±] 7	38 [±] 7	167 [±] 11
	Cut at 2 cm	26 [±] 4	13 [±] 2	40 [±] 10

The yield values given in Table 19 do not take account of the weight of discarded clippings and both treatments reduced the dry weight of both shoots and roots as compared with those of unclipped controls. Again as might be anticipated the shorter clipping had the greatest effect - (Table 19). Clipping at 6 cm did not reduce the yield of

Festuca ovina considerably because most of the herbage did not grow to the height of the cut. In all species the effect of herbage removal is reflected in reduced root production. Close clipping regularly at 2 cm from the sand surface resulted in scantier root development than cutting at greater height (6 cm) even in Agrostis tenuis which appeared to develop a vigorous shoot under both types of clipping. This result is in agreement with those obtained for prairie grasses, subjected to clipping or grazing, (Aldous, 1930; Weaver, 1930; and Parker and Sampson, 1930). Experiments with Poa pratensis by Graber (1931) also show that root development is inhibited by frequent defoliations. Harrison (1931) investigated several grass species and concluded that close clipping always resulted in small root development. Similar results were obtained by Dittmer (1973) when he subjected Bermuda grass (Cynodon dactylon) to various clipping treatments.

The data suggest that, of the three species, Arrhenatherum elatius is the least able to tolerate clipping. Although producing the highest yield when the plants were unclipped, (mean dry weights per plant for Arrhenatherum elatius, Agrostis tenuis and Festuca ovina were 9896 ± 333 mg, 6584 ± 415 mg, and 196 ± 22 mg respectively.), the species equalled Agrostis tenuis in yield when clipped at 6 cm (mean oven-dry weights per plant were 1849 ± 400 mg, 1890 ± 116 mg for Arrhenatherum elatius and Agrostis tenuis respectively.) However, when clipped at 2 cm, the yield of Arrhenatherum

Plates 60 - 68.

Appearance of representative plants of Arrhenatherum elatius (Plates 60 - 62) Agrostis tenuis (Plates 63 - 65) and Festuca ovina (Plates 66 - 68), which were subjected to different clipping treatments. Plants were photographed at final harvest.

Control	Unclipped plants.
T ₂	Clipped every week at 6 cm from soil surface.
T ₁	Clipped every week at 2 cm from soil surface.



A. ELATIUS
T.1

60



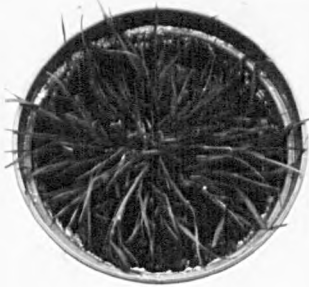
A. ELATIUS
T.2

61



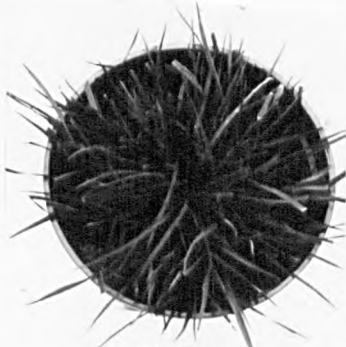
A. ELATIUS
CONTROL

62



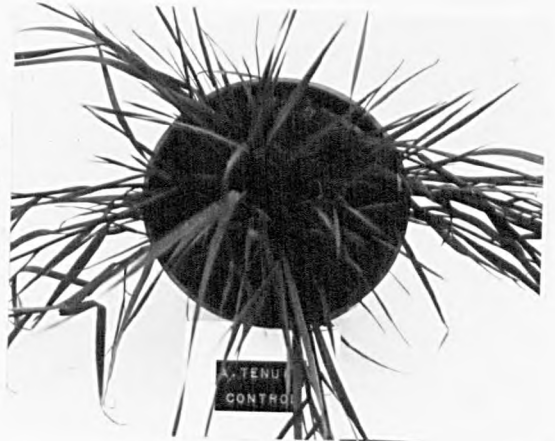
A. TENUIS
T.1

63



A. TENUIS
T.2

64



A. TENUIS
CONTROL

65



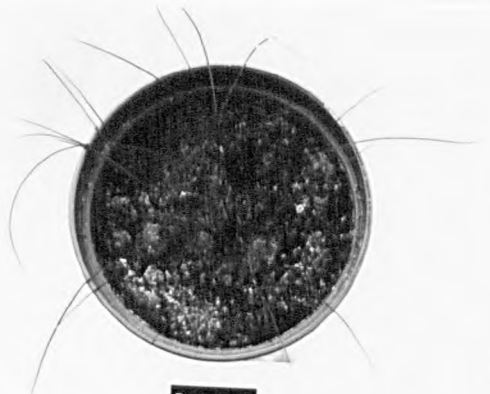
F. OVINA
T.1

66



F. OVINA
T.2

67



F. OVINA
CONTROL

68

elatus was less than half of that of Agrostis tenuis.

(390 \pm 151 mg and 885 \pm 116 mg were the oven-dry weights of Arrhenatherum elatus and Agrostis tenuis respectively.)

Plates 60 to 68 show the appearance of representative plants of the three species at final harvest.

Experiment B.

Experiment "A" was repeated in a controlled environment in a growth-room with the following objectives:- (a) to see whether the morphogenetic responses shown by Agrostis tenuis were maintained when the plants were subjected to close intensive clipping for a longer period, (b) to obtain a more complete account of dry matter production, by weighing the clippings, and (c) to examine the response to clipping of the prostrate forms of Arrhenatherum elatus, which were observed among the controls in experiment "A" (page 125) and to compare this response with that of Agrostis tenuis.

Materials and methods.

One-week-old seedlings were grown individually in sand culture in 18 cm diameter plastic flower pots, under standardized conditions in a growth room. The room provided the following environment: a temperature regime of 20°C by day and 15°C by night, a relative humidity of 70% and a light intensity of 3.3 cal cm⁻² h⁻¹ visible radiation and a day length of 18 hours. In order to avoid a possible accumulation of salts, the plants were watered alternately every three days with 100 ml of complete Hewitt solution and with 100 ml of distilled water.

The seedlings of each species were subjected to the following treatments:

- i.) "C" Unclipped control. In practice the plants were clipped once, at 2 cm from soil surface 50 days after commencement of the experiment. This was to avoid shading effects by the large control plants on adjacent clipped plants and to allow measurement of the vertical distribution of dry matter in unclipped plants (see Fig.32). The distribution of dry matter was analysed by a stratified clipping technique (Monsi and Saeki, 1953) in which the shoot canopy was separated into 2 cm horizontal strata, and the plant material within each stratum oven-dried and weighed.
- ii.) (T_1) Plants were clipped every three days at 2 cm from the soil surface.
- iii.) (T_2) Plants were clipped every three days at 6 cm from the soil surface.

Each treatment was replicated ten times.

Clipping commenced 25 days after planting. The clippings from successive cuts were collected from individual plants, oven-dried and weighed.

The pots were divided into two blocks, each block containing, for each species, representatives of half of each treatment. The treatments were fully randomized within each block.

Before clipping for the first time and at the final harvest, the number of tillers was counted. The plants were harvested after 70 days. The shoots and roots were oven-dried and weighed separately. On the day of harvest representative plants of the three species were photographed. (Plates 69 to 71).

Results.

The data obtained from this experiment supported the results of experiment "A" (page 128) in that Agrostis tenuis and Festuca ovina were better able to maintain growth under close clipping than Arrhenatherum elatius. Histograms in Fig. 30 show the mean dry weights of the shoot and root and also mean total dry weights of the three species at harvest.

The single clipping treatment (C) applied to the control plants after 50 days (a treatment perhaps not far removed from certain regimes of meadow and road-side management) caused only a temporary check on growth. Plants of Arrhenatherum elatius produced flowering shoots and the species slightly outyielded Agrostis tenuis. Repeated clipping at 6 cm reduced the yield of Arrhenatherum elatius to a value slightly lower than that of Agrostis tenuis. The performance of the species as reflected by the dry weights and general appearance of the shoot at final harvest suggested that frequent clipping at 2 cm had a most destructive effect on Arrhenatherum elatius in that the plant was reduced to a size comparable to that of the slow-growing species, Festuca ovina (Fig. 30).

Plates 69 to 71.

Appearance of representative plants of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina which were subjected to different clipping treatments. Plants were photographed at final harvest.

Treatments, from left to right:-

- a single clipping treatment applied after 50 days.
- repeated clipping treatment at 6 cm from soil surface.
- repeated clipping treatment at 2 cm from soil surface.

Plate 69. Arrhenatherum elatius.

Plate 70. Agrostis tenuis.

Plate 71. Festuca ovina.



69



70



71

Fig.30.

Yield of Arrhenatherum elatius, (A)
Agrostis tenuis (T) and Festuca ovina
(F).

- . (Cont.) = Clipped once at 2 cm.
- . T₂ = Clipped frequently at 6 cm.
- . T₁ = Clipped frequently at 2 cm.

95% confidence limits are included.

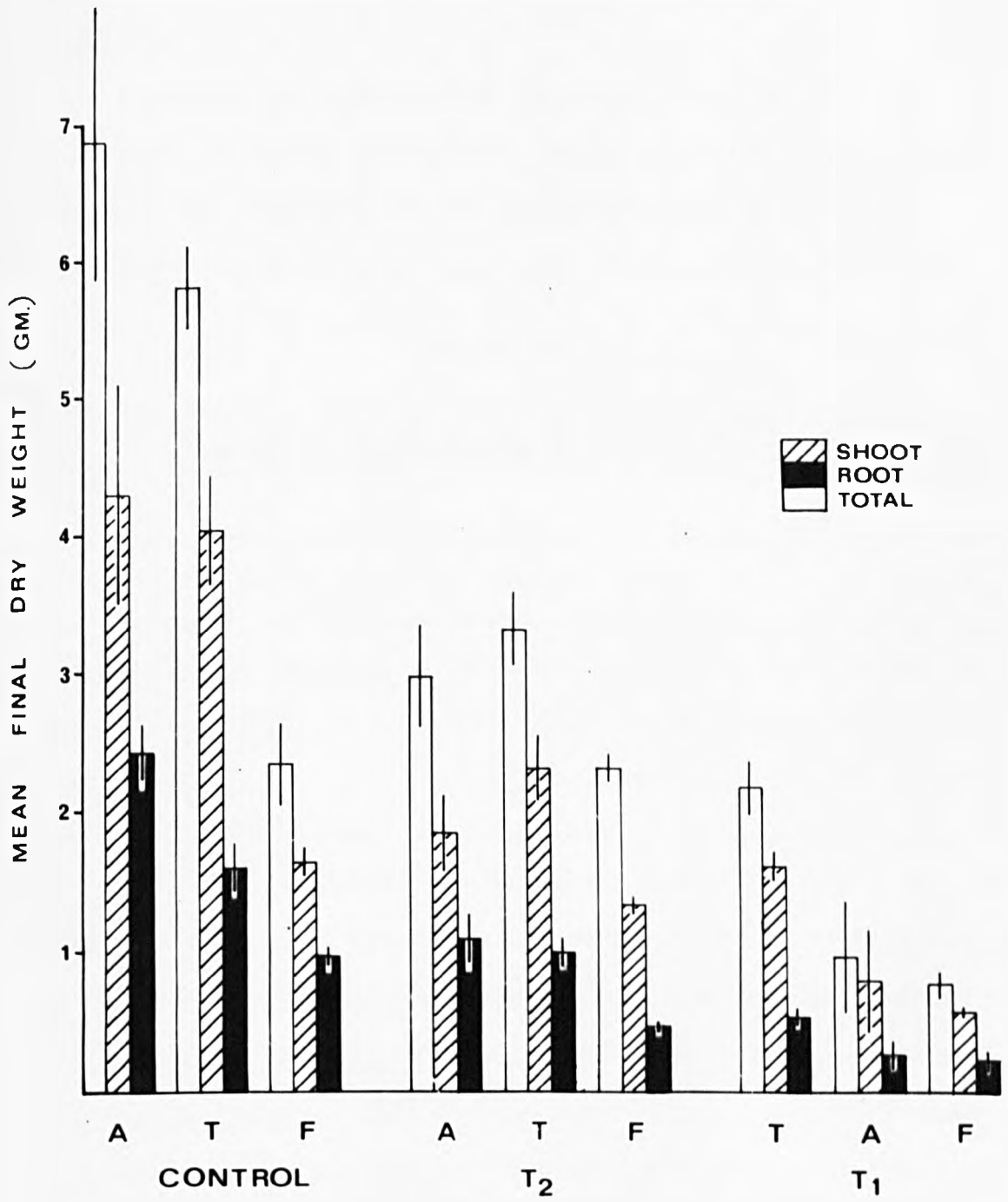


FIG.30

When clipped frequently at 2 cm, Agrostis tenuis outyielded the other two species in both shoot and root (Fig.30).

Differences between the three species in tolerance of different clipping treatments are evident when we examine the mean dry weights of the clippings collected from successive cuts (Fig.31) and also the totals in Table 20.

Table 20.

Mean dry weights (mg) of accumulated clippings from successive cuts of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina. 95% confidence limits are inserted in brackets.

Species	Cut at 6 cm	Cut at 2 cm
<u>Arrhenatherum elatius</u>	1049.70(± 116.94)	418.12(±74.67)
<u>Agrostis tenuis</u>	1329.31(± 45.24)	921.49(±56.88)
<u>Festuca ovina</u>	355.84(± 36.82)	249.59(±43.45)

The data presented in Table 20 show that under the most intensive clipping treatment the amount of the total clippings produced by Agrostis tenuis was more than double that produced by Arrhenatherum elatius and almost four times that produced by Festuca ovina. The mean oven-dry weights of the clippings collected from the successive cuts, presented in Fig.31 showed that, although Arrhenatherum elatius produced more clippings than the other two species at the beginning of the experiment (presumably because of its erect habit and its vigorous growth prior to clipping), the species produced a lower yield of

Fig.31. Dry weights of clippings collected at successive cuts from plants of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina, clipped at 6 cm (T_2) and 2 cm (T_1). 95% confidence limits are included.

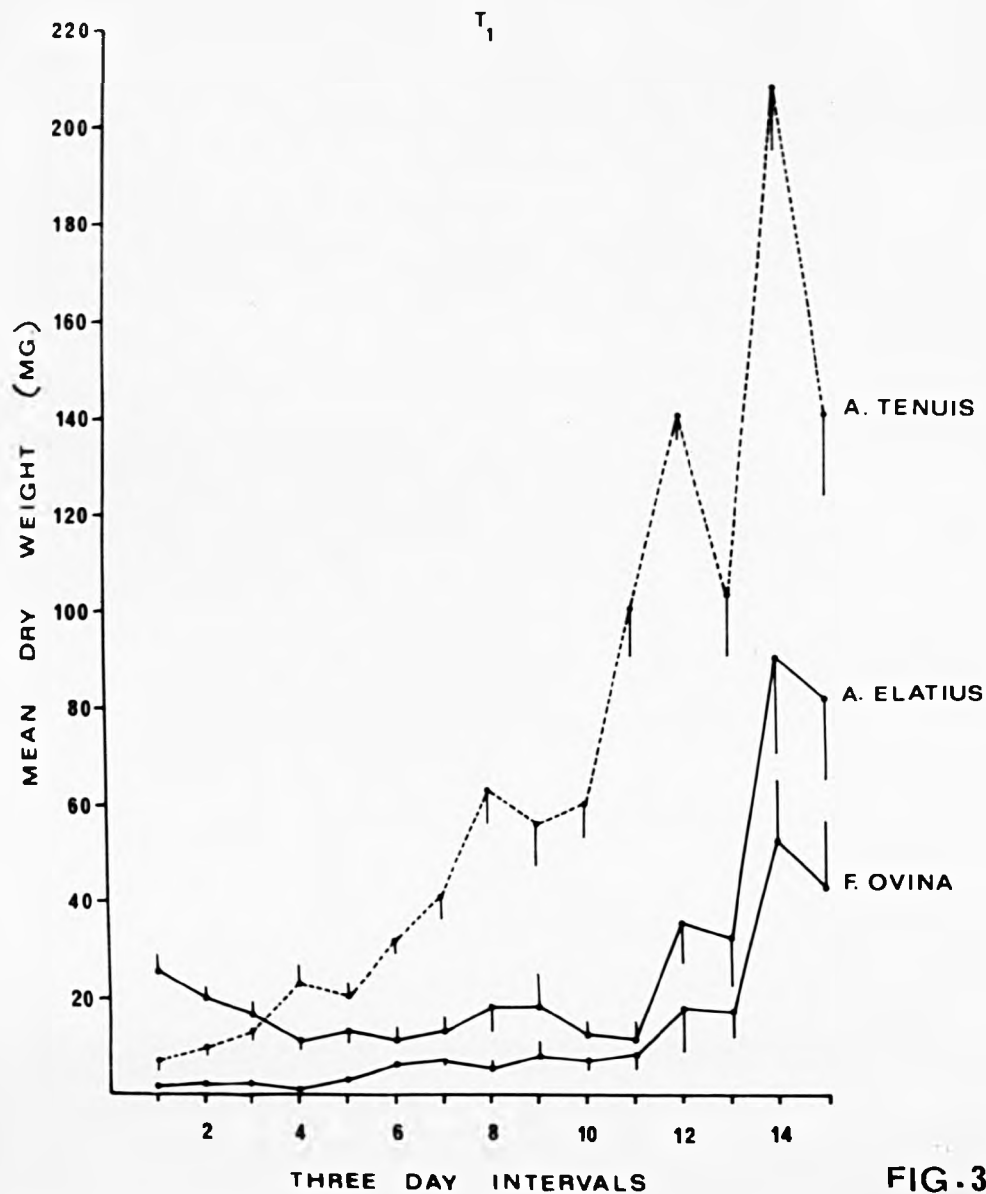
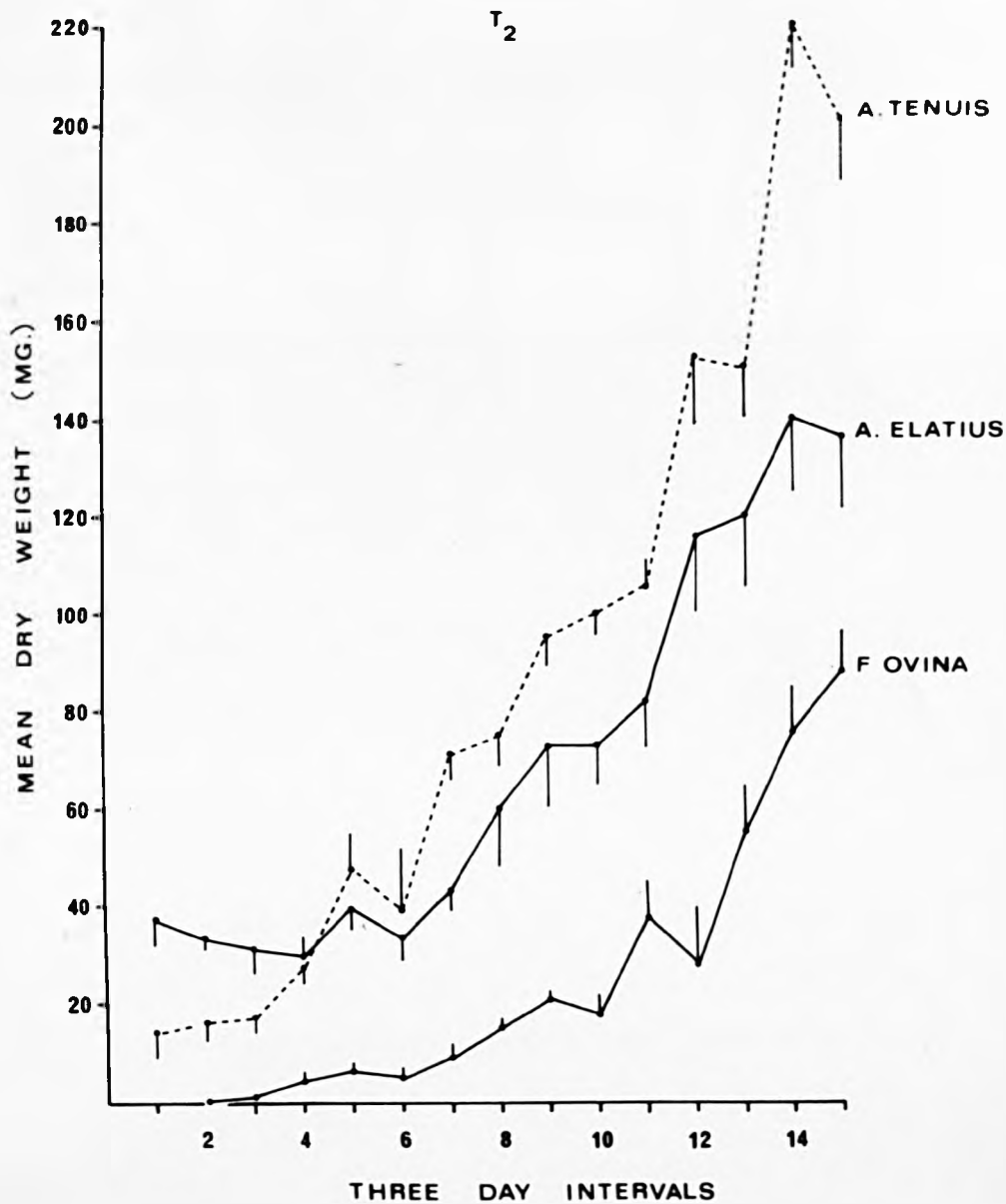


FIG. 31



clippings than Agrostis tenuis in the later stages of the experiment. In fact, by the end of the experiment the clippings produced by Arrhenatherum elatius were comparable in weight to those of Festuca ovina.

When the species were clipped at 6 cm Agrostis tenuis produced a greater dry weight of clippings than Arrhenatherum elatius. The dry weights of the clippings produced by these two species exceeded those of Festuca ovina. The curves in Fig.31 indicate that under this less intensive clipping all the species showed an increase in the yield of clippings with time. While the amount of clippings obtained from Arrhenatherum elatius in this treatment was almost double that produced when the species was clipped at 2 cm, the amount produced by Agrostis tenuis and Festuca ovina towards the end of the experiment was comparable to that produced when the two species were clipped at 2 cm.

Values for total production (estimated by adding the dry weight of the plants at harvest to the dry weight of the accumulated clippings) are presented in Table 21 and are clearly very much dependent on the height of clipping.

Table 21.

Mean total production (gm) of the three species when they were clipped at 6 cm and 2 cm. (95% confidence limits in brackets)

Species	Plants clipped at 6 cm.	Plants clipped at 2 cm.
<u>Agrostis tenuis</u>	6.624(±0.590)	3.069(± 0.208)
<u>Arrhenatherum elatius</u>	4.033(±0.527)	1.364(± 0.393)
<u>Festuca ovina</u>	2.161(± 0.467)	1.0213(±0.161)

Even in Agrostis tenuis which seemed to be relatively tolerant of defoliation, clipping at 2 cm reduced herbage production to half that obtained at the 6 cm height of clipping. However, Agrostis tenuis, outyielded Arrhenatherum elatius and Festuca ovina in the two clipping treatments. When clipped at 2 cm Arrhenatherum elatius had a comparable yield to that of Festuca ovina.

Table 22 illustrates the mean number of tillers present just before clipping commenced and at harvest.

Table 22.

Mean number of tillers of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina present just before clipping commenced and at harvest.
95% confidence limits are included.

Species	Treatment	Number of tillers just before clipping	Number of tillers at harvest
<u>Arrhenatherum elatius</u>	Control	28.2(±9.8)	48.9(±14.1)
	Cut at 6 cm	16.7(±7.9)	94.6(±22.1)
	Cut at 2 cm	14.0(±3.7)	39.9(±8.7)
<u>Agrostis tenuis</u>	Control	63.1(±8.1)	180.2(±22.9)
	Cut at 6 cm	56.8(±10.8)	207.4(±33.2)
	Cut at 2 cm	54.1(±12.3)	307.6(±11.9)
<u>Festuca ovina</u>	Control	36.8(±9.8)	167.3(±32.7)
	Cut at 6 cm	36.4(±10.8)	185.5(±32.6)
	Cut at 2 cm	31.3(±6.1)	204.5(±28.5)

It is clear from Table 22 that close clipping (at 2 cm) did not reduce the capacity of Agrostis tenuis and Festuca ovina to maintain tiller number as it did in the case of Arrhenatherum elatius.

It is worth mentioning that the prostrate growth forms of Arrhenatherum elatius which were recognized among the control

plants which were cut once at 2 cm (Treatment C) were observed to produce more tillers than the erect forms and maintained their superiority in tiller number after the single clipping. In this respect the prostrate plants resembled Agrostis tenuis, but they did not seem to approach the latter species in its potential for producing tillers. Table 23 shows the number of tillers of the two forms of Arrhenatherum elatius and Agrostis tenuis present just before clipping and at harvest.

Table 23.

Mean number of tillers of Arrhenatherum elatius, (prostrate and erect growth forms) and Agrostis tenuis in the control treatment, present just before clipping and at harvest. 95% confidence limits are included.

