Predicting the Impact of Hydrological Change on Wetland Vegetation

by

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Abstract

Wetlands are becoming increasingly recognised as important ecosystem units within the wider landscape. They provide a number of valuable ecological, biogeochemical and hydrological functions, including biodiversity support, groundwater discharge, recharge and amelioration, and natural flood defence. Despite legislation however, wetlands are still threatened on a global scale, and continue to be lost to agriculture, urbanisation, and pollution, both directly and indirectly.

Numerous studies of wetland ecosystems have highlighted predictive relationships between vegetation assemblages and underlying hydrology. More recently, predictive relationships have been formalised between traits of wetland vegetation (collective vegetation variables, and traits of the dominant populations) and underlying hydrology. In allied research, consistent functional trait groupings of wetland vegetation have also been defined over broad geographical regions in Europe.

During a three year field study (1997-2000) vegetation assemblages, collective vegetation variables, traits of dominant populations and hydrological and hydrochemical variables were repeat-sampled within seven wetland sites across Scotland and northern England. These ranged from the Insh Marshes, Inverness-shire in the north, to Tarn Moss, Cumbria at the southern extreme. Sampling was conducted at a total of fifty-six permanent sample stations located along a total of eleven transects. Vegetation groupings were defined using multivariate analyses, and were classified as various fen, mire, and swamp NVC community types. The various groups were characterised by the values for the range of variables measured, and significant differences were seen between a number of these variables for different groupings. In addition, certain separate groupings with the same community classifications were also seen to have significant variations between them in terms of trophic status, and canopy height and biomass values.

Collective vegetation variables and dominant population trait values were successfully predicted from physical and chemical variables measured within the groundwater and substrate during 1999. A number of specific models incorporating relatively large numbers of predictor variables were proposed alongside more general models incorporating fewer predictor variables. The greatest predictive power was $R^2 = 0.67$ ($p<0.001$) for a model predicting stem density (m^{-2}). Conversely, vegetation variables proved useful for predicting characteristics of the groundwater environment, for which specific and general models were

again proposed. In this instance, the greatest predictive power was $R^2 = 0.79$ ($p<0.001$) for a model predicting minimum water table level (i.e. maximum level of drawdown).

The models were tested using data collected during 2000 from repeat sites and independent sites. Whilst some of the variables were predicted within noisy limits, predicted values generally corresponded well to observed values.

Further models were constructed using the same measures of groundwater and substrate variables to predict the proportion of life forms and life history types per sample (and also of groundwater and substrate variable values from proportions of life form and life history types). The predictive power of the models produced was generally lower than for those produced using directly measured traits, but the approach was considered worthy of further investigation.

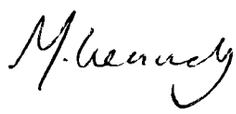
In addition to the field study, experiments were conducted using *Agrostis stolonifera*, *Deschampsia cespitosa* and *Phalaris arundinacea* (as test species with contrasting established phase strategies); competition and water level variation treatments were imposed. The main findings were that significant growth responses were seen in both *Agrostis* and *Deschampsia* in relation to increasing inundation, and that the strong competitive advantage of *Agrostis* over *Deschampsia* at a water level treatment of 7cm below soil surface level, was greatly reduced (almost completely so) at a water level treatment of 7cm above soil level.

In *Deschampsia* and *Phalaris* a number of growth responses were seen to differ between individuals for various water level fluctuation treatments. Rhizome production, plant height, and reproductive structure weight and number were some of the variables significantly reduced by treatments equating to the highest levels of stress.

It was concluded that the study represented a stage of progression in the application of trait-based assessments to the understanding of wetland ecology. Such approaches may be successfully applied as eco-hydrological tools, but there is an obvious need to complement a trait-based with a phytosociological approach if wetland management is to be best informed.

Declaration

I declare that the work described in this thesis has been carried out by myself unless otherwise acknowledged. It is entirely of my own composition and has not, in whole or part, been submitted for any other degree.



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Chapter 1: General introduction

1.1. Wetland ecosystems

Aquatic and swamp plant associations represent natural vegetation assemblages which form dynamic systems within the hydroseral succession from open water to dry land (Rieley and Page, 1990). The habitats supporting these plant communities are often characterised by flat terrain, rich alluvial soils, and plentiful water (Finlayson and Moser, 1991). By virtue of these characteristics, and of their position within the landscape, the relationship between wetlands and man is one with a substantial history. The value of wetlands in the provision of food and other tangible products such as building materials has long been recognised (Finlayson and Moser, 1991). Indeed, a range of archaeological evidence shows that a number of early settlements were founded in intimate association with water and wetland areas (e.g. Maltby, 1991; Coles and Coles, 1992; Bernick, 1998) and took advantage of the benefits associated with these areas.

Within more recent history wetlands have often been reviled as worthless and disease-ridden places (e.g. Maltby, 1986; Giblett, 1996), better subject to 'improvement' through drainage and conversion. Partly this reflected a desire to use wetlands for agricultural production (e.g. Gibbons, 1993), or to eradicate diseases such as malaria, still present within the fen areas of eastern England and northern Europe in the nineteenth century (Maltby, 1986). With the advent of the Ramsar Convention (Ramsar, Iran, 1971) for example, which aimed to foster international co-operation for the conservation of wetlands (see Maltby, 1991), it was hoped that decisions and attitudes concerning wetlands will become more enlightened. However, politically, contention still exists regarding the exact definition(s) of what a wetland is (Denny, 1985).

1.1.1. Freshwater wetlands

Globally, four main types of wetland are recognised (Etherington, 1983):

- *freshwater wetlands*
- *agricultural wetlands*
- *maritime saline wetlands*,
- *inland saline wetlands*

Within these umbrella classifications exist a myriad of types from tropical through to temperate and arctic regions, including lake littoral zones, floodplains, mangroves, shallow open waters and marshes (Gopal *et al.*, 2000). Of these, freshwater wetland ecosystems cover an estimated 8,558,000 km^2 (Williams, 1990), which approximates to 6% of the earth's land surface (Maltby, 1986). A general international nomenclature for wetlands has been proposed by Gore (1983) (Table 1.1.1).

Wetlands have been classified on the basis of numerous attributes, including shape, chemical properties of peat, floristic composition, and structure of the vegetation, although a majority of these classifications have focused upon vegetation types (Ross, 1995). Such classifications have aided in the appreciation of fine-scale differences within, and between wetlands (e.g. Tansley, 1939; McVean and Ratcliffe, 1962; Daniels, 1978).

The Ramsar Convention on Wetlands of International Importance (1971) proposed a generally broad classification of wetlands as "areas of marsh, fen, peat land or water whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish salt, inundating areas of marine water the depth at which low tide does not exceed six meters" (UNESCO, 1971). Through the Ramsar Convention, which was implemented in 1975, wetlands are an ecosystem type targeted for special international protection (Hills, 1994). Many of the waters contained within small lowland catchments in Europe are located in Special Areas of Conservation (SACs), and/or Special Protection Areas (SPAs). While the spirit of the Ramsar Convention has not been well served by a number of signatory states, where site designation has been slow (Gerakis and Kiriaki, 1998), Navid (1988) considers Ramsar as "an important conservation tool".

A number of other classifications have been proposed for wetlands, all of which are somewhat narrower than the all-embracing Ramsar definition, and which generally pertain to wetlands as land-water hydroseral ecotones (Hills, 1994). Wheeler (1999) argues that while there are valid reasons for broad classifications, in reality the hydrological processes of open waters, and those of 'wet land' transitional zones, are essentially different. Therefore, the term 'wetland' in the context of this study will follow the classification outlined by Wheeler (1999) (see Figure 1.1.1). This is based on the premise that the character of wetlands is strongly controlled by magnitude and duration of water table fluctuation, and that this factor is strongly reflected within their plant ecology (Wheeler, 1999). Within this classification of wetlands three main types are recognised: *permanent wetlands*, *seasonal wetlands*, and

fluctuating wetlands. However, Wheeler (1999) points out that these broad types are intergrading. At the community level, this grading between types and the related problems of classifying some associations is recognised by Rodwell (1995). Within the specific names given to freshwater ecosystem types (Figure 1.1.1), some variety exists. For example the term *fen* generally applies to areas with impeded drainage, often peat forming, but not exclusively so (Wheeler, 1999).

1.1.2. Wetland characteristics

The main characteristic underlying all wetland systems is that they are wet. As such, one of the primary drivers of the ecological processes which go on in wetlands is the underlying water regime (Etherington, 1983; Wheeler, 1999). The blanket term 'wetland' (in this context, freshwater) therefore lends itself to all those areas of land which are generally saturated, and which exist in the zone between fully aquatic and terrestrial ecosystems. Wheeler (1999), however, points out that the word 'wetland' is used widely, but not consistently. The presence of a water table at or around ground level, and the related physical and chemical properties (e.g. inundation, drawdown, reducing soils) are widely acknowledged determinants of species composition and community structure in wetlands (for example, see Goslee *et al.*, 1997; Wheeler, 1999). The inseparable link between groundwater-related factors such as pH and water level, and characteristics of peatland vegetation have been noted by Jeglum (1971), who successfully predicted water level and pH classifications of plant groups from trial studies within North American peatlands. Ellenberg (1974) also proposed a range of indicator values for plant species in continental Europe, including a soil moisture/water level requirement value termed 'F'; the system has been successfully applied to British species (Mountford and Chapman, 1993). Variations in vegetation assemblage for certain wetland types (e.g. tall-herb fens) have long been the subject of phytosociological study and interpretation (Rodwell, 1995). More recently studies have begun to interpret structural and functional aspects of vegetation in relation to groundwater dynamics (e.g. Hills, 1994; Hills *et al.*, 1994; Murphy *et al.*, 1994; Willby *et al.*, 1997). However, while variation in representative communities has been shown to exist within and between wetlands, Etherington (1983) has noted that a greater degree of similarity exists between vegetation types of wetland ecosystems, than within fully terrestrial systems, due to the more constricted nature of underlying environmental gradients.

