FUNCTIONAL ANALYSIS OF EUROPEAN WETLAND VEGETATION

A thesis submitted to the University of Glasgow for the degree of
Doctor of Philosophy in the Faculty of Science

by

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ABSTRACT

Riverine marginal wetland vegetation was studied at thirty-two hydrogeomorphic units of sites used by the European Community project "Functional Analysis of European Wetland Ecosystems", these units were situated in England, France, Ireland and Spain. Fieldwork was carried out between May 1991 and August 1993. The aim of the work was to develop a system of analysis of wetland vegetation using functional attributes which could be used to predict the effect of anthropogenic perturbation. Grime's C-S-D established-phase strategy theory was used as the framework for this study.

Analysis of plant species abundance, using DCA (detrended correspondence analysis) and PCA (principal components analysis), revealed the extent of variation in the plant species composition between the hydrogeomorphic units. A majority of the hydrogeomorphic units could be assigned to CORINE biotope categories (the European Community categorisation system of sites of nature conservation importance); most sites were water fringe vegetation (53) or humid grassland (37).

Eight morphological traits were measured from one hundred and forty-four common plant populations from the hydrogeomorphic units. Non-hierarchical classification of populations by traits was carried out using sum of squares and centroid dissimilarity algorithms. It was determined that the most efficient classification was into three groups. Each of these three groups was associated with different parts of the C-S-D strategy space. The results strongly suggested that morphological traits can be used to classify plants into functional groups which have differing ecological properties.

Using twelve traits, linear and multiple discriminant analysis were used to distinguish objectively between populations with *a priori*-selected strategies determined from the work of Grime. Competitive and stress-tolerant populations were found to be significantly different using twelve traits. Stepwise multiple regression identified the important traits for predicting competitive ability (C) and stress tolerance (S). Significant predictors of the C-strategy were height of plant and the dry weight of leaves; and of the S strategy, the dry weight of stems and the weight per seed. Use of these predictive equations permitted calculation of C and S for the one hundred and forty-four populations that were studied. The mean C and S scores of the populations present in each hydrogeomorphic unit were used to determine the functional vegetation type (FVT) in terms of competitiveness (CFVT) and stress-tolerance (SFVT). CFVT and SFVT were inversely correlated ($r = -0.73$, $P<0.001$).

A greenhouse experiment was carried out to determine the effect of competition (phytometer), disturbance (cutting) and stress (saturated soil conditions) on the morphology of six common wetland plants. The stress treatment was too weak to have much effect on the morphology of the species. The ranking of the species in terms of C and D (disturbance-tolerance) showed a degree of similarity with the strategy designation of Grime. The competitive ability of the test species, using the phytometry method, was significantly related to the field determined C score ($r = 0.80$, $P<0.05$).

Eleven state variables, defined as measurable variables of biotic communities which have a particular range of values for each type of vegetational community, were measured in the studied wetlands. Using PCA, the major gradient in state variables was most strongly correlated to biomass. However, using CCA (canonical correspondence analysis), constraining the axes to be linear combinations of CFVT and SFVT, a different gradient in state variables was identified. This gradient was related to a high canopy, large stem area with great distance between stems and dominated by a few species at high CFVT-low SFVT values and high stem density, species richness and density of reproductive structures at low CFVT-high SFVT values. Using stepwise multiple regression, state variables could significantly predict CFVT ($P<0.0001$).

Common CORINE biotopes were related to the CCA ordination diagram of FVT and state-variables. 3 biotopes (humid grassland, mesophile grassland and reed beds) were related to certain areas of the CFVT-SFVT gradient. Sedge beds ranged across much of the gradient, this could be due to the taxonomic diversity of the biotope. The results suggested a certain degree of comparability between the strategy, state-variable and phytosociological biotope units in the studied wetlands.

Four field experiments were set up to determine if the C score for populations and the CFVT score for communities (defined by state variables) responded to changes in stress and disturbance in the direction predicted by the C-S-D strategy model. In the seven cases where the C score was significantly different between treatments, the direction of change in the C score was the same as predicted by the C-S-D model. CFVT responded less to perturbations than C score, but when significant differences were found they were in the predicted direction. Significant differences in CFVT were found only in situations where there was a significant difference in C score. It was proposed that the C index represents a potentially useful framework for a predictive model of wetland vegetation.

A five point critique of the work is presented relating to; (1) the use of only above-ground morphology, (2) the use of morphological traits (3) the lack of disturbance tolerance indices (4) the short length of the experiments, and (5) the lack of use of environmental data. An analysis was carried out relating C scores to Ellenberg indicator values for species for nitrogen (N) and water class (F). No trends with C were identified suggesting that variation in C could be due to a complex set of environmental parameters.

It was proposed that competitive indices could potentially be valuable tools for land planners for the assessment and prediction of change in a wetland model. Competitive indices could be simplified into an information-rich, relational value which could down-load into impact statements about a set of wetland functions. Such a model would have general applicability as predictions could be applied to all possible types of environmental perturbation.

Two topological model systems, coupled with scientific rationale from this work, were proposed, one for wetland assessment and the other for wetland impact prediction.

DECLARATION

I hereby declare that this thesis is composed of work carried out by myself unless otherwise acknowledged and cited and that the thesis is of my own composition. The research was carried out in the period May 1991 to February 1994. This dissertation has not, in whole or part, been previously presented for any other degree.

ACKNOWLEDGEMENTS

This work was only possible with the help of a large number of people.
I would like to thank all the members of the "Functional Analysis of European Wetland Ecosystem" project, with many of whom good times were shared. Some deserve special mention, Dr. B. Clement and Isabelle Mouton (Univ. of Rennes, France) for helping and teaching me about plant identification and biotope designation, the Utrecht team (Netherlands) (Drs. Mark van Oorschot, Drs. Marianne van der Peijl and Dr. Jos Verhoeven) who were constantly professional and friendly and set up the wheely bin and fertilisation experiment which I used, David Hogan (Univ. Exeter, U.K.) for his patience and organisational skills, Allous Hoyer (University of Amsterdam, The Netherlands) for hard working days and amusing nights, Maximo Florin and Carmella Guerro for hospitality and introducing me to the Spanish study area, and Dr. Emmanuel Castella (University of Geneva, Switzerland) for discussions on the functional approach and multivariate methods.
I would like to thank all those who assisted me in the fieldwork; Aileen Adam, Magdi Ali, Susan Marrs, Anna Milligan, Karin Rossnagel, Andrew Spink and especially Vicky Abernethy with whom most of my field work in 92 and 93 was carried out with. I am also indebted to Kieth Watson who generously spent time helping with identification of difficult species.
Many of the ideas in this thesis arose from discussions with colleagues, in particular Magdi Ali, Susan Marrs, Ricqui Sabbatini and Andrew Spink. I am indebted to their insight and imagination. I am also indebted to Dr. B. Huntley (University of Durham, UK) who introduced and taught me about multivariate methods of analysis during my M.Sc and to Dr James Currall (University of Glasgow) who, besides being a mountain of useful information on mathematical analytical methods, always had a supply of amusing banter and coffee.
Over 60,000 miles were travelled in the course of this work. I would like to thank Air Lingus, Air France, Air UK, British Airways, British Midland, Iberia, KLM and Viva Air for relatively untroubled flights; and Arnold Clark, Avis and Budget for hire cars. Most of the reservations were made very efficiently by the members of Portman Travel at the University. License numbers IPMISC/13-15/91, for transportation of foreign plant samples back to the UK., were supplied by the Dept. of Agriculture and Fisheries for Scotland. I would also like to thank all the people who we have stayed with especially Seamus and Celine Grennan from Shannon Bridge in the Irish Republic who were always open-hearted and over-fed us, and the people of the house in Marzy of the Societe Ornithologique du Bec d'Allier who made us most welcome.
I have also received pratical support from the people at Glasgow University, Garscube field station, in particular Aileen, Mags, Bob, Jamie and Jim.
Most of all I would like to thank my supervisors at Glasgow University. Dr. Kevin Murphy (Botany) has been constantly supportive of me and my ideas throughout the last few years, without this support much less would have been achieved. Dr. I. Pulford and Dr. H. Flowers (Chemistry) advised me on the chemical aspects in the thesis. It was always a comfort to know that my personal supervisor, Prof. R. Cogdell, was available for informal chats and advice when necessary
On a more personal note, I would like to express my gratitude to Susan Marrs, and to my parents whose support has enabled me to have the privilege of 7 years of University education.

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INTRODUCTION

1.1 BACKGROUND TO THE "FUNCTIONAL ANALYSIS OF EUROPEAN WETLAND ECOSYSTEMS" PROJECT

1.1.1 Project organisation, aims and objectives

"Functional Analysis of European Wetland Ecosystems" (FAEWE) was a European Community research project funded by the "Science and Technology for Environmental Protection" (STEP) programme of DG XII, EC.. Funding for stage I was granted by the EC. from May 1991 to May 1994. The Chairperson of the project was Dr E. Maltby from the Department of Geography, University of Exeter. The project consisted of a multidisiplinary team from 9 scientific institutions from 6 European countries (Table 1.1).

The objective of the FAEWE project was "to develop science-based procedures for evaluating the functional characteristics of European wetland ecosystems" (Anon. 1992). The project methodology was summarised by Hogan & Maltby (1990):

"Procedures for the functional analysis of European wetlands will be developed by means of the investigation of the key processes operating in wetland ecosystems, their linkage to functioning and appropriate dynamic and predictive system modelling. Particular emphasis will be placed on the effects of ecosystem perturbation by anthropogenic activities such as drainage, altered flooding and ground water regime, fertiliser application and sedimentation. The work will be both field-based and laboratory-based and will involve process studies, modelling and model testing as well as the development of functional analysis systems".

The project end-product was stated to be a model system for the analysis of the effect of impacts on European wetland ecosystems, for a set of functions, using scientifically-determined predictors. It was proposed that the end-users of the model system would be land management organisations: the end-product was aimed to be used by a fieldworker with general scientific training.

Four institutions were involved with the work on wetland vegetation. Topics covered were: phytosociology (University of Rennes, France), productivity and nutrient cycling (University of Utrecht, The Netherlands) plant pattern and adaptation (University of Madrid (Computense), Spain) and trait and strategy analysis (University of Glasgow, UK). The work on trait and strategy analysis was carried out at Glasgow University by J.M. Hills with supervision from Dr. K.J. Murphy (Dept. of Botany), Dr. I. Pulford and Dr. H. Flowers (Dept. of Agricultural Chemistry).

Table 1.1 The Principal Investigators, institutions and research topics of members of the "Functional Analysis of European Wetland Vegetation" project.

Principle Investigator	**Institution**	**Research area**
B. Clement	University of Rennes, France	vegetation-phytosociology
B. Englen	University of Amsterdam, Netherlands	hydrology
R. Llamas Madurga & J. Sanz Donaire	University of Madrid (Autonomous & Computense), Spain	hydrology vegetation-adaptation
E. Maltby (Chairperson)	University of Exeter, UK.	soil nutrients
K. Murphy	University of Glasgow, UK.	vegetation - strategies
P. Obrdlik	WWF - Auen institute, Germany	invertebrates
J. Ryan	Irish Wildlife Service, Repbublic of Ireland	birds
J. Tellam	University of Birmingham, UK.	hydrogeology
J. Verhoeven	University of Utrecht, Netherlands.	vegetation - nutrient dynamics

1.1.2 The Glasgow University sub-project

The aim of the Glasgow sub-project was to develop a system of analysis of wetland vegetational communities using functional attributes which could be used to predict the effect of natural or anthropogenic impacts. It was envisaged that the end-product of this work would be suitable for use by a competent, but non-specialist scientist. To achieve this aim, three sequential objectives were identified:

1. To use community strategy analysis to classify the plant communities of European riverine wetlands into functional vegetation types.
2. To determine the potential of functional vegetation types as indicators of environmental perturbation.
3. To assess the value of the functional approach as a system for predicting the effect of environmental impact in wetland ecosystems.

In the Introduction (Chapter 1) a brief account is given of the relevant ecology of wetlands (definition, conservation issues and effect of flooding on soils and plants) and methods of describing vegetational communities. A more in depth analysis of survival strategy theory and its problems is made. Finally, a site summary and a description of studied sites by species is made.

In Chapter 2 the suitability of morphological plant traits for defining functional groups in the studied wetland communities, and the relationship of the functional groups to the C-S-D model of Grime (1979) is assessed. Chapter 3 describes a multivariate methodology to determine the strategy of plant populations and communities in terms of stress-tolerance and competitive ability. Chapter 4 uses data collected from the field and greenhouse experiments to search for general trends in biomass allocation and leaf morphology relationships in wetland plants. Chapter 5 introduces the idea of state-variables of communities, the relationship of these state-variables to community strategy scores and CORINE phytosociological units is determined. Chapter 6 describes four field experiments in which anthropogenic perturbations were imposed on wetland plant communities. The changes in indices of competitiveness are described and the degree to which the observed changes were similar to the predicted changes is discussed. Chapter 7 starts with a critique of the work described in the previous chapters and suggests further research priorities, following this, the potential of strategy indices as indicators and predictors of environmental change are discussed. Finally, the value of the strategies to the FAEWE wetland model is discussed and a model system proposed.

1.2 BACKGROUND TO WETLAND ECOSYSTEMS

1.2.1 Geographical extent, definition and conservation

Wetland ecosystems cover an area totalling 8,558,000km^2 (Williams 1990), representing 6% of the earth's land surface (Maltby 1988). All wetland ecosystems share two common characteristics. Firstly, they have an abundant and readily available water supply at sometime during the year, and secondly, the soil has a hostile chemical environment for the growth of plants (Etherington 1983). Beyond these two similarities a large amount of natural and anthropogenic variation is apparent within this ecosystem type. Attempts at a more precise definition of wetlands have been made, although attempting to delimit highly variable ecological units is notoriously difficult.

The "Convention on Wetlands of International Importance especially as Wildfowl Habitats" (also known as the Ramsar Convention), held in Iran (1971), defined wetlands as, "areas of marsh, fen, peat land or water whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, inundating areas of marine water the depth at which at low tide does not exceed six meters" (UNESCO 1971). The wide range of this definition was a consequence of the scope of the Ramsar Convention (Navid 1988). Zolta & Pollett (1983) included less variety of wet environments in their definition of Canadian wetlands: wetlands are "areas where wet soils are prevalent, having a water table near or above the mineral soil for most of the thawed season, supporting a hydrophilic vegetation and pools of open water less than two meters deep" (Zolta & Pollett 1983). Holland, Whigham & Gopal (1990) considered wetlands to be ecotones (i.e. a transitional zone between vegetation types, Risser 1990). They used the following definition: "lands transitional between terrestrial and aquatic systems where the water table is at or near the surface or the land is covered by shallow water". The I.B.P. (International Biological Programme) defined wetlands as ecosystems characterised by having emergent vegetation. Clearly, wetlands have been defined in different ways depending on the type of study and geographical area of the work. This study will utilise the relatively simple definition of wetlands, proposed by Williams (1990b) as, "lands with soil that periodically floods". Precise definition of wetlands is becoming more than just an academic exercise and is "now assuming legal importance" in land disputes (Gosselink & Maltby 1990).

Haslam (1973) suggested that in the British Isles wetlands are the "most threatened and vulnerable" of habitats. Throughout the world destruction of wetland environments has been taking place since before the present century (Maltby 1988). One of the statutes of the French Revolution was the formal abolition of all marshes in France (Purseglove 1991). Wet areas were considered to be bad for the populace and consequently drainage, for agricultural development and disease eradication, was considered to be public spirited (Gosselink & Maltby 1990). The rate of destruction of wetlands today is alarming. For example, in Ireland, 80,000 hectares of bog have been drained since 1946, and in Brittany (France) 40% of the coastal wetlands have disappeared (Maltby 1988). Bottom-land hardwood forest in the USA, found particularly around the Mississippi, annually lost 1% of its area between 1960 and 1975 (Abernethy & Turner 1987). Only 25% of the 24,000 hectares of mangrove swamps remain in Puerto Rico (Maltby 1988); the Philippines have less than half of their mangrove swamps remaining (Jara 1984, in Gosselink & Maltby 1990). In Central and South America nearly one fifth of internationally important wetlands are threatened with drainage. In view of the diminishing area of wetland ecosystem on the earth, management and conservation must be a priority.

Many wetlands have been managed, at least intermittently, for many centuries (Haslam 1973b). However the pressures imposed on wetlands today are greater than ever. Wetland plant communities commonly exhibit a "rather distinctive" elevational range in relation to the water table (Busch & Lewis 1984, Cook 1968, Holland *et al.* 1990), which is the main factor controlling many aspects of wetland vegetation (Haslam 1973b). Each community has a characteristic mean water table and a limited tolerance range (Spence 1964). Such an altitudinal zonation of plant communities with water table means that changes in the water regime can have major effects on the composition and functioning of the community. Much of the vulnerability of the wetland ecosystem to changes in the hydrological regime is a result of the existence of plant community zonations, which can be differentiated by only 1-2cm of water table, thus, "small interferences can have....enormously magnified biological consequences" (Etherington 1983). As a result, optimal management requires an intimate knowledge of the individual wetland system to avoid undue damage to the wetland habitat.

Due to their vulnerable nature, wetlands are the only ecosystems to be singled out for special international protection. The Ramsar Convention, a two tier conservation policy for wetlands, was implemented in 1975. This treaty involved firstly, an international advisory system to aid countries with national policy decisions, and secondly, a special list of "Wetlands of International Importance". By July 1986, forty contracting parties had signed the convention including France, Ireland, Spain and the United Kingdom, and 335 sites covering 20,000,000 hectares world-wide had been designated. Although problems such as lack of administrative provision and dependence upon moral rather than legal obligations of signatories have been noted, Ramsar is considered as an "important conservation tool" (Navid 1988).

Other wetland conservation initiatives have been apparent. As a follow-on from the International Biological Programme a list of wetlands, code named AQUA, with special limnological interest was drawn up. A programme, termed EDWIN, was set up by the World Wildlife Fund (WWF) at Leiden University (Netherlands) to create information on wetland development schemes, to evaluate the ecological soundness, and to propose recommendations to limit ecological damage. International co-operation has been growing with conferences such as the Heiligenhafen International Conference on the Conservation of Wetlands. Wetlands are also repeatedly mentioned in the World Conservation Strategy (IUCN-UNEP-WWF 1980). However, protection of the sites is only the first stage of the maintenance of wetlands. In the light of the anthropogenic pressures on wetlands throughout the modern world, management must be a priority. As Etherington (1983) warns, "a fence and time may convert the finest pond into a willow scrub".

1.2.2 The effect of waterlogging on soil and plants

Flooding has been defined as "the environmental situation when the water table rises above the soil level and is submerging a part of the shoot or the total shoot" (Ernst 1990). The impact of waterlogging on the plants and the soil will depend on the duration, intensity and the frequency of flooding. It is facile to regard flooding as a single stress to plants, as it has a set of effects on the soil environment (Davy, Noble & Oliver 1990). If no replacement of oxygen occurs following the onset of waterlogging, the remaining oxygen in the soil will generally be utilised within one day (Ernst 1990). Replenishment of the oxygen of the waterlogged soil is negligible as oxygen diffuses 10,000 times more slowly into waterlogged soil than air filled soil pores (Greenwood 1961). Consequently, with oxygen deficiency, the redox potential (a measure of the reduction state of the medium, quoted in millivolts, mV) of the soil will decrease and hypoxic (Davy *et al.* 1990) or anoxic (Fagerstedt & Crawford 1987) conditions will occur. This fall in oxygen concentration will cause reduction and changes in some soil chemicals (Ernst 1990) and redistribution of them between the soil reservoirs (Iu, Pulford & Duncan 1982).

With a lowered redox potential nitrate (NO_3^-) will be reduced to nitrous oxide (N_20) and nitrogen gas (N_2). Ernst (1990) suggested that the reservoir of nitrate in the soil would be depleted by the third day after the onset of waterlogging. Higher concentrations of nitrate reductase have been found in salt-marsh plants lower down the moisture gradient of a marsh, the nitrate content of the leaves was similar across the moisture gradient (Jeffries 1977, in Ernst 1990). The concentration and availability of nitrogen can be major determinants of the type of plant community (Verhoeven & Schmitz 1991).

Manganese (IV) is reduced to manganese (II), which is more readily available to plants, at a lower redox potential. Further decrease in redox potential with waterlogging causes ferric iron (Fe III) to reduce to the more soluble ferrous iron (Fe II). However, in close proximity to roots reddish/brown deposits of ferric hydroxide are produced (Ernst 1990). This ferric hydroxide plaque prevents phosphate uptake (PO_4^{3-}) and inhibits much of the absorption of iron into the plant. However, the plant tissue concentrations of iron and manganese increase with decreasing redox potential, which can affect chlorophyll synthesis (Ernst 1990).

At extremely low soil redox potential (-75 to -150 mV), found in permanently waterlogged soils, sulphate (SO_4^{2-}) is reduced to sulphide (S^{2-}). Although the iron plaque can cause precipitation of iron sulphide (FeS), once the iron precipitates, the concentration of sulphur in the plant tissue increases. High tissue sulphur concentration can limit the cellular availability of metals (Ernst 1990).

Waterlogging has a marked effect on the soil conditions, producing an "extremely severe" environment for plant growth (Heathcote, Davis & Etherington 1987). However, representatives of all the major groups of higher plants have retained the ability to inhabit flooded, hypoxic soils successfully (Davy *et al.* 1990). Wetland plants must consequently have certain attributes that enable them to cope with flooding which their terrestrial counterparts do not exhibit.

1.2.3 Wetland plants - variation and attributes

Different wetland species have a different tolerance to waterlogging. Some species e.g. *Carex elata* are found in stagnant water, whereas others are situated where there is ground-water flow e.g. *Cladium mariscus* (Haslam 1973b). Voesenek, Blom & Poowels (1988) concluded that three *Rumex* species (*R. acetosa*, *R. crispus* and *R. palustris*) had a different degree of flooding tolerance and this corresponded to their distribution in the field. The waterlogging tolerance of two species (*Epilobium hirsutum* and *Chamerion angustifolium*) were compared by Etherington (1984). He found that the speed of morphological adaptations to waterlogging differed between the two species. The difference in the tolerance to waterlogging of wetland species was the underlying cause of the highly zonal vegetation found in aquatic to terrestrial gradients (Spence 1964, Busch & Lewis 1984).

Variation in the flooding tolerance can be found in different populations of the same species e.g. barley cultivars (*Hordeum vulgare*) (Fagerstedt & Crawford 1987), *Nyssa sylvatica* (Keely 1979), *Festuca rubra* and *Agrostis stolonifera* (Davies & Singh 1983), *Carex flacca* (Heathcote *et al.* 1987) and *Veronica peregrina* (Linhart & Baker 1973). Thus, some wetland species display a degree of phenotypic plasticity in their ability to cope with the stresses of waterlogging (Heathcote *et al.* 1987).

Three theories have been put forward to explain the tolerance of these wetland plants to waterlogging (Ernst 1990):

1. Oxygen transport theory - when waterlogged conditions occur the plant structurally adapts so as to maintain the levels of oxygen in the root system suitable for aerobic metabolism. This is achieved by the production of an oxygen transport system within the tissues of the plant, which means that anoxia can be wholly or partly avoided in the plant.
2. Ion toxicity theory - the species have genetically adapted to tolerate the high levels of ionic concentrations (e.g. Mn, Fe) found in the waterlogged soil environment.
3. Metabolic adaptation theory - the plant avoids the production of ethanol by the formation of alternative organic acid end-products to the glycolosis metabolic pathway.

The attributes required by each of the above three theories for a plant to become tolerant have been found in the field or experimentally induced. Tolerance of waterlogged conditions by plants would thus appear to entail utilisation of one or more of the above.

To increase the flow of oxygen from the leaf to the root of a waterlogged plant special transporting vessels called aerenchyma can be found. Aerenchyma is tissue which contains large air-filled spaces (lacunae), formed from either schizogeny of intracellular spaces (e.g. in *Filipendula ulmaria*) or lysigeny of cells (e.g. *Juncus effusus*) (Smirnoff & Crawford 1983).. Aerenchyma is commonly found in wetland species to differing degrees of extent (Teal & Kanvisher 1966). Justin & Armstrong (1987) surveyed the aerenchyma and flooding tolerance of 91 plant species from wetlands, non-wetlands and intermediate habitats. They found that the wetland species were less affected by flooding than the non-wetland species (measured by decrease in shoot weight upon flooding), and tended to have a greater amount of aerenchyma tissue. However, Keeley (1979) noted that during periods of limited water supply, aerenchyma causes excessive water loss, and thus, having aerenchyma involves a "cost" if periods of drought are likely to occur.

Some species, upon flooding, substitute their deep roots for surface adventitious roots (Ernst 1990). Production of these roots takes 15 days for *Fraxinus pennsylvatica* seedlings, after which stomata re-open and normal photosynthesis resumes (Sena Gomes & Kozlowski 1980). The pruning of adventitious roots limits the growth rate of waterlogged plants (Etherington 1984).

Other adaptations to waterlogging are concerned with the biochemistry of the plant. These are less well understood. Linhart & Baker (1973) considered that malate storage, rather than conversion to ethanol, was a sign of flooding tolerance. Low levels of alcohol dehydrogenase (ADH) tend to be found in some waterlogged tolerant species (Ernst 1990, Davy *et al.* 1990).

1.2.4 Life form classification of wetland plants

Wetland plants have long been recognised as being different to their terrestrial counterparts. Raunkaier (1937) divided the cryptophytes (plants with dormant buds which survive periods of unfavourable environmental conditions) into geophytes (terrestrial), helophytes (inhabit soil saturated with water or water from which leaf and flower shoots emerge) and hydrophytes (only inflorescence above the water and with floating or submerged leaves). However, the helophytes did not include such common marsh species as *Equisetum*, as it is not an angiosperm, and *Mentha aquatica* as it is not strictly a cryptophyte (Denny 1985).

Clapham, Tutin & Warburg (1962) overcame this problem in the "Flora of the British Isles" by considering helophytes as swamp and marsh plants and hydrophytes as waterplants. Cook (1968), concentrating on wetland plants, divided wetland plants into hydatophytes (obligate water plants), tenagophytes (can live submerged but require an aerial phase for sexual reproduction) and trichophytes (terrestrial plants that can tolerate a degree of flooding). Using this classification, this project concentrates predominantly on the trichophytes of seasonally flooded wetland. However, the applicability of this type of life form-based plant classification is limited due to natural variation and a poor relationship with other aspects of plant communities (Denny 1985).

1.3 METHODS OF VEGETATION DESCRIPTION

1.3.1 Different approaches

Ever since the conception of ecology as a science attempts have been made to understand the large amount of variation in plant communities. To date, such work has led to three basic approaches to vegetation analysis (Denny 1985):

1. Classical methods. Tansley (1953) in "The British Isles and their Vegetation", divided up the wetland vegetation of the UK. into units e.g. marsh, fen, carr, using

differences in vegetation. Each unit was characterised by a group of plant species that were normally found in that habitat, and were considered to constitute a recognisable type of vegetation. This allowed comparison within and between these units, however, the delimitation of the communities was subjective.

2. Phytosociological methods. These methods divide up the community using differences in species abundances. Two schools of phytosociology are apparent. The Braun-Blanquet/Montpellier school (Braun-Blanquet 1932) uses a hierarchical classification method using a table work system. The method considers the "association" as the basic unit in plant community. An alternate school of phytosociology in the UK. and U.S.A. uses a similar method of analysis, however it relies more heavily on the dominance of the species to differentiate the communities. This method was considerably improved by the work of Poore (1955), who named the basic unit of vegetational communities the "nodum". A comprehensive survey over the last 15 years by the University of Lancaster has led to a phytosociological classification of terrestrial and aquatic British plant communities. The results of this survey are in the process of being published in five volumes (Rodwell *et al.* 1991a & b (vol. 1 & 2)).

The EC. formulated a phytosociological system for Europe, vegetational units being termed CORINE biotopes. A biotope was defined as "an area of land or a body of water which forms an ecological unit of Community significance for nature conservation regardless of whether this area is formally protected by legislation" (EC. 1991). To be of "community significance" the site must satisfy at least one of a set of conditions e.g. the site is one of 100 or fewer sites of its type in the Community, or one of the most important sites in a region for a threatened species (EC. 1991). The CORINE biotopes manual contains a set of biotopes which are of community significance. All biotopes have certain indicative species listed, further divisions of biotopes were made using other indicative species.

3. Multivariate methods. This group of methods improved the phytosociological approach by employing objective multivariate algorithms in computer-based programmes for classification e.g. TWINSPAN (Two Way Indicator Species Analysis) and CLUSTAN (Cluster Analysis), and ordination e.g., DCA (Detrended Correspondence Analysis). These programmes have been made more readily available due to the exponential increase in the utilisation of computers by ecologists in recent years (Gauch 1982).

Many studies of vegetation ecology have utilised multivariate methods. Adam (1978, 1981), analysed data from 3000 releves from 133 saltmarsh sites, using Principal Co-ordinates Analysis and Cluster Analysis. The British saltmarsh vegetation was divided into 10 noda, which constituted at a higher level three basic types of saltmarsh. Wheeler (1980) divided the plant communities of the rich fen system of England and Wales, using data from over 1500 releves in 298 sites, into nine main syntaxa. Prentice & Prentice (1975) divided the hill vegetation of North Hoy, Orkney, using Principal Components Analysis into recognisable habitat types. Marrs, Murphy & Hills (1993) described the aquatic vegetation of Loch Dee (Scotland) from 1904 to 1990 using Principal components analysis. The flora of the Loch in 1990 was more similar to the flora in 1904 than in the other surveys between these two dates, it was proposed that this could have been caused by selective liming between 1983 and 1985 (Marrs *et al.* 1993).

Such studies have invariably produced distinct groupings of vegetational communities, often recognisable on the ground, which can be related to management regimes and environmental factors. However, one of the main aims of contemporary ecology is to identify general models and principles (Day, Keddy, McNiell & Carleton 1988). The vegetation classifications described above are species (and consequently geographically) orientated descriptions of vegetational species assemblages. To appreciate general ecological processes and allow comparisons over a broad geographical range, the concept of functional groups (Day *et al.* 1988); also termed "strategies" (Grime 1979); or "life history types" (van der Valk 1981) could be potentially more valuable.

Thus, recently a fourth type of vegetational community analysis, termed strategy analysis, has been developed. This involves the division of communities into vegetational functional groups (e.g. Grime 1985, Murphy 1991, Murphy, Rorslett & Springuel 1990). Plant communities were compared on the basis of certain attributes and characteristics of the constituent species, rather than just species presence or abundance. These functional groups have been shown to change predictively over environmental gradients (e.g. the TRISTAR computer prediction package, unpublished, Hunt pers. comm.). The theory and practical work leading to this contemporary method of community analysis will now be introduced.

1.3.2 Survival strategy theory

All organisms must "struggle for existence" (Darwin 1859). To be successful in this "struggle", individuals must produce more individuals that reach reproductive maturity. To achieve this aim, the organism must have attributes that permit survival in the environment in which it inhabits. For any environment only certain sub-sets of attributes permit survival and reproductive success (Grime 1979). These attributes will be very different in a plant living, for example, in a desert and a plant living in a lake, but will also show a measurable degree of difference between plants occupying habitats showing less extreme differences in environmental condition.

Raunkiaer (1937) used plant morphological criteria to divide communities up into life forms. He created groups in which plants had a similar life form e.g. cryptophytes are species of plant that have dormant buds which survive unfavourable periods (Raunkiaer 1937). However, as Denny (1985) noted the "association of a life-form with a specific community is not rigid".

MacLeod (1894, in Hermy & Stieperaraere 1985) noted that plants had to make sacrifices in order to attract insects and suggested the use of the terms "capitalist" (large storage capability and pollinator attractant mechanisms), "proletarians" (early flowering, self fertilising with a short life-cycle) and a set of intermediates (e.g. "less rich capitalists" and "half capitalists"). Noble & Slayter (1979) employed a set of "vital attributes" of plants on which they based predictions of the course of succession and perturbations. However, such an approach has two problems concerned with general applicability (Grime, Hunt & Krzanowski 1987). Firstly, the same "vital attribute" could have a different significance in two different organisms and secondly, changes in the set of traits would be apparent with increasing specialisation.

MacArthur & Wilson (1967) proposed a model, extended by Pianka (1970), with two opposing strategies, "r" and "K" (r and K coming from the general population growth rate equation in a resource limited environment). Any organism tended to be either r or K selected. K-selected organisms have a long life cycle and produce a small number of offspring during their life cycle. Whereas r-selected organisms have short life cycles and devote a large proportion of their energy to the production of many offspring. r-selected organisms tend to colonise newly available habitats, and K-selected organisms are found in more stable environments later in the successional sere (MacArthur & Wilson 1967).

However, this theory has not made a "significant contribution" to the production of a general unified theory (Grime & Sibley 1986) and is thus "incomplete" (Stearns 1977). Two serious inconsistencies between the theory and the real world have been noted (Grime 1979):-

1. There was no strategy for stable but unproductive habitats. The strategy suitable for this environment has been termed "beyond K-selection" (Greenslade 1972), "S-selection" (Grime 1974) and "adversity selection" (Whittaker 1975). Thus, Grime concluded that the "primary mechanism controlling the nature and distribution of plant populations, species and communities, arises from three selection processes which operate in the present and have also exerted a dominant influence in the evolution of plants" (Grime *et al.* 1987).

2. Juveniles and adults of the same species were assumed to have the same traits. When Shipley *et al.* (1989) studied the strategies of juvenile and adult aquatic macrophytes, they found no association between juvenile and adult traits. They concluded that it was necessary to consider life-history strategies separately for different stages of the plant life cycle.

Stearns (1977) developed seven lines of criticism about the r-K selection theory. He commented that because K cannot be described using simple parameters, "calling K a population trait is an artefact of logistical thinking".

To achieve a broadly based theory with a general perspective, it appeared that a three strategy model in the adult phase was necessary, from which the juvenile phase was uncoupled. Grime (1974) proposed that two environmental factors were acting upon plants to reduce their biomass and consequently, their growth rate and reproductive success. He termed these two environmental factors disturbance and stress. All environments would have a mixture of these two environmental factors. If there was high stress and high disturbance then plants would not be able to grow in that habitat. If disturbance was small, but there was a lot of stress, then the plants would primarily have to posses a stress-tolerant strategy in order to survive. Alternatively, if a habitat had little stress but considerable disturbance, then the plant strategy would be disturbant tolerant. If a habitat was low in both stress and disturbance then a competitive strategy would be employed. Three basic strategies of plants are thus apparent, stress tolerant (S), disturbance tolerant (D) and competitive (C). Plants could be primarily of one strategy or a mixture of two (e.g. C-D) or of all three (C-S-D).

The term Grime uses for disturbance tolerance, "R", was not used in this study, an alternative term, "D", was used. R stands for ruderal, whereas, D represents disturbance tolerance. It was considered that a plant species with a strategy with a small compliment of disturbance tolerance was not necessarily partially ruderal (R), but it did have some degree of disturbance tolerance (D)

1.3.3 Grime's C-S-D theory

A primary requirement of any body of theory is that the terms or parameters utilised are defined precisely in the context of the model. Survival strategy theory has suffered somewhat a confusion over the terms used (Grime 1979) and has led to rather unnecessary disputes over the validity of the model in relation to other general theories on plants (Grace 1991). Thus, I propose to define the terms *sensu* Grime, namely:-

Strategy- "a grouping of similar or analogous genetic characteristics which recur widely among species or populations and causes them to exhibit similarities in ecology" (Grime 1979)

Competition- " the tendency of neighbouring plants to utilise the same photon of light, ion of mineral nutrient, molecule of water, or unit of space" (Grime 1979)

Disturbance- "any factor which actually destroys biomass and includes trampling, grazing and fire-damage" (Grime 1979)

Stress- "any factor which reduces the rate of accumulation of biomass and includes shortage of light, water and minerals" (Grime 1979)

Grime (1974, 1979) measured two traits of a variety of plant species around Sheffield (UK.), R_{max} (potential maximum rate of growth) and a morphology index (an assessment of the morphology of the plant); these two values were used to represent the disturbance tolerance (D) and the competitive ability (C) of the plant respectively. Grime plotted these two parameters on a triangular axis, with each side representing C, S or D. Due to the geometric requirements of the axis $C+S+D=1$, the stress-tolerance of the plant could be extrapolated from the C and D parameters. This method allowed the basic families of plants to be separated within the triangle. However the selection of the traits to determine the strategy was over-simple and thus, the model lacked definition (Grime 1979). Strategies would be better represented by "complex arrays" of traits (Grime 1985).

A more sophisticated strategy designation procedure was developed using a more complex set of traits (Grime, Hodgson & Hunt 1988). A dichotomous key was developed using indicative attributes or traits from the phenology, morphology and life history of plants to determine the degree of C, S and D tolerance of the plant species. Certain "marker" species were then selected which could be unquestionably placed into a primary or secondary strategy category. The species with the "pure" primary C, S and D strategies were used to define the limits of the three corners of the triangle. Axes were then created between these limits where species with secondary and tertiary strategies could be placed. An extensive survey of many of the habitats around Sheffield was carried out using $1m^2$ quadrats. The abundance of the species in relation to the "marker" species in these habitats was assessed, all species could then be placed in the triangle. If a species was found in quadrats with only stress-tolerant (S) "marker" species, the habitat was assumed to be stressed and the species considered to be exhibit a stress tolerant strategy. In this way, many common plant species could be placed into the triangle by their relationship with the marker species. This approach led the way to the publication of "Comparative Plant Ecology", in which the strategy and other plant-habitat relationships are outlined for a number of common British species (Grime *et al.* 1988).

Further work to assess the validity of aspects of the C-S-D model has been carried out. Gaudet & Keddy (1988), using *Lythrum salicaria* as an indicator of the competitive ability of test species (i.e. a phytometer), found that plant traits could predict the competitive ability of plants and that "size related variables are pervasive indicators of competitive dominance". Campbell & Grime (1989) found that plants exposed to periods of mineral nutrient enrichment fitted the predictions of the C-S-D model. Campbell & Grime (1992), using experimental nutrient and disturbance gradients, found that data on above-ground biomass and flowering responses were consistent with strategy theory predictions. Traits are assumed to have functional significance (Grime 1979) and some have "considerable predictive value" (Grime *et al.* 1987). A classification of 273 species using 30 traits found "objective support" for sets of traits characteristic of particular ecologies and the evidence was "consistent" with C-S-D theory (Grime *et al.* 1987). There was "from diverse schools of research already available a considerable amount of evidence in support of the view that......response to C, S and D are remarkably stereotyped" (Grime 1988). Murphy *et al.* (1990), studying adult phase aquatic macrophytes, considered that a C-S-D strategy approach provides an "objective means of assessing the strategy of populations and communities". Although not all aspects of the model have been fully tested, "for the present the most compelling evidence supporting the C-S-D model is the large number of very different ecological phenomena which appear to be explained by the theory" (Grime 1988).

As a broadly based theory with general perspective, C-S-D strategy theory, appeared to offer a contribution to understanding plant ecology. It provides a general framework for the "intimidating quantity" of plant-environment relationships (Grime 1979b). One of its main strengths was its extensive applicability to widely geographical areas and variety of habitat ecosystems. However, "it is important.......that we should not be seduced by the precision and elegance of current techniques into an extensive preoccupation with the detailed functioning of contemporary populations of amenable species" (Grime 1984). Or put another way, " in plant ecology as in golf there is a time for precision and a time for progression" (Grime 1985).

1.3.4 Problems and alternatives to the C-S-D theory

If one considers that the C-S-D theory constitutes a general model with a broad perspective, three problem areas are apparent. The first, concerned with the problems of terminology and definition is basically semantic, the other two areas represent, potentially, flaws in the ecological intuition behind the C-S-D model.

1. Problems of terminology and definition. Slobodkin (1986) wrote that one of the polemics of contemporary ecology is to fill verbally the gap between narrow ecological theory and the richness of nature. Metaphors were used to replace the empirical world and bandied around the scientific community, however precise definitions were forgotten. Useful scientific terminology maximises the information content related to the object under study, but minimises the importance of the object (Chapleau, Johnsen & Williamson 1988).

Chapleau *et al.* (1988) suggest that the term "strategy" should be used with care. They, suggest that use of the word "strategy" in some contexts tends to "glorify" the scope of the work; words such as "pattern" and "option" would be more appropriate. The idea of a strategy involves causation and some degree of purpose or aim, which is rare in natural systems. However, Grime precisely defines "strategy" in the context of the C-S-D theory (Grime 1979, and see above for definition) and thus problems of accepting the limited scope of this definition lie with the reader not with the definer.

Tilman (1977) introduced a general resource based theory of competition, which has been extended to environmental gradients and suites of traits. Apparent contradictions in the predictions of the model appear to be implicit. For example, Grime's theory proposes that plants gain competitive superiority from high resource uptake capacity, whereas Tilman suggests this is due to a lower equilibrium resource requirement. However, this apparently basic dispute can resolved by appreciating that the two authors utilise differing definitions (Grace 1991, 1993). Instead of being opposing theories, they are in actual fact predominantly complementary and the "primary differences between the theories are of perspective and emphasis" (Grace 1991).

2. C+S+D=1. One of the constraints of the early triangular ordinations using two parameters (R_{max} and morphology index) plotted on a triangle was that the third of the axes (i.e. the stress tolerance of the species) had to be 1-[C+D]. For example, if a plant scored 0.3 on the C axis, 0.3 on the D axis, the S score is constrained to be 0.4 (1-[0.3+0.3]=0.4).

This constraint assumes that there is a direct trade off between traits (Loehle 1988). For example, if a plant has traits suitable for a competitive life style, it cannot also have the traits suitable for a stress tolerant lifestyle without incurring some cost or loss from having traits which are not being exploited. If a competitive plant, which also had stress tolerant traits (if the traits were not mutually exclusive), tried to grow in a stressed community, the unused competitive traits would confer some disadvantage on it compared to a stress tolerant plant without them; it would thus have a diminished competitive ability. Grime (1988b) agreed with Loehle (1988) that the method for plotting species on the triangular axes should not "exclude the possibility of contingencies external to the triangle".

Certain trade-offs are apparent. In *Nyssa sylvatica,* a wetland deciduous tree, the use of aerenchyma for the internal transport of oxygen in waterlogged conditions carries a "cost" in terms of excessive water loss when water becomes scarce (Keeley 1979). However, the extent of the trade-off between traits or sets of traits has been little studied. Intuitively, because different plant species are found in different environments, plants would tend not to be successful in any more than a relatively narrow range of environments in which their traits confer survival i.e. the realised or the functional niche. Absolute commonness (i.e. density over a geographical area) would be a function of the availability of suitable habitats, rather than some plants being "better" than others (Hodgson 1989).

3. Species strategy or population strategy? Harper, in his Presidential address to the British Ecological Society in 1967, spoke of two main problems in plant demography, one of which is plasticity. As an example, he quoted *Chenopodium album* which as a mature adult might produce between 4 and 100,00 seeds (Harper 1967). If such variety is apparent within plant species, is the idea of a species strategy appropriate to the natural world?

Between-population variation in traits in plant species between has been widely reported (e.g. *Veronica peregrina*: Linhart & Baker 1973; *Festuca rubra* and *Agrostis stolonifera*: Davies & Singh 1983; *Carex flacca*: Heathcote, Davies & Etherington 1987; *Spartina patens*, Pezeshki & Delaune 1991). Verhoeven, Jacobs & van Vierssen (1982) proposed that genetically-defined characteristics occur in populations not species, and thus strategy should be considered at the level of population. However, this is contrary to the broad perspectives outlined by Grime (Grime 1979, 1984) of the C-S-D theory. Accepting that there is variation among populations within a species, the functional question should be, how does the amount of variation in traits between populations of the same species compare to the variation in traits between species? This vital question appears not to have been addressed.

1.3.5 Community predictions using survival strategy

The idea of a species strategy has recently been extended to a community strategy (also termed a functional vegetation type), whereby a plant community was assessed and the strategy of the community designated as a function of the constituent species strategies (Murphy, Rorslett & Springuel 1990). Thus, for example, in a stressed environment the plant species present would all be expected to exhibit stress tolerant strategies. However, the sets of traits exhibited by each constituent population would not necessarily be the same as there are a variety of evolutionary adaptations to overcome the same problem, but the traits would all be from the sub-set of stress tolerant traits (Grime 1988). Changes in community strategy along an environmental gradient have been found (Murphy 1991).

Stearns (1977) proposed that the r-K selection theory can be applied as a system of classification, as a model for explanation and as a model for prediction. One of the aims of this study is to examine further the idea that the C-S-D model of Grime applied to plant communities would allow classification, explanation and ultimately prediction of changes in plant communities.

1.4 DESCRIPTION OF THE FAEWE PROJECT SITES AND THEIR PLANT COMMUNITIES

1.4.1 Site and hydrogeomorphic unit selection

Four riverine wetland regions, encompassing much of the climatic range of Europe, were selected for study in England, France, Ireland and Spain. Sites were positioned in two areas from each riverine system:

1. Middle Shannon (Ireland)
    a) Little Brosna (53° 55' N, 7° 55' W)
    b) Clonmacnoise (53° 20' N, 7° 58' W)
2. Torridge headwaters (UK)
    a) Kismeldon (50° 55'N, 4°20W)
    b) Bradford Mill (50° 55'N, 4° 15'W)
3. Bec d'Allier (confluence of Loire and Allier, France)
    a)Apremont (46° 55' N, 3° 5'E)
    b)Decize (46° 55' N, 3° 28' E)
4. Giguela-Zancara headwaters of the Guadiana River (Spain)
    a) Masegar Reserve - wet area (39°20'N, 3°20'W)
    b)Masegar Reserve - dry area (39°20'N, 3°20'W)

Within each site three, four or five sites were selected on pedological criteria by David Hogan, Ed Maltby (University of Exeter) and others (Maltby 1990). Each of these sub-sites was termed a hydrogeomorphic unit. Hydrogeomorphic units were defined as "parcels of landscape which are more or less homogeneous in terms of slope angle and geometry, likely geomorphic processes together with the source, quantity and quality of water input / output" (Maltby & Hogan, in prep). Permanent hydrological and chemical instrumentation was installed in the hydrogeomorphic units during 1991. A 10m x 10m quadrat was selected within 5m of the instrumentation at each of the hydrogeomorphic units. A permanent radio-transponder was buried in the soil at the south-west corner of the quadrat so the quadrat could be located using a scanner on each subsequent sampling occasion.

A four digit system for naming each hydrogeomorphic unit was devised. The first letter represents the country of the hydrogeomorphic unit (England, France, Ireland or Spain).The next two letters refer to the site (Bradford Mill, KiSmeldon, APremont, DeCize, CLonmacnoise, Little Brosna, Masegar Wet and Masegar Dry). The fourth digit refers to the number of the hydrogeomorphic unit, the hydrogeomorphic unit closest to the river at each site was designated number 1. The number of the units increase as they become further away from the river. Thus, for example, "EKS1" refers to the hydrogeomorphic site closest to the river at Kismeldon Mill in England. Traits were measured at one additional site, named FAPS. This site was situated on a sand-bank on the edge of the R. Allier at Apremont, France.

1.4.2 Site descriptions

The Upper Torridge Catchment. The catchment of the Upper Torridge is situated in the north-west of Devon, UK. The catchment has a total area of 875km^{2} and covers an area of undulating plains with convex ridges up to 180m and broad basins with moderate slopes (Hogan & Maltby 1990). The climate is mild and wet with annual rainfall in the catchment of 1133mm (1941-1970), though there is some local variation. 43.6% of total rainfall falls between October and January, inclusive. The underlying rock is of Carboniferous age comprising mainly of sandstone and shales. A majority of the upper Torridge catchment is grassland, used predominantly for dairy farming, which has become increasingly intensive in recent years.

Bradford Mill (SS424078) is at the confluence of the Torridge and the Waldon. The soils are well drained brown alluvium and are seasonally flooded in winter and spring. The soils at Kismeldon Meadows (SS351171) are a complex of poorly drained loamy and clayey stagnogleys. Part of the site has been designated as a Site of Special Scientific Interest (SSSI) and is maintained under traditional management.

Loire / Bec d'Allier area: The Loire basin drains about 20% of France. The headwaters of the Loire and the Allier, the biggest tributary of the Loire, are in the slopes of the Massif Central. The width of the Loire reaches 1300m downstream of the confluence of the Loire and the Allier at the Bec d'Allier. The well preserved alluvial flood plains exhibit an array of braided channels, sand and gravel banks dead-arms and river islands. The upper geological strata consist of alluvial sediments comprising predominantly of sand and gravel. Extensive agriculture is the dominant land use on the banks of the Loire and Allier, however intensification of the agriculture is increasing in this area. The site at Apremont, on the river Allier has an uncontrolled flow regime whereas the site on the Loire at Decize has a set of dams upstream; the hydrological regime in both rivers is primarily governed by the Mediterranean winter rains.

The Shannon catchment: The catchment of the Shannon covers about 20% of the area of the Republic of Ireland and is 258km long, excluding the estuary. The area has an oceanic climate with rain falling one day in two (total of 1024mm of rain annually). The sites are situated on the "callows" a local word for the floodplain derived from the Irish word *cala* meaning a marshy meadow along a river. The soils of the callows are mainly alluvium and peat. The flow of the Shannon exceeds channel capacity for 15% of the time. Approximately 250,000 acres of land are affected by waterlogging in the Shannon catchment. Land use of the Callows is pasture with some meadows (23%). At the Little Brosna site there is considerable silt deposition, possibly due to peat stripping, which causes eutrophic conditions. At the other site at Clonmacnoise, less silt deposition is apparent, about 25% of the farmers apply NPK fertiliser (up to 30kg per hectare). High floods, which occur one year in 5, tend to remove applied fertiliser and thus decrease the economic value of fertilisation.

The Guadiana-Zancarra headwaters (Spain): Located in the central high plateau of Spain, the Spanish sites experience very hot summers, cold winters and little rain (76.4mm per annum, 1948-1982). The soils are of two main types; flooded areas with peat formation and saline soils in drier areas. The salinity of the soil in the dry areas is due to a lack of water for a long period of time and the presence of large amounts of soluble salts which the ground water is rich in. The wet site is located in the extensive wetlands around the Laguna Masegar. Increasing amounts of irrigation in the La Mancha region have led to a lowering of the water table (20m in the last 20 years according to the reserve warden in the

Masegar area). Laguna Masegar dried up in July/August 1992 and did not refill during 1993. The dry site on the banks of the Rio Giguela about 1km away have not flooded recently, a salt glaze covers the surface of the soil.

1.4.3 Vegetational analysis and description of hydrogeomorphic units

During the 1991 and 1992 field seasons, data on the abundance and cover of all species at each hydrogeomorphic unit were collected. Nomenclature follows Stace (1991), unless otherwise indicated. A 0.5m x 0.5m quadrat, divided into 25 equal squares, was used to determine the abundance of each species at each hydrogeomorphic unit. The quadrat was randomly placed in the area of the hydrogeomorphic unit. The presence of each species in each of the squares was recorded. This was repeated during the field season making a total of ten or more quadrats (or 250+ presence/absence data for each species).

At units with tall and dense stands, quadrating of vegetation was not possible. This was because the quadrat either crushed the vegetation or view of the lower storey of plants was obscured by the canopy. At these units estimates of abundance for each species were made; no error term was ascribed to these estimates.

A Harris pin frame was used to determine the cover of each species in each hydrogeomorphic unit. This piece of equipment consists of a tube held about 50cm above the ground with ten thin pins at 5cm intervals pushed through it pointing vertically to the ground. The pins pierce the vegetation that they encounter. Each species which was touching each of the ten pins was recorded. The pin frame was randomly placed ten times within the quadrat of the hydrogeomorphic unit.

Data on species frequency (and standard error) and cover of each species at each hydrogeomorphic unit were tabulated for reference (Appendix 1.1 for sites in England, Appendix 1.2 for France, Appendix 1.3 for Ireland and Appendix 1.4 for Spain).

These data were analysed using two ordination techniques available on the CANOCO programme of ter Braak (1987):

1. Detrended Correspondence Analysis (DCA)
2. Principal Components Analysis (PCA)

DCA is popular among field ecologists as it tends to provide an effective solution to the problem of exhibiting differences in communities due to species presence or abundance (Jongman, ter Braak & van Tongeren 1987). It uses a unimodal response model and is appropriate for long gradients with much species turnover. PCA uses a linear response model and is thus more appropriate for shorter gradients with little species turnover. PCA constructs a theoretical variable that minimises the total residual sum of squares after fitting straight lines to the species data; PCA is a multi-species extension of multiple, least-squares regression.

DCA was used to determine the relationship, using species, of all the hydrogeomorphic units in multidimensional space. Groups of sites that were positioned close together in DCA ordination were re-analysed by PCA to determine the within-group relationships.

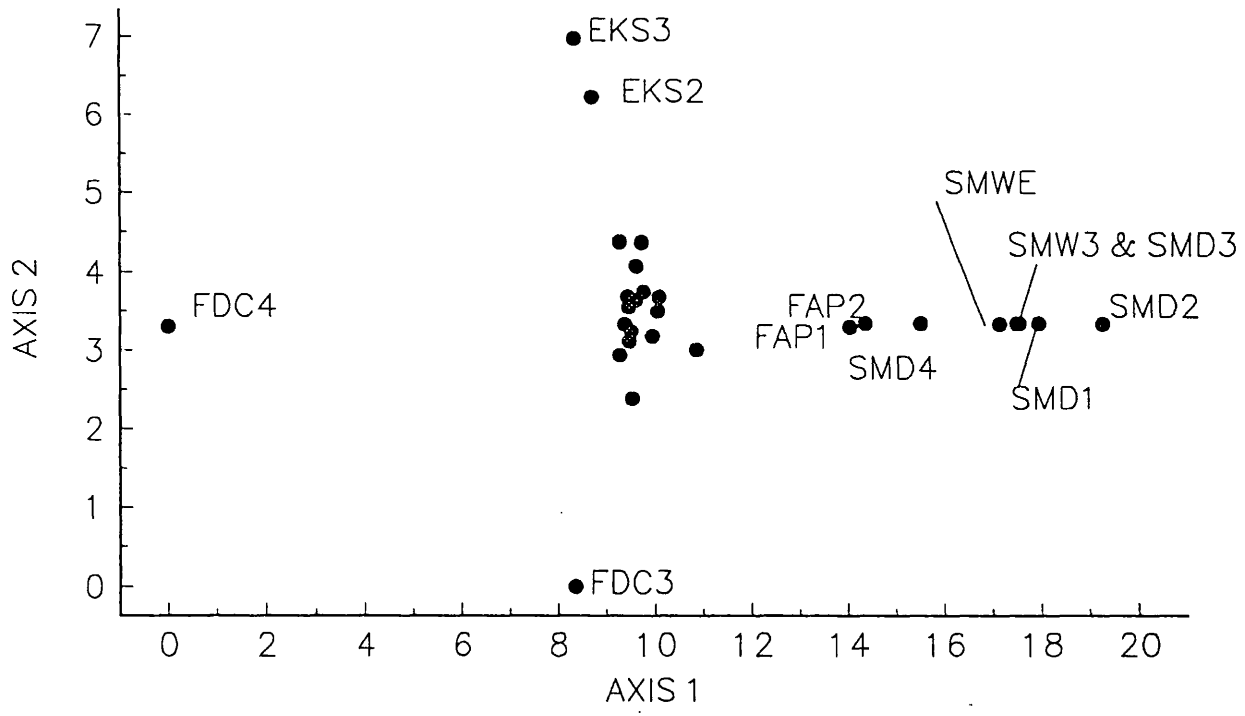
There was considerable variation in the plant species composition of the wetland sites. The first ordination axis ranged by nearly 20 standard deviations of species turnover, the second axis was over six standard deviation units long. The length of these axes suggest that the FAEWE wetland sites represent a wide range of plant communities. Eigenvalues, the maximised dispersion of the species scores on the ordination axis, were large in the first four axes, (0.98, 0.76, 0.63 and 0.57 for axes 1 to 4 respectively); all these axes were of importance.

A plot of the first and second DCA axes show that there was a central group surrounded in 4 orthogonal directions by outliers (Fig.1.1). Outliers represent communities which have little or no species association to the central group. All the 6 sites from Spain were found in the right-hand area of the plot. *Galium aparine* was the only species common between the Spanish site (SMD4) and other sites e.g. FAP1, FAP2 and FDC2 (central group). The presence of *Galium aparine* in SMD4 and 3 French sites represents the only link between the species composition of Spain and the other wetland sites. The Spanish wetland flora was, thus, very dissimilar to other target wetlands.

Two further French sites were represented as outliers, FDC3 and FDC4. FDC3, a lightly grazed grassland on sandy soils, was dominated by species common to other sites i.e. *Agrostis capillaris* and *Festuca ovina/rubra*. However, some less abundant species were not found in other studied sites e.g. *Eryngium campestre* and *Euphorbia cyparissias*. FDC4 also had a different species composition from the central group of sites - the unit is seasonally flooded, seasonally experiences drought, is grazed and trampled by cows. This unit experiences very different environmental conditions from the other sites surveyed.

The remaining two outliers (EKS2 and EKS3) are situated on a flood-plain slope. They probably never experience inundation, but, the soil is generally wet, maintained by through ground flow towards the River Torridge. They are both dominated by *Molinia caerulea*; with small *Carex* species, *Festuca rubra* and *Narthecium ossifragum* common in the case of EKS2 and *Agrostis canina*, *Anthoxanthum odoratum* and *Juncus acutiformis* in EKS3.

Fig. 1.1 DCA of hydrogeomorphic units by species
(eigenvalue axis 1 = 0.98, axis 2 = 0.76)



The central group, consisting of the remaining 16 units studied, was re-analysed using PCA (Fig. 1.2). The PCA was not particularly successful at summarising the units in a few dimensions. The first axis explained 23% of the variation in the species scores, axis two explained 19%. Interpreting the ordination in terms of environmental gradients led to an unclear picture. The first axis possibly represents a gradient from grasslands, with high positive scores, to riverside / wet units at the negative end of the axis. The relationship of the second axis to the environment is unclear. This group of units may experience a heterogeneous set of environmental conditions.

An attempt was made to assign each of the hydrogeomorphic units to a CORINE biotope (European Commission 1991). Most units could be classified into a CORINE category (Table 1.2). A majority of the sites were humid grassland (CORINE code 37) or water-fringe vegetation (53).

From the species-orientated descriptions of the vegetation of the FAEWE hydrogeomorphic units it can be concluded that the wetland sites support a range of plant communities, with a wide range of species composition. A central group of units with some overlapping species was apparent. Ordination of the 16 units in the central group was poor and environmental interpretation limited. This suggested that the sites experienced a highly heterogeneous set of environmental conditions. The outliers consisted of all the Spanish sites and some sites from France and England.

FIG. 1.2 PCA of central group of hydrogeomorphic units by species (eigenvalue, axis 1 = 0.23, axis 2 = 0.19)

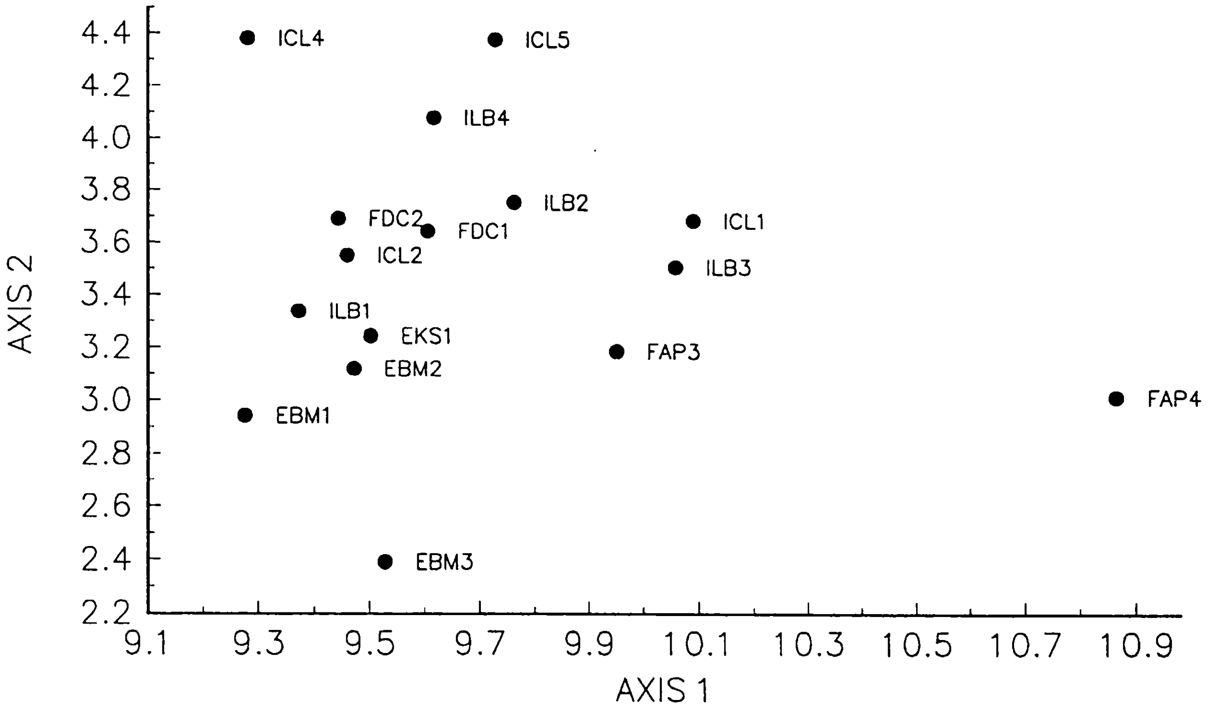


Table 1.2 CORINE biotope designation of FAEWE wetland sites ("?" represents communities without a clear bitope classification).

