THE FUNCTIONAL ECOLOGY OF EUHYDROPHYTE COMMUNITIES OF EUROPEAN RIVERINE WETLAND ECOSYSTEMS

A thesis submitted to the University of Glasgow for the degree of Doctor of Philosophy.

by
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DECLARATION

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

Terminology

Nomenclature follows Stace (1991) except non British species which follow Tutin *et al.* (1964-1980)

Abstract

To investigate the functional ecology of euhydrophyte communities in European riverine wetlands six study catchments were chosen. Of these, four were the target sites of a European Community research project investigating the 'Functional Analysis of European Wetland Ecosystems' to which this project was allied. These sites cover a range of climatic conditions from eu-oceanic to semi-arid. Within the six catchments, 37 sampling sites were located in total. Sampling sites exhibited a range of flow velocities, trophic states, water depths and water qualities.

During 1992 and 1993 a field survey involving repeated visits to all the sites was conducted. At each site, euhydrophyte plant communities were recorded, other plant species present below the water line were recorded, a suite of environmental variables was assessed, and morphological traits measured on selected species. Sites were visited between two and eight times over the two year period. A total of 54 euhydrophyte species were recorded.

TWINSPAN was used to classify sites by their constituent species, and was found to strongly reflect geographical location. Canonical Correspondence Analysis showed that no single environmental factor was controlling community composition, although the most influential of those measured were flow, conductivity, water phosphate levels, sediment texture, depth, sediment organic matter, level of light received at the substrate and pH. Species were ranked along selected gradients.

An extensive review of research published on euhydrophytes was used to compile a table of euhydrophyte traits and assign to them a fuzzy coded value. These included morphological, life history, physiological and regenerative traits. Traits concerned with the established phase of the life cycle were used to classify euhydrophytes into six groups, termed functional groups, using non-hierarchical clustering methods. The homogeneity of these groups was investigated using a Principal Components Analysis. A linear discriminant analysis provided equations, using a subset of the original traits, to predict functional group membership for new species. Morphological traits measured in the field survey were tested for their value as indicators of functional group, but were found to be poor descriptors.

Glasshouse experiments on established phase plants were used to investigate the response of selected species to the pressures of competition, stress and disturbance. Species responses were measured in terms of total biomass, plant length and biomass allocation. The results could be used to improve the knowledge of species strategy *sensu* Grime (1979).

Regenerative phase traits, taken from the published literature, were also used to classify euhydrophyte species using a non-hierarchical clustering method. Examination of these groups showed them to be quite heterogeneous in composition. Comparison with groupings achieved using established phase traits only and using established and regenerative phase traits in combination, showed a grouping from established phase traits to be most homogenous. This was attributed to the poor data available on regenerative phase traits. Few strong correlations existed between established and juvenile phase traits.

Two aspects of regenerative biology were investigated experimentally. The rooting rate of fragments did not show any correlation with flow velocity, stress index or disturbance index. The seed banks from a range of sites were quantified using seedling emergence techniques. Flooding depth had a severe effect on the numbers of seedlings emerging and on species richness. A permanent seed bank was demonstrated for a number of euhydrophytes. The contribution of the seed bank to population maintenance in euhydrophytes was found to be small, but potentially critical, particularly in seasonal water bodies or following natural catastrophe, or artificial disturbance. The seed bank of permanently submerged sites was higher than suggested from previous studies and may have potential for wetland restoration.

The contribution of each functional group was used to classify sites into Functional Vegetation Types (FVTs). Predictive equations were constructed, using linear discriminant analysis, to allow new sites to be assigned to an FVT on the basis of their functional group composition. These were found to be unrelated to geographical location. The FVTs showed recognisable associations to particular habitat conditions. In many sites a variety of the functional groups were present, possibly indicating within-site heterogeneity of environmental conditions.

A field survey was carried out in the Czech and Slovak Republics in 1994. Fifteen sites were visited and data on community composition, euhydrophyte morphological traits and environmental variables was collected. This was

comparable to the 1992/93 survey and was used as a test data set. Morphological traits measured in the field were again found to be inadequate indicators of functional group. The relationship of functional groups to environmental gradients described from the original survey was largely supported. The necessity for collection of comparable data on euhydrophyte traits, particularly regenerative traits is emphasised.

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Throughout this work I was lucky enough to travel to numerous beautiful and interesting places both for fieldwork and meetings, and I am grateful to many individuals and agencies for the support that made this possible. The project was funded by the Natural and Environmental Research Council in the United Kingdom. During the study I was based at the Department of Botany, University of Glasgow and I would like to thank Professor R. Cogdell and Dr C. Wheeler for use of the facilities. Scottish Natural Heritage, Royal Society for the Protection of Birds, Fundacion Jose Maria Blanc and Societé Ornithologique du Bec d'Allier allowed access to land and provided advice and accommodation.

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Chapter 1

INTRODUCTION

Chapter 1

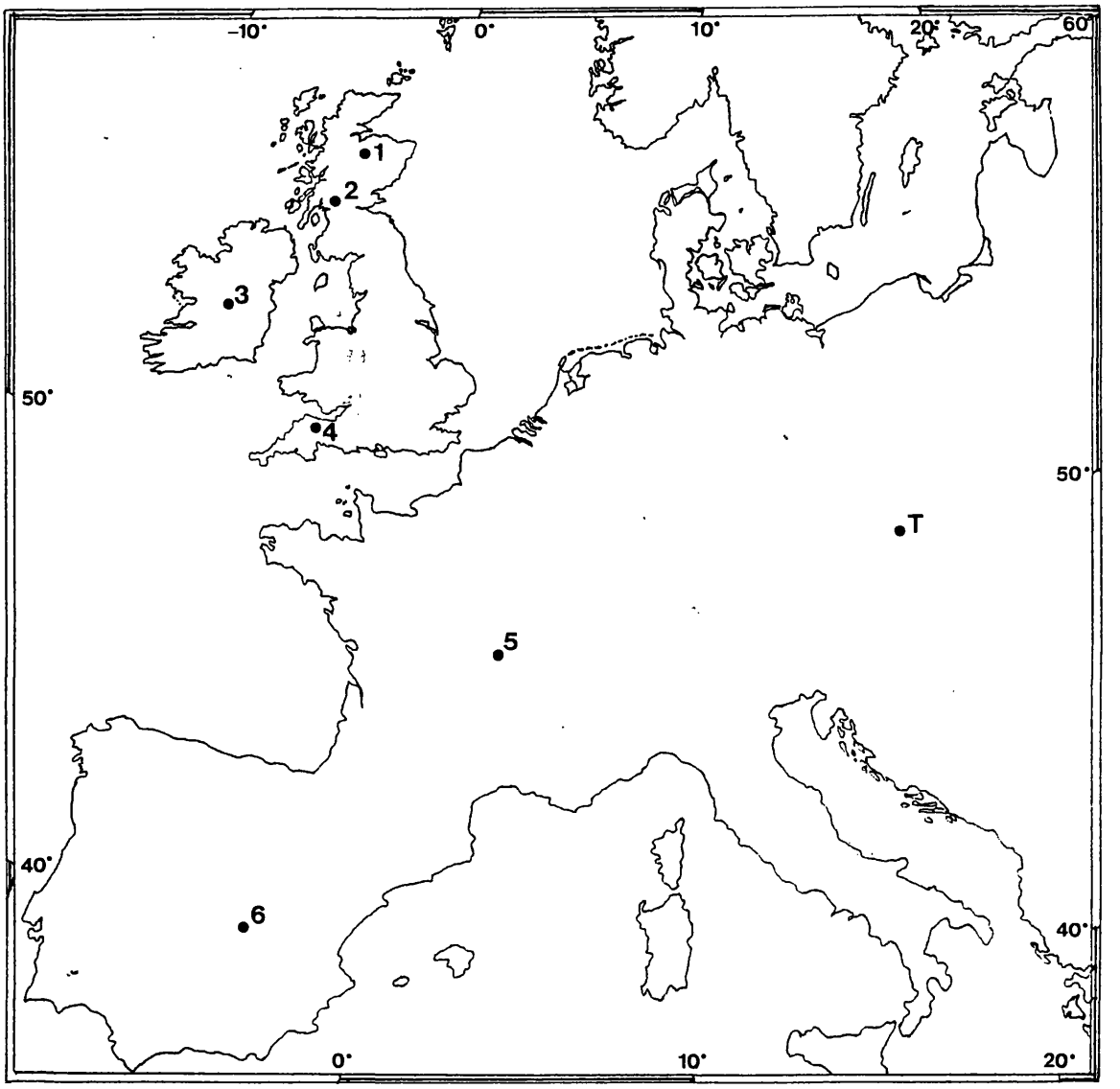
INTRODUCTION

1.1 Introduction

This project was run in association with a cross-disciplinary EC funded project investigating the functioning of European riverine wetlands, led by Dr E. Maltby at the University of Exeter. The present study concerns itself with the open water habitats (both temporary and permanent) associated with the wetlands, and as such was outside the direct scope of the EC project.

The original sites investigated covered a range of climatic and environmental conditions. Two sites were located in Ireland on the Rivers Shannon and Little Brosna. In Scotland the Endrick marshes at the south end of Loch Lomond, and the Insh marshes on the River Spey were studied. The English sites were associated with the River Torridge, in North Devon. In France wetlands on the River Loire and its tributary the Allier were visited, and in central Spain an area of wetland on the Giguela river. The sites in Ireland, England, France and Spain were part of the EC project. An additional and independent data set was collected in the Czech and Slovak Republics in May/June 1994, with the collaboration of the Institute of Hydrobotany, Czech Academy of Science, Trebon, Czech Republic. Figure 1.1 shows the location of the study areas in a European context.

Figure 1.1 Riverine wetland study sites and test sites



Key

1	Insh marshes, Strathspey
2	Endrick marshes, Loch Lomond
3	Clonmacnoise and Little Brosna callows, R. Shannon
4	R. Torridge headwaters
5	R. Loire and R. Allier floodplains
6	El Masegar, R. Giguela
T	Test sites in Czech and Slovak Republics

1.2 Aims

This study set out to examine aspects of the functional ecology of euhydrophyte plant communities in European riverine wetlands by assessing the applicability, to aquatic taxa, of an approach that has been widely and successfully used for terrestrial groups. Functional ecology can be divided into three basic components: 1) construction of trait matrices through screening; 2) exploration of empirical relationships among these traits; and 3) determination of the relationship between traits and environment. (Keddy 1992a). The research presented in this thesis covers these three components. In studies of community ecology there is frequently a lack of emphasis on clearly defined questions (Keddy 1987) so in this study I have attempted, from the outset, to clearly outline the questions and design a research programme aimed at resolving them. The basic questions to be addressed are as follows:

1. Can euhydrophyte plants be grouped into ecologically meaningful assemblages (functional groups) using functional and morphological traits?

2. How do the functional groups defined for euhydrophytes relate to the environment they are inhabiting and is this predictable?

3. Are the relative proportions of strategies displayed at a site (or functional vegetation types) as useful as full species composition for purposes of assessment and prediction?

1.3 Research outline

Four main areas of investigation were covered in this study:

1. A survey of plant communities in the wetland sites and the environmental characteristics of these sites.
2. A study of the established phase strategies of euhydrophyte plants using field measurements, greenhouse experiments and information from the published literature.
3. A study of juvenile phase traits using greenhouse experiments and information from the published literature. A study of regeneration from the seedbank addresses both the types of seed/propagule bank possessed by euhydrophytes, and the role of the seedbank in aquatic habitats.

4. Testing, at an independent site, the accuracy of predictions of aquatic plant strategies.

1. 4 Euhydrophyte ecology and classification

Water plants were defined by den Hartog and Segal (1964) as '*plants which are able to achieve their generative cycle when all vegetative parts are submerged or are supported by the water, or which occur normally submerged but are induced to reproduce sexually when their vegetative parts are dying due to emersion.*' This was the basis of the definition of the term 'euhydrophyte' proposed by Denny (1985) to include all plants that are either completely submerged (except for their inflorescences), whether rooted or free-floating; or have floating leaves which are anchored to the substrate. For the purposes of this study all free floating species are included as euhydrophytes. The use of the defined term euhydrophyte will avoid the ambiguity sometimes arising from the term macrophyte.

Early work on aquatic macrophyte ecology was undertaken by Arber (1920) and Butcher (1933). A thorough general ecology text was produced by Sculthorpe (1967), which is still a standard text. Guides to identification are provided by Haslam, Sinker and Wolsey (1975) and Cook *et al.* (1974). Other relevant works deal with general aquatic ecology (Hynes 1960; Reimer 1984; Symoens 1988; Moss 1988; Ellenberg 1988; Jeffries and Mills 1990), river ecology (Hynes 1970; Holmes and Whitton 1977; Whitton 1979; Haslam 1987), plants of standing waters (Palmer, Bell and Butterfield 1992) and management of aquatic weeds (Mitchell 1974, Pieterse and Murphy 1990). Relevant information is also available from work on euhydrophyte taxa in lake ecosystems (Hutchinson 1975, Spence 1967, 1982, Pearsall 1920). Spence (1964) and Palmer *et al.* (1993) deal particularly with aquatic macrophytes in Scotland.

As this work aims to derive a classification of aquatic plants based on functional attributes it is necessary to be fully aware of other criteria that have been used to group euhydrophytes. As noted by Sculthorpe (1967) '*it should be appreciated that the bewildering diversity of habit and plasticity of organisation sorely frustrate any attempt to construct a precise biological classification of this heterogeneous group.*' As a result, a number of classifications of aquatic macrophytes have been employed in the past. Those occurring most commonly in the literature are dealt with here. They are divided into three approaches by Hynes (1970); spatial,

Luther (1949) divides macrophytes into *rhizophytes* (rooted to the substrate), *haptophytes* (attached to, but not penetrating, a solid surface) and *planophytes* (free floating). *Planophytes* are sub divided into small *planktophytes* and large *pleustophytes*. But exchange can occur between these classes, for instance *Ceratophyllum* and *Utricularia* species (pleustophytes) can anchor themselves in silt and *Elodea* and *Myriophyllum* species (rhizophytes) behave as pleustophytes when fragmented (Sculthorpe 1967). Du Reitz (1931) used a system of growth form classification named by a representative genus, such as the isoetid form or the lemnid form. Barkman (1988) proposed a classification based mainly on morphological features which aimed to be a compromise between a practical and a logical system. Best (1988), Sculthorpe (1967) and Hutchinson (1975) provide reviews of classification and Hutchinson went on to devise his own ecological classification based on earlier schemes.

These various classifications are used in many works on euhydrophyte ecology but are not always a relevant way of grouping the populations under study. Taxonomic classifications are largely reliant on ecologically trivial characters (Grime and Hodgson 1987) while a functional classification aims to be more closely related to the ecology of the population regardless of its specific affinity. A functional classification can also be much more generally applicable than taxonomic studies, that are limited by the geographical ranges of species (Keddy 1992a). The theory behind this more recent approach will be dealt with in some detail in Chapter 4. Attribute-based approaches have only rarely been applied to aquatic river macrophyte vegetation (Wiegleb 1988). Hence this work is of an exploratory nature dealing with the viability of a functional classification of euhydrophyte species and the first stages of forming one.

Many studies in plant ecology are concerned with finding correlations between environment and community (whether it is described in functional or phytosociological terms); these studies, by their nature can only generate hypotheses. This approach cannot contribute to ecological theory unless current vegetation theories are considered in study design and experimental tests are also included (Austin 1987). The theories being explored are detailed in Chapter 4 while Chapter 9 tests the hypotheses laid out in the preceding chapters on an independent field data set. Chapter 5 presents an experimental approach that can be used to quantify the relationships postulated. While the hypotheses have been tested as far as possible, it is emphasised that more rigorous testing of individual parameters is necessary to verify the relations suggested.

Chapter 2

SITE DESCRIPTIONS

Chapter 2

SITE DESCRIPTIONS

2.1 Mid-Shannon, Ireland

Sites were situated in central Ireland, on the river Shannon and one of its tributaries, the Little Brosna. The climate is oceanic although drier than the rest of Ireland, with a mean annual rainfall under 850 mm (although increasing to over 1400mm in the Slieve Bloom mountains in the east of the catchment). The underlying rock is generally Carboniferous Limestone with some volcanic intrusions. Deep ground water flow occurs through the limestone, which influences water chemistry (Hoyer 1991). The flood plain is bounded in many places by esker ridges formed during the last Ice Age, which are in evidence at both the study sites. The extraction of gravel from pits in the eskers along the Little Brosna may have changed the composition of the groundwater in recent years, making it less calcareous. Following the Ice Age much of the present flood plain was covered with gravel and boulder clay and filled with melt waters forming a large lake. Lake clays were deposited first and as the water levels fell, calcareous lake marl was laid down. As the lake turned to swamp, peat development started and until early this century much of the lowland area consisted of raised bog. With the onset of mechanical cutting of the peat in the middle of this century the raised bogs were quickly fragmented and today only a small percentage remain. The area is sparsely populated and agriculture is extensive. Water management has been by individual farmer by means of ditches, which criss-cross the flood plain. In comparison to most European rivers the Shannon is relatively clean, with little industrial pollution (Heery 1993). The main pressures on water quality are sewage waste, which at present is low but may increase as the level of water-related tourism rises, and an increased load of organic sediment due to the peat cutting industry. At a lesser level, agricultural wastes spread on the land are quickly transported to the watercourse before they can become bound into the soil. Fertilizer use is currently relatively small, but increasing use, together with herbicides may contribute to future degradation of water quality. The chemistry of the Shannon is measured by the Environmental Research Unit of An Foras Forbatha (Dublin). They record gradients from Athlone to Portumna of conductivity (350-450 μScm^{-1}), total hardness (170-210 mgl^{-1} $CaCO_3$), NO_2 and NO_3 (0.4-0.8 mg l^{-1} N) and a pH varying around 8 (ERU 1990).

The two main study sites were located at Clonmacnoise (Plate 1) on the River Shannon (53°20'N, 7°58'W), and close to Newtown on the Little Brosna (53°8'N, 7°55'W) and both lie at an altitude of less than 40m. The sites are river 'callows' (from the Irish word 'caladh' meaning a river meadow, or alternatively a landing place (Heery 1993)). These are wetland areas that are drained to some extent and used for hay and pasture. Many Irish callows were lost to agricultural improvement between 1950 and 1970. The Shannon and Little Brosna callows remain, probably more due to the difficulties in taming them than anything else (Heery 1993). The callows flood regularly each autumn (Plate 2), and these floods can continue well into the following growing season. Water levels in winter can be two metres above the summer level. Flash floods in the summer months, with up to a metre change in level, are also a relatively common occurrence. Due to the flatness of the callows, during the flooding season (3 - 6 months), the width of the river expands by three quarters of a kilometre on average (Hoyer 1991). As a result of extensive peat cutting in the Shannon catchment during recent decades, the callows are now receiving a higher sediment load than previously. This could have a number of effects such as changing the nutrient levels, affecting the underwater light climate and silting up drains.

In terms of plant life the aquatic habitats of the callows have been given very little attention (Heery 1993). The sample sites selected for the present study are mainly on ditches in the callows (Plates 3 and 4). The character of these ditches varies with respect to flow, depth and width. In some the white lake marl is exposed at the surface, while in others it is overlain by dark peat deposits. A lot of emergent vegetation is also present in these ditches. As the water levels can fluctuate quite dramatically both within and between seasons, these ditches appear to support quite dynamic communities. Sample sites were also located in stretches of both rivers. An additional site was located at Bullock Island, which is a backwater of the Shannon close to Banagher.

Visits were made to the sites in April and June 1992 and May and July 1993.

Figure 2.1 a) Location of the study sites on rivers Shannon and Little Brosna.

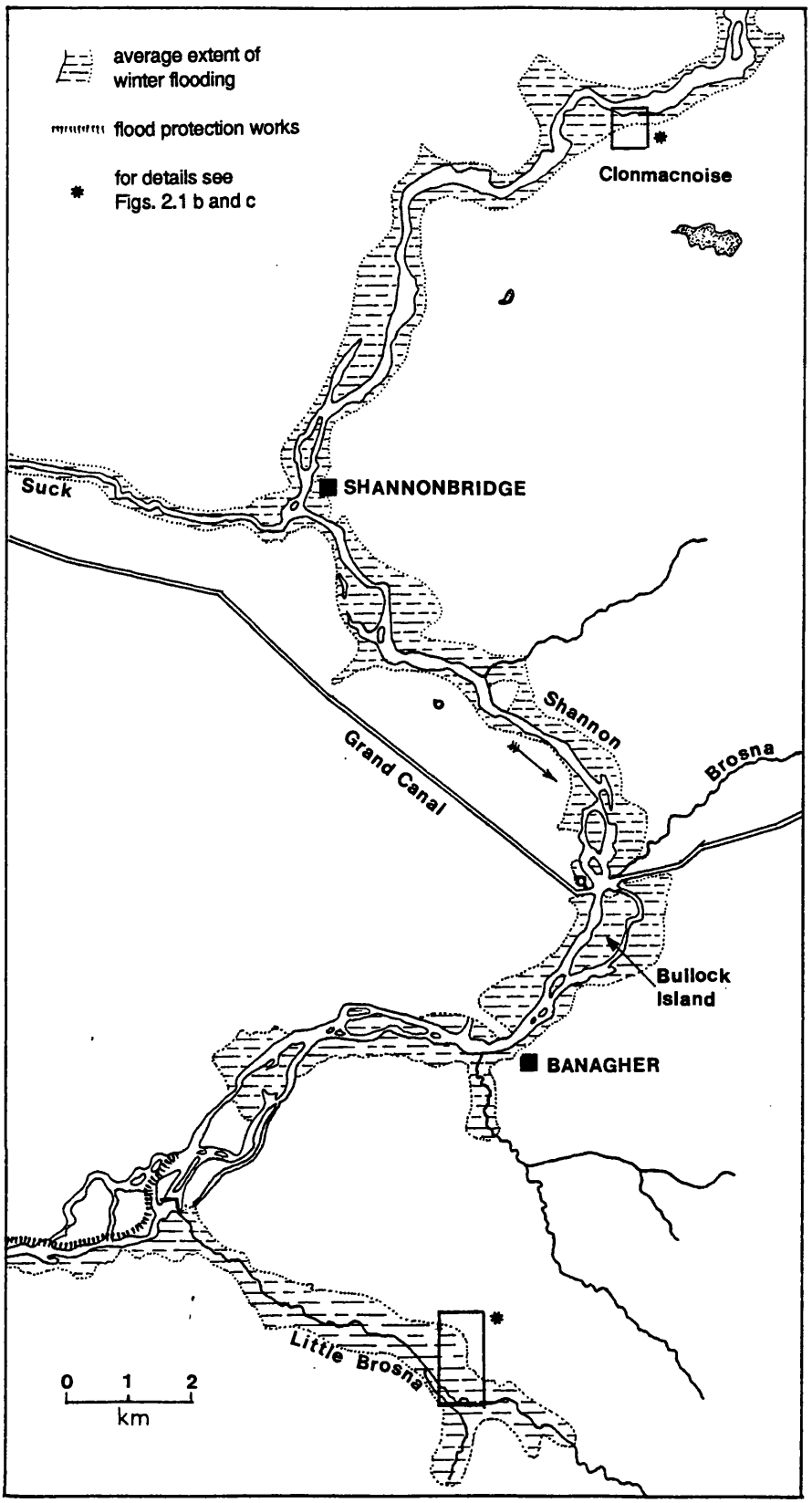


Figure 2.1 Shannon (b) and Little Brosna (c) callows showing location of sampling sites. For sampling site codes see Table 2.1

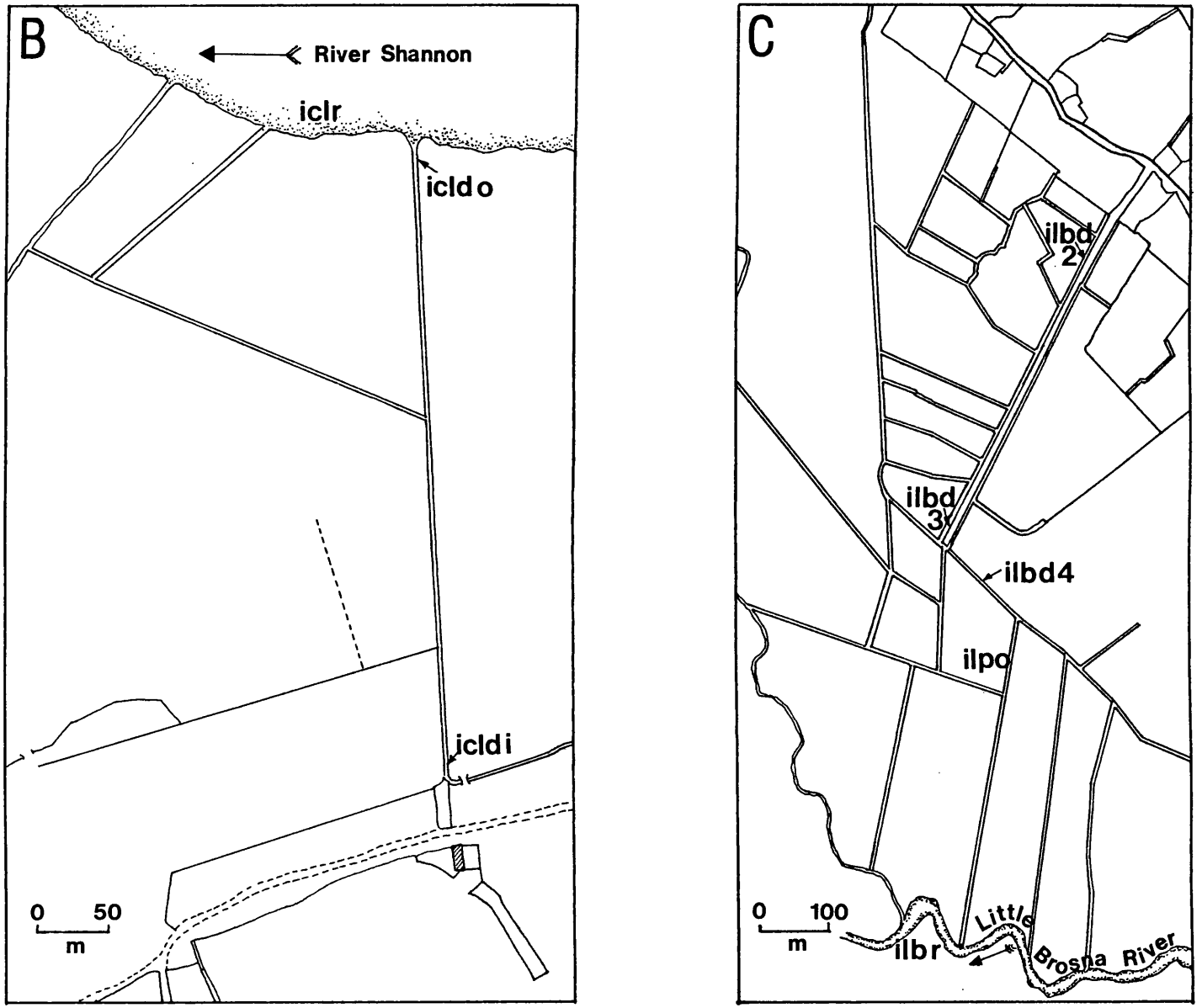


Plate 1: River callows at Clonmacnoise, Ireland. River Shannon in the background and drainage ditches running across the picture in the foreground. April 1992.

Plate 2: Little Brosna river **(ilbr)** in the foreground showing extensive flooding of callows on the opposite side of the river. September 1994. Photo N. Willby.

Plate 3: Top end of drainage ditch, Little Brosna callows **(ilbd2)**. Species include *Potamogeton coloratus, Baldellia ranunculoides, Chara hispida.*
Photo: N. Willby, July 1994.

Plate 4: Bottom of drainage ditch, Little Brosna callows **(ilbd3)**. Species include *Hippuris vulgaris, Myriophyllum verticillatum, Lemna minor, Hydrocharis morsus-ranae.*
Photo: N. Willby, July 1994.

Plate 5: River Torridge at Bradford Mill **(ebmr)** with *Ranunculus penicillatus* in the foreground. June 1992

2.2 Torridge Headwaters, England

The sites were located on the upper reaches of the River Torridge, Devon. The climate is wet and mild with a mean annual rainfall of 1113 mm, of which 43.6% falls between October and January (inclusive). The bioclimatic classification of the Upper Torridge is euoceanic, slightly cool, exposed and moderately moist. The underlying rocks are Upper Carboniferous Culm measures (sandstones and shales) overlain by head deposit. Much of the water movement is surface water flow intercepted by land drains and field ditches, or shallow ground water movement. Both pathways allow agricultural pollutants to move relatively quickly into the watercourse. The floodplain is susceptible to winter and spring flooding. The Upper Torridge catchment is in an area dominated by intensive dairy farming and water quality has declined markedly since the 1960's, possibly due to agricultural intensification (FAEWE 1990a). Chemical data for 1992 and 1993 were made available by the National Rivers Authority (South West region), and show nitrates present at up to 3.2 mg l^{-1} close to Bradford Mill. Ortho-phosphate did not exceed 0.14 mg $^{-1}$ and was generally lower than 0.05 mg l^{-1}. All the stretches of river surveyed are classed as NWC class 1B by the NRA.

Three study areas were used within the catchment, all at an altitude of around 55m. The Kismeldon site (50°55'N,4°20'W), on the south bank of the River Torridge, is a traditionally managed wet area with field ditches. Some parts are designated SSSI's for their botanical value. The second site (Plate 5), at Bradford Mill (50°55'N,4°15'W), is just downstream of the confluence of the Waldon (a major tributary) and the Torridge. It is a wet meadow area, prone to seasonal flooding in winter and spring. The last site is an oxbow at Hele Bridge (50°53'N,4°15'W), created in the early nineteenth century when the river was straightened to allow bridge construction (FAEWE 1990a). The adjacent land is arable, supporting mainly winter cereals. The variety of open water types associated with the Torridge wetland areas under study is less varied than in the other catchments. The flora is also less diverse. Sampling sites were established on four stretches along the Torridge, in a temporary oxbow in Kismeldon meadows and the larger oxbow at Hele bridge.

Visits were made to the sites in March, June and July 1992 and July 1993.

2.3 Insh Marshes, Scotland

The site (Plate 6) lies in the Badenoch district of Highland region, between Kincraig and Kingussie (57°0'N, 4°0'W), at an altitude of about 230 m (Ratcliffe 1977). Within the marshes there exists about 67 ha of open water and 16 ha of watercourse, of which 12 km is river and 9.25 km ditch (Wood and Evans 1989). The climate is cool with a mean annual rainfall of 1300 mm.

Attempts were made in the 19th century to drain the marshes and indeed by 1835 much of the area was well drained and could support rich cropping (Gibbons 1993). However the flood defence and engineering works gradually fell into disrepair (although much is still visible) and the area gradually assumed its former marshy character. The larger drainage ditches remain and are dredged on a 10 - 20 year cycle, but were not cleared during the period of study (or in the preceeding 3 years). The marshes are of relatively base-rich, rather than acid, peat and the lochans support a more diverse plant life than lochans on moorland peat (Charter 1988). The mosaic of open water bodies and wet fen and marsh communities comprise the largest single unit of poor-fen flood plain mire in Britain (Fojt 1988). There is a diverse range of freshwater plant species and communities present, with at least six major communities of freshwater plants (Murphy and Hudson 1991). A number of species rare or uncommon on a national basis, in particular *Pilulifera globulifera* L., *Nuphar pumila* (Timm) DC., *Potamogeton filiformis* Pers., and *Subularia aquatica* L. are mentioned in reserve records. This places the marshes in the nationally important category on freshwater botanical grounds. The site is recognised to be of international importance as a major European example of a little damaged riverine wetland with an unbroken gradient of plant communities on the sere from open water to fen and carr (Murphy and Hudson 1991; Commission of the European Community 1991). In a Scottish context (and even within the Spey valley), the Insh marshes constitute a unique assemblage of waterbodies (Charter 1988). The Spey itself is fast to moderate flowing, experiencing heavy spates in winter, with a stone and gravel bed, but the flow slows as the river approaches Loch Insh. It is mesotrophic in nature with *Myriophyllum alterniflorum* the dominant species (Ratcliffe 1977).

Most of the site lies within the RSPB reserve (Fig 2.2) and was designated an SSSI in 1963. A number of previous studies have been carried out on the marshes (Ratcliffe 1981; Page and Reiley 1985; Charter 1988; Fojt 1989; Wood and Evans 1989); the most recent, by Murphy and Hudson (1991), concentrates on the

aquatic plants present and brings together data from the previous surveys. Chemical information was made available by the North East River Purification Board. Relevant sampling points are located on the Spey at Kingussie, Insh drain at Insh and Farletter and on the River Tromie (which feeds the Spey above the marshes). The NERPB 1990 Annual Report assigns mean chemical indices of 91 and 84 to the drain at Insh and Farletter respectively (on a scale of 1 - 100 with 100 as clean). The Tromie and the Spey both scored 97. The Insh drain receives effluent from Insh sewage treatment works, with a resultant decline in water quality. In 1993 the mean water Quality Index of the drain was 92 upstream of the Insh surface water treatment works and 87 downstream. Overall, in the Upper Spey catchment, there has recently been a large increase in the number of water quality complaints, with inadequate sewage treatment facilities to cope with tourism and distillery effluents being mainly to blame. Charter (1988) records the rise of Aviemore as a tourist centre and the associated increase in water sports on Loch Insh as direct factors affecting the loch, but also notes land use changes in the catchment, particularly grassland improvement, an increase in conifer afforestation and some shift to arable farming as potential threats to water quality. In general the waters are of good quality, with a lower pH, conductivity and alkalinity than the second Scottish site associated with the River Endrick. Daily water level readings have been taken by the RSPB for the last 10 years. These raw data were made available and are presented graphically in Fig 2.3. showing the rapid, dramatic changes in water level that can be experienced particularly in the spring and autumn.

Recent proposals for a flood alleviation scheme have, to date, been refused but it seems likely that construction of such a scheme will take place in the near future, probably involving channelisation of the river. The impacts of this scheme on the aquatic macrophyte communities have been assessed by Murphy and Hudson (1991). They conclude that a change of $\leq \pm$ 0.1 m in low flow would be highly unlikely to produce any measurable impact on plant communities. A more substantial decrease in water levels (0.5 - 0.75 m in low flow) as predicted by some options of the flood alleviation scheme would lead to a decrease in the submerged macrophyte communities of lochs, lochans, ditches and temporary standing waters and a shift in habitat occupancy by the floating leaved community due to accelerated hydroseral effects. The ability of the community to cope with this movement would be largely dependent on the speed and amplitude of the water level change, and the occurrence of any compounding disturbance events, such as a severe drought.

The sampling sites (Fig 2.2) include both lentic and lotic habitats covering the river channel, an oxbow, two lochans (Plates 7), a stretch of the Insh drain which runs along one side of the marsh into Loch Insh and a small, shallow pond (Plate 8). This covers most of the water body types present on the marsh.

Visits to the site were made in October 1991, March, May, July and September 1992; June and July 1993.

Fig. 2.2 Map of Insh marshes showing location of sampling sites. For site codes see Table 2.1.

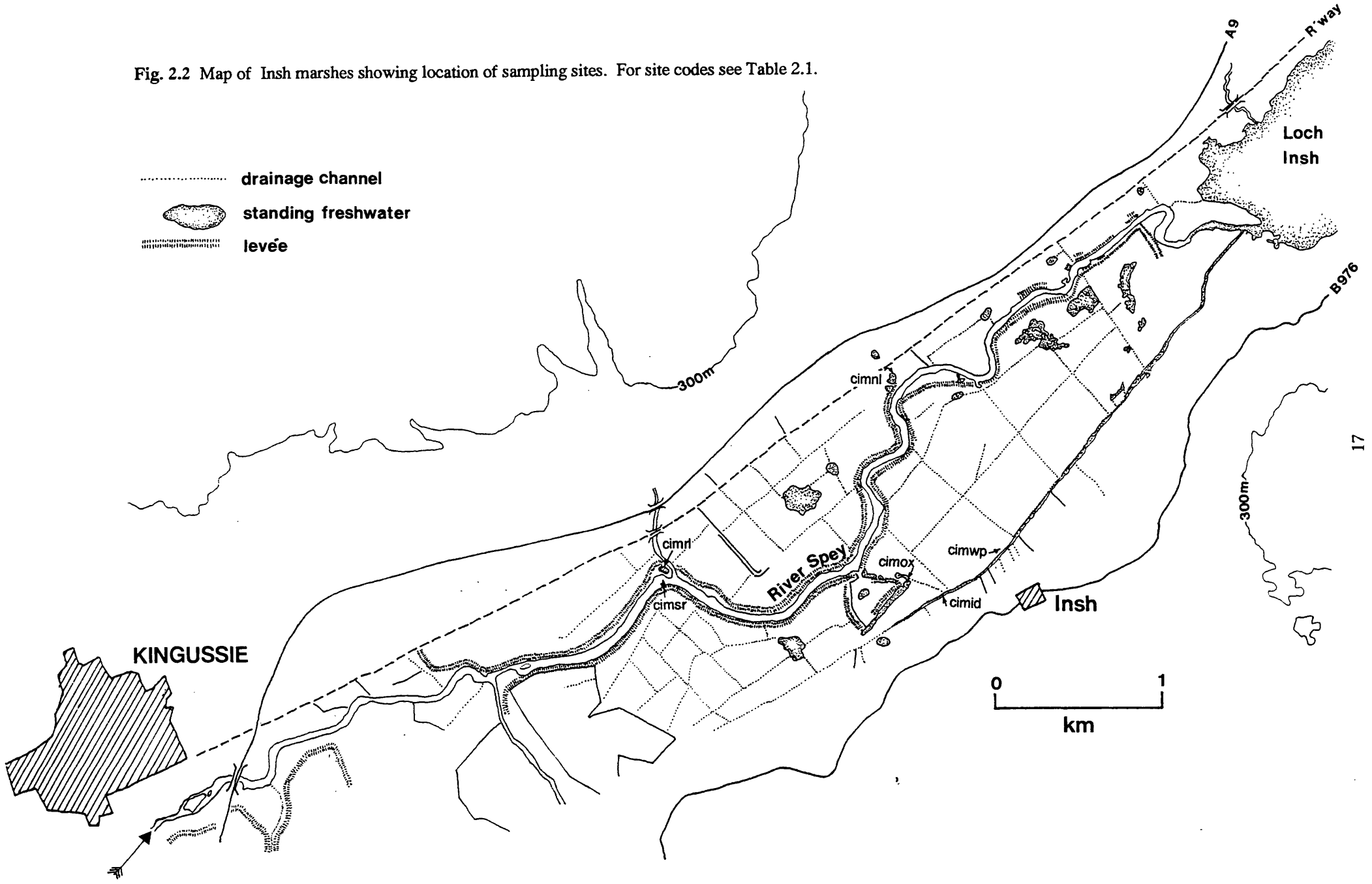


Fig 2.3 Water levels Insh Drain 1982 - 1992 (11 year average in bold)

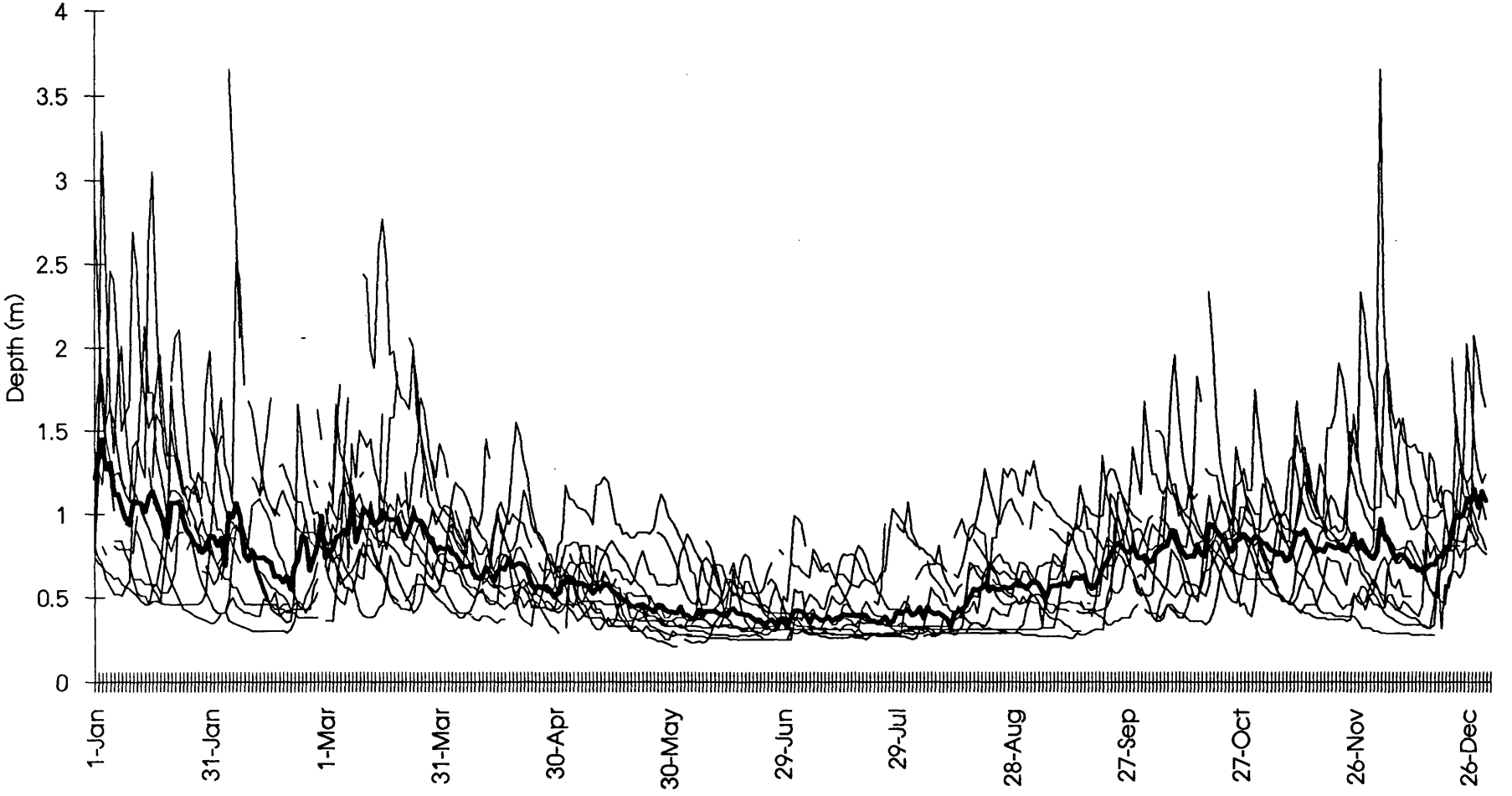
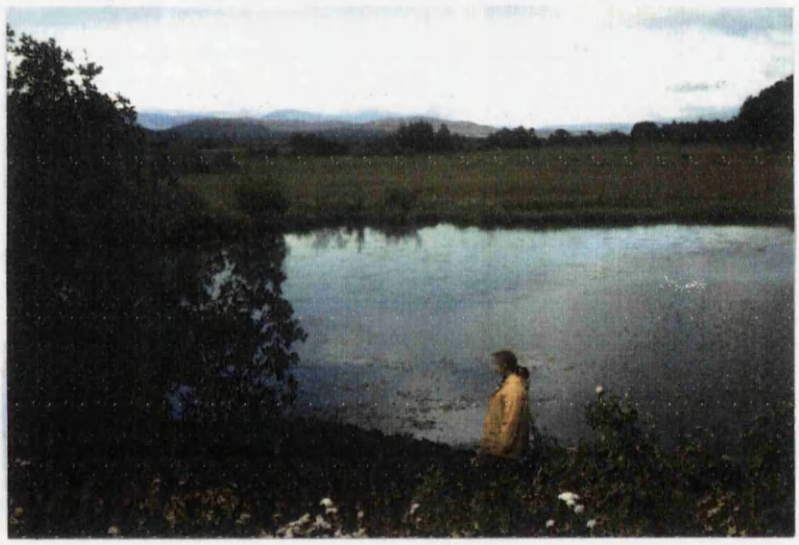


Plate 6: Insh marshes looking north from the B970. Insh drain in foreground. March 1992.

Plate 7: Lochan, Insh marshes, Scotland.
Photo: J. Hills, July 1993.

Plate 8: Shallow pool (**cimwp**), Insh marshes, Scotland.
Photo: J. Hills, July 1993



2.4 Endrick Marshes, Scotland.

The Endrick marshes (56°0'N, 4°25'W) are situated NW of Glasgow at an altitude of about 10m and have a climate fairly typical of west Scotland. It is cool and wet with air temperatures varying from just below freezing to about 25C and a mean annual rainfall of 1300 mm (Maitland 1966). In their review of internationally important waterbodies Luther and Rzóska (1971) consider Loch Lomond to be of importance for its relatively undisturbed nature and its use as a research resource.

The river has a catchment of 26,700 ha. The underlying rock is Old Red Sandstone mostly overlain by glacial and alluvial deposits. The substrate at the sampling sites is fine sand and silt as might be expected in the lower reaches of a river. The gradient as it flows through the marshes is 1 in 3000 (Ratcliffe, 1977). High water levels in spring and autumn can reduce the amount of work that can be undertaken, particularly at Wards Ponds, where access becomes difficult. This site is a diverse mixture of open water areas, including the river channel of Endrick Water itself, oxbow lakes, various drains, a large area of ponds and a small bay at the mouth of the Endrick which, although it is strictly a lacustrine habitat, has been included to provide an example of a community at the interface between river and lake systems.

The sites south of the river have been managed by Scottish Natural Heritage (previously the Nature Conservancy Council) as a National Nature Reserve since 1962, and the north side was designated in 1977. Drains were installed in the marshes in about 1835 but had largely fallen into disrepair by the 1920's. After this Wards ponds (Plate 9) were used as flighting ponds for wild fowling (as were areas to the south of the river). The drainage system has been repaired by Scottish Natural Heritage (Plate 10) with new embankments in the Aber bogs. Building of these embankments led to the creation of winning ditches as earth was excavated (John Mitchell, pers. comm.). Sluice gates allow control of the water levels in the marshes. Management of the surrounding farmland is quite different on either side of the river, with applications of fertiliser heavier on the more intensively managed land to the south. Although this land is presently given over to animal husbandry in the past it was under arable crops and was one of the most productive areas in the parish, and probably the most heavily fertilised. Silage production has also

largely replaced hay, with attendant threats of watercourse pollution (John Mitchell, pers. comm.).

Water quality data was supplied by the Clyde River Purification Board for its sampling stations at Drymen Bridge and Buchanan Castle. Data for the last five years at Buchanan castle show little change in water chemistry. In its second water quality report the Clyde River Purification Board (1985) describes the Endrick Water as a 'very clean river'. The main discharges it receives in this stretch are effluent from Drymen, Buchanan Castle and Gartocharn (via the Aber Burn) sewage treatment works. Pollution entering the river through the Aber Burn would not show up in the River Board monitoring as their last station is at Drymen Bridge upstream from the confluence. Concern has been expressed by the reserve warden over the impact of increased sewage loading on the Aber Burn from Gartocharn sewage works as the population of Drymen grows. To minimise the impact on the reserve the Aber Burn has been diverted to flow around the periphery of the reserve (John Mitchell, pers. comm.). A sampling site was located on the burn and heavy algal growth was noted in the summer months.

The sites chosen cover gradients in flow rate, depth and pollution. The drains in particular have varying loads of agricultural and sewage pollutants and the difference in the vegetation between those drains that carry sewage effluent from nearby Drymen and the cleaner drains at Balmaha is apparent. Six separate sampling locations have been used within the marshes (Fig 2.4).

Visits were made to the site in October 1991, June, August, September 1992, July and September 1993.

Figure 2.4 Map of the Endrick marshes showing sampling site locations. For site codes see Table 2.1.

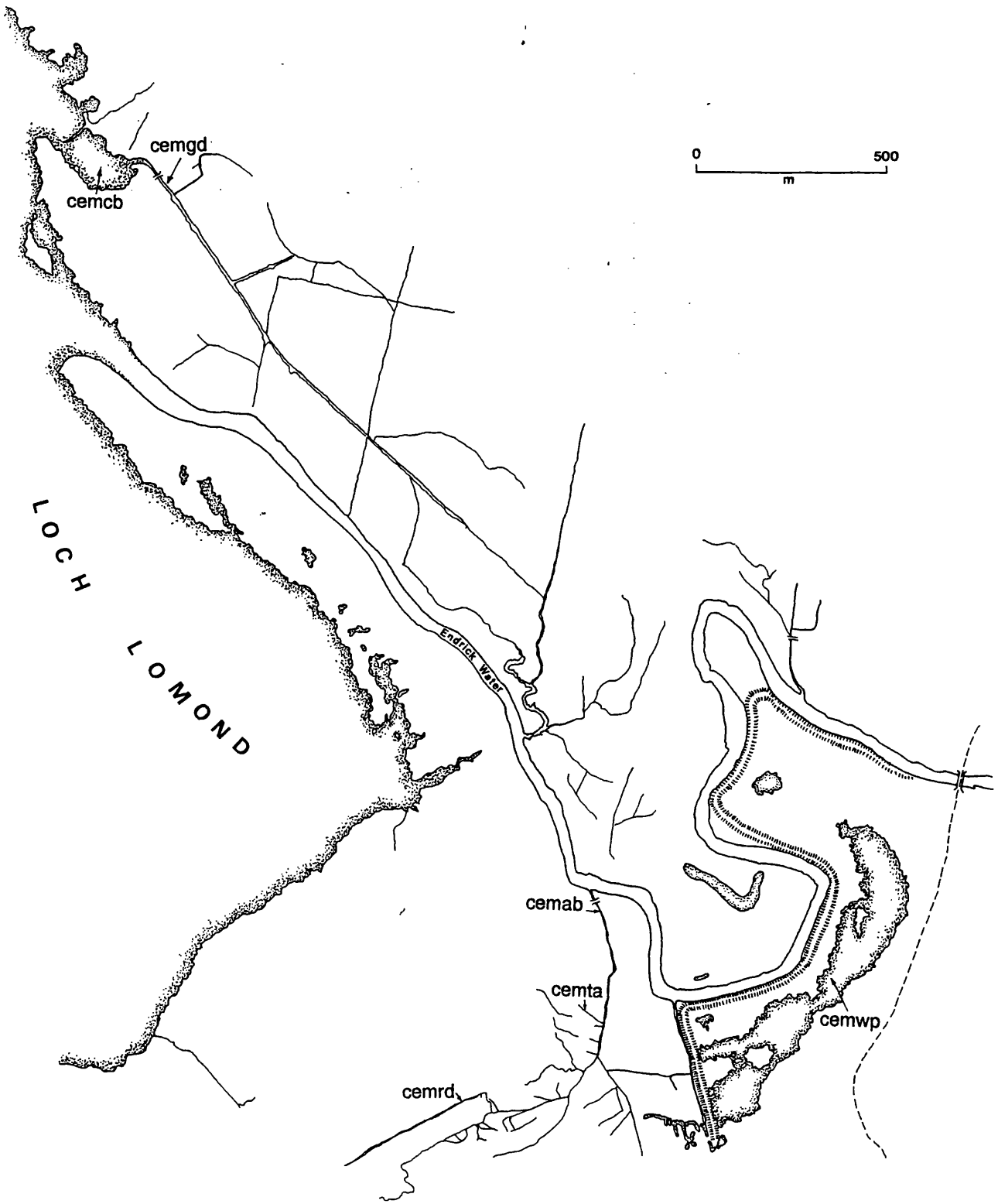
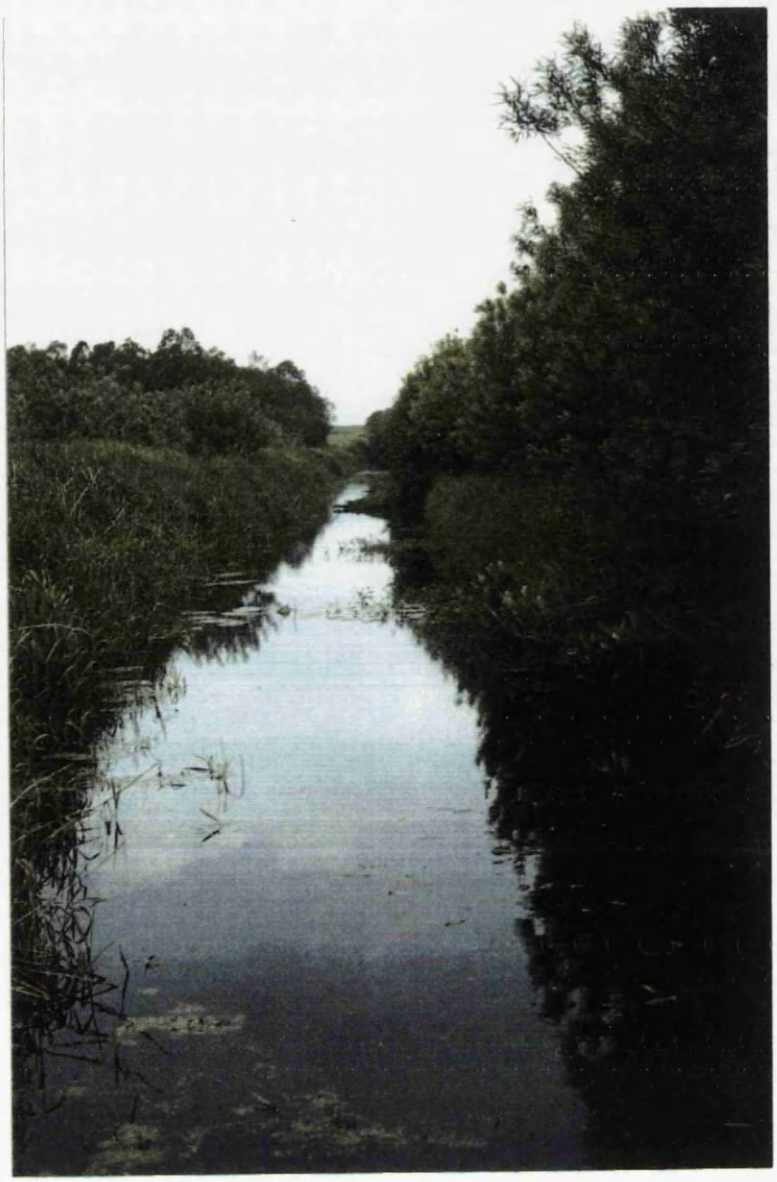


Plate 9: Wards ponds (**cemwa**), Endrick marshes, Scotland. August 1992.

Plate 10: Drainage ditch, Endrick marshes (**cemta**). June 1992



2.5 Giguela-Zancarra headwaters, Spain

The Spanish site differs in many environmental characteristics from the previous sites, and the flora exhibited is also unique to the area under consideration. The site is El Masegar wetland (Plate 11) close to Alcazar de San Juan in central Spain's La Mancha region. The water is semi-saline and of a strongly seasonal nature. In 1992 the lagunas and rivers were dry by July and had not yet filled by October. In the flood plains of the Giguela and Zancarra there are permanent and seasonal lakes. Those termed permanent are dry during July and August. Seasonal waters can dry up from late spring until early autumn (4-6 months). Ground water levels in La Mancha are falling very dramatically, and drought periods are becoming longer each year. This is attributed to the increase in sprinkler irrigation being employed to allow the expansion of viniculture in the region. El Masegar is a nature reserve managed by the private Fundacion Jose Maria Blanc, but with no national status. It comprises a large seasonal laguna (Plate 12) and adjacent areas that are seasonally flooded but in the dry season. Adjacent to it are wildfowling ponds which have been deepened as water levels drop. The reserve warden believes water is diverted from the Giguela river (Plate 13), which feeds El Masegar, to supplement these ponds. In 1992 an area of about 40km radius surrounding Masegar was surveyed, and of twenty one open water sites marked on local maps most were dry and supporting established terrestrial vegetation. In 1993 the lagunas at Masegar were dry nearly all summer (C. Guerrero pers. comm.).

Visits were made in May and October 1992. Data reported for June 1992 was collected by S.J. Marrs.

2.6 Loire-Allier confluence, France

The French study sites are located on the Rivers Loire and Allier, close to where they join at the Bec d'Allier. The area is very dry in the summer with the wetlands drying out drastically, and extensive sand banks appearing in the river channel. These support short lived annual communities through the summer. In the winter, Mediterranean rains can cause severe flooding. The surrounding area is extensive agriculture, mainly cattle rearing at present but a trend towards cereal culture and intensification is occurring. This includes increasing drainage of meadows and greater use of chemicals (FAEWE 1990b). Water from the river is extracted for both drinking water and irrigation. The main pressures on water

quality are sewage effluent which is often untreated. The Upper Loire is generally of poorer quality than the Allier and has higher concentrations of nutrients. Three dams in the area (Villerest, Grangut and Naussac I) affect the hydrology and sediment transport in the region. Two more dams and a weir are planned, although there is much controversy surrounding the plans and they may not be realised. Flow regulation is probably the biggest anthropogenic impact to be considered at this site. The Loire dams are designed to hold back flood water in winter and release it in summer (Purseglove 1991). This will drastically change the ecology of what has been described, by the pressure group Loire Vivante, as the last wild river in Europe.

The floodplains are well preserved, with areas of open water such as channels and backwaters. Three areas were investigated in the catchment. The first, near Apremont on the Allier (46°55'N,3°5'E), may become affected by the proposed weir upstream at Le Veudre, although construction has been suspended at present. The Allier is on limestone and marls covered by alluvial sands and gravels and some thin clay layers. The floodplain at Apremont includes a large oxbow lake, various drainage ditches and backwaters of the river. The view afforded from the chateau, which is sited on the ridge bordering the flooodplain, shows many depressions and meanders in the meadows which are now dry following improved drainage (Plate 14). The second site is on the Loire at Decize (46°55'N, 3°28'E). The only open water associated with the river is a dead arm surrounded by *Salix* woodland. The last site is a backwater of the Loire (Plate 15), and is found close to the village of Marzy (46°55'N,3°10'E), just downstream from the confluence at the Bec d'Allier (Plate 16). The backwater maintains a heavy and rapid flow of water during winter but in dry summers is of a seasonal nature. The majority of work was undertaken at Apremont, as it was by far the richer site, in terms of waterbody types. In particular the oxbow site at Apremont (Plate 17) supports an interesting flora. This is the major open water body associated with the river. Work was also carried out on the ditches leading into and out of the oxbow. Aquatic vegetation is largely absent in the main river channels (Plate 18). No vegetation was recorded in the Allier backwaters during the two year survey, although *Ranunculus* species had been observed in 1991 (J. Hills, pers. comm.)

Visits were made in June and August 1992 and April, June and August 1993.

Plate 11: El Masegar nature reserve, La Mancha, Spain, from the approach road. May 1992.

Plate 12: Maseger laguna (**smml1**), La Mancha, Spain . May 1992.

Plate 13: Giguela river, La Mancha, Spain, showing dense growth of charophytes. June 1992.

Plate 14: Allier floodplain at Apremont, with oxbow in the foreground (**faoxa**) and riverine flood forest to the left hand side. August 1992.

Plate 15: Backwater of River Loire near Marzy, France. August 1993.

Plate 16: Bec D'Allier; confluence of the rivers Loire and Allier. April 1993.

Plate 17: Side arm of oxbow at Apremont (**faoxd**), France, showing *Utricularia vulgaris* in flower. May 1993.

Plate 18: River Allier, Apremont, France, showing braiding of the river channel. August 1993.

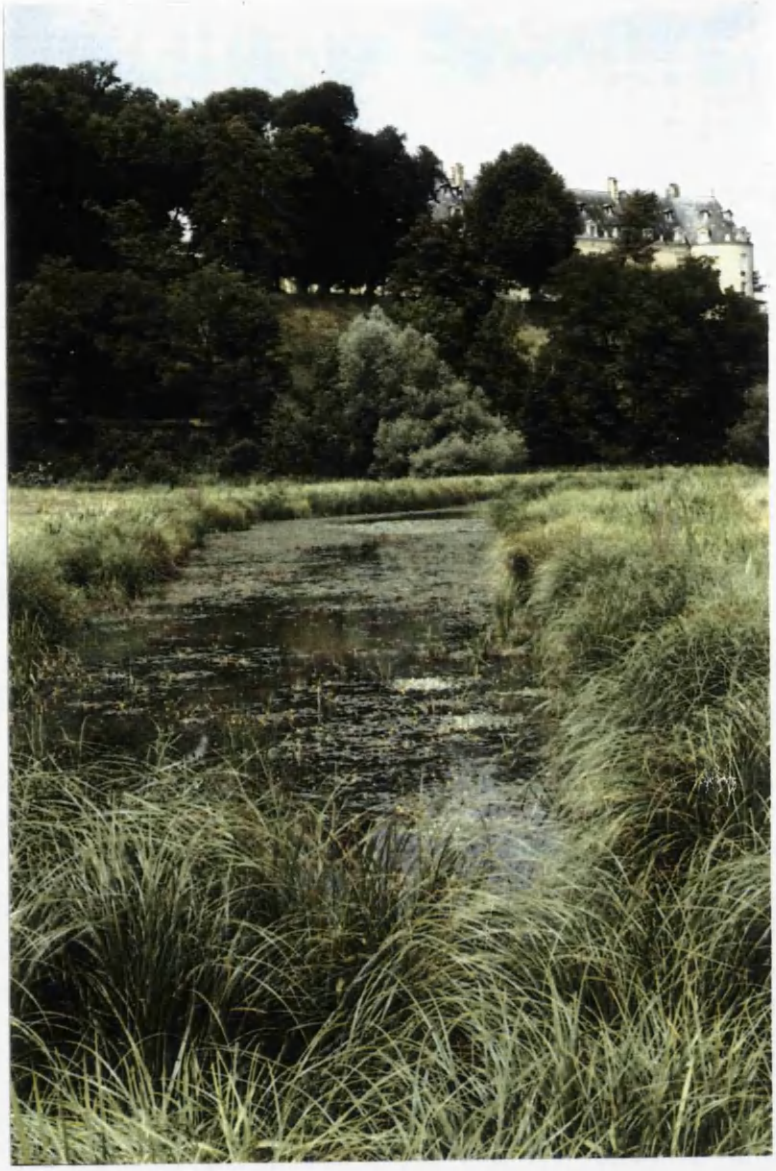


Table 2.1 Locations and descriptions of survey sites.

No.	Country	Area	Code	Description
1	Ireland	Little Brosna	ilbd2	shallow drainage ditch over marl sediments, steep banks.
2			ilbd3	medium depth drainage ditch over peat, quite dense emergent growth.
3			ilbd4	medium drainage ditch, dense emergent growth, steep high banks.
4			ilbpo	temporary shallow pond
5			ilbr	river channel
6		Clonmacnoise	icldi	shallow drainage ditch
7			icldo	medium shallow drainage ditch at outflow to river
8			iclr	river channel
9		Bullock island	ibipo	deep oxbow
10	England	Kismeldon	eksrf	river channel, shallow riffle reach
11			eksrr	river channel
12			eksrl	river channel, shaded riffle reach
13			eksox	seasonally flooded oxbow
14		Bradford Mill	ebmr	river channel, riffle reach
15		Hele Bridge	ehbox	deep oxbow heavily shaded by trees
16	Scotland	Insh marshes	cimsr	river channel
17			cimrl	deep lochan
18			cimnl	deep lochan connected to river
19			cimid	main drainage ditch
20			cimwp	shallow pond
21			cimox	oxbow
22		Endrick marshes	cemab	main drainage ditch, occasionally dredged
23			cemta	deep drainage ditch controlled by sluice gate.
24			cemwa	shallow, extensive ponds
25			cemrd	shallow drainage ditch controlled by sluice gate.
26			cemgd	main drainage ditch
27			cemcb	bay at mouth of river
28	Spain	Masegar	smgr	seasonal river channel
29			smml1	seasonal lagoon, shallow edge site
30			smml2	seasomal lagoon deep site.
31	France	Apremont	faoxa	deep oxbow main body
32			faoxd	deep oxbow side arm
33			fappo	shallow oxbow sidearm disconnected from main body during summer
34			fapdo	outflow ditch between oxbow and river
35		Decize	fdcbw	river backwater
36		Marzy	fmlbw	river backwater
37		Apremont	fapdi	shallow inflow ditch to oxbow

Chapter 3

FIELD SURVEY

Chapter 3

FIELD SURVEY

3.1 Introduction

This chapter

- presents the results of the vegetation survey undertaken in 1992 and 1993 and the results of the environmental parameters measured
- details multivariate techniques suitable for the analysis of data from vegetation surveys
- classifies sites according to their species composition
- relates species occurrence to environmental conditions and discusses these relationships
- compares these results to previous studies

When attempting to elucidate the response of plant communities to environment two approaches are possible: 1) direct experimentation varying one factor at a time and monitoring community response; and 2) looking at existing patterns of communities and relating this to the environment they inhabit. The latter can be used to generate hypotheses testable by direct experimentation (Dennison *et al.* 1993). In a short term study such as this, where the aim is to gain an insight into the factors affecting a wide range of sites, and if possible, to select which are the controlling factors, the first approach is not suitable. Ideally the work presented here should be followed up by more rigorous testing of the hypotheses generated (Austin 1987).

Therefore the aim of the field survey was to obtain a dataset comprising the communities growing in the aquatic phases of riverine wetland habitats, and the different environmental conditions in which they existed. This data set could then be analysed using a phytosociological or a functional approach and related to the measured environmental parameters. As this data set would be used to generate

hypotheses on the relationship of communities to environment, a varied environmental data set would allow wider predictions to be attempted. The sites themselves cover a wide climatic and geographical range, from euoceanic in Ireland to semi-arid in Central Spain. The choice of sites was largely confined to those sites already designated by the FAEWE project, but it was also possible to include two Scottish wetland sites. The Endrick marshes were chosen as they contained two areas of quite different nutrient status on either side of the river and both sides of the river contained a diverse set of open waterbodies. They also had good site records of water levels, and it would be possible to manipulate water levels in some of the ditches by use of the sluice gate system. Originally transplant experiments were planned for the second field season so this was a useful facility. These were later dropped as the fieldwork schedule would not allow for regular monitoring of the experiment. The Insh marshes were also selected as one of the larger riverine wetland sites within reach of Glasgow. Within all wetland sites waterbody types were chosen to be as diverse as possible, with ditches, river channels, dead arms, backwaters, oxbows, permanent and temporary ponds all represented .

The survey was carried out over two seasons and between two and five visits were made to each site each year (see Chapter 2), except to the Spanish field site where no visits were made in the second year because by June the waterbodies had still not refilled from the previous years' dry season. Repeated visits to the sites allowed a good picture of the environmental character of the site to be obtained. It also allowed accurate identification of difficult species as mature specimens could be examined on return visits. This was also important for the field trait measurements (see Chapter 4), as these were taken from fruiting specimens wherever possible, and repeated visits through the season allowed measurement of most populations that reached fruiting.

Throughout this work averages of environmental parameters and species frequencies for each site were used for analysis (Appendices 1 and 2).

3.2 Field survey methods

All survey work was carried out between March 1992 and September 1993 (see Chapter 2).

3.2.1 Vegetation survey

At each site the plant community was assessed using frequency as an estimate of abundance (Bannister 1966). In ditches, rivers and other linear water bodies a 20 m stretch was assessed. Oxbows, lochans and ponds were regarded as single ecological units (Seddon 1972), and the entire flora recorded (Appendices 2 & 3). Where the waterbody was wadeable transects were used across the water body width and species occurring on this transect were recorded. In deeper water bodies grapnel throws were used. Ten replicates were taken (either grapnel or transect) and the frequency of occurrence of individual species recorded. As species have individual phenology of growth (Jones 1956) and show remarkable changes in biomass through the season (Wiegleb 1981; Kunii and Maeda 1982), a single visit would not be representative of all species contributions to the community. For this reason species averages were taken over all visits. All species names, authorities and codes are given in Appendix 4.

3.2.2 Environmental survey

Parameter codes are given in brackets.

Depth (D)

Measured to the nearest cm by meter rule or by lowering a grapnel vertically into the water.

Conductivity (Cond)

Using a Whatman CDM600 portable electronic field meter recording in $\mu S\ cm^{-1}$.

Dissolved oxygen (DO%, DOmg)

Both saturation and concentration of oxygen were measured with a Jenway 9010 dissolved oxygen probe.

pH (pH) and Temperature

Both measured using a Jenway 3070 portable pH meter. pH measurements were taken between 10:00 and 14:00 whenever possible to obtain the maximal diurnal value.

Light net downward attenuation coefficient (K)

Photosynthetically active radiation (PAR) levels were measured at two or three depths in the water column using a Skye SKP2200 with two SKP 210 PAR sensors that take readings simultaneously. The hand held display can show either absolute readings from either sensor or the ratio between the two. From these readings the light extinction coefficient (k) was calculated (Moss 1988):

$$k\ m^{-1} = \log_e (Io/I) \ / \ d$$

where Io = subsurface PAR

I = PAR at depth (d)

d = depth (m)

These readings were also used to calculate the euphotic zone (Zeu) depth:

$$Zeu = 3.51 / k$$

The substrate light parameter **(SL)** is the euphotic zone depth divided by the actual depth. Therefore a record close to one indicates that the bed at a site is near to the euphotic limit for plant growth.

Water phosphate (Pw)

Measured using colorimetric methods, an Aquamerk 14661 field testing kit was used. This measured orthophosphate (PO_4^{3-}) from 0 - 3 mg l^{-1} in 0.25 mg l^{-1} increments.

Water nitrate (Nw)

Measured using colorimetric methods, a Merckoquant 10020 Nitrate test was used. The range of detection was 0 - 500 mg l^{-1} $N0_3^-$. The smallest increment was 10 mg l^{-1}. Nitrite interference can be a problem but where nitrite levels are high an indicator square is triggered and the effects can be corrected for (Hutton 1983).

Total hardness (TH)

Measured using colorimetric methods. Merckoquant 10046 total hardness kit measured from 0 - 30°e in 9°e increments. 1°e ≡ 14.30ppm $CaCO_3$.

Sediment phosphate (Ps)

Analysis of sediment phosphorus was carried out by the Department of Chemistry, University of Glasgow. Sediment samples were air dried and ground to < 2 mm. The samples were digested with nitric/perchloric acids, with a final digestion in perchloric acid for 2 hours at 180°C. The digests were analysed for phosphate using an automated phospho-vanado-molybdate method. Results are given in parts per million.

Sediment organic matter (OMs)

Organic matter content was determined by loss on ignition. Samples were air dried and ground to < 2 mm, they were then oven dried at 100C to ensure loss of soil moisture. Approximately 5g of soil was placed in a weighed crucible, re weighed and put in a muffle furnace at 500C for 6 hours, then cooled in a 100C oven and placed in a desiccator to cool. The final weight was determined and percentage organic matter calculated.

Sediment particle size (%a, %b, %c, %d)

Samples were thoroughly ground using a pestle and then sieved through a stack of sieves to determine the weight distribution of 4 size classes:

a - < 180 μm

b - 180 - 500 μm

c - 500 - 1000 μm

d - > 1000 μm

Flow (FL)

Initially in the Scottish sites measurements were taken using an OTT flow meter, however as it was too heavy to be feasible for some of the European trips the flow measurement was categorised into five classes that could be estimated in the field:

1 - still

2 - very sluggish flow, barely perceptible

3 - slow flowing

4 - moderate flow

5 - rapid flow

Drought (DR)

This was a categorical variable relating to the observed or reported periods of substrate exposure at a site

1 - permanent water
2 - dries up for a short time some years
3 - dries up most years for two or three months
4 - dry every summer for at least three months

Emergent cover (Ecover or EC)

Categories 1 - 10 refer to the percentage cover estimate of emergent vegetation to the nearest 10% (e.g. 1 = 10% emergent cover). Details of the emergent plants present at each site are given in Appendix 3. This refers only to emergent plants growing in the waterbody and not to bankside vegetation.

Tree cover (Tshade or TC)

This was also a categorical variable referring to the nearest 10% cover of tree shade when viewed from below the canopy. i.e. an estimation of the percentage of open sky obscured by tree foliage.

The environmental survey results are given in Appendix 1

3.3 Data Analysis

3.3.1 Background

Ordination and classification are complementary methods for analysing large multivariate ecological data sets. While classification of sites by species is somewhat artificial as it imposes structure on continuous data, it is convenient to simplify data and to objectively group similar sites without allowing investigator bias to influence the groupings. Interpretation of the analysis however involves an element of subjectivity, for example in deciding on how many divisions to include in a classification. Ordination allows interpretation of the whole data set, and in this case it is possible also to look at relationships with environmental parameters. It is also a useful visual tool with which to represent, in two dimensions, the complex relationships in a large ecological data set.

A popular method of classifying sites by their constituent species is Two-Way Indicator Species Analysis or TWINSPAN (Hill 1979). TWINSPAN is widely used in community ecology and it has a number of useful products. It stems from the ideas used in phytosociology to characterise groups of sites by differential species (Jongman *et al.* 1987), and uses both quantitative and qualitative data. The basis of TWINSPAN is correspondence analysis (Hill 1973), which is used to ordinate sites along an axis which is then divided at its centre of gravity, to produce a dichotomy. The two groups thus produced are reordered and subsequently divided and so on. The end product is a classification of the sites and an ordered two way table from the *species x sites* matrix. It also gives indicators at each division, and preferential species for the positive and negative groups. These can be used to produce a dichotomous key that can be used to classify new sites. TWINSPAN uses quantitative data by assigning pseudospecies. A pseudospecies is a species at a certain abundance (or frequency) range. These can be controlled by setting the number and position of the cut levels that delimit these ranges. For instance to assign more pseudospecies to low frequency classes the cut levels could be set at 1,2,3,5,7; while setting cut levels as 2,4,6 gives less fine tuning at low species frequencies. In interpretation of TWINSPAN groups it should be remembered that the classification is based on the artificial separation of a continuous gradient, and is not necessarily a natural grouping.

A widely used approach to the simplification of large ecological data sets is to use indirect ordination techniques such as detrended correspondence analysis (DCA) to ordinate the species with subsequent regression of site scores against measured environmental variables. DCA is based on correspondence analysis and assumes a unimodal response curve. The advantage of DCA is that it corrects the 'arching' effect that was sometimes encountered in CA, particularly on the second axis (Hill 1979; Hill and Gauch 1980). Where axis lengths are less than 2 standard deviations (s.d.) in a DCA ordination, the response is in effect monotonic and analysis based on a linear model (e.g. PCA) may be more suitable (ter Braak 1986). An axis length of 4 s.d. or more, would indicate that sites at either end of the axis have no species in common (ter Braak 1987a), this being the separation of the extremities of a normal distribution. This also indicates that the data is probably strongly non linear in response.

A complementary approach to DCA is to use canonical correspondence analysis (CCA), which is a direct gradient approach, since the axes are constrained by the measured environmental variables. CCA is appropriate where a DCA followed by

environmental gradient interpretation does not explain the main variation, as is often the case. Where more than one environmental variable is related to an axis it is easily recognised by the positions of the arrows on the biplot diagram. ter Braak (1986) has shown how CCA allows a quick appraisal of community composition variation with environment. Individual relationships can still be investigated by regression of site scores against single variables that may be highly influential.

The same arching effects that occur in CA (and are corrected in DCA), are possible in CCA, particularly if the number of environmental variables approaches the number of sites under analysis, or if several variables are strongly intercorrelated. Detrending can reduce this effect, but a more efficient way is to reduce the number of environmental variables by excluding those that are highly correlated with another variable. The second axis is most susceptible to arching, so variables that are highly correlated with this axis are most likely to be superfluous (ter Braak 1987a). CCA, DCA and TWINSPAN all share underlying assumptions with correspondence analysis, in particular weighted averaging to implement non-linear ordinations, which is preferable where a linear response model is inadequate. (ter Braak and Prentice 1988; Brown *et al.* 1993). CCA has been shown to perform well with skewed species distributions, quantitative noise in species abundance data, highly intercorrelated environmental variables and situations where the major factors determining species composition are not measured (Palmer 1993).

To interpret the CCA axes it is necessary to look at the intraset correlations and the canonical coefficients; their signs and magnitudes can be used to infer the relative importance of individual variables in explaining the community composition. Canonical coefficients define the ordination axes as linear combinations of the environmental variables (ter Braak 1986). Intraset correlations are defined as correlation coefficients between the environmental variables and the ordination axis (ter Braak 1986 1987a). Both measures relate to the rate of change in community composition per unit change in the corresponding (standardised) environmental variable (ter Braak 1986). They differ in that canonical correlations assume that other environmental variables are constant while the intraset correlations assume that the environmental variables covary in the manner particular to the data set (ter Braak 1987b). In a case where environmental variables are strongly correlated canonical coefficients are unstable, and should not be used for interpretation. Intraset correlations do not suffer from this problem.

If the environmental variables were mutually uncorrelated, the canonical coefficients and the intraset correlations would give the same information (ter Braak 1986).

In some cases indirect gradient analysis may be more informative than direct gradient analysis as environmental conditions are difficult to characterise exhaustively and species composition may be a more informative indicator of the total environmental character than the chosen environmental parameters. Comparison of the DCA and CCA eigenvalues is of interest as it provides an indication of how much of the species variance remains unexplained by the environmental parameters. Where the ratio of canonical to unconstrained eigenvalues is low it may be necessary to measure further environmental variables to give a feasible explanation of how the communities are being influenced.

3.3.2 Analysis

The TWINSPAN classification was run on the 1992/1993 euhydrophyte data set (Appendix 2). Data on emergent plants contribution to the communities was also available (Appendix 3). This was not used in this analysis as the emergent vegetation is subject to different environmental influences from the euhydrophytes (Palmer *et al.* 1992), and its inclusion may obscure relationships between euhydrophytes and the environmental characteristics of the aquatic environment. The TWINSPAN classification of the sites by their species composition is given in Fig. 3.1. Four levels of the analysis were used, except where the eigenvalue for the iteration was below 0.400, as this showed that the group was quite homogeneous. This resulted in eight groups of sites as shown. Site codes are given in Appendix 1. Species codes are given in Appendix 5, numbers in brackets indicate the pseudospecies.

The groups strongly reflected geographical location, with the French and Spanish sites both in discrete groups. This is not surprising in the case of the Spanish sites as the species set is completely different from any of the other sites. In the French sites there are many species in common with other sites, but the presence of *Ceratophyllum demersum* exclusively in these sites differentiates them from the rest. The Insh and Torridge sites overlap, as do the Irish and Endrick sites.

The DCA analysis was run initially with the Spanish sites included, but since the Spanish sites contained an exclusive set of species the first axis only served to

separate these sites from the rest of the data set and all the variation in the remaining sites had to be contained in the second axis. This did not give a very clear picture. As it is obvious that floristically the Spanish sites are a discrete and well separated group it is not necessary, or meaningful, to show them in relation to the other sites so the DCA was rerun without these sites. A summary of the DCA is given in Table 3.1 and the ordination is shown in Fig 3.2 with the TWINSPAN groups overlaid. The gradients of the first and second axis are quite long, justifying the use of correspondence analysis rather than a Principal Components Analysis, which assumes a linear response model. Both axes have high eigenvalues, but quite a low proportion of the species variation is explained (11.8% and 9.3% by axis 1 and 2 respectively). This reflects the diversity of the data set and also suggests that there is no strong underlying gradient that is controlling community composition.

The CCA was similarly run without the Spanish sites. The initial analysis included all environmental parameters in the run except water nitrate data as it was highly skewed. Depth and conductivity data were natural logarithm transformed to approximate better to a normal distribution. All continuous variables were standardised to zero mean and unit variance. To reduce any arching effects, the correlation matrix was examined to see if variables could be dropped from the analysis without serious reduction in the species-environment variance explained. Total Hardness was strongly correlated with conductivity ($r = 0.909$), as would be expected. Conductivity reflects a range of major ions therefore it was retained in preference to total hardness. Percentage saturation of dissolved oxygen and dissolved oxygen concentration were also very closely correlated ($r = 0.945$). Percentage saturation was retained as it is more straightforward to interpret. % 'd', being the last of four particle size classes, is a redundant variable, so was also excluded. Total hardness and % 'd' were run as passive variables. Passive analysis allows the variable to be placed on the ordination diagram without being used in the calculations that construct the ordination. Comparisons of the summary tables 3.2a and 3.2b show that the species environment correlations and the percentage of the species environment relation explained are little affected by dropping these variables.

Fig 3.1

TWINSPAN dendrogram showing sites classified in terms of species.

Indicator pseudospecies are shown at each division (See Appx 2 for codes)

Eigenvalues for each iteration are shown in bold type

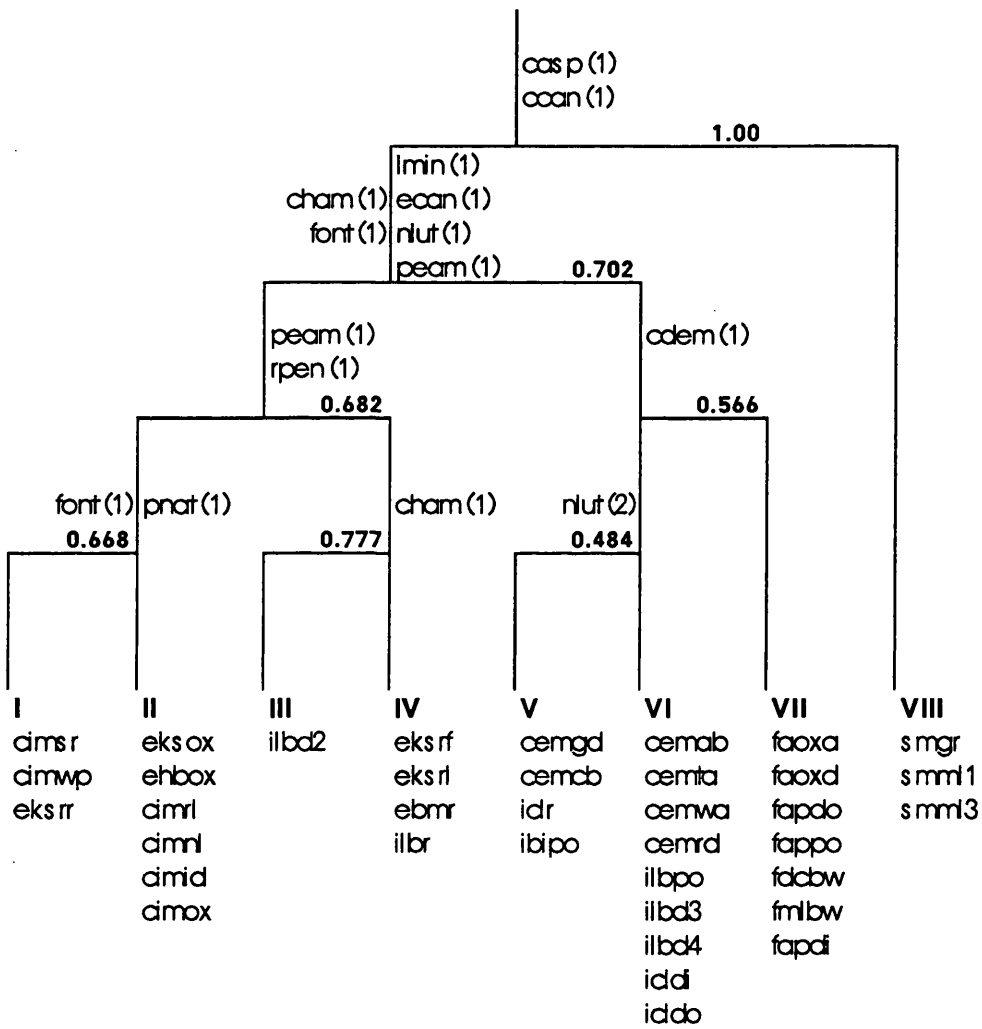


Fig 3.2 DCA ordination of 1992/1993 sites (except Spanish) using species composition. TWINSPAN groups delineated by dotted lines. For site codes see Table 2.1

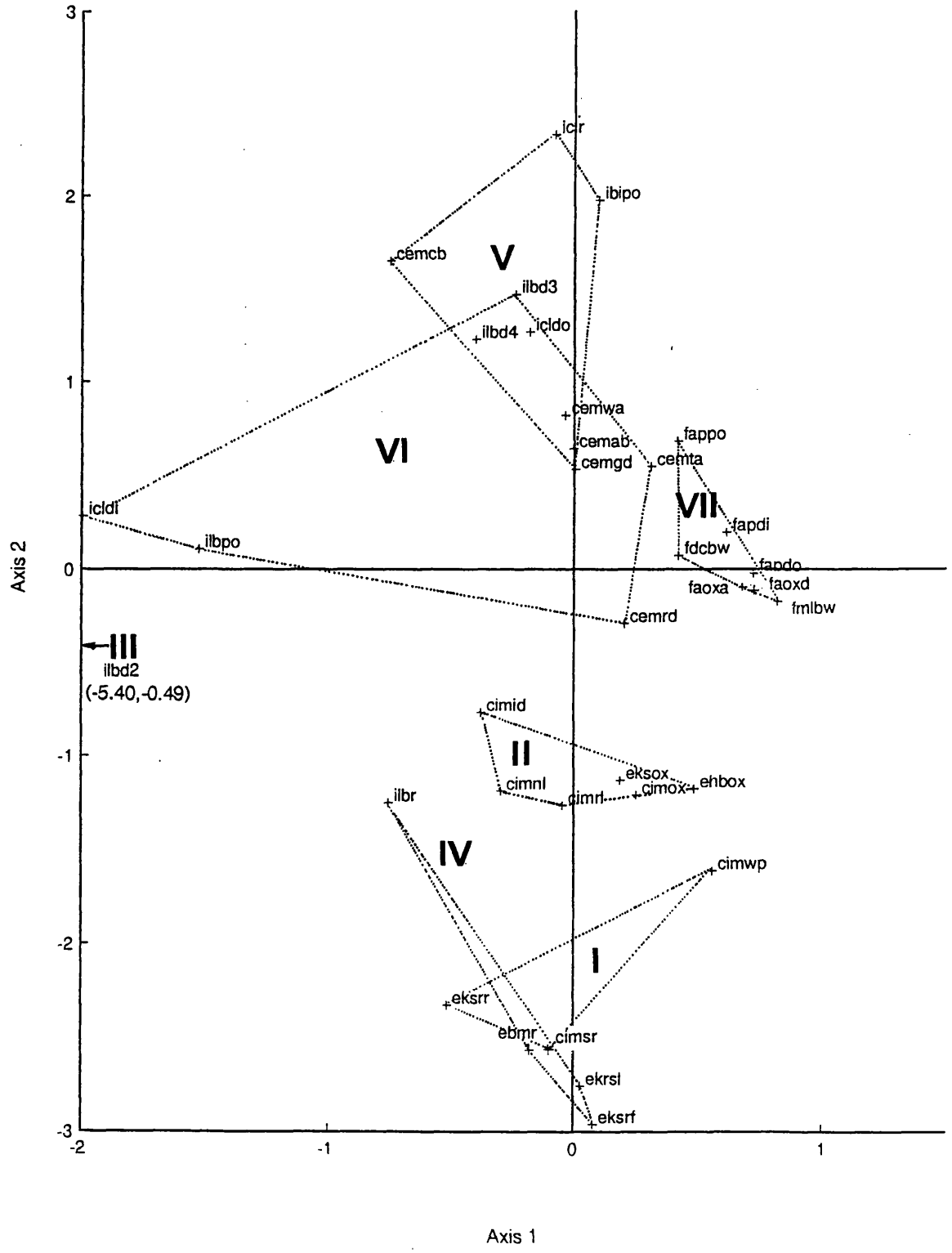


Table 3.1 DCA summary (Spanish field site excluded from analysis)

Axes	1	2	3	4	Total inertia
Eigenvalues	0.932	0.731	0.408	0.201	7.869
Lengths of gradient	6.224	5.293	3.387	3.202	
Species-environment correlations	0.838	0.825	0.865	0.666	
Cumulative percentage variance explained					
species data	11.8	21.1	26.3	28.9	
species-environment relation	10.3	19.6	0	0	
Sum of all unconstrained eigenvalues					7.869

Table 3.2a Summary of CCA including all environmental variables

Axes	1	2	3	4	Total inertia
Eigenvalues	0.769	0.688	0.565	0.473	7.869
Species-environment correlations	0.976	0.927	0.939	0.908	
Cumulative percentage variance explained					
species data	9.8	18.5	25.7	31.7	
species-environment relation	14.9	28.3	39.2	48.4	
Sum of all unconstrained eigenvalues					7.869
Sum of all canonical eigenvalues					5.158

Table 3.2b Summary of CCA excluding correlated environmental variables

Axes	1	2	3	4	Total inertia
Eigenvalues	0.769	0.660	0.558	0.452	7.869
Species-environment correlations	0.976	0.910	0.943	0.897	
Cumulative percentage variance explained					
species data	9.8	18.2	25.3	31.1	
species-environment relation	16.2	30.2	42	51.5	
Sum of all unconstrained eigenvalues					7.869
Sum of all canonical eigenvalues					4.736

The summary of the final ordination (Table 3.2b) confirms some of the hypotheses suggested by the DCA. The eigenvalues of each axis are high, indicating good species separation, but only 30.2% of the species-environment correlation is contained in the first two axes. The ratio between the sum of canonical and the sum of unconstrained eigenvalues is high, showing that the environmental variables measured are responsible for a high proportion of the displayed species variation. A Monte-Carlo test was used to test if the species were significantly related to the environmental variables. The test is carried out by randomly permuting the sample numbers in the environmental data and then randomly linking these to the species data, thereby creating a random data set. CANOCO then calculates the test statistic, in this case for all the environmental variables (termed the 'trace' statistic). 100 permutations were carried out and test statistics calculated. If the test statistic from the real data is among the highest 5% of those from the random data then the species are significantly related to the environmental variables. In this case the test statistic was highly significant (in the highest 1%). Remaining variation will also take in the variation attributable to chance distribution of aquatic flora (Godwin 1923) for which there is no environmental basis. A plot of the eigenvalues over the first four axes (Fig. 3.3) shows that there is only a gradual decrease, again showing that the variation cannot be attributed to one or two strong gradients. The ordination biplot of site scores and environmental arrows is shown in Fig. 3.4a and the species scores in Fig. 3.4b. Individual sites names are not given, instead the TWINSPAN groups are shown.