Wetlands are among the most productive ecosystems on earth (Holland *et al.*, 1990). Estimates of primary productivity in marsh and swamp ecosystems run from 125 g m^{-2} yr^{-1} in

Molinia caerulea in Swedish systems, to 2500 g m^{-2} yr^{-1} in *Phragmites australis* dominated systems in northern Britain (Gore, 1983). In addition, below-ground standing crop has been estimated at up to 4418 g m^{-2} within Czechoslovakian *Phragmites* dominated vegetation (Gore, 1983).

Table 1.1.1 International terminology used in the naming and description of wetlands (adapted from Gore, 1983). *Apart from in North American usage, the term is used to include both Mires and Marshes.

General Term	Wetland Types Included	Environmental Conditions
Mire	- Bog.	Ombrotrophic nutrient supply (atmospheric deposition only).
	- Fen, Carr.	Minerotrophic water supply (from soils, rocks, sometimes lakes, rivers). May be eutrophic, mesotrophic or oligotrophic.
Swamp*/ Marsh	Less specific words apparent in popular usage.	Implies eutrophic conditions; Marsh often confined to wetlands with more or less mineral soils.

Table 1.1.2 River marginal wetland functions (from Maltby *et al.*, 1993).

Type of Function	Importance
Hydrological (Water Quantity)	- Flood water control - Groundwater recharge - Groundwater discharge - surface water generation
Biogeochemical (Water Quality)	- Nutrient removal - Nutrient retention - Sediment retention - Peat accumulation
Ecological (habitat)	- Ecosystem maintenance - Food web support

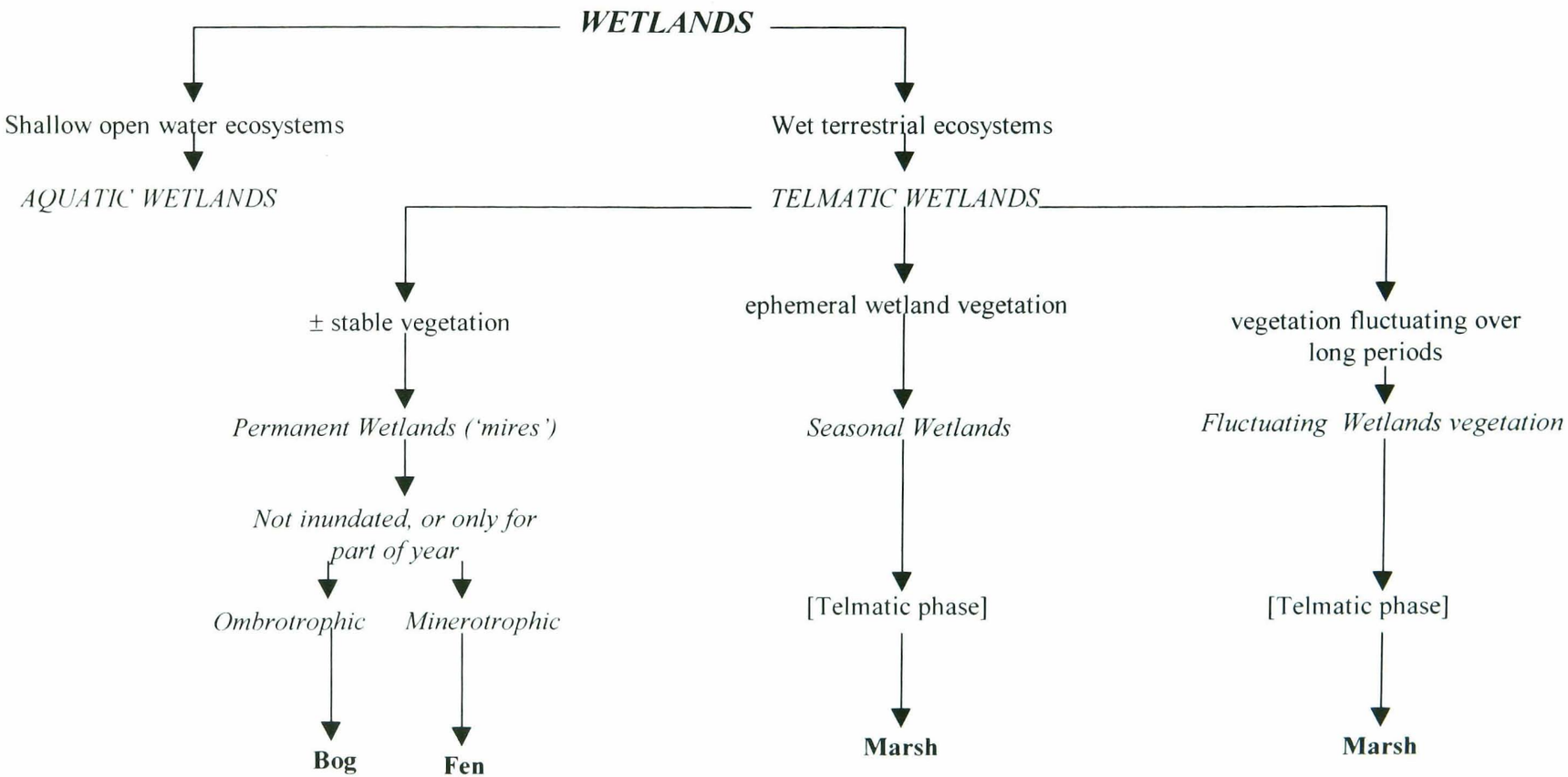

Figure 1.1.1 wetland types in relation to groundwater characteristics (adapted from Wheeler, 1999).

All wetlands are underpinned by water, but the specific inputs and balances of water into wetlands vary. The flood pulse concept proposed by Junk et al. (1989) suggests that low levels of riverine inundation equates to low levels of physical stress (Grime, 1979b; Dickinson and Murphy, 1998), with low inputs of nutrients, sediment, or allochthonous seed material, thereby allowing domination by competitive species. Vegetation assemblages are controlled in such cases by site-specific hydrological variation. Intermediate levels of inundation lead to an increased input of seed and nutrient sources, and in combination with intermediate levels of stress more diverse species assemblages are favoured. High levels of inundation allow little opportunity for deposition of allochthonous loads, or suspended silt and mineral nutrients. In addition, species without considerable stress-tolerant components within their survival strategies (Grime, 1979a; Grime *et al.*, 1988), are unable to establish within regularly flushed, high-stress environments, leading to domination by a few species. Recent germination studies of deposited propagule banks along disturbance gradients in riverine floodplain habitats (Abernethy and Willby, 1999) have shown a greater number of wetland generalist species to be characteristic of areas with intermediate levels of disturbance. While species richness was higher overall in terms of those represented in the propagule bank in the most disturbed habitats, the number of hydrophyte species was lower.

1.1.3. The values and functions of wetlands

The value of wetlands as distinct ecological units within their wider catchment is now becoming increasingly recognised (Ramsar Convention Bureau, 1990), as are a number of the specific functions they perform (see Table 1.1.2). They are essential to the survival of many plant species, migratory birds and other animals (e.g. Etherington, 1983; Pickess, 1989; Greenwood *et al.*, 1995). They also mediate and provide wider catchment functions; for example, sediment accretion and water mediation (Hey *et al.*, 1991). Mitsch (1994) regards floodplain wetlands as the "kidneys" of the catchment, through their role in water purification. Within a number of Greek Ramsar sites Gerakis and Kiriaki (1998) consider the main functions of these wetlands to be nutrient removal, sediment retention, flood alteration and groundwater discharge. The primary values are considered to be biodiversity support, fishing, hunting and recreation.

In terms of biodiversity support afforded by wetlands, Britain is regarded as internationally important for over-wintering and nesting waterfowl, due to the presence of extensive areas of wetland (including estuaries in this context) (Cranswick *et al.*, 1997). Specific habitats such as wet grasslands are also recognised for their importance to feeding and nesting birds

(Tickner and Evans, 1991). However, Gopal and Junk (2000) point out that globally, waterfowl species richness readily attracts attention, but other biota, such as occurs in the *varzea* wetlands of the Amazon basin are much less studied, or understood. The River Paraná in Brazil is one of the largest, yet most regulated rivers in the world. Even so, studies within various areas of the last remaining unregulated stretches, and of the associated *varzea* wetlands have uncovered high levels of diversity for a range of organisms (Agostinho *et al.*, 2000; Murphy *et al.*, 2001) (Table 1.1.3). As a function of the biodiversity support inherent within wetland ecosystems, a number of values are provided which are of direct benefit to man. These include the provision of spawning grounds for a range of fish species within both coastal and freshwater wetlands, which in turn provides benefits for commercial fisheries on a global scale (Maltby, 1986).

1.1.4. Threats to wetland functioning

Many wetlands are now afforded relatively high levels of protection, for example, as sites of international importance within the Ramsar Convention (RAMSAR Convention Bureau, 1990); via inclusion by the Natura 2000 network of the European Union[1] (see Gerakis and Kiriaki (1998), for example); or more locally (in a UK context) as SACs, SSSIs and local nature reserves (e.g.[2,3]). However, it is still evident that wetlands are amongst the habitats which are most vulnerable to disruption by human interference, both intentional and accidental (Etherington, 1983).

For example, in Australia, Boon and Brock (1994) indicate that only a very small proportion of scientific research specific to inland wetlands is disseminated to the appropriate audiences via journal publication. This situation is highly likely to be replicated globally; meaning that the application of informed management through appropriate knowledge may not be applied to its full potential in the context of protecting, or restoring, wetland habitats and their biota.