SITE CODE	CORINE UNIT	FURTHER CORINE CLASSIFICATION
EBM1	MESOPHILE GRASSLAND (38)	MESOPHILE PASTURE (38.1)
EBM2	HUMID GRASSLAND (37)	EUTROPHIC HUMID GRASSLANDS (37.2)
EBM3	HUMID GRASSLAND (37)	EUTROPHIC HUMID GRASSLAND (37.2)
EKS1	HUMID GRASSLAND (37)	MEADOWSWEET STANDS (37.1)
EKS2	HUMID GRASSLAND (37)	OLIGOTROPHIC HUMID GRASSLANDS (37.3)
EKS3	HUMID GRASSLAND (37)	OLIGOTROPHIC HUMID GRASSLANDS (37.3)
FAP1	RUNNING WATER (24)	RIVER MUD BANKS (24.5)
FAP2	TALL HERB COMMUNITIES (37)	HUMID TALL HERB FRINGES (37.7)
FAP3	HUMID GRASSLANDS (37)	FLOOD SWARDS (37.24)
FAP4	WATER FRINGE VEGETATION (53)	GREATER POND SEDGE BEDS (53.213)
FDC1	WATER FRINGE VEGETATION (53)	REED BEDS (53.1)
FDC2	ALLUVIAL WET FOREST (44)	RIPARIAN WILLOW FORMATION (44.1)
FDC3	DRY SILICEOUS GRASSLANDS (35)	SAND SEDGE GRASSLANDS (35.15)
FDC4	MAN-MADE FRESH WATER BODIES (22)	BUR MARIGOLD COMMUNITIES (22.23)
ICL1	WATER FRINGE VEGETATION (53)	BOTTLE AND BLADDER SEDGE BEDS (53.214)
ICL2	HUMID GRASSLAND (37)	MEADOWSWEET STANDS (37.2)
ICL3	HUMID GRASSLAND (37)	MEADOWSWEET STANDS (37.2)
ICL4	HUMID GRASSLAND (37)	MEADOWSWEET STANDS (37.2)
ICL5	FENS, MIRES & SPRINGS (54)	ACIDIC FENS (54.4)

Table 1.2 continued

ILB1	MESOPHILE GRASSLANDS (38)	MESOPHILE PASTURES (38.1)
ILB2	WATER FRINGE VEGETATION (53)	LARGE SEDGE COMMUNITIES (53.2)
ILB3	WATER FRINGE VEGETATION (53)	LARGE SEDGE COMMUNITIES (53.2)
ILB4	?	
SMD1	WATER FRINGE VEGETATION (53)	REED BEDS (53.1)
SMD2	?	
SMD3	?	
SMD4	WATER FRINGE VEGETATION (53)	REED BEDS (53.1)
SMW3	WATER FRINGE VEGETATION (53)	REED BEDS (53.1)
SMWE	WATER FRINGE VEGETATION (53)	REED BEDS (53.1)

FUNCTIONAL GROUPS OF PLANTS: A CLASSIFICATION OF WETLAND PLANT POPULATIONS USING TRAITS

2.1 INTRODUCTION

Classification of objects by humankind is a common and fundamental activity (Gauch 1982). Botanists are no different and have for a long while been attempting to classify individuals of the plant kingdom of the world into groups. Theophrastos of Eresos (371 - 286 BC) constructed one of the earliest life-form classifications by distinguishing between trees, shrubs, half-shrubs and herbs. Many other classifications of plants followed (e.g. Drude 1886, Warming 1909, Clements 1920, Braun Blanquet 1928, Du Rietz 1931, Raunkiaer 1937).

When data are voluminous and complex the human brain can experience difficulty in identifying groups or patterns within the data (Gordon 1981). Recent advances in computer technology and associated software have allowed patterns and relationships in large data sets to be elucidated. Modern classifications of plants have exploited this potential, using both more species or samples and more descriptive characteristics of plants. For example, Grime, Hunt and Krzanowski (1987) classified 273 species of plant using 30 attributes and Leishman & Westoby (1992) classified 300 species of plant into groups on the basis of 43 traits.

Recent work has suggested that traits or characteristics associated with plant size are fundamentally related to many ecological aspects of plants. Al-Mufti, Sydes, Furness, Grime & Band (1977) found that dominant plants tended to have greatest biomass, Givnish (1982) proposed that plants with leaves higher up in the canopy would be more competitive for light. Menges & Waller (1983) found that maximum plant height was related to fast growing competitive species. Kautsky (1988) divided aquatic soft-bottomed macrophytes into 4 groups on the basis of predominantly size-related criteria. Epp & Aarssen (1988) suggested that rapid growth rate, tall plant height, large shoot biomass and large root biomass are among a set of attributes that have been demonstrated to confer competitive ability on plants. Keddy (1990) reviewed a number of papers which suggested that height of plant was related to the degree of competition intensity in the environment. It would thus appear that aspects related to the size of the plant, in particular height, are of fundamental significance in determining the ecology of plant species.

The work presented here uses non-hierachical clustering techniques to classify established-phase plant populations on the basis of morphological traits. The aim was to determine to what extent morphological trait data can be used as an indicator of plant strategy and other generalities about the ecological behaviour of plants. Three objectives were identified:

1. To formulate the "best" classification of plant populations into groups.
2. To determine the relationship of the "best" classification to the C-S-D strategy groups of Grime *et al.* (1988).
3. To analyse differences in traits and ecology between groups.

2.2 METHODS

2.2.1 Trait measurement

Between April and October 1991 and 1992, a selected set of traits was measured for a variety of plant populations in the FAEWE study wetlands in England, Ireland, France and Spain. In each hydrogeomorphic unit a number (approximately 4) of common plant species present were selected for trait measurement. The work presented here was carried out at the population level. If different units had similar species composition, then traits of the populations (i.e. a species at a hydrogeomorphic unit) were measured in each of those units. This field analysis was carried out around the time of reproductive maturity for each plant species. Eight traits were measured for each species in each 10 x 10m hydrogeomorphic unit. Four traits were measured in the field, the other four traits required the harvesting and transportation of samples back to the laboratory at Glasgow University, UK..

Four traits were measured in the field; height of plant, area of the plant canopy, number of leaves and the number of seeds per plant.

1. Height of plant (HT). The height of the plant was measured using a ruler (± 0.5cm) *in situ*. Care was taken not to disturb the position of the plant in the canopy while the measurement was being taken. A plant that drooped or had a creeping habit would have a height measurement smaller than its total length if the plant was harvested and measured straight along a ruler.
2. Area of the plant canopy (AREA). A transparent quadrat with 5cmx5cm squares was held over the top of the plant. The number of squares in which pieces of stem, leaves or reproductive structures were present, when observed from above, were counted. The structure of the plant canopy was not disturbed during this operation. If other plants obscured the view of the individual being measured, minor adjustments were made to the canopy to permit a complete view.
3. Number of leaves (LEAVES). The number of leaves of ten studied individuals was counted. Leaves were considered to be separate and counted as two if any piece of stem was apparently dividing them. Immature leaves were counted as long as an area of photosynthetic leaf tissue was observed. Dead or dying leaves

were also counted if any area of green photosynthetic tissue was still remaining on their surface.

4. Number of seeds (SEEDS). For ten individuals the total number of seeds produced was counted. For plants that produced large numbers of seed, the number of reproductive structures (e.g. number of seed heads) and the number of seeds in each reproductive structure was counted for ten of the structures. The mean number of reproductive structures, and the mean number of seeds in the reproductive structure were multiplied together to give an estimate of the number of seeds.

Ten individuals for each study species in each quadrat were harvested, with most of the root system intact to maintain their freshness during transport. The individuals were placed in a cool box and transported back to Glasgow University. Further traits were then measured:-

5. Dry weight of leaves (WTLEAF). The leaves from each individual were placed in tissue paper and left in a drying oven at 55°C for one to two weeks. The dry weight of each individual sample was subsequently weighed.

6. Dry weight of stem (WTSTEM). The stems were placed in tissue paper and dried for one to two weeks. Dry weights were measured.

7. Dry weight of reproductive structures (WTREPRO). Reproductive structures, including structural tissue for the support of sexual organs, were dried for one to two weeks and the dry weight measured.

8. Seed weight (WTSEED). Between 30 and 50 seeds were removed from the dry reproductive structure and weighed (more seeds were used if the seeds were extremely small). The weight of one seed was calculated.

The above traits were measured for a total of 144 plant populations from 32 hydrogeomorphic units. So distributions of traits approximated to normal, traits were natural logged prior to classification analysis (Jongman, ter Braak & van Tongeren 1987).

2.2.3 Statistical Analysis

The primary objective of this work was to divide the 144 plant populations into groups using morphological traits. Non-hierachical classification methods were selected for three reasons:

1. The general pattern of the data, as opposed to the hierachical structure of groups, was required (Gauch 1982).
2. Non-hierachical classification permits *a posteri* assessment of the classification success.

3. Grime *et al.* (1987) proposed that "since it is less likely that co-evolution of plant attributes will have occurred in response to fine interrelations between closely similar species than it is that it has followed broader axes of evolutionary progress" a non-hierachical method of classification was appropriate.

The sum of squares non-hierachical classification method enables classification of objects which can be represented as points in Euclidean space in a number of dimensions i.e. each object is described by a set of continuous variables. The method aims to partition the set of n objects into g groups so as to minimise the total within-group sum of squares about the g centroids. An iterative relocation (or k- means) algorithm was used whereby an initial partition of the objects into g groups is modified by the reallocations of objects until a minimum sum of squares is reached i.e. until the movement of further objects does not decrease the sum of squares. Two initial partitions were used:

1. Random partition. In this case g even-sized groups were formed from the data set. The first group was the first g/n (where n = the total number of objects) set of objects in the data list, subsequent groups were the following g/n set of objects.
2. Height partition. An initial partitioning procedure of height was used; g groups were initially classified by height values.

Sum of squares classifications were run for both initial partitions with $g = 3$ to 8 using GENSTAT (version 5). All the classifications should permit the placing of 144 objects into g groups, however further work was necessary to determine which of the classifications was "best".

All classifications carried out caused a decrease in the sum of squares from the sum of squares prior to classification, ss_o, compared to the sum of squares after the classification, ss_c. However, the difference between ss_o and ss_c is not a good measure of classification effectiveness because when $g = n$, $ss_c = 0$, and when $g = 1$ then $ss_c = ss_o$. An index could be derived to counteract this tendency but the effect of g on the difference between ss_o and ss_c is not clear, particularly when g is small (<5).

The residual sum of squares, ss_r, (where $ss_r = ss_{total} - ss_c$) is the remaining sum of squares after the objects have been classified into g groups (ss_{total} was defined as the ss_c when $g = 1$). The difference in ss_r from g to g+1 would be expected to decline with increasing g. However, if there is an atypically small difference moving from ss_r of g to ss_r of g+1, then the expected effect of moving from g to g+1 has not occurred. This suggests that the g classification was rather more effective in decreasing the sum of squares than the g+1 classification. The first point of inflexion in the curve of differences in ss_r between g and $g = 1$ would be the most important as groups with a greater g would tend to be sub-sets of the g

classification. This assessment of residual sum of squares was carried out for the initial starting procedure that was most effective at decreasing ss_C.

A further clustering technique was used to identify the changes in group membership and to produce a classification of wetland plants that tends to emphasise the differences between groups. A special case of the general agglomerative algorithm which optimises the dissimilarity between groups, the centroid algorithm, was used. A classification from the random partitioned sum of squares classification where $g = 8$ was used as the starting point of the centroid dissimilarity classification. The method was run from $g = 8$ to 2. At each stage the group with its centroid closest to another group centroid is removed. The objects from the destroyed group are then iteratively relocated in the remaining groups so as to optimise the dissimilarity between the group centroids.

The optimum of g value (determined from differences in the residual in the sum of squares) of the centroid dissimilarity classification was plotted on the first and second axis of a PCA of the natural-logged traits to determine the degree of internal cohesion and external isolation and to compare the differences in group members between the optimum g value classifications of the centroid dissimilarity method and the sum of squares classification method.

2.2.4 The relationship of the classification using morphological traits to the strategy model of Grime.

The strategies of 98 out of the 144 plant populations studied in this work are given (though at species level) by Grime *et al.* (1988). They proposed that much of the ecology, for example maximum relative growth rate or life form, of a species could be summarised by the placing of it into a strategy model based on the degree of stress and disturbance in the environment (Grime 1979, Grime *et al.* 1988). The extent to which the morphological classifications carried out in this work were related to the groups proposed by Grime was determined.

The proportion of populations in each of the strategy categories defined by Grime *et al.* (1988) were calculated. If the strategy was an intermediate, for example C / C-S-D, the population was scored as 0.5 C and 0.5 C-S-D. The distribution of all the 98 populations between the strategy categories of Grime was termed the null model. Each group of the classification can be similarly related to the strategy categories. A null hypothesis was generated proposing that the distribution of group g is not significantly different to the distribution of the null model. The null hypothesis can be tested using χ^2 tests. The members of each strategy category of group g were multiplied by a factor to make the group size equal to the null model (where $n = 98$). g χ^2 tests were carried out to determine if any of the g groups had a significantly different distribution to the null model.

2.3. RESULTS

2.3.1 Sum of squares classification.

All 12 sum of squares classifications caused a decrease in the sum of squares compared to the starting positions. The groups resulting from the classifications were in tighter groupings than the initial partitions. As expected, the remaining sum of squares after classification, ss_c, was smaller when g was higher (Table 2.1) The more groups that the objects were classified into, the smaller the sum of squares of the groups. In 5 out of the 6 classifications, the initial partition by height was able to decrease the sum of squares after classification more than a random initial partition (Table 2.1). The initial grouping formed by partition by height, thus, had a greater relationship to the final sets of group members than the random partition. Because partitioning by height generally produced tighter clusters, assessment of the effect of varying g was carried out on this set of classifications.

To assess which of the specified g value classifications was particularly effective at producing tight groups, the difference in the residual sum of squares between g and $g+1$ was calculated. A plot of ss_r with changes in group number should show an asymptotic form. This would be produced because the effect of adding one more group when g was small would be proportionally greater than adding one more group when g is large. A plot of ss_r against change in group number (Fig. 2.1) approximated to an asymptotic form, however the ss_r when changing from 3 to 4 was below the general line of the curve. Thus, when $g = 3$, a particularly small difference between the ss_r when $g = 3$ and $g = 4$ was observable; this suggests that the clusters were relatively tight with 3 groups.

This apparent low value of the 3 to 4 ss_r could be somewhat exaggerated however, because the ss_r value of 2 to 3 was greater than it should be from the best-fit decay curve of ss_r with g (Fig. 2.1.). This would be due to the observation that because 3 was a "good" group number, the difference between the ss_r of $g = 2$ and $g = 3$ would be large, as $g = 3$ had a unusually low ss_r. The initial decay of the asymptotic curve would then not appear so steep. However, even if that was the case, the difference between the ss_r values of $g = 3$ and $g = 4$ was somewhat smaller. Initial partitioning by height into 3 groups would thus appear to be a particularly efficient sum of squares classification for the data set.

Table 2.1 The remaining sum of squares in the *g* groups following classification (ss_c) using a random initial partition and an initial partition by height.

Number of groups (*g*)	Random partition	Height partition
3	1225.9	1224.5
4	1095.2	1099.2
5	983.5	950.1
6	962.3	859.0
7	810.1	806.0
8	780.3	750.3

Table 2.2 Changes in group membership with changes in group number (*g*) for a centroid dissimilarity classification of 144 plant populations (values shown as group code followed by number of members of that group in brackets).

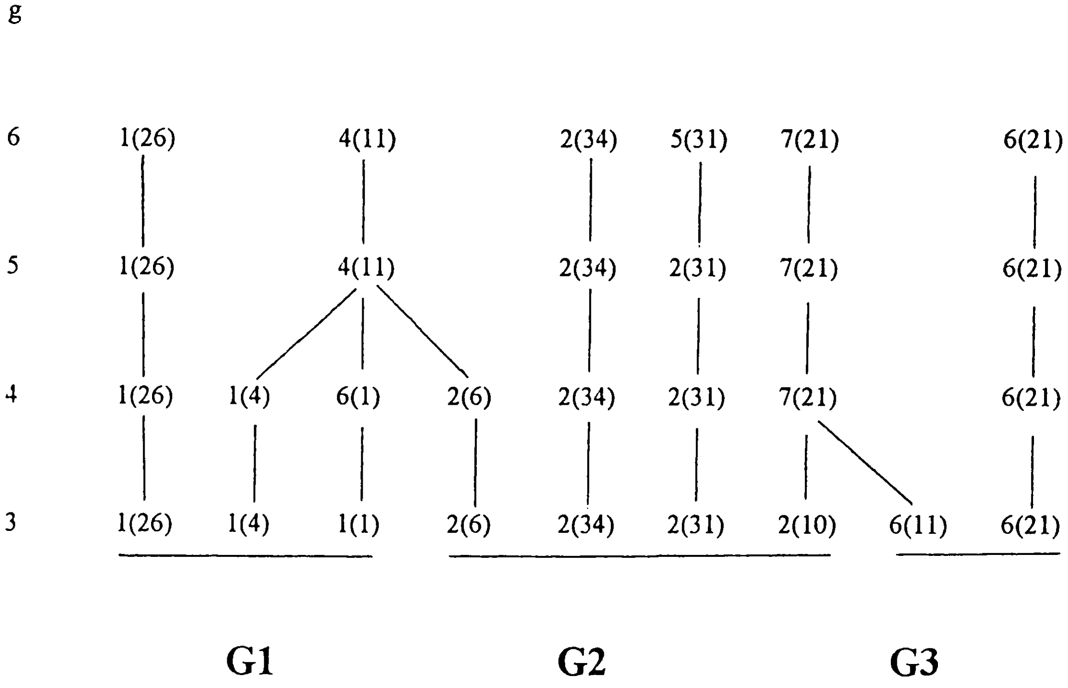
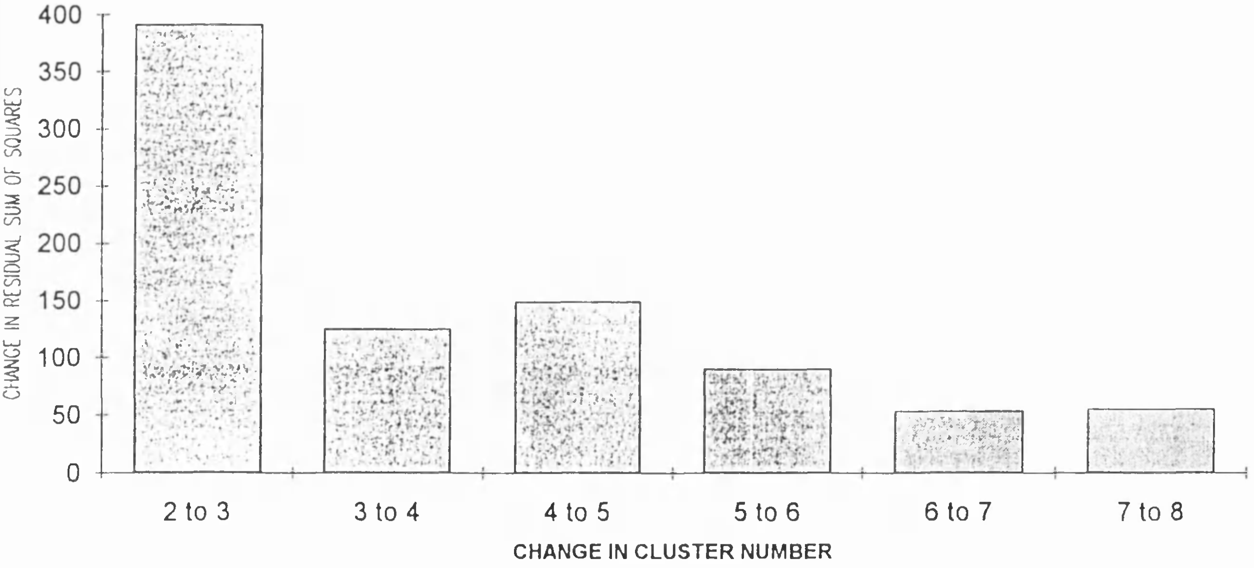


Fig. 2.1 Changes in residual sum of squares with different number of clusters.



2.3.2 Centroid dissimilarity classification

Centroid dissimilarity classification tends to produce group centroids, and consequently group members, that are most distant in Euclidean space as opposed to sum of squares which aims to minimise within-group variance. Centroid dissimilarity classification was carried out from $g = 8$ to 3. The $g = 8$ classification starting with random partitioning was used as it is nearly as efficient as the $g = 8$ height partition ($ss_C = 780$ and 750, for random and height partition respectively (Table 2.1)) and it assumed nothing about relationships within the data set.

Two groups, 3 ($n = 5$) and 8 ($n = 8$), were immediately removed and the members iteratively relocated because the group size was less than 10. The relocation of members from removed groups was mapped (Table 2.2). At the $g = 6$ to 5 stage, group **5** was removed, all previous members of group **5** were placed into group **2**. Moving from $g = 5$ to 4 group **4** was removed, the 11 members of group **4** were distributed in a variety of ways. Six members of the removed group **4** were relocated in group **2** and four members were placed in group **1**. The remaining member of the removed group **4** was placed in group **6** , however this object was relocated at the next stage (moving from $g = 4$ to $g = 3$) to group **1**. This object was the only case out of the 144 objects that moved out of one of the final groups at (1, 2 and 6) once it was placed in one. This object, number 100 in the data set, was plainly difficulty to classify, and is discussed later.

Objects displayed a strong fidelity to their groups, as only one object was moved more than once. If these data did not have some pattern in the groups more changes between groups would be expected. Groups were relatively stable from $g = 6$ to $g = 3$. The final groups were **1** ($n = 31$), **2** ($n = 81$) and **6** ($n = 32$), subsequently termed G1, G2 and G3 respectively.

2.3.3 Comparison of sum of squares and centroid dissimilarity classification methods.

Two methods of classification produced two clusters, with $g = 3$. However, it would be important to find out if the members of the groups in each classification were identical, similar or highly dissimilar. To determine how similar the two classifications were, a Principal Components Analysis (PCA) was carried out for the 144 objects using 8 traits. The objects from the sum of squares classification were plotted on axis 1 and axis 2 of the PCA using different point markers for the 3 groups (Fig. 2.2a.). Samples that were classified differently between the centroid dissimilarity method and the random start sum of squares method were plotted (Fig. 2.2b).

FIG. 2.2a Position of the 3 groups from the sum of squares classification plotted on axes 1 and 2 of a PCA of the 8 traits.

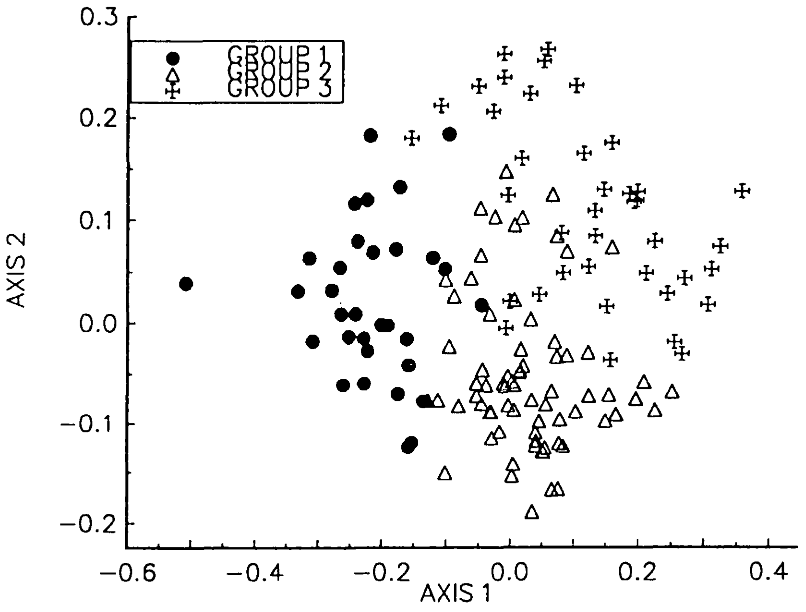
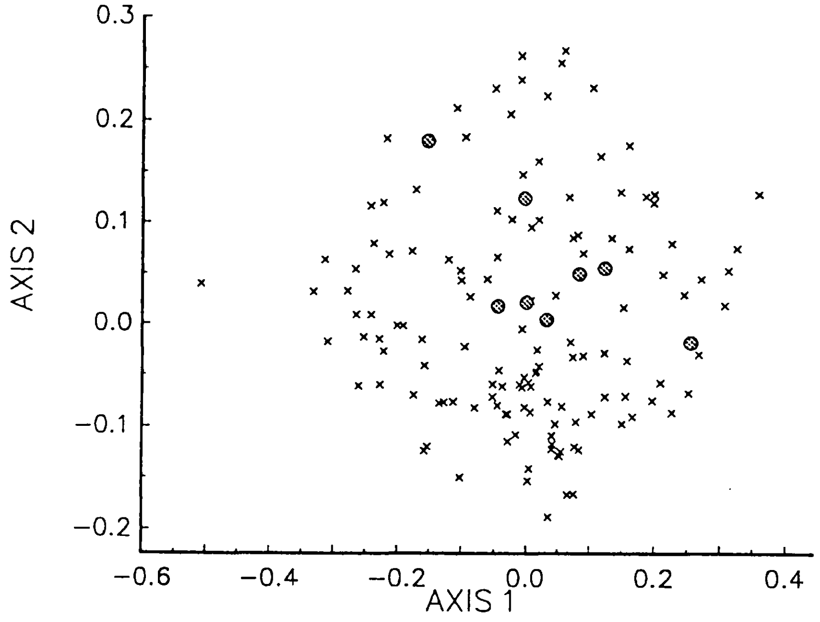


Fig.2.2b Position of populations classified differently between sum of squares classification and centroid classification (solid circles).



The groups tended to be distributed in different areas of the ordination space. Little overlap between groups was apparent (Fig. 2.2a) Eight objects (5.6% of the total) were classified differently between the centroid dissimilarity and sum of squares classification methods (Fig 2.2b). The main area of differences in classification (7 objects) was between group 2 and group 3 where the border between the groups was undistinguished. One object was placed centrally on axis 1 but high on axis 2; this object was sample number 100, the only object that was relocated more than once in the centroid dissimilarity classification. The two methods, using different optimality criteria for defining groups, tended to come up with a similar classification of the 144 objects.

Gordon (1981) proposed two desirable characteristics of clusters, internal cohesion and external isolation; the algorithms of the sum of squares and centroid dissimilarity classification methods address these characteristics respectively. The above analysis has considered these two properties and the clusters produced would appear to have internal cohesion and external isolation (though the boundary between group 2 and 3 was not well defined). They would thus appear to be a "good" classification of the objects.

2.3.4 Ecological significance of clusters

So far the mathematical properties of clustering have been discussed. Due to the fact that classification techniques generally will cluster any data set, however un-dissectable the objects are in reality, *a posteri* assessment is an important and largely neglected step of classification procedures (Gordon 1981). In this case a "good" classification, defined in terms of internal cohesion and external isolation, of wetland plants by functional attributes has been achieved. Now it is important to assess the ecological attributes of the groups identified.

The sum of squares classification produces means for the k variables used to describe the objects (k = 8 throughout this analysis). The mean value for each variable for each group can be plotted, this was done for the classification $g = 3$ with height partition (Fig. 2.3a-h). Differences in the mean values are clear between the groups. Group 1 (G1) had greater mean plant height, plant area, number of seeds, dry weight of stems and leaves. These plant thus tend to be large plants. Species in this group include *Phragmites australis*, *Phalaris arundinacea* and *Urtica dioica* (Table 2.3). G3 (equivalent to group 6 of the centroid dissimilarity classification) was composed of plants that had a small number of light-weight seeds and low weight reproductive structures (Fig. 2.3). Plants in G3 include species such as *Hydrocotyle vulgaris*, *Carex aerenaria* and *Cynodon dactylon* (Table 2.3). G2 tended to be intermediates between G3 and G1 and

Fig. 2.3 The mean value (± standard error) for the eight morphological traits for G1, G2 and G3 from the sum of squares classification.

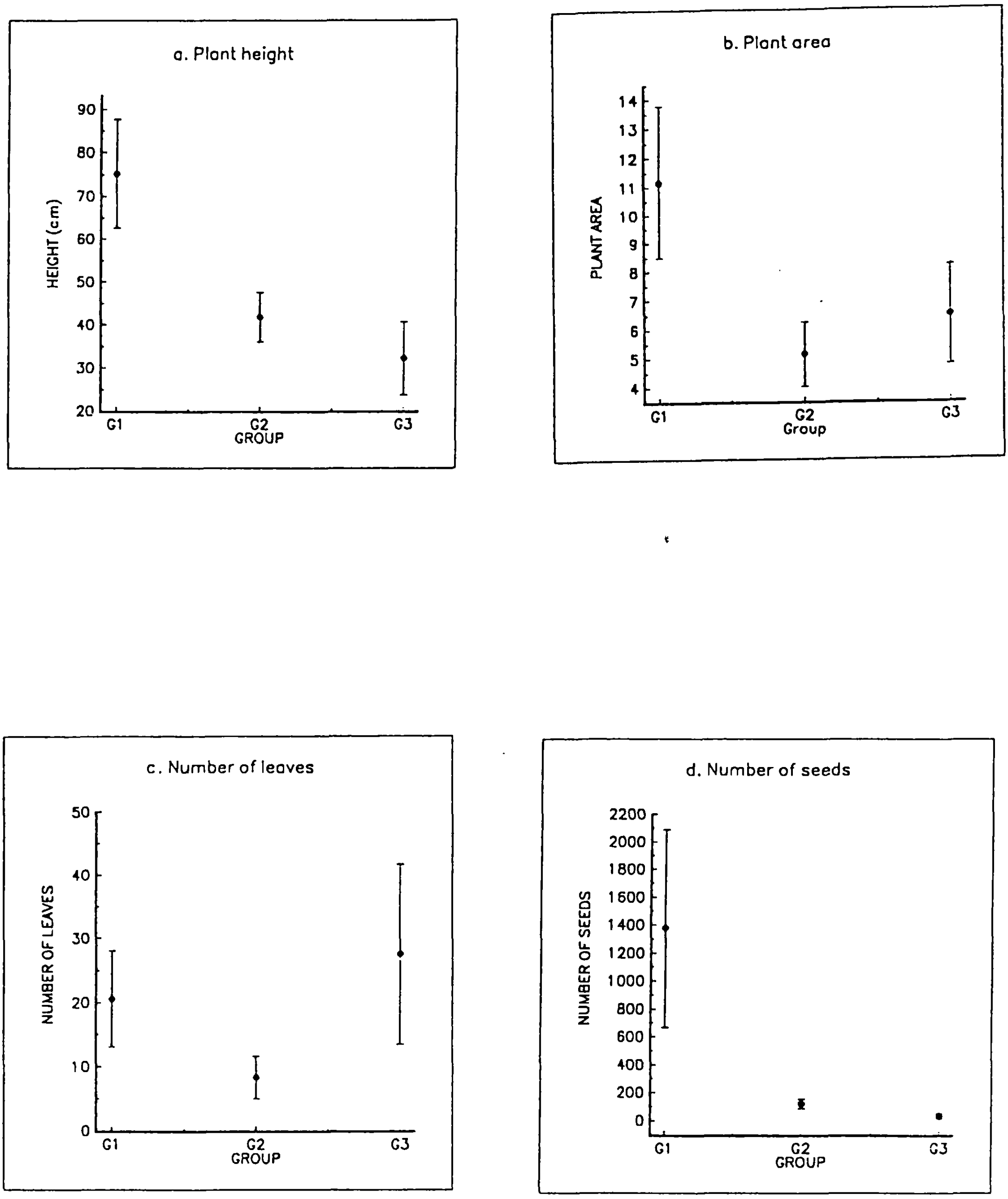
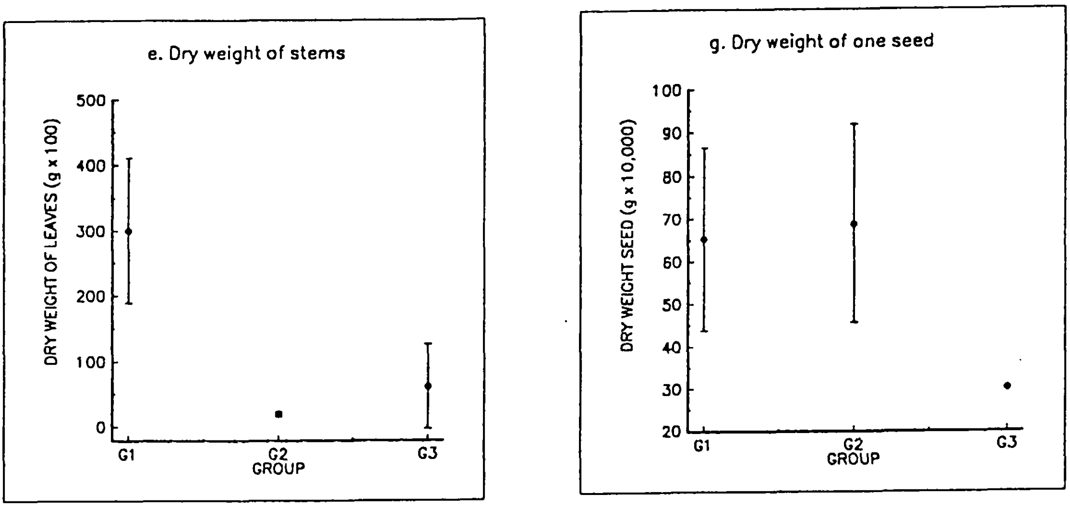


Fig. 2.3 continued.



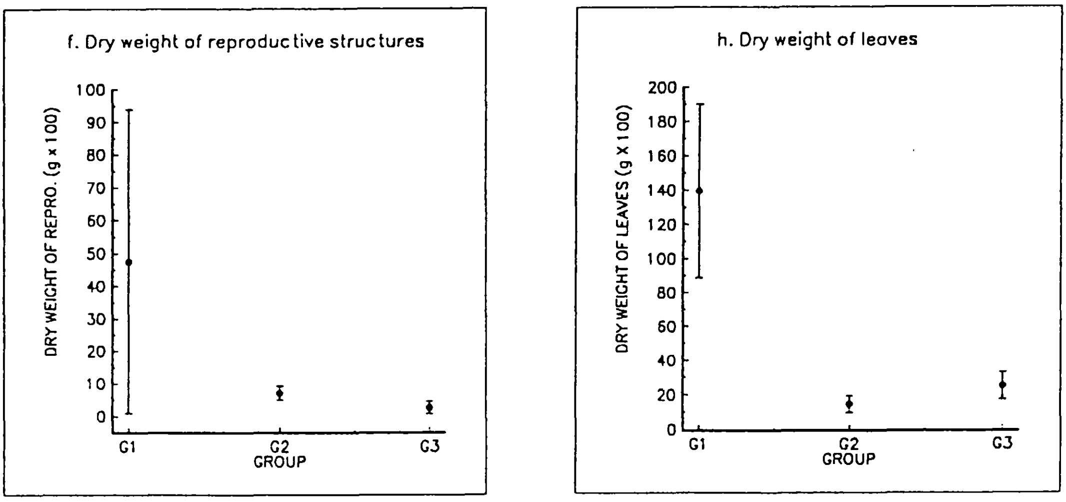


Table 2.3 The species found in G1, G2 and G3 of a non-hierachical classification of wetland plant populations using morphological traits.

GROUP 1	GROUP 2	GROUP 3
Centaurea nigra	*Agrostis canina*	*Aeluropus sp.*
Cirsium arvense	*Agrostis capillaris*	*Agrostis stolonifera*
Cyperus longus	*Cynosurus cristatus*	*Carex acutiformis*
Deschampsia cespitosa	*Cyperus nigra*	*Carex arenaria*
Echinochloa crus-gali	*Danthonia decumbens*	*Carex disticha*
Eryngium campestre	*Eleocharis palustris*	*Umbelliferae*
Filipendula ulmaria	*Euphorbia cyparissus*	*Carex elata*
Lamium maculatum	*Gaudinia fragilis*	*Carex nigra*
Leontodon autumnalis	*Gnaphalium album*	*Cynodon dactylon*
Mentha aquatica	*Holcus lanatus*	*Eleocharis palustris*
Phalaris arundinacea	*Juncus inflexus*	*Elymus sp.*
Phragmites australis	*Mentha pulegium*	*Erica tetralix*
Plantago lanceolata	*Molinia caerula*	*Galium aparine*
Puccinellia festuciformis	*Narthecium ossifragum*	*Galium palustre*
Rumex acetosa	*Phleum pratense*	*Glyceria fluitans*
Rumex conglomeratus	*Plantago lanceolata*	*Hydrocotyle vulgaris*
Rumex crispus	*Poa trivialis*	*Lathyrus palustris*
Senecio aquaticus	*Sagina rubra*	*Lotus pedunculatus*
Solidago canadensis	*Alopecurus geniculatus*	*Phalaris arundinacea*
Urtica dioica	*Bromus sp.*	*Phragmites australis*
	Caltha palustris	*Poa trivialis*
	Cardamine pratensis	*Potentilla anserina*
	Carex echinata	*Ranunculus aquatilus*
	Carex vulpina	*Ranunculus bulbosus*
	Frankenia laevis	*Ranunculus repens*
	Galium aparine	*Salix alba*
	Galium verum	*Saxifraga sp.*
	Hordeum marinum	*Stellaria graminea*
	Juncus maritimus	*Urtica dioica*
	Limonium sp.	
	Luzula campestre	
	Lychnis flos-cuculi	
	Poa pratensis	
	Ranculus acris	
	Ranunculus repens	
	Rhinanthus minor	
	Schoenus nigricans	
	Mentha aquatica	
	Dactylis glomerata	
	Deschampsia cespitosa	
	Carex acutiformis	
	Lolium perenne	
	Juncus effusus	
	Anthoxanthum odoratum	
	Carex nigra	
	Carex distica	
	Carex panicea	
	Phalaris arundinacea	
	Veronica sp.	

contains species such as *Anthoxanthum odoratum*, *Agrostis capillaris* and *Holcus lanatus*.

Classification by morphology alone takes account of only part of the variation in plants that is possible to describe using traits. However, the extent to which a morphological classification is related to other aspects of the plant's ecology is poorly understood. To determine the degree to which the classification presented here can be used to extrapolate further ecological aspects of the species, the groups were related to the strategy database of Grime *et al.* (1988).

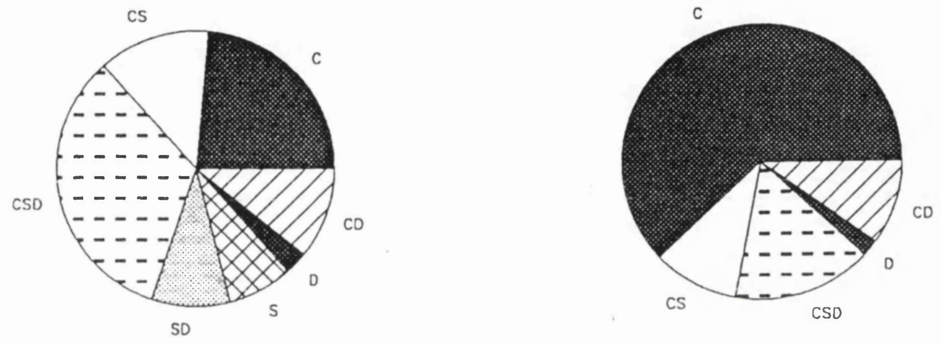
2.3.5 The relationship of the morphological classification to the strategy model of Grime.

The proportion of the populations in each of the strategy categories of Grime was calculated for the all the 98 populations (the null model) (Fig. 2.4a.) and for G1, G2 and G3 (Fig 2.4b, c and d respectively). The R (ruderal) category of Grime was removed from statistical analysis because the expected value of the χ^2 was less than 5. Using χ^2 tests all of the 3 groups were significantly different to the null model (G1 $\chi^2 = 82.2$, $P < 0.001$; G2 $\chi^2 = 23.6$, $P<0.01$ and G3 $\chi^2 = 126.1$, $P<0.001$; all with df = 5). Thus, each group has significantly more plants of a certain strategy or strategies among their members than would be expected through randomness.

G1 contains many C strategists, over 75% of the total. A majority of the remaining members were from CS and CD categories. Thus, G1 compared well to the competitive plants of Grime *et al.* (1988) (Fig. 2.4b.). G2 was dominated by C-S-D strategy plants, containing over 80% of all the intermediate (C-S-D) plants in the total data set. The remaining plants in G2 were drawn from all strategy categories (Fig. 2.4c.). G3 consisted mainly of plants of an intermediate to competitive strategy, the CD group was proportionally well represented (70% of the total) and C, CS and C-S-D making up most of the remainder (Fig. 2.4d.).

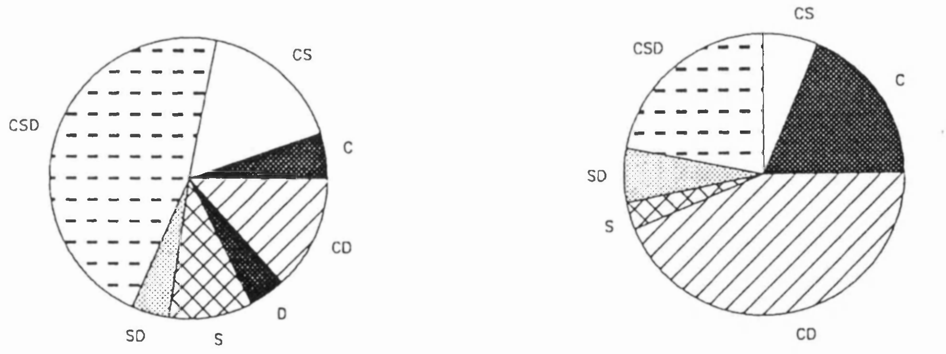
Classification using morphological traits produced groups which were interpretable in terms of strategies, *sensu* Grime. The competitive element was strongest in the null model with C, CD, CS and C-S-D constituting over 80% of all studied plant populations. As a result all three groups showed a tendency toward dominance by C-characteristics, with G1 being dominated by competitive plants, G2 by (C-S-D) intermediates. G3 was a more heterogeneous group consisting of plants of an intermediate to competitive nature more closely related to G2 than G1 and with a stronger D component than G1 or G2.

Fig. 2.4 The proportion of the populations in the strategy categories of Grime for the null model of the whole data set and for G1, G2 and G3 from the sum of squares classification.



a. Null model

b. G1



c. G2

d. G3

The ecological attributes of the groups can be inferred from information contained in Grime *et al.* (1988). For example the plants in G1 would tend to have a high dense canopy of leaves, extensive lateral spread above and below ground, a rapidly ascending monolayer, well defined peaks of production, high mean potential growth rate and little storage of photosynthate and mineral nutrients (Grime *et al.* 1988, pp. 23-24). The results suggested strongly that morphological traits can be used to classify plants into functional groups which have differing ecological properties. Morphological traits covary with other aspects of the plant's life-history and physiology and thus can be validly used as the basis of classification systems of plants.

2.4 DISCUSSION

The analysis above highlighted a strong association between the morphological traits measured in this study and C-S-D strategy groups. To an extent, the association between these differently-defined functional classifications was not unexpected. Grime *et al.* (1988) used some morphological measures in their dichotomous key for definition of the strategy of the "marker" species. Thus, the morphologically-defined groups and the C-S-D strategy groups were not fully independent. In addition to morphology, Grime *et al.* (1988) used information on the phenology and life-history of the "marker" species to determine plant strategy. However, in this case a similar classification was obtained without the phenological and life-history data utilised by Grime *et al.* (1988). This suggests that in the case of the wetland plant populations studied, differences in phenology and life-history were relatively unimportant or largely redundant compared to the variation in the morphology.

Grime *et al.* (1987) in a classification of 273 plant species from the Sheffield area using vegetative attributes, found that morphological vegetative attributes were important determinants of strategy groups. In a "conservative" classification (where g was between 2 and 6) three groups were selected. Although one group was almost exclusively annual species, the division between the other two predominantly perennial groups was on the basis of morphological features. Much of the differentiation between the seven groups of the "liberal" classification (where g was from 7 to 12) was on the basis of morphological features, especially height.

Leishman & Westoby (1992) calculated the degree of association between traits of species from Australian semi-arid woodlands using the Bray-Curtis dissimilarity index. A re-analysis was carried out of Table 3. (p. 420, Leishman & Westoby

1992) which displayed the degree of associations between vegetative, life-history, phenological and seed biology traits. The re-analysis showed that, besides the presence of shallow roots and soft leaves, plant height (defined as the maximum height to the nearest cm) was the trait most associated with the other vegetative traits (Table 2.4a). The association for each trait with all the 55 other traits was calculated as a percentage. Plant height was seventh equal (with summer flowering) in its degree of association with 55 traits associated with vegetative, life-history, phenology and seed biology; it had a Bray-Curtis dissimilarity index of greater than 0.6 in 34% of its associations with other traits (Table 2.4b). Height was thus one of the more important traits used to classify the semi-arid plant species.

Moore & Noble (1990) in the FATE (Functional Attributes in Terrestrial Ecosystems) model of vegetation stand dynamics noted that although the model uses plant age as the determinant of their competitive and reproductive status, they were "aware that the size of a plant may be a better quantity to use , and that combining age and size would be better still" (Moore & Noble 1990).

Literature evidence suggests that plant size is related to aspects of the ecology of plant species. Keddy (1990) found that plant height was related to competition intensity in the community. Menges & Waller (1983) concluded that plant height was related to growth rate and competitiveness. Poorter & Remkes (1990), in a study on seedlings found specific leaf area to correlated to relative growth rate.

It is paramount, however, to note that although morphological / ecological associations have been found, these are only correlative. It could be proposed that plant morphology was actually the end result of the physiological actions of the plant. The underlying process determinating the ecology of a plant species would be its physiology, the plant morphology being related to the resultant physiological processes of the plant.

The overall aim of this work was to produce a functional assessment of plant communities using simply measurable variables. Thus, in this case, although physiological traits would potentially be of more fundamental value, they would require too much specialist expertise. It was thus decided to try to use the relatively simply measured morphological traits, and their underlying association with physiology, as the data source for a functional assessment. This work showed that there was a strong relationship between plant morphology and aspects of a plant's ecology. The next chapter develops a methodology for the description of plant populations and communities using morphological traits.

Table 2.4a The percentage of strong associations between each vegetative trait and all the other vegetative traits (adapted from Leishman & Westoby (1992). *Journal of Ecology*, 80, 417-424).

Vegetative trait	% of strong associations
Soft leaves	45
Shallow roots	42
Height	**38**
Forb	33
Leaf area	31
Hairiness	31
Deep roots	17
Tree	11
Subshrub	11
Succulent leaves	9
Stiff leaves	9
Grass	0
Spines	0
Shrub	0

Table 2.4b The ten traits most associated with the other 55 traits and their percentage of strong associations (from data in Leishman & Westoby (1992)).

Trait	% of strong associations
Shallow roots	56
Flowering in spring	53
C3 physiology	52
Resprout ability	48
Seed release in spring	48
Germination in autumn	35
Height	**34**
Flowering in summer	34
Unassisted dispersal	33
Flowering in autumn	32

A METHOD FOR CLASSIFYING EUROPEAN RIVERINE WETLAND ECOSYSTEMS USING FUNCTIONAL VEGETATION GROUPS.

3.1 INTRODUCTION

Much evidence supporting the validity of the C-S-D strategy theory as a general framework contributing to the understanding of plant-environment relationships has been collected (e.g. Campbell & Grime 1989; Grime 1984; Grime 1988; Grime *et al.* 1987; Murphy *et al.* 1990). Other papers have concentrated on finer understanding of certain aspects of the general principles of the C-S-D strategy theory; for example Campbell, Grime, Mackey & Jalili (1991) and Grime & Sibley (1986) in relation to nutrient use and dynamics.

The potential of using the C-S-D strategy theory as the basis of a classification system, or as an explanatory model of plant communities has, so far, been little realised. However, a few examples where the general principles of the C-S-D theory have been applied to attempt to understand the pattern and functioning of plant communities are apparent. Kautsky (1988) used an adapted version of the C-S-D theory, which included a fourth strategy (termed biomass storers), to create a general framework on which to consider both terrestrial and aquatic plants. Murphy *et al.* (1990) used a strategy approach to assess the vegetation - environment relationship in four geographically distinct lakes. They suggest that the strategy approach "may prove valuable both in selecting appropriate management measures and in predicting their effect on the target community" (Murphy *et al.* 1990). The movement away from multivariate, species-orientated descriptions to models of general applicability is "one of the current challenges in community ecology" (Day *et al.* 1988).

It was shown in the previous chapter that morphological traits of wetland plants were strongly associated with the C, S and D strategy categories assigned to species by Grime *et al.* (1988). The work presented in this chapter uses plant morphological attributes to formulate a model of vegetation in terms of plant functional status, with general applicability to European riverine wetland ecosystems. The approach differs from other work because it attempts to objectively determine the traits associated with strategies, and uses a continuous scale of variation in strategies.

This work has three primary objectives:

1. To identify a set of easily-measurable plant traits which are associated with the C, S and D strategy types.
2. To use this sub-set of traits as a basis of a determination of the strategy characteristics of adult plant populations.

3. To extend the use of population strategy characteristics to classify riverine European wetland plant communities into functional vegetation types.

3.2 METHODS

3.2.1 Trait measurement

During the April to October 1991 and 1992 data on 12 traits was recorded from hydrogeomorphic units. Eight traits were the same as those used in the classification analysis in Chapter 2, i.e.:

1. Height of plant (HEIGHT).
2. Area of the plant canopy (AREA).
3. Number of leaves (LEAVES).
4. Number of seeds (SEEDS).
5. Dry weight of leaves (WTLEAF)
6. Dry weight of stem (WTSTEM)
7. Dry weight of reproductive structures (WTREPRO).
8. Seed weight (WTSEED).

One further morphological trait was measured:

9. Total leaf area (LEAFAREA). The total area of the leaves of each individual was measured, in cm^2, using a calibrated Delta video area meter. The leaf area of the individual as found in the natural situation was measured, no attempt was made to flatten leaves that were naturally curved or creased.

Three chemical traits were recorded for the plant populations (see Appendix 3.1 for methods):

10. Nitrogen concentrations in the leaf (NCONC).
11. Phosphorus concentrations in the leaf (PCONC).
12 Potassium concentrations in the leaf (KCONC).

The 12 traits measured were summarised in Table 3.1.

3.2.2 Data analysis

Due to the nature of the trait data, a multivariate method was required for data analysis. Many multivariate statistical methods consider the equality between populations, searching for similarities or differences between sets of multivariate data (Krzanowski 1988). This procedure would be rather uninteresting as the intuitive *a priori* distinction between two or more groups (e.g. sets of plant species with different survival strategies) suggested that they were different. A more positive approach would be to attempt to describe and interpret differences

Table 3.1 Summary information on the twelve measured traits.

TRAIT	CODE	MEASUREMENTS PER POPULATION	PLACE OF MEASUREMENT	UNITS
Height of plant	HEIGHT	10	FIELD	cm
Area of plant canopy	AREA	10	FIELD	5x5cm squares
Number of leaves	LEAVES	10	FIELD	-
Number of seeds	SEEDS	10	FIELD	-
Total leaf area	LEAFAREA	10	LABORATORY	cm^2
Dry weight of leaves	WTLEAF	10	LABORATORY	$10^{-2}g$
Dry weight of stem	WTSTEM	10	LABORATORY	$10^{-2}g$
Dry weight of reproductive structures	WTREPRO	10	LABORATORY	$10^{-2}g$
Weight per seed	WTSEED	1	LABORATORY	$10^{-5}g$
N conc. in leaves	NCONC	1	CHEMISTRY LABORATORY	% of dry weight
Pconc. in leaves	PCONC	1	CHEMISTRY LABORATORY	% of dry weight
K conc. in leaves	KCONC	1	CHEMISTRY LABORATORY	% of dry weight

between characters of two or more populations. This was carried out using discriminant analysis.

An *a priori* selection of studied plant populations with predominantly competitive, stress-tolerant and intermediate (C-S-D) strategies was made from the listings by Grime *et al.* (1988). None of the studied species had a predominantly disturbance-tolerant survival strategy, so this strategy-type was eliminated from the analysis. In total, 23 populations (7 primarily competitive and 6 primarily stress-tolerant and 10 intermediate) were utilised, consisting of 15 species (Table 3.2). A linear discrimination analysis was carried out between seven competitive and six stress-tolerant species using the 12 measured traits. A multiple discriminant analysis was carried out between the competitive, stress-tolerant and intermediate groups using the 12 measured traits. All analyses were carried out using SPSSx.

The plant populations that were designated as competitors (C) by Grime *et al.* 1988, were arbitrarily given a score of 10 for competitive ability and 0 for stress-tolerance. Stress-tolerant plants were given a score of 10 for stress-tolerance and 0 for competitive ability. Intermediate strategists (C-S-D) were given a score of 5 for both stress-tolerance and competitive ability. Multiple regression was used to determine which of the traits important in distinguishing competitive plants and stress-tolerant plants, identified using discriminant analysis, were the most important in predicting the designated strategy scores of the 23 plant populations. The predictive equations from the multiple regressions were subsequently utilised to produce C and S values for all the 144 plant populations sampled.

3.3 RESULTS

At the start of the linear discriminant analysis between the C and S groups, one variable (KCONC) was selected out because it did not pass the tolerance test (set at $P<0.001$). Prior to discrimination, the probability that the two *a priori* samples were from the same population was $P<0.001$ ($\chi^2 = 33.864$, df = 12), the C and S populations were thus significantly different using the remaining 11 descriptor variables.

The linear discrimination function distinguished between the C and the S groups. Over 28 canonical discriminant function units separate the C and S populations; the groups were thus highly distinguished (Fig. 3.1). The traits that discriminated for competitive and stress-tolerant groups were ranked in order of discriminatory power (Table 3.3).

The canonical correlation for the discriminant function, a measure of association which measures the degree of relatedness between the groups and the discriminant function (on a scale of 0, for no correlation, to 1 for a perfect correlation) , was

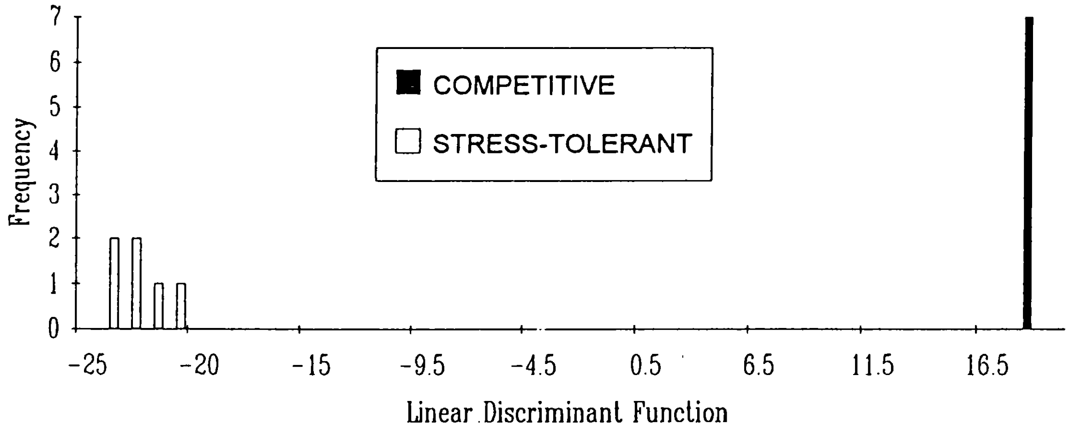
Table 3.2 Competitive (C), stress-tolerant (S) and intermediate strategy (C-S-D) a priori selected plant populations.

STRATEGY	PLANT SPECIES	SITE CODE
C	*Cirsium arvense* (L.) Scop.	EBM1
C	*Phalaris arundinacea* L.	EBM2
C	*Phalaris arundinacea* L.	FAP4
C	*Phalaris arundinacea* L.	FDC1
C	*Urtica dioica* L.	FAP1
C	*Urtica dioica* L.	FAP2
C	*Urtica dioica* L.	FDC2
S/D/CSD	*Anthoxanthum odoratum* L.	EKS3
SC/S	*Carex nigra* (L.) Reichard	ICL5
SC/S	*Carex nigra* (L.) Reichard	ILB4
S	*Carex panicea* L.	EKS2
S	*Danthonia decumbens* (L.) DC	ILB1
S	*Deschampsia cespitosa* (L)Beauv.	ICL2
C-S-D	*Agrostis capillaris* L.	EBM1
C-S-D	*Agrostis capillaris* L.	FAP3
C-S-D	*Agrostis canina* L.	EKS3
C-S-D	*Cynosurus cristatus* L.	ILB1
C-S-D	*Eleocharis palustris* (L.) Roemer & Schultes	ILB2
C-S-D	*Holcus lanatus* L.	EBM3
C-S-D	*Holcus lanatus* L.	EKS1
C-S-D	*Holcus lanatus* L.	ICL5
C-S-D	*Hydrocotyle vulgaris* L.	ILB4
C-S-D	*Rumex acetosa* L.	EBM1

Table 3.3 The importance of twelve traits in discriminating between competitive (C) and stress-tolerant (S) plant populations.

DISCRIMINATING FOR C	DISCRIM. FUNCTION
1. Dry weight of leaves	26.3
2. Height of plant	20.5
3. N conc. in leaves	8.3
4. P conc. in leaves	8.3
5. Number of seeds	1.5
DISCRIMINATING FOR S	
6. Dry weight of repro. structures	-15.0
7. Area	-9.9
8. Dry weight of stem	-8.8
9. Number of leaves	-8.7
10. Area of leaves	-6.3
11. Dry weight of a seed	-2.4
REDUNDANT	
12. K conc. in leaves	

Fig. 3.1 The frequency of occurence of competitive and stress-tolerant plants on a linear discriminant function axis, using twelve descriptive variables.



0.9989. The discriminant function therefore provides a powerful means of distinguishing between the C and S groups. Retrospective classification of the 13 populations utilised in this analysis, using the discriminant function, resulted in correct assignment of all populations to their *a priori*-defined C or S groups.

To determine the position of the intermediate (C-S-D) populations a multiple discriminant analysis was carried out between the C, S and C-S-D groups of plant populations (Fig. 3.2). Initially, the three groups were significantly different ($P<0.01$, $\chi^2=55.1$, df = 22). However, after the first discriminant function they were not significantly different ($P=0.26$, $\chi^2=13.45$, df=22). The first discriminant function had a canonical correlation of 0.973. WTLEAF, HEIGHT and KCONC were the three most important variables that discriminated for competitive plants. Separation of stress-tolerant plants and plants with an intermediate strategy was not clear on the first discrimination axis.

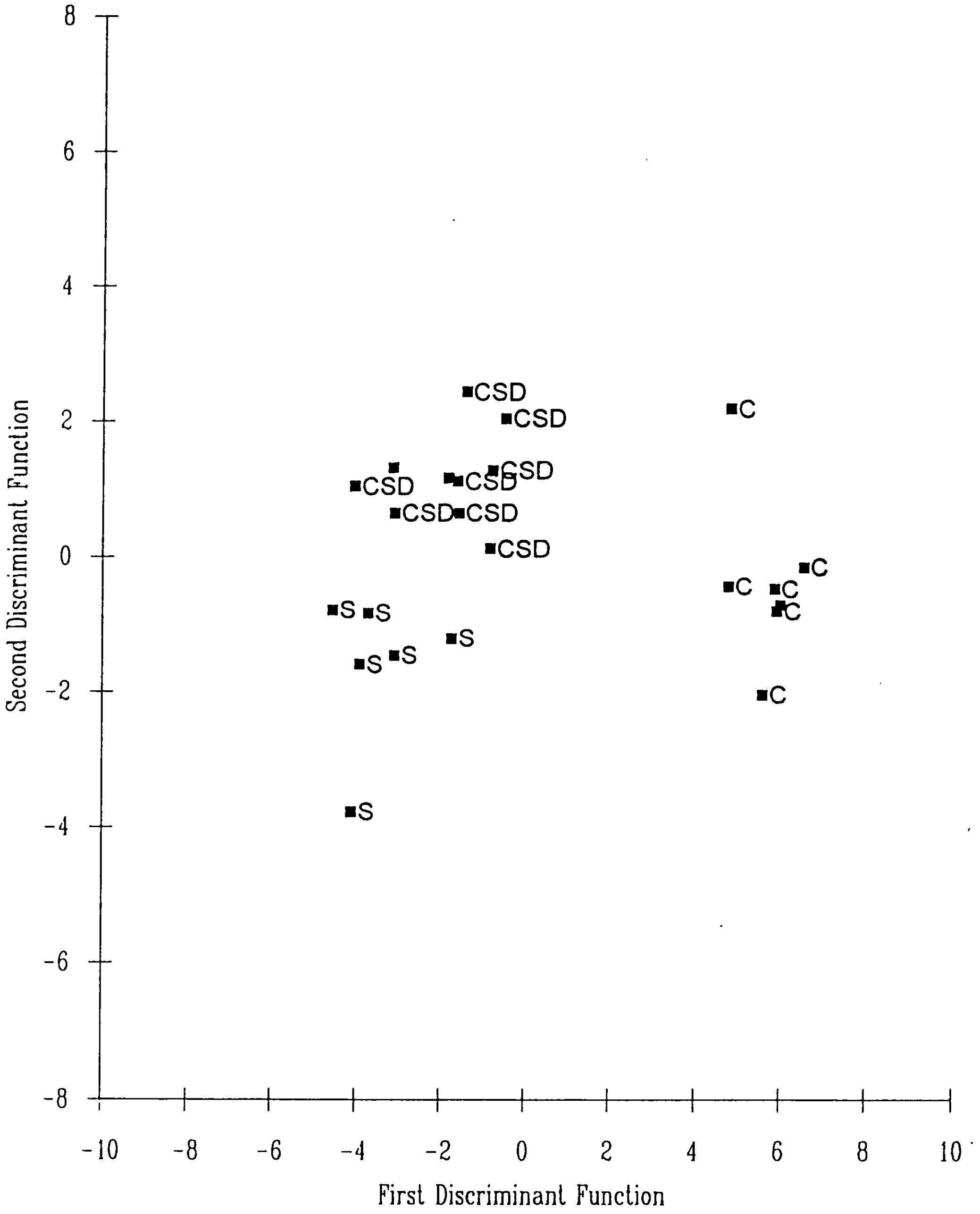
The second axis was much less powerful in its ability to discriminate between the three groups of plants. It explained only 8.4% of the variance, as opposed to the first discriminant function which explained 91.6% of the variance. The canonical correlation of the second axis was 0.778.

Using the discriminant functions of the first and second axes, the 23 plant populations were retrospectively classified 100% correctly. The competitive plants were highly distinct from the stress-tolerant plants and plants with an intermediate strategy, being found at the positive end of the first axis (Fig. 3.2). Stress-tolerant plants and plants with an intermediate strategy, although distinct, were closer together (Fig. 3.2). Distinction between S and C-S-D was gained predominantly from the second discriminant axis. On the first axis the plants with an intermediate strategy were placed between the stress-tolerant and the competitive plants.