Species	Number of plants	Number of tillers just before clipping	Number of tillers at harvest
<u>Arrhenatherum elatius</u> (prostrate)	4	37.4(\pm 6.24)	65.6(\pm 8.4)
<u>Arrhenatherum elatius</u> (erect)	6	14.0(\pm 3.14)	32.2(\pm 2.38)
<u>Agrostis tenuis</u>	10	63.1(\pm 8.1)	180.0(\pm 22.9)

The results of the stratified clipping of the control plants show that Agrostis tenuis and Festuca ovina were closely similar in terms of the vertical distribution of shoot dry weight and there was little variation between replicates. In contrast, the distribution of dry matter in individual plants of Arrhenatherum elatius, confirmed the presence of distinct growth forms.

Fig.32 illustrates the distribution of dry matter in different strata of three representative plants of Agrostis tenuis,

Fig.32. Distribution of dry matter in horizontal (2 cm) strata in three representative plants of each of Arrhenatherum elatius (1), Agrostis tenuis (2), Festuca ovina (3). Note the difference between the three growth forms of Arrhenatherum elatius.

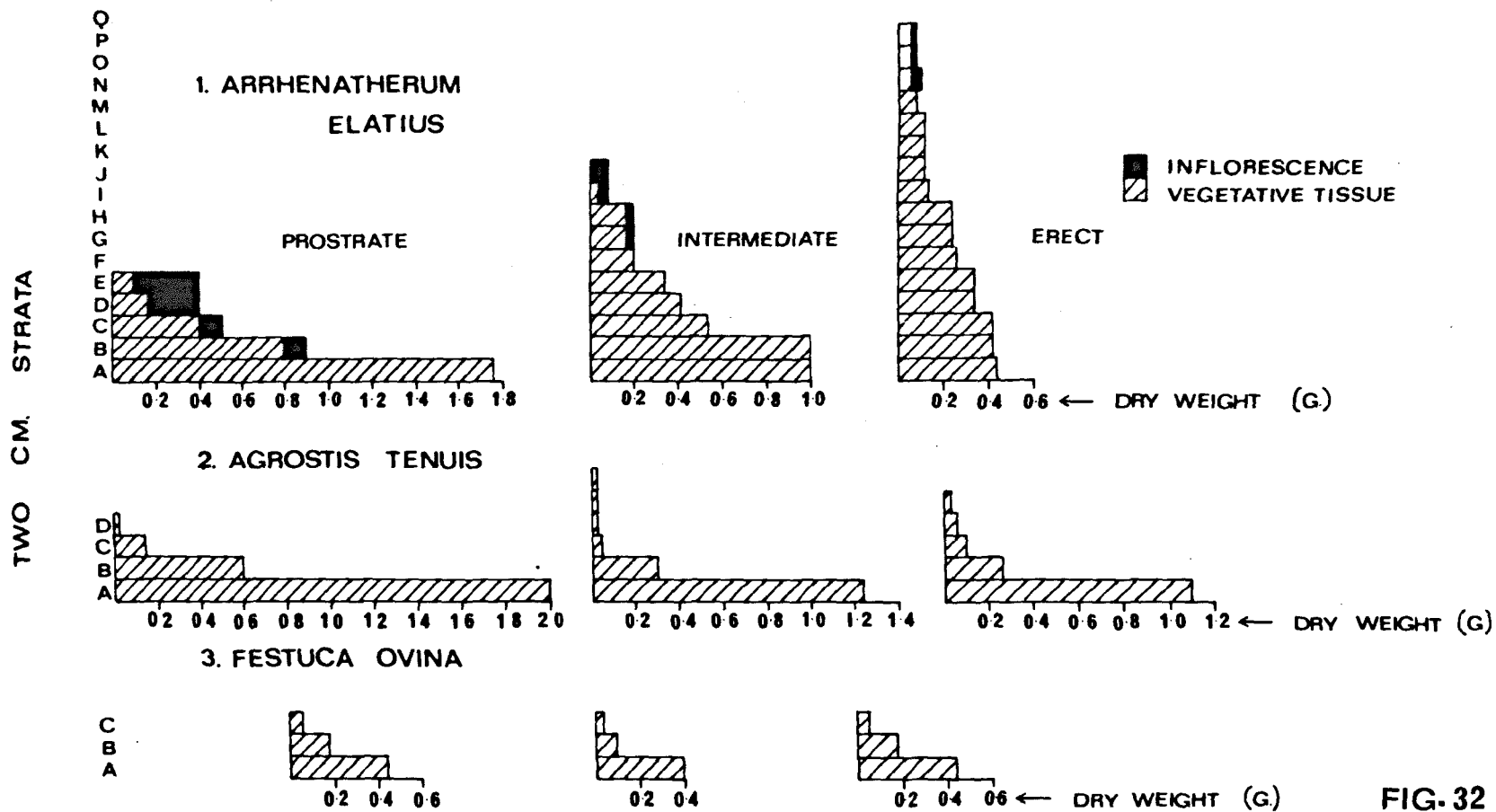


FIG-32

Festuca ovina and Arrhenatherum elatius. Three growth forms of Arrhenatherum elatius (prostrate, semi-prostrate and erect) are represented.

Experiment "C"

Responses of the different growth forms of Arrhenatherum elatius to clipping.

It was observed in previous experiments (pages 125 and 135) that variation occurs in the growth form of Arrhenatherum elatius i.e. populations contain prostrate and erect forms, and it was found that even in the absence of clipping, the former produced more tillers (page 135). It was suspected that the greater potential for tillering may give the more prostrate forms an advantage over the erect plants in heavily grazed or managed sites and that the latter are more susceptible to destruction and elimination under conditions of defoliation. In order to examine this hypothesis the response of two different grown forms of Arrhenatherum elatius to clipping was investigated in an experiment.

Materials and methods.

100 seedlings of similar age were grown individually in sand culture in polyethylene tubes similar to those used in experiments involving growth of plants at different temperatures (Chapter 5, page 54). The environment and methods of cultivation were similar to those used in experiment B (page 129).

When the plants were four weeks old, a range of growth forms could be distinguished and seedlings conforming to three

arbitrarily defined groups were selected:

- a) A form in which all the shoots were almost erect,
- b) A prostrate growth form in which all the shoots approached the horizontal;
- c) Forms intermediate between (a) and (b). In this group were included plants in which most of the shoots are upright, but with some oblique and plants in which most of the shoots were subtended at angles between 30° and 60° to the horizontal.

The differences in growth form were evident at an early stage of seedling development, i.e. in the first tillers. In the most prostrate forms the first tiller approached the horizontal. Plate 72 provides an illustration of a marked difference in growth form evident in two-week-old seedlings. These differences in growth form were pronounced throughout the vegetative stage of development. However, with the onset of flowering the more prostrate plants were observed, as in experiment A, to form upright culms despite the fact that the vegetative shoots remained in a horizontal position.

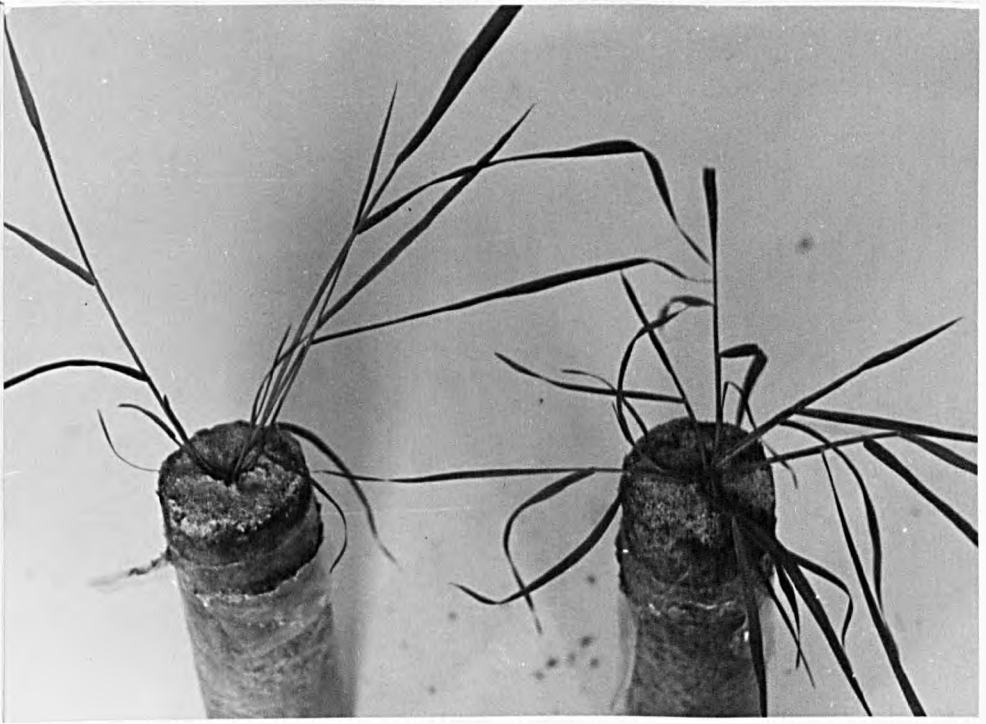
Six plants of each group were selected, transplanted into 23 cm plastic flower pots and placed in a growth-room. After eight weeks of growth all the plants came into flower over a period of one week and no difference in flowering time was associated with growth form. At this time all the plants were clipped at 2 cm above the soil surface. Clipping was then repeated at intervals of three days. The plant material collected from the successive cuts was oven-dried and weighed. The number of living tillers on each plant was counted before the first and last cut.

Plate 72.

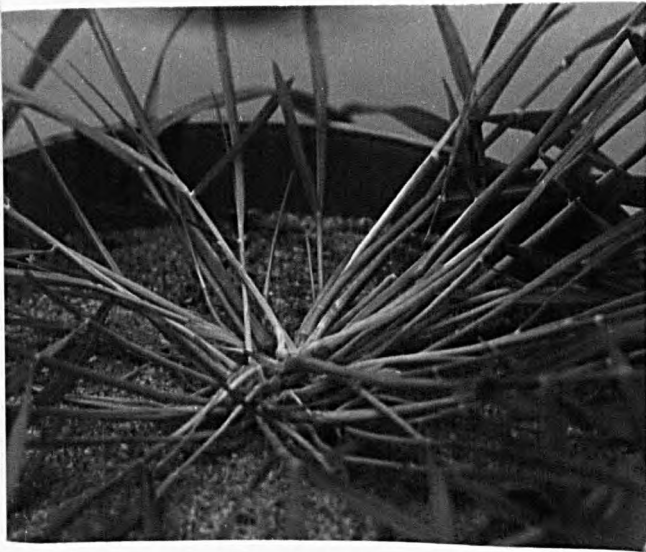
Two-week old seedlings of the erect (left) and prostrate (right) growth forms of Arrhenatherum elatius.

Plates 73 and 74.

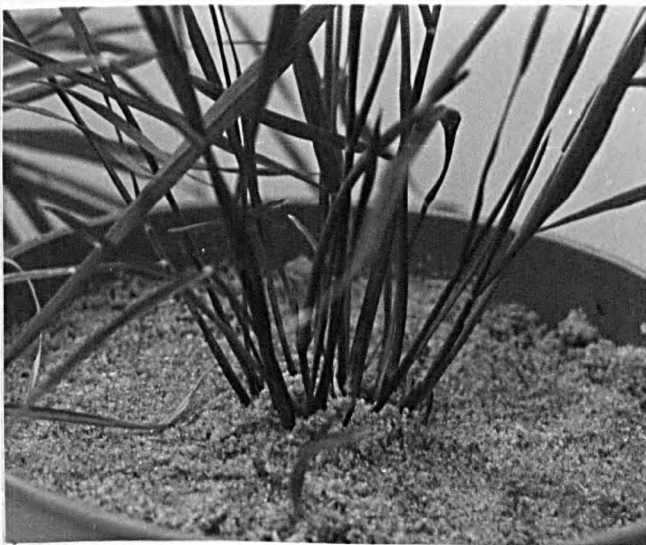
Unclipped representative plants of the prostrate (Plate 73) and erect (Plate 74) growth forms of Arrhenatherum elatius. Note the difference in tiller number between the two forms.



72



73



74

Results

Values for the mean number of tillers per plant in each treatment are presented in Table 24.

Table 24.

Mean number of living tillers in three growth forms of Arrhenatherum elatius before first cut (after 8 weeks of growth) and before the last cut (after 26 weeks of growth) 95% confidence limits are given in brackets.

Growth form	Mean number of living tillers before first cut.	Mean number of living tillers before last cut.
Very erect	20.2(\pm 4.2)	All tillers were dead
Intermediate	37.2(\pm 3.7)	134.4(\pm 14.4)
Very prostrate	50.4(\pm 5.7)	210.3(\pm 11.9)

It is evident that, before clipping, plants with prostrate and intermediate growth forms were better tillering than plants of the erect growth habit; the plants with the very prostrate growth form displayed a significantly greater capacity for producing tillers than plants of the intermediate growth form. Plates 73 and 74 show representative plants of the very erect and very prostrate growth forms before the plants were cut for the first time. Plants of the very prostrate and intermediate forms responded to clipping similarly to Agrostis tenuis, that is, they produced numerous small tillers which carried very small leaves and could easily be mistaken for the latter species in a closely clipped or grazed turf. After 16 cuts had been carried out none of the erect growth forms had living shoot material and subsequent examination showed them to be dead.

Plates 75 and 76 depict representative plants of the prostrate and erect growth forms respectively, photographed 3 days after the 16th clipping.

Table 25 contains the mean oven-dry weight of the plant material obtained from the initial clip of the plants at the different growth forms.

Table 25.

Mean oven-dry weights of plant material collected from the first clip of the plants of the different growth forms of Arrhenatherum elatius. 95% confidence limits are included.

Growth form	Mean oven-dry weight (g) of initial clipping per plant
Very erect	5.44 \pm 0.64
Intermediate	3.16 \pm 0.70
Very prostrate	4.00 \pm 0.44

The curves in Fig.33 show the mean dry weights of the clippings from successive cuts for the three different forms of Arrhenatherum elatius.

As might be expected, plants of the erect growth form lost more material in the initial clip (Table 25) and the first two subsequent clips (Fig.33) than the plants of the other two forms. After the 7th cut, however, these plants showed a steep decline in yield of clippings and shoot growth had ceased in all plants by the 16th cut (Fig.33, and Plate 76). The yield of clippings of the prostrate and intermediate forms was comparable and showed a similar course throughout the experiment (Fig.33).

Plates 75 and 76. Representative plants of the prostrate (Plate 75) and erect (Plate 76) growth forms of Arrhenatherum elatius after cutting every three days at 2 cm from soil surface. The plants were photographed after the 16th clipping. Observe the tufted growth of the prostrate growth form and also its narrow leaves.



75



76

Fig.33. Dry weights of clippings collected at successive cuts from plants representing the three growth forms of Arrhenatherum elatius. 95% confidence limits are included.

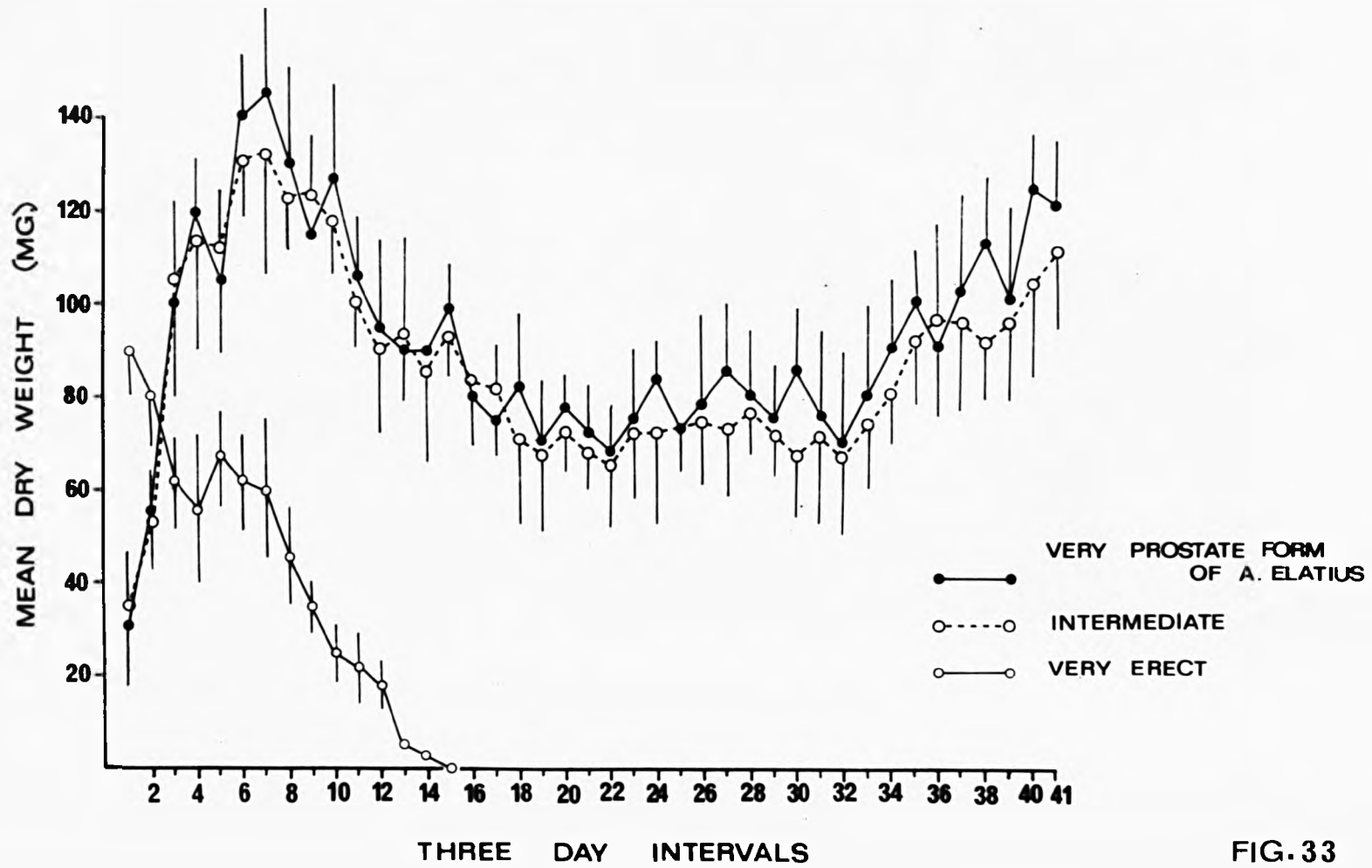


FIG. 33

It appears that the greater number of tillers of the prostrate and intermediate forms is due to the existence of auxilliary buds which are placed either at the base of old shoots or underneath the soil. It is suspected that it is the presence of these buds which enables the prostrate and intermediate growth forms to withstand defoliation. The failure of the erect growth forms to withstand clipping is possibly due to the scarcity of auxilliary buds and in addition due to the greater damage sustained under close clipping.

These results strongly suggest that the prostrate growth form is an adaptation to defoliation.

A comparison of the response to clipping of the very erect plants in this experiment with those in experiment B, page 130 indicates that clipping affects Arrhenatherum elatius more severely if it is started at a later stage in the life of the plant (after flowering). In experiment B, (page 130) plants were clipped when they were in early vegetative phase. While all the plants of the erect growth form in this experiment died after 16 cuts, and most of them showed signs of deterioration well before that, none of the plants in experiment B died.

The findings of this investigation on the response of the different species to clipping suggests that for a species to tolerate intensive close clipping, it must probably have one or both of the following morphological characteristics:-

- i) a capacity for producing numerous tillers. Species in which there is a stock of auxilliary buds able to develop into tillers, to replace the tillers killed by clipping have a better chance of survival under clipped or mowed situations.
- ii) a growth habit which reduces the magnitude of the damage caused by clipping. Plants with a prostrate shoot and which have the ability to produce numerous basal leaves, below the level of cutting, possess an obvious advantage. Plants with erect growth forms are subject to severe defoliation under close clipping which causes a severe reduction in photosynthetic output.

PART 3.

COMPETITION EXPERIMENTS.

CHAPTER 10.

COMPETITION BETWEEN ARRHENATHERUM ELATIUS
AGROSTIS TENUIS AND FESTUCA OVINA AT TWO
LEVELS OF FERTILITY.

Introduction.

To remain within a plant community a species must be able to survive the stress imposed by the physical and biological environment associated with that community. In many circumstances survival will depend upon the competitive ability of the species, i.e. its ability in the presence of other species to draw adequately upon the resources of the environment. This in turn depends upon a number of morphological and physiological characteristics of the species.

In this chapter an investigation is conducted under semi-controlled conditions to assess the intrinsic factors which affect the competition between Arrhenatherum elatius, Agrostis tenuis and Festuca ovina and to study the effect of factors of soil fertility upon the competitive ability of these species.

Materials and methods.

Each species was placed in a 50/50 mixture with each of the other two species on a productive medium (sand culture watered with complete Hewitt solution in which nitrogen was 170 ppm) and in an unproductive medium in which the nitrogen level was reduced to 5 ppm). Monocultures of each

species provided controls at two fertility levels. The plants were grown in 35.0 x 35.0 x 30.0 cm hard plastic tubs containing 16 cm of sand. Drainage holes were provided on the bottom of each tub which was lined with glassfibre cloth. The tubs were arranged in four replicate blocks.

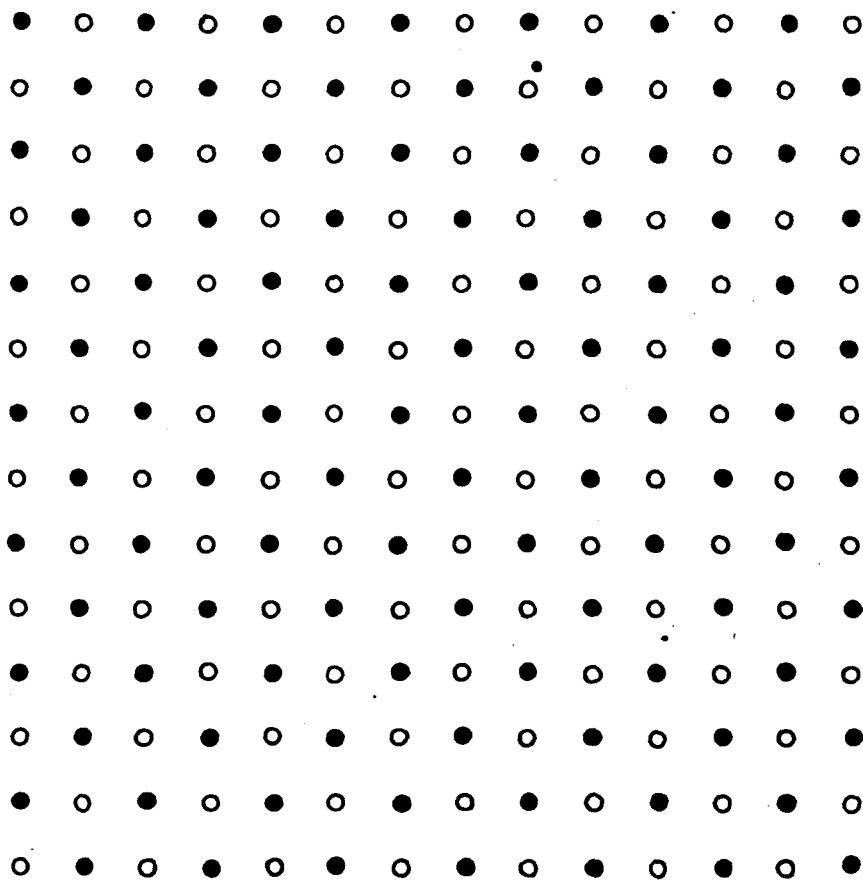
Preparation of plant material.

Seeds were germinated on moist nylon cloth in transparent plastic boxes. One-week-old seedlings of comparable size were planted in seed trays containing sand watered with complete Hewitt solution. The number of seedlings planted in the seed trays outnumbered that required for the experiment by 100 seedlings. Several seed trays were used for each species. The seed trays were left in a growth room in which the following environment was maintained: day length of 18 hours, temperature 20°C by day and 15°C by night, a light intensity of $3.3 \text{ cal cm}^{-2} \text{ h}^{-1}$ visible radiation and a relative humidity of 79%. After ten days the seedlings were transplanted to the experiment; by this time the seedlings developed enough roots and attained a size which made manipulation easier and ensured no loss of seedlings during the early establishment phase.