The intimate relationship between wetlands and their wider catchment is highlighted by a number of studies detailing the practices which threaten them. Examples include pressure from agriculture (Lemly, 1994), drainage (Haslam, 1973; Sheil and Wells, 1983), and flood control management (Washitani *et al.*, 1997). Grazing pressure from introduced exotic

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[1] Directive on the Conservation of Wild Birds (79/409/EEC)

[2] Glasgow District Council (1985) *Woodend Loch Site of Special Scientific Interest, notification: Strathclyde region*

[3] Glasgow District Council (1985) *Woodend Loch Site of Special Scientific Interest, notification: Strathclyde region*

species such as coypu (*Myocaster coypus* Molina) was linked to reedbed losses in the Norfolk Broads during population peaks in the 1950's and 1960's (Boorman and Fuller, 1981). A review by Gerakis and Kiriaki (1998) states that approximately two thirds of the wetland area of Spain, France, Italy and Greece had been drained during the last two generations, with an estimated 28,500 km^2 of wetlands now remaining in the Mediterranean basin. Within Greece, it was considered that irrigation represented the most negative influential factor upon the functions and values of a number of Ramsar sites, followed by cropland expansion and overgrazing. Other forms of anthropogenic impacts, whether direct or indirect, represent threats to wetlands. For example, the gross heavy metal pollution from mine waste of the World Heritage Site *Guadalquivir Marshes* near Seville, in southern Spain, in April 1998 (Osborn *et al.*, 1999), formed a significant threat to that ecosystem. In Ireland, road building as a result of economic development currently poses a threat to the hydrology of some of the most extensive (yet protected by legislation) calcium-rich fen habitats in western Europe (Mills, 2001).

Water level changes resulting from dam construction or groundwater abstraction for drinking water, and drainage for agriculture, represent threats to formerly stable wetland systems (Heathwaite, 1995). Such changes can shift the overall range of fluctuation within a wetland beyond those that can be tolerated by the representative species. In such a situation competition and invasion may come from species more suited to the new conditions (Newbold and Mountford, 1997), thereby altering species assemblages. In addition to potential changes in plant communities following hydrological change, Greenwood *et al.* (1995) observed a reduction in the species richness of spider communities of the River Trent floodplain in the UK in relation to river channel management and related floodplain drying. As potential impacts of hydrological change upon wetland plant communities, and the wider wetland ecosystem have been recognised (e.g. Cadbury, 1976; Burgess, 1991; Murphy and Hudson, 1991; Wheeler and Shaw, 1992; Murphy, 1994; Murphy, 1995; Moustafa *et al.*, 1998), so also has been recognised the need to be able to predict the impacts of such changes on wetland vegetation (Keddy, 1992a; Gowing *et al.*, 1998).

1.1.5. The wetland environment

Waterlogging and/or flooding may be relatively permanent (marshes and bogs), seasonal (floodplain wetlands and fens), or short term, within a range of ecosystems following heavy rainfall (Ernst, 1990). Davy *et al.* (1990) however, point out that "it would be facile to regard flooding as a single selection pressure [stress] on plants": the effect of waterlogging will

depend on duration, intensity and frequency of flooding, and timing in relation to critical growth stages, and will have a set of effects on the soil environment (Hills, 1994). With regard to the plant life present, the main ecological characteristic of waterlogging is the reduced availability of oxygen to the roots, where oxygen diffuses 10 000 times more slowly in water than in air (Greenwood, 1961). In well-drained soils gas exchange by diffusion between the atmosphere and oxygen-consuming organisms is largely unlimited. However, upon flooding a majority of the soil pores are filled with water and gaseous diffusion is greatly reduced. Aerobic soil organisms will deplete the oxygen present, producing a steep oxygen gradient, with oxidised soils for the few surface millimetres only, if at all. Oxygen becomes limited in the lower layers, and aerobic microbial processes will be replaced by anaerobic processes (Laanbroek, 1990). Due to the low diffusion rate of oxygen in water, following the onset of flooding, soil oxygen will generally be utilised within one day (Ernst, 1990), or potentially, within a few hours (Ponnamperuma *et al.*, 1966). Redox (oxidisation-reduction) potential (measured in millivolts; mV) is a quantitative measure of the intensity of the reduction of soils (Ponnamperuma *et al.*, 1966). Following flooding, redox potential will decrease, resulting in hypoxic (anaerobic) conditions (Davy *et al.*, 1990). A fall in soil oxygen concentration will result in complex changes in a number of soil chemicals, and a redistribution of them between relative soil reservoirs (Iu *et al.*, 1982). Facultative anaerobes, followed by strict anaerobes will utilise oxidised soil components such as nitrate (NO_3^-) as electron acceptors for respiration (Ponnamperuma *et al.*, 1966). Through microorganism activity and root respiration, waterlogging changes the speciation of a number of nutrients from an oxygenated to a reduced state. This follows the thermodynamic sequence: NO_3^- > Mn^{4+} >Fe^{3+} > SO_4^{2-} >CO_2, producing NH^+_4, N_2, Mn^{2+}, Fe^{2+}, H_2S, S^-, S^0 and CH_4 (Ernst, 1990). Anaerobic reduction processes, which are dependent upon appropriate electron acceptors therefore occur in a fixed sequence rather than simultaneously. Laanbroek (1990) relates these processes to relative redox potential (Table 1.1.4).

With lowered redox potential, nitrate (NO_3^-) will be reduced to nitrous oxide (N_2O) and nitrogen gas (N_2), with soil nitrate usually being depleted within three days of the onset of flooding (Ernst, 1990). Ernst (1990) also reviews the case of increased nitrate reductase (NR) activity at the lower end of a water depth gradient within an English salt marsh, where the concentration and availability of nitrogen can be a major determinant of the plant community present.

Table 1.1.3 Biodiversity support within the upper Paraná River and associated *varzea* floodplain wetlands of southern Brazil (Adapted from Agostinho *et al.*, 2000). *systematic surveys of large areas of floodplain only since 1997

	Total number of taxa recorded
Phytoplankton	300
Zooplankton	329
Periphyton	228
Zoobenthos	80
Aquatic macrophytes*	48
Fish	170 (c.151 endemic)

Table 1.1.4 Soil reduction dynamics and related redox potential (adapted from Laanbroek, 1990).

Process	Redox (E_0) (mV).
Disappearance of oxygen	+330
Disappearance of nitrate	+220
Appearance of manganous ions	+200
Appearance of ferrous ions	+120
Disappearance of sulphate	-150
Appearance of methane	-250

Under lower redox potential conditions, manganese is reduced from Mn (IV) to Mn (II). Mn (II) is more available to plants, but waterlogged plants appear to have a greater ability to exclude manganese (Ernst, 1990). Further decreasing redox potential leads to the reduction of the relatively insoluble ferric (III) form of iron to the very mobile ferrous (II) form. While aerenchyma and high root porosity are a prerequisite for radial oxygen loss (see section 1.1.6), the formation of a reddish-brown ferric hydroxide plaque may prevent excessive iron uptake. A trade-off in this situation may be reduced phosphate (PO_4^{3-}) uptake by plants (Ernst, 1990). Desiccation of leaves, and a greater inhibition of photosynthesis in waterlogging-intolerant plants may be explained to some degree by Fe (II) uptake, and also by the reduced interaction of the relevant forms of iron and manganese in chlorophyll synthesis (Ernst, 1990).

Once redox potentials reach values of –75 to –150 mV, sulphate (SO_4^{2-}) becomes unstable and is reduced to sulphide (S^{2-}). At such low redox potentials, even radial oxygen loss is insufficient to oxidise the rhizosphere, and porewater sulphide may diffuse into the root tissue.

Sulphide may precipitate as iron sulphide (FeS) at the root surface if an iron plaque has formed previously under less-reducing conditions. However, once the iron precipitates, sulphide may enter the plant freely as it is metabolically uncontrolled, and concentrations in the plant will then increase (Ernst, 1990).

Submergence and waterlogging produces soil conditions that are markedly different from those of well-drained soils (Patrick and Mahapatra, 1968). There are many examples in the literature of the implications for plant growth and community structure in relation to the redox systems outlined above. Pearsall (1952) related general pH ranges to loosely classified vegetation types (e.g. acid woodlands, blanket bogs), and considered pH to be 'the most useful single measurement that can be made for ecological purposes'. Redox potential is known to influence pH values, as are products of anaerobic soils such as elevated CO_2. These factors in turn have been shown to effect rice growth (Ponnamperuma *et al.*, 1966).

1.1.6. Wetland species adaptation to flooding

The wetland environment is hostile to a great number of plant species, but is also one to which a great number of species are very well adapted. These species have characteristically evolved mechanisms to tolerate the conditions associated with waterlogging (Davy *et al.*, 1990; Ernst, 1990). All wetlands, freshwater included, contain assemblages of plants which have evolved the ability to tolerate water tables which fluctuate around, or above the soil surface for at least a part of the year (Etherington, 1983). The tolerance of wetland species to inundation can be attributed to a number of mechanisms. These mechanisms may relate to structural and anatomical adaptations (waterlogging avoidance), physiological adaptations to the plant's immediate environment (e.g. oxygen transfer), or an ability to tolerate aspects of an anaerobic environment and/or anaerobic metabolism. This may include traits relating to morphology or internal biochemistry, selected for pressures exerted by the relevant wetland environment (Ernst, 1990; Wheeler, 1999). Different species can be expected to show different degrees of tolerance to waterlogging (Hills, 1994). This has been the subject of much research (e.g. Newbold and Mountford, 1997).