The next step was to use stepwise multiple regression to determine which of the traits were good predictors of C and S strategies. The traits used to predict competitive ability were the variables that distinguished for competitive plants in the linear discriminant analysis (Table 3.3). The first independent variable selected by the stepwise multiple regression to predict competitive ability was height of the plant (HEIGHT) ($P<0.01$, df = 22); 36% of the variation in the strategy score was explained by this relationship. The second variable selected by the stepwise multiple regression was the dry weight of the leaf (WTLEAF). The significance of the relationship was improved by the addition of the second variable ($P<0.0001$, df = 22), 59% of the variation in the C strategy score was explained by the two independent variables. The predictive equation was:

$$\text{Competitive ability} = (\text{HEIGHT} \times 0.0602) + (\text{WTLEAF} \times 0.0181) + 0.4690$$

Fig. 3.2 Plot of the first and second axes of a multiple discrimination analysis used to distinguish between competitive (C), stress-tolerant (S) and intermediate strategy (CSD) plants.



Stepwise multiple regression was used to predict the stress-tolerance of the same 23 plant populations. The first variable selected was weight of stem (WTSTEM). The relationship between the designated stress scores and the dry weight of the stem was highly significant ($P<0.001$, df = 22), and 49% ($r^2 = 0.49$) of the variation in the stress-tolerance scores was explained. The relationship between the dependent and independent variable was inverse ($B = -0.011$): stress-tolerant plants tend to have a small dry weight of stems. The second variable selected by the regression was the weight of a seed, the predictive power of the relationship improved ($P<0.0001$, df = 22) and 62% of the variation in the stress-tolerance scores was explained ($r^2 = 0.62$). No further variables were significantly related ($P<0.05$) to the residual variation of the scores of stress-tolerance. The equation for the prediction of stress-tolerance was:

$$\text{Stress-tolerance} = (\text{WTSTEM} \times -0.0101) + (\text{WTSEED} \times 0.0097) + 5.4456$$

The use of discriminant analysis coupled with stepwise multiple regression identified traits associated with the primary strategies of competitive ability and stress-tolerance in populations of wetland plants, and permitted the assigning of C and S scores to each of the 144 populations studied. Competitive ability varied between 18.0 (*Phragmites australis*, SMW4) and 0.6 (*Aeluropus sp.*, SMD2). Stress-tolerance varied from 12.3 (*Danthonia decumbens*, ILB1) to -3.2 (*Urtica dioica*, FDC2) (Table 3.4). Negative scores were possible for plant populations if the population had traits which were less competitive or stress-tolerant then the original marker species. The few populations which could not be positively identified to species level were still used in the further analyses as the aim of the study was to describe vegetation in terms of strategy not taxonomy; other groups within the project were dealing with the taxonomy. Populations of the same species, from different wetland locations tended to have similar strategies. For example, in 1991 *Holcus lanatus* was measured at eight hydrogeomorphic units in England, France and Ireland. The C value varied from 3.0 to 5.2 and the S value from 5.3 to 6.5 for these eight populations (Table 3.4).

Individual plant populations were grouped together into species assemblages per hydrogeomorphic unit and mean of the C and S scores were used to produce CFVT and SFVT (Competitive ability of Functional Vegetation Type, and Stress-tolerance of Functional Vegetation Type) values (Table 3.5). CFVT values ranged from 18.3 (SMW4) to 1.0 (FDC4, FAPS and SMD2), and SFVT values ranged from 6.9 (ILB1) to -1.8 (SMW4).

Table 3.4 Species names, competitive ability and stress-tolerance scores for each plant population studied (* after a species name denotes plant populations that were used to predict the survival strategy of the other listed species) (nomenculature as Appendices 1.1-1.4).

a. Data collected in 1991

Species name	**Quadrat code**	**Competitive ability**	**Stress-tolerant ability**
Agrostis canina L.*	EKS3	3.7	5.5
Agrostis capillaris L.*	EBM1	3.7	5.4
" "	EBM1	3.2	6.2
Anthoxanthum odoratum L.*	EKS3	3.0	5.8
Carex nigra (L.) Reichard	EKS2	1.5	5.4
Carex panicea L.*	EKS2	2.4	7.6
Cirsium arvense (L.) Scop.*	EBM1	10.5	1.0
Dactylis glomerata L.	EBM2	3.0	5.4
Deschampsia caespitosa (L.) Beauv.	EBM2	7.6	5.4
Filipendula ulmaria (L.) Maxim	EBM3	10.6	3.7
" "	EKS1	6.7	3.9
Holcus lanatus L.	EBM1	5.3	5.3
" "	EKS3	4.2	5.4
" " *	EBM3	4.8	5.6
" " *	EKS1	4.4	5.8
Juncus effusus L.	EBM2	8.1	6.1
" "	EBM3	8.2	6.0
" "	EKS1	4.7	5.5
Juncus inflexus L.	EKS1	5.6	5.6
Molinia caerulea (L.) Moench.	EKS2	2.4	5.6
" "	EKS3	4.0	6.0
Narthecium ossifragum (L.) Hudson.	EKS2	1.6	5.4
Phalaris arundinacea L.*	EBM2	8.5	3.7
Poa trivialis L.	EBM3	4.0	5.4
Rumex acetosa L.*	EBM1	3.7	5.2
Agrostis capillaris L. *	FAP3	2.7	3.4
Carex arenaria L.	FDC3	0.8	5.4
Carex elata All.	FAP3	2.0	5.4

Carex otrubae Podp.	FAP4	3.5	6.6
Cynodon dactylon (L.) Pers.	FAP3	1.1	5.1
Cyperus longus L.	FDC1	6.0	4.9
Cyperus fuscus L.	FAPS	0.8	5.3
Echinochloa crus-galli (L.) Beauv.	FDC1	5.5	3.9
Eryngium campestre L.	FDC3	7.6	3.4
Euphorbia cyparissias L.	FDC3	1.4	5.1
Gaudinia fragilis (L.) Beauv.	FDC3	2.4	6.0
Gnaphalium luteo-album L.	FAPS	1.3	5.8
Holcus lanatus L.	FAP3	3.0	5.5
Mentha pulegium L.	FDC4	1.0	5.7
Phalaris arundinacea L.*	FDC1	9.0	2.9
" " *	FAP4	6.1	3.8
Potentilla anserina L.	FAP4	1.5	5.4
Rumex crispus L.	FAP4	3.8	3.0
Sagina nodosa (L.) Fenzl.	FDC4	0.9	5.5
Salix alba L.	FAPS	1.9	5.4
Solidago canadensis L.	FAP1	4.6	4.8
Urtica dioica L.*	FAP1	8.5	1.8
" " *	FAP2	9.7	-0.4
" " *	FDC2	11.4	-3.2
Veronica sp.	FAPS	1.0	7.4
Agrostis stolonifera L.	ICL1	1.9	5.4
Anthoxanthum odoratum L.	ICL5	3.5	6.3
" "	ICL5	3.5	6.3
Carex acutiformis Ehrl.	ILB3	6.5	4.3
" "	ICL1	3.8	5.2
Carex disticha Hudson	ILB2	3.2	5.4
" "	ILB3	3.5	6.2
" "	ILB3	3.7	5.3
" "	ICL2	2.9	5.8
" "	ICL4	3.7	5.3
Carex nigra (L.) Reichard	ICL4	1.9	6.2
" "*	ICL5	1.9	6.3
" " *	ILB4	2.4	7.0
Cynosurus cristatus L.*	ILB1	3.2	6.2
Danthonia decumbens (L.) DC.*	ILB1	3.3	12.3
Deschampsia caespitosa (L.) Beauv.*	ICL2	6.6	5.0
" "	ICL2	6.6	5.0

Eleocharis palustris (L.) Roemer & Schultes.	ICL1	4.2	5.6
" " *	ILB2	3.7	5.5
Filipendula ulmaria L.	ILB4	5.7	4.6
Holcus lanatus L.	ILB1	4.2	5.6
" "	ICL4	4.3	6.5
" " *	ICL5	4.8	5.4
Hydrocotyle vulgaris L. *	ILB4	1.5	5.4
Leontodon autumnalis L.	ILB4	4.8	4.9
Lolium perenne L.	ILB1	4.4	7.7
Mentha aquatica L.	ICL1	3.9	5.4
" "	ICL2	4.2	5.0
" "	ILB3	2.9	4.9
Phalaris arundinacea L.	ILB3	5.2	5.3
Phleum pratense L.	ILB1	3.5	5.2
" "	ICL2	3.5	5.2
Plantago lanceolata L.	ILB1	3.6	7.5
" "	ICL2	3.4	5.9
Poa pratensis L.	ICL2	3.7	5.2
Ranunculus acris L.	ICL2	2.8	7.1

Table 3.4 b. Data from 1992

Species name	Quadrat code	Competitive ability	Stress-tolerant ability
Centaurea nigra L.	EBM1	6.69	3.79
Erica tetralix L.	EKS2	1.67	5.37
Holcus lanatus L.	EBM1	6.67	5.27
Lotus pedunculatus non. Cav.	EBM3	5.48	4.78
Molinia caerula (L.) Moench.	EKS2	1.84	5.44
Poa trivialis L.	EBM1	3.07	5.39
Senecio aquaticus Hill.	EBM3	7.67	8.04
Agrostis capillaris L.	FAP3	0.98	5.42
Alopecurus geniculatus L.	FAP4	3.84	5.45
Carex vulpina L.	FAP4	3.96	5.40
Galium aparine L.	FAP2	4.41	5.15
" "	FDC2	5.48	4.99
Galium verum L.	FDC3	1.87	5.35
Glyceria fluitans (L.) R. Br.	FDC4	1.27	5.26
Luzula campestris (L.) DC.	FDC3	1.11	5.82
Phalaris arundinacea L.	FAP4	3.07	5.12
Poa trivialis L.	FDC4	0.91	5.52
Ranunculus aquatilis L.	FDC3	0.78	5.43
Ranunculus bulbosus L.	FDC3	1.74	5.23
Ranunculus repens L.	FAP3	3.34	4.77
" "	FAP4	4.54	4.66
Rumex conglomeratus Murray	FAP4	15.39	6.72
Saxifraga sp.	FDC3	1.78	5.35
Stellaria graminea L.	FDC3	1.14	5.42
Urtica dioica L.	FAP2	3.82	2.19
" "	FDC2	8.21	1.22
Agrostis stolonifera L.	ILB2	1.60	5.42
Caltha palustris L.	ILB2	2.59	5.34
Cardamine pratensis L.	ICL4	1.45	5.62
Carex disticha Hudson	ILB2	5.00	5.52
" "	ILB4	1.87	5.40

Carex echinata Murray	ICL4	1.45	5.62
Carex nigra (L.) Reichard	ILB4	1.45	5.90
Galium palustre L.	ICL5	2.14	5.40
Lathyrus palustris L.	ICL5	2.91	5.16
Lychnis flos-cuculi L.	ICL4	3.06	5.21
Molinia caerula (L.) Moench	ICL3	4.17	5.46
" "	ILB1	3.69	5.56
Plantago lanceolata L.	ILB1	2.32	5.61
Ranunculus repens L.	ILB4	1.83	5.82
Rhinanthus minor L.	ICL4	2.22	6.34
Aeluropus sp.	SMD2	0.57	5.44
Bromus sp.	SMD3	2.16	6.83
Bromus sp.	SMD4	2.11	5.74
Elymus repens (L.) Gould	SMD4	1.90	5.28
Frankenia laevis L.	SMD2	1.13	5.52
Galium aparine L.	SMD4	5.39	5.70
Hordeum murinum L.	SMD3	1.92	5.75
Juncus maritimus Lam.	SMD1	1.31	5.52
Limonium sp.	SMD1	3.07	5.97
Phragmites australis (Cav.) Trin.	SMD4	12.56	2.84
" "	SMW2	9.49	2.62
" "	SMW3	10.04	3.94
" "	SMW4	18.03	-1.84
" "	SMWE	9.45	1.13
Puccinellia sp.	SMD1	11.98	4.32
Schoenus nigricans L.	SMWE	4.04	5.56
Umbellifera sp.	SMD4	4.91	5.16

Table 3.5 Competitive and stress-tolerant functional vegetation type scores (FVT) for hydrogeomorphic units (standard deviation in brackets).

Unit	Number of plant populations studied	CFVT (Standard deviation)	SFVT (Standard deviation)
EBM1	8	5.43 (2.46)	4.70 (1.64)
EBM2	4	6.79 (2.58)	5.16 (1.01)
EBM3	6	6.77 (2.50)	5.56 (1.45)
EKS1	4	5.33 (1.05)	5.20 (0.80)
EKS2	6	1.91 (0.42)	5.75 (0.82)
EKS3	4	3.76 (O.54)	5.74 (0.26)
FAP1	2	6.55 (2.70)	3.30 (2.1)
FAP2	4	5.96 (1.02)	2.30 (2.79)
FAP3	8	2.71 (1.17)	5.36 (0.30)
FAP4	8	5.22 (4.20)	5.08 (1.30)
FAPS	3	1.22 (0.60)	6.02 (0.78)
FDC1	3	6.82 (1.90)	3.89 (1.00)
FDC2	4	7.75 (2.68)	2.61 (3.85)
FDC3	9	2.19 (2.08)	5.23 (0.72)
FDC4	5	0.97 (0.18)	5.48 (0.16)
ILB1	8	3.42 (0.76)	6.85 (2.39)
ILB2	6	3.29 (1.14)	5.43 (0.07)
ILB3	4	4.56 (1.60)	5.03 (0.38)
ILB4	8	2.74 (1.60)	5.75 (0.87)
ICL1	4	3.46 (1.10)	5.39 (0.14)
ICL2	8	4.20 (1.50)	5.53 (0.72)
ICL3	1	4.17 (NA)	5.46 (NA)
ICL4	8	2.62 (0.95)	6.10 (0.58)
ICL5	3	3.27 (1.34)	5.33 (0.15)
SMD1	3	5.45 (5.70)	5.27 (0.85)
SMD2	2	0.85 (NA)	5.35 (NA)
SMD3	2	2.04 (NA)	6.29 (NA)
SMD4	4	5.37 (4.3)	4.94 (1.20)
SMW2	1	9.49 (NA)	2.62 (NA)
SMW3	1	10.04 (NA)	3.94 (NA)
SMW4	1	18.03 (NA)	-1.84 (NA)
SMWE	2	6.75 (NA)	3.35 (NA)

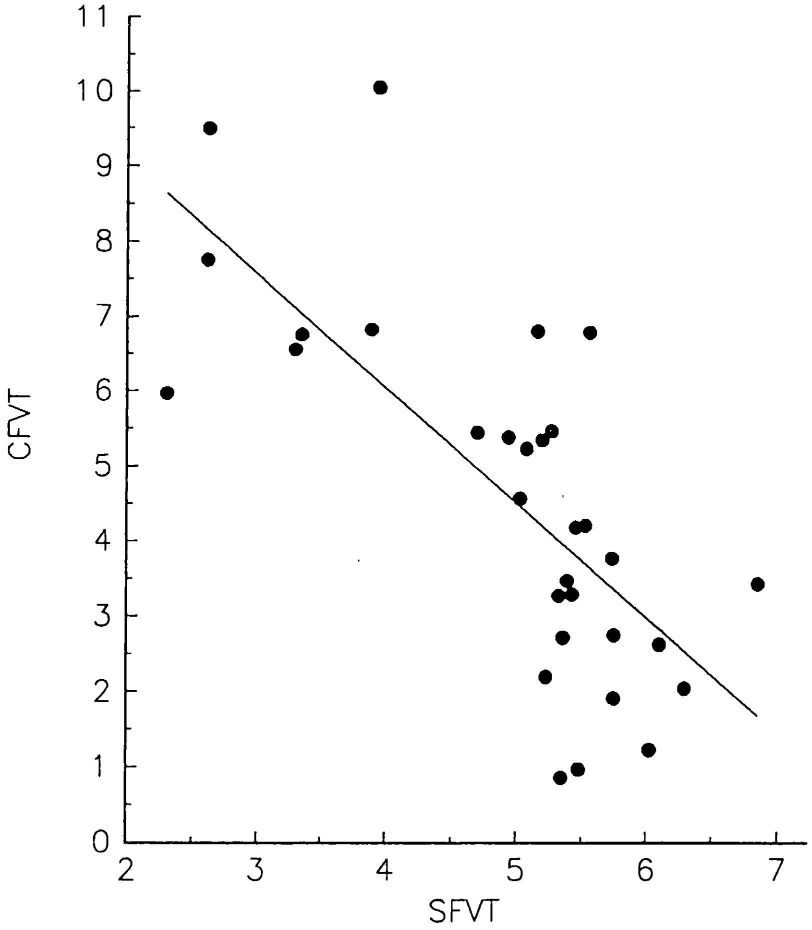
A significant inverse relationship was found between the two independent parameters of CFVT and SFVT for the 32 hydrogeomorphic units (Fig. 3.3). The Pearson product-moment correlation coefficient for the relationship between SFVT and CFVT was $r = -0.73$ ($P<0.001$, df = 31). Thus, a hydrogeomorphic unit with a high CFVT value (i.e. a set of plants in the community with a mean high competitive ability) tends to have a low value of SFVT (i.e. a set of plants with low stress-tolerant ability).

3.4 DISCUSSION

From the predictive stepwise multiple regression equation used to predict competitive ability, it appears that wetland plant populations that were tall and had a large dry weight of leaves tended to have a high competitive ability. In the literature, plant height consistently occurs as a trait positively related to competitive ability of the plant. In the competitive index (CI) used by Grime (1974) to determine the competitive ability of plant species, maximum height of leaf canopy (scored in 10 categories from <12cm to >112cm) was one of three components of the index. In a more recently devised dichotomous key to determine the strategies of herbaceous plant species, the possession of tall and laterally extensive shoots was the character which divided the strategies "competitive" (with) and "intermediate" (without) (Grime *et al.* 1988). Gaudet & Keddy (1988), using a modified additive design in a greenhouse experiment, found a significant negative relationship ($P<0.001$) between the biomass of a phytometer (*Lythrum salicaria*) and height of the test species; taller plants being able to suppress the biomass of the phytometer more than could lower-growing plants. Keddy & Shipley (1989) reworked the data of a lake-shore experiment by Wilson and Keddy (1986) and found that 37% of the variation in competitive ability could be explained by plant height. Menges & Waller (1983) found that the tallest and most competitive of flood plain forest herbs tend to be found in high-elevation areas which were relatively infrequently flooded. The work presented here work supports the idea that there is a positive relationship between height and competitive ability.

From the multiple stepwise regression the residual variation in competitive ability, after regression with height of plant, was best explained by the dry weight of leaves (WTLEAF). Relatively large dry weight of leaves was associated with large residual variation in competitive ability. The structural costs in being tall can be offset by the phytosynthetic gains of having leaves in a relatively unshaded area of sunlight (Givnish 1982), which is conducive to the efficient capture and utilisation of light in competitive environments (Grime 1974). Both plant height and dry

Fig. 3.3 Relationship of CFVT and SFVT of units (r=−0.73, n=32, P<0.001)



weight of leaf are characteristics important in the ability of plants to exploit resources. Grace (1990) proposed that "exploiter" would be a more appropriate term for this group of plants than "competitor" (*sensu* Grime).

Although only above-ground parts of the plant were measured in this study, evidence suggests a positive relationship between competitiveness above-, and below-ground in herbaceous plants. Campbell, Grime, Mackey & Jalili (1991) found a "consistent positive association" between the foraging characteristics of shoots and roots. They proposed that there was a strong interdependence of competitive abilities for exploiting light and minerals.

Stress-tolerance was highly related to certain survival traits of the plants. The dry weight of the stem was the most important trait in determining stress-tolerance of the population. Stress-tolerant plants tend to be small in stature (Grime 1974), have short shoots and are not laterally extensive (Grime *et al.* 1988). Stress-tolerant plants are, thus, morphologically constrained to a low stem dry weight. The ecological significance of a large seed weight, the second selected variable in the stepwise multiple regression, is less obvious. Boorman (1982) noted that a large seed can give an initial advantage to the establishment of a seedling even if the relative growth rate of a competitor is greater. Boorman found that the dry weight of a *Cynoglossum officinale* seedling germinated from a relatively large seed was greater than the dry weight of a *Lactuca virosa* seedling for 27 days, although the relative growth rate of *Cynoglossum* was lower. The functional significance of seed weight in relation to stress-tolerant plant success is not associated with the established-phase strategy of the species on which this study is based. Further work on the regenerative phase of the plant life-cycle would be necessary to elucidate this relationship.

The ability to predict the strategy of plant populations, in terms of competitive ability and stress-tolerance, appears to be possible on the basis of simple trait data. A population-based, field method using continuous data, has led to objective selection of fundamental traits for wetland plant populations. The functional significance of these traits is supported by evidence from other workers. None of the plant populations studied had a high S-high C value, or a low S-low C value. Thus, a plant population cannot exhibit competitiveness <u>and</u> stress-tolerance. There is a trade-off between emphasis on C-favouring and S-favouring traits. This trade-off is paramount to Grime's view of competition; "it is this basic trade-off and its attending physiological constraints that result in a division between 'competitive' and 'stress-tolerant' species" (Grace 1990).

Grime *et al.* (1988) used three axes to describe the strategy of a plant species; competitive, stress-tolerance and disturbance-tolerance. The work presented here has used two axes, competitiveness and stress-tolerance, to describe the plant strategies of riverine wetland plants. None of the common species studied were of primary disturbance-tolerant strategy, or strongly disturbance-tolerant as described by Grime *et al.* (1988). Without purist D strategists, marker species could not be designated in a similar fashion to C and S. Disturbance-tolerance was considered to be of less importance, compared to stress-tolerance and competitive ability, for the wetland plants included in this study. Some of the study sites undeniably suffer some disturbance from sources such as grazing and flooding. However, intuitively, the sites would be low in disturbance compared to, for example, the regular rigorous disturbance common in agricultural systems.

The traits measured in this study may be of little use to predict disturbance tolerance. Keddy (1990) noted that disturbed wetland sites can exhibit a large array of life forms and morphologies compared to fertile and undisturbed sites. However, in highly disturbed situations an ephemeral life-history would appear to be the almost universal solution to selection forces. Life-history traits, as opposed to morphological traits measured in the work presented here, would tend to be more closely correlated to disturbance-tolerance in plants.

Most of the work involving the demarcation of competitive, stress-tolerant and disturbance-tolerant strategies has tended to select the traits which subsequently determine the strategy. For example, Grime *et al.* (1988) produced a dichotomous key of plant traits to determine the strategy of the plant species under study. Murphy *et al.* (1990) selected between four and seven traits to determine the level of C, S and D in submerged lake macrophytes. In these approaches the value of traits has been pre-set, the workers having made assumptions about the functional significance of certain attributes.

An alternative approach, outlined in the work presented here, made an *a priori* decision about the strategy of plant populations but not on the functional significance of traits. Although *a priori* plant strategies were taken from Grime *et al.* (1988) in this work, other sources could be used to determine the strategy of the selected populations e.g. ranking of sites in terms of soil fertility or the screening of populations in laboratory based experiments. This would be important if the work was being carried out in an area with a flora the strategies of which were less well described than for the species included in Grime *et al.* (1988).

Functional groups have previously been identified using descriptive multivariate methods applied to sets of trait data. Shipley, Keddy, Moore & Lemky (1989) used principal co-ordinate analysis of 13 traits to identify adult functional groups in aquatic macrophytes. Leishman & Westoby (1992) used a multivariate clustering procedure on 43 traits of Australian semi-arid species to produce five main groups. The nature of the interaction of the functional groups to the environment is diffuse, as no environmental information is implicit or explicit in the analysis. One of the significant aspects of Grime's model of plant strategies is that the functional groups (C, S and D) are implicitly interconnected with aspects of the environment as they are, by definition, derived from the two main forces in nature acting on plant survival, stress and disturbance. The model of Grime, thus, has general applicability to vegetational systems, and provides a solid basis for the development of strategy models.

Work with functional groups tends to be at the general process and pattern level, more specific than state variables e.g. biomass and species richness, but less specific than species-oriented site and region descriptions (Keddy 1990). Evidence from the work presented here suggests that the C-S-D model provides a valid framework on which to base information on plant functional groups at this general process level. Although the implicit environmental information in the Grime strategy model is non-site specific, simplistic predictions of environmental perturbation can be made from communities in terms of C and S. For example, the addition of fertiliser would tend to make the plants in the community, and thus the community strategy, more free from stress (-S) and favour those which are more competitive (+C). For more refined predictions, sub-divisions of disturbance and stress in the environment may be necessary. The ability to predict is of major importance in ecology, "the test for ecology is not logical consistency, aesthetic appeal or mathematical precision, but the accuracy and utility of its predictions" (Peters 1980). Further work should explore the potential of functional plant groups to predict the effect of environmental perturbation.

BIOMASS ALLOCATION AND LEAF MORPHOLOGY - THEIR RELATIONSHIP TO PLANT STRATEGIES

4.1 INTRODUCTION

The previous two chapters have developed the idea that morphological characteristics of plants can be used as an indicator of strategy. Chapter 2 showed that plants classified on morphological traits were placed in groups which correspond to the strategy groups of Grime *et al.* (1988). Chapter 3 identified a method which permitted the scoring of plant populations in terms of C and S strategy, using a small number of indicative traits. The selected traits indicated that competitive plants tended to have a taller stature and be of greater biomass than stress-tolerant plants. The strategy of the plant was primarily determined by plant size. Although the literature supports this conclusion, many studies have been more concerned with the relative proportions of biomass allocated to different parts of the plant.

Plants operate under certain rules of cost and benefit, under which they adjust their rates of resource acquisition and patterns of resource partitioning (Bloom, Chapin & Mooney 1985). Plants have been considered as similar to a commercial company and economic theory has been used to analyse resource partitioning in plants (Bloom *et al.* 1985). However, complications arise in this approach because money does not have a simple analogue in plants, consideration must be made of not just carbon, but nutrients and water (Bloom *et al.* 1985). Although analysis may not be simple, Schultze & Chapin (1987) wrote that "a key process by which plants respond to changes in their environment is the partitioning of resources into production of new leaves, stems, roots and reproductive structures".

Givnish (1982) proposed that competition for light should be a significant selection pressure on leaf height in forest herbs. A trade-off between photosynthetic gains and structural costs was proposed in which the proportion of above ground biomass in the leaves decreased in relation to leaf height i.e. allocation was proportionally greater to stems as the plant became taller. Givnish (1982) confirmed that this relationship for herbaceous foliage in a mesic floodplain forest. Korner & Renhardt (1987) compared biomass allocation in 47 herbaceous species, 22 species from lowland (~600m) and 27 from high altitude areas (2600 - 3200m) in the Austrian Alps. They found that the average proportion of total dry matter allocated to leaves and storage organs did not change with elevation, but allocation was different between the two altitudes for stems and flowers (Korner & Renhardt 1987). Pickett & Bazzaz (1978) concluded from a study of six early successional weed species that competitive and abiotic stresses were generally absorbed by morphological plasticity, though this could be a characteristic of the opportunistic pioneers that were studied and not a general trend in plants.

Tilman's mechanistic model of plant growth and biomass, called ALLOCATE (Tilman 1988), attempted to explain large scale patterns of plant morphology and vegetational structure. One of the assumptions in the model was that the maximum relative growth rate was negatively related to the ratio of non-photosynthetic tissues to photosynthetic tissues (i.e. root to shoot ratio). To test this assumption, Shipley & Peters (1990) measured the root to shoot ratio and growth rate of 68 wetland herbaceous angiosperms and found that the results did not agree with Tilman's assumption. They proposed that more work should be directed at general predictive relationships among plant traits over measurable environmental gradients. Campbell *et al.* (1991) found a "consistent positive association" between the foraging characteristics of roots and shoots and thus, an interdependence of competitive ability for light and mineral nutrients.

From a survey of the ecological literature it appears that general models of variation in plant biomass allocation, formulated from data, are notably lacking. Two workers have proposed such models Tilman (described above) and Grime (Grime 1979, Grime *et al.* 1988). Grime *et al.* (1988) proposed that competitive plants form a high dense canopy of leaves with extensive spread and respond rapidly to resource depletion by morphogenic responses involving the redistribution of leaf and root biomass. Although such intuitive descriptive generalisations may be true, further work using data and more deterministic analysis would be necessary to clarify these issues.

One area of research that has proceeded, through both laboratory and field-work, has been that of leaf morphological relationships. Poorter & Remkes (1990) found that the leaf area ratio (LAR; the ratio of leaf area and total plant weight) was positively correlated to the relative growth rate (RGR), a characteristic of competitive plants (Grime 1979), for 24 wild plant species. The correlation was predominantly due to specific leaf area (SLA; the ratio of leaf area and leaf weight), rather than the leaf weight ratio (LWR; the proportion of the total biomass allocated to the leaves). The authors postulated that natural selection in a nutrient rich environment favoured species with a high SLA and LWR (Poorter & Remkes 1990). The rate of photosynthesis, expressed on a leaf area basis, was not correlated with RGR, however there was a correlation with leaf photosynthesis expressed per unit leaf weight (Poorter, Remkes & Lambers 1990). Further experiments, using the same species, found that seedlings with a high RGR accumulated more organic N-compounds, organic acids and minerals; although the cost for 1g of plant biomass, in terms of C for C-skeletons and as total glucose costs, was similar for fast and slow growing species (Poorter & Bergkotte 1992). Russell & Grace (1978) found that in controlled conditions there was a correlation between LAR and wind speed (mainly due to the SLA component of LAR) for two grass species. Woodward (1983) from a survey of *Festuca ovina* and *Carex bigelowii* at different altitudes found a significant decline in SLA for both species with altitude, however, the relative effect of temperature and wind speed on this relationship was not clear.

This chapter attempts to assess the applicability of biomass allocation parameters, as opposed to the overall size or biomass considered in the two previous chapters, as a general model for the description and classification of wetland plants. Two areas of morphology will be considered. Firstly, the proportion of above ground allocation to stems and leaves. No root data was collected so root to shoot ratios cannot be considered. The reason for this was that, although root biomass data could be collected for greenhouse grown species, it was not possible to collect such data with a suitable degree of accuracy in the wide range of soil types that the fieldwork for this study used. The overall aim of this work is to produce field-based assessment procedures for wetlands, this necessitates the use of measurable parameters. Secondly, leaf morphology will be considered in terms of LAR, LWR and SLA..

The aim of the work was to answer two questions:

1. Do species have a stereotyped response in terms of biomass allocation to changes in environmental conditions? This question was addressed using a greenhouse experiment involving growing 6 species under a range of treatments representing differing environmental conditions. The environmental perturbations used represented changes in competition, stress and disturbance. From the experimental data, it was aimed to produce indices for C, S and D. This was possible because the treatments represented changes in the balance of stress, disturbance and competition pressures acting on the plants. The indices for C, S and D, calculated from the experiment were related to the values determined in Chapter 3 and by Grime *et al.* (1988).
2. Can a general model of changes in biomass allocation and leaf morphology be determined for mature plants in a range of wetland habitats? A data set of traits collected from 85 populations from FAEWE field sites will be used to attempt to construct a general model of biomass allocation and leaf morphology.

4.2 GREENHOUSE EXPERIMENT

4.2.1 Methods

Malanson (1993) proposed that there were two major gradients in riparian areas; a stress gradient related to moisture and a disturbance gradient formed from dynamic fluvial geomorphology, these two factors represent stress and disturbance respectively. These two factors were simulated in a greenhouse experiment. In addition to a stress and a disturbance treatment, a measure of competitive ability was made following the method of Gaudet & Keddy (1988). This method uses ability of a test species to depress the phytometer biomass as an index of competitive ability of the test species. The experiment was thus designed to have a control (with plentiful water), a stressed treatment (saturated soil moisture), a disturbed treatment (periodic cutting) and a competitive treatment (growth with a phytometer).

Six species of plant were selected on the following criteria:

1. They were found in the FAEWE study sites.
2. They were included in the listings of Grime *et al.* (1988).
3. They were important species in defining CORINE biotopes.

The six species were (with the code in brackets):

1. *Agrostis capillaris* (*Ac*)
2. *Agrostis stolonifera* (*As*)
3. *Cynosurus cristatus* (*Cc*)
4. *Holcus lanatus* (*Hl*)
5. *Lolium perenne* (*Lp*)
6. *Phalaris arundinacea* (*Pa*)

Seeds were purchased from Herbiseed (Billingbear Park, Wokingham, UK.). Seeds were placed in germination containers in potting compost (ICI Growers potting and bedding compost) which were placed in the greenhouse. Natural lighting was supplemented by mercury vapour lamps giving a light intensity providing 13 W m^{-2} for 16 hours a day (Spink 1992). Temperature was thermostatically controlled, and was set to 20°C. After 2 weeks the seedlings were planted out individually into 1 litre plant plots which were full of potting compost. A piece of filter paper was placed over the holes in the bottom of the pot to prevent the compost falling through. Each pot was placed into a 4-litre white, rectangular plastic container (15cm x 21cm and 15cm high). The water level in the bottom of the container was maintained at 3cm by daily watering. The seedlings were left for two weeks to allow them to become established. If any individual died during the first two weeks after planting out, it was removed and a replacement seedling, from the germination tray, was planted in its place. Treatments commenced in week 4.

Three treatments were used:

1. Soil saturation (code: SAT). The water level was maintained by daily watering to the height of the soil in the pot; soil was maintained at 100% saturation..
2. Disturbance (CUT). Every two weeks the plant was cut to 5cm using a pair of blunt scissors.
3. Phytometer (PHYTOM). Each species was grown against a phytometer using the method of Gaudet & Keddy (1988). The phytometer used was *Phalaris arundinacea*. One individual *Phalaris arundinacea* seedling was placed in the middle of a one litre pot, four individuals of the test species were planted about 1cm from the edge of the pot in a square surrounding the phytometer.

6 replicates of each treatment and 6 controls (maintained at 3cm water in the base of the plastic container) were used. They were arranged in a block with each row having one of each treatment (SAT, CUT & PHYTOM) and a control randomly assigned to a position. Due to the lack of space in the greenhouse, it was not possible to grow all species simultaneously. Thus, the start date for each had to be species was staggered.

Treatments were continued for 12 weeks (week 16). At week 18 plants were harvested, data on the dry weight of leaves and the dry weight of stem were taken from the control, disturbed and flooded treatments. From the phytometer treatment the biomass of phytometer and of the test species was recorded.

Statistical analysis was carried out using the AXUM computer package.

4.2.2 Results

4.2.2.1 Differences between treatments

Treatments had an effect on the total plant biomass (Fig. 4.1 a - f). In general the biomass of the flooding treatment was similar to the control, both the phytometer treatment and the disturbance treatment were lower than the control or flooded treatment.

ANOVA's were carried out for the stem biomass, leaf biomass, total biomass and leaf to stem ratio for the test species (except for *As*, which was accidentally not divided into separate biomass components during harvesting; separate stem and leaf biomass were not available) between the control, flooded and disturbed treatment (Table 4.1). For *Ac*, *Hl*, *Lp* and *Pa* significant differences were found between the stem, leaf and total biomass between treatments. However, no difference was found between the leaf to stem ratio for these four species, although the results for *Hl* and *Lp* were very close to being different (P = 0.06 and

Fig. 4.1 Differences between treatments in above-ground biomass for the 6 test species (with standard error bars).

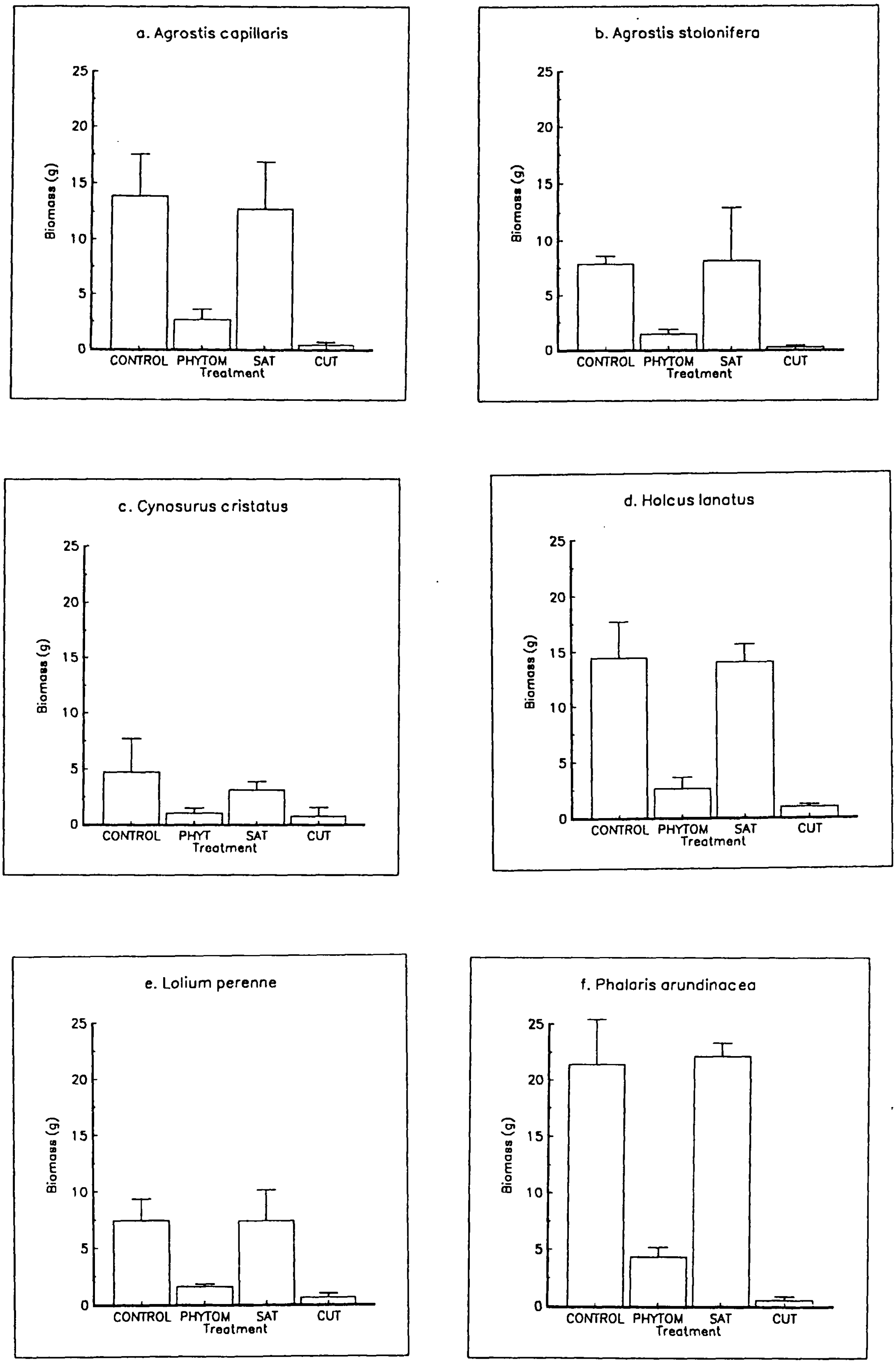


Table 4.1. Results of ANOVA's for the six studies species between the control, disturbance and stress for biomass of stem, biomass of leaf, above-ground biomass and leaf to stem ratio.

	Stem biomass	Leaf biomass	Above-ground biomass	Leaf to stem ratio
Agrostis capillaris	***	***	***	NS
Agrostis stolonifera	-	-	NS	-
Cynocurus cristatus	NS	NS	NS	NS
Holcus lanatus	***	***	***	NS
Lolium perenne	**	***	***	NS
Phalaris arundinacea	***	***	***	NS

Notation:
NS = not significant
** = P<0.01
*** = P<0.001
- = data unavailable

0.09, respectively). For *Cc* no significant differences were found between stem biomass, leaf biomass, total biomass and leaf to stem ratio. These results show that although changes in plant size were apparent between the different treatments, the ratio of allocation to leaves and stems did not significantly differ. The treatments affected the size, in 4 out of the 5 cases, rather than allocation between the leaves and stems.

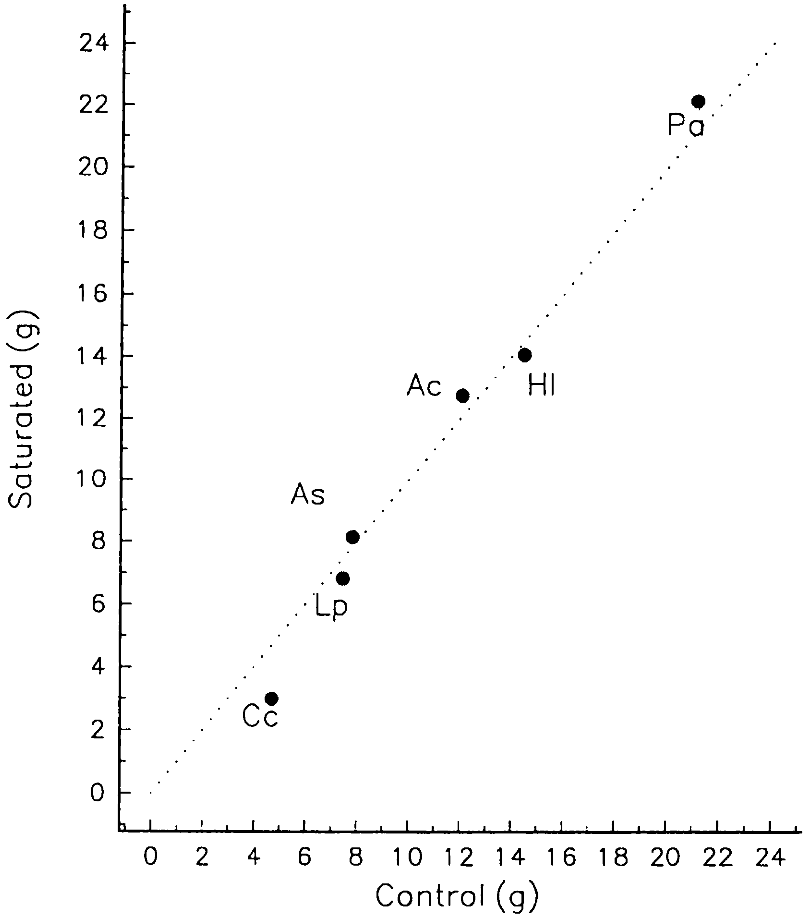
4.2.2.2 The effect of treatments

1. **Stress tolerance** - soil saturation can be considered to be a stress (*sensu* Grime); it was assumed that the flooded species were growing in more stressed conditions than the controls. The difference between the biomass of the 6 species when grown in control and flooded conditions was plotted (Fig. 4.2). Deviation away from the line where control biomass equals flooded biomass was minimal for all of the six species. In the case of *As*, *Ac* and *Pa*, the mean biomass in flooded conditions was higher than in the controls. Using ANOVA, the biomass between the control and the flooded conditions was not different for the 6 species ($P = 0.59$). No differences were found between the biomass of stem ($P = 0.69$) and leaf to stem ratio ($P = 0.40$). The biomass of leaves was significantly different between the control and the flooding treatment ($P<0.03$).

It would appear that the effect of the stress was too small to have much effect on the morphology of the species. No index of stress-tolerance derived from the greenhouse experiment could be derived. Possibly, because the species tend to be found in wetland or moist habitats, tolerance to soil saturation would be expected to some degree. The biomass of leaves was greater in the controls than the flooded pots, however the difference could have not been great because neither total biomass nor the leaf to stem ratio were different between treatments. It is proposed that the degree of stress would need to be greater for the implications of stress on morphology to be investigated. This could be carried out using a water table above the level of the soil, as opposed to at the soil level.

2. **Disturbance tolerance**. Two way ANOVA's (by treatment and species) were carried out for 5 species for which data was available, between the control and the disturbed treatments for leaf, stem and total above ground biomass and leaf to stem ratio. Significant differences were found for these four parameters for both treatment and species. The repeated removal of a significant part of the plant would be expected to bring about a decrease in biomass. The disturbance treatment had a significant effect, compared to the control, on the leaf to stem ratio of the plants ($P<0.001$). The leaf to stem ratio was lower in the disturbed treatments than the controls (*Ac*, 0.24 compared to 0.18; *Cc*, 3.86 / 1.35; *Hl*, 0.81

Fig. 4.2 Relationship between control and flooded biomass (dotted line represents situation where control = saturated biomass).



/ 0.53 and *Lp*, 1.01 / 0.13) except for *Pa* (0.44 / 0.48). The degree to which this was a trend caused by disturbance (*sensu* Grime) or a trend associated with the specific disturbance carried out was not clear. The disturbance involved the removal of biomass above 5cm, this would have been predominantly leaves; the biomass of leaves would be expected to decrease. A further experiment could clarify this issue, for example the removal of all above ground biomass at a certain ontogeny or the non-selective crushing of above ground biomass. The disturbance used here was more akin to large herbivore grazing than the effect of disturbance from flood waters.

The degree of disturbance tolerance was calculated from the results of this experiment. The total biomass production of the disturbed individuals was calculated by the addition of the weight of the fortnightly cuttings to the final weight at the end of the experiment. The ratio of the total biomass production in disturbed conditions to the final above ground biomass of the controls (which was the total production as no abscission of dead leaves was observed throughout the experiment) was calculated. Species that were tolerant of the disturbance would be able to maintain biomass production when under the influence of disturbance; the ratio of disturbed production to control production would be lower than a species which could only poorly tolerate disturbance.

The species were ranked in relation to their tolerance of disturbance from the most disturbant tolerant to the least (production ratio in parentheses):

Lp (0.38) > Hl (0.30) > As (0.29) > Cc (0.23) > Ac (0.14) > Pa (0.12)

Grime *et al.* (1988) proposed the following categorisation for the grasses, they were ranked in terms of decreasing D component:

As (CD) < *Lp* (CD / CSD) < *Ac* = *Cc* = *Hl* (CSD) < *Pa* (C)

Data were too small to permit a Kendal's rank correlation. From visual inspection, the indications were that some form of association between the two classifications was apparent, though with so little data this would be only tentative. *Pa* was ranked bottom in both classifications and *As* and *Lp,* the two most disturbant tolerant species of Grime, were in the top three of the classification from the greenhouse experiment. A larger number of species, particularly from strongly disturbed habitats, would need to be tested in such a way to objectively determine the degree of association between these two methods. It was noted in Chapters 2 and 3 that the degree of disturbance tolerance at the FAEWE wetland sites was considered to be small.

3. **Competitive ability**. The phytometer biomass (PB) was different between species ($P<0.05$); the six species were having differing effects on the biomass of the phytometer. A graph of the relationship between the test species biomass

(TSB) and the PB was constructed (Fig. 4.3), the relationship was not significant ($r = -0.43$, NS).

Gaudet & Keddy (1988) found the relationship between TSB and PB to be significant. However, the TSB axis ranged from 0 to 25g, in the work presented here the range was only 0 to 5g. The variation in the 0 to 5g area of the graph of Gaudet & Keddy (1988) was large. It would be possible that the small TSB values and the limited number of species studied (6 as opposed to 44 species used by Gaudet & Keddy) help to make the relationship statistically non-significant.

Gaudet & Keddy (1988) define competitive ability of a species as the "relative ability of each species to suppress the growth of a common indicator species, or phytometer". Following this definition, competitive ability was calculated as the inverse of the weight of the phytometer; a more competitive plant would have a larger competitive ability score. The relationship between the C score from the field (a mean C value was used if the population was sampled more than once) and the competitive ability determined from the phytometer was significant ($r = 0.80$, $P<0.05$) (Fig. 4.4). The species which had a more competitive morphology measured in the field were more able to depress the growth of the phytometer in the greenhouse experiment. This was considered as independent confirmation of the value of the results of the methodology outlined in Chapter 3, in terms of competitive ability.

The rank of the species in competitive ability was determined from the experiment with the phytometer. In terms of decreasing competitive ability the rank was:

$Pa > Lp > As > Hl > Cc > Ac$

Grime *et al.* (1988) rank the species, in terms of competitiveness:

$Pa > As > Lp > Hl = Cc = Ac$

A Kendal's rank correlation between the two rankings was not carried out due to too few samples. However, a good degree of similarity between the rankings was apparent, although *As* and *Lp* were ranked differently.

Fig. 4.3 Relationship between the biomass of test species and the biomass of the phytometer ($r = -0.43$, NS.)

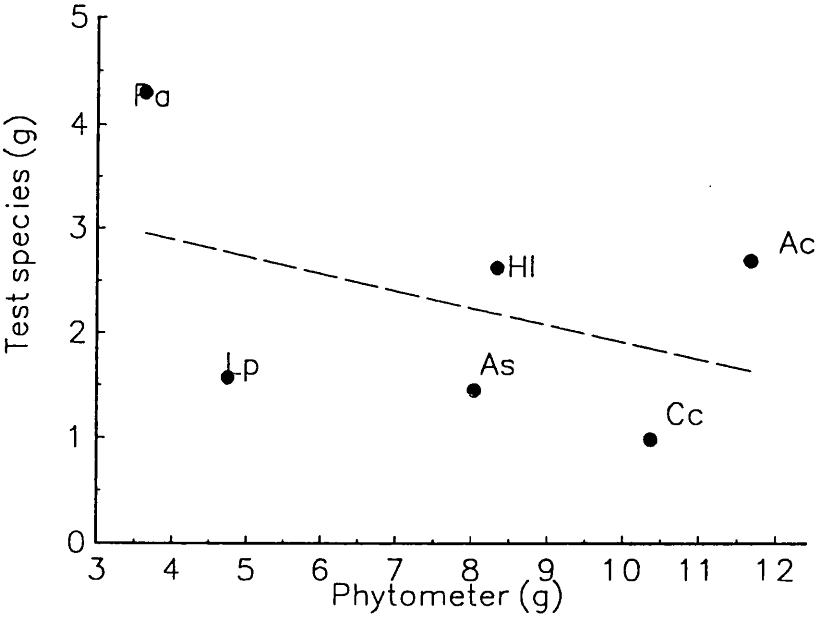
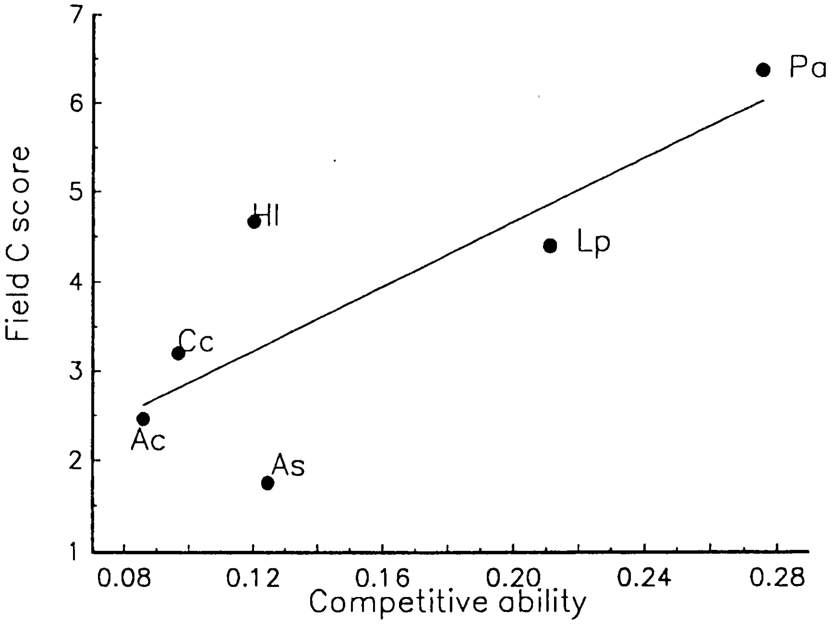


Fig. 4.4 Relationship between the competitive ability from greenhouse experiments and the field C score ($r = 0.80$, $P<0.05$).



4.3 FIELD DATA - A GENERAL MODEL OF BIOMASS ALLOCATION AND LEAF MORPHOLOGY.

4.3.1 Methods

Data collected in 1991 on the traits of 85 plant populations (see Table 3.4a) in the FAEWE wetland study sites were used for the analysis. Data consisted of measurements of leaf, stem and reproductive biomass, height, leaf area and concentration of nitrogen in the leaves, Trait measurement methods were outlined in Chapters 2 and 3. Using these data further traits could be calculated:

1. Total above ground biomass by addition of the leaf, stem and reproductive parts of the plant.
2. SLA, the ratio of leaf area to leaf weight.
3. Above ground leaf weight ratio (AGLWR), the ratio of weight of leaves to the above ground biomass of the plant.
4. Above ground leaf area ratio (AGLAR), the ratio of area of leaves to the above ground biomass of the plant.

A sub-set of 45 of the 85 plant populations studied were included in the listings of Grime *et al.* (1988). Data for these populations on seedling relative growth rate (RGR) were collected from Grime *et al.* (1988). Seedling RGR data was related to traits of established plants.

Statistical analysis was carried out using AXUM.

4.3.2 Results

Plants with a greater biomass of above ground parts had a greater biomass of leaves ($r = 0.84$, $P<0.001$; data non-independent). On plotting this relationship a majority of the above ground biomass data were less than 3g. To counteract this by getting a more even spread of points above ground biomass was natural-logged; the relationship with leaf biomass was significant ($r = 0.69$, $P<0.001$; Fig. 4.5). The leaves consisted of approximately 30% of above ground biomass irrespective of total above ground biomass. Plants with a greater above ground biomass also had a larger area of leaves ($r = 0.78$, $P<0.001$; with biomass natural logged, $r = 0.73$, $P<0.001$; Fig. 4.6). Leaf area and leaf weight were positively correlated ($r = 0.63$, $P<0.001$). However, AGLAR was not significantly related to above ground plant biomass ($r = -0.08$, NS,). The SLA and AGLWR were not significantly related to above ground plant biomass ($r = -0.01$, NS and $r = -0.02$, NS, respectively). These results mean that although plants with a greater above ground biomass have a greater leaf area, the morphology of the leaf in terms of AGLAR, AGLWR and SLA did not change with above ground biomass. Plants

Fig. 4.5. Relationship between the above ground biomass of a plants and the biomass of leaves (r = 0.69, P<0.001, data non-independent).

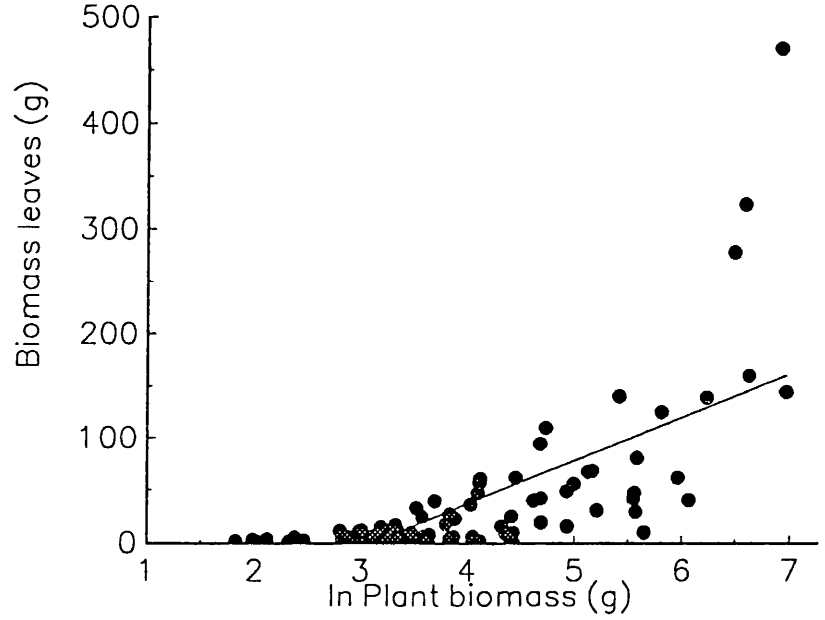
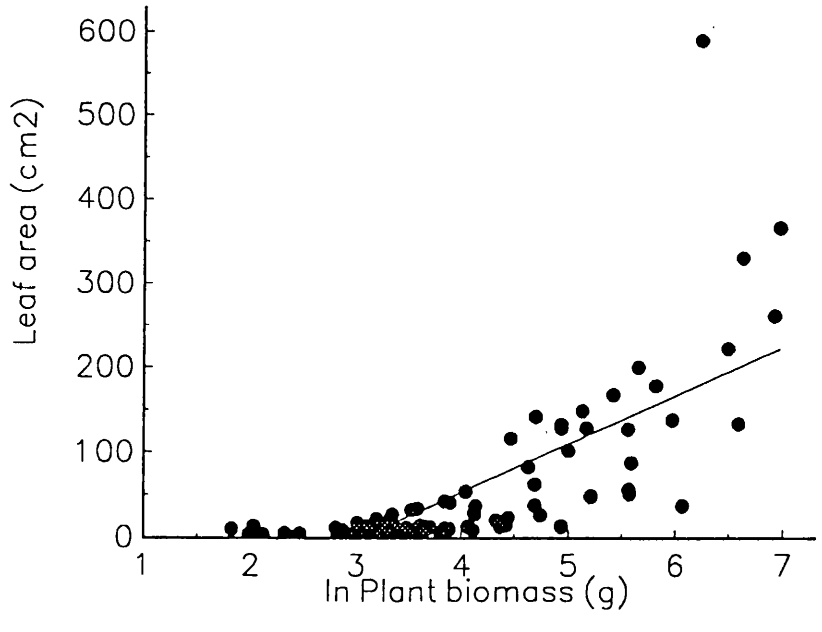


Fig. 4.6. Relationship between the above ground biomass of plants (natural logged) and leaf area (r = 0.73, P<0.001).



allocate a similar percentage of biomass to leaves, irrespective of their above ground biomass. Leaf area increases at approximately 35cm^2 for each additional gram of above ground biomass.

It is possible that the area of a leaf is not a good representation of the photosynthetic capacity of the leaf. Field (1983) noted that, for a wide variety of plants, leaf nitrogen content and photosynthetic capacity were highly correlated. Lambers & Poorter (1992) suggest that leaf organic nitrogen may be used as a good approximation of the "efficiency and size of photosynthetic machinery". Thus, rather than using leaf weight, leaf nitrogen weight was calculated by multiplication of the % N-nitrogen (Kjeldahl) per dry leaf weight by the leaf biomass. This was carried out for leaf weight and SLA (coded SLA-N)(it was not appropriate to AGLAR and AGLWR because they do not involve leaf weight). Leaf area and the total weight of leaf nitrogen were significantly correlated ($r = 0.87$, $P<0.001$). However, SLA-N was not significantly correlated to above ground biomass ($r = -0.08$, NS).

Givnish (1982) proposed that the proportion of above ground biomass allocated to leaves was less in taller plants in floodplain forest herbs. Using the data set collected from FAEWE wetlands, this relationship did not appear to have general applicability to wetland plants ($r = -0.09$, NS). There is no relationship in the proportion of above ground biomass allocated to leaves in relation to height. Niklas (1992) notes that "since shape influences the distribution of mechanical stresses within a structure, and since the size of a structure influences the magnitude of self-imposed mechanical stresses, the conditions of self loading are continuously modified as organs grow". Thus, the relationship proposed by Givnish (1982) concerning increased structural costs with height could be a poor approximation of the fundamental forces maintaining structure in plants. The type and ontogeny of the material and the shape of the structural members must be considered. Biomass of the stem would be a poor reflection of the ability of plants to maintain a leaf canopy in a variety of plants from different growth forms and habitats.

The seedling relative growth rates for 45 of the 85 populations studied above were obtained from Grime *et al.* (1988). Values for the 45 populations were in 4 of the 6 classes (range 0.5 week^{-1}) used by Grime *et al.* (1988). Due to the categorical nature of the data, one-way ANOVA's were carried out between the RGR in the four classes and mature plant trait data. Above ground biomass ($F = 22.02$, $P<0.001$), plant height ($F = 3.49$, $P<0.05$) and leaf area ($F = 37.91$, $P<0.001$) were significantly different between RGR classes. However, in the case of above ground biomass of plant and leaf area, no trend with increasing RGR was apparent (data displayed in Fig. 4.7a and c). A trend was apparent in the relationship between height and RGR, though there was much variation; values from the lowest RGR class overlapped the height values of the highest RGR class (Fig. 4.7b). There was no difference between RGR classes for the leaf to stem ratio ($F = 0.27$, $P = 0.84$), leaf area ratio ($F = 1.75$, $P = 0.17$) and the specific leaf area ($F = 0.37$, $P = 0.77$). From these results, it appears that there was little relationship between the seedling RGR and certain traits related to plant size and biomass allocation in mature plants. Although the data analysed were poor, in the sense that only broad RGR classes were available, the compound nature of RGR over time would be expected to create gross differences. Russell & Grace (1978) noted that if the RGR for a plant differs by only 0.001g day^{-1}, then the dry weight would differ by 13% after 14 days. Even though growth rates would tend to decline as maturity was reached, the maintenance of a disparity between two species over the course of a growing season should create major differences in species in size related traits. The data did not support this contention, thus, some degree of uncoupling between the nature of seedling and mature ecology must be apparent. This important point will be considered further in the discussion.

4.4 DISCUSSION

The data presented in this chapter are related to aspects of variation in plant biomass allocation, leaf morphology and strategy. A synthesis follows using the conclusions from the above data and other published sources. It covers firstly the relationship between the greenhouse results and the field-determined strategies (section 4.4.1), then the relationship of structural components to photosynthetic organs (4.4.2), the next two sections discuss the topics of leaf morphology (4.4.3) and growth rate relationships (4.4.4). The final section assesses the potential value of the use of biomass allocation as a indicator of the general ecology of plant species.

4.4.1 Field and greenhouse determined strategies.

In addition to competition, the greenhouse experiments were designed to imitate the two major gradients in riparian areas, stress and disturbance (Malanson 1993). The stress treatment (soil saturation) was not great enough to cause any change in the above ground biomass in the studied species. Differences in disturbance tolerance were found between the species, however, due to the limited presence of disturbance tolerant species in the FAEWE study sites, no field-value was determined. Only competitiveness could be compared between the greenhouse experiment and field data.

Fig. 4.7a The relationship between the above ground biomass of plants and RGR.