Procedure

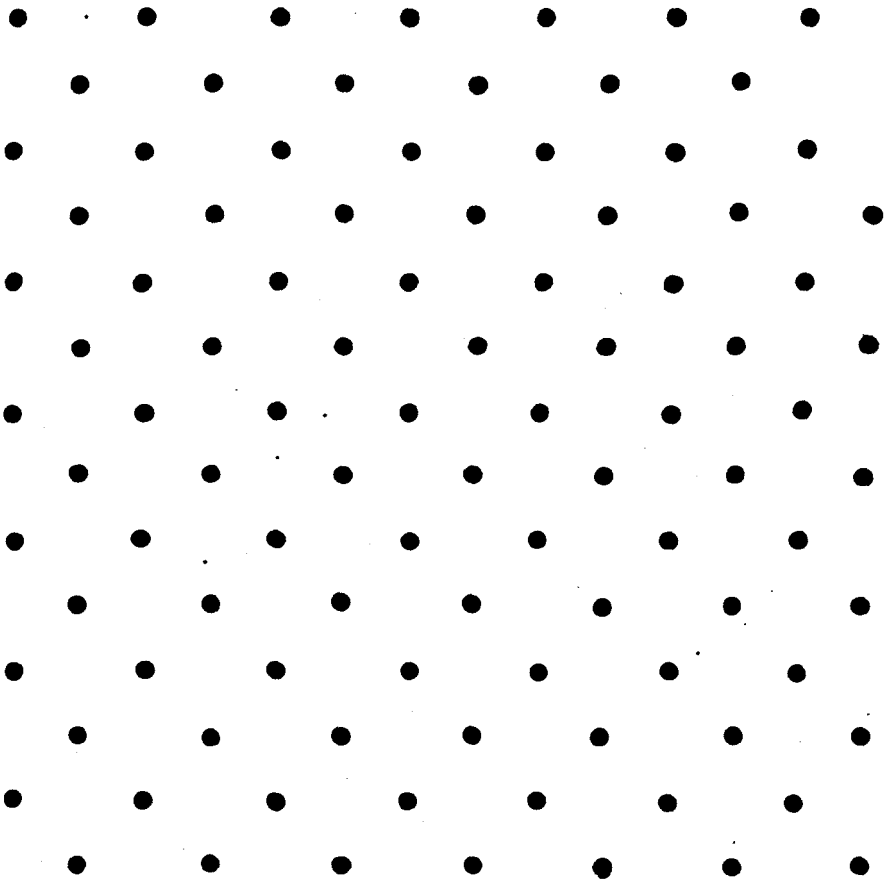
Seedlings of the two species which composed the mixture were arranged alternately and were placed 2.5 cm apart. With the exception of the plants at the margin, each individual was therefore surrounded by four individuals of the other

Fig.34. Pattern of planting of seedlings of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina in mixtures (a) and control (b).



a

FIG. 34



b

species. (Fig.34a). In monoculture, the individual plants were arranged in the same pattern in which they occurred in the mixtures. The areas corresponding to those occupied by the other species in the mixture were left bare (Fig.34b). This arrangement was preferred to the monoculture systems in which the sowing density is maintained constant. This "true" control differs from the experimental (mixed) treatment in only one factor and permits a comparison between the yield of each species in the presence and in the absence of another species. Before the seedlings were introduced, the sand in each container was watered with 4 litres of the appropriate nutrient solution. The plants were watered with 3 litres of the appropriate nutrient solution every three weeks and every three days with an equal quantity of tap water. The tubs were allowed to stand in shallow trays to collect the runoff and to prevent contamination of low fertility treatments by neighbouring high fertility treatments.

The plants were grown in a heated greenhouse with an automatic ventilation system, to maintain the temperature within the range of 20°C by day and 15°C by night. On sunny days, temperatures of +25°C were recorded for short periods. A day length of 18 hours was maintained throughout by using when necessary mercury vapour lamps.

Netlon garden netting supported to 80 cm by wooden stakes was used to prevent the plants grown at high fertility from spreading and shading neighbouring tubs.

The plants were harvested after one year. During the harvest it was found very difficult, if not impossible, to separate individual plants of Arrhenatherum elatius and Agrostis tenuis, grown at high fertility, because they formed a solid mass. It was therefore decided to harvest the standing crop and then to separate the two component species (but not individual plants), in each mixture. The vegetation was cut two inches below the sand surface and the turf was removed on masse. The sand was then washed from the roots and the turfs were placed in polyethylene bags and stored in the cold room at 5° C while sorting was in progress. The roots were severed, and the shoots were washed and dried for 48 hours in 105° C oven and weighed. Plants grown at low productivity remained identifiable and were removed easily from the tubs. Again the total shoot produced by each species was oven dried and weighed.

Results.

Differences in the fertility levels produced two distinct types of turf. Low fertility resulted in an open turf, where individual plants remained identifiable, and produced very little foliage much of which was pale green in colour. From visual inspection it appeared that very little aerial interference was taking place. At high fertility closed turfs were produced. Arrhenatherum elatius produced tall massive plants (about 150 cm high) which formed very large quantities of litter and flowered twice during the experiment. Profilerous inflorescences were observed. In the control treatments

Agrostis tenuis produced large (about 50 cm high) plants with very long stolons. Plate 77 compares the growth of this species at the two fertility levels. Agrostis tenuis produced much larger taller plants than those of Festuca ovina and exceeded the latter species in litter production. Festuca ovina responded to high fertility by producing large compact plants (about 20 cm high) with long fleshy succulent leaves. Both Agrostis tenuis and Festuca ovina produced small amounts of litter in comparison with Arrhenatherum elatius. The mean dry weight of the litter produced by plants in the control treatments was 120.7 ± 19.7 g, 47.5 ± 12.4 g and 10.24 ± 6.5 g for Arrhenatherum elatius, Agrostis tenuis and Festuca ovina respectively.

Histograms (Fig.35.a) show the dry weights of the living shoots of each species in monoculture and mixtures at high fertility levels. There was no significant difference between the yield of Arrhenatherum elatius when it was growing in monoculture and in mixture with Agrostis tenuis or Festuca ovina; the latter two species were completely eliminated by Arrhenatherum elatius. Festuca ovina was completely excluded from mixtures containing Festuca ovina and Agrostis tenuis. The yield of Agrostis tenuis in the mixture with Festuca ovina was not significantly different from the yield of the species in monoculture.

The fatal result of competition to Agrostis tenuis and Festuca ovina when these species were grown in mixtures with Arrhenatherum elatius could clearly not have been the effect

Plate 77.

Plants of Agrostis tenuis grown at high fertility (left) and low fertility (right) Observe the long stolons. The vertical scale is 100 cm in length.

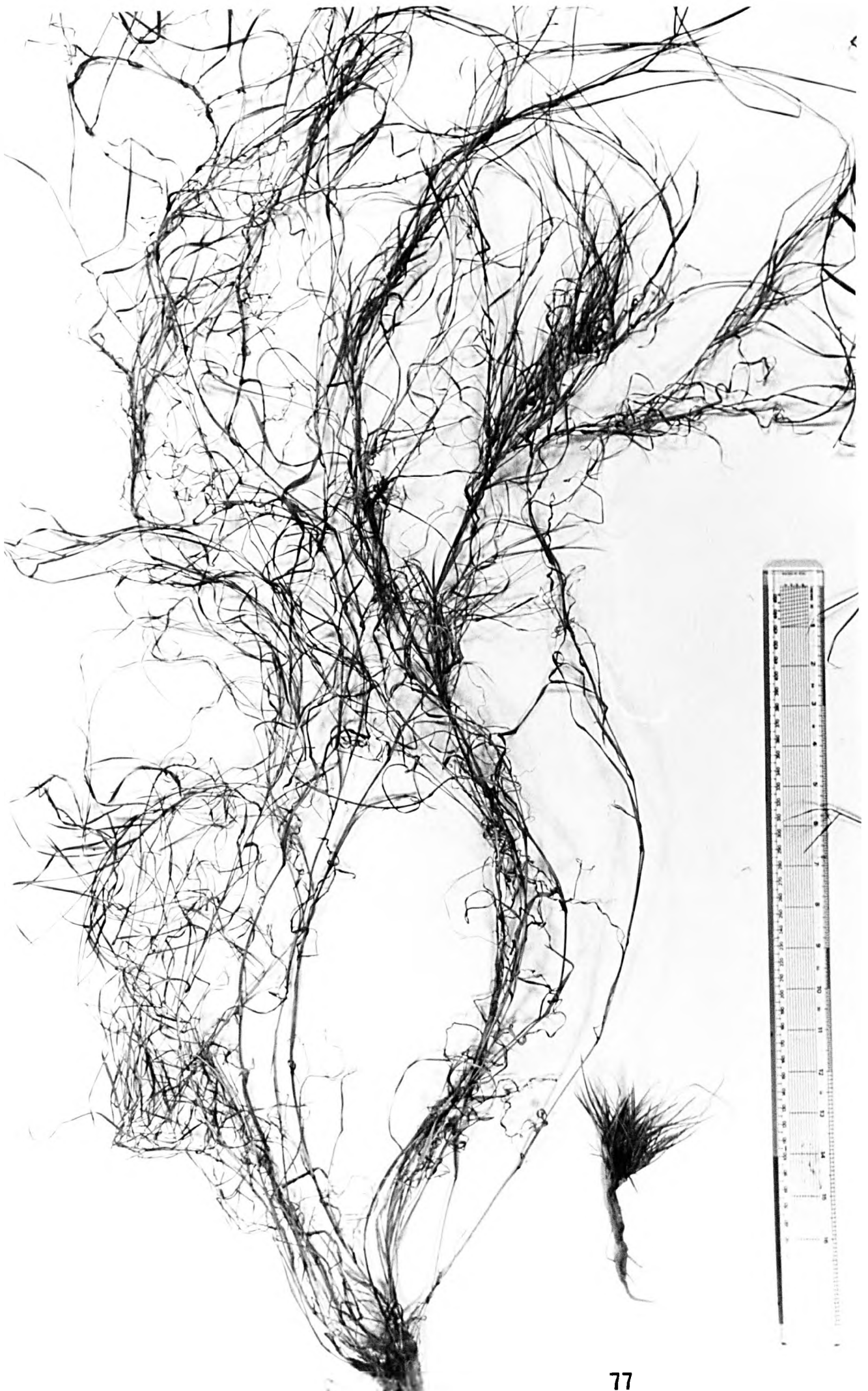
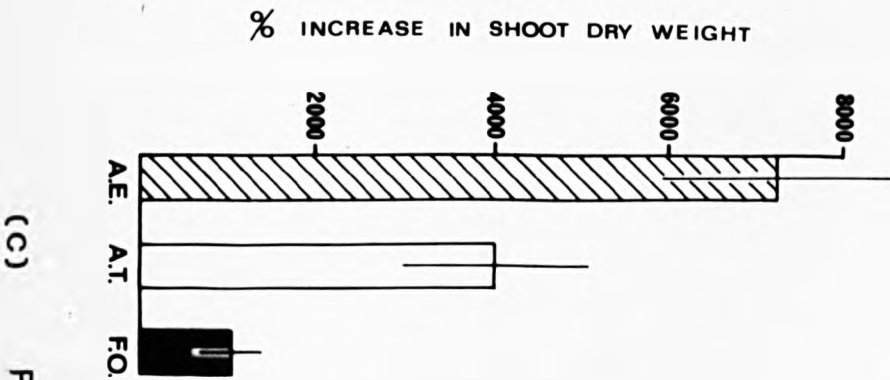
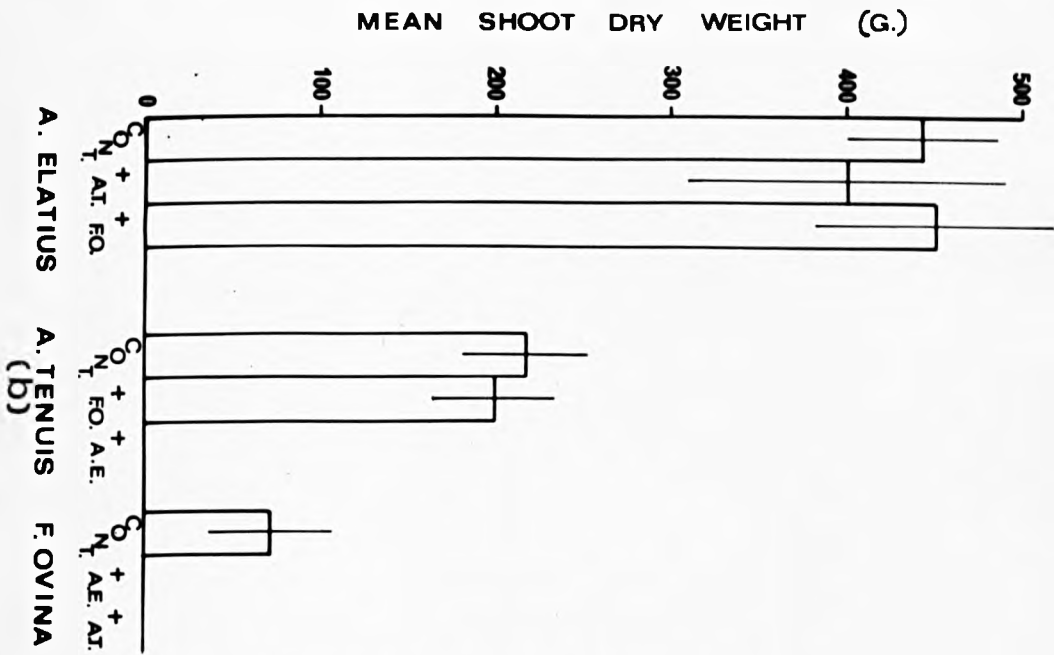
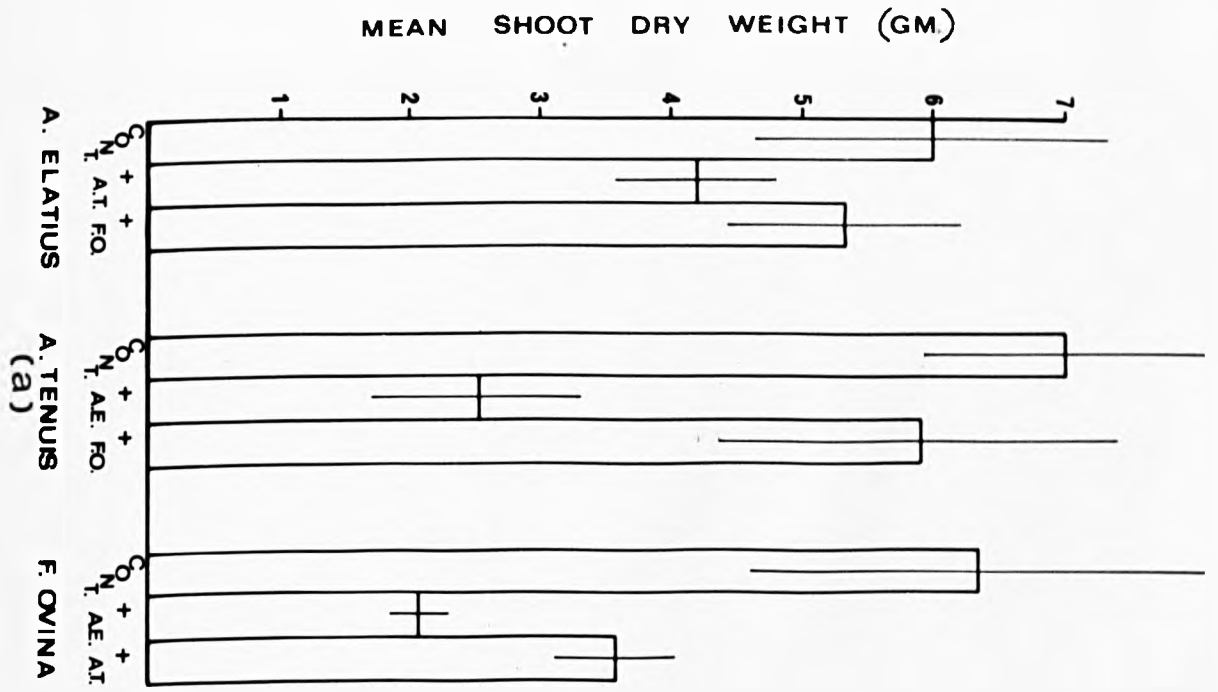


Fig.35 (a and b)

Dry weights of shoots of each of Arrhenatherum elatius (A.E.), Agrostis tenuis (A.T.) and Festuca ovina (F.O.) in monoculture (Cont.) and mixtures (+) at high fertility (Nitrogen = 176 ppm - Fig.a) and low fertility (Nitrogen = 5 ppm, Fig.b).

(c)

Percentage increase in dry matter production of plants of the former species grown in monoculture when high nitrogen treatment is compared with low nitrogen. 95% confidence limits are included.



(C) FIG. 35

of root competition for nutrient and water per se since these were supplied in excess.* It is certainly a result of smothering of the smaller plants of Agrostis tenuis and Festuca ovina by the taller growth of Arrhenatherum elatius. The exclusion of Festuca ovina from mixtures containing species with Agrostis tenuis can be similarly explained. It appears that the following morphological characters of plants are important competitive attributes, (a) tall stature (b) an expanded structure which allows extensive exploration of the environment above the ground and (c) a tendency to develop a dense layer of litter. The order of the three species in respect to the magnitude of each of these attributes is Arrhenatherum elatius > Agrostis tenuis > Festuca ovina.

When the plants grown under conditions of low fertility are considered (Histograms Fig. 35b), a different picture emerges. In monoculture, the yield of Arrhenatherum elatius and Agrostis tenuis, the two species with high potential for dry matter production, were drastically reduced. The histograms in Fig. 35 c which show the percentage increase in dry matter production of plants of the three species grown in monoculture, when the high nitrogen treatment is compared

*Although the possibility cannot be discounted that interactions above ground were affected by factors such as the relative efficiency of mineral nutrient uptake in the competing species (Donald 1958, Grime 1973).

with the low nitrogen treatment indicate that all the species responded to increased fertility by producing much larger plants.

When the plants were grown in mixtures, at low fertility the presence of either of Agrostis tenuis and Festuca ovina, did not significantly reduce the yield of Arrhenatherum elatius below its yield in the control. Arrhenatherum elatius caused a marked and comparable reduction in yield of Agrostis tenuis and Festuca ovina and outyielded them. The superior performance of Arrhenatherum elatius on the nitrogen-deficient medium is in agreement with the results obtained in Chapter 8 (see Fig.26 a). The yield of Agrostis tenuis when grown in mixtures with Festuca ovina was not significantly different from the yield of the species in monoculture. When grown in mixtures with either Arrhenatherum elatius or Agrostis tenuis, the yield of Festuca ovina was significantly reduced below the control, but this effect was less pronounced in the Festuca ovina: Agrostis tenuis mixture. It is of interest to note that the order of dry matter production (Arrhenatherum elatius > Agrostis tenuis > Festuca ovina on this nitrogen-deficient medium is in agreement with the results obtained in Chapter 8 (see Fig. 26a).

CHAPTER 11.

THE INFLUENCE OF COMPETITION ON

LATERAL VEGETATIVE SPREAD

OF ARRHENATHERUM ELATIUS, AGROSTIS TENUIS AND FESTUCA OVINA.

In a previous experiment factors which affect the interaction of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina were examined by growing the plants in intimate mixtures composed of pairs of species (Chapter 10). Plants, especially where seedling establishment is of rare occurrence, frequently impinge by lateral expansion of the fronts and under conditions of grazing, mowing etc. lateral spreading may be of primary importance. In the experiment described in this chapter an attempt was made to measure the extent to which this capacity is affected by the presence of another grass species in the area under colonization.

Materials and methods.

The experiment was carried out in a growth-room providing the following conditions: $3.3 \text{ cal cm}^{-2}\text{h}^{-1}$ visible radiation, temperature 20°C (day) 15°C (night), R.H. 70% and day length 18 hours.

Combinations of seedlings of the three species:

Arrhenatherum elatius, Agrostis tenuis and Festuca ovina and also monocultures of each species were set up in 30 cm diameter pots, containing 18 cm acid-washed sand which was enriched with complete Hewitt solution prior to planting.

Procedure

One-week-old seedlings of each species were used in the experiment. In the combined sowing, the seedlings were arranged as in Fig.36a. In this pattern 16 seedlings of each species were distributed over a sector equivalent to one-third of the sand surface and each species occupied two fronts, one opposite each of the other two species. Plate 78 shows the plants in position in one of the pots at an early stage of growth. As controls, monocultures of each species were set up. These contained 16 plants of one species and except for the absence of seedlings of the other two species they resembled the combined sowing in every respect. (Fig.36b). Each treatment was replicated twice.

The pots were placed on a plastic-coated heavy-gauge steel grill. The latter was supported by a metal frame. This arrangement facilitated completely free drainage from each pot. The pots were arranged in two randomized blocks, one on each side of the growth room. Each block contained one mixture and one monoculture for each species.

Each pot was watered, alternately every three days with an aliquot (1800 ml) of complete Hewitt solution and distilled water. To ensure uniform distribution of nutrients or water, each sector received one-third of the liquid applied. Watering was carried out by sprinkling the surface sand from a plastic rose. The plants in monoculture were similarly treated, the two initially bare sectors receiving two-thirds of the liquid.

Fig.36 (a and b) Pattern of planting of seedlings of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina in mixtures (a) and controls (b).

Plate 78. Plants of Arrhenatherum elatius, Agrostis tenuis, and Festuca ovina in one of the mixed pots, photographed at an early stage of growth, in order to illustrate the sowing positions.

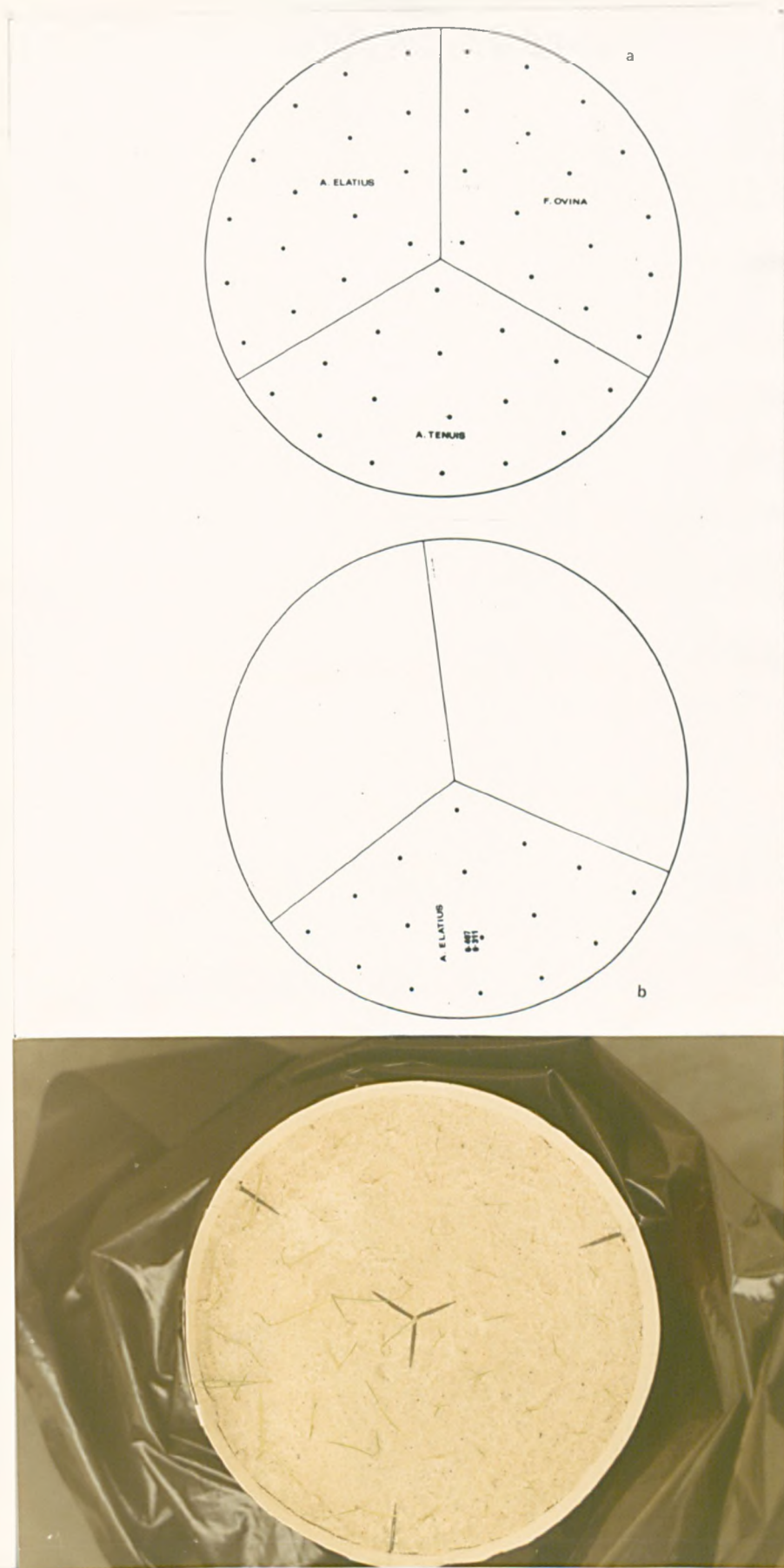


Fig.36

Plants were clipped every three days at 6 cm from the soil surface. Clipping commenced three weeks after the start of the experiment. The experiment was terminated after four months. On the harvest day, but before the plants were removed from the pots, the areas into which shoots of each of the three species had ramified in each of the mixed turfs was mapped by placing a white woollen string on top of the turfs circumscribing the furthest extensions of the shoot. The turfs were then photographed from above. From these photographs the area occupied by each species in each turf was calculated using a planimeter. The area occupied by each species in monoculture was also measured. Plates 83, 84 and 85 show the areas occupied by Agrostis tenuis, Arrhenatherum elatius and Festuca ovina respectively in one of the mixed turfs. The triangular sector in each photograph marks roughly the original sowing position of each species. Plates 79, 80 and 81 illustrate the appearance of the monocultures of Agrostis tenuis, Arrhenatherum elatius and Festuca ovina respectively at harvest. The individual plants both in the combined sowing and also in the monocultures were identified and tagged and harvested in order to examine the effect of sowing position upon yield. The shoot of each individual plant was oven-dried and weighed. Although the plants at the margin of the pots were harvested and their yields are included in Fig. 37a and 37b, they were not used in any calculations.