Variation in flooding tolerance can also be found in different populations of the same species e.g. *Festuca rubra* and *Agrostis stolonifera* (Davies and Singh, 1983), and *Carex flacca* (Heathcote *et al.*, 1987). Phenotypic plasticity in relation to water level has been investigated for a number of wetland species (e.g. Heathcote *et al.*, 1987; Legg *et al.*, 1995a; Vretare, *et al.* 2001). Within *Phalaris arundinacea*, which can only tolerate limited periods of anoxia,

and hence grows in relatively shallow water (Brix and Sorrell, 1996), 11 week treatments saw mean root porosity (per volume of root) at 29.9% under flooding, and 9.7% under drained conditions (Smirnoff and Crawford, 1983). Waterlogging tolerance in plants has been outlined in the form of four main theories by Wheeler (1999), echoing those above, and as described by Ernst (1990), and Hills (1994):

1. *Waterlogging avoidance:* within stable wetlands with relatively shallow water tables, colonisation of tussock vegetation (e.g. *Carex paniculata*) by shrub species may occur. Particular species such as *Drosera anglica, Viola palustris,* and members of the Orchidaceae only root within the upper substrate layer. Alternatively, rooting depth may increase only in relation to increased aeration at depth (e.g. *Molinia caerulea*).
2. *Oxygen transfer:* plants structurally adapt under waterlogging to allow oxygen transport systems (and structures such as lacunae, aerenchyma and respiratory roots), to maintain oxygen levels within root systems. Oxygenation of the anaerobic rhizosphere by *Radial Oxygen Loss* (ROL) is undertaken by a number of species (e.g. *Phragmites australis, Scirpus lacustris*), either by radial diffusion of oxygen through the cortex, or by enzymatic oxidation on the root surface. Both the season and the age of plants have been shown to effect methane (CH_4) oxidation.
3. *Anaerobic metabolism:* metabolic adaptations to anoxia survival may stimulate stem elongation via ethylene production, or the development of oxygenating structures within certain species (e.g. *Acorus calamus*), although specific toxin tolerance in certain species is under debate. Metabolic adaptation may also allow the plants to avoid the production of ethanol by producing alternative organic acid end products within the glycolysis metabolic pathway (e.g. *Alnus glutinosa, Nyssa sylvatica*).
4. *Seed survival and establishment:* the production of buoyant propagules may allow seedling establishment at the upper limit of a tidal wetland, thereby avoiding conditions of total anoxia (e.g. *Centaurium littorale* and *Samolus valerandi*, found within seasonally flooded dune slacks). Some seasonal wetlands have persistent seed banks which can survive several years of above average flooding, although evidence for this is limited (Wheeler, 1999).

Wetland vegetation is generally controlled by a combination of some or all of these factors, with the relative importance of each contributing to a species level of waterlogging tolerance. Specific morphological adaptation may include the production of adventitious 'surface' roots upon flooding, which undertake the role of nutrient acquisition, while 'deep' roots provide

anchorage. This mechanism may help overcome nutrient deficiency under anoxic conditions where excessive nitrogen occurs (Koncalová, 1990). The definite ability of various species to tolerate toxin accumulation is still under debate (Wheeler, 1999), and ideas about the ability to compartmentalise toxins in older leaves which are to be discarded, and away from reproductive structures are now being proposed (Ernst, 1990; Wheeler, 1999). In addition, limited evidence exists for the expulsion of toxic compounds via volatile emissions; for example Nriagu *et al.* (1987) found that up to 30% of sulphur emissions in remote areas of Canada came form biogenic emissions from boreal wetlands. Justin and Armstrong (1987) found that the shoot weight of wetland species was generally less affected upon flooding than were those of non-wetland species, and that they tended to have more aerenchyma. Keeley (1979) however did identify a 'cost' of excessive water loss from aerenchyma if drought were to occur.

Oxygen supply is the key factor in the maintenance of an aerobic metabolism in waterlogging tolerant plants. Alcohol dehydrogenase (ADH) is an enzyme which is synthesised in hypoxic plant tissue, catalysing the final step in the synthesis of ethanol (Ernst, 1990). Species of *Nymphaea* and *Nuphar* are rooted in highly reducing sediments and allow ethylene production when oxygen supply is restricted to the roots at night. However, these periods are limited in duration, and an extensive lacunar system allows root aeration during the day (Smits *et al.*, 1990). In species less adapted to anoxic conditions high ADH activity may indicate a sub-optimal metabolism (Ernst, 1990). For example, ADH activity is highest in roots at depth in *Filipendula ulmaria*, indicating the small airspaces and low oxygen transport capacity of this species; other species in waterlogged soils such as *Ranunculus repens*, *Poa trivialis*, and *Juncus articulatus* exhibit lower ADH activity, indicating more extensive aerenchyma, and oxygen transport systems (Ernst, 1990).

1.2. Eco-hydrological studies

1.2.1. Wetland hydrology and hydrochemistry

To define hydrology simply as 'the science of water' would perhaps be too broad and misleading, and usage of the term has tended to refer to the study of water in relation to its occurrence on, over, and under the surface of the earth as stream flow, water vapour, precipitation, soil moisture and groundwater (Ward, 1967). Implied within more recent definitions is the need to understand 'how water cycles and cascades through the physical and biological environment', and also that we must be able to 'account for all inputs and outputs to and from the system as well as all stores within the system (Baird and Wilby, 1999). Ward (1967) points out that while it was not until the 19th century that the first textbook on hydrology was published (Nathaniel Beardmore's *Manual of Hydrology*), the close association of Man and water had been evident since at least the time of the ancient Egyptians. Indeed historical figures proposed a number of theories, all of which bore some level of plausibility: e.g. Aristotle (384-322 B.C.) explained precipitation, while da Vinci (1452-1519) had some concept of the principle of flow in open channels. Ward (1967) considers that the principles of the modern science of hydrology were laid towards the end of the 17th century by the work of Pierre Perrault and Edmé Mariotte on drainage basins, and the English astronomer Edmund Halley, and his observations of flow in springs and rivers. Baird and Wilby (1999) considers that today hydrology is still largely an engineering discipline concerned with water supply, waste water disposal and flood prediction.

The understanding of wetland hydrology has advanced since Godwin published his work on the hydrology of Wicken Fen (Godwin, 1931; Godwin and Bharucha, 1932). However, wetland hydrological processes are still poorly understood, and generally little researched (Baird, 1995). The complex nature of the wetland environment is highlighted by Gilman (1994), who states that the wetland water balance must take account of all of the inputs, outputs and storage in the hydrological system. For these, groundwater and surface water inflows and outflows must be represented. From this basis, Gilman (1994) states that the water balance of a wetland site can be expressed as:

$$P + G_{in} + Q_{in} = E + G_{out} + Q_{out} + \Delta s$$

Where, P = precipitation; G_{in} = groundwater inflow; Q_{in} = surface inflow; E = actual evaporation from the wetland; G_{out} = groundwater outflow; Q_{out} = surface outflow; and Δs =

change in water storage, usually seen as a change in water level or the water table. Grieve *et al.* (1995) consider that recently there has been an increasing recognition of the importance of groundwater inputs into the hydrology and hydrochemistry of floodplain wetlands. These are in addition to the riverine and hill-slope inputs, which were originally regarded as the main sources. A study of the hydrological processes within Catfield Fen in the Norfolk Broads, UK, by Gilvear *et al.* (1997) uncovered a complex system, which was perhaps not as reliant upon riverine influences as previously thought. This was also a view previously put forward by Giller and Wheeler (1986).

That plants require 15-20 essential elements for growth is well known. The three primary elements for structural and energy storage purposes are C, H, and O. The remaining are divided into macronutrients (e.g. P, K, S, Ca, N, Mg) required in relatively large amounts, and micronutrients (Cu, Zn, B, Cl, Mo, Mn, Fe, Si) required in smaller amounts. While atmospheric nitrogen (N_2) is fixed as organic N via microbial loops, all the other nutrients are generally soil-derived (for rooted macrophytes, though not, of course, for free-floating macrophytes and phytoplankton); although rainfall may be the sole source of S and Cl to plants under extreme conditions on ombrogenous substrates (Etherington and Armstrong, 1982). The availability of certain of these nutrients due to the relative redox potentials of waterlogged soils is variable, as discussed in section 1.1.5.

The complex hydrological properties of wetlands, in conjunction with the specific origins of water sources, and to a degree *in situ* transformations, determine their organic and inorganic chemical composition. Ross, (1995) considers the four principle hydrological characteristics which determine the nature of the hydrochemistry of a particular wetland to be:

1. *Whether the system is permanently or periodically inundated*: seasonal fluctuations in the degree of waterlogging will influence redox potential, and hence nutrient availability (especially nitrogen, due to the early onset of its reduction and depletion in waterlogged soils; see section 1.1.5).
2. *The source of water*: nutrient status is largely dependent on whether wetlands are fed by groundwater which has been in contact with rocks and soil (telluric), or are wholly rainwater fed (meteoric). The nutrient status of telluric systems is variable, depending on the type of bedrock (e.g. insoluble quartz and granites, or soluble calcites).
3. *Whether the water is free flowing or stagnant*: while macrophytes actively slow flowing waters, they also act as oxygenators, and trap suspended sediments. British *Phragmites*

and *Typha* reedswamps are examples of wetlands whose nutrient uptake is predominantly from organic and mineral substrates.

4. *The substrate hydraulic conductivity*, which determines porewater retention times: British wetland soils comprise two main groups; *Gleys*, which may be derived from alluvial, estuarine, or lacustrine clay or silt mineral deposits; or *Peats*, derived from organic deposits. The main characteristic that differentiates peats from mineral soils is the high pH dependent cation exchange capacity (CEC), and high total nitrogen (N) values within the organic content. While hydraulic conductivities have been found to be very variable, they are at the lower end of possible values for soils, and not thought to have a major influence over hydrochemical dynamics. Further work needs to be undertaken on the influence of specific wetland soil properties on hydraulic conductivity (e.g. the compression and expansion of accumulated gas due to pore water pressure) (Baird, 1995).

Within a single wetland the dynamic and influence of relative inputs can vary substantially. Grieve *et al.* (1995), for example, observed significant differences between sample stations across Insh Marshes, Scotland. Valley side runoff increased dissolved organic carbon and Al in the shallow groundwater, while groundwater upwellings increased pH and Ca concentrations, and river inundation decreased the base status and increased Cl and Al.