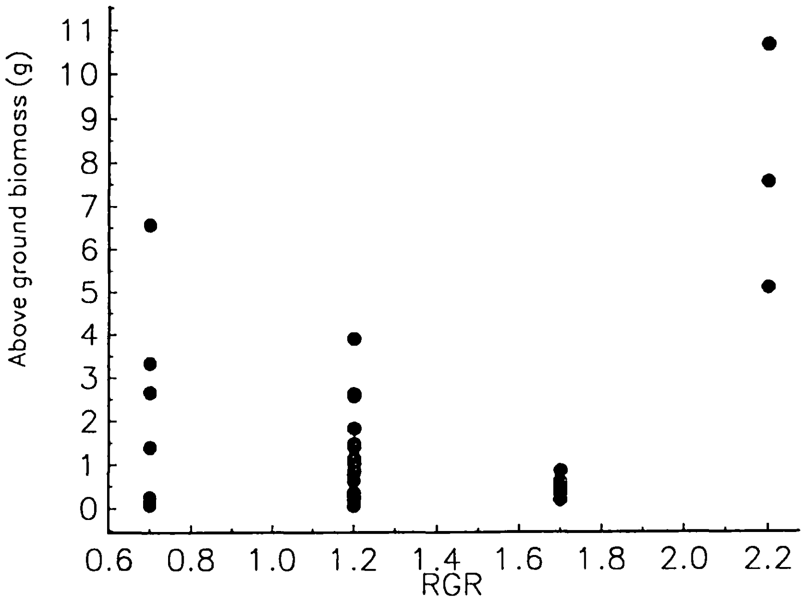
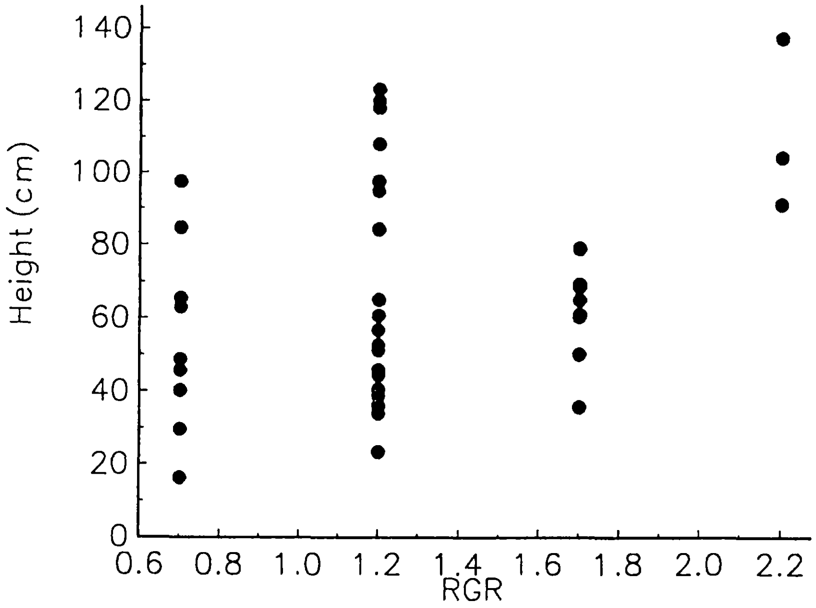
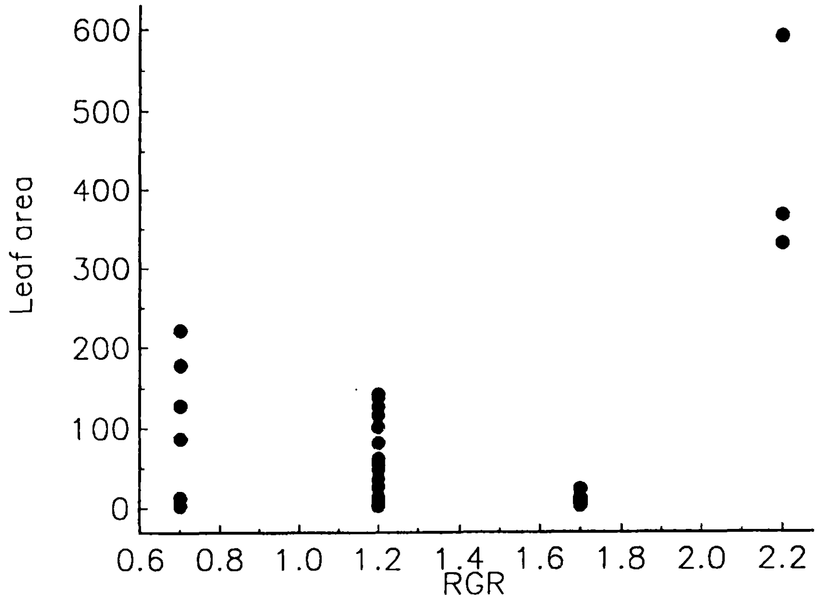


Fig. 4.7b The relationship between the height of plants and RGR.



4.7c The relationship between leaf area and RGR.



Keddy (1990) proposed that competitive ability of a plant was strongly associated with its morphology and physiology, he reviewed experimental data which showed that competition varies in a predictable manner in plant communities. If this is the case, then association between the greenhouse and the field should be apparent. In the work, presented here two methods of determining competitiveness (greenhouse, following Gaudet & Keddy (1988) and determined from the field, adapted from Grime (1979), Grime *et al.* (1988) and Chapter 3, this thesis) were significantly correlated. This association between traits and competitive ability is not new. Gaudet & Keddy (1988) found an association between competitive ability and traits, particularly above ground biomass and height. Epp & Aarssen (1988) listed a number of traits associated with competitive ability in three stages of a plant's life (seed - seedling, juvenile -adult and reproductive). They suggested that, in the juvenile to adult phase, the pre-emption of resources is important thus, morphological characters become increasingly important (Epp & Aarssen 1988). Such relationships exist for intraspecific as well as interspecific competition; Benjamin (1984) found in carrot monocultures that the difference in plant competitiveness can be reasonably explained by differences in plant height.

However, one problem critical to the assessment of competitive ability in the context of community process / organisational studies is that it can vary within a species. Snaydon (1971) studied populations of *Trifolium repens* from two acid and two calcareous sites and found that the competitive ability of the acid populations was greater than the calcareous populations when in acid conditions and vice-versa in calcareous conditions. The designation of a competitive ability to a species would appear as a generalisation. Different outcomes of competition between two species would be possible depending on the environmental conditions of the habitat. Variation has been shown in competitive ability depending on, for example, fertilisation level (Remison & Snaydon 1978). These factors would tend to complicate the formation of competitive hierarchies for species.

A powerful analysis was carried out by Keddy & Shipley (1989) to attempt to determine the extent to which plants could be placed into competitive hierarchies. Keddy & Shipley (1989) analysed data from six competition studies from a variety of environment types and concluded that competitive networks were primarily asymmetric (species *i* would tend to exclude species *j*) and transitive (species *i* would exclude *j* and *k*, and that *k* would not exclude *j* or *i*), as opposed to intransitive (although *i* excludes *j* and *j* excludes *k*, *i* does not exclude *k*), in relation to null models. They suggested that asymmetrical, transitive competitive networks were common in herbaceous plant communities and that they provide a conceptual framework and a set of useful and testable assumptions which can be addressed using experiments. It should be noted however, that the data selected for the analysis by Keddy & Shipley (1989) were selected from experiments which, although using the same ontogeny, used also the same environmental conditions for each of the 6 data sets. Although the general concept of competitive networks was proposed, the degree to which this would become unstable with different environmental conditions requires further consideration.

The approach taken in this work overcomes the problems of different environmental conditions. Instead of using a species as a unit as Keddy & Shipley (1989) do, a population approach was used. The competitive scores for 144 populations (Table 3.4) were a function of the species score and the environmental conditions at the site in which they were measured. Further work could clarify the effect of different environmental conditions on the overall C score, possibly along the gradients of generalised stress and disturbance, and determine the effect on the degree of asymmetry and transiveness on the competitive network. The degree to which the plants response to differing environmental conditions would be species-specific or trait-specific (e.g. a 10cm reduction in height for plants between 80cm and 120cm) could be determined. If height, for example, which has frequently been associated with competitive ability, changed in a predictable way with stress, then a whole series of species do not need to be screened. The transitive network could be determined from the known effect of the stress on the height of a plant. Work in this direction could determine the degree of predictability of the outcome of competitive interactions for a variety of environments.

4.4.2 Structural components and photosynthetic organs.

Caldwell (1987) wrote that, " in the competition for light, plants are balancing their investment in leaves, which are the prime photosynthetic and shading organs, and supporting structures such as stems and petioles that place the leaves in the most advantageous position for competition". Givnish (1982) found that floodplain herbs do in fact put proportionally more of their above ground biomass (leaves + stems) into stems as they become taller. It was found that a 7% increase in herbaceous cover, where competition for light would be more intense, was related to a doubling in maximum leaf height.

The results from the FAEWE wetland sites do not support this contention. The data represent both mono- and dicotyledons from a variety of different habitats, not just mesic floodplain forest as studied by Givnish (1982). This trend does not appear to be generally applicable to wetland environments. Possibly, competition for light is not so important in some of the grasslands surveyed in this project. The requirement to get leaves at the top of the canopy, and suffering the inevitable costs in terms of biomass allocation to supporting structures, may not have been so crucial to survival. In addition, Niklas (1992) makes the point that materials change as a result of development, thus a gram of biomass does not necessarily have the ability to support a constant amount of photosynthetic tissue.

Korner & Renhart (1987) in a study of species from lowland and upland areas in the Austrian Alps, found that allocation to flowers and stems was significantly different between low altitude (mean 35.3% biomass) and high altitude species (mean 18%). However, no trend of biomass allocation to flowers and stems with plant weight was apparent for low or high altitude species. Although no data were presented on plant height, if it was assumed that heavier plants were taller, then these results, from a stressed habitat do not support the findings of Givnish (1982). Wall & Morrison (1990) in a two year study on biomass allocation in *Silene vulgaris* found that in the establishment phase increased biomass to stem tissue was concomitant with a decline in the biomass to leaf tissue. However, Colosi & Cavers (1984) found for the same species that during reproduction the biomass of the plant did not change, however there was a strong negative correlation between biomass allocated to stems and number of capsules per plant. This removal of biomass away from the stem while still able to maintain structure, suggests that the allocation of biomass to the stem was not the most efficient in terms of biomass allocation, necessary to maintain the structure.

It is possible that the model proposed by Givnish was suitable to describe biomass allocation for certain groups of plants in environments with a strong competition for light. However, as a general model of biomass allocation for non-woody plants it does not appear to hold. The effect of age and shape of the supporting structures and the degree to which the plant minimises biomass allocation to supporting structures confounds the relationship.

4.4.3 Leaf morphology

Schulze & Chapin (1987) noted that competitive ability for light was the major environmental variable that determines succession. The response of plants to light is well documented, and involves reactions such as changing the proportion of leaves and the morphology of the leaves (e.g. LAR, LWR & SLA) (Chapin 1980). The work presented here found no change in the leaf biomass allocation (leaves represent ~30% of above ground biomass irrespective of size) or morphology (an increase in the above ground biomass of 1g was associated with an increase in leaf area of ~35cm^2, irrespective of size). Using the amount of organic nitrogen in the leaves as a rough indicator of the photosynthetic potential of the leaf (Lambers & Poorter 1982, Field 1983) no changes in leaf morphology with plant size were found, although the amount of leaf nitrogen increased with area. The relationship of leaf nitrogen to photosynthetic capacity could be related to the age of the leaf (Field & Mooney 1983), though, this would be modified by the nitrogen and phosphorus availability (Shaver & Melillo 1984). Species-specific changes have been found in species in different environmental conditions (Russell & Grace 1978 and Woodward 1983). Whether such relationships hold for a range of species needs further work.

Lambers & Poorter (1992) suggest that fast growing species of a similar life form tend, per unit leaf weight, to have higher rates of photosynthesis than slow growing ones per unit leaf weight. If we assume that a faster growing species will attain a larger size than a slower growing species (see section 4.4.4 for a discussion of this), and that proportional biomass allocation to leaves does not change with plant biomass, then, following the above generalisation of Lambers & Poorter (1992), larger plants will photosynthesise proportionally more per unit leaf weight (or per above ground biomass) than smaller plants. Thus, a species would tend to be large (and consequently, probably more competitive) because the photosynthetic apparatus is more efficient, although biomass allocation to leaves would be similar to a small plant. This line of argument does not however, agree with Poorter & Remkes (1990) who note a positive relationship between the RGR of 24 wild species and SLA; fast growers producing leaves with a low investment in biomass.

Considering that leaves are the photosynthetic, and thus production orientated, organs of the plant, relatively few general patterns relating leaf allocation and morphology to ecology are apparent. Comparisons between seedlings (the work of Poorter *et al.*) and adult plants seem poor. This is discussed further in the next section. However, it is known that *Urtica dioica* loses and replaces its leaves about 3 times during the growing season, whereas leaf turnover is much lower in slower growing plants (Lambers & Poorter 1992); this must have a significant effect on biomass allocation patterns. Further work using many species and studying many aspects of physiology and ecology over the whole growing season would be necessary before the ecological significance of leaf biomass allocation and morphology could be interpreted.

4.4.4 Relationship between seedling growth rate and mature plant traits.

Much variation in RGR for different species of plant has been recorded. Hunt (1984) suggested that overall within-species variability between the RGR of plant species studied around Sheffield (UK.), tends to vary approximately tenfold; differences between a genet, population or ramet vary approximately twofold. Such a variation in RGR for similar individuals of the same population tends to lead to a log normal frequency distribution of RGR (Hunt 1984). Relationships between RGR and morphological, physiological and chemical characteristics of plants have been recorded (Poorter & Remkes 1990, Poorter *et al.* 1990 and Poorter & Bergkotte 1992). Analysis of data collected from the work at the FAEWE study sites did not support many of these relationships. It should be noted however, that the traits measured in the work presented here differ from Poorter's data in that they were from mature plants.

There is evidence in the literature to suggest that the traits of seedlings and mature plants are not related. Shipley *et al.* (1989) explicitly tested the degree of correspondence between adult and juvenile traits. Using 7 juvenile and 13 adult traits for 25 wetland species, the authors found that there was no association between the adult and juvenile traits. They proposed that life-history stages must be dealt with separately (Shipley *et al.* 1989). The results from this work support the conclusions of Shipley *et al.* (1989) in terms of the relationship between seedling RGR and mature plant traits.

Grime & Hunt (1975) using a different growth rate parameter, R_{max} (the maximum growth rate achieved by the plant; in many cases R_{max} = RGR), suggested that plants with a low R_{max} (<1.0 week^{-1}) would be small in stature both as seedlings and as mature plants. Species with an R_{max} of greater than 1.5 week^{-1} were heterogeneous with respect to the form of the mature plant, but could be classed into those with a large stature and capacity for lateral spread and those which have a rapid completion of life-cycle. From the data presented here, comparison of the extremes would tend to support the proposals of Grime & Hunt (1975), though the species with a high RGR were from the large stature group. However, the trend is not borne out by the intermediate species for traits related to the stature of the mature plant (weight and height of plant and leaf area).

Possibly the most important stage of the life during which the success of an individual is determined is the seedling phase (Cavers 1983, Epp & Aarssen 1988), traits such as germination rate and seedling RGR would be important for survival. However, as the plant becomes juvenile, the necessity to forage for resources becomes increasingly important, thus, morphological characters become more significant (Epp & Aarssen 1988). The lack of dependence between seedling and mature plant traits could be a reflection of these two different processes; establishment and competitive success. Further work is necessary to elucidate this issue, involving the measurement of traits throughout the life cycle of the plant, from the seedling stage to flowering. Although, the evidence at present seems to suggest that the growth rate of a seedling is not necessarily a good indicator of the ecology of the mature plant, it may have been an important factor in getting the individual established in the first place.

4.4.5 The potential of biomass allocation and leaf morphology as indicators of strategy.

From the above work it appears that trends in biomass allocation and leaf morphology do not appear to be valuable indicators of mature plant strategy in wetlands. The main variation in the FAEWE plant traits was in size and this was related to the C and S strategies of Grime (1979) (Chapters 2 & 3). General patterns of biomass allocation and leaf morphology were not related to this gradient in the studied wetland plants.

A majority of the cases where differences have been found in biomass allocation and leaf morphology were found were comparisons between either species, (e.g. Poorter & Remkes 1990) or, environmental conditions (e.g. Woodward 1983). The FAEWE data set considers both variation in species and site simultaneously, by utilising populations as opposed to species. It appears that such a data set is too heterogeneous for relationships of biomass allocation and leaf morphology to apply. Thus, they appear to be poor general indicators of plant strategy although, they are probably ecologically important.

HOW DO TRAITS AND SURVIVAL STRATEGIES RELATE TO COMMUNITY-WIDE STATE VARIABLES?

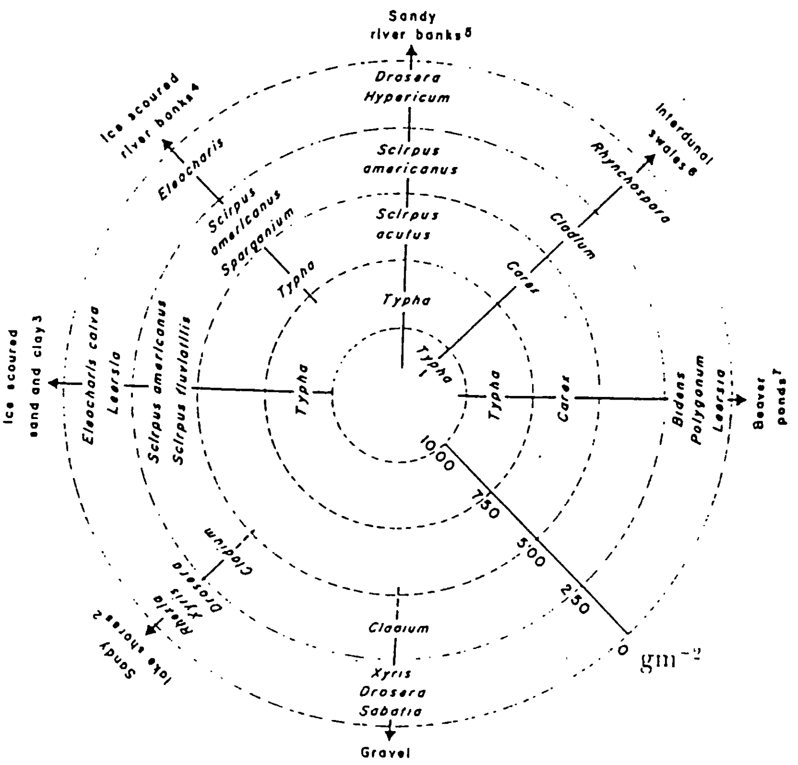
5.1 INTRODUCTION

Following observations of desert rodents, Rosenweig & Abramsky (1986) proposed a model of centrifugal community organisation. In this model they identified what they termed a core habitat which, even at low population densities, was being exploited by rodents. They also identified peripheral habitats which were only used when rodent population densities increased. As population densities increased, a greater variety of habitats was utilised; this was the centrifugal effect after which the model was named. Keddy (1990) proposed a similar model for herbaceous wetland communities. The model was formulated using two simple constructs, firstly that plant communities are structured by competitive hierarchies and secondly, that competition is most intense in high biomass sites. The central core consisted of a species poor - high biomass community. From the core a set of possible paths along an axis of decreasing biomass was proposed, each of which was defined as a habitat with a particular set of environmental conditions e.g. intertidal swales or gravel lake shores. On each path a small number of species-specific communities exist at certain biomass ranges. As biomass decreased the number of species or life-forms increased (see Fig. 5.1).

Keddy (1990) introduced the concept of state variables although they were not defined. He used them as community-wide descriptors of biotic assemblages. In physics, a state function is defined as a "quantity in thermodynamics which has a unique value for each state of the system" (Walker 1991). The definition of "state variable" used in this work will follow this definition, and the sense that Keddy used it in, and be defined as "a measurable variable of a biotic community which has a particular range of values for each type of vegetational community." It was proposed by Keddy (1990) that "biomass may produce changes in other state variables such as the total species pool, alpha diversity and number of vegetation types" and that the use of biomass in the centrifugal model " integrates a number of state variables of interest" (Keddy 1990). The relationship between biomass and other state variables remains largely untested.

The proposal by Grime (1973) and Tilman (1988) that high species richness occurs at intermediate points along environmental gradients was tested by Wisheu & Keddy (1988). They found that, although species richness tended to follow the predicted pattern for low-medium biomass, at higher biomass species richness did not decline as predicted, (though this was possibly due to the fact that there were

Fig. 5.1 Model of centrifugal community organisation in herbaceous wetland communities, showing changes in dominant plant species with varying biomass (gm^{-2}) for a selection of wetland habitat types (taken from Keddy 1990).



no really high standing crop sites). The species richness-standing crop relationship at each of the Wisheu & Keddy's four lake shore sites was significantly different.

The centrifugal model of Keddy (1990) was based on data on wetland plant communities (although general applicability was proposed and the model has been related to forest communities by Keddy & MacLellan (1990)). However, community descriptions were in the form of dominant species taxonomic names. To achieve more general applicability and to transcend taxonomic barriers, the use of functional groups would be appropriate.

This chapter aims to relate the functional classification of wetland communities (in terms of CFVT and SFVT, Chapter 3) to a set of state variables. It is proposed that there is a relationship between state variables of a community and it's functional vegetation type. If a relationship is apparent then a complementary method for the determination of functional groups, related to competitiveness and stress-tolerance, could be constructed without the necessity of measuring plant traits. This could potentially be of value in the wetland predictive model as independent confirmation of the CFVT and SFVT values determined from plant traits or as a stand-alone indicator of environmental change.

The objectives of this chapter are:

1. To determine the relationship between state variables and CFVT and SFVT values.
2. To determine the degree of association between state variables and CORINE biotopes.
3. To assess the potential of state variables as predictors of CFVT and SFVT.
4. To test the assertion by Keddy (1990) that biomass represents the major gradient in state variables of wetland communities.

5.2 METHODS

5.2.1 Measurement of state variables

In total, 26 samples of 11 state variables were measured from FAEWE wetland sites. All state variables were variables measured for the whole community, rather than traits which were measured for certain constituent populations. Eleven units were measured twice in a season or once in 1992 and once in 1993; the two records for each unit were considered as independent samples, although, for some measures it is accepted that the second value of the pair may be influenced by the first.

The eleven state variables measured were:

1. Species richness (**SPP**) was the mean number of species present in a 30cm x 30cm quadrat placed randomly ten times in the hydrogeomorphic unit.

2. Community dominance (**DOM**) was determined using Simpson's index. All diversity indices have two components; species richness and evenness. However, Simpson's index is a diversity index which is particularly sensitive to unevenness (or dominance) in the species composition of the community. The tendency of Simpson's index to give relatively heavy weight to dominant species means that it is primarily an index of dominance.

The number of squares in which each species was present within a transparent quadrat (consisting of 36, 5cm x 5cm squares) was recorded. Simpson's index was used to determine the dominance of the plant community, where DOM = $\sum (p_i)^2$, where p = the proportion of squares that a species is present in and i = each of the species found in the quadrat. The value of Simpson's index varies from between 0 (high diversity, high evenness) and 1 (low diversity, high dominance).

3. The density of stems per area (**DEN**) in a 10cm x 10cm quadrat was recorded ten times in each quadrat. A "stem" was considered to be any piece of plant material that was rooted in the soil and had one or more shoots above ground. If the density of stems was low (<15 per 10cm x 10cm) then the density of stems from a larger area of ground was recorded and results mathematically adjusted to 10 x 10cm quadrats.

4. The distance (mm) from a randomly selected shoot to its nearest neighbour (**DIS**) was recorded at ground level. This was repeated ten times at each hydrogeomorphic unit.

5. The diameter of ten randomly selected stems was recorded (mm) and the cross-sectional area of each stem (**STA**) calculated, assuming the stem was circular.

6. Canopy height (**CAN**) was determine using a metre ruler (cross-section 2.5 x 0.5cm) placed in random positions vertically at the soil surface. The height from the ground to the highest piece of vegetation touching the ruler was recorded.

7. The density of reproductive structures (**REPD**) was recorded in 30 x 30cm quadrats. All flower buds, flowers and seed-heads were recorded.

8. The cover of vegetation from the soil surface to 10cm (**C0-10**) was recorded using a Harris pin frame with each pin marked at 10cm. The mean number of "hits" per pin was calculated.

9. The cover of vegetation from 10cm above the soil surface to 20cm above the soil surface (**C10-20**).

10. The cover of vegetation above 20cm was also recorded (**C20+**).

11. The total above ground living biomass (**BIO**) was harvested from plots of between 100cm^2 and 1600cm^2. The size of the harvested plot depended on the type of vegetation, homogeneous grassland plots were smaller than heterogeneous *Urtica* of *Phragmites* dominated communities. It was necessary to harvest small

plots as travel back to Glasgow from field sites was not possible with large amounts of wet biomass. Whole biomass samples were dried and weighed. Values were expressed in g/m^2 dry weight.

5.2.2 Data analysis

Canonical correspondence analysis (CCA) was used for some of the data analysis. This multivariate method, an extension of Correspondence analysis, permits the linking a set of "species" data to a set of "environmental" data. It simultaneously uses ordination and multiple regression to produce a plot of species in relation to environmental variables, plotted as biplot arrows. The axes are not the axes of maximum variation, as in PCA or CA, but are constrained to be linear combinations of the environmental variables (Jongman *et al.* 1987, ter Braak 1987). CCA is available as an option on the CANOCO programme (ter Braak 1987).

5.3 RESULTS

5.3.1 Relationships between state variables

A table of product moment correlation coefficient significances between each of the state variables was constructed (Table 5.1). Although this is statistically non-valid due to the large number of individual significances employed, it does give a first impression of relationships between the variables. If these data were random, one would expect that only 5% of the relationships to be significant at the $P<0.05$ level or higher. However, in this case 47% (26 out of 55) of the relationships were significant; this suggests some degree of covariance in these variables. This, however, is not suprising as variables like species richness (SPP) and dominance (DOM) should be related to some degree.

Due to the degree of covariance in these data, PCA was used to find the main axes of variation in these data. The PCA was highly successful at explaining the variation in these data; the eigenvalues were 0.902, 0.013 and 0.004 for axes 1, 2 and 3 respectively. To determine which state variables were related to the first and second axes of the PCA, product moment correlation coefficients were calculated between the state variables and PCA axes 1 and 2, and the significance recorded (Table 5.2). The first axes, explaining by far most of the variation in the state variables, was significantly related to biomass ($P<0.001$) and to a lesser extent the density of shoots ($P<0.01$); the second axis was related to distance between shoots ($P<0.001$) and the species richness ($P<0.05$). Much of the variation in the state variables could be explained in two axes. The predominant axis was most strongly related to biomass and the secondary axis to the distance between shoots. The

Table 5.1 The significances of product moment correlation coefficient between the 11 measured state variables.

	SPP	DOM	DEN	DIS	STA	CAN	REP-D	C0-10	C10-20	C20+
SPP										
DOM	***									
DEN	***	***								
DIS	***	***	***							
STA	**	*	-	***						
CAN	-	-	-	-	**					
REPD	***	-	-	-	-	-				
C0-10	***	-	***	**	*	-	**			
C10-20	***	*	***	-	-	-	-	***		
C20+	-	-	*	-	-	***	-	-	-	
BIO	-	-	*	-	***	***	-	-	-	**

- = not significant at $P<0.05$
* = $P<0.05$
** = $P<0.01$
*** = $P<0.001$

Table 5.2 The significance of the product moment correlation coefficients (and the sign of the correlation in brackets) for the relationships between axes 1 and 2 of a PCA of state variables and state variables.

	AXIS 1	AXIS 2
SPP	-	* (-)
DOM	-	-
DEN	** (+)	-
DIS	-	*** (+)
STA	-	-
CAN	-	-
REP	-	-
C0-100	-	-
C10-20	-	-
C20+	-	-
BIO	*** (+)	-

- = not significant at P<0.05
* = P<0.05
** = P<0.01
*** = P<0.001
(+) = positive relationship
(-) = inverse relationship

importance of biomass as the variable that best explains variation in most of the other state variables supports the idea of Keddy (1990) who used biomass as the basic unit for structural organisation of plant communities in the centrifugal model.

5.3.2 Relationship between state variables, FVT's and CORINE biotopes

A further ordination procedure was carried out with the state variables data as species and the axes constrained to be linear combinations of SFVT and CFVT. The degree of relationship between the FVT values and the state variables can then be assessed. This was carried out using Canonical Correlation Analysis (CCA).

The eigenvalues of the CCA were relatively low (axis 1 = 0.128; axis 2, 0.058), this means that a majority of variation in the state variables could not be explained by CFVT and SFVT. However, the use of a Monte Carlo permutation test, which tests the significance of the species-environment relationship by testing it against a set of random permutations, found the relationship to be significant overall (99 permutations, F ratio = 2.86, $P < 0.05$) although the first axis was not quite significant (99 permutations, F ratio = 3.75, $P = 0.06$). A plot was constructed between the scores of the state variables and the FVT values (Fig. 5.2a). The CFVT and SFVT biplot arrows pointed in nearly opposite directions, suggesting a strong inverse correlation between the two variables (see section 3.3 and Fig. 3.3). Competitive FVT's tended to have a great distance between stems (DIS), a tall canopy (CAN), large stem areas (STA) and tend to be dominated (DOM). Stress-tolerant FVT's tend to have a high density of stems (DEN), a high species richness (SPP) and high density of reproductive structures (REPD). There appears to be a set of state variables related to both CFVT and SFVT.

Biomass has a position close to the origin, this suggests that the variation in biomass was not an important variable in determining the relationship between the FVT values and the state variables. In the PCA carried out prior to this analysis, biomass was the state variable most strongly related to axis 1. Thus, although biomass would appear to be a variable which explains much of the variation in the other state variables, when it is constrained to be related to FVT values it becomes less important.

Biomass was significantly related to CFVT ($r = 0.37$, $P<0.05$, Fig. 5.3) though not as well as other state variables. Sites with plant populations exhibiting strongly competitive strategies tend to have high biomass. This agrees with one of the assumptions of the centrifugal model of Keddy (1990) that competition is more intense in sites with greater biomass.

Fig. 5.2a CCA diagram showing the scores for state variables and the position of biplots for CFVT and SFVT.

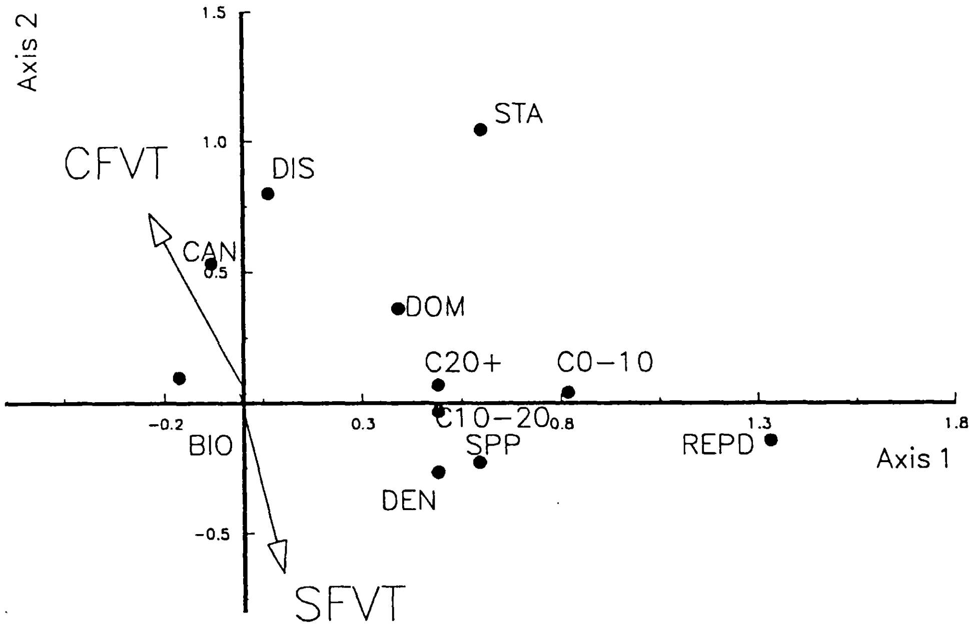
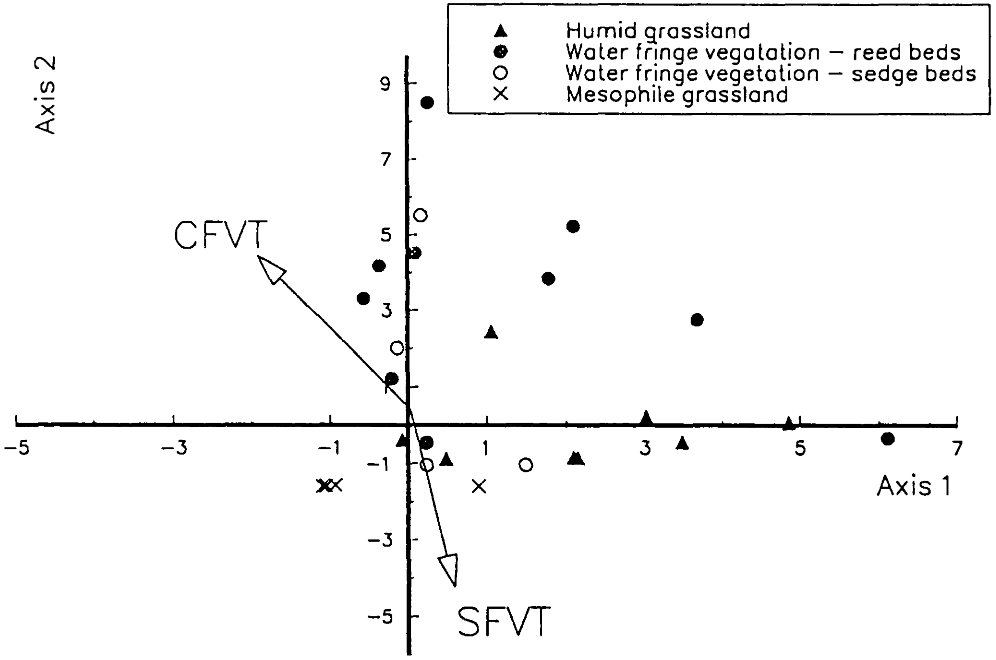


Fig. 5.2b CCA diagram showing CORINE biotopes described by state variables in relation to CFVT and SFVT.



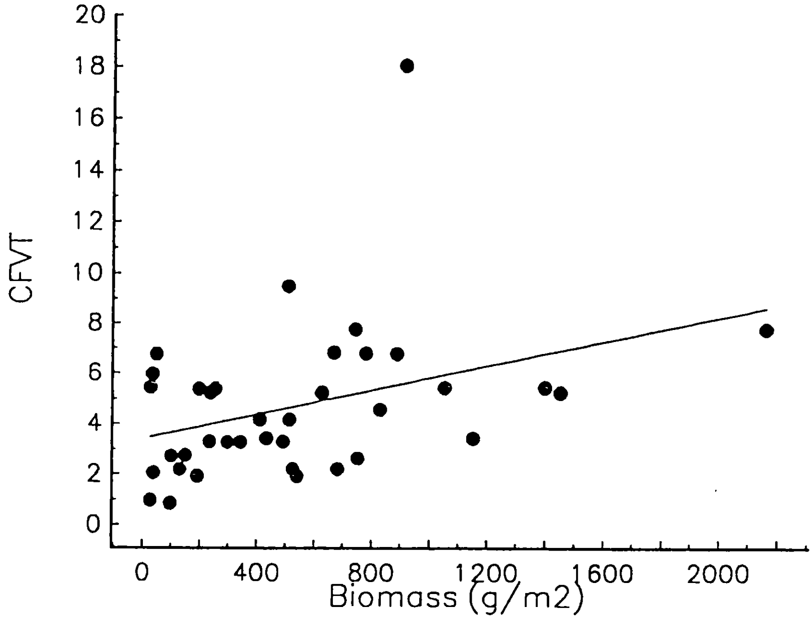


Fig. 5.3 Relationship between CFVT and biomass (r = 0.37, P<0.05).

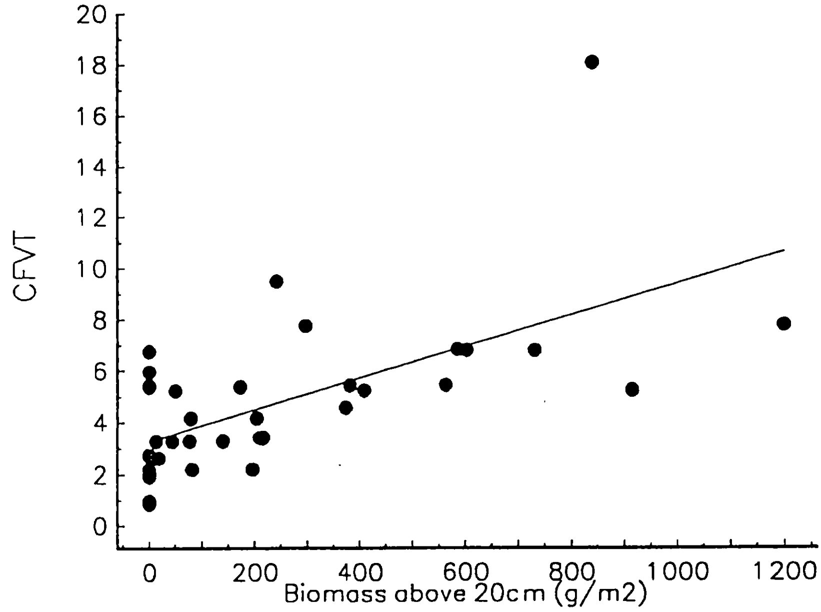


Fig. 5.4 Relationship between the biomass above 20cm and the CFVT value (r = 0.56, P<0.001).

The ability to overtop a potential competitor and reduce or remove the light available to the competitor has been related to competitive ability (Keddy 1990). The proportion of biomass in the zone above 20cm in the plant communities (BIO20+) was calculated from the state variable data. The total biomass of the plant community was multiplied by the proportion of the pin frame hits in the 20cm+ zone (i.e. BIO20+ = BIO x {C20+ / C0-10 + C10-20 + C20+}) . A significant positive relationship was found between the calculated biomass above 20cm (BIO20+) and CFVT ($r = 0.56$, $P<0.001$, Fig. 5.4). This means that more competitive plants tend to have a greater biomass in the zone above 20cm, they thus tend to have a greater potential to outshade neighbouring potential competitors.

To test whether different CORINE biotopes had different state variables and FVT values associated with them, CORINE biotopes were displayed on the CCA diagram at the site scores (Fig. 5.2b). Only CORINE biotopes which were present at four, or more, study sites were used in this analysis. The four biotopes used were humid grassland (CORINE code 37), water fringe vegetation - reed beds (53.1), water fringe vegetation - sedge beds (53.2) and mesophile grasslands (38). Distinct groupings of units in the CCA ordination space were found for three out of the four CORINE biotopes.

The humid grassland biotopes tended to be found in the stressed area of the CFVT-SFVT axis, they tended to have site scores ranging from near the origin to high on the first axis; the scores were related to high species richness, reproductive density and plant cover from 0-10cm, 10-20cm and 20cm+. The reed beds were found at the positive end of the CFVT axis associated with high canopy height, a large distance between stems and high stem area. The 4 mesophile grassland samples were found mid-way along the SFVT biplot; they were associated with a high biomass, density of stems and species richness. The fourth CORINE biotope category, sedge beds, was found to range across a large part of the CCA diagram, particularly on the second axis; the association to FVT and state variables could not be determined. Some of the more important associations between CORINE biotopes and, FVT values and state variables are summarised in Table 5.3.

The CCA analysis showed that there was a relationship between FVT values and state variables, certain state variables being associated with CFVT and SFVT. Three of the four CORINE biotopes, described by state variables, formed distinctive groups in the CCA diagram. This means that these CORINE biotopes have certain values for state variables measured here which can be used to distinguish them from other biotopes. In addition, these biotopes tend to be found

Table 5.3 The range of values of FVT and indicative high values for state variables for 4 CORINE biotopes.

	Mesophile grassland	Reed bed	Sedge bed	Humid grassland
CFVT	L	H	H-L	L
SFVT	M	L	M-L	M
SPP	H			
BIO	H			
DEN	H			
DIS		H		
STA		H		
CAN		H		
DOM		H		H
C0-10				H
C10-20				H
C20+				H
REPD				H

L = low value
M = medium value
H = high value

in certain areas of the CFVT-SFVT axis. From these results it appears that there was a strong degree of complementarity between strategy (FVT scores), community-wide descriptors (state variables) and phytosociological units (CORINE biotypes).

The CCA analysis suggested that there was a relationship between the CFVT and SFVT scores and state variables. To elucidate this relationship more simply and to produce a predictive equation, a stepwise multiple regression was carried out between CFVT and the state variables. As CFVT and SFVT were strongly related, only one needed to be related to the state variables, and because the experiments of Chapter 4 had supported the C scores, CFVT was selected instead of SFVT. The first variable selected in a stepwise multiple regression between CFVT and state variables was the distance between stems (DIS); this variable explained 46% of the variation in the CFVT value ($P<0.00001$). The second variable was the cover above 20cm (C20+), together these two variables explained 59% of the variation in CFVT ($P<0.00001$). The final variable selected was the dominance (DOM), which added a further 7% to the relationship making a total of 66% of the variation in CFVT explained ($P<0.00001$). The final predictive equation was:

$$CFVT = (DIS \times 0.0455) + (C20+ \times 0.336) + (DOM \times 3.575) + 0.7802$$

From these results it seems that there was a highly significant relationship between CFVT and certain state variables. The variable which best explained the variation in CFVT was distance between stems, more competitive plants tend to be found in communities where there is a large distance between stems. This predictive equation permits the determination of CFVT from state variables with a high degree of accuracy.

The measurement of DIS in the field was not easy due to the difficulty of getting the ruler at ground level without disturbing the vegetation coupled with the requirement to measure the nearest neighbouring shoot, which was not always obvious. The degree of accuracy which DIS could be measured in the field by a non-specialist scientist would be under question. Thus, the stepwise multiple regression was run without DIS, to find the best predictive equation excluding DIS. The predicted CFVT value was termed CFVT-S; the "-S" denoting that a sub-set of state variables were used in the predictive equation. The first variable selected by the regression was DOM, which explained 28% of the variation in CFVT-S ($P<0.001$). The next variable selected was C20+, which increased the percentage of CFVT-S explained to 41% ($P<0.0001$). No further variables were significantly related to the remaining variation in CFVT-S. Without DIS, the competitive FVT could be significantly predicted from state variables. The predictive equation for CFVT-S was:

CFVT-S = (DOM x 6.22) + (C30+ x 0.352) + 0.75

5.4 DISCUSSION

5.4.1 The centrifugal model of community organisation

The data collected from FAEWE wetland sites supported Keddy's (1990) contention that biomass "integrates a number of state variables of interest". This suggested that biomass was a good baseline on which to place ecological data about plant communities. However, it should be noted that although biomass was the state variable most closely related to the first PCA axis of the state variables, it is possible that other state variables which were not measured would be better related to this axis. However, due to the significance of biomass as an indicator of ecological functioning and its common use in ecological studies, biomass remains the best state variable on which to base such a model.

When the axes of the ordination were constrained in the CCA analysis to be linear combinations of state variables, biomass was not the most important variable. In the stepwise multiple regression, biomass was not selected as the first descriptor variable of CFVT, although it was significantly related to CFVT (Fig. 5.3). The distance between stems was found to be the best descriptor of CFVT. It can be concluded from these results that the main axis of variation in the state variables was not the main axis of variation in the FVT values. The degree to which the addition of other state variables would affect the relationship between axes of variation in the state variables and FVT is not known.

The two assumptions used by Keddy in the construction of the hierarchical model were supported by these data. Firstly, he assumed that competitive ability was highest at sites with the highest biomass. If it is assumed that more competitive plants are found in communities with more intense competition, then competition was found to be most intense in high biomass sites.

Secondly, Keddy also assumed that plant communities were structured by competitive hierarchies (Keddy 1990). Evidence for this is given by Keddy & Shipley (1989) who found that competitive networks in plants tend to be transitive. They wrote that "mechanisms of plant competition appear to be related to variables implicated in plant size" (Keddy & Shipley 1989). This hypotheses was supported by the work with phytometers of Gaudet & Keddy (1988), in which it was found that competitive ability was related to attributes connected with plant size, and that larger plants were more able to suppress the growth of a competitive phytometer than smaller plants. More competitive, and consequently larger plants, were found to live in communities that had a greater amount of biomass in the zone above 20cm. Smaller plants (and consequently less competitive) would find growth and survival in such communities difficult due to exclusion from part of the light resource by larger plants. From these data it appears that a structure related to competitiveness was apparent in wetland communities, with competitive plants living in more competitive situations than less competitive plants. Places where competitive plants grow also tend to have certain state variables which are related to the large growth form of the plant e.g. high biomass, great amount of biomass above 20cm, high canopy, great distance between stems, and larger stem areas.

The data presented here agrees with the centrifugal model of Keddy (1990) (Fig. 5.1). However it is argued that the model is basically a restructuring of the C-S-D triangle model of Grime. The central core of the centrifugal model consists of competitive plant species. As the biomass decreases, the plants tend to become less competitive and more adapted to survive certain habitat types. These habitat types experience more disturbance or stress then the central core e.g. "ice scoured sand and clay" or "gravel lake shores"; the peripheral habitats thus represent the stress and disturbance corners of the Grime triangle. This can be considered as a restructured version of the "Grime triangle". The core of the centrifugal model represents the competitive area and the periphery represents the stressed and / or disturbed areas of the Grime triangle.

The important difference between the models of Keddy and Grime is however, that they come from two different sets of assumptions. Grime made assumptions about the stress and disturbance at a site, and if both of these were low then competition was assumed to be the major structuring component. Keddy, on the other hand, started with competition, making assumptions about the nature of competition in communities in relation to the biomass. Keddy proposed that intensity of competition and biomass became less when the habitat became more peripheral (i.e. stress or disturbed). The work presented here has shown a degree of complementarity between the two models with changes in competitiveness (*sensu* Grime) related to changes in biomass and other state variables. Further work could concentrate on developing a hybrid of the Grime strategy model and Keddy's centrifugal model.

5.4.2 CORINE biotopes, state variables and FVT values.

A strong degree of complementarity was found between the three approaches used to describe vegetational communities; the phytosociological CORINE biotope units, the community-wide state variables and the mean population competitive and stress-tolerance scores or FVT's (see Table 5.3). These three methods of vegetational description represent a hierarchy of approaches from individual populations (strategy), through species abundance's within communities (CORINE) to community-wide variables related to size, diversity and architecture. Three CORINE biotopes were found to have a distinct combination of state variable values, and differences in the FVT values. One CORINE biotope, sedge beds, was found to be wide ranging in terms of state variables and FVT values. This could have been due to the taxonomic diversity within the sedge bed biotope, with both bottle and bladder sedge beds (53.214) and greater pond sedge beds (52.213) being present in the studied sites. However, it is possible that a further division of this biotope into subunits would lead to distinct groups; the data for this was not available.

To improve the relationship between biotopes and FVT values, more sites should be used, particularly from higher biomass areas. A better idea of the biotope centroid, the range of the biotope in terms of FVT values and state variables, and the degree of distinction from other biotopes could be determined.

Two potential uses of state variables as indicators and predictors of change in wetlands can be formulated:

1. The state variables provide a second, independent and accurate method for the determination of CFVT in wetlands. This could potentially be useful as a check, built into the wetland model system, on the CFVT value determined by the measurement of traits from plant populations. Or as a stand-alone method which does not even require the drying of plant samples in an oven as the population trait method does. CFVT values could be quickly determined on site following a simple calculation using the field-measured state variables identified in the stepwise multiple regressions. This process would take a mater of minutes.

2. State variables provide the potential starting point for disturbance to be investigated, following the model of Grime. In the FAEWE wetland sites disturbance was found to be of less importance than either stress-tolerance or competitive ability. It was also argued (section 3.4) that the traits which would be good indicators of disturbance tolerance would be more related to reproductive variables and life-form, and less related to morphological features; these traits would be difficult to measure in the field. However, in many cases the evidence for disturbance in the past would still be apparent (e.g. the removal of biomass by grazing or the presence of bare areas at the edge of wave-washed lake shores). State variables related to such observations could be determined and used as

predictors of the degree of disturbance at the site, this could lead to the calculation of a DFVT index.

DO POPULATION AND COMMUNITY STRATEGY INDICES RESPOND PREDICTABLY TO ENVIRONMENTAL PERTURBATION?

6.1 GENERAL INTRODUCTION

The work presented so far, has used morphological traits to describe species and communities. Changes in trait and strategy over environmental gradients have been recorded. Two independent strategy measurements, one for stress-tolerance and one for competitive ability were found to be significantly correlated. This suggests that a number of morphological traits covary predictably with the environmental gradients within and between the FAEWE sites.

If one of these morphological traits, *T*, was measured in plant communities with different species composition over a wide range of environmental conditions, then trait *T* would be expected to change in predictable manner with a change in environmental conditions. It is proposed that a similar relationship occurs within a species. Thus, if trait *T* was measured for one species at a number of sites where it occurred, a relationship between *T* and the environmental conditions would be expected. Unfortunately, the nature of the "environment" is highly diffuse and constitutes a "panchestron" (Peters 1991). The measurement of even a large number of environmental variables, followed by ordination or regression would not necessarily reduce the environment to constituent environmental parameters of importance to plants.

If the environment of a number of sites studied changed by only one factor, *F*, then the only difference in environmental conditions between sites would be *F* (*F* could be a factor such as moisture content of the soil or soil fertility). This controlled situation can be achieved through the use of experiments. A change in *F* of the environmental conditions should bring about a predictable change in *T*. For example, if a fertiliser was applied to a site (assuming that the site was nutrient-limited) then a particular species should tend, within certain limits, to become less stress-tolerant and more competitive, in terms of *T*. There is good evidence, for example, that plant height is positively correlated to the competitive ability of plant species (e.g. Caldwell 1987, Epp & Aarssen 1988, Keddy 1990). Thus, a likely response to the relaxation of stress due to nutrient limitation would be that individuals within a plant population would tend to become taller.

In this model, each species can have a variety of trait values, and consequently strategy values. It is well known that a species can vary in morphology. Classical strategy theory tends to consider a strategy for a species fixed (Grime 1979, Grime *et al.* 1988). For example, Grime *et al.* (1988) designated the established strategy of *Holcus lanatus* to be C-S-D. However, this strategy score was actually the centroid of all the positions of the species in the triangle. In the survey carried out around Sheffield (UK.), *Holcus lanatus* was found in over 90% of the area of the C-S-D triangle. Many of the other species covered in Grime *et al.* (1988) were present in over 50% of the C-S-D triangle space.

In the framework discussed here, two forms of strategy space can be identified. They will be termed the potential strategy and the expressed strategy. The potential strategy represents the range of strategies that the plant species exhibits. Wide ranging, common plants, such as *Holcus lanatus*, would tend to have a wide potential strategy space. A species, specialised to a certain habitat type, would tend to have a narrow strategy space. The potential strategy will tend to have a genetic base. Expressed strategy is the strategy that the species is expressing at a particular site at a particular time (i.e. the displayed phenotype), this is more akin to the idea of a population strategy as used throughout this study. The expressed strategy must be included in the potential strategy range. To detect environmental change within a species using the strategies approach, the expressed strategy rather than the potential strategy must be utilised.

The work had two general objectives:

1. To determine if competitive index showed measurable change in response to anthropogenic perturbation.
2. To determine if the competitive indices responded in the way predicted by strategy theory.

The aim of the following four experiments was to determine the value of strategy indices as indicators of environmental change. The competitive index was chosen (C score for populations and CFVT-S for communities) because greenhouse experiments had confirmed that there was a significant relationship between the C score from field measurements and competitive ability determined from the phytometry method of Gaudet & Keddy (1988) (see section 4.2 and Fig. 4.4). Predictions about the effect of the impact, in terms of the direction of change in the competitiveness of the population or the community, were made. If the treatment increased stress or disturbance then the competitive index was predicted to become less competitive. If however, the treatment diminished stress or disturbance, then the competitive index would be predicted to become increasingly competitive.

6.2 MANIPULATION OF WATER REGIME: A MESOCOSM EXPERIMENT.

6.2.1 Introduction

This experiment was designed to investigate the effects of flooding and drought on two wetland communities from central France. Manipulation of water regime in the field was impractical, thus a controlled experiment was designed in which plots were removed from the wetland sites and kept in greenhouse conditions.

This experiment was carried out in conjunction with Drs. Mark van Oorschot, Dr. A Spink and Dr. J. Verhoeven at the Department of Ecology and Evolutionary Biology, University of Utrecht, The Netherlands. In the whole experiment three types of data were recorded:

1. Environmental monitoring (e.g. soil moisture, water level, leaf water stress)
2. Vegetation studies (species abundance, phytometer response, biomass, strategies and N & P content of plants).
3. Soil processes (N mineralization, denitrification, P dynamics).

This section will report on only the strategies section of the vegetation studies.

The experiment had three aims:

1. To determine if changes in water regime had any measurable effect on the C-score and CFVT-S.
2. To assess if the changes were in the direction predicted by the strategy model.
3. To determine the degree of complementarity between the C-score index for populations and the CFVT-S index for communities.

6.2.2 Methods and statistical analysis

15 grassland turfs (0.5m x 0.5m and 0.3m deep) were dug in December 1992 from two French FAEWE wetland sites; Decize (FDC3) and Apremont (FAP3). They were transported back to the greenhouses at the University of Utrecht (The Netherlands) and kept in an unheated greenhouse. In February 1993, the turfs were installed in approximately 1m high polypropylene containers (wheely bins) with the base of the vegetation level with the top of the container. The space beneath the turf in each bin was filled with sand.

In April 1993 differential water regimes were commenced, the three regimes used were:

1. Dry: water table 10cm or just below the base of the container.
2. Wet: water table at soil level or just below.
3. Control: water table 20cm below soil surface or just below.

To achieve these water regimes, holes were drilled in the sides of the bins at the appropriate height for each treatment. Water was added daily from the base, via a piezometer tube, if the water level was more than 10cm below the desired level. Evapotranspiration meant that water was lost from the bins, thus, over the 24 period between watering the water level would fall. Water quality was similar to river water from the French sites (van Oorschot, pers. com.). Water was also supplied weekly from above in a similar amount that the vegetation would receive in central France in a dry year (10mm each week), with longer intervals between watering during the summer. On the 12/3/93 all the turfs were cut close to ground level. Trait and state variables were measured between 22-26/7/93.

Measurements were taken to determine the C-score and CFVT-S. The C-score was calculated for the most common species, *Agrostis capillaris*, in each of the turfs and involved the measurement of the traits; plant height and the dry weight of leaves. Traits were recorded 10 times for each turf and a mean was taken. CFVT-S was calculated from dominance and the vegetation cover above 20cm (see 5.2.1 for methods).

Analysis of these data to determine if the treatments had significant effect on the competitive index were carried out using analysis of variance (ANOVA). However, ANOVA only tests if the treatments had a significant effect, it does not permit differences between 2 treatments to be assessed (unless, of course, the experiment only had 2 treatments). Least significance difference (L.S.D), a fixed range test for comparison between two sample means, and multiple range tests (e.g. Duncans new multiple range test (Alder & Roessler 1977)) for comparisons between a set of sample means have been commonly used for analysis of biological data. These two types of test are, however, *a posteriori* tests, to be used following inspection of the results and identification of interesting comparisons (Sokal & Rolfe 1981). The aim of the experiment was to determine the predictability of the competitive index in response to treatments. Only a subset of possible comparisons between treatment means are of interest; those comparisons about which predictions can be made by the strategy model. Thus, an *a priori*, or pre-planned, test was required; the comparisons to be determined before the data was analysed.

It was considered that setting up pairwise comparisons "blind" i.e. before data about the treatment perturbation had actually been analysed, would be a more rigorous test of the predictive potential of the C index. It was accepted that some treatments which retrospectively appeared to be significantly different would not be uncovered using "blind" comparisons. However, it was considered that the advantages of using a "blind" comparison method, which better represents the situation when predictions are made, outweighed the potential loss of significance between treatments.

One method which permits comparisons of a set of pre-planned comparisons, within the ANOVA analysis is orthogonal comparisons. Orthogonal comparisons are pre-planned or *a priori* comparisons of different treatments, or sets of treatments, which are identified of being of interest before the results of the experiment are obtained. The treatment sum of squares are decomposed into separate user-defined parts with sum of squares and degrees of freedom pertaining to them, this allows the determination of the variance ratio and consequently the F probability. Two assumptions must be met for orthogonal comparisons to work; firstly the sum of the degrees of freedom of the comparisons must not exceed the degrees of freedom of the treatments and secondly, the planned comparisons must be orthogonal (see Sokal & Rolfe 1981; pp. 236-237 for further explanation). If the number of samples were different between the two groups of the orthogonal comparisons, a weighting method was applied following Sokal & Rolfe (1981; pp. 537-538).

All ANOVA analyses with orthogonal contrasts were carried out using Genstat 5 on PC.

The percentage of variation explained by the treatments (R^2_{adj}) was calculated from:

$$R^2_{adj} = 1 - [\text{ residual m.s.} / \text{total m.s.}]$$

Total m.s. was calculated by dividing the total s.s. by the total d.f. (Jongman *et al.* 1987)

6.2.3 Results

Apremont: The treatments had a significant effect on the C-score of *A. capillaris* ($P<0.05$) (Table 6.1a). The dry treatment had a lower C-score than the control, and the wet treatment had a slightly higher mean C-score than the control (Fig. 6.1a). Treatments explained nearly 40% of the variation in C-score between treatments ($R^2_{adj} = 0.39$). From the orthogonal comparisons there was no difference between the control and the two treatments together. This was because the dry treatment C-score was lower than the control and the wet treatment was higher than the control. The mean of the treatments would be similar to the control (and also have a large amount of variation), thus the treatment and control means would not be significantly different. The C-score of the dry treatment and the wet treatment were significantly different ($P<0.05$) with the dry having a lower C-score than the wet treatment (Table 6.1a, Fig. 6.1a).

Table 6.1 Results from analysis of variance of the C score, with orthogonal contrasts, for the bin experiment

a. Apremont

Source of variation	**d.f**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	2	0.59	0.30	5.03	*
control vs treatments	1	0.06	0.06	1.11	NS
dry vs wet	1	0.52	0.53	9.04	*
RESIDUAL	10	0.59	0.06		
TOTAL	12	1.18			

b. Decize

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	2	0.61	0.30	7.64	**
control vs treatments	1	0.08	0.08	2.11	NS
dry vs wet	1	0.52	0.52	13.17	**
RESIDUAL	12	0.47	0.04		
TOTAL	14	1.1			

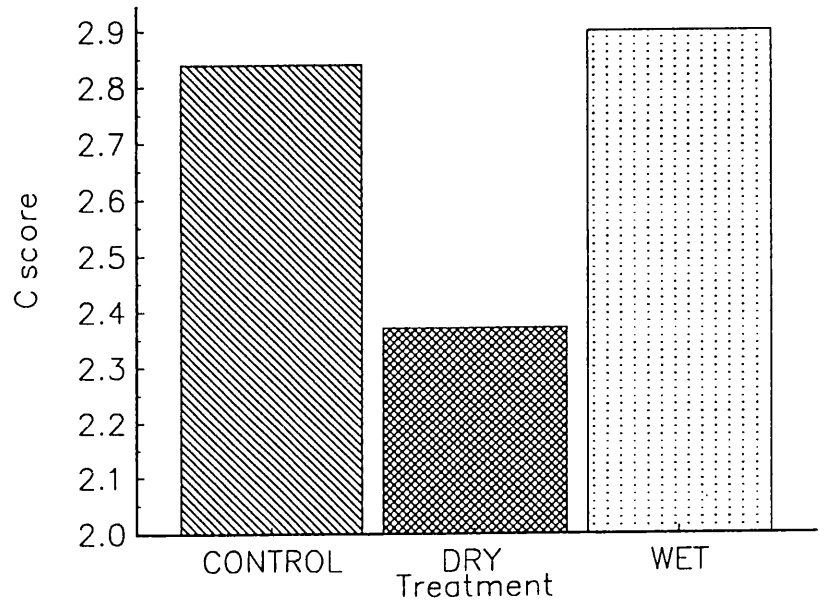


Fig. 6.1a The effect of treatments on the mean C score of the Apremont bin experiment ($P<0.05$).

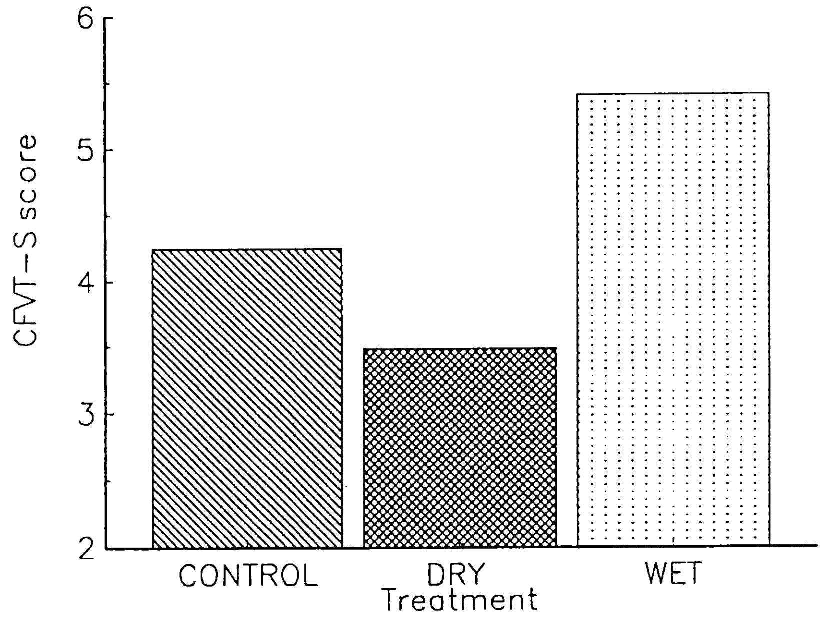


Fig. 6.1b Effect of treatments on the CFVT-S score of the Apremont bin experiments ($P<0.05$).