In order to assess the capacity of the three grasses for lateral vegetative spread, a comparison was made between the areas occupied by each species in the mixtures and monocultures. The extent to which the capacity of a species for lateral vegetative spread was affected by the presence of the other species was measured by calculating the percentage reduction in area occupied by the species when comparing the areas occupied by the species in the control and the mixed sowing turfs. When calculating this percentage reduction in area, or subsequently in yield, two separate estimates are carried out in each species, i.e. control and mixture were compared in each of the two blocks.

The gross effect of competition on the yield of each species was assessed by comparing the total weight of shoot produced by each species in mixtures and controls.

In order to assess the impact of the different species on each other, on a dry weight basis, a comparison was made between the mean dry weight of shoot per plant in the fronts in mixed sowing and that of plants of the same species in the centre of the sector. In this assessment data from the two replicates were pooled.

Effects of interspecific competition were also assessed by comparing the mean dry weight of the shoot of plants in the fronts in mixtures with the mean dry weights of shoots in the same position in the controls.

Results

Each of the three species responded to high fertility and clipping by producing dense turfs.

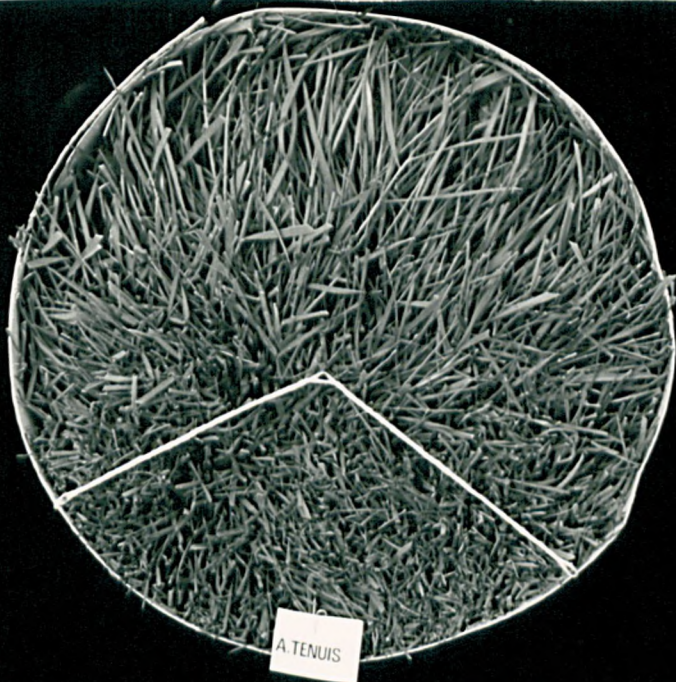
In the monocultures, it was noticed that Agrostis tenuis spread laterally much more rapidly than the other two species and after three months extended throughout the pot; in contrast some sand remained unoccupied by Arrhenatherum elatius and Festuca ovina at the time of harvest. It may be observed in plates 79, 80 and 81, that in Agrostis tenuis shoot apices had reached the farthest ends of the pots, while in the non-stoloniferous Arrhenatherum elatius and Festuca ovina the lateral spread was mostly effected by leaves. The data for areas occupied by each species in the control treatment are presented in Table 26.

Table 26.

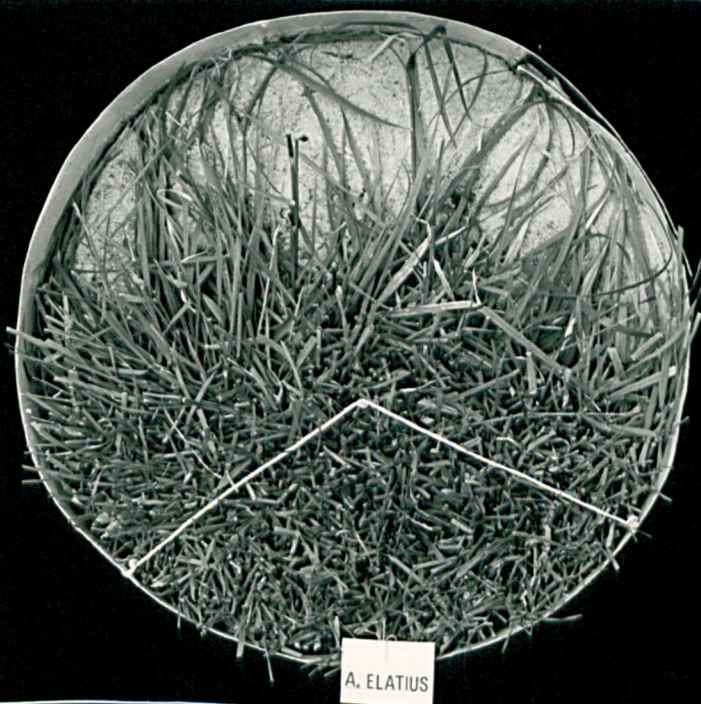
Area (cm²) occupied by each of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina in the control treatment.

Species	Area cm ² occupied by species in replicate 1.	Area cm ² occupied by species in replicate 2.	Mean
<u>Agrostis tenuis</u>	60.0	60.5	60.3
<u>Arrhenatherum elatius</u>	57	47	52.0
<u>Festuca ovina</u>	54.0	54.5	54.3

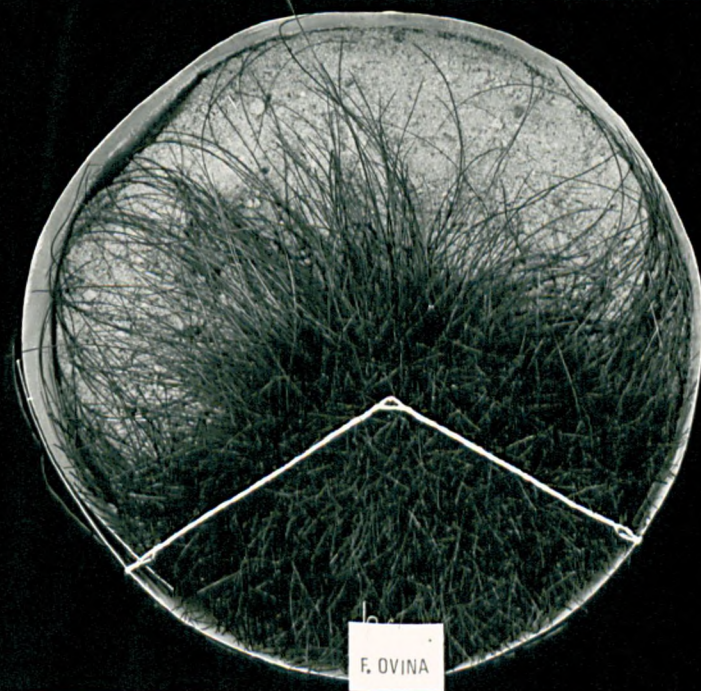
Plates 79 to 81. The area occupied by Agrostis tenuis (Plate 79), Arrhenatherum elatius (Plate 80) and Festuca ovina (Plate 81) after four months of growth in control treatments. The triangular sector in each pot marks roughly the initial area occupied by the species.



79



80



81

In mixed sowing treatments mutual encroachment by the species impinging at the fronts could be observed after four weeks (Plate 82). By the end of the experiment a closed turf had been established in both replicates. The areas exploited by each species are presented in Table 27.

Table 27.

Area (cm²) occupied by each of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina in the mixed turfs.

Species	Area cm ² occupied by species in replicate 1.	Area cm ² occupied by species in replicate 2.	Mean
<u>Agrostis tenuis</u>	43	48	45.5
<u>Arrhenatherum elatius</u>	29.0	27.0	28.0
<u>Festuca ovina</u>	26.5	29.0	27.8

It is apparent that Agrostis tenuis was able to spread laterally in the combined sowing treatment to an extent greater than that of the two other species.

The data for percentage reduction in total area occupied by each species in mixtures as compared with monoculture are presented in Table 28.

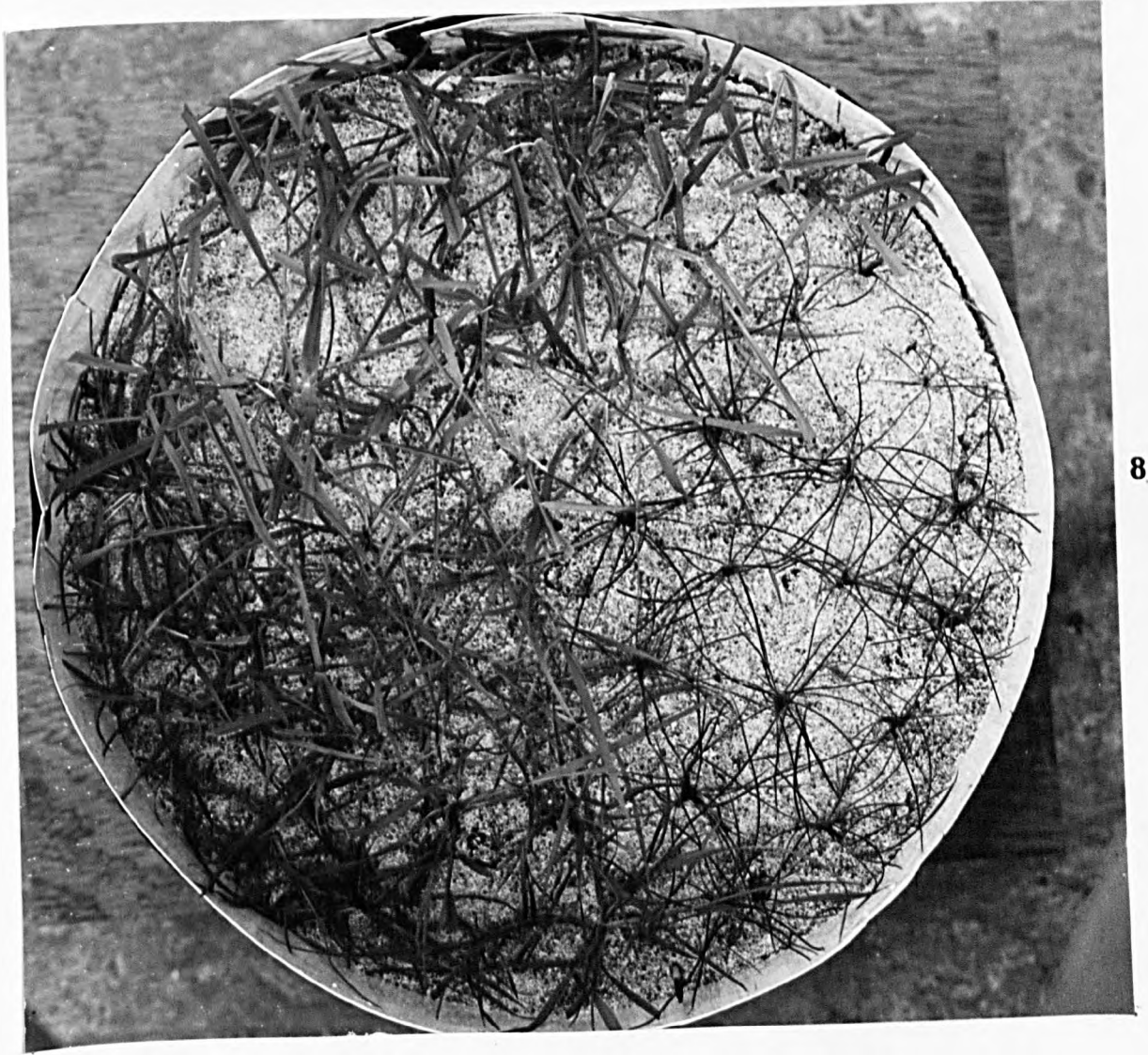
Table 28.

Percentage reduction in total area occupied by each of Arrhenatherum elatius, Agrostis tenuis, Festuca ovina in mixtures as compared with monocultures.

Species	Percentage reduction in total area.		
	Replicate 1.	Replicate 2.	Mean
<u>Festuca ovina</u>	50.9	46.7	48.8
<u>Arrhenatherum elatius</u>	49.1	42.5	45.8
<u>Agrostis tenuis</u>	28.3	22.6	24.4

Plate 82.

Appearance of plants of
Arrhenatherum elatius, Agrostis
tenuis and Festuca ovina in one
of the mixed sowing treatments,
after four weeks of growth.
Observe the mutual encroachment
by the species impinging at the
fronts.

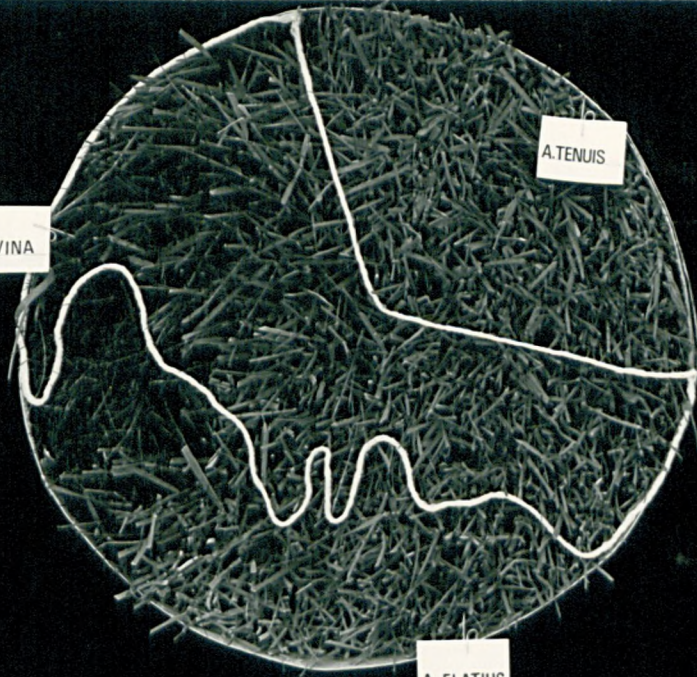


Plates 83 to 85.

The areas occupied by plants of Agrostis tenuis (Plate 83), Arrhenatherum elatius (Plate 84) and Festuca ovina (Plate 85) at harvest, in one of the mixed sowing treatments (after four month of growth). The white line circumscribes the areas into which shoots of each species had ramified in the turf. The triangular sector in each plate marks roughly the original sowing position of each species.

F. OVINA

A. TENUIJS

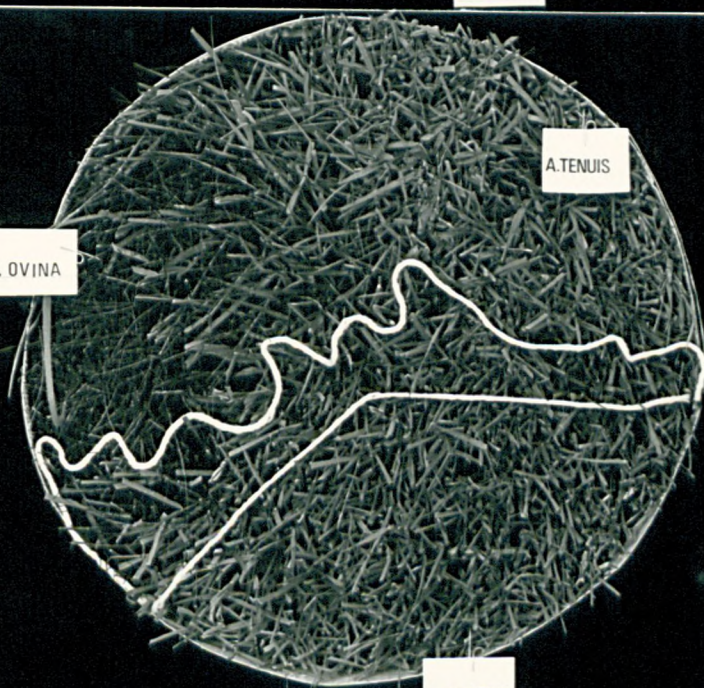


A. ELATIUS

83

F. OVINA

A. TENUIJS

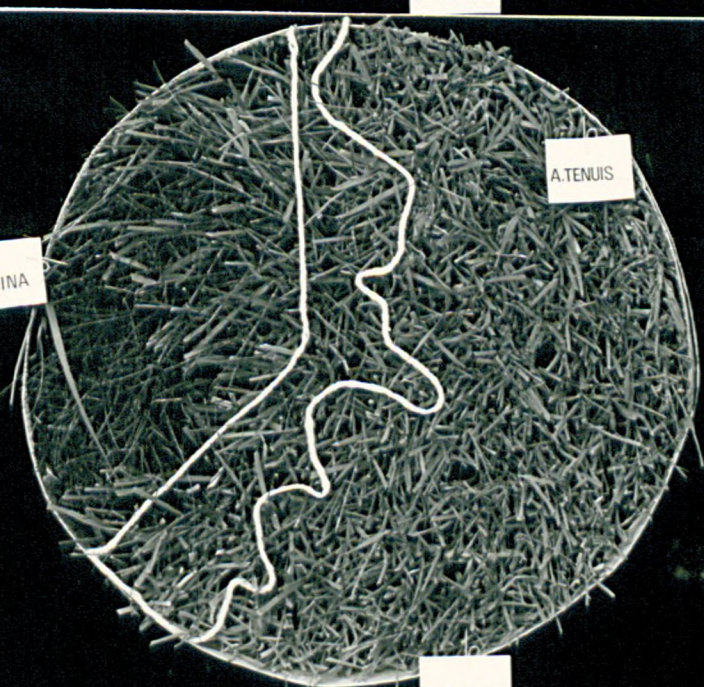


A. ELATIUS

84

F. OVINA

A. TENUIJS



A. ELATIUS

85

The data in Table 28 show that, in Agrostis tenuis, the presence of the other two species caused a relatively small reduction in the potential capacity for lateral vegetative spread. However, it is to be noted that the value obtained for Agrostis tenuis is an underestimate since the shoot of this species extended throughout the control pots after only three months' growth. It is of interest to note that in Arrhenatherum elatius and Festuca ovina, lateral vegetative spread was reduced to a comparable extent by interspecific competition.

Yields.

Fig.37a and 37b, illustrate the yield (g) of the individual plants in monocultures and mixtures respectively. The total dry weights of shoot material produced by each species in monocultures and mixtures are presented in Table 29.

Table 29.

Dry weights (g) of total shoot produced by Arrhenatherum elatius, Agrostis tenuis and Festuca ovina in monocultures and mixtures.

Species	Monoculture			Mixtures		
	Dry wt.g of total shoot Replicate (1)	Dry wt.g of total shoot Replicate (2)	Mean	Dry wt.g of total shoot Replicate (1)	Dry wt.g of total shoot Replicate (2)	Mean
<u>Agrostis tenuis</u>	21.42	21.88	21.65	9.42	9.61	9.22
<u>Arrhenatherum elatius</u>	13.27	13.46	13.37	4.85	5.34	5.10
<u>Festuca ovina</u>	10.28	11.39	10.84	3.33	3.15	3.24

The data in Table 29 show that Agrostis tenuis produced the highest yield both in monocultures and mixtures.

Fig.37 (a and b)

Yield of individual plants of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina in monoculture (a) and mixed sowing (b). The two figures above each dot refer to the yield (g) of the plant sown at that position in the two replicates.

Arrhenatherum elatius and Festuca ovina produced comparable yield - Arrhenatherum elatius slightly higher. It was interesting to note that the yield of Agrostis tenuis in the mixed sowing was greater than the total yield of both Arrhenatherum elatius and Festuca ovina and only slightly less than the yield of either of these two species in monocultures.

The percentage reduction in the total yield of shoot material brought about by interspecific competition is presented for each species in Table 30.

Table 30.

Percentage reduction in total yield of shoot material of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina brought about by interspecific competition.

Species	Percentage reduction in total yield		
	Replicate 1.	Replicate 2.	Mean
<u>Festuca ovina</u>	67.5	72.3	69.9
<u>Arrhenatherum elatius</u>	63.7	60.3	62.0
<u>Agrostis tenuis</u>	56.0	55.60	55.8

As expected, all three species when grown in mixed turfs, suffered a reduction in yield by more than 50%. Festuca ovina and Arrhenatherum elatius experienced a greater reduction than Agrostis tenuis, Festuca ovina being the most affected.

The data presented in Table 31 illustrate the mean dry weight of shoot in plants along the fronts and at the centre of the sectors in control treatments, and in mixture.

Table 31.

Mean dry weight of shoot per plant of each of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina along the fronts and at the centre of the sectors in control treatments and in mixtures.

Species	Control		Mixture	
	Mean dry weight of shoot per plant along fronts	Mean dry weight of shoot per plant in centre of sector	Mean dry weight of shoot per plant along fronts	Mean dry weight of shoot per plant in centre of sector
<u>Agrostis tenuis</u>	3.54 [±] 0.73	0.98 [±] 0.36	1.25 [±] 0.17	0.81 [±] 0.20
<u>Arrhenatherum elatius</u>	2.09 [±] 0.37	0.72 [±] 0.27	0.61 [±] 0.19	0.50 [±] 0.14
<u>Festuca ovina</u>	1.70 [±] 0.40	0.51 [±] 0.11	0.22 [±] 0.03	0.49 [±] 0.02

The data in Fig.37a and Table 31 showed that, of the three species, Agrostis tenuis, in monoculture produced the largest plants along the fronts initially adjoining bare sand. The mean dry weights of shoot per plant along these fronts were 3.54 ± 0.730 g, 2.09 ± 0.37 g and 1.70 ± 0.40 g for Agrostis tenuis, Arrhenatherum elatius and Festuca ovina respectively. The mean dry weights at the centre of the sector were 0.98 ± 0.36 g, 0.72 ± 0.27 g and 0.51 ± 0.11 g for Agrostis tenuis, Arrhenatherum elatius and Festuca ovina respectively.

It is clear from Fig.37b and Table 31 that in mixtures the largest plants of Agrostis tenuis were produced in individuals growing at the fronts.

The mean dry weight of shoot per plant of plants harvested along the fronts was 1.25 ± 0.17 g. The mean dry weight of the shoot per plant in the centre of the sector was 0.81 ± 0.20 g.

For Arrhenatherum elatius, the mean dry weight of shoot per plant along the whole length of the fronts was 0.61 ± 0.19 g. The species produced comparatively smaller plants in its front with Agrostis tenuis than with Festuca ovina (Fig.37b).

It is possible that at the front with Agrostis tenuis, the shoots of Arrhenatherum elatius were deflected upwards by the rather compact foliage of Agrostis tenuis and consequently subjected to more defoliation. If this did occur, it probably reduced the ability of the species to compete for light. The mean dry weight of the shoot per plant in the centre of the sector was 0.50 ± 0.14 g. Festuca ovina produced comparatively smaller plants along the length of the species fronts with Agrostis tenuis and Arrhenatherum elatius than in the centre of its own block. The mean dry weight of the shoot per plant along the length of the species front was 0.22 ± 0.03 g while that at the centre of the block was 0.49 ± 0.02 g.

The data in Table 32 represents the percentage reduction in yield when plants harvested along the fronts in mixtures were compared with plants harvested from similar positions in controls.

Fig.32.

Percentage reduction in yield of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina when yield of plants harvested along the fronts in the mixtures are compared with yields of plants harvested from similar positions in the controls.

Species	Percentage reduction in yield		Mean
	Replicate (1)	Replicate (2)	
<u>Festuca ovina</u>	85.4	85.1	85.2
<u>Arrhenatherum elatius</u>	65.9	69.8	67.8
<u>Agrostis tenuis</u>	58.3	61.3	59.8

As expected, Festuca ovina showed the greatest reduction in yield as compared to the other species. Arrhenatherum elatius showed comparatively higher percentage reduction than Agrostis tenuis.

The results of this experiment reflect two general biological features of these grasses.

1. Under this experimental régime (i.e. high soil fertility and frequent clipping), the species showed differences in tolerance of clipping which were reflected on their yields. Agrostis tenuis outyielded each of Arrhenatherum elatius and Festuca ovina both in mixtures and monocultures. The higher yields of Agrostis tenuis were probably due to (a) capacity of the species to tolerate clipping and produce more tillers under intensive clipping, a feature shown by the species in monoculture experiments (Chapter 9.), (b) capacity of the species to form denser turf below the level of clipping and (c) lateral spreading capacity. Since previous experiments in fertile unclipped monocultures and competition experiments show Arrhenatherum elatius to be potentially higher yielding, the fall in the yield of this species to values comparable to those of the inherently slow-growing species, Festuca ovina, must be due to clipping. Festuca ovina appears to be more tolerant of clipping than Arrhenatherum elatius.
2. Agrostis tenuis has a capacity for lateral vegetative spreading by producing stolons, while lateral vegetative spreading capacity of Arrhenatherum elatius and Festuca ovina

is restricted both by the tussock growth form and especially in case of Arrhenatherum elatius by the destruction of shoot by clipping. Therefore because of this morphogenetic characteristic, Agrostis tenuis is well equipped to colonize bare soil or to invade the territory of less competitive species (e.g. Festuca ovina) or of species whose competitive ability is reduced by clipping (e.g. Arrhenatherum elatius).

CHAPTER 12.