1.2.2. Eco-hydrology

Ward (1967) recognised that the applications of hydrology had broadened to include issues of urban hydrology and of interactions with vegetation during the main period of its development. Baird (1995) however states that there has been a general lack of work to attempt to quantify and model relationships between ecology and wetland hydrology.

Ellenberg (1974) formulated relationships between plant species and their environment, effectively delimiting their ranks. Goslee *et al.* (1997) indicated that the identification of species to indicate wetland water source could be useful in the development of tools for wetland management.

In a review by Wheeler and Shaw (1995), the authors considered that: "conservationists would generally welcome a clear understanding of the interrelationships between mire vegetation and hydrology, to help them predict the likely effects of hydrological change upon vegetation.....or to determine desirable water environments for attempts at re-wetting damaged sites.....however, despite quite a large number of studies.....the relationship

between the hydrology of fens and the composition of their vegetation is not at all well understood, except in gross terms". Such tools would comfortably fit the ethos of eco-hydrology, which is regarded by Wassen and Grootjans (1996) as "an application-driven discipline ...[which]...aims at a better understanding of hydrological factors determining the natural development of wet ecosystems, especially in regard of their functional value for nature protection and restoration". This application to management and restoration was underlined in special issue of *Vegetatio* (vol. 126; 1996): *Consequences of changes in the water cycle for ground water and surface water fed ecosystems: eco-hydrological approaches.*

The application of applied eco-hydrological concepts is important under the European Water Framework Directive[4], due to be implemented in 2003. The directive recognises that "aquatic ecosystems .....equilibrium is strongly influenced by the quality of the inland waters flowing into them...", and the overall purpose of the directive is "to establish a framework for the protection of inland surface waters, transitional waters, coastal waters and groundwaters...".

[4] Establishing a framework for community action in the field of water policy (2000/60/EC)

1.3. Plant ecology

Begon *et al.* (1996) define ecology as 'the scientific study of the interactions between organisms and their environment'. Within this definition, individual organisms of the same species coexisting as *populations*, and numbers of populations existing as *communities* are all of interest to the ecologist; as are the varying complexities of the inherent interactions.

1.3.1. Plant community ecology

Plant communities, existing as a set of populations of representative species, are subject to environmental controls. Rieley and Page (1990) consider a number of abiotic and biotic factors whose variability influences the structure and composition of plant communities. Abiotic factors may include *light, temperature, water, CO_2 supply, wind, nutrient supply* and *fire*. Biotic factors include *Dispersal, species-species interactions* (for a review of competition see section 5.1.3, Chapter 5), and *succession*. Such definitions can be regarded as a simplification, and as Rieley and Page (1990) argue, the division of biotic and abiotic factors is somewhat simplistic. For example, a reduction in light (abiotic) to ground flora can occur as a function of succession. It should also be noted that within habitats regarded as man-made (e.g. golf courses), 'ecology' still operates (Begon *et al.*, 1996). The difference however, is that a number of factors are being actively selected for (e.g. fertiliser application; regular cutting), and as such, may preferentially benefit one species within a plant community over another.

1.3.2. Plant community definition

In relation to the science of taxonomy, ecology is relatively new (Grime, 1998). However, plant community ecology as a branch of this science is relatively old, and from its conception, disputes stemming from differences in opinion and approach have abounded (Kent and Coker, 1995). Crawley (1986) suggests that a good deal of these disputes relate to scale and positioning issues within sampling; as simple as how big and where exactly samples should be. While the volumes of the *British Plant Communities* (Rodwell, 1991 *et seq.*) prescribe ranges for nested quadrats within various community types, Sparks *et al.* (1997) suggest that within semi-natural and other habitats, appropriate sample size estimation may be inherently subject to errors where there is no prior information regarding the expected variability within an area. Wilby and Schimel (1999) point out that scale issues now constitute a growing body of research, and have been identified in the U.S. as a research priority. (Crawley, 1986)

considers that differing approaches to sampling makes comparisons, and agreement upon basic ecological concepts difficult.

At the beginning of the twentieth century much debate centred on the concept of the plant community within a spatial setting. Perhaps the most notable of these differing opinions was that between the American ecologists Frederic Clements, and H.A. Gleason. Clements (1916; 1928) proposed the *Organismic concept*, with vegetation communities comprising definable components within the overall cover of vegetation. He also regarded these associations to represent climax communities given long-term stability. Generally regarded to be at odds with Clements ideas, was the *Individualistic concept* proposed by Gleason (1917; 1926; 1939), whereby plant species respond individually to environmental parameters. While different species exist within groups at any one point, within a wider spatial framework individuals would vary independently, and therefore pre-defined 'groups' could not be considered to repeat over space. While Kent and Coker (1995) consider the emphasis to have been placed largely upon plant ecology at the community level previous to 1975, they indicate an increase in work related to individual plant strategies (e.g. Grime, 1979b) and plant population biology (e.g. Harper, 1977; Silvertown, 1987). Crawley (1986) considers that latterly, opinions have moved towards Gleason's '*individualistic*' concept of the plant community.

1.3.3. Vegetation description

During the early part of the twentieth century Moss (1910) recognised a lack of uniformity within the subject of plant ecology, with different names being given to similar, or identical plant associations. With the development of plant ecology as an academic discipline came a number of differing approaches to the description of vegetation (Kent and Coker, 1995). Denny (1985) describes the three main approaches to date:

1. *Classical methods:* vegetation was divided into units, and the units then considered separately, with the initial divisions based upon habitat and/or life-form and morphology of representative populations of plants. The 'life-form' classifications proposed by Raunkaier (1937), were related to broad environmental gradients, and the status of the perennating organs relative to the ground level. The main characteristics of the major categories are listed in Table 1.3.1; further sub-divisions were however recognised. Tansley (1939) also proposed classifications for communities of British vegetation (e.g. *Marsh, Fen* and *Carr*), and a variety of structural classifications have followed thereafter (Kent and Coker, 1995). Characterisation of such units was on the basis of groups of

plant species normally found within the habitat, and this approach allowed a subjective discrimination between communities (Hills, 1994).

2. *Phytosociological methods:* a number of schools of phytosociology developed during the latter half of the 19th and the first half of the 20th century (Kent and Coker, 1995), and were based upon the principle that vegetation communities were divided up on the basis of differences in species abundances, following the approach favoured by Clements (1916) (see Section 1.2.2). Denny (1985) considers the two main approaches to be the Zurich-Monpellier (Braun-Blanqet) school of subjective classification (Braun-Blanquet, 1932), which resulted from a convergence of the methods of a number of European workers (Kent and Coker, 1995), and the approach developed in the UK. and U.S.A.. The Zurich-Montpellier school uses a hierarchical classification, and considers the 'association' as the fundamental unit of vegetation. While the British/American system is similar, it relies more heavily upon the dominance of species to differentiate communities. While Kent and Coker (1995) indicate that problems exist with the clarity of methods in the Zurich-Montpellier approach, the British/American approach has been developed since 1975 as the basis of a national-scale classification of British plant communities, published as the National Vegetation Classification (NVC) (Rodwell, 1991 *et seq.*).

   A similar approach is the CORINE (Co-ordination of information on the environment) phytosociological system (Devillers *et al.*, 1991), which utilised the biotopes concept to draw up a vegetation framework for Europe. Biotopes are defined as "an area of land or a body of water which forms an ecological unit of community significance for nature conservation regardless of whether they are formally protected by legislation". Biotopes have indicative species listed, with further sub-divisions based on other indicative species.

3. *Multivariate methods:* methods employing objective multivariate algorithms for hierarchical classification (e.g. TWINSPAN: Two Way Indicator Species Analysis) and ordination (e.g. DCA: Detrended Correspondence Analysis) of species assemblage and abundance data have been developed since the mid 1970's (Hills, 1994). Gauch (1982) comments that the use of such methods has been aided by the increased availability of computers, and considered them at the time to be the best techniques for analysing complex sample-by-species data arrays. The method of ordination mentioned above allows an interpretation of environmental controls (gradients) only as a retrospective process, and is termed 'indirect gradient analysis'. A development of the multivariate approach now however allows a 'direct gradient analysis', whereby quantitative species scores are ordinated on the basis of underlying environmental values (ter Braak and Prentice, 1988; Jongman *et al.*, 1995); the principle and application of these methods are

discussed further in Chapter 3. Multivariate procedures have been vital to the production of the NVC (see Rodwell, 1991 *et seq.*), and in packages produced in order to assign vegetation samples to existing NVC categories (e.g. MATCH; Malloch, 1999).

Table 1.3.1 Major categories of Raunkaier's life-form classification (Raunkaier, 1937), showing main characteristics for those groups containing species of interest in the context of this study*.

Group	Main Sub-Groups and Characteristics
Phanerophytes	Perennating buds emerging from aerial parts of plants (>2m)
Chamaephytes	Perennating buds emerging from aerial parts of plants close (<2m) to the ground
Hemicryptophytes	Perennating buds borne at ground level; aboveground parts die back
Cryptophytes*	Perennating buds/shoot apices survive unfavourable season below ground/underwater (a) Geocryptophytes or geophytes including forms with: (i) rhizomes; (ii) bulbs, (iii) stem tubers, (iv) root tubers (b) Marsh plants (helophytes) (c) Aquatic plants
Therophytes (Annuals)	Perennating as seeds

1.3.4. Plant survival strategies and traits

Species based methods of vegetation analysis and description, are inherently subject to geographical variation. Keddy (1992b) argues that models to predict vegetation response to environmental perturbation are increasingly needed, however, due to the large number of species on the planet, models based upon species taxonomy would have a limited applicability (for example, species are likely to differ greatly between UK and south-east Asian wetlands). However, models based upon aspects of traits which species globally have in common (e.g. the relative diameter of aerenchyma), are more applicable, due at its simplest to the fact that the models necessarily must deal with these shared traits. Keddy (1992b) points to the work of van der Valk (1981): a simple trait such as the ability to germinate under flooded conditions means that those species lacking this ability can only regenerate under drawdown conditions. Noble and Slatyer (1980) employed "vital attributes" of plants to predict succession and

perturbation in plant communities. Functional groups have also been defined; for example, species with an isoetid life form (e.g. *Isoetes lacustris*, *Litorella uniflora*, and *Lobelia dortmanna*) are found at the margins of oligotrophic lakes, and are phylogenetically unrelated. However, all produce leaves in robust rosettes to withstand wave action, and have extensive root systems to pump nutrients from deep within gravelly substrates (Dickinson and Murphy, 1998). Semenova and van der Maarel (2000) review the development of 'trait-based' approaches in assessing vegetation. They consider that while a good deal of progress has been made of late, confusion still ensues, and a clarification of the terminology is needed. It is suggested that the term 'plant functional types' (PFT's) be used, and that a consistent framework is required for these PFT's to be compared and interpreted. Similarly, a review by Duckworth *et al.* (2000), suggests that the use of PFT's in plant ecology requires increased consistency. It is also stated that the potential for future development lies in the identification of a minimum set of useful plant functional traits to optimise efficiency.