The dry treatment caused *A. capillaris* to have a lower C-score, and consequently become less competitive when compared to the control. Drought can be considered as a stress, and with no change in disturbance, caused the plant to exhibit a less competitive and consequently more stress-tolerant strategy. The wet treatment and the control had similar mean values, although the wet was slightly greater. The mean 20cm difference between the water tables of the two treatments appeared to have little effect on the C-score, this maybe due to the presence of roots down to the 20cm level in the control which could maintain supply of water to the above ground vegetation. It was recorded in a previous chapter (see section 4.2.2.2) that the effect of flooding *A. capillaris* to the soil surface did not appear to affect the biomass production of the plant compared to individuals maintained at a water level ~8cm below the soil surface. These results support this previous contention that the saturation of water to the soil surface does not impose a stress on *A. capillaris* compared to a moist soil.

Treatments had a significant effect on the CFVT-S values ($P<0.05$) (Table 6.2a, Fig. 6.1b). The dry treatment had a lower CFVT-S score than the control, the score for the wet treatment was greater than the control. Although the control and the two treatments together were not different, due to the means of the wet and dry treatments being either side of the control, there was a difference between the dry and wet treatment ($P<0.01$).

The effect of the treatments described in terms of a competitive index for the population and the community were similar (compare Fig. 6.1a and b). The dry treatment being lower than the control, and the wet treatment higher than the control. The similarity of effect of treatments was obtained from two independent data sources, traits and state variables. This suggests that both the C-score and CFVT-S were responding in a similar way to the water regime. It should be noted that the CFVT-S index value was about 40% higher than the corresponding C-score, possible reasons for this will be discussed later.

<u>Decize:</u> The C-score was different between the treatments ($P<0.01$) (Table 6.1b); the treatments explained nearly 50% of variation in the C-score ($R^2_{adj} = 0.49$). The dry treatment was lower than the wet, which was similar to the control (Fig. 6.2a). No difference between the control and the treatments was found, however, there was a significant difference between the dry and wet treatments ($P<0.01$), the dry having a lower C-score than the wet. There was little difference between the wet treatment mean C-score and the control. As with the results from Apremont, it appeared that *A. capillaris* was not greatly affected by soil

Table 6.2 Results from analysis of variance of CFVT-S, with orthogonal contrasts, for the bin experiment.

a. Apremont

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	2	9.38	4.69	4.81	*
control vs treatments	1	0.12	0.12	0.13	NS
dry vs wet	1	9.25	9.26	9.49	**
RESIDUAL	12	11.07	0.98		
TOTAL	14	21.08			

b. Decize

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	2	1.75	0.88	0.71	NS
control vs treatments	1	0.06	0.06	0.05	NS
dry vs wet	1	1.69	1.69	1.37	NS
RESIDUAL	12	14.83	1.23		
TOTAL	14	16.59			

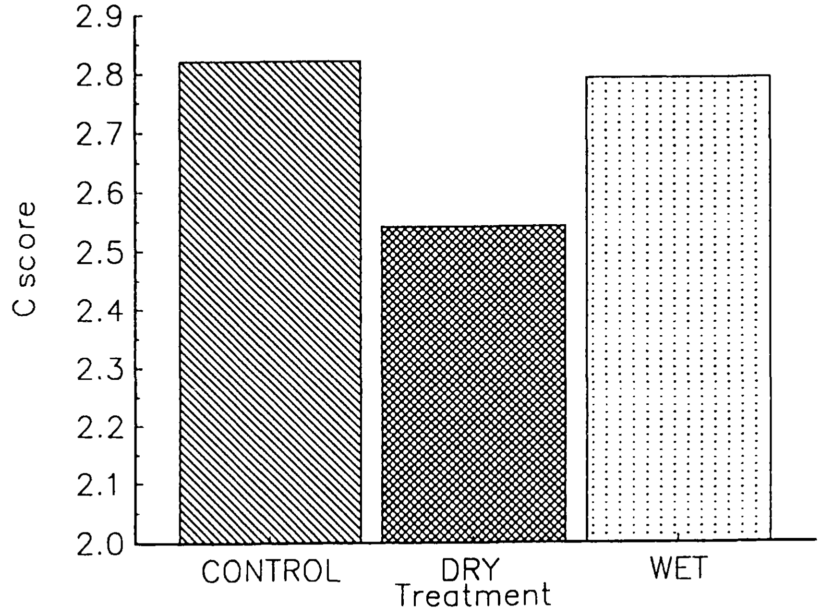


Fig. 6.2a Effect of treatments on the C score of the Decize bin experiment (P<0.01).

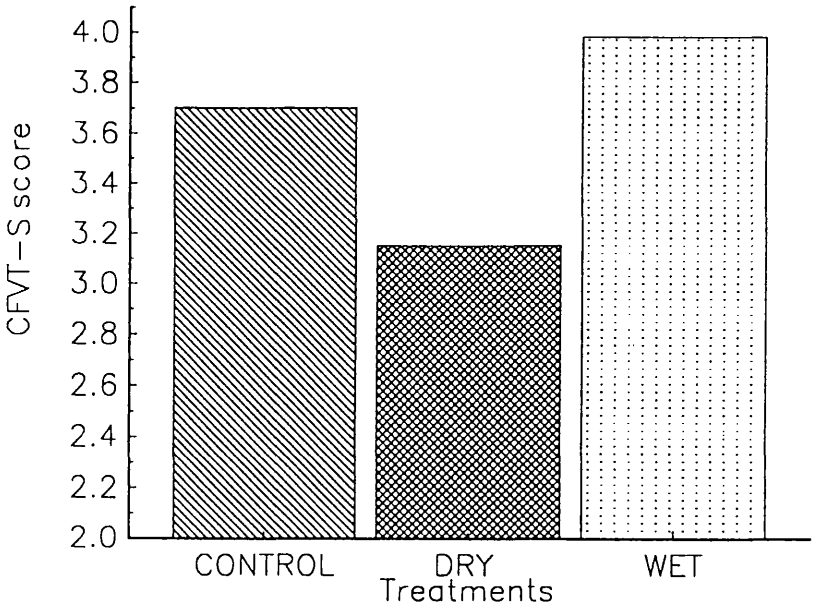


Fig. 6.2b Effects of treatments on the CFVT-S score of the Decize bin experiments (P= not sig.).

saturation. The C-score for *A. capillaris* decreased with the dry conditions, the stress of drought causing a decrease in competitiveness.

No significant differences were found between treatments overall or for orthogonal contrasts for the CFVT-S score (Table 6.2b). Although, the mean effect of treatments was similar to the C-score for Decize (compare 6.2a and b), statistical differences were obscured by too much variation. The high variation in the CFVT-S scores could have been due to inadequate sampling or much variation in CFVT-S within the plots.

From the results for Apremont and Decize it was apparent that the treatment was having similar effects on the vegetation from the two sites. The dry treatment tended to decrease the competitiveness of one of the common plant species and the community, the wet treatment having less of an effect than the dry treatment but generally causing a small rise in the competitive indices.

6.2.4 Discussion

A strong similarity in the direction of response to the effect of water regime on the C-score and the CFVT-S score was apparent. Although CFVT-S was formed from the CFVT value (the mean C-score at a hydrogeomorphic unit), state variables, related to diversity and architecture rather than traits, were used to determine its value. The C-score and CFVT-S are, thus, independent but related. The stepwise multiple regression of CFVT with state variables to produce CFVT-S was carried out using the whole range of FAEWE wetland sites. The variation in CFVT-S in this experiment was small compared to the wide range of sites from which the index was derived. However, the CFVT-S index responded within one season to the non-catastrophic treatments related to water level. This supports the suggestion that CFVT-S may be a potentially useful indicator of vegetation change.

A difference in the actual value between CFVT-S and the C-score was noted, with the C-score being about 40% lower than the CFVT-S score. This was somewhat unexpected as the scale of the CFVT-S index should be similar to that of the C-score. The difference in scales could be due to the problems associated with the statistical reductionism carried out in the stepwise multiple regression stage used to derive CFVT-S; only two state variables were selected to be used as predictors of CFVT-S. However, from the CCA analysis between FVT values and state variables it was noted that certain biotopes were associated with high values in certain state variables (see Table 5.3). In the regression stage of the formulation of CFVT-S, this pattern of indicative state variables was lost, because linear regression techniques describe the best fit line between a dependent variable and one or a set of independent variables. Stepwise multiple regression would thus tend to find the variable(s) which describes best the variation in the dependent variables rather than determining the variables which have certain indicatively high values for certain types of community; this would potentially cause error in determining the CFVT-S score. Thus, the CFVT score would not necessarily be closely related to the CFVT-S score in certain circumstances.

An alternative and simpler explanation of the difference in value between the CFVT-S and the C-score could be related to *A. capillaris* having a lower C-score than the mean of the community. This would mean that the CFVT-S value would automatically be higher than the corresponding C-score. However, if plants were arranged in competitive hierarchies (Keddy 1990) then the presence of a population with a lower competitive ability than the surrounding constituent species of the community would be an anomaly. To fully explain the difference between CFVT-S and C-score further work would be necessary in a range of environments. However, the important result from the experiment was that CFVT-S and C-score responded in a similar fashion to similar treatments.

Dry treatment experimental plots were consistently less competitive (in terms of both C-score and CFVT-S) than controls. A less competitive C-score entails a greater stress-tolerant score, as the two indices are highly negatively related (see Fig 3.3). Thus, the dry treatments responded predictably in relation to the treatment. The wet treatments responded little compared to the control, though both Apremont and Decize samples had a greater C-score. The predicted effect of the wet treatment was more difficult as it was not known if the *A. capillaris* was suffering from drought stress in the control or if the wet treatment would cause a flooding stress due to e.g. anaerobic soil conditions. The results tend to support the idea that *A. capillaris* was more stressed in the control treatment than the wet treatment.

6.2.5 Summary

1. Changes in water regime had a significant effect on the values of the C-score for *A. capillaris* from turfs from Apremont and Decize and on the CFVT-S value for the whole community the Apremont turfs.
2. Both CFVT-S and C-score changed in the predicted manner following the dry treatment. The wet treatment had little effect compared to the control and the direction of the prediction was not clear.
3. The treatments affected CFVT-S and the C-score in a similar manner.

6.3 THE EFFECT OF FERTILISATION AND DISTURBANCE.

6.3.1 Introduction

To determine the effect of fertilisation and disturbance on the vegetational community of a river marginal wetland, a two-year experiment was set up. It was predicted that the addition of fertiliser would tend to increase the competitive indices (the C-score and CFVT-S) of the treated plots, whereas the disturbance would tend to make the community less competitive.

The aims of the experiment were:

1. To determine if the C-score and CFVT-S could detect changes in the vegetation due to perturbation affecting the balance of stress and disturbance influencing it.
2. To assess if the measured competitive indices responded in the predicted manner.

6.3.2 Methods

Five exclosure cages (to stop grazing by cows in the field) were randomly placed no more than 5m apart in the FAEWE site FDC3 (Decize, France). Each cage was oriented north-south. At the level of the soil, cages were 1.3m wide and 5.2m long, the top was semi-circular and was 0.8m above ground at its apex. The frame of the cages was made out of tubular galvanised steel, the frame was covered in wire netting. The cages were pinned to the ground using stakes which were only removed when measurements were taken. Each of the five cages were equally divided into 3 areas, the central 1m x 1m of the 1.4m x 1.3m plot was the treated zone.

Four treatments were randomly assigned to the 15 plots. One treatment however was stopped after the first application due to unknown effects on environmental monitoring equipment located in close proximity. The plots with this treatment could no longer be used in the experiment due to the possible effect of the first treatment. Thus, the experiment was carried on with 3 treatments in 11 plots. The treatments were:

1. Fertilisation - application of 100g m^{-2} granulated NPK fertiliser (15:10:20) (Engrais Fraisiers NFU 42.001 made by ICI) (n = 4).
2. Disturbance - roughly cutting to 5cm using hand-operated shears (n = 3).
3. Control (n = 4).

Treatments were applied 3 times in 1992 (10/5/92, 27/6/92 and 13/8/92) and twice in 1993 (28/4/93 and 26/6/93). Morphological traits (height, weight of stem, weight of leaves and weight of reproductive structures) of *A. capillaris* were measured in June and August in 1992 and 1993 i.e.

1. Sampling time 1 - 22-26/6/92

2. Sampling time 2 - 10-12/8/92
3. Sampling time 3 - 22-25/6/93
4. Sampling time 4 - 3-6/8/93

State variables to determine the CFVT-S score for the community were measured at the start and the end of the experiment (sample times 1 and 4) (see section 5.2.1 for method).

6.3.3 Results

C-score: In 1992, significant differences were found between the C-score for *A.capillaris* in the different treatments. At sample time 1, although the treatments did not have a significant effect overall, there was a difference between the disturbance treatment and the uncut treatments (control and fertiliser) (Table 6.3a). The disturbance treatment had a lower C-score than the control (Fig. 6.3a), this agrees with the prediction that an increase in disturbance would cause a decrease in competitive ability, assuming that stress was constant. The fertiliser tended to increase the C-score for *A. capillaris*, although the difference was not significant.

The differences between the plots due to treatments were greater later on in the 1992 growing season (sampling time 2). The treatments had a significant difference on the C-score ($P<0.01$) (Table 6.3b). A similar pattern was observed to sampling time 1, with the C-score of the fertiliser treatment having a greater, though, not significantly, C-score than the control and the disturbed treatment having a lower mean value than the control (Fig. 6.3b). The response of *A. capillaris* followed the prediction that disturbance would decrease the competitive ability of the plant, however, although the mean of the fertilised treatment was higher than the control it was not significantly different.

During the sampling periods 3 and 4 in 1993, no differences were found overall or between orthogonal contrasts (Table 6.3c & d).

CFVT-S: CFVT-S was measured at the start of the experiment (sampling time 1) and at the end of the experiment (sampling time 4), on both of these occasions there were no differences between treatments for the CFVT-S value (Table 6.4a & b).

The treatments appeared not to have a cumulative effect on the C-score from 1992 to 1993 as no differences were found in 1993. The difference in effect between 1992 and 1993 due to the treatments could have been caused by:

1. A difference in another factor between 1992 and 1993 e.g. climatic conditions.

Table 6.3 Results from analysis of variance of the C score, with orthogonal contrasts, for the exclosure cage experiment at Decize.

a. Sample time 1.

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	2	1.92	0.96	3.92	NS
control vs fert.	1	0.15	0.14	0.59	NS
cut vs uncut	1	1.78	1.78	7.24	*
RESIDUAL	8	1.84	0.25		
TOTAL	10	3.90			

b. Sample time 2.

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	2	3.60	1.80	15.08	**
control vs fert.	1	0.08	0.08	0.67	NS
cut vs uncut	1	3.52	3.52	29.5	***
RESIDUAL	8	0.96	0.11		
TOTAL	10	4.55			

c. Sample time 3.

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	2	0.11	0.06	0.623	NS
control vs fert.	1	0.01	0.01	0.81	NS
cut vs uncut	1	0.10	0.10	0.37	NS
RESIDUAL	8	0.89	0.11		
TOTAL	10	1.01			

d. Sample time 4.

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	2	0.86	0.43	2.38	NS
control vs fert.	1	0.00	0.00	0.00	NS
cut vs uncut	1	0.86	0.86	4.76	NS
RESIDUAL	8	1.45	0.18		
TOTAL	10	2.31			

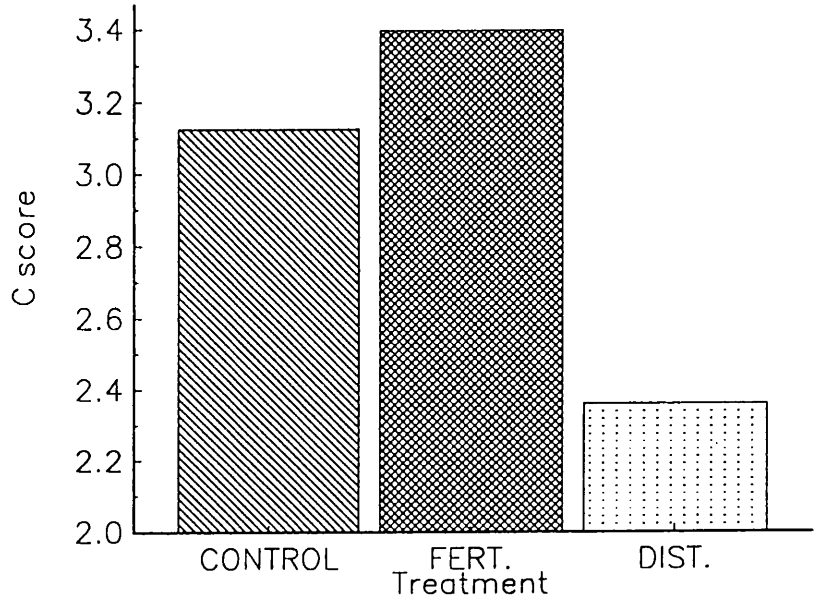


Fig. 6.3a Effect of treatments on the C score of the exclosure cage experiment, sampling time 1 (P not sig.).

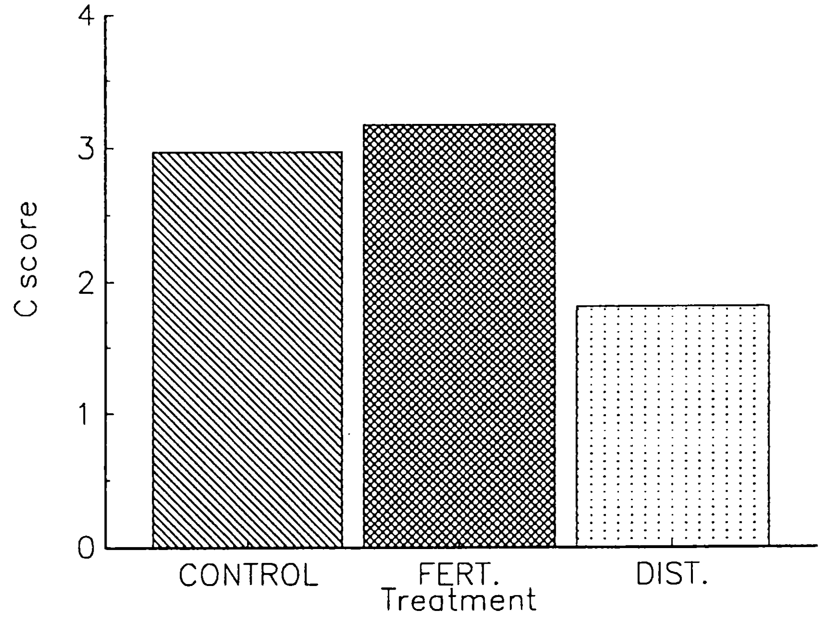


Fig. 6.3b Effect of treatments on C score of exclosure cages, sampling time 2 (P<0.01).

Table 6.4 Results of analysis of variance of CFVT-S, with orthogonal contrasts, for the exclosure cage experiment at Decize.

a. Sample time 1.

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	2	3.72	1.85	2.22	NS
control vs fert.	1	0.87	0.87	1.03	NS
cut vs uncut	1	2.85	2.85	3.40	NS
RESIDUAL	8	6.71	0.84		
TOTAL	10				

b. Sample time 4.

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	2	0.60	0.30	0.09	NS
control vs fert.	1	0.29	0.29	0.09	NS
cut vs uncut	1	0.315	0.31	0.10	NS
RESIDUAL	8	26.28	3.29		
TOTAL	10	26.89			

2. An adaptation by *A. capillaris* to the treatments making them more resistant to these treatments in the following season.

It would be difficult to test explicitly whether the differences between the years in response to treatments was due to one or the other possible explanations. However, a further analysis indicated that the explanation concerning some difference in an unknown factor between 1992 and 1993 could partly explain the difference between years.

The null hypothesis that there were no differences in morphology between 1992 and 1993 in June and in August was tested using two-way ANOVA. The two "treatments" in the ANOVA were the C-scores for 1992 and 1993, the 3 treatments were considered as blocks so as to remove the variation in C-score due to the treatments. Comparisons were made separately for June and August.

Differences were found in June between the C-score between 1992 and 1993 ($P<0.001$), the mean C-score for 1992 being over 1 C-score unit below 1993 (3.01 compared to 4.06). The plants in 1993 were more competitive than in 1992, this suggests, consequently, that they were less stressed or disturbed. Assuming that the level of disturbance was the same between the years, which was true for large herbivore grazing and flood disturbance but largely unknown concerning the effects of insect and small mammal grazing, the difference in competitiveness could be explained by a reduction in the degree of stress in the environment. No significant differences were found between the C-score for 1992 and 1993 in August.

Using the same design of ANOVA as with the C-score, a set of morphological traits were assessed for differences between 1992 and 1993 in June. All of the tested morphological traits were significantly different between 1992 and 1993, in all cases the traits were significantly larger in 1993 (height, $P<0.001$; weight of stem, $P<0.001$; weight of leaves, $P<0.001$ and weight of reproductive structures, $P<0.01$). These results provide some indirect evidence that 1993 was a more productive year than 1992. Data from biomass samples in both 1992 and 1993 would be needed to confirm this notion.

If 1993 was considered to be a more productive year than 1992 for *A. capillaris*, one of the possible explanations for the difference in the C-score between 1992 and 1993, outlined above, was that the increase in productivity was due to some adaptation in the plant. However, the results suggest that the increased productivity and competitiveness occurred irrespective of the treatment, as the variation due to treatment was removed prior to the ANOVA (using the BLOCK command in Genstat 5). Thus, the adaptations to both disturbance and fertiliser would have had to occur in a manner that had a similar effect on the morphology of *A. capillaris*. In addition, the control plot was more competitive in 1993 compared to 1992 (C-score mean of 3.13 in 1992 compared to 4.09 in 1993); the adaptation explanation cannot be invoked in this case as no treatment was applied. Thus, the difference between the years was due to some unknown factor which had an effect in the early part of the season but which had little effect later on in the season. Strong drought conditions are frequently experienced at this site during the summer, due partly to the sandy soil on which it is based and partly to the sites continental position close to the centre of France. Due to the tendency for the site to dry up in early in the growing season, a possible explanation for the above data could a relatively moist early summer in 1993. Further evidence would be needed to confirm this hypothesis. Soil moisture data from the monitoring stations should become available during Phase II of the FAEWE project.

6.3.4 Discussion

In 1992, predictions concerning the effect of disturbance on *A. capillaris* were correct. The predictions that fertiliser would increase the competitiveness of the plant were not correct, although the mean C-score value was greater in the fertilised compared to the control plots. No differences were found in 1993, which was possibly a more productive year for *A. capillaris*. Further work would be necessary to determine why there was no change in the more productive year. It could be possible that in more productive conditions the plant was more able to cope with the pressures imposed on it by stress and disturbance factors. It could also be possible that the fertiliser had little effect on the C-score because it was not the factor that was limiting growth at that time; although the soil was nutrient poor at the site the sudden greenness of the field following summer rainfall suggests some degree of water stress. To test these assertions a greenhouse experiment could be set up with the disturbance and fertiliser treatments with different water regimes. This experiment would really be a synthesis of the previous experiment concerning water regime in bins and this experiment, however it would allow the effects of interactions between water and perturbations to be determined.

The CFVT-S index did not respond to treatments, even when the C-score was significantly different. The reasons for this were not apparent. Though logically, for change to occur in structure and species abundance, individual plants would already have morphologically adapted. Thus, changes in the C-score would be expected prior to changes in CFVT-S.

6.3.5 Summary

1. In June and August 1992, *A. capillaris* was less competitive compared to controls following a disturbance treatment. No differences were found in 1993.
2. No differences were found between the controls and the fertilised plots in 1992 and 1993 in terms of C-score for *A. capillaris*.
3. No differences were found in CFVT-S in June 1992 or August 1993.
4. Using morphological traits of *A. capillaris*, it was found that June 1993 was a more productive season than June 1992. It was hypothesised that the reasons for this could be related to water availability in the early summer.

6.4 THE EFFECT OF FERTILISATION .

6.4.1 Introduction

As part of the investigation on the functioning of riparian wetlands in the FAEWE project a fertiliser experiment was set up by a team from the Department of Landscape Ecology and Evolutionary Biology, University of Utrecht, The Netherlands (the team consisted of Drs. M. van Oorschot, Drs. M. van der Peijl and Dr. J.T.A. Verhoeven). The main aims of the experiment were to supply the dynamic nutrient model, being constructed as part of the project by Drs. M. van der Peijl and Dr. J.T.A. Verhoeven (University of Utrecht), with curves describing the response of several processes to elevated nutrient levels and to test predictive systems in a controlled field experiment. However, the experiment could also be used to investigate the effect on the vegetational community of different levels and different types of fertilisation using population and community competitive indices as indicators of vegetational change.

6.4.2 Methods

Two FAEWE wetland areas were selected for study:

1. Site EKS2 from the Kismeldon meadows (SSSI) on the Torridge catchment, Devon, England.
2. Site ICL3 from the floodplain of the Shannon in the Republic of Ireland.

Six treatments were used:

1. control
2. P1 (10kgP/ha/year)
3. P2 (25kgP/ha/year)
4. N1 (40kgN/ha/year)
5. N2 (100kgN/ha/year)
6. N2P2 (100kgN/ha/year + 25kgP/ha/yr)

Phosphorus was added in the form NaH_2PO_4 and nitrogen in the form NH_4NO_3; all treatments were applied in solution form to obtain a more even application within plots Treatments were applied in April in 1992, and again in 1993. The fertiliser treatments were added in two applications, at least 3 days apart, to avoid excessive leaching and possible toxic effects on micro-organisms and plants.

The experimental design was in the form of a Latin square. An area with 6 x 5 plots was set up, with a single replicate of each treatment in each of the five rows; the rows being parallel with the river. Plots were 1m x 1m (except for the control plot which was 1.5m x 1.5m). Plots within a row were 1m apart and the distance between rows was 2m. The area in England was fenced off to prevent grazing from the cattle which were let into the field in some summers. There was no grazing on the Irish site.

Data were collected in July 1992 and 1993 on traits to produce the C-score for *Agrostis capillaris* in the Irish area, and *Molinia caerulea* in the England area. State variables were recorded to determine the CFVT-S index for each plot in both England and Ireland.

The ANOVA's carried out were two-way, one-way for treatment effects and one-way for block effects (a block in this experiment being a row).

6.4.3 Results

England: In July 1992, neither the block nor the treatments had significant effect on the C-score of *Molinia caerulea*. One of the five orthogonal contrasts was significantly different. The C-score of the N2P2 treatment was significantly greater than the score of the P2 and N2 treatments (1.86 compared to 1.74; P<0.05) (Table 6.5a). This result suggests that the application of N2P2 had a greater effect than just the addition of high levels of P or N on the C-score. The mean C-score values of both the N2 and P2 treatments were higher than the control treatment (1.74, 1.74 and 1.52 respectively), however the addition of N2 compared to N1 and P2 compared to P1 did not have a significant effect in either case (though again the means were greater in the high treatment compared to he low treatment) (Table 6.5a).

In July 1993, there was no significant difference between the treatments (Table 6.5b). There was a difference between the C-score for the N1 treatment and the N2 treatment. The mean C-score value of the N2 treatment was higher than the mean of the N1 treatment (2.79 compared to 2.41), suggesting that the higher addition of nitrogen had increased the competitiveness of *Molinia* compared to the low application level.

The orthogonal relationship with the highest P value of the variance ratio, after the N1 / N2 comparison, was between N2P2 and N2 and P2 (P=0.16). The pattern of this comparison, the only orthogonal contrast significant in 1992, was similar to the previous year with the N2P2 treatment having a greater C-score (2.77) compared to the N2 and P2 treatments (2.38). The differences however, were not great enough to be significantly different.

In both 1992 and 1993, the treatment did not have any significant effect on CFVT-S overall or using the same orthogonal contrasts as in Table 6.5.

Ireland: In 1992, treatments were found to have a significant effect on the C-score of *A. capillaris* (P<0.01) (Table 6.6a). Only one orthogonal contrast was

Table 6.5 Results from analysis of variance of C score, with orthogonal contrasts, for the fertiliser experiment in England.

a. Sample 1 (07/92)

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
BLOCK	4	0.13	0.03	0.84	NS
TREATMENT	5	0.52	0.10	2.70	NS
control vs N	1	0.14	0.13	3.57	NS
control vs P	1	0.02	0.02	0.53	NS
N1 vs N2	1	0.02	0.02	0.57	NS
P1 vs P2	1	0.12	0.12	3.20	NS
N2P2 vs P2 & N2	1	0.21	0.21	5.63	*
RESIDUAL	20	0.77	0.04		
TOTAL	29	1.41			

b. Sample 2 (07/93)

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
BLOCK	4	0.33	0.08	1.17	NS
TREATMENT	5	0.54	0.11	1.52	NS
control vs N	1	0.00	0.00	0.03	NS
control vs P	1	0.03	0.03	0.49	NS
N1 vs N2	1	0.35	0.35	4.93	*
P1 vs P2	1	0.00	0.00	0.01	NS
N2P2 vs N2 & P2	1	0.15	0.15	2.13	NS
RESIDUAL	20	1.42	0.07		
TOTAL	29	2.29			

Table 6.6 Results from the analysis of variance of the C score, with orthogonal contrasts, for the fertiliser experiment in Ireland.

a. Sample 1 (07/92)

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
BLOCK	4	0.39	0.10	1.78	NS
TREATMENT	5	1.16	0.23	4.17	**
control vs N	1	0.04	0.04	0.80	NS
control vs P	1	0.21	0.21	3.75	NS
N1 vs N2	1	0.23	0.23	4.03	NS
P1 vs P2	1	0.66	0.66	11.74	**
N2P2 vs N2 & P2	1	0.03	0.03	0.50	NS
RESIDUAL	20	1.11	0.06		
TOTAL	29	2.68			

b. Sample 2 (07/93)

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
BLOCK	4	0.70	0.18	2.66	NS
TREATMENT	5	0.14	0.03	0.43	NS
control vs N	1	0.00	0.00	0.00	NS
control vs P	1	0.10	0.10	1.53	NS
N1 vs N2	1	0.02	0.02	0.24	NS
P1 vs P2	1	0.00	0.00	0.03	NS
N2P2 vs N2 & P2	1	0.02	0.02	0.36	NS
RESIDUAL	20	1.32	0.07		
TOTAL	29	2.17			

significant, the comparison between the low and the high application levels of P. The mean C-score for *A. capillaris* at the higher application level of P was higher than the mean C-score at the lower P application (3.70 compared to 3.20). This pattern was similar to the results obtained in the English plot, where in significantly different orthogonal contrasts the higher application always had a higher C-score compared to the lower application..

No differences were found in the C-score of *A. capillaris* in 1993, or in the CFVT-S index in 1992 or 1993.

6.4.4 Discussion

Few differences were found due to the effects of fertilisation in these fertilisation experiments over two years. Both communities were humid grassland CORINE biotopes, the English site was an oligotrophic humid grassland (37.3) whereas the Irish site was a meadow-sweet stand (37.2) (see Table 1.2). Their CFVT values were relatively low compared to the range in the FAEWE sites, with a value of 1.91 for the English site and 4.17 for the Irish site (See Table 3.5). These two indicators suggest that the sites were relatively nutrient poor, the plant assemblages being adapted to low levels of nutrients.

Grime (1979) suggested that competitive plant species have more potential for plasticity in their morphology than either strongly stress-tolerant or disturbant-tolerant plants. The relatively stress-tolerant plants growing in the oligotrophic conditions in the two experimental plots were possibly unable to exploit the nutrient additions and exhibit morphological change. One way to test this hypothesis would be to carry out the experiment, in an identical manner, but in a more competitive habitat type and compare the changes in C-score for a common species and CFVT-S to the results obtained for these two oligotrophic sites.

It was possible that much of the fertiliser failed to reach the plants. In Ireland, problems of heavy rain (not an unusual occurrence) and a water table at or slightly above the soil level at times could have lead to some leaching or ground flow of nutrient additions. In England, the experimental plot was situated on a gentle slope, it being possible that some of the nutrient seeped down-slope before it could be utilised by the plants. This, however was unlikely as there was no evidence for any block effects in the experimental design.

The main aim for the design of the experiment for the Utrecht team, was to produce data for relationships in the nutrient model. Thus, studies on soil nutrient processes were carried out throughout the course of the experiment. These data are not yet available, but would permit a more objective analysis of the processes occurring producing the patterns detected. The data would answer the question as to whether the nutrients were actually available to the plant. One of the main aims of Phase II FAEWE, starting in May 1994, will be to bring together data from the different research groups to allow a greater understanding of wetland functioning.

6.4.5 Summary

1. Few differences due to N and P fertiliser treatments were found in the C-score for *A. capillaris* in Ireland, or for *M. caerulea* in England.
2. In all cases where differences were found between treatments, higher levels of treatments caused a higher C-score. This follows the prediction that fertilisation tends to make plants more competitive.
3. No significant changes were found in the CFVT-S index in either 1992 or 1993.
4. Both experimental plots were from oligotrophic grassland CORINE biotopes, it was hypothesised that the plant assemblage showed little change in morphology because the species were relatively stress-tolerant and could not exploit the nutrient additions. Data from soil process studies will help further interpretation of the results.

6.5 THE EFFECT OF STRESS AND DISTURBANCE ON GRASSLAND COMMUNITY.

6.5.1 Introduction

An experiment was organised by J. Hills (Glasgow University, UK.), Dr. A. Spink (University of Utrecht, The Netherlands) and I. Mouton (University of Rennes, France). The aim of the experiment was to compare three methods of identification of vegetational change, namely;

1. Competitive strategy indices (J. Hills)
2. Phytometers (*Phalaris arundinacea* and *Epilobium hirsuta*) (A. Spink)
3. Phytosociological techniques (I. Mouton)

The results for the approaches 2 and 3, were not available at the time of writing, thus only the results from the competitive strategy indices will be reported.

The experiment was aimed to determine if indicators of change could identify change within one growing season, using a stress factor and a disturbance factor, both singly and together The experiment was run over the growing season of 1993. The objective of the work on competitive indices was to determine if changes in competitive indices could be determined within one growing season and if those changes were in the direction predicted by the strategy model.

6.5.2 Method

The experiment was carried out at site FDC3. On April 16th, 1993, a fence was constructed around 25 1.5m x 1.5m plots arranged in a 5 x 5 pattern. There was a distance of 1.5m between an outside plot and the fence, and a 1m distance between plots. As the grassland appeared to be homogeneous with respect to vegetation and gradient, treatments were allotted randomly to 24 plots (one plot was left spare in case of mistakes in treatment applications).

Four treatments were used:

1. Control
2. Salt - 100g of salt per m^2 (code S).
3. Disturbance - cutting of sward to 5cm using shears (D).
4. Stress and disturbance - both treatments 2 and 3 (SD).

Treatments were applied on the 24th of April and two months later on the 24th of June. Sampling occurred three times during the year:

1. Pre-treatment sample - before the application of treatments (16-24/4/93).
2. Sampling time 1 - before the application of the second treatments (19-23/6/93).
3. Sampling time 2 (7-12/8/93).

Due to the range of time over which the experiment was being sampled and the necessity to sample plants around the point of reproductive maturity, different plant species had to be sampled at different times in the year. In the pre-treatment sample *Luzula campestris* was sampled, at sampling time 1 *Cynosurus cristatus* was sampled and at sampling time 2 *Agrostis capillaris* was used. State variables to determine CFVT-S were measured at sampling time 2.

6.5.3 Results

The pre-treatment data were collected to test if there were no differences between the plots before the treatments were applied. Analysis of variance, with orthogonal contrasts did not confirm that there were no differences between plots prior to treatment application. The treatments plots were significantly different before treatments were applied ($P<0.05$) (Table 6.7a). From the orthogonal contrasts there was found to be a difference between the control and the D plots ($P<0.01$). These results suggest that the random design did not suitably counteract environmental variation.

At sampling time 1, no differences in C-score were found between treatments (Table 6.7b). At sampling time 2 differences between treatments were found (Table 6.7c). However, because differences were found before the treatments were applied, interpretation of these results would be misleading.

Differences were found in the CFVT-S score sampled at time 2 (Table 6.8). However, due to the pre-treatment differences ecological interpretation of these results was not carried out. It would be interesting to note however, that the treatments which were different in the CFVT-S score were also different in the C-score for *A. capillaris* at sampling time 2 (Table 6.7c). This can be considered as evidence that the C-score and the CFVT-S index can respond in a similar manner to stress and disturbance (Fig. 6.4a and b).

6.5.4 Discussion.

Due to differences prior to treatment applications, little ecological interpretation can be made from this experiment, except that it represents further evidence that CFVT-S and the C-score respond in a similar manner to some stresses and disturbance. However, the experiment does highlight the problems of field experiments and experimental design.

There were four botanists present when the decisions about experimental design were made, the view was that a Latin square or a block design were not necessary as the area appeared to be homogeneous. This, however was not the case. Only through pre-treatment assessment of the plots was the inadequate experimental design uncovered. If no pre-treatment survey was carried out, the results would have fitted the hypotheses being tested well. No differences would have been

Table 6.7 Results of analysis of variance of C score, with orthogonal contrasts, for the Decize fence experiment.

a. Pre-treatment

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	3	0.16	0.05	3.84	*
control vs S	1	0.00	0.00	0.17	NS
control vs D	1	0.16	0.15	10.57	**
SD vs S & D	1	0.01	0.01	0.77	NS
RESIDUAL	20	0.29	0.01		
TOTAL	23	0.45			

b. Sample time 1.

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	3	0.52	0.17	1.88	NS
control vs S	1	0.30	0.30	3.21	NS
control vs D	1	0.02	0.02	0.25	NS
SD vs S & D	1	0.20	0.20	2.17	NS
RESIDUAL	20	1.86	0.09		
TOTAL	23	2.38			

c. Sample time 2.

Source of variation	**d.f.**	**s.s.**	**m.s.**	**v.r.**	**F prob.**
TREATMENT	3	5.67	1.89	14.85	***
control vs S	1	0.48	0.48	3.77	NS
control vs D	1	4.27	4.27	33.55	***
SD vs S & D	1	0.92	0.92	7.23	*
RESIDUAL	20	2.54	0.12		
TOTAL	23	8.21			

Table 6.8 Results of analysis of variance of CFVT-S, with orthogonal contrasts, form Decize fence experiment at sample 2.

Source of variation	d.f.	s.s.	m.s.	v.r.	F prob.
TREATMENT	3	6.51	2.17	7.99	**
control vs S	1	0.31	0.31	1.17	NS
control vs D	1	2.10	2.10	7.72	*
SD vs S & D	1	4.09	4.09	15.09	***
RESIDUAL	20	5.43	0.27		
TOTAL	23	11.95			

Fig. 6.4a Effect of treatments on the C score of the Decize fence experiment, sampling time 2 (P<0.001)

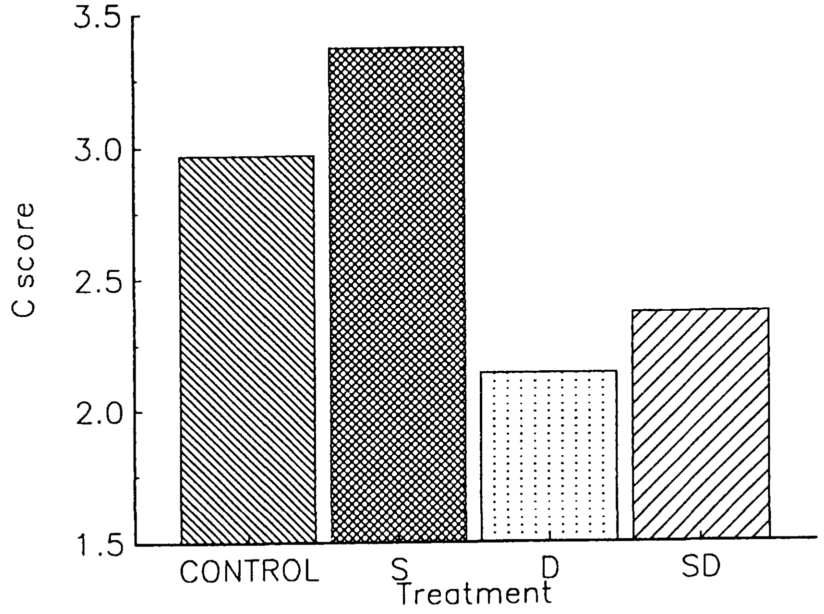
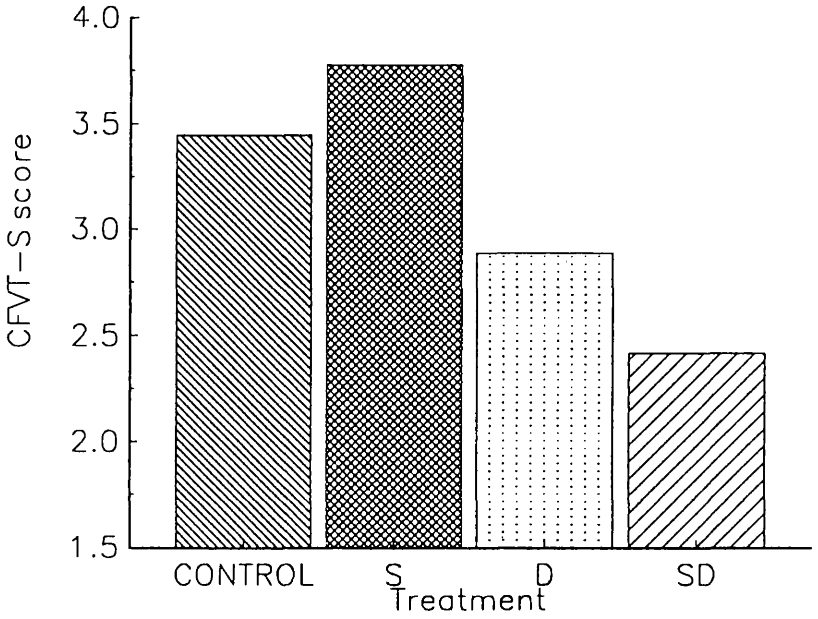


Fig. 6.4b Effect of treatments on the CFVT-S score of the fence experiment at Decize, sampling time 2 (P<0.01).



found after the first treatment (Table 6.7b), however differences would have been found at sampling time 2 (Table 6.7c). This, however, would have been a misrepresentation of the real differences in the data due to the design.

A guideline for future field experiments can be drawn from this experiment. Even if experimental areas subjectively appear to be homogeneous, an experimental design which allows the possibility of underlying environmental gradients to be uncovered is necessary.

6.5.5 Summary

1. Differences in plots prior to treatment applications made interpretation of further results difficult.
2. A similarity in CFVT-S and the C-score for *Agrostis capillaris* was found at sampling time 2.
3. A guideline for using experimental designs which allow environmental gradients, not perceived by the experimenter, to be addressed was proposed.

6.6 GENERAL RESULTS

In all the experiments, significant differences were found between treatments. A summary table was constructed, for the significantly different orthogonal contrasts, showing the predicted and actual direction of change (Table 6.9). The prediction of the direction of change in the C score was correct in 100% of the predictions. It would appear from these results that the C score responds in a similar fashion to that predicted using strategy theory.

The CFVT-S index appeared to change in response to treatments in a similar fashion to the C score. In the cases where there was a significant difference between orthogonal contrasts of the CFVT-S, there was also a significant difference between the C scores.

A majority of the orthogonal comparisons for the C score were not significantly different. The possible reasons for this are discussed below.

6.7 GENERAL DISCUSSION

6.7.1 The constraint of time

The main constraint on testing the effect of anthropogenic effect of treatments on strategy indices such as C score and CFVT-S, was time. Funding for this project was for three years, the realistic maximum length of field experiments being 2 years. It would be easy to create differences within these time lengths, but to do so, the treatments would have to be so powerful that either the community would be wiped out (and thus recolonisation would be studied) or the prediction of the effect would be plainly obvious. Thus, I attempted to use treatments which would have more subtle effects on the vegetational community. A lot of the treatments would thus not be significant because they were too weak, either in the amount of repetitions each year or in intensity. Whether differences between treatments were due to the weak strength of the treatments, or the insensitivity of the indices to environmental change, could not be determined.

Temporal differences, for example between early and late season, could not be assessed due to the small number of experiments (4 in total) and the number of years over which they were followed (1-2 years). Further experiments could possibly determine the time in the season when differences in treatments, in terms of competitive indices, were the greatest. However, this possibly would vary between habitats.

6.7.2 Prior state and prediction accuracy

The direction of prediction, in terms of C, for all the treatments which were significantly different, using orthogonal comparisons, agreed with the actual

Fig. 6.9 Similarity in the direction of change between predicted and the actual changes in C score between treatments from the orthogonal contrasts which were significantly different (the + or - notation for the prediction and actual response refer to if the first treatment of the treatment contrast was higher (+) or lower (-) than the second treatment).

EXPERIMENT	SITE (SAMPLE TIME)	TREATMENT CONTRAST	PREDICTION	ACTUAL RESPONSE	PREDICTION CORRECT
6.2	Apremont	dry vs wet	-	-	yes
	Decize	dry vs wet	-	-	yes
6.3	Decize (1)	uncut vs cut	+	+	yes
	Decize (2)	uncut vs cut	+	+	yes
6.4	England (1)	N2P2 vs N2 & P2	+	+	yes
	England (2)	N1 vs N2	-	-	yes
	Ireland	P1 vs P2	-	-	yes

direction of change in all cases. This suggests that the direction of response of populations to simple environmental perturbations was predictable, and that the C score represents a good method for determining the effect of the environmental perturbation. Thus, it appears that if differences were significant, the direction of change was predictable, however, the main problem was predicting if change was going to occur.

A change in the environmental regime would not necessarily have an effect on the vegetation. For example, the addition of NPK fertiliser to the cages in Decize seemed to have no significant effect. This could be due to the situation that the vegetation was actually water limited (rather than nutrient), and thus the addition of fertiliser would not increase growth. Some consideration must be made of the state of the plants prior to change. It was originally predicted that in the bin experiment, both the dry and the wet treatments were stresses, compared to the moist control. However, the actual case was that the control and wet treatments were similar, the wet being different to the dry treatment. Water logging had little effect on the studied plants.

6.7.3 Complementarity between population and community competitive indices

Treatments brought about similar responses in CFVT-S and the C score. This may not be too suprising, as CFVT-S and the mean C score for the constituent common species (CFVT) were highly correlated. However, it would appear that the state variables used to define CFVT-S and the traits used to determine the C score responded in a similar direction and similar amount to the same treatment. In some cases the C score was different but there was no difference in the CFVT-S index. This suggests that CFVT-S responds slightly slower than the C score; this could be due to the requirement for morphological trait change to bring about change in state variables.

6.8 GENERAL SUMMARY

1. Treatments were found to have an effect on competitive indices of populations and communities.
2. If significant differences between treatments were found, then the direction of measured change was the same as the predicted direction of change in 100% of cases
3. Some treatments did not have a significant effect on the competitive indices, and the possible reasons for this are discussed.

4. There was a strong degree of complementarity between the response of CFVT-S and C score. CFVT-S probably changed to a lesser degree than the C score, suggesting that C score was a more sensitive indicator of environmental change.

A DISCUSSION OF ACADEMIC AND MODELLING ASPECTS OF THE PROPOSED FUNCTIONAL APPROACH METHODOLOGY.

7.1 Introduction

This final chapter is divided into three sections. The first section is a critique of the work carried out at Glasgow as part of the FAEWE project; five main criticisms are outlined and discussed. The next section discusses the potential value of the proposed methodology to give predictions in terms of strategy indices. The ecological meaning of strategy indices, their link with other biotic and abiotic factors, and the characteristics of strategy indices as predictors, are discussed. After a brief discussion of philosophical aspects of ecological modelling, the final section considers the modelling aspects of the FAEWE project. A topological structure, with scientific rationale, for an assessment and a prediction model is proposed and the way in which this sub-model could fit into the overall FAEWE model design is considered.

7.2 A CRITIQUE

7.2.1 Introduction

Many aspects of the preceding work can be criticised. The work was carried out under a set of constraints which were pre-set as part of the FAEWE project. Criticism of these pre-set constraints would be unproductive, thus critical analysis is confined to aspects of the work which could have been controlled by the author. Four pre-set constraints on the work, of relevance to the following critique, are worth reiterating:

1. The field assessment was to be carried out by a competent scientist, without specialist training in any particular scientific discipline. Many potential end-user organisations do not have the resources for a specialist botanist / ecologist.
2. The time for field assessment was to be kept small, a matter of minutes rather than hours, for each predictor. Lengthy follow-up work in the office or laboratory was unacceptable.
3. A "product" from the constituent groups was expected within the three years of the FAEWE project. The "product" was to be in the form of a scientifically-formulated predictor(s) which was considered to respond in a predictable way following a proposed anthropogenic perturbation.
4. The predictive "product" was required to be related to other environmental processes, thus permitting a cohesive and nested set of predictors for important aspects of the wetland ecosystem to be fitted together into the assessment model.

7.2.2 Five criticisms

1. The work only considered above-ground characteristics of the plant populations. Throughout the work only traits related to the above-ground part of the plant were measured. A large part of the plant, below the soil surface, was left unstudied. The trophic design of herbaceous plants means that most of the photons of light and carbon dioxide are captured by above ground parts, whereas water and mineral nutrients are intercepted by roots (Grime 1979). A classification system of plants based on morphology not related to water and mineral nutrition would be incomplete.

Early on in the project attempts were made to dig up root systems in the field and subsequently rinse the soil off them. In certain conditions this was possible, for example on the sandy soils of FDC3, however when hard and dry soils were predominant (e.g. units at the dry area of Masegar), or plants had extensive root systems (e.g. *Phragmites australis*), root systems could not be harvested with accuracy. In addition to the physical difficulties, it was a very time consuming process to achieve a suitable number of replicated samples.

Trade-offs, due to the limited synthetic capacity of the plant, between root and shoots have been proposed (Huston & Smith 1987). Theories related to the root-shoot partitioning have been become collectively known as the "resource-ratio hypotheses" (e.g. Huston & Smith 1987, Tilman 1988). Resource-ratio hypotheses tend to distinguish two functional types of competitors, those with large shoots which are strongly competitive for light and those with large root systems which are strong competitors for below-ground resources.

Support for the resource-ratio hypothesis was gained from a set of experiments (e.g. Corre 1983, Hunt & Nicholls 1986) in which increasing the degree of stress imposed on the plants (through low mineral nutrition or shade treatments) caused a change in the root-shoot ratio. The results suggested that plants from fertile and infertile soils, or shaded and unshaded habitats, would differ in root-shoot ratio. However, more recently, further experiments have not supported this contention (Berendse & Elberse 1989; Shipley & Peters 1990; Aerts, Boot & van der Aart 1991 and Campbell *et al.* 1991).

Two problems with the study of root-shoot ratios in experimental conditions are apparent. Firstly, environment situations can occur were there is more than one limiting factor, for example a vegetation stand which is on nutrient-poor soil and which is also shaded. Secondly, in experiments, the resource tends to be experimentally limited in a uniform manner which is not similar to the spatially dynamic resource concentration in the environment. Further experiments are necessary using more complex resource patterns to fully determine the validity of resource-ratio hypotheses.

On a biochemical level there would be limits to the trade-off between roots and shoots. Growth requires chemical constituents from both the root and the shoot. Chemical analysis of plants has revealed that the ratio of root and shoot derived elements remains relatively constant across a wide range of ecologies (Grime 1991). In addition, species with the capacity for high rates of photosynthesis and dry matter production have higher concentrations of leaf nitrogen (Sharkey 1985, Field & Mooney 1986) and, are thus dependent on high rate of nutrient capture by the root system. A strong interdependence between root and shoot competitive abilities could thus be suggested.

The degree of importance of the lack of root data in the functional analysis methodology is not known. The literature on resource-ratio hypotheses does not offer a simple answer. However, some literature suggests that there is a strong interdependence between root and shoot competitive ability. Thus, a competitive hierarchy of plants using above-ground traits could well be similar to a hierarchy using both above- and below-ground traits; root traits could possibly be largely redundant.

Although, data on root systems would have been valuable, the time involved in obtaining suitable data and the proposed degree of interdependence in the competitive abilities of roots and shoots both suggest that the lack of root data does not represent a serious flaw in this work.

2. The traits measured were all simple morphological measurements, related to size or biomass. These traits represent only a "very small window into the rich landscape of traits" (Keddy 1992). The use of more traits or traits which were more functionally determined (e.g. plant water potential) may have produced a different classification of plant populations. Much of the variation in plants and the methods of adaptation which permit survival is lost using just morphological traits.

It is undoubtedly correct, that the addition of more traits to the analysis would produce a better basis for the grouping of plant populations into functional groups. However, this is the case with any similar classification procedure of a highly heterogeneous set of samples. The important point is that the traits that were measured could be used to describe a suitable degree of variation in the plant populations. The more traits used, the greater would be the degree of redundancy. Although this in itself is not a problem, redundancy of data means that effort in producing data has been largely wasted.

The aim of the work was to produce a general predictive model, rather than a specific accurate model for a certain habitat type. To elucidate general relationships between strategy types, a large number of units, representing a wide range of environmental conditions, was used (Glasgow University was the only institution in the FAEWE project to work in all the 4 European countries where units were designated). The measurement of a larger number of traits at the number of sites studied was not possible due to the short length of the project.

It could be argued that the model would be improved, not with more traits, but with more functionally determined traits. For example, the ability to withstand drought could be an important variable in determining stress in wetlands with drought problems. The methods for measuring drought resistance, and over 60 other ecological traits, can be found in Hendry & Grime (1993). Two problems would arise from the use of such traits:

i. The degree of generality is lost as the traits are closely linked to certain ecological phenomena e.g. drought tolerance. The only way to increase the generality would be to increase the number of traits used to cover, for example, all the possible stress conditions that the wetland plant is likely to experience. This was not possible due to the time limitations.

ii. The results for such tests are not immediate and require much specialist equipment. In the case of drought resistance, the plants have to be grown in controlled conditions for 32 days, subsequent further analysis has to be carried out on protein, chlorophyll and malonylaldehyde concentration. This chemical analysis would require a certain amount of time and much specialist, technical and expensive equipment.

It would be possible, through screening procedures, to measure the scores of these traits for a set of common wetland plants. This database of traits could then be used, following a field survey, to assess the plants for strategy components. However, this would entail an accurate species list for the common species at the unit under study, which in turn would require the field operator to have a certain degree of specialist knowledge on plant identification. In addition, it was shown in the previous chapter that change in strategy indices within a species are valuable indicators of environmental change. The use of a dataset using species scores would not permit analysis at the population level.

The morphological parameters measured as part of the FAEWE project were valuable in functionally classifying plant populations (Chapter 2). Certain traits were particularly valuable at predicting C and S scores; the predictive equations for C and S from traits were both highly significant (Chapter 3). This suggests that the morphological traits were closely related to the strategy groups. Height of plant was found to be most closely related to competitive ability of the plant, this was supported by the literature (e.g. Menges & Waller 1983; Gaudet & Keddy 1988; Keddy & Shipley 1989). Simple morphological parameters can thus be valuable indicators of ecological character and strategy; they are thus valid for a general predictive framework.

3. The strategy model of Grime had 3 strategy components C, S and D (Grime 1979). In the preceding work, only two of the strategy components were addressed, C and S. It was apparent that disturbance factors were occurring at some of the hydrogeomorphic units e.g. grazing, cutting and flooding. Is it valid to have a strategy model with an important part of the model missing?

The importance of D, compared to C and S, of common species inhabiting the FAEWE hydrogeomorphic units was found to be low. Not one of the 144 measured populations was found to have a D strategy in Grime *et al.* (1988). The regression equation for C was constructed using pure C strategists, intermediates (C-S-D) and none or negligible C component; the equation for S was developed in a similar fashion. This method was not possible for D.

Three methods were proposed to formulate a measure for D:

1. To use the residual variation from the best fit regression line of C and S, for each population, as an indicator of D. The idea was that the unexplained variation in terms of C and S would be D. This assumes however, that trade off between C, S and D was perfect and that there was no error in the C and S strategy determinations. Neither of these assumptions could be upheld, thus the method was considered to be poor.
2. Using evidence of past disturbances, as state variables, could be potentially lead to the formulation of a state variables derived DFVT index. State variable data could include variables such as % of shoots grazed (see section 5.4.2). Some forms of disturbance would, however, not be apparent in the community, for example the powerful scouring action of winter floods. The degree to which disturbance could be assessed in a site visit would need to be tested.
3. To obtain pure D strategist populations, plants not in FAEWE sites could be measured, for example, from arable fields or trampled roadways. This was considered as a valid approach and if time had allowed this would have been carried out. However, the fact would still remain that pure D strategists had not been found in the FAEWE sites. If the FAEWE sites signify a representative sample of the variation in vegetation of European wetlands, the importance of D in the wetland model would be small. Thus the missing D component does not detract away from the C-S model presented in the preceding chapters. If the

model was to be extended to be valid within the catchment landscape, rather than the riverine marginal wetland habitat, then it would be important to include the D component in the model. It might be necessary to use other traits to determine the D score related more to life-cycle and reproductive effort.

From the work it was found that the competitive index was probably the most useful as it was significantly correlated to easily measurable traits which the literature supported and a correlation between competitive ability in the greenhouse and field-determined scores was apparent. Competitive ability can be considered as a negative indicator of the combination of both stress and disturbance. If both D and S were low, then C would be high, if both D and S were high then C would be low. Both D and S cause a decrease in C, thus the measurement of C gives an indication of the amount of D and S, although the individual components cannot be separated. Evidence suggests that wetland plants are organised along competitive hierarchies (Keddy 1990), and thus indices related to C (and inversely related to the combination of D and S) would be the most valuable.

The lack of D in the preceding work meant that certain aspects of the strategy model were not addressed, the importance of this omission is not known. However, if wetland plants are organised along competitive hierarchies, then C indices would be expected to show up as the most useful strategy indicators of general ecological functioning.

4. The length of time of the field experiments in was only 1-2 years. Is this a suitable time for changes in vegetation to occur in response to environmental perturbation?

The simple answer to the above question is "no". The necessity of short field experiments, due to the funding structure of the project, meant that vegetation could still be changing as a result of environmental perturbation, even after the experiment had stopped. Alternatively, the plant community could have been reacting slowly to the environmental perturbation and was still in the "lag phase" (Hairston 1989). The results of the field experiments should not thus be used to determine the absolute degree of change or the speed of change in strategy indices to the environmental perturbations. However, the field experiments do indicate the degree of predictability in the direction of change, in terms of strategy, following perturbation. In all cases where significant changes were found between treatments, the direction of change in the C score was always in the predicted direction (Table. 6.8).

Field experiments are of great value in many of the topical issues in ecological research as they do not, unlike greenhouse experiments, require so much abstraction of results to the "real" field situation. However, time-scales must be suitably long for the dynamics of change to be detected, e.g. the 5 year experiment of Wedin & Tilman (1993).

5. All the work in the thesis was concerned with details of plant and community variables of a biotic nature. Major gradients in biotic variables and indices were found, however, the way in which they relate to major abiotic gradients e.g. moisture class of soil, or nitrogen gradient, was not considered.

The original plan of the project was for the groups monitoring abiotic factors to disseminate the data, through the University of Exeter, to the other interested groups. This system broke down, and no environmental data was circulated. One of the major aims of Phase II of the project will be to relate together data obtained by the different research groups. It is proposed that the strategy indices would be related to environmental data at all of the hydrogeomorphic units; initial analysis would use canonical correlation analysis (CCA).

7.3 THE MEANING AND VALUE OF FUNCTIONAL INDICES

7.3.1 What do functional indices tell a wetland planner?

To improve the degree of wetland planning, in terms of nature conservation, water quality or any other wetland function, a planner would want to know the likely effect of the plan on the wetland ecosystem. This means that some prediction of the proposed impact of the plan must be made. The prediction could come from two possible sources:

1. From subjective assessment techniques using the prior knowledge and experience of "experts" or "consultants". Often reports from such assessments are accompanied by a pack of "pseudo-science" in the form of species lists or NVC designations which can play little part in the decision making process of the "expert".
2. From objective scientifically-determined expert- or model-systems, which contain much of the "knowledge" of experts or a group of experts, but have a simple user-interface which can be used by planners and other non-specialist scientists.

The FAEWE project aims to produce an expert system. However, to communicate to planners about the predicted impact of a certain plan, system output must be summarised in readily understandable statements or values which can be interpreted. Functional predictors would be of value for 3 reasons:

1. A single value could summarise a community. Although the NVC categorises communities using a single category value, the values are not relative. Using functional indices, values are all relative, thus, a change from 1.5 to 2.5 represents the same magnitude of change as from 5.0 to 6.0. This relativity of values allows the size of the predicted change to be assessed by the planner; this is vital as the planners are the people trained to make value judgements on the effect of predicted impacts.

2. The functional index can download into a set of wetland functions. Three examples will be used to illustrate this point:

i. The work has shown that there was a relationship between CFVT and CORINE biotopes (chapter 5); thus, functional indices represent a method whereby a planner can determine biotope type. This can be useful as certain biotope types may be of major significance in the impacted area e.g. recreational or agricultural potential.

ii. Functional indices can also be downloaded into parameters related to nature conservation. A strong relationship was found between the CFVT values and dominance, an index related to the species richness and equality of communities. Biodiversity is of major conservation importance.

iii. The potential of the community for water quality management could also be assessed. Communities with high CFVT values having high biomass values, tall canopies and dominated by a few species would be of greater potential for the removal of certain anthropogenic inputs e.g. sewage.

3. The strategy indices can be used for all impacts. The "environment" is summarised in the strategy model into C, S and D components, and it is assumed that the response to disturbance will be similar whatever the exact nature of disturbance e.g. grazing or flooding. This possibly could be an over generalisation, however, some summary of the environment is necessary as all environmental variables cannot be measured.

In summary, it is proposed that functional indices are of value to a planner for two reasons:

1. They represent a relative scale on which the scale of change can be simply determined. The scale of change in the functional indices for a set of proposals can be calculated and the option corresponding to least change can be identified.

2. The functional indices can download into a set of functions which may be of great importance in the planners decision-making process.

7.3.2 The relationship between functional indices of vegetation and other biotic indicators.

Within the FAEWE project, work was carried out on two other aspects of the biotic community which can be related to the functional indices; phytosociology and functional description of hoverflies (Syrphidae). Both these studies were carried out on a descriptive rather than a predictive framework. Murphy, Castella, Clement, Hills, Obrdlik, Pulford, Scheider & Speight (1994) (Appendix 2.2) attempted to link the three approaches of vegetation phytosociology and functional indices and functional traits of hoverflies. The authors found that: " there is a reasonable degree of comparability between the results of the analyses of wetland hydrogeomorphic units based upon plant-community data and upon analysis of the biological traits of the populations of plant species comprising those communities" and that " comparison of the FVT analysis, with the results of the linked site-trait analysis of hoverfly fauna for hydrogeomorphic units within the target wetlands provides a further indication that the strategy-based approach may have potential for further development as an indicator of wetland functioning......Given that the sets of traits used to analyse the strategies of the two groups of organisms are completely different, and the differences in computation used by the two methods, this outcome gives us confidence in the basic validity of the strategy-based approach as a means of indicating wetland ecosystem functioning" Murphy *et al.* (1994).