COMPETITION BETWEEN AGROSTIS TENUIS AND
PROSTRATE FORM OF ARRHENATHERUM ELATIUS
IN A CLIPPED TURF

When plants were grown singly in monoculture and were subjected to close frequent clipping the prostrate form of Arrhenatherum elatius resembled in morphology plants of Agrostis tenuis and were found to be more tolerant of defoliation (Page 138). Agrostis tenuis is, however a common species in heavily grazed pastures, yet Arrhenatherum elatius is infrequent in these situations. One possible explanation for the scarcity of Arrhenatherum elatius from grazed sites is that other species, e.g. Agrostis tenuis, which are more tolerant of defoliation and have a greater capacity for lateral spread in grazed turf, exclude both the erect and the prostrate forms of Arrhenatherum elatius by competition. To test this hypothesis an experiment was set up in which prostrate individuals of Arrhenatherum elatius were allowed to compete with Agrostis tenuis in clipped turfs.

Materials and methods

Two hundred, one-week-old seedlings of Arrhenatherum elatius and the same number of Agrostis tenuis were planted in sand culture in 12.5 cm diameter plastic flower pots, The plants were placed in a growth room and were watered alternately every three days with 50 ml of Hewitt complete nutrient solution and 50 ml of distilled water.

The objective of this initial stage of the experiment was to obtain seedlings of the prostrate growth form of Arrhenatherum elatius of equal age to those of Agrostis tenuis. Unfortunately the seedling population did not include the required number of the prostrate forms. It was therefore decided to use tillers instead of seedlings. Thirty seedlings of each of Agrostis tenuis and Arrhenatherum elatius (prostrate) were transplanted individually to 23 cm diameter plastic flower pots in a growth room. After five weeks, the plants produced numerous tillers from which a uniform selection could be made for use in the experiment. By means of these tillers turfs were established in sand culture in 30 x 30 x 15 cm plastic containers. In the mixtures the tillers of the two species were arranged alternately and were placed 2.5 cm apart. With the exception of those at the margin, the tillers of each species were surrounded by four of the other species. The controls were monocultures, in which tillers of one species were planted in the positions occupied in the mixture; i.e. the area occupied by the other species in mixture were left as gaps. Four containers were used for the mixtures, and four containers for the monocultures of each of the two species. The containers were arranged in four randomized blocks. Each container was watered every three weeks with two litres of complete Hewitt solution and twice a week with two litres of tap water. The plants were grown in a growth-room and

were clipped at 2 cm every three days for one year. Clipping started four weeks after planting, by which time the tillers were well established. At harvest time, the plants in each container formed a uniform closed turf. It was difficult to separate the individual plants, so it was decided to use the total yield of shoot material in the container to give an estimate of the performance of each species in monocultures and mixtures. The percentage reduction in yield of Arrhenatherum elatius resulting from the presence of Agrostis tenuis and vice versa was calculated by comparing the yield of each species in the mixture with its yield in monoculture in the same block.

Results

Table 33 shows the mean oven-dry weights of the total shoot of each species and also the mean percentage reduction in yields of each species.

Table 33.

Mean dry weights of total shoot, of Agrostis tenuis and Arrhenatherum elatius (prostrate) and mean percentage reduction in yields of the two species; 95% confidence limits are given in brackets.

Species	Treatment	Mean oven dry weight (grams) of total shoot	Percentage reduction in yield
<u>Arrhenatherum elatius</u> (prostrate)	Monoculture	23.45(± 5.96)	70.8%(± 13.0)
	Mixture	5.92(± 2.00)	
<u>Agrostis tenuis</u>	Monoculture	30.35(± 4.03)	21.25(± 11.4)
	Mixture	23.77(± 6.99)	

The data included in Table 33 show that Arrhenatherum elatius was very much suppressed by Agrostis tenuis.

Evidence from previous experiments in which the plants of Agrostis tenuis and Arrhenatherum elatius (prostrate growth form) were grown singly in monoculture and were clipped at 2 cm, showed that the potential tillering capacity of these plants was not seriously affected by clipping and that Agrostis tenuis possessed greater tillering capacity than Arrhenatherum elatius (page 135). This difference in potential capacities for tiller production, and the ability of Agrostis tenuis to spread by producing stolons could perhaps account for the superiority of the species and the suppression of Arrhenatherum elatius.

CHAPTER 13.

EFFECT OF CUTTING AND SOIL FERTILITY ON THE
STATUS OF ARRHENATHERUM ELATIUS, AGROSTIS
TENUIS AND FESTUCA OVINA IN AGRASS MIXTURE

To study the effect of management and fertility on the competitive ability of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina in various types of grassland communities, turfs were synthesized from standardized seed mixtures containing the three grasses together with Agropyron repens, Dactylis glomerata, Holcus lanatus, Lolium perenne, Festuca rubra, Anthoxanthum odoratum and Zerna erecta. These species represented a wide range in competitive ability. In Table 34, the species selected for the experiment are allocated values based on a competitive index, devised by Grime (1973), and which is derived from scores for each of four consistent features of competitive species namely: (1) tall structure, (2) a growth form (usually large densely branched rhizome or expanded tussock structure which allows extensive exploration of the environment above and below the ground (3) a high maximum growth rate, (4) a tendency to deposit a dense layer of litter at the ground surface. He scored plant species with respect to each of these features and used the sum of scores to provide a competitive index over a score of 0 - 10. According to this system the species used in this experiment are rated as in Table 34.

Table 34.

Species	Competitive index
<i>Arrhenatherum elatius</i>	8.0
<i>Agr^oropyron repens</i>	8.0
<i>Dactylis glomerata</i>	7.0
<i>Holcus lanatus</i>	6.5
<i>Lolium perenne</i>	6.5
<i>Agrostis tenuis</i>	6.5
<i>Festuca rubra</i>	6.0
<i>Zerna erecta</i>	5.5
<i>Anthoxanthum odoratum</i>	5.0
<i>Festuca ovina</i>	4.0

Materials and methods.

The turfs were established in sand culture in hard plastic tubs, (35 x 35 x 30 cm); the sand was 6" deep. The sand in all containers was watered with two litres of complete Hewitt solution before the seeds were introduced. The seed stocks used in the experiment gave approximately 100% germination when tested on filter paper prior to the experiment. 100 seeds of each species were introduced in each container. The seeds were buried in very shallow furrows on the moist sand and in order to avoid drying of the sand surface each tub was covered by a sheet of polyethylene. Each tub was provided with a drainage tray which allowed the tubs to be watered from below. After 10 days, seedling establishment was assessed by measuring the "rooted frequency" of each species, that is, a 35 x 35 cm grid which was divided into 2.5 cm square grids, was placed over the central area of the sand surface and the number of subdivisions containing seedlings of the species

was recorded. The assessment showed that there was a high rate of establishment of all the species. Table 35.

Table 35.

Mean percentage rooted frequency of seedlings of the different species used in the experiment.

Species	Mean percentage rooted frequency
<i>Arrhenatherum elatius</i>	89.3
<i>Agropyron repens</i>	91.2
<i>Dactylis glomerata</i>	90.0
<i>Holcus lanatus</i>	89.5
<i>Lolium perenne</i>	86.2
<i>Festuca rubra</i>	86.2
<i>Anthoxanthum odoratum</i>	90.5
<i>Zerna erecta</i>	90.0
<i>Festuca ovina</i>	90.6

The tubs (32 in all) were divided into two equal groups. To each tub in one group excess equal quantities of water were added so as to leach nutrients from the sand. Each tub was then watered with two litres of Hewitt solution in which the nitrogen level was reduced to 5 ppm. These tubs represented the low fertility treatment. At the same time the second group of tubs which represented the high fertility treatment were watered each with two litres of complete Hewitt solution in which the nitrogen level was 170 ppm. The tubs were watered every three weeks with two litres of the appropriate nutrient solutions, and were also watered twice a week with equal quantities of water. The tubs were arranged into 4 blocks, each block containing four tubs of the high fertility treatment and four of the low fertility treatment.

At high and low nitrogen treatments cutting treatments were applied (uncut control, cut every 6 weeks, every 3 weeks and weekly). The plants were cut at 6 cm.

The experiment was carried out in a heated greenhouse, with an automatic ventilation system to maintain the temperature within the range of 20°C day and 15°C by night. In sunny days temperatures of 25 were recorded for short periods. A long day period was maintained by using large mercury vapour lamps.

Netlon garden netting (80 cm high), supported by wooden stakes was placed around certain tubs to prevent the unclipped plants grown at high fertility from spreading and shading neighbouring turfs.

The experiment was allowed to run for seven months. The turfs were then harvested in the same manner as in Chapter 10, and were stored in the cold room at 5°C in large polyethylene bags while sorting was in progress. The shoot material of each species was separated, oven-dried and weighed.

Results.

The differences in fertility levels produced two distinct types of turfs. In all the treatments at high fertility levels, the turfs were dense and green; the unclipped plants reached the height of about 60 cm and Arrhenatherum elatius flowered. At low fertility, the turfs were open, the plants were yellowish green, and the uncut plants were very much shorter (about 20 cm high) as compared to those in fertile treatment, and none of the plants flowered.

The histograms in Fig 38a and b show the dry weight of the shoot of each species in each treatment; yields and confidence limits are represented as percentages of standing crop transformed to angles. The contribution of each species to the turf varies with the fertility of the growing medium and the frequency of cutting (Fig. 38a and b).

The histograms in Fig. 38a show the yield of each species in the mixtures when the plants were grown under conditions of high fertility under the different cutting regimes. In the unclipped turfs Arrhenatherum elatius produced the greatest yield and a number of other species of high competitive index (Dactylis glomerata, Agropyron repens, Holcus lanatus, and Lolium perenne) became major constituents. Species of low competitive index (e.g. Festuca ovina) were either eliminated or became very minor components. Infrequent clipping (every 6 weeks) reduced the yield of Arrhenatherum elatius and the contribution of this species was not significantly different from that of Dactylis glomerata, and Holcus lanatus. Dactylis glomerata, Arrhenatherum elatius, Holcus lanatus were main contributors to the total herbage in all the treatments. Though Agropyron repens was among the dominants in the unclipped turfs, the contribution of the species to the total herbage decreased sharply at the two most frequent rates of clipping. Agrostis tenuis and Festuca ovina responded similarly in that their contribution to the total herbage increased with increased clipping, although under all clipping treatments, Agrostis tenuis out-

Fig.38(a and b)

Histograms comparing the effect of soil fertility and clipping upon the species composition of a turf synthesized from a standardized seed mixture. Yields (shoots only) and confidence limits are represented as percentages of standing crop transferred to angles. Histograms in (a) high fertility (170 ppm N) and (b) low fertility (5 ppm N).

- A: *Arrhenatherum elatius*
- D: *Dactylis glomerata*
- F: *Festuca ovina*
- G: *Agropyron repens*
- H: *Holcus lanatus*
- L: *Lolium perene*
- N: *Nardus stricta*
- R: *Festuca rubra*
- T: *Agrostis tenuis*
- Z: *Zerna erecta*

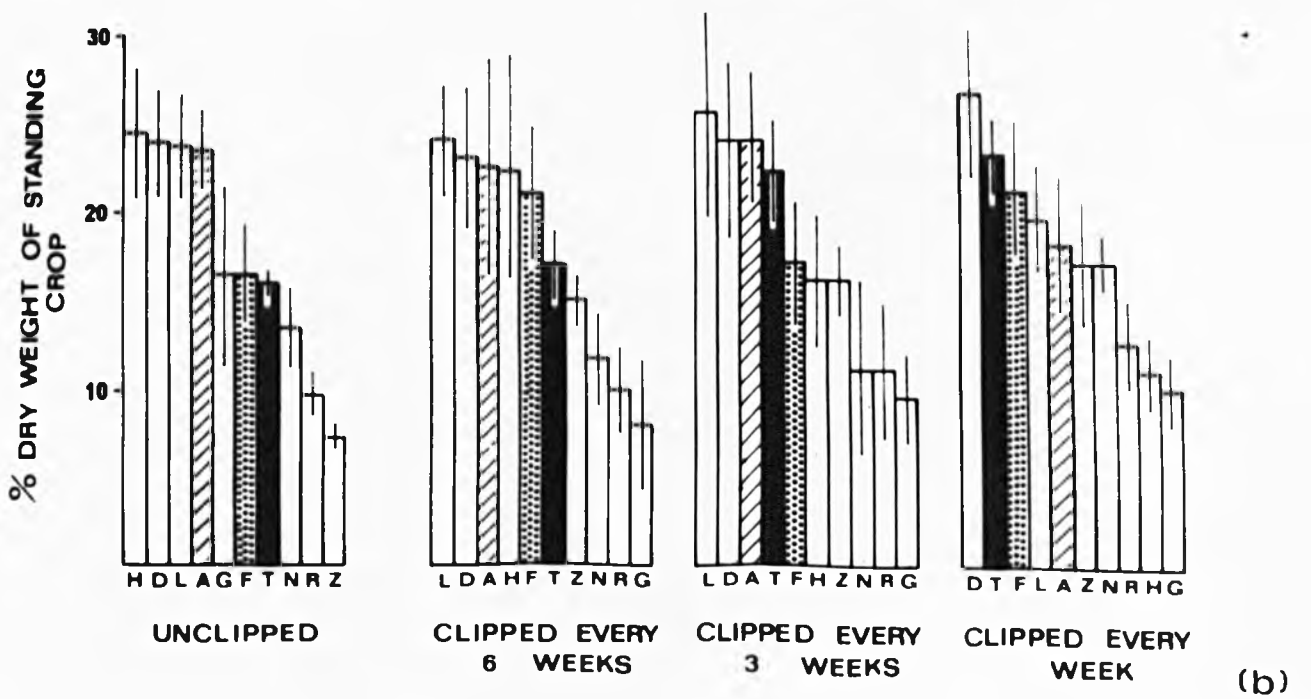
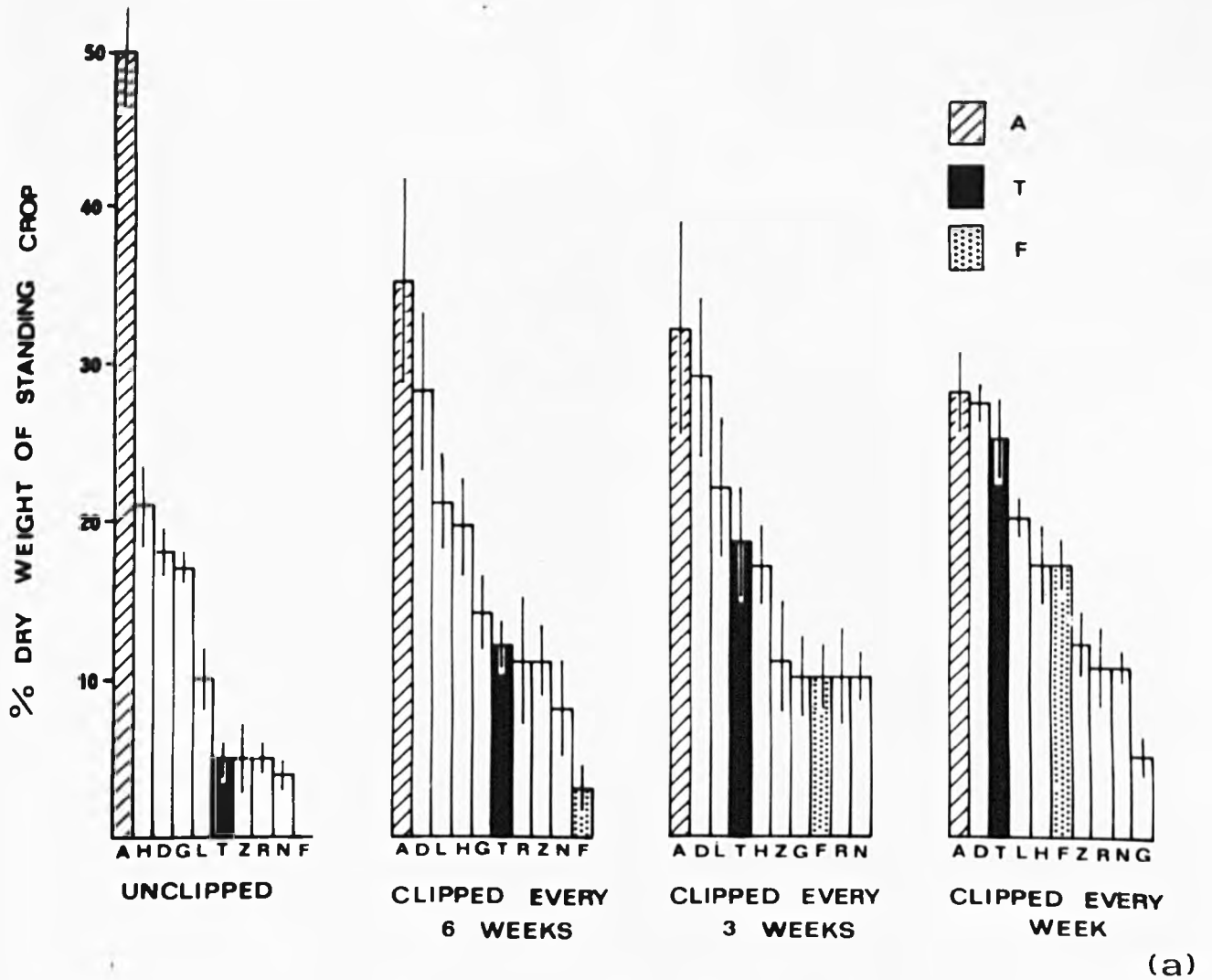


FIG. 38

yielded Festuca ovina. The behaviour of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina agrees with the predictions based on the responses of these grasses in monoculture to clipping. Arrhenatherum elatius being sensitive to clipping, had a reduced yield as the intensity of clipping increased, while Agrostis tenuis and Festuca ovina which are more tolerant of clipping than Arrhenatherum elatius increased their contribution to the total herbage as the intensity of clipping increased, and Agrostis tenuis outyielded Festuca ovina.

Histograms in Fig.38b describe the yield of shoot material in each species in the low fertility treatments. In the unclipped low fertility treatment, the yield of Arrhenatherum elatius was closely similar to that of Holcus lanatus, Dactylis glomerata, and Lolium perenne. Festuca ovina and Agrostis tenuis became more important components of the turf. Low productivity when accompanied by intensive clipping resulted in a more uniform performance of the species.

It is worth mentioning that, although the performance of the Species in this experiment did not agree in each species with predictions based upon the competitive index, it was clear that at high fertility and in unclipped treatments, Arrhenatherum elatius which is a species of high competitive ability, attained dominance over the other species and Dactylis glomerata, Agropyron repens, Holcus Lanatus and Lolium perenne became important components. Zerna erecta Festuca ovina and Anthoxanthum odoratum which have low

competitive indices were suppressed. However, it is clear from the results that the "competitive" attributes are advantageous only under conditions of rather high fertility and low intensity of forms of management, e.g. clipping which damage the shoots.

The results of this experiment and of the experiment described in Chapter 10 forward an interesting phenomenon which is worth mentioning here. In these experiments there is evidence that species of high competitive ability are suppressed differentially by certain forms of management (here represented by repeated cutting) and also by environmental stress (in this case, nitrogen deficiency). It is of interest to compare the effects of these two rather different factors in the present experiment. The results suggest that both are capable of promoting species diversity by debilitation of the most competitive species. It appears that species of high competitive ability approach their maximum size and vigour under conditions of fertility and low degree of management and tend in these conditions to exclude species of lower competitive ability.

DISCUSSION

A major objective of this work has been to attempt to recognise measurements which when carried out under laboratory conditions enable the most convenient and accurate prediction of features of plant distribution and ecology evident at the level of the species. Measurements have been carried out on plants grown in monoculture and refer to a variety of attributes. In this discussion an attempt is made to examine the usefulness of predictions based on selected laboratory characteristics used singly or in various combinations.

1. Seed weight and size.

The three species differ in the size of the seed and quantity of reserves contained therein. Arrhenatherum elatius seed is the largest (mean weight 4.5 mg) Festuca ovina is intermediate (mean weight 1.2 mg) and Agrostis tenuis comparatively the smallest (mean weight 0.10 mg). From this difference in seed size we may predict that the seeds are likely to differ in penetration into the soil surface. In fact the seed of Agrostis tenuis appears to be small enough to penetrate into quite small crevices.

The significance of seed size in relation to survival of seedlings in different environmental conditions was first realized by Salisbury (1942). However, more precise work on the ecological significance of this plant attribute has been pioneered and developed by Harper et al. (1963, 1965 and 1967).

The differences in seed size and weight between Arrhenatherum elatius, Agrostis tenuis and Festuca ovina are likely to be associated with differences in the rate and success of emergence of seedlings from deep burial in the soil. It is expected that rapid and successful emergence of seedlings of Agrostis tenuis will be restricted to seeds germinating nearest to the soil surface, but seedlings of Arrhenatherum elatius will be capable of establishment from more deeply buried seeds. Harper and Obeid (1967) studying the germination of three species of oil-seed and three fibre flaxes (Linum usitatissimum) showed that seedlings from the largest seeds emerged most quickly from deep sowing and those from small seeds most quickly from shallow sowing. It seems likely that seedlings of Agrostis tenuis arising from buried seed will have a comparatively smaller chance of survival during soil penetration than seedlings of the two larger seeded grasses. Even if exhaustion of the reserves of the small seed does not occur the seedlings penetrating the soil from deep burial will lose vigour and temporarily will be at a disadvantage in competition with seedlings of large seeded plants. Black (1956, 1957, and 1958) emphasized the role of seed size in the establishment and vigour of Trifolium subterraneum. He showed that the area of cotyledons produced by the seedlings decreased with increasing depth of sowing and with decreasing seed size.

Differences in rates of emergence of seedlings could be of major importance for the success of a species in competitive situations. Harper (1965) emphasized the role of the time of germination and establishment in success of a species in competition. However, it is to be noted that we are dealing here with perennial species and that competition between seedlings may be less important than competition between established plants or between established plants and seedlings.

It is therefore expected that under field conditions, physical or biological agencies which disturb the soil and bring the buried viable seeds of Agrostis tenuis to shallow burial result in rapid emergence and more successful establishment of Agrostis tenuis. Spray (in preparation) showed that soil samples collected from Derbyshire Dales contained numerous viable seeds of Agrostis tenuis and Festuca ovina. When these soils are transferred to pots in the greenhouse and watered regularly, seedlings of Agrostis tenuis and Festuca ovina were always present among the flora. When the seedlings were removed and the soil disturbed further crops of seedlings of these species appeared.

A further prediction arising from differences in the size of the seeds relates to the ability of the seedling to establish in a closed turf. It appears most likely that the large seed reserves of Arrhenatherum elatius will permit the species to produce a large seedling even under conditions of intensive competition for light and mineral nutrients. In particular it is to be expected that rapid initial height

growth will allow the shoot to gain access to the light even in a closed turf. Confirmation of this prediction is available from examination of the data showing the response of the species to shade (Chapter 6, Page 82) and the plates 31 to 38. The experimental evidence of Grime and Jeffery (1965) and the observations of Pigott (Page 82) also support this prediction. In view of the small seed size of Agrostis tenuis, it seems extremely doubtful that establishment in a closed turf is possible in this species. Kershaw (1958) concluded on the basis of field observations that successful invasion by seedlings of Agrostis tenuis is entirely dependent upon the availability of an area of bare ground suitable for germination and establishment. At Ffridd, N. Wales he observed that overgrazing of a productive pasture, mainly composed of Dactylis glomerata, resulted in exposure of a considerable number of small patches of bare mineral soil and that this favoured the invasion and spread of Agrostis tenuis. After 5-6 years a fairly uniform Agrostis tenuis sward was established and subsequently even under heavy conditions of sheep grazing little bare soil was exposed. Kershaw suggests that at this stage seedling establishment by Agrostis tenuis was of rare occurrence.

2. After-ripening of seeds.

The freshly collected seeds of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina have no dormancy, but they seem to require a short period of after-ripening before rapid germination of a high percentage of seeds is possible (Page 33).

This suggests that providing that there is no dormancy imposed by environmental conditions, germination is possible in all three species soon after detachment from the plants. Field observations (J.P. Grime and J. Hodgson) confirm that in the Sheffield area large numbers of seedlings of Arrhenatherum elatius are to be found soon after seed is shed in the summer and early autumn.

However, the presence of abundant buried viable seeds of Agrostis tenuis and Festuca ovina in the soil (Milton, 1935, 1939; and ... Spray, in preparation), suggests that conditions in the soil (possibly, the presence of high concentrations of carbon dioxide) induce a secondary dormancy in the seeds of these two species. It is not clear whether the failure of at least some of the seeds of Agrostis tenuis and Festuca ovina to germinate in the autumn is due to later seed production, retention of seed on the plant or to relatively easy penetration of the seeds of these two species into the soil (See page 48).

3. Response of germination to temperature.

With respect to the germination of fully ripened seeds, the three species showed different responses to temperature. Seeds of Arrhenatherum elatius germinated to a high percentage over a wide range of temperature (5 - 25°C) and 15°C was the temperature treatment closest to the optimum. Percentage germination declined with a rise in temperature above 25°C and fell steeply when the temperature approached 35°C. In contrast the percentage germination of seeds of Agrostis

tenuis was markedly low at 5°C and 35°C, but responses to the other temperatures were similar to those of Arrhenatherum elatius, except that the optimum temperature for germination was rather higher (about 20°C).