1.3.4.1. Survival theories

For a plant attempting to grow and reproduce in a given environment, only certain sub-sets of attributes will permit survival and reproductive success (Grime, 1979a), with the environment having had a 'filtering effect' upon the traits represented (Diaz *et al.*, 1998).

r-K selection

MacArthur and Wilson (1967) proposed a model with opposing "*r*" and "*K*" strategies (from the general population growth rate in a limited environment), which was later extended by Pianka (1970). The deterministic factors of the model related *r*-selection to earlier maturity, with larger reproductive effort and shorter life, and *K*-selection to later maturity, lower reproductive effort, and longer life (MaCarthur and Wilson, 1967). Inconsistencies of the model were regarded by Grime (1979a) as:

1. the theory made no provision for a successful strategy to occupy stable but unproductive habitats.
2. juveniles and adults of the same species were assumed to have the same traits.

Although the r-K framework has proved useful in understanding the ecology of many organisms, particularly animals, Grime and Sibley (1986) considered that the theory had not made a "significant contribution to the production of a unified strategy theory", while Stearns (1977) considered it incomplete.

Grime's C-S-R theory

Grime (1974; 1979a) proposed a triangular ordination model with axes for competitive ability (C), stress tolerance (S), and disturbance tolerance (R, sometimes also rendered as D) for a variety of plant species around Sheffield, UK. In his framework theory, Grime (1979a) laid down the following definitions:

Strategy = "a grouping of similar or analogous characteristics which recur widely among species or populations and causes them to exhibit similarities in ecology".

Competition = "the tendency of neighbouring plants to utilise the same photon of light, ion of mineral nutrient, molecule of water, or unit of space".

Disturbance = "any factor which destroys biomass and includes trampling, grazing and fire-damage".

Stress = "any factor which reduces the rate of accumulation of biomass and includes shortage of light, water and minerals".

Traits relating to R_{max} (maximum potential growth rate) and various morphological parameters were measured, to provide indicators of the disturbance tolerance (D: also given as R = "ruderal qualities") and competitive ability (C). These were plotted onto two sides of the ordination, and from these, stress tolerance (S) could be extrapolated. This came from the geometric requirements of the triangular ordination, whereby C+S+D=1, and allowed species to be separated in the ordination.

Grime (1985) however considered that strategies would be better represented by a "complex array of traits". Hence, a more sophisticated strategy theory was produced (Grime *et al.*, 1988), with a dichotomous key based upon attributes and traits from phenology, morphology and life history. "Marker" species were also selected which could be placed unquestionably into a primary, or secondary strategy. Intermediate strategies could therefore also be described, where for example, plants exhibited elements of stress tolerance and competitive ability, giving a C-S strategist. Other strategies such as competitive ruderal (C-R), stress tolerant ruderal (S-R), and intermediate (C-S-R) could also be assigned (Grime *et al.*, 1988). However, while intermediates could be described, it was apparent that factors of high stress and high disturbance would effectively exclude plant life.

The theory was considered to have a good generality, providing a framework for describing plant-environment relationships (Grime, 1979b), and has been tested by several workers. Gaudet and Keddy (1988) found that traits such as a rhizomatous nature could be used to predict the competitive ability of plants. Murphy *et al.* (1990) considered that the C-S-D strategy approach could be applied objectively to populations and communities of aquatic macrophytes in order to describe their strategies. Hills *et al.* (1994) also proposed three main functional groups within European wetland vegetation, with a trade-off between competitive ability and stress tolerance. Spink (1992) applied the theory to describe the strategies of aquatic *Ranunculus* species, while Abernethy (1994) applied it to European euhydrophyte communities. Further work by Grime *et al.* (1997) has produced evidence for functioning being predictable from traits relating to aspects of reproduction and evolutionary strategies in roots and shoots.

Problems with the C-S-D framework

Potential problems with the theory have been aired (Hills, 1994). However Grace (1991) considers that a good deal of unnecessary debate has simply arisen from the definition of the terms used in the development of theories. While Grime's theory supports the concept that plants gain competitive superiority from high resource uptake capacity, Tilman (e.g. see Tilman, 1987) suggests that competitive superiority is due to a lower equilibrium resource requirement. However, the specific definition of competition varies between the authors, and Grace (1991) suggests that the theories are actually largely complementary rather than opposing.

Two further problems relating to (1) the constraints of a triangular ordination, and (2) cases of extreme morphological plasticity within a single species are outlined by Hills (1994):

1. Loehle (1988) argues that the constraints of a triangular ordination assume a direct trade off between traits; where C+S+D=1, axes scores for C and D of 0.3 each (=0.6 in total), would constrain the species to have a S axis score of 0.4. Some work in this area (e.g. Hills and Murphy, 1996) has shown that a direct trade off between strategies can be observed. However, the assumption that species will always fall within the constraints of the triangular ordination should not be taken as implicit. We need to remember that one of the axes is a composite extrapolation of the measured components of competitive ability (C), and stress tolerance (S). In response to criticism of the theory by Loehle (1988), Grime (1988) has agreed that the possibility of species being plotted external to

the triangular ordination should not be excluded. The theory does however form a good basis of a consistent strategy framework.

2. Arguments abound for a good deal of variation occurring within populations, as well as between species, with genetic variation being defined at the population level. However the perspectives put forward by Grime (1979a) are broad, and accept the fact that variation within species will occur. The functional question of which traits delimit which species, and what is the degree of variation in functional traits between, and within species, can therefore be addressed.

1.3.4.2. Trait differentiation in relation to the environment

Rozenzweig and Abramsky (1986) proposed a model of centrifugal community organisation based on observations of desert rodents, whereby they identified a 'core' habitat, which, even at low population densities was exploited by rodents. Peripheral habitats were also identified which were only utilised in times of increased population density, whereby as densities increased, a greater number of habitats was utilised; this being the centrifugal effect. In a similar vein, Keddy (1990) and Keddy and MacLellan (1990), proposed a model for herbaceous wetland and forest communities; using the constructs of (I) plant communities being structured as competitive hierarchies, and (II) that competition is more intense in high biomass sites. From a species poor - high biomass core, a set of possible paths, defined by a particular set of environmental conditions was proposed, with these being related to an axis of decreasing biomass.

With these proposals, Keddy and MacLellan (1990) also introduced the concept of 'state variables', whereby "biomass may produce changes in other state variables such as the total species pool, alpha diversity and number of vegetation types", and that the use of biomass in centrifugal models "integrates a number of state variables of interest". While these state variables were undefined by Keddy, Hills (1994) regarded them as "a measurable variable of a biotic community which has a particular range of values for each type of vegetation community". Keddy (1992b) considered that "as ecology matures and the world's environmental problems multiply, the need for general predictive models also grows". He then went on to point out that models based on traits would have a more general applicability than those based on taxonomic divisions. Further to this, both Keddy (1992b) and Diaz *et al.* (1998) regard traits as being filtered through the effect of climate, disturbance, and biotic conditions.

Examples of relationships between species composition and underlying environmental gradients are numerous in the literature, and are outlined elsewhere in this chapter. Hills (1994) suggests relationships between biomass and other state variables remain largely untested. However, recent work within the Rio Paraná *varzea* wetlands (Murphy *et al.*, 1999; Murphy *et al.*, 2001) has begun to address this deficiency. Regression equations show that macrophyte biomass can be predicted from the variables, light extinction coefficient, total oxidised nitrogen in the water, and sediment redox potential. Recently there have been examples of the use of state variable within vegetation as indicators of hydrological processes (Willby *et al.* 1997). Some examples successfully extend this approach to organisms other than plants (e.g. Murphy *et al.*, 1994), but examples of such work are limited.

1.4. Project outline

1.4.1. A background to the project

Past work carried out at the Universities of Glasgow and Stirling has emphasised functional relationships between the vegetation of wetland and aquatic habitats, and the underlying hydrological regime(s) (e.g. Abernethy, 1994; Murphy, 1994; Murphy, 1995; Sabbatini and Murphy, 1996; Willby *et al.*, 1997; Ross *et al.*, 1998; Ali *et al.*, 1999; Ross, 1999; Murphy *et al.*, 2001).

The work of Hills (1994), which contributed to the wider FAEWE (Functional Analysis of European Wetland Ecosystems) project (see Maltby *et al.*, 1993), concentrated on a functional analysis of European wetland vegetation. The work was undertaken by studying hydrogeomorphic units within study sites, in order to produce a system by which analysis of wetland vegetation could be used to predict the effects of anthropogenic perturbation. From this baseline work, which used the C-S-D established-phase strategy theory as its framework (Grime *et al.* 1988), Hills *et al.* (1994) developed predictive equations to determine the importance of C and S strategy elements for 78 plant populations. The work has since been verified over a range of sites (Hills and Murphy, 1996), and the principles have been successfully extended to act as indicators of wetland functioning (Murphy *et al.*, 1994; Murphy *et al.*, 2001), and as indicators of biodiversity within Scottish agricultural land (Abernethy *et al.*, 1996).