Clearly this area of complementarity between descriptive methods of biotic functioning needs further work. However, the association of trait-based models from different trophic levels identified by Murphy *et al.* (1994) suggests that such models are valid descriptors of wetland ecosystems. With further work, it could be possible to have independent, but complementary, trait-based assessment procedures for more than one trophic level.

7.3.3 The linking of functional vegetation indices to the abiotic environment.

At the time of writing no data about the abiotic environment of the hydrogeomorphic units were available. The interaction of predictors with abiotic factors will be studied in Phase II of FAEWE. Although no measured values of environmental variables are available, a simple analysis could possibly elucidate the relationship between the functional indices and the environment using published information on the type of environmental conditions which plant species tend to grow in.

Ellenberg (1988) gave indicator values for a set of ecological characters for a number of common plant species found in central Europe. Two indicator values were of interest in this study; water value (F) and nitrogen value (N). The F and N values were aimed to represent the type of environment in which the particular species was commonly found in (Ellenberg 1988).

The value of N varies from 1 (sites poor in available nitrogen) to 9 (extremely rich situations). Of the 144 plant populations studied, Ellenberg gives N values (at the species level) for 112 populations. The N values ranged from 1 to 8, covering most of the N gradient identified by Ellenberg. The mean value was 4.33 (SD = 2.01, n = 112). No clear relationship between the population C score and the N value was apparent, although at the highest N value the C scores seemed to be rather higher than the lower N values (Fig. 7.1a). From these data it appeared that the C score was not strongly related to the Ellenberg N value.

Ellenberg designed the scale for F to vary from 1 (extreme dryness) to 12 (submerged plants). Of the 144 populations studied, 111 could be designated F scores (at the species level). The mean F score was 7 (SD = 1.93, n = 111), which was described as "damp site indicators, mainly on constantly damp, but not wet soils" (Ellenberg 1988). No relationship between the C score and F was apparent (Fig. 7.1b). These data suggest that there was little relationship between C score and F.

The analysis between Ellenberg indicator values and C scores lacked sensitivity. However, it did show that there was no simple relationship between two important gradients in wetlands, water and nitrogen status, and the C score. The environment is highly complex in terms of abiotic factors and only a small proportion of abiotic factors can feasibly be measured; these may not be the important variables to which the plants respond (Peters 1991). It is possible that even the measurement of a large number of environmental variables would not be able to explain a significant amount of the variation in the C score. The complexities of the abiotic gradient can be further confounded by temporal dynamics. van der Valk (1981) suggested that the environment acted like a "sieve" on the propagules in the ecosystem, permitting only certain species to survive; he warned, however, that the "sieve" changes over time. Gaudet (1977) found that papyrus (*Cyperus papyrus*) swamps were only formed following a particular set of hydrodynamic fluctuations over a number of years.

Before judgements on the relationship between functional indices and abiotic variables can be made, monitoring data from the project must be analysed. However, the use of Ellenberg indicators suggested that the relationship between the C scores and environmental gradients is not simple. It is proposed that a multivariate method should be utilised, using as many environmental variables as

Fig. 7.1 a Distribution of C scores with Ellenberg nitrogen values (N).

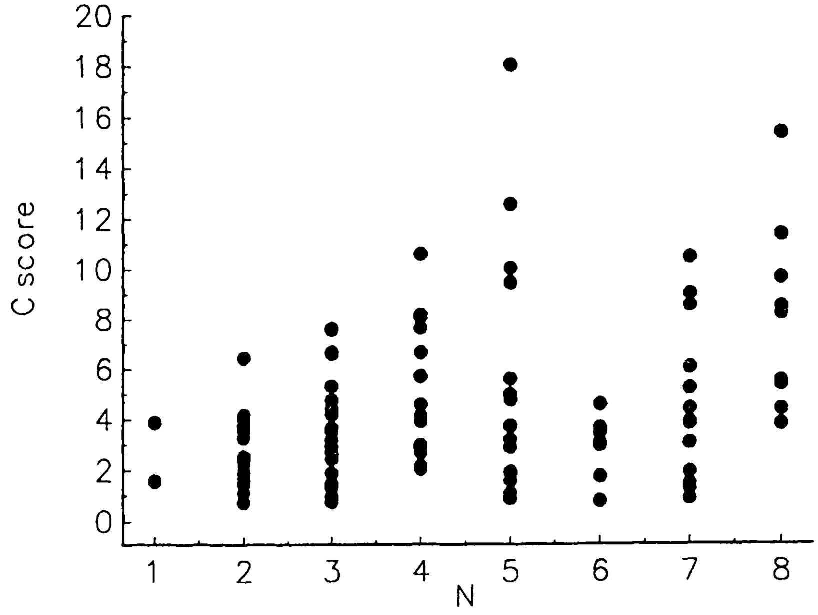
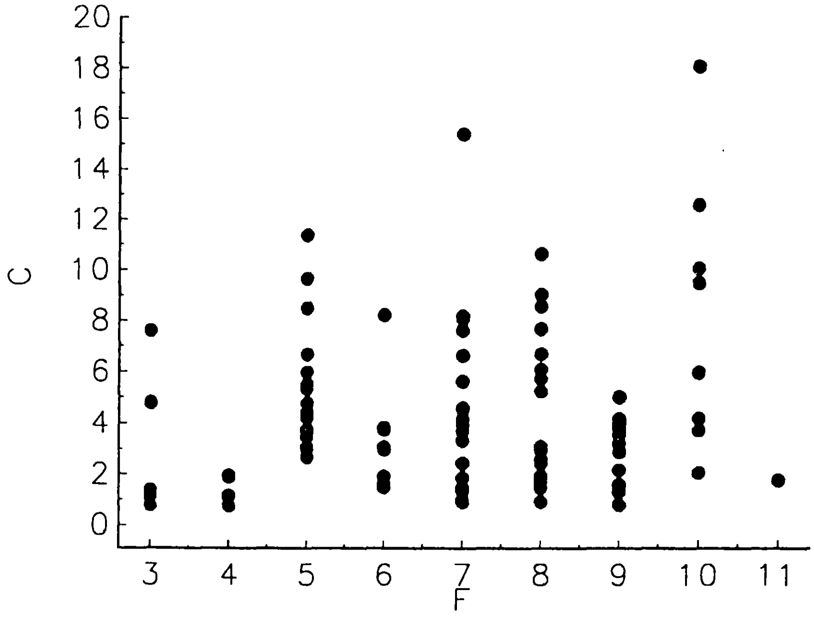


Fig. 7.1 b Distribution of C-scores with Ellenberg water values (F)



available; variables which were subsequently not important or redundant could then be discarded.

7.4 MODEL DEVELOPMENT: PHILOSOPHICAL CONSIDERATIONS

G.S. Innis, director of the US/IBM grassland simulation model, suggested that a major lesson should be derived from the development and analysis of models. He proposed that the recognition of the need for clear definition and usage of a sound philosophical structure for modelling was vital (Innis 1978). Scientific philosophy represents the framework of study underlying all "scientific" actions. Although scientific philosophy is implicit in science, it is rarely explicitly stated. Recently, following the inability of ecology to address environmental problems sufficiently, a renewed interest in scientific philosophy has come about (Peters 1991). Books have recently appeared attempting to highlight areas of weakness and to strengthen scientific philosophy in ecology e.g. *A critique for ecology* (Peters 1991) and *Method in conservation - strategies for conservation* (Shrader-Frechette & McCoy 1993). The aim of this section is to provide a brief review of relevant philosophical subjects in order to build up a framework for the model development section which follows.

"Mathematics is the language of science" wrote Lambert & Brittan (1970). They suggest that mathematics is useful as it allows precise expression of empirical hypotheses and methods for the teasing out results or patterns (Lambert & Brittan 1970). However, mathematics is the "world of conceivable possibilities, not a world of actuality" (Skellam 1972). Thus mathematical statements are almost void of empirical content and these uninterpreted tautologies are not genuinely informative. Skellam (1972) warns of "barren formalism" and "worship to the new electronic gods". Science represents a way in which value and meaning can be formed from the mathematical language.

Ecology can use two forms of mathematics; formal or logic-system maths with stated axioms and/or statistics (sensu Fischer) (Nelder 1972). Peters wrote that "statistical models are faster cheaper, simpler and better predictors than their representational competitors, because their sole purpose is to make the best possible estimate" (Peters 1991). Although this is maybe a rather narrow view of the value of statistics, it does make the point that statistics are a useful mathematical tool for the modelling of ecological systems. This contention was supported by Pomeroy, Hargrove & Alberts (1988) who wrote that; "Probabilistic statements are the bread and butter of current ecosystem studies. They tell us, under a defined set of circumstances, what we can expect to happen most of the time, at least in that small corner of the universe we have observed. The search for methods that tell us what happens all of the time is a wholly different business, one we have likened to the search for the Holy Grail". The authors suggest that the search for the Holy Grail is a "pleasant and genteel occupation" but with little chance of success (Pomeroy *et al.* 1988). Statistics, rather than, logic statements have been used throughout this thesis. The author attempted to keep ecological interpretation of statistical results straight-forward; expansive arguments following one of many possible lines of interpretation using unsubstantiated assumptions were not undertaken.

Pomeroy *et al.* (1988) suggest there are two basic approaches to study of ecology:

1. Theoretical approaches which attempt to determine universal laws.
2. Historical approaches in which statements are made about events related to laws.

Shrader-Frechette & McCoy (1993) suggest that the theoretical approach looking for universal applicable theories is "ambiguous, value laden and often untestable". They support the second "bottom-up" approach and suggest that it is more fruitful for ecological explanation. The results presented in this thesis were obtained using a "bottom up approach", fitting together a set of field studies into a wetland model.

The aim of the FAEWE was a predictive model rather than an explanatory model. However, prediction (not to be confused with retrodiction e.g. retrodiction of the big-bang from observations today) and explanation have a similar structure in philosophy (Lambert and Brittan 1970). "The only difference between them concerns the time at which the explanation or prediction is made. Other things being equal, if one derives a description of an event prior to its having taken place, the event has been predicted: if the description has been derived after the event has taken place, it has been explained" (Lambert & Brittan 1970). Explanation and prediction are thus similar processes, but they are delineated with respect to time. However, prediction and explanation do not always have to be similar. For example explanation has to be true, whereas a prediction does not necessarily have to be true and a predictive statement does not necessarily have potential explanatory power (Lambert & Brittan 1970).

The work in this thesis has predominantly been explanatory. For example, the similarity between the competitive score for *Dactylis glomerata* and *Holcus lanatus*, could be used as an explanation for their co-occurrence at sites. However, due to the complementarity between explanation and prediction, predictions could be made from an explanatory model (e.g. the direction of change in field experiments; chapter 6).

Model confirmation involves the production of positive instances where the model appears to offer something useful to the user (Lambert & Brittan 1970). Although the status of "confirmations" in ecology was suggested to be problematic, partly due to the inadequate understanding of basic ecological processes (Shrader-Frechette & McCoy 1993) Confirmation of the model means that the possibility that it is an accidental generalisation becomes diminished, the model is then believed to become more akin to a set of lawlike statements. However, confirmation of a model is only one part of the notion of acceptability. Lambert & Brittan (1970) suggest that there are two other factors which aid acceptance:

1. Simplicity, which makes the model easier to understand, communicate and remember.
2. Theoretical connection to generally accepted laws or theories. This tends to decrease conflict, and needs very strong support if it is to oust previously accepted doctrine.

For Phase II, scientific confirmation of the FAEWE model would not be enough for acceptability. It must have a degree of simplicity and theoretical connection for acceptance to follow.

In summary, from a philosophical point of view the work presented in this thesis has been:

1. Strongly reliant on mathematical procedures.
2. Used the statistical form of mathematics.
3. It used a "bottom up" (empirical) approach from historical data rather than theoretical assertions.
4. The approach was explanatory rather than predictive, however, the complementarity between explanation and prediction means that it can easily be transposed into a predicative framework.
5. A degree of scientific confirmation was carried out, though this should be increased
6. It is based on a generally accepted theory (Grime C-S-D theory) and can be communicated to non-experts; both these factors could aid acceptability.

It thus follows, from the preceding philosophical treatment of the thesis, that the work disposes itself favourably to being part of a model system for wetlands.

7.5 PROVISIONAL MODEL TOPOLOGY AND SCIENTIFIC RATIONALE

Some initial thoughts of the author, KJM and IDP are outlined in this section on how to use the strategy-based methods, developed by Glasgow during FAEWE, for assessing plant response to stress and disturbance in European riverine wetlands. These ideas were presented to the FAEWE workshop in Madrid in February 1994 for further discussion and development. An overall topology of the wetland assessment system was proposed by the FAEWE project (Fig. 7.2). Further system designs were proposed for the desk-study and hydrogeomorphic (HGMU) delineation system (Figs. 7.3 and 7.4 respectively).

It is proposed that the strategy model topology presented here fits into the first or second level of the overall assessment system topology i.e. qualitative / quantitative assessment (Fig. 7.2). It is aimed that the ideas presented here represent the skeleton of a module within the overall functional assessment scheme, which the user would reach at some point after the hydrogeomorphic unit has been defined. The user is assumed to know that he is assessing a piece of wetland forming a defined unit (HGMU), and wants now to know the answers to one or more of three basic questions at this stage, which will either allow him to progress further through the system, or lead him to specific answers about the wetland unit of interest:

(i) how can I easily define the vegetation type of this HGMU ?

(ii) how can I find out if the vegetation indicates signs of ecosystem perturbation (stress, disturbance or both) affecting this HGMU ?

(iii) how can I use the information which the plants are telling me to determine or predict impacts of perturbation on specified wetland functions ?

Answers to the first two questions can provide an assessment of current status of the HGMU. Answers to the third question can provide a means of using the vegetation of the wetland HGMU(s) to predict the impacts of perturbation on certain wetland functions, or to compare intensities of such impacts between HGMUs in time and/or space.

Examples of use might include:

(i) the broad survey approach: e.g. assessing the relative degree of perturbation affecting riverine wetlands across an area of interest (e.g. an NRA Region), while also providing a quick overall assessment of the vegetation of HGMUs present within each site; and providing a prediction of potential impact of any known or suspected causes of perturbation on the functioning of the wetland

Fig. 7.2 System design for the overall wetland assessment model system.

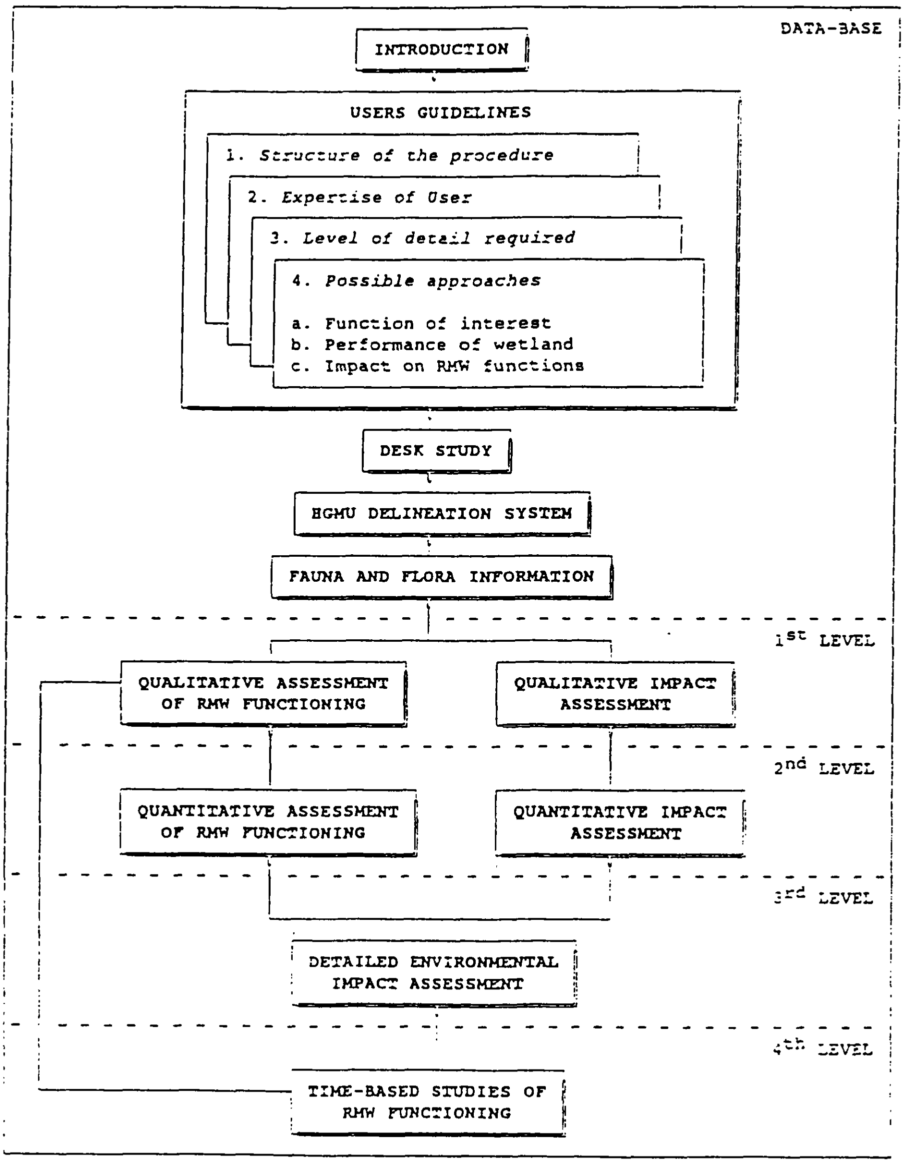


Fig. 7.3 System design for information sources for desk study stage of assessment procedure

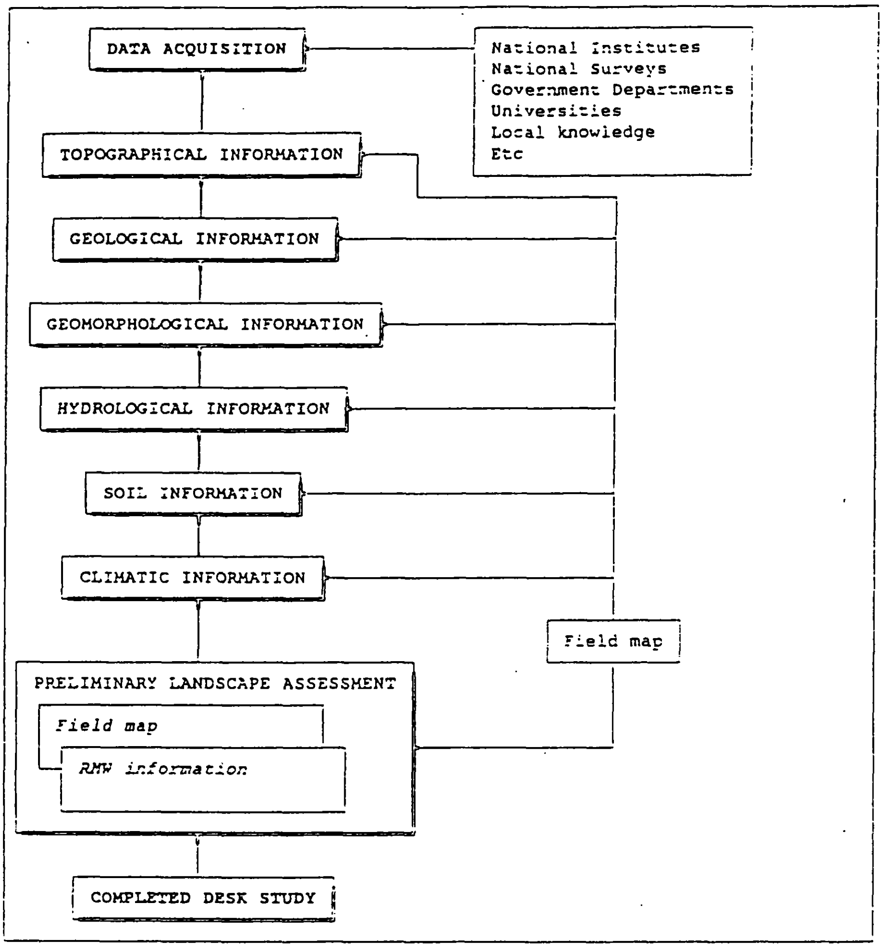
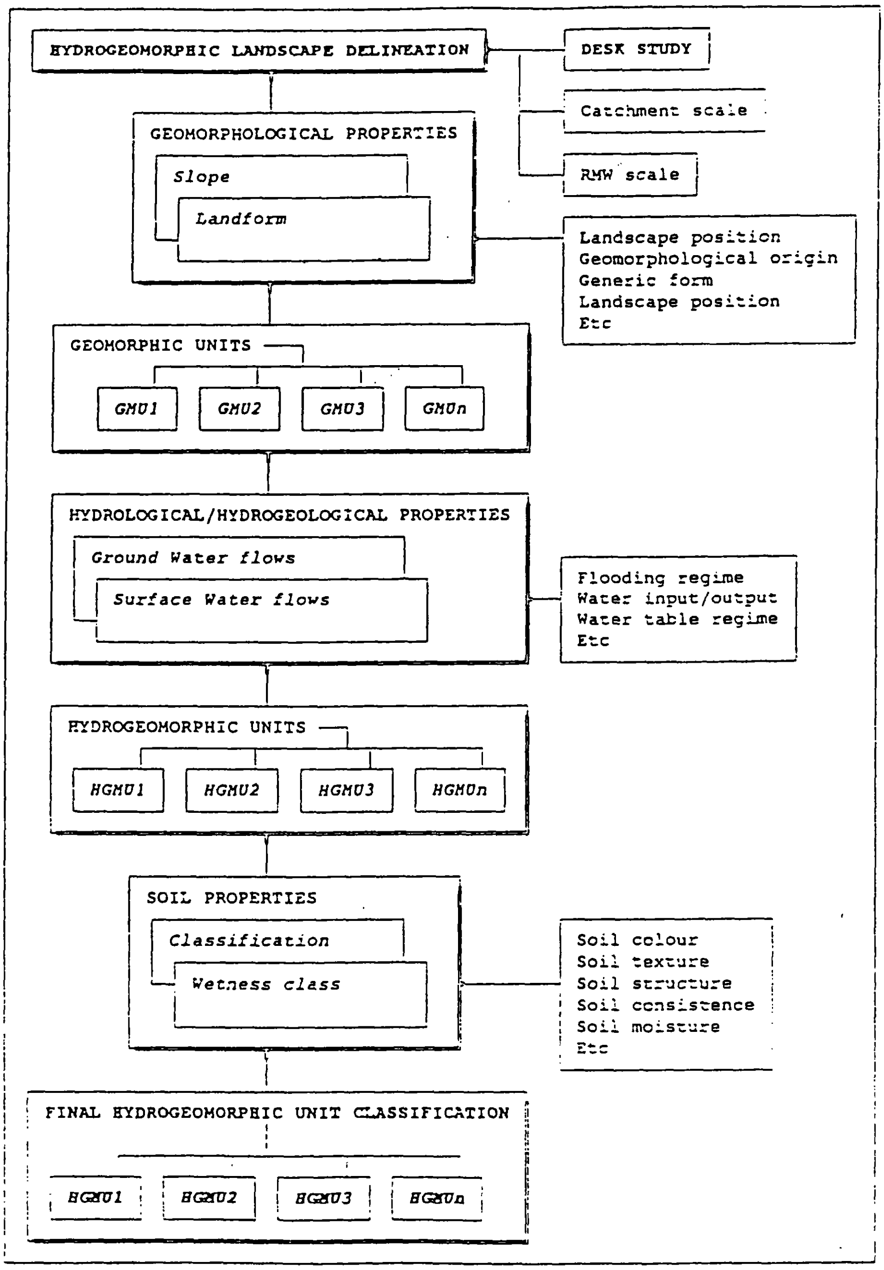


Fig. 7.4 Procedure for the delineation of hydrogeomorphic units.



(ii) a more intensive assessment of changes affecting a key wetland site: e.g. a SSSI site impacted by groundwater abstraction which has lowered water tables since SSSI status was granted, where vegetation has been surveyed (within known areas of the site - which may or may not correspond to HGMUs!) at intervals over a period of years. The method could provide a "hindcasted" assessment of likely intensity of perturbation on each survey occasion, to give an indication of trend within the vegetation of the site, which might in turn be related to current and/or hydrological (or other relevant environmental) data. Application of our technique could also provide a prediction of likely impacts of further intensification of any perturbation trend picked up by the analysis - both on vegetation and on those aspects of wetland functioning which the plants are capable of indicating.

(iii) comparative predictive studies of the impacts of planning decisions likely to affect several wetland sites within a given area: e.g. the effects of moving a borehole providing water supply capability for a rural area containing a number of riverine wetlands. What would be the implications for water table changes affecting these wetlands? Assuming that the hydrological implications can be modelled to give predicted changes in mean summer water table for each site, then our method could provide predictions of changes in intensity of perturbation affecting each site. If current vegetation data were available for each site (usually the case for most of Europe), then predictions of likely change in vegetation type might also be made.

It was proposed that two model systems would be appropriate; the first for wetland assessment, and the second for the prediction of the effect of perturbation(s) on wetland vegetation.

The wetland assessment model permits the placing of each HGMU into a CORINE biotope and Perturbation Band (PB), calculated from the CFVT value (Fig. 7.5). Further values can then be calculated from predefined state variable-CFVT relationships, relating to production and diversity. Output statements for each HGMU assessed would be generated.

In the scheme for prediction of impact on wetland functioning (Fig. 7.6), the starting point is the calculated value of CFVT (or Perturbation Band) obtained from the assessment system (Fig. 7.5). We assume that the user is faced with a situation in which he knows that some change in conditions is likely to occur, which he is worried might affect the site of interest. Two questions would be relevant:

Fig. 7.5 Provisional system design for the assessment procedure of wetland vegetation in terms of CORINE biotope, Perturbation Band and state variables.

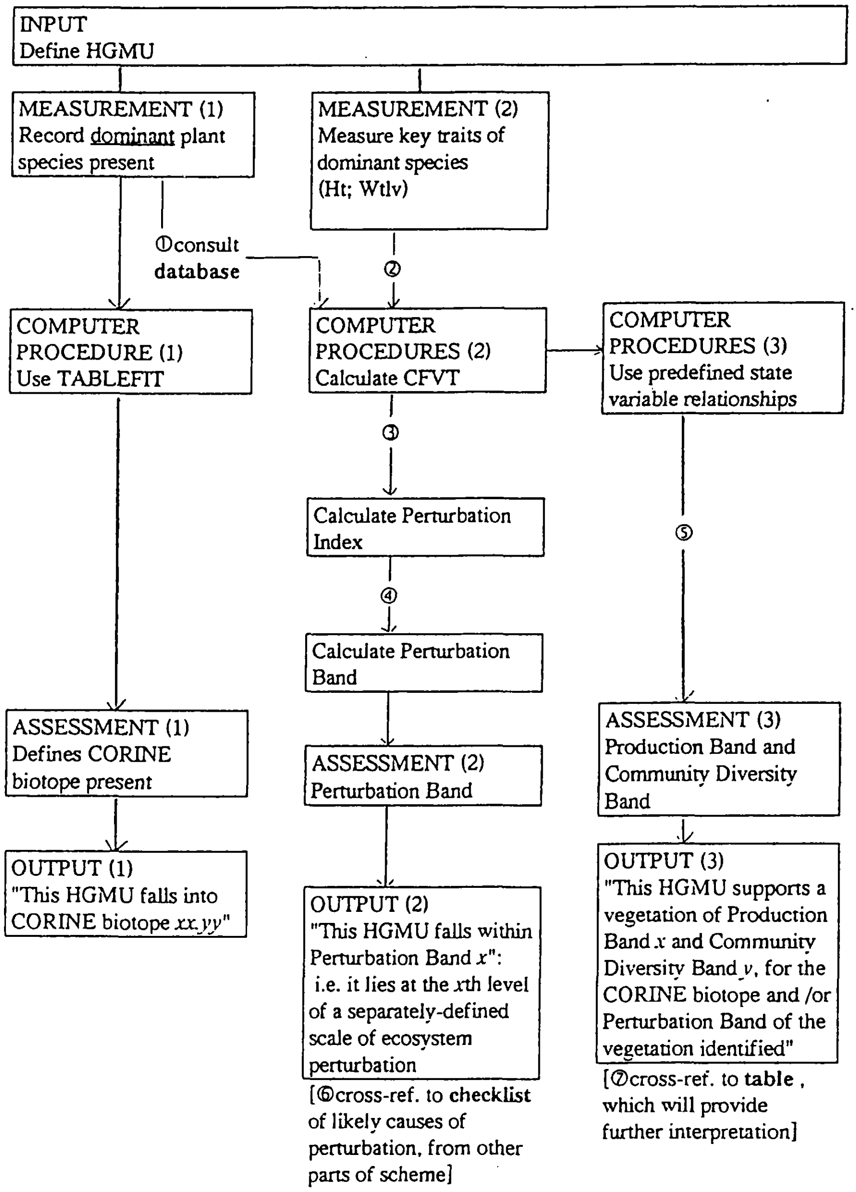


Fig. 7.5 (contd.) footnotes:

① consult **database** (given within scheme as appendix to printed version, and as look-up table on disk) for defining CFVT from dominant wetland plant species present: at this stage this route will only be possible for a limited set of species because of the small number of HGMUs so far examined; however the database will build up as the scheme is developed)

② first calculate C score for each of n dominant species present:

$$C = [HT \times 0.0602] + [WTLV \times 0.0181] + 0.469$$

then sum species C scores and divide by total number of species used to calculate Functional Vegetation Type index for competitiveness of vegetation (CFVT score):

$$CFVT = \Sigma C/n$$

③ Calculate perturbation index (P) as inverse of CFVT score, multiplied by 100 to get rid of decimal places:

$$P = 100(1/CFVT)$$

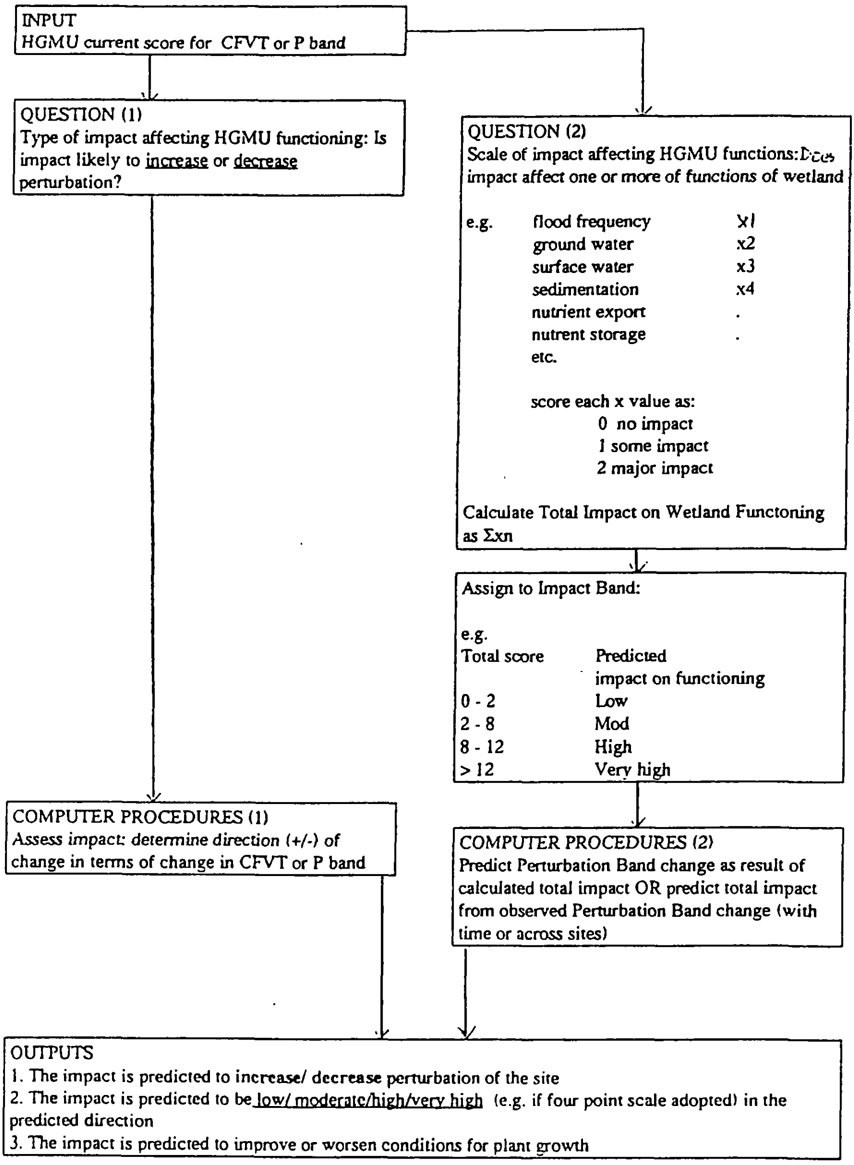
④ Place HGMU into one of 5 (?) predefined bands for P index described verbally (e.g. "high perturbation" down to "low perturbation")

⑤ $CFVT = [DOM \times 6.22] + [C30 \times 0.352] + 0.75$

⑥ cross-ref. to **checklist** of likely causes of perturbation, from other parts of scheme: this would refer user back to hydrological and chemical assessments made, or to other more subjective assessments of impacts on HGMU (or site as a whole), from which likely causes of perturbation as measured by vegetation might be made

⑦cross-ref. to **table** , which will provide further interpretation: here, we envisage the user getting information which will permit some refinement of the basic CORINE biotope and P banding of the HGMU. For example: application of the scheme to HGMU located in a frequently-flooded RMW might thus far, in applying the scheme, have produced a result suggesting that CORINE biotope 53.112 ("water fringe vegetation: dry *Phragmites beds*") is present, with a perturbation band P3 ("moderately perturbed") implying that the HGMU is undergoing moderate levels of stress and/or disturbance, then application of this part of the procedure will allow an assessment of whether the HGMU is experiencing a reduction in either production or community diversity, below that which would be <u>expected</u> for the vegetation type. This could be as simple as a designation into "as expected" v. "degraded" category", or it might be something more sophisticated. The intention is to help the user assess the degree of ecosystem damage exhibited within the HGMU.

Fig. 7.6 Provisional system design for the prediction module of wetland vegetation relating to direction and scale of change in vegetation in response to perturbation.



INPUT
HGMU current score for CFVT or P band

QUESTION (1)
Type of impact affecting HGMU functioning: Is impact likely to <u>increase</u> or <u>decrease</u> perturbation?

QUESTION (2)
Scale of impact affecting HGMU functions: Does impact affect one or more of functions of wetland

e.g.
flood frequency x1
ground water x2
surface water x3
sedimentation x4
nutrient export .
nutrent storage .
etc.

score each x value as:
0 no impact
1 some impact
2 major impact

Calculate Total Impact on Wetland Functoning as Σxn

Assign to Impact Band:

e.g.

Total score	Predicted impact on functioning
0 - 2	Low
2 - 8	Mod
8 - 12	High
> 12	Very high

COMPUTER PROCEDURES (1)
Assess impact: determine direction (+/-) of change in terms of change in CFVT or P band

COMPUTER PROCEDURES (2)
Predict Perturbation Band change as result of calculated total impact OR predict total impact from observed Perturbation Band change (with time or across sites)

OUTPUTS
1. The impact is predicted to increase/ decrease perturbation of the site
2. The impact is predicted to be <u>low/ moderate/high/very high</u> (e.g. if four point scale adopted) in the predicted direction
3. The impact is predicted to improve or worsen conditions for plant growth

(i) the simplest question might be "What is the likely direction of change (in terms of increased or decreased intensity of perturbation), likely to result from the predicted change?"

To answer this the user starts with the calculated CFVT score or Perturbation Band for each HGMU within the site, and consults either a database or look-up table of predicted effects of a set of likely environmental changes affecting riverine wetlands. In a very simple form this might look something like this:

Likely change	**Perturbation Band of HGMU**				
	Low perturbation→High perturbation				
	I	II	III	IV	V
Summer water table drops	+	+	+	+	0
Summer water table rises	0	-	-	-	-
Nutrient inputs increase	+	+	+	0	0
Nutrient inputs decrease	0	-	-	-	-
Recreational use increases	+	+	+	0	0
etc.					

(+ = increase in PB status of HGMU predicted; - = decrease in PB status of site predicted; 0 = no effect on PB status of site predicted)

This might be refined if it is possible to input some information on existing environmental conditions for each HGMU of site: for example if user knows existing summer water table conditions and existing Perturbation Band status of the HGMUs within site, a matrix predicting direction of PB change produced by predicted increase in water table for each combination of pre-existing conditions could be drawn up.

(ii) the second question of interest would be to predict the effects on Perturbation Band status of the sites which might be caused by the impacts of the "likely change in conditions" on functioning of the wetland. Again the user starts by calculating the current PB status of the wetland, HGMU by HGMU, by following the assessment procedure (Fig. 7.5). Assume, as an example, that he is interested in assessing the likely impacts of an increase in summer water table brought about by halting use of a nearby borehole. The existing PB status of HGMUs within the wetland varies from III to IV, i.e. the site currently shows signs of moderate to high perturbation (associated with drying out in summer). The first part of the scheme has told him to expect a reduction in PB status of HGMUs within the site as a result of the likely change in conditions: i.e. the intensity of perturbation is likely to be reduced (intuitively obvious for an easy example like this, but may be less so for other causes of perturbation - all of which we could include in the matrix).

The scheme would rely on the existence of a set of look-up tables, or matrices, giving the total likely impact on wetland functioning resulting from each "likely change in conditions" which we decide to include (certainly one of these would be predicted increase in summer water table):

e.g.	some impact likely on flood frequency:	score 1
	major impact on ground water availability	score 2
	some impact on surface water availability	score 1
	no impact on nutrient export	score 0

etc.

The sum of the values from the impact matrix could be used to determine a Total Impact on Functioning (TIF) score for the HGMU. Assign this to a Total Impact Band (TIB) which will give an overall prediction of scale of impact on wetland functioning for the predicted change in conditions a (very simply this might be from "low" to "very high").

The final stage would be to relate the TIB to the PB of the HGMU. This would be carried out using a computer procedure which would relate the TIF to the CFVT score from the assessment module for each HGMU. It is proposed that the computer procedure would take the form:

$$\text{CFVT}_{(\text{assessment})} \pm \text{TIF} = \text{CFVT}_{(\text{predicted})}$$

This would however, be more simply represented in the user-interface as:

$$\text{PB}_{(\text{assessment})} \pm \text{TB} = \text{PB}_{(\text{predicted})}$$

The choice of "+" or "-" TIF, would be determined by the likely effect of the proposed impact on the HGMU, in terms of increase or decrease in perturbation (i.e. Question 1, Fig. 7.6).

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9. APPENDICES

Appendix 1.1a. Plant species frequency (%) (and standard error in brackets) and cover (%) for Bradford Mill, England.

SPECIES	EBM1	EBM2	EBM3
1 Achillea millefolium L.	+ (+) +		
4 Agrostis capillaris L.	52 (12) 17		23 (10) +
5 Agrostis stolonifera L.		43 (15) 7	62 (14) 17
6 Ajuga reptans L.			+ (+) 2
8 Anthoxanthum odoratum L.	12 (6) 6		1 (1) +
15 Cardamine pratensis L.		+ (+) 1	+ (+) 1
24 Carex nigra (L.) Reichard		+ (+) 9	
26 Carex panicea L.			35 (16) 2
30 Cirsium arvense (L.) Scop.	36 (4) 11		
31 Cirsium dissectum (L.) Hill	+ (+) 7		
35 Dactylis glomerata L.	15 (6) 31		
37 Deschampsia cespitosa (L.) P. Beauv.	74 (12) 86		
40 Equisetum fluviatile L.		+ (+) 2	
45 Festuca rubra L.	76 (13) 51		22 (13) 4
46 Filipendula ulmaria (L.) Maxim		4 (4) 2	
48 Galium palustre L.			+ (+) 1
55 Glyceria fluitans (L.) R.Br.		19 (+) +	+ (+) 2
59 Holcus lanatus L.	72 (5) 26	6 (6) +	37 (8) 8
64 Juncus effusus L.		65 (13) 26	78 (11) 84
65 Juncus inflexus L.		2 (8) +	68 (11) 41
68 Lathryrus pratensis L.	+ (+) 6		
72 Lotus corniculatus L.	8 (5) +	+ (+) 4	7 (5) 4
75 Lychnus flos-cuculi L.		1 (1) +	+ (+) 2
77 Lysimachia nummularia L.	4 (3) +		1 (+) +
83 Myosotis scorpoides L.		4 (3) +	+ (+) 1
87 Phalaris arundinacea L.		45 (16) 37	
88 Phleum pratense L.	+ (+) 1		
92 Poa trivialis L.	24 (10) 28	2 (5) 4	+ (+) 4
100 Ranunculus acris L.	1 (1) +		
102 Ranunculus flammula L.			8 (5) 1
103 Ranunculus lingua L.		1 (1) +	+ (+) 5
104 Ranunculus repens L.	4 (3) 1	+ (+) +	25 (4) 28
111 Rumex acetosa L.	4 (2) 22		
114 Rumex obtusifolius L.			5 (3) 4
117 Senecio aquaticus Hill		2 (1) +	5 (4) +
119 Sium latifolium L.	1 (1) +		
122 Stellaria palustris Retz.			+ (+) 12
126 Trifolium repens L.	2 (2) 1		
130 Veronica chamaedrys L.	+ (+) 7		4 (3) +
141 Angelica sylvestris L.		2 (2) +	
142 Persicaria maculosa Gray			+ (+) +

+denotes value less than 1

Appendix 1.1b. Plant species frequency of occurence(%)(and standard error in brackets) and cover estimate for sites at Kismeldon, England.

SPECIES	EKS1	EKS2	EKS3
2 Achillea ptarmica L.	+ (+) 2		2 (2) +
3 Agrostis canina L.			76 (16) +
4 Agrostis capillaris L.	12 (8) +		
6 Ajuga reptans L.	+ (+) 3		
8 Anthoxanthum odoratum L.	2 (1) 3	10 (5) +	40 (8) 7
9 Stachys officinalis (L.) Trev. St. Leon	2 (2) +		
12 Calluna vulgaris (L.) Hull			3 (3) 3
13 Caltha palustris L.			1 (1) +
19 Carex echinata Murray			+ (+) 2
22 Carex hostiana DC.		+ (+) 3	4 (3) +
24 Carex nigra (L.) Reichard		32 (11) +	2 (2) 3
26 Carex panicea L.		82 (10) 15	23 (5) 11
31 Cirsium dissectum (L.) Hill		25 (5) +	
32 Cirsium palustre (L.) Scop.	+ (+) 1		
34 Dactylorhiza fuchsii (Druce) Soo		+ (+) 1	
36 Danthonia decumbens (L.) DC.			6 (2) +
37 Deschampsia cespitosa (L.) P. Beauv.	10 (10) 4		2 (2) +
42 Erica tetralix L.		28 (10) 17	
45 Festuca rubra L.	27 (16) 17	60 (10) 12	
46 Filipendula ulmaria (L.) Maxim	52 (10) 63		
48 Galium palustre L.	8 (5) 4		
49 Galium ulignosum L.	2(2) 3		
52 Genista anglica L.		20 (8) 9	2 (2) 1
59 Holcus lanatus L.	53 (13) 47	3 (2) +	
60 Hydrocotyle vulgaris L.	+ (+) +		
62 Juncus acutiflorus Ehrh. ex Hoffm.	16 (10) 11		40 (9) 14
64 Juncus effusus L.	63 (14) 16		
65 Juncus inflexus L.		8 (3) 4	
68 Lathyrus pratensis L.	2 (1)+		
73 Lotus pendunculatus Cav.		5 (2) +	
74 Luzula campestris (L.) DC.		5 (2) +	5 (2) 6
82 Molinia caerula (L.) Moench		92 (5) 82	90 (9) 75
84 Nardus stricta L.			2 (1) +
85 Narthecium ossifragum (L.) Hudson		33 (13) 10	
86 Pedicularis palustris L.		1 (1) 2	1 (1) 3
89 Plantago lanceolata L.	5 (3)+		
92 Poa trivialis L.	12 (5) +		1 (1) 2
93 Polygala serpyllifolia Hose			1 (1) +
98 Potentilla erecta (L.) Raeusch.	1 (1) +	6 (2) 4	
100 Ranunculus acris L.			1 (1) +
104 Ranunculus repens L.	14 (1)		
111 Rumex acetosa L.	6 (2) 12		
118 Serratula tinctoria L.	+ (+) +		7 (2) +
122 Stellaria palustris Retz.	1 (1) 2		+ (+) 3
123 Succisa pratensis Moench.	2 (2) +		18 (5) 17

124 Taraxacum sect. Ruderalia Kirschner, Oellgaard & Stepnek.	1 (1) +	
128 Valeriana officinalis L.	10 (5) 10	+ (+) 3
135 Viola palustris L.	1 (1) 2	
138 Trifolium pratense L.	2 (1) +	

"+" denotes value less than 1.

Appendix 1.2a. Plant species frequency (%) (and standard error in brackets) and cover (%) for Apremont, France.

SPECIES	FAP1	FAP2	FAP3	FAP4
4 Agrostis capillaris L.			+ (+) 3	
5 Agrostis stolonifera L.			92 (5) 84	14 (7) +
7 Alopecurus geniculatus L.			2 (2) 3	+ (+) 1
13 Caltha palustris L.				+ (+) +
14 Calystegia sepium (L.) R. Br.				6 (4) +
20 Carex elata All.				8 (4) +
21 Carex hirta L.			8 (4) +	
25 Carex otrubae Podp.				18 (7) 21
27 Carex vesicaria L.				+ (+) 16
35 Dactylis glomerata L.			+ (+) 6	
38 Digitaria sanguinalis (L) Scop.			8 (5) +	
47 Galium aparine L.	51 (NA) 20	12 (NA) 5		
50 Galium verum L.			+ (+) 2	
53 Geranium dissectum L.			2 (3) 3	
59 Holcus lanatus L.			54 (6) 31	
61 Iris pseudacorus L.				20 (13) +
71 Lolium perenne L.			+ (+) 2	
72 Lotus corniculatus L.			4 (3) +	
76 Lycopus europaeus L.	7 (NA) 10			
77 Lysimachia nummularia L.	1 (NA) +			7 (4) 8
79 Lythrum salicaria L.				+ (+) 1
81 Mentha arvensis L.				+ (+) +
87 Phalaris arundinacea L.			+ (+) 2	84 (8) 67
88 Phleum pratense L.			1 (1) +	
92 Poa trivialis L.				+ (+) 1
97 Potentilla anserina L.				10 (4) +
99 Potentilla reptans L.			2 (4) +	16 (10) +
104 Ranunculus repens L.			22 (8) 28	+ (+) 10
109 Rubus caesius L.	23 (NA) +			
111 Rumex acetosa L.			+ (+)+	
113 Rumex conglomeratus Murray				1 (3) +
116 Scutellaria galericulata L.	8 (NA) +			
121 Stellaria graminea L.			+ (+) 3	
126 Trifolium repens L.			+ (+) +	+ (+) 1
127 Urtica dioica L.	53 (NA) 63	100 (NA) 77		
133 Vicia sativa L.			+ (+) +	
134 Vicia tetrasperma (L.) Schreber			1 (2) +	

"+" denotes value less than 1

"*NA*" standard error non-applicable as plant species frequency estimated as quadrating of vegetation was impossible.

Appendix 1.2b. Plant species frequency (%) (and standard error in brackets) and cover (%) for Decize, France.

SPECIES	FDC1	FDC2	FDC3	FDC4
1 Achillea millefolium L.			5 (5) 4	
4 Agrostis capillaris L.			30 (10) 66	
5 Agrostis stolonifera L.	100 (NA) 1			+ (+) 1
7 Alopecurus geniculatus L.				83 (12)
8 Anthoxanthum odoratum L.			+ (+) +	
14 Calystegia sepium (L.) R. Br.	+ (+) 1	1 (NA)+		
17 Carex arenaria L.			46 (15) 41	
20 Carex elata All.	+ (+) 4			
29 Chenopodium sp.	72 (NA) 12			
33 Cynosurus cristatus L.			5 (4) 2	
38 Digitaria sanguinalis (L.) Scop.				+ (+) 1
39 Eleocharis palustris (L.) Roemer & Schultes				+ (+) +
43 Euphorbia cyparissias L.			26 (6) 29	
44 Festuca ovina L.agg			30 (15) 55	
45 Festuca rubra L.			+ (+) 9	
47 Galium aparine L.		24 (NA) 20		
50 Galium verum L.			+ (+) +	
51 Gaudinia fragialis (L.) P. Beauv.			2 (1) 10	
54 Glechoma hederacea L.		4 (NA) 40		
55 Glyceria fluitans (L.) R.Br.				23 (16)
56 Gnaphalium sp.	8 (NA) +			
57 Gnaphalium uliginosum L.				3 (3) +
66 Lamium maculatum (L.) L.		4 (+) +		
71 Lolium perenne L.			3 (3) 9	
72 Lotus corniculatus L.			6 (6) 6	
74 Luzula campestre (L.) DC.			2 (2) 10	
77 Lysimachia nummularia L.	1 (NA) 2			
79 Lythrum salicaria L.	+ (+) 1			
83 Myosotis scorpoides L.	12 (NA) +			
87 Phalaris arundinacea L.	48 (NA) 46			
89 Plantago lanceolata L.			5 (3) 6	3 (2) +
90 Poa annua L.				76 (15)
94 Polygonum aviculare L.				49 (17)
96 Polygonum hydropiper (L.) Spach	+ (+) 2			
101 Ranunculus aquatilis L.				3 (1) +
104 Ranunculus repens L.	+ (+) 1			
105 Ranunculus sardous Crantz				30 (19)
107 Rorippa amphibia (L.) Besser	28 (NA) 10			
108 Rorippa sylvestris (L.) Besser	+ (NA) 19			+ (+) +
110 Rubus fruticosus L. agg.		1 (NA) 10		
112 Rumex acetosella L.			+ (+) 1	
114 Rumex obtusifolius L.	+ (+) 1			
115 Sagina procumbens L.				+ (+) 2
120 Solanum dulcamara L.	10 (NA) 1			
125 Trifolium dubium Sibth.				
126 Trifolium repens L.			+ (+) +	2 (1) +
127 Urtica dioica L.		100 (NA) 100	+ (+) 5	
133 Vicia sativa L.			27 (7) 24	
136 Vulpia bromoides (L.) Gray			2 (6) +	

142 Persicaria maculosa Gray	+ (+) 3	
143 Cynodon dactylon (L.) Pers.	44 (7) 4	
144 Eryngium campestre L.	5 (3) 4	
145 Ranunculus bulbosus L.	1 (2) 8	
146 Rumex crispus L.		2 (1) +
147 Mentha pulegium L.		26 (5)

"+" denotes value less than 1.
"NA" where standard error non-applicable as plant species frequencies were estimated as quadrats were impossible.

Appendix 1.3a. Plant species frequency (%) (and standard error in brackets) and cover (%) for units ICL1, ICL2 and ICL3 at Clonmacnoise, Ireland.

SPECIES	ICL1	ICL2	ICL3
5 Agrostis stolonifera L.	40 (20) 43	92 (6) 33	163(8) 10
8 Anthoxanthum odoratum L.		6 (3) +	4 (2) 8
13 Caltha palustris L.	7 (5) 14		
15 Cardamine pratensis L.			+ (+) +
18 Carex disticha Hudson		92 (6) 65	33(7) 18
19 Carex echinata Murray			24 (4) 29
24 Carex nigra (L.) Reichard			10 (2) 31
27 Carex vesicaria L.	100 (0) 38		
28 Centaurea nigra L.		+ (+) 2	
37 Deschampsia cespitosa (L.) P. Beauv.		62 (12) 40	53(12)34
39 Eleocharis palustris (L.) Roemer & Schultes	40 (22) 11		
40 Equisetum fluviatile L.	55 (10) 8		
46 Filipendula ulmaria (L.) Maxim.		54 (8) 46	
49 Galium ulignosum L.	49 (13) 18		
55 Glyceria fluitans (L.) R. Br.		4 (4) +	
59 Holcus lanatus L.			
60 Hydrocotyle vulgaris L.	42 (24) +	1 (0) +	
61 Iris pseudacorus L.	7 (6) +		
68 Lathryrus pratensis L.	22 (11) 1	14 (5) 8	
70 Leontodon autumnalis L.		8 (8) 6	
77 Lysimachia nummularia L.		20 (5) 3	3(+)+
80 Mentha aquatica L.	22 (8) 7		
83 Myosotis scorpoides L.	22 (13) 3	1 (1) +	
86 Pedicularis palustris L.			1 (+) 1
87 Phalaris arundinacea L.	100 (0) 4		
88 Phleum pratense L.		62 (9) 35	
89 Plantago lanceolata L.		64 (10) 60	43 (5) 12
92 Poa trivialis L.		9 (5) +	
95 Persicaria amphibia (L.) Gray	7 (7) +		
100 Ranunculis acris L.		60 (7) 31	
104 Ranunculus repens L.	50 (18) 25	+(+) 10	2 6(2) 19
111 Rumex acetosa L.		3 (2) 1	2 (2) +
119 Sium latifolium L.	+ (+) 1		
126 Trifolium repens L.		4 (2) +	
131 Vicia cracca L.			3 (+) 2

"+" denotes value less than 1.

Appendix 1.3a (contd.). Plant species frequency (%) (and standard error in brackets) and cover (%) for units ICL4 and ICL5 at Clonmanoise, Ireland.

SPECIES	ICL4	ICL5
5 Agrostis stolonifera L.	14 (8) +	84 (4) 22
6 Ajuga reptans L.	+ (+) 2	
8 Anthoxanthum odoratum L.	50 (5) 38	
15 Cardamine pratensis L.	+ (+) +	
18 Carex disticha Hudson	97 (3) 64	
19 Carex echinata Murray	24 (4) 29	
23 Carex lasiocarpa Ehrh.		72 (12) 76
24 Carex nigra (L.) Reichard	11 (4) 65	64 (12) 30
26 Carex panicea L.	17 (3) 32	47 (14) 58
33 Cynosurus cristatus L.	+ (+) +	
40 Equisetum fluviatile L.		+ (+) +
45 Festuca rubra L.	100 (0) 45	
46 Filipendula ulmaria (L.) Maxim.	46 (5) 4	46 (14) 48
49 Galium uliginosum L.	20 (8) 11	58 (11) 37
59 Holcus lanatus L.	92 (6) 56	4 (4) +
67 Lathyrus palustris L.		10 (6) 7
72 Lotus corniculatus L.		2 (1) +
74 Luzula campestris ((L.) DC.	17 (5) 7	
75 Lychnis flos-cuculi L.	8 (5) 2	
77 Lysimachia nummularia L.		+ (+) 2
86 Pedicularis palustris L.	1 (1) 1	
87 Phalaris arundinacea L.		+ (+) 4
89 Plantago lanceolata L.	23 (5) 3	
91 Poa pratensis L.	+ (+) 10	
98 Potentilla erecta (L.) Raeusch	2 (2) 2	
100 Ranunculis acris L.	60 (6) 6	44 (14) 9
102 Ranunculus flammula L.		5 (3) 2
104 Ranunculus repens L.	2 (2) 12	40 (7) 24
106 Rhinanthus minor L.	6 (3) 2	
111 Rumex acetosa L.	2 (2) +	
122 Stellaria palustris Retz.		2 (2) 1
126 Trifolium repens L.		19 (7) 7
131 Vicia cracca L.	3 (2) 2	

"+" denotes value less than 1.

Appendix 1.3b. Plant species frequency (%) (and standard error in brackets) and cover (%) for Little Brosna, Ireland (nomenclature following Stace 1991).

SPECIES	ILB1	ILB2	ILB3	ILB4
5 Agrostis stolonifera L.		70 (15) 10	100 (0) 72	73 (13) 60
8 Anthoxanthum odoratum L.				+ (+) 2
10 Briza media L.				4 (4) 2
13 Caltha palustris L.	23 (10) +		3 (2) 8	
15 Cardamine pratensis L.		2 (1) +		
16 Carex acutiformis Ehrh.			79 (27) 92	
18 Carex disticha Hudson	80 (14) 62	78 (15) 100	96 (4) 64	66 (12) 67
21 Carex hirta L.	21 (8) +			
24 Carex nigra (L.) Reichard	4 (2) 4	22 (13) 3	3 (3) +	100 (0) 68
33 Cynosurus cristatus L.	12 (4) 4			
36 Danthonia decumbens (L.) DC.	45 (16) 24			
39 Eleocharis palustris (L.) Roemer & Schultes		75 (16) 42	8 (6) 29	
40 Equisetum fluviatile L.			2 (3) +	
41 Equisetum palustre L.	3 (2) 2		9 (4) +	
45 Festuca rubra L.	100 (1) 70			100 (0) 80
46 Filipendula ulmaria (L.) Maxim	61 (8) 66	11 (6) +	12 (8) 3	32 (40) 4
48 Galium palustre L.		18 (6) 26	48 (16) 24	8 (7) 11
59 Holcus lanatus L.	17 (12) 16			4 (3) 1
60 Hydrocotyle vulgaris L.			+ (+) 1	88 (5) 37
61 Iris pseudacorus L.		6 (6) +		
63 Juncus articulatus L.		+ (+) 4		
69 Leucojum aestivium L.	1 (1) +			
70 Leontodon autumnalis L.				32 (12) 34
71 Lolium perenne L.	52 (15)26			
72 Lotus corniculatus L.				8 (8) +
77 Lysimachia nummularia L.	13 (5) +	+ (+) 3	10 (5) 5	32 (10) 2
80 Mentha aquatica L.		24 (11) 18	21 (10) +	1 (1) +
87 Phalaris arundinacea L.		28 (16) 4	64 (22) 61	
88 Phleum pratense L.	54 (16) 48		20 (44) +	
89 Plantago lanceolata L.	32 (10) 18		5 (4) +	3 (3) 4
91 Poa pratensis L.			2(4) +	15 (5) 7
95 Persicaria amphibia (L.) Gray		6 (4) 1	12 (7) 3	
97 Potentilla anserina L.				47 (12) 19
98 Potentilla erecta (L.) Raeusch		+ (+) 1		
100 Ranunculis acris L.	23 (7) +			14 (5) +
104 Ranunculus repens L.	14 (4) 16	11 (4) 2	63 (9) 34	20 (3) 18
111 Rumex acetosa L.	12 (4) +			
119 Sium latifolium L.	2 (2) +			+ (+) +
124 Taraxacum sect. Ruderalia Kitscher, Oellgaard & Stepanek.	23 (8) 8	2 (1) +	2 (1) +	
126 Trifolium repens L.	35 (9) 22	1 (1) +	1 (1) +	14 (6) 10
129 Veronica catenata Pennell		10 (8) 7		
131 Vicia cracca L.	10 (4) +		6 (6) +	
137 Cerastium fontanum ssp. holosteoides (Fries) Salman, Ommering & Voogd	4 (2) 4			+ (+) +
138 Trifolium pratense L.	+ (+) 28			

139 Festuca arundinacea Schreber	11 (5) 30
140 Potentilla palustris (L.) Scop.	1 (1) +

"+" denotes value less than 1.

Appendix 1.4a Plant species frequency (%) (and standard error in brackets) and cover (%) for hydrogeomorphic sites SMD1, SMD2 and SMD3 from Spain (nomenclature from Flora Europaea).

SPECIES	SMD1	SMD2	SMD3
148 Aeluropus littoralis (Govan) Parl.			22(6)5
152 Cirsium sp.			1(+)+
156 Elymus repens L. (Gould)			56(11)26
157 Frankenia laevis L.		60(13)2	
158 Hordeum murinum L.	14(2)2		
159 Juncus maritimus Lam.	13(8)29	8(4)+	29(8)8
160 Limonium sp.	42(7)+	1(+)+	
161 Phragmites australis (Cav.) Trin ex. Steudel	30(5)8	+(+)6	
162 Puccinellia festuciformis (Host) Parl.	24(9)43		
163 Salicornia sp.	4(3)+	4(+)2	
165 Suaeda fruticosa auct.	4(2)+		
166 Valeriana sp.			1(+)+
167 Bassia sp.		3(+)0	

+ denotes value less than 1.

Appendix 1.4b. Provisional plant species frequency (%) (and standard error in brackets) and cover (%) for hydrogeomorphic sites SMD4, SMW3 and SMWE from Spain (nomenclature from Flora Europaea).

SPECIES	SMD4	SMW3	SMWE
148 Aeluropus littoralis (Govan) Parl.	+(+)+		
149 Bromus hoderaceous L.	32(16)15		
150 Bromus madritensis L.	12(4)6		
152 Cirsium sp.	12(4)+		
154 Convolvus arvensis L.			60(7)0
155 Dorycnium pentaphyllum Scop.		23(5)5	
156 Elymus repens L. (Gould)	12(8)+	56(11)17	5(4)9
47 Galium aparine L.	24(8)8		
158 Hordeum murinum L.	8(4)13		
159 Juncus maritimus Lam.		11(6)+	
161 Phragmites australis (Cav.) Trin ex. Steudel	32(8)+	36(8)5	25(7)4
164 Schoenus nigricans L.	100(0)94		
166 Valeriana sp.	12(4)5		
168 Typha latifolia L.			52(8)40

+ denotes value less than 1.

Appendix 2. Publications related to the FAEWE project

2.1 Hills, J.M., Murphy K.J., Pulford I.D. & Flowers T.H. (1994) A method for classifying European riverine wetland ecosystems using functional vegetation groups. *Functional Ecology* (in press).

A METHOD FOR CLASSIFYING EUROPEAN RIVERINE WETLAND ECOSYSTEMS USING FUNCTIONAL VEGETATION GROUPS.