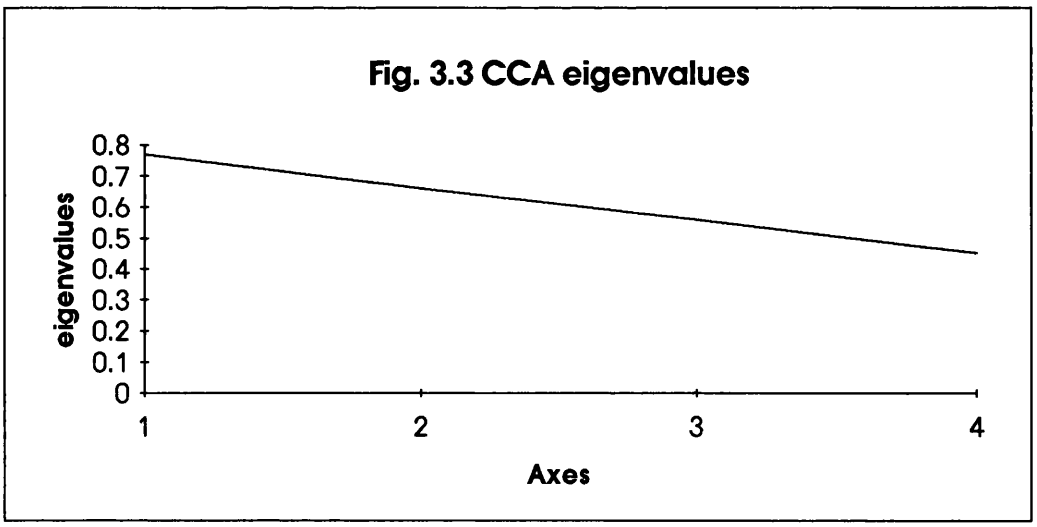


Table 3.3 Comparison of vegetation classifications for the surveyed sites

Site	Group	National Vegetation Classification	CORINE
cimsr	I	A14 Myriophyllum alterniflorum	C24.41
cimwp	I	A14 Myriophyllum alterniflorum	C22.433
eksrr	I	A14 Myriophyllum alterniflorum	C24.41
eksox	II	A16a Callitriche stagnalis Callitriche spp.	C22.432
ehbox	II	A7a Nymphaea alba Species-poor	C22.431
cimrl	II	A9 Potamogeton natans	C22.431
cimnl	II	A9 Potamogeton natans	C22.431
cimid	II	A9b Potamogeton natans Elodea canadensis	C22.431
cimox	II	A7 Nymphaea alba	C22.431
ilbd2	III	A11a P. pectinatus-M. spicatum P. pusillus (poor)	C24.42
eksrf	IV	A17 Ranunculus penicillatus	C24.43
eksrl	IV	A17 Ranunculus penicillatus	C24.43
ebmr	IV	A17 Ranunculus penicillatus	C24.43
ilbr	IV	A8b Nuphar lutea Callitriche stagnalis - Z. palustris	C24.4
cemgd	V	A9 Potamogeton natans	C22.431
cemcb	V	A10 Polygonum amphibium	C22.4315
iclr	V	A8a Nuphar lutea Species-poor	C22.431
ibipo	V	A8 Nuphar lutea	C22.431
cemab	VI	A15 Elodea canadensis	C22.422
cemta	VI	A15 Elodea canadensis	C22.42
cemwa	VI	A15 Elodea canadensis	C22.42
cemrd	VI	A15 Elodea canadensis	C22.422
ilbpo	VI	A19 Ranunculus aquatilis	C22.432
ilbd3	VI	A2b Lemna minor-Lemna trisulca	C22.411
ilbd4	VI	A2b Lemna minor-Lemna trisulca	C22.411
icldi	VI	A16a Callitriche stagnalis Callitriche spp.	C22.432
icldo	VI	A15 Elodea canadensis	C22.42
faoxa	VII	A5a Ceratophyllum demersum Ranunculus circinatus	C22.42
faoxd	VII	A5 Ceratophyllum demersum	C22.42
fapdo	VII	A5 Ceratophyllum demersum	C22.42
fappo	VII	A4 Hydrocharis morsus-ranae - Stratiotes aloides	C22.431
fdcbw	VII	A10 Polygonum amphibium (poor)	C22.431
fmlbw	VII	A5 Ceratophyllum demersum	C22.42
fapdi	VII	A3 Spirodela polyrhiza - Hydrocharis morsus-ranae	C22.411
smgr	VIII	No classification	C22.44
smml1	VIII	No classification	C22.44
smml3	VIII	No classification	C22.44

Overlaying the TWINSPAN groups on the CCA species-environment biplot (Fig 3.4a) suggests that using level four of the classification may be introducing artificial groupings, with groups divided in level four strongly overlapping. However as separation was clear on the DCA it may be that some factor that I have not measured may be dividing the groups at this level. Table 3.3 shows a comparison of my groups with the National Vegetation Classification and CORINE biotopes. The CORINE database gives a classification of biotopes of major importance for nature conservation in the European Community (Commission of the European Community 1991). NVC classes were assigned using the program TABLEFIT (Hill 1993). The programme showed a poor goodness of fit for some sites (where goodness of fit was especially low it is noted on the table). In the European sites this may be due to species or associations not occurring in Britain. Problems may also arise through the delimiting of communities; the inclusion of emergent vegetation resulted in the classification of some of the communities as water margin vegetation, with improved goodness of fit. As the publication concerning the NVC classification of aquatic communities is not yet available it was difficult to judge the accuracy of the NVC communities assigned by TABLEFIT. Den Hartog and Segal (1964) argue for classifying pleustophytes and rhizophytes separately. In this case pleustophytes are not indicator species at any of the TWINSPAN divisions and do not seem to be unduly influencing the analysis, so this recommendation was not followed. However problems concerning the strong stratification present in aquatic systems may also have contributed to the poor goodness of fit. It should also be noted that the programme was written mainly for terrestrial systems where, generally speaking, species richness is considerably higher than in aquatic systems. In species poor communities relatively small changes in the abundance of one or two key species may produce a poor match with the suggested community. It has also been noted in phytosociological studies that species exclusively bound to one association are rare amongst water plants and their exclusiveness is often a local feature (Den Hartog and Segal 1964). This feature of aquatic plant sociology may also contribute to difficulty in assigning communities with certainty.

Groups I and II (the Insh marshes and some of the Torridge sites) tend to be deep sites, shaded by trees to some extent, with low conductivity, but quite high sediment phosphorus and high dissolved oxygen levels, characterised by nymphaeid species. A9 (*Potamogeton natans)* and A14 (*Myriophyllum alterniflorum)* are the main communities, with A7 (*Nymphaea alba*) and A16 (*Callitriche stagnalis*) also represented.

Groups III and IV are quite discrete on the diagram. Group III contains the single site **ilbd2** a shallow drain in the Little Brosna callows with *Chara hispida* and *Potamogeton coloratus* as co-dominants. This community is not represented at any other sites, and does not correspond well with any NVC category, with the closest fit being A11a, although this does not seem appropriate, since the preferential species are either rare or absent. The community seems to favour conditions of high substrate light and high conductivity. The CORINE classification of C24.42 lime-rich oligotrophic river vegetation is characterised by *P. coloratus* and *C. hispida* and is a perfect match. However, the NVC classification does not have a community that can be cross referenced with this. The site is in a shallow drain over exposed marl. Group IV comprises fast flowing shallow river sites on the Torridge and the larger, deeper Little Brosna river in Ireland. These sites are slightly shaded, fast flowing with large particle size substrate, and highly saturated with dissolved oxygen. Characterised by *Ranunculus penicillatus, Fontinalis antipyretica* and *Callitriche hamulata*, these sites all correspond to A17 of the NVC.

Groups V and VI are the Endrick marshes and the Shannon callows sites (with the exception of **ilbd2**). While group V seems to be a subset of Group VI, it is quite tightly clustered on the ordination. These sites are the deeper sites, dominated by *Nuphar lutea, Persicaria amphibia* and *Potamogeton natans* (NVC categories A8, A9 and A10). Group VI is almost exclusively composed of drainage ditches, with a temporary pond on the callows and the more extensive Wards Ponds completing the group. These sites also have high substrate light potential, with a high cover of emergent species and silty sediment. Conductivity and pH are quite high and the sites tend to be shallow. *Glyceria fluitans, Myriophyllum verticillatum*, lemnids and narrow leaved *Potamogeton* species are all well represented at these sites. This group corresponds to A15 of the NVC with A2b and A19 also represented.

Group VII contains all the French sites, with no other areas represented. These sites have a medium sediment texture, high water phosphate levels and quite turbid water. There is also some degree of droughting in many sites. *Ceratophyllum demersum* is ubiquitous, with *Potamogeton nodosus, Ranunculus circinatus* and *Myriophyllum spicatum* also present. This is represented by quite a spread of NVC classes. These may not accurately reflect the communities as *Potamogeton nodosus,* which was abundant in many sites, being rare in Britain is not present in the NVC classification. Many sites are variations of the A5 (*Ceratophyllum*

demersum) community, with A3 and A4 in the ditches. *C. demersum* has previously been reported to occur frequently in oxbows that are permanently filled with water during the growing season, being replaced by *Potamogeton lucens* in periodically drying out water bodies (Adamec *et al.* 1993). The backwater at Decize did not fit well into any category, with A10 showing a very poor goodness of fit. This is a species poor site and difficult to assign to a class.

Group VIII comprises the Spanish sites which are very different from the other study sites, as discussed above. The NVC does not have a classification that covers *Chara* and *Nitella* carpets, the CORINE classification of these sites is algal carpets at the bottom of unpolluted lime-rich lakes.

As the NVC classification was devised specifically for the British Isles its applicability in a European context is doubtful, this may be exacerbated by the northern bias in the aquatic dataset on which the NVC was based (Palmer *et al.* 1992). However in general the communities of aquatic plants that occur over Europe are less dissimilar over the geographic range than their terrestrial counterparts, so the NVC classification has some use for preliminary classification.

Fig 3.4a CCA biplot (excluding Spanish sites) showing site scores and environmantal biplots. TWINSPAN groups delineated by dotted lines (Individual site codes not indicated).

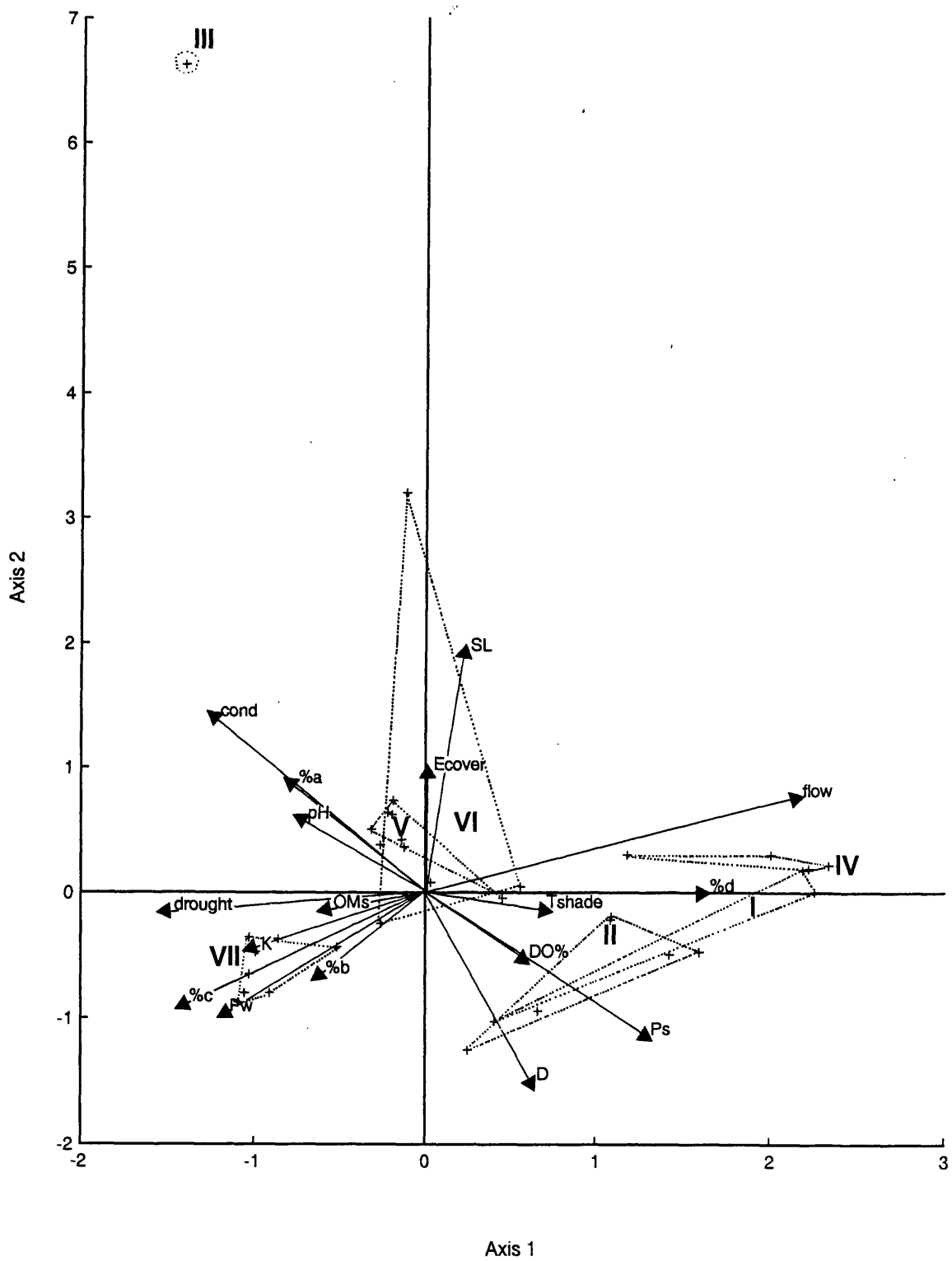
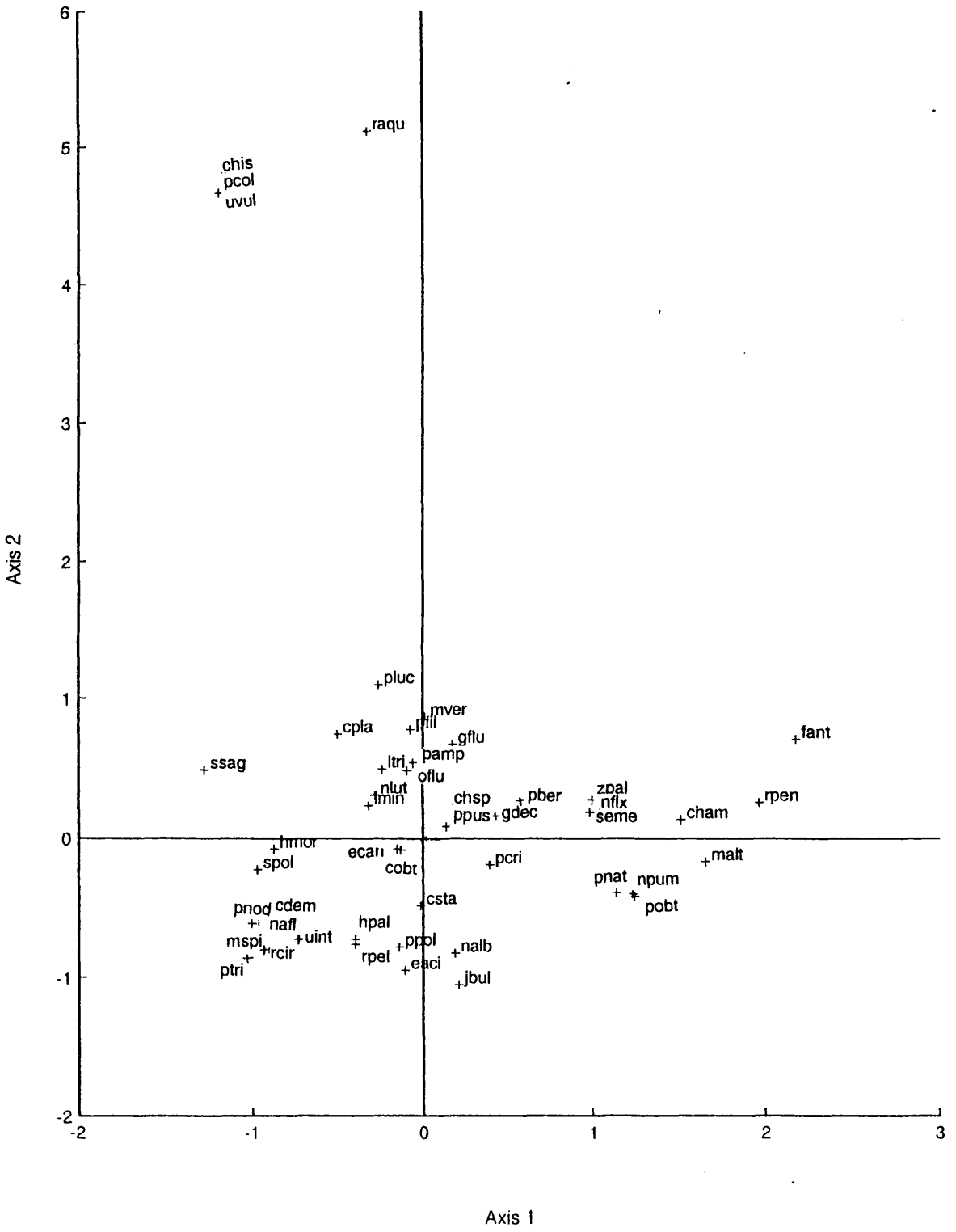


Fig 3.4b CCA ordination (excluding Spanish sites) showing species scores. For species codes see Appendix 2.



Examination of the intraset correlations (Table 3.4) show flow rate and large particle size (%'d') to be correlated with Axis 1. Drought, % 'c' particle size and conductivity are all negatively correlated to the same axis. With regard to the second axis, substrate light, and conductivity were positively correlated and depth and sediment phosphate negatively correlated. Except for the positive correlations with Axis 1, where flow and % 'd' were much more highly correlated than other variables, there tended to be a number of variables all quite weakly correlated with the axes. The significance levels of these correlations cannot be assessed by a straightforward t-test as intraset correlations and canonical correlations have different properties from a normal correlation (ter Braak 1988), one of which is an increased variation. The t-values given by CANOCO for intraset correlations can only be used in an exploratory manner in direct gradient analysis (ter Braak 1988). Correlations marked ** are most significant ($p < 0.01$ for a conventional t-test) and * of secondary significance ($p < 0.05$ for a conventional t-test).

Table 3.4 Intraset correlations of environmental variables with axes

	Axis 1	Axis 2
Sediment organic matter	-0.186	-0.041
Depth	0.200 **	-0.456
Sediment phosphate	0.043	-0.342
Conductivity	-0.400 **	0.424
Dissolved oxygen (% saturation)	0.186	-0.161
pH	-0.235	0.176
Water phosphate	-0.380 **	-0.285
Light extinction coefficient	-0.323 **	-0.140
Flow	0.699 **	0.233 *
Drought	-0.484	-0.045
Tree shade	0.222 *	-0.037
Emergent cover	0.005 *	0.298
Substrate light	0.077 *	0.580 *
% 'a'	-0.252	0.263 **
% 'b'	-0.202	-0.199
% 'c'	-0.458	-0.266
% 'd'	0.528	-0.007

Running CANOCO using forward selection of the environmental variables allows each one to be added sequentially to the model starting with the variable which

explains the greatest variation in the species data. A Monte-Carlo permutation test can then be run on each variable to test its significance in explaining the remaining variation in the data set. This method of analysis shows which variables are redundant (i.e. do not explain a significant proportion of the variation once the variation attributable to the most influential variables has been extracted). Flow, conductivity, water phosphate, % 'a', depth and sediment organic matter all independently explained significant variation ($p < 0.05$) and the variation explained by substrate light and pH was significant at $p < 0.1$.

Inferred ranking of the species along the more influential environmental variables can be made by dropping perpendicular lines from the species co-ordinates to the environmental arrows. Table 3.5 gives these rankings for flow, conductivity and substrate light in ascending order (i.e. the uppermost species is found at high values of the parameter in question).

Table 3.5 Inferred species rankings along major environmental gradients from CCA

Flow	Conductivity	Substrate light
F. antipyretica	C. hispida	R. aquatilis
R. penicillatus	P. coloratus	C. hispida
M. alterniflorum	U. vulgaris	P. coloratus
C. hamulata	R. aquatilis	U. vulgaris
P. obtusifolius	S. sagittifolia	F. antipyretica
N. pumila	C. platycarpa	P. lucens
P. natans	P. lucens	M.verticillatum
Nitella flexilis	L. polyrhiza	P. filiformis
Z. palustris	H. morsus-ranae	G. fluitans
S. emersum	P. nodosus	R. penicillatus
R. aquatilis	C. demersum	C. platycarpa
P. berchtoldii	P. trichoides	Z. palustris
G. declinata	R. circinatus	P. amphibia
P. crispus	L. trisulca	C. hamulata
G. fluitans	P. filiformis	Nitella flexilis
M.verticillatum	Najas flexilis	O. fluviatile
P. pusillus	M.verticillatum	S. emersum
Chara sp.	L. minor	L. trisulca
P. filiformis	N. lutea	P. berchtoldii
P. amphibia	M. spicatum	G. declinata
O. fluviatile	O. fluviatile	M. alterniflorum
N. alba	P. amphibia	N. lutea
J. bulbosus	U. intermedia	L. minor
P. lucens	G. fluitans	P. pusillus
C. stagnalis	E. canadensis	Chara sp.
L. trisulca	C. obtusangula	S. sagittifolia
C. obtusangula	H. palustris	N. pumila
E. canadensis	R. peltatus	P. crispus
N. lutea	P. pusillus	P. natans
C. hispida	Chara sp.	P. obtusifolius
P. coloratus	C. stagnalis	E. canadensis
U. vulgaris	P. polygonifolius	C. obtusangula
L. minor	G. declinata	H. morsus-ranae
P. polygonifolius	E. acicularis	L. polyrhiza
E. acicularis	P. berchtoldii	C. stagnalis
C. platycarpa	P. crispus	N. alba
H. palustris	N. alba	P. polygonifolius
R. peltatus	J. bulbosus	H. palustris
U. intermedia	Z. palustris	C. demersum
H. morsus-ranae	S. emersum	R. peltatus
M. spicatum	Nitella flexilis	P. nodosus
C. demersum	P. natans	U. intermedia
L. polyrhiza	C. hamulata	Najas flexilis
Najas flexilis	N. pumila	M. spicatum
R. circinatus	P. obtusifolius	E. acicularis
P. nodosus	M. alterniflorum	R. circinatus
P. trichoides	F. antipyretica	J. bulbosus
S. sagittifolia	R. penicillatus	P. trichoides

3.4 Discussion

3.4.1 Classification

As this chapter is concerned with the classification of aquatic communities the necessity for classification exercises should also be examined. When systems such as the National Vegetation Classification and CORINE exist is there any need for further attempts at classification? It was deemed necessary in this work partly to enable direct comparison with the functional classification of the same sites carried out by the same statistical processes (Chapter 8) and partly to compare a classification of exclusively riverine wetland communities with the broader classification of the NVC to see if useful subdivisions arose. As emphasised by Whittaker (1962) *'Classifications develop and are improved through continuing interaction of ecologists and natural communities and growing understanding of significant relations of ecosystems. The form of a given classification is determined by no simple verisimilitude or fidelity to nature, but by a complex system of inter balanced value judgements.'*

While the present classification was as far as possible objective, some value judgements were used (e.g. in deciding on the number of final TWINSPAN groups). One way of assessing the value of this classification is to compare it with other existing classifications (Table 3.4). In most cases the TWINSPAN groups showed a sensible relationship to the distribution of NVC categories, with similar or identical NVC classes in each TWINSPAN group. One or two anomalies were apparent. The occurrence of **ilbr** in group IV seemed incongruous, group V may be more appropriate. With the exception of **cemgd** all A9 NVC communities were in group II. The CORINE classification also shows a good relationship with the TWINSPAN analysis. Some groups (I, III, VII) are exclusively of one CORINE type, while II, IV and V have only one member differing. CORINE C22.4 corresponds to still freshwater sites. These comparisons serve to reassure that the TWINSPAN classification displayed is a sensible and meaningful one in terms of grouping like communities. TWINSPAN is, in fact, becoming an indispensable tool for ecologists dealing with large data sets containing species occurrence data (Holmes 1989). It also reinforces the NVC as a good working classification. Inspection of the groups suggest geographical location to be a strong influencing classification, this may be obscuring within-catchment patterns. The NVC classification distinguishes more subtle within-catchment differences. As the TWINSPAN was limited to only dividing groups with more than four members, some of the NVC groups are merged into one TWINSPAN class.

3.4.2 Community and species variation with environment.

The relationship of communities to environment is complex because communities, such as the ones I have defined, are in reality continuous and each constituent species of a community has its own range of chemical tolerances (Moyle 1945). However problems are experienced when attempting to relate individual species distributions to environmental parameters due to the wide ecological amplitude of many aquatic species (Swindale and Curtis 1957; Seddon 1972; Pip 1979, 1984; Kadono 1982a; Carbiener *et al.* 1990). Aquatic plant communities may be more consistent in their relationship to the environment, and are considered by some workers to have more value as bioindicators than species (e.g. Carbiener *et al.* 1990). The combination of TWINSPAN and CCA analysis (Figs 3.4 and 3.5) allows consideration of both community and species relations with the environmental parameters measured. Many workers have emphasised water chemistry as the controlling factor in macrophyte distribution (Moyle 1945; Spence 1967; Seddon 1972), particularly in limnological studies. Additionally depth (Spence 1967), substrate type (Pearsall 1920; Misra 1938) and altitude (Lundh 1951) have all been recognised as influential. In a riverine wetland context preferences are further obscured by the effects of flow. Dennison *et al.* (1993) reported a lack of appreciable correlation between water quality parameters and survival of macrophytes and supported the use of multiple habitat requirements to predict survival. In the present analysis flow, conductivity and light levels at the substrate were all influential in ordinating the communities. These factors will be discussed individually.

3.4.2.1 Effects of flow rates

Flow was identified as an important factor for riverine wetland euhydrophyte communities. Forward selection of the environmental variables, in CCA, selected flow as the parameter explaining the highest proportion of the variation. This has been noted as influential to both species distribution and abundance (Westlake 1973; Haslam 1978; Bornette and Amoros 1991; Chambers *et al.* 1991; Spink 1992). The variety of flow rates in aquatic sites in a floodplain range from still ponds, through ditches and streams to the river channel. The confounding effects of spates and droughts, mean that aquatic ecosystems of a river floodplain are more complex than those found in lacustrine habitats (Bornette and Amoros 1991). The flow ranking presented correlates well with previous findings with a few exceptions

such as *M. spicatum* which is usually associated with moderate flow (Haslam 1978; Holmes 1989).

Flow velocity affects plants in a number of ways. Physical damage such as uprooting or breaking of stems can be considered a disturbance *sensu* Grime (1979). Individual species, such as *Callitriche hamulata* and *Ranunculus penicillatus* are well adapted to high flow velocity through a flexible streamlined growth form and stems resistant to breakage in turbulent flow (Haslam 1978; Spink 1992) or firm rooting. It is difficult from field observations to separate the direct effects of flow rate (e.g. physical damage) from indirect effects (e.g. changes in sediment texture), but it is likely that both have an effect (Chambers *et al.* 1991). Species with adaptations that confer tolerance of a wide range of flow velocities (e.g. *Sparganium emersum* (Bornette and Amoros 1991)) will be able to exploit a range of wetland habitat types. In this study *S. emersum* was observed in deep still lochans, ditches and fast flowing rivers. Its appearance near the top of the flow ranking is probably not reflecting its inability to exist in still waters, but rather the inability of many other species to tolerate high velocity. This highlights the complications present in interpreting species rankings along environmental gradients. Location at the top or bottom of a gradient does not necessarily mean exclusion from the other extremity. For instance species at the bottom of trophic rankings are often not intolerant of high trophic conditions but rather are outcompeted in such conditions (Seddon 1972). Sudden increases in flow velocity, such as winter and spring flooding can lead to severe damage to plant populations in the form of uprooting and physical damage (Brierley *et al.* 1989). This can be particularly damaging in sites where normal flow velocity is moderate or slow and plants are poorly adapted to faster flows.

Flow velocity also affects the ability of plants to take up inorganic carbon because in conditions of high, turbulent flow the boundary layer resistance to uptake is reduced. In dense beds of macrophytes in still waters acute carbon depletion can occur (Van *et al.* 1976). In this way low flow velocity could be considered a stress, reducing the rate of photosynthesis (Haslam 1978; Spink 1992). The ability of a species to utilise bicarbonate will also influence its distribution (Hutchinson 1975). Many *Potamogeton* species are bicarbonate users and common in alkaline systems (Barko *et al.* 1986). Other methods of carbon gain, including crassulacean acid metabolism and use of sediment CO_2, will also influence species occurrence in systems low in free CO_2 (Maberly and Spence 1983; Sand-Jensen 1983; Boston *et al.* 1989).

In conclusion the displayed species ranking seems ecologically sensible in the light of field experience and published work, and can be considered analogous to a disturbance ranking with high flow corresponding to high disturbance.

3.4.2.2 Conductivity and nutrients

Conductivity cannot be regarded as a factor in itself as it reflects the concentration of several major ions, but can be used as a general index of the nutrient status of the water (Swindale and Curtis 1957; Kadono 1982). Many authors regard the water chemistry of a lake as determining which species can inhabit it (Moyle 1945; Spence 1967; Seddon 1972), but recognise the difficulties in precisely determining preferences of all but very restricted species, due to confounding effects of variation in all chemical factors. In addition to the problems of disentangling the effects of multiple parameters in field data many aquatic macrophytes have wide amplitudes with regard to water chemistry (Swindale and Curtis 1957; Seddon 1972; Newbold and Palmer 1979; Pip 1979, 1984; Kadono 1982a). Pip (1979) found that the most significant species affinities to water chemistry parameters in central Canadian waterbodies to be to total alkalinity and total filterable residue although some species showed affinity to pH. Pip also noted that species that showed a significant result for a parameter still tended to have a wide tolerance, but the species occurrence tended to be concentrated to one end of the range. Seddon (1972) considered species of eutrophic waters to be obligate species restricted to the habitat by physiological demands, while species found in dystrophic and oligotrophic sites had a wide range of tolerance but were excluded from the sites of higher trophic status by competition.

The ranking of species along a conductivity gradient (Table 3.5) conforms quite well to published studies concerning trophic preferences (Seddon 1972; Newbold and Palmer 1979; Cernohous and Husak 1986; Caffrey 1986; Palmer *et al.* 1992), although *P. coloratus* is in a misleadingly high position due to its preference for hard waters. *U. vulgaris* and *R. aquatilis* are also surprisingly high; while *P. crispus, Z. palustris* and *S. emersum* would be expected to appear higher in the ranking. These anomalies may be, in part, due to wide tolerance displayed by these species. Seddon's description of species preferences for trophic status of water, shows consistent similarities with the present ranking. While the variety of definitions of terms such as eutrophic and oligotrophic may lead to confusion when comparing studies dealing with trophic relations, they consistently represent a fertility series and, as such, can be used in discussion of rankings. Those species

listed by Seddon as not being influenced by solute concentration all occurred in the middle or bottom of the list suggesting that in some cases they had an advantage over less widely tolerant species in nutrient poor waters. Eutrophic and meso-eutrophic species were ranked between the middle and the top of the series, with the exception of *P. crispus* which was surprisingly low in the ranking. The extreme position of site **ilbd2** on the ordination seems to be ecologically logical rather than the effect of an aberrant data point. The site is a shallow ditch over marl on the Little Brosna callows, supporting the association *Potamogeton colorati.* This has been recognised to occur in sites with a supply of meso-oligotrophic hard water (Carbiener *et al.* 1990; Hoyer 1991), which holds true in this location. The presence also of large quantities of *Chara hispida* at **ilbd2** similarly conforms to the observations of Swindale and Curtis (1957) who also recorded *Chara* spp as abundant in water of high conductivity and restricted to sites with a marl bottom (although *Chara* spp do also occur in non-marl sites). Low conductivity may reflect a stress in the form of limited nutrient availability. High conductivity (as encountered in the Spanish sites, but omitted in the construction of the ranking due to their extreme nature) is also a stress in brackish sites where only a few species of macrophyte can survive (e.g. *Chara, Ruppia, Zannichellia, Potamogeton pectinatus* (Grillas 1990)).

Nutrient enrichment of water exerts an effect through the increased growth of phytoplankton, periphitic algae and some macrophyte species leading to possible shading effects on submerged macrophytes (Phillips *et al.* 1978; Hough *et al.* 1989; Roelofs 1983). This is confirmed by the similar location of the arrows for K and Pw in Fig 3.4. The effects of high turbidity are discussed in 3.4.2.3. This direction of variation can also be considered a form of stress with high values of K corresponding to high stress sites.

pH often exerts an influence on macrophyte distribution through its relationship with dissolved inorganic carbon, water hardness and calcium concentration (Spence 1967). Many species occur in quite a wide pH range (Kadono 1982a), although Hutchinson (1975) noted that at pH <6 some species show limited occurrence. These extremes of low pH were not encountered, and pH seemed to be of little consequence in this data set.

The relationship of species to nutrient status of the water has been shown to correspond well to previously published work, but the influence of sediment nutrition should also be considered. The role of the sediment in providing major

nutrients is discussed only for the sediment chemical parameters measured in this survey i.e. sediment P (**Ps**) and organic matter content (**OMS**). Sediment organic matter content has been shown to be positively correlated with N and P levels in the sediment (Chambers 1987), however, in the ordination **OMs** and **Ps** had different influences from each other, so inferences about N and P nutrition were not made from the relationship of **OMs** and species scores. It is generally accepted that rooted macrophytes can satisfy their phosphorus requirements from the sediment (Best and Mantai 1978; Barko and Smart 1980; Carignan and Kalff 1980; Barko *et al.* 1986). Chambers *et al.* (1989) found that submersed river macrophytes obtain 70% of their phosphorus from the sediments. This would suggest that water phosphate levels are of lesser importance than sediment phosphate in most macrophyte distributions (Pip 1979). In oligotrophic water most phosphorus is taken up from the sediment, while in eutrophic water, water-soluble P probably plays a part in nutrition (Carignan and Kalff 1980; Rattray *et al.* 1991), there is also significant uptake of nitrogen from the sediment (Nichols and Keeney 1976; Best and Mantai 1978). Sediment phosphorus levels and water phosphorus levels do not have a parallel effect, as can be inferred from the CCA biplot. Enrichment of the sediment can encourage luxuriant growth of rooted macrophytes and enrichment of the water promotes pleustophytes, phytoplankton and epiphytic algae (Roelofs 1983). In both cases there is a shading effect on rosette and bottom dwelling species. It has been recognised that sediment composition has an important influence on macrophyte community composition (Barko and Smart 1991), and it is also apparent that sediment characteristics are as much a product of macrophyte growth as a controlling factor (Barko *et al.* 1991). There is little known about lower levels at which N may become limiting, however high sediment organic matter contents can inhibit submerged species (Barko and Smart 1983, 1986); emergent plants are less inhibited possibly due to their greater ability to oxidise the rhizosphere and overcome toxicity problems (Armstrong 1979).

Sediment texture can be important both in influencing rooting success and nutrient availability (Haslam 1978). In larger water bodies sediment texture and organic matter content has been shown to be closely related to the degree of exposure to wind/wave action with plant zonation along exposure gradients (Keddy 1982). It is difficult to separate the effects of exposure, organic matter content and sediment texture. In the small water bodies sampled in this study, exposure is unlikely to be an important consideration so the effect of sediment texture can be discussed in isolation. Some species show distinct textural preferences (Butcher 1933; Haslam 1978; Holmes 1983). For instance *Potamogeton coloratus* seems to prefer fine

sediments (Bornette and Amoros 1991). Stony or sandy substrates are nutritionally poor and growth may be limited, but low levels of organic matter addition can stimulate growth on sandy soils (Sand Jensen and Søndergaard 1979). In this analysis sediment texture did not play a significant role with the exception of % 'a' (fine sediment), which showed a close relation to conductivity and seems to also indicate high nutrient status sites.

3.4.2.3 Light

Light is stressed as an important factor in the distribution of macrophytes (Spence 1967; Spence and Crystal 1970a; Best 1982; Barko *et al.* 1986). The depth to which a species can extend is influenced by light quantity and quality (Chambers and Kalff 1987; Duarte and Kalff 1988; Chambers and Prepas 1988). Light is suggested as the limiting factor with increasing depth in this study. The influence of depth is almost directly opposite to the influence of substrate light availability, suggesting that in this study depth does not have any strongly limiting effects (such as pressure) on the plant, other than light attenuation. Compared with terrestrial shade species submersed aquatic vegetation has a high minimal light requirement (Dennison *et al.* 1993), so light can often be a limiting factor if water clarity is poor.

The influence of light is examined using two parameters in the survey; light extinction coefficient (K), a measure of turbidity; and substrate light levels (SL), a measure of light received at the substrate. The two parameters show different effects in the analysis. As floating-leafed and surface free-floating plants are, to a large extent, independent of this parameter (although it is influential for the former group in the juvenile phase), their occurrence will not be correlated with this parameter, thus reducing its importance in the overall analysis. In river sites changes in turbidity can be frequent, rapid and extreme in response to incidents of spate, erosion or pollution (Westlake 1966). I attempted to obtain reasonable estimates of the average turbidity of river sites by using repeated visits. As well as light attenuation by dissolved and suspended material in the water, self-shading is also important in macrophyte communities where only 0.1% of surface light may penetrate to the bottom of a dense weed-bed (Westlake 1966). Light availability principally affects vegetation abundance, but because species are differentially adapted to low light intensities it also affects community composition.

The morphological adaptations that enhance light capture (both whole plant morphology and individual leaf morphology) are responsive to light regime in submersed macrophytes. Generally plants produce fewer, longer shoots and longer

leaves with a greater surface area when irradiance is reduced (Barko *et al.* 1986; Abernethy *et al.* 1995 subm). Those species that can produce a dense surface canopy (e.g. *Myriophyllum spicatum*) may grow at greater depths in turbid waters than submerged prostrate species (Titus and Adams 1979). Specific leaf area has also been correlated with depth of occurrence for *Potamogeton* species (Spence and Crystal 1970b). Nymphaeid species, possessing strong petioles and floating leaves, may be particularly successful in turbulent and turbid waters (Vermaat and De Bryne 1993).

Shading by trees and emergent plant cover may also reduce euhydrophyte abundance especially in narrow water bodies (Dawson and Haslam 1983; Canfield and Hoyer 1988).

3.4.2.4 Drought and water level fluctuations

Although drought was not as influential as the preceding factors in the final analysis it seemed to be having an extreme effect in determining the species present at the Spanish sites (that were dropped from the final analysis). The effect of drought will be considered together with the influence of fluctuating water levels. Fluctuations in water level were not calculated directly but were evidently of high magnitude at some sites (e.g. Insh marshes, Apremont); they are considered as a similar type of disturbance pressure to droughting.

Grillas (1990) found that in marshes in the Camargue flooding period was the controlling factor with conductivity also correlating to species variation. *Chara aspera* was found in sites characterised by a long dry period (the flood duration and conductivity ranges reported are similar to the conditions found in El Masegar). *Chara* species often appear following a disturbance event (Nichols 1984), persist for a season or two and are then replaced by other macrophytes, but are also recorded as persisting as stable communities for longer than 50 years (Wood 1950). In some cases this is where the community is subject to regular, or annual disturbance. The *Chara* lawns observed in El Masegar, seem to be an example of such a community that is stable in the long term due to the seasonal nature of the habitat which prevents the establishment of other macrophytes in the community. Whether this will continue if the drought periods get longer and the refilling is not annual, or predictable, remains to be seen. Local extinctions are rare in species of temporary water as the species are well adapted to surviving unfavourable conditions (Williams 1987).The persistence of *Chara* oospores in the sediment can be quite long term (Allen 1950), and they can tolerate freezing, drying and ingestion

by birds (Procter 1967; Blindow 1992a), which may allow for re-establishment even after prolonged drought. Oospore germination is also stimulated by a period of desiccation (Allen 1950) and the alternating wetting/drying regime at El Masegar is therefore likely to promote *Chara* dominance.

Chara species are not restricted to the deeper waters as often recorded, but can occur below, amongst or above other macrophyte communities on a depth gradient (Wood 1950; Blindow 1992b) . The species show significant ecological differences and exhibit zonation according to species. Much is missed by grouping the stoneworts as *Chara* spp. A zonation of *Chara* species was recorded in the present study with different species growing in different depth zones of the laguna. The extreme clarity of the water allowed this zonation to be clearly observed from a boat and indeed seemed to be sensitive even to the depth difference resulting from tractor ruts persisting from the dry season. *Chara hispida* var. *major* was ubiquitous, occurring even in the shallowest water depths. *Chara canescens* occurred in the slightly deeper waters and *Chara aspera* was found in the deeper more central areas, and in the deeper ditches surrounding the laguna. Stross (1979) has postulated that the depth boundaries of *Nitella* are determined by a photomorphogenetic switch mechanism at some critical point in the life cycle. This also mediates oospore production and internode length, with longer internodes and less oospore production with increasing depth (Stross 1979; pers obs.).

Water level fluctuations can destroy biomass by exposing plant parts to desiccation if water levels fall, or by decreased light, or dissolved gas availability if water levels dramatically increase. Large water level variations can result in a reduction in community diversity or a shift of peak production to deeper waters (Rørslett 1984), although moderate fluctuations of 1 - 3m $year^{-1}$ can result in a diverse flora (Rørslett 1991). r - strategy species increase with increasing fluctuations (Rørslett 1984). Species better able to survive fluctuating water levels in the form of inundation (e.g. flooding from the river) include *Persicaria amphibia* and *Oenanthe aquatica* (van der Brink *et al.* 1991). Nymphaeids were able to survive a moderate level of inundation. The effects of inundation are both physical (especially associated with summer flooding) and through the effects of changes in water chemistry and turbidity. Data on inundation frequency at the sites is not available, but at the sites where water level fluctuations appear to be a factor (Insh marshes, Apremont) nymphaeids, *P. amphibia* and *Oenanthe* spp were all recorded. Brock (1988) reported that a flexible life cycle pattern and morphological plasticity can enhance survival in widely fluctuating environments. Distribution of standing water

in time and space is the most important factor for macrophytes in temporary water habitats. (Williams 1987).

Both drought and water level fluctuations constitute a form of disturbance, but as the most severely droughted sites were not included in the ordination its effect was not significant so a species ranking was not constructed. The superior disturbance tolerance of the Characeae is however readily apparent.

3.4.3 Species distribution and Grime's CSR model

A detailed description of the model is given in Chapter 4, the basic premise being species tolerance to the three factors competition (C), stress (S) and disturbance(R). The environmental parameters can be used to construct an index of stress and disturbance for each site (Spink 1992). The criteria used to construct these indices are shown below.

Parameter	Stress score	Disturbance score
Tree shade >50%	1	0
Flow = 0	1	0
Flow = 4	0	3
Flow = 5	0	4
SL < 3	1	0
K > 3	1	0
Cond < 100	1	0
Pw = 0	1	0
Ps <500	1	0
Drought = 3	0	1
Drought = 4	0	3

While this is a fairly crude method of characterising the sites in these terms, it serves to explore the relationship of species to these forces. Competition has not been addressed in this discussion as there was no measure of competitive pressure made in the field. The general applicability of Grime's model to aquatic macrophytes will be discussed further in Chapter 10.

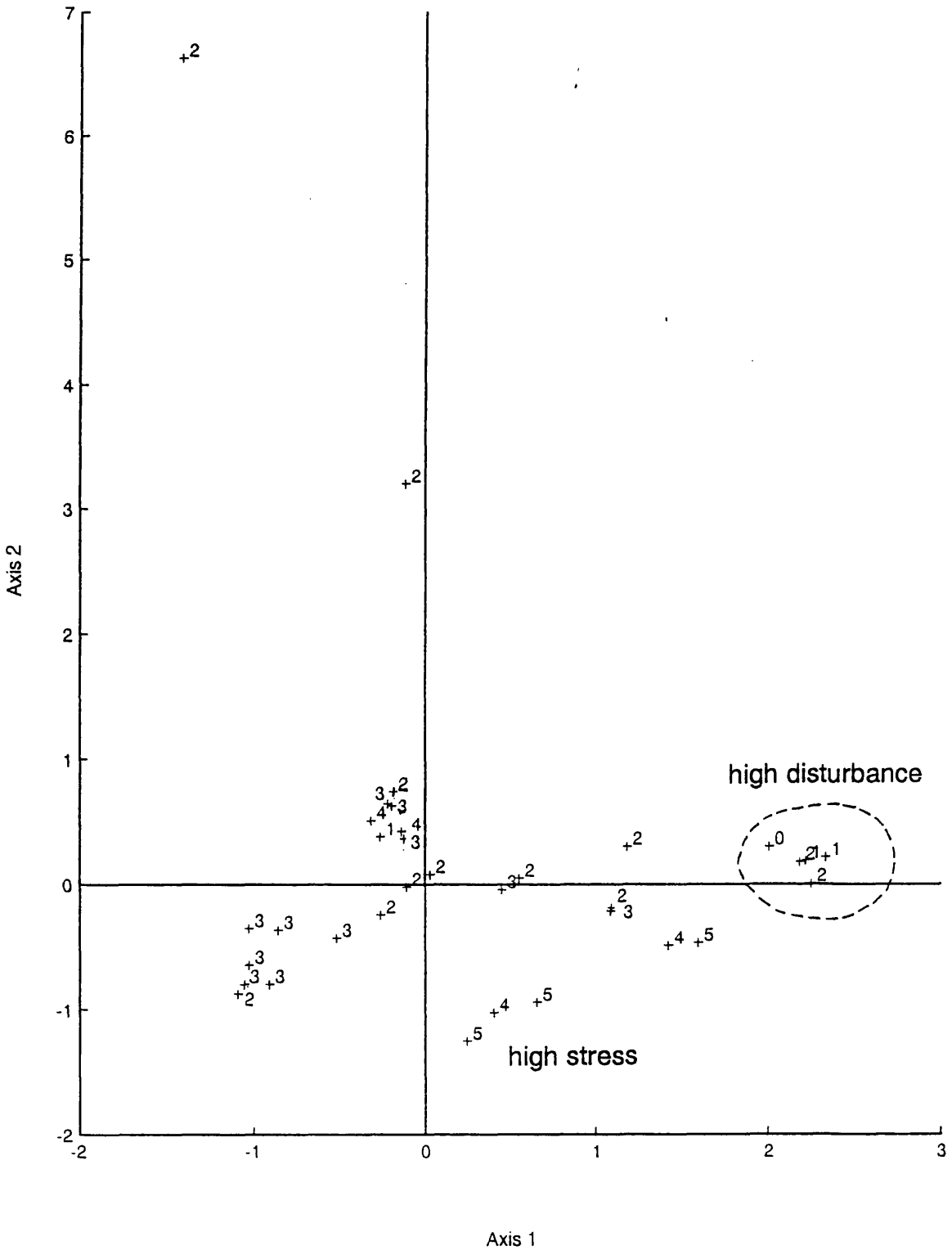
If the CCA ordination is re-examined with the site codes replaced with the stress index scores and the area of high disturbance index indicated (Fig 3.5) the species can be related to these indices. The stress index is shown beside the corresponding site co-ordinate, the disturbance index values were only above zero in the area

indicated (although the highly disturbed Spanish sites are not represented). A visual comparison of this figure with Fig 3.4b suggests the following species as particularly tolerant of stress or disturbance:

Stress	**Disturbance**
J. bulbosus	*F. antipyretica*
N. alba	*R. penicillatus*
N. pumila	*C. hamulata*
P. natans	*M. alterniflorum*
P. obtusifolius	
M. alterniflorum	

As discussed above *Chara* spp are also tolerant of high levels of disturbance. Of these Grime *et al.* (1988) designate strategy classes for only three: *J. bulbosus* SR/CSR; *P. natans* C/SC; *R. penicillatus* C?. The first two both display the stress tolerant elements noted in this study. *J. bulbosus* is given an element of disturbance tolerance by Grime *et al.* (1988), this may reflect its ability to withstand water level fluctuations. *R. penicillatus* is classified C? with no recognition of its tolerance of disturbance. This does not seem to be an accurate appraisal of this species, which has been noted as disturbance tolerant (Spink 1992).

Fig 3.5 CCA ordination (excluding Spain) showing site scores. Site codes replaced by stress index values. Areas with high disturbance index indicated.



3.4.4 Environmental character and species diversity

The negative effects of large water level fluctuations and the diverse flora associated with moderate fluctuations have been noted above. Bornette and Amoros (1991) attributed the species paucity of some zones of their study to periodic flood disturbance and high flow velocity. This type of impoverished community was present in the backwaters of the river Loire also prone to high velocity spring floods. Studies of regulated and unregulated lakes (Wilcox and Meeker 1991) found that sites experiencing natural frequencies and magnitudes of water level fluctuations had the most diverse communities. Too little disturbance gave stable but species poor communities at permanently flooded depths, while too much disturbance allowed only species capable of surviving the physical disturbance or newly established ruderal species to exist.

In their study of a braided river floodplain, Bornette and Amoros (1991) found the most complex macrophyte community in a zone affected by several allogenic processes, including underground and seepage water, periodic river overflow with high nutrient contents and alluvial deposition. Such sites represent a dynamic equilibrium between successional changes and the effects of floods (Bornette *et al.* 1994) They suggested that the thick alluvial deposit may explain the abundance of macrophytes, providing nutrients and root support. In this survey the richest macrophyte communities were found in the sites on the floodplain of the river Allier at Apremont. This site is subject to the processes described by Bornette and Amoros and seems to support their contention. A negative correlation has been observed between species richness and frequency of inundation in still waters associated with rivers in the Netherlands. Negative correlations between species richness and orthophosphate concentration and nitrate concentration in the ambient water and species richness and turbidity of the ambient water were also demonstrated (van der Brink *et al.* 1991).

3.5 Summary

Sites were successfully classified by their species composition into groups that corresponded well to existing classifications.

There was no single factor controlling community composition in the survey but the most influential were flow, conductivity, water phosphate, proportion of fine sediment particles, depth, sediment organic matter and substrate light availability.

It was difficult to relate species or communities to environmental factors with precision due to the amplitude of species tolerances and the confounding effects of the measured environmental parameters. Rankings of the species to some of the more influential parameters gave similar results to previous studies.

An estimation of species tolerance of stress and disturbance pressures was made by using integrated indices.

Species diversity was highest in sites with a range of allogenic processes resulting in thick alluvial deposition. To achieve high diversity sites should also be free from excessive disturbance (e.g. by inundation) or high nutrient concentrations in the ambient water.

Chapter 4

DEFINING FUNCTIONAL GROUPS FROM ESTABLISHED PHASE TRAITS

Chapter 4

DEFINING FUNCTIONAL GROUPS FROM ESTABLISHED PHASE TRAITS

4.1 Introduction

This chapter

- discusses the relevance of the growth strategy approach both in general terms and in relation to the selection pressures peculiar to an aquatic environment.

- uses analyses of field-measured and literature-based traits to construct a functional grouping of euhydrophytes in the established phase.

- selects key traits or predictors for the functional groups

- discusses the validity and ecology of the functional groups

4.1.1 Strategy Theory.

The use of species nomenclature as the basic framework for botanical studies has for a long time been dominant. Within ecological research the European phytosociological approach is based on description of species assemblages. While recognising the species as a `useful vehicle for communication between ecologists' Grime (1984) saw a need for estimations of the ecological amplitude of each species and a functional classification within which to locate these species. Earlier this century the development of a life forms classification by Raunkiaer (1939) was a move away from the predilection for individual species to a more functional classification.

Much present work on methods for functional classification of vegetation arises from the r-K continuum proposed by MacArthur and Wilson (1967) to summarise the large diversity of plant and animal life strategies. The extremes are r - selected species that have short life spans and allocate a large proportion of their resources to reproduction early in life, and K - selected organisms that have superior competitive ability in stable environments and allocate less resources to rapid population growth. While the value of this model as a positive step towards the

understanding of many ecological processes was accepted, several workers found its single axis of variation unsatisfactory. An additional axis, termed adversity (Whittaker 1975; Southwood 1977) or stress (Grime 1979), was proposed. A debate in `Nature' marked the beginning of Grime's involvement in the development of strategy theory (Grime 1973a 1973b, 1974; Newman 1973). Sibly and Grime (1986) later presented a mathematical model to show adversity selection, using the supply of mineral nutrients to roots as an example. Southwood (1977) proposed a 2-D representation with one axis representing r-k and the other adversity. Grime's strategies arise from the relative contributions of three forces on a plant or plant community. (Objection has been made to the use of the term strategies as it has teleological implications. However it has become widely used in this context and while there is clear understanding of its meaning as a set of genetically defined characteristics, it is a convenient term to employ.)

These forces are defined as; 'stress', the external constraints which limit the rate of dry matter production of all or part of the vegetation; 'competition', the tendency of neighbouring plants to compete for the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space; 'disturbance' the mechanisms which limit the plant biomass by causing its partial or total destruction (Grime, 1979). Of these, stress and disturbance are environmental factors that are present at different degrees in a habitat. If we simplify their occurrence to either 'high' or 'low' intensity there are four resultant combinations of the two factors. Grime considered high intensity of both factors to result in an environment too hostile for plant growth. The remaining combinations gave rise to three corresponding plant strategies; C = competitor (low disturbance + low stress), S = stress tolerator (low disturbance + high stress) and R = ruderal (high disturbance + low stress).

The relationship of these strategies with more traditional life history theories based on plant demography has been investigated by Silvertown *et al.* (1992), and while they failed to find a relationship between CSR strategies and chosen demographic variables they also admitted that current demographic work could benefit from a more comparative approach. Grubb (1985) added to the definition of disturbance the caveat that senescence of individual plants is excluded. Criticism has also been made of the use of the word 'stress' in this context. Grubb (1985) argues that it reflects productivity only and many other stresses can be defined. Rørslett (1989) objects to the definition of disturbance as it is a biological effect rather than a cause. Verhoeven *et al.* (1982) also criticised the vague definition of environmental factors and highlighted the difficulties in quantifying them.

The three strategies described above are termed primary strategies by Grime (1979). He also described four secondary strategies; competitive ruderals (CR), stress-tolerant ruderals (SR), stress tolerant competitors (SC) and CSR strategists. As noted by Grime *et al.* (1988) *'In the real world the C-S-R equilibrium varies from place to place, even within a plant community, and on diurnal, seasonal and successional time scales, for this reason communities often contain species of widely differing strategy.'*

A different approach to understanding plant community structure is presented by Tilman (1977), based on resource acquisition. His theory attempts to predict competitive success as a function of the concentration of limiting resources. A number of contradictions arise from these two models, but it has been argued that many of these are due to differences in perspective, emphasis and terminology, and that there is much general agreement between the two theories (Grace 1991). In this work the theories outlined by Grime (1979) and Grime *et al.* (1988) serve as a starting point. These were preferred over Tilman as they do not concentrate exclusively on competition as a structuring force. The role of competition in structuring macrophyte communities may be minor (Best 1988; Wilson and Keddy 1991), so a broader based approach is preferred.

The other innovation to the r-K model proposed by Grime (1979), was the uncoupling of regenerative and established phase characteristics, following problems in linking the two phases. This recognises that different selection forces and design constraints are pertinent in the regenerative phase in comparison to those in the established phase. Grime (1979) assigned five categories to the regenerative phase; vegetative expansion; seasonal regeneration; persistent seed or spore bank; numerous widely dispersed seeds or spores; persistent juveniles. He found that the established phase strategies were not consistently linked with any of the regenerative phase categories, and so dealt with the two phases separately. This has been confirmed for emergent aquatic plants by Shipley *et al.* (1989), and semi-arid communities (Leishman and Westoby 1992). Wiegleb and Brux (1991) found no correlation between reproductive strategies in *Potamogeton* and environmental conditions expressed as stress and disturbance. In this study the two phases were examined separately and then the relationship between the two investigated. Chapters 6 and 7 deal with regenerative phase strategies.

Grime (1979) introduced a triangular ordination, the three axes representing the relative importance of three basic 'strategies', as a convenient and visually accessible way of representing a species strategy. The process of ordinating species on the triangular diagram (concentrating here on the established phase) has been refined since its inception. Early ordinations (Grime 1979) used measures of Relative Growth Rate and a Morphology Index to represent competition and stress as co-ordinates for ordination. These crude methods were much criticised, although they served the purpose of establishing a framework to be improved upon. More recent ordinations (Grime 1988) use a more elaborate system based upon the recognition of a number of plant 'traits' (genetic characteristics) which correspond to the three basic life strategies. In the current work plant traits have not been attached to a particular strategy so an ordination such as this is not feasible. A general discussion of traits associated with each functional group is given in its place.

Grime and co-workers identified six principles which have proved useful in the task of identifying the ecological and evolutionary significance of particular traits (Grime *et al.* 1988). These are outlined in brief, and their relevance to this study discussed.

1. *Mechanisms excluding an organism or reducing its abundance in a particular habitat may be suggested on the basis of differences in requirements or in tolerance which distinguish it from other organisms which are more successful in the habitat.*

2. *Comparisons between species of contrasted ecology reveal many differences and it is difficult to determine which, if any, are of ecological significance. Attention should be confined to the more consistent differences between successful and unsuccessful species.*

3. *Where available, populations of the same species drawn from contrasted habitats may provide opportunities to examine variation with respect to a smaller number of potentially critical characteristics. It is advisable to review the evidence from intra-specific studies within the context provided by broader inter-specific comparisons.*

4. *It is rarely profitable to examine variation in a single attribute without reference to other characteristics of the organism under study.*

5. *Care must be taken in the choice of attributes to be measured. In some plants development is extremely plastic making extrapolation of data unrealistic.*

6. *Studies involving large numbers of species may provide opportunities for comparison and interpretation. This may extend beyond the identification of traits that have been the subject of natural selection, to the recognition of components which have a limited capacity for phenotypic adjustment. These aspects have probably been a recurrent focus for selection pressures and are internal constraints limiting the potentiality of particular taxonomic groups.*

Principles 1 and 2 can be used to draw up lists of traits relevant to the populations under study. Grime *et al.* (1988) have established a set of traits they found useful in the study of the herbaceous plants in the Sheffield area and this has subsequently been adapted to apply to aquatic macrophytes (Rørslett 1989; Murphy *et al.* 1990). Use of species rather than populations has been criticised (Verhoeven *et al* 1982), and principle 3 draws attention to this point. In this study field measurements were taken at the population level making it possible to analyse and compare intra- and inter-specific variation. Analysis should involve the examination of variation in a set of independent traits (principle 4). In this work suites of characteristics falling under a single general category (e.g. morphology, phenology) have been used. Initial analysis is executed on the entire set of traits, with clustering and ordination dependent on the variation in all traits. Care must be taken in choosing traits as plasticity in a trait may be just the feature that makes it significant to a particular strategy. For example the plastic response of roots in response to nutrient concentrations may be of significance to a competitive strategy (Grime *et al.* 1986; Sutherland and Stillman 1988). In covering a high proportion of the European euhydrophyte flora there is scope for interpretation of both proximal and ultimate determinants in aquatic species. There may be significant internal constraints in this species set limiting the capacity for phenotypic adjustment but these may be recognised when comparisons of traits are made with a terrestrial species group. Within the aquatic environment, evolutionary adaptation to current stress and disturbance forces will have followed a different path to terrestrial counterparts.

Once traits have been identified they can be used in a number of approaches. Grime *et al.* (1988) classified each species according to the ratio of traits belonging to each strategy. They then classified the most consistent species into seven strategy types (three primary and four intermediate) by use of a dichotomous key based on life history characteristics. These marker species were then used to ordinate each

vegetation sample. The marker species were weighted according to their abundance. The vegetation samples (2008 in all) were grouped into hexagons within the triangular representation and the percentage occurrence of a species in each hexagon plotted. These values can then be used to plot contours and assign a centroid for each species. This gives a visual representation of the species strategy and its ecological amplitude. This approach is not appropriate for a smaller scale study such as this, and so the method used to group species was based more directly on the traits possessed by the euhydrophytes.

So far this discussion has been limited to a species level, the next step is to analyse at a community level (see chapter 8). Various workers have attempted this (Grime 1984; Rørslett 1989; Murphy *et al.* 1990; Hills *et al.* 1994). This can be by means of a strategy index (Rørslett 1989; Murphy *et al.* 1990), which assesses the relative importance of each strategy element in the set of populations making up the whole community. It uses the strategies assigned to each population and weights them according to abundance. For each element the index lies between 0-1 and the summation of all elements is 1. An alternative and complementary approach is to plot percentage occurrence of each strategy type into the appropriate element of the triangular representation (Murphy *et al.* 1990). This can be used for visual comparison between communities and highlights the contribution of the intermediate strategies. Grime (1984) plotted constituent species in the triangular ordination by the centre of their contour diagram, to show the orientation and spread of the community. The value of using a strategy approach at the community level was clearly explained by Grime *et al.* (1988), *'the classification of plant communities with respect to the strategies of their component species is also valuable, because it provides a means of predicting the rate and direction of any cyclical or successional change. Knowledge of strategies also allows prediction of the resilience of vegetation to climatic fluctuation, herbivore or human disruptive influences.'*

Now the basic concept of strategy analysis has been covered, a number of recommendations and criticisms are appropriate. Grime *et al.* (1988) identify four points relating to the model which are summarised and discussed below.

1.*'It provides a compact framework in which to connect disparate threads of ecological information and a basis on which to predict the direction and rate of floristic response to alterations in the nature or intensities of stress or disturbance.'*

This is of interest in a study designed to investigate the response of euhydrophyte communities to anthropogenic pressures. An evaluation of the validity and resilience of the approach in riverine wetland communities, and an indication of any modification to previous approaches, will be useful for future studies in similar habitats.

2.*'A central assertion of the triangular model is that the intensity of competition for resources (C) declines progressively with increasing intensities of stress (S) and/or disturbance (D). This equilibrium is a major determinant of vegetation structure and species composition at any site. Opportunities for analysis and description may be expected , therefore, wherever it proves possible to recognise measurable plant characteristics which vary in relation to the prevailing intensities of C, S or D.'*

Loehle (1988) criticised the geometry of the triangular model, and in particular the validity of the three axes summing to one. Grime's model however is based on the use of relative measures of the three environmental variables and as such is a convenient way of showing the influences of these variables and the strategies they give rise to. The summation to one implies a trade off between traits, as is stated by Grime (1985) and in the herbaceous vegetation in the Sheffield area this has so far been the case. However Grubb (1985) gives the example of *Elymus flavescens,* a plant that exists on sand dunes which are regularly and severely disturbed by sand storms (D) and subject to severe drought (S). This is a condition of high S and high D that Grime regarded as inimical to plant survival. Another example is *Phragmites australis* in Egypt, which can withstand severe disturbance in the form of burning, cutting or ploughing and the severe stress of highly saline soil (M. M. Ali, pers. comm.). Results from strategy analysis of aquatic macrophyte communities show some similar anomalies (Kautsky 1988), including the common occurrence of isoetid vegetation in the high stress and disturbance environment created in oligotrophic, wave disturbed lakes (Farmer and Spence 1988). However it is difficult to delimit when a stress or disturbance changes from moderate to high levels. The difficulty of measuring C, S and D intensities has been noted by Verhoeven *et al.* (1982).

3. *'In any analysis of vegetation it is necessary to distinguish between the selection forces which have determined its essential characteristics, ultimate determinants, and those which are operating at the present time, proximal determinants.'*

The selection forces that led to adaptations for existence in aquatic habitats are just such ultimate determinants. Although both selection forces are relevant to strategy analysis while working in a particular community, proximal determinants will be governing the fine scale tuning of the community. The inability of strategy theory to address itself to small scale changes has been criticised (Harper 1982), however a community may, for example, be basically stress tolerant (e.g. Arctic-alpine plant communities) but the small scale variations in strategy are governed by the proximal selection forces of stress, disturbance and competition.

4. *'Except in extreme conditions it is unlikely that plant communities will be composed exclusively of species of similar strategy, due to seasonal, successional and spatial changes altering the balance in the C-S-D equilibrium both spatially and temporally.'*

There are quite dramatic differences in species diversity displayed at the survey sites. Some are virtually monospecific while others have a large number of species with no clear dominant. It will be revealing to see if this is reflected in strategy terms, or if one strategy type is dominant. The range of different strategies (as well as the ecological amplitudes of constituent species) exhibited by a community may give an indication of its resilience to change. Work in terrestrial systems suggests it is unusual to have only one strategy type in a community. Grime (1988), in reviewing the implications of strategy theory, suggests that *'analysis of the strategic diversity within a plant community will... provide clues to the mechanisms which permit co-existence and control the relative abundance of species.'* Comparisons of the strategic diversity displayed by environmentally different sites may provide further clues to these mechanisms.

Although Grime advocates investigating variation of strategies between populations of a species his results are reported on a species basis with the range of species characteristics shown. Murphy *et al.* (1990) designed their analysis on a population basis (although the range of populations was limited) but, since they uncovered no differences, found it convenient to adopt a species based approach. This may not always be the case however, because well delimited sets of genetically defined characteristics occur in populations rather than species (Verhoeven *et al* 1982). Bearing this in mind, in this study initial field measurements were undertaken at a population level.

Despite the criticisms levelled at it, strategy analysis is useful to ecologists as a simple and easily understood way of presenting a complex set of data on adaptive traits (Murphy *et al.* 1990). Southwood (1988) encouraged research into strategy theories but suggested three improvements:

1. Further rigour in the quantitative definition of axes of templets.
2. Explicit models of life history strategy to explore the trade off between the various tactics.
3. More holistic studies on communities and organisms along one or other of the axes to test the systems and predictions that have been made. Combinations of field observations with information from the literature may be a powerful comparative approach.

While all three recommendations are valid, the third recommendation has been particularly noted, and this approach is the basis of the work presented in this chapter. However, Bradshaw (1987) described three limitations to the inferences that could be drawn from comparative studies: 1) There is no way of determining the generality; a very large number of comparisons is needed. 2) An asymmetry of proof exists (i.e. Popperian principles dictate that only disproving a hypothesis is possible), therefore imagination is needed to create testable hypotheses. 3) There are problems in attributing particular effects to particular causes, because of confounding variables. All of these limitations are noted and there implications discussed as the results of the study are presented.

4.1.2 The predictive use of strategy theory

A clear statement of the potential application of this approach is given by Shipley and Parent (1991); *'community ecology requires a set of predictive relationships that transcends taxonomic boundaries and allows one to extrapolate from the particular to the general. It is therefore important to know how general the relationships are that we now possess and how accurately these relationships can predict.'* Various predictive relationships between individual plant traits, or strategies, and environmental gradients have been reported. Shipley and Keddy (1988) found a positive correlation between sensitivity to nutrient stress and relative growth rate. This would be expected from Grime's theories, with competitive plants having high relative growth rates, but high vulnerability to nutrient stress; while

stress tolerant plants have lower relative growth rates but are less sensitive to nutrient stress. They suggested that this may allow the prediction of the response of species to suboptimal resource levels. Shipley *et al.* (1989) documented increasing exhibition of competitive traits in wetland plants along a gradient of increasing soil fertility and increasing incidence of stress tolerant traits along a gradient of increasing water depth. Gaudet and Keddy (1988) noted a relationship between competitive ability and morphological plant traits. Of particular importance were plant biomass, plant height, canopy diameter, canopy area and leaf shape. Franz and Bazzaz (1977) used 'niche differentiation' as a statistic of a population which represents a holistic response to the environmental complex. They relate this to a single environmental factor, flooding probability. While this is a species based model it uses a functional characteristic to define the species changes. Duarte and Roff (1991) developed a predictive model based on plant traits, of submersed macrophyte community response to environmental change. Montavalo *et al.* (1991) recorded a change in morphological and functional traits along an altitudinal gradient in the Central Spanish mountains. Day *et al.* (1988) described variation in strategies (or functional groups) along fertility and disturbance gradients in a marsh. The variation of the functional groups delimited in this chapter is discussed in relation to environmental character in Chapter 8.

In concluding this evaluation of strategy approaches we must bear in mind that while the approach is a useful descriptive, and to some extent predictive tool, it should not be concentrated on to the exclusion of autecological research. Without background knowledge of the organisms under study the points illuminated by the analysis will not be understood. While some studies find the three strategy model too simplistic (Menges and Waller 1983), Day *et al.* (1988) conclude that, in the modelling of plant communities, at one extreme there are simple multivariate descriptions of vegetation based upon species that are site specific with low generality; at the other extreme are broad conceptual models that may not apply to specific communities or small scale variation. By shifting viewpoints along this continuum it is possible to detect principles that would be missed by insisting on one or the other. This would appear to be the case for a study of riverine wetland euhydrophytes, where existing broad models do not seem applicable, yet a mere cataloguing of vegetation types seems inadequate for the purpose of generalised predictions.

4.1.3 Applications of a functional approach to aquatic vegetation.

At present strategy analysis (or a functional approach) has not been widely applied to riverine euhydrophytes since most of the work carried out has been on herbaceous species, and in particular those of grasslands. Grime *et al.* (1988) did not include aquatic species in their work because '*criteria were not available*'.

Recent applications of strategy theory to aquatic vegetation have been have been largely confined to data from lacustrine habitats or emergent communities (Boston 1986; Farmer and Spence 1986; Day *et al.* 1988; Kautsky 1988; Shipley *et al.* 1989; van Vierssen 1990; Murphy *et al.* 1990; Springuel and Murphy 1991) leaving little detailed investigation of the validity of the approach in riverine euhydrophyte communities. Day *et al.* (1988) proposed five strategies from the Ottawa River: clonal dominants; gap colonisers; stress tolerators; reeds; ruderals. These were arrived at by measuring environmental traits and grouping species according to them, before commenting on the traits of the resulting groups. Rørslett (1989) adapted Grime's set of traits for aquatic plants and used these to analyse the relationship between the strategy elements and increasing water fluctuations. As would be expected from strategy theory, species possessing ruderal traits predominated where fluctuations were high. Rørslett related this finding to the occurrence of a transient niche as discussed in Rørslett and Agami (1987).

Murphy *et al.* (1990), using the same set of traits developed by Rørslett (1989), found a high incidence of stress tolerant traits in plants occurring in habitats characterised by low nutrient availability and low pH, and a higher occurrence of disturbance-tolerant and competitive traits in plants found in productive lakes impacted by fluctuating water levels. They concluded that a strategy approach is valid for highlighting differences in environmental pressures influencing lake habitats and went on to suggest that the strategy approach might also help pinpoint the relative importance and contribution of anthropogenic and natural pressures. For example the increased mineral ion loading in one loch was not reflected in gross chemical changes over a 58 year time period, but changes in the community strategy were still apparent.

Duarte and Roff (1991) used submersed macrophyte architecture and life history strategies to develop a predictive model for community response to environmental change. Using architectural and life history characteristics they were able to predict successfully species dominance, absence and rank at sites along a productivity gradient. Kautsky (1988) recognised four primary strategies for aquatic

macrophytes in the Baltic Sea. Light was chosen as the primary stress factor and exposure as a measure of disturbance. The plant traits measured were maximum net production and a 'morphology index' based on height of canopy and lateral spread. Kautsky divided Grime's stress tolerator strategy into 'biomass storers' and 'stunted strategy' to give her four strategies. These last two categories of plants exploited low disturbance + high stress and high disturbance + high stress respectively, although she agreed with Grime that under conditions of extreme stress combined with extreme disturbance plant survival would not be possible. Kautsky (1988) went on to outline the key morphological, physiological and life history traits of her four strategies.

Wiegleb and Brux (1991) in an investigation of the genus *Potamogeton* do not consider that strategies, or individual plant traits, are strictly correlated to a particular habitat condition (conceptualised as predictability and severeness of habitat). They consider that the same environmental pressure can be resisted by different traits (e.g. heavily disturbed sites can be colonised by various regenerative strategies: perennial rhizomes, fragments, mobile turions or a permanent seed bank). They concede that traits can be considered vital attributes and may allow predictions on the future persistence of those plants, as suggested by Noble and Slatyer (1980) and expanded by Wiegleb *et al.* (1991). They also highlight the advantages of undertaking research at different levels of organisation (e.g. population, genet, clone, patch, shoot complex, vertical shoot, modular unit) as some traits (e.g. life span), require different levels of research and cannot always be generalised at species level. Wiegleb *et al.* (1991) attempted to explain decline and maintenance of *Potamogeton* species in lowland rivers and streams in terms of life history characteristics. They based their choice of life history characters on the assumption that fitness in a clonal plant such as *Potamogeton* is determined by optimally allocating resources to fragmentation, vertical and horizontal growth. The characters they chose were mobile turions, unspecialised winter buds and re-rooting fragments, relating to vegetative reproduction; perennating rhizomes, perennating stolons, fast growing stolons and emergency turions, relating to horizontal growth; infinite growth, phenotypic plasticity, synchronous shoot polymorphism and regrowth from reserve buds, relating to vertical growth. They suggested that mobile turions, rooting shoot fragments, regrowth from reserve buds, a perennating rhizome, phenotypic plasticity and synchronous shoot polymorphism were key characters under conditions of intense disturbance. Bornette *et al.* (1994) found that species traits could be used to explain macrophyte distribution in a river floodplain, although they did not restrict themselves to euhydrophytes.

Many characters of aquatic plant strategies (and general plant strategies) have been dealt with in detail individually (Al-Mufti *et al.* 1977; Raven 1981; Grime and Mowforth 1982; Grime *et al.* 1985; Givnish 1987; Sondergaard 1988; Duarte and Kalff 1990); these and other sources are used to compile the list of species attributes analysed in this chapter. A list of suitable traits for investigation can be compiled by looking at the basic functions of the organism and looking for traits related to these functions; by looking for traits related to an investigator defined function; or by listing as many measurable traits as possible from the study and then investigating the patterns. The latter approach has been commended as pragmatic for exploratory studies (Keddy 1992a) and as this work is looking for a generalised classification this is most applicable.

4.2 Methods

As outlined above the approach used was a complementary analysis of a traits obtained from the published literature and field measured traits.

4.2.1 Literature derived traits.

Information was taken from the literature on a wide range of species and species traits. This was synthesised down to a list of traits on which information was available for most species. Over 70 works were used in producing this list (see Bibliography). 18 traits were used, but for the purposes of analysis some traits were divided into attributes which allowed them to be presence/absence coded (Leishman and Westoby 1992). This resulted in 34 attributes in total, which are given in Table 4.1. Scores of 0, 1, 2 were allocated to each attribute with 0 indicating absence of the attribute, 2 indicating presence of the attribute and 1 indicating conflicting evidence or only occasionally exhibited. The species by traits matrix is shown in Appendix 5. The 45 species included were those encountered in the 1992 field survey, which covers the majority of species encountered over the entire survey period, with the exception of those few unique to the 1993 survey.

4.2.2 Field measured traits

Field measurement of traits was carried out between April and October 1992, and April to September 1993.

The field traits measured were morphological, and all measurements were done at the ramet scale of organisation. A ramet is defined as a modular unit of a clone, that may follow an independent existence if separated from the parent organism (Lincoln *et al.* 1982). A description of each measure is given in Table 4.2. Values are based on 10 replicate measurements taken from independent ramets. Where this was not possible, or was considered too destructive, smaller numbers of replicates were used, to a lower limit of 5. Where possible measurements were taken on fruiting specimens to ensure that plants were mature. Measurements were taken at the population level (5-10 replicates per population) and the mean of these measurements used at the species level. Between one and seven populations were quantified for each species. The species by traits matrix (population level) is given in Appendix 6.

Table 4.1 Established phase traits taken from the published literature

No.	Trait	Attribute	Code
1	Growth form	free floating surface	ffsur
		free floating submerged	ffsub
		submerged rooted	subr
		submerged and floating leaved	subf
		floating leaved only	flo
2	Wintergreen		wg
3	Potential annual		a
4	Canopy former		cf
5	Amphibious		amp
6	Heterophyllous		het
7	Pollen vector	wind	win
		water	wat
		insect	ins
		self	self
9	High below : above ground ratio		bta
10	Lacunal air spaces		lac
11	Extensive lateral spread		lat
12	Vigorous seed production		vsp
13	Shoot architecture	single stem, few or no branches	snonb
		multiple stems arising from base	mult
		single stem, many branches	sinb
14	Plant size	small 0-10cm	pls
		medium 10-40cm	plm
		large 40cm+	pll
15	Leaf type	rigid	lr
		soft	ls
		waxy	lw
16	Leaf area	small	las
		medium	lam
		large	lal
17	Flowering phenology	early (april/may)	ear
		mid (june/july)	mid
		late (august/september)	late
18	Bicarbonate user		hco3

Table 4.2 Established phase traits measured in the field

No	Trait	Method	Units	Code
1	Proportion floating leaves	no floating leaves divided by total number of leaves	%	%fl
2	Total no. leaves	no. leaves per ramet	integer	tlv
3	Leaf length	callipers	mm	lvl
4	Leaf breadth	callipers	mm	lvb
5	Leaf thickness	micrometer	mm	lvt
6	Internode distance	callipers	cm	int
7	Leaves per node	count	integer	lpern
8	No.sexual reproductive structures	no. reproductive structures discretely separated on the stem (e.g. spike)	integer	norep
9	Stem thickness	micrometer	mm	st
10	Stem length	maximum stem length	cm	sl
11	Biomass of stem	stem dry weight	g	bios
12	Biomass of leaves	total leaves dry weight	g	biol
13	Biomass of sexual reproductive parts	total fruit/flower dry weight	g	bior
14	Biomass allocation	Proportion of dry weight in stems, leaves, sexually reproductive parts	%	%s,%l,%r
15	Total biomass	dry weight of entire ramet	g	tbio
16	No. of seeds	Total number of seeds	integer	nseed
17	Leaf area	DELTA T video leaf area meter.	mm^2	la

Dry weights were measured, as an indicator of biomass (Harper 1977), to four decimal places on a Precisa 125A digital balance, after drying to constant weight at 60°C. Leaf areas were measured to the nearest mm^2 on a Delta-T area measuring video system . Image analysis based techniques such as these have been compared against calliper measures and other techniques and give significantly better results especially for dissected leaved species (Gerber *et al.* 1994). Leaf length and breadth and internode distance were measured using callipers. The middle internode and leaves of a plant were chosen for measurement. Leaf thickness and stem thickness were quantified using a micrometer. Stem thickness was measured 5 cm above the sediment level. Leaf thickness was measured as close as possible to the centre of the leaf but not over a vein. Stem length was taken as the length of the shoot when fully extended.

4.3 Data Analysis

4.3.1 Defining functional groups

The aim of analysis of the large data sets produced by field measurements and by literature review was to group the populations and species into a set of ecologically sensible groups using the attributes they possess. The concept of grouping species or communities is a construction of ecologists and it is a matter of debate whether variation in ecological communities occurs as discrete, discontinuous classes or as continuous community variation (Gauch 1982). It is also unclear how the variation of species attributes is structured. What obviously is important is not to rigorously impose an artificial structure on the data, but to try to reflect the true patterns of variation as far as possible, although it is accepted that, for practical purposes, arbitrary dissections must sometimes be imposed on essentially continuous community variation (Whittaker 1962). Gauch (1982) recommends that if variation is discontinuous then classification is a natural framework but if it is continuous then ordination is more natural. He therefore advocates the complementary use of both methods.

In the analysis of the established phase traits I did not predefine groups or 'strategies' to which the species must conform, but rather the data was used to form ecologically sensible groupings of species which could then be examined and categorised. Botkin (1975) defines functional groups as sets of plants which have common physiological, reproductive and life history characteristics and where variation in each characteristic has specific, ecologically predictive value. While physiological traits have not been given much emphasis in this work, it is recognised that this is not ideal and it is accepted that they play an important role in any functional classification. It is hoped that grouping by the selected traits will reflect some of the underlying physiological characteristics of the group. MacMahon *et al.* (1981) adopt a more holistic outlook, defining a functional group as '*all organisms which perform the same investigator defined ecosystem function*'.

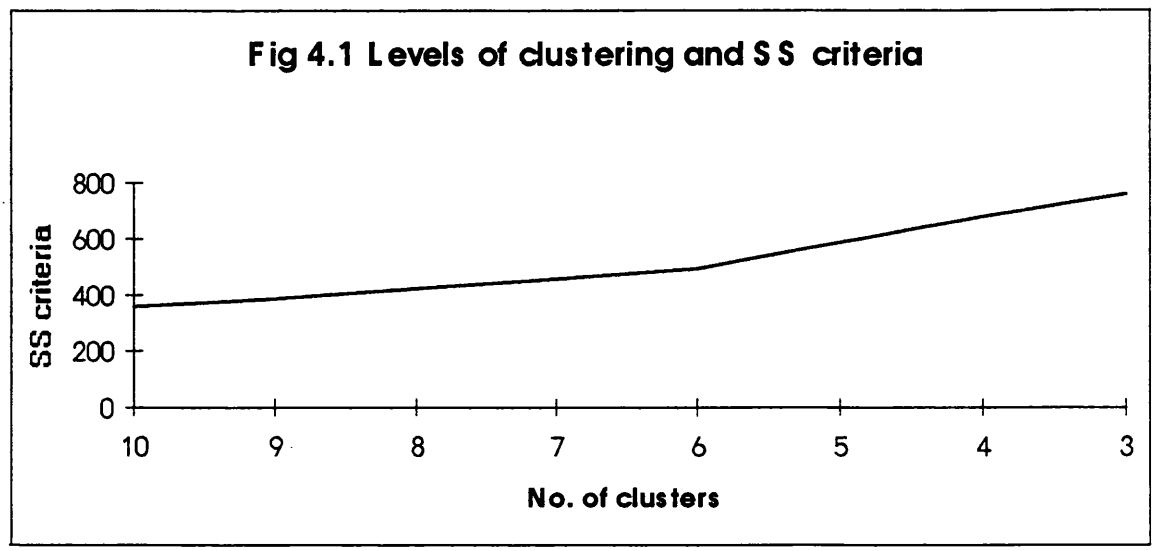
The initial analysis was carried out on the data taken from the literature, as this covered a larger range of species and traits. This could then be compared with the field measurements. The data consisted of a matrix of 45 species by 34 attributes, as shown in Appendix 5. Leishman and Westoby (1992) found it necessary to weight attributes where certain attribute categories were over represented. In the present study no weightings have been assigned, as it was felt that these could as easily introduce bias as eliminate it. Montavalo *et al.* (1991) used a relatively high number

of phenotypic characteristics (60) and felt this was sufficient to give a broad characterisation of species without an *a priori* assumption that some attributes are more important than others.

The first step was to cluster the data into homogeneous groups as far as possible. The technique used was non-hierarchical clustering, using the GENSTAT statistical package. This technique is more appropriate for data where an underlying gradient is not assumed to exist. In this case the relative adaptive significance of traits is unknown, therefore a hierarchical structure is not appropriate (Orshan 1980). Where sets of mutually exclusive traits are used one is dropped from the analysis to avoid the computational problems of redundant data. The 10 starting groups were chosen using a TWINSPAN classification (see Chapter 3). TWINSPAN is a hierarchical divisive polythetic technique of classification (Hill 1979). As this also assumes a gradient, it is not the most appropriate method for the type of data set in question, however it is adequate to make a sensible initial grouping of the data, which allows the subsequent non-hierarchical clustering to function optimally. A number of clustering runs were performed using slightly different starting groups so as to ascertain their effect on the end result. In all cases the final clusters were identical, which allayed apprehensions about the influence of starting groups on the clusters. A number of criteria can be used to delimit clusters, and, as they are independent, it is not possible to optimise all of them so a choice of clustering criteria must be made. In this case the ratio of within groups sum of squares to between groups sum of squares was used (hereafter labelled SS criteria). The SS criteria was then plotted against the number of groups (Fig. 4.1). The SS criteria rises sharply after 6 clusters (i.e. the groups get much less homogeneous) which suggests that this is the optimal grouping of the data. After examination of the composition of the groups produced by 5, 6 and 7 clusters, 6 clusters also seemed to be ecologically sensible and so were used as preliminary functional groups for the continuing analysis. The species distribution amongst these groups is shown in Table 4.3.