Hydrological and hydrochemical regimes have long been recognised as being amongst the most important factors in determining the vegetation associations found within wetlands (Godwin and Bharucha, 1932; Sjors, 1950; Gorham, 1953; Ingram, 1967; Damman and Dowhan, 1980; Malmer, 1986; Keddy *et al.*, 1994; Brown and Scott, 1997). Hydrochemical-vegetation interactions have been studied with reference to floodplain mires by Giller and Wheeler (1988), Wassen *et al.* (1990), Wassen and Barendregt (1992), and Willby *et al.* (1997). However, it is only recently that attempts have been made to quantify the specific water level requirements of wetland species (Newbold and Mountford, 1997), going some way to filling the gap in such quantitative information which had been earlier recognised (Mountford and Chapman, 1993).

Many wetlands have hydrological systems which are both complex and variable (Grieve *et al.*, 1995; Gilvear *et al.*, 1997). However, with the exception of the work of Willby *et al.* (1997)

little work has been carried out on the relationships of functional vegetation groups to localised hydrological and hydrochemical conditions within wetlands.

The main aim of this project is to determine the main environmental pressures driving diversity, vegetation structure, and functional characteristics of the dominant plant populations in different assemblages within a number of representative freshwater wetland systems across northern Britain. In conjunction with experimental work, this will hopefully permit identification of traits within the vegetation with the potential to act as predictors of hydrological variation, and also to allow the prediction of what changes, if any, might occur in the vegetation as a result of altered hydrological regimes. Increased knowledge of ecohydrological interactions is considered important in informing the management of these important habitat types.

1.4.2. Thesis outline

- *Chapter 2* describes the selection of the seven wetland sites used during the fieldwork component of the study, and gives a background to each of these sites. The hydrological instrumentation employed is described, as are the vegetation composition and structure, and environmental ranges measured within each of the seven sites.
- *Chapter 3* discusses the phytosociological aspects of the field study, in terms of the floristic assemblages found at each of the sites, and their classification as National Vegetation Classification (NVC) community types. By means of multivariate analyses the community types are characterised (and differentiated) in terms of parameters relating to their underlying environmental regimes, and to a number of traits measured within either the collective species complement, or the dominant species present. A number of sites, which were repeat sampled for either two or three years, allow for a temporal focus to be placed on this aspect of the study.
- *Chapter 4* – investigates eco-hydrological relationships within the wetland vegetation studied. Ecological gradients which drive the composition of each sample are determined. Differences between these samples are also characterised by investigating differentiation in predominant traits. Using a trait-based approach, predictive models of vegetation response and relationship to measured environmental parameters are constructed, and tested. In addition, predictive models are proposed which utilise attribute data gleaned from the literature as predictors of hydrological regime.
- *Chapter 5* – investigates the response of selected wetland species to ground-water stress and competitive interaction within an experimental framework. Species with contrasting

established phase strategies (*sensu.* Grime, 1988) are employed in various combinations of treatments, and a number measurements are made of vital attributes (e.g. leaf and reproductive structure production) in relation to these treatments.

- *Chapter 6* –contains a general synthesis and discussion of the results obtained, and of their potential implications for the general science of freshwater wetland plant ecology. Suggestions for development of the work are discussed.

Chapter 2: Field study sites; floristic composition and hydrological characteristics

2.1. Introduction

2.1.1. Selection of study sites

During the winter of 1998, prior to the first field season of this study, a number of freshwater wetland sites were identified, and their potential for inclusion as study sites was assessed. Assessments were based on a number of factors, including representation of a number of perceived groundwater regimes and vegetation types. Physical ease of access and land ownership issues were also considered, to allow for the setting up of permanent instrumentation (see Section 2.2.1.2) at fixed stations along each of the transects. Two sites were chosen for the field study in the first year (Table 2.1.1) and sampling visits were made at approximately monthly intervals (Appendix 1) from May until September.

A similar protocol was used for the 1999 and 2000 field site selection (Table 2.1.1), but sampling visits were reduced in number (Appendix 1). The number and geographical range of sites sampled was however increased for the 1999 and 2000 field seasons, in order to increase the envelope of applicability of models which were to be generated from the field data collected (Dickinson and Murphy, 1998). This would also provide a suitable range of model test data (see Chapter 4).

None of the sites studied were subject to grazing pressure imposed by management practices. However, it is likely that native and/or feral animals such as deer could have grazed the sites.

In this Chapter a general overview of study sites used during 1998-2000 (Figure 2.1.1) is presented, the plant species recorded at each site are listed, and the ranges of the environmental variables measured are outlined. An analysis of plant community composition and measured groundwater characteristics is covered in Chapter 3, and an analysis of the eco-hydrological interrelations of these variables is covered in Chapters 3 and 4.

In summary, this Chapter:

- Introduces, and gives a background to the wetland study sites used for this work.
- Gives details of the field instrumentation and methodologies used to collect the vegetation data and hydrological, hydrochemical and other environmental data.
- Characterises the various sites used in terms of the plant species occurring, and the underlying hydrological and hydrochemical regimes.

Figure 2.1.1 Field site locations in Scotland and Northern England sampled during 1998-2000. *IM* = Insh Marshes; *EM* = Endrick Marshes; *GM* = Glen Moss; *LW* = Lochwinnoch Reserve; *NW* = Nether Whitlaw Moss; *WOC* = Wood of Cree; *TM* = Tarn Moss.

Table 2.1.1 Study sites sampled, and the year(s) in which they were sampled, showing NGR centred upon all transects for each site (see section 2.1.2 for start and finish NGRs for each transect).

Site Name	NGR*	Reserve Area (ha)**	Region Within UK	Height Above Sea Level* (meters)	Number of Transects			Total Number of Stations		
					1998	1999	2000	1998	1999	2000
Endrick Marshes	NS435875	27	Dumbartonshire, Scotland	9	-	-	1	-	-	6
Glen Moss	NS368699	19.5	Renfrewshire, Scotland	150	-	2	-	-	6	-
Insh Marshes	NH793014	844[†]	Inverness-shire, Scotland	220	2	3	1	17	20	8
Lochwinnoch	NS364584	39.5[††]	Renfrewshire, Scotland	31	-	2	-	-	6	-
Nether Whitlaw Moss	NT508295	4	Selkirkshire, Scotland	274	1	1	-	6	6	-
Tarn Moss	NY400275	16.8	Cumbria, England	274	-	1	-	-	5	-
Wood of Cree	NX375718	32.4[†††]	Wigtownshire, Scotland	31	-	-	1	-	-	6

*From OS 1:50000 map series; **From SSSI notifications and site management information; [†]Largely floodplain, but includes some farmland, woodland and moorland under RSPB ownership; [††]Includes wet grassland, marsh and tall fen areas of reserve only; [†††]Includes fen and swamp area combined, of which approximately 3 ha. is fen

2.1.2. A background to the study sites

Endrick marshes (Aber Bog)

Aber Bog, along with other areas of the Endrick Marshes, is managed by Scottish Natural Heritage (SNH), and forms part of the larger Loch Lomond NNR (National Nature Reserve), designated in 1962; the marshes act as an important site in winter for migratory White-Fronted Geese (*Anser albifrons*) and support a number of rare plant species. The mesotrophic site comprises an area of fen whose vegetation was formerly harvested. This practice however was abandoned in the mid 1930's, allowing encroachment by *Phalaris arundinacea* (Reed Canary-grass), and colonisation by Willow (*Salix* spp.) (Mitchell, 2000). The site underwent major rehabilitation works during the period 1978-1989, including redirection of polluted drainwater, creation of open water bodies, and the introduction of sluices to actively control water levels. The ten years following completion of the scheme saw the spread of *Phalaris* curbed, coupled with a resurgence of growth of *Carex* species. The site was designated as a SSSI in 1983, as part of the larger Endrick River Mouth SSSI, and falls within the proposed designation for the new Loch Lomond and Trossachs National Park (Scottish Natural Heritage, 2000).

The transect was intersected between stations 3 and 4 by a drainage ditch. Stations 1-3 were based on a mineral substrate, with there being little or no peat deposit present (John Mitchell, pers. com., 1999). The vegetation taken in by stations 3-6, while still being underlain by mineral deposits, tended to form a floating mat 50-75cm above the underlying substrate. The transect ran from NS434873 – 438877.

Glen Moss

Glen Moss (Plate 2.1), a Scottish Wildlife Trust (SWT) site, is a mixed basin and valley mire containing sedge-dominated plant communities with an area of shallow open water. The sedge beds provide nesting sites for breeding ducks such as Teal (*Anas crecca*) and Shoveller (*A. clypeata*); the site is considered entomologically interesting due to the presence of a variety of moths, butterflies, damsel flies and dragonflies (Glen Moss Site of Special Scientific Interest: File reference 605/22WYG; Scottish Natural Heritage, Clydebank). The site is also a [local] stronghold for sedge warbler (*Acrocephalus schoenobaenus*) and Reed Bunting (*Emberiza schoeniclus*), with 5-10, and 4-5 pairs respectively in 1996 (Garratt, 1996).

The site has one drainage outlet, which is currently controlled by a sluice (date unknown). In the latter part of the 19th century a sluice was put in place to allow winter flooding of the

moss for the use of the local curling club; during this time the moss was also drained in spring to allow cattle grazing, and reeds were cut in autumn on a yearly basis. The original sluice had fallen into disuse by the 1950's and the curling club no longer used the moss. For a short while during the 1960's, groundwater was abstracted from the site in order to water the nearby golf greens, but this practice was later discontinued (Garratt, 1996). The site is currently designated as a SSSI, with the most recent designation being in 1984, under the 1981 Wildlife and Countryside Act.