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Running title: Riverine wetland plant functional groups

SUMMARY

The aim of this work is to formulate a methodology for the use of trait analysis to classify European riverine wetlands into functional vegetation types. Plant species and data on biological traits and survival strategy were collected from sites in England (Bradford Mill and Kismeldon: River Torridge), France (R. Allier at Apremont and the R. Loire at Decize) and Ireland (R. Shannon at Clonmacnoise and the Little Brosna near Banagher) during 1991.

Linear and multiple discriminant analysis were used to distinguish objectively between plant populations with *a priori*-selected strategies. There appeared to be very little variation in disturbance-tolerance (D) between the wetland plant populations studied. Competitive and stress-tolerant plants were found to be significantly different by linear discriminant analysis using twelve descriptive parameters. Multiple discriminant analysis permitted a distinction to be drawn between competitive (C), stress-tolerant (S) and intermediate strategy plants, and retrospectively classified the populations in accordance with the strategies suggested for them by previous work .

Stepwise multiple regression was used to identify the important survival traits for predicting competitive ability and stress-tolerance. Significant predictors of the C-strategy were the height of the plant and the dry weight of the leaves; and of the S-strategy the dry weight of stems and weight per seed. Use of the predictive equations permitted the importance of the C and S strategy elements to be determined for 78 plant populations.

Weighted for plant cover, mean C and S scores of the plant populations present in each sample unit of vegetation were utilised to determine the functional vegetation type (FVT) in terms of competitiveness (CFVT) and stress-tolerance (SFVT).

Vegetation samples were ordinated using CFVT and SFVT values. CFVT and SFVT values were highly inversely correlated: a trade-off between competitive ability and stress tolerance in wetland plants was apparent.

INTRODUCTION

To succeed in the "struggle for existence" (Darwin 1859) an organism must have attributes permitting survival in the environment which it inhabits. For any given environment only certain sub-sets of attributes permit survival and reproductive success (Grime 1979). The limited set of attribute-combinations which permit success in any environment has formed the basis of descriptions and models in plant ecology.

Plants have long been classified into groups on the basis of functional attributes. Raunkaier (1934) created categories of plants according to similarities in life form: for example, "cryptophytes" are species of plant that have dormant buds which survive unfavourable periods beneath soil or water surfaces. Noble & Slayter (1970) employed a set of "vital attributes" of plants on which they based predictions of the course of succession and perturbation. Australian semi-arid vegetation was classified, by Leishman & Westoby (1992), into 5 main groups using 43 traits associated with vegetative character, life-history, phenological and seed-biology characters. MacArthur & Wilson (1967) proposed a model of life-history types with two opposing strategies, "r" and "K" (descriptors derived from the general population growth rate equation in a resource-limited environment). The r-K strategy model has been applied to plant species (Gadgil & Solbrig 1972; McNaughton 1975). However, Stearns (1977), in a review of the r-K continuum theory found it to be "incomplete", and according to Grime & Sibley (1986) it has not made a "significant contribution" to the advancement of plant ecology theory.

An alternative approach to the delineation of functional groups in plants was taken by Grime (1974). He identified two major forces in the environment, stress and disturbance, and considered the consequences of the interaction of these forces for plant species. Environments were classified according to the degree of stress (any factor which reduces the rate of accumulation of biomass: including shortage of light, water and mineral nutrients), and disturbance (any factor which destroys biomass: including trampling, grazing and fire damage), into three main types where plant growth was possible: high stress-low disturbance, low stress-high disturbance and low stress-low disturbance (Grime 1979). The plant strategy successful in these environment types would be stress-tolerators (S), disturbance-tolerators (D) and competitive (C), respectively. Plants could be of a pure strategy (e.g. C) or of an intermediate strategy (e.g. C-S or C-S-D). The strategy approach to describing the success of plants introduces the concept of a common currency or link between plant species which greatly reduces the need to rely on taxonomic and habitat descriptors of plant communities.

Much evidence supporting the validity of the C-S-D strategy theory as a general framework contributing to the understanding of plant-environment relationships has been collected (e.g. Campbell & Grime 1989; Grime 1984; Grime 1988; Grime, Hunt & Krazanowski 1987; Murphy, RØrslett & Springuel 1990). More recent publications have tended to concentrate on a finer understanding of certain aspects of the general principles of the C-S-D strategy theory; for example, Campbell, Grime, Mackey & Jalili (1991) and Grime & Sibley (1986) in relation to nutrient use and dynamics. However, the potential of using C-S-D strategy theory as the basis of a classification system, or as an explanatory model of plant communities has, so far, been little realised (though see Kautsky 1988 and Murphy *et al.* 1990 for aquatic macrophytes). The movement away from multivariate, species-oriented vegetation descriptions to models of general applicability is, "one of the current challenges in community ecology" (Day, Keddy, McNeill & Carleton 1988).

The work presented here uses plant attributes to formulate a model of vegetation in terms of plant functional groups, with general applicability to European riverine wetland ecosystems. This work has three primary objectives. First, to identify a set of easily measurable plant traits which are associated with the C, S and D strategy types. Second, to use this sub-set of traits as a basis of a determination of the strategy characteristics of adult plant populations. And finally, to extend the use of population strategy characteristics to classify riverine European wetland plant communities into functional vegetation types.

MATERIALS AND METHODS

Study sites

Three riverine wetland regions, encompassing much of the climatic range of Europe, were selected for study in England, Ireland and France. Sites were positioned in two areas from each riverine system :

a) Torridge headwaters (England): at Kismeldon (50°55'N, 4°20'W; site code; EKS) and Bradford Mill (50°55'N, 4°15'W; code EBM).

b) Middle Shannon (Ireland): the Little Brosna near Banagher (53°8'N, 7°55'W; code ILB) and the Shannon River at Clonmacnoise (53°20'N, 7°58'W; code ICL).

c) Loire valley (France): on the River Allier at Apremont (46°55'N, 3°5'E; code FAP) and the River Loire at Decize (46°55'N, 3°28'E; code FDC), France.

Within each site three, four or five 10 x 10m quadrats were positioned in hydrologically and pedologically distinct areas of the riverine system (Hogan & Maltby 1990). Transponders (CTT1, A. & P. Chambers Ltd., Kaluna House, Nairnside, Inverness, UK.) were buried beneath the soil surface to permit relocation of the quadrat during subsequent visits. Site codes were numbered in ascending order with distance from the river, except for one quadrat on a temporary sand-bank at Apremont in France which was coded FAPS.

Cover assessment

A Harris pin frame was used to determine the cover of all species in each quadrat. The pin frame was placed randomly ten times in each of the 10 x 10m quadrats and any plant species touching each pin was recorded. Values for each species were expressed as percentage cover.

Trait measurement

During the summer of 1991, a selected set of survival traits was measured for a variety of plant populations in each study wetland. In each quadrat between one and seven (mean = 3.6) of the common plant species present were selected for trait analysis. The work presented here was carried out at population level, thus, common species were measured in more than one quadrat. Field analysis was carried out around the time of reproductive maturity for each plant species (i.e. when flowers or seeds were present). Measurements were taken from individual shoots unconnected above-ground to other shoots. Twelve traits were measured for each studied species in each 10 x 10m quadrat. Four traits were measured in the field, the other eight traits required the harvesting and transportation of samples back to the laboratories at Glasgow University. In total twelve traits (Table 1) were measured from 78 populations situated in 22 10 x 10m quadrats in riverine systems from England, Ireland and France.

Four traits were measured in the field:

1. Height of plant (HEIGHT). The *in situ* height of the plant above ground was measured using a ruler. Care was taken not to disturb the position of the plant in the canopy while the measurement was being taken.

2. Area of the plant canopy (AREA). A transparent quadrat with 5cm x 5cm squares was held over the top of individual ramets of the plant. The number of squares in which pieces of stem, leaves or reproductive structures were present, when observed from above, was counted. The structure of the plant canopy was not disturbed during this operation. If other plants obscured the view of the individual being measured, minor adjustments were made to the canopy to permit a complete view.

3. Number of leaves (LEAVES). The number of leaves of individual ramets was counted. Immature leaves were counted as long as an area of green photosynthetic leaf tissue was observed. Dead or dying leaves were also counted if any area of green photosynthetic tissue was still remaining on their surface.

4. Number of seeds (SEEDS). The total number of seeds produced was counted for ten individuals. For plants that produced large numbers of seed, the number of reproductive structures (e.g. number of seed heads) and the number of seeds in each reproductive structure was counted for ten of the structures. The mean number of reproductive structures, and the mean number of seeds in the reproductive structure were multiplied together to give an estimate of the number of seeds.

Eight traits were measured in the laboratory:

Ten individuals of each study species in each quadrat were harvested, with most of the root system intact to maintain freshness during transport. The individuals were placed in a cool box and transported back to Glasgow University.

Further traits were then measured:-

Botanical parameters:
5. Total leaf area (LEAFAREA). The total area of the leaves of each individual was measured using a calibrated Delta video area meter. The leaf area of the individual as found in the natural situation was measured, no attempt was made to flatten leaves that were naturally curved or creased.

6. Dry weight of leaves (WTLEAF) was recorded for leaves from each individual. Leaves were placed in tissue paper and left in a drying oven at 55°C to constant weight.

7. Dry weight of stem (WTSTEM) was recorded for stems placed in tissue paper and dried to constant weight.

8. Dry weight of reproductive structures (WTREPRO). Reproductive structures, including structural tissue for the support of sexual organs, were dried to constant weight.

9. Seed weight (WTSEED). Between 30 and 50 seeds were removed from the dry reproductive structure and weighed (more seeds were used if the seeds were extremely small). The mean weight per seed was calculated.

Chemical parameters:

10. Nitrogen concentrations in the leaf (NCONC).

11. Phosphorus concentrations in the leaf (PCONC).

12 Potassium concentrations in the leaf (KCONC).

Plant leaf tissue was analysed to determine the concentration of nitrogen, phosphorus and potassium. The Kjeldahl method for digestion of dried plant material was used with a salicylic acid pre-digestion to ensured complete oxidation of nitrate-N and nitrite-N (Bremner & Mulvaney 1982). The concentrations of nitrogen and phosphorus in the acid digests were determined colorimetrically using a Technicon AutoAnalyser II system. Potassium concentration in the digests was measured using a flame photometer.

Data analysis

One of the primary aims of this paper is to determine the traits which are associated with different survival strategies in wetland plants. Clearly, due to the nature of the data, a multivariate method was required. Many multivariate statistical methods consider the equality between populations, searching for similarities or differences between sets of multivariate data (Krzanowski 1988). This procedure would be rather uninteresting as the intuitive *a priori* distinction between two or more groups (e.g. sets of plant species with different survival strategies) suggested that they were different. A more positive approach would be to attempt to describe and interpret differences between characters of two or more populations. This was carried out using discriminant analysis.

An *a priori* selection of studied plant populations with predominantly competitive, stress-tolerant and intermediate (C-S-D) strategies was made from the listings by Grime, Hodgson & Hunt (1988). None of the studied species had a predominantly disturbance-tolerant survival strategy, so this strategy-type was eliminated from the analysis. In total, 23 populations (7 primarily competitive and 6 primarily stress-tolerant and 10 intermediate) were utilised, consisting of 15 species (Table 2). A linear discrimination analysis was carried out between seven competitive and six stress-tolerant species using the 12 measured traits. A multiple discriminant analysis was carried out between the competitive, stress-tolerant and intermediate groups using the 12 measured traits. All analyses were carried out using SPSSx.

The plant populations that were designated as competitors (C) by Grime *et al.* 1988, were arbitrarily given a score of 10 for competitive ability and 0 for stress-tolerance. Stress-tolerant plants were given a score of 10 for stress-tolerance and 0 for competitive ability. Intermediate strategists (C-S-D) were given a score of 5 for both stress-tolerance and competitive ability. Multiple regression was used to determine which of the traits important in distinguishing competitive plants and stress-tolerant plants, identified using discriminant analysis, were the most important in predicting the designated strategy scores of the 23 plant populations. The predictive equations from the multiple regressions were subsequently utilised to produce C and S values for all the 78 plant populations sampled.

RESULTS

At the start of the linear discriminant analysis between the C and S groups, one variable (KCONC) was selected out because it did not pass the tolerance test (set at $P<0.001$). Prior to discrimination, the probability that they were from the same population was $P<0.001$ ($\chi^2 = 33.864$, df = 11), the C and S populations are thus significantly different using the remaining 11 descriptor variables.

The linear discrimination function distinguished between the C and the S groups. Over 28 canonical discriminant function units separate the C and S populations; the groups are thus highly distinguished (Fig. 1). The traits that discriminated for competitive and stress-tolerant groups were ranked in order of discriminatory power (Table 3).

The canonical correlation for the discriminant function, a measure of association which measures the degree of relatedness between the groups and the discriminant function (on a scale of 0, for no correlation, to 1 for a perfect correlation) , was 0.9989. The discriminant function therefore provides a powerful means of distinguishing between the C and S groups. Retrospective classification of the 13 populations utilised in this analysis, using the discriminant function, resulted in correct assignment of all populations to their *a priori*-defined C or S groups.

To determine the position of the intermediate (C-S-D) populations a multiple discriminant analysis was carried out between the C, S and C-S-D groups of plant populations (Fig. 2). Initially, the three groups were significantly different ($P<0.01$, $\chi^2=55.1$, df = 24). However, after the first discriminant function they were not significantly different ($P=0.26$, $\chi^2=13.45$, df=11). The first discriminant function had a canonical correlation of 0.973. WTLEAF, HEIGHT and KCONC were the three most important variables that discriminated for competitive plants. Separation of stress-tolerant plants and plants with an intermediate strategy was not clear on the first discrimination axis.

The second axis was much less powerful in its ability to discriminate between the three groups of plants. It explained only 8.4% of the variance, as opposed to the first discriminant function which explained 91.6% of the variance. The canonical correlation of the second axis was 0.778.

Using the discriminant functions of the first and second axes, the 23 plant populations were retrospectively classified 100% correctly. The competitive plants were highly distinct from the stress-tolerant plants and plants with an intermediate strategy, being found at the positive end of the first axis (Fig. 2). Stress-tolerant plants and plants with an intermediate strategy, although distinct, were closer together (Fig. 2). Distinction between S and C-S-D was gained predominantly from the second discriminant axis. On the first axis the plants with an intermediate strategy were placed between the stress-tolerant and the competitive plants.

The next step was to use stepwise multiple regression to determine which of the traits were good predictors of C and S strategies. The traits used to predict competitive ability were the variables that distinguished for competitive plants in the linear discriminant analysis (Table 3). The first independent variable selected by the stepwise multiple regression to predict competitive ability was height of the plant (HEIGHT) ($P<0.01$, df = 22); 36% of the variation in the strategy score was explained by this relationship. The second variable selected by the stepwise multiple regression was the dry weight of the leaf (WTLEAF). The significance of the relationship was improved by the addition of the second variable ($P<0.0001$, df = 22), 59% of the variation in the C strategy score was explained by the two independent variables. The predictive equation was:

$$\text{Competitive ability} = (\text{HEIGHT} \times 0.0602) + (\text{WTLEAF} \times 0.0181) + 0.4690$$

Stepwise multiple regression was used to predict the stress-tolerance of the same 23 plant populations. The first variable selected was weight of stem (WTSTEM). The relationship between the designated stress scores and the dry weight of the stem was highly significant ($P<0.001$, df = 22), and 49% ($r^2 = 0.49$) of the variation in the stress-tolerance scores was explained. The relationship between the dependent and independent variable was inverse ($B = -0.011$): stress-tolerant plants tend to have a small dry weight of stems. The second variable selected by the regression was the weight of a seed, the predictive power of the relationship improved ($P<0.0001$, df = 22) and 62% of the variation in the stress-tolerance scores was explained ($r^2 = 0.62$). No further variables were significantly related ($P<0.05$) to the residual variation of the scores of stress-tolerance. The equation for the prediction of stress-tolerance was:

$$\text{Stress-tolerance} = (\text{WTSTEM} \times -0.0101) + (\text{WTSEED} \times 0.0097) + 5.4456$$

The use of discriminant analysis coupled with stepwise multiple regression identified traits associated with the primary strategies of competitive ability and stress-tolerance in populations of wetland plants, and permitted the assigning of C and S scores to each of the 78 populations studied. Competitive ability varied between 11.4 (*Urtica dioica*, FDC2) and 0.0 (*Carex elata*, FAP3). Stress-tolerance varied from 12.3 (*Danthonia decumbens*, ILB1) to -0.4 (*Urtica dioica*, FAP2) (Table 4). Populations of the same species, from different wetland locations tended to have similar strategies. For example *Holcus lanatus* was measured in seven quadrats in England, France and Ireland. The C value varied from 3.0 to 5.2 and the S value from 5.3 to 5.8 for these seven populations (Table 4).

Individual plant populations were grouped together into species assemblages per quadrat and a weighted mean of the C and S scores was used to produce CFVT and SFVT (Competitive ability of Functional Vegetation Type, and Stress-tolerance of Functional Vegetation Type) values (Table 5). The mean was weighted using vegetational cover, whereby the contribution of the population to the quadrat mean strategy value (CFVT and SFVT) was directly related to its cover in the quadrat. CFVT values ranged from 11.4 (FDC2) to 1.0 (FDC4 and FAPS), and SFVT values ranged from 8.6 (ILB1) to -3.2 (FAP2). The proportion of the total vegetation cover occupied by the studied populations varied from 100% at quadrat FAPS, to 5% at FDC4 (Table 5). Low percentage figures were found in species-rich sites where the limited number (mean of 3.6) of plant populations studied comprised only a small proportion of the total number of species present.

A significant inverse relationship was found between the two independent parameters of CFVT and SFVT for the 22 hydrogeomorphic units (Fig. 3). The Pearson product-moment correlation coefficient for the relationship between SFVT and CFVT was $r = -0.74$ ($P<0.001$, df = 21). Thus, a quadrat with a high CFVT value (i.e. a set of plants in the community with a mean high competitive ability) tends to have a low value of SFVT (i.e. a set of plants with low stress-tolerant ability).

DISCUSSION

From the predictive stepwise multiple regression equation used to predict competitive ability, it appears that wetland plant populations that were tall and had a large dry weight of leaves tended to have a high competitive ability. In the literature, plant height consistently occurs as a trait positively related to competitive ability of the plant. In the competitive index (CI) used by Grime (1974) to determine the competitive ability of plant species, maximum height of leaf canopy (scored in 10 categories from <12cm to >112cm) was one of three components of the index. In a more recently devised dichotomous key to determine the strategies of herbaceous plant species, the possession of tall and laterally extensive shoots was the character which divided the strategies "competitive" (with) and "intermediate" (without) (Grime *et al.* 1988). Gaudet & Keddy (1988), using a modified additive design in a greenhouse experiment, found a significant negative relationship ($P<0.001$) between the biomass of a phytometer (*Lythrum salicaria*) and height of the test species; taller plants being able to suppress the biomass of the phytometer more than could lower-growing plants. Keddy & Shipley (1989) reworked the data of a lake-shore experiment by Wilson and Keddy (1986) and found that 37% of the variation in competitive ability could be explained by plant height. Menges & Waller (1983) found that the tallest and most competitive of flood plain forest herbs tend to be found in high-elevation areas which were relatively infrequently flooded. Our work supports the idea that there is a positive relationship between height and competitive ability.

From the multiple stepwise regression the residual variation in competitive ability, after regression with height of plant, was best explained by the dry weight of leaves (WTLEAF). Relatively large dry weight of leaves was associated with large residual variation in competitive ability. The structural costs in being tall can be offset by the phytosynthetic gains of having leaves in a relatively unshaded area of sunlight (Givnish 1982), which is conducive to the efficient capture and utilisation of light in competitive environments (Grime 1974). Both plant height and dry weight of leaf are characteristics important in the ability of plants to exploit resources. Grace (1990) proposed that "exploiter" would be a more appropriate term for this group of plants than "competitor" (*sensu* Grime).

Although only above-ground parts of the plant were measured in this study, evidence suggests a positive relationship between competitiveness above-, and below-ground in herbaceous plants. Campbell, Grime & Mackey (1991) found a "consistent positive association" between the foraging characteristics of shoots and roots. They proposed that there was a strong interdependence of competitive abilities for exploiting light and minerals.

Stress-tolerance was highly related to certain survival traits of the plants. The dry weight of the stem was the most important trait in determining stress-tolerance of the population. Stress-tolerant plants tend to be small in stature (Grime 1974), have short shoots and are not laterally extensive (Grime *et al.* 1988). Stress-tolerant plants are, thus, morphologically constrained to a low stem dry weight. The ecological significance of a large seed weight, the second selected variable in the stepwise multiple regression, is less obvious. Boorman (1982) noted that a large seed can give an initial advantage to the establishment of a seedling even if the relative growth rate of a competitor is greater. Boorman found that the dry weight of a *Cynoglossum officinale* seedling germinated from a relatively large seed was greater than the dry weight of a *Lactuca virosa* seedling for 27 days, although the relative growth rate of *Cynoglossum* was lower. The functional significance of seed weight in relation to stress-tolerant plant success is not associated with the established-phase strategy of the species on which this study is based. Further work on the regenerative phase of the plant life-cycle would be necessary to elucidate this relationship.

The ability to predict the strategy of plant populations, in terms of competitive ability and stress-tolerance, appears to be possible on the basis of simple trait data. A population-based, field method using continuous data, has led to objective selection of fundamental traits for wetland plant populations. The functional significance of these traits is supported by evidence from other workers. None of the plant populations studied had a high S-high C value, or a low S-low C value. Thus, a plant population cannot exhibit competitiveness and stress-tolerance. There is a trade-off between emphasis on C-favouring and S-favouring traits. This trade-off is paramount to Grime's view of competition; "it is this basic trade-off and its attending physiological constraints that result in a division between 'competitive' and 'stress-tolerant' species" (Grace 1990).

Grime *et al.* (1988) used three axes to describe the strategy of a plant species; competitive, stress-tolerance and disturbance-tolerant. The work presented here has used two axes, competitiveness and stress-tolerance, to describe the plant strategies of riverine wetland plants. None of the common species studied were of primary disturbance-tolerant strategy, or strongly disturbance-tolerant as described by Grime *et al.* (1988). Thus, disturbance-tolerance was considered to be of minimal importance, compared to stress-tolerance and competitive ability, for the wetland plants included in this study. Some of the study sites undeniably suffer some disturbance from sources such as grazing and flooding. However, intuitively, the sites would be low in disturbance compared to, for example, the regular rigorous disturbance common in agricultural systems.

The traits measured in this study may be of little use to predict disturbance tolerance. Keddy (1990) noted that disturbed wetland sites can exhibit a large array of life forms and morphologies compared to fertile and undisturbed sites. However, in highly disturbed situations an ephemeral life-history would appear to be the almost universal solution to selection forces. Life-history traits, as opposed to morphological traits measured in the work presented here, would tend to be more closely correlated to disturbance-tolerance in plants.

Most of the work involving the demarcation of competitive, stress-tolerant and disturbance-tolerant strategies has tended to select the traits which subsequently determine the strategy. For example, Grime *et al.* (1988) produced a dichotomous key of plant traits to determine the strategy of the plant species under study. Murphy *et al.* (1990) selected between four and seven traits to determine the level of C, S and D in submerged lake macrophytes. In these approaches the value of traits has been pre-set, the workers having made assumptions about the functional significance of certain attributes.

An alternative approach, outlined in the work presented here, made an *a priori* decision about the strategy of plant populations but not on the functional significance of traits. Although *a priori* plant strategies were taken from Grime *et al.* (1988) in this work, other sources could be used to determine the strategy of the selected populations e.g. ranking of sites in terms of soil fertility or the screening of populations in laboratory based experiments. This would be important if the work was being carried out in an area with a flora the strategies of which were less well described than for the species included in Grime *et al.* (1988).

Functional groups have previously been identified using descriptive multivariate methods applied to sets of trait data. Shipley, Keddy, Moore & Lemky (1989) used principal co-ordinate analysis of 13 traits to identify adult functional groups in aquatic macrophytes. Leishman & Westoby (1992) used a multivariate clustering procedure on 43 traits of Australian semi-arid species to produce five main groups. The nature of the interaction of the functional groups to the environment is diffuse, as no environmental information is implicit or explicit in the analysis. One of the significant aspects of Grime's model of plant strategies is that the functional groups (C, S and D) are implicitly interconnected with aspects of the environment as they are, by definition, derived from the two main forces in nature, stress and disturbance. The model of Grime, thus, has general applicability to vegetational systems, and provides a solid basis for the development of strategy models.

Work with functional groups tends to be at the general process and pattern level, more specific than state variables e.g. biomass and species richness, but less specific than species-oriented site and region descriptions (Keddy 1990). Evidence from the work presented here suggests that the C-S-D model provides a valid framework on which to base information on plant functional groups at this general process level. Although the implicit environmental information in the Grime strategy model is non-site specific, simplistic predictions of environmental perturbation can be made from communities in terms of C and S. For example, the addition of fertiliser would tend to make the plants in the community, and thus the community strategy, more free from stress (-S) and more competitive (+C). For more refined predictions, sub-divisions of disturbance and stress in the environment may be necessary. The ability to predict is of major importance in ecology, "the test for ecology is not logical consistency, aesthetic appeal or mathematical precision, but the accuracy and utility of its predictions" (Peters 1980). Further work should explore the potential of functional plant groups to predict the effect of environmental perturbation.

ACKNOWLEDGEMENTS

The authors would like to thank V. Abernethy, M. Ali, J. Currall and A. Spink for comments on this work and all the people who have helped with field-work. License numbers IP/MISC/13-15/91 for transportation of samples back to the UK. were provided by the Department of Agriculture and Fisheries for Scotland. This work was carried out as part of the European Community funded project "Functional Analysis of European Wetland Ecosystems".

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TABLE 1 SUMMARY INFORMATION ON THE TWELVE TRAITS MEASURED

TRAIT	CODE	MEASURE-MENTS PER POPULATION	PLACE OF MEASUREMENT	UNITS
Height of plant	HEIGHT	10	FIELD	cm
Area of plant canopy	AREA	10	FIELD	5x5cm squares
Number of leaves	LEAVES	10	FIELD	-
Number of seeds	SEEDS	10	FIELD	-
Total leaf area	LEAFAREA	10	LABORATORY	cm^2
Dry weight of leaves	WTLEAF	10	LABORATORY	$10^{-2}g$
Dry weight of stem	WTSTEM	10	LABORATORY	$10^{-2}g$
Dry weight of reproductive structures	WTREPRO	10	LABORATORY	$10^{-2}g$
Weight per seed	WTSEED	1	LABORATORY	$10^{-5}g$
N conc. in leaves	NCONC	1	CHEMISTRY LABORATORY	% of dry weight
Pconc. in leaves	PCONC	1	CHEMISTRY LABORATORY	% of dry weight
K conc. in leaves	KCONC	1	CHEMISTRY LABORATORY	% of dry weight

TABLE 2 COMPETITIVE (C), STRESS-TOLERANT(S) AND INTERMEDIATE STRATEGY (C-S-D) *A PRIORI* SELECTED PLANT POPULATIONS.

STRATEGY	PLANT SPECIES	SITE CODE
C	*Cirsium arvense* (L.) Scop.	EBM1
C	*Phalaris arundinacea* L.	EBM2
C	*Phalaris arundinacea* L.	FAP4
C	*Phalaris arundinacea* L.	FDC1
C	*Urtica dioica* L.	FAP1
C	*Urtica dioica* L.	FAP2
C	*Urtica dioica* L.	FDC2
S/D/CSD	*Anthoxanthum odoratum* L.	EKS3
SC/S	*Carex nigra* (L.) Reichard	ICL5
SC/S	*Carex nigra* (L.) Reichard	ILB4
S	*Carex panicea* L.	EKS2
S	*Danthonia decumbens* (L.) DC	ILB1
S	*Deschampsia cespitosa* (L)Beauv.	ICL2
C-S-D	*Agrostis capillaris* L.	EBM1
C-S-D	*Agrostis capillaris* L.	FAP3
C-S-D	*Agrostis canina* L.	EKS3
C-S-D	*Cynosurus cristatus* L.	ILB1
C-S-D	*Eleocharis palustris* (L.) Roemer & Schultes	ILB2
C-S-D	*Holcus lanatus* L.	EBM3
C-S-D	*Holcus lanatus* L.	EKS1
C-S-D	*Holcus lanatus* L.	ICL5
C-S-D	*Hydrocotyle vulgaris* L.	ILB4
C-S-D	*Rumex acetosa* L.	EBM1

TABLE 3. THE IMPORTANCE OF TWELVE TRAITS IN DISCRIMINATING BETWEEN COMPETITIVE (C) AND STRESS-TOLERANT (S) PLANT POPULATIONS.

DISCRIMINATING FOR C	DISCRIM. FUNCTION
1. Dry weight of leaves	26.3
2. Height of plant	20.5
3. N conc. in leaves	8.3
4. P conc. in leaves	8.3
5. Number of seeds	1.5
DISCRIMINATING FOR S	
6. Dry weight of repro. structures	-15.0
7. Area	-9.9
8. Dry weight of stem	-8.8
9. Number of leaves	-8.7
10. Area of leaves	-6.3
11. Dry weight of a seed	-2.4
REDUNDANT	
12. K conc. in leaves	

TABLE 4 SPECIES NAMES, COMPETITIVE ABILITY AND STRESS-TOLERANCE SCORES FOR EACH PLANT POPULATION FROM QUADRATS IN ENGLAND, IRELAND AND FRANCE (* after a species name denotes plant populations that were used to predict the survival strategy of the other listed species) (nomenclature as Clapham, Tutin & Moore 1987).

Species name	Quadrat code	Competitive ability	Stress-tolerant ability
Agrostis canina L.*	EKS3	3.7	5.5
Agrostis capillaris L.*	EBM1	3.7	5.4
Anthoxanthum odoratum L.*	EKS3	3.0	5.8
Carex nigra (L.) Reichard	EKS2	1.5	5.4
Carex panicea L.*	EKS2	2.4	7.6
Cirsium arvense (L.) Scop.*	EBM1	10.5	1.0
Dactylis glomerata L.	EBM2	3.0	5.4
Deschampsia caespitosa (L.) Beauv.	EBM2	7.6	5.4
Filipendula ulmaria (L.) Maxim	EBM3	10.6	3.7
" "	EKS1	6.7	3.9
Holcus lanatus L.	EBM1	5.3	5.3
" "	EKS3	4.2	5.4
" " *	EBM3	4.8	5.6
" " *	EKS1	4.4	5.8
Juncus effusus L.	EBM2	8.1	6.1
" "	EBM3	8.2	6.0
" "	EKS1	4.7	5.5
Juncus inflexus L.	EKS1	5.6	5.6
Molinia caerulea (L.) Moench.	EKS2	2.4	5.6
" "	EKS3	4.0	6.0
Narthecium ossifragum (L.) Hudson.	EKS2	1.6	5.4
Phalaris arundinacea L.*	EBM2	8.5	3.7
Poa trivialis L.	EBM3	4.0	5.4
Rumex acetosa L.*	EBM1	3.7	5.2
Agrostis capillaris L.*	FAP3	2.7	3.4
Carex arenaria L.	FDC3	0.8	5.4

Carex elata All.	FAP3	2.0	5.4
Carex otrubae Podp.	FAP4	3.5	6.6
Cynodon dactylon (L.) Pers.	FAP3	1.1	5.1
Cyperus longus L.	FDC1	6.0	4.9
Cyperus fuscus L.	FAPS	0.8	5.3
Echinochloa crus-galli (L.) Beauv.	FDC1	5.5	3.9
Eryngium campestre L.	FDC3	7.6	3.4
Euphorbia cyparissias L.	FDC3	1.4	5.1
Gaudinia fragilis (L.) Beauv.	FDC3	2.4	6.0
Gnaphalium luteo-album L.	FAPS	1.3	5.8
Holcus lanatus L.	FAP3	3.0	5.5
Mentha pulegium L	FDC4	1.0	5.7
Phalaris arundinacea L.*	FDC1	9.0	2.9
" " *	FAP4	6.1	3.8
Potentilla anserina L.	FAP4	1.5	5.4
Rumex crispus L	FAP4	3.8	3.0
Sagina nodosa (L.) Fenzl.	FDC4	0.9	5.5
Salix alba L	FAPS	1.9	5.4
Solidago canadensis L.	FAP1	4.6	4.8
Urtica dioica L.*	FAP1	8.5	1.8
" " *	FAP2	9.7	-0.4
" " *	FDC2	11.4	-3.2
Veronica sp.	FAPS	1.0	7.4
Agrostis stolonifera L	ICL1	1.9	5.4
Anthoxanthum odoratum L	ICL5	3.5	6.3
Carex acutiformis Ehrl.	ILB3	6.5	4.3
" "	ICL1	3.8	5.2
Carex disticha Hudson	ILB2	3.2	5.4
" "	ICL2	2.9	5.8
Carex nigra (L.) Reichard*	ICL5	1.9	6.3
" " *	ILB4	2.4	7.0
Cynosurus cristatus L.*	ILB1	3.2	6.2
Danthonia decumbens (L.) DC.*	ILB1	3.3	12.3
Deschampsia caespitosa (L.) Beauv.*	ICL2	6.6	5.0
Eleocharis palustris (L.) Roemer & Schultes.	ICL1	4.2	5.6
" " *	ILB2	3.7	5.5
Filipendula ulmaria L	ILB4	5.7	4.6
Holcus lanatus L.	ILB1	4.2	5.6
" " *	ICL5	4.8	5.4
*Hydrocotyle vulgaris L.**	ILB4	1.5	5.4
Leontodon autumnalis L	ILB4	4.8	4.9
Lolium perenne L	ILB1	4.4	7.7
Mentha aquatica L.	ICL1	3.9	5.4
" "	ICL2	4.2	5.0
" "	ILB3	2.9	4.9
Phalaris arundinacea L.	ILB3	5.2	5.3
Phleum pratense L	ILB1	3.5	5.2
" "	ICL2	3.5	5.2
Plantago lanceolata L.	ILB1	3.6	7.5
" "	ICL2	3.4	5.9
Poa pratensis L	ICL2	3.7	5.2
Ranunculus acris L.	ICL2	2.8	7.1

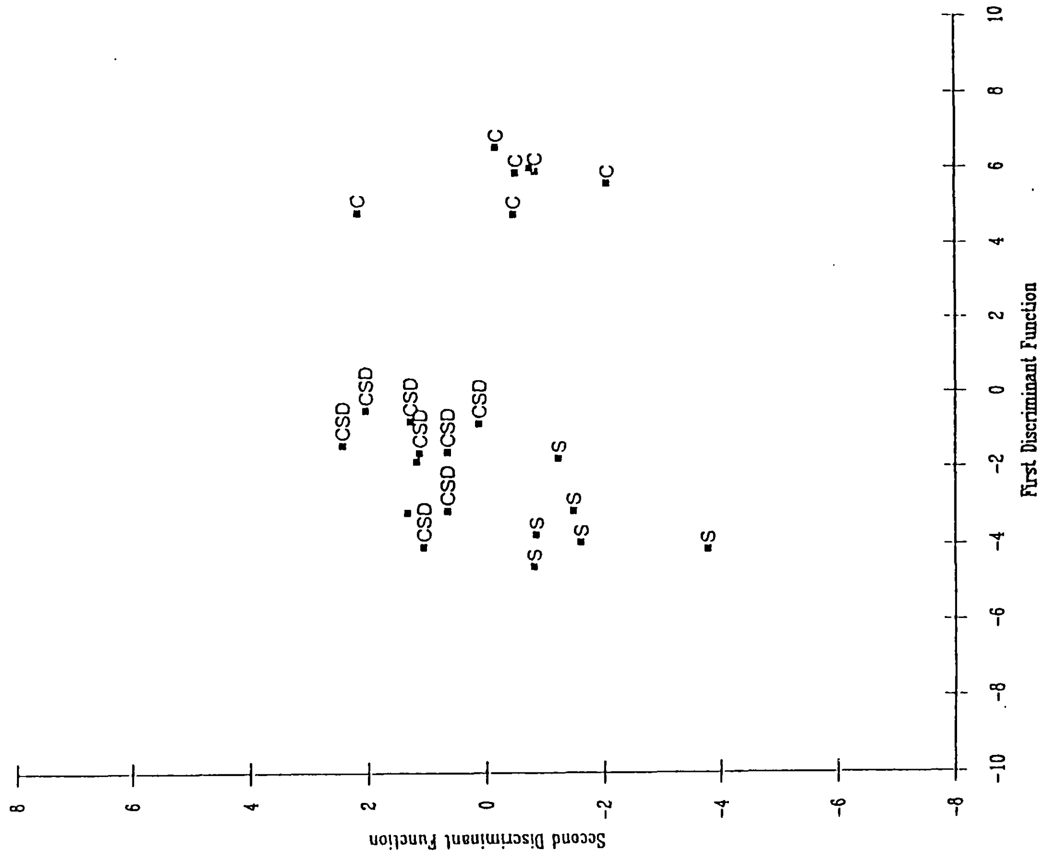
TABLE 5 COMPETITIVE (CFVT) AND STRESS-TOLERANT (SFVT) COMMUNITY STRATEGY SCORES AND THE PROPORTION OF THE TOTAL VEGETATION COVER USED TO DETERMINE THE SCORES FOR QUADRATS IN ENGLAND, FRANCE AND IRELAND.

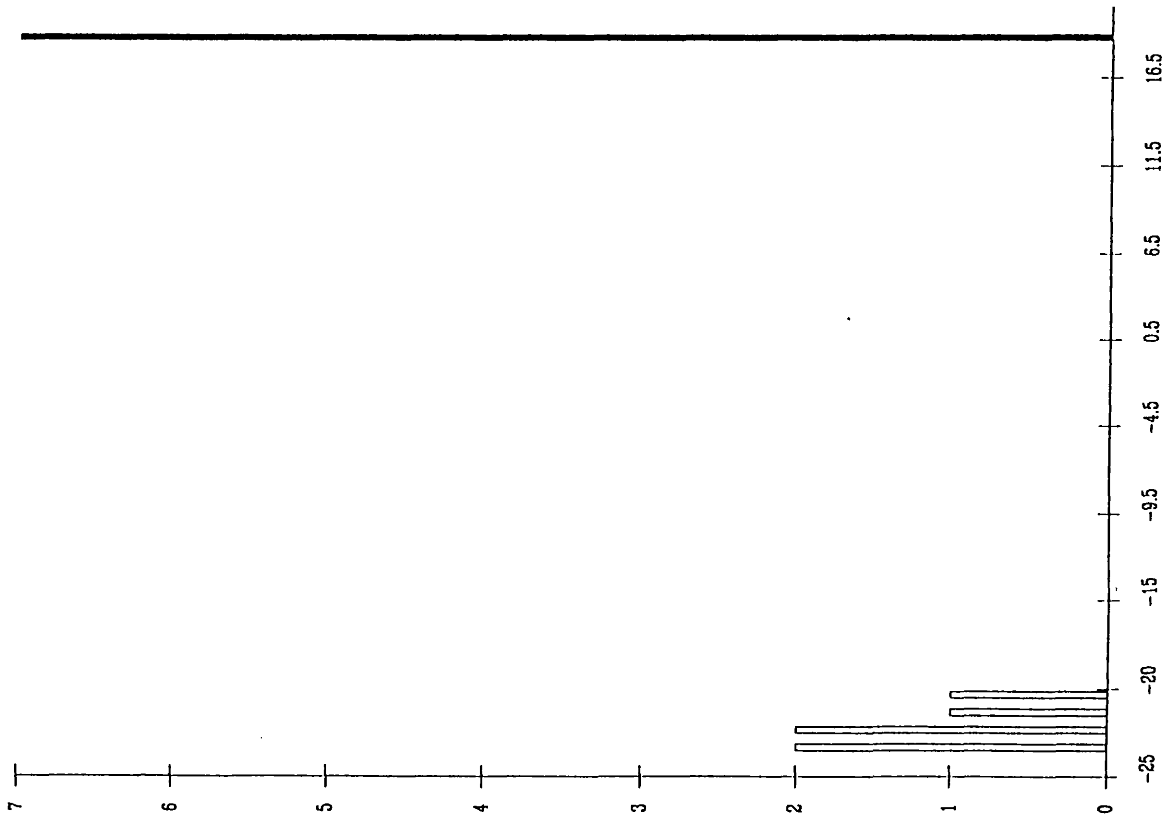
Quadrat code	Competitive ability (CFVT)	Stress-tolerant ability (SFVT)	Proportion total cover (%)
EKS1	5.6	4.8	57
EKS2	2.3	5.9	64
EKS3	3.9	6.0	54
EBM1	4.6	4.6	30
EBM2	7.9	5.1	84
EBM3	7.8	6.0	43
FAP1	8.4	1.9	69
FAP2	9.7	-0.4	94
FAP3	2.8	5.5	22
FAP4	5.4	4.5	68
FAPS	1.0	7.0	100
FDC1	8.9	3.0	42
FDC2	11.4	-3.2	6
FDC3	1.5	5.3	26
FDC4	1.0	5.7	5
ICL1	3.0	5.4	56
ICL2	3.9	5.6	59
ICL4	3.2	6.5	40
ILB1	3.9	8.6	20
ILB2	3.4	5.4	44
ILB3	5.1	5.0	62
ILB4	2.8	6.0	31

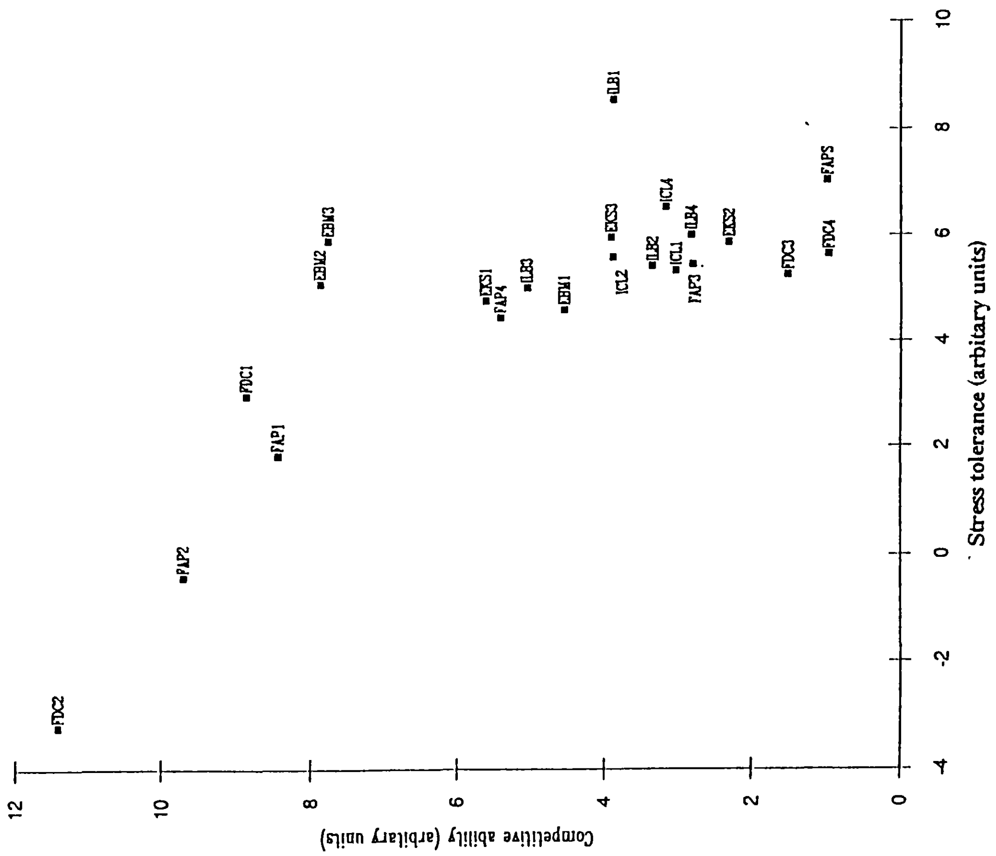
Figure 1. The frequency of occurrence of 13 competitive (unshaded bars) and stress-tolerant (shaded bars) plant populations on a linear discriminant function axis, using 12 descriptive variables.

Figure 2. Plot of the first and second axes of a multiple discriminant analysis used to distinguish between competitive (C), stress-tolerant (S) and intermediate strategy (C-S-D) plant populations.

Figure 3. Functional Vegetation Types (FVT) of European riverine wetland plant communities plotted on a competitive and stress-tolerant axes ($r = 0.74$, $P<0.001$, $df = 21$).


Second Discriminant Function
8
6
4
2
0
-2
-4
-6
-8
First Discriminant Function
-10
-8
-6
-4
-2
0
2
4
6
8
10
C
C
C
C
C
C
CSD
CSD
CSD
CSD
CSD
CSD
CSD
CSD
CSD
S
S
S
S
S
S
S


Frequency
7
6
5
4
3
2
1
0
Linear Discriminant Function
-25
-20
-15
-9.5
-4.5
0.5
6.5
11.5
16.5


Competitive ability (arbitary units)
Stress tolerance (arbitary units)
0
2
4
6
8
10
12
-4
-2
0
2
4
6
8
10
FDC2
FAP2
FAP1
FDC1
EBM2
EBM3
EKS1
FAP4
DLB3
EBM1
ICL2
EKS3
DLB2
ICL1
FAP3
DLB4
ICL4
EKS2
DLB1
FDC3
FDC4
FAP5

Appendix 2.2 Murphy K.J., Castella E., Clement B., Hills J.M., Obrdlik P., Pulford I.D., Scheidner E. & Speight M.C.D. (1994) Biotic indicators of riverine wetland ecosystem functioning. *Global wetlands - old and new* (ed. W. Mitsch). Elsevier (in press).

Biotic indicators of riverine wetland ecosystem functioning

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Abstract

An analysis is provided of the relationship between strategies of species as indicators of environmental conditions, and independently defined (in hydrological and geomorphic terms) units of riverine wetlands in Europe. Two contrasting groups of organisms were targeted: wetland plants and wetland hoverflies (Syrphidae). The strategy concept was used to classify each group of target organisms on the basis of their possession of sets of similar or analagous genetic traits, which permit tolerance of similar sets of environmental pressures affecting their survival in riverine wetlands. The results of these strategy analyses were then linked to analyses of distribution data for the groups of species concerned, to permit definition of functional groupings of organisms in relation to habitat characteristics. Both plant and adult Syrphid assemblages showed some potential for distinguishing independently-defined hydrogeomorphic units of the target wetlands. The use of functionally-defined groupings, which linked trait and distribution data for each set of organisms, proved effective in indicating differing hydrological and geomorphic conditions likely to produce differing intensities of stress affecting plants and invertebrates occurring within a riverine wetland. There was a reasonable degree of congruity between the results obtained using plants, and those obtained using hoverflies to indicate riverine wetland ecosystem functioning at the target sites.

1. INTRODUCTION

In this paper we outline an approach to analyzing the functioning of riverine wetland ecosystems based upon the use of vascular plants, and macroinvertebrates, as indicator organisms. The study forms part of a large-scale multidisciplinary programme "Functional Analysis of European Wetland Ecosystems" (FAEWE), funded by the Commission of the European Communities (Maltby *et al.* 1992).

Our approach utilises the strategy concept of Grime (1979) to classify the target organisms on the basis of their possession of sets of similar or analagous genetic traits, which permit tolerance of similar sets of environmental pressures affecting the survival of organisms within riverine wetlands. Analysis of biological trait data ("strategy analysis": Murphy *et al.* 1990) may be linked to analysis of distribution data ("community analysis" - for example, phytosociological analysis of vegetation: Westhoff & van der Maarel 1973) to define functional groupings of organisms in relation to the environmental characteristics of the wetland habitat (Hills *et al.* 1993 in press; Wu *et al.* 1992; Obrdlik *et al.* 1992). Such functionally-defined groups of organisms may play a useful role as indicators of ecosystem status, or ecosystem response to changing environmental conditions in riverine wetlands.

Vascular plants and macroinvertebrates were chosen as target organisms because they provide both comparable and contrasting ecological features. These include the following points of interest:

(i) Plants are much less mobile than invertebrates. The mobility of invertebrates has major implications for their susceptibility to environmental stress (any factor which impairs physiological functioning critical to the organism's survival: e.g. photosynthetic carbon fixation in the case of plants) or environmental disturbance (any factor which destroys or damages either the biomass, or the habitat of the organism).

(ii) Wetland macroinvertebrates have a much higher taxonomic diversity than vascular plants, on a unit area basis. This precludes inclusion in the analysis of all the invertebrate species occurring on a site. For the purposes of this paper we selected one group, the family Syrphidae (hoverflies) of the Diptera for comparison with vascular plants. Additional data are however available for other invertebrate groups, to provide a reasonable sample of the range of trophic levels and dispersal abilities of riverine wetland invertebrates (Speight 1986).

(iii) The amount of knowledge available on the life cycles, biological traits and survival strategies of wetland invertebrates is less than that available for wetland plants. Absence of information on the biology (e.g. even fundamental data such as the location of the larval stages for some species) of invertebrates is a constraint on the applicability of identical approaches to analysis of botanical and zoological data from wetland systems.

(iv) Plants are producers while invertebrates are consumers - with obvious fundamental differences between the two groups in terms of resource requirements from the wetland ecosystem. The Syrphidae comprise a group closely associated with vegetation, from ground-layer to tree canopy. They have flower-feeding adults, which play a significant role in pollination. Their larvae are divided among plant-feeding, predatory and saprophagic life- styles.

2. SITE INFORMATION

Information included in this paper was derived from field studies conducted during 1991 at riverine wetland sites in France, Ireland and England:

Country	Catchment and sites (SITE CODE)	Lat. & Long.
Ireland	Middle Shannon:	53°N, 7°W
	a) R. Shannon at Clonmacnoise (ICL1,2,4,5)	
	b) Little Brosna (ILB1-4)	
France	Loire:	47°N, 3°E
	a) R. Loire at Decize (FDC1-4)	
	b) R. Allier at Apremont (FAP1-4; FAPS)	
England	Torridge:	51°N, 5°W
	a) R. Torridge at Kismeldon (EKS1-3)	
	b) R. Torridge at Bradford Mill (EBM1-3)	

Within each site three, four or five site-units were selected for sampling on hydrological and pedological criteria, and termed hydrogeomorphic units (criteria for defining and selecting hydrogeomorphic units were described by Maltby *et al.*, 1992). Units were numbered in order away from the river channel. FAPS was an additional site set up on a sandbank in the main river channel of the R. Loire.

3. HOVERFLIES AS BIOTIC INDICATORS OF ECOSYSTEM FUNCTIONING

3.1. Field data

Field sampling was carried out during May 1991 in France, and August 1991 in Ireland, at a total of 18 site-units. The Irish sites were at Clonmacnoise on the R. Shannon (ICL1-5), and at a site on a small tributary of the Shannon, the Little Brosna (ILB1-5). The French sites were at Decize on the R. Loire (FDC1-4), and at Apremont on the R. Allier (FAP1-4), a major tributary of the Loire. Flying adults of the Syrphidae were sampled using Malaise traps (Southwood 1978). Two traps were installed and operated for 10 days within each hydrogeomorphic site-unit under investigation by the FAEWE study, except FAP4 and FDC4 (1 trap), and FDC3 (3 traps). Fuller details of methodology are given by Obrdlik *et al.* (1992). The 63 species encountered are listed in Table 1.

3.2. Biological traits of wetland Syrphid species

Seven traits were chosen as being *a priori* related to the ability of the species to colonize, survive and reproduce in riverine wetland conditions (Table 2). Each trait is categorised using a four-level fuzzy coding system, ranking from 0 (no affinity of the species for this category of the trait) to 3 (high affinity). The concept of fuzzy sets, where "elements may be partial members of a set, rather than either being members or non-members" (Roberts 1989a) is appropriate to the variability of ecological systems, and has been successfully applied to a range of ecological datasets (e.g. Roberts 1989b; Equiha 1990). Building on earlier attempts by Usseglio-Polatera (1991) and Bournaud *et al.* (1992 in press), the coding of species biological traits used here represents an effort to transcribe into a numerically-processable form a body of information derived from diverse sources, which may be scattered through the literature, or available from experts' individual knowledge and experience. Conveniently, for most of the Syrphidae trapped in this study, the relevant data had already been summarised by Speight & Lucas (1992).

3.3. Data analysis

A three-step procedure was used:

(i) qualitative species distribution data (presence or absence of each species per hydrogeomorphic site-unit: 63 species x 18 units) were processed using Correspondence Analysis (CA)

(ii) fuzzy-coded biological traits (63 species x 25 categories of the 7 traits) were processed using a Fuzzy Multiple Correspondence Analysis (FMCA), following the technique of Bournaud *et al.* (1992 in press) and Doledec & Chessel (1992).

(iii) the linkage between the two datasets, i.e. the relationship between the ordination of sites and the ordination of biological traits was described using a simultaneous ordination method: "co-structure analysis" (Mercier 1991; Chessel & Mercier 1992 in press; Doledec and Chessel 1992).

All computations were carried out using the ADE software package of Chessel & Doledec (1991).

3.4. Community analysis by ordination of hydrogeomorphic site-units in terms of Syrphid assemblages

The first three axes of the CA of Syrphid species presence data provided a clear ordination of the 18 site-units (Fig. 1). The French and Irish sites were clearly separated along Axis F1 (accounting for 17% of inertia). The Irish sites proved to be a much more homogeneous dataset than the French sites. Axis F2 (12.3%) tended to segregate the Loire and Allier sites, within the French sites. Axis F3 (12.2%) suggested a trend of variation within the French sites which may be related to habitat-type, with river-margin sites (FAP1, FDC1), woodland (FAP2, FDC2), wet depression (FAP4, FDC4), and pasture (FAP3, FDC3) succeeding each other along this axis.

3.5. Strategy analysis by ordination of Syrphid species in terms of biological traits

The first two axes of the FMCA (Fig. 2) of traits (respectively accounting for 23.3% and 15% of inertia) provided a reasonable depiction of the ordination of the 63 Syrphid species. Traits apparently most important in contributing to the observed species-ordination were:

(i) F1: inundation tolerance (74% of variability explained); migration status (66%); food type (46%); and stratum occupied (46%)

(ii) F2: inundation tolerance (75%); food type (40%); and migration status (30%)

Less important were traits for length of developmental phase (33% on F1); number of reproduction cycles per year (39% on F1); and overwintering phase (36% on F1).

The detailed representation of the categories of two of the most important contributory traits (inundation and larval food type), plotted on the F1 x F2 framework, suggests possible explanations for the distribution of species within the ordination (Fig. 2D).

3.6. Linkage of site and trait ordinations

The simultaneous ordination (Fig. 3) of the two data sets provided a direct assessment of the relationship between the site ordination and the biological traits of the Syrphid species occurring at these sites (Figs. 3D and 3E). The co-structure described on the first factorial plane of the simultaneous ordination (Fig. 3D) is similar to the F1 x F3 site ordination (Fig. 3B), but is intermediate between the first two axes of the trait ordination (Fig. 3C).

The main patterns of this co-structure appear to be related to the structural and hydrological characteristics of the sites. The absence of trees from the Irish sites prevents the occurrence of species with tree-dwelling larvae (stratum category 1), whilst the wet soils and presence of permanently-filled ditches at the Irish sites favour species with aquatic larvae (stratum category 4). Sites with permanent tree cover, such as FAP1 and FAP2 in France harbour species with a long developmental stage (>1 year: development category 4), and a correlated low number of reproduction cycles per year (cycles category 1). These traits are entirely absent from species present at the Irish sites.

4. VASCULAR PLANTS AS BIOTIC INDICATORS OF ECOSYSTEM FUNCTIONING

4.1. Field data

(i) A vegetation survey of 25 relevés was carried out during 1991 at each of two sites (EKS, EBM) on the R. Torridge, following a standard Zürich-Montpellier approach (Braun-Blanquet 1925). Plant assemblage characterisation by this method is based on the concept of "degree of fidelity" of plant species (Moravec 1992) in an association or community. Relevés were selected on the ground for homogeneity of vegetation type, and all species present within the relevé were identified. Plant species were quantified using a semi-qualitative abundance-dominance index (+ to 5) and by frequency category (I to V).

(ii) Field sampling to acquire data for plant strategy analysis was carried out between April - October 1991, with 3 visits to each of 22 site-units during this period. Sampling was confined to ground-cover vegetation. A 10 x 10 m permanent quadrat (marked by a set-frequency miniature radiotransponder buried in the soil) was set up within each unit. Within this, % frequency of species occurrence was determined using a random sub-divided quadrat (0.5 x 0.5 m) sampling technique. Percentage cover data were acquired using a random pin-frame sampling method, with 10 replicate samples per permanent quadrat. Fuller details of methodology were given by Hills *et al.* (1993 in press). In total 147 vascular plant species were recorded, of which 78 were selected for inclusion in the strategy analysis procedure (Table 3).

4.2. Biological traits of wetland plants

Plant survival strategy theory (Grime 1979) divides plant habitats into three basic categories, defined by the balance of environmental pressures affecting them. Disturbed (D) habitats are those where there is a high probability of destruction of plant biomass (corresponding to the "R" (= "ruderal") habitat type defined by Grime (1979)). Stressed (S) habitats are unproductive, with a low rate of accumulation of biomass. Competitive habitats (C) are both undisturbed and productive, with the main threat to a plant's survival coming from competition for resources from other plants: C-strategists are therefore resource-capture specialists. Plants occupying these habitat-types, or intermediates, must have evolved appropriate sets of survival traits ("strategies": for tolerance of stress, disturbance or competition, or intermediate combinations of these strategy elements) to permit growth and reproduction under the prevailing conditions. Successful species may be defined as those with the most appropriate strategy for the current set of pressures influencing a given site. Adult ("established-phase") and juvenile ("regenerative-phase") stages of the plant life-cycle are recognised as having differing responses to environmental pressures, and therefore different strategies. In this paper we deal only with the established-phase strategies of riverine wetland plant populations. Further work is needed to incorporate the regenerative-phase into the approach outlined here.

It is possible to assign traits *a priori* to C, S or D strategy elements, as was done by Murphy *et al.* (1990) for lake vegetation. A better approach is to make no pre-assignment of traits into strategy elements, but rather to use objectively quantified biological traits as the basis for assessing the strategy of a plant population.

Twelve traits were measured quantitatively (Table 4: see also Hills *et al.* 1992), for 78 selected plant populations present in the permanent quadrats sampled in 21 hydrogeomorphic units during 1991.

4.3. Community analysis of wetland vegetation

4.3.1. *Phytosociological classification and ordination of vegetation data within the R. Torridge wetland sites.*

Two-Way Indicator Species Analysis (TWINSPAN: Hill 1979) and Correspondence Analysis (CA) were used respectively to classify and ordinate the dataset of 50 relevés in terms of species assemblage (Thioulouse 1989). A standard Braun-Blanquet table-rearrangement procedure was used to derive a synoptic table (Table 5) of vegetation units for comparison with the results of the multivariate analyses (Braun-Blanquet 1925).

Two main groupings of relevés were detected by the TWINSPAN analysis within the R. Torridge wetlands (Fig. 4), which may be divided into a sub-set of two phytosociological units, labelled A and B; and a sub-set of three phytosociological units (B - E). A small intermediate group (C + D) was made up of 3 relevés located on an area disturbed by old drainage work. This group was left out of the subsequent analysis. CA ordination of the same dataset (Fig. 5), depicted on the Axis 1 - Axis 2 plane, suggested little evidence for any major between-site differences. Phytosociological units D and E were quite clearly separated from each other, and from a more homogeneous group comprising A + B + C. When the ordination was replotted on the Axis 1 - Axis 3 plane (Fig. 6), it became clear that this large group was in fact separable into its three component relevé-groupings along the z axis of the ordination plot.

There was thus reasonably good evidence from the multivariate anaysis of the data for the existence of 5 vegetation types (phytosociological units) within the R. Torridge wetlands, which may be characterised (Table 6) in terms of "differential" species for each unit.

These units can be described by reference to the standard CORINE list of biotopes within the European Community (Devillers *et al.* 1991). Units A and B are typical of oligotrophic humid grasslands. Unit A is a heath rush meadow type found in oligotrophic acidic fens. Unit B is related to the purple moorgrass (*Molinia caerulea*) meadow type, typically on less oligotrophic and less-peaty soils than type A.

The remaining groups were more characteristic of nutrient-richer humid grasslands. Unit C belongs to the meso-eutrophic humid grasslands, developed on nutrient-rich alluvial wet soils, often inundated (at least in winter and spring). A variant with *Carex paniculata* indicates seepage areas, with local base-enrichment of the substrate. Unit D is a mesophile grassland, regularly grazed, on well-drained alluvial soils. Unit E is related to humid tall-herb fringes, nitro-hygrophilous, developing along the shaded side of wooded stands and hedges

4.3.2. *Ordination of vegetation data from R. Torridge, R. Loire and R. Shannon wetland sites*

The plant community data (% frequency) collected from all six wetland sites were processed using Detrended Correspondence Analysis (DCA: Hill & Gauch 1980) using the CANOCO software package of ter Braak (1988, 1989), to produce an ordination of hydrogeomorphic site-units in terms of vegetation.

DCA produced an ordination of the plant population frequency data from permanent quadrats located in 21 of the hydrogeomorphic units sampled, shown in Fig. 7. A central, fairly homogeneous set of site-units, comprising all the Irish sites, and most of the French and English sites was identified. Three groups of outliers were apparent, with vegetation very different from that of the central set. The DCA ordination of data from three widely-separated sets of riverine wetlands provided an indication of the considerable variation in plant community, but with evidence for the existence of at least four clearly-separate main vegetation types. To take this approach further, environmental data (e.g. hydrology and physico-chemistry for each hydrogeomorphic unit) are required. These data (collected at the target sites by other members of the FAEWE team: see Tellam *et al.* (1992); Maltby (1992); van Oorschot (1992) but not available at the time of writing) may be used to establish correlative relationships, and their significance, between vegetational gradients as expressed along the DCA axes, and gradients of environmental variation. Alternatively, once environmental data are available, a reanalysis of the complete vegetation-environment dataset, using Canonical Correspondence Analysis (ter Braak 1986) may be undertaken to permit direct assessment of statistical relationships between plant community and wetland environmental characteristics.