Table 4.3 Functional group (FG) membership for 6 clusters formed by non-hierarchical clustering of species using published literature traits.

FG1	FG2	FG3
H. palustris	C. demersum	G. declinata
O. fluviatilis	E. canadensis	G. fluitans
R. aquatilis	J. bulbosus	P. coloratus
R. penicillatus	M. alterniflorum	P. lucens
R. peltatus	M. spicatum	P. natans
R. trichophyllus	M. verticillatum	P. nodosus
R. circinatus	P. pectinatus	P. polygonifolius
	P. berchtoldii	S. emersum
	P. crispus	S. angustifolium
	P. obtusifolius	
	P. pusillus	
	P. trichoides	
	U. vulgaris	
	U. intermedia	
	Z. palustris	
FG4	**FG5**	**FG6**
C. hamulata	N. alba	E. acicularis
C. stagnalis	N. lutea	H. morsus-ranae
C. obtusangula	N. pumila	L. minor
C. platycarpa	P. amphibia	L. polyrhiza
	S. sagittifolia	L. trisulca



The next step was to examine the classifications within the framework of an ordination. A Principal Components Analysis (PCA), using the UNISTAT statistical package, was carried out to ordinate the species. The first four components

contained 52.7% of the variation in the data set. The species ordination on Components 1 and 2 is shown in Fig. 4.2. Component 1 contains 17.2% of the total data set variation, component 2 takes up a further 13.6%. The functional groups are overlaid on the ordination. These two components divide the 6 groups well, with each group distinct in space. Species ordination by components 3 and 4 is shown in Fig. 4.3 with the functional groups again overlaid. The separation is obviously poorer than on the first two components, but still shows distinct grouping. Components 3 and 4 contain 12.1% and 9.7% respectively of the variation in the entire data set. Where individual traits are completely uncorrelated a PCA would not be expected to simplify the data set. Where many traits are correlated to some degree much of the variation will be contained in the first few components of the analysis. Where this is the case a PCA is an efficient tool to elucidate a complicated data set. In this case the traits are not highly inter-correlated, but the first four axes still offer a useful insight into the data. The subsequent components each only explain a small percentage (< 8%) of the total variation and have therefore not been considered.

From these two complementary assessments (non-hierarchical clustering and PCA), a classification into 6 groups was accepted for further analysis. This classification is as objective as possible, but as agreed by Foran *et al.* (1986) *'judgements on the basis of experience are still an integral part of the process.'* So, while not allowing prior knowledge of the species to unduly influence the actual clustering process, the classification was accepted as workable on the basis of ecological experience.

To examine the influence of individual traits on the clusters, two analyses were conducted:

1. Examination of the correlation of traits:

a) with each other

b) with the first four principal components.

2. A linear discriminant analysis to look at the discriminant power of individual traits and also their use as predictors for new cases.

Fig 4.2 Plot of Component 1 and Component 2 from the PCA of species established phase traits. Functional groups delineated by dotted lines (for species codes see Appendix 2).

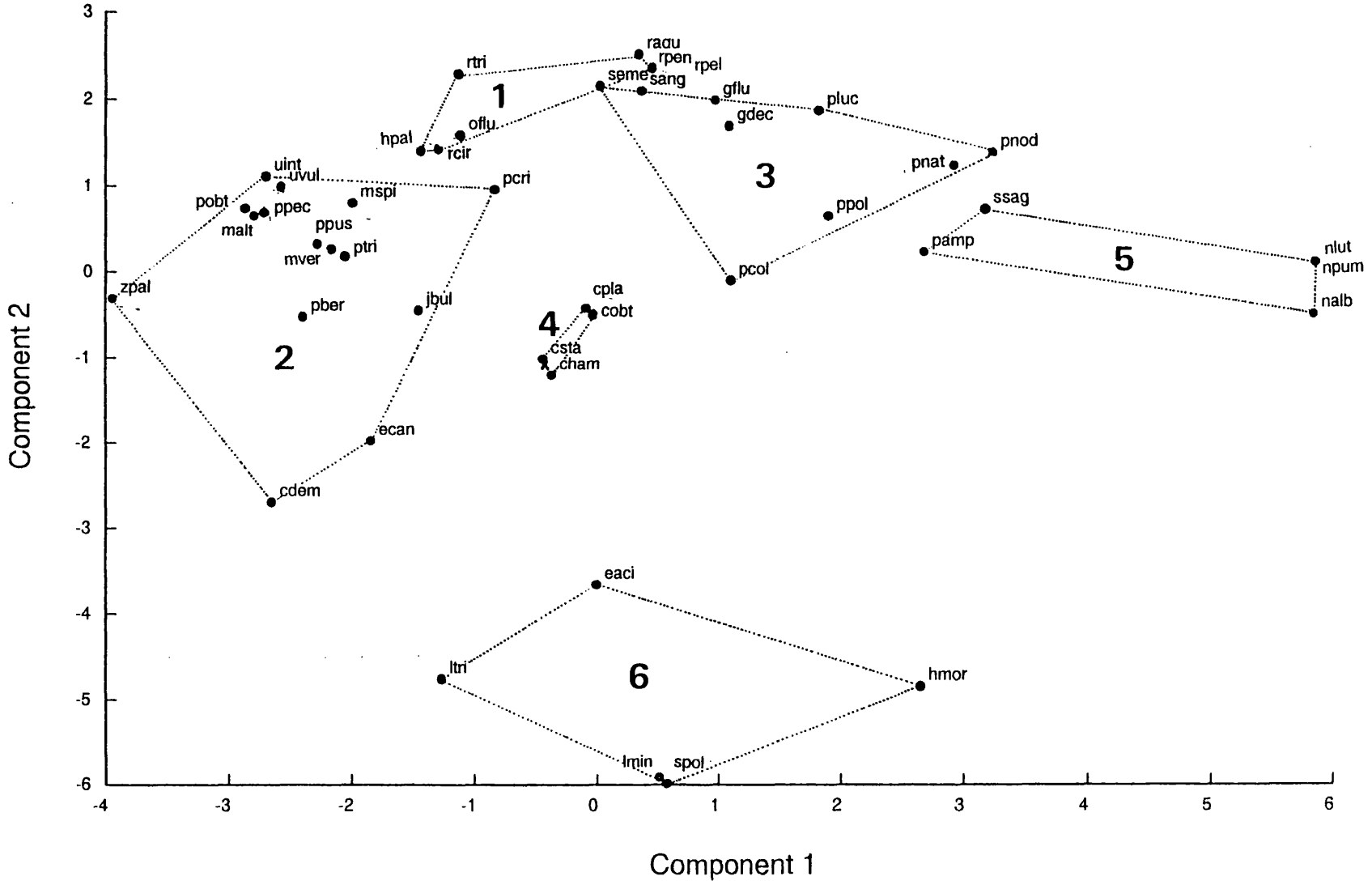
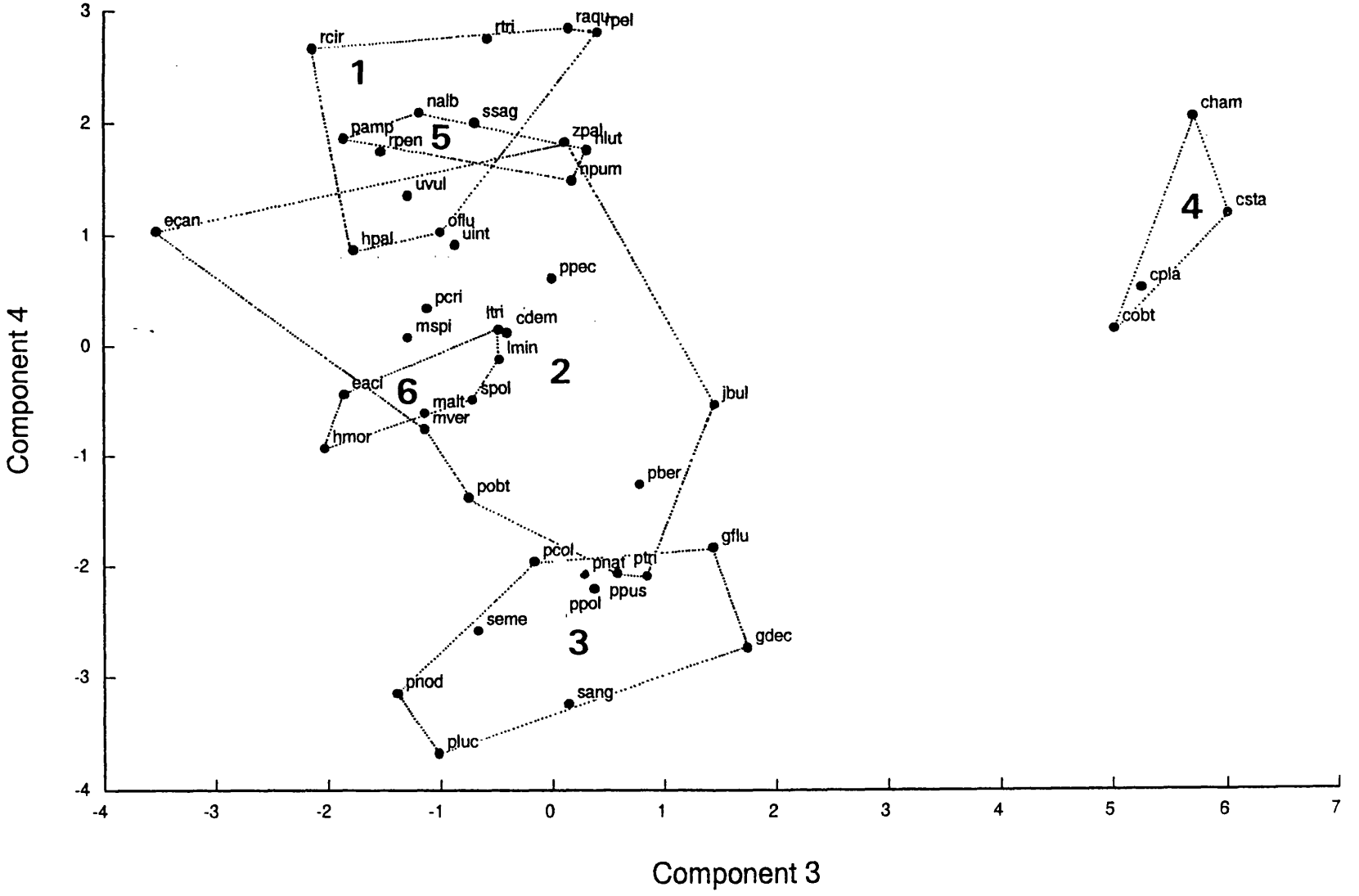


Fig 4.3 Plot of Component 3 and Component 4 from the PCA of species established phase traits. Functional groups delineated by dotted lines (for species codes see Appendix 2).



The correlation coefficient used was Spearman's Rank Correlation with a significance level of $p < 0.001$ unless otherwise stated. Table 4.4 lists the strongest inter trait correlations. These do not include negative attribute correlations within trait 'sets' (e.g. growth form; leaf area). Few traits were highly correlated ($r > 0.6$), so weaker trait correlations ($r = 0.5 - 0.6$) are also shown. High correlations are hard to obtain for data measured on a three point scale as a trait scored as 2 for a particular species will be uncorrelated with a trait scoring 1. On a more detailed scale the same traits may score 8 and 6 respectively, substantially strengthening the correlation. Some of these correlations could have been predicted from experience of aquatic plant ecology. For instance, the positive correlation between free floating surface plants and a small plant size, or between heterophylly and a submerged and floating leaved growth form are not surprising. Similarly, the negatively correlated relationship between canopy formers and a submerged growth form or between small plant size and large lateral spread were to be reasonably expected. The recognition of these correlations lends weight to the less obvious correlations found (although this does not necessarily guarantee their ecological significance). Correlations such as those between large plant size and vigorous seed production or large leaf area and high below:above ground biomass are of possible functional significance.

None of the PCA axes were very strongly correlated with a single trait, as might be expected from the relatively low percentage variation explained by individual axes of the PCA, but the strongest correlations are listed. Principal component 1 (PC 1) was correlated with large ($r = 0.568$), rigid ($r = 0.573$), waxy ($r = 0.651$) leaves; the ability to form a canopy ($r = 0.575$); large lateral spread ($r = 0.509$) and a high above : below ground biomass ratio ($r = 0.539$). Looking at these correlations within the context of Grime's model for terrestrial plant strategies, some have been recognised as pertinent to a particular plant strategy. A high, dense canopy; extensive lateral spread above and below ground; a proportion of photosynthate stored to form the capital for next seasons growth, have all been found to characterise a competitive strategy (Grime *et al.* 1988). The possibility that PC 1 may, to some extent, reflect competitive ability (*sensu* Grime) should be noted, while bearing in mind that the functional significance of Grime's chosen characteristics in an aquatic environment is not proven. PC 1 was also negatively correlated with small leaves ($r = -0.733$); a submerged growth form ($r = -0.617$) and a single many branched stem ($r = -0.608$). PC 2 was correlated with a large plant size ($r = 0.767$); medium sized leaves ($r = 0.674$) and vigorous seed production ($r =$

0.669). Negative correlations were found with small plant size (r = -0.544) and small leaf area (r = -0.530). Grime associates vigorous seed production with a ruderal strategy, but small plant size is also associated with this strategy. PC 2 is less clearly correlated with a particular strategy (as defined by Grime 1979). PC 3 was correlated with a submerged and floating leafed growth (r = 0.569) and negatively correlated with the occurrence of lacunal air spaces (r = -0.541). PC 4 was correlated with insect pollination (r = 0.697) and an annual life history (r = 0.577); and negatively correlated with wind pollination (r = -0.783) and a little branched stem (r = -0.672). Other studies have found correlations between morphology, attachment and regeneration potential in macrophytes (Bornette *et al.* 1994)

Table 4.4 Correlations between published traits, using Spearman's rank correlation coefficient. Probabilities are $p \leq 0.001$ (unless otherwise indicated), n = 45.

r	Positive correlations	Negative correlations
r > 0.6	free floating surface / plant size small (r = 0.756)	single many branched stem / large lateral spread (r = 0.666)
	single many branched stem / HCO_3^- user (r= 0.664)	
	heterophyllous / submerged and floating leaved (r = 0.622)	
	leaf area large / large lateral spread (r = 0.617)	
	plant size large / vigorous seed production (r = 0.609)	
	Leaf area large / high below:above ground biomass (r = 0.601)	
r = 0.5 - 0.6	multiple stems / self pollinated (r = 0.578)	HCO3- user / multiple stems (r = 0.563)
	submerged and floating leafed / single non branching (r =0.535)	Lacunal air spaces / water pollinated (r = 0.512)
	amphibious / self pollinating (r = 0.527)	canopy former / submerged growth form (r = 0.512)
	early flowering / potential annual (r = 0.526)	plant size small / large lateral spread (r = 0.512)
	single few branched stem / wind pollinated (r = 0.522)	plant size small / vigorous seed production (r = 0.512)
	leaf area medium / single non branching stem (r = 0.518)	HCO_3^- user / self pollinated (r = 0.502)
	single few branching / below : above ground high (r = 0.506)	
	high below:above ground biomass / rhizomes (r = 0.504)	

The relationship of the field measured traits to the defined functional groups was examined next. 51 populations of 28 species were measured in the field (appendix 6). The data used are the mean for each species. In addition to multivariate analysis of the entire trait set, individual species responses can also be examined and related to overall trends. For instance, many species are represented across the range of sites (e.g. *Elodea canadensis, Lemna minor, Persicaria amphibia*). One avenue of interest is to look at the trait variation between populations of the same species in different habitats. This comparative approach has been encouraged by Bradshaw (1987), as the differences may relate more readily to the environment currently being inhabited and not be obscured by the past acquisition of characters with little relation to the present environment. Verhoeven *et al.* (1982) also argue that investigation should be at the population level. As the functional grouping has been executed at the species level, field measured traits will also be considered at the same level. A PCA of the population level field-measured traits (Fig. 4.4) showed replicates of each species to be quite closely grouped. This confirmed the decision to undertake the analysis at a species level.

The species were again ordinated by their field measured traits using a Principal Components Analysis (Fig. 4.5) and overlaid by the 6 functional groups defined by the previous traits analysis. The PCA was performed on a set of traits standardised to mean and unit variance distribution to avoid undue influence of traits with a high magnitude. The separation is not as clear as with the literature-based traits, suggesting that they are not powerful descriptors for the functional groups defined. Much of the variation was contained in the first axis (42.9%) indicating that some of the traits are highly correlated. This is perhaps unsurprising for a trait set based on mainly morphological measurements, which by their very nature are interrelated. The first four axes of this PCA explained 78.9% of the data set variation so were quite an efficient way of reducing the original array of 17 variables. As much of this variation is contained in the first two axes (57.7%), subsequent axes scores are not plotted.

Fig 4.4 Plot of Component 1 and Component 2 from the PCA of field-measured traits: population level. Numbers represent species and letters represent populations (see Appendix 6).

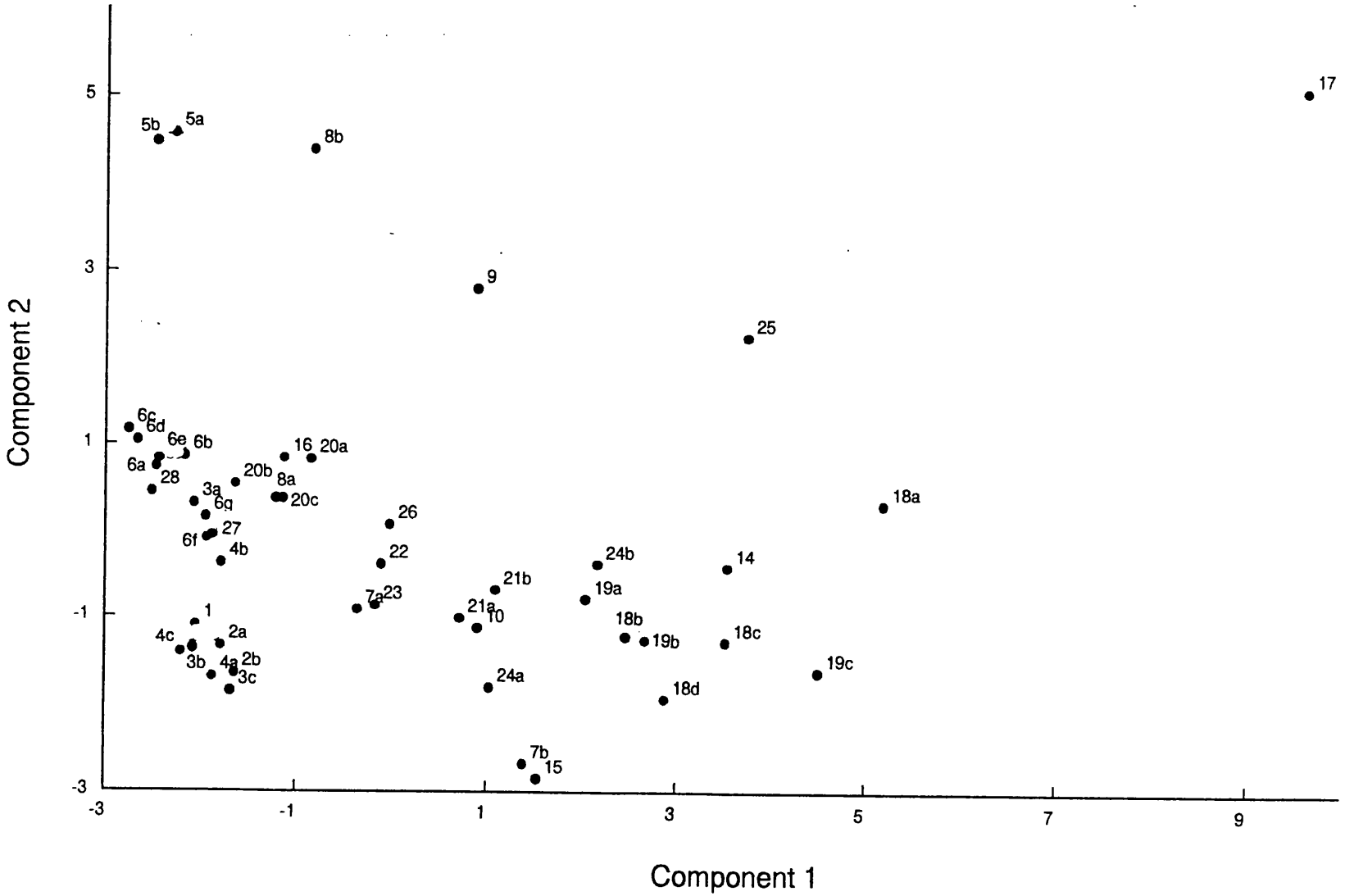
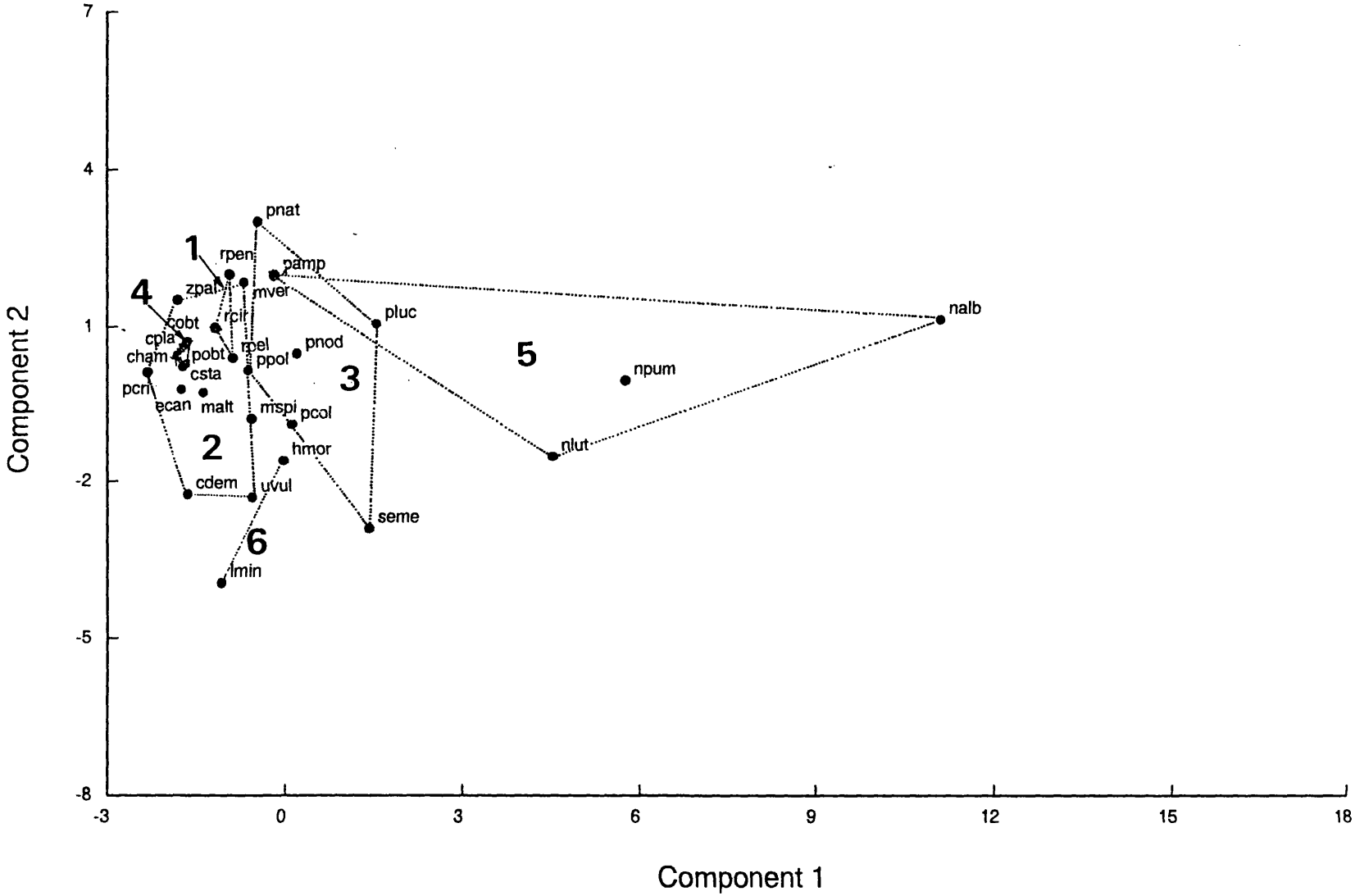


Fig 4.5 Plot of Component 1 and Component 2 from the PCA of species field-measured traits. Functional groups delineated by dotted lines (for species codes see Appendix 2).



The correlation between field traits and also their correlation with the first four Principal Components was examined. The correlation coefficient used was Spearman's Rank Correlation, and $p < 0.001$, unless otherwise stated. Table 4.5 gives the strongest inter trait correlations. Where several attributes are highly correlated one should be discarded, and it is sensible to discard those which are less easily recognised or measured in the field (Friedel *et al.* 1988). All four traits based on biomass measurements were highly correlated being all basically reflections of size, and so correlations between them have not been shown. Similarly the negative correlations between the biomass allocation traits are not shown as they are just reflecting the necessary trade-off between these parameters. Inter-trait correlations for the field measured traits were much stronger than for the published traits. No strong negative correlations were found. Correlations $r < 0.7$ are not shown.

Table 4.5 Between trait correlations for field measured traits. $p < 0.001$, $n = 28$

	Positive correlation
$r > 0.8$	leaf area / leaf breadth (r=0.88)
	No. seeds / reproductive weight (r = 0.83)
	Stem thickness / leaf breadth (r = 0.81)
r = 0.7 - 0.8	Stem thickness / stem weight (r = 0.78)
	Stem thickness / leaf weight (r = 0.78)
	No. seeds / % reproductive (r = 0.76)
	Stem thickness / total biomass (r = 0.76)
	Total biomass / leaf breadth (r = 0.76)
	Reproductive weight / leaf breadth (r = 0.75)
	Leaf area / leaf length (r = 0.75)
	Reproductive weight / leaf breadth (r = 0.75)
	Leaf breadth / stem weight (r = 0.74)
	Leaf breadth / Leaf weight (r = 0.74)
	Stem thickness / leaf length (r = 0.73)
	Stem thickness / leaf area (r = 0.70)
	Stem thickness / leaf thickness (r = 0.70)

The traits that are highly correlated with PC1 are leaf breadth (r = 0.923); stem thickness (r = 0.816); leaf area (r = 0.768); total biomass (r = 0.748); reproductive weight (r = 0.776). PC 2 is correlated with % stem biomass (r=0.830); % leaf

biomass (r=0.786); internode distance (r=0.664). These two axes contain 62.4% of the data set variation.

4.3.2 Defining key traits for functional group descriptors

Linear discriminant analysis was performed on the 6 functional groups to see which traits were most influential in defining them. The analysis was carried out using the MINITAB statistical package.

Linear discriminant analysis and cluster analysis present a useful dichotomy where classification is difficult. In many cases (as this one), the two approaches are complementary (Everitt and Dunn 1991). The most commonly used method is Fisher's linear discriminant function, which is the method used here. To successfully use discriminant analysis one assumption that must be satisfied is that the covariance matrices must be similar for each group. Exploratory analysis of the covariance matrices showed no reason to doubt this assumption. Further tests of similarity are possible but were not considered necessary.

The published traits were first examined to see if smaller subsets of traits could be used to successfully discriminate the functional groups. The cross validation option was used, as this gives a more realistic error rate which better reflects the performance of the discriminant function on new cases. This is a widely used way of estimating the misclassification rate of a discriminant function without requiring a new data set. A discriminant function is derived from the data while omitting one case. This function is then used to classify the individual not included. This process is repeated for each individual. The smallest useful subset comprised 6 traits (from the original 18): growth form, shoot architecture, plant size, leaf area, leaf type, below:above ground biomass ratio. This gave 100% success on the original data set (n=48) and 89% success with cross validation. The linear discriminant function using these traits is shown in Table 4.6. Only slightly inferior success was achieved when the number of traits used was reduced to 5 by omitting the below:above ground biomass ratio. The initial success rate was still 100%, but cross validated classification success fell to 87%.

It was also found possible to discriminate the groups completely without reference to the size related traits (i.e. using growth form, leaf type, HCO_3^- user, wintergreen, potential annual, canopy former, amphibious, heterophyllous,

below:above ground biomass ratio, lacunal air spaces, flowering phenology, lateral spread, vigorous seed producer, pollen vector). The size traits reflect the same characters as some of the field-measured traits, although this discriminant analysis grouped the species independently of these measures. With cross validation the success rate fell to 64%. Dropping the lacunal air spaces trait from this analysis brought the success rate up to 76%. The linear discriminant function in Table 4.6 (6 traits) was selected for testing (Chapter 9) as this gave the highest success rate. The species misclassified by these equations are shown in Table 4.7.

Table 4.6 Linear Discriminant Function using 6 trait groups (for attribute codes see Table 4.1).

		Functional Group					
Trait	**Attribute**	**FG1**	**FG2**	**FG3**	**FG4**	**FG5**	**FG6**
	Const.	-136.60	-232.36	-105.89	-134.48	-178.93	-96.44
Growth form	ffsur	28.60	35.15	24.81	19.72	37.68	39.51
	ffsub	36.62	44.42	32.34	27.35	44.51	35.23
	subr	22.05	26.46	21.41	18.42	31.54	21.91
	subf	22.09	50.24	65.40	79.19	29.70	-7.36
	flo	49.11	54.66	51.81	52.39	83.98	41.15
Below:above ground	bta	25.97	39.49	37.08	30.97	28.19	9.93
Leaf area	las	49.00	88.75	48.65	76.43	45.44	26.74
	lam	9.89	8.78	11.02	11.89	7.47	-0.44
	lal	-22.98	-42.65	-25.08	-28.26	-11.57	-13.97
Plant size	plm	7.18	8.00	6.92	8.33	5.12	0.62
	pll	20.09	28.79	21.60	20.20	17.68	6.56
Shoot architecture	mult	53.59	92.55	47.91	68.72	50.61	32.05
	sinb	52.66	85.84	46.54	60.66	41.72	22.83
Leaf type	ls	23.27	2.14	-17.35	-29.47	29.11	37.55
	lr	9.60	-12.82	-24.95	-39.99	19.05	32.47

Table 4.7 Species incorrectly classified by the linear discriminant function based on traits from the published literature.

Species	**True functional group**	**Predicted group**
Eleocharis acicularis	6	1
Lemna trisulca	6	1
Persicaria amphibia	5	1
Potamogeton crispus	2	1
Ranunculus circinatus	1	2

4.3.3 Using field measured traits as functional group descriptors

A similar analysis was carried out using the field measured traits in a linear discriminant analysis, to see which field traits were useful descriptors. This could only include the 28 species for which morphological measurements had been collected (Appendix 6). As with the PCA analysis above, the data used was the average from populations in a number of sites. It was not possible to use the whole trait set as the traits were too strongly correlated. The first analysis used leaf area, total leaves, % floating leaves, leaf breadth, leaf length, leaf thickness, stem length, internode distance and number of seeds. This set, while containing some inter-trait correlation was independent enough to allow the analysis to function. The linear discriminant analysis achieved 100% success with the original data, and 76% success with cross validation. It was possible to drop stem length from this set without reducing the effectiveness of the cross validated classification. The linear discriminant function for this smaller set is shown in Table 4.8. No smaller subset of traits was found that achieved a higher classification success. Misclassifed species are shown in Table 4.9.

Table 4.8 Linear Discriminant Function using a subset of field measured traits (for trait codes see Table 4.2)

	Functional Group					
Trait	FG1	FG2	FG3	FG4	FG5	FG6
Constant	-20.155	-5.773	-43.140	-3.139	-35.112	-60.691
la	-0.004	-0.002	-0.001	-0.001	-0.001	0.001
tlv	0.004	0.004	0.002	0.002	0.003	-0.000
%fl	-0.033	-0.055	0.810	0.104	0.467	1.085
lvb	6.857	2.938	4.325	1.209	6.308	-0.572
lvt	-3.202	3.437	11.100	9.839	13.868	38.505
nseed	0.016	0.010	-0.047	-0.006	-0.035	-0.081
int	4.091	2.006	0.740	0.997	1.637	-2.557
lvl	-0.074	-0.054	1.135	0.135	0.480	1.286

Table 4.9 Species incorrectly classified using a linear discriminant function based on field measured traits

Species	True functional group	Predicted group
Elodea canadensis	2	4
Nymphaea alba	5	3
Persicaria amphibia	5	3
Potamogeton crispus	2	4
Potamogeton lucens	3	5
Ranunculus peltatus	1	2
Sparganium emersum	3	6

The linear discriminate functions used to predict functional group from field traits and from published traits are further tested for their effectiveness in Chapter 9, on an independent set of data collected in the Czech Republic, containing both previously classified and new species.

4.4 Discussion

4.4.1. Classification methods

The data analysis has permitted classification of the species set in as objective a manner as possible. The combination of classification and ordination techniques produced a classification that can be adequately utilised with a smaller subset of characteristics. That the classification can be discriminated without reference to the morphological traits shows that it is reflecting more than these traits alone. The field traits were not as successful at discriminating the groups. This is partly a reflection of the plasticity of aquatic plants with regard to the traits measured. It also reflects the inadequacy of using morphological traits, in isolation, to classify species. Spink (1992) found correlations between plant strategy (defined in terms of habitat utilisation) and morphological characters, but did not attempt to use these to discriminate between groups. Although data on some aspects of aquatic plant biology is sparse, it is preferable to utilise the available knowledge and refine classifications as the data increase. Some traits are more straightforward to assign than others, for instance, bicarbonate use can be considered as a gradient response affected by environmental conditions, rather than a simple presence/absence character (Allen and Spence 1981). The situation in which a species is assigned this trait needs to be more carefully defined. One prudent warning arose from Friedel *et al.* (1988), that data should not be collected solely at the functional group level until the autecology of all species is well known, but that species data should be collected and classifications then made, allowing misclassifications to be rectified as knowledge of the autecology improves. This should be particularly heeded in studies of aquatic vegetation as the background of autecological information is not as comprehensive as for many terrestrial taxa. For example in the University of Bath Ecological Flora Database, of the 132 ecological characteristics available some aquatic species had very few entries (e.g. *Utricularia australis* 27; *Potamogeton lucens* 37; *Potamogeton coloratus* 43). Of the 225 species covered to date by the Biological Flora of the British Isles only 10 are euhydrophtye species. Bornette *et al.* (1994) also noted how greatly the published information on their chosen species traits varied between macrophyte species, from quite sparse (e.g. *Luronium natans*) to well documented (e.g. *Nuphar lutea*). A similar spread was apparent in this data set.

4.4.2 Misclassified species

Examining the location of the five species misclassified by the LDA (literature-based traits) on the PCA ordination diagrams aids interpretation of the analysis. Both *P. crispus* and *R. circinatus* are close to the boundary between group 1 and 2, probably with many characters common to both groups. The misclassification of *E. acicularis, L. trisulca* and *P. amphibia* to Group 1 is surprising, but reflects the choice of characters in the LDA. While these characters gave the best possible overall discrimination, those characters that are most influential in separating these species from functional group 1 species on the ordination cannot have been included.

4.4.3 Ecological significance of functional groups

The six groups appear to be statistically robust, so at this point an examination of the key attributes of each group (Table 4.10) can be used to define its probable ecological significance. Leishman and Westoby (1992) found that groupings reflected well established, major growth form groups and went on to look for any evidence of further natural groupings than those previously recognised. Bornette *et al.* (1994) classified macrophytes by species traits with a result that differed from taxonomic groupings, but their groups reflected growth forms. Whilst my groups do not rigorously adhere to one or other growth form there does seem to be a preponderance of a single growth form in some groups. Group 6 is dominated by free floating species; Group 2 by submerged species; Groups 1, 3, 4 and 5 are species with submerged/floating leaves. While they have similar growth forms the latter groups show differences in leaf area and plant length. It could be postulated that size and growth form were the controlling traits in the analysis but it should also be remembered that the groups can be well discriminated without reference to either of these characters. Growth form could be considered as a morphological expression of a number of traits. For the further analysis of community strategy in Chapter 8 an additional functional group termed FG0 was included which contained non-vascular species encountered in the survey.

Comparisons of previous classifications can also be made (Table 4.11). Comparisons are also possible with the recent classification of Bornette *et al.* (1994), a classification similarly derived from species traits without prior assumptions about strategies. However their work includes helophytes and results in a more coarse classification that, roughly speaking, only serves to separate emergents, submerged macrophytes and free floating plants. Their classification does not aim to look in detail at the differences in the ecology of euhydrophytes

alone. The classifications of both Grime *et al.* (1988) and Murphy *et al.* (1990) are based on the three strategy CSR model of Grime (1979). Murphy *et al.* (1990) used the proportion of 'strategy elements' possessed by a species to classify it. Strategy elements were based on Grime's predictions (with some adaptations (Rørslett 1989)). The present classification avoids introducing that bias at such an early stage. However the groups, once constructed, can be discussed in the context of Grime's theories. Of the traits used, some can be directly associated with a Grime strategy (Grime *et al.* 1988; Murphy *et al.* 1990) as shown below:

Competitive	Stress tolerant	Ruderal
extensive lateral spread	wintergreen	potential annual
canopy former	leaf area small	vigorous seed production
rigid leaves?	high below: above ground biomass	early flowering
bicarbonate use		

These do not allow a strategy to be straight-forwardly assigned to each functional group although FG5 seems to possess a combination of traits in keeping with a CSR strategy; FG1 approximates most closely to a CR strategy; FG2 and FG6 contain both S and C elements; and FG4 displays only recognisably stress tolerant (S) characters. FG3 did not have any dominant characters that could be easily matched with a particular strategy type. Before any further interpretation of the groups is made the role of regenerative strategies must be examined. While Grime (1979) emphasised the uncoupling of juvenile and established phase traits, he still associates particular regenerative strategies with his three primary established phase strategies (Grime *et al.* 1988). Omitting regenerative strategies from this analysis has important implications. For instance the suggestion that FG6 may consist of SC plants is without reference to the outstanding ability of lemnids to reproduce vegetatively and rapidly cover areas of open water. Until the correlation of regenerative strategies with the functional groups defined is understood, further discussion is misplaced. To prevent the analysis from being dominated by preconceptions and to minimise subjectivity, ecological interpretations will be reserved for the final stages of the investigation (Chapter 9); consequently no detailed analysis, or predictions, of the response of groups to environmental stresses or disturbances, are made at this stage.

Table 4.10 Traits associated with functional groups of euhydrophytes. Traits are common to at least 75% of group members; traits in brackets are possessed by more than 50% of the group members.

Functional Group	Traits
1	plant length (medium) long submerged rooted with/without floating leaves soft, medium sized leaves single stem, many branches insect pollinated flowers early flowering (potential annual) (canopy former)
2	submerged rooted small (soft) leaves single stem, many branches medium/large length plants (late flowering) (wind pollinated) (HCO3 user)
3	submerged and floating leaved wind pollinated single stem, few branches large plant length medium (large) leaves (vigorous seed production) (canopy former)
4	amphibious submerged and floating leaved heterophyllous medium plant length small, soft leaves long flowering period single stem, few branches (wintergreen) (wind pollinated)
5	submerged/floating leaves large, rigid, waxy leaves large length plants multiple stems arising from base canopy former insect pollinated (below:above ground biomass high) (vigorous seed production) (large lateral spread)
6	free floating small plants small, rigid (waxy) leaves (canopy formers)

Table 4.11 Comparison of functional groups with previous classifications.

	Functional group	Grime et al. 1987	Murphy et al. 1990
Chara aspera	0		CSR
C. canescens	0		CSR
C. hispida	0		CSR
C. hispida var. major	0		CSR
Chara spp	0		CSR
Fontinalis antipyretica	0		
Nitella flexilis	0		CSR
Hottonia palustris	1		
Oenanthe fluviatilis	1		
Ranunculus aquatilis	1		
R. peltatus	1	R/CSR	CSR
R. penicillatus	1	?C	
R. tricophyllus	1		CR
R. circinatus	1		
Ceratophyllum demersum	2		CR
Elodea canadensis	2	CR	CR
Juncus bulbosus	2	SR/CSR	CS
Myriophyllum alterniflorum	2		CS
M. spicatum	2	CSR	CR
M. verticillatum	2		
Najas flexilis	2		CSR?
Potamogeton berchtoldii	2		CSR
P. crispus	2	CR	CR
P. filiformis	2		
P. obtusifolius	2		
P. pectinatus	2		CR
P. pusillus	2		CR
Potamogeton trichoides	2		CR
Utricularia intermedia	2		
U. vulgaris	2		CS
Zannichellia palustris	2		CR
Glyceria declinata	3		
G. fluitans	3	CR	
P. coloratus	3		
P. lucens	3		
P. natans	3	C/SC	
P. nodosus	3		CR
P. polygonifolius	3		CSR
Sparganium angustifolium	3		
S. emersum	3	CR	
Callitriche hamulata	4		CR
C. stagnalis	4	R/CR	
C. platycarpa	4		
C. obtusangula	4		
Nuphar lutea	5	C/CSR	
N. pumila	5		
Nymphaea alba	5		
Persicaria amphibia	5	CR	
Sagittaria sagittifolia	5		
Eleocharis acicularis	6		
Hydrocharis morsus-ranae	6		
Lemna minor	6	CR	
L. trisulca	6	S	
Spirodela polyrhiza	6		

4.5 Summary

Euhydrophytes of European riverine wetlands included in the survey are classified into functional groups on the basis of possession of a range of traits.

A linear discriminant function, based on a subset of these traits, is devised that can be used to classify further species.

Morphological traits measured in the field are found to be inadequate indicators of these functional groups, probably due to the plasticity displayed by many species.

The ecological relevance of these groups is discussed.

Functional groups cannot be adequately related to strategies (as defined by Grime) without reference to regenerative strategies.

Chapter 5

GLASSHOUSE EXPERIMENTS ON ESTABLISHED PHASE PLANTS

Chapter 5

GLASSHOUSE EXPERIMENTS ON ESTABLISHED PHASE PLANTS

5.1 Introduction

The analysis presented in Chapter 4 showed one method of classifying euhydrophyte species using a functional approach. One problem arising from this approach is that the resultant broad categorisations of species are not always subtle enough to recognise specific differences in growth strategy which occur at a finer, but still potentially important, scale. Quantification of species responses, in terms of traits, is necessary to advance an effective functional classification.

A series of glasshouse experiments was devised to quantify species response to stress, disturbance and competitive pressures. These experiments used seven euhydrophyte species (*Callitriche stagnalis, Elodea canadensis, Myriophyllum spicatum, Myriophyllum alterniflorum, Potamogeton berchtoldii, Potamogeton crispus, Potamogeton pectinatus*). Competitive experiments compared growth in pure and mixed species stands. Cutting was used to produce disturbance. Reduction of PAR by shade material was used as a stress pressure. These experiments were carried out in collaboration with M.R. Sabbatini (Dept of Botany, University of Glasgow). Some of the results below and additional results from the experimental series have been reported by MRS. The responses of *Elodea canadensis* and *Myriophyllum spicatum* are presented in a joint publication (Abernethy, Sabbatini and Murphy 1995, *subm.*; Appendix 11).

This chapter:

- investigates the possibility of quantifying euhydrophyte tolerance to the three factors (C, S and D) of Grime's model.

- uses the results of the series of experiments to contrast the survival strategy of two widespread species.

- discusses the advantages of accurate, empirical, quantification of species strategy and the problems in achieving this.

5.2 Methods

Four large scale experiments were carried out between May 1992 and December 1993. All experiments used plant stock collected from field sites in England and Scotland. The origins of experimental plants are given in sections 5.2.1 to 5.2.4 below. All experiments were carried out in the greenhouse at a temperature of 20°C ± 3°C. Natural light was supplemented by 400 watt Navilux flood lights (16hr day $^{-1}$) giving an average PAR above the tanks of 918 μmols m^{-2} s^{-1}at midday. In all experiments, plants were grown in 30 l black polypropylene tanks aerated with electric air pumps to aid plant growth and reduce epiphytic algae (Robson 1974). Experiments 5.2.2 and 5.2.4 were conducted in a macrophyte culture system consisting of interconnected tanks, a pump to circulate water and a gravel filter (described in Marrs 1994), which helped to reduce variability in water quality between tanks. Experiments 5.2.1 and 5.2.3 were carried out in isolated tanks. The rooting sediment throughout was well mixed river sediment collected from the River Kelvin, Glasgow. In aquatic macrophytes the importance of nutrient uptake by the roots has been realised (Denny 1980), and therefore the production of a substrate with adequate nutrients is important. The use of natural sediments rather than culture solutions has been shown to reduce the occurrence of algal blooms in experimental situations (Smart and Barko 1985). The luxuriant growth of macrophytes in the River Kelvin also indicated a medium with adequate nutrients for plant growth. Plants were grown in tap water: the mains supply in the Glasgow area is of very constant and high quality, coming directly from an oligotrophic highland loch source (Loch Katrine). Plants were established as 12 cm stem sections and buried 4 cm deep into the rooting medium in line with methods used successfully by Barko and Smart (1981a) and Smart and Barko (1985). The experimental design differed over the four experiments and is outlined below.

On harvesting, the plant length was measured to the nearest mm. In some experiments plants were subdivided into stem, leaf and root components and in others the plant was retained intact (see results). The plant, or plant parts, were dried at 60°C to a constant weight and the final weight recorded for biomass comparisons.

5.2.1. Response to competition

The target species were *Elodea canadensis* (origin Insh marshes, Scotland) and *Myriophyllum spicatum* (origin Solway drainage area, Cumbria). An additive design was adopted (Martin and Snaydon 1982). The additive design was preferred over a more complex replacement series design (de Wit 1960) for ease of use and simplicity of interpretation. Additive designs have been criticised because they confound changes in the relative frequency of the component with changes in overall density (Harper 1977), but recent work suggests that they produce results at least as useful as, and often more so than, replacement series experiments (Connolly 1983; Snaydon and Satorre 1989). While alternative approaches to competition experiments can provide additional information (for example on the relative contribution of above- v. below-ground interactions in the case of competition partitioning (Wilson 1988)), the purpose of this trial was simply to rank the interacting populations in terms of relative response to pressure from competitor plants. For this purpose a simple additive design was considered adequate. 'PURE' consisted of 25 plants of one or other species grown in monoculture in a 360 x 220 x 60 mm deep tray; 'MIXED' consisted of 25 plants of each species grown together in a 360 x 220 x 60mm deep tray. Each tray was placed in a separate polypropylene tank. The experiment ran for 84 days before harvesting.

5.2.2 Response to cutting

The target species were *Elodea canadensis* (origin Insh marshes, Scotland) and *Myriophyllum spicatum* (origin Solway drainage area, Cumbria). In this experiment plants were grown in individual pots. 11 pots were placed in each polypropylene tank and 18 tanks were used. This gave a total of 99 plants of each species. A control and two frequencies of cutting were used with 33 replicates of each. Treatments were randomly allocated. 'Control' plants were uncut; '1 cut' plants were cut 5cm from the sediment surface 35 days after planting; '2 cut' plants were cut 5cm from the sediment surface 35 and 66 days after planting. Plants were harvested 122 days after planting.

5.2.3 Response to shade

Target species were *Elodea canadensis* (origin Insh marshes, Scotland), *Myriophyllum spicatum* (origin Solway drainage area, Cumbria), *Myriophyllum alterniflorum* (origin Insh marshes, Scotland), *Potamogeton crispus* (origin Solway drainage area, Cumbria) and *Callitriche stagnalis* (origin Solway drainage area, Cumbria). Plants were grown in individual pots with 2 pots of each species giving a total of 10 pots per polypropylene tank. Nine tanks were used. A control and two

levels of shading were used with treatments randomly allocated to tanks (i.e. six replicates per species per treatment). 'Control' tanks had no shade imposed; 'low shade' tanks were covered with one layer of white nylon shade material which reduced PAR by 23%; 'high shade' tanks were covered by two layers of white nylon shade material which reduced PAR by 40%. Plants were harvested 77 days after planting.

5.2.4 Response to combinations of cutting and shade

The target species were *Elodea canadensis* (origin Insh marshes, Scotland), *Myriophyllum spicatum* (origin Solway drainage area, Cumbria), *Potamogeton crispus* (origin Solway drainage area, Cumbria), *Potamogeton pectinatus* (origin River Kelvin, Glasgow) and *Potamogeton berchtoldii* (origin Solway drainage area, Cumbria). Plants were grown in individual pots with two replicates of each species per tank. 24 tanks were used, with one of six treatments (including a control), imposed on each tank (giving eight replicates per species per treatment). 'Control' was uncut and unshaded; '1 cut' and '2 cut' were as 5.2.2; 'low shade' and 'high shade' were as 5.2.3; 'low shade + 1 cut' entailed shading with a single layer of shade material and one cutting treatment. The experiment was harvested after 74 days.

5.3 Results

Data were analysed using GENSTAT. All experiments were subject to ANOVA followed by orthogonal mean separation using Tukey's Least Significant Difference except 5.2.4 where a two-way ANOVA using orthogonal contrasts was required followed by the same mean separation test. The results were treated as significant at $p < 0.05$. Histograms show treatment means for each species with standard errors indicated by bars. For the purposes of discussion mean percentage changes were calculated.

5.3.1 Response to competition

E. canadensis showed a significant reduction (25%) in plant length when grown in competition with *M. spicatum,* but no significant biomass response (Figs 5.1a and b). In contrast *M. spicatum* showed a significant biomass response (33% reduction) but no significant change in plant length under competitive pressure.

5.3.2 Response to cutting

Both treatments were compared with untreated controls (Figs 5.2a and b). For *E. canadensis* no significant change in length was apparent after one cut, but biomass was significantly reduced by 41%. Two cuts resulted in a 44% reduction in length and a 59% reduction in biomass. *M. spicatum* showed a poorer recovery from cutting with significant reductions in length and biomass after a single cut (22% and 45% respectively) and large, significant reductions in length and biomass after two cuts (70% and 90% respectively).

5.3.3 Response to shade

Three out of the five species showed no significant length or biomass response to shade (Figs. 5.3a and b). *M. spicatum* and *M. alterniflorum* were the species to show a significant response. In *M. spicatum* there was a significant increase in length with high shading (19%) but no significant biomass change compared with the control. In *M. alterniflorum* there was a significant biomass decrease with shade.

Changes in biomass allocation were also measured in this experiment. *E. canadensis, C. stagnalis* and *M. alterniflorum* showed no significant changes. *M. spicatum* (Fig 5.3c) showed an increase in stem biomass at the expense of the roots, but no change in leaf biomass. *P. crispus*, despite showing no significant overall change in biomass with high shade showed a significant loss of root biomass with an associated gain in stem biomass (Fig 5.3d).

5.3.4 Response to combinations of cutting and shade

No replicates of *P. pectinatus* survived, with initial establishment of cuttings very poor. Experiments with this species may be more successful when the plant is grown from tubers rather than stem fragments (Y. Filizadeh, pers. comm.). The significant length and biomass reductions (%) for 5 orthogonal contrasts are shown in Tables 5.1 and 5.2 respectively.

Table 5.1 Percentage length reductions in the four species to the contrasts shown. Only reductions significant at $p < 0.05$ are indicated.

Comparison	*P. crispus*	*P. berchtoldii*	*E. canadensis*	*M. spicatum*
control v. low shade	NS	NS	NS	NS
low shade v. high shade	NS	NS	NS	NS
control v. low shade + 1cut	NS	NS	NS	62
control v. 1cut	NS	NS	37	NS
1cut v. 2cut	NS	49	43	66

Table 5.2 Percentage total biomass reductions in the four species to the contrasts shown. Only reductions significant at $p < 0.05$ are indicated.

Comparison	*P. crispus*	*P. berchtoldii*	*E. canadensis*	*M. spicatum*
control v. low shade	NS	NS	NS	53
low shade v. high shade	72	68	77	NS
control v. low shade + 1cut	NS	NS	49	85
control v. 1cut	NS	NS	38	38
1cut v. 2cut	NS	NS	88	83

Fig 5.1a Length response of Elodea and Myriophyllum to additive competition (standard error indicated)

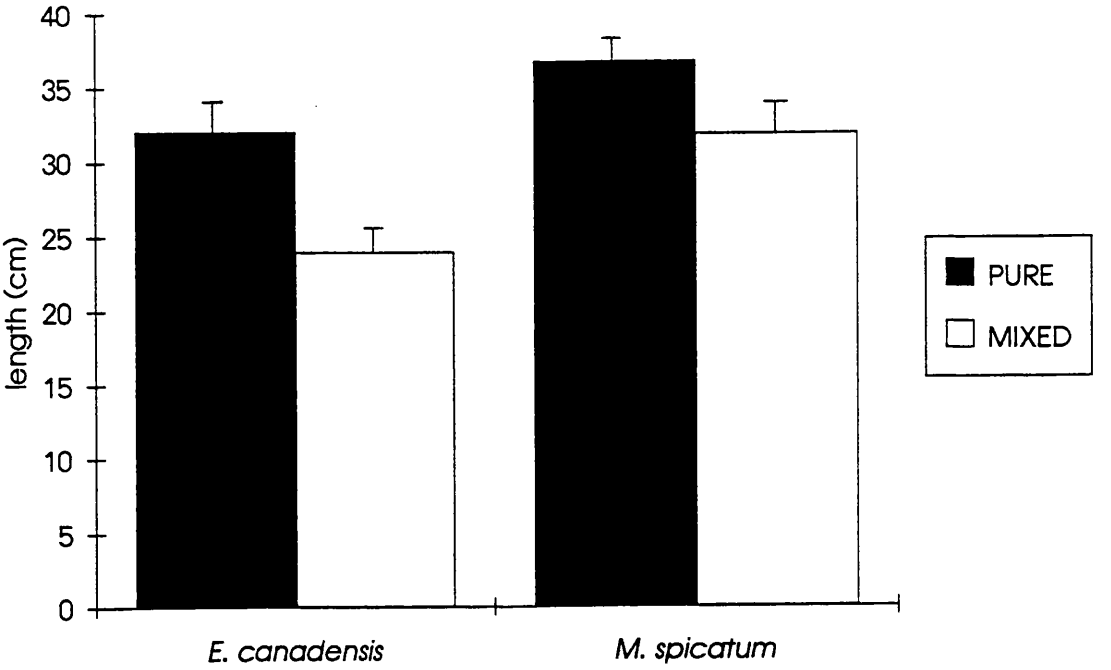


Fig 5.1b Biomass response of Elodea and Myriophyllum to additive competition (standard errors indicated)

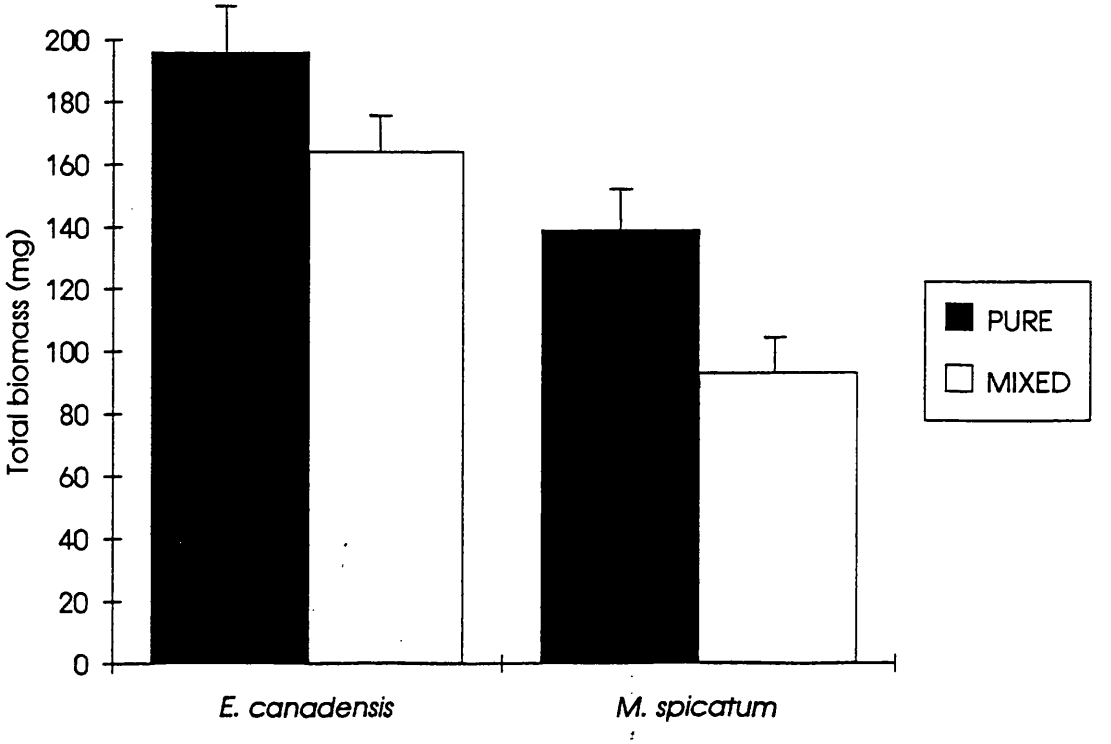


Fig 5.2a Length response of Elodea and Myriophyllum to different cutting regimes

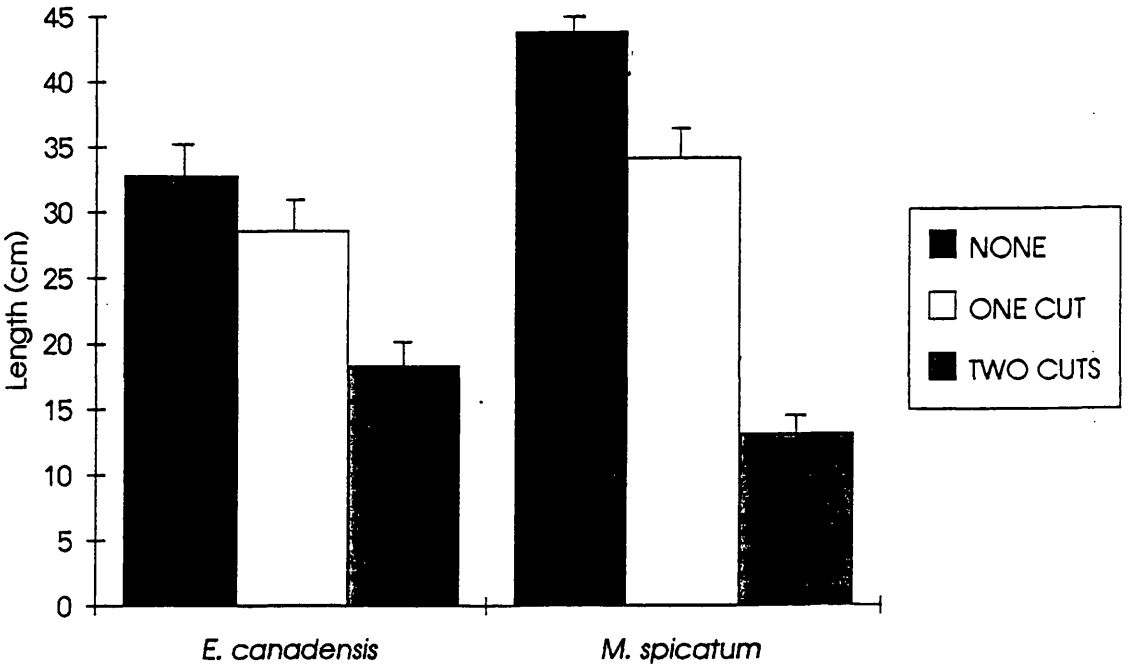


Fig 5.2b Biomass response of Elodea and Myriophyllum to different cutting regimes

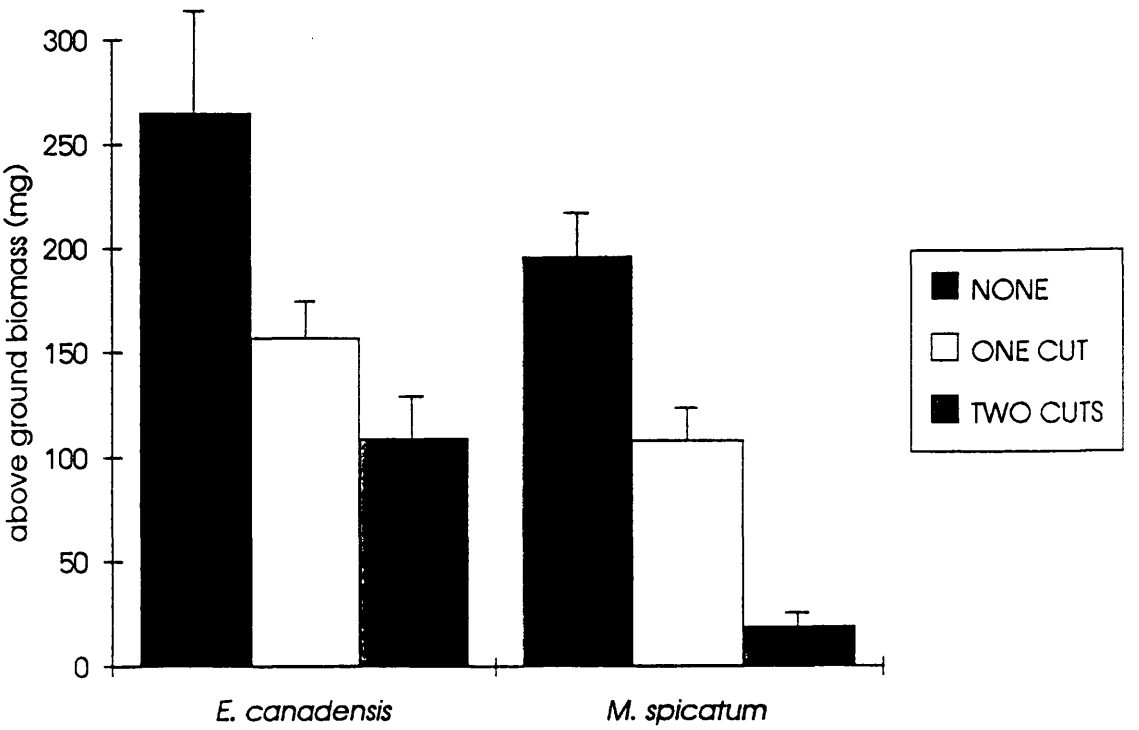


Fig 5.3a Length response to shading for five euhydrophytes (standard errors indicated)

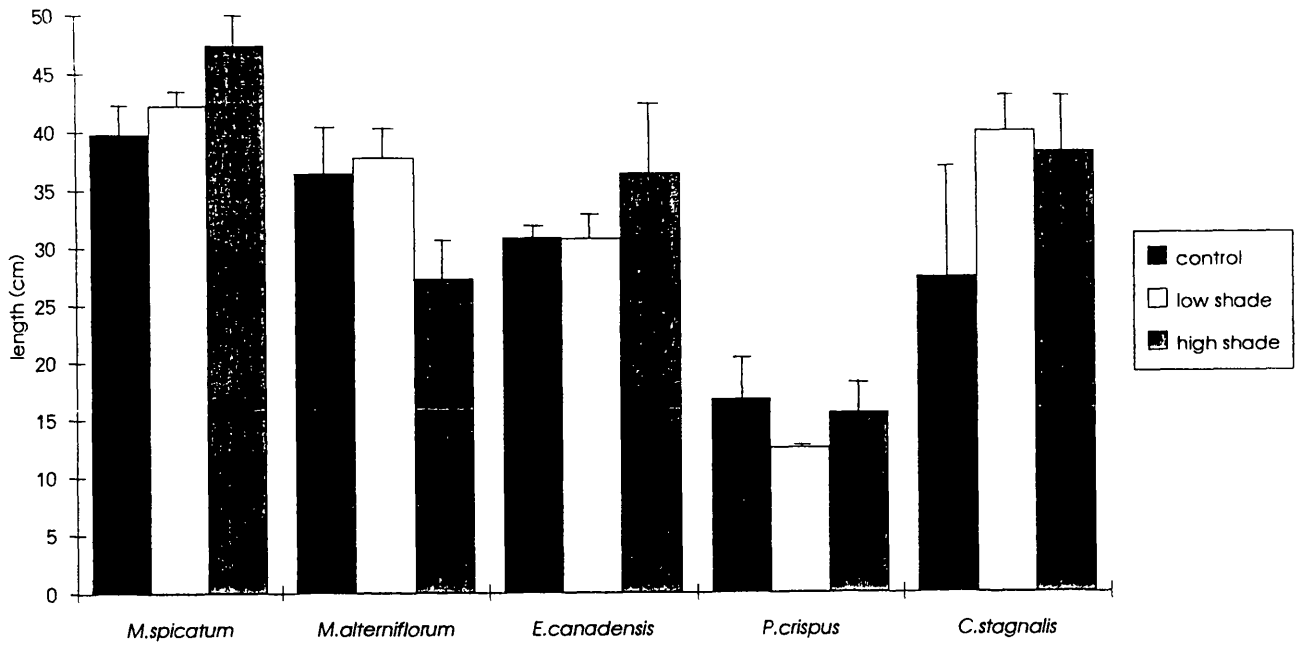


Fig 5.3b Biomass response to shade in five euhydrophytes (standard errors indicated)

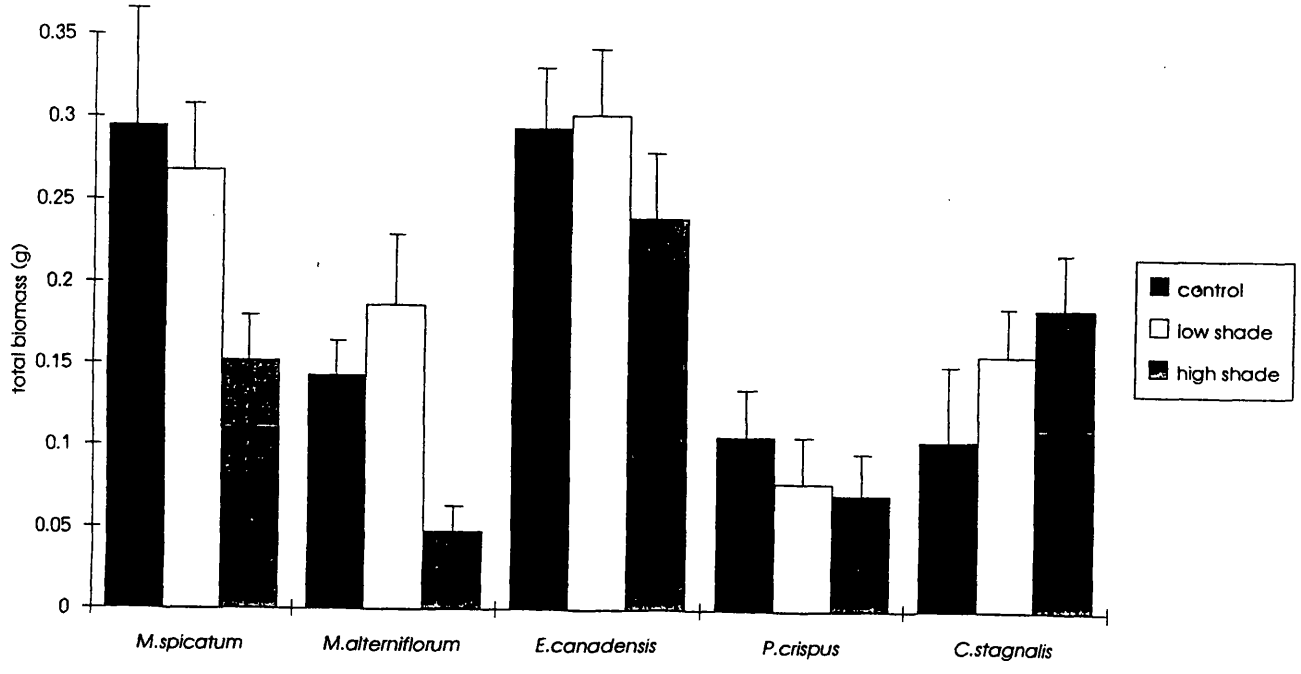


Fig 5.3c Myriophyllum spicatum biomass allocation in response to shade (standard errors indicated)

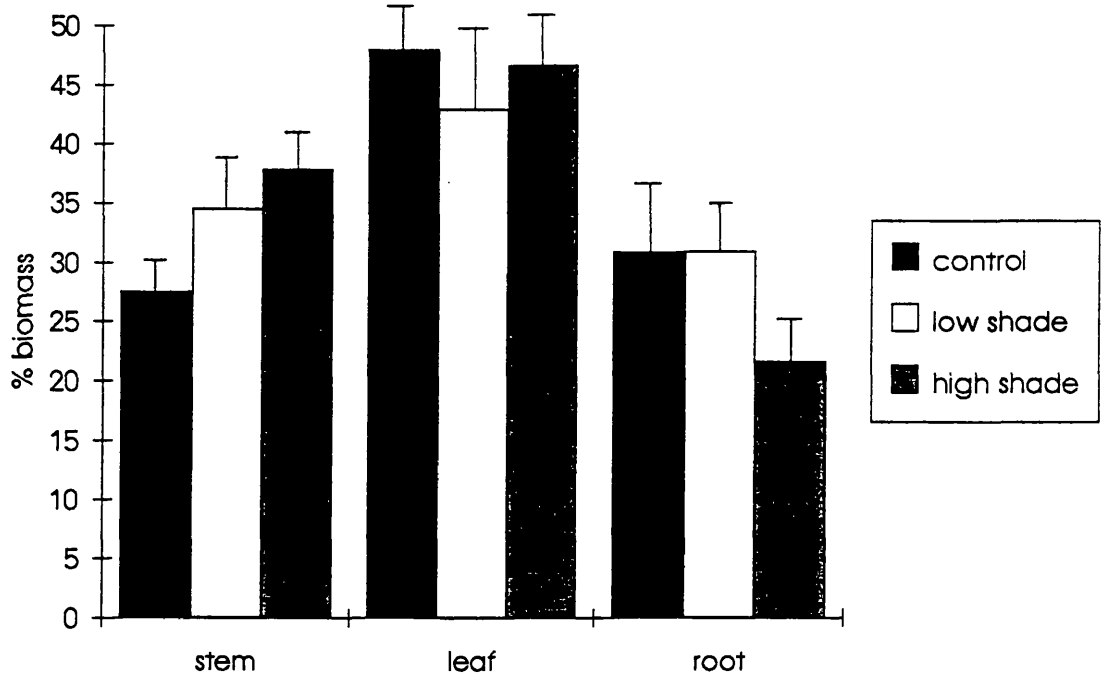


Fig 5.3d Potamogeton crispus biomass allocation in response to shade (standard errors indicated)

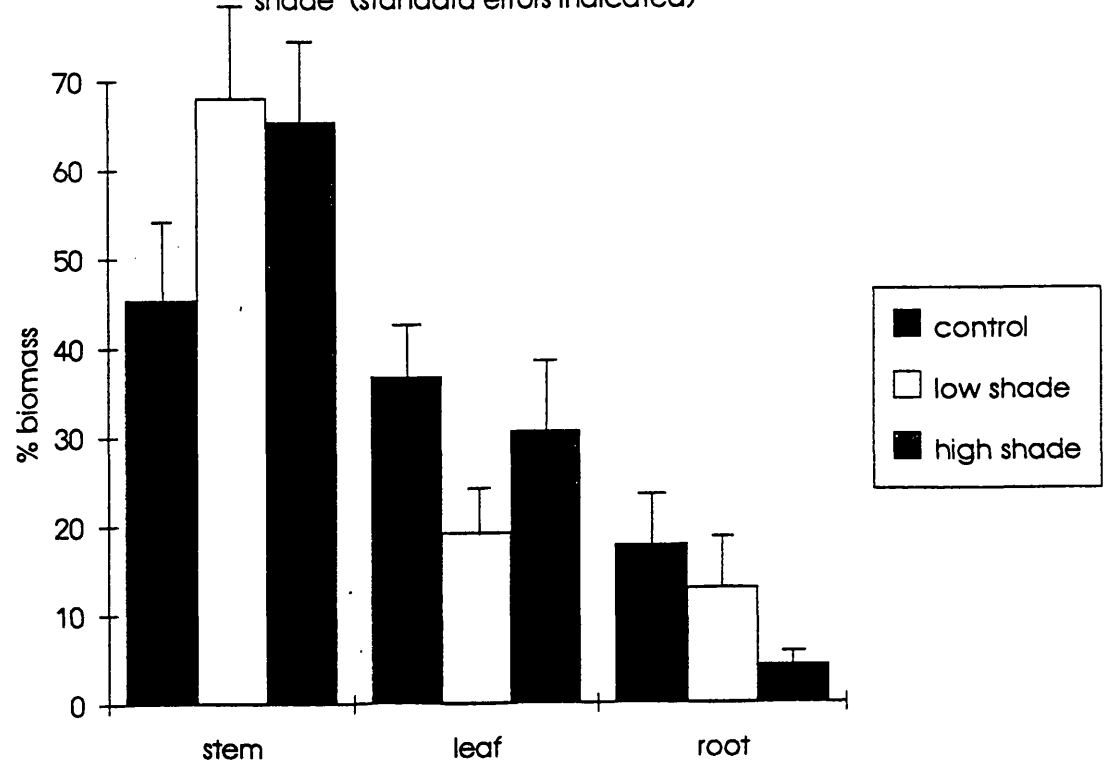


Fig 5.4a Length response of four euhydrophyte species to combinations of shade and cutting (standard errors indicated)

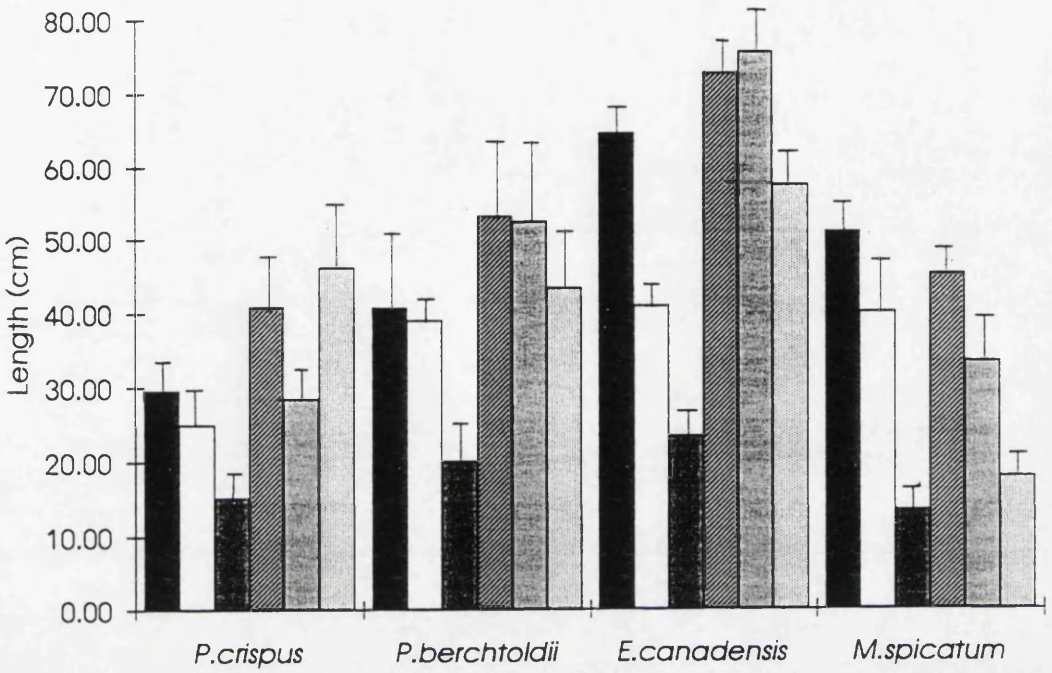
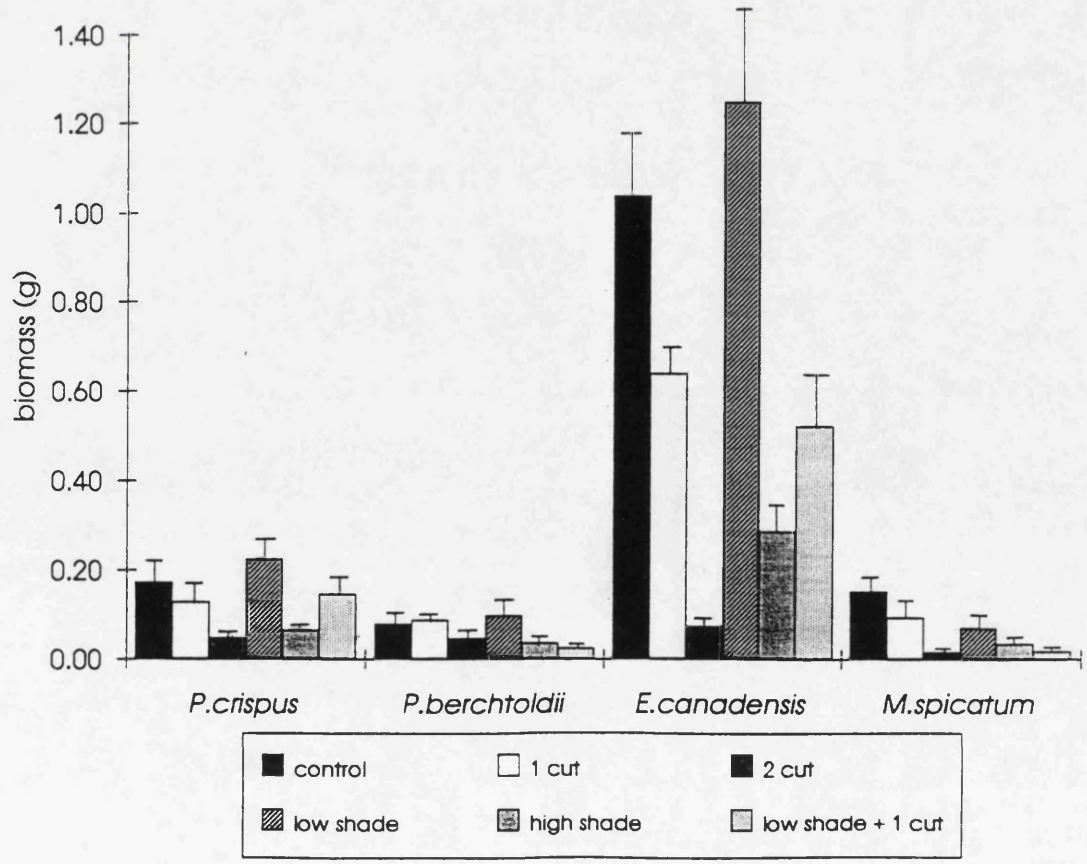


Fig 5.4b Biomass response of four euhydrophytes to combinations of shade and cutting (standard errors indicated)



5.4 Discussion

In general the biomass response is taken as a more reliable indicator of plant response to the treatments. However plant length is of use in shade experiments where a plastic growth response shows poor stress tolerance (Grime 1979; Spink 1992).

5.4.1 Competitive ability

While there was a decrease in length in *E. canadensis*, the biomass comparisons suggests that it is a superior competitor to *M. spicatum* in this situation. The poorer competitive performance of *M. spicatum* in comparison with *E. canadensis* has not been observed in field situations where *M. spicatum* is reported to out-compete *E. canadensis* (Madsen *et al.* 1991). The reduction in biomass recorded for *M. spicatum* may be due in part to sloughing of shoot fragments at high temperature (over 24°C) that has been reported in this species (Barko and Smart 1981a). This phenomenon was observed in the experiment where stem fragments were found floating in the experimental tanks. As there was no significant reduction in plant length this response to temperature may also involve etiolation of the stem.

5.4.2 Response to cutting (or disturbance tolerance)

These results strongly suggest that *M. spicatum* is less tolerant of cutting than *E. canadensis*. Even at low frequencies of cutting it makes a poor recovery and a second cutting treatment has severe effects on the plant with little recovery evident even eight weeks after the cut.

5.4.3 Response to shade (or stress tolerance)

There was no significant response from *E. canadensis, P. crispus* and *C. stagnalis,* suggesting them to be tolerant of stress in this form. The tolerance of *Callitriche* spp to shade has been noted (Spence and Chrystal 1970b; Haslam 1978). *E. canadensis* has been reported to show increases in shoot length with decreasing light levels (Barko *et al.* 1984), but that was not supported at the light intensities in this experiment. It has been suggested that it is disadvantaged by turbidity (Barko *et al.* 1984). However in experiment 5.2.4 a significant reduction in biomass was noted in *P. crispus* and *E. canadensis* at the higher level of shading. Experiment 5.2.4 was carried out in winter when ambient light levels are possibly lower (despite the flood lights) and the high shade treatment may therefore have resulted in light levels at the lower limit of tolerance of these species. *P. crispus* usually occurs in

clear waters in Britain (Haslam *et al.* 1975), but has been shown to be tolerant of low light levels (Tobiessen and Snow 1983).

M. spicatum showed a significant increase in length and no biomass changes. This would suggest a poor response to stress (Grime 1979). In experiment 5.2.4 a biomass decrease was evident in *M. spicatum* at the low shade level (although there was no further significant reduction with increasing shade). Chambers and Kalff (1985) concluded that irradiance was less important than sediment composition in determining *M. spicatum* growth, but this only examined biomass changes. The lower leaves of *M. spicatum* are adapted to shade (Adams *et al.* 1974), to accommodate the effects of self shading due to the dense surface canopy frequently formed. The biomass allocation patterns displayed by *M. spicatum* seem to show a short term adaptation to shade, possibly unsustainable in the long term. *P. crispus* shows a similar allocation pattern, suggesting that it too may not be as tolerant to shade as suggested from the total biomass results. It also seems to be adopting a quick fix response that is unsustainable under prolonged stress conditions. *M. alterniflorum* is also poorly tolerant of shade, as befits its usual occurrence in clear water, upland rivers and oligotrophic lakes.

5.4.4 Response to a combination of stress and disturbance.

This experiment had two objectives. Firstly to show how species responded to the combined effects of stress and disturbance and secondly to support the results of the previous experiments. As discussed under 5.4.3 the shade responses differed in the two experiments and this is thought to be due to the slightly lower ambient light levels in this experiment.

In response to cutting this experiment showed both *E. canadensis* and *M. spicatum* responded in a similar way, with poor recovery after two cuts.

The combination of the two factors showed no significant effect on *P. crispus* and *P. berchtoldii*. *E. canadensis* and *M. spicatum* both showed significant (near additive) biomass reductions on combining the two factors. In *M. spicatum* the reduction was especially severe, probably due to its poorer tolerance of shade stress. By contrast, in *Elodea* most of the combined effect appears to be the result of an adverse biomass response to cutting. The combination of stress and disturbance had a similar effect on *M. spicatum* as 2 cuts, whereas for *Elodea* the effect of two cuts was more severe than the combined treatment.

5.4.5 Discussion of species strategies in the light of experimental evidence.

The experimental species have all been classified previously according to their established phase strategy in previous studies. The classifications of Grime *et al.* (1988) and Murphy *et al.* (1990) are shown below.

	Grime *et al.* (1988)	Murphy *et al.* (1990)
C. stagnalis	R/CR	-
E. canadensis	CR	CR
M. alterniflorum	-	CS
M. spicatum	CSR	CR
P. berchtoldii	-	CSR
P. crispus	CR	CR

These classifications can be examined in the light of the experimental evidence reported here. It is accepted that this series of experiments is only a preliminary step in the refinement of knowledge of aquatic plant strategies. The strategies of terrestrial plants covered by Grime *et al.* (1988), are supported by an extensive screening programme that has been underway many years. This is the type of rigorous experimentation necessary to bring the understanding of the ecology of aquatic plants into line with their terrestrial counterparts. A large scale programme using standard conditions for all experiments and investigating a wide range of populations (to examine concurrently intraspecific variation in response to factors), a variety of pressures and a wide range of response variables, would greatly advance functional study of this group. The following redefinition of strategies shows how such a programme could be interpreted.

C. stagnalis should have an element of stress tolerance included in its strategy, reflecting its shade tolerance, redefining it as SR/CSR.

P. crispus is probably correctly classified CR since its stress response is not sustainable.

P. berchtoldii's CSR strategy can also not be rejected on the evidence of these experiments.

M. spicatum has an S component included by Grime *et al.* (1988) which does not seem to be justified and I would rather agree with the CR classification of Murphy *et al.* (1990).

E. canadensis, in contrast, seems to have a greater S element than it has previously been credited with and could be redefined in the light of these experiments as CSR.

A more detailed examination of the two species common to all the experiments (*M. spicatum* and *E. canadensis*), can be used to separate two species with a reportedly similar strategy (Abernethy *et al.* 1994 *subm.* see Appendix 11). *Myriophyllum spicatum* displays a lower tolerance to shade stress, a similar or slightly weaker recovery from cutting and a poorer competitive ability than *Elodea canadensis*. These results suggest that weed control practices based on stress or disturbance measures, that have given a poor result with *Myriophyllum* (Smith and Barko 1990), are likely to show even worse results when applied to *Elodea,* a superior stress and disturbance tolerator.

5.5 Summary

An experimental programme can be used to refine knowledge of species established phase strategies.

Six species strategies are examined, of which four are redefined in light of the experimental evidence.

The way in which a quantitative screening programme can be used to separate species of similar ecology is demonstrated.

Chapter 6

DEFINING FUNCTIONAL GROUPS FROM REGENERATIVE PHASE TRAITS

Chapter 6

DEFINING FUNCTIONAL GROUPS FROM REGENERATIVE PHASE TRAITS

6.1 Introduction

The uncoupling of juvenile and established phase traits has been suggested by Grime (1979) and since confirmed for wetland plants (Shipley *et al.* 1989) and some taxa of aquatic plants (Wiegleb and Brux 1991). Other workers have considered the two phases of development concurrently (Murphy *et al.* 1990; Bornette *et al.* 1994), which prevents their relationships from being separated. The present analysis looks at established and juvenile phase traits both separately and concurrently and compares the utility of the different analyses.

The approach taken for the juvenile phase was similar to that covered in Chapter 4 for the established phase. This chapter provides an analysis of the regenerative phase based on traits taken from the published literature. Species are grouped according to their regenerative phase traits and the robustness of this classification is assessed. The relationship between the two phases can be examined by i) comparing the two classifications; ii) examining correlations between established and regenerative phase traits; and iii) examining which regenerative traits, if any, are consistently associated with the established phase FG's outlined in Chapter 4. Chapter 7 complements this chapter, presenting the results of experimental work focused on the regenerative phase.