Seeds of Festuca ovina germinated to a high percentage over the whole range of temperatures investigated (5 - 35°C). The species germinated more rapidly and to higher percentages at the upper temperature range (15 to 35°C) than at the lower range (5 - 10°C) and the most favourable temperature occurred at the upper end of the range (between 25 - 30°C).

The capacity of the seeds of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina to germinate at low temperature (5 - 10°C) could be of special ecological significance. In places where winters are hard, this characteristic of the seed may reduce the efficiency of sexual reproduction in these species. In the cold regions, the seeds will be shed in the late summer and will start to germinate when they are shed and there is a danger that the seedlings might not be able to survive the winters. The reliability of this prediction would be improved considerably if data were available concerning the tolerance of the seedlings of these species to frost. Davison (1964) showed that by the end of November, seedlings of species including Agrostis tenuis sown in plots in the Derbyshire Dales, showed distinct signs of frost damage followed by a collapse of the leaves on thawing.

Arrhenatherum elatius is probably more exposed to these effects than Agrostis tenuis and Festuca ovina since the seeds

of the former species ripen before the seeds of the last two species and are shed very quickly. Plants of Festuca ovina and Agrostis tenuis tend to retain seeds in the inflorescence and it is possible that many of the seeds are shed at a time when soil temperatures do not favour their germination and that seeds are washed into soil during the winter. This possibility of seeds being shed at times when soil temperatures are not suitable for germination tends to be supported by the abundance of buried seeds in the soil. The stock of buried viable seeds of Festuca ovina and Agrostis tenuis in the soil may represent an adaptation for survival in extreme conditions: if seedlings are killed by cold weather or other environmental hazards, a reservoir of buried viable seeds can allow further regeneration. However, lack of dormancy and germination to a high percentage at low temperatures could be an advantage to the species, if the seedlings can survive subsequent cold weather conditions. Species with seeds which can germinate at lower temperatures and survive the winter as seedlings will have an initial advantage over species which have similar growth rates but start growth later in the season because they require higher temperatures for germination.

It is perhaps rather surprising that Festuca ovina germinates more rapidly and to a higher percentage at the upper temperature range (30 - 35°C) than Agrostis tenuis, a species with which it is commonly associated in the field. However, reference to the world distribution of the two

species (Plates 5 and 6) does not indicate that Festuca ovina extends further than Agrostis tenuis into warmer regions.

The high percentages of germination (more than 60%) attained by the three species at high temperatures (25 - 30°C) which occur only for short periods in their natural habitat in the United Kingdom suggests that the seed physiology of these species retains characteristics evolved in a climate distinct from that experienced in Derbyshire Dales today.

4. Response of seed germination to light.

The three species, Arrhenatherum elatius, Agrostis tenuis and Festuca ovina differ in their germination responses to light. Seeds of Agrostis tenuis are highly sensitive to light in that seeds which were incubated at suitable temperatures in the dark germinated very rapidly almost to 100% but continuous illumination by white light strongly inhibited rate and reduced final percentage germination. The seeds of Arrhenatherum elatius germinated to equally high percentages in the dark and in continuous white light, but the seeds which were incubated in the dark germinated at a slightly faster rate than the seeds germinated in continuous white light. The seeds of Festuca ovina incubated in the dark and in continuous white light germinated to equally high percentages and at similar rates when other suitable conditions for germination prevailed.

It is difficult to assess the ecological significance of the germination responses to light. One obvious advantage

arising from regulation of germination by light would be, in seeds having different light requirements, in adapting them to their habitat. Thus a light requirement may prevent germination of seeds when they are buried under the soil or leaf litter, or promote it when they fall on the soil surface or are unearthed. Such behaviour may determine how well a seedling will subsequently be able to establish itself. (Mayer and Poljakoff-Mayber 1963). Thus a light requirement for germination could be an advantage in preventing exposure of the seedling to a degree of shading, e.g. under canopies or litter. Light requirement is frequently associated with small seeds. It is generally assumed that, because the seeds are small and therefore contain little reserve materials, in order to lead to successful establishment they must germinate under conditions where photosynthesis occurs very soon after germination. In this context, the capacity of seeds of Agrostis tenuis to germinate to a high percentage when light is excluded cannot be of any ecological advantage to the plant.

5. Height of the vegetative shoot.

In a number of experiments carried out under productive conditions in the greenhouse (Pages 146 and 147) and growth-room (plates 11 to 22, and Plates 31 to 33), growth in height by Arrhenatherum elatius, Agrostis tenuis and Festuca ovina could be compared. The order in height of the three species is Arrhenatherum elatius > Agrostis tenuis > Festuca

ovina. From these observations, it could be predicted that under conditions in which potential height growth can be realised or nearly so (i.e. on fertile soils and under a low intensity of these forms of management which damage shoots e.g. grazing or clipping) Arrhenatherum elatius will prevail over Festuca ovina and Agrostis tenuis and that the last species will prevail over Festuca ovina. The fatal results of competition to Agrostis tenuis and Festuca ovina when these species were grown in mixtures with Arrhenatherum elatius, under productive conditions and the smothering of Festuca ovina by Agrostis tenuis (Pages 147 and 148) are in agreement with this prediction. However, examination of the data in Fig. 38a Chapter 13) suggests that it may be dangerous to predict the outcome of competition on potential height growth alone. Arrhenatherum elatius and Agropyron repens have roughly comparable height but the former species was considerably more successful in the competition experiment described on page 166 to 172. At least in some cases attributes other than height must be taken into consideration. In the case of Arrhenatherum elatius V. Agropyron repens, competition in the short term seems to favour Arrhenatherum elatius, perhaps because of its rapid development of massive impenetrable tussocks. Other considerations such as the patterns of dry matter allocated above and below the ground could help in resolving this situation. Plants of Agropyron repens derived from seed have been found to allocate a high proportion of the dry matter to underground parts in pure stands and this effect

was even more pronounced when the plants were grown in mixed stands (Tripathi and Harper 1973). As advocated by these two authors, study of the changes in allocation pattern of dry matter and associated form of growth of the two species in mixtures would help our understanding of this particular competition. However in the long term Agropyron repens may be favoured by toxic exudates from the litter (Welbank, 1960 and 1963).

6. Capacity for lateral vegetative spread.

The control treatments of the competition experiment (Page 154, Table 26) permitted measurements of rate of lateral vegetative spread in fertile conditions under clipping. In monoculture, it was noticed that Agrostis tenuis spread laterally much more rapidly than the other two species and three months after planting extended throughout the pots; in contrast some sand remained unoccupied by Arrhenatherum elatius and Festuca ovina after four months. It was noted that, in Agrostis tenuis, shoot apices had reached the distant margin of the pots, whilst in the non-stoloniferous Arrhenatherum elatius and Festuca ovina the lateral spread was mostly effected by leaves (Plates 79 to 81). It is expected that under fertile conditions in which Arrhenatherum elatius cannot exert its advantage in height growth (i.e. under intensive grazing or cutting) Agrostis tenuis will prevail at the expense of the other two species. The superiority of Agrostis tenuis (both in area occupied and yield) in the combined sowing treatment (page 155,

Table 27, page 156, Table 29, and page 158, Table 31) is probably due to this morphological characteristic. In this experiment the superiority of Agrostis tenuis over Arrhenatherum elatius could be in part due to better adaptation of Agrostis tenuis to clipping. However the suppression by Agrostis tenuis of the prostrate form of Arrhenatherum elatius (page 165), whose responses in monoculture to intensive defoliation are similar to those of Agrostis tenuis (page 138), when grown in mixtures under productive conditions and subjected to repeated close clipping, is at least partly due to the superior capacity of Agrostis tenuis to spread laterally.

Because of this morphogenetic characteristic therefore, Agrostis tenuis appears to be well equipped to colonize bare soil or to invade territory of less competitive species (e.g. Festuca ovina) or of species whose competitive ability is reduced by defoliation.

The unusual capacity for lateral vegetative spread under grazing conditions provides an explanation for an observation made by Kershaw (1958) in Aber, North Wales. He found that overgrazing by sheep caused a sward containing Dactylis glomerata and Lolium perenne to be invaded by Agrostis tenuis, the last eventually forming a reticulum with a few isolated patches of Dactylis glomerata and Lolium perenne.

7. Rate of dry matter production under fertile conditions.

Opportunities have arisen in several experiments to compare the three species with respect to dry matter production

under fertile conditions. The order in rate of dry matter production was found to be Arrhenatherum elatius > Agrostis tenuis > Festuca ovina. Differences between Arrhenatherum elatius and Agrostis tenuis in terms of absolute growth rate (g/unit time) are due to differences in initial embryonic capital and food reserves. In terms of RGR, Arrhenatherum elatius and Agrostis tenuis exceed Festuca ovina. It is unlikely that potential maximum growth rates will be achieved except very briefly in the field but nevertheless differences are likely to reflect differences in ability to respond to productive (but suboptimal) field conditions.

It is expected that when the species compete under fertile conditions as established plants, Arrhenatherum elatius and Agrostis tenuis will prevail over Festuca ovina. On this basis it is possible to predict that the application of fertilizers to Festuca ovina turf will lead to its displacement in favour of faster growing species. The work of Milton (1940) who showed that the application of N.P.K. to ungrazed plots increased the ratio of Agrostis tenuis/Festuca ovina, confirms this prediction.

It is expected that when Arrhenatherum elatius and Agrostis tenuis compete as established plants under fertile conditions, factors other than potential growth rate e.g. height of plant, litter accumulation, response to management, will dictate the outcome of competition.

It is to be noted that RGR does not only influence the rate of production of foliage in experiment, but also the amount

of litter accumulation. However, it is dangerous to extrapolate too readily to field conditions since litter accumulation depends upon the balance between rate of decomposition and rate of incorporation.

8. Mineral nutrient concentration for optimal growth.

When plants of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina were grown at different concentrations of potassium (Fig.25) the yields of the species increased significantly as the concentration of potassium increased from 0.13 ppm to 0.78 ppm and further increases in potassium concentration to 7.8 and 78 ppm resulted in correspondingly increased yield of Arrhenatherum elatius and Agrostis tenuis but not of Festuca ovina.

When the plants of Arrhenatherum elatius, Agrostis tenuis (grassland (G) and lead-heap (L.H.) populations) and Festuca ovina were grown at different levels of nitrogen (2.5 - 100 ppm) all the species except Festuca ovina showed an increase in yield to a maximum followed by a plateau (Fig.26a). The maximum yield was attained at 2.5, 5, 7.5 and 20 ppm in Festuca ovina, Agrostis tenuis (L.H.) Agrostis tenuis (G) and Arrhenatherum elatius respectively.

An obvious feature of these results is the correlation between the level of potassium or nitrogen necessary for optimal growth and the potential growth rate of the species (whether expressed as RGR . (max) or as absolute growth rate). This correlation between the potential growth rate and nutrient demand has been noted previously by Hunt, (1970). There is reason therefore to examine further the possibility that at

least crude predictions of mineral nutrient demands may be based upon measurements of $RGR_{(max)}$ rather than more elaborate experiments in which the plant's response to varied nutrient levels is examined.

The level of potassium and nitrogen at which the maximum yield is attained could be of ecological significance. Festuca ovina which is least responsive to increased potassium and nitrogen concentrations and which produced the least yield is expected to be associated with soils of low fertility where competition from other more productive species is checked by limiting fertility levels.

The fact that Agrostis tenuis (L.H.) reaches its maximum yield at lower concentration of nitrogen (5 ppm) than Agrostis tenuis (G) (7.5 ppm) can clearly be correlated with the nutrient-deficient habitat from which this population was obtained.

In view of the comparatively higher nutrient concentrations required for optimal growth in Arrhenatherum elatius and Agrostis tenuis it is possible to suggest that these two species can extend onto communities growing on more fertile soils than Festuca ovina and the lead-heap population of Agrostis tenuis.

9. Response to low rate of mineral nutrient supply.

The order of dry matter production at 0.13 ppm potassium (Fig.25) was Arrhenatherum elatius > Festuca ovina > Agrostis tenuis. At 0.78 ppm the order was Arrhenatherum elatius > Agrostis tenuis > Festuca ovina, and at 78 ppm K, the order was Arrhenatherum elatius > Agrostis tenuis > Festuca ovina (Fig.25).

The order of dry matter production at 2.5 ppm N was Arrhenatherum elatius > Agrostis tenuis (L.H.) > Agrostis tenuis (G) > Festuca ovina (at 100 ppm N. the order was Arrhenatherum elatius > Agrostis tenuis (G) > Agrostis tenuis (L.H.) > Festuca ovina. (Fig.26a).

In view of the higher nutrient concentrations required for optimal growth in Arrhenatherum elatius it is perhaps surprising to find this species outyielding the others at low concentrations of K and N. This is not merely due to the larger initial seed size of the seedling, i.e. a seed-size effect. A comparison of the size of the seedlings at the time which they were placed in the experiment and at harvest confirms that a higher dry matter production was sustained. In the absence of chemical analysis of the plant (which is desirable but was not carried out because of lack of time) it is not clear whether this was due to more effective absorption of nutrients or to the ability to grow despite low internal concentrations. However, foliar analysis carried out by the Nature Conservancy Unit at Sheffield reveal comparatively higher levels of all major nutrients in ^{leaf material} the turfs of Arrhenatherum elatius even in samples collected from nutrient deficient grasslands in which Festuca ovina exhibits low levels of major nutrients.

The performance of Arrhenatherum elatius exposed to low external concentrations of potassium and nitrogen indicates that the species has the potential to extend onto sites of low fertility. Arrhenatherum elatius is in fact a pioneer of limestone scree and at the present time appears to be invading

many of the derelict limestone pastures in Derbyshire previously dominated by Festuca ovina (Grime and Lloyd, 1973).

A conclusion that mineral nutrient stress per se does not exclude Arrhenatherum elatius from infertile soils is also suggested by the unpublished results of an experiment in which J.P. Grime and A. Curtis followed the fate of seedlings of Arrhenatherum elatius and Festuca ovina on unmanaged nutrient deficient Festuca ovina grassland in Millers Dale, Derbyshire. In this experiment, seedlings of both species were severely stunted by nutrient stress (attributed to phosphorus deficiency) but differential mortality of Arrhenatherum elatius was restricted to unwatered plots. This finding suggests that whilst nutrient stress may here be contributing to the failure of Arrhenatherum elatius a more critical difference between Festuca ovina and Arrhenatherum elatius may lie in their susceptibility to drought.

The fact that plants of Agrostis tenuis (G) did not show nutrient-deficiency symptoms when grown at low levels of potassium (0.78 ppm) and nitrogen (2.5 ppm) and that they significantly outyielded Festuca ovina at these low concentrations indicates that the growth of the species can extend onto habitats similar to those of Festuca ovina, Agrostis tenuis is in fact, frequently associated with Festuca ovina in acidic grasslands (Bradshaw et al., 1960; Lloyd, 1972). A comparison of the size and yields of plants of Agrostis tenuis (G) and Festuca ovina when plants were grown at 0.78 ppm K (Plates 52 and 56 and Fig.25) and also the yields of these

two species at 2.5 ppm N (Fig.26a), suggests that Agrostis tenuis will do better than Festuca ovina at fairly low levels of nutrients. The fact that Festuca ovina is commoner in soils of low fertility (Hubbard, 1968) suggests that these soils must be remarkably deficient in soil nutrients or that other phenomena (e.g. drought) swing the balance in favour of Festuca ovina. The superiority of Festuca ovina over Agrostis tenuis, both in size and yield, when plants of the two species were grown at 0.13 ppm K (Plates 51 and 55, and Fig.25) perhaps indicates the magnitude of nutrient stress required to favour Festuca ovina over Agrostis tenuis.

10. Susceptibility to aluminium and manganese toxicities.

The results of the experiments described in Chapter 7 confirm that predictions of the extent to which Arrhenatherum elatius, Agrostis tenuis and Festuca ovina will occur on acidic soils can be made by measurements of the degree of tolerance of the toxic elements aluminium and manganese whose solubility is known to increase with increased acidity of the soil.

The comparative study of the degree of tolerance of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina to aluminium toxicity (pages 90 to 101) showed Festuca ovina and Agrostis tenuis to be more tolerant than Arrhenatherum elatius. A comparison of the concentrations of aluminium which caused 50% reduction in total root length of these species with values obtained by Hodgson (1970) for other calcicolous and calcifugous grassland species (Table 13) placed Arrhenatherum

elatus among the calcicoles and Festuca ovina and Agrostis tenuis among the calcifuges. Festuca ovina seemed to be more tolerant than Agrostis tenuis.

When the yields of Deschampsia flexuosa, Festuca ovina, Agrostis tenuis and Arrhenatherum elatius were expressed as a function of manganese in solution (Fig.21) three levels of susceptibility were evident. Deschampsia flexuosa and Festuca ovina, were extremely resistant, Agrostis tenuis was intermediate in sensitivity, while Arrhenatherum elatius was very susceptible. The yields of Deschampsia flexuosa and Festuca ovina were not significantly reduced with increasing manganese concentrations (5-200 ppm), while the yields of Agrostis tenuis was reduced markedly only when the concentration of manganese in solution reached 100 ppm. The yields of Arrhenatherum elatius were reduced markedly at 25 ppm manganese.

The species which were more tolerant of aluminium toxicity (Deschampsia flexuosa, Festuca ovina and Agrostis tenuis) were also tolerant of manganese toxicity. The order of tolerance of these four species of aluminium and manganese (Deschampsia flexuosa, > Festuca ovina > Agrostis tenuis > Arrhenatherum elatius) is in agreement with the edaphic conditions under which these species normally flourish. Deschampsia flexuosa is a strict calcifuge which has a high frequency of occurrence at sites of low pH, Arrhenatherum elatius is a calcicolous species which is common in habitats with moderate or high pH. Agrostis tenuis which is more common in habitats of moderate pH seems

to be less tolerant of aluminium and manganese toxicities than Festuca ovina (a species more frequent in soils of low pH).

Since the seeds of both calcifuges and calcicoles used in this experiment had previously been found to be capable of germination in very acidic soils (pH 3-4) (Grime unpublished data), it seems that the low frequency of occurrence of the calcicolous species Arrhenatherum elatius in very acidic soils is due at least in part to the failure of seedling establishment in these habitats.

Although measurement of resistance to aluminium or manganese toxicity appears to allow predictions of edaphic tolerance, other factors must be taken into account in order to explain the success or failure of species on acidic soils (see Chapter 7, page 90). The limitations on plant growth in acidic soils are likely to be due to combinations of factors including deficiencies of major plant nutrients and the presence, in high concentrations, of aluminium and manganese.

11. Response in vegetative growth to temperature.

Vegetative growth of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina is very much affected by temperature. Several measures of growth (tiller number, yield, relative growth rate, shoot height, etc.) indicate that for all these species, the optimum temperature for growth lies between 20-25°C. The broad similarities between these species in their temperature responses is in agreement with their distribution in Britain. All occur more or less within similar altitude and are ubiquitous in the British Isles.

The capacity of the three species to maintain optimum growth between 20 - 25°C, temperatures which occur only for short periods in their natural habitats in Britain, suggests that provided that other environmental factors are not limiting the vegetative growth of these species is adapted to temperature conditions extending beyond the limits of the temperature range commonly experienced in Britain. The ability of the species to attain optimum growth at a comparatively high temperature is not surprising in view of the wide spread occurrence of these species in the Mediterranean countries where (as reported by Cooper and Tainton 1965) the mean day temperatures in summer exceed 30°C and winter daily maxima exceed 15°C. Eagle (1967) showed differences between Norwegian and Mediterranean populations of Dactylis glomerata in their growth responses to temperature and that the Mediterranean populations have higher temperature optima for growth.

12. Height growth in shade.

Arrhenatherum elatius produced seedlings in both control and shaded treatments which were tall in comparison with the seedlings of Agrostis tenuis, Festuca ovina and Deschampsia flexuosa. (page 82, Plates 31 to 33). This superiority in height growth was especially evident at lower light intensities (page 86, Plates 35 to 37). The rapid initial height growth of Arrhenatherum elatius in shade (Table 9) appears to be related to the combination of a comparatively large seed weight (page 26, Table 4) with the capacity to produce a long erect first leaf.

It seems reasonable to suggest that the shade response of Arrhenatherum elatius facilitates seedling establishment in a closed sward, and that the absence of a comparable response in Agrostis tenuis, and Festuca ovina may restrict successful establishment to shorter or broken turf.

Arrhenatherum elatius is, in fact, of common occurrence in tall closed communities and seedlings of this species are frequently observed beneath the parent plants in the summer and autumn (P.J. Grime and J. Hodgson pers. Comm.) However, there is, as yet, no clear proof that seedlings of Arrhenatherum elatius can establish in a closed sward.

It is to the rapid initial height growth that Professor C.D. Pigott attributed the colonization of stabilized scree by Arrhenatherum elatius in Derbyshire, England (Grime and Jeffrey 1965). He showed that seeds of Arrhenatherum elatius were washed down between the rocks and germinated in humid pockets which may be a considerable distance below the scree surface. From this position the first leaf grows upwards to the light through a distance of up to 10 cm.

13. Light intensity compensation point.

The experiments described in pages 84 to 89 permit a calculation of the light intensity at which, under the experimental conditions of temperature and day length, respiration losses balance photosynthetic gain. Agrostis tenuis and Festuca ovina were found to have light intensity compensation points considerably higher than those of Arrhenatherum elatius

and Deschampsia flexuosa (Fig.18). The prediction arising from this difference, i.e. that the latter two species are likely to be more frequent in shaded habitats, is confirmed by field observation (J.P. Grime, pers. comm.).

Although Arrhenatherum elatius and Deschampsia flexuosa seem to have similar light intensity compensation points (in fact lower in Arrhenatherum elatius than Deschampsia flexuosa), Arrhenatherum elatius loses weight more rapidly below the compensation point than Deschampsia flexuosa. This is consistent with the field ecology of the two species. Deschampsia flexuosa extends further than Arrhenatherum elatius into deeply shaded habitats. Results consistent with those of the present investigation were obtained by Hutchinson (1967) who found that seedlings of Deschampsia flexuosa were able to tolerate continuous darkness for a much longer period than those of Arrhenatherum elatius.

14. Response to clipping.

The data obtained from experiments in which Arrhenatherum elatius, Agrostis tenuis and Festuca ovina were grown under productive conditions in monoculture and subjected to various clipping treatments revealed consistent differences in response between the species.

The data from experiments A and B (pages 124 to 136) suggest that of the three species, Arrhenatherum elatius is the least tolerant of defoliation. Although producing the highest yield when plants were unclipped, the species equalled Agrostis tenuis in yield when clipped every week at 6 cm.

Clipping at 2 cm reduced the yield of Arrhenatherum elatius to less than half that of Agrostis tenuis (Table 19). However, the plant showed a rapid recovery after a single clipping treatment at 2 cm applied 50 days after germination, the plants producing flowering shoots and slightly outyielding Agrostis tenuis after a further 18 days' growth. Repeated clipping at 6 cm reduced the yield of Arrhenatherum elatius to a value slightly lower than that of Agrostis tenuis. Repeated clipping at 2 cm reduced Arrhenatherum elatius to a size much below that of Agrostis tenuis and comparable to that of the slow growing species Festuca ovina (page 131, and Fig.30).

These differences in response to clipping are probably due to the different amounts of damage caused to the plants due to differences in morphology. The more erect plants of Arrhenatherum elatius are more vulnerable to loss of photosynthetic tissue than the other two comparatively short grasses. Furthermore unlike Arrhenatherum elatius, both Agrostis tenuis and Festuca ovina possess morphogenetic responses to clipping which enable these two species to sustain growth under close repeated defoliation. Under close repeated clipping Agrostis tenuis and Festuca ovina produce numerous tillers (Fig.28, and page 134, Table 22) and have a tufted growth form which maintains photosynthetic canopy below the level of the clipping regime. (Plates 86 and 87).

The data concerning the responses of these three species to the different clipping treatments suggest that defoliation is particularly harmful to Arrhenatherum elatius and that

Plates 86 and 87. The appearance of plants of Agrostis tenuis and Festuca ovina which were clipped every three days at 2 cm from soil level.

Note the tufted growth of the two species and the comparatively larger plants of Agrostis tenuis.



86



87

forms of management which involve repeated defoliation close to the soil surface will be most destructive to the species. It is possible that it is due to this inability of Arrhenatherum elatius to withstand close defoliation that the species is scarce in situations which are subjected to repeated defoliation either by clipping or grazing.

The rapid recovery of Arrhenatherum elatius from a single close clipping at 2 cm, suggests that the plant can survive rotational cutting and grazing and probably explains the persistence of large plants of Arrhenatherum elatius under rotational grazing and forms of road verge maintenance which involve only low intensity of mowing.

The responses of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina in monoculture to clipping suggests that in managed grassland the status of Arrhenatherum elatius will be expected to decrease with increased frequency of defoliation and/or decreased height of clipping. The data in Fig.37(a) agree with this prediction. In unclipped turf growing under productive conditions, Arrhenatherum elatius was the highest contributor to the turf, but with increased frequency of clipping (every week) the contribution of the species was reduced to that of Dactylis glomerata and Agrostis tenuis.