4.4. Strategy analysis of wetland vegetation

The strategy analysis procedure entailed three steps, summarised below:

(i) Linear (LDA) and multiple (MDA) discriminant analyses were used to distinguish respectively between subsets of 13 and 23 wetland populations of plant species (chosen because information was available on their strategies in Grime *et al.* (1988)), using 12 biological traits as descriptor variables. These populations were drawn from three C species (*Cirsium arvense*, *Phalaris arundinacea*, *Urtica dioica*), five species with strategies including a strong element of stress-tolerance (*Carex nigra*, *Carex panicea*, *Danthonia decumbens*, *Anthoxanthum odoratum*, *Deschampsia caespitosa*), and seven intermediate strategy (C-S-D) species (*Agrostis canina*, *Agrostis capillaris*, *Cynosurus cristatus*, *Eleocharis palustris*, *Holcus lanatus*, *Hydrocotyle vulgaris*, *Rumex acetosa*), present at the wetland sites in 1990.

(ii) Stepwise multiple regression was used to quantify the relationships between biological traits predictive of competitive ability (C score) and stress- tolerance (S score) for 78 wetland plant populations.

(iii) The functional vegetation type (FVT) present in each hydrogeomorphic unit was assessed in terms of competitiveness (CFVT) and stress-tolerance (SFVT), by calculating a weighted mean (using plant cover as the weighting factor) of C and S scores derived from the regression analysis for each population. A functional vegetation type is here considered to be a unit of vegetation which is relatively homogeneous in terms of a set of functional traits which are exhibited by the plant assemblage, and which are relevant to the survival of those plants under prevailing environmental conditions. In relation to plant strategy theory, an FVT may be considered to be a unit of vegetation which is defined in terms of traits for survival of stress, disturbance and competition pressures acting on plant survival.

Technical details of the strategy analysis approach used above to determine FVTs of wetland vegetation are given in more detail by Hills *et al.* (1993 in press).

The discriminant analysis approach showed that plants previously categorised as C, S or intermediate (C-S-D) strategists by Grime *et al.* (1988) showed significant differences when compared in terms of up to 12 descriptive biological traits. The most important traits (see Table 4) discriminating for the competitive-strategy were in descending order: WTLEAF, HEIGHT, NCONC, PCONC, and SEEDS. Traits discriminating for stress-tolerance in the wetland species tested were, in descending order: WTREPRO, AREA, WTSTEM, LEAVES, LEAFAREA, and WTSEED. MDA clearly separated the subset of 23 wetland plant populations into three groups, when biological traits were used as discriminant variables . Overlaying the strategy allocated by Grime *et al.* (1988) for each species (Fig. 8) on the ordination of plant populations from the target wetland sites it is apparent that this technique succeeded in grouping together populations of similar strategy (C, S or C-S-D). An approach based upon the utilisation of the 12 biological traits measured for wetland plants therefore appears promising as the basis of a method for analyzing the strategies of wetland vegetation.

The 23 populations included in the MDA analysis were assigned numerical scores on a fuzzy coding system where S-strategists were assigned a score of 10 for stress-tolerance and 0 for competitiveness; C-strategists a score of 10 for competitiveness and 0 for stress-tolerance; and intermediate strategists a score of 5 for both stress-tolerance and competitiveness. A stepwise multiple regression procedure was then used to determine the relationship between stress-tolerance scores of the 23 plant populations (as dependent variable) and the six traits identified by discriminant analysis as important in defining stress tolerance (as independent predictive variables). This process was repeated using competitive ability scores and the five traits discriminating most strongly for the C-strategy. The result was a pair of predictive equations for the importance of biological traits in determining strategy scores, for a sample of 23 populations of wetland plants. These equations were then used to predict the C and S strategy scores of the remaining 55 plant populations in the data set.

For each hydrogeomorphic unit sampled, the mean C and mean S score was calculated for the set of plant populations present, weighted by cover score, to derive a value for CFVT (competitive ability of functional vegetation type) and SFVT (stress-tolerance ability of functional vegetation type). CFVT and SFVT scores were plotted against each other to provide an indication of the functional vegetation type of each hydrogeomorphic unit, defined in terms of C and S strategy elements (Fig. 9).

The results indicate a significant inverse relationship between stress-tolerant and competitive strategies within plant assemblages characteristic of wetland hydrogeomorphic units (SFVT v. CFVT: $r = -0.74$; $p<0.001$). This is in line with the postulate of strategy theory that there is a trade-off between these two elements within the strategy of plant populations (Grace 1990).

The 23 hydrogeomorphic units ordinated in Fig. 9 appear to fall into two main groups: a group in which FVT is dominated by populations of plant species in which traits for competitive ability are important; and a larger group in which the importance of the C strategy-element is variable, but lower than in the first group, and traits for stress-tolerance are more important. Units EBM2 and EBM3 are to some extent intermediate between the two FVT categories identifiable for this dataset.

5. THE POTENTIAL OF INVERTEBRATES AND VASCULAR PLANTS AS BIOTIC INDICATORS OF RIVERINE WETLAND FUNCTIONING

5.1. Hoverflies

From the results of applying the approach described here to a test dataset from only two riverine wetland areas, it is clear that community analysis based on adult Syrphid assemblages has a high indicator potential for distinguishing between sites and sub-sites with differing ecological characteristics. The high homogeneity of the Irish sites is in sharp contrast with the more heterogeneous French wetland sites. Despite the mobility of the organisms concerned, the adult Syrphid assemblages are capable of distinguishing quite clearly between different hydrogeomorphic units of the target wetlands.

The invertebrate strategy analysis approach, and the attempt to couple this to community analysis, together show promise as a means of characterising wetlands in terms of functional units. The flexibility and potential of the statistical methods employed here can form the basis for further development of this technique, particularly by improving the description and coding of species biological traits. Distinguishing between the strategies of larval and adult organisms appears to be a requirement, as these two life history stages are unlikely to be equally affected by any given perturbation of the host system. It would also be sensible in future development to differentiate between traits pertaining to single morphological or physiological features of the species (e.g. life span; food type), and more holistic traits incorporating several interacting behavioural or biological features (e.g. flooding tolerance).

The next steps required toward incorporation of invertebrates in a model for the assessment of riverine wetland ecosystem responses to perturbation are:

(i) comparison of the results so far described for the Syrphidae with complementary analyses of community and strategy data for contrasting macroinvertebrate groups: the Carabid beetles and Mollusca;

(ii) incorporation of data from field sampling undertaken under differing seasonal and hydrological conditions; and

(iii) establishment of the relationship between unit-strategy associations for macroinvertebrate groups, and the variability of the physico-chemical and vegetational parameters measured for each hydrogeomorphic unit of the target riverine wetlands.

5.2. Plants

The phytosociological approach can produce a classification of the wetland habitats which may be superimposed on the hydrogeomorphic concept to indicate variation in environmental conditions. For example, within the R. Torridge wetland sites, the same hydrogeomorphic unit ("gentle slope") is occupied by two different plant communities, comprising Units A and B at Kismeldon (EKS) and Units B and C at Bradford Mill (EBM). These differences are indicators of differing trophic status of the two sites, together with differences in soils and hydrology.

The approach has potential in translating findings from the regional to the national or international level, because of the enormous pre-existing body of phytosociological information, and its widespread use in preparing classification schemes for vegetation, e.g. Rieley & Page (1990) on British vegetation; Devillers *et al.* (1991) on European vegetation.

Plant assemblages, summarised in phytosociological terms as outlined here, may have a limited capability for assessing wetland response to perturbation, caused either by human or natural changes. For example, Fig. 5 provides evidence for a gradient of disturbance from heavily-grazed grasslands (Unit D) to ungrazed tall-herb fringes (Unit E) along Axis 2. The relative position of an individual relevé or stand of vegetation along this axis might be expected to alter if the level of disturbance were to change.

The concept of FVT as outlined here is based on data for only two of the three strategy-elements proposed by Grime (1979) as important in defining the survival strategies of established-phase plants. Incorporation of the disturbance-tolerance element in the approach requires further work. On the results outlined above, however, it is apparent that vegetation present in a defined locality (here defined in hydrological and geomorphic terms, as a "unit" of the riverine wetland ecosystem) at a given point in time, can be described very simply, using only two numbers (CFVT and SFVT scores) for the plant assemblage. Changes in the plant assemblage which are big enough to affect the FVT coordinates, can be tracked across the FVT plot. Alternatively, comparisons can be made between plant assemblage FVT scores from different localities, sampled during a given period of time. In either case FVT values provide a simple but information-rich package which might be used as a biotic indicator of conditions affecting the functioning of a wetland ecosystem.

For example, a change in nutrient status, or hydrological conditions within the wetland might be expected to have measurable effects on the functioning of a wetland, specifically by altering stress conditions influencing the plant populations present. Strategy analysis provides the basis of a method for assessing the importance of any such changes, using the response to the changed conditions of plant populations (which will comprise some combination of increased or reduced growth or extinction of species already present, or colonization of new species), as expressed in their contribution to the FVT of the assemblage.

The next stage in developing the strategy analysis technique is to link FVT information and environmental data for the target wetland hydrogeomorphic units, in order to quantify the relationships between FVT score (based on biological traits for tolerance of environmental stress and competition for environmental resources), and environmental factors causing such stresses or providing such resources. On completion of this work it should be possible to place limits on the potential value of the FVT concept as an indicator of change or functioning in riverine wetland ecosystems.

Three final points should be made:

(i) there is a reasonable degree of comparability between the results of the analyses of wetland hydrogeomorphic units based upon plant-community data (community analysis), and upon analysis of the biological traits of the populations of plant species comprising those communities (strategy analysis). When Figs. 7 and 8 are compared, it is clear that certain plant assemblages occupy extreme positions in both analyses (examples are FAP1, FAP2 and FDC3). In both analyses, the remaining sites tend to cluster together, suggesting a strong degree of homogeneity in the vegetation, both in terms of species present, and their survival strategy. This is so both for sites which were close to each other on the ground (the Irish sites providing a particularly close-knit grouping), and also for sites which may be widely separated geographically. EKS1, FAP4 and ILB3 provide a good example: closely similar in terms of both plant community (Fig. 7) and FVT (Fig.9).

(ii) further work is needed to calculate FVT values for other riverine wetland plant communities. The CORINE list (Devillers *et al.* 1991) provides the essential plant community data for the basic types of vegetation which characterise such wetlands in Europe. Similar phytosociological data may be obtained for riverine wetlands elsewhere in the world. Given the widespread availability of such data, and also the strong base of autecological data detailing traits of wetland plant species available in the literature (and increasing in accessibility, with the advent of on-line ecological databases, such as the UK Ecological Flora database, which lists 124 ecological characteristics for 1777 British plant species: Fitter & Ford 1993) it should in principle be possible to calculate FVT values for a wide cross-section of riverine wetland habitats, without the need for additional fieldwork (although clearly better results will always be obtained if traits are measured for the actual set of plant populations present in a given wetland vegetation type). This approach may provide a potentially useful link between phytosociologically-defined plant communities and strategy-defined vegetation types.

(iii) comparison of the FVT analysis (Fig. 9), with the results of the linked site-trait analysis of hoverfly fauna (Fig. 3) for hydrogeomorphic units within the target wetlands provides a further indication that the strategy-based approach may have potential for further development as an indicator of wetland ecosystem functioning. Although the hoverfly analysis included no data from the two English wetlands, we consider that there is a degree of congruity in the outcome of the two analyses for the remaining sites. In particular, the Irish sites show considerable homogeneity for both indicator groups (though more so for the hoverfly-based approach). Outlier units tend to be the same: FAP1, FAP2 and FDC 1 are clearly very different both in terms of plant community strategy and hoverfly community strategy from the other sites. FDC3 also occupies an outlier position far-distant from other hydrogeomorphic units in both analyses. Given that the sets of traits used to analyze the strategies of the two groups of organisms are completely different, and the differences in computation used by the two methods, this outcome gives us confidence in the basic validity of the strategy-based approach as a means of indicating wetland ecosystem functioning.

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Table 1. Identifications of 63 Syrphid (hoverfly) species recorded at 18 hydrogeomorphic units of wetland sites in France and Ireland.

1 Baccha elongata (Fab.)
2 Brachyopa bicolor (Fall.)
3 Brachypalpoides lenta (Mg.)
4 Brachyopa scutellaris R.-D.
5 Caliprobola speciosa Rond.
6 Cheilosia albitarsis
7 Chrysotoxum arcuatum (L.)
8 Cheilosia bergenstammi Beck.
9 Chrysotoxum cautum (Harr.)
10 Cheilosia impressa Lw.
11 Chalcosyrphus nemorum (Fab.)
12 Cheilosia pagana (Mg.)
13 Chailosia variablis (Panz.)
14 Cheilosia velutina Lw.
15 Chrysotoxum vernale Lw.
16 Criorhina asilica (Fall.)
17 Criorhina berberina (Fab.)
18 Episyrphus balteatus (Deg.)
19 Epistrophe eligans (Harr.)
20 Epistrophe nitidicollis (Mg.)
21 Epistrophe ochrostroma (Zett.)
22 Eristalis arbustorum (L.)
23 Eristalis intricarius (L.)
24 Eristalis pertinax Scop.
25 Eristalinus sepulchralis (L.)
26 Eupeodes corollae (Fab.)
27 Eupeodes latifasciatus (Macqt.)
28 Eupeodes latilunulatus (Coll.)
29 Eupeodes luniger (Mg.)
30 Eumerus tuberculatus Rond.
31 Ferdinandea cuprea (Scop.)
32 Helophilus hybridus Lw.
33 Helophilus pendulus (L.)
34 Lejogaster metallina (Fab.)
35 Meligramma cincta (Fall.)
36 Melanostoma mellinum (L.)
37 Melanostoma scalare (Fab.)
38 Meligramma triangulifera (Zett.)
39 Myathropa florea (L.)
40 Neoascia geniculata (Mg.)
41 Neoascia podagrica (Fab.)
42 Neoascia tenur (Harr.)
43 Paragus bicolor (Fab.)
44 Paragus majoranae Rond.
45 Pipizella viduata (L.)
46 Platycheirus albimanus (Fab.)
47 Platycheirus angustatus (Zett.)
48 Platycheirus clypeatus (Mg.)
49 Platycheirus europaeus Goeldlin, Maibach & Speight
50 Platycheirus granditarsus (Foerst.)
51 Platycheirus manicatus (Mg.)
52 Platycheirus scutatus (Mg.)
53 Rhingia campestris (Mg.)
54 Sericomyia silentis (Harr.)
55 Sphaerophoria interrupta (Fab.)
56 Sphaerophoria scripta (L.)
57 Syrphus ribesii L.
58 Syrphus vitripennis Mg.
59 Temnostoma bombylans (Fab.)
60 Temnostoma vespiforme (L.)
61 Volucella bombylans (L.)
62 Xylota abiens (Mg.)
63 Xylota segnis (L.)

Table 2. Biological traits and trait-categories used in analysis of Syrphid strategy.

1. Duration of developmental phases	1. < 2 months
	2. 2 - 6 months
	3. 6 - 12 months
	4. > 1 year
2. Number of reproduction cycles per year	1. < 1
	2. 1
	3. 2
	4. > 2
3. Migratory status	1. not known to migrate
	2. recorded migrant
	3. strongly migratory
4. Habitat stratum of larvae	1. trees and shrubs
	2. low-growing plants
	3. litter layer/ grass root zone
	4. aquatic
5. Inundation tolerance of larvae	1. high
	2. moderate
	3. low
	4. none
6. Overwintering phase	1. larva
	2. puparium
	3. adult
7. Food type of larvae	1. microphagous
	2. living plants
	3. animals

Table 3. Plant taxa recorded in permanent 100 m^2 quadrats located within 22 hydrogeomorphic units of 6 riverine wetland sites in Europe (names follow Stace 1991).

1 Achillea millefolium L.	2 Achillea ptarmica L.
3 Agrostis canina L.	4 Agrostis capillaris L.
5 Agrostis stolonifera L.	6 Ajuga reptans L.
7 Alopecurus geniculatus L.	8 Anthoxanthum odoratum L.
9 Stachys officinalis (L.) Trev. St. Leon	10 Briza media L.
11 Bromopsis erecta (Hudson) Fourr.	12 Calluna vulgaris (L.) Hull
13 Caltha palustris L.	14 Calystegia sepium (L.) R. Br.
15 Cardamine pratensis L.	16 Carex acutiformis Ehrh.
17 Carex arenaria L.	18 Carex disticha Hudson
19 Carex echinata Murray	20 Carex elata All.
21 Carex hirta L.	22 Carex hostiana DC.
23 Carex lasiocarpa Ehrh.	24 Carex nigra (L.) Reichard
25 Carex otrubae Podp.	26 Carex panicea L.
27 Carex vesicaria L.	28 Centaurea nigra L.
29 Chenopodium L.	30 Cirsium arvense (L.) Scop.
31 Cirsium dissectum (L.) Hill	32 Cirsium palustre (L.) Scop.
33 Cynosurus cristatus L.	34 Dactylorhiza fuchsii (Druce) Soo
35 Dactylis glomerata L.	36 Danthonia decumbens (L.) DC.
37 Deschampsia cespitosa (L.) P. Beauv.	38 Digitaria sanguinalis (L.) Scop.
39 Eleocharis palustris (L.) Roemer & Schultes	40 Equisetum fluviatile L.
41 Equisetum palustre L.	42 Erica tetralix L.
43 Euphorbia cyparissias L.	44 Festuca ovina L. agg.
45 Festuca rubra L.	46 Filipendula ulmaria (L.) Maxim
47 Galium aparine L.	48 Galium palustre L.
49 Galium uliginosum L.	50 Galium verum L.
51 Gaudinia fragilis (L.) P. Beauv.	52 Genista anglica L.
53 Geranium dissectum L.	54 Glechoma hederacea L.
55 Glyceria fluitans (L.) R.Br.	56 Gnaphalium L.
57 Gnaphalium uliginosum L.	58 Pilosella Hill.
59 Holcus lanatus L.	60 Hydrocotyle vulgaris L.
61 Iris pseudacorus L.	62 Juncus acutiflorus Ehrh. ex Hoffm.
63 Juncus articulatus L.	64 Juncus effusus L.
65 Juncus inflexus L.	66 Lamium maculatum (L.) L.
67 Lathyrus palustris L.	68 Lathyrus pratensis L.
69 Leucojum aestivum L.	70 Leontodon autumnalis L.
71 Lolium perenne L.	72 Lotus corniculatus L.
73 Lotus pedunculatus Cav.	74 Luzula campestris (L.) DC.
75 Lychnis flos-cuculi L.	76 Lycopus europaeus L.
77 Lysimachia nummularia L.	78 Lysimachia vulgaris L.
79 Lythrum salicaria L.	80 Mentha aquatica L.
81 Mentha arvensis L.	82 Molinia caerulea (L.) Moench
83 Myosotis scorpoides L.	84 Nardus stricta L.
85 Narthecium ossifragum (L.) Hudson	86 Pedicularis palustris L.
87 Phalaris arundinacea L.	88 Phleum pratense L.
89 Plantago lanceolata L.	90 Poa annua L.
91 Poa pratensis L.	92 Poa trivialis L.
93 Polygala serpyllifolia Hose	94 Polygonum aviculare L.
95 Persicaria amphibia (L.) Gray	96 Persicaria hydropiper (L.) Spach.
97 Potentilla anserina L.	98 Potentilla erecta (L.) Raeusch.

Table 3 (continued). Plant taxa recorded in permanent 100 m^2 quadrats located within 22 hydrogeomorphic units of 6 riverine wetland sites in Europe (names follow Stace 1991).

99 Potentilla reptans L.
100 Ranunculus acris L.
101 Ranunculus aquatilis L.
102 Ranunculus flammula L.
103 Ranunculus lingua L.
104 Ranunculus repens L.
105 Ranunculus sardous Crantz
106 Rhinanthus minor L.
107 Rorippa amphibia (L.) Besser
108 Roroppa sylvestris (L.) Besser
109 Rubus caesius L.
110 Rubus fruticosus L. agg.
111 Rumex acetosa L.
112 Rumex acetosella L.
113 Rumex conglomeratus Murray
114 Rumex obtusifolius L.
115 Sagina procumbens L.
116 Scutellaria galericulata L.
117 Senecio aquaticus Hill
118 Serratula tinctoria L.
119 Sium latifolium L.
120 Solanum dulcamara L.
121 Stellaria graminea L.
122 Stellaria palustris Retz.
123 Succisa pratensis Moench
124 Taraxacum sect. Ruderalia Kirschner, Oellgaard & Stepanek
125 Trifolium dubium Sibth.
126 Trifolium repens L.
127 Urtica dioica L.
128 Valeriana officinalis L.
129 Veronica catenata Pennell
130 Veronica chamaedrys L.
131 Vicia cracca L.
132 Vicia L.
133 Vicia sativa L.
134 Vicia tetrasperma (L.) Schreber
135 Viola palustris L.
136 Vulpia bromoides (L.) Gray
137 Cerastium fontanum ssp. holosteoides (Fries) Salman, Ommering & Voogd
138 Trifolium pratense L.
139 Festuca arundinacea Schreber
140 Potentilla palustris (L.) Scop.
141 Angelica sylvestris L.
142 Persicaria maculosa Gray
143 Cynodon dactylon (L.) Pers.
144 Ranunculus bulbosus L.
145 Rumex crispus L.

Table 4. Biological traits quantified for wetland plant populations. Measurements were usually based on 10 replicate ramets per sampling unit.

Trait code	Description	Notes
1. HEIGHT	Mean height of plant	Field
2. AREA	Area of plant canopy	Field
3. LEAVES	Number of leaves/ramet	Field
4. SEEDS	Number of seeds/ramet	Field
5. LEAFAREA	Total area of leaves/ramet	Lab
6. WTLEAF	Dry weight of leaves/ramet	Lab
7. WTSTEM	Dry weight of stem/ramet	Lab
8. WTREPRO	Dry weight of reproductive structures/ramet	Lab
9.WTSEED	Mean individual seed dry weight	Lab
10. NCONC	Leaf ammonium-N content	Lab
11. PCONC	Leaf P content	Lab
12. KCONC	Leaf K content	Lab

Notes: Field measurements were conducted on non-destructively sampled ramets in the field; Lab measurements were made on destructively-sampled whole plants returned to the laboratory for analysis (see Hills *et al.* 1993 in press, for more detail).

Table 5. Example of synoptic table for relevé vegetation samples taken from one riverine wetland site (R. Torridge: Kismeldon) in 1991.

Location	K	K	K	K	K	K	K	K	K	K	K	K	
N° relevé	35b	33	36	40	41b	41	42	35	39	27	31	37	
Surface relevé (m2)	60	80	80	80	60	60	30	30	100	50	120	30	
Hauteur végétation (cm)	40	50	30	60	60	60	60	50	60	40	40	60	
Recouvrement herbacé (%)	98	98	100	98	95	95	98	100	100	100	98	95	
Recouvrement muscinal (%)	<5	0	<5	10	10	50	10	0	<5	<5	<5	0	
Nombre d'espèces	25	31	24	30	29	28	27	30	37	28	37	30	29.6
Differentials of group A													
Carex pulicaris	2	2	2	2	2	2	2	2	2	+	1	1	V
Festuca tenuifolia	1	2	1	2	1	1	1	3	1	2	2	.	V
Festuca ovina	1	1	1	2	2	2	2	1	3	1	1	1	V
Pedicularis sylvatica	2	1	1	2	1	1	2	+	1	1	1	.	V
Danthonia decumbens	2	2	2	2	2	2	2	2	1	.	1	.	V
Erica tetralix	2	1	2	1	1	2	.	1	1	.	+	+	V
Calluna vulgaris	1	1	1	1	1	1	+	2	1	.	.	1	V
Genista anglica	2	+	2	+	2	.	.	+	+	.	.	1	IV
Nardus stricta	2	1	2	.	2	1	.	1	.	.	+	.	III
Salix repens	1	+	+	.	.	.	.	+	.	.	+	.	III
Polygala serpyllifolia	.	.	.	+	+	1	+	.	.	.	.	.	II
Narthecium ossifragum	1	+	2	.	.	.	.	.	.	.	.	.	II
Differentials of groups A + B													
Molinia caerulea	3	3	2	4	3	3	4	3	4	3	3	4	V
Agrostis canina	2	2	2	2	3	2	2	2	2	2	1	3	V
Carex panicea	3	3	3	2	3	2	2	2	2	3	2	1	V
Cirsium dissectum	3	3	2	2	3	1	+	+	2	1	3	2	V
Dactylhorhiza maculata	2	1	1	2	1	1	1	+	2	1	1	+	V
Potentilla erecta	2	1	1	1	2	2	1	2	2	2	1	1	V
Serratula tinctoria	1	+	+	1	2	2	2	.	+	1	2	+	V
Succisa pratensis	.	2	+	3	3	2	2	1	3	3	3	1	V
Carex demissa	1	2	2	+	1	.	+	.	.	.	+	.	III
Carex echinata	.	1	.	1	2	2	2	.	+	.	.	.	III
Carex nigra	.	.	.	+	.	+	+	.	1	.	.	.	II
Differentials of variant													
Angelica sylvestris	.	.	.	.	.	.	.	.	1	+	+	+	II
Valeriana officinalis	.	.	.	.	.	.	.	.	+	+	+	1	II
Deschampsia caespitosa	.	.	.	.	.	.	.	.	+	+	.	+	II
Filipendula ulmaria	.	.	.	.	.	.	.	.	+	.	+	+	II
Compagnion species													
Anthoxanthum odoratum	1	2	1	2	2	3	2	2	2	3	2	1	V
Juncus acutiflorus	1	2	1	2	3	3	2	.	2	3	2	1	V
Holcus lanatus	+	1	.	+	+	+	+	.	1	1	+	+	V
Poa trivialis	+	+	+	+	1	+	.	+	1	+	+	+	V
Luzula multiflora	.	1	+	1	1	1	.	1	2	2	1	1	V
Ranunculus acris	.	+	.	+	+	+	+	.	1	1	1	.	IV
Lotus uliginosus	.	.	.	2	1	1	1	.	1	1	1	.	III
Achillea ptarmica	.	.	.	+	.	+	+	.	1	1	+	.	III
Juncus conglomeratus	.	1	.	.	+	.	.	.	1	1	+	+	III
Cirsium palustre	.	.	.	.	+	+	+	.	+	+	+	1	III
Rumex acetosa	.	.	.	.	.	.	.	+	+	.	+	.	II
Salix aurita	.	+	.	.	.	.	.	.	+	.	+	.	II
Trifolium cf medium	.	.	.	.	.	.	.	1	+	.	.	+	II
Juncus effusus	.	.	.	+	.	.	.	.	.	.	+	.	I
Lotus corniculatus	.	+	.	.	.	.	.	1	.	.	.	.	I
Ranunculus flammula	.	.	.	.	.	.	.	.	.	+	+	.	I
Galium palustre	.	.	.	.	.	.	.	.	+	+	.	.	I
Equisetum fluviatile	.	.	.	.	.	.	+	.	.	+	.	.	I
Plantago lanceolata	.	.	.	.	.	.	.	1	.	.	+	.	I
								1			.	3	I

Table 6. Synoptic table summarising results of phytosociological analysis of vegetation data from two wetland sites on the R. Torridge (Kismeldon, Bradford Mill), showing division into five phytosociological units (A - E).

TORRIDGE UNITS	A	B	C	D	E
N relevés	12	17	10	9	6
Kismeldon	12	11	1	2	4
Bradford	0	6	9	7	2
N species (mean)	29.6	26.8	23.3	33.6	30.6
Differentials of unit A					
Carex pulicaris	V	r	.	.	.
Pedicularis sylvatica	V	r	.	.	.
Danthonia decumbens	V	I	.	.	.
Erica tetralix	V	.	.	.	.
Genista anglica	IV	.	.	.	.
...					
Differentials of units A + B					
Molinia caerulea	V	V	I	.	.
Agrostis canina	V	V	II	.	.
Potentilla erecta	V	IV	.	r	.
...					
Differentials of units B + C					
Lychnis flos cuculi	.	III	IV	.	.
Potentilla palustris	.	II	II	.	.
...					
Differentials of unit C					
Senecio aquaticus	.	II	V	.	r
Stellaria alsine	.	r	III	.	.
Glyceria fluitans	.	r	II	.	.
...					
Differentials of unit D					
Agrostis capillaris	.	.	.	V	I
Lolium perenne	.	.	.	V	.
Festuca rubra	r	I	.	V	.
Plantago lanceolata	I	.	.	V	.
Centaurea nigra	I	.	.	V	r
...					
Differentials of units D + E					
Dactylis glomerata	r	r	.	IV	III
Veronica chamaedrys	.	.	.	III	II
Differentials of unit E					
Galium aparine	.	.	.	r	V
Galeopsis tetrahit	.	.	.	.	V
Silene dioica	.	r	.	.	V
Urtica dioica	.	.	.	r	V
...					
Meso-eutrophic species					
Epilobium tetragonum	.	I	IV	II	III
Rumex conglomeratus	.	.	III	III	V
...					
Oligo-mesotrophic species					
Anthoxanthum odoratum	V	V	r	V	.
Juncus acutiflorus	V	V	IV	III	.
Luzula multiflora	V	V	r	II	.
...					
Compagnion species					
Holcus lanatus	V	V	IV	.	II
Poa trivialis	V	II	III	V	V
Deschampsia caespitosa	II	V	V	IV	II
...					

Captions to Figures

Fig. 1. Correspondence Analysis of distribution data, as presence/absence for 63 Syrphid species in 18 hydrogeomorphic units of wetland sites in France and Ireland.
A: eigen values of the factorial axes; B: F1 x F2 ordination of the units; C: F1 x F3 ordination of the units.

Fig. 2. Fuzzy Multiple Correspondence Analysis of the biological traits (63 Syphid species ; 25 categories belonging to 7 traits). A: eigen values of factorial axes; B: F1 x F2 ordination of the 63 species (see Table 1 for species identifications); C: F1 x F2 ordination of the 25 categories grouped according to the seven traits (see Table 2 for list of trait-categories); D: representation of the categories of two traits (flood tolerance and larval food type) overlaid on F1 x F2 ordination of the species.

Fig. 3. Simultaneous ordination of the Syrphid distribution data and biological traits. A: eigen values of the factorial axes; B: projection of the factorial axes of the distribution analysis on the F1 x F2 plane of the simultaneous ordination; C: projection of the factorial axes of the trait analysis on the F1 x F2 plane of the simultaneous ordination; D: F1 x F2 ordination of the 18 hydrogeomorphic units in the simultaneous ordination; E: F1 x F2 ordination of the 25 trait-categories grouped according to the seven traits (see Table 2).

Fig. 4. Classification of 50 vegetation relevés from R. Torridge wetland sites: Bradford Mill (EBM) numbered 1 - 25, and Kismeldon (EKS) numbered 26 - 50, using TWINSPAN analysis, to give five phytosociological units (A - E).

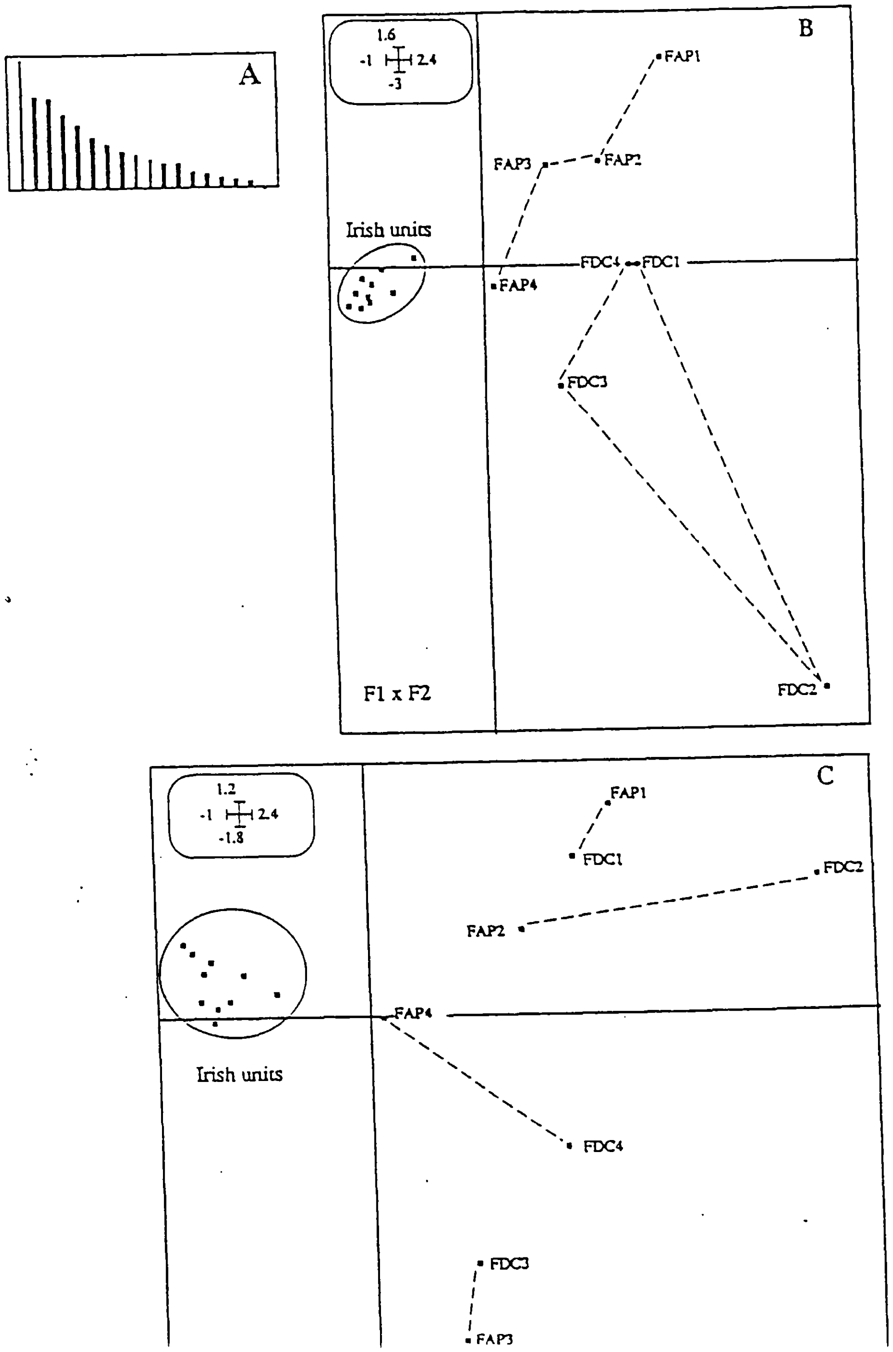
Fig. 5. Ordination of R. Torridge relevés (B: Bradford Mill; K: Kismeldon) on the F1 x F2 plane, showing grouping into three vegetation types, corresponding to phytosociological units A - E derived from TWINSPAN classification (see Fig. 4).

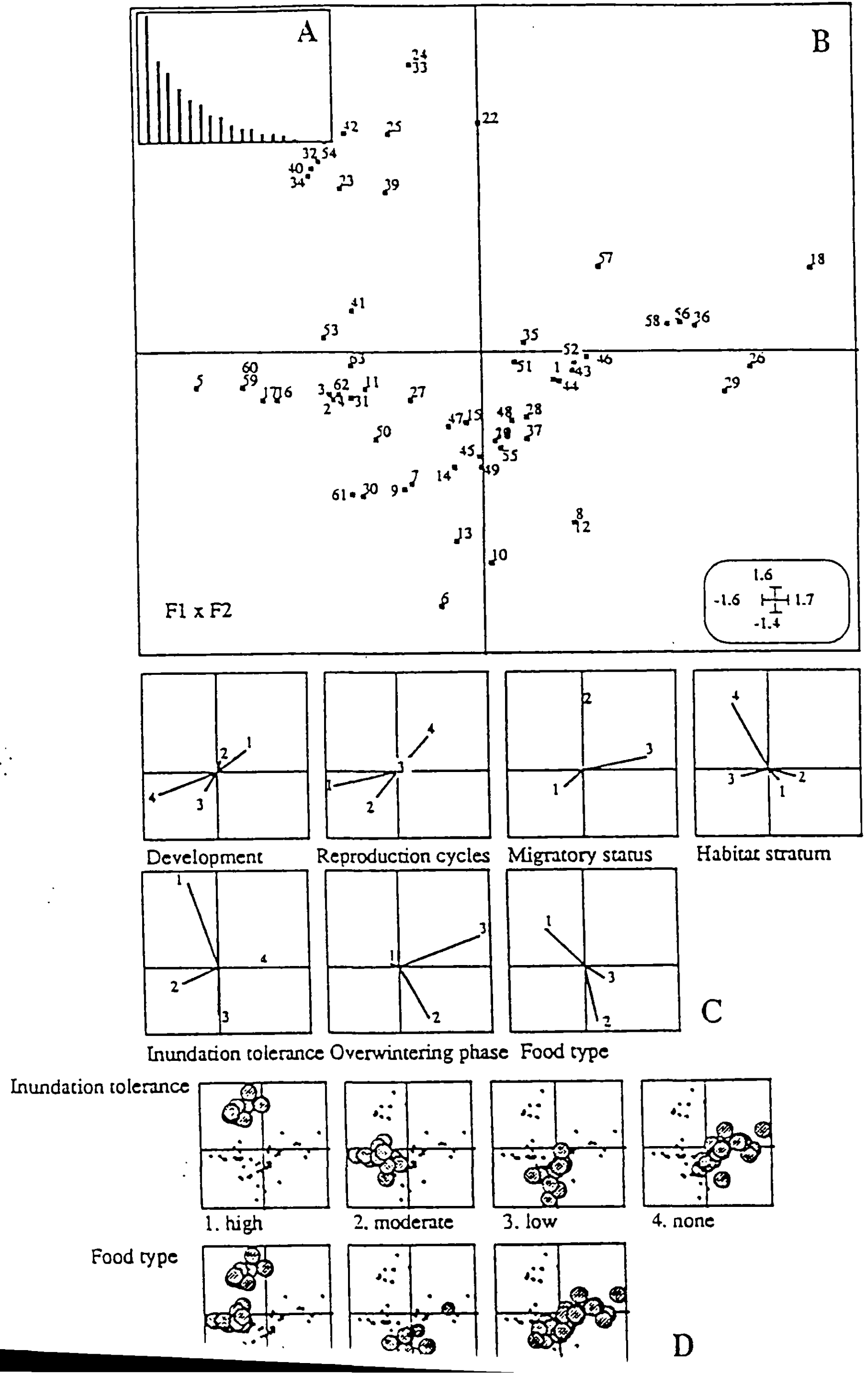
Fig. 6. Ordination of R. Torridge relevés (B: Bradford Mill; K: Kismeldon) on the F1 x F3 plane, showing separation of phytosociological units along the z axis of the ordination.

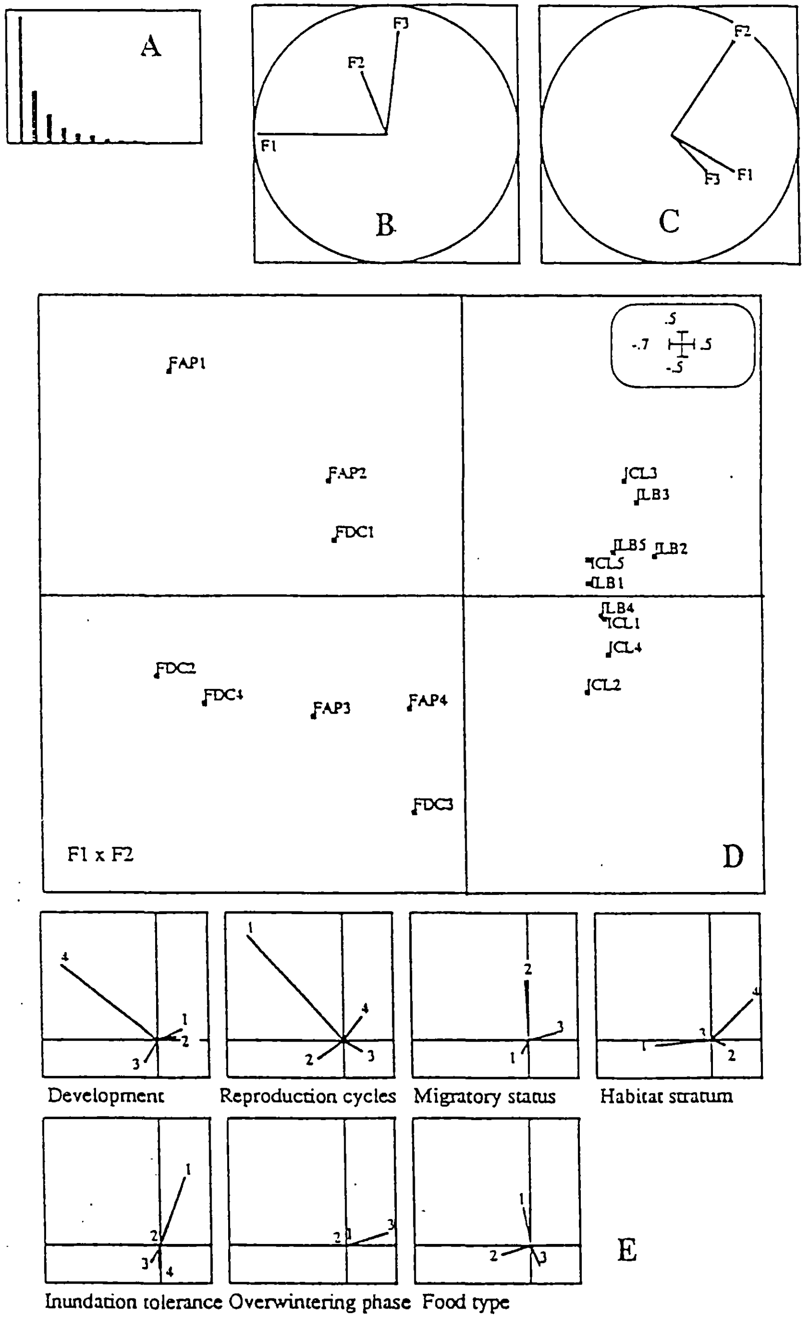
Fig. 7. Detrended Correspondence Analysis (DCA) ordination on F1 x F2 plane of 21 hydrogeomorphic units from English (EBM, EKS), Irish (ICL, ILB) and French (FAP, FDC) riverine wetland sites in terms of 145 plant species recorded (see Table 3). Axis units: standard deviations of species turnover; eigen values: F1 axis 0.91; F2 axis 0.65.

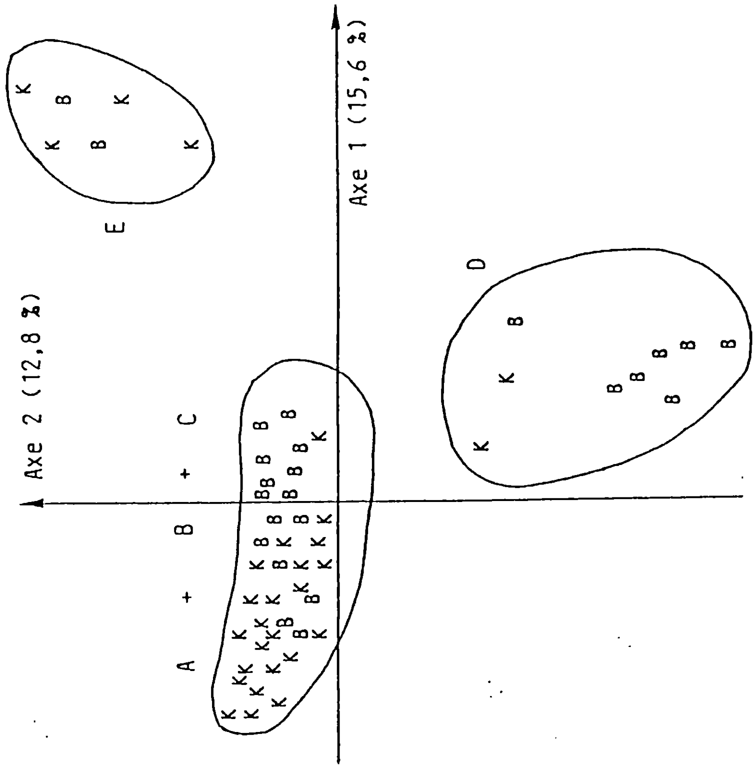
Fig. 8. Plot of first and second axes of a multiple discriminant analysis used to distinguish between 23 populations of plant species defined by Grime *et al.* (1988) as having competitive (C), stress-tolerant (S), or intermediate (CSD) strategy.

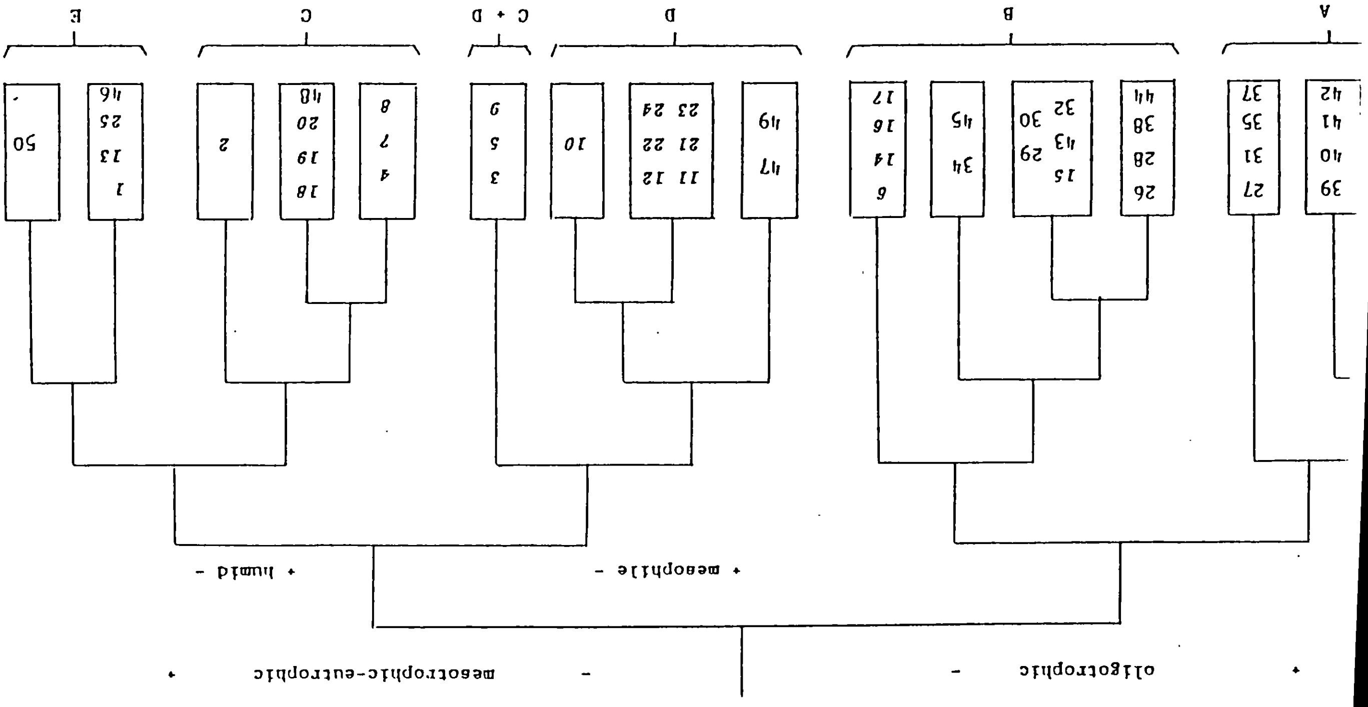
Fig. 9. Functional Vegetation Type (FVT) defined for 22 hydrogeomorphic units of in six European riverine wetlands (see Fig. 7) using relative competitiveness (CFVT) and stress-tolerance (SFVT) of constituent plant populations.

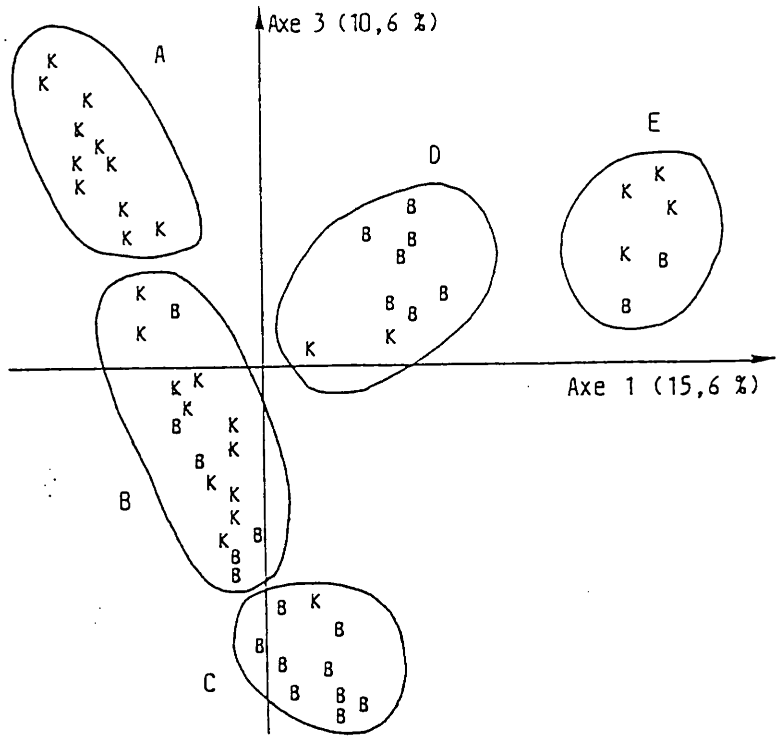


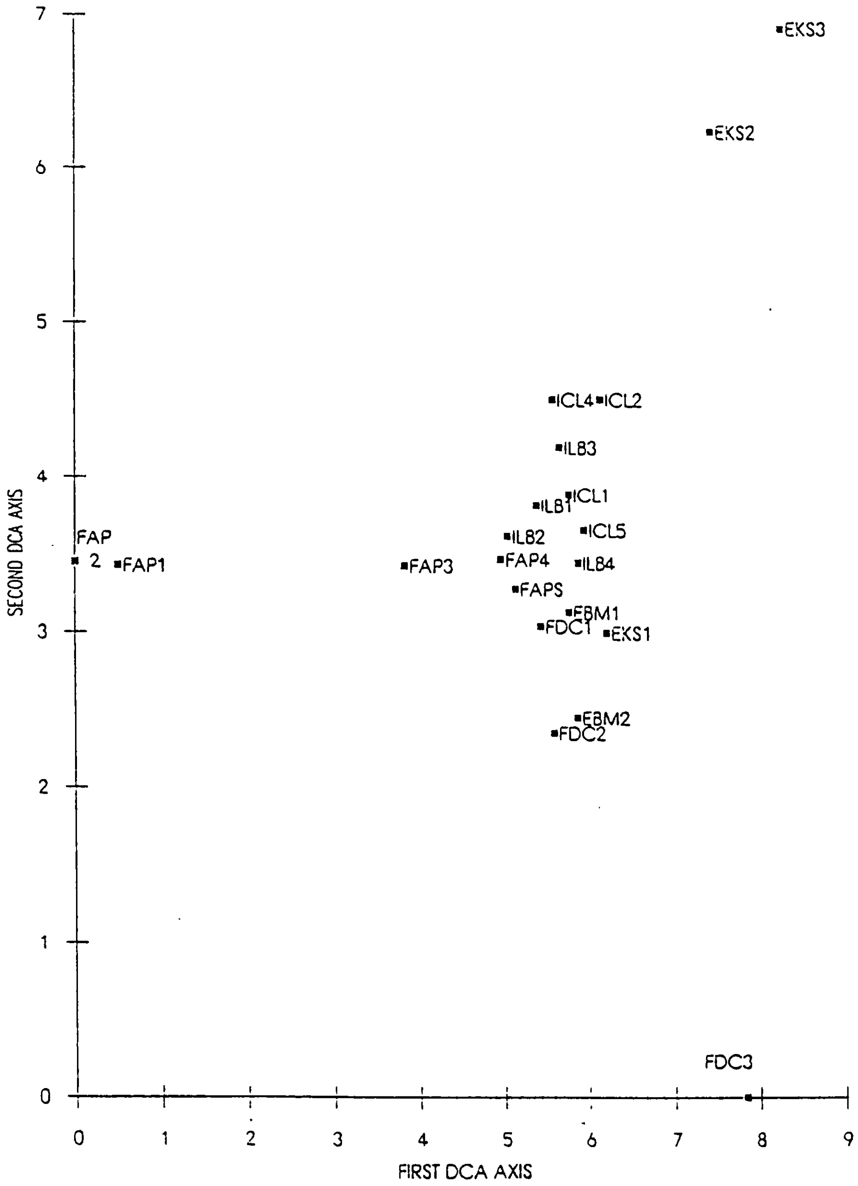

A
B
F1 x F2
1.6
-1.6
1.7
-1.4
Development
Reproduction cycles
Migratory status
Habitat stratum
Inundation tolerance
Overwintering phase
Food type
C
Inundation tolerance
1. high
2. moderate
3. low
4. none
Food type
D

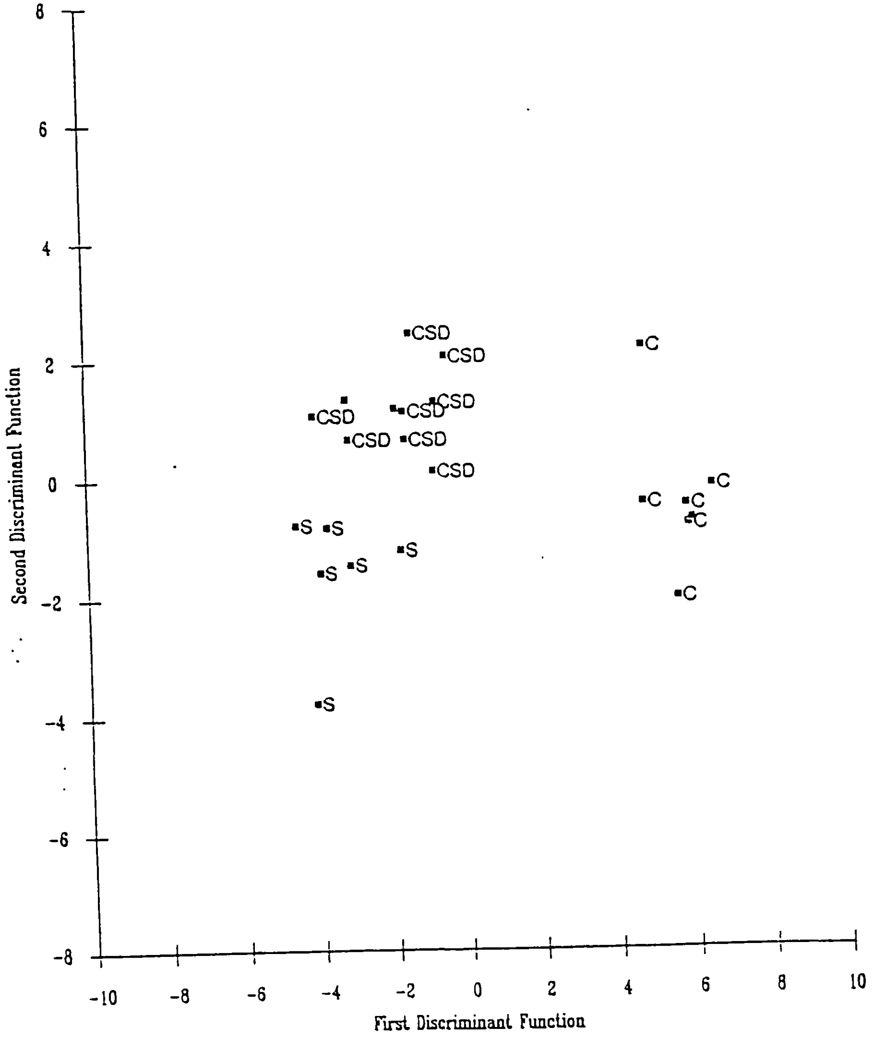

A
F1
F2
F3
B
C
FAP1
FAP2
FDC1
JCL3
JLB3
JLB5
JLB2
JCL5
JLB1
JLB4
JCL1
JCL4
JCL2
FDC2
FDC4
FAP3
FAP4
FDC3
.5
-.7
.5
-.5
F1 x F2
D
Development
Reproduction cycles
Migratory status
Habitat stratum
Inundation tolerance
Overwintering phase
Food type
E

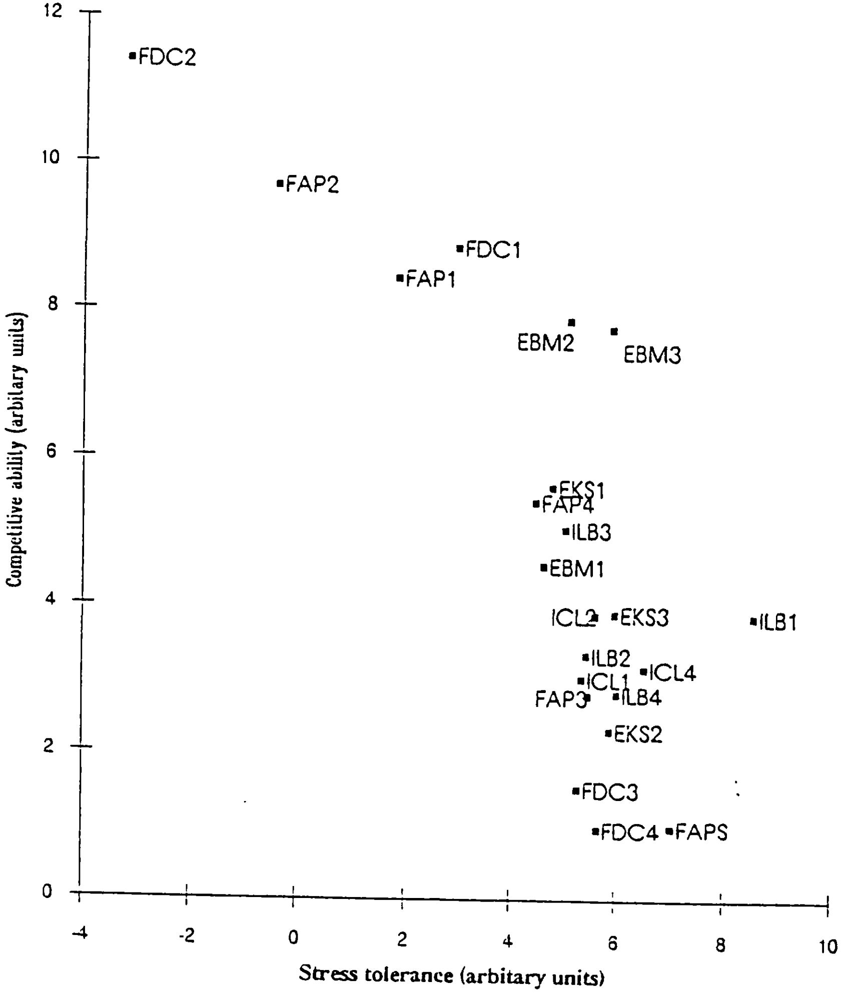

Axe 1 (15,6 %)
Axe 2 (12,8 %)
A + B + C
D
E
K
B


+ oligotrophic -
- mesotrophic-eutrophic +
+ mesophile -
+ humid -
A
B
D
C + D
C
E
39 40 41 42
27 31 35 37
26 28 38 44
15 29 43 30 32
34 45
9 14 16 17
47 49
11 12 21 22 23 24
10
3 5 6
4 7 8
18 19 20 48
2
1 13 25 46
50


Axe 3 (10,6 %)
Axe 1 (15,6 %)
A
B
C
D
E
K
B


SECOND DCA AXIS
FIRST DCA AXIS
0
1
2
3
4
5
6
7
8
9
EKS3
EKS2
ICL4
ICL2
ILB3
ICL1
ILB1
ICL5
ILB2
FAP
2
FAP1
FAP3
FAP4
ILB4
FAPS
FBM1
FDC1
EKS1
EBM2
FDC2
FDC3


Second Discriminant Function
8
6
4
2
0
-2
-4
-6
-8
-10
-8
-6
-4
-2
0
2
4
6
8
10
First Discriminant Function
CSD
CSD
CSD
CSD
CSD
CSD
CSD
CSD
CSD
C
C
C
C
C
C
S
S
S
S
S
S
S


Competitive ability (arbilary units)
12
10
8
6
4
2
0
-4
-2
0
2
4
6
8
10
Stress tolerance (arbitary units)
FDC2
FAP2
FDC1
FAP1
EBM2
EBM3
EKS1
FAP4
ILB3
EBM1
ICL2
EKS3
ILB1
ILB2
ICL4
ICL1
FAP3
ILB4
EKS2
FDC3
FDC4
FAPS

Appendix 3.1 Method used for determination of nitrogen, phosphorus and potassium in the leaves of plants.

Plant leaf tissue was analysed to determine the concentration of nitrogen, phosphorous and potassium. The Kjeldahl method for digestion of dried plant material was selected as this permits quantitative measurement of nitrogen (N), phosphorus (P) and potassium (K) from the same digest. One of the problems of traditional Kjeldahl digests is the limited recovery of N in the form of nitrate-N and nitrite-N. The amount of nitrate-N reduced to ammonia is variable (Pruden, Kalembsa & Jenkinson 1985). Nelson & Summers (1973) found that between 21 and 55% of nitrate-N was oxidised from plant material. Wilkoff & Moraghan (1985) found a partial recovery or nitrate-N in soil of 56.3%. A salicylic acid pre-digestion was used to ensured complete oxidation of nitrate-N and nitrite-N.

Dry leaves from each species of plant studied for survival traits were ground until they had the consistency of a coarse powder. A sub-sample of the ground leaf, was accurately weighed (+/- 0.0001g) and placed at the bottom of a Kjeldahl boiling tube.

A 5ml aliquot of concentrated hydrochloric acid and salicylic acid (25g of salicylic acid in $1dm^3$ of c.H_2SO4) was added to the plant material in the Kjeldahl boiling tube and left to stand for one hour. 0.5g of sodium thiosulphate pentahydrate was added to the mixture, it was gently heated, shaken and left to cool. 1.0g of a ground mixture of sodium sulphate and copper(II) sulphate (10:1 by weight) was added. The digests were placed in a block digestor for one hour and twenty minutes at 375^{o}C, cooled, made up to 100ml with deionised water and filtered.

Determination of the concentration of ammonium-N (NCONC- trait 10)and P (PCONC-trait 11) in the digests was carried out using a Tecnicon Autoanalyser 2 System. Analysis of K (KCONC-trait 12) was carried out using a flame photometer. The flame photometer was calibrated up to 100 ppm K.