Grime *et al.* (1988) classified regeneration strategies for terrestrial herbaceous vegetation, assigning five classes, as shown in Table 6.1. This classification was based on experience of terrestrial herbaceous species. The vegetative category, in particular, does not appear to reflect adequately the range of regenerative strategies displayed by aquatic vegetation. Vegetative reproduction is thought to play a significant and effective role in the maintenance and dispersal of many aquatic plant populations (Grace 1993; Spencer and Bowes 1990). For instance, in an aquatic environment subject to flow or some other form of disturbance, vegetative fragmentation is an effective means of dispersal and regeneration. Grouping together all methods of vegetative reproduction ignores the differences in dispersal, seasonality, and degree of independence represented by the various mechanisms (as recognised by Leakey 1981). Bearing in mind these drawbacks, while still retaining

the basic idea of classifying mechanisms of regeneration in functional terms, an alternative classification is proposed (Table 6.2). The category of persistent juveniles used by Grime *et al.* (1988) has not been included. This is due, firstly, to the difficulty of recognising such a strategy in the field, and secondly the low likelihood of encountering it in the framework of riverine aquatic habitats. These are in general quite productive and with at least some degree of disturbance, and are unlikely to produce the combination of low productivity and low intensities of disturbance under which this strategy is normally exhibited. Limited data exist on the persistence of aquatic seed banks and it is hard to distinguish between persistent seed banks and seeds of limited persistence. This question is addressed in Chapter 7, but for the purposes of this analysis the available published studies have been utilised. Definitions of rhizomes and stolons follow Clapham, Tutin and Moore (1987); a rhizome is an underground stem lasting more than one growing season; a stolon is a creeping stem of short duration produced by a plant which has a central rosette or an erect stem and when used without qualification is above ground.

Table 6.1 Regenerative strategies in terrestrial vegetation (after Grime *et al.* 1988)

Strategy	**Functional characteristics**	**Conditions where strategy seems to enjoy competitive advantage**
Vegetative expansion (V)	New shoots vegetative in origin and remaining attached to parent plant until well established. Capable	Productive or unproductive habitats subject to low intensities of disturbance
Seasonal regeneration (S)	Independent offspring (seeds or vegetative) produced in a single cohort	Habitats subject to seasonally predictable disturbance by climatic or biotic factors
Persistent seed or spore bank (B_s)	Viable but dormant seeds or spores present throughout the year; some persisting more than 12 months	Habitats subject to temporally unpredictable disturbance
Numerous widely distributed seeds or spores (W)	Offspring numerous and buoyant in air; widely dispersed and often of limited persistence	Habitats subjected to spatially unpredictable disturbance or relatively inaccessible
Persistent juveniles(B_j)	Offspring derived from an independent propagule but seedling capable of long term persistence in a juvenile state	Unproductive habitats subjected to low intensities of disturbance

Table 6.2 Regenerative categories used in the analysis and their functional significance.

Strategy	Functional significance	Proposed conditions where strategy may have an advantage
Rhizomes	new shoots vegetative remaining attached until well established. Capable of perennation and dispersal.	productive or unproductive habitats; low intensity and frequency of disturbance. Possibly light limited at sediment surface.
Fragmentation (including shoot fragmentation and budding)	new shoots vegetative in origin but capable of dispersal	productive or unproductive habitats; moderate intensity and frequency disturbance
Seasonal vegetative propagules (tubers; turions)	vegetative propagules produced in a single cohort, capable of dispersal	habitats subjected to seasonal disturbance possibly light limited at the sediment surface
Stolons	new shoots vegetative remaining attached until well established, rapid spread	productive or unproductive habitats; low intensity and frequency of disturbance.
Seasonal seed production	seeds produced in a single cohort no dormancy mechanisms	productive habitats subject to seasonal disturbance.
Persistent seed or spore bank	viable but dormant seeds or spores present throughout the year; some persisting throughout the year	Habitats subject to temporally unpredictable disturbance (such as occasional drought)

When proposing the conditions under which the strategy may have a selective advantage, both the frequency and intensity of disturbance have been considered. For instance, drought can be considered as a disturbance since it destroys aquatic plant biomass. However if the fluctuations are not rapid or frequent then species employing creeping stems will be able to keep pace with the fluctuations. Dramatic changes in water level are better exploited by seasonal (vegetative or seed) reproduction where they are predictable, or persistent seed or spore banks where they are not. Frequent changes in water level are possibly best coped with by fragmentation or efficient seed dispersal, that allows the offspring to establish quickly in favourable conditions. Also, when adhering to the terms used in Grime's framework, it should be considered that *'the essential elements of natural disturbances are their stochasticity and the fact that they change resource availability suddenly (whether they destroy plant matter or not)'* (Moore and Noble 1990). As with the established phase, it is expected that different relationships will exist between regenerative strategies and habitat conditions than those documented for terrestrial habitats. For example, a seed in a productive habitat, with nutrient-rich sediment and/or water, may experience difficulties in establishment due to the light limiting effects of phytoplankon and luxurious macrophyte growth. It will have an advantage conferred upon it as a vegetative propagule (such as a turion), in

that it will have the resources to germinate and reach the surface. In this case what is a good habitat for an established plant poses some problems for the regenerative phase. Grace (1993) made preliminary models of the trade off between different regenerative factors and also their suitability in different habitat conditions, but emphasised that his system represented an approach rather than an exhaustive treatment.

This chapter aims to:

- group selected euhydrophyte species according to their juvenile traits.
- assess the validity of this grouping
- compare this grouping with that arising from established phase traits.
- look at both groupings compared to a single analysis of all traits
- select the most coherent and valid method of functionally grouping the euhydrophyte species.

6.2 Methods

A list of traits pertaining to the juvenile phase was drawn up and data on these traits drawn from the literature. The traits are listed in Table 6.3 and the values for the species are given in Appendix 5.

Table 6.3 Juvenile traits taken from the published literature

Trait	Attribute	Code
Mode of reproduction	rhizome	rhi
	fragmentation	fra
	turions and tubers	tur
	stolons	sto
	persistent seed bank	psb
	transient seed bank	tsb
Rate of seed production	none	sbn
	low	sbl
	medium	sbm
	high	sbh
Seed buoyancy	seed buoyant	buo
Seed size	< 1mm	sss
	1 - 3mm	ssm
	> 3mm	ssl

6.3 Data Analysis

6.3.1 Clustering using regenerative phase traits

An initial grouping was achieved using TWINSPAN. The TWINSPAN classification showed very low eigenvalues for each division, indicating that the groups are not well separated and may not even be statistically significant different. Nonetheless this initial grouping could be used for the start of a non-hierarchical clustering of the species. (See Chapter 4 for detail of data analysis techniques). Non-hierarchical clustering was performed using the GENSTAT programme. The SS criteria for different numbers of clusters is shown in Fig 6.1. 6 groups and 5 groups both appeared to show some improved coherence. Examination of the species distributions in both clusterings showed no difference between group composition except the merging of two groups to reduce the clusters to five. Six groups were chosen for further analysis. The species distribution between these six groups is shown in Table 6.4.

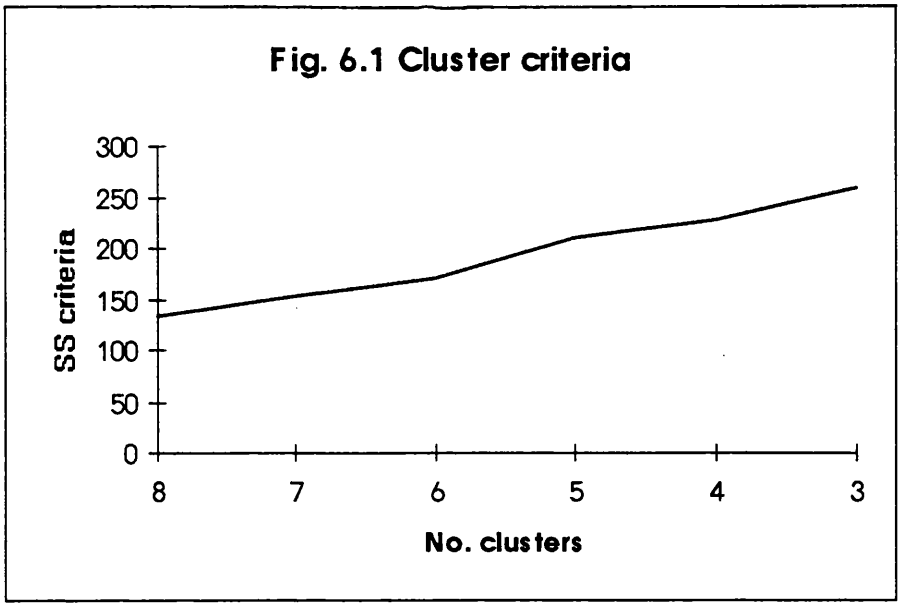


Table 6.4 Species distribution between the groups defined by juvenile traits

1	2	3
H. palustris	C. demersum	M. alterniflorum
N. lutea	P. lucens	M. spicatum
N. pumila	P. natans	M. verticillatum
O. fluviatile	P. nodosus	P. amphibia
S. emersum	P. obtusifolius	P. berchtoldii
S. angustifolium	P. pectinatus	P. coloratus
		P. crispus
		P. polygonifolius
		P. pusillus
		P. trichoides
		Z. palustris
4	**5**	**6**
G. fluitans	C. hamulata	J. bulbosus
G. declinata	C. obtusifolius	L. trisulca
N. alba	C. platycarpa	L. minor
R. aquatilis	C. stagnalis	S. polyrhiza
R. circinatus	E. acicularis	U. intermedia
R. penicillatus	E. canadensis	U. vulgaris
R.peltatus	H. morsus-ranae	S. sagittifolia
R. trichophyllus		

To investigate the validity of these groups a Principal Components Analysis of the species by their traits was overlaid by the groups (Fig 6.2). Principal component 1 contained 24.1% of the variation and Principal component 2, 17.8%. Only partial separation of these groups was achieved using the first two axes. The groups showed quite good separation between groups 5, 6 and the remaining four.

However distinguishing between groups 1, 2, 3 and 4 was not possible on the first axis and while groups 1, 2 and 3 could be distinguished on Axis 2, group 4 could not. So while these groups are the most coherent available, it seems that they are not distinctly separated in terms of juvenile traits.

6.3.2 Comparison with groups from the established phase.

The species membership of the groups arising from the established phase trait and the juvenile traits can be compared in Table 6.5. The juvenile phase groups do not seem consistently to correspond to particular established phase groups, although in some established phase groups (e.g. FG1, FG4, or FG6) there does appear to be a preponderance of one juvenile group. This general lack of coherence between the two phases is consistent with the findings of Grime (1979).

To further investigate the relationship between the juvenile and established phase the correlations between the two sets of traits were calculated. Pearsons Rank correlation coefficient was calculated and, unless otherwise stated, $p < 0.01$, $n = 48$. In general, there was little correlation between established and juvenile phase traits. Correlation coefficients $r > 0.5$ are shown in Table 6.6. Correlations between small plant size and no, or low, seed production are strong, and conversely there is negative correlation between large plant size and low seed production. Given the above it was not surprising that small plants were also unlikely to form persistent seed banks. Free floating plants also showed a correlation with no seed production. High seed production, as would be expected, is correlated with the trait labelled vigorous seed production in the established phase (and negatively correlated with low, or no, seed production). This trait was included in the established phase to reflect the amount of energy invested in seed production by mature plants. There is not complete correlation between high seed production and vigorous seed production as some of the 'vigorous seed production' species will be categorised as medium seed production in the more detailed classification used in the juvenile phase trait set. Low seed production was also correlated with water pollination, suggesting that, despite the plants being emersed in the aquatic medium, it is not a reliable method of pollination. Buoyant seeds were correlated with large plants and negatively correlated with a multiple stem growth form. A high below : above ground biomass ratio was correlated with the use of rhizomes as a means of reproduction.

Table 6.5 Comparison of Functional Groups derived from different sets of traits.

	Functional group	Juvenile group	All traits group
Hottonia palustris	1	1	2
O. fluviatilis	1	1	2
Ranunculus aquatilis	1	4	1
R. peltatus	1	4	1
R. penicillatus	1	4	1
R. tricophyllus	1	4	1
R. circinatus	1	4	1
Ceratophyllum demersum	2	2	2
Elodea canadensis	2	5	2
Juncus bulbosus	2	6	4
Myriophyllum alterniflorum	2	3	2
M. spicatum	2	3	2
M. verticillatum	2	3	2
Potamogeton pectinatus	2	2	2
P. berchtoldii	2	3	4
P. crispus	2	3	2
P. obtusifolius	2	2	2
P. pusillus	2	3	4
P. trichoides	2	3	4
Utricularia intermedia	2	6	2
U. vulgaris	2	6	2
Zannichellia palustris	2	3	2
Glyceria declinata	3	4	3
Glyceria fluitans	3	4	1
P. coloratus	3	3	3
P. lucens	3	2	3
P. natans	3	2	3
P. nodosus	3	2	3
P. polygonifolius	3	3	3
Sparganium angustifolium	3	1	3
S. emersum	3	1	3
Callitriche hamulata	4	5	4
C. stagnalis	4	5	4
C. platycarpa	4	5	4
C. obtusangula	4	5	4
Nuphar lutea	5	1	3
N. pumila	5	1	3
Nymphaea alba	5	4	3
Persicaria amphibia	5	3	3
Sagittaria sagittifolia	5	6	1
Eleocharis acicularis	6	5	5
Hydrocharis morsus-ranae	6	5	5
Lemna minor	6	6	5
L. trisulca	6	6	5
Spirodela polyrhiza	6	6	5

Fig 6.2 Plot of Component 1 and Component 2 from the PCA of species regenerative phase traits. Clusters assembled using regenerative phase traits delineated by dotted lines (for species codes see Appendix 2).

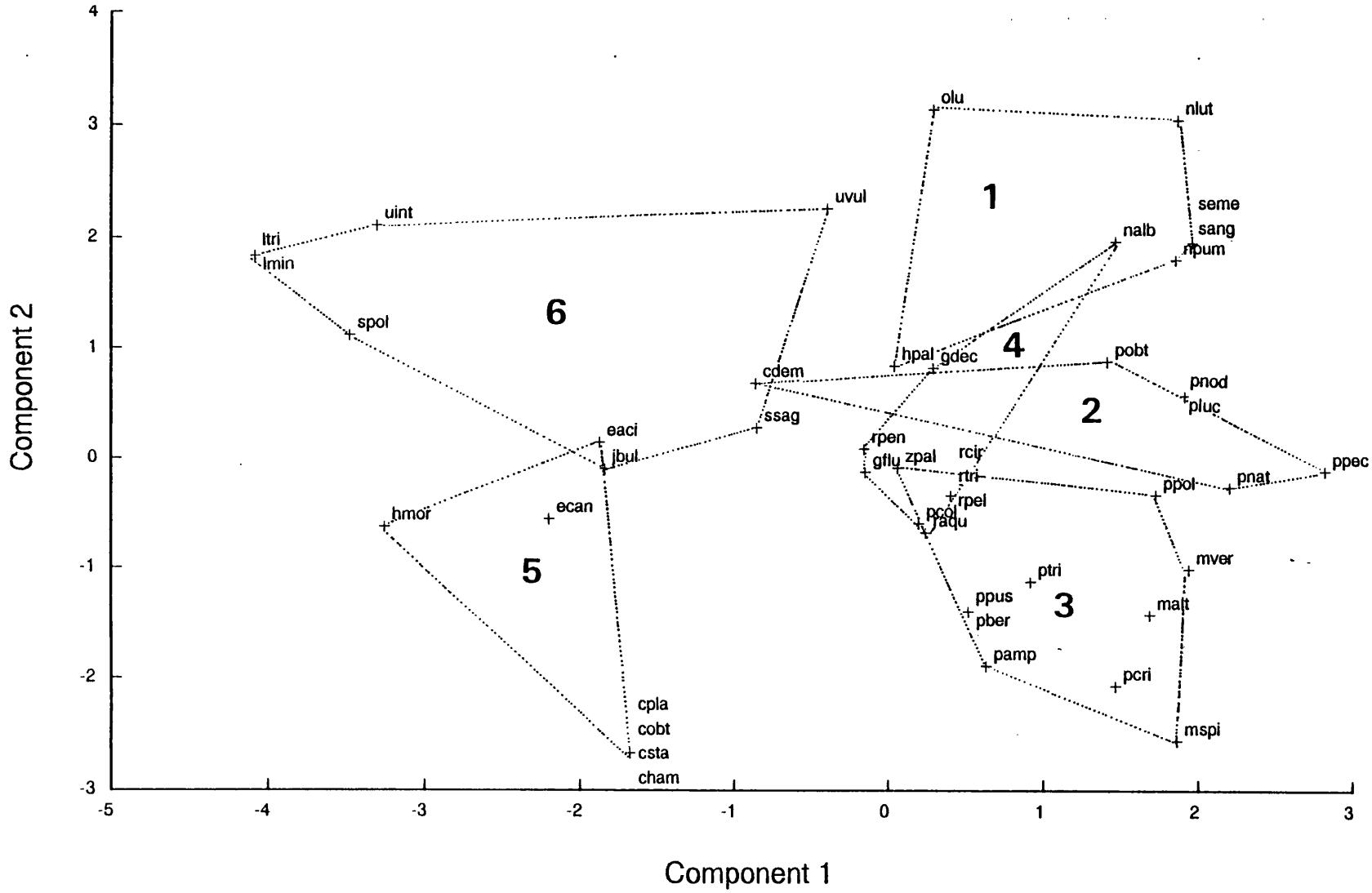


Table 6.6 Significant correlation coefficients for established and juvenile phase traits

Established trait	Juvenile trait	Correlation
Small plant	No seed production	0.743
Vigorous seed production	Seed production high	0.674
Free floating plant	No seed production	0.562
Large plant	Buoyant seeds	0.538
Small plant	Seed production low	0.524
Water pollinated	Seed production low	0.507
Below : above ground high	Rhizomes	0.504
Large plant	Seed production low	-0.588
Vigorous seed production	Seed production low	-0.584
Multiple stems	Buoyant seeds	-0.519
Vigorous seed production	Seed production none	-0.508
Small plant	Persistent seed bank	-0.508

Within the set of juvenile traits the only significant correlation was a negative relationship between buoyant seeds and low seed production ($r = -0.648$).

As there was no clear relationship between the two sets of traits the next step was to perform the same exercise of clustering and ordination on the entire trait set comprising both the established and regenerative phase traits. For the non-hierarchical clustering the initial groups used were the same as for the established phase analysis. The SS criteria (Fig 6.3) shows a slight change at 5 clusters and these were examined. Group membership is shown in Table 6.6 alongside a comparison of this grouping with the previous two. In general, the classification corresponds quite well with the established phase groups.

A Principal Components Analysis of the species using all the traits was run. Principal component 1 contained 14.9% of the variation in trait data and component 2 contained 13.1%. The ordination is shown overlain by the juvenile trait grouping, the established trait grouping and the entire trait grouping in Fig 6.4a, b, and c respectively. From these diagrams, it seems that the established phase grouping (Fig 6.4b) is still showing the most coherent pattern, even when both sets of traits are under consideration. The analysis of juvenile phase traits does not seem to result in a robust classification independent of the established phase, and as clustering of all traits does not produce an improved result, the analysis of the relationship of

species traits to environment, and the assessment of functional vegetation type will be continued with the established phase grouping. An examination of the regeneration traits associated with these groups can be made as no uncoupling has been proved or disproved. In Table 6.7, Table 4.10 has been amended to include regenerative traits.

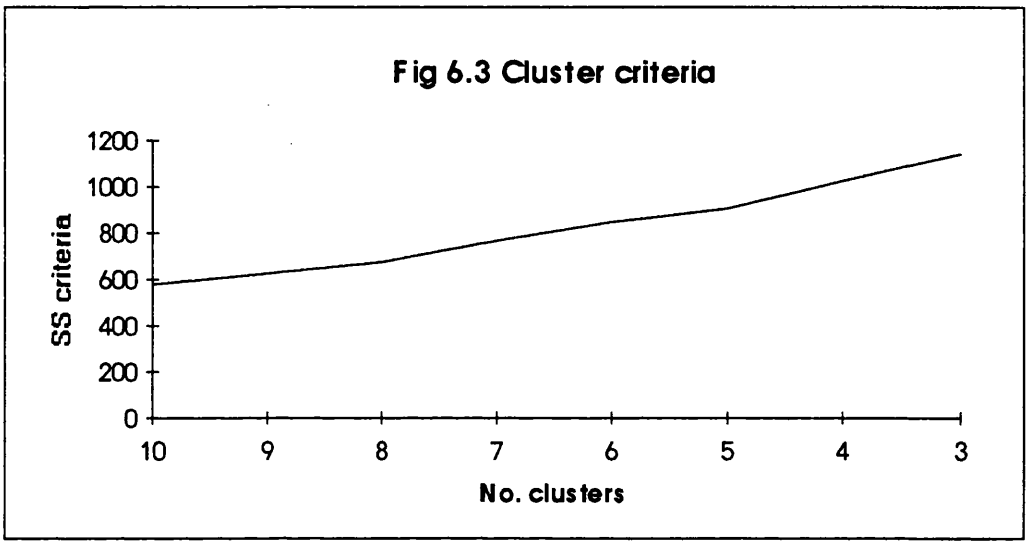


Fig 6.4a Plot of Component 1 and Component 2 from the PCA of species established and regenerative phase traits. Clusters assembled using regenerative phase traits delineated by dotted lines (individual species codes not indicated).

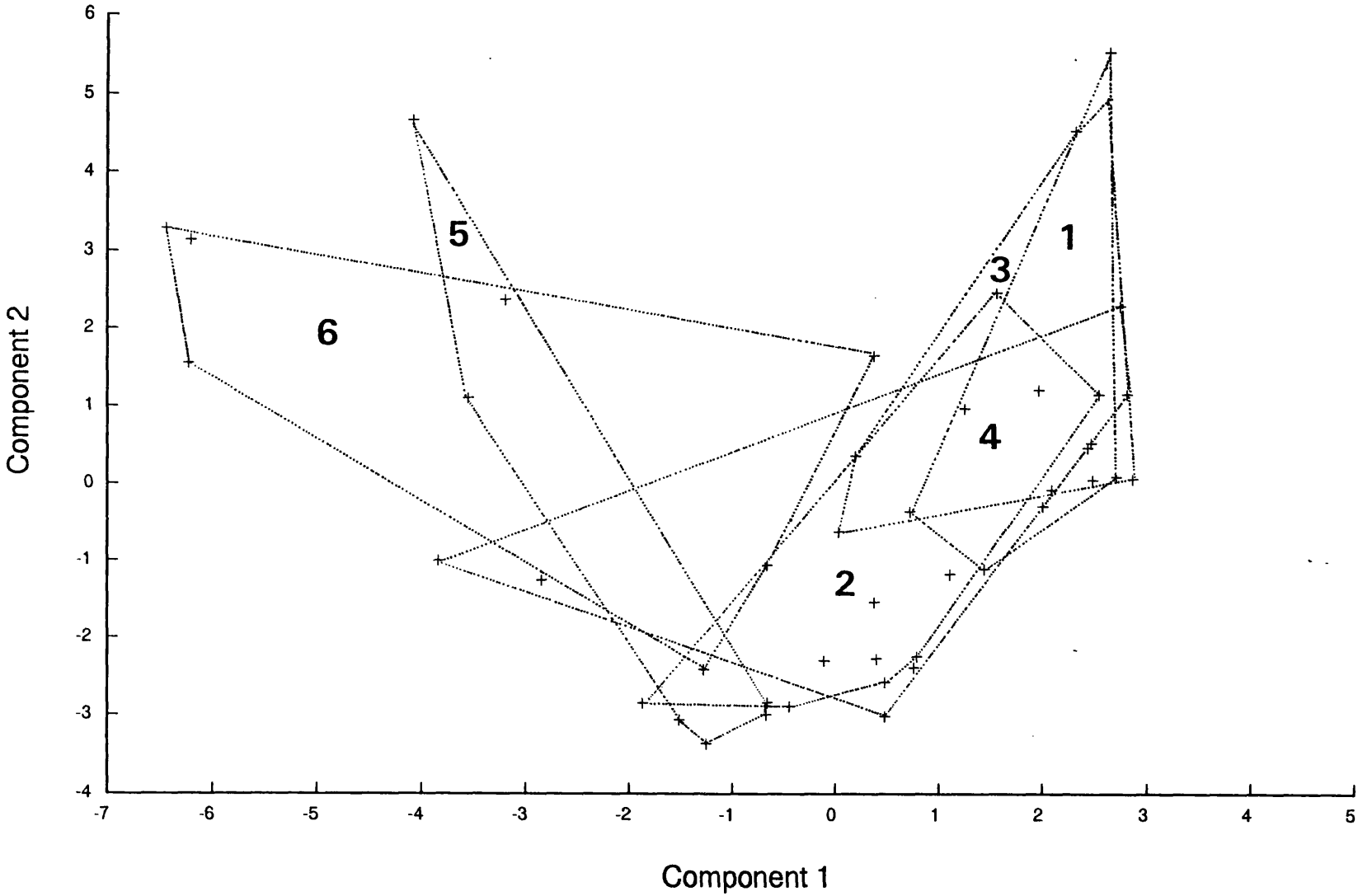


Fig 6.4b Plot of Component 1 and Component 2 from the PCA of species established and regenerative phase traits. Clusters assembled using established phase traits delineated by dotted lines (individual species codes not indicated).

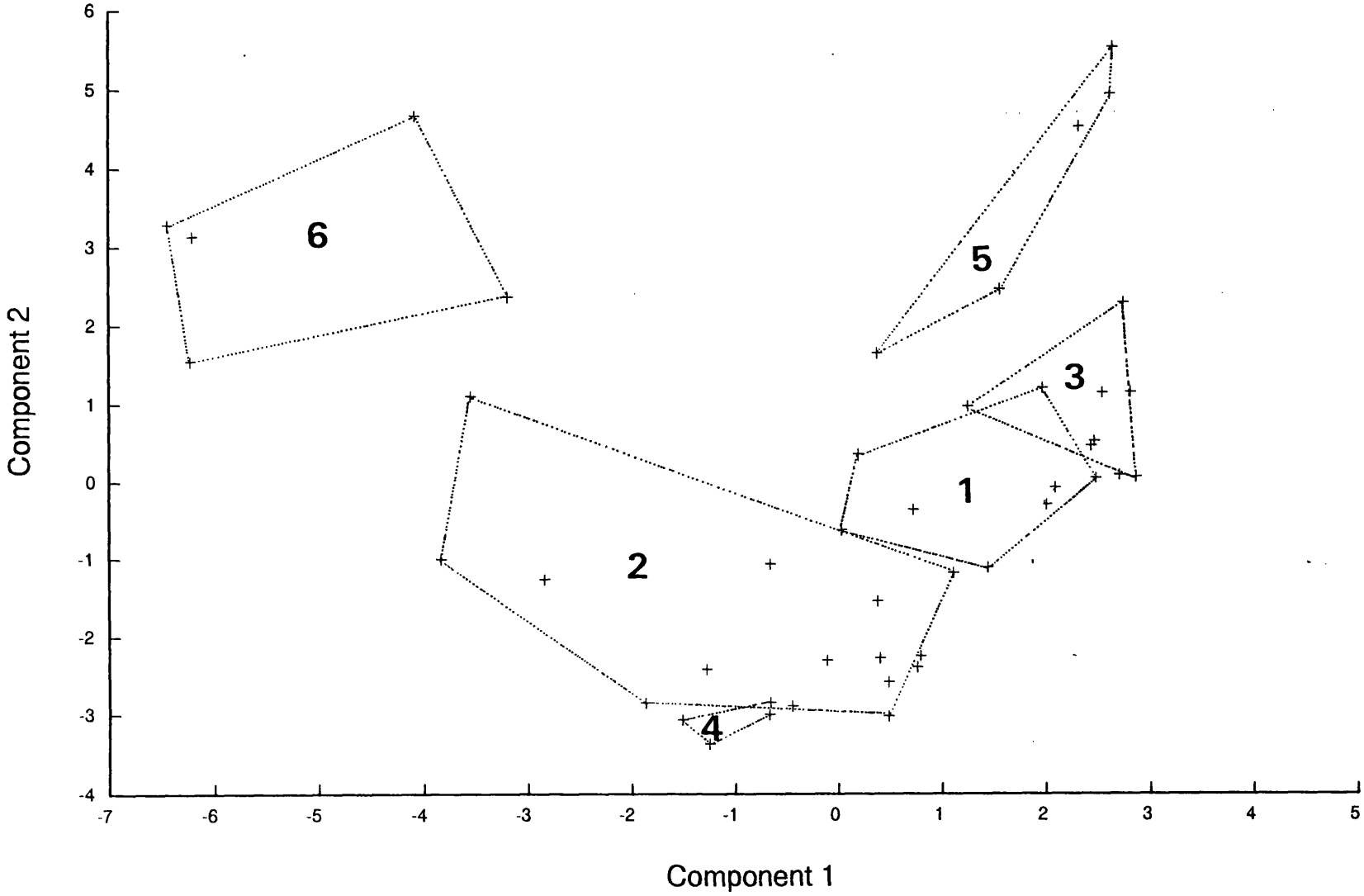


Fig 6.4c Plot of Component 1 and Component 2 from the PCA of species established and regenerative phase traits. Clusters assembled using regenerative and established phase traits delineated by dotted lines (individual species codes not indicated).

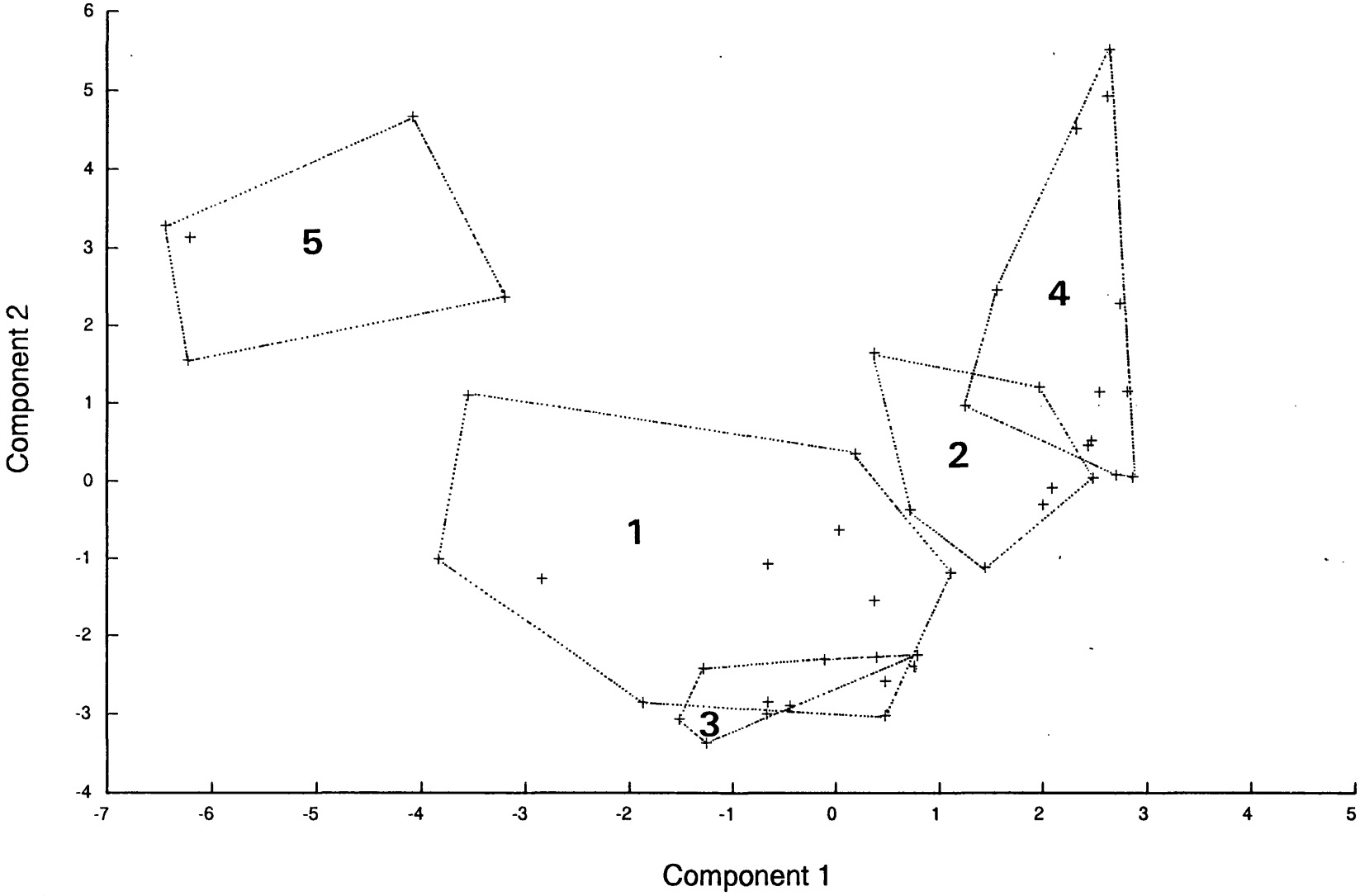


Table 6.7 Functional groups and their associated established and regenerative phase traits. Traits are common to at least 75% of group members except those in parentheses which are common to at least 50% of members.

Functional Group	Established phase traits	Regenerative phase traits
1	plant length (medium) long submerged rooted with/without floating leaves soft, medium sized leaves single stem, many branches insect pollinated flowers early flowering (potential annual) (canopy former)	buoyant seeds medium/large seeds (transient seed bank)
2	submerged rooted small (soft) leaves single stem, many branches medium/large sized plants (late flowering) (wind pollinated) (HCO3 user)	(rhizomes) (turions) (seed production moderate) (buoyant seeds)
3	submerged and floating leaved wind pollinated single stem, few branches large plant size medium (large) leaves (vigorous seed production) (canopy former)	rhizomes buoyant seeds medium large seeds
4	amphibious submerged and floating leaved heterophyllous medium sized plant length small, soft leaves long flowering period single stem, few branches (wintergreen) (wind pollinated)	fragmentation stolons low/medium seed production persistent seeds medium size seeds
5	submerged/floating leaves large, rigid, waxy leaves large plants multiple stems arising from base canopy former insect pollinated (below:above ground biomass high) (vigorous seed production) (large lateral spread)	rhizomes transient seed bank seed production med/high
6	free floating small plants small, rigid (waxy) leaves (canopy former)	fragmentation no/low seed production

6.4 Discussion

A number of explanations may be given for the failure of the juvenile traits to produce either coherent groupings or firm relationships with the established phase:

1) The juvenile phase is truly uncoupled from the established phase.
2) The parameters used were not a good reflection of variation in juvenile phase strategy, particularly through the placing of too much emphasis on aspects of sexual reproduction.
3) The information available on reproductive biology of euhydrophyte species was inadequate, giving too many '1' coded attributes that may be obscuring trends.

The above analysis appears tentatively to lend some weight to the hypothesis of (Grime 1979), that the established and juvenile phase strategies are not directly related. However, the influence of the latter two factors on the analysis is judged, retrospectively, to be quite high. Regeneration traits need to be more carefully defined with specific reference to euhydrophytes and with more attention paid to vegetative reproduction mechanisms. A framework needs to be established for detailed research on individual species to improve the quality of the data set. Autecological research such as that conducted by Titus and Hoover (1991) into the reproductive success of *Vallisneria americana*, if extended to a wider range of species would provide ideal comparative data. Meanwhile the relationships between the traits need exploring in a more rigorous manner, by direct experimentation, before the hypothesis of uncoupling of the juvenile and established phase can be confirmed or rejected for euhydrophytes.

Few species exhibit high seed production and this could be due to the substantial costs of flowering in an aquatic environment and the hazards of elevating aerial flowers (Leaky 1981), which need to be balanced by a selective advantage (Kay 1987) as flowering competes with vegetative reproduction for resources. Floral limitation may be the principal limiting step for sexual reproduction, but ineffective pollination, failure of seeds to germinate and the challenges of seedling establishment all reduce its efficiency (Titus and Hoover 1991). Asexual regeneration may be so economical, safe and effective in an aquatic medium that the selective value of sexual reproduction may be reduced (Kay 1987; Grace 1993) and

this may lead to a reliance on vegetative propagation (Sculthorpe 1967). The generally expressed view is that vegetative reproduction is the prevalent mode, but this is supported by qualitative, rather than quantitative, field observations (Titus and Hoover 1991)

It has been suggested that the clonal adaptations of aquatic angiosperms have functional significance to the plants and can be related to habitat conditions (Grace 1993). Functional characteristics of clonal reproduction have been recognised as numerical increase; resource acquisition, storage; protection; and anchorage (Grace 1993). The various mechanisms of clonal reproduction have different capacities for these functions e.g. fragmentation is associated with numerical increase, dispersal and resource acquisition. Some of these characters will have negative correlations with each other, e.g.. dispersal and storage. Aspects of both established phase and regenerative phase correlation with habitat conditions will be considered in Chapter 8.

6.5 Summary

Using the species grouping defined by the established phase traits seemed to be the most coherent way of organising the data.

Data on regenerative biology is sparse and the traits selected could have over represented sexual reproduction, with a biasing influence on the classification.

Regenerative traits are recognised as associated with particular established phase groups.

On the basis of the available information, coupling or uncoupling of established and regenerative phase traits in euhydrophytes cannot be proved.

Chapter 7

EXPERIMENTAL WORK ON THE REGENERATIVE PHASE

Chapter 7

EXPERIMENTAL WORK ON THE REGENERATIVE PHASE

7.1 Introduction

In Chapter 6 an analysis of regenerative phase traits taken from the literature was presented. Chapter 7 describes experimental work conducted to improve the understanding of regenerative strategies in euhydrophytes. Both sexual and vegetative means of reproduction were investigated. I concentrated on one aspect of vegetative reproduction: fragmentation, selected because it is a prominent form of propagation in these communities (Sculthorpe 1967; Leakey 1981; Grace 1993). Fragments can either be separated naturally, by decay of connective tissues, by active abscission (which occurs during the formation of turions) or by physical damage. The latter is particularly common in fast flowing waters. In water plants, fragmentation provides an asexual method for dispersal, which, in most terrestrial plants can be accomplished only by energetically costly seed production. It is well suited to the aquatic medium by the protection and buoyancy offered. The numerical increase attained by fragmentation can also be exceedingly high; in an experiment on *P. crispus,* 23250 dormant apices were produced from a single dormant apex over one growing season (Yeo 1966). The ability to regrow from shoot fragments in the field is associated with the rapid production of roots in laboratory trials (Hodgson and Pearce 1993).

It has been suggested that sexual reproduction plays a small role in the maintenance and dispersal of euhydrophyte plant populations (Sculthorpe 1967; Aiken *et al.* 1979; Hutchinson 1975; Frankland *et al.* 1987) despite quite high rates of seed production in some species (Gopal 1986; Smith and Barko 1990) but little direct experimentation has been reported (as noted by Titus and Hoover 1991). However, van der Valk and Davis (1978) showed that some euhydrophytes (e.g. *Potamogeton pectinatus, Lemna minor, Najas flexilis, Ceratophyllum demersum, Utricularia vulgaris*) do regenerate from seed or propagule following drawdown and these propagules must, therefore, be able to survive for at least a year in unfavourable conditions.

The role of sexual regeneration was investigated by a study of the seed bank found in aquatic habitats of wetlands. This approach is an indirect means of estimating the role of sexual regeneration by simulating conditions that are deemed to be of

importance in the field and quantifying the germination response. This includes persistent and non persistent seeds (the term 'seed' is used here for true seeds and fruits) and spores and seasonal vegetative propagules (the 'bud bank' *sensu* Harper 1977). This use of the term seed bank has been used in a number of frequently cited studies (van der Valk and Davis 1978; van der Valk 1981; van der Valk and Verhoeven 1988). Aquatic plants which can germinate from turions or other non seed propagules include species of Lemnaceae (van der Valk and Davis 1979); Potamogetonaceae (Rogers and Breen 1980; Sastroutomo 1981); and Characeae (van der Valk and Davis 1979; Kadlec and Smith 1984). Turions and tubers are usually formed as dormant organs (Frankland *et al.* 1987) and like seeds require a special environmental cue for germination (Bartley and Spence 1987). In their physiology and ecology, turions resemble seeds remarkably closely (Bartley and Spence 1987; Leck 1989). It is very difficult to distinguish between plants arising from sexual propagules and those arising from vegetative ones (Muenscher 1936; Scribailo and Posluszny 1985; Leck 1989), so I did not attempt to separate the two in this study. In addition little is known about the influence of the component of the seed bank that is not true seeds (particularly spore producers such as *Chara*) on wetland vegetation dynamics (Leck and Simpson 1987b). The relationship of the true seed bank and the bud bank is illustrated along with their role in vegetation dynamics in Fig 7.1. The trials involved collecting sediment cores which were then germinated in the laboratory (Smith and Kadlec 1985; van der Valk and Davis 1978) and the seedlings counted (Chancellor 1965). This technique has been used in wetland and terrestrial systems with success (Grillas, van Wijck and Boy 1992; Gross 1990; van der Valk and Davis 1979). Although the approach may underestimate seed density (Roberts 1981; van der Valk and Verhoeven 1988), as a comparative technique across sites it is adequate. It is a good measure of the 'ecologically active component' of the seed bank rather than an absolute measure of the seed bank size.

While many studies have been published on wetland seedbanks (Leck 1989), little information exists on the seedbanks of submerged sites, possibly due to the difficulty experienced in obtaining samples. Few studies have taken permanently submerged freshwater sediments as their subject, and those that have are concerned with lacustrine habitats (Rodgers and Breen 1980; Keddy and Reznicek 1982; Haag 1983). Kautsky (1990) also used germination trials, combined with seed and tuber counts, to assess the seed bank of brackish aquatic habitats. Wetland studies have examined the relationship of the seedbank to established vegetation (e.g. Milton 1939; van der Valk and Verhoeven 1988), to zonation patterns (van der Valk and

Davis 1978, 1979; Keddy and Reznicek 1982; Smith and Kadlec 1983; Kadlec and Smith 1984; McCarthy 1987), to succession (van der Valk 1981), to species diversity (Pederson 1981, Leck *et al.* 1988, 1989) and to establishment and recruitment patterns (Leck and Simpson 1987a). Studies of consecutive horizons can provide insight into seed longevity and vegetation history (van der Valk and Davis 1979). Repeated, comparative sampling visits to a site can be used to investigate seasonal variations in the composition and size of the seed bank (Thompson and Grime 1979; Titus 1988). The effects of environmental variation, such as water level fluctuation (van der Valk 1981; Keddy and Reznicek 1986) and salinity (Grillas, van Wijck and Boy 1992) on recruitment from the seed bank have been reported. The characteristics of seed banks of aquatic habitats can be compared to these studies. Information on seed banks of submerged aquatic macrophytes is relatively scarce (van Wijk 1989) and there is also a need for comparative study of wetland seed banks (Leck 1989).

Thompson and Grime (1979) investigated seed banks in ten contrasting habitats, but did not include aquatic habitats in their study. From this study they classified terrestrial species seed banks into four categories set out below:

I Species with transient seed banks present during the summer.
II Species with transient seed banks present during the winter
III Species with persistent seed banks, many seeds germinate soon after release (like type I), the remainder form part of the seed bank.
IV Species which form a persistent seed bank, few seeds germinate immediately following release.

(I and II correlate with seasonal seed banks and III and IV correspond to permanent seed banks in the proposed regeneration classification shown in Table 6.2). Types III and IV can be difficult to distinguish and may be a single type (Thompson and Grime 1979).

In their study Thompson and Grime did not attempt to enumerate the seed banks under study but rather their aims were to classify the seed banks of herbaceous species, and to analyse their functional significance in contrasted vegetation types. They contended that to realise these aims methods which did not involve complete recovery of the seed flora were adequate. They used comparison of samples taken throughout the year, and at different depths, to classify the species seed bank types. Germination studies have also been used to evaluate life history traits and relate

them to environmental parameters such as water regime (Grillas, van Wijck and Bonis 1991). From an applied view point the most interesting aspect of a seed bank study is its role in determining future vegetation after natural or anthropogenic disturbance.

This chapter

- investigates the efficiency of fragmentation as a means of propagation in selected populations.

- relates the above results to the types of habitats from which the populations originated.

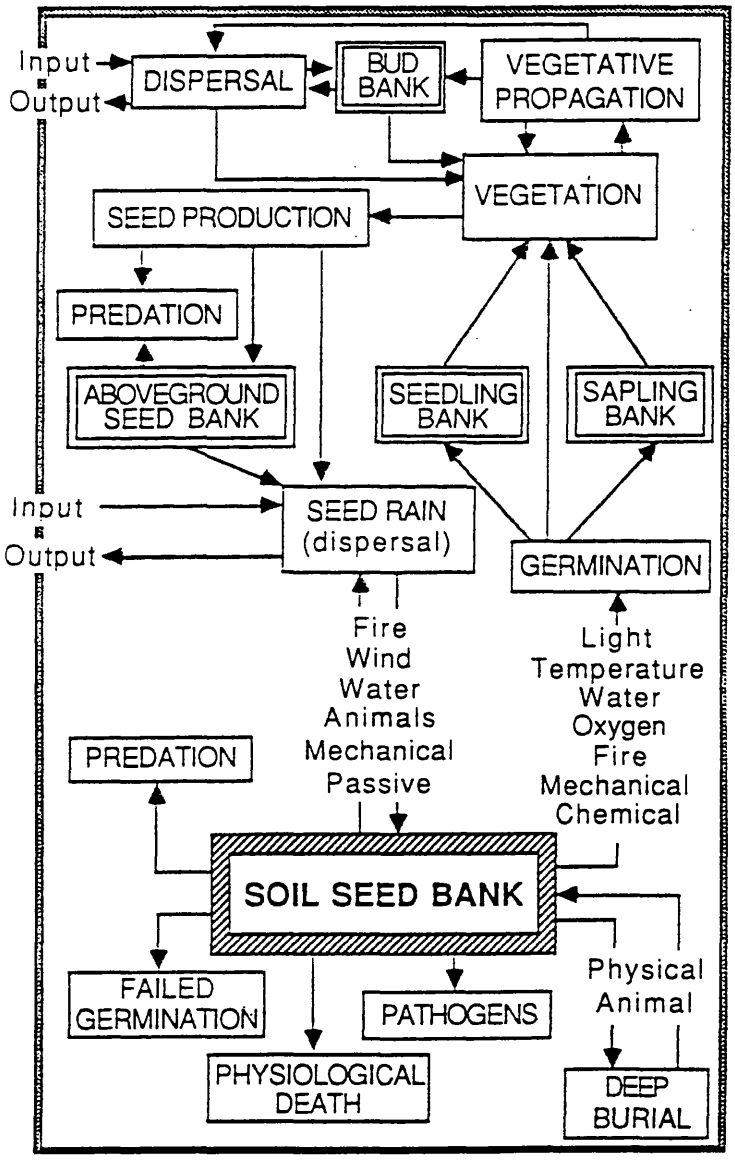
- investigates the role of the seed/propagule bank in aquatic habitats of wetland ecosystems.

- investigates the influence of various environmental parameters on recruitment from the seed/propagule bank.

- relates the above to environmental parameters observed in the field

- discusses the importance of sexual reproduction to euhydrophyte species

Fig 7.1 A general model of seed bank and vegetation dynamics (from Simpson *et al.* 1989).



7.2 Regeneration by Fragmentation - Methods

The method used was adapted from experiments described by Hendry and Grime (1993) to compare the adventitious rooting of cuttings in terrestrial plants. Three-node apical stem sections were collected from plants in the field and transported to the laboratory in cool boxes. For 'rosette' species, such as *Sparganium*, a whole rosette was used and the basal roots excised. 10 replicates were taken from each population examined. Where possible, non flowering material was used, and collections were made in June, July and August 1993. The stem fragments were floated in varying quantities of tap water depending on size. Fragments up to 10 cm long were floated in 400ml, fragments larger than this were allowed 1000ml tap water. Each fragment was floated in a separate shallow container with water depth approximately 15mm. The water was replenished daily, and changed every 4 days. Fragments were put into the greenhouse where a temperature of 20°C was maintained and there was a 16hr daylight regime of natural light supplemented by 400 watt Navilux flood lights. Fragments were checked daily for roots. The number of days taken for 50% of the population to form roots was recorded (T_{50}). If this had not been achieved after 60 days the experiment was terminated.

7.3 Regeneration by Fragmentation - Results

In total 22 populations were screened for rooting ability. The results are shown in Table 7.1 together with information on the species and sites. No correlation existed between the T_{50} of a population and the flow at the collection site, the stress index of the site or the disturbance index of the site. Collection date also had no strong correlation with T_{50}. Some trends can be suggested between Functional Group and T_{50}, but these are not certain. It seemed that species from FG 1 and FG 4 had quite short rooting times, while those from FG 2 and FG 3 were slower, or did not produce roots at all.

Table 7.1 Results of rooting trials.

Species	FG	Collection		Site Indices			T50 (days)
		site	date	Stress	Disturb.	Flow	
Callitriche stagnalis	4	fappo	28-Jun	3	1	1	2
Callitriche obtusangula	4	icldi	04-Jun	3	0	2	4
Callitriche hamulata	4	cimsr	17-Jun	2	4	5	4
Callitriche obtusangula	4	ilbd4	04-Jun	4	0	2	5
Ranunculus peltatus	1	fappo	28-Jun	3	1	1	5
Sparganium emersum	3	cimid	14-Jul	2	0	3	7
Ranunculus penicillatus	1	eksrf	24-Jul	1	4	5	8
Zannichellia palustris	2	ilbr	30-Jul	2	0	4	10
Myriophyllum spicatum	2	faoxa	11-Aug	3	0	1	12
Myriophyllum alterniflorum	2	cimsr	09-Jul	2	4	5	13
Potamogeton nodosus	3	fapdo	28-Jun	3	0	1	14
Elodea canadensis	2	fappo	11-Aug	3	1	1	14
Callitriche hamulata	4	eksrl	24-Jul	1	4	5	19
Myriophyllum spicatum	2	eksrl	24-Jul	1	4	5	19
Elodea canadensis	2	cimid	17-Jun	2	0	3	27
Potamogeton lucens	3	ibipo	31-Jul	4	0	1	28
Ranunculus circinatus	1	faoxa	28-Jun	3	0	1	46
Potamogeton coloratus	3	ilbd2	04-Jun	2	0	2	nr
Potamogeton obtusifolius	2	cimnl	13-Jul	4	0	1	nr
Potamogeton crispus	2	ilbr	30-Jul	2	0	5	nr
Myriophyllum verticillatum	2	ilbd3	04-Jun	3	0	2	nr
Myriophyllum verticillatum	2	ilbd3	30-Jul	3	0	2	nr

7.4 Regeneration by Fragmentation - Discussion

The T_{50} recorded for the various populations did not appear to be closely related to environmental parameters or species functional group. A negative correlation with flow might be expected as establishment of fragments in such an environment would be difficult, although high flow velocity may promote the initial formation of fragments. Grace (1993) has associated fragmentation of free floating plants with lakes and slow moving waters. Fragmentation is well suited to productive water where the ability of fragments for maximum resource acquisition can be exploited. This trial involved a number of parameters that could be influencing the rate of root production, including collection date, collection site location, collection site environmental conditions and species phenology and more extensive trials, dealing

with each in isolation, are required to separate species ability to regenerate by fragmentation from other parameters. While samples were only collected from mature non-flowering specimens, more subtle differences in phenology may influence root production. In *M. spicatum* the rate of fragmentation increases dramatically after peak biomass has been attained (Madsen *et al.* 1988). The rate of rooting is probably related to hormonal changes in the plant during this period. The functions of regeneration by fragmentation can be characterised as dispersal, numerical increase and the ability for resource acquisition (Grace 1993). Madsen *et al.* (1988) found the fragments of *M. spicatum* to be suitable for long distance dispersal as they were capable of survival for at least 36 days and they grew in both length and weight in this time. Grace (1993) suggested that fragmentation would not be suited to habitats subject to disturbance, such as desiccation, due to the poorly protected nature of the propagules. However the strategy is still advantageous in a wide variety of habitats and I may have been looking for too simplistic a relationship with environmental conditions.

7.5 Regeneration from Buried Seeds and Propagules - Methods

Sediment cores were collected in Scotland, France and Ireland during 1993. The collection dates at each site and the germination period are shown in Table 7.2. Within each site cores were taken from random locations. Cores were collected (Plate 19) using a sediment corer (diameter 100mm) designed for use in aquatic habitats (Sutton 1982). Cores were taken to a depth of 10 cm and divided into two horizons (a = 0 - 5cm ; b = 5 - 10 cm below surface). A lower limit of 10 cm was deemed adequate as decline with depth is usually exponential (Leck 1989) and most reports for lakeshores, temporary ponds and freshwater tidal wetlands have revealed a shallow seed bank with more than 80% of seeds located in the top 5 cm (Nicholson and Keddy 1983; Leck 1989). Cores were transported from the field sites to the laboratory in cool boxes and stored at 5°C until the start of the trial. Species chilling requirements can vary between a few days to several months (Grime 1979; Smits and Wetzels 1986). This period of chilling should satisfy the chilling requirement of most species, particularly as the majority of samples were collected in the early spring, after the winter chill period. In the laboratory samples were thoroughly mixed and detritus removed (adhering sediment was washed back into the sample). Samples were spread over 20mm of washed aquarium sand in plastic trays (130mm x 190mm x 155mm deep) giving a sediment depth of approximately 15mm (following Van der Valk & Davis 1978). Sediment flats were

left to dry out before imposing the different treatments. The samples were left to germinate in the greenhouse at about 20°C with natural light supplemented by 400 watt Navilux sodium lights for 16hr per day (Plate 20). Diurnal temperature fluctuations, which are known to stimulate germination in many cases (Frankland *et al.* 1987), were in the order of 5 - 6°C. Conditions of 16 hr day at 20°C and 8 hr night at 15°C have been found to be suitable for germination of a wide range of native species (Grime *et al.* 1980). High, fluctuating temperatures and a high light intensity are conducive to the germination of both annuals and emergents (Galinato and van der Valk 1986). These conditions applied to marsh vegetation have been shown to result in 100% germination of the seed bank of many species and a large proportion of the seed bank of the remainder (ter Heerdt and Drost 1994). Various treatments were applied to the germination trays and various levels of replication were used (Table 7.2). Fifteen replicates per site are recommended for the reliable estimation of the seed bank in terrestrial habitats (Gross 1990). An alternative recommendation states that 400cm^3 of soil is sufficient to detect most species of ecosystems in the early stages of succession (Numata *et al.* 1964). In this study over 3000 cm^3 were used in each treatment (A horizon only), which should therefore be ample to detect all species. The treatments were different at each site and were devised with the pressures salient to the site in mind. The combination of a period of cold stratification, ample light, some diurnal fluctuation in temperature, and a variety of water levels should satisfy the germination conditions for the majority of species. Germination methods were favoured over physical separation by sieving and floating for seed bank assessment as 1) seedlings represent viable seeds and are thus a better functional estimation of the seed bank, 2) seedlings are easier to identify, 3) tiny seeds are not overlooked. A comparative study of the two techniques concluded that germination provided a more reliable determination of the species composition of the viable seed bank (Gross 1990) as elutriation methods can yield extremely high numbers of nonviable seeds.

The 'control' treatment consisted of keeping the sediment moist by daily watering, often referred to as drawdown conditions (near optimum conditions for germination). '2 cm' and '12 cm flood' entailed permanently inundating the sediment by the indicated depth of water. 'Fluctuations' entailed three days of 12 cm flood followed by three days in control conditions. 'Flood + shade' was 12 cm flood conditions combined with a shading effect achieved by covering the tray with white nylon shading fabric which reduced PAR by 23%.

The number of seedlings germinating was counted frequently (at least weekly) to insure that seedlings did not emerge and die between counts. Most germination occurred in the first two months (as noted by Grime and Thompson 1979). Germination trials continued for up to fourteen months, to allow for accurate identification of the species. Species were refereed where identification was uncertain.

Table 7.2 Details of collection and treatment of sediment samples for the seed bank study.

Site	Code	Collection date	Germination observed	Treatments	Code	Replicates per treatment
fmlbw	M	17/04/93	27/04/93 - 18/06/94	control 2 cm flood 12 cm flood	A B C	5
fapoxa	O	18/04/93	27/04/93 - 18/06/94	control 2 cm flood 12 cm flood	A B C	5
fapdi	D	18/04/93	27/04/93 - 18/06/94	control 2 cm flood 12 cm flood	A B C	5
fdcbw	Z	13/08/93	14/10/93 - 18/06/94	control 2 cm flood fluctuations	A B D	4
cemta	E	15/08/93	14/10/93 - 18/6/94	control 12 cm flood	A C	5
icldo	C	22/05/93	05/06/93 - 18/06/94	control 12 cm flood flood + shade	A C E	4
ilbd3	L	24/05/93	05/06/93 - 18/06/94	control 12 cm flood flood + shade	A C E	4
cimid	Ma	04/05/93	11/01/94 - 18/06/94	control 12 cm flood	A C	5
cimid	Au	17/08/93	11/01/94 - 18/06/94	control 12 cm flood	A C	5
cimid	Oc	20/10/93	11/01/94 - 18/06/94	control 12cm flood	A C	5

7.6 Regeneration from Seed - Results

The full results are given in Appendix 10. In general no significant difference was apparent between the horizons, so discussion concentrates on the effects of site, treatment and season on the A horizon results. Total seed densities and species richness were compared using one way analysis of variance and Tukey's honestly significant difference (HSD) test. Significant differences reported correspond to $p < 0.01$ unless otherwise stated. At all sites *Lemna* and *Spirodela* species are only included in the species richness counts. This is because of the difficulty in quantifying the number of turions that were present in the sediment from the numbers observed in the germination. The number of plants present at the first count was recorded and the lemnids were then removed. Floristic differences were analysed using multivariate methods (as recommended by Benoit *et al.* 1992).

7.6.1 Total seedling germination

Germination totals are given as number of seedlings m^{-2} for a 5cm horizon. Total seedling germination differed little over the sites (Fig 7.2) with no significant differences between any pair of sites in control conditions as a result of the high variability of replicates. In flooded treatments the Marzy backwater (M) had significantly higher germination than all the other sites except the Decize backwater (Z).

The treatments showed quite a dramatic effect on total germination within sites. (Figs 7.3 - 7.5). The results from the Endrick marshes are not presented as the treatment showed no significant effect on total germination. In the French sites the two backwater sites (M, Z) showed no significant difference due to flooding treatment. At the oxbow (O) there was also no significant difference over the treatment set but the numbers germinating in flooded conditions were significantly lower than at Marzy. The ditch (D) showed a significant lowering in seedling emergence between the control and a 12 cm flood. There was a less significant difference ($P < 0.05$) between the control and fluctuating water levels. The samples from the Clonmacnoise. ditch showed a very dramatic reduction in seedling germination due to a 12 cm flood, with a significant mean reduction from 6079 seedlings m^{-2} to 637 seedlings m^{-2}. Adding shade to flooding did not give a further significant reduction. The reduction observed from the Little Brosna cores

was not significant. The Insh marshes cores also showed significant reduction with flooding in May and August (Fig 7.5).

Seasonal variation was examined from the Insh marshes cores but no significant difference in germination was recorded over the season in either treatment. (Fig 7.5).

7.6.2 Species richness

The variation in species richness was also examined. (Fig 7.6). The Decize backwater (Z) was significantly more species rich than the Endrick and Insh marshes samples which had the most species poor germination. It was also significantly richer ($p < 0.05$) than the Apremont oxbow and the Clonmacnoise samples. The Apremont ditch also possessed a more varied seedbank than the Insh samples (May and August). While the oxbow was the least species rich site of the French catchments, it was still richer ($p < 0.05$) than the Insh marshes (May).

Species richness also varied with treatment (Figs 7.7 - 7.9). At the French sites no difference was observed from the oxbow cores (O), but the backwater sites and the ditch all showed a significant lowering of species diversity with a 12 cm flood. At a lower level of significance ($p < 0.05$), the backwaters also showed a reduction between a 2 cm flood and 12 cm flood, but no difference between a shallow flood and the control. From the ditch, the 12 cm flood and fluctuating water levels showed no significant difference, but both were different from the control ($p < 0.05$). From the Irish cores there was a significant difference in species richness between the control and both treatments at both sites. However adding shade to the flooding treatment did not reduce species diversity significantly. From the Endrick marsh cores there was no treatment effect on diversity of seedlings. From the Insh marshes there was a significant difference in August and October but the reduction in species richness with flooding from the May cores was only significant at $p < 0.05$.

Between the seasons there was no significant difference in species richness (Fig 7.9).

Fig 7.2 Comparison of seed germination from each site (A horizon)

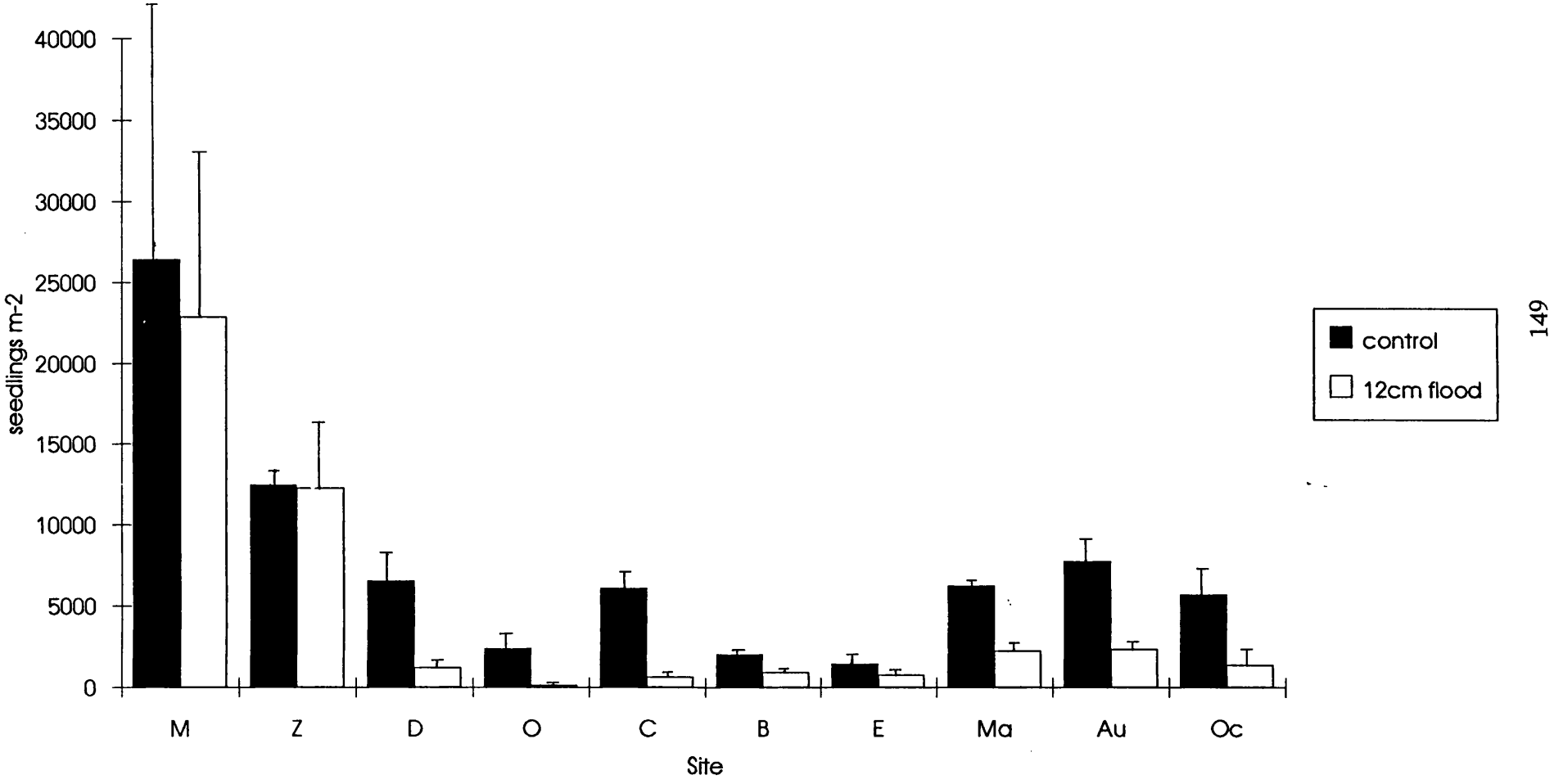


Fig 7.3 Seed germination from French sites

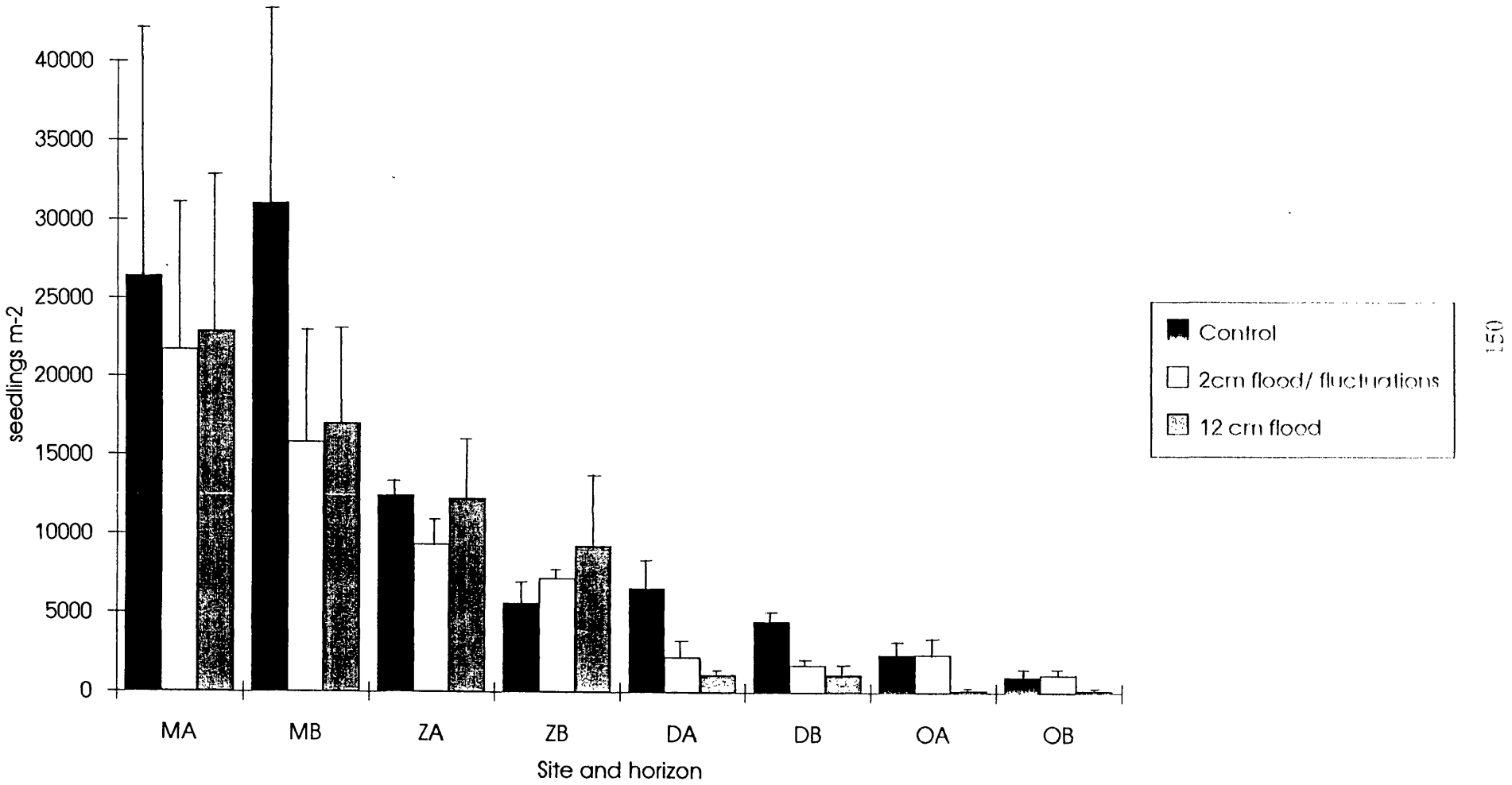


Fig 7.4 Seed germination from Irish sites

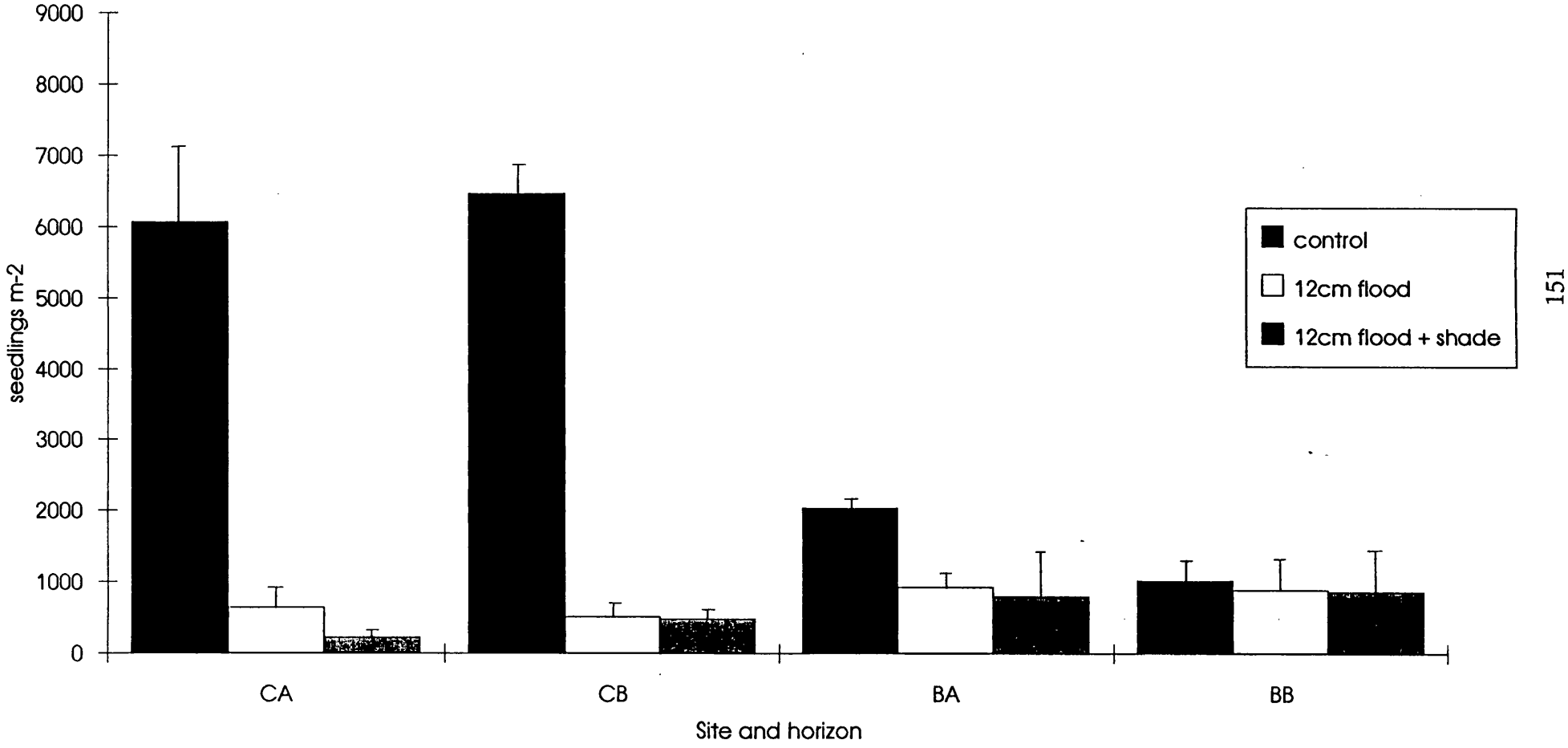


Fig 7.5 Seed germination from Insh marshes (seasonal study)

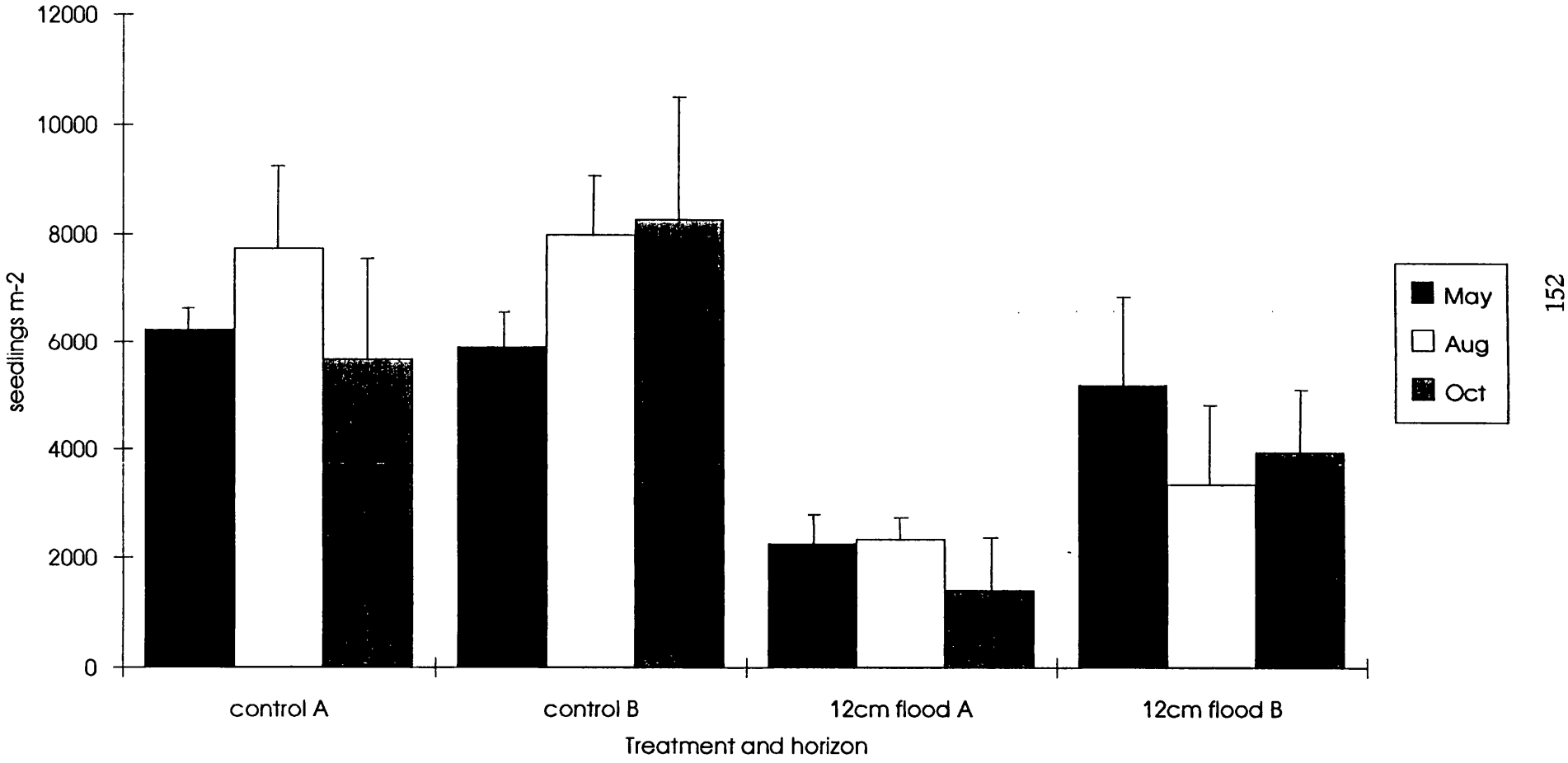


Fig 7.6 Comparison of species richness from each site (A horizon)

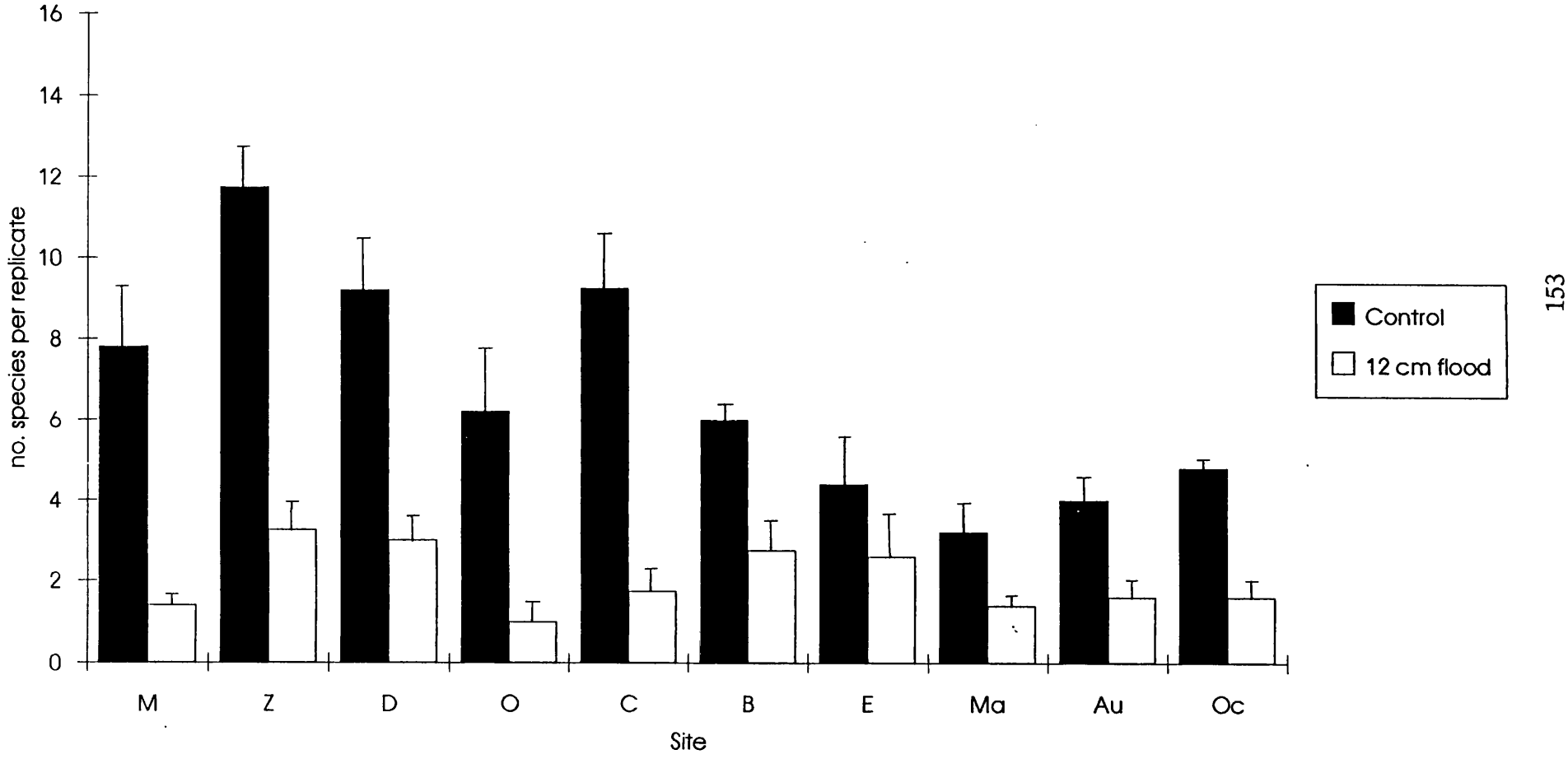


Fig 7.7 Seed germination from French sites

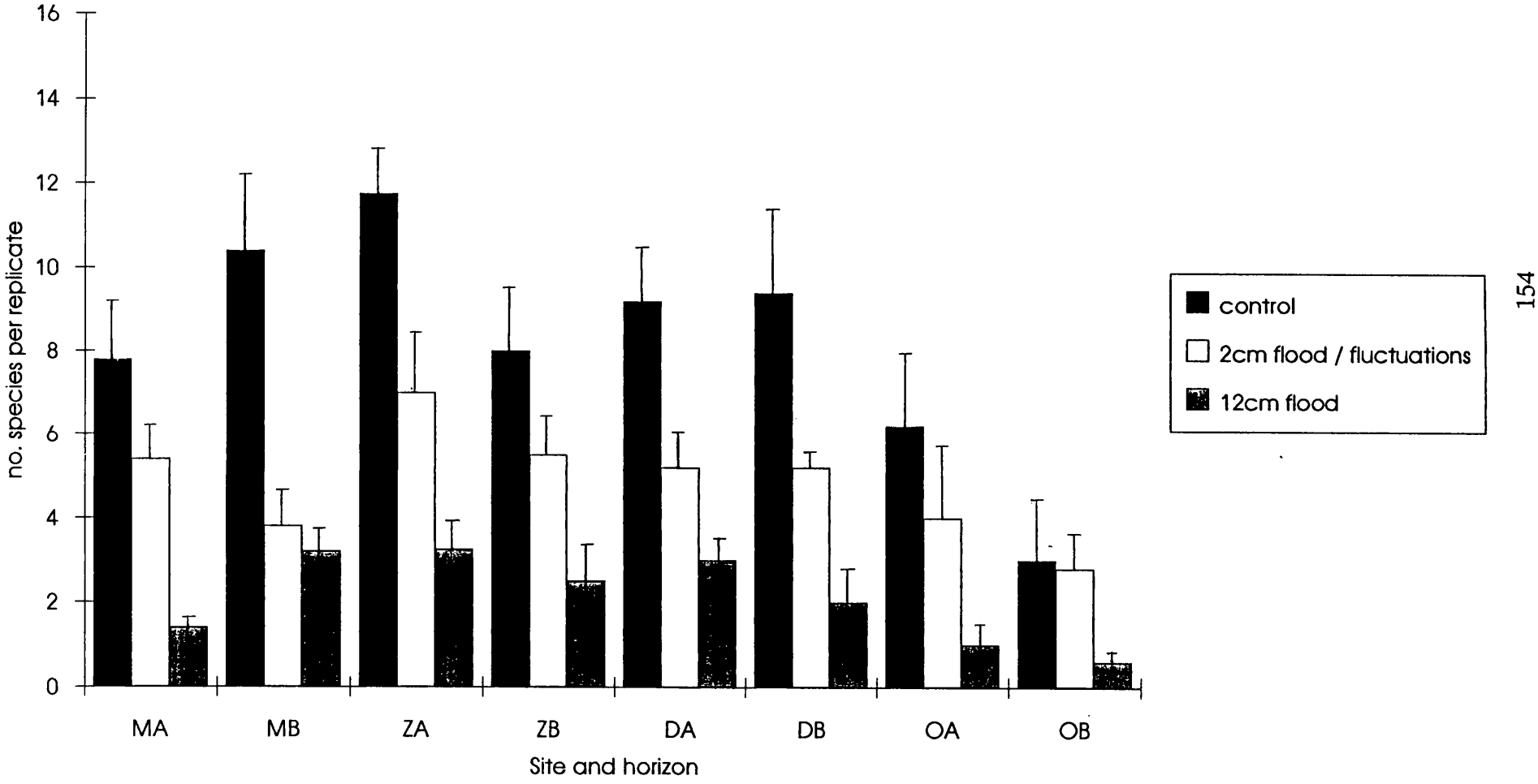


Fig 7.8 Seed germination from Irish sites

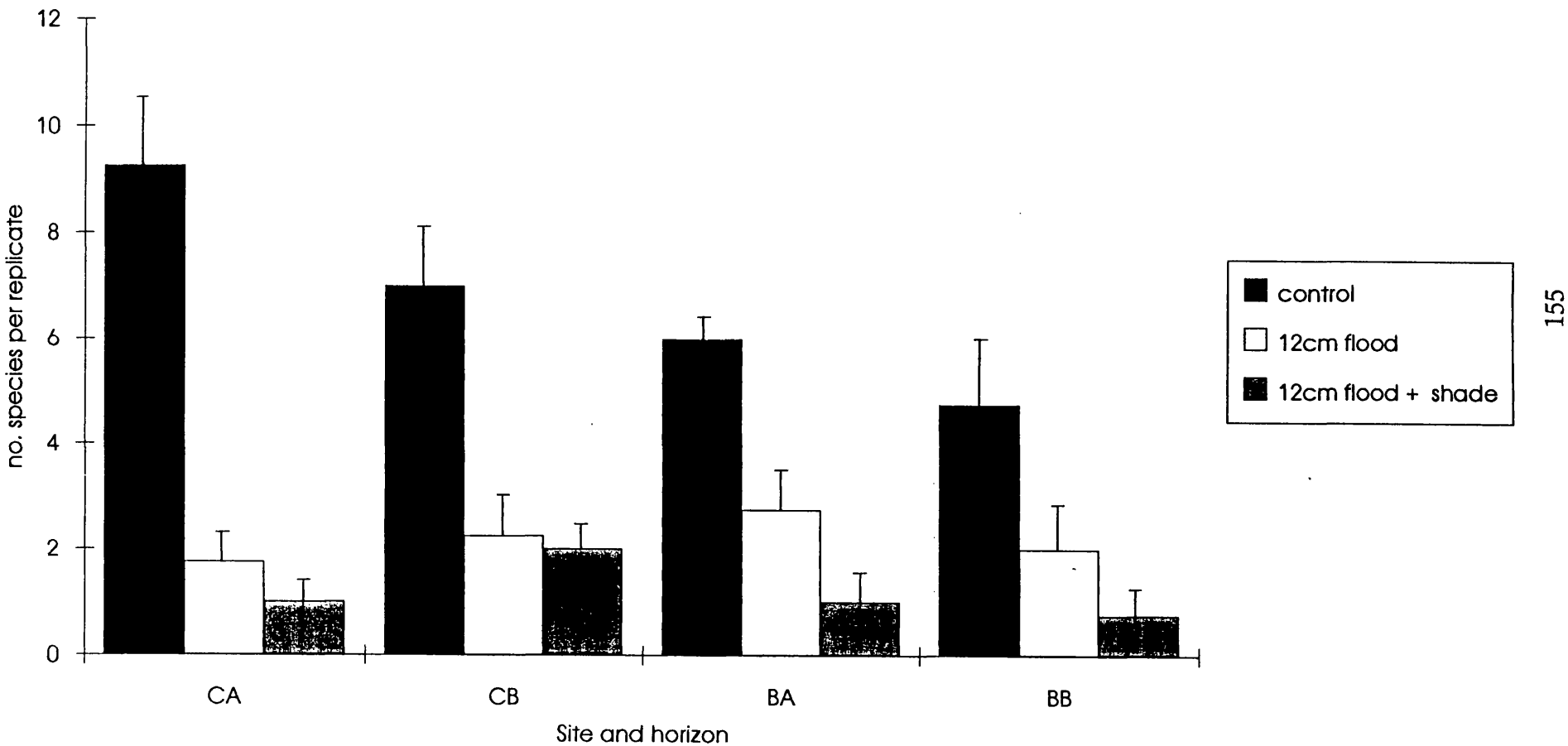
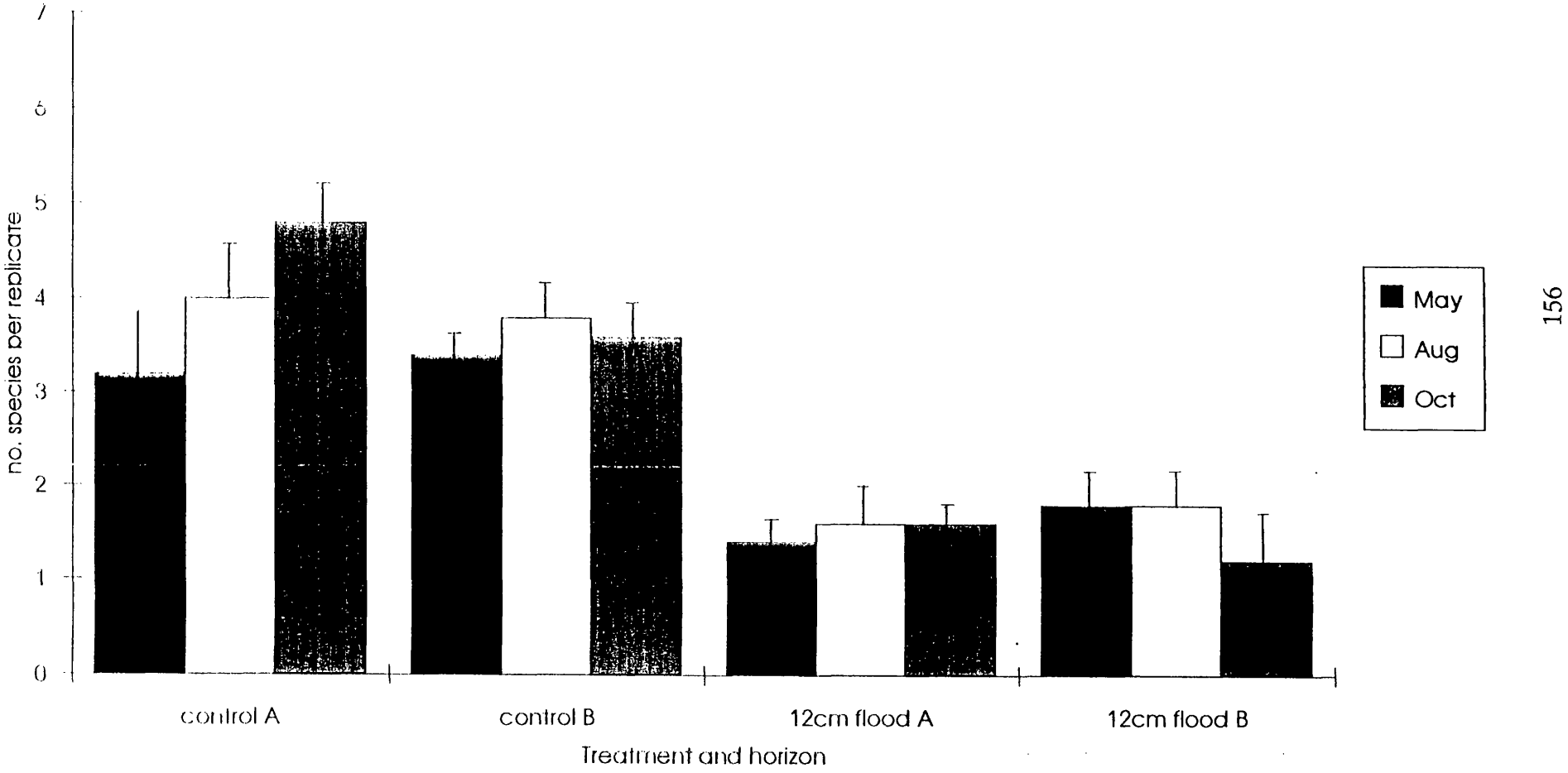


Fig 7.9 Seed germination from Insh marshes (seasonal study)



7.6.3 Species composition

The majority of species that germinated could be categorised into three types: mud flat species (e.g. *Persicaria, Bidens, Cyperus, Carex*); emergent species (e.g. *Typha, Sagittaria, Phalaris*); and euhydrophytes (e.g. *Ceratophyllum, Potamogeton, Lemna*). Of these mud flats made up the highest proportion followed by emergents and then euhydrophytes. To compare the species composition in the cores Detrended Correspondence Analysis (DCA) was used. A separate analysis is presented for each site (Figs 7.10 - 7.13), as the species present in the French and Scottish sites differed almost completely meaning that between site differences obscured treatment and seasonal changes. In all figures the sample labelling shows site, treatment, horizon in that order. The full species list for all sites is shown in Table 7.3, and species labels follow the same convention used in Chapter 3 (one letter for genus, three for species; for taxa only identified to genus, two genus letters followed by 'sp'). Ambiguities are resolved as follows;

Carex sp	= cxsp
Callitriche sp	= casp
Chara sp	= chsp
Chenopodium sp	= cpsp
Mentha aquatica	= maqu
Myosoton aquaticum	= myaq
Poa trivialis	= ptri
Potamogeton trichoides	= potr
Salix sp	= sxsp
Sonchus asper	= sasp
Senecio aquaticus	= saqu
Subularia aquatica	= suaq

Table 7.3 Species germinating from sediment cores and their strategies (from Grime *et al.* 1988)

Species	Established strategy	Regenerative strategy	Seed bank type
Agrostis stolonifera L.	CR	V, Bs	III
Alisma plantago-aquatica L.	CR/R	V, Bs	IV?
Anthemis spp			
Apium spp			
Berula erecta (Hudson) Coville	CR	(V), S?	II
Bidens cernua L.			
Bidens tripartita L.			
Callitriche hamulata Kutz ex Koch			
Callitriche sp			
Callitriche stagnalis Scop.	R/CR	V, Bs?	III/IV?
Caltha palustris L. ?	S/CSR	V, S?	II
Cardamine pratensis L.?	R/CSR	Bs,(V)	III?
Carex chordorhiza L. fil.			
Carex dioica L.			
Carex disticha Hudson			
Carex limosa L.			
Carex nigra (L.) Reichard	S/SC	V, Bs	IV?
Carex sp			
Carex vesicaria L.			
Centaurea nigra L.	S/CSR	V, S	?
Ceratophyllum demersum L.			
Chara spp			
Chara vulgaris var. *longibractea*			
Chenopodium polyspernum L.			
Chenopodium spp			
Cyperus fuscus L.			
Echinochloa crusgalli (L.) P. Beauv.			
Eleocharis palustre (L.) Roemer and Schultes	CSR	V, ?	?III/IV
Epilobium ciliatum Rafin.	CR	(V), W, Bs	III
Epilobium obscurum Schreber	CSR	(V), W, Bs	III
Equisetum fluviatile L.	SC	V,W	I
Festuca sp.			
Galium palustre L.	CSR/CR	V, Bs	IV
Galium sp.			
Glyceria fluitans (L.) R.Br.			
Glyceria maxima (Hartman) O.Holumb.	C	V, Bs	III
Gnaphalium sp.			
Gnaphalium uliginosum L.	R	Bs	III?
Hydrocharis morsus-ranae L.			
Juncus articulatus L.	CSR	V, Bs	IV
Juncus bufonius L.	R	Bs	IV?
Juncus bulbosus L.			
Juncus conglomeratus L.	CS/CSR	V, Bs?	IV?
Juncus effusus L.	C/SC	V, Bs	IV
Juncus spp			
Leersia oryzoides (L.) Sw			
Lemna minor L.	CR	V	
Lemna trisulca L.	S	V	
Limosella aquatica L.			