In contrast, the status of Agrostis tenuis and Festuca ovina may be expected to increase with increased frequency of defoliation and/or decreased height of clipping. The data in Fig.37(a) show that even in the presence of highly competitive species and at high fertility levels, the contribution of

Agrostis tenuis and Festuca ovina to the total herbage increased with increased intensity of defoliation. It is possible that the increased status of these two short species in mixed turfs is related, in addition to the stimulated tillering under clipping, to the low amounts of photosynthetic tissues removed from these short plants. By comparison the tall more erect species Arrhenatherum elatius and Agropyron repens suffered excessive losses and were debilitated. It seems reasonable to conclude therefore that excessive forms of management tend to affect severely the vegetative growth of taller species and favour the spread of Agrostis tenuis and Festuca ovina.

Judging by the yield of Agrostis tenuis and Festuca ovina (Fig.30, T₁) and the size of the plants (Plates 86 and 87), one would predict that turfs containing Agrostis tenuis and Festuca ovina which are growing under productive conditions, and are subjected to excessive defoliation (i.e. by intensive grazing or clipping), would be dominated by Agrostis tenuis. For Festuca ovina to become more abundant than Agrostis tenuis, other factors of the environment which limit the growth of Agrostis tenuis (e.g. drought, limiting levels of nutrients) must be operative in combination with clipping. The work of Milton (1940) who showed by a series of fertilizer trials on grazed plots that the application of fertilizers reduce the Festuca ovina/Agrostis tenuis ratio agrees with this prediction.

It was found only in Arrhenatherum elatius (because the other two species did not flower during the short time of experiments included in pages 124 to 136) that close frequent clipping has a more destructive effect when applied after flowering than when applied in early seedling stage (page 140). This implies, that in attempting to estimate the magnitude of the effects of defoliation on vegetation, the time of defoliation seems to be equally important, as height and frequency of the treatment.

The responses of species in monoculture to clipping suggest that for a species to tolerate close repeated defoliation, it probably possesses one or both of the following morphological characteristics:-

- a) Capacity of producing numerous tillers. Species in which there is a stock of auxilliary buds, able to develop into tillers to replace the shoots killed by clipping, have a better chance of survival in grazed or mowed situations.
- b) a growth habit which reduces the magnitude of the damage caused by clipping. Plants with a prostrate shoot and which have the ability to produce numerous basal leaves below the level of cutting treatment possess an advantage. Plants with erect growth forms are subject to severe reduction in photosynthetic output and to a rapid decline in performance.

Agrostis tenuis, Arrhenatherum elatius (prostrate form) and Festuca ovina seem to possess both of the above characteristics to greater or lesser degree and seem to be more tolerant of clipping than the erect growth form of Arrhenatherum elatius,

which has even in unclipped plants a poorer tillering capacity than Arrhenatherum elatius (prostrate) (Plates 73 and 74), Agrostis tenuis, and Festuca ovina (Table 25). Under close clipping Agrostis tenuis, Arrhenatherum elatius (prostrate form) and Festuca ovina produced short tufted plants with numerous short tillers (Plates 86, 75 and 87) respectively, while erect plants of Arrhenatherum elatius were killed (Plate 76). This similarity in response to clipping between Agrostis tenuis, Arrhenatherum elatius (prostrate) and Festuca ovina suggests that the prostrate form of Arrhenatherum elatius is an adaptation to grazing and it is not unreasonable to expect a high frequency of Arrhenatherum elatius (prostrate) in grazed or mowed turfs. However, field data (Lloyd, Grime and Rorison 1971) seems to agree on the low incidence of Arrhenatherum elatius from heavily grazed pastures. This suggests that other factors of the environment in addition to defoliation (e.g. competition from other species such as Agrostis tenuis which are tolerant of defoliation and have a greater capacity for lateral vegetative spread, trampling) are excluding the species in these situations. The result of the competition experiment between the prostrate form of Arrhenatherum elatius and Agrostis tenuis (page 162 to 165) which showed a suppression of the plants of Arrhenatherum elatius suggest competition as a factor contributing to the scarcity of Arrhenatherum elatius in heavily grazed pastures.

It is to be noted that the data presented in this thesis were obtained as a result of investigations carried out on plant material derived from a single field population. It was realised from the beginning that predictions based on the laboratory characteristics of plant material derived from a single field population involve a major difficulty in the need to account for intraspecific variations. The work embodied in this thesis has indicated that in native plants genetic variations may exist even in populations raised from seeds derived from a single plant population (e.g. morphological differences between growth forms of Arrhenatherum elatius). Physiological differences (e.g. differences in responses to mineral nutrients) have been recognized between populations of Agrostis tenuis (lead-heap and grassland populations). Physiological differences in lead-tolerance have been reported to occur between populations of Agrostis tenuis (Bradshaw, 1963) and for Festuca ovina (Wilkins, 1957).

However, despite the evidence of genetic differences within the species it is concluded from the results obtained in this investigation that there are certain attributes which are less subject to variation, which control the broad ecology of the species and which are measureable in the laboratory.

CHAPTER 15.

SUMMARY

An attempt has been made to recognise laboratory characteristics of three common British grasses, Arrhenatherum elatius (L.) Beauv. ex J. and C. Presl, Agrostis tenuis Sibth. and Festuca ovina L. which allow features of their ecology to be predicted. Experimental work was carried out under controlled and semicontrolled conditions to investigate responses to selected environmental factors. The studies involved considerations of plant morphology and measurements of responses in germination and growth to light and temperature and responses to nutrient stress, metal toxicity and defoliation. In some experiments, additional species, Deschampsia flexuosa, and Zerna erecta were included in order to provide a wider basis for comparison.

Predictions of the field ecology were evaluated by reference to published accounts of field studies on these species and by carrying out competition experiments.

Various plant attributes used singly or in combination were found to provide a useful basis for predictions and provide an insight into the mechanisms operating in the field. Attributes which appear to have a predictive value in the species investigated include, seed weight, lack of dormancy, response of the germination and vegetative growth to temperature, maximum potential growth rate under productive conditions, litter production features related to seedling growth under

conditions involving nutrient stress, or aluminium and manganese toxicity, extension growth in shade, the light intensity compensation point and tiller production under continuous clipping.

The freshly collected seeds of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina were found to exhibit no dormancy but required a short period of after-ripening before rapid germination to a high percentage was possible.

The three species showed major differences with respect to longevity of seeds. Germination tests carried out on seeds stored at room temperature showed Agrostis tenuis to have a longer life-span than those of the other two species. This was consistent with the reported abundance of buried viable seeds in Agrostis tenuis grasslands. In marked contrast seeds of Arrhenatherum elatius lost viability readily and do not appear to occur in buried seed flora of native soils.

With respect to the germination of the fully ripened seeds, the three species showed differences in response to temperature and light. Seeds of Arrhenatherum elatius germinated to a high percentage over a wide range of temperature (5 - 25°C) and 15°C was the temperature approaching the optimum. The percentage germination of Agrostis tenuis was notably low at 5°C, and at 35°C, but responses to other temperatures were similar to those of Arrhenatherum elatius, except that the optimum temperature is slightly higher (about 20°C).

The seeds of Festuca ovina germinated to a high percentage over the temperature range (5 - 35°C) but in contrast to the

other species, Festuca ovina germinated more rapidly and to a higher percentage at the upper temperature range (15 - 35°C) than at the lower range (5 - 10°C).

Continuous illumination by white fluorescent light strongly reduced the rate and final percentage germination of seeds of Agrostis tenuis. The significance of this phenomenon is rather obscure. No major effect of light was apparent in the germination of Festuca ovina and Arrhenatherum elatius.

Vegetative growth of the three species was strongly influenced by temperature. Several attributes of growth (tiller number, shoot height, leaf area, yield, relative growth-rate) indicated that for the three species the optimum temperature for growth lay between (20 - 25°C).

The broadly similar responses to temperature in germination and vegetative growth of the three species are in agreement with their geographical distribution in the United Kingdom; all are ubiquitous in the British Isles and occur within similar altitudinal range.

The capacity of the species to germinate at high percentages (>60%) at high temperature (25-30°C) and to attain optimum growth between (20-25°C), temperatures which occur for short periods in their natural habitat in Britain imply that the physiology of the seed and vegetative growth may be preadapted to temperature conditions such as those of Southern Europe parts of which fall within the present distribution of the species.

The order of tolerance of the four species investigated (Deschampsia flexuosa > Festuca ovina > Agrostis tenuis > Arrhenatherum elatius) to aluminium and manganese toxicities enables a prediction to be made of the extent to which each will extend onto acidic soils.

When Arrhenatherum elatius, Agrostis tenuis, Festuca ovina and Deschampsia flexuosa were grown under artificial shade, Arrhenatherum elatius produced tall seedlings in comparison with those of the other species. This rapid height growth of seedlings of Arrhenatherum elatius in response to shade probably confers the ability to establish in closed turf. In Agrostis tenuis, Deschampsia flexuosa and Festuca ovina, the absence of a comparable response appears to restrict establishment of these species to shorter or broken turf.

Under the experimental conditions used Agrostis tenuis and Festuca ovina were found to have light intensity compensation points considerably higher than those of Arrhenatherum elatius and Deschampsia flexuosa. From this, it may be predicted that the latter two species will be more frequent in shaded habitats. This prediction is confirmed by reference to field survey data.

Comparison of the responses of the three species to different rates of supply of nitrogen and potassium in solution-culture experiments revealed that the potentially faster-growing species (Arrhenatherum elatius and Agrostis tenuis) require higher external concentrations than Festuca

ovina in order to attain maximum yield. This may in part explain the success of Festuca ovina in nutrient deficient habitats. However, at very low external concentrations of nitrogen and potassium, Festuca ovina was outyielded by Arrhenatherum elatius. This implies that factors other than nutrient stress restrict the distribution of Arrhenatherum elatius in the field. It is clear that Arrhenatherum elatius has the potential to extend onto sites of low fertility. Such a conclusion is consistent with recent evidence of widespread invasion of the derelict limestone pastures of Derbyshire by the species.

At low levels of potassium (0.78 ppm) and nitrogen (2.5 ppm) Agrostis tenuis outyielded Festuca ovina. It is suggested therefore, that the greater success of Festuca ovina on nutrient-deficient calcareous pastures can only be attributed to major nutrient deficiencies where the levels of available nutrients are extremely low. It is suggested that other factors notably droughting may be exerting a more important effect upon the Agrostis:Festuca ratio of daleside pastures.

The data obtained from experiments in which individual plants of Arrhenatherum elatius, Agrostis tenuis and Festuca ovina were grown under productive conditions and were subjected to different clipping treatments showed that of the three species Arrhenatherum elatius, is least tolerant of defoliation. Repeated clipping at 6 cm reduced the yield of Arrhenatherum elatius to a value below that of Agrostis

tenuis. Repeated clipping at 2 cm reduced the yield of Arrhenatherum elatius to a value below that of Agrostis tenuis and comparable to that of Festuca ovina.

The experimental results suggest that forms of management which involve repeated defoliation close to the soil surface will eliminate or suppress Arrhenatherum elatius. However, the rapid recovery of Arrhenatherum elatius from a single clipping applied at 2 cm, indicates the ability of Arrhenatherum elatius to survive rotational cutting or grazing and probably explains the persistence of large plants of Arrhenatherum elatius in meadows, lightly grazed pastures and road verges subject to a low intensity of mowing.

The resistance of Agrostis tenuis and Festuca ovina to close repeated clipping appears to be related to two morphological characteristics. The first is the capacity to produce numerous tillers. In Agrostis tenuis, in particular, there appears to be a large stock of axillary buds, able to develop into tillers to replace the shoot material removed by clipping. The second characteristic is a growth habit which reduces the magnitude of the damage caused by clipping. The semi-prostrate shoots of Agrostis tenuis have the ability to produce numerous basal leaves below the level of cutting and providing a dense canopy close to the ground surface.

Populations of seedlings of Arrhenatherum elatius raised in the laboratory were found to be polymorphic, containing both erect and prostrate growth forms. In clipping

experiments, the prostrate forms were found to be more tolerant of defoliation and have a superior tillering capacity.

By comparison of the absolute growth rates of the three species, together with their potential for vertical height and lateral growth of the shoot and for litter production, it was found to be possible to predict the outcome of competition experiments in which the species were grown under fertile conditions and in absence of clipping. Under these circumstances the order in competitive ability was Arrhenatherum elatius > Agrostis tenuis > Festuca ovina. Further competition experiments, showed that it was possible to predict shifts in the relative importance of the species in treatments involving clipping or mineral nutrient stress.

The data on which predictions have been based were derived from investigations carried out on a single field population of each species. Evidence of the need to take account of interspecific variation was obtained in the present study; it was necessary to carry out additional experiments to investigate the significance of morphological variations in Arrhenatherum elatius. It is concluded, however, that whilst genetic variation within the species may have an important influence, the laboratory characteristics of plants drawn from a single field population frequently revealed attributes which control the broad ecology of the species.

REFERENCES

- Albertson, F.W., Riegel, A., and Launchbaugh, J.L. (1953). Effects of different intensities of clipping on short grasses in west-central Kansas, *Ecology*, 34, 1-20.
- Aldous, A.E. (1930). Effect of different clipping treatments on the yield and vigour of prairie grass vegetation. *Ecology*, 11, 752-759.
- Aspinall, D. (1961). The control of tillering in barley plants. 1. The pattern of tillering and its relation to nutrient supply. *Aust.J.Biol.Sci.*, 14, 493-505.
- Baker, K.F. (1946). Observations on some Botrytis disease in California. *Pl. Dis. Repr.* 30, 145-155.
- Baker, H.K. (1957b). Studies on the root development of herbage plants. 111. The influence of cutting treatments on the root, stubble and herbage production of a perennial ryegrass sward. *J. Brit. Grassland Soci.* 12, 197-208.
- Balme, O.E. (1953). Edaphic and Vegetational zoning on the Carboniferous Limestone of the Derbyshire Dales. *J. Ecol.* 41, 331-344.
- Barnes, W.C. (1936). Effects of some environmental factors on growth and colour of carrots. *Connell Univ. Agr. Expt. Sta. Mem.* 186, 36.
- Benedict, H.M. and Brown, G.D. (1944). The growth and carbohydrate responses of Agropyron smithii and Bouteloa gracilis to changes in nitrogen supply. *Pl. Physiol., Lancaster*, 19, 481-494
- Black, C.A. (1957) *Soil plant relationships.* New York.
- Black, J.N. (1956). The influence of seed size and depth of sowing on pre-emergence and early vegetative growth of subterranean clover (Trifolium subterraneum L.), *Aust.J.Agr.Res.* 7, 98-109.
- Black, J.N. (1957). The early vegetative growth of three strains of subterranean clover (Trifolium subterraneum L.) in relation to size of seed. *Aust. J.Agr.Res.* 8, 1-14.

- Black, N.J. (1958) Competition between plants of different initial seed size in swards of subterranean clover (Trifolium subterraneum L.) with particular reference to leaf area and the leaf micro-climate. Aust.J. Agric.Res. 9, 299-318.
- Black, N.J. (1960). The significance of petiole length, leaf area, and light interception in competition between strains of subterranean clover (Trifolium subterraneum L.) grown in sward. Aust.J. Agr. Res. 11, 277-291.
- Blackman, G.E. and Black, J.N. (1959). Physiological and ecological studies in the analysis of plant environment. XI. A further assessment of the influence of shading on the growth of different species in the vegetative phase. Ann. Bot. N.S. 23, 51-63.
- Blackman, G.E. and Wilson, G.L. (1951). Physiological and ecological studies in the analysis of plant environment. VII. An analysis of the differential effects of light intensity on the net assimilation rate, leaf area ratio, and relative growth rate of different species. Ann. Bot. N.S. 15, 373-408.
- Blackman, G.E. and Wilson, G.L. (1954). Physiological and ecological studies in the analysis of plant environment. IX. Adaptive changes in the vegetative growth of Helianthus annuus induced by an alteration in light level. Ann. Bot. 18, 71-94.
- Blair, A.W. and Prince, A.L. (1923). Studies on the toxic properties of soils. Soil Sci. 15, 109-130.
- Böhning, R.H. and Burnside, C.A. (1956). The effect of light intensity on rate of apparent photosynthesis in leaves of sun and shade plants. Am.J.Bot. 43, 557-561.
- Boissier, E. (1884). Flora Orientalis Lyon.
- Bourdeau, P.F. and Laverick, M.L. (1958). Tolerance and photosynthetic adaptability to light intensity in white pine, red pine, hemlock and ailanthus seedlings. Forest Sci. 4, 196-207.

- Borriss, H. (1941). "Über die inneren Vorgänge bei der Samenkeimung und ihre Beeinflussung durch Außenfaktoren. Jb. wiss. Bot. 89, 254-339.
- Borriss, H., Arndt, M. (1967). Die genetischen Grundlagen der Samenruhe bei Agrostema githago. Physiologie Ökologie und Biochemie der Keimung. (Ed. by H. Borriss), pp.393-404, Greifswald, University.
- Bosemark, N.O. (1954). The influence of nitrogen on root development. Physiologia Pl. 7, 497-502.
- Bortner, C.E. (1935). Toxicity of manganese to Turkish tobacco in acid Kentucky soils. Soil Sci. 39, 15-33.
- Boyd, D.A. and Lessels, W.J. (1954). Influence of fertility levels on grassland output. J. Brit. Grassland Soci. 9, 7-15.
- Bradshaw, A.D. (1963). Populations of Agrostis tenuis resistant to lead and zinc poisoning. Nature, Lond. 169, 1098.
- Bradshaw, A.D., Chadwick, M.J., Jowett, D., Lodge, R.W. and Snaydon (1960b). Experimental investigations into the mineral nutrition of several grass species. III. Phosphate level. J. Ecol. 48, 631-637.
- Bradshaw, A.D., Chadwick, M.J., Jowett, D. and Snaydon, R.W. (1964). Experimental investigation into the mineral nutrition of several grass species. IV. Nitrogen level. J. Ecol. 52, 665-667.
- Bradshaw, A.D., Lodge, R.W., Jowett, D. and Chadwick, M.J. (1958). Experimental investigations into the mineral nutrition of several grass species. I. Calcium level. J. Ecol. 46, 749-757.
- Bradshaw, A.D., Lodge, R.W., Jowett, D. and Chadwick, M.J. (1960a). Experimental investigation into the mineral nutrition of several grass species. II. Calcium and pH. J. Ecol. 48, 143-150.
- Brooks, E.G. (1908). Observations on the botany of Botrytis cinerea. Ann. Bot. 22, 479-487.
- Brouwer, R. (1966). Root growth of grasses and cereals. The Growth of Cereals and Grasses (Ed. by F.L. Milthorpe and D.J. Ivins), pp.153-166. Butterworths, London.

- Brown, E.M. (1939). Some effects of temperature on the growth and chemical composition of certain grasses. Res.Bull. Mo. Agri. Expt. Sta., 299, 276.
- Clapham, A.R., Tutin, J.G. and Warburg, E.F. (1957). Flora of the British Isles, Cambridge University Press, London.
- Clarkson, D.T. (1965). The effect of aluminium and other trivalent metals on cell division in the root apices of Allium cepa. Ann. Bot. N.S. 29, 309-315.
- Clarkson, D.T. (1966a). Aluminium tolerance in species within the genus Agrostis J.Ecol.54, 167-178.
- Clarkson, D.T. (1966b). Effect of aluminium on the uptake and metabolism of phosphorous by barley seedlings. Pl. Physiol., Lancaster, 41, 165-172.
- Clymo, R.S. (1962). An experimental approach to part of the calcicole problem. J.Ecol., 50, 701-731.
- Cooper, J.P., and Edwards, K.J.R. (1961). The genetic control of leaf development in Lolium perenne.
1. Assessment of genetic variation. Heredity, 16, 63-82.
- Cooper, J.P. and Tainton, N.M. (1965). Light and temperature requirements for growth of tropical and temperate grasses. Herb. Abstr. 38, 167-176.
- Connors, D. and Sears, O.H. (1922). Aluminium salts and acids at varying hydrogen ion concentrations in relation to plant growth in water culture. Soil Sci. 13, 23-34.
- Crocker, W. and Barton, L.V. (1957). Physiology of Seeds, pp.114. Waltham, Mass. U.S.A.
- Culley, M.J., Campbell, R.S. and Canfield, R.H. (1933). Values and limitations of clipped quadrats. Ecology, 14, 35-39.
- Curtis, O.F. and Clark, D.G. (1950). An Introduction to Plant Physiology. 1st ed. McGraw-Hill Book Co. Inc. New York.
- Daji, J.A. (1948). Manganese toxicity as a probable cause of the band disease of Areca palms. Curr.Sc. 17, 259-260.

- Darrow, R.A. (1939). Effects of soil temperature, pH, and nitrogen nutrition on the development of Poa pratensis. Bot. Gaz. 101, 109-112.
- Davison, A. (1964). Some factors affecting establishment on calcareous soil. Ph.D. thesis. Sheffield University.
- Davison, R.L. (1969b). Effect of soil nutrients and moisture on root/shoot ratios in Lolium perenne L. and Trifolium repens L. Ann.Bot.33, 571-577
- Dittmer, H.J. (1973). Clipping effects on Bermuda grass biomass. Ecology, 54, 217-219.
- Donald, C.M. (1958). The interaction of competition for light and for nutrients. Aust.J. Agri.Res. 9, 421-435.
- Eagle, C.F. (1967). The effect of temperature on vegetative growth in climatic races of Dactylis glomerata in controlled environments. Ann. Bot. N.S. 31, 31-39.
- El-Shargawy, M., Hesketh, J. and Muramoto, H. (1965). Leaf photosynthetic rates and other growth characteristics among 26 species of Gossypium. Crop Sci. 5, 173-175.
- Evans, M.W. (1927). The life history of timothy. U.S.D.A. Bull. 1450, 1-56.
- Evans, G.E. and Hughes, A.P. (1961). Plant growth and aerial environment. 1. Effect of artificial shading on Impatiens parviflora. New Phytol. 60, 150-180.
- Ewart, A.J. (1930). Flora of Victoria. Melbourne, University press.
- Foster, R.E. and Walker, J.C. (1947). Predisposition of tomato to Fusarium wilt. J. Agri. Res. 74, 165-185.
- Gilbert, B.E., and Pember, F.R. (1931). Tolerance of certain weeds and grasses to toxic aluminium. Soil Sci., 39, 425-430.
- Graber, L.F. (1931). Food reserves in relation to other factors limiting the growth of grasses. Pl. Physiol. 6, 43-71.
- Gregory, R.P.G. and Bradshaw, A.D. (1965). Heavy metal tolerance in populations of Agrostis tenuis Sibth. and other grasses. New Phytol. 64, 131-143.

- Grime, J.P. (1965). Shade tolerance in flowering plants. *Nature, Lond.*, 208, 161-163.
- Grime, J.P. (1966). Shade avoidance and shade tolerance in flowering plants. Light as an ecological factor (Ed. by R. Bainbridge, G.C. Evans, and R. Rackham), pp. 187-207, Oxford.
- Grime, J.P. (1968). The creative approach to nature conservation. The future of Man. (Ed. by F.J. Ebling, and G.W. Heath), pp.47-54, Academic Press, London. New York.
- Grime, J.P. (1973). Control of species density in herbaceous vegetation. *Journal of environmental management* 1, 151-167.
- Grime, J.P. and Hodgson, J.G. (1969). An investigation of the ecological significance of lime-chlorosis by means of large-scale comparative experiments. *Ecological Aspects of the Mineral Nutrition of Plants* (Ed. by I.H. Rorison). pp.67-99, Blackwell, Oxford.
- Grime, J.P. and Jeffrey, D.W. (1965). Seedling establishment in vertical gradients of sunlight. *J. Ecol.* 53, 621-642.
- Grime, J.P. and Lloyd, P.S. (1973). *An Ecological Atlas of Grassland Plants.* Arnold, London.
- Hacket, C. (1965). Ecological aspects of the nutrition of Deschampsia flexuosa (L.) Trin. II. The effect of Al., Ca, Fe, K, Mn, N, P, and pH on the growth of seedlings and established plants. *J. Ecol.* 53, 299-314.- 333
- Hacket, C. (1967). Ecological aspects of the nutrition of Deschampsia flexuosa (L.) Trin. III. Investigation of the phosphorous requirement and response to aluminium in water culture and a study of growth in soil. *J. Ecol.* 55, 831-840.
- Hamilton, H.H. (1948). A developmental study of the apical meristem in four varieties of Avena stiva grown at two temperatures. *Amer. J. Bot.* 35, 656-665.
- Hargreaves, J.W. (in preparation). A comparative study of root plasticity in native plant species. M.Sc. thesis, University of Sheffield.