Table 7.3 (cont.)

Species	Established strategy	Regenerative strategy	Seed bank type
Lindernia dubia (L.) Pennel.			
Ludwigia palustris (L.) Elliott			
Lysimachia thrysiflora L.			
Lythrum portula (L.) D. Webb	R/SR	Bs	IV
Lythrum salicaria L.	CR/CSR	Bs	IV
Mentha aquatica L.	C/CR	V, Bs	IV?
Mentha pulegium L.			
Myosotis laxa Lehm.			
Myosotis scorpiodes L.	CR	V, Bs	III?
Myosoton aquaticum (L.) Moench			
Myriophyllum spicatum L.	CSR	(V), Bs?	IV?
Nitella spp			
Oxalis sp			
Panicum ?capillare L.			
Persicaria hydropiper (L.) Spach	R	Bs	IV
Persicaria maculosa Gray	R	Bs	IV
Persicaria sp.			
Phalaris arundinacea L.	C	V, Bs	III/IV?
Plantago major L.	R/CSR	Bs	IV
Poa pratensis L.	CSR	V, Bs?	III?
Poa trivialis L.	CR/CSR	V/Bs	III
Potamogeton crispus L.	CR	S, Bs	IV
Potamogeton nodosus Poiret			
Potamogeton obtusifolius Mert & Koch			
Potamogeton trichoides Cham & Schldl.			
Ranunculus circinatus Sibth.			
Ranunculus flammula L.			
Ranunculus peltatus Schrank	R/CSR	V, Bs	III/IV?
Ranunculus repens L.	CR	(V), Bs	III
Ranunculus sceleratus L.	R	Bs	IV?
Rorippa islandica (Oeder ex Murray)			
Rorippa sp			
Rorippa x *anceps* (Wahlenb.) Reichb.			
Rumex sp.			
Sagittaria sagittifolia L.			
Salix sp.			
Samolus valerandi L.			
Senecio aquaticus Hill	R/CR	W	?
Sonchus asper (L.) Hill	R/CR	W, Bs?	III
Sonchus sp.			
Sparganium emersum Rehmann	CR	(V), Bs	III
Spirodela polyrhiza (L.) Schleiden			
Stellaria sp.			
Subularia aquatica L.			
Thalictrum flavum L.			
Trifolium repens L.	CR/CSR	(V), Bs	IV
Typha latifolia L.	C	V, W, Bs	III
Urtica dioica L.	C	V, Bs	IV
Veronica beccabunga L.	CR	V, Bs	IV
Veronica catenata Pennell			
Veronica spp			

The DCA summaries (Table 7.4a - d) show that high percentages of the species variation are represented in these diagrams. They also tend to show a high proportion of the variation explained on the first axis with subsequent axes explaining small amounts of the species variations. This confirms that one strong gradient exists in the species composition which is shown by the sample locations to be the effect of the experimental treatments.

Table 7.4a Summary of DCA on French samples

Axes	1	2	3	4	Total inertia
Eigenvalues	0.670	0.443	0.198	0.105	3.445
Lengths of Gradient	3.733	4.031	2.078	1.940	
Cumulative percentage variance explained					
species data	19.5	32.3	38.1	41.1	
Sum of unconstrained eigenvalues					3.445

Table 7.4b Summary of DCA on Irish samples

Axes	1	2	3	4	Total inertia
Eigenvalues	0.618	0.165	0.053	0.035	1.872
Lengths of Gradient	2.655	1.926	1.922	1.881	
Cumulative percentage variance explained					
species data	33.0	41.8	44.7	46.6	
Sum of unconstrained eigenvalues					1.872

Table 7.4c Summary of DCA on Endrick marshes samples

Axes	1	2	3	4	Total inertia
Eigenvalues	0.586	0.106	0	0	0.995
Lengths of Gradient	2.682	1.234	0	0	
Cumulative percentage variance explained					
species data	58.8	69.5	0	0	
Sum of unconstrained eigenvalues					0.995

Table 7.4d Summary of DCA on Insh Marshes samples

Axes	1	2	3	4	Total inertia
Eigenvalues	0.105	0.037	0.016	0.009	
Lengths of Gradient	0.618	0.429	0.199	0.238	
Cumulative percentage variance explained					
species data	40.3	54.4	60.7	64.3	
Sum of unconstrained eigenvalues					0.261

At the French sites (Figs 7.10a & b) there is a clear division on the DCA between the Loire sites (both backwaters) and the sites on the Allier floodplain. Nine euhydrophyte species germinated (excluding *Lemna minor* and *Spirodela polyrhiza*) and these were confined to the Allier sites. For the Loire samples, which formed a very tight group, it is difficult to distinguish between site, horizon or treatment by species composition. In the Allier samples the composition of seedlings arising in the 12 cm flooded sites differs from other treatments (divided by the dotted line). Not surprisingly most of the euhydrophytes are found in this area of the ordination, although some that are capable of germinating in emergent conditions (such as *Callitriche stagnalis* and *Ranunculus peltatus*) are on the borderline. There does not seem to be a difference between the community arising in controlled, shallow flooded or fluctuating water conditions in the Allier sites.

The Irish sample scores and the species scores are plotted simultaneously (Fig. 7.11). Only three euhydrophytes germinated (*Sparganium emersum, Callitriche* sp and *Chara* sp). The control samples are in the bottom left of the diagram with the flooded and shade + flooded samples difficult to separate from each other. The Clonmacnoise and Little Brosna sites can also be separated with the Clonmacnoise samples to the left and the Little Brosna samples to the right.

The Endrick marshes sites (Fig 7.12) also showed differences in species composition with treatment, with euhydrophytes represented in the flooded treatments.

For the Insh marshes trials little difference in species composition was evident through the season. Differences were observed between flooded and control samples, with control samples to the left hand side and flooded samples to the left hand side. The flooded samples showed a high representation of euhydrophyte species.

Fig 7.10a DCA ordination of species composition from seed germination trial of French sediment samples: Sample scores. Hard line shows division between Loire and Allier samples, dotted line shows division between treatments of Allier samples. Inset shows detail of the Loire samples. (Label = site, treatment, horizon. See Table 7.2)

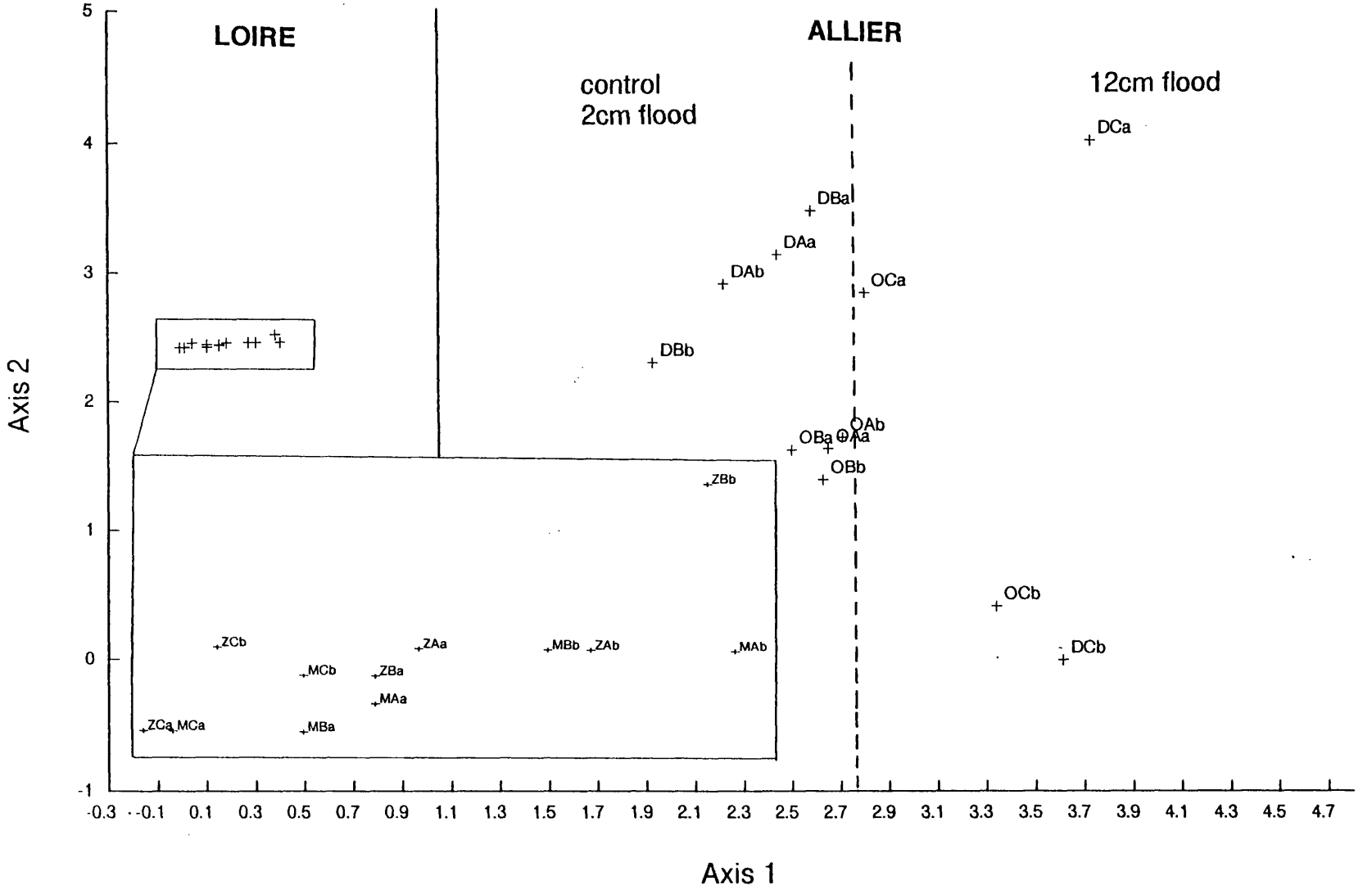


Fig 7.10b DCA ordination of species composition from seed germination trials of French sediment samples: Species scores. Hard line shows division between Loire and Allier samples, dotted line shows division between treatments of Allier samples. Inset shows detail of the Loire samples. (Species codes see Appendix 4, euhydrophytes underlined).

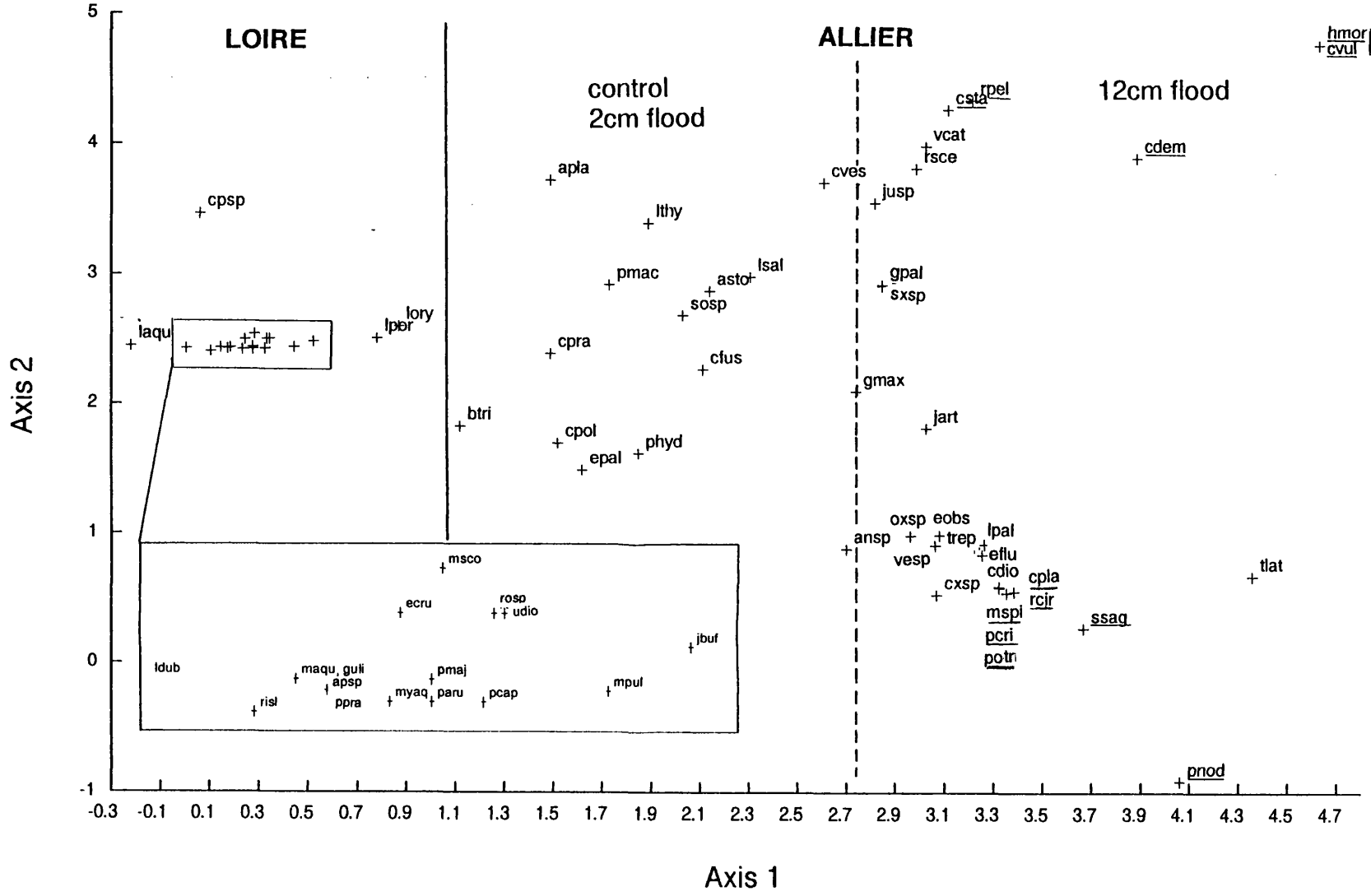


Fig 7.11 DCA ordination of species composition from seed germination trials of Irish sediment samples: Sample and species scores. (For species codes see Appendix 4, euhydrophytes underlined; for sample codes see Table 7.2).

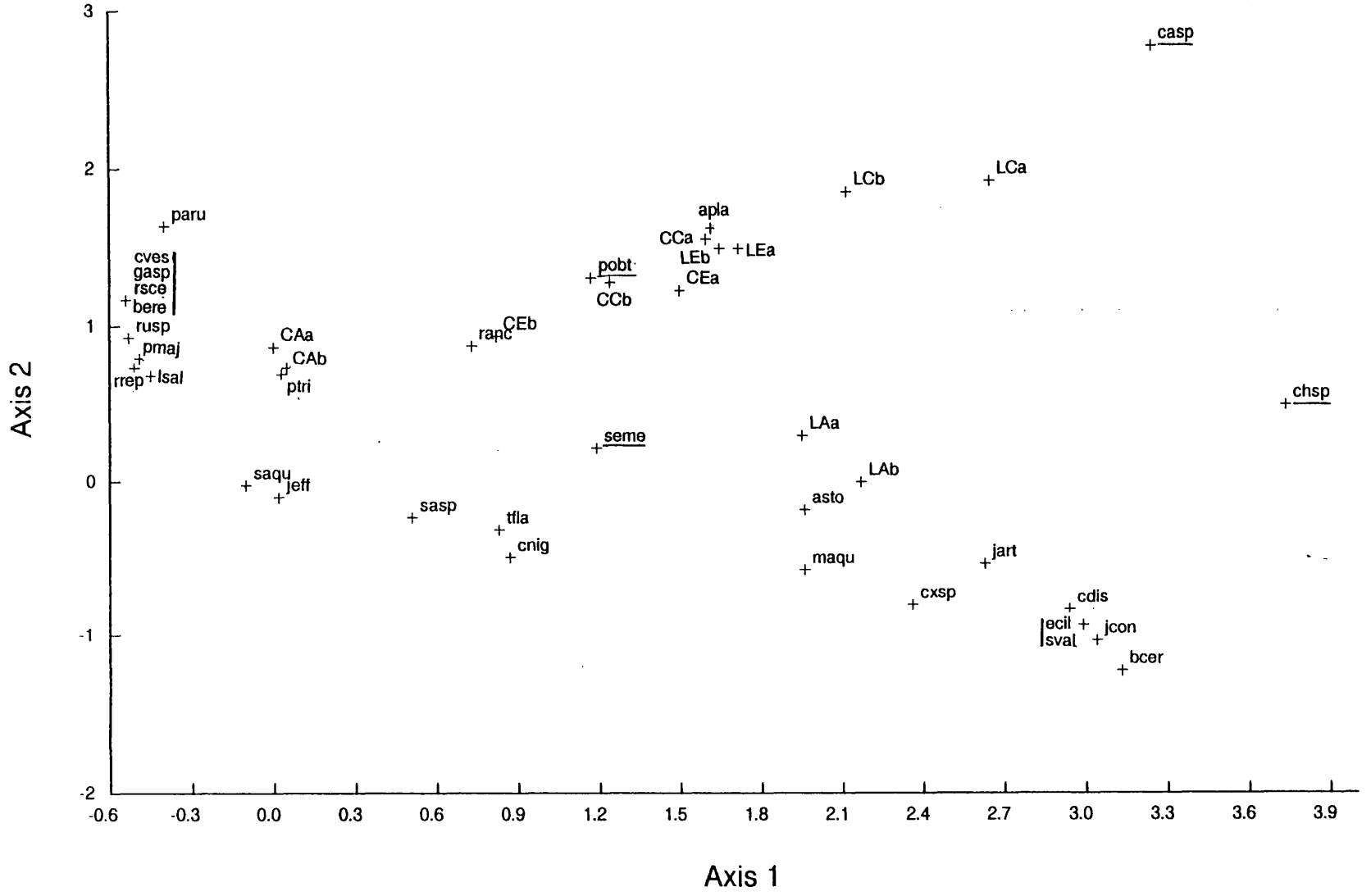


Fig 7.12 DCA ordination of species composition from seed germination trials of Endrick sediment samples: Sample and species scores. (For species codes see Appendix 4, euhydrophytes underlined; for sample codes see Table 7.2).

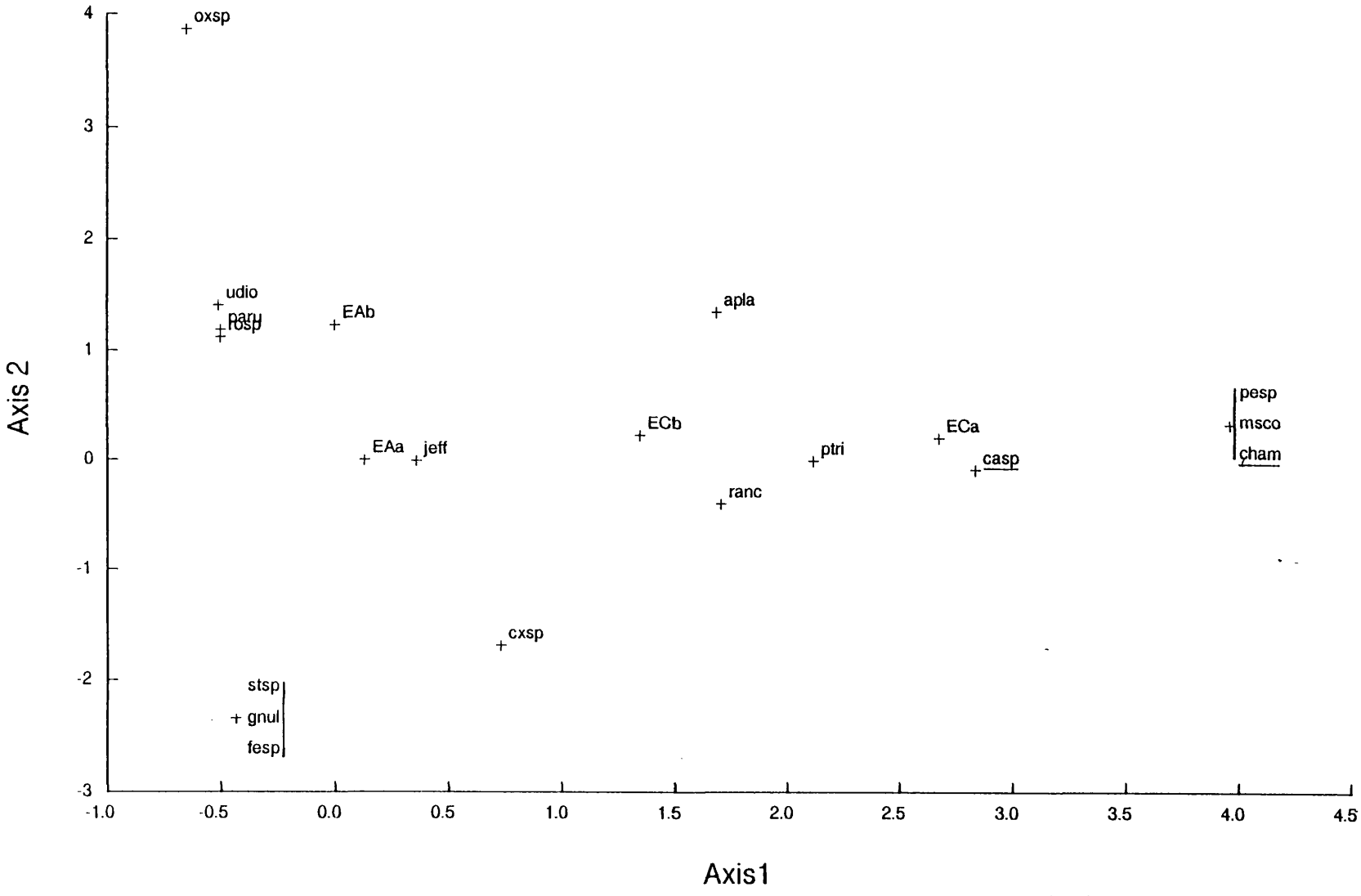
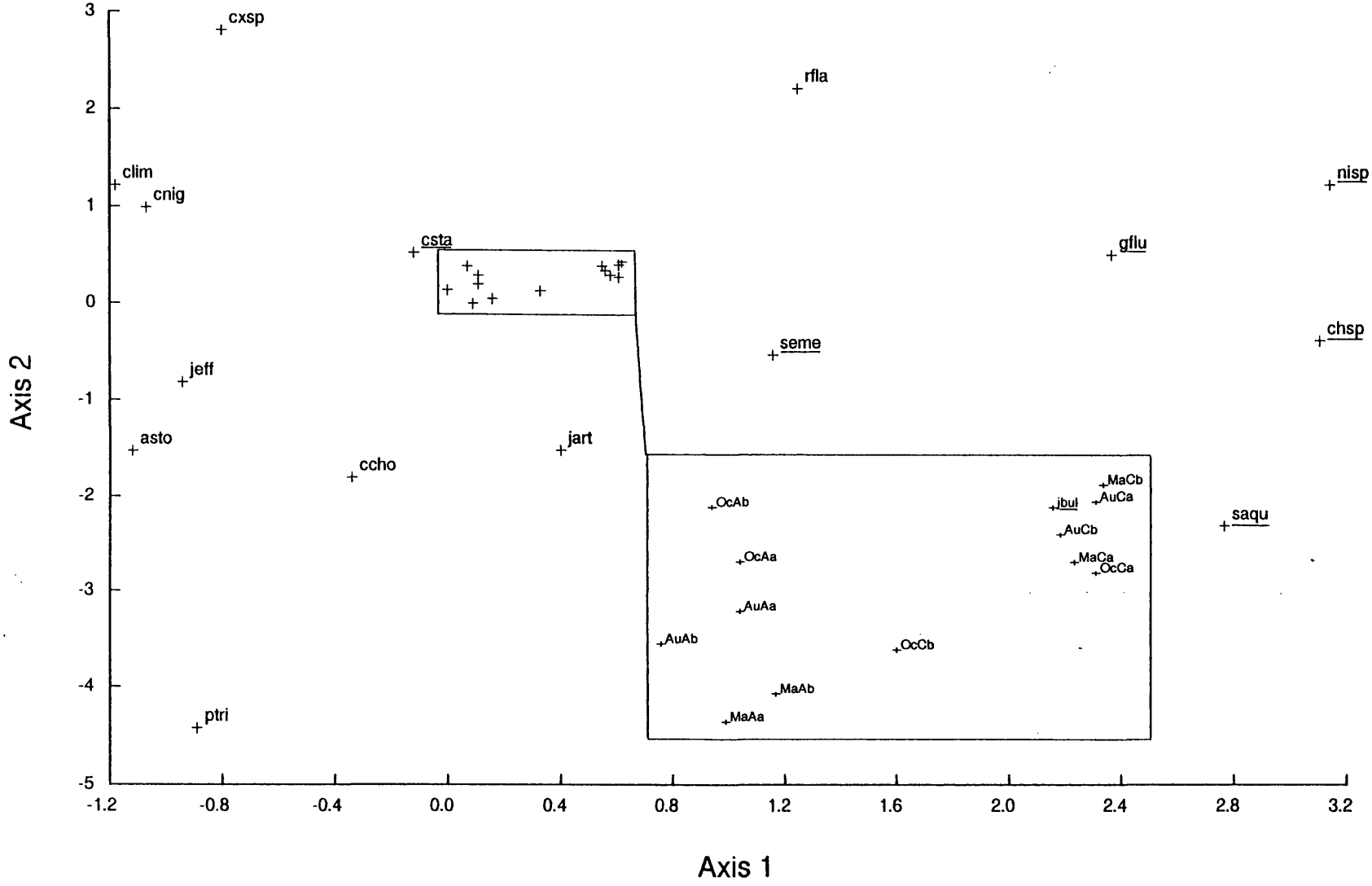


Fig 7.13 DCA ordination of species composition from seed germination trials of Insh sediment samples: Sample and species scores. Inset shows detail of sample scores (For species codes see Appendix 4, euhydrophytes underlined; for sample codes see Table 7.2).



7.6.4 Comparison with existing vegetation

Comparisons can be made between the surface vegetation and the seed bank flora. Comparisons were made only with species presence and absence, and three comparisons were made (Table 7.5):

1) The percentage of the seed bank flora also recorded by my 1992/93 survey of existing vegetation. This includes both the euhydrophytes and the emergent species growing below the waterline.

2) The percentage of the seed bank flora also recorded by Hills (1994) in a survey of the floodplain flora adjacent to the FAEWE sites.

3) The percentage of the species present at the site in my 1992/93 survey that were represented in the seed bank.

Table 7.5 Comparison of seed bank flora and existing vegetation. (na = no data available)

Site	No. of species in seed bank	% seed bank species in survey	% seed bank species recorded by Hills 1994	% survey species present in seed bank
fmlbw	28	4	na	13
fdcbw	30	17	36	56
fapoxa	30	33	17	43
fapdi	35	26	11	62
icldo	25	52	40	48
ilbd3	21	19	33	18
cemta	16	19	na	33
cimid	17	47	na	58

Plate 19: Collecting sediment cores at site **fmlbw**, a backwater of the River Loire. April 1993

Plate 20: Seed bank samples from Clonmacnoise germinating in the greenhouse (four months after start of trial).

Plate 21: Natural regeneration observed in the backwater at Marzy. August 1993.

7.7 Regeneration from seed - Discussion

For the purpose of this discussion the seed bank size at each site is taken to be the mean number of seeds germinating in drawdown (control) conditions. Recruitment from this seedbank, under the different conditions imposed, compares the difference between control and treatment numbers and species. Three aspects of variation will be discussed, differences in seed bank size and composition between the sites; effects of the treatments on recruitment; effects of season on seed bank size and composition.

7.7.1 Seed bank variation between sites

Species composition differed greatly between the different areas studied, reflecting geographical patterns of species distribution. While many wetland and aquatic taxa have wide geographical ranges (Darwin 1859; Sculthorpe 1967), probably as a result of effective dispersal mechanisms (Ellenberg 1986), a low proportion of species were found in common between the seed banks from different catchments.

While little significant difference was apparent between the total germination in the wetland sites studied, the test used for comparison of means (Tukey's HSD) was highly conservative and less conservative tests showed significant difference between a number of sites. Differences can be due to a number of factors such as seed longevity, existing vegetation, seed rain, hydrological regime and environmental variations in the substrate. In riverine wetlands, isolation of the site is not the limiting factor that it can be in other freshwater wetland types due to the transport function of the river channel itself. van der Valk and Davis (1976) noted differences in floristic composition between marshes but few differences within sites (even different vegetation types) in a marsh. Wind, water and animal dispersal of seeds allow species to reach most areas in a catchment.

The total numbers of seedlings observed in the control, or drawdown conditions, can be compared to other wetland studies where germination trials have adopted the same conditions. Wetland habitats generally have a high buried seed density (Keddy and Reznicek 1986) and wetland seed rain can be high (van der Valk and Davis 1979). In comparison with other habitats, wetlands show seed banks an order of magnitude higher than forests but are much smaller than the seed banks of agricultural fields (van der Valk and Davis 1978). Darwin (1859) reported 537 seedlings emerging from 3 tablespoons of pond soil. Schneider and Sharitz (1986)

reported a mean of 2,576 m^{-2} (depth 10cm), with a range from 759 to 4,392 m^{-2}, for riverine wetlands in South Carolina. Titus (1988) gives a lower mean of 276 m^{-2} (depth 10cm) with a range of 76 - 611 m^{-2} in Florida. These studies show figures lower than reported here, but demonstrate the high variability experienced in this type of sampling, with a tenfold difference between samples being not uncommon.

The Loire samples showed a particularly high density of seeds compared to other wetland studies (see review in van der Valk and Verhoeven 1988; Leck 1989). The highest values in other studies have been found for lakeshores, particularly the littoral zone (Keddy and Reznicek 1982) and the transition zone between aquatic and marsh habitats (van der Valk and Davis 1978). Seedling densities may be highest in these habitats due to the combination of submersed and emersed conditions that allow seeds to be deposited in situ or accumulate by water transport, and also slows their rate of decay (Keddy and Reznicek 1982). Means comparable to those reported here for the Loire backwaters have been observed at temporary ponds in New Jersey (McCarthy 1987), with a mean of 17,943 m^{-2} (depth 5cm) and a range of 11,455 to 24,430 m^{-2}. Seed banks in Iowa marshes (van der Valk and Davis 1978) ranged from 21,440 to 42,620 m^{-2} in 5cm depth. Along channels, the buoyant nature of many aquatic and wetland species leads to increased seed densities on emergent substrates, where emergent vegetation occurs, or in still, sheltered waters (van der Valk and Davis 1976, 1978; Smith and Kadlec 1983; Titus 1988). The braided river channel, characteristic of the Loire, gives just such emergent substrates on which seeds can accumulate during the summer periods of low flow or drought, although seeds that remain on the soil surface will be lost with the return of high flow in winter. For these sites dispersal phenology needs to coincide with the periods of low flow.

Fewer seeds are generally found in sites that are permanently inundated (Rodgers and Breen 1980; Smith and Kadlec 1983; Leck 1989), a fact that is supported here by the especially low means recorded from the Apremont oxbow, the ditch at Little Brosna and the Endrick marshes drain. However the assertion that the seeds of the majority of land plants lose their viability if submerged for long periods (Hook 1984) is contradicted by the presence of viable terrestrial plant seed in the B horizon of the oxbow sediments. The sites that regularly dry up (Marzy and Decize backwaters) show the highest means. This fits with the theory that a decline in seed numbers is expected with decreasing disturbance (Thompson 1978). Sites that may dry up in some years (Apremont drain and Clonmacnoise drain) both show quite

high seed densities. The variability of the samples means that conservative tests will place many samples as homogeneous, but it seems that, in general, samples from temporary (disturbed sites) display a high density of seeds, while less disturbed sites on riverine wetlands have a lower number. This is consistent with the scheme presented by Thompson (1978) that shows buried seed density increasing with disturbance and decreasing with stress. One of the few studies involving samples taken from open water sites also reported few species and low species densities (Smith and Kadlec 1983). In large, permanent, open water sites there are few physical barriers and seeds may float some distance until they meet emergent vegetation or some other obstacle which causes them to sink (Smith and Kadlec 1985).

Dominance of herbaceous species over graminoids, and of both of these groups over woody species, was noted by Leck (1989) and is also apparent in this study. Dominance of one or two species is also apparent, particularly in the high density samples in which *Lindernia dubia* and *Leersia oryzoides* were especially prevalent, although neither of these species had high representation in the surface vegetation at the site. *Lindernia dubia* was not recorded at any site and *Leersia oryzoides* was recorded in low frequency at one site only (**fapdi**). Seed rain decreases with distance from source plants (Haag 1983), which is one factor influencing representation, but seed production rates, seed longevity, seed dispersal mechanisms and herbivory all complicate this relationship.

7.7.2 Treatment effect

The relevance in the field of the treatment effects observed in this experiment, as with many glasshouse experiments, must be extrapolated with care. Light and temperature are important germination cues that will differ in the field and have not been investigated here. In addition, in a wetland ecosystem, the influences of substrate, water flow and water turbidity will also influence recruitment and establishment. As the treatments imposed on samples from each site differed and the seed flora were quite different between catchments the results from each catchment will be discussed in turn.

In the French samples the treatment that had the greatest effect was the deep flood conditions where a significant reduction in seedling number and species richness

was noted for several sites. This effect has also been recorded in a number of studies (van der Valk and Davis 1979; Smith and Kadlec 1983; Leck and Simpson 1987a). Shallow flooding seemed to fulfil the germination requirements of many species, with mud flat, emergent and euhydrophyte species all represented. Shallow flooding rather than total drawdown in managed wetlands will allow germination of marsh and aquatic species and also combat problems of increasing soil salinity sometimes encountered with drawdown (Smith and Kadlec 1983). In the Carmargue, partial drawdown of a marsh allowed the re-oxidation of metal phytotoxins in the sediment and promoted germination of *Potamogeton pectinatus* seedlings (van Wijk *et al.* 1993). Fluctuations in water level produced a similar community to drawdown conditions. Although there was no significant difference in species richness or seed density between the shallow and drawdown treatments, statistical tests fail to detect the more subtle differences in the representation of the different groups that can be suggested by familiarisation with the data. The DCA ordination for the French site (Fig. 9a and b) illustrate features of these systems. The two rivers are separated along the first axis by species composition. The two group centroids are separated by almost 3 s.d., indicating very different, though not quite discrete floras. This may not, however, represent a compositional difference in the seed flora of the two river flood plains as the Loire sites were all backwaters. These sites were all very closely grouped on the ordination. Examination of the species plot shows a similar pattern, with the species characteristic of the Loire sites being tightly grouped. No clear separation of the treatments is possible from species composition. This suggests that many species are following the pattern illustrated by *Lindernia dubia* (see below) with no discernible effect of treatment on germination. Many wetland species have broad tolerance of water levels during recruitment (Keddy and Ellis 1985). These species must be able to tolerate the low concentrations of oxygen that will be present under waterlogged or submerged conditions. Few terrestrial plants can germinate in these anaerobic conditions (Frankland *et al.* 1987), Those species that can are ideally adapted for this seasonally fluctuating environment. As well as individual species adaptations, the combination of mud flat species, emergents and euhydrophytes displayed is a community adaptation to the cyclical environment and a schematic diagram can be used to represent the role of the seed bank in these changes.

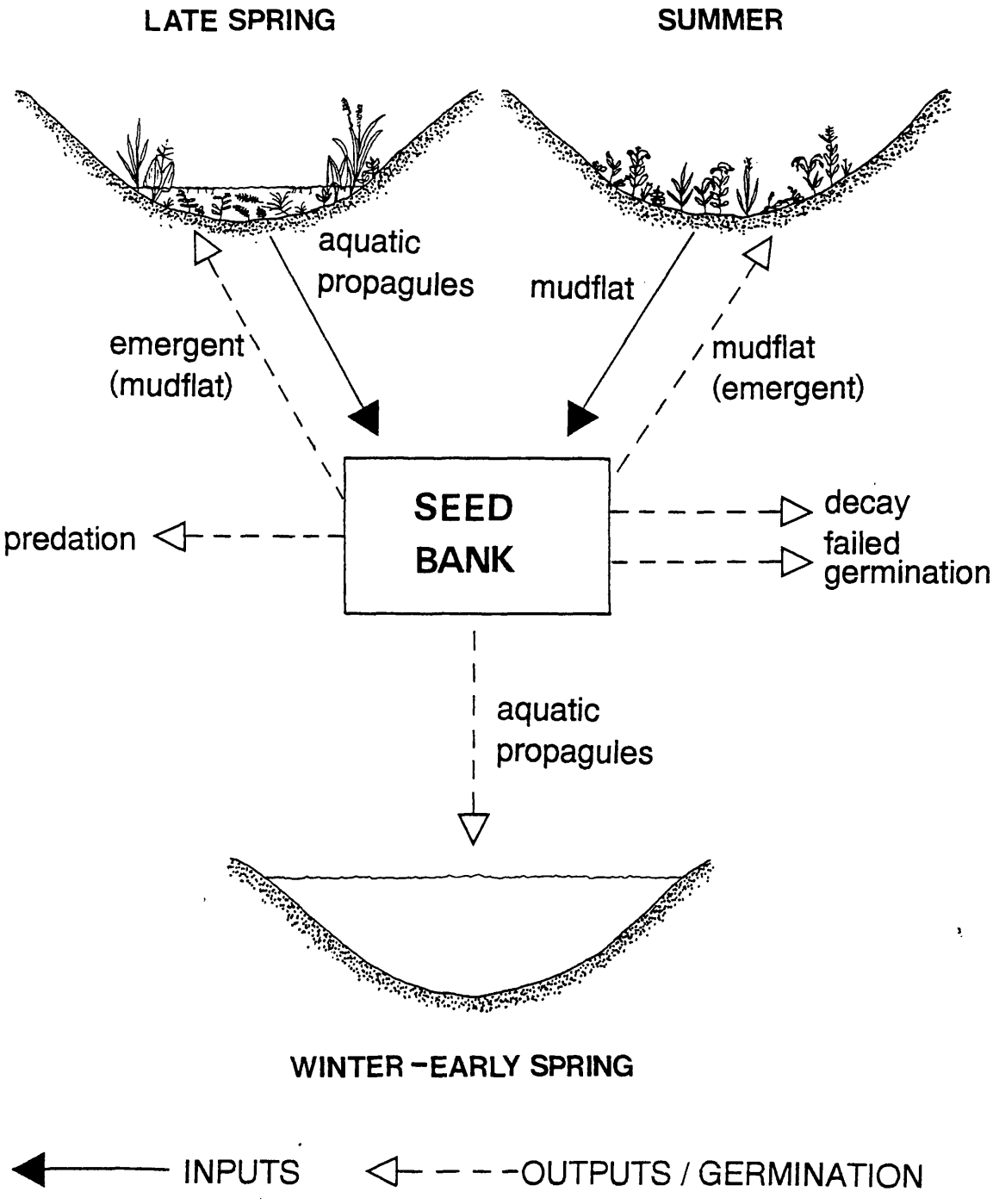


Figure 7.14 A schematic representation of seed bank dynamics in Loire backwaters

With changes in the hydrology of the river (caused, for example, by barrages) water levels and the phenology of fluctuations may change. The seed bank will not be maintained if inputs are reduced. Predation and decay will further reduce the seed reservoir and change the vegetation dynamics. This could have knock-on effects, such as an increased rate of sediment erosion, if mud flat annuals are not able to colonise and stabilise the sand banks during summer (see Plate 21).

The sparseness of vegetation observed in the temporary backwaters may be attributable to the short period of time available each year for occupation. The very warm temperatures of unshaded shallow waters may also be a contributing factor (Lippert and Jameson 1964). Submerged vegetation that is to survive in seasonally flooded habitats must produce propagules early in the growing season and in large quantities (Grillas 1990; Grillas *et al.* 1991). Seeds of true aquatic plants rapidly lose viability in the absence of water (Frankland *et al.* 1987). In seasonally flooded habitats mud flat species that are able to germinate in shallow water will gain an immediate competitive advantage over those that cannot commence growth until the water recedes (Hook 1984). A functional model was presented by van der Valk (1981) using just three life history characters to predict species presence or absence in a wetland following change. The life history traits he used were life span, propagule longevity and propagule establishment requirements. This model has been found to give accurate predictions in the long term, but has found to be inaccurate in the short term (ter Heerdt and Drost 1994). It has been suggested that incorporating the effects of season and drought would strongly improve the model (ter Heerdt and Drost 1994). However, until the regenerative biology of aquatic species is better documented his model cannot be tested for this group.

Individual species responses to the treatments can also be examined. As species differed so greatly between the study areas these will be discussed separately. In the French sites few mud flat species were exclusive to the moist treatment (e.g. *Lythrum portula*), as many could tolerate a shallow flood (e.g. *Lythrum salicaria, Ludwigia palustris, Cyperus fuscus*). Most euhydrophytes could germinate in 2cm of water (e.g. *Potamogeton crispus, P. nodosus, P. trichoides Ranunculus circinatus, Myriophyllum spicatum*) and indeed seemed to perform better in shallow water than under deep flood where a weak germination response was noted. *Ceratophyllum demersum* and *Hydrocharis morsus-ranae* were the only euhydrophytes restricted to this treatment. *Callitriche* spp. were capable of

germinating in drawdown conditions. Some species were ubiquitous over the treatments. For example *Lindernia dubia* germinated from the Loire samples under all conditions and its abundance did not differ significantly with treatment. However, over the year that these samples were observed, the population in the moist and shallow flooded samples completed their life cycle, while the population in the deep flooded samples remained as persistent juveniles not reaching the water surface or producing flowers. This seems an ideal strategy to tolerate years of exceptional flood where water levels remain elevated well into the growing season. Remarkably this plant can germinate under water and remain as a persistent juvenile until the water levels recede, even if this is a matter of months. Some mud flat species that were observed to germinate under flooded conditions died out after a few days to weeks (e.g. *Lythrum salicaria, Chenopodium alba*).

In the Irish sites the 2cm flood was not included and therefore species tolerances of a shallow depth of flooding could therefore not be examined. *Potamogeton obtusifolius* and *Sparganium emersum* were the only species exclusive to flooded germination conditions. Shading the flooded sites reduced species germination still further and *Alisma plantago-aquatica* was the only species consistently tolerant of these conditions. Clonmacnoise samples show a much more dramatic reduction in seedling density with flooding than Little Brosna sites. The Little Brosna site can remain flooded until quite late in the year and flooding can resume as early as September (see Plate 2). Due to microtopological differences and a slightly higher floodplain elevation, flooding at Clonmacnoise seems to recede more quickly, possibly explaining the poorer tolerance of flooding observed in the seed flora at this site. On the DCA ordination the species composition was sufficient to distinguish the two sites, with the few euhydrophyte species tending to the Little Brosna sites.

The Endrick marshes samples showed the lowest seed density and one of the lowest species diversities of all the sites. Some compositional differences were evident from the DCA such as an increase in *Alisma, Callitriche* and *Myosotis* species with deep flooding. The correlation between survey species and seed bank flora was low, indicating a negligible role of the seed bank at this site, in terms of contributing to the established vegetation. The high light extinction coefficient ($k = 4.77$) and the permanently high water level in the drain (maintained by a sluice gate) make it unlikely that germination would be possible in field situations. The drain supports a dense population of *Potamogeton polygonifolius* which was observed to fruit quite

profusely. However, it seems unlikely from these results that sexual regeneration is maintaining this population.

The samples from the Insh drain show a small reduction in species richness and seedling germination with a flood treatment. The differences in species composition with flooding are also slight. The representation of the euhydrophyte taxa is biased towards the flooded samples, but species dominant in the seed bank (e.g. *Juncus bulbosus*) are not reduced by the flood treatment. This site can be subject to prolonged spring flooding and the capacity of species to germinate under water is an advantage. The representation of a number of euhydrophytes in the seed bank (*Glyceria fluitans, Callitriche stagnalis, Sparganium emersum, Subularia aquatica, Nitella* sp.) will aid recovery of the flora after the periodic dredging that the drain receives. The co-dominant *Potamogeton natans* does not appear to maintain a large permanent seed bank and may spread vegetatively from adjacent sites.

7.7.3 Seasonal differences in seed bank size and composition

At the site chosen for this study (Insh drain, Insh marshes) little differences in the seed bank size or composition were evident between May, August and October. This suggest that the seedbank is a permanent one, probably consisting largely of Type IV species. Of the fourteen species identified at the site; 7 were unclassified by Grime *et al.* (1988); 3 were classified Type III; 1 was classified III/IV; and 3 were classified Type IV. The species with the highest representation in the seed bank were *Juncus bulbosus* and *Juncus effusus*. *Carex nigra, Carex limosa* and *Juncus articulatus* were the next most frequent species (though much less abundant than the two dominants). All these species were evenly represented in both horizons of the sediment. Of these *J. effusus* and *J. articulatus* were classified by Grime *et al.* (1988) as Type IV and *C. nigra* as Type IV?. It would seem reasonable to update this classification and place *C. nigra* definitely in Type IV, and add *J. bulbosus*, and *C. limosa*. The inclusion of *J. bulbosus* in this Type can be well assured due to the large representation throughout the season and at depth; *C. limosa* shows a lower representation and its classification should be more tentative.

While much of the permanent seed bank will decay, some species show extremely long viability. *Juncus effusus* seeds have been suggested to have a longevity exceeding 75 years (Leck and Simpson 1994). Seeds of *Nelumbo nucifera* have

been found to remain viable for between 150 and 250 years (Exell 1931 in Harper 1977) and seeds of *Chenopodium alba* may still be viable after 1600 years (Odum 1965). Harper (1977) reviewing the literature on seed longevity, presents the following generalisations. 1) Long lived seeds are characteristic of disturbed habitats. 2) Most long lived seeds are annuals or biennials. 3) Small seeds tend to have greater longevity than large ones. 4) Aquatic plants may have great seed longevity and the conditions in mud overlain by water may inhibit decay.

7.7.4 Seedbank type

Species composition of the seed bank can be discussed in the context of seed bank types as defined by Grime and Thompson (1979) (Fig 7.15). To type all species present is not possible as seasonal studies were not feasible at all sites. Most of the germination is likely to be from the permanent seed bank as my sampling regime could only pick up Type I seeds in the summer and autumn samples from the Insh marshes (although none of this type were observed in these samples). As previous works have suggested that wetland seed banks are predominantly permanent in nature (Leck 1989) it was assumed that few species would be excluded. Type II seed banks should still be present in early spring samples. A tentative way of separating Type III and Type IV seed banks is to see if the species is represented in the surface vegetation. In Type III many of the seeds germinate soon after release and only a small proportion are incorporated into the seed bank (Thompson and Grime 1979). Where a species is present in the seed bank and not present in the surface vegetation it is fairly likely to be Type IV. However, the inverse situation does not allow for such a clear assumption. Type IV species probably also have a higher representation in the lower horizons of the soil (Thompson and Grime 1979).

Leck (1989) agreed with observations by Grime and Thompson (1979) on the morphological and physiological characteristics associated with these seed bank types (as these become refined they may prove to be useful indicators of seed bank type):

Type I: Large seeds (> 0.5mg), often with projections, such as awns, that germinate readily lacking dormancy mechanisms and with the ability to germinate in a wide range of conditions.

Type II: Relatively large seeds that escape burial by floating for extended periods or by projections on the seed coat. Capable of germination in dark or light conditions and at low temperature.
Type III and IV: Require light for germination, often require alternating temperature regime, may require drying or scarification to break dormancy; germination is affected by oxygen availability.
Type IV Seed banks can be recognised by the greater numbers of seeds in lower horizons (Thompson and Grime 1979).

Of the species that have been previously classified by Grime *et al.* (1988) all, except three, are Type III and IV, of a persistent nature (Table 7.3). Those that are not are present in very low numbers (although sampling timing may have excluded some type I and II species). This was also noted for wetland seedbanks (Leck 1989) with 66 Type III and 28 Type IV species from a total of 97 species; for prairie glacial marshes (van der Valk and Davis 1978; van der Valk 1981) and for exposed mud (Salisbury 1970). However, in tidal wetlands, where inundation is predictable, a large component of the seed bank was transient (Leck and Simpson 1994). Thompson (1992) considered that 'species typical of open water do not accumulate persistent seed banks'. This study allows some previously unclassified species to be typed and is able to verify some tentative classifications of Grime *et al.* (1988) (Table 7.6). Species are typed by examination of the surrounding vegetation and their representation in the lower horizons. Species with only a few occurrences cannot be reliably typed.

Grime and Hillier (1992) advocated the use of regenerative functional types to advance the analysis of regenerative processes. However, this was based on an allusion to the increasing availability of data banks on the regenerative strategies of individual species. Here the lag in knowledge of individual species strategies for aquatic plants again becomes apparent and reiterates the need for a comprehensive screening programme to yield data that can be utilised in functional analyses such as those presented by Grime and Hillier (1992) for terrestrial communities.

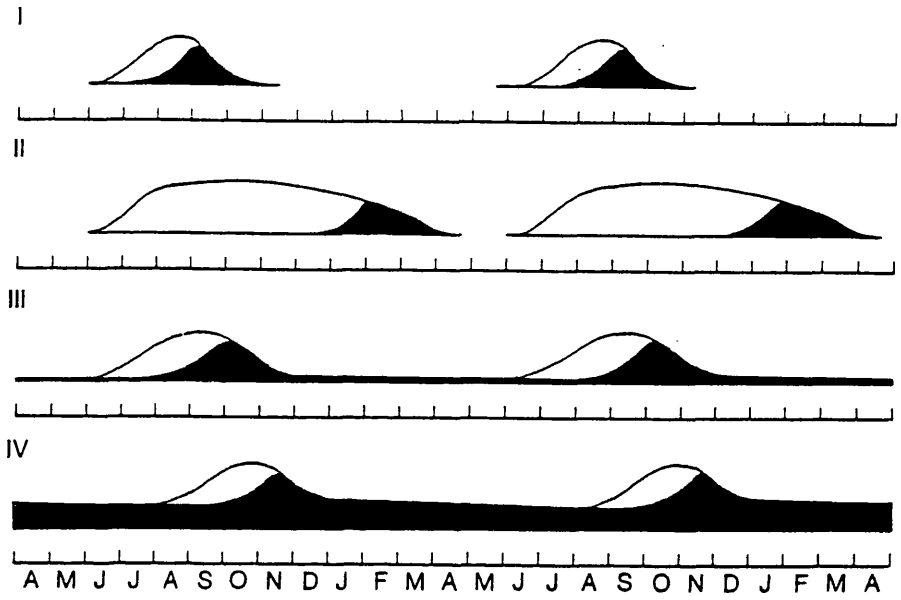


Fig 7.15 A diagrammatic representation of the four types of seed bank.

Shaded areas: seeds capable of germinating immediately after removal to suitable laboratory conditions. Unshaded areas: seeds viable but not capable of immediate germination. I Annual and perennial grasses of dry and disturbed habitats capable of immediate germination. II Annual and perennial herbs, colonising vegetation in the early spring. III Annual and perennial herbs, mainly germinating in the autumn but maintaining a small seed bank. IV Annual and perennial herbs and shrubs with large persistent seed banks. (From Thompson and Grime 1979).

Table 7.6 Seed banks typed in the light of this survey

Species	Type (Grime et al 1988)	Type (this study)
Carex dioica	-	III/IV?
Carex limosa	-	IV?
Carex vesicaria	-	III/IV?
Cyperus fuscus	-	IV
Echinochloa crusgalli	-	IV
Leersia oryzoides	-	IV
Limosella aquatica	-	IV
Lindernia dubia	-	IV
Ludwigia palustris	-	III/IV?
Myosoton aquaticum	-	IV
Potamogeton nodosus	-	III/IV?
Potamogeton trichoides	-	III/IV?
Ranunculus circinatus	-	III/IV?
Rorippa islandica	-	IV
Sagittaria sagittifolia	-	III/IV?
Samolus valerandi	-	IV
Senecio aquaticus	-	IV
Veronica catenata	-	IV?
Callitriche stagnalis	III?IV?	IV
Carex nigra	IV?	IV
Juncus conglomeratus	IV?	IV

7.7.5 Comparison with existing vegetation

The relationship between the existing vegetation and the seed bank flora in this study was variable, but generally low. Van der Valk and Verhoeven (1988) found a closer correlation between the species present in the seed banks of quaking fens and their seed banks. Of 48 species in the seed bank 40 were to be found in the surface vegetation (83%) and of the 59 species in the surface vegetation 39 possessed a seed bank (65%). Harper (1977) noted a remarkable lack of close correlation between the surface vegetation and the seed flora in the studies he reviewed. Thompson and Grime (1979) also noted a similar lack of correlation. Leck and Graveline (1979) and van der Valk and Davis (1978) both found good correlation

between seed bank and field flora. Smith and Kadlec (1983) found that seed bank and field data did not reflect similar species composition in a Utah marsh. This is indicative of a predominance of seed bank of Type IV. A high proportion of weed seeds (e.g. *Echinochloa crusgalli*) was present, and this has also been reported in marsh seed bank studies in Hungary (Hunyandi and Pathy 1976). Salisbury (1921) showed that species rare in the vegetation, can suddenly occur in large quantities following drought. He attributed this to the long viability of macrophyte seeds that allows seeds to remain viable after established plants had for some reason disappeared; and the requirement for desiccation of many species (e.g. *Alisma plantago-aquatica*). *A. plantago-aquatica* germinated in quite significant quantities in the Endrick marshes samples, although it was not recorded in the vegetation. In habitats where the dry season is prolonged and most species are annual, the correlation between existing and seed bank flora is much higher (Grillas *et al.* 1993). This relationship was not found in the most temporary of the sample sites, the Loire backwaters. However, this could largely be due to the timing and methodology of sampling. Established vegetation at these sites was recorded while there was still water present, and the sampling methodology allowed only species occurring below the waterline to be recorded.

Differences between the existing vegetation and the seed bank may be caused by transport of seeds from other sites by river flow, by winter flooding and by animal vectors; the small contribution of some dominant species (often C strategists with a low seed production); or dormancy which was not broken by the experimental conditions (van der Valk and Davis 1976, 1978, 1979; Smith and Kadlec 1983). Furthermore different specific germination requirements of light, temperature and moisture can lead to very different established floras in sites with almost identical seed bank composition (Galinato and van der Valk 1980).

In many of the less disturbed sites the existing vegetation may be of a later successional stage, consisting of more competitive species, while the seed bank is dominated by pioneer colonists that will facilitate the subsequent development of more competitive species.

7.7.6 Importance of the seed bank to aquatic plant populations

In previous studies (Titus and Hoover 1991) differences in germination results have been reported between glasshouse and field experiments on the same species, but not consistently in one direction. This observation implies that the results of greenhouse experiments should be interpreted with care and ideally consolidated by in situ field studies. Bearing this in mind this study has suggested the seed bank to be of small importance to euhydrophytes in European riverine wetlands. This supports the work of Kautsky (1990) who concluded that, except for a few annual species, such as *Najas marina,* the seed bank played a minor role in brackish water communities. However, there are a number of reasons why the existence of euhydrophyte seed banks is none the less significant. True seeds that do germinate represent a genetically different population giving the species an enhanced ability to survive changing environmental conditions. The seed bank provides a long term reservoir for the species in case of a period of extreme adverse conditions (e.g. drainage, unpredictable drought). For example, *R. peltatus* has been observed to germinate from seed and become dominant in a chalk stream, where it was previously uncommon, following a period of drought (Ladle and Bass 1981). *Potamogeton crispus* appears to increase fruit production as a response to lowering water levels (Hunt and Lutz 1959), which will allow it to re-establish after a period of drought. Wade (1993) noted the rapid re-establishment of aquatic vegetation in recently dredged ditches. In certain habitats, such as seasonal water bodies, the ability to survive as a propagule over the adverse season will allow long term survival (Grillas 1990).

For some aquatic species (e.g. *Myriophyllum spicatum, Potamogeton pectinatus*) germination has been successfully achieved in the laboratory (Madsen and Boylen 1989; van Wijk 1989; Hartleb *et al.* 1993) and observed in the field (Hartleb *et al.* 1993). In *M. spicatum* germination is inhibited by low temperature, low light and high levels of sediment deposition (Madsen and Adams 1988; Hartleb *et al.* 1993). The germination of turions (e.g. *Hydrocharis morsus-ranae, Potamogeton crispus, Potamogeton trichoides*) has also been demonstrated to require light (Richards and Blakemore 1975; Kadono 1982b; van Wijk and Trompenaars 1985) and to possess other dormancy mechanisms that only allow germination in favourable conditions (Patten 1955). Many other species of aquatic plants have been shown to exhibit prolonged dormancy (of 5 years or more (Guppy 1897)) and long viability (Sculthorpe 1967; Harper 1977; Leck 1989; Salisbury 1970). Some aquatic species have been demonstrated to possess hard seed coats, impermeable to water

(Teltscherová and Hejný 1973), which in some species disintegrates rapidly (e.g. *Potamogeton pusillus*), but in others may result in dormancy for some time. Muenscher (1936) reported that cold storage in water for one year resulted in the best germination from *Potamogeton* seeds. The environmental tolerance of seedlings is also much narrower than that of established plants and these requirements may seldom be met in the field (Patten 1955). It has also been demonstrated that, for some aquatic species, successful germination occurs only in calm, sheltered waters, usually found in lacustrine systems (Hartleb *et al.* 1993); this could lessen, still further, the role of sexual regeneration in the more disturbed habitats found in riverine wetlands. The combination of delayed germination and slow rate of decay in permanently submerged soils will favour the existence of a long-lived seed bank that, while not critical to population maintenance, has certain relevance to survival particularly in the event of catastrophe. Conversely the key advantages of vegetative reproduction are that it enables the multiplication of proven clones and appears to give a better chance of survival in these habitats than sexual reproduction (Leakey 1981).

Potamogeton nodosus, Potamogeton trichoides, Ranunculus circinatus and *Sagittaria sagittifolia* are all postulated to have permanent Type IV seed banks from the results of this study. It seems reasonable to expect that, in the future, many more euhydrophytes will be shown to have permanent seed banks, even if these turn out to play only a minor role in population maintenance.

7.8 Conclusions

While these studies have confirmed that the seed bank is playing a small role in the population dynamics of euhydrophyte populations, much insight has been gained into the functioning of the seed bank of riverine wetland systems. The seed bank of permanently inundated sites may be larger than previously supposed from models based on lacustrine data. Seed banks can be central to wetland plant survival (van der Valk and Davis 1978; 1979; van der Valk 1981; Smith and Kadlec 1985; van der Valk and Verhoeven 1988). The long viability of seeds in permanently inundated areas may make them important reservoirs for the restoration of floodplains that have been long drained or are isolated from other wetlands and are an important functional component, particularly at sites where water level fluctuations can lead to summer droughting, because emergents and mud flat annuals are then recruited from the seed bank. As water levels rise the mud flat

species can no longer survive but the germination of euhydrophytes (from seed or propagule) is facilitated. If levels continue to rise, the emergent component will also decline. So, while the aquatic seed bank is limited, it has a role to play particularly in systems where drought and inundation cycles are regular and predictable. The French sites were the only ones that conformed to this hydrological regime and were indeed the samples that possessed the highest proportion of euhydrophyte regeneration. In the more permanently flooded sites aquatic plant populations can be maintained by vegetative means and the possession of a permanent seed bank is not a critical survival trait.

7.9 Summary

Fragmentation rates were not found to be correlated to flow, stress index, or disturbance index.

The highest seed densities were found in the most disturbed sites i.e. backwaters that dry up in summer.

Some species of previously untyped seed bank were classified according to the framework of Thompson and Grime (1979).

The majority of species contributing to the seed bank were classified as type III or IV (permanent seed bank).

Flooding depth had a severe effect on seedling germination and species richness in many sites. Effects were less severe in sites where spring flooding recedes and an emergent and mud flat flora adapted to the phenology of flooding becomes established.

A persistent seed bank was demonstrated for some euhydrophytes, but it is confirmed to be of low importance in maintenance of existing populations.

The seed bank at permanently submerged sites was not as low as suggested from other studies.

The seed bank in permanently inundated sites is suggested as potentially useful for wetland restoration.

Chapter 8

DEFINING FUNCTIONAL VEGETATION TYPES AND INVESTIGATING THEIR RELATIONSHIP TO HABITAT CONDITIONS

Chapter 8

DEFINING FUNCTIONAL VEGETATION TYPES AND INVESTIGATING THEIR RELATIONSHIP TO HABITAT CONDITIONS

8.1 Introduction

Having defined the functional groups in Chapter 4 and 6, it is now possible to investigate their relationship to the environmental parameters measured during the field survey. It is also possible to construct Functional Vegetation Types (FVTs) based on the composition of the communities in terms of functional groups.

Various analyses are possible with the data available. The contribution of each of the groups at a site can be used to assign the site's Functional Vegetation Type (Murphy *et al.* 1990). This can then be examined in relation to environment. One of the simplest alternatives is to represent the proportion of each group at a site graphically, to give a visual estimation of the FVT. For example Murphy *et al.* (1990) plotted their functional groups into a triangle following Grime's approach. To prevent the analysis from being dominated by preconceptions and to minimise subjectivity, ecological interpretations should be left as late as possible, therefore at present no judgements have been made as to how the functional groups correspond, or not, to Grime's three axes model. Ordination on the triangular framework is not possible but a similar representation of the group contribution at each site can be made.

An effective method of analysis is to construct a matrix of sites by proportion of functional group and then ordinate and classify this matrix (Friedel *et al.* 1988), in much the same way as the analysis of species data in Chapter 3. This is a useful way to examine broad trends of functional group with environment.

One method, that is to some extent a combination of both phytosociological principles and a functional approach, is that devised by Den Hartog and Segal (1964), who classified water plant communities not only by the traditional Braun-Blanquet system using floristic composition, but also incorporating life form spectrum, physiognomy, stratification, and ecology of the vegetation. A comparison of the FVT's recognised in this study and Den Hartog and Segal's classification is made. A comparison of the functional assessment that arises from this study with

one based on phytosociological principles (as outlined in Chapter 3), will be made in Chapter 10.

This chapter

- classifies the sites into functional vegetation types according to the composition of functional groups

- uses ordination techniques to examine the relationship of both functional groups and functional vegetation type to the environment

- uses linear discriminant analysis to construct predictive equations to allow classification of new sites into functional vegetation types

Table 8.1 Proportions of Functional Groups at each site.
(see Appendix 1 for site codes)

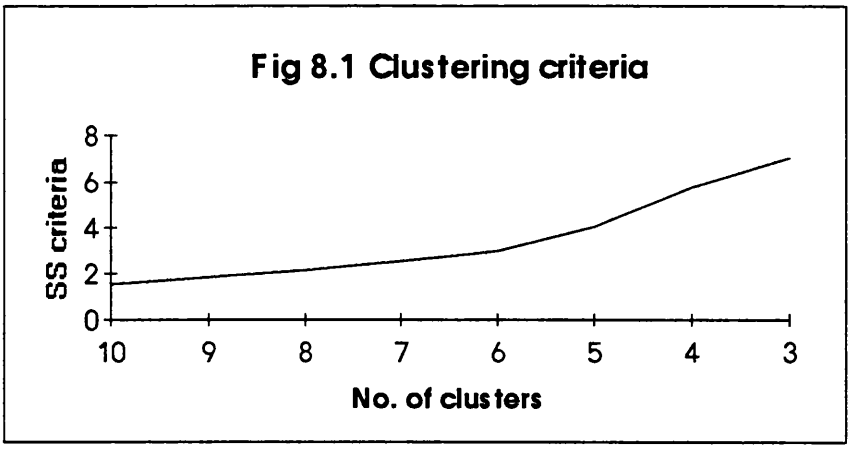
Site	FG1	FG2	FG3	FG4	FG5	FG6	FG0
1	0.02	0.06	0.49	0.00	0.02	0.00	0.41
2	0.03	0.26	0.04	0.01	0.04	0.62	0.00
3	0.04	0.07	0.09	0.07	0.04	0.69	0.00
4	0.75	0.00	0.13	0.00	0.13	0.00	0.00
5	0.01	0.31	0.16	0.19	0.12	0.01	0.20
6	0.16	0.00	0.21	0.44	0.05	0.14	0.00
7	0.00	0.38	0.02	0.06	0.17	0.38	0.00
8	0.00	0.47	0.02	0.00	0.47	0.04	0.00
9	0.00	0.14	0.13	0.00	0.27	0.46	0.00
10	0.38	0.09	0.00	0.38	0.00	0.00	0.15
11	0.00	0.00	0.30	0.20	0.00	0.00	0.50
12	0.29	0.15	0.01	0.41	0.01	0.00	0.12
13	0.00	0.00	0.10	0.90	0.00	0.00	0.00
14	0.44	0.00	0.16	0.36	0.00	0.04	0.00
15	0.00	0.00	0.00	0.00	1.00	0.00	0.00
16	0.00	0.38	0.12	0.15	0.00	0.00	0.35
17	0.00	0.13	0.70	0.14	0.00	0.00	0.02
18	0.00	0.30	0.48	0.01	0.21	0.00	0.00
19	0.00	0.42	0.51	0.03	0.00	0.00	0.04
20	0.00	0.71	0.27	0.00	0.00	0.01	0.01
21	0.00	0.44	0.10	0.00	0.41	0.03	0.01
22	0.00	0.43	0.13	0.23	0.03	0.17	0.00
23	0.00	0.40	0.27	0.00	0.05	0.27	0.00
24	0.00	0.53	0.14	0.03	0.00	0.20	0.11
25	0.00	0.50	0.17	0.31	0.00	0.03	0.00
26	0.02	0.04	0.47	0.02	0.40	0.05	0.00
27	0.00	0.00	0.00	0.00	1.00	0.00	0.00
28	0.20	0.00	0.00	0.00	0.00	0.00	0.80
29	0.00	0.00	0.00	0.00	0.00	0.00	1.00
30	0.00	0.00	0.00	0.00	0.00	0.00	1.00
31	0.05	0.61	0.12	0.01	0.12	0.10	0.00
32	0.02	0.56	0.27	0.00	0.05	0.10	0.00
33	0.16	0.45	0.00	0.10	0.08	0.22	0.00
34	0.01	0.47	0.21	0.00	0.03	0.28	0.00
35	0.00	0.24	0.00	0.18	0.12	0.47	0.00
36	0.00	0.97	0.03	0.00	0.00	0.00	0.00
37	0.00	0.25	0.13	0.00	0.11	0.51	0.00

8.2 Data Analysis

8.2.1. Defining Functional Vegetation Types

The species distribution amongst the six groups defined in Chapter 4 is shown in Table 4.3. The average species frequency was used (see chapter 3) at each site to calculate the proportion of each group making up the community at a site. This information is given in Table 8.1. This then gives us a *functional groups x sites* matrix that can be classified and ordinated in a similar way to the *species x sites* matrix analysed in Chapter 3. It can also be related to the measured environmental parameters given in Appendix 1. An additional group, labelled functional group 0 (FG0), has been included for analysis purposes. This group contains non vascular aquatic species, such as Charophytes and aquatic mosses, that had not been included in the trait analysis from which the functional groups were derived. It was considered necessary to use this group in the current analysis as in some sites non vascular species make a large contribution to community biomass. FG0 is not a true functional group as it has not been formed using its group members traits. Some vascular species that had not been included in the trait analysis were present in the survey (these are species that were recorded later in the second field season, after the trait analysis had been completed, and were not present at large frequencies, or in many sites). These species were assigned to functional groups using the linear discriminant functions of the published traits calculated in Chapter 4.

A preliminary classification of the sites by their functional group composition can be achieved by a TWINSPAN analysis (Hill 1979) option in the VESPAN statistical package (see Chapter 3). As in Chapter 4, a non - hierarchical clustering was then used to group the sites. This was preferred to a TWINSPAN classification as it does not assume the functional groups are showing a gradient based response. The number of clusters formed ranged from 3 - 10 and the sum of squares criteria for these clusters is displayed in Fig 8.1. The most coherent grouping appeared to be six clusters. This was confirmed by examination of the site distribution into 7 clusters and 5 clusters. Increasing to 7 clusters only served to isolate a single site into an additional cluster, while 5 clusters amalgamated two clusters that seemed to be more appropriate as discrete entities.



The distribution of the sites within the six groups is shown in Table 8.2. These will now be referred to as Functional Vegetation Types (FVTs).

Table 8.2 Sites ordered into functional vegetation types by non-hierarchical cluster analysis.

I	II	III	IV	V	VI
ehbox	ilbd3	ilbr	eksrr	ilbd2	ilbpo
cemcb	ilbd4	iclr	smgr	cimrl	icldi
	icldo	cimsr	smml1	cimnl	eksrf
	ibipo	cimwp	smml3	cimid	eksrl
	fdcbw	cimox		cemgd	eksox
	fapdi	cemab			ebmr
		cemta			
		cemwa			
		cemrd			
		faoxa			
		faoxd			
		fappo			
		fapdo			
		fmlbw			

The next treatment of the data was to ordinate the sites by their functional group contributions. To do this a Detrended Correspondence Analysis (DCA) was performed using the CANOCO programme. The site scores are plotted in Fig 8.2, and overlaid by the FVTs. A summary of the DCA analysis is shown in Table 8.3. A feature of DCA is that the axes are expressed as standard deviations and can be

used to check the validity of assuming a unimodal response curve in the functional group abundance. The length of the first two DCA axes are 3.901 s.d. and 1.995 s.d. respectively. An axis length of 4.0 s.d. or more, would indicate that sites at either end of the axis have no species in common (ter Braak 1987a), and that the data is probably strongly non linear in response. In the present analysis sites at either end of the first axis will, therefore, have few functional groups in common and the assumptions underlying CA based techniques seem to be valid.

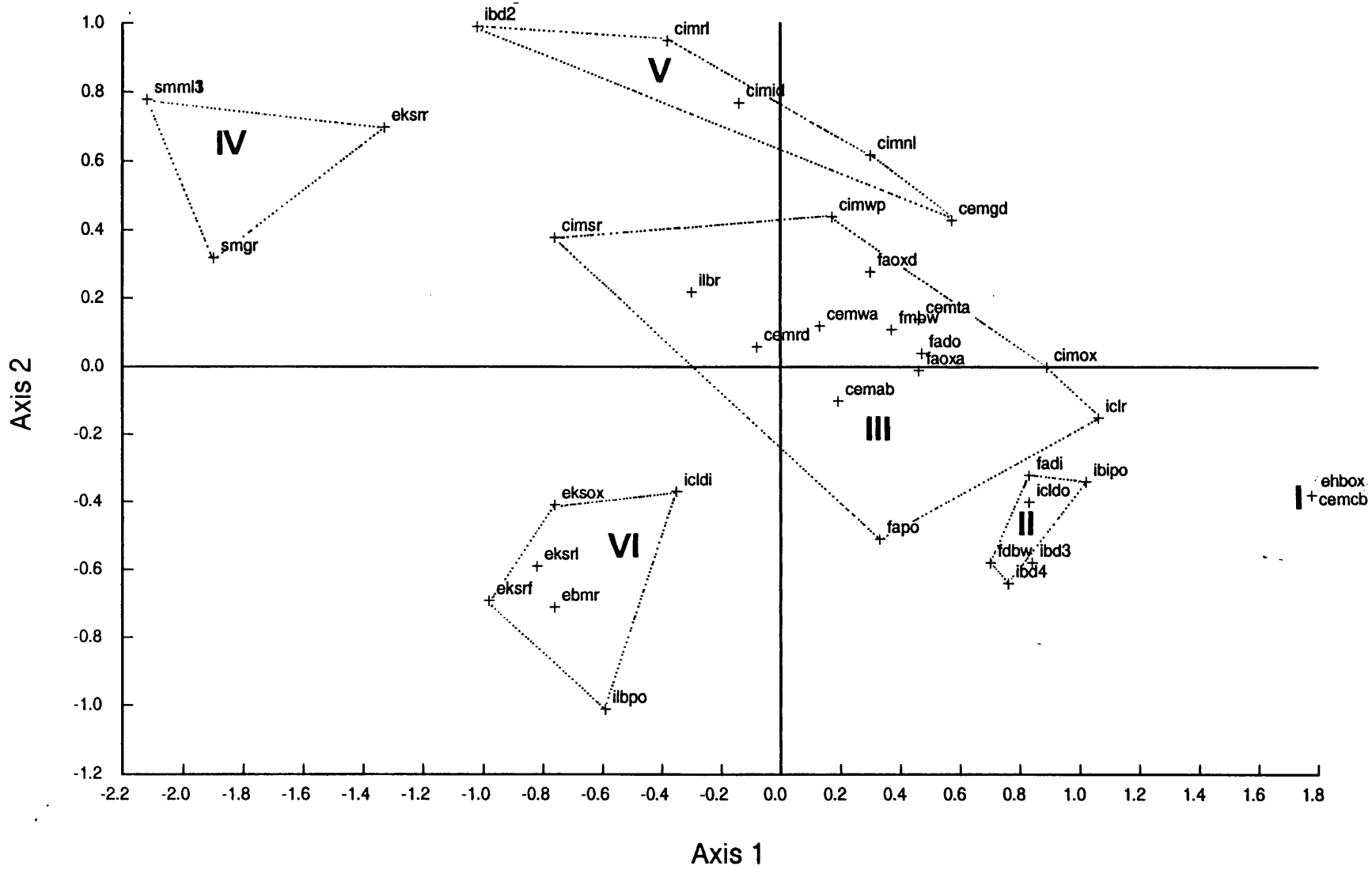
Table 8.3 Summary of DCA

Axes	1	2	3	4	Total inertia
Eigenvalues	0.690	0.268	0.112	0.073	2.344
Length of gradient	3.901	1.995	2.531	2.062	
Species-environment correlations	0.877	0.666	0.837	0.720	
Cumulative percentage variance					
species data	29.4	40.9	45.6	48.7	
species-environment relation	39.5	45.3	0.0	0.0	
Sum of all unconstrained eigenvalues					2.344
Sum of all canonical eigenvalues					1.506

When interpreting a DCA diagram, it should be noted that species (or in this case functional groups) that lie between the central area and the extreme edges are most likely to show a clear relation to the axis. Species at the extremes are often rare, sometimes because they prefer extreme environmental conditions. Species at the centre of the diagram may be unimodally distributed with their optima at the centre of the diagram, but may also be either bimodal or unrelated to the displayed axes.

The separation of the six Functional Vegetation Types on the DCA diagram was quite clear, with no overlap between the types. FVTs I and IV are clearly separated from the others on the first axis but it is necessary to use the second axis to separate the remaining four types. The eigenvalue of axis 1 is more than double that of axis 2 and quite a large percentage of the functional group variation and species - environment relation is explained by it (Table 8.3). FVTs I and IV are very different in terms of their environmental requirements to the other types, which may be closer in habitat utilisation.

Fig 8.2 DCA ordination of 1992/1993 sites using functional group composition. Functional vegetation types delineated by dotted lines.



The next step was to look at the relationship between the functional groups, the FVTs and the measured environmental parameters. A Canonical Correspondence Analysis (CCA) was performed using the CANOCO programme (see chapter 3). The first run included all sites. The environmental parameters that were shown in 3.3.2 to be highly correlated or skewed were not used. CANOCO gives warnings of sites and particular variables that are having an extreme influence on the ordination. At site **ilbpo** the combination of clear and a very shallow water (12cm) gave rise to a very high substrate light level that led this site to dominate the ordination with a 72.8x influence. Rather than exclude the potentially important substrate light variable from the analysis, this site was dropped. The position of **ilbpo** on the DCA ordination indicates that, in terms of functional groups, it is close to the other sites of type VI. A comparison of analysis summaries with and without the site (Tables 8.4a and 8.4b respectively), shows that although the eigenvalue and species-environment relation of axis 2 are reduced, an overall improvement in the proportion of variation explained by the first two axes is evident. Consequently all subsequent references to CCA ordinations, in this chapter, refer to the analysis with **ilbpo** excluded from the data set.

A summary of the analysis (including eigenvalues) is given in Table 8.4b. The eigenvalue (which can range from 0 - 1) is equal to the dispersion of the species scores on the axis, and so reflects the importance of the axis (ter Braak 1987a). The eigenvalue for the first axis is high (> 0.3 is to be expected for ecological data (ter Braak 1988)), while the eigenvalue for axis 2 is considerably lower, but still quite high. A high eigenvalue generally indicates good separation along the axis. However some of this is due to the extreme position of the three Spanish sites, which consequently leads to compression of the other sites along the first axis. CCA can usually cope with sites such as these, that are species-poor and contain rare species (Palmer 1993). The species environment correlations were also very high. This correlation is a measure of association between species and the environment, but is not ideal; axes with a small eigenvalue may have a misleadingly high species-environment correlation (ter Braak 1987a).

The site scores for axis 1 and 2 are plotted in Fig 8.3, individual sites are not labelled, instead FVTs are marked by the dotted lines. The functional group scores and the gradients of greatest change in the environmental variables (shown as arrows) are displayed as a biplot (Fig 8.4). Subsequent axis scores are not plotted as the eigenvalues are low. 28.2% of the variance in the functional group data was

explained by axis 1 and 43.6% of the species-environment relation. FVT II and FVT IV are clearly separated on this axis. The second axis is separating FVT VI and I. It contains 13.6% of the functional group variance and 21.1% of the species-environment relation. FVT III and V are difficult to separate on either axes. The ratio of the unconstrained eigenvalues to the canonical eigenvalues indicates that a lot of the variation of the functional group data expressed in the DCA, is explained in the CCA using the environmental variables.

Table 8.4a Summary of CCA: all sites

Axes	1	2	3	4	Total inertia
Eigenvalues	0.599	0.320	0.244	0.167	2.344
Species-environment correlations	0.940	0.814	0.818	0.745	
Cumulative percentage variance					
species data	25.5	39.2	49.6	56.7	
species-environment relation	39.8	61.0	77.2	88.2	
Sum of all unconstrained eigenvalues					2.344
Sum of all canonical eigenvalues					1.506

Table 8.4b Summary of CCA: without ilbpo

Axes	1	2	3	4	Total inertia
Eigenvalues	0.628	0.303	0.179	0.162	2.228
Species-environment correlations	0.956	0.788	0.711	0.724	
Cumulative percentage variance					
species data	28.2	41.8	49.8	57.1	
species-environment relation	43.6	64.7	77.1	88.3	
Sum of all unconstrained eigenvalues					2.228
Sum of all canonical eigenvalues					1.440

The intraset correlations (see 3.3.2) for the first two axes are shown in Table 8.5.

Fig 8.3 CCA ordination of 1992/1993 sites using functional group composition. Functional vegetation types delineated by dotted lines.

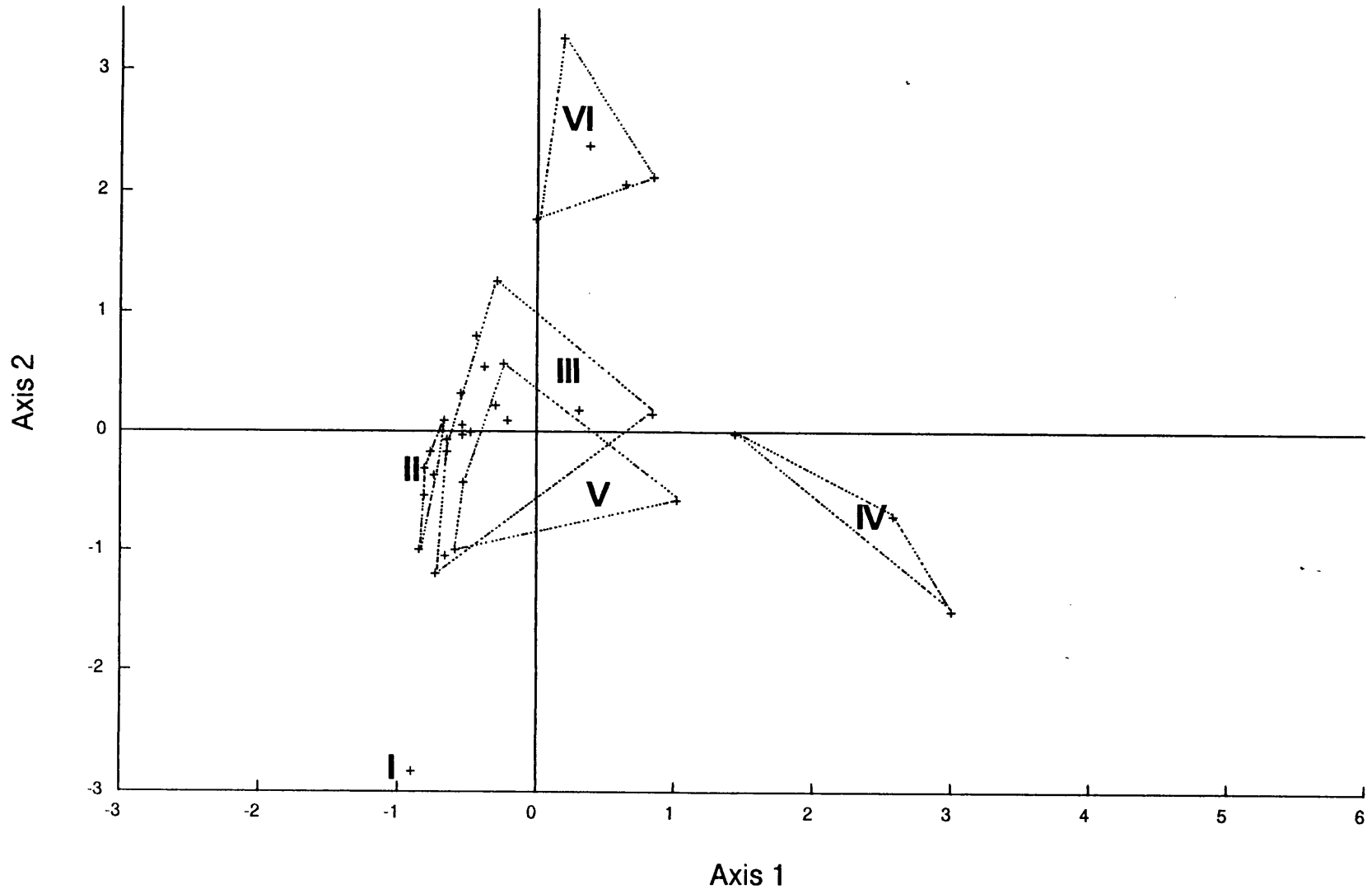


Fig 8.4 CCA biplot of 1992/1993 data showing functional group scores (filled circles) and environmental variables (arrows).

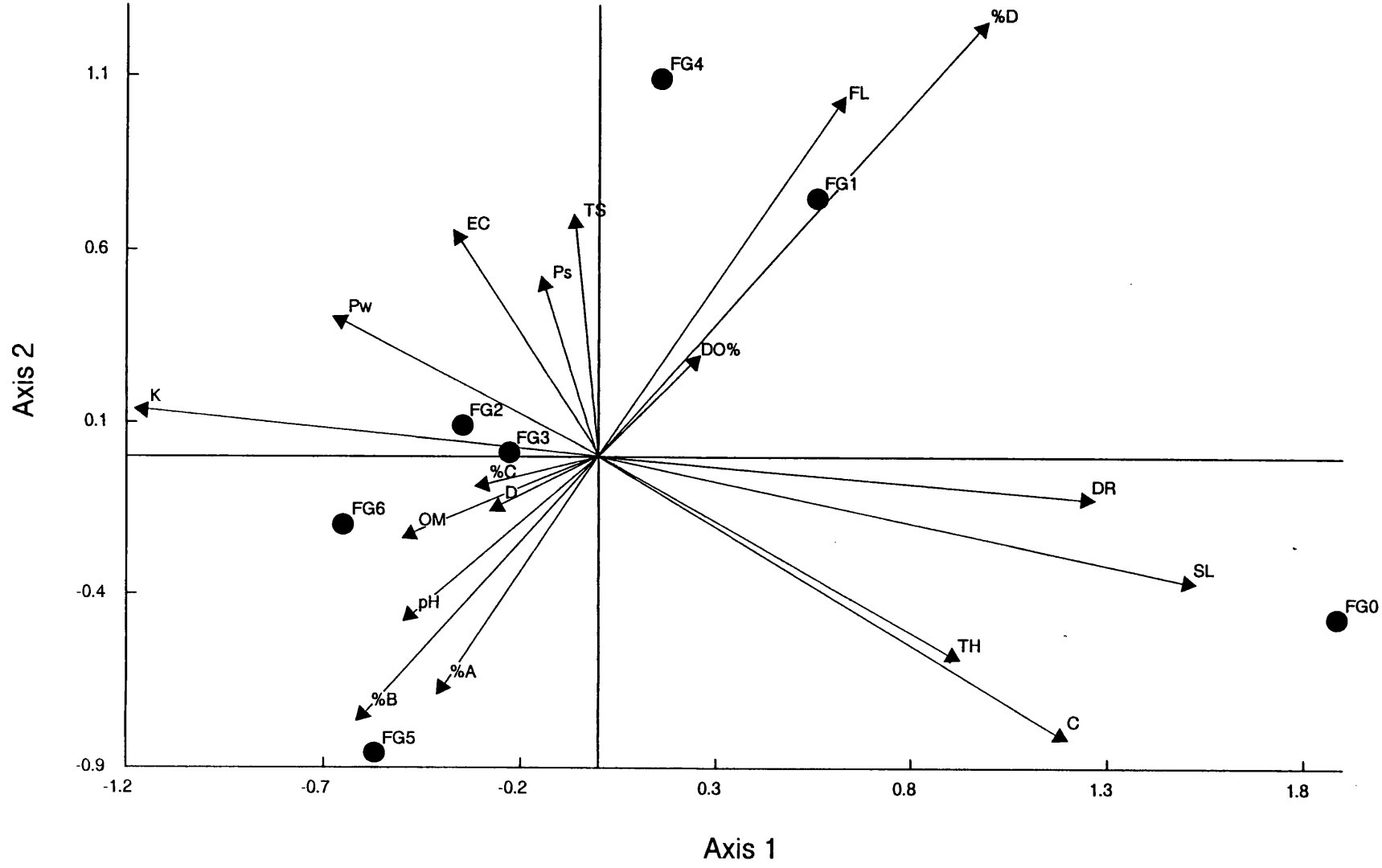


Table 8.5 Intraset correlations (Environmental variables with axis)

Correlations marked ** are most significant (approximating to $p < 0.01$), those marked * are of secondary significance (approximating to $p < 0.05$).

Parameter and code	Axis1		Parameter and code	Axis2	
Light at substrate (SL)	0.713	**	Flow	0.402	
Drought (DR)	0.595	**	% 'd'	0.359	
Conductivity (Cond)	0.568		Tree shade (Tshade)	0.269	
% 'd'	0.347		Emergent cover (Ecover)	0.249	*
Flow	0.294		Sediment P (Ps)	0.200	
% dissolved oxygen (DO%)	0.116		Water phosphate (Pw)	0.159	
Sediment P (Ps)	-0.064		% dissolved oxygen (DO%)	0.108	
Depth (D)	-0.127	**	Depth (D)	0.059	
% 'c'	-0.145		Light extinc. coeff. (K)	0.055	
Emergent cover (Ecover)	-0.173		% 'c'	0.029	
% 'a'	-0.194		Drought (DR)	-0.046	
pH	-0.228		Sed. organic matter (OMs)	-0.085	
Sed. organic matter (OMs)	-0.231		Light at substrate (SL)	-0.144	
Tree shade (Tshade)	-0.240		pH	-0.182	
% 'b'	-0.284		% 'a'	-0.256	
Water phosphate (Pw)	-0.319		% 'b'	-0.291	
Light extinc. coeff. (K)	-0.550		Conductivity (Cond)	-0.315	

Significance levels are exploratory (see section 3.2.2) and variables that are correlated with another variable may have low 'significance'. These values are of greatest use where the aim is to reduce the number of environmental variables under consideration. The intraset correlations show substrate light levels ($r = 0.713$), drought ($r = 0.595$), light extinction ($r = -0.550$) and conductivity ($r = 0.568$) to be most strongly correlated with axis 1. No single environmental variable is dominating the axis. Conductivity may rise due to the concentration of ions with droughting, where the drought effect is due to evaporation. Axis 2 shows strong correlations with flow ($r = 0.402$) and %'d' (large) particle size ($r = 0.359$); conductivity ($r = -0.315$) shows a negative correlation. The correlation of flow and large particle size to the same axis is unsurprising, as smaller particle size classes will not be deposited in faster flowing waters. Axis 2 is also correlated with tree shading ($r = 0.269$) and emergent cover ($r = 0.249$). The relative position of arrows, functional groups and sites on the diagram is also relevant. Percentage

saturation of dissolved oxygen follows the direction of flow and large particle size as high oxygen saturation levels are found particularly in turbulent fast flowing rivers. Sediment phosphate concentration does not seem to be related to sediment organic matter concentration, as might be expected (Chambers 1987). Sediment phosphate concentration and water soluble orthophosphate concentration are showing the same directional influence.

The interpretation of the relationships of the functional groups to these variables is clearer for some groups than others. As noted previously in relation to DCA, species lying in the centre of the diagram are less easy to interpret in relation to the axes. Inferred rankings of the functional groups with respect to the environmental variables can be constructed by dropping perpendicular lines from the functional group co-ordinates to the environmental arrows and noting the ranking (as in 3.3.2). The inferred rankings for flow, conductivity, substrate light level and light attenuation coefficient are given in Table 8.6 in descending order (i.e. the top group is associated with a high value of the particular variable). FG1 and FG4 tolerate high flow conditions. FG1 is dominated by Batrachian *Ranunculus* species often associated with fast flowing rivers (Haslam 1987; Spink 1992). FG4 (exclusively *Callitriche* species) differs from FG1 in that it also tends towards sites with low conductivity. FG4 also seems to occur where shading by trees is heavy. Members of this group have been noted to be tolerant of shade (Spence and Crystal 1970b; Haslam 1978). FG5 and FG6 are both at the bottom of the flow ranking. These groups are dominated by nymphaeids and lemnids respectively. FG5 tends to relatively still, unshaded sites with small sediment particle size and high pH. FG6 occurs in still waters where sediment organic matter is high. This is observable in the field with lemnid species often exhibiting vigorous growth in still, nutrient rich sites (e.g. Caffrey 1986). Their decay may contribute directly to the high organic matter concentrations. Both these groups also show a negative response to substrate light levels and can occur in water of high turbidity (high K). This allows the dominance of these groups at sites where the low light climate may preclude submerged species for example in sluggish, lowland clay rivers (Holmes 1983) or in phytoplankton rich eutrophic lakes (e.g. Moss 1988). FG5 and FG6 can also occur in deeper sites than the other groups, lemnids being able to occur independent of water depth and nymphaeids possessing large underground rhizomatous reserves that aid petiole extension to the surface. FG0 occurs in sites of high conductivity, with high substrate light levels and experiencing frequent and often prolonged drought. FG2 and FG3 are less easy to interpret being closer to the centre of the diagram. Assuming this is due to their optima being located here rather than being

uncorrelated to the axis or showing bimodal distribution these groups occur at moderate flow, conductivity and light levels. These displayed preferences are tested in Chapter 9.

Table 8.6 Inferred functional group rankings along environmental gradients (In descending order)

Flow	Conductivity	Drought	Substrate light	Extinction coeff.
FG4	FG0	FG0	FG0	FG6
FG1	FG1	FG1	FG1	FG5
FG0	FG5	FG4	FG4	FG2
FG3	FG3	FG3	FG3	FG3
FG2	FG2	FG2	FG2	FG4
FG6	FG4	FG5	FG5	FG1
FG5	FG6	FG6	FG6	FG0

Examination of the position of FVTs on the diagrams (Figs 8.3 and 8.4) show FVT II lying to the extreme left of axis 1, indicating greatest abundance at sites where drought is infrequent, light levels may be low and sediment organic matter and water phosphate levels may be above average. Axis 1 also clearly separates FVT IV from the other FVTs, with this type occurring mostly in sites prone to drought with high conductivity and light levels. The remaining groups occur at intermediate drought, conductivity and light levels but can be separated along Axis 2. FVT VI shows a strong inclination to fast flowing sites. FVT 1 occurs at still sites with silty sediment and low dissolved oxygen levels. FVT III and V are not discretely separated, but FVT III tends to slightly more turbid locations with more shade and emergent cover while FVT V occurs at sites with higher conductivity and improved light climate. While visual descriptive interpretation of a CCA plot may seem crude, it is adequate to generate testable hypotheses. The statistical significance of eigenvalues, species-environment correlations and canonical coefficients needs further work (ter Braak 1986).

The results of the DCA and the CCA both show FVT VI, IV and I to be easily distinguishable on two axes. II, V and III are less easily separated. There species composition can be used to separate them (Fig 8.2) but the environmental conditions in which they are found are similar (Fig 8.3). The comparison of the unconstrained and constrained eigenvalues in the final CCA also show that a high proportion (65%) of the functional group variation is accounted for by the known environmental variation.

Fig 8.5 a- f represent the functional group composition at each site, organised by catchment, showing the diversity of functional groups in most catchments. This can be compared with Fig 8.6 a- f showing the sites grouped into FVTs. Visual representation makes it easy to see the importance of different functional groups to the particular FVT. FVT I is exclusively composed of FG5 and comprises only two sites. FVT II shows a more mixed composition with FG6 and FG2 prevalent, and no representation of FG0. FVT III shows the greatest diversity with a dominance of FG2 but representation of all functional groups. FG0 is almost exclusive in FVT IV. FVT V has a more varied representation of Functional Group but is dominated by FG3. FVT VI shows dominance of FG1 and FG4.

Fig 8.5a Functional group composition: Ireland (Site numbers 1-9)

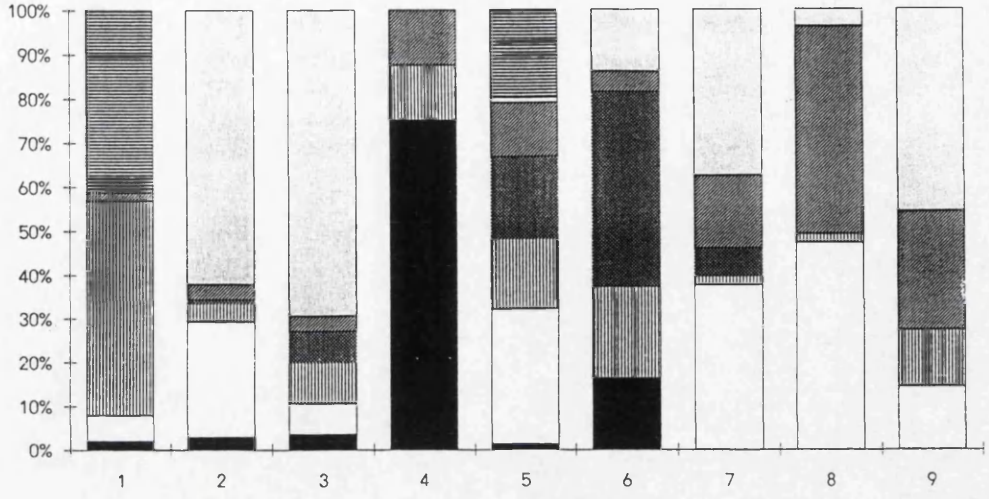


Fig 8.5b Functional group composition: Torridge (Site numbers 10 - 15)

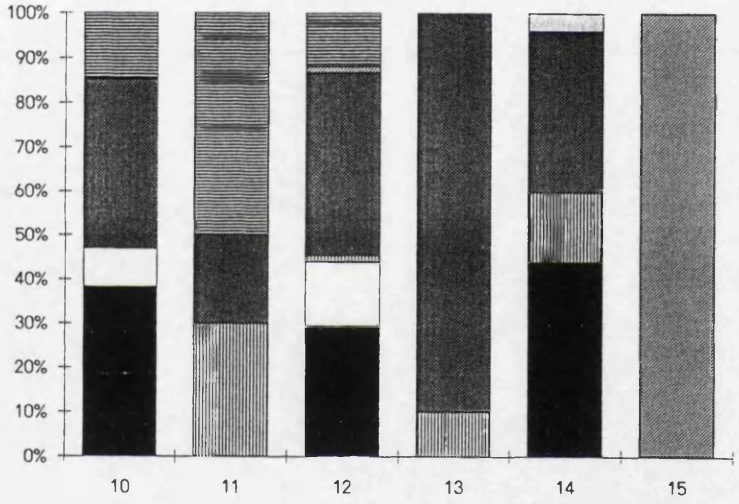


Fig 8.5c Functional group composition: Insh marshes (Site numbers 16 - 21)

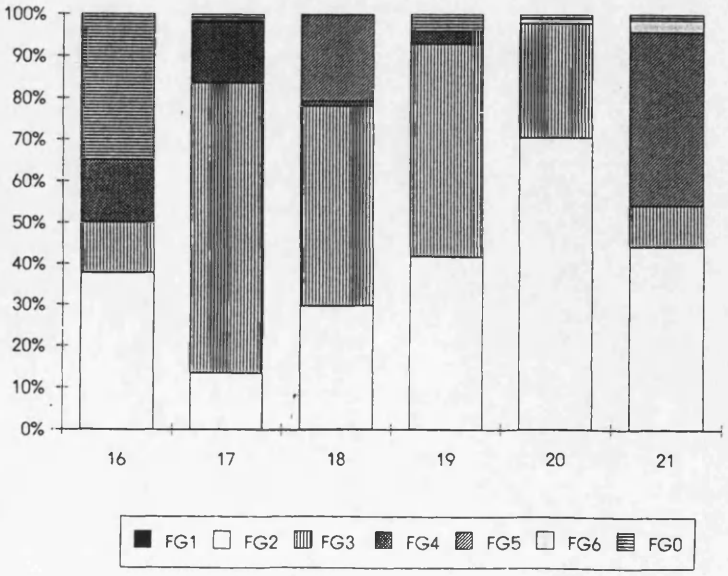


Fig 8.5d Functional group composition: Endrick marshes (Site numbers 22-27)

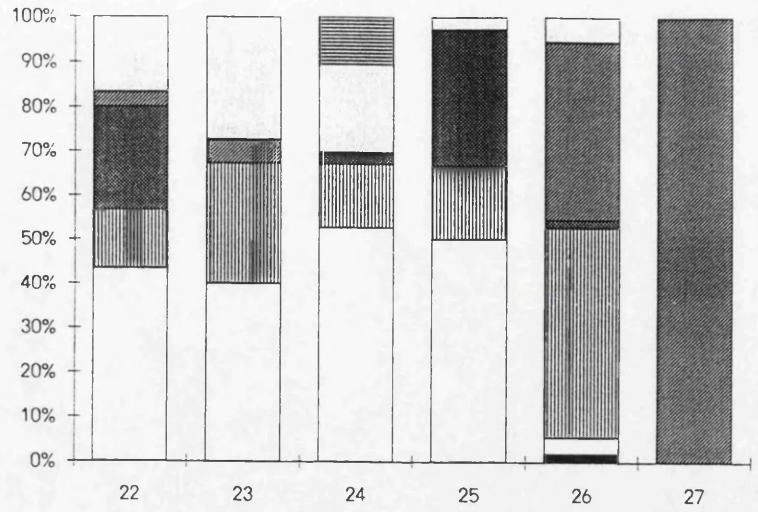


Fig 8.5e Functional group composition: Spain (Site numbers 28 - 30)

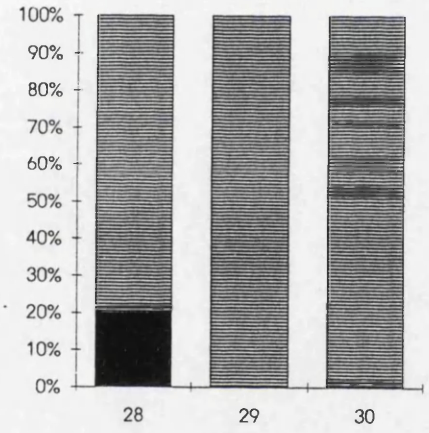


Fig 8.5f Functional group composition: France (Site numbers 31 - 37)

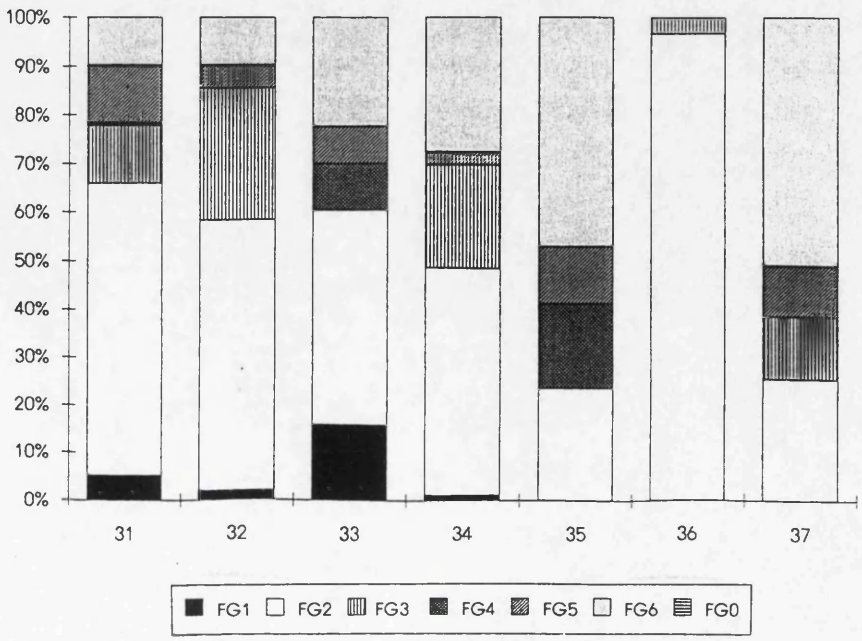


Fig 8.6a Functional vegetation type I

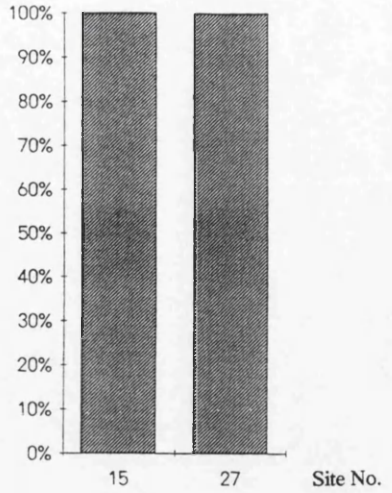


Fig 8.6b Functional vegetation type II

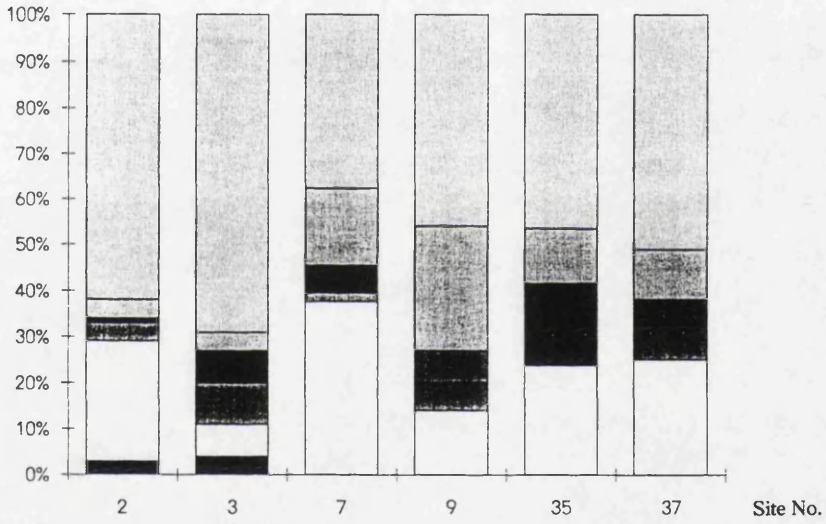


Fig 8.6c Functional vegetation type III

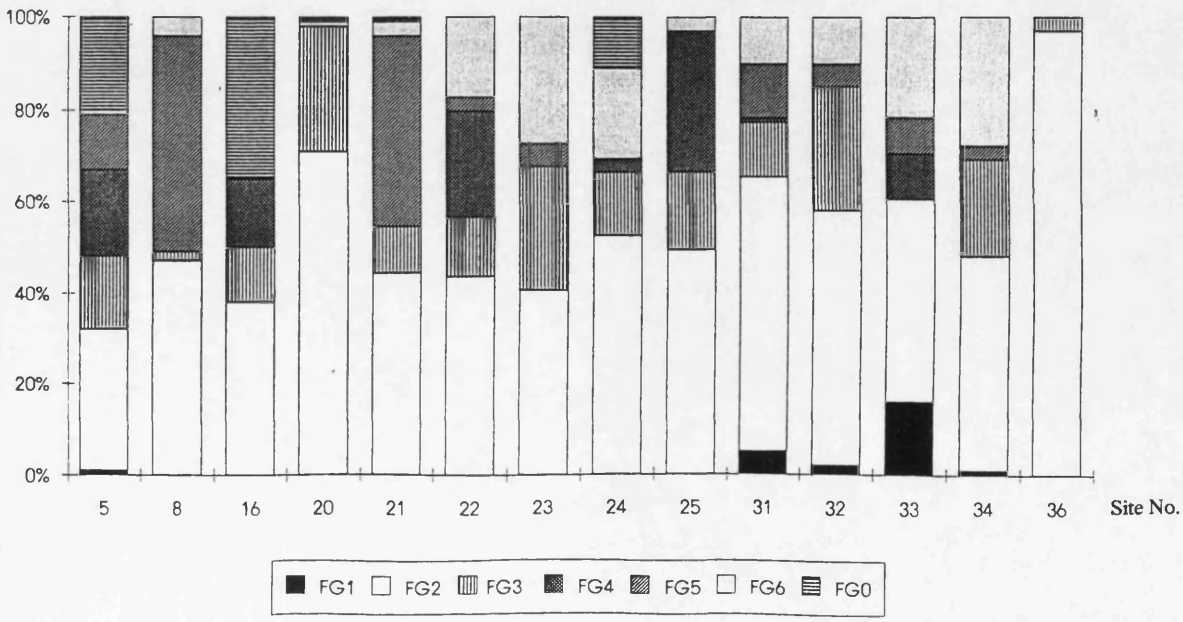


Fig 8.6d Functional vegetation type IV

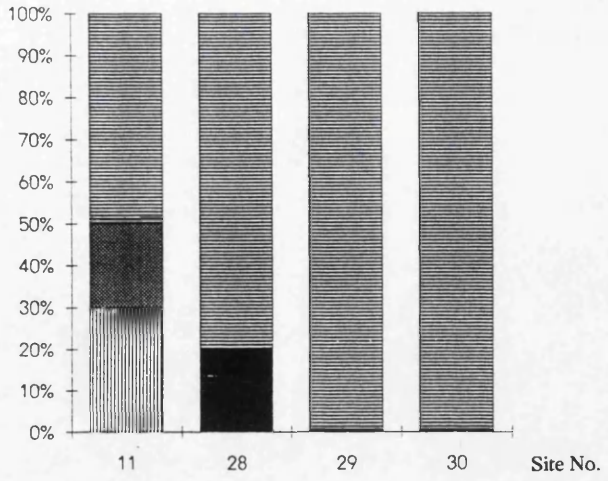


Fig 8.6e Functional vegetation type V

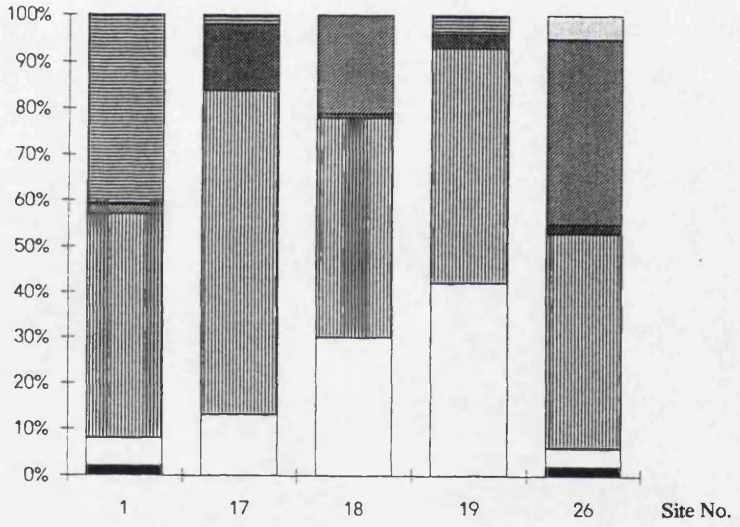
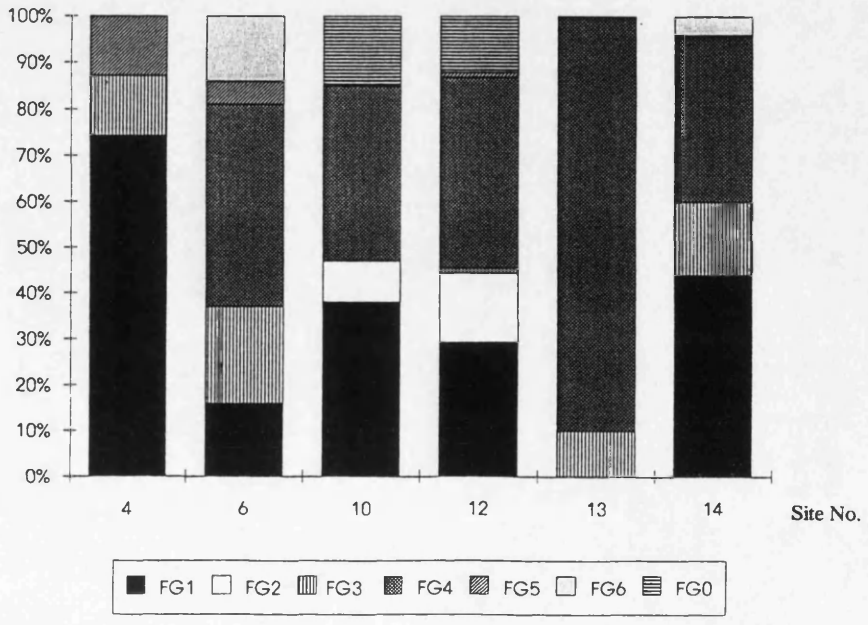


Fig 8.6f Functional vegetation type VI



8.2.2 Predicting Functional Vegetation Type from functional group composition

To develop predictive equations for categorising new sites into Functional Vegetation Types a linear discriminant analysis was used. The cross validation option was used as this gives a better indication of the predictive value of the analysis. The linear discriminant functions for each FVT are given in Table 8.7

Table 8.7 Linear discriminant functions for Functional Vegetation Types

FVT	I	II	III	IV	V	VI
Constant	-17852	-17897	-17674	-17756	-17846	-17279
FG1	34556	34611	34414	34481	34565	34084
FG2	35310	35376	35176	35219	35318	34741
FG3	35979	36013	35824	35907	36042	35395
FG4	35096	35149	34943	35006	35092	34587
FG5	35705	35709	35496	35560	35661	35073
FG6	35707	35827	35558	35607	35689	35122
FG0	35611	35660	35455	35569	35627	35033

Using the entire data set these equations achieved 100% success and with cross validation achieved 95% success. The sites that were misclassified were 11 **eksrr** (assigned to V instead of IV) and 33 **fappo** (assigned to II instead of III). Inspection of the DCA shows both these sites to be at the extreme edges of their groups in the ordination diagram. These equations are used in Chapter 9 to assign sites from an independent data set to Functional Vegetation Types.

8.3 Discussion

In contrast to the classification of sites achieved using species composition (Chapter 3), classification by functional group is relatively independent of geographical location (Table 8.8). Comparisons are also made in this table with den Hartog and Segal's (1964) classification that contained some functional characters (Table 8.8). The functional classification shows more similarities with this classification than with the classification based exclusively on species composition, although FVT III contains a variety of classes under both classifications. FVT III has a high proportion of sites from the Order Parvopotemetalia but other groups are also well represented. The comparison of FVT II is confused by the separation of layers of vegetation used by den Hartog and Segal. It seems that the functional classification presented in this work is more detailed than that of den Hartog and Segal, with for example, the alliance Callitricho-Batrachion apparent in a spread of FVTs, and is better suited to picking up differences between sites in a riverine wetland context.

Table 8.8
Comparison of functional and species based classifications

	Den Hartog and Segal 1964 (species-based)			Present study	
Site	Class	Order	Alliance	FVT	Species
ehbox	Potametea	Magnopotametalia	Nymphaeion albae	I	2
cemcb	Potametea	Magnopotametalia	Nymphaeion albae	I	5
ilbd3	Lemnetea	Lemnetalia		II	6
	Potametea	Parvopotametalia	Parvopotamion		
ilbd4	Lemnetea	Lemnetalia		II	6
	Potametea	Parvopotametalia	Callitricho - Batrachion		
icldo	Potametea	Parvopotametalia	Callitricho - Batrachion	II	6
fdcbw	Lemnatea	Ceratophylletea	Ceratophyllion	II	7
fapdi	Potametea	Parvopotametalia		II	7
	Lemnatea				
cimsr	Potametea	Parvopotametalia	Callitricho - Batrachion	III	1
cimwp	Potametea	Luronio-potametalia		III	1
cimox	Potametea	Magnopotametalia	Nymphaeion albae	III	2
ilbr	Potametea	Parvopotametalia		III	4
iclr	Potametea	Magnopotametalia		III	5
cemab	Potametea	Parvopotametalia	Callitricho - Batrachion	III	6
cemta	Potametea	Parvopotametalia		III	6
cemwa	Potametea	Parvopotametalia		III	6
cemrd	Potametea	Parvopotametalia		III	6
faoxa	Potametea			III	7
	Lemnatea	Ceratophylletea	Ceratophyllion		
faoxd	Potametea	Parvopotametalia		III	7
	Lemnatea	Ceratophylletea			
fapdo	Potametea	Parvopotametalia		III	7
	Lemnatea	Lemnatalia			
fappo	Potametea	Parvopotametalia		III	7
fmlbw	Lemnatea	Ceratophylletea	Ceratophyllion	III	7
eksrr	Potametea	Luronio-potametalia?		IV	1
smgr	Charatea	Charetalia	Charion	IV	8
smml1	Charatea	Charetalia	Charion	IV	8
smml3	Charatea	Charetalia	Charion	IV	8
cimrl	Potametea	Magnopotametalia		V	2
cimnl	Potametea	Magnopotametalia		V	2
cimid	Potametea	Parvopotametalia?		V	2
ilbd2	Charatea	Charetalia	Charion	V	3
cemgd	Potametea	Magnopotametalia		V	5
eksox	Potametea	Parvopotametalia	Callitricho - Batrachion	VI	2
eksrf	Potametea	Parvopotametalia	Callitricho - Batrachion	VI	4
eksrl	Potametea	Parvopotametalia	Callitricho - Batrachion	VI	4
ebmr	Potametea	Parvopotametalia	Callitricho - Batrachion	VI	4
ibipo	Potametea	Magnopotametalia	Magnopotamion	VI	5
ilbpo	Potametea	Parvopotametalia	Callitricho - Batrachion	VI	6
icldi	Potametea	Parvopotametalia	Callitricho - Batrachion	VI	6

The proportion of the functional group-environment relation explained by the first two axes of the CCA (64.7%) is much higher than the proportion of the species-environment relation explained by the first two CCA axes in Chapter 3 (30.2%). This shows the CCA diagram arising from analysis of functional groups (i.e. by reference to the species traits) is more useful in explaining variation attributable to the measured environmental variables, than a conventional sociological approach. The functional groups could be used to define well-separated Functional Vegetation Types, with distinct habitat preferences. An examination of Functional Vegetation Types with respect to average site stress index and average site disturbance index show FVT IV and FVT VI to occupy the most disturbed sites while FVT I and FVT V occupy the most stressed sites. Habitat preferences of the functional groups have been indicated but detailed discussion of habitat preferences of both FG's and FVT's will be postponed until the testing of the classifications is presented in Chapter 9.

The majority of FVTs are dominated by one functional group, with the exception of FVT III which is the most varied in functional group composition. This is also the FVT with the highest occurrence. As discussed in the review of strategy theory in Chapter 4, communities can contain species of widely differing strategy. While the functional groups have not been aligned to a particular Grime strategy, it does seem that some sites (e.g. members of FVT III) can contain a variety of strategies. This diversity of functional groups in many riverine wetland habitats is probably reflecting the varying pressures of C, S, and D present at these sites. These include diurnal, seasonal and spatial variations, all combining to result in a habitat where a wide variety of functional groups coexist. Seddon (1972) remarked that submerged species of comparable growth form occur rarely in the same lake. While sites of FVT III often conform to this pattern this is not always the case in the sites studied with, for example, *Ceratophyllum demersum* and *Utricularia vulgaris* in the Apremont oxbow (site 31; **faoxa**). Sites of other FVTs, with less diverse FG composition, are more likely to have species of similar growth form. Wiegleb and Brux (1991) found that for *Potamogeton* species, strategies, or individual plant traits, were not strictly correlated to a particular habitat condition (conceptualised as predictability and severeness of habitat). They considered that the same environmental pressure can be resisted by different traits. For example, herbivory can be resisted by terrestrial plants by molecular defences (e.g. production of poisons); morphological defences (e.g. spines; protected meristems) or physiological defences (e.g. incorporation of Si to 'harden' foliage). This also seems to be true for the selected species in this study. If this were not the case it would

seem likely that Functional Vegetation Types would all be composed exclusively of a single functional group. Furthermore, if there were a single optimum trait solution for any given environmental pressure, the obvious diversity of aquatic plant growth forms would not have evolved Analysis of the manner in which individual traits varied with environment would help to clarify this point.

In this study, Functional Vegetation Types have been defined from the representation of functional groups at a site. These FVT's are therefore based on the possession of the species attributes analysed in Chapter 4. In this study the entire community is used to assign the FVT, rather than a few dominant member species (Hills *et al.* 1994), which could be misleading particularly in communities such as FVT III where a variety of strategies appear to be present. Friedel *et al.* (1988) noted several advantages when using the relative proportions of functional groups to define conditions in arid rangelands:

a) using attributes to numerically define the functional groups eliminated variations in the way an ecologist may assign species to groups

b) it simplified complex species data sets down to ecologically sensible groups that were then more easily understood, particularly in the forum of vegetation change

c) the technique was robust enough for the workers scoring the attributes to be able to do so without a detailed knowledge of the species autecology.

These are important considerations for a useful assessment technique. Subjectivity is reduced by the numerical basis of the classification and data sets are clarified without loss of ecologically important information. However, unless morphological traits are found that are better indicators than those tested, the third statement cannot be supported for euhydrophytes on the present evidence. A sound knowledge of species autecology would seem to be the best basis on which to build a classification (Friedel *et al.* 1988), and the plasticity of aquatic plant morphology reduces the viability of morphological traits as indicators. When comparing their range assessment with a study of the same sites using full species data Foran *et al.* (1986) found very similar classes were assigned. This was not the case here perhaps due to the broad geographical range covered. Friedel *et al.* (1988), discussing the use of functional groups in assessing range condition, state *'Our ultimate purpose is to ensure that field data are sufficiently simplified that their implications are understood and applied in a practical management context.'* When assessing the approach it is important to keep in mind that the aim is to simplify the data and make it more clearly and readily understandable.

8.4 Summary

Functional groups can be used objectively to delimit Functional Vegetation Types, and new sites can be classified using a linear discriminant function.

These FVTs give a site classification that is not obscured by geographical location.

Functional groups (and Functional Vegetation Types) display recognisable habitat preferences.

In riverine wetland sites it is common to find a diverse representation of functional groups at a single site, due to the variable nature of the habitats in terms of C, S and D pressures.

Chapter 9

TESTING THE APPROACH IN AN INDEPENDENT SET OF FIELD SITES

Chapter 9

TESTING THE APPROACH IN AN INDEPENDENT SET OF FIELD SITES

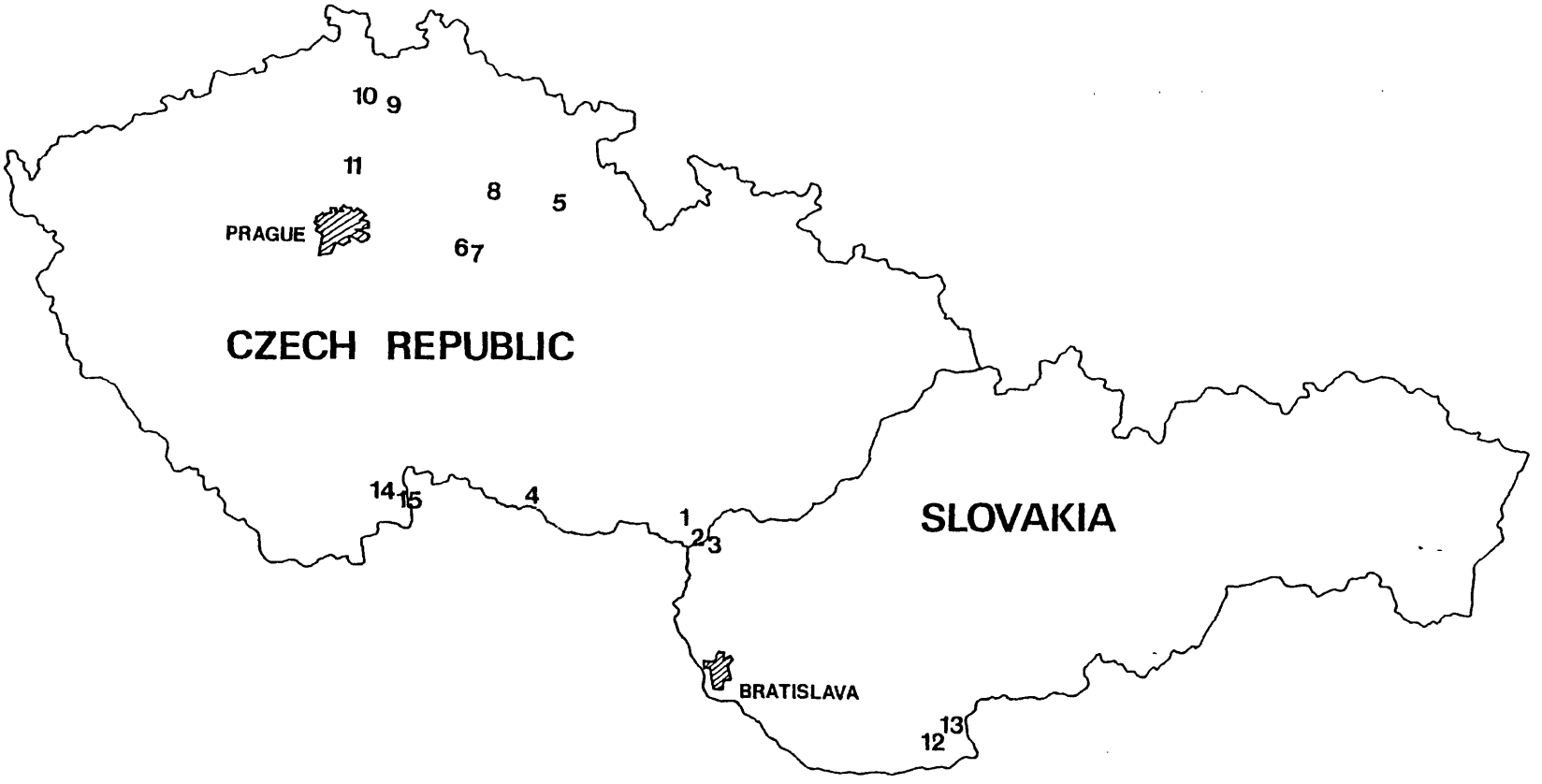
9.1 Introduction

To test the ideas generated in the preceding chapters an independent field data set was necessary. Links were established with the Institute of Hydrobotany, Czech Academy of Sciences, Trebon, Czech Republic. While many of the country's artificially created ponds have been given recognition by the Ramsar convention, the wetlands of the greatest biogeographical interest are the river flood plains, particularly those of South Moravia and the adjacent areas in south west Slovakia (IUCN 1993). East and North East Bohemia has the richest macrophytic vegetation of the region (Cernohous and Husák 1986) and this has been attributed to the diversity of water biotopes in this area. These areas are covered in the test data set, as well as other areas of lowland floodplain. An accelerated rate of eutrophication has been suggested as the cause for the documented loss of macrophytes in some Czech waterbodies (Dykyjova *et al.* 1985; Cernohous and Husák 1986). Eutrophication rates are particularly high in the densely stocked fishponds and rivers running through towns or close to centres of livestock production. Areas of low economic interest, such as upper reaches of rivers and old oxbows, are therefore important for conservation as most rare aquatic plant communities are now confined to these waterbodies (Cernohous and Husák 1986).

Fieldwork was undertaken in the Czech and Slovak Republics between May 24 and June 9 1994. The sites covered a range of waterbody types in riverine wetlands (Plates 22, 23 and 24), including the channels of large (River Dyje) and small (e.g. River Luznice) rivers, channellised rivers and brooks, oxbows and small ponds associated with the rivers and extensive wetlands associated with major rivers (the Pariske wetlands associated with the River Danube in Slovakia). The locations of the sites are shown in Fig 9.1 and listed in Table 9.2. 15 sites were visited but at site **cz2**, a large oxbow, two sets of data were collected as two distinct communities were present. Data were collected on community composition, environmental character and morphological traits.

Figure 9.1 Location of the test sites in the Czech and Slovak Republics.

Individual site descriptions are given in Table 9.2 where each site is given the prefix cz.



This chapter

- presents a brief phytosociological analysis of the communities present at each site.

- classifies species previously unrecorded in this project into functional groups by reference to traits from the published literature, using the linear discriminant function devised in Chapter 4.

- tests the efficiency of the field-measured morphological traits as descriptors of these groups.

- classifies the sites into Functional Vegetation Types on the basis of their functional group composition, using the linear discriminant function devised in Chapter 8.

- tests the relationship of FVTs and FGs to habitat conditions described in Chapter 8.

- constructs a more generally applicable model of FVT variation in response to selected environmental parameters in European riverine wetlands

9.2 Methods

9.2.1 Field survey

The field survey followed the same methodology as that outlined in Chapter 3. At each site the community composition was recorded (Appendix 8), environmental parameters measured (Appendix 7), water and sediment samples collected for further analysis in the laboratory, and plant samples collected for measurement of morphological traits (Appendix 9). The species that were chosen for measurement of morphological traits, included species that had been previously recorded and their morphological traits measured; species that had been previously recorded in this project but without morphological trait measurement; and species that had not been previously recorded (see Table 9.1). The traits measured were the same as those described in Chapter 4.

The environmental parameters measured (Appendix 7) were not identical to those in the 92/93 survey, due to problems in transporting equipment and samples. However all the parameters selected as key variables in Chapters 3 and 8, were recorded and methodology is as in Chapter 3. In addition total sediment C and N were measured, and levels of PO_4^{3-}, NO_3^-, NH_4^+ and NO_2^- in the water were quantified. Chemical analysis of water and sediment samples was carried out by the Institute of Hydrobotany at Trebon.

Plate 22: Site **cz14** with patches of *Ranunculus aquatilis*.

Plate 23: Site **cz3** dominated by *Nuphar lutea*.

Plate 24: Site **cz3** with *Lemna minor,* and *Spirodela polyrhiza* overlying *Potamogeton lucens* .

Table 9.1 Euhydrophyte species recorded in the Czech and Slovak Republics: showing species already recorded in the 92/93 field survey of FAEWE sites, and those which had morphological measurements taken in the 92/93 FAEWE survey and in the 94 Czech survey.

Species	Recorded 92/93	Morphological traits measured 92/93	Morphological traits measured 94
Callitriche cophocarpa			x
Callitriche hamulata	x	x	x
Ceratophyllum demersum	x	x	x
Chara spp	x		
Eleocharis acicularis	x		
Elodea canadensos	x	x	x
Fontinalis antipyretica	x		
Glyceria fluitans	x		
Hottonia palustris	x		x
Hydrocharis morsus-ranae	x	x	x
Juncus bulbosus	x		x
Lemna minor	x	x	
Lemna polyrhiza	x		
Lemna triscula	x		
Nymphaea alba	x	x	
Nuphar lutea	x	x	x
Oenanthe aquatica			
Potamogeton alpinus			x
Potamogeton crispus	x	x	
Potamogeton lucens	x	x	x
Potamogeton trichoides	x		x
Ranunculus aquatilis	x		x
Ranunculus circinatus	x	x	x
Ranunculus fluitans			x
Ranunculus penicillatus	x	x	x
Sagittaria sagittifolia	x		x
Sparganium emersum	x	x	x
Stratiotes aloides			x
Utricularia australis			x
Utricularia vulgaris	x	x	x
Zannichellia palustris	x	x	x

Plate 25: *Potamogeton alpinus* and *Utricularia australis* at site **cz5**.

Plate 26: *Lemna minor* mat with *Utricularia vulgaris* flowers at site **cz13.**

9.3 Data Analysis

9.3.1 Phytosociological analysis

The species composition was assigned to an NVC and CORINE community type using the TABLEFIT programme as in Chapter 3. The same problems, outlined previously, apply in using this programme with a European data set. The site codes, descriptions and NVC and CORINE classifications are given in Table 9.2.

Table 9.2 Czech and Slovak field sites with habitat descriptions and vegetation classifications.

Code	Description	NVC type	CORINE type
cz1	shady oxbow, R. Dyje, nr Ladná	A8 Nuphar lutea	C22.4311 Waterlily carpets
cz2	1st oxbow, R. Morava, nr Tvrdonice	A4 Hydrocharis- Stratiotes	C22.413 Water soldier rafts
cz2b	1st oxbow, R. Morava river, nr Tvrdonice	A5 Ceratophyllum demersum	C22.422 Small pondweed communities
cz3	2nd oxbow, R. Morava river, nr Tvrdonice	A5a Ceratophyllum demersum- Ranunculus circinatus (poor)	C22.421 Large pondweed beds
cz4	R. Dyje main channel, riffle reach, nr Vranhov n. Dyji	A18 Ranunculus fluitans	C24.44 Eutrophic river vegetation
cz5	shallow shaded pond, R. Orlice, nr Belec	A24 Juncus bulbosus	C22.45 Peatmoss-bladderwort bog pools
cz6	oxbow, Špackova jerezo, R. Labe, nr St Kolín	A8 Nuphar lutea	C22.4311 Waterlily carpets
cz7	oxbow, Špackova jerezo, R. Labe, nr St Kolín	A8c Nuphar lutea - Nymphaea alba	C22.4311 Waterlily carpets
cz8	R. Cidlina, shallow brook, nr Cerneves	A8 Nuphar lutea	C24.4 Submerged river vegetation?
cz9	Panenský brook, riffle reach,nr Mimon	A17 Ranunculus penicillatus	C24.4 Submerged river vegetation?
cz10	still sidewater, R. Ploucnice, nr Melník	A15 Elodea canadensis	C22.422 Small pondweed communities
cz11	R. Pšovka (channellised), nr Melník	A8b N. lutea - Cal stag - Zan pal (poor)	C24.44 Eutrophic river vegetation
cz12	drainage channel, Parízske mociare, nr Gbelce, SK	A2b Lemna minor + A11 P. pectinatus-M.spicatum?	C22.411 Duckweed covers + C22.422 Small pondweed communities
cz13	Paríz brook, Parízske mociare, nr Gbelce, SK	A4 Hydrocharis morsus-ranae- Stratiotes aloides	C22.414 Bladderwort colonies+ C22.411 Duckweed covers
cz14	oxbow, R. Luznice, nr Halámky	A19 Ranunculus aquatilis	C22.432 Shallow water floating communities
cz15	river channel, R. Luznice, nr Tušt	A19 Ranunculus aquatilis (poor)	C24.4 Submerged river vegetation

A spread of community types was apparent. As this chapter is designed to test the functional approach, a classification of the Czech sites by species will not be presented. However, from the results of Chapter 3, it would seem reasonable to assume that a classification would group species of a similar NVC type together (for example the subcommunities of A8 would be in one class, as would be those of A5). It should be noted here, as a warning for future classifications of aquatic communities, that two problems arose persistently, here and in Chapter 3 with respect to the use of the NVC. 1) Problems in assigning NVC categories where *Lemna* mats overlay a well established submerged community. Although the NVC allows for a submerged community under *Lemna* mats (classes A2 and A4), it seems that where this is well developed, the submerged communities are undervalued in the NVC description. 2) Cross referencing NVC and CORINE classes needs care, especially when using the TABLEFIT programme. Many communities from streams and rivers are cross referenced to a C22 community (standing water); this is a problem associated with cross referencing a vegetation based system (NVC) with a habitats (or biotopes) system (CORINE) as many vegetation types can occur in more than one type of habitat, just as one biotope may contain several different vegetation classes.

9.3.2 Classifying Previously Unrecorded Species

There were 6 new species in the Czech data set that had not been previously encountered; *Callitriche cophocarpa, Oenanthe aquatica, Potamogeton alpinus* (Plate 26), *Ranunculus fluitans, Stratiotes aloides* and *Utricularia australis*. These, therefore, required classifying, by their established phase traits (taken from the literature), into functional groups. The traits for these species are shown in Appendix 5. The linear discriminant functions derived in Chapter 4 (Table 4.6) were used to place the species into groups. The function that gives the minimum score is the assigned group. With cross validation these functions had given an 89% success rate on the 92/93 data set (Chapter 4). The calculations were done using MINITAB, Release 9. All species were classified with 100% probability, implying that there were no borderline cases, but that the species clearly conformed to a particular group. The classification results were as follows:

C. cophocarpa	Functional group 4
O. aquatica	Functional group 4
P. alpinus	Functional group 3
R. fluitans	Functional group 1
S. aloides	Functional group 6

U. australis Functional group 2

All species surveyed were now assigned to one of the seven functional groups defined in Chapter 4.

9.3.3 Testing the use of morphological traits as descriptors of functional group.
The efficacy of field measured morphological traits as descriptors of these groups can now be tested. The linear discriminant function derived in Table 4.7 was used to classify the species. This used a subset of the morphological traits. This achieved 76% success when used on the 92/93 dataset with cross-validation. The classification of the Czech species from these functions and their true groups are shown in Table 9.3. This classification correctly assigned 57% of the species to their functional groups. Of the misclassified species 2 were also misclassified in Chapter 4. These were *E. canadensis,* which was incorrectly assigned to FG 4 in Chapter 4, and *P. lucens,* which was incorrectly assigned to FG 5. These may be species that are borderline between functional groups and, therefore, more prone to being misclassified. Of the remaining seven misclassified species, two (*R. circinatus* and *Z. palustris*) had previously been correctly classified (4.3.3) using morphological traits. The other five had not been classified before using morphological traits. Looking at the position of the misclassified species on the PCA of species published traits (Fig 4.2) helps to explain some of the misclassifications. Both *E. canadensis* and *J. bulbosus* are at the extreme left hand side of group 2, close to group 4. However, it is surprising that *Z. palustris* and *U. vulgaris* were misclassified into Group 4 as they are to the right of Group 2. *H. palustris* and *R. circinatus* are also at the extremity of Group 1, close to Group 2. The misclassification of *P. lucens* and *S. sagittifolia* is surprising in the context of this diagram. *P. alpinus* was not recorded in the 92/93 survey and, therefore, not included in the PCA.

Table 9.3 Classification of species which had morphological traits measured using the linear discriminant function derived in Chapter 4. Misclassified species are marked *.

Species	Misclassified	Predicted group	True group
Callitriche cophocarpa		4	4
Callitriche hamulata		4	4
Ceratophyllum demersum		2	2
Elodea canadensis	*	4	2
Hottonia palustris	*	2	1
Hydrocharis morsus-ranae		6	6
Juncus bulbosus	*	4	2
Nuphar lutea		5	5
Potamogeton alpinus	*	4	3
Potamogeton lucens	*	1	3
Potamogeton trichoides		2	2
Ranunculus aquatilis		1	1
Ranunculus circinatus	*	2	1
Ranunculus fluitans		1	1
Ranunculus penicillatus		1	1
Sagittaria sagittifoia	*	4	5
Sparganium emersum		3	3
Stratiotes aloides		6	6
Utricularia australis	*	4	2
Utricularia vulgaris		2	2
Zannichellia palustris	*	4	2

9.3.4 Defining Functional Vegetation Types for the Czech and Slovak sites.

The data could now be used to group the sites into Functional Vegetation Types using the proportions of functional groups at each site (Table 9.4). The linear discriminant equation devised in 8.2.2 can be used for this purpose and the results are given in the final column of Table 9.4. These equations had given 95% correct classifications using cross validation on the 92/93 data set. The classification could be verified to some extent by overlaying a DCA ordination of site scores (derived from their functional group composition) with the FVTs (Fig 9.2). This shows clear separation of the FVTs. The first axis strongly discriminates between FVT IV and the other FVTs. This is similar to Fig 8.2 showing the DCA ordination for the 92/93 data. In both diagrams FVT V is at the top of Axis 2 and the remaining groups are distinguished along Axis 2. The analysis summary (Table 9.5) shows that Axis 1 has a much higher eigenvalue than Axis 2 and contains almost twice the percentage variance of the FG data. FVT VI is not very coherent in the test data. Site **cz11** is

possibly a borderline member of this FVT showing similarities to groups V and II. Its relationship to the environmental parameters may serve to clarify its type. The functional classification does not separate the sites in the same manner as might have been expected from a community composition classification; for example **cz14** and **cz15**, both A19 communities, are from different FVTs and **cz6** and **cz7**, both A8 communities, are also from different FVTs. This is in accordance with the comparisons made in Table 8.8 showing a poor relationship between classifications based on species composition and those based on functional characters.

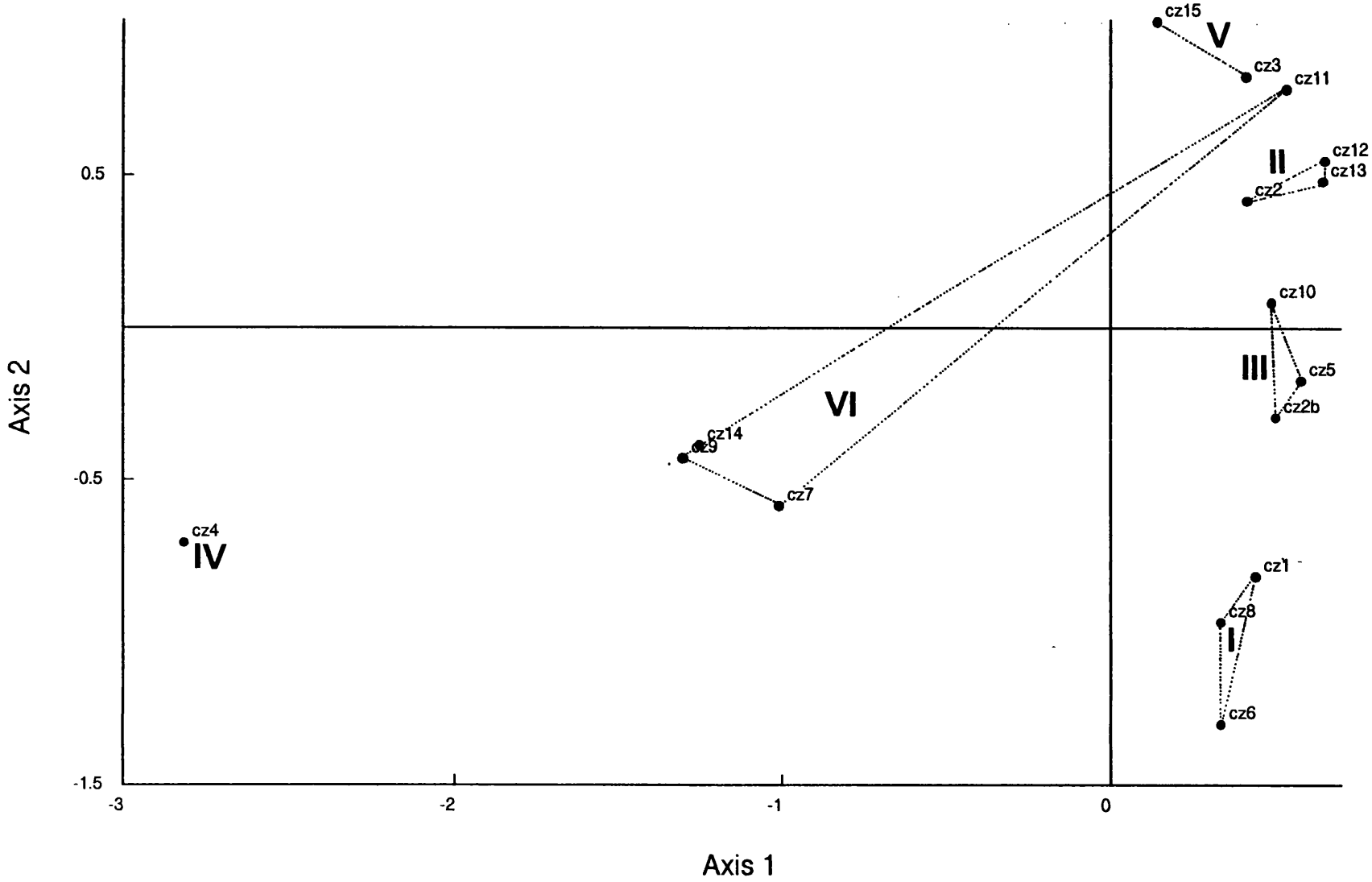
Table 9.4 Proportions of Functional groups at each site

Site	FG1	FG2	FG3	FG4	FG5	FG6	FG0	Predicted FVT
cz1	0	32	0	1	61	6	0	1
cz2	12	24	0	0	0	64	0	2
cz2b	5	95	0	0	0	0	0	3
cz3	5	6	47	0	0	42	0	5
cz4	5	0	0	0	0	0	95	4
cz5	0	92	7	1	0	0	0	3
cz6	0	0	0	0	100	0	0	1
cz7	82	0	0	0	18	0	0	6
cz8	0	0	14	0	86	0	0	1
cz9	100	0	0	0	0	0	0	6
cz10	0	71	15	5	0	7	2	3
cz11	0	42	5	53	0	0	0	6
cz12	0	26	0	0	0	74	0	2
cz13	0	30	0	1	0	69	0	2
cz14	97	0	3	0	0	0	0	6
cz15	15	0	57	28	0	0	0	5

Table 9.5 DCA summary

Axes	1	2	3	4	Total inertia
Eigenvalues	0.929	0.576	0.188	0.027	3.489
Lengths of Gradient	3.469	2.297	2.028	2.276	
Species-environment correlations	1.000	0.976	0.986	0.967	
Cumulative percentage variance					
of species data	26.6	43.2	48.5	49.3	
of species-environment relation	31.6	45.8	0	0	
Sum of unconstrained eigenvalues					3.489
Sum of canonical eigenvalues					3.021

Fig 9.2 DCA ordination of Czech and Slovakian sites using functional group composition. Functional vegetation types delineated by dotted lines. (For site codes see Table 9.2)



9.3.5 Testing hypotheses of FVT and functional group relationships to environmental parameters.

A canonical correspondence analysis was carried out using functional group composition and the environmental variables measured. It is not possible to analyse the dataset including the full range of environmental variables because the number of sites is much lower. To run a canonical correspondence analysis the number of sites must be greater than the number of species (functional groups) + the number of environmental variables + 1. So, in this case, no more than 7 environmental variables can be used. Using the highest possible number of variables can lead to instability in the analysis. The environmental variables that were having the most influence on functional group composition in Chapter 8 were flow, conductivity, drought period, substrate light level and light extinction coefficient. Drought period has not been quantified for the Czech sites as data were unavailable, so the remaining four variables were used for the canonical analysis.

An initial run showed the substrate light level for **cz10** to be having a high influence on the analysis, so this site was omitted. The CCA biplot is shown in Fig. 9.3. The analysis summary is given in Table 9.6. A comparison with the CCA diagram showing the relationship between functional group composition and environment for 92/93 data (Figs 8.3 and 8.4) show the FVTs to be placed in extremely similar positions in both cases. This simplifies comparison of the effects of the environmental variables on FVT as direction and magnitude of environmental arrows can be compared directly between diagrams. Substrate light levels and light extinction coefficient are having a similar influence on both sets of sites. The influence of flow was similar along Axis 1 but in the opposite direction along Axis 2. Conductivity was in the opposite direction along Axis 1 and the same direction along Axis 2. Axis 1 contains 50.1% of the variance of the species environment relation while Axis 2 contains 30.5%.

Conductivity is the only variable that is acting differently from expected along Axis 1. However it is also the variable with the lowest correlation to the axis (Table 9.7), so it will not be greatly influencing the distribution of functional groups. The difference in response of FVTs to conductivity between the two data sets is almost certainly attributable to the extreme effect which the Spanish sites have in the 92/93 analysis. None of the sites encountered in the Czech or Slovak Republics have such elevated conductivity levels. The relationship between conductivity and FVT demonstrated by the Czech and Slovak data sets is probably more representative of

that existing in European riverine ecosystems than the hypothesis generated by the FAEWE dataset. The correlation of flow with Axis 2 is also quite low (-0.261) and so its influence on FVT distribution along this axis is low.

A high proportion of the species-environment relation was explained by the displayed axes (80.6%). This relationship only accounts for the measured environmental parameters. Comparison of the unconstrained and the canonical eigenvalues shows that the four environmental variables used are explaining over one third of the total variation in the functional group data. In Fig 8.4 about two thirds of the variation is explained by all the environmental parameters, so it seems that reducing the environmental variables to four key variables results in a large loss in explained variation. This implies that while the four variables selected are the key variables in these systems a lot of variation is still explained by other environmental parameters (e.g. depth).

The same diagrams can be used to compare the position of functional group and environmental gradients. The inferred rankings (Table 9.8) can be compared with those in Table 8.6. The substrate light and extinction coefficient rankings compare well between the two analyses. FG6 can tolerate low substrate light conditions in turbid water, while FG0 requires a high level of radiation at the substrate. FG 3 and FG4 are intermediate for both parameters. FG5 appears in the intermediate range of all the parameters. Conductivity shows a different pattern in the two surveys, again due to the influence of the Spanish wetlands in 92/93. FG0 (algae and mosses) is at the top in Table 8.6. In the Czech sites these plants tended to the lower conductivity sites. In both cases FG6 preferred still sites while FG4 and FG0 were in faster flowing systems. In the Czech survey FG1 plants were located in stiller waters than in the FAEWE survey, and FG5 plants in faster flowing waters than previously recorded.

Table 9.6 CCA summary

Axes	1	2	3	4	Total inertia
Eigenvalues	0.679	0.415	0.225	0.038	3.562
Species-environment correlations	0.906	0.790	0.742	0.326	
Cumulative percentage variance					
of species data	19.1	30.7	37.0	38.1	
of species-environment relation	50.1	80.6	97.2	100.0	
Sum of unconstrained eigenvalues					3.652
Sum of canonical eigenvalues					1.357

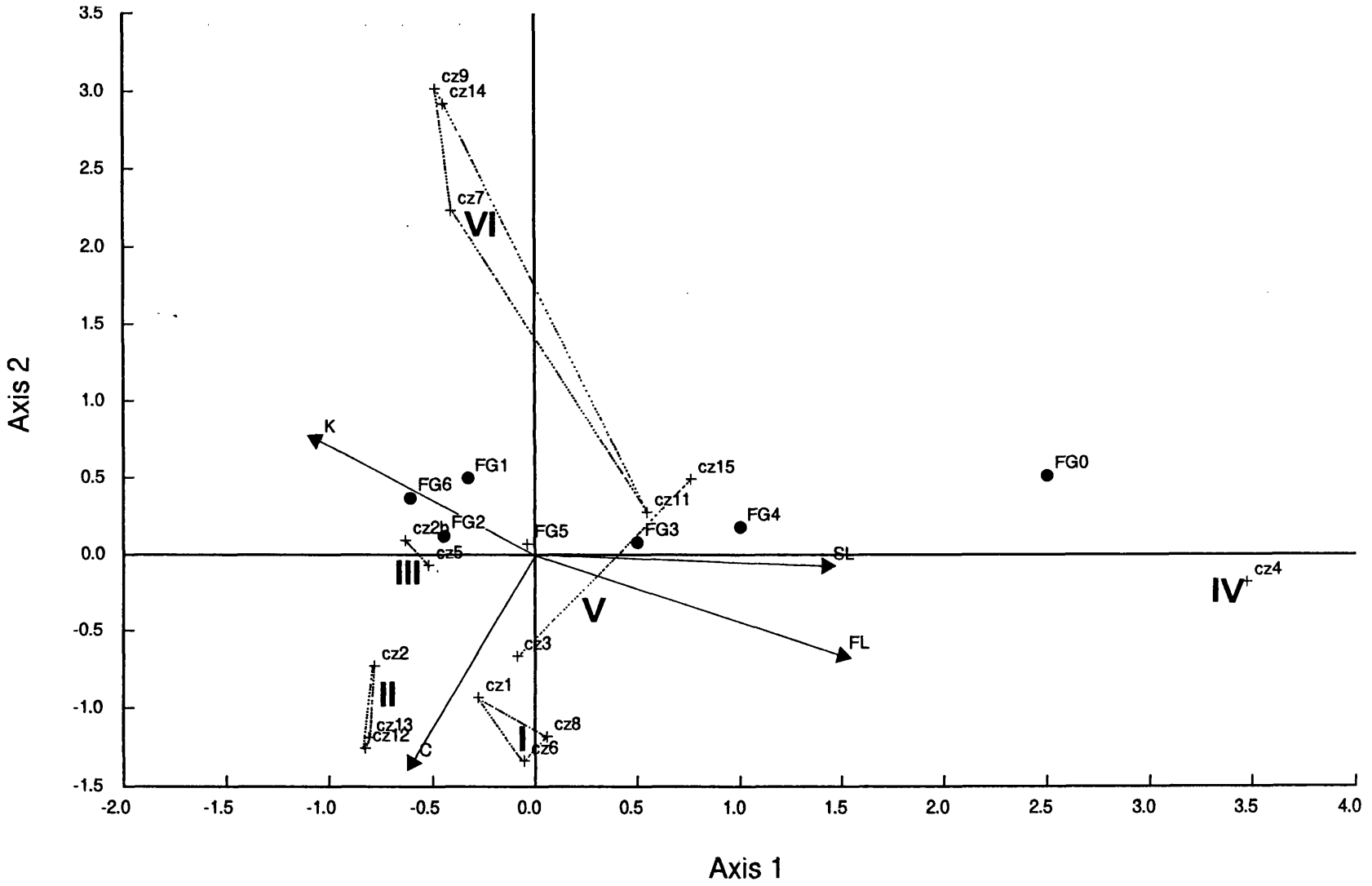
Table 9.7 Intraset correlations of environmental variable with axis (exploratory significance shown as ** $p < 0.05$ * $p < 0.01$. See section 3.3.2.for an explanation of these values)

Parameter	Axis 1		Axis2	
Flow	0.677	**	-0.261	*
Substrate light	0.646		-0.290	*
Conductivity	-0.273	**	-0.533	
Extinction coefficient	-0.480		0.298	*

Table 9.8 Inferred rankings of functional groups with environmental gradients (in descending order)

Flow	Conductivity	Substrate light	Extinction coefficient
FG0	FG2	FG0	FG6
FG4	FG6	FG4	FG1
FG3	FG5	FG3	FG2
FG5	FG1	FG5	FG5
FG2	FG3	FG1	FG3
FG1	FG4	FG2	FG4
FG6	FG0	FG6	FG0

Fig 9.3 CCA biplot of Czech and Slovakian sites showing functional group scores (filled circles), site scores (see Table 9.2) and environmental variables (arrows).



9.4 Improved Analysis of European Riverine Wetlands

The hypotheses from the FAEWE data of functional group variation with environment are consolidated by the Czech and Slovak data. Along the major axis of variation only conductivity does not show a consistent pattern. However all the data can be combined to give improved hypotheses that will be more applicable to European riverine wetlands.

DCA of the whole data set still shows good separation of the six FVTs especially along Axis 1 (Fig 9.4) with FVT I and IV very distinct. Some overlap occurs between the remaining types but they still show quite coherent grouping on the ordination. FVTs V, III and VI show the greatest variation over the first two axes which indicates a wider ecological amplitude for these types.

In the Spanish wetlands the degree of drought experienced is severe, with no water in the laguna for several months; no other sites experience this class of droughting. The conductivity of these sites is also considerably greater than any other, and the light extinction coefficient is low. The CCA was run without the Spanish sites as these compress the ordination due to the extreme nature of these variables. While these sites are recognised as a type of riverine wetland community to be found in Europe, and should therefore be included in the analysis, it was felt that omission of these sites would produce a model more applicable to the majority of European riverine wetland systems (i.e. those in the NW and central part of the region). As the Spanish sites are so different (both in terms of habitat conditions and floristic composition) from any of the other sites in the project and are influencing the analysis so heavily, either a larger number of sites from this type of wetland should be included, or some sites representing wetlands intermediate in, for example, drought period and conductivity, should included. This would give a more robust model. Sites **ilbpo** and **cz10** were also omitted as they were having extreme influence through single variables. Only environmental variables that the two surveys had in common could be utilised. This distilled the total environmental variable list down to eight variables; depth, conductivity, percentage saturation dissolved oxygen, pH, orthophosphate, light extinction coefficient, flow and substrate light. A CCA biplot shows these variables and the functional group scores (Fig 9.5). The summary table (Table 9.9) shows that these explain a low proportion (just over one quarter) of the total variation in the functional group data. However a Monte-Carlo test using the trace statistic shows that this is a significant proportion ($p = 0.05$).

Table 9.9 CCA summary (Analysis of full data set)

Axes	1	2	3	4	Total inertia
Eigenvalues	0.346	0.151	0.099	0.066	2.525
Species-environment correlations	0.781	0.637	0.489	0.431	
Cumulative percentage variance					
of species data	13.7	19.7	23.6	26.2	
of species-environment relation	51.0	73.3	87.9	97.7	
Sum of unconstrained eigenvalues					2.525
Sum of canonical eigenvalues					0.677

Table 9.10 Intraset correlations of environmental variables with axis (exploratory significance shown as ** $p < 0.05$ * $p < 0.01$. See section 3.3.2.for an explanation of these values)

Parameter	Axis 1		Axis 2	
% saturation dissolved oxygen	0.547	*	-0.242	
Flow	0.531	**	0.109	*
Substrate light	0.523	**	-0.023	
pH	-0.103		-0.369	**
Depth	-0.224		0.025	
Conductivity	-0.248		0.020	**
Dissolved orthophosphate	-0.300		-0.003	
Light extinction coefficient	-0.395		0.042	

Examination of the intraset correlations (Table 9.10) shows dissolved oxygen saturation level, flow and substrate light are all positively correlated with Axis 1. Significance levels are only exploratory as explained in 3.3.2. On Axis 2 flow is positively correlated and pH is negatively correlated; conductivity is almost uncorrelated with this axis. It seems surprising that flow and substrate light are showing similar influences along axis 1, but this is maybe due to the shallow water depth in many of the fast flowing riffle reaches of low turbidity river channels that were sampled. Much of the species environment relation is contained in the first axis (51%) as is obvious from the ordination. The functional vegetation types show a gradual change along this axis:

FVT II → FVT I and III → FVT V and VI → FVT IV

Functional groups are spaced out along this axis implying habitat preferences of these groups indicated by this axis:

FG6 → FG5 → FG2 → FG1 → FG3 → FG4 → FG0

Inferred rankings of functional groups along selected variables are given in Table 9.11. As so much of the variation attributable to the measured variables is contained in this axis these rankings correspond closely to the ranking along axis one, or to the inverse of it.

Table 9.11 Inferred rankings (full data set) in descending order

Flow and dissolved oxygen	**Substrate light level**	**pH and conductivity**
FG0	FG0	FG6
FG4	FG1	FG5
FG1	FG4	FG2
FG3	FG3	FG3
FG2	FG2	FG1
FG5	FG5	FG4
FG6	FG6	FG0

Fig 9.4 DCA ordination of 1992/1993 sites and Czech and Slovakian sites using functional group composition. Functional vegetation types delineated by dotted lines. Individual sites not labelled.

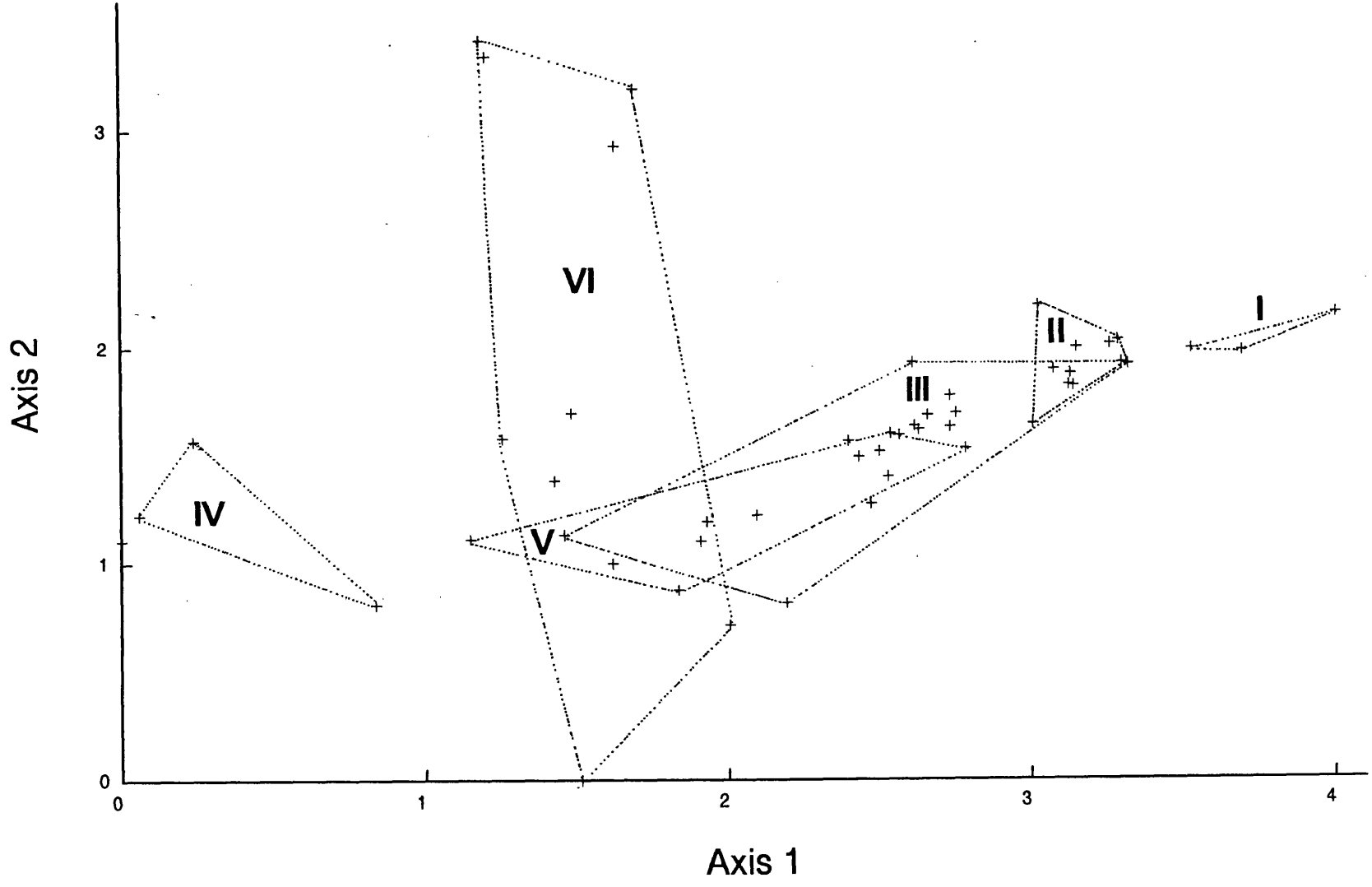
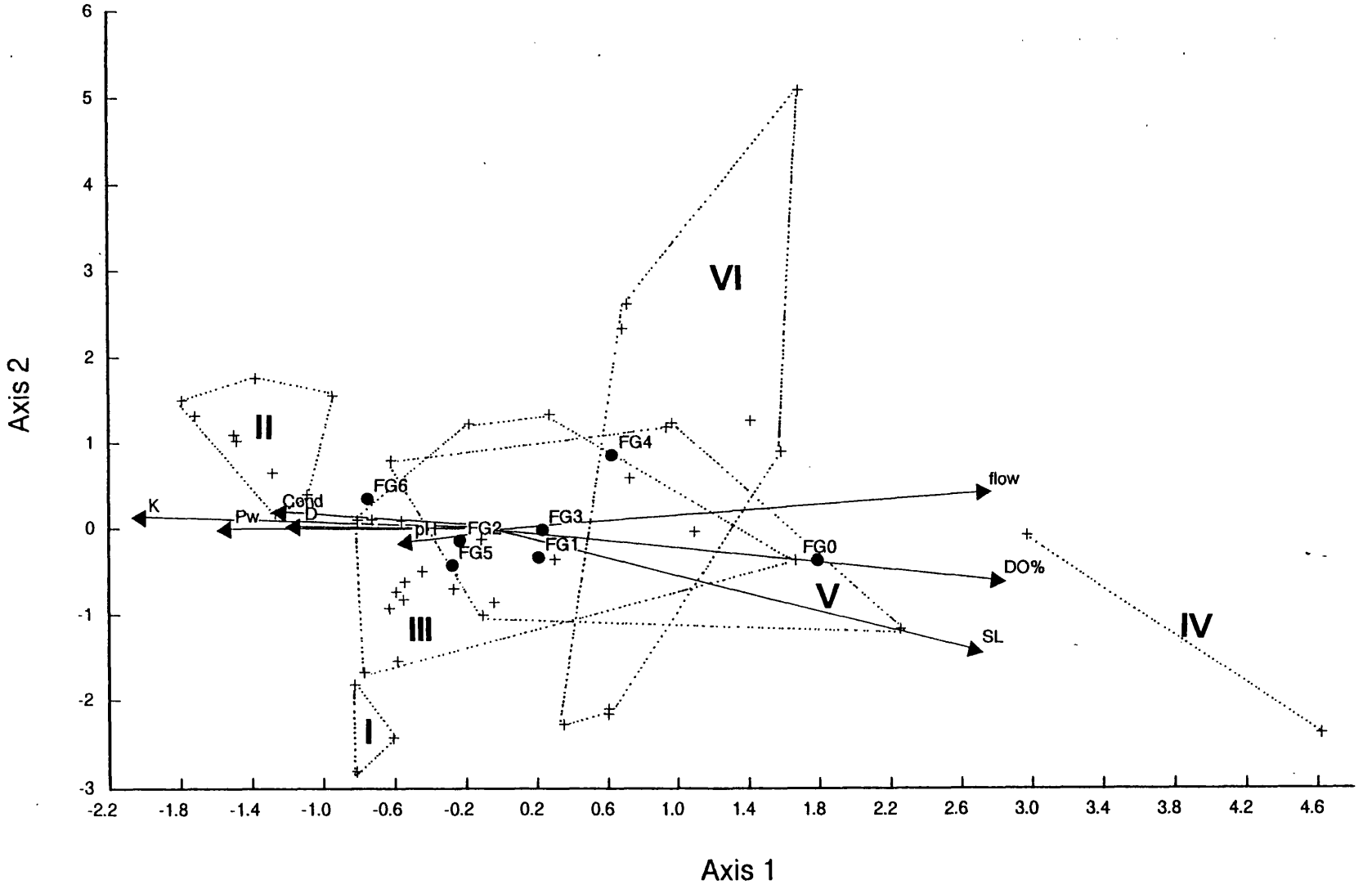


Fig 9.5 CCA biplot of all sites (1992/1993 and Czech/Slovak sites) except Spanish, showing functional group scores (filled circles), site scores (not individually labelled) and environmental variables (arrows). Functional vegetation types delineated by dotted lines.



9.5 Discussion

9.5.1 Published traits and field measured traits as group descriptors.

The field measured traits were successful descriptors for some group members, but misclassified many borderline species. The low percentage success on a test data set precludes the use of these traits as a method of assigning species to functional group. Although it had been recognised that using the field measured traits alone excluded many important aspects of the species autecology, it was hoped that they would reflect underlying characters. This does not appear to be the case in euhydrophytes, however, probably largely due to their plasticity of morphology.

The subset of published traits used were adequate to classify new species correctly. This subset contained all morphological characters (growth form, stem architecture, plant height, leaf area, leaf type, below:above ground biomass), but, in contrast to the field traits, seemed to be reflecting better the whole suite of traits that had been used to classify the species. The wide categories employed to assign these traits may also be more appropriate to the species set than continuous data, by allowing for quite a wide degree of plasticity within one category. This data could easily be collected in the field, thus giving the basis for collection of field data at a functional level. However, the warnings that have been made earlier, about the wisdom of doing this without collection of other data until the methodology has been refined, should be kept in mind.

9.5.2 The relationship of functional groups and Functional Vegetation Types to habitat conditions

This work, in contrast to other published works concerning the description of communities by species attributes (Murphy *et al.* 1990; Hills *et al.* 1994) has made no initial assumptions about species strategy or the functional significance of certain traits. The functional interpretation of the classification is reserved until these last stages. Other analyses of terrestrial vegetation have favoured this approach (Shipley *et al.* 1989; Leishman and Westoby 1992) and while it has been criticised for having no environmental information implicit in the analysis (Hills *et al.* 1994) the advantages are that it does not carry over assumptions from previous studies, which can be particularly dangerous where the assumptions are based on limited geographical spread and limited species groups (e.g. Grime *et al.* 1988).

The functional groups show better resilience of relationship to habitat conditions than the FVTs, when the two data sets are combined. This indicates that the Functional Vegetation Types defined are probably not robust enough for prediction purposes. FVTs, however, were not redefined using the combined data set, which may give a better typing. This would not be possible to test with the data available, so it has not been attempted. However, predictions can be made in shifts of dominance of functional group with environmental change, which is essentially what FVT changes reflect. Areas intermediate in character along axis 1 will have a Functional Vegetation Type of mixed composition, while extremes will show dominance of particular functional groups.

Table 9.12 shows the functional groups, their characteristic traits and their habitat preferences. This can only include the variables common to the two surveys. It is difficult to pick out a strong pattern from this table although some traits are associated with particular habitat characters (for instance rigid leaves occur in slow or still water). There are several possible explanations for this lack of strong pattern:

1) An environmental pressure can be resisted by more than one trait (Wiegleb and Brux 1991).

2) Trait functions, rather than the actual mechanism, may be correlated with habitat conditions, as has been demonstrated for regenerative traits (Grace 1993).

3) The traits are related to some environmental variable other than that included in this analysis (e.g. sediment nutrients; water level fluctuations; drought duration).

4) Gaps in the data for species traits (i.e. where a species is assigned a score of 1 for a trait) are obscuring trends.