- Harper, J.L. (1965). Establishment, aggression and cohabilitation in weedy species. Genetics of colonizing species (Eds. H.G. Baker, and G.L. Stebbins). pp.243-265, New York: Academic.
- Harper, J.L. and Clatworthy, J.N. (1963). The comparative biology of closely related species. VI. Analysis of the growth of Trifolium repens and T. fragiferum in pure and mixed populations. J. Exp.Bot. 14, 172-190.
- Harper, J.^L~~P~~. and Obeid, M. (1967). Influence of seed size and depth of sowing on the establishment and growth of varieties of fiber and oil-seed flax. Crop Si. 7, 527-532.
- Harrison, C.M. (1931). Effect of cutting and fertilizer application on grass development. Pl. Physiol. 6, 669-684.
- Harrison, C.M. (1934). Responses of Kentucky bluegrass to variation in temperature, light, cutting and fertilizing. Pl. Physiol., Lancaster, 9, 83-106.
- Hartwell, B.L. and Pember, F.R. (1918). The presence of aluminium as a reason for the difference in the effect of so-called acid soils on barley and rye. Soil Sci. 6, 259-279.
- Heinrichs, D.H. and Clark, K.W. (1961). Clipping frequency and fertilizer effects on productivity of five grasses. Can.J.Agr. Sci. 34, 97-108.
- Hiesey, W.M. and Milner, H.W. (1965). Physiology of ecological races and species. An. Rev. Pl. Physiol. 16, 203-216.
- Hergert, G., Zillinsky, F.J. and Kemp, J.K. (1966). An Aspirator for cleaning small seed samples. Can.J. Pl. Sci. 46, 570-572.
- Hewitt, E.J. (1946). The resolution of the factors in soil acidity. Some effects of manganese toxicity. Ann. Rep. Long-Ashton Res. Sta. 50-61.
- Hewitt, E.J. (1948). The resolution of the factors in soil acidity. The comparative effects of manganese and aluminium toxicities on some farm and market garden crops. Ann.Rep. Long Ashton Res. Sta. 58-65.

- Hewitt, E.J. (1966). Sand and water culture methods used in the study of plant nutrition. Comm. Agr. But. Tech. Comm. Bur. Hort. 22 (2nd edn.)
- Hultén, E. (1950). Atlas Över Växternas Utbredning i Norden Stockholm.
- Hultén, E. (1964). The Circumpolar plants. Almqvist and Wiksell, Stockholm.
- Hodgson, J.G. (1972). A comparative study of seedling root growth with respect to aluminium and iron supply, Ph.D. thesis, University of Sheffield.
- Hubbard, C.E. (1968). Grasses, 2nd edn. Penguin, Harmondsworth.
- Hunt, R. (1970). Relative growth rate: its range and adaptive significance in a local flora. Ph.D. thesis, University of Sheffield.
- Hunt, R. and Parsons, I.T. (1974). A computer programme for deriving growth functions in plant growth-analysis. J. Appl. Ecol. 11 (Submitted).
- ✓ Hutchinson, T.C. (1967). Comparative studies of the ability of species to withstand prolonged periods of darkness. J. Ecol. 55, 291-299.
- Isikawa, S. (1957). Interaction of temperature and light in the germination of *Nigella* seeds. Bot. Mag. (Tokyo) 70, 264-275.
- Jacobson, H.G.M. and Swanback, T.R. (1932). Manganese content of certain Connecticut soils and its relation to the growth of tobacco. J. Am. Soc. Agron. 24, 327-345.
- Jefferies, R.L. and Willis, A.J. (1964). Studies on the calcicole-calcifuge habit. 11. The influence of calcium on the growth and establishment of four species in soil and sand culture. J. Ecol. 52, 691-707.
- Kershaw, K.A. (1958). An investigation of the structure of a grassland community. 1. the pattern of *Agrostis tenuis*. J. Ecol. 46, 571-492.
- Koller, D. (1957). Germination - regulating mechanisms in some desert seeds. 1V. *Atriplex dimorphostegia* Kar. et Kiv. Ecology, 38, 1-13.
- Koller, D. and Negbi, M. (1959). The regulation of germination in *Oryzopsis miliacea* Asch. et Schw. Ecology, 40, 20-36.

- Kotowski, F. (1926). Temperature relations to germination of vegetable seeds. Proc. Amer. Soc. Hort. Sci. 23, 176-184.
- Lawer, E. (1952). "Über die Keimungstemperatur von Ackerunkräutern und deren Einfluss von Unkrautgesellschaften. Flora. Jena. 14, 551-95.
- Ligon, W.R., and Pierre, W.H. (1932). Soluble aluminium studies. 11. Minimum concentration of aluminium found to be toxic to corn, sorghum and barley in culture solutions. Soil Sci. 34, 307-321.
- Lloyd, P.S. (1968). The ecological significance of fire in Limestone grassland communities of the Derbyshire Dales. J. Ecol. 56, 811-826.
- Lloyd, P.S. (1972). The grassland vegetation of the Sheffield region. 11. Classification of grassland types. J. Ecol. 60, 739-776.
- Lloyd, P.S., Grime, J.P., Rorison, I.H. (1971). The grassland vegetation of the Sheffield region. 1. General features. J. Ecol. 59, 863-866.
- Loach, K. (1967). Shade tolerance in tree seedlings. 1. Leaf photosynthesis and respiration in plants raised under artificial shade. New Phytol. 66, 607-621.
- Lovvorn, R.L. (1945). The effect of defoliation soil fertility, temperature, and length of day on the growth of some perennial grasses. J. Am. Soc. Agro? 37, 370-382.
- Luckwill, L.C. (1960). The physiological relationships of root and shoot. Scint. hort. 14, 22-26.
- Magisted, O.C. (1925). The aluminium content of the soil solution and its relation to soil reaction and plant growth. Soil Sci. 20, 181-226.
- Matsumura, J. (1905). Index Plantarum Japonicum. Tokyo, Marizen.
- Maitre, R. (1953). Flore de L'Afrique du Nord, Paris.
- May, L.H. (1965). Quantitative studies of root development. 1. The influence of nutrient concentration. Aust. J. Biol. Sci. 18, 25-35.
- Mayer, A.M. and Poljakoff-Mayber, A. (1963). The germination of seeds. pp.194. A Pergamon Press Book, Macmillan Company, New York.

- McLean, F.H. and Gilbert, B.E. (1927). The relative aluminium tolerance of crop plants. *Soil Sci.* 20, 163-175.
- Milton, W.E.J. (1935). The buried viable seeds of enclosed and unenclosed Hilland. *Bull. Welsh Plant Breeding St. Ser. H. No. 14*, 58-84.
- Milton, W.E.J. (1939). The occurrence of buried viable seeds in soil at different elevations and on a salt marsh. *J. Ecol.* 27, 149-159.
- Milton, W.E.J. (1940). The effect of manuring, grazing and cutting on the yield, botanical and chemical composition of natural hill pastures. *J. Ecol.* 28, 328-356.
- Mitchell, K.J. (1956). Growth of pasture species under controlled environment. 1. Growth at various levels of constant temperature. *N.Z.J. Sci. Tech.* 38, 203, 216.
- Monsi, M. and Saeki, T. (1953). Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jap.J.Bot.* 14, 22-52.
- Moss, C.E. (1913). *Vegetation of the Peak District.* University Press, Cambridge.
- Muramoto, H., Hesketh, J. and El Sharkawy, M. (1965). Relationships among rate of leaf area development, photosynthetic rate, and rate of dry matter production among American cultivated cottons and other species. *Crop Sci.* 5, 163-166.
- Myerscough, P.J. and Whitehead, F.H. (1967). Comparative biology of Tussilago farfara L. Chamaenerion angustifolium (L.) Scop. Epilobium montanum L. and Epilobium adenocaulon Hauskin. *New Phytol.* 66, 785-823.
- Neiland, B.M. and Curtis, J.L. (1959). Differential responses to clipping of six prairie grasses in Wisconsin. *Ecology*, 37, No.2. 355-365.
- Newman, E.I. (1966). A method of estimating the total length of root in a sample. *J. Appl. Ecol.*, 3, 139-145.

- Nielsen, K.F. and Cunningham, R.K. (1964). The effect of soil temperature, form and level of nitrogen on growth, chemical composition of Italian ryegrass. Proc. Soil Sci. Soc. Am. 28, 213-218.
- Okali, D.U.U. (1972). Growth-rates of some west African forest tree seedlings in shade. Ann. Bot. 36, 953-959.
- Parker, K.W., and Sampson, A.W. (1930). Influence of leafage removal on anatomical structure of Stipa pulchra and Bromus hordeaceus. Pl. Physiol. 5, 543-553.
- Parlatore, F. (1948). Flora Italiana florenze Le Monnier.
- Pfitzenmyer, C.D. (1962). The autecology of Arrhenatherum elatius (L.) J. and Presl. and its inter-generic relationships. M.Sc. thesis, University of Wales.
- Piere, W.H., Pohlman, G.G. and McLlwaine, T.C. (1932). soluble aluminium studies. 1. The concentration of aluminium in the displaced soil solution of naturally acid soils. Soil Sci. 34, 145-160.
- Pigott, C.D. (1970). Soil formation and development on the Carboniferous Limestone of Derbyshire. 11. The relation of soil development to vegetation on the plateau near Coombs Dale, J. Ecol. Vol.58, 529-541.
- Ratcliff, D. (1961). Adaptation to habitat in a group of annual plants. J. Ecol. 49, 187-203.
- Read, D.J. (1963). Dieback disease in pines. Ph.D. thesis, University of Hull.
- Rorison, I.H. (1958). The effect of aluminium on Legume nutrition. In Nutrition of Legumes. (Ed. by E.H. Hallsworth), 43-61, London.
- Rorison, I.H. (1960a). Some experimental aspects of the calcicole-calcifuge problem. The effects of competition and mineral nutrition upon seedlings growth in the field. J. Ecol. 48, 585-599.

- Rorison, I.H. (1960b). The calcicole-calcifuge problem.
11. The effects of mineral nutrition on
seedling growth in solution Culture
J. Ecol. 48, 679-688.
- Rorison, I.H. (1964). A double shell plant growth cabinet.
New Phytol. 63, 358-362.
- Salisbury, E.J. (1929). The biological equipment of species
in relation to competition. J. Ecol. 17,
197-222.
- Salisbury, E.J. (1942). The Reproductive Capacity of Plants.
London. Bell. pp.244.
- Sharman, B.C. (1942). Developmental anatomy of the shoot of
Zea mays. L. Ann. Bot. N.S. 6, 245-282.
- Sharman, B.C. (1945). Leaf and bud initiation in the
Gramineae. Bot. Gaz. 106, 269-289.
- Shibles, R.M., and MacDonald, H.A. (1962). Photosynthetic
area and rate in relation to seedling vigor
of bird-shoot trefoil (Lotus corniculatus L.)
Crop Sci. 2, 299-302.
- Snaydon, R.W. and Bradshaw, A.D. (1961). Differential
responses to Calcium within the species
Festuca ovina L. New Phytol. 60, 219-234.
- Soper, K. (1957). Effects of changes in light and temperature
on roots of perennial ryegrass. (Lolium
perenne L.). N.Z. J.Sci.Tech. A.38, 783-792.
- Soper, K. and Mitchell, K.J. (1956). The developmental
anatomy of perennial ryegrass (Lolium
perenne L.) N.Z. J.Sci.Tech. 37 A, 484-504.
- Soriano, A. (1953). Estudios Sobre Germinacion. I. Rev.
Invest. Agri.(Buenos Aires) 7, 315-340.
- Sparling, J.H. (1967). The occurrence of Schoenus nigricans L.
in blanket bogs. 11. Experiments on the
growth of Schoenus nigricans L. under
controlled conditions. J. Ecol. 55, 15-31.
- Spray, M. (in preparation). An investigation of the factors
controlling species diversity in herbaceous
vegetation. Ph.D. thesis, University of
Sheffield.

- Stoddart, L.A. (1946). Some physical and chemical responses of Agropyron spicatum to herbage removal at various seasons. Utah Agri. Exp. Sta. Bul. 324.
- Sucharnkov, K.T. (1956). The physiology of immunity of some agricultural plants. Proc. 2nd Intern. Con. Plant Protect. Fernhurst Research Sta., Engl. 42-51. Academic Press, New York.
- Thompson, P.A. (1968). Germination of Species of Caryophyllaceae at low temperature in relation to geographical distribution. Nature, Lond. 217, 1156-1157.
- Thompson, P.A. (1970). Germination of species of Caryophyllaceae in relation to their geographical distribution in Europe. Ann. Bot. N.S. 34, 427-449.
- Thompson, P.S. (1970b) Changes in germination responses of Silene secundiflora Otth. in relation to the climate of its habitat. Physiologie Pl. 23, 739-746.
- Toole, E.H. and Toole, U.K. (1939). Germination of some Brassica types at different temperatures, Proc. Int. Seed Test. Ass. 11, 51-56.
- Tripathi, R.S. and Harper, J.P. (1973). The comparative biology of Agropyron repens (L.) Beauv. and A. caninum (L.) Beauv. 1. The growth of mixed populations established from tillers and from seeds. J. Ecol. 61, 353-368.
- Troughton, A. (1956). Cessation of tillering in young grass plants, Nature, 176, 514.
- Vaartaja, O. (1952). Forest humus quality and light conditions as factors influencing damping-off. Phytopathology, 42, 501-506.
- Vaartaja, O. (1953). Disease caused by weak parasites associated with shade in seedbeds. Biomon. Prog. Rep. Dir. Forest Biol., Ottawa, 9, 3-4.
- Vaartaja, O. and Cran, H.W. (1956). Damping-off pathogens of conifers and of caragana in Saskatchewan. Phytopathology, 46, 391-397.
- Vaartaja, O. (1962). The relationship of fungi to survival of shade tree seedlings. Ecology, 43, 547-549.

- Voisin, A. (1959). Grass Productivity. London.
- Voisin, A. (1960). Better Grassland Swards. Lond.
- Wagner, R.H. (1967). Application of a thermal gradient bar to the study of germination patterns in successional herbs. American Midland Naturalist, 77, 86-92.
- Wallace, T. (1951). The diagnosis of mineral deficiencies in plants by visual symptoms: a colour atlas and guide. London.
- Watson, D.J. (1952). The physiological basis of variation in yield. Advanc. Agron. 4, 101-145.
- Watson, D.J. (1956). Leaf growth in relation to crop yield. The growth of leaves. (Ed. by F.L. Milthorpe), pp.178-191. Butterworths. London.
- Watt, A.S. (1955). Bracken versus heather, a study in plant physiology. J. Ecol. 43, 490-506.
- Weaver, J.E. (1930). Underground plant development in its relation to grazing. Ecology, 11, 543-557.
- Wellbank, P.J. (1960). Toxin production from Agropyron repens. The Biology of Weeds. (Ed. by J.L. Harper). pp.158-164. Blackwell Scientific Publications, Oxford.
- Wellbank, P.J. (1963). Toxin production during decay of Agropyron repens (Couchgrass) and other species. Weed Res. 3, 205-214.
- Went, F.W. (1957). The experimental control of plant growth. Chronica bot. 17.
- Wilkins, D.A. (1957). A technique for the measurement of lead tolerance in Plants. Nature, London, 180,37.
- Wilson, D.B. and McGuine, W.S. (1961). Effect of clipping and nitrogen on competition between three pasture species. Canad. J. Plan. Sci. 41, 631-643.

APPENDICES

Appendix 1.

MEAN SHOOT HEIGHT AT FOUR TEMPERATURE TREATMENTS OF ARRHENATHERUM ELATIUS, AGROSTIS TENUIS, FESTUCA OVINA,

DESCHAMPSIA FLEXUOSA AND ZERNA ERECTA, AT FOUR HARVESTS.

95% CONFIDENCE LIMITS ARE INCLUDED.

Species	Temp.	Parameter	1st harvest	2nd harvest	3rd harvest	4th harvest	Species	Temp.	Parameter	1st harvest	2nd harvest	3rd harvest	4th harvest
Arrhenatherum Elatius	15°C	Shoot height	11.72 [±] 1.81	14.54 [±] 0.34	21.98 [±] 5.61	20.71 [±] 6.48	Deschampsia Flexuosa	15°C	Shoot height	4.57 [±] 0.50	6.28 [±] 0.84	7.14 [±] 0.90	9.15 [±] 1.31
	20°C	Shoot height	18.42 [±] 2.14	27.54 [±] 4.01	35.71 [±] 4.72	38.14 [±] 4.36		20°C	Shoot height	5.50 [±] 0.68	10.14 [±] 0.34	10.42 [±] 1.22	11.61 [±] 1.56
	25°C	Shoot height	21.82 [±] 1.42	32.12 [±] 1.64	42.24 [±] 4.14	63.72 [±] 4.84		25°C	Shoot height	5.12 [±] 0.34	6.71 [±] 0.68	11.00 [±] 0.90	12.35 [±] 0.68
	30°C	Shoot height	13.55 [±] 1.42	23.21 [±] 0.56	28.84 [±] 6.62	41.51 [±] 4.31		30°C	Shoot height	3.14 [±] 0.48	6.57 [±] 1.02	5.09 [±] 1.03	5.75 [±] 0.97
Agrostis Tenuis	15°C	Shoot height	3.28 [±] 0.432	4.42 [±] 0.96	8.21 [±] 0.81	16.14 [±] 2.87	Zerna Erecta	15°C	Shoot height	9.07 [±] 1.92	12.14 [±] 1.46	14.28 [±] 2.34	17.00 [±] 1.04
	20°C	Shoot height	7.20 [±] 0.82	14.52 [±] 1.73	21.28 [±] 4.31	29.31 [±] 5.85		20°C	Shoot height	12.85 [±] 1.78	17.7 [±] 1.12	25.28 [±] 1.24	32.91 [±] 3.66
	25°C	Shoot height	9.45 [±] 0.68	16.64 [±] 0.87	22.09 [±] 1.31	30.55 [±] 5.05		25°C	Shoot height	13.57 [±] 1.14	21.41 [±] 1.34	35.00 [±] 3.66	41.57 [±] 2.73
	30°C	Shoot height	7.00 [±] 1.34	14.44 [±] 1.83	19.42 [±] 3.56	20.50 [±] 3.80		30°C	Shoot height	13.20 [±] 2.39	15.00 [±] 2.75	26.81 [±] 2.85	25.71 [±] 2.85
Festuca Ovina	15°C	Shoot height	3.21 [±] 0.56	3.44 [±] 0.54	3.81 [±] 0.81	5.71 [±] 0.41							
	20°C	Shoot height	5.58 [±] 0.68	7.61 [±] 1.84	9.71 [±] 2.60	14.64 [±] 2.41							
	25°C	Shoot height	8.08 [±] 0.66	10.77 [±] 0.488	13.0 [±] 1.30	19.58 [±] 0.66							
	30°C	Shoot height	6.64 [±] 0.90	8.07 [±] 1.18	11.45 [±] 1.40	13.60 [±] 1.22							

Appendix 2.

FITTED LEAF AREA RATIOS AND FITTED UNIT LEAF RATES FOR ARRHENATHERUM ELATIUS, AGROSTIS TENUIS, FESTUCA OVINA, DESCHAMPSIA FLEXUOSA

AND ZERNA ERECTA, AT FOUR HARVESTS AND AT FOUR TEMPERATURE TREATMENTS.

VALUES FOR STANDARD ERROR ARE INCLUDED.

	Temperature	LEAF AREA RATIO ($m^2 g^{-1} \times 10^2$)				UNIT LEAF RATE ($g m^{-2} week^{-1}$)			
		2 weeks	3 weeks	4 weeks	5 weeks	2 weeks	3 weeks	4 weeks	5 weeks
<i>Arrhenatherum Elatius</i>	15°C	2.11 ± 6.20	2.19 ± 0.18	2.35 ± 0.19	1.27 ± 0.123	46.99 ± 3.78	45.24 ± 3.83	42.06 ± 4.28	77.91 ± 9.88
	20°C	2.38 ± 0.13	2.03 ± 0.16	1.34 ± 0.07	1.29 ± 0.07	97.88 ± 10.37	65.75 ± 4.67	72.51 ± 7.57	96.33 ± 20.68
	25°C	2.38 ± 0.20	1.34 ± 0.12	1.53 ± 0.14	1.24 ± 0.10	126.22 ± 16.00	104.3 ± 8.95	55.11 ± 11.43	106.63 ± 35.83
	30°C	2.41 ± 0.23	1.09 ± 0.116	1.38 ± 0.14	1.34 ± 0.13	111.97 ± 15.85	94.51 ± 12.56	46.68 ± 12.50	114.70 ± 39.03
<i>Agrostis Tenuis</i>	15°C	2.50 ± 0.01	1.80 ± 0.08	1.70 ± 0.08	1.43 ± 0.06	42.79 ± 9.38	87.64 ± 5.40	81.91 ± 6.29	34.64 ± 16.97
	20°C	2.89 ± 0.34	2.55 ± 0.22	2.36 ± 0.21	2.27 ± 0.26	79.15 ± 9.17	70.41 ± 7.00	55.51 ± 5.28	36.07 ± 8.33
	25°C	2.85 ± 0.13	2.69 ± 0.14	2.70 ± 0.14	1.49 ± 0.06	85.52 ± 7.85	55.70 ± 2.59	44.93 ± 4.63	106.51 ± 18.61
	30°C	1.57 ± 0.18	1.36 ± 0.18	1.66 ± 0.33	1.39 ± 0.16	131.30 ± 18.73	118.05 ± 17.69	43.35 ± 6.28	50.36 ± 17.48
<i>Festuca Ovina</i>	15°C	2.26 ± 0.16	2.45 ± 0.22	1.23 ± 0.11	0.83 ± 0.06	30.51 ± 5.67	37.67 ± 3.85	93.3 ± 9.52	166.28 ± 16.0
	20°C	1.59 ± 0.12	1.26 ± 0.08	1.35 ± 0.09	1.97 ± 0.15	92.77 ± 7.06	93.12 ± 11.85	64.23 ± 5.15	28.64 ± 12.08
	25°C	3.00 ± 0.16	1.52 ± 0.08	1.76 ± 0.09	1.09 ± 0.05	43.30 ± 7.97	55.20 ± 5.29	60.73 ± 5.81	178.6 ± 25.93
	30°C	1.36 ± 0.17	1.42 ± 0.15	1.29 ± 0.24	1.35 ± 0.17	60.39 ± 6.13	57.85 ± 6.58	36.01 ± 5.21	61.03 ± 11.36
<i>Deschampsia Flexuosa</i>	15°C	1.05 ± 0.10	0.75 ± 0.06	1.00 ± 0.08	0.89 ± 0.08	89.78 ± 7.78	125.18 ± 10.83	94.64 ± 9.04	106.42 ± 11.85
	20°C	1.68 ± 0.15	1.81 ± 0.17	0.99 ± 0.09	1.24 ± 0.11	90.58 ± 9.34	71.98 ± 7.33	109.64 ± 10.93	70.76 ± 11.64
	25°C	1.47 ± 0.12	1.42 ± 0.13	2.07 ± 0.20	1.33 ± 0.11	68.11 ± 6.07	70.63 ± 7.26	48.34 ± 5.01	75.09 ± 6.87
	30°C	1.35 ± 0.16	1.09 ± 0.08	0.89 ± 0.07	0.72 ± 0.09	48.25 ± 6.04	59.4 ± 6.66	73.18 ± 9.92	94.12 ± 16.39
<i>Zerna Erecta</i>	15°C	1.59 ± 0.09	1.26 ± 0.04	1.00 ± 0.63	0.79 ± 0.04	45.23 ± 3.26	57.10 ± 3.91	72.07 ± 5.69	90.98 ± 9.03
	20°C	1.61 ± 0.08	1.56 ± 0.05	1.50 ± 0.04	1.45 ± 0.07	68.64 ± 3.22	66.98 ± 2.66	69.41 ± 3.18	71.93 ± 4.56
	25°C	1.79 ± 0.07	1.56 ± 0.05	1.31 ± 0.04	1.07 ± 0.04	73.67 ± 6.23	70.42 ± 3.48	66.64 ± 3.81	60.90 ± 9.25
	30°C	1.59 ± 0.12	1.45 ± 0.08	1.32 ± 0.08	1.19 ± 0.09	69.86 ± 7.74	63.33 ± 6.17	55.05 ± 4.92	44.62 ± 13.58

APPENDIX 3.

DISTRIBUTION OF THE DIFFERENT GROWTH
FORMS OF *Arrhenatherum elatius* IN THE FIELD.

From the experimental evidence on page 138 it may be suggested that *Arrhenatherum elatius* has evolved prostrate growth forms which are comparatively resistant to defoliation. In an additional experiment, an attempt was made to determine whether the prostrate growth forms are associated with habitats subjected to grazing.

Materials and methods.

Populations were raised from seeds collected from Lathkilldale (recently derelict pasture), Norton Sports field (ungrazed wasteland), from a roadside (ungrazed but probably mown once every growing season) and from plants in an experimental garden, but originally from ungrazed wasteland at Hooper Hall. 50 seedlings from each of the above mentioned populations were grown singly in sand culture each in an 18 cm diameter plastic flower pot. The experiment was set up in a heated greenhouse. The plants were watered alternately every three days with 100 ml. of Hewitt solution and 100 ml. of distilled water.

Results

After five weeks growth forms conforming to the three classes recognised previously (very erect, intermediate and very prostrate) could be recognised. Each type of growth form was found to be represented, although at different

percentages, in all four populations. The percentages of each form in each population are presented in Table 36.

Table 36.

% of the different forms of Arrhenatherum elatius in populations raised from seeds collected from contrasting habitats.

Growth form	% in population from Lathkilldale	% in population from Roadside	% in population from Experimental Garden.	% in population from Norton Sports Field.
Very prostrate	20%	14%	10%	16%
Intermediate	10%	6%	8%	12%
Very erect	70%	80%	82%	72%

It appears that the prostrate form of Arrhenatherum elatius, shown to be tolerant of defoliation in experiment 'C' page 136-141. is widely distributed and is not restricted to grazed or mown habitats. It is possible that the populations sampled in these contrasting habitats had been grazed or mown in the past and that the prostrate plants present in these seed collections are relics from a prexistent short turf.