Other studies of macrophytes have uncovered clearer correlations of species traits with environment. Bilby (1977) found plant exposed to strong currents possessing smaller leaves, shorter petioles, shorter internodes and producing fewer floating leaves. Bornette *et al.* (1994) showed that macrophyte species distribution in the Upper Rhône floodplain could be explained by species traits. While the system studied contains habitats comparable to those from which my data was drawn, the authors included the full range of species present (emergents, bank species, submerged and floating plants). A correspondingly wider array of growth forms seems, perhaps not surprisingly, to have enabled them to correlate traits with habitat conditions. This is the only comparable study of riverine euhydrophyte species strategies and does not succeed in separating habitat preferences of euhydrophytes

in terms of traits. Studies of individual traits may show more success, and these individual studies may gradually uncover suites of traits that can be recognisable in the field. With the current, incomplete state of knowledge of species traits only broad predictions can be made. Rørslett (1984), for example, found that larger water level fluctuations in lake systems favoured r - strategists over K strategists, but quantification of the trait-environment relationship was not attempted. Chambers (1987) found that along gradients of increasing sediment fertility the proportion of total aquatic plant biomass contributed by canopy producers/erect plants increased and rosette and bottom dwellers decreased. These correspond to the S strategy assigned to aquatic macrophytes by Kautsky (1988).

Table 9.12 Functional groups and their characteristic traits and habitat preferences. Traits shown are possessed by at least 75% of group members, except those in parentheses which are possessed by at least 50% of members.

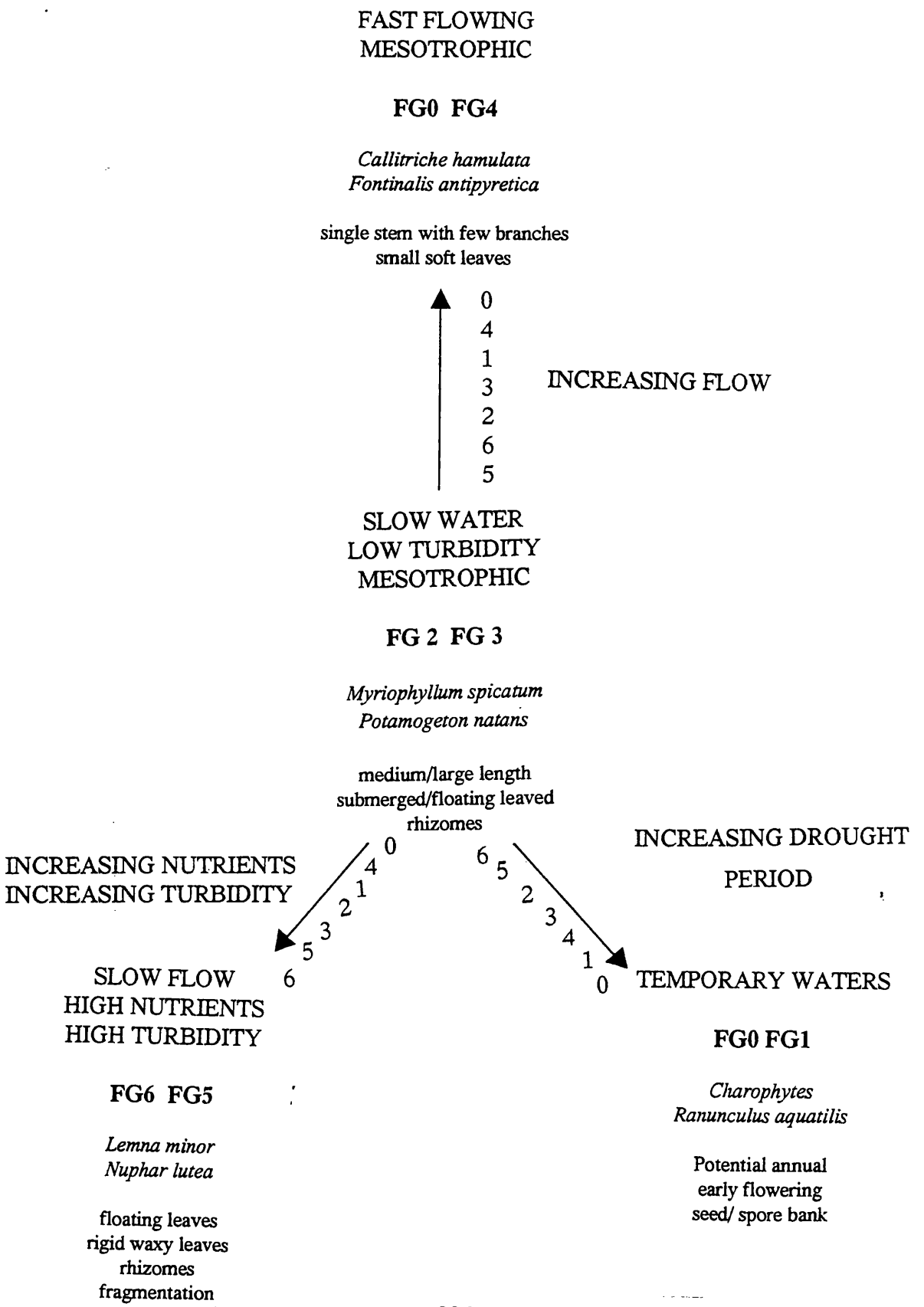
Functional Group	Established phase	Regenerative phase	Habitat preference
1	plant height (medium) large submerged rooted with/ without floating leaves soft, medium sized leaves single stem, many branches insect pollinated flowers early flowering (potential annual) (canopy former)	buoyant seeds medium/large seeds (transient seed bank)	moderate to fast flow low turbidity meso-oligotrophic moderately shallow sites
2	submerged rooted small (soft) leaves single stem, many branches medium/large plant height (late flowering) (wind pollinated) (HCO3 user)	(rhizomes) (turions) (seed production moderate) (buoyant seeds)	moderate flow tolerant of some turbidity meso-eutrophic
3	submerged and floating leaved wind pollinated single stem, few branches large plant height medium (large) leaves (vigorous seed production) (canopy former)	rhizomes buoyant seeds medium large seeds	moderate flow tolerant of some turbidity mesotrophic moderate depth
4	amphibious submerged and floating leaved heterophyllous medium plant height small, soft leaves long flowering period single stem, few branches (wintergreen) (wind pollinated)	fragmentation stolons low/medium seed production persistent seeds medium size seeds	moderate to fast flow meso-oligotrophic low turbidity shallow to medium depth
5	submerged/floating leaves large, rigid, waxy leaves large plant height multiple stems arising from base canopy former insect pollinated (below:above ground biomass high) (vigorous seed production) (large lateral spread)	rhizomes transient seed bank seed production moderate/high	moderate to slow flow meso-eutrophic tolerates high turbidity medium to deep sites
6	free floating small plants small, rigid (waxy) leaves (canopy former)	fragmentation no/low seed production	slow to still flow eutrophic tolerates high turbidity medium to deep sites

9.5.3 *Predictions of Functional Vegetation Type with changes in habitat conditions.*

The use of functional groups in some sort of predictive, rather than merely descriptive, way has been examined in various vegetation types (e.g. Day *et al.* 1988; Moore and Noble 1990; Duarte and Roff 1991). A description of principles involved in using plant attributes in a widely applicable, predictive way is given in Noble and Slatyer (1980). This hinges on the use of 'vital attributes' to predict replacement sequences following a disturbance. Day *et al.*(1988) used TWINSPAN to give five wetland vegetation types, which were then described in functional terms. These were superimposed on a DCA ordination with the axes related to environmental variables using canonical redundancy analysis. While the model successfully arranged the vegetation types showing the main 'structuring forces', it is still based in taxonomy, rather than offering an attribute based classification of the functional groups. Moore and Noble (1990) produced a model for terrestrial vegetation dynamics using functional groups to simplify vegetation description and the parameters used in the model were functional attributes. These successful attempts in other vegetation types, make it a reasonable hope that, with improved trait knowledge, a similarly useful result could be obtained for freshwater macrophytes. With the present results only a simple model can be postulated which, if nothing else, demonstrates the way forward, and gives a basis for refinement or rejection.

The relationships of functional group (and associated traits) to environment variables observed for this data set can be used to predict likely vegetation shifts with changes in certain environmental parameters (Fig 9.6). This is based on the data of Chapter 8 and 9, to be able to include data on drought periods. It is difficult to represent more than two factors in two dimensional space (hence the need for CANOCO ordinations), but this diagram serves to give an overview of the findings of the last two chapters. With descriptions of habitat conditions are given the dominant functional groups, examples of species characteristic of these groups and traits that may be enabling survival in these circumstances. This can be compared with the idea of centrifugal community organisation in wetland vegetation proposed by Keddy (1990). The central set of habitat conditions could be regarded as the preferred set of conditions, with habitats along the three described gradients peripheral. Species have different abilities to occupy these peripheral habitats and these can be well described by functional groups.

Fig. 9.6 Predicted functional dynamics of euhydrophytes in European riverine wetlands. Changing dominance of functional groups is shown along the environmental gradients. Functional groups dominant under particular habitat conditions are shown in bold. Examples of species from dominant functional groups are given. Traits that the groups possess and are likely to be advantageous in these situations indicated in small type.



9.6 Summary

Field measured morphological traits were not found to be adequate descriptors of functional group

Functional groups showed quite a constant relationship with environmental parameters except to conductivity where the extreme nature of some sites had influenced the analysis.

A broad model of functional vegetation changes with environmental change is presented for riverine wetlands

The value of autecological research on euhydrophyte species to improve the scope and accuracy of this model is emphasised.

Chapter 10

GENERAL DISCUSSION

Chapter 10

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10.1 How does the study answer the original questions?

This study was designed to address the specific questions outlined in Chapter 1. As with most research, aspects other than those under primary consideration attracted interest and revealed avenues of study not originally considered. However, the original aims were adhered to, and the study concludes by answering these questions and discussing additional aspects covered.

10.1.1 Can euhydrophyte plants be grouped into ecologically meaningful assemblages using functional and morphological traits?

The study succeeds in constructing functional groups that have ecologically recognisable functions and can be defined using a subset of the original traits. While the chosen field measured traits did not emerge as useful descriptors of these groups, analysis of the more coarsely coded traits from published work, suggests that morphological traits have potential as indicators of functional groups that can be used in the field. Care must be exercised in this type of analysis, as from a large set of data such as this, some sort of grouping, meaningful or otherwise, will inevitably emerge. The ease with which many complex analyses can be executed, using modern computer based multivariate techniques, makes it easy to ignore the underlying principles and assumptions. In the sections concerned with data analysis, detail has been given at each step and explanations of the rationale behind using various techniques. This was considered necessary to avoid the ambiguities arising from a 'black box' approach. The other trap involved in this type of analysis is the risk of 'garbage in; garbage out'. While the principles of the work required no implicit assumptions of species strategy in the analysis, a sound knowledge of species ecology is required to be able to decide whether the end result is worth further consideration. Although groups that emerge are, I feel, reasonable ones, the value of improved autecological data cannot be over emphasised, and it is fully accepted that a better classification may arise as this information becomes available.

Throughout the study, the necessity for better trait data has been mentioned. This, I feel, is one of the strongest points to emerge from the study. Aquatic plant ecology would be able to advance along the same lines as have been achieved in terrestrial

ecology (e.g. Grime *et al.* 1988; Keddy and Boutin 1993) with the establishment of a comprehensive comparative study of individual species ecology. At present there is an increasing body of information on various aspects of euhydrophyte biology (although it is severely biased towards invasive and weed species), but it exists in a fragmented and therefore relatively incomparable form. A functional approach encourages collection of individual trait data that may be more directly comparable, especially if a common format can be established early on. The classification presented here is achieved by the best possible utilisation of the limited available data.

10.1.2 How do the functional groups relate to the environment they are inhabiting and is this predictable?

This study is trying to discover what relationship, if any, exists between environmental parameters and species traits. In this way the habitat is being considered as a templet for ecological response. Other studies have reported failure to apply existing ecological templets to lotic systems (Resh *et al.* 1994). It has been suggested that poor matches between species traits and environmental parameters may be due to a) the history of the environment and the chance dispersal of organisms which may mask the effect of a habitat templet and b) species interactions (e.g. competition) which could intervene between the direct match of an organism and its environment (Townsend and Hildrew 1994). While this analysis has not uncovered clear examples of habitat conditions being correlated with species traits it has started to investigate the state of knowledge for aquatic macrophytes and has highlighted the advantages a more rigorous screening programme designed to collect information on euhydrophyte traits would bring.

It would be possible, and tempting, to present models for predicting vegetation change with alterations in stress or disturbance, but I feel this is extrapolating the data beyond its useful limits and would be misleading; therefore only likely shifts in functional groups are presented. Some of the information contained in the 92/93 survey is not included in Fig 9.6 as it was not common to the Czech survey. This meant that predictions could be made only for a limited set of environmental gradients. While this illustrates how data sets such as these can be used in a predictive manner it is recognised that, while prediction for key variables such as drought duration are not included, the model is incomplete.

Flow has emerged as the factor most influential to functional group composition. Wetlands containing aquatic habitats covering a wide flow spectrum will support a

functionally varied aquatic flora. Such an area will contain species that, due to the possession of a varied pool of traits, should be better able to recover from various perturbations (as demonstrated by Tilman (1988) in disturbed grasslands. In contrast to many limnological studies of macrophyte distribution (e.g. Spence 1967), depth did not appear to be an influential factor. This is probably due to both the narrower depth range experienced in riverine wetland habitats and the fluctuations that most of the communities occupying these habitats must be adapted to cope with.

10.1.3 Are functional vegetation types as useful as full species composition for purposes of assessment and prediction?

A life history theory, such as this, can be evaluated on three levels (Grace 1993): as a system for classifying biological diversity, as a way of understanding the variability amongst organisms, and as a means of predicting the relationships between organisms and environment.

On the first of these levels both functional and species based assessments have advantages. A functional assessment will allow comparisons across a wide range of sites. A species based comparison may give a more detailed inventory of biodiversity and may be more relevant in certain situations, e.g. to assess the conservation importance of a site. The approach chosen will depend upon the objectives of the study. At the second level, a functional based approach has obvious advantages in explaining variability and similarity in terms of traits. At the third level, a functional approach offers scope for prediction and allows these predictions to be generally applicable. Such predictions at a species level require extremely thorough knowledge of a species autecology and distribution. In some circumstances a functional prediction may have more relevance. It may, for example, be more useful for a manager to know that canopy forming species will dominate, following a particular environmental perturbation, than to be given more precise estimates of likely species composition.

While the traditional species based approach tends to be dominated by geographical divisions (produced by variation in species across the range); the functional approach was able to transcend these divisions and produce a model that is more easily applied to a geographically separated range of sites. This approach is therefore particularly useful for large scale studies. The assessment value of systems based on species recognition (e.g. Holmes 1983; Wiegleb 1981) can be only locally applicable. Even systems that are based on less geographically limited features, such

as structure or rarity, can present problems when making comparisons across a range of biotopes (de Lange and van Zon 1983).

Problems experienced in relating phytosociological communities to environmental parameters (Wiegleb 1984; Haslam 1978) may be due to difficulties in syntaxonomy of aquatic communities (Carbiener *et al.* 1990), rather than lack of a relationship between community and environmental character, but the relationships may still be only locally applicable. Communities have been shown to be better than species for environmental monitoring or classification (Carbiener *et al.* 1990); these have some predictive value (Tremolieres *et al.* 1994; Carbiener *et al.* 1990) but are still limited in application, as shown by the difficulties in applying the NVC to European data.

There may be scope, using a functional approach, for defining groups with a particular goal in mind. For example, when considering aquatic weed management, attributes that are a response to cutting or herbicides could be used exclusively, or weighted more heavily, when forming groups. Functional guilds have also been suggested as a subjective and predictive method of survey for the purposes of Environmental Impact Assessment (Johnson 1980). These applications utilise the definition of functional groups as given by MacMahon *et al.* (1981) *'all organisms which perform the same investigator defined ecosystem function'*.

The current approach can be used for both assessment and prediction. A functional classification system can be applied to any aquatic vegetation, world-wide. Although at the present time its predictive value is limited to the areas in which it has been tested (i.e. European riverine wetlands), and is of a fairly coarse nature, it seems reasonable to hope that, through gradual refinement of the predictive relationships by study of individual parameters and traits, more precise and generally applicable predictions will become possible.

10.2 What is the role of the regenerative phase?

The lack of comparable data concerning the regenerative phase of euhydrophytes has been the biggest obstacle to this work. The available data was shown in Chapter 6 to be of little use in improving the functional classification. However, it seems inevitable that this is due to the poor data rather than to the negligible importance of regenerative traits to the plants' ecology, particularly in view of the effective dispersal and colonising abilities of many euhydrophytes. The experimental work presented here, while providing new data on the seed banks occurring in aquatic habitats and giving useful results concerning more generalised wetland ecology, only served to confirm the relatively minor role of sexual regeneration in aquatic plants. It did demonstrate however, that a permanent seed bank probably exists for many euhydrophytes. Considerably more work is needed to quantify other regenerative phase traits before their relationship with the established phase, or their correlation to environmental conditions can be fully elucidated. Grace (1993) demonstrated a lack of perfect correspondence between clonal attributes and plant distribution and suggested that this was due to the environmental requirements being met by traits not associated with clonal reproduction. Similarly low correlation between regenerative traits and measured environmental variables was demonstrated here, again probably due to the lack of good data.

Life history studies to investigate the effort invested in different methods of reproduction and the losses at different stages (e.g. Titus and Hoover 1991) present a valuable quantitative approach that should be utilised in future studies (e.g. screening trials).

10.3 Do euhydrophyte strategies conform to the theories of Grime (1979)?

Grime's model is not easy to fit to this group of plants. Many traits outlined by him are difficult to measure in the field (e.g. potential relative growth rate, response to resource depletion) and experimental data is at present unavailable. The functional groups defined here do not possess suites of traits that correspond clearly to Grime's strategies. Bearing in mind the extreme differences between the aquatic and terrestrial environments, and their effects on adaptations, it seems unlikely that euhydrophytes would conform to the trait-environment relationships described by

Grime. However, the concepts he used can be adapted for the aquatic situation. The forces of stress, disturbance and competition can be used as a framework, although they must obviously take different forms in an aquatic medium. Similarly, traits that have evolved to resist these forces are also different. I am inclined to the view of Wiegleb and Brux (1991), who consider that a stress can be met by a number of adaptations. I think it is also true that the different forms of stress may not all be equally well resisted by a species. An example from this study is *Myriophyllum alterniflorum* which showed a poor response to shade under experimental conditions, but in the field however, was found to tolerate low nutrient conditions. For these reasons the concepts of stress, disturbance and competition, while providing a useful framework for study, need to be subdivided into different forms for study, before generalisations concerning species response to them are made.

Habitat preferences have been discussed in relation to the characteristics of functional groups (Table 9.12), and no strong pattern was observed. However, the role of individual traits in the analysis needs closer study. Their relation to environmental pressures could be examined by regression of individual morphological traits (e.g. leaf area) with the environmental parameters measured concurrently in the field. Another avenue of investigation is to look at the variation between populations of the same species in different habitats (e.g. Marrs 1994). This comparative approach has been advocated by Bradshaw (1987), as the differences observed may relate more readily to the environment currently inhabited and not be obscured by the past acquisition of characters which have little relation to the present environment. Verhoeven *et al.* (1982) also argue that investigation should be at the population level.

The variety of functional groups that can be found at a particular site (particularly those of FVT III) can make it difficult to fit particular groups (or strategies) to environmental types, although preferences can be recognised. This representation of a number of strategies at one site is in concurrence with Grime *et al.* (1988) who attribute it to the variation of C-S-R equilibrium on diurnal, seasonal and successional time scales. While this explanation is plausible, it also brings the value of attributing stress or disturbance values to a site into question. The problems of quantifying stress and disturbance, as previously discussed, contribute to the difficulties in using this, theoretically, useful framework.

Boutin and Keddy (1993) identified five questions for the early stages of functional classification. These same questions emerged as this study progressed, some have been answered in whole or in part, some have yet to be addressed:

1) What are the best traits for measuring the functional roles of plants in vegetation?
An answer to this could be attempted using the information available from this analysis, but this would not necessarily identify the best traits, as only a subset of the myriad plant traits has been examined. While I tried to investigate a range of traits information in some areas is weaker than in others. Regenerative biology, as noted above, needs much more attention, and these traits are likely to prove significant in any functional classification. Physiological ecology was largely neglected, and also requires more thorough attention.

2) What are the minimum number of traits we need to measure to produce accurate and useful classifications of functional groups?
In this analysis six traits were adequate to predict functional group membership (growth form, leaf area, plant length, stem architecture and below to above ground biomass ratio). These are all morphological traits, but this may be reflecting the morphological bias of the trait set, rather than actual descriptive value. However, many studies have found morphological traits, particularly height and lateral spread, to be indicative of a species ability to dominate in fertile, undisturbed habitats (Grime 1979; Givnish 1982; Day *et al.* 1988; Gaudet and Keddy 1988; Shipley *et al.* 1989; Hills *et al.*1994). In disturbed or stressed sites it seems that a wider array of morphologies occurs (Keddy 1990). The key descriptors identified here may not be adequate for a more refined classification based on traits obtained from screening experiments.

3) What are the most efficient methods for screening for the above traits?
The volume of data on aquatic plant traits is lower than that on terrestrial groups and as yet no integrated programme is underway to remedy this. A possible screening programme is outlined below (10.4).

4) How many functional groups are necessary for particular levels of accuracy?
It has been shown at various points in this study that the three strategy model of Grime (1979) is inadequate at this level of investigation. Six functional groups are adequate for describing differences in site ecology in a European riverine wetland context, and to classify sites into functional vegetation types, but other levels of accuracy have not been explored.

5) Across how many vegetation types can one extrapolate a particular model?
It seems unlikely that models developed in an aquatic environment can be usefully extrapolated to terrestrial habitats. This may be inferred partly from the lack of success experienced in attempts to fit models developed in the terrestrial environment to the aquatic situation, as discussed above. The present work is focused on riverine wetland euhydrophytes and could be tested for its applicability to other aquatic systems. Traits, other than those defined as key here may be influential. For example in regulated lakes and the Nile river in Egypt, competitive traits were of prime importance with disturbance traits also important. Stress tolerance was of the least importance (Springuel and Murphy 1991). Relationships between traits and environmental pressures may also differ between systems, for example, *Najas flexilis,* as a free CO2 requirer, is a better competitor than HCO_3^- users such as *Potamogeton pectinatus* in turbid lakes with lower pH (Hough and Forwall 1988). Most workers contend that the ability to assimilate HCO_3^- directly confers a competitive advantage in hard water (Hutchinson 1975; Raven 1970).

While these data may not be easily equitable with Grime's theories, the utility of a general model should not be discarded, rather a system-specific sub model may be the solution (Keddy 1990). This could take the form of a set of strategies (or functional groups) particular to euhydrophytes a level of organisation below the more generalised models of Grime (1979). This work favours such an approach, with the results showing that Grime's strategies do not lead to a significantly improved understanding of the community (the majority of species being lumped together as CR strategists). The functional groups presented here are the first steps to such a sub model. Assembly rules have been suggested (Keddy 1992b) as a means of unifying community ecology. The environment can be considered to act as a filter (van der Valk 1981; Keddy 1992b) removing all species lacking certain combinations of traits. The objective of assembly rules is to identify which traits (and so which species) occur in a given environment, for a given species pool (Keddy 1992b). This study has gone some way in the search for these rules, by generating hypotheses about the traits that may be associated with a particular

environment. The next step is to test these hypotheses in the light of improved trait data. (At a species level this could be compared with the community composition and environmental data of the present survey to generate hypotheses). These must then be tested on an independent set of data.

10.4 Future work.

1) Quantitative screening of euhydrophyte species for a range of traits.
A wide range of quantitatively defined traits is necessary to uncover trait environment relationships. For example, while photosynthetic capacity of floating leaved plants is high, their biomass accumulation is quite low. This has been related to the high leaf turnover rate in these plants (Tsuchiya 1991). Quantitative measurement of leaf life span would help to clarify the relationships between biomass accumulation and habitat conditions. Leaf life span has also been tentatively related to the degree of stress in an environment, with leaf life span increasing in nutrient poor or low light habitats (Tsuchiya 1991). Studies such as those of Kadono (1984) into the growth form and life cycle of Japanese *Potamogeton* could be extended to included a wide range of species, but conducted along the same comparative lines. The main requisite of such a programme is that it should be comparable. The experimental conditions used should be standardised as far as possible and the traits must be measured using a previously agreed, identical methodology on each species. This has been carried out on a wide range of terrestrial species by workers at the Unit of Comparative Plant Ecology in Sheffield. A similarly ambitious approach to aquatic species is required to advance their functional classification.

2) The hypotheses generated here are at present confined to the relationships observed in riverine wetland habitats. While relationships observed in terrestrial situations have been found to be applicable over a wide of range habitats (Grime *et al.* 1988), it is preferable to investigate the trait-environment relationships in other aquatic habitats before extrapolating the present hypotheses to them.

3) As comparative data is collected the hypotheses generated in this thesis could be tested, or euhydrophytes reclassified by applying the approach presented here to a new set of trait data. The final goal is to establish assembly rules for aquatic communities, that can be used for predictive purposes.

10.5 Conclusions

Detailed conclusions have been given at the end of each chapter, but several points deserve reiteration. This study has presented a method of functional analysis of euhydrophyte communities. This type of analysis has proved useful in various situations and seems likely to be profitable in aquatic habitats. However, throughout this thesis the recurrent problem of lack of comparable data on various aspects of euhydrophyte biology is emphasised, and the need for an integrated screening programme to provide these data is stressed. This would seem to be the next step forward in this field. As simple morphological traits have been shown to be of relatively limited use it will not be possible to progress this line of investigation without better knowledge of macrophyte traits. Quantitative data on regenerative characters is particularly lacking, and an increase in the volume and quality of data in this area would be especially valuable.

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APPENDICES

Appendix 1

1992 & 1993 field survey: Environmental parameters

Site codes see Table 2.1
Parameter codes and units see section 3.2.2

Site	Code	D	Ps	Cond	DO%	DOmg	pH	Pw	Nw	TH	K	flow
1	ilbd2	0.08	42	944	63	6.7	7.4	0	0	35	2.88	2
2	ilbd3	0.32	547	590	23	3.8	7.1	0	0	27	6.91	2
3	ilbd4	0.38	440	672	33	3.35	7.47	0	0	27	3.07	2
4	ilbpo	0.12	763	652	37	3.9	8	0	0	22	0.59	1
5	ilbr	1.53	367	578	74	7.45	8.4	0.25	0	27	2.79	4
6	icldi	0.31	620	441	35	3.5	7.3	0	0	27	5.14	2
7	icldo	0.13	1165	459	39	3.95	7	0	0	22	3.96	3
8	iclr	0.69	332	369	75	7.45	7.8	0.25	0	15	2.82	4
9	ibipo	0.77	313	652	49	4.6	7.5	0	0	27	3.7	1
10	eksrf	0.27	763	192	92	9.05	7.28	0	10	9	2.12	5
11	eksrr	0.49	763	194	91	9.55	6.99	0	10	0	1.62	4
12	eksrl	0.21	763	192	92	9.7	7.05	0	10	0	2.12	5
13	eksox	0.51	763	101	66	6.1	5.8	0	10	0	1.88	1
14	ebmr	0.33	763	206	92	9.8	6.9	0.25	10	9	2.35	5
15	ehbox	1	763	424	50	5.6	7.2	0	0	9	3.6	1
16	cimsr	0.51	763	53	84	9.96	6.62	0	0	0	1.44	5
17	cimrl	2.01	763	82	52	6	6.45	0	0	0	5.05	1
18	cimnl	1.75	1189	242	69	7.53	6.79	0	0	0	5.34	1
19	cimid	0.37	505	91	75	8.99	6.81	0	0	0	2.03	3
20	cimwp	0.44	811	57	80	8.96	6.73	0	0	0	2.73	1
21	cimox	0.58	411	84	79	9.67	6.9	0	0	0	2.33	1
22	cemab	1.01	1846	270	70	7.03	7.13	0.5	0	9	3.73	3
23	cemta	0.64	1885	101	24	2.23	6.5	0.5	0	0	4.77	2
24	cemwa	0.43	949	161	100	10.34	7.44	0.25	0	9	3.03	2
25	cemrd	0.38	1578	161	29	2.55	6.65	0.5	0	9	5.64	3
26	cemgd	0.65	139	171	86	9.25	6.88	0.25	0	9	3.92	2
27	cemcb	0.15	763	92	78	9.5	7	0	0	0	2.94	1
28	smgr	0.27	763	3905	60	6	6.75	0	0	35	1.43	4
29	smml1	0.7	763	3905	56	4.9	7.2	0	0	35	0.55	1
30	smml3	0.5	763	2980	58	5.7	6	0	0	35	0.55	1
31	faoxa	0.94	687	317	99	9.55	7.25	0.25	0	9	3.56	1
32	faoxd	0.39	763	296	71	6.85	7.7	0.25	0	9	3.55	1
33	fappo	0.57	1026	233	24	4	6.95	0.25	0	9	9.9	1
34	fapdo	0.51	872	265	85	6.6	7.35	0.25	0	9	3.59	1
35	fdcbw	1.26	680	279	90	9	6.7	0.25	10	9	2.01	1
36	fmlbw	0.39	443	314	70	5.95	7.3	0.25	0	15	2.88	2
37	fapdi	0.2	703	260	52	4.95	7.07	0.25	0	9	6.71	1

Site	Code	drought	Tshade	Ecover	SL	% 'a'	% 'b'	% 'c'	% 'd'	OMs
1	ilbd2	2	0	3	15.23	74	17	8	1	5.7
2	ilbd3	1	0	4	1.59	56	30	9	5	48.3
3	ilbd4	1	1	7	1.07	45	41	12	2	28
4	ilbpo	3	0	1	49.58	38	28	14	20	16.4
5	ilbr	1	0	1	0.82	63	36	0	0.5	3.5
6	icldi	2	2	3	2.20	23	31	21	25	22.1
7	icldo	2	4	6	6.82	21	26	46	7	56.1
8	iclr	1	0	0	1.80	38	28	14	20	16.4
9	ibipo	1	0	1	1.23	70	23	4	3	12.2
10	eksrf	1	3	0	6.13	2	5	10	83	1
11	eksrr	1	8	0	4.42	3	8	12	77	2.4
12	eksrl	1	4	0	7.88	2	5	9	84	1.4
13	eksox	3	9	5	3.66	38	28	14	20	16.4
14	ebmr	1	2	1	4.53	5	12	12	71	1.9
15	ehbox	1	8	0	0.98	38	28	14	20	16.4
16	cimsr	1	0	0	4.78	2	5	10	83	0.7
17	cimrl	1	0	1	0.35	38	28	14	20	16.4
18	cimnl	1	0	1	0.38	75	22	3	0.6	17.1
19	cimid	1	1	3	4.67	31	62	5	2	11.1
20	cimwp	1	0	0	2.92	48	33	19	0.4	64
21	cimox	1	0	1	2.60	29	68	3	0.2	1.4
22	cemab	1	1	1	0.93	81	16	3	0.4	18.7
23	cemta	1	1	1	1.15	54	43	3	0	18.7
24	cemwa	2	0	1	2.69	78	19	3	0.2	14.6
25	cemrd	2	3	6	1.64	56	30	13	1	19
26	cemgd	1	0	2	1.38	20	44	27	9	1.1
27	cemcb	1	0	0	7.96	38	28	14	20	16.4
28	smgr	4	0	2	9.09	38	28	14	20	16.4
29	smml1	4	0	0	9.12	38	28	14	20	16.4
30	smml3	4	0	0	12.76	38	28	14	20	16.4
31	faoxa	1	0	0	1.05	24	30	37	9	3.5
32	faoxd	2	0	0	2.54	38	28	14	20	16.4
33	fappo	3	0	1	0.62	38	35	27	0.4	35.4
34	fapdo	2	2	1	1.92	47	29	21	3	11.3
35	fdcbw	2	9	0	1.39	26	31	35	8	14.6
36	fmlbw	2	0	0	3.13	2	6	12	80	0.6
37	fapdi	3	1	1	2.62	47	29	21	3	14.6

Appendix 2

1992 & 1993 field survey: Euhydrophyte species frequencies

Site numbers see Table 2.1
Frequencies shown are averages of all site visits (see section 3.2.1)

Code	EUHYDROPHYTES	Site 1	2	3	4	5	6	7	8	9	10
cham	*Callitriche hamulata*	0.00	0.25	0.25	0.00	5.00	0.00	0.00	0.00	0.00	6.50
csta	*C. stagnalis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cpla.	*C. platycarpa*	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00
cobt	*C. obtusangula*	0.00	0.00	1.25	0.00	0.00	6.33	0.00	0.00	0.00	0.00
cdem	*Ceratophyllum demersum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
casp	*Chara aspera*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ccan	*C. canescens*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
chis	*C. hispida*	5.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cmaj	*C. hispida var major*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
chsp	*Chara spp*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
eaci	*Eleocharis acicularis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ecan	*Elodea canadensis*	0.00	0.75	1.50	0.00	0.67	0.00	4.50	1.33	4.50	0.00
fant	*Fontinalis antipyretica*	0.00	0.00	0.00	0.00	1.33	0.00	0.00	0.00	0.00	2.50
gdec	*Glyceria declinata*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
gflu	*Glyceria fluitans*	0.00	0.00	0.00	1.00	0.00	3.00	0.25	0.00	0.00	0.00
hpal	*Hottonia palustris*	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
hmor	*Hydrocharis morsus-ranae*	0.00	2.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
jbul	*Juncus bulbosus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
lmin	*Lemna minor*	0.00	9.75	7.50	0.00	0.00	2.00	2.75	0.33	7.00	0.00
ltri	*L. triscula*	0.00	9.25	7.25	0.00	0.33	0.00	1.75	0.33	9.00	0.00
malt	*Myriophyllum alterniflorum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.50
mspi	*M. spicatum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
mver	*M. verticillatum*	0.00	7.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nafl	*Najas flexilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nflx	*Nitella flexilis*	0.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00
nlut	*Nuphar lutea*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.33	9.50	0.00
npum	*N.pumila*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nalb	*Nymphaea alba*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
oflu	*O. fluviatilis*	0.25	1.00	0.50	0.00	0.33	2.33	0.00	0.00	0.00	0.00
pamp	*Persicaria amphibia*	0.25	1.25	0.75	1.00	3.33	0.67	2.00	1.67	0.00	0.00
pber	*Potamogeton berchtoldii*	0.00	1.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pcol	*P. coloratus*	6.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pcri	*P. crispus*	0.00	0.00	0.00	0.00	2.67	0.00	0.00	0.00	0.00	0.00
pfil	*P. filiformis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.67	0.00	0.00
pluc	*P. lucens*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.50	0.00
pnat	*P. natans*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pnod	*P. nodosus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pobt	*P. obtusifolius*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ppec	*P. pectinatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ppol	*P. polygonifolius*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ppus	*P. pusillus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ptri	*Potamogeton trichoides*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
raqu	*Ranunculus aquatilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rpel	*R. peltatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rpen	*R. penicillatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.50
rtri	*R. tricophyllus*	0.00	0.00	0.00	6.00	0.00	0.00	0.00	0.00	0.00	0.00
rcir	*R. circinatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ssag	*Sagittaria sagittifolia*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sang	*Sparganium angustifolium*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
seme	*Sparganium emersum*	0.25	1.50	2.00	0.00	4.33	0.00	0.00	0.33	0.00	0.00
spol	*Spirodela polyrhiza*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
uint	*Utricularia intermedia*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
uvulg	*U. vulgaris*	0.75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
zpal	*Zannichellia palustris*	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00

Code	EUHYDROPHYTES	Site 11	12	13	14	15	16	17	18	19	20
cham	*Callitriche hamulata*	0.50	7.00	2.50	2.25	0.00	2.00	2.00	0.29	0.25	0.00
csta	*C. stagnalis*	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.38	0.00
cpla	*C. platycarpa*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cobt	*C. obtusangula*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cdem	*Ceratophyllum demersum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
casp	*Chara aspera*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ccan	*C. canescens*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
chis	*C. hispida*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cmaj	*C. hispida var major*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
chsp	*Chara spp*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
eaci	*Eleocharis acicularis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17
ecan	*Elodea canadensis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00
fant	*Fontinalis antipyretica*	1.25	2.00	0.00	0.00	0.00	4.63	0.29	0.00	0.13	0.17
gdec	*Glyceria declinata*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.29	0.00	0.00
gflu	*Glyceria fluitans*	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	1.00	0.00
hpal	*Hottonia palustris*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
hmor	*Hydrocharis morsus-ranae*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
jbul	*Juncus bulbosus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.83
lmin	*Lemna minor*	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
ltri	*L. triscula*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
malt	*Myriophyllum alterniflorum*	0.00	2.50	0.00	0.00	0.00	5.00	0.00	0.00	0.25	4.00
mspi	*M. spicatum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
mver	*M. verticillatum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nafl	*Najas flexilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nflx	*Nitella flexilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.63	0.00
nlut	*Nuphar lutea*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
npum	*N.pumila*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.43	0.00	0.00
nalb	*Nymphaea alba*	0.00	0.00	0.00	0.00	1.00	0.00	0.00	1.43	0.00	0.00
oflu	*O. fluviatilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pamp	*Persicaria amphibia*	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pber	*Potamogeton berchtoldii*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00
pcol	*P. coloratus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pcri	*P. crispus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pfil	*P. filiformis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pluc	*P. lucens*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pnat	*P. natans*	0.00	0.00	0.00	0.00	0.00	0.00	9.71	7.43	5.13	0.00
pnod	*P. nodosus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pobt	*P. obtusifolius*	0.00	0.00	0.00	0.00	0.00	0.00	1.86	7.00	3.88	0.00
ppec	*P. pectinatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ppol	*P. polygonifolius*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.33
ppus	*P. pusillus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ptri	*Potamogeton trichoides*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
raqu	*Ranunculus aquatilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rpel	*R. peltatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rpen	*R. penicillatus*	0.00	5.00	0.00	2.75	0.00	0.00	0.00	0.00	0.00	0.00
rtri	*R. tricophyllus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rcir	*R. circinatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ssag	*Sagittaria sagittifolia*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sang	*Sparganium angustifolium*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.57	0.00	0.00
seme	*Sparganium emersum*	0.75	0.25	0.00	1.00	0.00	1.63	0.00	0.00	3.63	0.00
spol	*Spirodela polyrhiza*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
uint	*Utricularia intermedia*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.33
uvulg	*U. vulgaris*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
zpal	*Zannichellia palustris*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Code	EUHYDROPHYTES	Site 21	22	23	24	25	26	27	28	29	30
cham	*Callitriche hamulata*	0.00	0.00	0.00	0.00	5.50	0.00	0.00	0.00	0.00	0.00
csta	*C. stagnalis*	0.00	2.33	0.00	0.40	0.00	0.25	0.00	0.00	0.00	0.00
cpla	*C. platycarpa*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cobt	*C. obtusangula*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cdem	*Ceratophyllum demersum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
casp	*Chara aspera*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	2.00
ccan	*C. canescens*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.33	5.00
chis	*C. hispida*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cmaj	*C. hispida var major*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	10.00
chsp	*Chara spp*	0.00	0.00	0.00	1.60	0.00	0.00	0.00	0.00	0.00	0.00
eaci	*Eleocharis acicularis*	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ecan	*Elodea canadensis*	0.00	4.33	7.33	6.40	9.00	0.50	0.00	0.00	0.00	0.00
fant	*Fontinalis antipyretica*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
gdec	*Glyceria declinata*	0.00	0.00	0.00	0.00	2.00	0.75	0.00	0.00	0.00	0.00
gflu	*Glyceria fluitans*	0.29	1.00	0.00	0.40	1.00	0.00	0.00	0.00	0.00	0.00
hpal	*Hottonia palustris*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
hmor	*Hydrocharis morsus-ranae*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
jbul	*Juncus bulbosus*	1.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
lmin	*Lemna minor*	0.00	1.67	5.00	3.00	0.50	0.75	0.00	0.00	0.00	0.00
ltri	*L. triscula*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
malt	*Myriophyllum alterniflorum*	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
mspi	*M. spicatum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
mver	*M. verticillatum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nafl	*Najas flexilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nflx	*Nitella flexilis*	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nlut	*Nuphar lutea*	0.00	0.00	1.00	0.00	0.00	5.25	8.00	0.00	0.00	0.00
npum	*N.pumila*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nalb	*Nymphaea alba*	4.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
oflu	*O. fluviatilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pamp	*Persicaria amphibia*	0.00	0.33	0.00	0.00	0.00	0.25	8.00	0.00	0.00	0.00
pber	*Potamogeton berchtoldii*	0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pcol	*P. coloratus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pcri	*P. crispus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pfil	*P. filiformis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pluc	*P. lucens*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pnat	*P. natans*	0.71	0.00	0.00	0.20	0.00	5.50	0.00	0.00	0.00	0.00
pnod	*P. nodosus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pobt	*P. obtusifolius*	1.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ppec	*P. pectinatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ppol	*P. polygonifolius*	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ppus	*P. pusillus*	0.00	0.00	0.00	1.60	0.00	0.00	0.00	0.00	0.00	0.00
ptri	*Potamogeton trichoides*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
raqu	*Ranunculus aquatilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rpel	*R. peltatus*	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
rpen	*R. penicillatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rtri	*R. tricophyllus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.50	0.00	0.00
rcir	*R. circinatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ssag	*Sagittaria sagittifolia*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
sang	*Sparganium angustifolium*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
seme	*Sparganium emersum*	0.00	0.33	0.00	1.60	0.00	0.25	0.00	0.00	0.00	0.00
spol	*Spirodela polyrhiza*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
uint	*Utricularia intermedia*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
uvulg	*U. vulgaris*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
zpal	*Zannichellia palustris*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Code	EUHYDROPHYTES	Site 31	32	33	34	35	36	37
cham	*Callitriche hamulata*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
csta	*C. stagnalis*	0.25	0.00	5.00	0.00	1.00	0.00	0.00
cpla	*C. platycarpa*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cobt	*C. obtusangula*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cdem	*Ceratophyllum demersum*	9.75	7.33	6.00	10.00	1.00	8.33	8.33
casp	*Chara aspera*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ccan	*C. canescens*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
chis	*C. hispida*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
cmaj	*C. hispida var major*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
chsp	*Chara spp*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
eaci	*Eleocharis acicularis*	0.25	0.00	0.00	0.00	0.00	0.00	0.00
ecan	*Elodea canadensis*	4.50	2.00	6.50	4.00	0.00	0.67	0.33
fant	*Fontinalis antipyretica*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
gdec	*Glyceria declinata*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
gflu	*Glyceria fluitans*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
hpal	*Hottonia palustris*	0.00	0.00	3.00	0.00	0.00	0.00	0.00
hmor	*Hydrocharis morsus-ranae*	2.50	1.67	1.00	4.25	0.00	0.00	7.33
jbul	*Juncus bulbosus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
lmin	*Lemna minor*	0.50	0.67	4.50	3.25	0.00	0.00	4.67
ltri	*L. triscula*	0.00	0.00	5.50	0.00	0.00	0.00	0.00
malt	*Myriophyllum alterniflorum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
mspi	*M. spicatum*	8.75	5.33	3.00	3.25	0.00	0.67	0.00
mver	*M. verticillatum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nafl	*Najas flexilis*	0.25	0.00	0.00	0.00	0.00	0.00	0.00
nflx	*Nitella flexilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nlut	*Nuphar lutea*	2.00	1.00	4.00	0.25	0.00	0.00	2.00
npum	*N.pumila*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
nalb	*Nymphaea alba*	2.75	0.00	0.00	0.00	0.00	0.00	0.33
oflu	*O. fluviatilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pamp	*Persicaria amphibia*	1.00	0.67	0.00	1.00	0.67	0.00	1.00
pber	*Potamogeton berchtoldii*	0.00	0.00	0.00	0.00	0.33	0.00	0.00
pcol	*P. coloratus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pcri	*P. crispus*	0.00	0.00	2.00	0.00	0.00	0.00	0.00
pfil	*P. filiformis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pluc	*P. lucens*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pnat	*P. natans*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
pnod	*P. nodosus*	5.75	9.33	0.00	9.75	0.00	0.33	5.33
pobt	*P. obtusifolius*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ppec	*P. pectinatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ppol	*P. polygonifolius*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ppus	*P. pusillus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ptri	*Potamogeton trichoides*	1.50	1.00	0.00	0.00	0.00	0.00	0.00
raqu	*Ranunculus aquatilis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rpel	*R. peltatus*	0.00	0.00	5.00	0.00	0.00	0.00	0.00
rpen	*R. penicillatus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rtri	*R. tricophyllus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
rcir	*R. circinatus*	2.50	0.67	0.00	0.50	0.00	0.00	0.00
ssag	*Sagittaria sagittifolia*	0.00	0.00	0.00	0.00	0.00	0.00	1.00
sang	*Sparganium angustifolium*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
seme	*Sparganium emersum*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
spol	*Spirodela polyrhiza*	1.50	1.00	0.50	5.25	2.67	0.00	9.00
uint	*Utricularia intermedia*	4.50	3.67	5.50	4.50	0.00	0.00	1.67
uvulg	*U. vulgaris*	0.00	0.00	0.00	0.00	0.00	0.00	0.00
zpal	*Zannichellia palustris*	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 3

1992 & 1993 field survey: Non euhydrophyte species frequencies

Site numbers see Table 2.1
Frequencies shown are averages of all site visits (see section 3.2.1)
Species were only recorded if rooted in water.

Species	Site 1	2	3	4	5	6	7	8	9	10
Agrostis stolonifera L.	4.75	3.75	2.00	1.00	0.33	3.33	4.75	0.00	0.00	0.00
Alisma lanceolatum With.	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A. plantago-aquatica L.	0.00	3.75	0.00	0.00	0.00	0.33	4.00	0.00	0.00	0.00
Apium inundatum (L.) H.G. Reichb.	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
A. nodiflorum (L.) Lag.	0.25	0.00	0.00	0.00	2.00	0.33	0.00	0.00	0.00	0.50
Baldellia ranunculoides (L.) Parl.	3.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Berula erecta (Hudson) Cov.	4.00	1.00	8.25	0.00	0.33	0.33	1.00	0.00	0.00	0.00
Butomus umbellatus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Caltha palustris L.	0.25	0.50	0.75	1.00	0.00	0.00	0.50	0.00	0.50	0.00
Cardamine pratensis L.	0.25	0.00	0.00	0.00	0.00	0.33	0.75	0.00	0.00	0.00
Carex acutiformis Ehrh.	1.75	2.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. flacca Schreber	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. otrubae Podp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. rostrata Stokes	3.00	8.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00
C. vesicaria L.	0.00	0.00	0.00	0.00	0.00	0.00	3.25	0.00	0.00	0.00
C. viridula ssp oedocarpa (Anderson) B. Scmhmid	2.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Epilobium ciliatum Raf.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Epilobium sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
Equisetum fluviatile L.	2.25	6.50	3.50	1.00	0.00	0.67	0.50	0.67	4.50	0.00
E. palustre L.	1.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eriophorum angustifolium Honck	0.75	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Galium palustre L.	0.00	3.75	0.75	0.00	0.33	3.67	2.75	0.00	0.00	0.00
Glyceria maxima (Hartman) O. Holmb.	0.00	4.75	7.50	0.00	0.00	2.33	6.00	0.00	0.00	0.00
Hippuris vulgaris L.	0.25	6.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydrocotyle vulgaris L.	0.25	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hypericum/lysimachia	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Iris pseudocorus L.	0.25	0.25	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juncus articulatus L.	5.75	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
J. effusus L.	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00
J. inflexus L.	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leersia oryzoides (L.) Sw.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ludwigia palustris (L.) Elliott	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lycopus europeaus L.	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00
Lythrum salicaria L.	0.00	0.00	0.00	0.00	0.00	0.00	1.50	0.00	2.00	0.00
Mentha aquatica L.	6.75	1.25	4.25	0.00	1.00	0.67	2.50	2.00	1.00	0.00
Menyanthes trifoliata L.	0.00	2.25	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00
Myosotis scorpiodes L.	0.00	0.25	0.00	1.00	0.00	2.00	1.25	0.00	0.00	0.00
Oenanthe fistulosa L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pedicularis palustris L.	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Persicaria hydropiper (L.) Spach	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00
Phalaris arundinacia L.	0.00	0.00	0.50	0.00	0.67	0.33	5.00	0.00	0.00	0.00
Phragmites australis (Cav.) Trin. ex Steudel	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	5.50	0.00
Potentilla palustre (L.) Scop.	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ranunculus acris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00
R. flamula L.	0.25	0.25	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
R. repens L.	0.50	0.25	0.00	1.00	0.00	0.33	0.25	0.00	0.00	0.00
R. sceleratus L.	0.00	0.00	0.00	0.00	0.00	0.67	0.25	0.00	0.00	0.00
Rorippa amphibia (L.) Besser	0.25	0.00	0.00	0.00	0.33	0.33	6.75	0.00	0.50	0.00
R. nasturtium-aquatica (L.) Hayek	0.00	0.00	0.00	1.00	0.00	7.00	1.50	0.00	0.00	0.00
R. sylvestris (L.) Besser	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rumex aquaticus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. hydrolaplathum Hudson	0.00	0.00	0.00	0.00	0.33	0.67	0.50	0.00	0.00	0.00
Rumex obtusifolius L.	0.00	0.25	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00
Schoenoplectus sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
Sium latifolia L.	0.25	0.50	0.00	1.00	0.00	0.00	1.25	0.00	5.50	0.00
Sparganium erectum L.	0.50	0.75	6.50	0.00	0.00	0.67	1.50	0.00	1.50	0.00
Teucrium scordium L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Triglochin palustre L.	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Typha latifolia L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Urtica dioica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Veronica anagallis-aquatica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
V. beccabunga L.	0.00	0.00	0.00	0.00	2.67	0.00	0.00	0.00	0.00	0.00

Species	Site 11	12	13	14	15	16	17	18	19	20
Agrostis stolonifera L.	0.00	0.25	0.00	0.00	0.00	0.25	0.50	2.25	0.00	0.00
Alisma lanceolatum With.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A. plantago-aquatica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Apium inundatum (L.) H.G. Reichb.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A. nodiflorum (L.) Lag.	0.00	0.25	0.00	0.25	0.50	0.00	0.00	0.00	0.00	0.00
Baldellia ranunculoides (L.) Parl.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Berula erecta (Hudson) Cov.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Butomus umbellatus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Caltha palustris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cardamine pratensis L.	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00
Carex acutiformis Ehrh.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. flacca Schreber	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.33
C. otrubae Podp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. rostrata Stokes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.17
C. vesicaria L.	0.00	0.00	0.00	0.00	0.00	0.00	2.75	4.50	1.63	1.50
C. viridula ssp oedocarpa (Anderson) B. Scmhmid	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Epilobium ciliatum Raf.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Epilobium sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Equisetum fluviatile L.	0.00	0.00	0.00	0.00	0.00	0.00	12.00	2.50	1.13	0.17
E. palustre L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eriophorum angustifolium Honck	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Galium palustre L.	0.00	0.00	0.00	0.00	0.00	0.13	1.75	2.00	0.38	0.50
Glyceria maxima (Hartman) O. Holmb.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
Hippuris vulgaris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
Hydrocotyle vulgaris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hypericum/lysimachia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Iris pseudocorus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juncus articulatus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
J. effusus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
J. inflexus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
Leersia oryzoides (L.) Sw.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ludwigia palustris (L.) Elliott	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lycopus europeaus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lythrum salicaria L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mentha aquatica L.	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00
Menyanthes trifoliata L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.13	0.00
Myosotis scorpiodes L.	0.00	0.00	0.00	0.00	0.50	0.38	0.00	2.00	0.38	0.00
Oenanthe fistulosa L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pedicularis palustris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Persicaria hydropiper (L.) Spach	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Phalaris arundinacia L.	0.00	0.50	0.00	0.00	0.00	0.25	0.00	0.50	0.00	0.00
Phragmites australis (Cav.) Trin. ex Steudel	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Potentilla palustre (L.) Scop.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.63	1.17
Ranunculus acris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. flamula L.	0.00	0.00	0.50	0.00	0.00	0.25	0.00	0.00	0.50	0.83
R. repens L.	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. sceleratus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rorippa amphibia (L.) Besser	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. nasturtium-aquatica (L.) Hayek	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. sylvestris (L.) Besser	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rumex aquaticus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. hydrolaplathum Hudson	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rumex obtusifolius L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Schoenoplectus sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sium latifolia L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sparganium erectum L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.50	2.25	0.50
Teucrium scordium L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Triglochin palustre L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Typha latifolia L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Urtica dioica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Veronica anagallis-aquatica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
V. beccabunga L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Species	Site 21	22	23	24	25	26	27	28	29	30
Agrostis stolonifera L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00
Alisma lanceolatum With.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A. plantago-aquatica L.	0.00	0.00	0.00	0.20	0.00	3.25	0.00	0.00	0.00	0.00
Apium inundatum (L.) H.G. Reichb.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A. nodiflorum (L.) Lag.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Baldellia ranunculoides (L.) Parl.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Berula erecta (Hudson) Cov.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Butomus umbellatus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Caltha palustris L.	0.00	0.00	0.33	0.00	0.00	0.75	0.00	0.00	0.00	0.00
Cardamine pratensis L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex acutiformis Ehrh.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. flacca Schreber	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. otrubae Podp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. rostrata Stokes	1.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. vesicaria L.	2.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. viridula ssp oedocarpa (Anderson) B. Scmhmid	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Epilobium ciliatum Raf.	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00
Epilobium sp	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00
Equisetum fluviatile L.	2.14	0.33	0.33	0.40	0.00	1.50	0.00	0.00	0.00	0.00
E. palustre L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eriophorum angustifolium Honck	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Galium palustre L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Glyceria maxima (Hartman) O. Holmb.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hippuris vulgaris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydrocotyle vulgaris L.	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
Hypericum/lysimachia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Iris pseudocorus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juncus articulatus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
J. effusus L.	0.29	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00
J. inflexus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leersia oryzoides (L.) Sw.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ludwigia palustris (L.) Elliott	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lycopus europeaus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lythrum salicaria L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mentha aquatica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Menyanthes trifoliata L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Myosotis scorpiodes L.	0.00	0.67	3.67	1.60	5.50	1.00	0.00	0.00	0.00	0.00
Oenanthe fistulosa L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pedicularis palustris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Persicaria hydropiper (L.) Spach	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Phalaris arundinacia L.	0.00	1.00	0.67	0.20	1.00	1.50	0.00	0.00	0.00	0.00
Phragmites australis (Cav.) Trin. ex Steudel	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.50	0.00	0.00
Potentilla palustre (L.) Scop.	0.29	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
Ranunculus acris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. flamula L.	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. repens L.	0.00	0.00	0.00	0.00	0.00	0.50	1.00	0.00	0.00	0.00
R. sceleratus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rorippa amphibia (L.) Besser	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. nasturtium-aquatica (L.) Hayek	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. sylvestris (L.) Besser	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rumex aquaticus L.	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. hydrolaplathum Hudson	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rumex obtusifolius L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Schoenoplectus sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sium latifolia L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sparganium erectum L.	0.00	0.67	0.00	1.20	0.00	4.25	0.00	0.00	0.00	0.00
Teucrium scordium L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Triglochin palustre L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Typha latifolia L.	0.00	0.00	0.00	0.00	0.50	0.00	0.00	2.50	0.00	0.00
Urtica dioica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Veronica anagallis-aquatica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
V. beccabunga L.	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00

Species	Site 31	32	33	34	35	36	37
Agrostis stolonifera L.	0.75	0.00	0.00	0.00	0.00	0.00	0.00
Alisma lanceolatum With.	0.00	0.00	1.50	0.00	0.00	0.00	0.00
A. plantago-aquatica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Apium inundatum (L.) H.G. Reichb.	0.00	0.00	0.50	0.00	0.00	0.00	0.00
A. nodiflorum (L.) Lag.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Baldellia ranunculoides (L.) Parl.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Berula erecta (Hudson) Cov.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Butomus umbellatus L.	0.00	0.00	1.50	0.25	0.00	0.00	0.00
Caltha palustris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cardamine pratensis L.	0.25	0.00	0.00	0.00	0.00	0.00	0.00
Carex acutiformis Ehrh.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. flacca Schreber	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. otrubae Podp.	0.00	0.00	1.00	0.00	0.00	0.00	0.00
C. rostrata Stokes	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. vesicaria L.	0.25	0.00	0.00	0.00	0.00	0.00	1.33
C. viridula ssp oedocarpa (Anderson) B. Scmhmid	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Epilobium ciliatum Raf.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Epilobium sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Equisetum fluviatile L.	0.25	2.33	0.00	0.00	0.00	0.00	0.00
E. palustre L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Eriophorum angustifolium Honck	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Galium palustre L.	0.25	0.00	0.50	0.50	0.67	0.00	0.00
Glyceria maxima (Hartman) O. Holmb.	0.00	0.00	2.50	0.00	0.00	0.00	2.67
Hippuris vulgaris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydrocotyle vulgaris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hypericum/lysimachia	0.00	0.00	0.00	0.00	0.33	0.00	0.00
Iris pseudocorus L.	0.00	0.00	0.50	0.00	0.00	0.00	0.00
Juncus articulatus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
J. effusus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
J. inflexus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leersia oryzoides (L.) Sw.	0.00	0.00	0.00	0.00	0.00	0.00	0.33
Ludwigia palustris (L.) Elliott	0.25	0.00	0.50	0.00	0.00	0.00	0.00
Lycopus europeaus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lythrum salicaria L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mentha aquatica L.	0.50	0.67	0.00	0.00	0.00	0.00	0.00
Menyanthes trifoliata L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Myosotis scorpiodes L.	0.50	0.00	0.50	0.25	3.67	0.00	0.00
Oenanthe fistulosa L.	0.00	0.00	0.50	0.00	0.00	0.00	0.00
Pedicularis palustris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Persicaria hydropiper (L.) Spach	0.00	0.00	3.50	0.00	0.00	0.00	0.33
Phalaris arundinacia L.	0.00	0.00	0.00	0.00	1.00	0.00	0.33
Phragmites australis (Cav.) Trin. ex Steudel	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Potentilla palustre (L.) Scop.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ranunculus acris L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. flamula L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. repens L.	0.00	0.00	0.00	0.00	0.33	0.00	0.00
R. sceleratus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rorippa amphibia (L.) Besser	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. nasturtium-aquatica (L.) Hayek	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. sylvestris (L.) Besser	0.00	0.00	0.00	0.00	0.00	0.33	0.00
Rumex aquaticus L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
R. hydrolaplathum Hudson	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rumex obtusifolius L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Schoenoplectus sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sium latifolia L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sparganium erectum L.	0.00	0.00	0.50	0.00	0.00	0.00	0.00
Teucrium scordium L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Triglochin palustre L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Typha iatifolia L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Urtica dioica L.	0.00	0.00	0.00	0.00	0.33	0.00	0.00
Veronica anagallis-aquatica L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
V. beccabunga L.	0.00	2.33	0.00	3.50	0.00	0.00	0.00

Appendix 4

Scientific names, authorities, common names and codes of all species recorded in surveys and experimental work.

Species	Common name	code
Agrostis stolonifera L.	creeping bent	asto
Alisma lanceolatum With.	narrow-leaved water-plantain	alan
Alisma plantago-aquatica L.	common water -plantain	apla
Anthemis spp	chamomile species	ansp
Apium inundatum (L.) H.G. Reichb.	lesser marshwort	ainu
Apium nodiflorum (L.) Lag.	fool's water-cress	anod
Apium spp		apsp
Baldellia ranunculoides (L.) Parl.	lesser water-plantain	bran
Berula erecta (Hudson) Coville	lesser water-parsnip	bere
Bidens cernua L.	nodding bur-marigold	bcer
Bidens tripartita L.	trifid bur-marigold	btri
Butomus umbellatus L.	flowering-rush	bumb
Callitriche cophocarpa		ccop
Callitriche hamulata Kutz ex Koch	intermediate water-starwort	cham
Callitriche obtusangula Le Gall	blunt-fruited water-starwort	cobt
Callitriche platycarpa Kuetz	various-leaved water-starwort	cpla
Callitriche stagnalis Scop.	common water starwort	csta
Callitriche spp	starwort species	casp
Caltha palustris L.	marsh marigold	cpal
Cardamine pratensis L.	cuckooflower	cpra
Carex acutiformis Ehrh.	lesser pond-sedge	cacu
Carex chordorhiza L. fil.	string sedge	ccho
Carex dioica L.	dioecious sedge	cdio
Carex disticha Hudson	brown sedge	cdis
Carex flacca Schreber	glaucous sedge	cfla
Carex limosa L.	bog-sedge	clim
Carex nigra (L.) Reichard	common sedge	cnig
Carex otrubae Podp.	false fox-sedge	cotr
Carex rostrata Stokes	bottle sedge	cros
Carex vesicaria L.	bladder-sedge	cves
Carex viridula ssp oedocarpa (Anderson) B. Schmid	yellow-sedge	cvir
Carex spp	sedge species	cxsp
Centaurea nigra L.	common knapweed	ceni
Ceratophyllum demersum L.	rigid hornwort	cdem
Chantransia chalybaea		
Chara aspera Deth. ex Willd	stonewort	casp
Chara canescens Desv. & Lois.	stonewort	ccan
Chara hispida L.	stonewort	chis
Chara hispida var major (Hartm.) R.D. Wood	stonewort	cmaj
Chara vulgaris var longibractea (Kutz.) J. Groves & Bullock-Webster	stonewort	cvul
Chara spp	stonewort	chsp
Chenopodium polyspernum L.	many-seeded goosefoot	cpol
Chenopodium spp	goosefoot species	cpsp
Cladophora glomerata (L.) Kutz.	blanket weed	
Cyperus fuscus L.	brown galingale	cfus
Echinochloa crusgalli (L.) P. Beauv.	cockspur	ecru
Eleocharis acicularis (L.) Roemer and Schultes	needle spike-rush	eaci
Eleocharis palustre (L.) Roemer and Schultes	common spike-rush	epal
Elodea canadensis Michaux	Canadian waterweed	ecan
Epilobium ciliatum Rafin.	American willowherb	ecil
Epilobium obscurum Schreber	short-fruited willowherb	eobs
Epilobium sp	willowherb species	epsp
Equisetum fluviatile L.	water horsetail	eflu
Eriophorum angustifolium Honck	common cottongrass	eang
Festuca sp.		fesp
Fontinalis antipyretica Hedw.		fant
Galium palustre L.	common marsh-bedstraw	gpal
Galium sp.	bedstraw species	gasp
Glyceria declinata Breb.	small sweet-grass	gdec
Glyceria fluitans (L.) R.Br.	floating sweet-grass	gflu
Glyceria maxima (Hartman) O. Holumb.	reed sweet-grass	gmax
Gnaphalium uliginosum L.	marsh cudweed	guli

Species	Common name	code
Gnaphalium sp.	cudweed species	gnsp
Hippuris vulgaris L.	mare's-tail	hvul
Hottonia palustris L.	water-violet	hpal
Hydrocharis morsus-ranae L.	frogbit	hmor
Hydrocotyle vulgaris L.	marsh pennywort	hyvu
Iris pseudacorus L.	yellow iris	ipse
Juncus articulatus L.	jointed rush	jart
Juncus bufonius L.	toad rush	jbuf
Juncus bulbosus L.	bulbous rush	jbul
Juncus conglomeratus L.	compact rush	jcon
Juncus effusus L.	soft rush	jeff
Juncus inflexus L.	hard rush	jinf
Juncus spp	rush species	jusp
Leersia oryzoides (L.) Sw	cut-grass	lory
Lemna minor L.	common duckweed	lmin
Lemna trisulca L.	ivy-leaved duckweed	ltri
Limosella aquatica L.	mudwort	laqu
Lindernia dubia (L.) Pennel		ldub
Ludwigia palustris (L.) Elliott	Hampshire-purslane	lpal
Lycopus europeaus L.	gypsywort	leur
Lysimachia thrysiflora L.	tufted loosestrife	lthr
Lythrum portula (L.) D. Webb	water-purslane	lpor
Lythrum salicaria L.	purple-loosestrife	lsal
Mentha aquatica L.	water mint	maqu
Mentha pulegium L.	pennyroyal	mpul
Menyanthes trifoliata L.	bogbean	mtri
Myosotis laxa Lehm.	tufted forget-me-not	mlax
Myosotis scorpiodes L.	water forget-me-not	msco
Myosoton aquaticum (L.) Moench	water chickweed	myaq
Myriophyllum alterniflorum DC.	alternate water-milfoil	malt
Myriophyllum spicatum L.	spiked water-milfoil	mspi
Myriophyllum verticillatum L.	whorled water-milfoil	mver
Najas flexilis (Willd.) Rostkov & W. Scmidt	slender naiad	nafl
Nitella flexilis (L.) Agardh	stonewort	nflx
Nitella spp	stonewort	nisp
Nuphar lutea (L.) Smith	yellow water-lily	nlut
Nuphar pumila (Timm) DC.	least water-lily	npum
Nymphaea alba L.	white water-lily	nalb
Oenanthe aquatica (L.) Poiret	fine-leaved water-dropwort	oaqu
Oenanthe fistulosa L.	tubular water-dropwort	ofis
Oenanthe fluviatilis (Bab.) Coleman	river water-dropwort	oflu
Oxalis sp	wood sorrel species	oxsp
Panicum capillare L.	witch-grass	pcap
Pedicularis palustris L.	marsh lousewort	ppal
Persicaria amphibia (L.) Gray	amphibious bistort	pamp
Persicaria hydropiper (L.) Spach	water-pepper	phyd
Persicaria maculosa Gray	redshank	pmac
Persicaria sp.		pesp
Phalaris arundinacia L.	reed canary-grass	paru
Phragmites australis (Cav.) Trin. ex Steudel	common reed	paus
Plantago major L.	greater plantain	pmaj
Poa pratensis L.	smooth meadow-grass	ppra
Poa trivialis L.	rough meadow-grass	ptri
Potamogeton alpinus Balbis	red pondweed	palp
Potamogeton berchtoldii Fieber.	small pondweed	pber
Potamogeton coloratus Hornem.	fen pondweed	pcol
Potamogeton crispus L.	curled pondweed	pcri
Potamogeton filiformis Pers.	slender-leaved pondweed	pfil
Potamogeton lucens L.	shining pondweed	pluc
Potamogeton natans L.	broad-leaved pondweed	pnat
Potamogeton nodosus Poiret	loddon pondweed	pnod
Potamogeton obtusifolius Mert & Koch	blunt leaved pondweed	pobt

Species	Common name	code
Potamogeton pectinatus L.	fennel pondweed	ppec
Potamogeton polygonifolius Pourret	bog pondweed	ppol
Potamogeton pusillus L.	lesser pondweed	ppus
Potamogeton trichoides Cham & Schldl.	hairlike pondweed	potr
Potamogeton spp	pondweed species	posp
Potentilla palustre (L.) Scop.	marsh cinquefoil	popa
Ranunculus acris L.	meadow buttercup	racr
Ranunculus aquatilis L.	common water-crowfoot	raqu
Ranunculus circinatus Sibth.	fan-leaved water-crowfoot	rcir
Ranunculus flammula L.	lesser spearwort	rfla
Ranunculus fluitans Lam.	river water-crowfoot	rflu
Ranunculus peltatus Schrank	pond water-crowfoot	rpel
Ranunculus penicillatus (Dunmort.) Bab	stream water-crowfoot	rpen
Ranunculus repens L.	creeping buttercup	rrep
Ranunculus sceleratus L.	celery-leaved buttercup	rsce
Ranunculus trichophyllus Chaix	thread-leaved water-crowfoot	rtri
Rorippa amphibia (L.) Besser	great yellow-cress	ramp
Rorippa islandica (Oeder ex Murray) Borbas	northern yellow-cress	risl
Rorippa nasturtium-aquatica (L.) Hayek	water-cress	rnas
Rorippa sylvestris (L.) Besser	creeping yellow-cress	rsyl
Rorippa x anceps (Wahlenb.) Reichb.	hybrid yellow-cress	ranc
Rorippa sp	water-cress species	rosp
Rumex aquaticus L.	Scottish dock	ruaq
Rumex hydrolaplathum Hudson	water-dock	rhyd
Rumex obtusifolius L.	broad-leaved dock	robt
Rumex sp.	dock species	rusp
Sagittaria sagittifolia L.	arrowhead	ssag
Salix sp.	willow species	sxsp
Samolus valerandi L.	brookweed	sval
Schoenoplectus sp	club-rush species	scsp
Senecio aquaticus Hill	marsh ragwort	saqu
Sium latifolia L.	greater water-parsnip	slat
Sonchus asper (L.) Hill	prickly sow-thistle	sasp
Sonchus sp.	sow-thistle species	sosp
Sparganium angustifolium Michaux	floating bur-reed	sang
Sparganium emersum Rehmann	unbranched bur-reed	seme
Sparganium erectum L.	branched bur-reed	sere
Spirodela polyrhiza (L.) Schleiden	greater duckweed	spol
Stellaria sp.	stitchwort species	stsp
Stratiotes aloides L.	water soldier	salo
Subularia aquatica L.	awlwort	suaq
Teucrium scordium L.	water germander	tsco
Thalictrum flavum L.	common meadow-rue	tfla
Trifolium repens L.	white clover	trep
Triglochin palustre L.	marsh arrowgrass	tpal
Typha latifolia L.	reedmace	tlat
Ulothrix zonata		
Urtica dioica L.	common nettle	udio
Utricularia australis R.Br.	bladderwort	uaus
Utricularia intermedia Hayne	intermediate bladderwort	uint
Utricularia vulgaris L.	greater bladderwort	uvul
Veronica beccabunga L.	brooklime	vbec
Veronica anagallis-aquatica L.	blue water-speedwell	vana
Veronica catenata Pennell	pink water-speedwell	vcat
Veronica spp	speedwell species	vesp
Zannichellia palustris L.	horned pondweed	zpal

Appendix 5

Euhydrophyte species traits taken from the published literature

Species codes see Appendix 2
Trait codes see Table 4.1

0 = attribute absent
1 = conflicting evidence/occasionally exhibited
2 = attribute present

Species codes	Trait codes ffsur	ffsub	subr	subf	flo	wg	a	cf	amp	het	win	wat
Cham	0	0	0	2	0	2	2	1	2	2	0	2
Csta	0	0	0	2	0	2	2	1	2	2	2	2
Cobt	0	0	0	2	0	1	1	1	2	2	2	0
Cpla	0	0	0	2	0	1	2	1	2	2	2	0
Cdem	0	2	0	0	0	1	0	1	0	0	0	1
Eaci	0	0	2	0	0	1	0	0	0	0	1	0
Ecan	0	0	2	0	0	2	0	1	0	0	0	0
Gdec	0	0	0	2	0	2	0	1	0	0	2	0
Gflu	0	0	0	2	0	2	0	1	2	0	2	0
Hpal	0	0	2	0	0	0	0	0	0	0	0	0
Hmor	2	0	0	0	0	0	0	2	0	0	1	0
Jbul	0	0	2	0	0	2	0	0	2	0	2	0
Lmin	2	0	0	0	0	1	1	2	0	0	0	1
Ltri	0	2	0	0	0	1	0	2	0	0	0	1
Malt	0	0	2	0	0	0	0	1	0	0	2	0
Mspi	0	0	2	0	0	2	0	2	2	0	2	0
Mver	0	0	2	0	0	1	0	2	0	0	2	0
Nlut	0	0	2	2	0	2	0	2	2	2	0	0
Npum	0	0	0	2	0	1	0	2	2	2	0	0
Nalb	0	0	0	0	2	1	0	2	2	0	0	0
Oflu	0	0	2	0	0	1	2	0	0	0	0	0
Pamp	0	0	0	0	2	1	0	2	2	0	0	0
Pber	0	0	2	0	0	0	0	0	0	0	2	0
Pcol	0	0	0	2	0	1	0	1	2	0	2	0
Pcri	0	0	2	0	0	2	2	0	0	0	2	0
Pluc	0	0	0	2	0	0	0	2	0	0	2	0
Pnat	0	0	0	2	0	0	0	2	2	2	2	0
Pnod	0	0	0	2	0	0	0	2	0	2	2	0
Pobt	0	0	2	0	0	0	0	0	0	0	2	0
Ppec	0	0	2	0	0	0	1	2	0	0	0	2
Ppol	0	0	0	2	0	0	0	2	0	2	2	0
Ppus	0	0	2	0	0	0	0	0	0	0	2	0
Ptri	0	0	2	0	0	0	0	0	0	0	2	0
Raqu	0	0	0	2	0	1	2	2	2	2	0	0
Rpel	0	0	0	2	0	1	2	2	2	2	0	0
Rpen	0	0	0	2	0	2	0	2	0	2	0	0
Rtri	0	0	2	0	0	1	2	2	2	0	0	0
Rcir	0	0	2	0	0	2	1	0	0	0	0	0
Ssag	0	0	2	2	0	0	2	0	2	2	0	0
Sang	0	0	0	2	0	1	0	1	0	0	2	0
Seme	0	0	2	2	0	1	0	1	0	0	2	0
Spol	2	0	0	0	0	1	0	2	0	0	0	1
Uint	0	0	2	0	0	1	0	0	0	0	0	0
Uvul	0	0	2	0	0	1	0	0	0	0	0	0
Zpal	0	0	2	0	0	1	2	0	0	0	0	2
Callitriche cophocarpa	0	0	0	2	0	1	2	1	2	2	0	2
Oenanthe aquatica	0	0	0	2	2	1	2	1	2	2	0	0
Potamogeton alpinus	0	0	0	2	0	0	0	1	0	2	2	0
Ranunculus fluitans	0	0	2	0	0	2	2	2	2	0	0	0
Stratiotes aloides	2	2	0	0	0	2	0	1	0	0	1	1
Utricularia australis	0	2	0	0	0	1	0	0	0	0	0	0

Species codes	Trait codes ins	self	bta	lac	lat	vsp	snonb	mult	sinb	pls	plm	pll
Cham	0	2	0	0	1	1	2	0	0	0	2	0
Csta	0	2	0	0	1	1	2	0	0	0	2	0
Cobt	0	2	0	0	1	1	2	0	0	0	2	0
Cpla	0	2	0	0	1	1	2	0	0	0	2	0
Cdem	0	0	0	0	1	0	0	0	2	0	2	1
Eaci	0	0	0	2	2	0	0	2	0	2	1	0
Ecan	0	0	0	2	2	0	0	0	2	0	2	1
Gdec	0	2	1	0	1	2	2	0	0	0	0	2
Gflu	0	0	1	0	1	2	2	0	0	0	0	2
Hpal	2	0	0	1	1	1	0	0	2	0	0	2
Hmor	1	0	0	1	2	0	0	2	0	2	0	0
Jbul	0	0	1	2	1	1	0	2	0	0	2	0
Lmin	0	0	0	0	1	0	0	0	0	2	0	0
Ltri	0	0	0	0	1	0	0	0	0	2	0	0
Malt	0	0	0	1	1	1	0	0	2	0	0	2
Mspi	0	0	0	2	1	1	0	0	2	0	0	2
Mver	0	0	0	1	1	1	0	0	2	0	0	2
Nlut	2	2	2	1	2	2	0	2	0	0	0	2
Npum	2	2	2	1	2	2	0	2	0	0	0	2
Nalb	2	2	2	1	2	2	0	2	0	0	0	2
Oflu	2	0	1	1	1	0	0	0	2	0	0	2
Pamp	2	2	1	2	1	1	0	0	2	0	1	1
Pber	0	0	0	1	1	1	0	0	2	0	2	1
Pcol	0	0	1	1	1	0	2	0	1	0	2	0
Pcri	0	0	1	1	1	1	0	0	2	0	2	2
Pluc	0	0	2	1	2	1	2	0	1	0	0	2
Pnat	0	0	1	1	2	1	2	0	1	0	1	2
Pnod	0	0	2	1	2	1	2	0	1	0	0	2
Pobt	0	0	0	1	1	1	0	0	2	0	1	2
Ppec	0	0	1	1	1	2	0	0	2	0	1	2
Ppol	0	0	1	1	1	1	2	0	1	0	2	1
Ppus	0	0	1	1	1	1	0	0	2	0	2	0
Ptri	0	0	1	1	1	1	0	0	2	0	2	0
Raqu	2	0	0	1	1	2	0	0	2	0	2	2
Rpel	2	0	0	1	1	2	0	0	2	0	2	2
Rpen	2	0	0	2	1	2	0	0	2	0	0	2
Rtri	2	0	0	1	1	2	0	0	2	0	2	2
Rcir	2	0	0	1	1	2	0	0	2	0	2	2
Ssag	2	0	1	1	1	1	0	2	0	0	0	2
Sang	0	0	1	1	1	2	2	0	0	0	0	2
Seme	0	0	1	1	1	2	2	0	0	0	0	2
Spol	0	0	0	0	1	0	0	0	0	2	0	0
Uint	2	0	0	1	1	2	0	0	2	0	2	2
Uvul	2	0	0	1	1	2	0	0	2	0	2	2
Zpal	0	0	0	1	1	0	0	0	2	0	2	2
Callitriche cophocarpa	0	0	0	0	1	0	2	0	0	0	2	0
Oenanthe aquatica	2	0	0	2	1	2	0	0	2	0	0	2
Potamogeton alpinus	0	0	1	1	1	1	2	0	0	0	2	0
Ranunculus fluitans	2	2	0	1	1	2	0	0	2	0	0	2
Stratiotes aloides	1	1	0	2	1	0	0	2	0	0	2	0
Utricularia australis	2	0	0	1	1	0	0	0	2	0	1	2

Species codes	Trait codes ls	lr	lw	las	lam	lal	hco3	ear	mid	late	rhi	fra
Cham	2	0	0	2	0	0	0	2	2	2	0	2
Csta	2	0	0	2	0	0	0	2	2	2	0	2
Cobt	2	0	0	2	0	0	0	2	2	2	0	2
Cpla	2	0	0	2	0	0	0	2	2	2	0	2
Cdem	0	2	0	2	0	0	2	0	2	2	0	2
Eaci	0	2	0	0	0	0	0	0	1	1	2	0
Ecan	0	2	0	2	0	0	2	0	0	0	2	2
Gdec	2	0	0	0	2	0	0	0	2	2	0	2
Gflu	2	0	0	0	2	0	0	2	2	0	0	2
Hpal	2	0	0	0	2	0	0	2	2	0	0	0
Hmor	0	2	2	0	2	0	0	0	2	0	0	2
Jbul	2	0	0	2	0	0	0	0	2	2	0	0
Lmin	0	2	2	2	0	0	0	0	2	0	0	2
Ltri	0	2	0	2	0	0	2	2	2	0	0	2
Malt	2	0	0	2	0	0	2	2	2	0	2	2
Mspi	2	0	0	2	0	0	2	0	2	0	2	2
Mver	2	0	0	2	0	0	1	0	2	0	2	1
Nlut	2	2	2	0	0	2	0	0	2	0	2	0
Npum	2	2	2	0	0	2	0	0	2	0	2	0
Nalb	0	2	2	0	0	2	0	0	2	0	2	0
Oflu	2	0	0	0	2	0	0	0	2	2	0	0
Pamp	0	2	2	0	2	0	1	0	2	2	2	2
Pber	2	0	0	2	0	0	1	0	2	2	0	2
Pcol	0	2	0	0	2	0	1	0	2	0	2	0
Pcri	0	2	0	1	2	0	2	2	2	2	2	0
Pluc	2	0	0	0	1	2	2	0	2	2	2	2
Pnat	1	2	2	0	2	0	0	2	2	2	2	1
Pnod	1	2	2	0	2	1	2	0	2	2	2	2
Pobt	2	0	0	2	1	0	1	0	2	2	0	1
Ppec	2	0	0	2	0	0	2	2	2	2	2	1
Ppol	1	2	2	0	2	0	0	2	2	2	2	0
Ppus	2	0	0	2	0	0	2	0	2	2	0	2
Ptri	2	0	0	2	0	0	1	0	2	2	1	1
Raqu	2	2	0	0	2	0	2	2	2	0	0	2
Rpel	2	2	0	0	2	0	1	2	2	0	0	1
Rpen	2	2	0	0	2	0	2	2	2	0	0	2
Rtri	2	0	0	0	2	0	1	2	2	0	0	1
Rcir	0	2	0	1	2	0	2	2	2	0	0	1
Ssag	2	2	2	0	2	2	1	0	2	0	0	0
Sang	2	0	0	0	2	0	1	0	2	2	2	0
Seme	2	0	0	0	2	0	1	0	2	0	2	0
Spol	0	2	2	2	0	0	0	0	2	0	0	2
Uint	2	0	0	2	0	0	1	0	2	2	0	0
Uvul	2	0	0	2	0	0	1	0	2	0	0	0
Zpal	2	0	0	2	0	0	2	2	2	0	2	0
Callitriche cophocarpa	2	0	0	2	0	0	0	2	2	2		
Oenanthe aquatica	2	0	0	0	2	0	1	0	2	2		
Potamogeton alpinus	1	0	1	0	2	0	1	0	2	2		
Ranunculus fluitans	2	0	0	0	2	0	1	0	2	0		
Stratiotes aloides	0	2	2	0	0	2	1	0	2	0		
Utricularia australis	2	0	0	2	0	0	1	0	2	0		

Species codes	Trait codes tur	tsb	psb	sto	sbn	sbl	sbm	sbh	buo	sss	ssm	ssl
Cham	0	0	1	2	0	1	1	0	0	0	2	0
Csta	0	0	1	2	0	1	1	0	0	0	2	0
Cobt	0	0	1	2	0	1	1	0	0	0	2	0
Cpla	0	0	1	2	0	1	1	0	0	0	2	0
Cdem	1	1	1	0	0	1	0	0	0	0	0	2
Eaci	0	1	0	2	2	1	0	0	1	0	2	0
Ecan	1	0	0	2	2	0	0	0	0	0	0	0
Gdec	0	2	0	0	0	0	0	1	2	0	2	0
Gflu	0	1	0	2	0	0	0	2	2	0	2	0
Hpal	0	1	1	2	0	1	1	1	1	0	0	2
Hmor	2	1	0	2	2	1	0	0	0	0	2	0
Jbul	0	0	2	2	1	1	1	1	1	2	0	0
Lmin	0	1	0	0	2	2	0	0	1	2	0	0
Ltri	0	1	0	0	2	2	0	0	1	2	0	0
Malt	0	1	1	0	0	0	2	0	2	0	2	0
Mspi	0	0	2	0	0	0	2	0	2	0	2	0
Mver	2	1	1	0	0	0	2	0	2	0	2	0
Nlut	0	2	0	0	0	0	1	2	1	0	0	2
Npum	0	2	0	0	0	0	2	0	1	0	0	2
Nalb	0	2	0	0	0	0	0	2	2	0	2	0
Oflu	1	2	0	0	1	1	1	1	2	0	0	2
Pamp	0	0	1	0	0	0	1	0	1	0	2	0
Pber	2	1	1	1	0	0	1	0	2	0	2	0
Pcol	2	1	1	2	0	1	0	0	2	0	2	0
Pcri	2	0	1	2	0	0	2	0	2	0	2	0
Pluc	2	1	1	0	0	0	1	0	2	0	0	2
Pnat	1	0	2	0	0	0	1	0	2	0	0	2
Pnod	2	1	1	0	0	0	1	0	2	0	0	2
Pobt	2	1	1	0	0	0	1	0	2	0	0	2
Ppec	2	0	2	0	0	0	2	1	2	0	0	2
Ppol	2	1	1	0	0	0	1	0	2	0	2	0
Ppus	2	1	1	1	0	0	1	0	2	0	2	0
Ptri	0	1	1	1	0	0	1	0	2	0	2	0
Raqu	0	1	1	1	0	0	0	1	2	0	2	0
Rpel	0	1	1	1	0	0	0	1	2	0	2	0
Rpen	0	2	0	2	0	0	0	1	2	0	2	0
Rtri	0	1	1	1	0	0	0	1	2	0	2	0
Rcir	0	1	1	1	0	0	0	1	2	0	2	0
Ssag	2	1	1	2	0	0	1	0	1	2	0	0
Sang	0	1	1	0	0	0	0	1	2	0	0	2
Seme	0	1	1	0	0	0	0	1	2	0	0	2
Spol	2	0	0	0	2	1	0	0	1	2	0	0
Uint	2	1	1	0	2	2	0	0	1	2	0	0
Uvul	2	1	1	0	0	0	0	2	1	2	0	0
Zpal	0	1	1	0	0	1	0	0	1	0	2	0
Callitriche cophocarpa												
Oenanthe aquatica												
Potamogeton alpinus												
Ranunculus fluitans												
Stratiotes aloides												
Utricularia australis												

Appendix 6

Euhydrophyte traits measured in the field 1992 & 1993: Population level

Site codes see Table 2.1
Trait codes and units see Table 4.2
Where populations were sampled in both years the average has been used.

			trait code									
code	species	site	%fl	tlv	lvl	lvb	lvt	int	lpern	norep	st	sl
1	*C.hamulata*	ekrf	9	94	2.96	0.21	0.1	1.32	2	6	0.46	26
2a	*C.obtusangula*	icdi	13	61	1.67	0.51	0.2	3.7	2	10	0.87	18
2b	*C.obtusangula*	ibd4	8	154	2.82	0.31	0.2	2.12	2	15	0.6	52
3a	*C.platycarpa*	ilbr	0	20	1.76	0.5	0.2	4.56	2	0	0.5	25
3b	*C.platycarpa*	icdo	10	144	2.46	0.19	0.1	1.36	2	8	0.5	27
3c	*C.platycarpa*	fappo	35	31	1.3	0.44	0.24	2.14	2	12	0.53	33
4a	*C.stagnalis*	icdi	20	43	1.4	0.58	0.1	4.2	2	17	0.81	38
4b	*C.stagnalis*	ekox	0	29	2.99	0.13	0.24	3.88	2	0	0.58	24
4c	*C.stagnalis*	ceab	33	55	1.34	0.48	0.1	2.44	2	11	0.34	28
5a	*C.demersum*	faoa	0	2485	1.89	0.14	0.1	2.09	8	3	0.85	69
5b	*C.demersum*	fmbw	0	2373	1.7	0.62	0.1	1.94	10	0	0.99	57
6a	*E.canadensis*	icdo	0	86	0.94	0.33	0.1	0.87	3	0	1.04	15
6b	*E.canadensis*	ciid	0	150	0.99	0.3	0.1	1.22	3	0	1.36	35
6c	*E.canadensis*	ceab	0	76	1	0.25	0.1	1.12	3	0	0.98	21
6d	*E.canadensis*	ceta	0	104	1.01	0.34	0.1	0.96	3	0	1	23
6e	*E.canadensis*	cewp	0	176	1.2	0.18	0.1	0.77	3	0	1.24	28
6f	*E.canadensis*	fapdo	4	197	0.97	0.3	0.1	0.55	3	0	1	41
6g	*E.canadensis*	fappo	2	221	0.86	0.25	0.1	0.56	3	2	1.22	42
7a	*H.morsus-ranae*	fapdo	100	5	2.86	2.76	0.36	0.01	1	0	1.3	8
7b	*H.morsus-ranae*	fapdi	100	5	3.4	3.6	0.39	0.01	1	3	1.88	9
8a	*M.alterniflorum*	cisr	0	482	1.29	0.97	0.1	0.96	4	4	1.15	59
8b	*M.alterniflorum*	eksrl	0	2673	1.63	0.73	0.1	0.8	4	0	2	65
9	*M.spicatum*	faod	0	399	2.03	1.03	0.26	2.33	4	2	2.6	84
10	*M.verticilatum*	ibd3	3	154	2.64	2.14	0.3	1.7	4	1	1.98	93
11	*N.lutea*	ibip	22	9	18.2	14.6	0.3	0.72	1	1	8	72
12	*N.pumila*	cinl	21	13	11.6	10.5	0.53	0.8	1	2	4.25	25
13	*N.alba*	ciox	89	9	18.94	17.18	0.82	0.16	1	6	7.24	52
14	*P.amphibia*	fapdl	36	144	11.32	3.62	0.28	3	1	2	2.74	93
15	*P.coloratus*	ibd2	100	9	5.06	2.98	0.22	2.05	1	3	1.85	15
16	*P.crispus*	ilbr	0	30	5.6	0.78	0.28	4.44	1	1	1.3	58
17	*P.lucens*	ibip	21	28	25.2	4.21	0.2	3.22	1	1	5	196
18a	*P.natans*	cirl	62	13	7.7	3.95	0.37	8.4	1	0	2.74	157
18b	*P.natans*	ciid	86	6	7.68	3.42	0.39	6.9	1	0	1.12	98
18c	*P.natans*	cegd	86	7	7.43	3.36	0.31	6.32	1	1	1.83	99
18d	*P.natans*	cegd	75	4	6.84	2.96	0.24	4.18	1	1	1.58	95
19a	*P.nodosus*	faoa	68	6	6.04	2.64	0.41	0.72	1	1	2.12	67
19b	*P.nodosus*	faod	56	5	7.18	3.3	0.39	0.65	1	1	2.12	79
19c	*P.nodosus*	fado	83	6	11	4.16	0.5	2.58	1	2	2.36	72
20a	*P.obtusifolius*	cirl	0	44	10.28	0.42	0.1	8.08	1	0	1.08	109
20b	*P.obtusifolius*	ciid	0	51	7.85	0.41	0.1	1.88	1	1	0.93	39
20c	*P.obtusifolius*	cinl	0	39	8.67	0.35	0.16	5.84	1	1	1.07	59
21a	*P.polygonifolius*	ciwp	87	8	8.76	2.14	0.28	3.46	1	1	1.82	37
21b	*P.polygonifolius*	ceta	96	5	7.06	3.1	0.3	3.38	1	0	1.44	60
22	*R.circinatus*	faoa	0	34	1.12	2.28	0.4	6.22	1	2	1.14	63
23	*R.peltatus*	faod	7	45	1.86	3.11	0.17	2.8	1	6	1.56	48
24a	*R.penicillatus*	ekrf	21	28	6.75	1.92	0.28	7.14	1	9	2.04	72
24b	*R.penicillatus*	ebmr	14	50	11.52	2.42	0.3	9.76	1	8	2.36	118
25	*S.emersum*	ciid	11	9	55.58	6	0.47	0.01	1	0	6.36	56
26	*U.vulgaris*	faoa	0	58	2.56	2.7	0.1	0.11	1	1	0.8	40
27	*Z.palustris*	ilbr	0	48	6.33	0.1	0.19	5.5	2	8	0.82	56
28	*L.minor*	ilbd3	100	3	0.5	0.2	0.2	0.01	1	0	0.01	0.4

			trait code								
code	species	site	bios	biol	bior	%s	%l	%r	tbio	nseed	la
1	*C.hamulata*	ekrf	0.07	0.06	0.01	52	47	1	0.14	24	24
2a	*C.obtusangula*	icdi	0.07	0.08	0	47	53	0	0.15	40	36
2b	*C.obtusangula*	ibd4	0.31	0.31	0	50	50	0	0.62	60	14
3a	*C.platycarpa*	ilbr	0.02	0.04	0	34	66	0	0.06	5	31
3b	*C.platycarpa*	icdo	0.14	0.14	0	51	49	0	0.28	32	31
3c	*C.platycarpa*	fappo	0.04	0.04	0	50	50	0	0.08	24	31
4a	*C.stagnalis*	icdi	0.04	0.05	0	47	53	0	0.09	68	27
4b	*C.stagnalis*	ekox	0.03	0.03	0	50	50	0	0.06	0	27
4c	*C.stagnalis*	ceab	0.03	0.05	0	36	64	0	0.08	11	27
5a	*C.demersum*	faoa	1.2	5.5	0.01	18	82	0.1	6.7	31	1
5b	*C.demersum*	fmbw	0.92	4.82	0	16	84	0	5.74	0	1
6a	*E.canadensis*	icdo	0.06	0.11	0	35	65	0	0.17	0	23
6b	*E.canadensis*	ciid	0.21	0.33	0	39	61	0	0.54	0	23
6c	*E.canadensis*	ceab	0.06	0.1	0	37	63	0	0.16	0	23
6d	*E.canadensis*	ceta	0.1	0.15	0	41	59	0	0.24	0	23
6e	*E.canadensis*	cewp	0.16	0.18	0	47	53	0	0.33	0	23
6f	*E.canadensis*	fapdo	0.32	0.32	0	50	50	0	0.64	0	23
6g	*E.canadensis*	fappo	0.35	0.42	0.01	45	54	1	0.78	0	23
7a	*H.morsus-ranae*	fapdo	0.15	0.34	0	31	69	0	0.49	0	704
7b	*H.morsus-ranae*	fapdi	0.3	0.68	0.13	27	61	11	1.1	322	704
8a	*M.alterniflorum*	cisr	0.83	1.03	0.15	41	51	7	2.01	41	1
8b	*M.alterniflorum*	eksrl	5.2	6.5	0	44	56	0	11.7	0	8
9	*M.spicatum*	faod	3.13	9.3	0.18	25	74	1	12.61	60	10
10	*M.verticilatum*	ibd3	2.11	1.33	0.11	59	37	3	0.71	319	5
11	*N.lutea*	ibip	5.49	25.35	2.76	16	75	8	33.6	418	20500
12	*N.pumila*	cinl	27.6	54.8	8.05	31	61	8	90.45	85	8800
13	*N.alba*	ciox	40.04	60.5	10.05	36	55	9	110.59	1700	27200
14	*P.amphibia*	fapdi	5.78	3.58	0.23	60	37	3	9.59	70	1776
15	*P.coloratus*	ibd2	0.54	0.91	0.29	31	52	17	1.74	168	888
16	*P.crispus*	ilbr	0.55	1.14	0.01	32	67	1	1.78	23	201
17	*P.lucens*	ibip	12.96	23.3	0.39	35	64	1	36.65	94	4190
18a	*P.natans*	cirl	11.2	5.53	0	67	33	0	16.73	0	1932
18b	*P.natans*	ciid	3.32	2.16	0	61	39	0	5.43	0	1931
18c	*P.natans*	cegd	4.11	3.07	0.32	55	41	4	7.5	57	1930
18d	*P.natans*	cegd	2.83	1.36	0.32	63	30	7	4.51	89	1930
19a	*P.nodosus*	faoa	2.29	2.73	0.18	44	53	3	5.2	57	1500
19b	*P.nodosus*	faod	1.85	2.07	0.37	43	48	9	4.29	56	1500
19c	*P.nodosus*	fado	3.77	4.04	0.41	46	49	5	8.22	235	2098
20a	*P.obtusifolius*	cirl	0.33	0.63	0	34	66	0	0.96	0	120
20b	*P.obtusifolius*	ciid	0.45	0.91	0.01	33	66	1	1.37	28	100
20c	*P.obtusifolius*	cinl	0.56	0.87	0.01	39	60	1	1.44	28	106
21a	*P.polygonifolius*	ciwp	0.79	1.21	0.05	39	59	2	2.05	24	1300
21b	*P.polygonifolius*	ceta	1.54	2.07	0	43	57	0	3.61	0	1300
22	*R.circinatus*	faoa	0.82	1.2	0.02	40	59	1	2.04	24	112
23	*R.peltatus*	faod	0.95	1.23	0.05	43	55	2	2.23	126	165
24a	*R.penicillatus*	ekrf	1.53	1.22	0.18	52	42	6	2.93	70	206
24b	*R.penicillatus*	ebmr	3.4	4.17	0.12	44	54	2	7.69	100	206
25	*S.emersum*	ciid	0.18	1.43	0	11	89	0	1.61	0	2312
26	*U.vulgaris*	faoa	0.45	2.69	0.43	13	75	12	3.57	95	13
27	*Z.palustris*	ilbr	0.18	0.16	0.01	52	47	1	0.35	20	8
28	*L.minor*	ilbd3	0	0.01	0	0	100	0	0.01	0	4

Appendix 7

1994 field survey (Czech and Slovak Republics): Environmental parameters

Site codes see Table 9.2
Parameter codes and units see section 3.2.2

Site	Map ref.	Date	Time	D	Temp C	Cond	DO%	DOmg	pH	Pw	Nw
cz1	38 e4	27/05/94	13:00	0.77	19	630	51	4.6	7.25	420	85.5
cz2	38 f4	28/05/94	10:00	0.58	17.8	462	32	2.7	7.36	103	6.12
cz2b	38 f4	28/05/94	10:30	0.96	17.8	462	32	2.7	7.36	103	6.12
cz3	38 f4	28/05/94	11:00	1.12	19.2	498	97	9.1	7.37	19.4	17
cz4	36 f2	28/05/94	15:00	0.25	15	410	127	9.1	7.86	39.6	6660
cz5	16 c1	30/05/94	13:00	0.48	17	690	90	9.3	7.5	13.7	95.4
cz6	15 e1	30/05/94	17:00	0.71	17	659	34	3.2	7.09	24.6	12.1
cz7	15 e1	30/05/94	18:00	0.8	18	679	50	4.6	7.6	14.2	28.9
cz8	15 c2	31/05/94	08:30	0.24	13	790	80	8.4	8.23	139	3505
cz9	07 c3	31/05/94	11:10	0.31	13	270	86	8.6	7.57	22	2295
cz10	06 d4	31/05/94	12:15	0.28	13	437	120	12.4	7.88	14.2	1280
cz11	13 b3	31/05/94	15:25	0.32	15	980	81	8.1	7.23	15.3	4065
cz12	62 c4	04/06/94	11:00	1.2	19	1120	12	0.9	7.7	76.3	116
cz13	62 c4	04/06/94	15:55	0.5	22	970	26	2.2	7.68	37	1228
cz14	35 e2	06/06/94	13:00	0.55	15	148	86	8.4	7.42	46.3	13.1
cz15	35 e2	06/06/94	14:00	0.56	13	248	90	9.2	7.44	50.5	229

Site	K	Secchi cm	flow	Tshade	Ecover	SL	NH4-N(w)	NO2-N(w)	C sed	N sed
cz1	2.56	137	1	10	0	1.780641	1146	38.4	1.568	0.15
cz2	4.38	58+	1	0	0	1.381672	434	0.533	2.809	0.263
cz2b	2.65	96+	1	0	0	1.379717	434	0.533	4.41	0.351
cz3	1.39	112+	1	0	0	2.254625	814	1.48	12.339	1.069
cz4	1.31	m	5	20	0	10.71756	811	65.9	0.551	0.052
cz5	3.47	48+	1	40	0	2.107349	452	1.32	1.305	0.128
cz6	1.86	71+	1	30	0	2.657883	374	2.89	0.586	0.036
cz7	3.05	80+	1	0	5	1.438525	986	8.55	2.734	0.235
cz8	2.94	24+	4	10	10	4.97449	1164	128	0.41	0.024
cz9	2.35	31+	4	30	0	4.818119	530	47.5	0.681	0.041
cz10	0.24	28+	3	40	10	52.23214	764	35.6	5.208	0.452
cz11	0.7	32+	3	0	2	15.66964	604	47.7	14.662	0.783
cz12	4.38	120+	3	0	20	0.667808	540	59.5	4.701	0.418
cz13	3.94	50+	3	0	15	1.781726	596	0.218	7.026	0.539
cz14	5.49	28	1	0	2	1.162444	730	15.8	5.423	0.514
cz15	3.94	m	4	20	2	1.590827	890	53.5	6.205	0.563

Appendix 8

1994 field survey (Czech and Slovak Republics): Vegetation survey

Site codes see Table 9.2
All species rooted in water recorded, although only the euhydrophytes were used in subsequent analysis
Values shown are species frequencies converted from cover values (Bannister 1966)

	Site														
	cz1	cz2	cz2b	cz3	cz4	cz5	cz6	cz7	cz8	cz9	cz10	cz11	cz12	cz13	cz14	cz15
Agrostis stolonifera												1				
Berula erecta												1				
Callitriche cophocarpa	1															
C. hamulata												1				2
Callitriche spp						1					1					
Ceratophyllum demersum	5	3	8	1							1		1	2		
Chara spp											1					
Eleocharis acicularis											1					
Elodea canadensis											3					
Fontinalis antipyretica					7											
Glyceria fluitans															1	
Hottonia palustris		2	1					5								
Hydrocharis morsus-ranae													1	2		
Juncus bulbosus						9										
Lemna minor	1	1		1							1		10	10		
L. trisulca		6		1									9	3		
Mentha aquatica								1								
N. alba							1	1								
N. lutea	9						6	1	6							
Oenanthe aquatica														1		
Phalaris arundinacea											1					1
Phragmites australis									3				1	1		
Potamogeton alpinus						1										
P. crispus		1											1			
P. lucens				9												
Potamogeton spp											1					
P. trichoides		1	2	1									6			
Ranunculus aquatilis										2					9	1
R. circinatus				1												
R. fluitans					1					3						
R. penicillatus ssp. *pseudofluitans*										5						
Rorippa amphibia		1												2		
R. nasturtium-aquatica												1				
Sagitaria sagittifolia									1							
Sparganium emersum									1		1	1				3
Spirodela polyrhiza	1	2		6							1					
Stratiotes aloides		3														
Typha latifolia													2			
Utricularia australis						5										
U. vulgaris														4		
Veronica anagallis-aquatica												1				
Zannichellia palustris												1				
Chantransia chalybaea					1											
Cladophora glomerata					2											
Ulothrix zonata					1											
moss sp.					4											

Appendix 9

Euhydrophyte traits measured in the field 1994: Population level

Site codes see Table 9.2
Trait codes and units see Table 4.2

	Trait codes										
	site	fl lv	%fl	tlv	M	Mb	lt	int	lpem	norep	st
C. cophacarpa	cz1	2	3	69	2.4	00.15	0.1	1.4	2	0	0.5
C. hamulata	cz11	6	17	36	2.1	00.22	0.1	2.6	2	2	0.64
C. hamulata	cz15	0	0	92	2.5	00.14	0.1	3	2	12	0.5
C.demersum	cz1	0	0	1107	1.5	00.25	0.4	3	9	0	0.84
C.demersum	cz3	0	0	2660	1.2	00.32	0.4	2.8	10	9	1
C.demersum	cz10	0	0	360	1.2	00.20	0.3	1.8	9	0	1
E. canadensis	cz10	0	0	81	0.7	00.30	0.1	0.8	3	0	1.2
H. palustris	cz2	0	0	54	1.9	01.40	0.2	1.01	1	0	2.4
H. palustris	cz7	0	0	325	3.9	02.40	0.1	0.7	1	19	3.4
H. morsus-ranae	cz5	5	100	5	3.9	03.90	0.45	0.1	1	0	1.8
J. bulbosus	cz5	2	40	5	11.2	00.08	0.8	6.4	1	1	1.2
N. lutea	cz6	2	18	11	25.5	22.90	0.3	0.1	1	2	8.7
N. lutea	cz8	0	0	9	17	16.60	0.25	0.1	1	2	5.5
P. alpinus	cz5	0	0	15	12.6	01.90	0.1	1.2	1	0	2.8
P. lucens	cz3	0	0	45	13.5	03.90	0.3	5	1	1	3.22
P. trichoides	cz2	0	0	38	3.8	00.06	0.1	6.6	1	0	0.5
P. trichoides	cz12	0	0	27	4.7	00.08	0.1	7.2	1	0	0.6
R. aquatilis	cz9	7	27	26	6.3	03.40	0.3	10.5	1	6	2.2
R. aquatilis	cz14	25	60	42	1.5	02.20	0.24	6.8	1	31	2.2
R. aquatilis	cz15	16	14	115	5.7	01.32	0.2	7.5	1	11	1.9
R. circinatus	cz3	0	0	20	1.3	02.40	0.6	4.2	1	2	1.4
R. fluitans	cz4	0	0	12	8.3	00.18	0.9	2.2	1	0	1.8
R. fluitans	cz9	0	0	8	31.1	00.44	0.9	24	1	2	2.2
R. penicillatus	cz9	0	0	17	11	00.96	0.5	9.4	1	1	2.3
S. sagittifolia	cz8	0	0	8	20	00.95	0.3	0.1	1	0	0.4
S. emersum	cz8	3	38	8	30.5	00.48	0.2	0.1	1	0	4.5
S. emersum	cz10	1	17	6	32	00.30	0.2	0.1	1	0	2.6
S. emersum	cz15	0	0	8	44	00.47	0.4	0.1	1	0	4.9
S. polyrhiza	cz3	4	100	4	0.06	00.04	0.3	0	1	0	0
S. aloides	cz2	40	100	40	30	02.10	0.9	0.1	1	3	7
U. australis	cz5	0	0	35	0.9	00.52	0.1	0.67	1	0	0.6
U. vulgaris	cz13	0	0	1348	3.4	02.80	0.1	0.7	1	2	1.5
Z. palustris	cz11	0	0	28	6.4	00.08	0.2	1.6	2	2	0.9

	Trait codes									
	sl	bios	biol	bior	%s	%l	%r	tbio	nseed	la
C. cophacarpa	16	0.00	0.02	0.00	20	80	0	0.02	0	19
C. hamulata	21	0.01	0.01	0.00	50	50	0	0.02	8	23
C. hamulata	48	0.01	0.02	0.00	31	63	6	0.03	48	37
C.demersum	73	0.17	0.66	0.00	20	80	0	0.83	0	9
C.demersum	153	0.30	1.21	0.01	20	79	1	1.52	67	9
C.demersum	32	0.04	0.12	0.00	25	75	0	0.16	0	9
E. canadensis	28	0.03	0.04	0.00	43	57	0	0.07	0	23
H. palustris	18	0.12	0.22	0.00	35	65	0	0.34	0	80
H. palustris	95	0.77	1.50	0.06	33	64	3	2.33	950	186
H. morsus-ranae	10	0.06	0.13	0.00	32	68	0	0.19	0	997
J. bulbosus	26	0.02	0.02	0.01	52	35	13	0.05	9	45
N. lutea	41	4.78	5.95	0.13	44	55	1	10.86	836	21734
N. lutea	29	1.74	3.31	0.30	32	62	6	5.35	836	22968
P. alpinus	27	0.98	0.03	0.00	97	3	0	1.01	0	1467
P. lucens	11	3.70	4.68	0.13	43	55	2	8.52	94	3384
P. trichoides	78	0.04	0.01	0.00	86	14	0	0.04	0	23
P. trichoides	75	0.03	0.01	0.00	71	29	0	0.05	0	37
R. aquatilis	72	0.20	0.32	0.01	38	61	2	0.53	72	148
R. aquatilis	98	0.97	0.39	0.16	64	26	11	1.52	372	110
R. aquatilis	172	1.56	2.53	0.05	38	61	1	4.14	132	129
R. circinatus	40	0.05	0.08	0.01	37	58	5	0.13	12	75
R. fluitans	25	0.05	0.08	0.00	37	63	0	0.12	0	109
R. fluitans	113	0.16	0.27	0.01	36	63	1	0.43	24	492
R. penicillatus	95	0.22	0.30	0.00	42	58	1	0.52	12	535
S. sagittifolia	33	0.23	0.33	0.00	41	59	0	0.56	0	1520
S. emersum	46	0.07	0.19	0.00	26	74	0	0.26	0	1464
S. emersum	46	0.02	0.04	0.00	33	67	0	0.06	0	960
S. emersum	65	0.02	0.17	0.00	8	92	0	0.19	0	2060
S. polyrhiza	0	0.00	0.01	0.00	0	100	0	0.01	0	17
S. aloides	36	0.44	13.24	0.42	3	94	3	14.10	36	5452
U. australis	10	0.01	0.02	0.00	26	74	0	0.02	0	3
U. vulgaris	64	0.14	0.47	0.04	21	72	7	0.65	250	55
Z. palustris	17	0.00	0.02	0.00	18	81	0	0.02	6	71

Appendix 10

Seedling regeneration from sediment cores from selected sites under various germination conditions

Site codes see Table 2.1
Treatment explanations see section 7.5

Site	fmlbw									
Treatment	12 cm flooding									
Replicate and horizon	1a	1b	5a	5b	9a	9b	10a	10b	14a	14b
Agrostis stolonifera L.				3						
Alisma plantago aquatica L.										3
Anthemis spp										
Apium spp										
Bidens tripartita L.										
Callitriche stagnalis Scop.										
Caltha palustris L. ?										
Cardamine pratensis L.?										
Carex dioica L.										
Carex vesicarisa L.		3								
Carex spp										
Ceratophyllum demersum L.										
C. vulgaris var longibractea										
Chenopodium polyspernum L.				1						
Chenopodium spp										
Cyperus fuscus L.										1
Echinochloa crusgalli (L.) P. Beauv.										3
Eleocharis palustre (L.) (L.) Roemer and Schultes										
Epilobium obscurum Schreber										
Equisetum fluviatile L.										
Galium palustre L.										
Glyceria maxima (Hartman) O. Holumb.										
Gnaphalium uliginosum L.										
Hydrocharis morsus-ranae L.										
Juncus articulatus L.						1				
Juncus bufonius L.										
Juncus spp										
Leersia oryzoides (L.) Sw					16	37		9	5	6
Lemna minor L.								11		
Spirodela polyrhiza (L.) Schleiden										
Limnosella aquatica L.										
Lindernia dubia	1	3	260	257	427	152	141	152	45	33
Ludwigia palustris (L.) Elliott										
Lythrum portula (L.) D. Webb										
Lythrum salicaria L.										
Lysimachia thyrisflora L.										
Mentha aquatica L.										
Mentha pulegium L.										
Myosotis scorpiodes L.										
Myosoton aquaticum (L.) Moench										
Myriophyllum spicatum L.										
Oxalis spp										
Panicum ?capillare L.										
Persicaria hydropiper (L.) Spach										
Persicaria maculosa Gray		2	1		1		2			
Phalaris arundinacea L.										
Plantago major L.										
Poa pratensis L.										
Potamogeton crispus L.										
Potamogeton nodosus Poiret										
Potamogeton trichoides Cham & Schldl.										
Ranunculus circinatus Sibth.										
Ranunculus peltatus Schrank										
Ranunculus sceleratus L.										
Rorippa islandica (Oeder ex Murray)										
Rorippa spp.										
Sagittaria sagittifolia L.										
Salix sp.										
Sonchus sp.										
Trifolium repens L.										
Typha latifolia L.										
Urtica dioica L.										
Veronica catenata Pennell										
Veronica spp										
unidentified	3	3							1	

Site	fmlbw									
Treatment	2 cm flooding									
Replicate and horizon	2a	2b	6a	6b	7a	7b	11a	11b	15a	15b
Agrostis stolonifera L.										
Alisma plantago aquatica L.										
Anthemis spp										
Apium spp										
Bidens tripartita L.					1					
Callitriche stagnalis Scop.										
Caltha palustris L. ?										
Cardamine pratensis L.?										
Carex dioica L.										
Carex vesicarisa L.										
Carex spp			1							
Ceratophyllum demersum L.										
C. vulgaris var longibractea										
Chenopodium polyspernum L.			1	2						
Chenopodium spp										
Cyperus fuscus L.	3	4	3	6	5	7	3	2	1	1
Echinochloa crusgalli (L.) P. Beauv.	3		3	5	4	1				
Eleocharis palustre (L.) (L.) Roemer and Schultes							2			
Epilobium obscurum Schreber										
Equisetum fluviatile L.										
Galium palustre L.										
Glyceria maxima (Hartman) O. Holumb.										
Gnaphalium uliginosum L.										
Hydrocharis morsus-ranae L.										
Juncus articulatus L.								2		
Juncus bufonius L.										
Juncus spp										
Leersia oryzoides (L.) Sw	1		42	123	3	6	4	4	1	
Lemna minor L.							22			
Spirodela polyrhiza (L.) Schleiden										
Limnosella aquatica L.										
Lindernia dubia	29	6	300	145	334	225	51	54	35	19
Ludwigia palustris (L.) Elliott										
Lythrum portula (L.) D. Webb										
Lythrum salicaria L.			1	2						
Lysimachia thyrisflora L.										
Mentha aquatica L.										
Mentha pulegium L.										
Myosotis scorpiodes L.										
Myosoton aquaticum (L.) Moench										
Myriophyllum spicatum L.										
Oxalis spp										
Panicum ?capillare L.										
Persicaria hydropiper (L.) Spach							1	1		
Persicaria maculosa Gray	1			3			1			
Phalaris arundinacea L.										
Plantago major L.										
Poa pratensis L.										
Potamogeton crispus L.										
Potamogeton nodosus Poiret										
Potamogeton trichoides Cham & Schldl.										
Ranunculus circinatus Sibth.										
Ranunculus peltatus Schrank										
Ranunculus sceleratus L.										
Rorippa islandica (Oeder ex Murray)										
Rorippa spp.										
Sagittaria sagittifolia L.										
Salix sp.										
Sonchus sp.										
Trifolium repens L.										
Typha latifolia L.										
Urtica dioica L.										
Veronica catenata Pennell										
Veronica spp										
unidentified	3	6								

Site	fmlbw									
Treatment	moist									
Replicate and horizon	3a	3b	4a	4b	8a	8b	12a	12b	13a	13b
Agrostis stolonifera L.			3	2						
Alisma plantago aquatica L.										
Anthemis spp										
Apium spp										
Bidens tripartita L.				5	1					
Callitriche stagnalis Scop.										
Caltha palustris L. ?										
Cardamine pratensis L.?	2	2		3	2			1		
Carex dioica L.										
Carex vesicarisa L.										
Carex spp						2				
Ceratophyllum demersum L.										
C. vulgaris var longibractea										
Chenopodium polyspernum L.		5	1	3			1			
Chenopodium spp										
Cyperus fuscus L.	1	7		62	10	6	2	1	7	3
Echinochloa crusgalli (L.) P. Beauv.				10	4					2
Eleocharis palustre (L.) (L.) Roemer and Schultes								1		2
Epilobium obscurum Schreber										
Equisetum fluviatile L.										
Galium palustre L.										
Glyceria maxima (Hartman) O. Holumb.										
Gnaphalium uliginosum L.	2	15	1	5	18	4	1			1
Hydrocharis morsus-ranae L.										
Juncus articulatus L.						3				
Juncus bufonius L.					1	1				
Juncus spp					2					3
Leersia oryzoides (L.) Sw			12	54	45	187	2		1	12
Lemna minor L.										6
Spirodela polyrhiza (L.) Schleiden										
Limnosella aquatica L.										
Lindernia dubia	49	30		172	600	360	109	73	117	109
Ludwigia palustris (L.) Elliott										
Lythrum portula (L.) D. Webb		1	4				1			
Lythrum salicaria L.		3	1	3	5	3		2	1	
Lysimachia thyrisflora L.			1						1	1
Mentha aquatica L.						1	2			
Mentha pulegium L.				1						1
Myosotis scorpiodes L.										
Myosoton aquaticum (L.) Moench										
Myriophyllum spicatum L.										
Oxalis spp										
Panicum ?capillare L.			3	4		2		2		
Persicaria hydropiper (L.) Spach			1	3						
Persicaria maculosa Gray	2			4	2	2				
Phalaris arundinacea L.										
Plantago major L.			2	24	12	3				,
Poa pratensis L.										
Potamogeton crispus L.										
Potamogeton nodosus Poiret										
Potamogeton trichoides Cham & Schldl.										
Ranunculus circinatus Sibth.										
Ranunculus peltatus Schrank										
Ranunculus sceleratus L.										
Rorippa islandica (Oeder ex Murray)										
Rorippa spp.										
Sagittaria sagittifolia L.										
Salix sp.										
Sonchus sp.										1
Trifolium repens L.										
Typha latifolia L.										
Urtica dioica L.										
Veronica catenata Pennell										
Veronica spp										
unidentified		16	7					1	1	

Site	fapoxa									
Treatment	12 cm flooding									
Replicate and horizon	1a	1b	5a	5b	9a	9b	10a	10b	14a	14b
Agrostis stolonifera L.										
Alisma plantago aquatica L.										
Anthemis spp										
Apium spp										
Bidens tripartita L.										
Callitriche stagnalis Scop.										
Caltha palustris L. ?										
Cardamine pratensis L.?										
Carex dioica L.										
Carex vesicarisa L.										
Carex spp										
Ceratophyllum demersum L.	1		1							
C. vulgaris var longibractea										
Chenopodium polyspernum L.										
Chenopodium spp										
Cyperus fuscus L.										
Echinochloa crusgalli (L.) P. Beauv.										
Eleocharis palustre (L.) (L.) Roemer and Schultes								1		
Epilobium obscurum Schreber										
Equisetum fluviatile L.										
Galium palustre L.										
Glyceria maxima (Hartman) O. Holumb.										
Gnaphalium uliginosum L.										
Hydrocharis morsus-ranae L.										
Juncus articulatus L.										
Juncus bufonius L.										
Juncus spp										
Leersia oryzoides (L.) Sw			1							
Lemna minor L.										
Spirodela polyrhiza (L.) Schleiden										
Limnosella aquatica L.										
Lindernia dubia										
Ludwigia palustris (L.) Elliott									1	
Lythrum portula (L.) D. Webb										
Lythrum salicaria L.									1	
Lysimachia thyrisflora L.										
Mentha aquatica L.										
Mentha pulegium L.										
Myosotis scorpiodes L.										
Myosoton aquaticum (L.) Moench										
Myriophyllum spicatum L.										
Oxalis spp										
Panicum ?capillare L.										
Persicaria hydropiper (L.) Spach										
Persicaria maculosa Gray										
Phalaris arundinacea L.										
Plantago major L.										
Poa pratensis L.										
Potamogeton crispus L.										
Potamogeton nodosus Poiret		1								
Potamogeton trichoides Cham & Schldl.										
Ranunculus circinatus Sibth.										
Ranunculus peltatus Schrank										
Ranunculus sceleratus L.										
Rorippa islandica (Oeder ex Murray)										
Rorippa spp.										
Sagittaria sagittifolia L.										
Salix sp.										
Sonchus sp.										
Trifolium repens L.										
Typha latifolia L.						1				
Urtica dioica L.										
Veronica catenata Pennell										
Veronica spp										
unidentified						2				

Site	fapoxa									
Treatment	2 cm flooding									
Replicate and horizon	2a	2b	6a	6b	7a	7b	11a	11b	15a	15b
Agrostis stolonifera L.										
Alisma plantago aquatica L.										
Anthemis spp		1								
Apium spp										
Bidens tripartita L.										
Callitriche stagnalis Scop.										
Caltha palustris L. ?										1
Cardamine pratensis L.?										
Carex dioica L.										
Carex vesicarisa L.										
Carex spp				1						
Ceratophyllum demersum L.			2		1					
C. vulgaris var longibractea										
Chenopodium polyspernum L.										
Chenopodium spp										
Cyperus fuscus L.	1	1			1		1	3		
Echinochloa crusgalli (L.) P. Beauv.										
Eleocharis palustre (L.) (L.) Roemer and Schultes										
Epilobium obscurum Schreber										
Equisetum fluviatile L.										
Galium palustre L.										
Glyceria maxima (Hartman) O. Holumb.										
Gnaphalium uliginosum L.										
Hydrocharis morsus-ranae L.										
Juncus articulatus L.	1	1						4		
Juncus bufonius L.										
Juncus spp										
Leersia oryzoides (L.) Sw	3									
Lemna minor L.										
Spirodela polyrhiza (L.) Schleiden	5									
Limnosella aquatica L.										
Lindernia dubia	4	1								1
Ludwigia palustris (L.) Elliott	2				2			1	2	
Lythrum portula (L.) D. Webb										
Lythrum salicaria L.	1									
Lysimachia thyrisflora L.										
Mentha aquatica L.										
Mentha pulegium L.										
Myosotis scorpiodes L.										
Myosoton aquaticum (L.) Moench										
Myriophyllum spicatum L.			2							
Oxalis spp										
Panicum ?capillare L.										
Persicaria hydropiper (L.) Spach	1									
Persicaria maculosa Gray										
Phalaris arundinacea L.										
Plantago major L.										
Poa pratensis L.										
Potamogeton crispus L.					1					
Potamogeton nodosus Poiret	1		1		1	1				
Potamogeton trichoides Cham & Schldl.								1		
Ranunculus circinatus Sibth.	1			2				1		
Ranunculus peltatus Schrank										
Ranunculus sceleratus L.										
Rorippa islandica (Oeder ex Murray)										
Rorippa spp.										
Sagittaria sagittifolia L.										
Salix sp.										
Sonchus sp.										
Trifolium repens L.										
Typha latifolia L.										
Urtica dioica L.										
Veronica catenata Pennell										
Veronica spp										
unidentified			27	15	39	10		1		

Site	fapoxa									
Treatment	moist									
Replicate and horizon	3a	3b	4a	4b	8a	8b	12a	12b	13a	13b
Agrostis stolonifera L.					1				1	
Alisma plantago aquatica L.										
Anthemis spp					*1*					
Apium spp										
Bidens tripartita L.									1	
Callitriche stagnalis Scop.										
Caltha palustris L. ?										
Cardamine pratensis L.?									1	
Carex dioica L.	1									
Carex vesicarisa L.		1								
Carex spp	2			1						
Ceratophyllum demersum L.										
C. vulgaris var longibractea										
Chenopodium polyspernum L.					2				1	
Chenopodium spp										
Cyperus fuscus L.		1	9	6			1	1	2	1
Echinochloa crusgalli (L.) P. Beauv.										
Eleocharis palustre (L.) (L.) Roemer and Schultes										
Epilobium obscurum Schreber							1		1	
Equisetum fluviatile L.									1	
Galium palustre L.										
Glyceria maxima (Hartman) O. Holumb.										
Gnaphalium uliginosum L.										
Hydrocharis morsus-ranae L.										
Juncus articulatus L.		*1*	1	2	1					
Juncus bufonius L.										
Juncus spp										
Leersia oryzoides (L.) Sw			1						1	
Lemna minor L.										
Spirodela polyrhiza (L.) Schleiden										
Limnosella aquatica L.										
Lindernia dubia									1	
Ludwigia palustris (L.) Elliott	6	4	25	2	5			6	2	
Lythrum portula (L.) D. Webb										
Lythrum salicaria L.	2		6	4	8				1	
Lysimachia thyrisflora L.										
Mentha aquatica L.										
Mentha pulegium L.										
Myosotis scorpiodes L.										
Myosoton aquaticum (L.) Moench										
Myriophyllum spicatum L.										
Oxalis spp			2	1					1	
Panicum ?capillare L.										
Persicaria hydropiper (L.) Spach					1					
Persicaria maculosa Gray										
Phalaris arundinacea L.										
Plantago major L.										
Poa pratensis L.										
Potamogeton crispus L.										
Potamogeton nodosus Poiret										
Potamogeton trichoides Cham & Schldl.										
Ranunculus circinatus Sibth.										
Ranunculus peltatus Schrank										
Ranunculus sceleratus L.										
Rorippa islandica (Oeder ex Murray)										
Rorippa spp.										
Sagittaria sagittifolia L.										
Salix sp.										
Sonchus sp.										
Trifolium repens L.				1						
Typha latifolia L.										
Urtica dioica L.										
Veronica catenata Pennell										
Veronica spp				1						
unidentified		7	2						1	

Site	fapdi									
Treatment	12 cm flooding									
Replicate and horizon	1a	1b	5a	5b	9a	9b	10a	10b	14a	14b
Agrostis stolonifera L.										
Alisma plantago aquatica L.										
Anthemis spp										
Apium spp										
Bidens tripartita L.										
Callitriche stagnalis Scop.			4		3				3	
Caltha palustris L. ?										
Cardamine pratensis L.?										
Carex dioica L.										
Carex vesicarisa L.							1			
Carex spp										5
Ceratophyllum demersum L.	2									
C. vulgaris var longibractea									1	
Chenopodium polyspernum L.										
Chenopodium spp										
Cyperus fuscus L.										
Echinochloa crusgalli (L.) P. Beauv.										
Eleocharis palustre (L.) (L.) Roemer and Schultes										
Epilobium obscurum Schreber										
Equisetum fluviatile L.										
Galium palustre L.										
Glyceria maxima (Hartman) O. Holumb.										
Gnaphalium uliginosum L.										
Hydrocharis morsus-ranae L.							9			
Juncus articulatus L.					2					
Juncus bufonius L.										
Juncus spp										
Leersia oryzoides (L.) Sw										
Lemna minor L.										3
Spirodela polyrhiza (L.) Schleiden		9	7			3	35	11	10	25
Limnosella aquatica L.										
Lindernia dubia										
Ludwigia palustris (L.) Elliott										
Lythrum portula (L.) D. Webb										
Lythrum salicaria L.							1			
Lysimachia thyrisflora L.										
Mentha aquatica L.										
Mentha pulegium L.										
Myosotis scorpiodes L.										
Myosoton aquaticum (L.) Moench										
Myriophyllum spicatum L.										
Oxalis spp										
Panicum ?capillare L.										
Persicaria hydropiper (L.) Spach										
Persicaria maculosa Gray										
Phalaris arundinacea L.										
Plantago major L.										
Poa pratensis L.										
Potamogeton crispus L.										
Potamogeton nodosus Poiret										5
Potamogeton trichoides Cham & Schldl.										
Ranunculus circinatus Sibth.										
Ranunculus peltatus Schrank										
Ranunculus sceleratus L.										
Rorippa islandica (Oeder ex Murray)										
Rorippa spp.										
Sagittaria sagittifolia L.				6	1	1				
Salix sp.										
Sonchus sp.										
Trifolium repens L.										
Typha latifolia L.										
Urtica dioica L.										
Veronica catenata Pennell										
Veronica spp										
unidentified	5	7	2			2		2	16	16

Site	fapdi									
Treatment	2cm flooding									
Replicate and horizon	2a	2b	6a	6b	7a	7b	11a	11b	15a	15b
Agrostis stolonifera L.										
Alisma plantago aquatica L.	1									
Anthemis spp										
Apium spp										
Bidens tripartita L.										
Callitriche stagnalis Scop.			18		28				1	
Caltha palustris L. ?										
Cardamine pratensis L.?										
Carex dioica L.										
Carex vesicarisa L.		1								
Carex spp								2		
Ceratophyllum demersum L.										
C. vulgaris var longibractea										
Chenopodium polyspernum L.										
Chenopodium spp										
Cyperus fuscus L.	2	5	2	1	2	5			4	6
Echinochloa crusgalli (L.) P. Beauv.										
Eleocharis palustre (L.) (L.) Roemer and Schultes										
Epilobium obscurum Schreber								1		
Equisetum fluviatile L.										
Galium palustre L.										
Glyceria maxima (Hartman) O. Holumb.								1		1
Gnaphalium uliginosum L.										
Hydrocharis morsus-ranae L.										
Juncus articulatus L.	1				1	5				
Juncus bufonius L.										
Juncus spp										
Leersia oryzoides (L.) Sw		6	6	2	6	4		5	1	6
Lemna minor L.							10			
Spirodela polyrhiza (L.) Schleiden	20	24	21	68	10	32	17	3	20	23
Limnosella aquatica L.										
Lindernia dubia										
Ludwigia palustris (L.) Elliott									2	
Lythrum portula (L.) D. Webb										
Lythrum salicaria L.			3	2	4	6				2
Lysimachia thyrisflora L.										
Mentha aquatica L.										
Mentha pulegium L.										
Myosotis scorpiodes L.										
Myosoton aquaticum (L.) Moench										
Myriophyllum spicatum L.										
Oxalis spp										
Panicum ?capillare L.										
Persicaria hydropiper (L.) Spach										
Persicaria maculosa Gray										
Phalaris arundinacea L.										
Plantago major L.										
Poa pratensis L.										
Potamogeton crispus L.										
Potamogeton nodosus Poiret										
Potamogeton trichoides Cham & Schldl.										
Ranunculus circinatus Sibth.										
Ranunculus peltatus Schrank									1	
Ranunculus sceleratus L.										
Rorippa islandica (Oeder ex Murray)										
Rorippa spp.										
Sagittaria sagittifolia L.				1		2		1	1	
Salix sp.										
Sonchus sp.										
Trifolium repens L.										
Typha latifolia L.										
Urtica dioica L.										
Veronica catenata Pennell					1		1			
Veronica spp										
unidentified	1			1			1	2		

Site	fapdi									
Treatment	moist									
Replicate and horizon	3a	3b	4a	4b	8a	8b	12a	12b	13a	13b
Agrostis stolonifera L.			3	1	1		3			
Alisma plantago aquatica L.										
Anthemis spp										
Apium spp										
Bidens tripartita L.										
Callitriche stagnalis Scop.	1		8	3	12	1	2	1	27	13
Caltha palustris L. ?										
Cardamine pratensis L.?	2									
Carex dioica L.										
Carex vesicarisa L.	1			2		1		1		2
Carex spp		2			1					
Ceratophyllum demersum L.										
C. vulgaris var longibractea										
Chenopodium polyspernum L.				2						
Chenopodium spp										
Cyperus fuscus L.	8	16	19	11	8	1		3	3	2
Echinochloa crusgalli (L.) P. Beauv.			1							
Eleocharis palustre (L.) (L.) Roemer and Schultes										
Epilobium obscurum Schreber										
Equisetum fluviatile L.										
Galium palustre L.										2
Glyceria maxima (Hartman) O. Holumb.										2
Gnaphalium uliginosum L.										
Hydrocharis morsus-ranae L.										
Juncus articulatus L.	1		2	3	1					
Juncus bufonius L.										1
Juncus spp	3	11	22	4	2	8	1	3		3
Leersia oryzoides (L.) Sw	1	6	13	6	3	10		3	3	3
Lemna minor L.										
Spirodela polyrhiza (L.) Schleiden	28		12				23		12	59
Limnosella aquatica L.										
Lindernia dubia										
Ludwigia palustris (L.) Elliott	3								1	1
Lythrum portula (L.) D. Webb										1
Lythrum salicaria L.	9		17	9	22	4	4	4	8	7
Lysimachia thyrisflora L.			2							
Mentha aquatica L.										
Mentha pulegium L.										
Myosotis scorpiodes L.										
Myosoton aquaticum (L.) Moench										
Myriophyllum spicatum L.										
Oxalis spp										
Panicum ?capillare L.										
Persicaria hydropiper (L.) Spach				2		2				
Persicaria maculosa Gray			1							2
Phalaris arundinacea L.										
Plantago major L.										
Poa pratensis L.										
Potamogeton crispus L.										
Potamogeton nodosus Poiret										
Potamogeton trichoides Cham & Schldl.										
Ranunculus circinatus Sibth.										
Ranunculus peltatus Schrank										
Ranunculus sceleratus L.	2		1							1
Rorippa islandica (Oeder ex Murray)										
Rorippa spp.										
Sagittaria sagittifolia L.	1			1						
Salix sp.				1						
Sonchus sp.								1		
Trifolium repens L.										
Typha latifolia L.										
Urtica dioica L.				1						
Veronica catenata Pennell					5	1	1		4	2
Veronica spp										
unidentified	7	1	14	4		3	2			

Site	fdcbw							
Treatment	12cm flooding							
Replicate and horizon	3a	3b	5a	5b	7a	7b	8a	8b
Agrostis stolonifera L.								
Alisma plantago aquatica L.								
Anthemis spp								
Apium spp								
Bidens tripartita L.								
Callitriche stagnalis Scop.		2		1				1
Caltha palustris L. ?								
Cardamine pratensis L.?								
Carex dioica L.								
Carex vesicarisa L.								
Carex spp								
Ceratophyllum demersum L.								
C. vulgaris var longibractea								
Chenopodium polyspernum L.								
Chenopodium spp								
Cyperus fuscus L.								
Echinochloa crusgalli (L.) P. Beauv.	1							
Eleocharis palustre (L.) (L.) Roemer and Schultes								
Epilobium obscurum Schreber								
Equisetum fluviatile L.								
Galium palustre L.								
Glyceria maxima (Hartman) O. Holumb.								
Gnaphalium uliginosum L.								
Hydrocharis morsus-ranae L.								
Juncus articulatus L.								
Juncus bufonius L.	1		1					
Juncus spp								
Leersia oryzoides (L.) Sw								2
Lemna minor L.								
Spirodela polyrhiza (L.) Schleiden								
Limnosella aquatica L.	2				4		3	2
Lindernia dubia	43	10	38	24	150	93	135	150
Ludwigia palustris (L.) Elliott								
Lythrum portula (L.) D. Webb								
Lythrum salicaria L.								
Lysimachia thyrisflora L.								
Mentha aquatica L.								
Mentha pulegium L.								
Myosotis scorpiodes L.							2	
Myosoton aquaticum (L.) Moench								
Myriophyllum spicatum L.								
Oxalis spp								
Panicum ?capillare L.								
Persicaria hydropiper (L.) Spach								
Persicaria maculosa Gray	1				2			4
Phalaris arundinacea L.								
Plantago major L.								
Poa pratensis L.								
Potamogeton crispus L.								
Potamogeton nodosus Poiret								
Potamogeton trichoides Cham & Schldl.								
Ranunculus circinatus Sibth.								
Ranunculus peltatus Schrank								
Ranunculus sceleratus L.								
Rorippa islandica (Oeder ex Murray)								
Rorippa spp.								
Sagittaria sagittifolia L.								
Salix sp.								
Sonchus sp.								
Trifolium repens L.								
Typha latifolia L.								
Urtica dioica L.								
Veronica catenata Pennell								
Veronica spp								
unidentified		1		1		1		

Site	fdcbw							
Treatment	fluctuating water levels							
Replicate and horizon	2a	2b	9a	9b	10a	10b	12a	12b
Agrostis stolonifera L.								
Alisma plantago aquatica L.								
Anthemis spp								
Apium spp								
Bidens tripartita L.								
Callitriche stagnalis Scop.							1	3
Caltha palustris L. ?								
Cardamine pratensis L.?								
Carex dioica L.								
Carex vesicarisa L.								
Carex spp							1	
Ceratophyllum demersum L.								
C. vulgaris var longibractea								
Chenopodium polyspernum L.								
Chenopodium spp								
Cyperus fuscus L.								
Echinochloa crusgalli (L.) P. Beauv.			1		1			
Eleocharis palustre (L.) (L.) Roemer and Schultes								
Epilobium obscurum Schreber								
Equisetum fluviatile L.								
Galium palustre L.								
Glyceria maxima (Hartman) O. Holumb.								
Gnaphalium uliginosum L.	1							
Hydrocharis morsus-ranae L.								
Juncus articulatus L.								
Juncus bufonius L.			1		1			
Juncus spp								
Leersia oryzoides (L.) Sw	4	2			3	1		3
Lemna minor L.								
Spirodela polyrhiza (L.) Schleiden			11	2				
Limnosella aquatica L.					1			
Lindernia dubia	85	43	64	45	42	10	57	49
Ludwigia palustris (L.) Elliott			1					
Lythrum portula (L.) D. Webb								
Lythrum salicaria L.	8	16	3	1		8		2
Lysimachia thyrisflora L.								
Mentha aquatica L.								
Mentha pulegium L.								
Myosotis scorpiodes L.	3	2	1	2	1	7		
Myosoton aquaticum (L.) Moench			1					1
Myriophyllum spicatum L.								
Oxalis spp						1		
Panicum ?capillare L.								
Persicaria hydropiper (L.) Spach	1		2					
Persicaria maculosa Gray						3		
Phalaris arundinacea L.								1
Plantago major L.	3							1
Poa pratensis L.								
Potamogeton crispus L.								
Potamogeton nodosus Poiret								
Potamogeton trichoides Cham & Schldl.								
Ranunculus circinatus Sibth.								
Ranunculus peltatus Schrank								
Ranunculus sceleratus L.								
Rorippa islandica (Oeder ex Murray)	2				1			
Rorippa spp.								1?
Sagittaria sagittifolia L.								
Salix sp.								
Sonchus sp.								
Trifolium repens L.								
Typha latifolia L.								
Urtica dioica L.	1							
Veronica catenata Pennell								
Veronica spp								
unidentified	1				3	1		

Site Treatment Replicate and horizon	fdcbw moist 1a	1b	4a	4b	6a	6b	11a	11b
Agrostis stolonifera L.		1					1	
Alisma plantago aquatica L.								
Anthemis spp	1							
Apium spp				2	1			
Bidens tripartita L.								
Callitriche stagnalis Scop.								
Caltha palustris L. ?								
Cardamine pratensis L.?								
Carex dioica L.								
Carex vesicarisa L.							1	
Carex spp		1						
Ceratophyllum demersum L.								
C. vulgaris var longibractea								
Chenopodium polyspernum L.								
Chenopodium spp	4		5				3	
Cyperus fuscus L.	1			4				
Echinochloa crusgalli (L.) P. Beauv.	3					1	2	1
Eleocharis palustre (L.) (L.) Roemer and Schultes								
Epilobium obscurum Schreber								
Equisetum fluviatile L.								
Galium palustre L.								
Glyceria maxima (Hartman) O. Holumb.								
Gnaphalium uliginosum L.	5		4		1		4	1
Hydrocharis morsus-ranae L.								
Juncus articulatus L.								
Juncus bufonius L.		1			1			
Juncus spp						1		
Leersia oryzoides (L.) Sw	8	1	3	1			4	
Lemna minor L.								
Spirodela polyrhiza (L.) Schleiden		8					4	
Limnosella aquatica L.							2	
Lindernia dubia	48	33	78	56	57	15	91	20
Ludwigia palustris (L.) Elliott								
Lythrum portula (L.) D. Webb								
Lythrum salicaria L.	3	2	4	3	4		3	7
Lysimachia thyrisflora L.								
Mentha aquatica L.								
Mentha pulegium L.								
Myosotis scorpiodes L.				1			3	
Myosoton aquaticum (L.) Moench	1	1	2	2	3	3		
Myriophyllum spicatum L.								
Oxalis spp								
Panicum ?capillare L.				1				
Persicaria hydropiper (L.) Spach				1	1			
Persicaria maculosa Gray		2	1		1		2	
Phalaris arundinacea L.	3			1	1	3		2
Plantago major L.			1		1	1		
Poa pratensis L.					2	1		
Potamogeton crispus L.								
Potamogeton nodosus Poiret								
Potamogeton trichoides Cham & Schldl.								
Ranunculus circinatus Sibth.								
Ranunculus peltatus Schrank								
Ranunculus sceleratus L.								
Rorippa islandica (Oeder ex Murray)	2			1			1	
Rorippa spp.		1			1			
Sagittaria sagittifolia L.								
Salix sp.								
Sonchus sp.								
Trifolium repens L.								
Typha latifolia L.								
Urtica dioica L.	5		7				1	
Veronica catenata Pennell								
Veronica spp								
unidentified		1					2	10

Site	icldo								icldo							
Treatment	moist								12 cm flooding							
Replicate and horizon	2a	2b	5a	5b	9a	9b	10a	10b	1a	1b	6a	6b	7a	7b	12a	12b
Agrostis stolonifera					1		1	1								
Alisma plantago aquatica	1	6	21	7	1	1		1	4	2		1	3		8	2
Berula erecta							1									
Bidens cernua																
Callitriche spp			1												1	2
Carex disticha																
Carex nigra	1	1														
Carex vesicaria	1															
Carex spp	1															
Centurea nigra					7	4	1									
Chara spp																
Epilobium ciliatum																
Galium sp.	1															
Juncus articulatus		1														
Juncus conglomeratus																
Juncus effusus?		2			2	7	5	1						2		
Lemna minor																
Lemna trisulca																
Lythrum salicaria	31	9	15	16	16	8	10	10								
Mentha aquatica	1				1											
Phalaris arundinacea	16	3	1	2	2		1	1								
Plantago major		1	2	2												
Poa trivialis?					10		2	2						2	1	
Potamogeton obtusifolius																1
Ranunculus repens	1		1					1								
Ranunculus sceleratus	1				5											
Rorippa x anceps				1										1		1
Rumex sp.	4			1												
Samolus valerandi																
Senecio aquaticus	2	1	1	2				1								
Sonchus asper?		1					1									
Sparganium emersum									1							
Thalictrum flavum	1															
Veronica beccabunga?																
unidentified	2	2	11		4	4	3	9			1			2	1	

Site	icldo								ilbd3							
Treatment	12 cm flooding and shade								moist							
Replicate and horizon	3a	3b	4a	4b	8a	8b	11a	11b	3a	3b	5a	5b	8a	8b	11a	11b
Agrostis stolonifera									3				1	1	2	
Alisma plantago aquatica				1	3	4	2	1	4		8	3	6	4	3	
Berula erecta																
Bidens cernua																1
Callitriche spp														1		
Carex disticha										1	5	1	1	1		
Carex nigra												1	1			
Carex vesicaria																
Carex spp														1	3	2
Centurea nigra																
Chara spp																
Epilobium ciliatum											1			1		
Galium sp.																
Juncus articulatus									2	1			3	3	1	
Juncus conglomeratus										1	1	1				
Juncus effusus?														2		
Lemna minor											5					
Lemna trisulca																
Lythrum salicaria		2		2				1								
Mentha aquatica									3	2	2					
Phalaris arundinacea																
Plantago major																
Poa trivialis?															1	
Potamogeton obtusifolius																
Ranunculus repens																
Ranunculus sceleratus																
Rorippa x anceps																
Rumex sp.																
Samolus valerandi												1	1			
Senecio aquaticus											1					
Sonchus asper?									1							
Sparganium emersum	1			2		2	1									
Thalictrum flavum																
Veronica beccabunga?															1	
unidentified									4		1	2	1		3	1

Site	ilbd3								ilbd3							
Treatment	12 cm flooding								12 cm flooding and shade							
Replicate and horizon	4a	4b	6a	6b	10a	10b	12a	12b	1a	1b	2a	2b	7a	7b	9a	9b
Agrostis stolonifera	1					1						2				
Alisma plantago aquatica	3	2	4		4	14					2	6	21	19		
Berula erecta																
Bidens cernua																
Callitriche spp	1	8	4		2		6	1								
Carex disticha																
Carex nigra																
Carex vesicaria																
Carex spp																
Centurea nigra																
Chara spp			4								1					
Epilobium ciliatum																
Galium sp.																
Juncus articulatus		1														
Juncus conglomeratus																
Juncus effusus?																
Lemna minor		1														
Lemna trisulca	1		1													
Lythrum salicaria																
Mentha aquatica													1			
Phalaris arundinacea								1								
Plantago major																
Poa trivialis?																
Potamogeton obtusifolius																
Ranunculus repens																
Ranunculus sceleratus																
Rorippa x anceps																
Rumex sp.																
Samolus valerandi																
Senecio aquaticus																
Sonchus asper?																
Sparganium emersum																
Thalictrum flavum																
Veronica beccabunga?																
unidentified																

Site	cemta									
Treatment	moist									
Replicate and horizon	4a	4b	7a	7b	8a	8b	9a	9b	10a	10b
Alisma plantago aquatica		2	2	1						
Callitriche hamulata										
Callitriche sp	1	1	1		1	2				
Carex sp	3									
Festuca sp.	8									
Gnaphalium sp.	1									
Juncus ?effusus		1	2		4	1	2		5	2
Myosotis scorpiodes										
Oxalis sp.						2				
Persicaria sp.										
Phalaris arundinacea	4	4	2	1	4	1	3	1	2	1
Poa trivialis	1									
Rorippa sp	3	2							1	
Rorippa x anceps?									1	
Stellaria sp.	1									
Urtica dioica	3	1		1						
unidentified							2			

Site	cemta									
Treatment	12 cm flood									
Replicate and horizon	1a	1b	2a	2b	3a	3b	5a	5b	6a	6b
Alisma plantago aquatica	3	2			2			1		2
Callitriche hamulata	3									
Callitriche sp			1	1	1		2		8	1
Carex sp	1									
Festuca sp.										
Gnaphalium sp.										
Juncus ?effusus		1		1				8		
Myosotis scorpiodes	2									
Oxalis sp.										
Persicaria sp.	1									
Phalaris arundinacea										
Poa trivialis	2	5	1	1						
Rorippa sp										
Rorippa x anceps?		1	1			1				
Stellaria sp.										
Urtica dioica										
unidentified				1		1			3	

Site and month	cimid May									
Treatment	moist									
Replicate and horizon	1a	1b	6a	6b	7a	7b	8a	8b	10a	10b
Agrostis stolonifera										
Callitriche stagnalis										
Carex chordorhiza								1		
Carex limosa	3				1	2				
Carex nigra		4								
Carex spp										
Chara spp						1				
Glyceria fluitans										
Juncus articulatus	1	3	1	1	2			2	1	1
Juncus bulbosus	17	26	44	34	26	42	49	37	21	23
Juncus effusus	21	14	10	8	16	20			19	11
Myosotis caespitosa					1					
Nitella spp										
Poa trivialis										
Ranunculus flamula										
Sparganium emersum										
Subularia aquatica										
unidentified	1	2			11					

Site and month	cimid May									
Treatment	12 cm flooding									
Replicate and horizon	2a	2b	3a	3b	4a	4b	5a	5b	9a	9b
Agrostis stolonifera										
Callitriche stagnalis										
Carex chordorhiza										
Carex limosa										
Carex nigra										
Carex spp						1				
Chara spp										1
Glyceria fluitans										
Juncus articulatus							2			
Juncus bulbosus	11	7	3	13	8	73	13	13	29	34
Juncus effusus										
Myosotis caespitosa										
Nitella spp										3
Poa trivialis										
Ranunculus flamula		1								
Sparganium emersum										
Subularia aquatica			1							
unidentified	12	58	10							

Site and month	cimid August									
Treatment	moist									
Replicate and horizon	1a	1b	3a	3b	4a	4b	5a	5b	10a	10b
Agrostis stolonifera		1					2			
Callitriche stagnalis	1	1								
Carex chordorhiza										
Carex limosa		3							6	16
Carex nigra			2		13	6	4	6		
Carex spp	1									
Chara spp										
Glyceria fluitans										
Juncus articulatus					1		1	1		
Juncus bulbosus	28	14	24	31	80	76	44	35	33	36
Juncus effusus	10	18	10	27	11	6	4	8	21	18
Myosotis caespitosa										
Nitella spp										
Poa trivialis										
Ranunculus flamula										
Sparganium emersum				2		1	1			
Subularia aquatica										
unidentified			7					8		

Site and month	cimid August									
Treatment	12 cm flooding									
Replicate and horizon	2a	2b	6a	6b	7a	7b	8a	8b	9a	9b
Agrostis stolonifera										
Callitriche stagnalis										
Carex chordorhiza										
Carex limosa										
Carex nigra										
Carex spp										
Chara spp										
Glyceria fluitans			2							
Juncus articulatus		1		1						
Juncus bulbosus	15	14	7	10	26	9	23	21	17	72
Juncus effusus										
Myosotis caespitosa										
Nitella spp										
Poa trivialis										
Ranunculus flamula			1							
Sparganium emersum				1		2	1			
Subularia aquatica										
unidentified						1				

Site and month	cimid October									
Treatment	moist									
Replicate and horizon	3a	3b	4a	4b	6a	6b	8a	8b	9a	9b
Agrostis stolonifera										
Callitriche stagnalis	1									
Carex chordorhiza										
Carex limosa				5		5	12	9		
Carex nigra	1				10				2	10
Carex spp			4							18
Chara spp										
Glyceria fluitans										
Juncus articulatus			1		2	2				1
Juncus bulbosus	2	7	4	5	74	81	26	66	50	52
Juncus effusus	1	10	7	5		5	14	23	10	10
Myosotis caespitosa										
Nitella spp										
Poa trivialis	1									
Ranunculus flamula								2		
Sparganium emersum										
Subularia aquatica										
unidentified			1	9						

Site and month	cimid October									
Treatment	12 cm flooding									
Replicate and horizon	1a	1b	2a	2b	5a	5b	7a	7b	10a	10b
Agrostis stolonifera										
Callitriche stagnalis										
Carex chordorhiza										
Carex limosa										
Carex nigra										
Carex spp										
Chara spp					1					
Glyceria fluitans				1						
Juncus articulatus			1	1				1	1	1
Juncus bulbosus	1	3	4	27		7	1	18	38	14
Juncus effusus										14
Myosotis caespitosa										
Nitella spp										
Poa trivialis										
Ranunculus flamula										
Sparganium emersum									1	
Subularia aquatica										
unidentified	1				1	27	5	41		

Appendix 11

Publication

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RESPONSE OF *ELODEA CANADENSIS* MICHX. AND *MYRIOPHYLLUM SPICATUM* L. TO SHADE, CUTTING AND COMPETITION IN EXPERIMENTAL CULTURE

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Abstract

Elodea canadensis Michx. and *Myriophyllum spicatum* L. are widespread nuisance aquatic plant species. Their ecology is regarded as similar. Both species have been previously classified in terms of established-phase survival strategy as "competitive disturbance-tolerant" species. Experimental data are presented to show that although this broad categorisation of strategy is probably correct for the two species, it is possible to demonstrate significant differences in terms of response to disturbance and competition. Less difference was discernible in their comparative response to stress. The drawbacks of applying broad descriptive terminology when dealing with two species of similar strategy are addressed. The results help explain reports of variable success in attempting to manage these two species using disturbance-based weed control measures, and suggest that *Elodea* is even less susceptible to such measures than *Myriophyllum.*

Introduction

Elodea canadensis Michx. and *Myriophyllum spicatum* L. are two submerged macrophyte species, which have successfully crossed the Atlantic during the past century, in the former case from North America to Europe, and in the latter from Europe to North America, to cause weed problems in a range of freshwater systems (Murphy *et al.* 1990a; Anderson 1990; Steward 1990; Simpson 1984). Despite their differing provenances, both species are currently problem aquatic weeds in Europe.

The ecology of the two species is usually considered to be quite similar. Their established phase strategies both show strong elements of competitiveness and disturbance-tolerance (Grime *et al.* 1988; Murphy *et al.* 1990b). The two species tend to occur in similar freshwater habitats, and occur under broadly similar sets of physico-chemical environmental conditions (Simpson 1984; Smith & Barko 1990). The available evidence (as, for example, reviewed by Nichols & Shaw 1986) therefore suggests that populations of the two species exhibit rather similar sets of phenotypically-expressed traits for tolerance of stress, disturbance and

competition from other species (*sensu* Grime 1979). When in direct competition there is some evidence that one species may successfully displace the other, but field observations are far from consistent (e.g. Madsen *et al.* 1991).

The question arises whether the application of management measures (which impose artificial stress or disturbance on weed populations) is likely to have similar effects on *E. canadensis* and *M. spicatum*, and whether such effects are modified in the presence of competitor plant populations.

The aims of the study were:

(i) to determine, under standardised experimental glasshouse conditions, the response of *Elodea canadensis* and *Myriophyllum spicatum* to artificially-imposed stress, disturbance, and interspecific competition; and

(ii) to use the information gained to refine knowledge of the established-phase survival strategy of the two species.

Methods

In all experiments plants were grown in tapwater, in aerated 30 l black polypropylene tanks, under 16 hr light regime (Navilux 400W sodium floodlights augmenting natural daylight) in a heated glasshouse (20 C). The rooting medium was well-mixed natural river sediment. Plants were established as 12 cm stem sections, each with a viable bud, and subjected in a series of experiments to varying intensities of stress, competition, and disturbance. A random-block design was used as standard, with 3 blocks; except in Experiment 4 where an incomplete factorial design was used, with 4 blocks. Variables measured were plant length, biomass per plant, and resource allocation, (as biomass per stem, leaves and roots: Experiment 1 only). For each variable, and each species, % changes compared to untreated controls were calculated. Four experiments were conducted:

Experiment 1. Effects of stress caused by shade

Plants were grown in individual pots (1 plant/pot), with 2 plants of each species per tank. Individual tanks were shaded with one or more layers of shade material, or left unshaded (9 tanks used), to give a design with 3 levels of the treatment factor: UNSHADED, LOW (23% reduction in photosynthetically-active radiation, measured using a Skye PAR meter at water level in the tank), and HIGH shade (40% reduction in PAR).

Experiment 2. Effects of disturbance caused by cutting

Plants were grown in individual pots (1 plant/pot), with 11 pots/tank (18 tanks, each containing a random mix of treatment units). Cutting treatments were

standardised to reduce individual plant length to 5 cm after each treatment. Two frequencies of cutting were used, to give a design with 3 levels of the treatment factor: UNCUT, LOW (cut 35 days after start of experiment) and HIGH cutting frequency (cut both 35 and 66 days after start).

Experiment 3. Effects of interspecific competition

An additive approach (Martin & Snaydon 1982) was used to compare MIXED v. PURE stands of *Elodea canadensis* and *Myriophyllum spicatum.* Either 25 plants of each species in monoculture, or 25 + 25 plants of each species in mixed culture, were planted in trays (360 x 220 mm), with 1 tray/tank.

Experiment 4. Combined effects of shade stress and disturbance caused by cutting

The experiment was set up with plants grown in individual pots at a density of 10 plants per tank, of which 2 replicates per tank of each species were harvested. In total there were 6 treatment-combinations: untreated (UNTR), low shade (LS), high shade (HS), single cut (C1), two cuts (C2), and low shade + single cut (LS/C1). Shade treatments were as in Experiment 1.

Statistical treatments

Data were analyzed using GENSTAT, as follows: Experiments 1 - 3: ANOVA followed by orthogonal mean separation using Tukey's LSD test; Experiment 4: two-way ANOVA with orthogonal contrasts (UNTR v. LS; UNTR v. C1; LS v. HS; C1 v. C2; LS/C1 interaction). In the results outcomes are treated as significant at $P<0.05$ throughout.

Results

Experiment 1. Effects of stress caused by shade

Data shown in Fig. 1 are 77 days from start of the experiment. Shade stress produced little significant response by either species. Both showed no significant change in length per plant (except for *Myriophyllum* under high shade: 19% increase) in response to reduced light availability. There were no significant effects on biomass per plant for either species. In terms of resource allocation no significant response was observed by either *Elodea* or *Myriophyllum* in biomass allocation to stem or leaves as a result of shading. For *Elodea* there was no change in root biomass either, but *Myriophyllum* showed a significant (71%) reduction in root biomass at high shade, compared with unshaded controls. The results for *Myriophyllum spicatum* mirror the findings of previous work, for example by Barko & Smart (1981).

Experiment 2. Effects of disturbance caused by cutting

Data shown in Fig. 2 are 123 days from start of the experiment. Compared with untreated controls *Myriophyllum* showed a significant response to both single and double cut treatments: for both biomass (45 and 90% reduction after 1 and 2 cuts respectively), and length per plant: (22 and 70% reduction). For *Elodea* the effect was less, especially for length response, where there was no significant change after 1 cut, and only 44% reduction after two cuts. The biomass response of *Elodea* was more marked, with reductions of 41 and 59% after 1 and 2 cuts respectively.

Experiment 3. Effects of interspecific competition

Data shown in Fig. 3 are 84 days post-treatment. The two species responded differently to interspecific competition. Compared with growth in monoculture, there was a significant reduction (25%) in plant length of *Elodea*, but no significant reduction in plant biomass, when grown with *Myriophyllum.* The converse was seen for the two variables measured in *Myriophyllum*: a significant reduction (33%) in plant biomass, but with no significant reduction in plant length, when grown with *Elodea.*

Experiment 4. Combined effects of shade stress and disturbance caused by cutting

The results shown in Table 1 are % changes, for the orthogonal comparisons shown, two for variables measured 74 days after treatment. A stronger response to shade stress was seen in *Myriophyllum,* with biomass being significantly reduced by LS treatment, whereas no significant response was observed under low shade conditions for *Elodea*. Adding in cutting disturbance to low shade stress produced a greater effect on *Myriophyllum* than on *Elodea*. The effect on *Myriophyllum* was similar to that of high-disturbance treatment; much less for *Elodea.* The effects of cutting disturbance alone were similar for both species.

Discussion and conclusions

Tolerance of stress and disturbance

Myriophyllum showed a more plastic growth response to shade stress: by reducing resource allocation to roots, and increasing its length. These results are suggestive of a rather low tolerance of stress (Grime 1979). The results of Experiment 4 also suggested that *Elodea* was slightly more tolerant of shade stress than *Myriophyllum.*

Elodea was slightly more disturbance-tolerant than *Myriophyllum.* In both Experiments 1 and 4 the responses of *Myriophyllum*, in terms of biomass-reduction, and reduced plant length, were usually similar to, or greater than for

Elodea. *Elodea* was more tolerant than *Myriophyllum* of combined stress and disturbance, at moderate intensities of both pressures.

These results are of relevance when considering the response of the two species to weed control measures based on stress and disturbance. *M. spicatum* has frequently been observed to respond positively to disturbance produced by cutting or harvesting (Smith & Barko 1990). The results of our study suggest that applying disturbance-based weed control to *Elodea canadensis* is likely to produce an even worse result in weed control terms.

Competitiveness

From the results of Experiment 3, *Elodea* was the more competitive of the two species when grown in mixed culture with each other under standard glasshouse conditions. Although *Elodea* produced shorter plants in competition with *Myriophyllum*, *Elodea* showed no significant loss of biomass compared with monoculture controls. In contrast, *Myriophyllum* plants competing with *Elodea* showed significant biomass loss.

Separation of strategies of Elodea *and* Myriophyllum

The two freshwater plant species studied here, both of which act as opportunistic weeds, and which tend to occur in similar habitats (Nichols & Shaw 1986), had measurably different responses to stress, disturbance and competition, under standardized experimental conditions.

Field evidence from comparison of drainage channel habitats of the two species in Britain (Sabbatini & Murphy, these Proceedings) has suggested that there is a tendency for *Elodea* to occur in slightly higher-stress conditions than *Myriophyllum*. Sheldon & Boylen (1979) found that *E. canadensis* had the deepest maximum depth (compared with *M. spicatum* and *Potamogeton crispus*) in US lakes. Nichols & Shaw (1986) considered that *E. canadensis* is the "most efficient" of these three submerged macrophyte species in surviving low light conditions. There is further evidence in the literature that *M. spicatum* is only poorly-tolerant of shade stress (e.g. Chambers & Kalff, 1985). In neither species, however, does stress-tolerance seem to play a major role in established-phase strategy. Much more important are traits for disturbance-tolerance and competitiveness.

The established-phase strategies of these two species are certainly close (for most populations of the two species, probably competitive disturbance-tolerant CD), but there are interspecific differences in response to environmental pressures on survival, which indicate that their strategies can be separated. This highlights the problem of relying on a descriptive terminology for plant strategy, such as that put forward by Grime (1979). When two species have closely-similar strategies, as in the case of *Elodea canadensis* and *Myriophyllum spicatum*,

classification into broad categories such as "competitive disturbance tolerator" do not adequately reflect the functional differences between the species. What is needed is a numerically-based methodology to describe strategy and functional type of plant species, which would allow better quantification of the differential responses of plants to pressures on their survival and reproduction. An increasing amount of work is currently being devoted to developing functional analysis methods along these lines, for aquatic and wetland vegetation as well as terrestrial plants (e.g. Hills *et al.* 1994; Abernethy 1994 in prep.; Pantou & Arens 1994; Bornette *et al.* 1994; Hendry & Grime 1993). The appropriate application of approaches such as these may lead to an improved understanding of both the ecology, and susceptibility to control measures, of nuisance species such as *Elodea canadensis* and *Myriophyllum spicatum.*

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Table 1. Percentage response of *Elodea canadensis* and *Myriophyllum spicatum* length and biomass per plant for 5 orthogonal comparisons. Treatment codes are given in text. NS: not significant (P>0.05); other values are significant at P<0.05 for comparison)

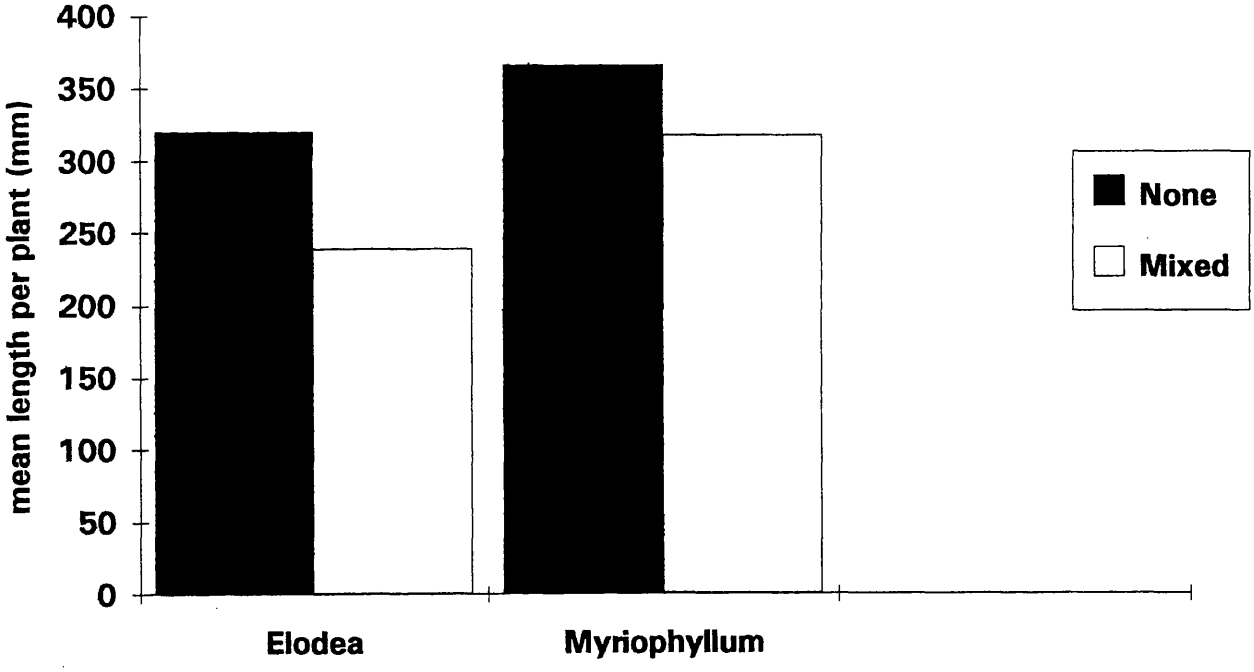
Treatment comparison	Reduction (%)			
	Elodea		*Myriophyllum*	
	Length	Biomass	Length	Biomass
UNTR v. LS	NS	NS	NS	53
LS v. HS	NS	77	NS	NS
UNTR v. LS/C1	NS	49	62	85
UNTR v. C1	37	38	NS	38
C1 v C2	43	88	66	83

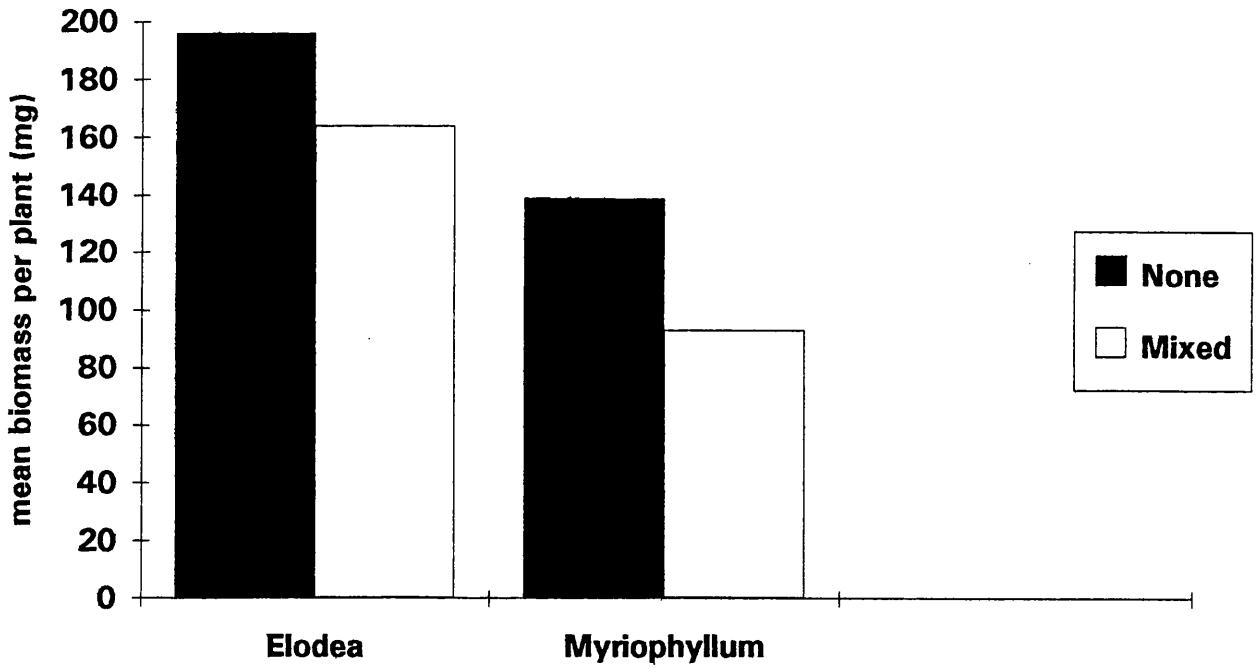
Figure captions

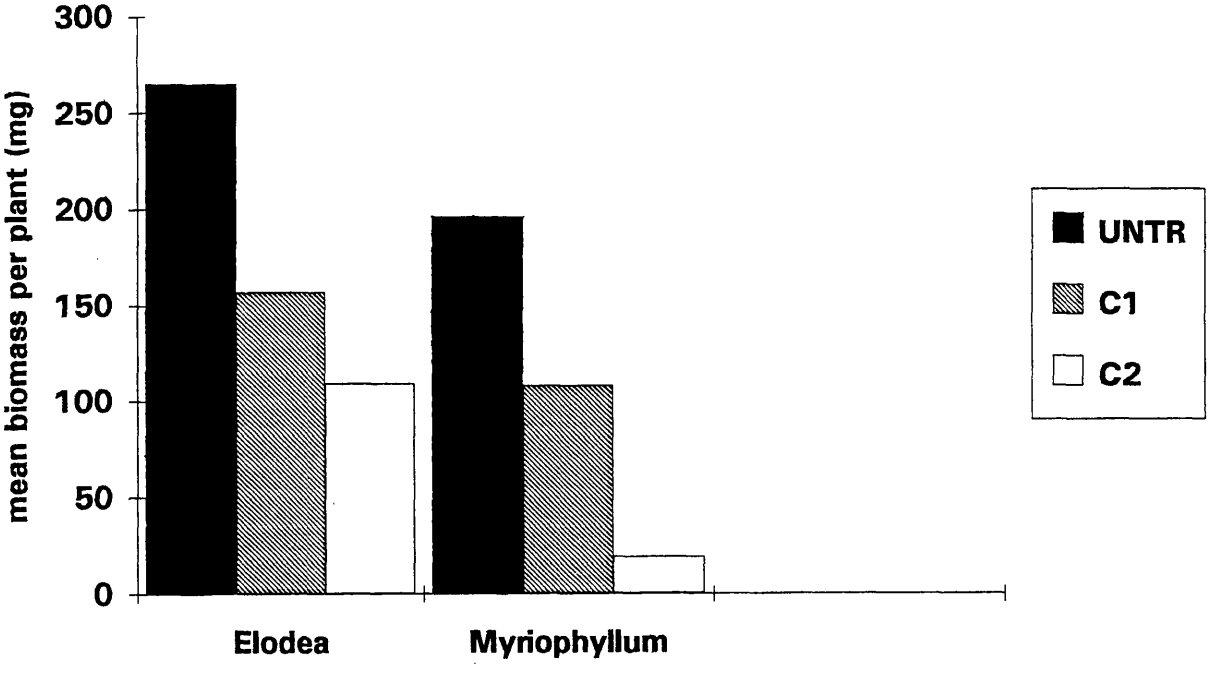
Fig. 1. Effects of stress caused by shade on (a) length, and (b) biomass per plant of *Elodea canadensis* and *Myriophyllum spicatum.*

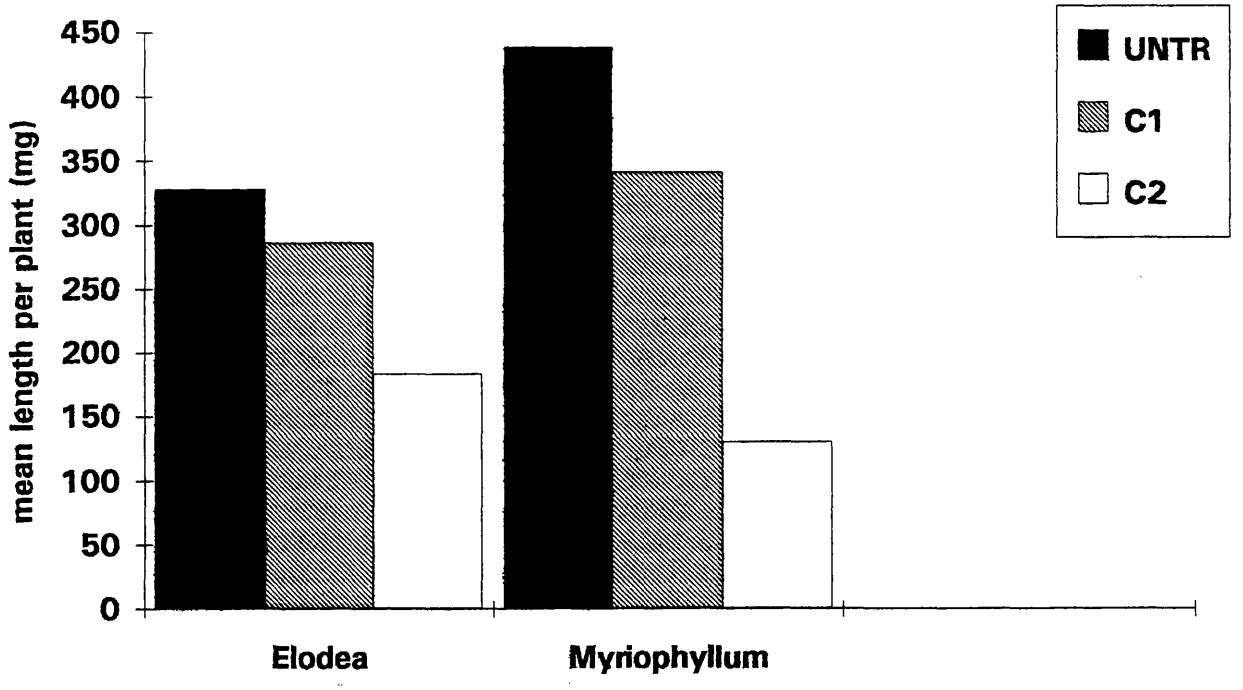
Fig. 2. Effects of disturbance caused by cutting on (a) length, and (b) biomass per plant of *Elodea canadensis* and *Myriophyllum spicatum.*

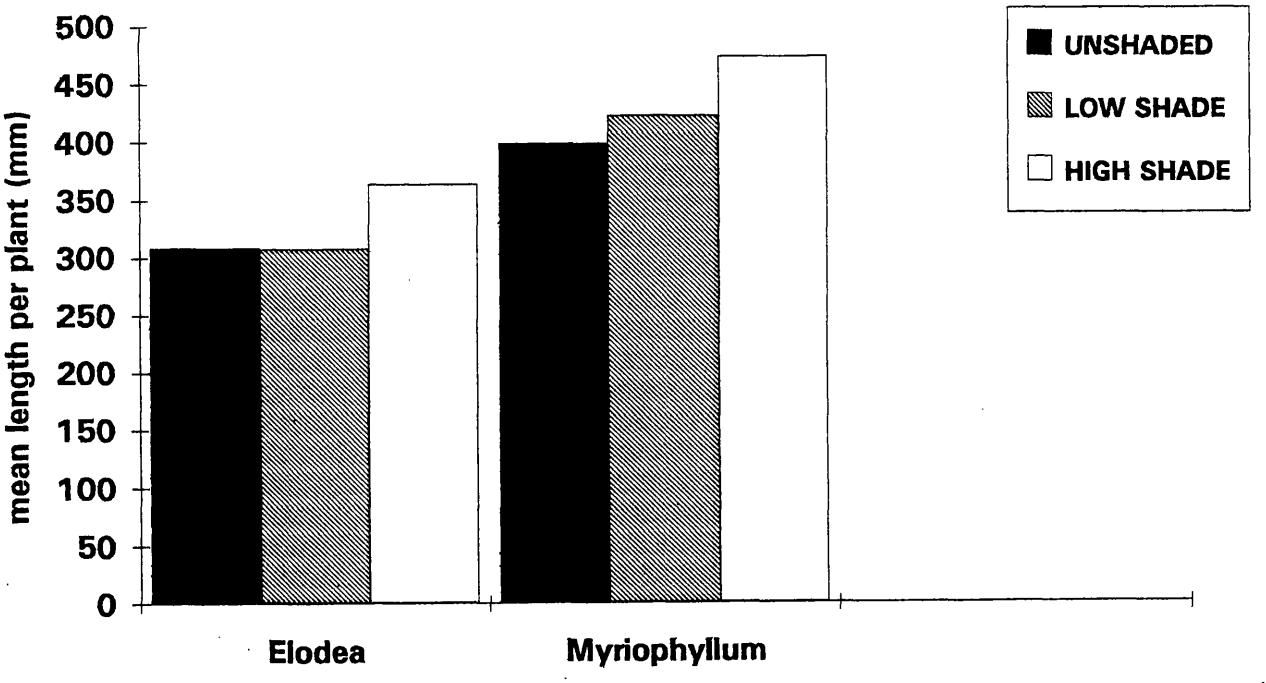
Fig. 3. Effects of interspecific competition on (a) length, and (b) biomass per plant of *Elodea canadensis* and *Myriophyllum spicatum*, grown in pure and mixed culture.


400
350
300
250
200
150
100
50
0
mean length per plant (mm)
None
Mixed
Elodea
Myriophyllum


mean biomass per plant (mg)
200
180
160
140
120
100
80
60
40
20
0
Elodea
Myriophyllum
None
Mixed


300
250
200
150
100
50
0
mean biomass per plant (mg)
Elodea
Myriophyllum
UNTR
C1
C2


mean length per plant (mg)
450
400
350
300
250
200
150
100
50
0
UNTR
C1
C2
Elodea
Myriophyllum


500
450
400
350
300
250
200
150
100
50
0
mean length per plant (mm)
UNSHADED
LOW SHADE
HIGH SHADE
Elodea
Myriophyllum