The two transects used, consisting of three fixed sample stations each (Table 2.1.1), took in areas of vegetation on either side of a raised, wooded, central area, and were both based on peat substrate. Transect 1 ran from NS367696 – 368698, and transect 2 ran from NS366697 – 366699. Two transects were used due to the rounded shape of the reserve, with a central wooded area, rather than due to its size.

Insh Marshes (Balavil Fen, Insh Fen, Tromie Fen)

This Royal Society for the Protection of Birds (RSPB) reserve (see Plate 2.2), mostly comprising an area of floodplain of the River Spey, is regarded as a nationally and internationally important site (Gibbons, 1993). The site has a grade 1 SSSI, and also a RAMSAR designation. The wetlands are home to a wide range of rare breeding and wintering birds, and also a number of rare plant species. *Carex chordorrhiza* (String sedge) (Jermy *et al.*, 1982; Legg *et al.*, 1995b) is particularly note-worthy, only being recorded in one other Scottish (and UK) site, in Sutherland.

Subsequent botanical surveys of the wetlands (Wood, 1987; Loizou, 1997) have classified the main communities as swamp and poor fen, with scattered and infrequent mire and scrub communities. Due to the diverse and large areas of intact swamps and fen, Loizou (1997; pp.2) considers the site to be:

"...probably the finest example of a floodplain mire in the whole of Britain....the site has national as well as international importance".

The importance of the Insh Marshes as a wetland habitat is undeniable, and while little documented history exists for the valley pre-18th century, it is thought to have been wooded, apart from scattered open water bodies (Gibbons, 1993). By 1835, much drainage of the valley had taken place, and crops were being grown; this was achieved by lowering the level of the largest water body, Loch Insh, and through the construction of embankments to prevent flooding from the river Spey. Embankments however, began to deteriorate from the

mid 19th century onwards, and drainage ditches became less effective. Recent work, undertaken by Grieve *et al.* (1995) suggests that a complex system of hydrological inputs and balances including valley side runoff, groundwater upwelling, and riverine inundation (Plate 2.3), underpin the functioning of the marshes.

The use of three transects at Insh Marshes was intended to take account of variations in perceived water level regime, and of spatial variation within vegetation over the greater area of the site. Transects were numbered as follows: (1) *Insh Fen*: south of the River Spey, with nine permanent sampling stations (reduced to eight during 2000); (2) *Tromie Fen*: south of the Spey, with eight permanent sampling stations (reduced to seven during 1999, and not sampled during 2000); and (3) *Balavil Fen*: north of the Spey, with four permanent sampling stations (sampled during 1999 only). Transect 1 (NH812023 – 805029) was underlain variously by mineral soils, and mineral soils overlain by peat; transect 2 (NH775001 – 774005) was generally peat based with areas of floating mat vegetation; transect 3 (NH793022 – 796019) consisted of floating mat vegetation overlying approximately 50cm of water, which in turn stood over an impermeable clay-based substrate (Tom Prescott, RSPB., pers. com., 1998).

Lochwinnoch (Aird Meadow)

The main wetland areas of the RSPB Lochwinnoch Reserve (Plate 2.4) comprise marsh and fen vegetation fringing shallow, eutrophic, open water (Castle Semple Loch and Barr Loch; these being the result of flooding of former water meadow systems). The wetland areas are in turn fringed by areas of scrub and mixed deciduous woodland, and include large areas dominated by *Carex aquatilis* (Water Sedge). The main fen and marsh areas are thought to be a relatively recent development following a loss of hydrological control via sluices, since the 1950's (Bhatia, 1999).

The reserve as a whole is regarded as an important example of lowland eutrophic wetland, which has supported breeding populations of four red data book listed bird species, and wintering populations of up to nine amber listed bird species in recent years (Bhatia, 1999). However, it is considered that an active management of water levels within the reserve would increase the value of the habitat, and potentially result in an expansion of areas of marsh, wet grassland and fen, and reedswamp. To this end, hydrological assessments and studies of potential water level control within the reserve have been undertaken in recent years (e.g. Gilvear, 1994; Heffernan and Mansell, 1998).

The majority of the reserve is designated a SSSI with the most recent designation being in 1985, under the 1981 Wildlife and Countryside Act.

Transect 1, consisting of three fixed sample stations, took in an area of floating-mat vegetation, with little or no peat or mineral substrate present; transect 2, also consisting of three stations, took in an area with mineral substrate. Transect 1 ran NS364585 – 365587), and transect 2 ran NS361585 – 362585). Two transects were used as the two distinct wetland areas (floating-mat, and those areas based on mineral substrate) were physically separated by sections of open water and scrub.

Nether Whitlaw Moss

Nether Whitlaw Moss (Plate 2.5), along with 3 other sites (*Blackpool Moss, Beanrig Moss* and *Murder Moss*) are managed by SNH, and form the Whitlaw Mosses NNR, which also has SSSI designation. These mosses have recently been proposed as part of a larger Special Area of Conservation (SAC) under the European Habitats and Species Directive (1992), which will allow the target type of 'transition mires and quaking bogs' to be maintained at a 'favourable conservation status' (Gilvear, 1998).

All of the mosses within the Whitlaw Mosses NNR occupy shallow basins within underlying Silurian shales, which are locally calcareous, resulting in base rich groundwater and localised upwelling springs (welleyes). Nether Whitlaw Moss itself is a small elongate basin surrounded by agricultural fields, which are known to drain into the basin, and comprises a mix of rich and poor fen communities with scattered birch scrub. During the 15th-16th century, the site was subject to peat removal, and also possibly marl extraction (Gilvear, 1998).

The length of the transect (NT506294 – 511295) took in areas of mineral substrates, and floating mat vegetation over wet peat/water.

Tarn Moss

Tarn Moss (Plate 2.6), which is owned by English Nature (EN), is a basin mire formed within a glacial hollow, and is largely devoid of tree or scrub cover. The site is unusual in having characteristics of an acid mire, interspersed within a nutrient-poor fen (EN information leaflet). Management has been minimal at the site, but has included the damming of drains to maintain water levels, and the construction of other drains to take road water away from the site. The site is designated as an NNR.

The length of the transect (NY398274 – 402276) took in peat based substrates.

Wood of Cree

The Wood of Cree fen forms part of a larger reserve which is owned and managed by RSPB, and which comprises mainly of ancient broad-leaved woodland, with scattered areas of swamp on the River Cree. The fen is characterised by a gradual gradation from *Salix* woodland to open (standing) water, and is occassionaly inundated by water from the river. Previous surveys have described the site as a good example of a transitional fen system (Paul Collin, RSPB., pers. com. 2000).

The length of the transect (NX 375719 – 376717) took in areas of mineral substrate, peat substrate, and floating mat vegetation over open water.

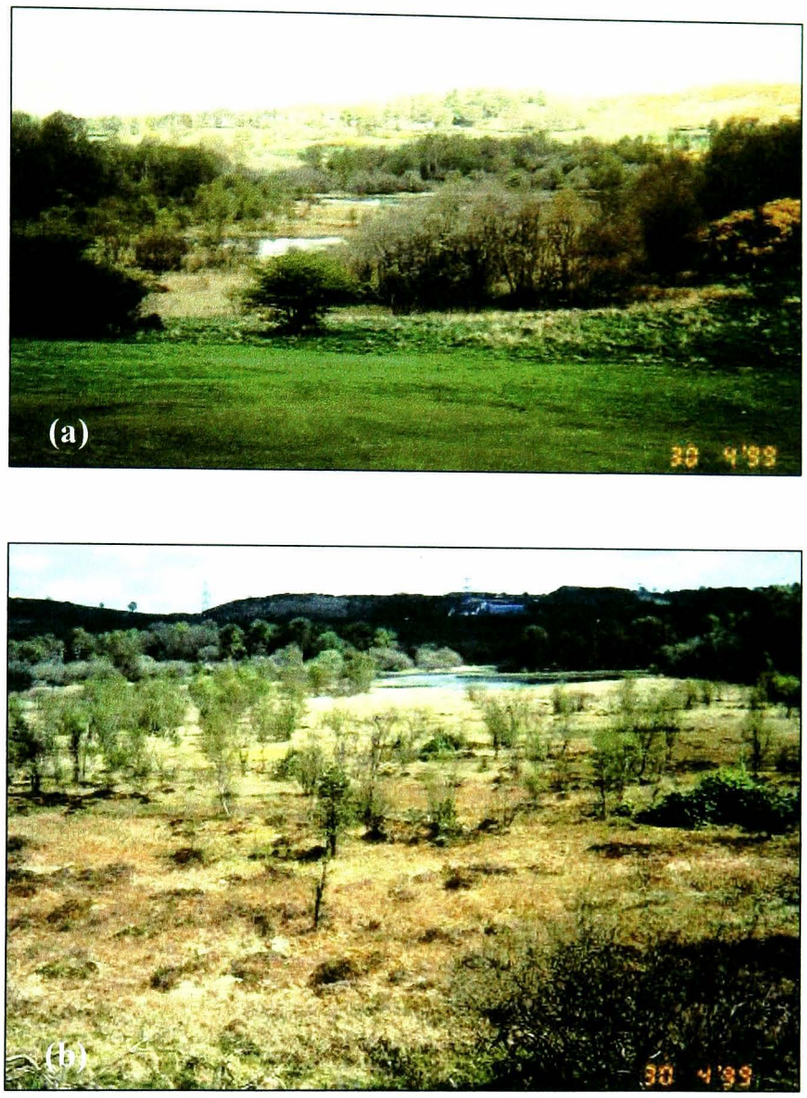


Plate 2.1 Glen Moss. (a) Transect 1, running left to right behind the foremost large patch of birch, showing areas of shallow, open water; (b) Transect 2, showing an area dominated by *Eriophorum angustifolium* in the foreground, with scattered scrub and open water beyond.

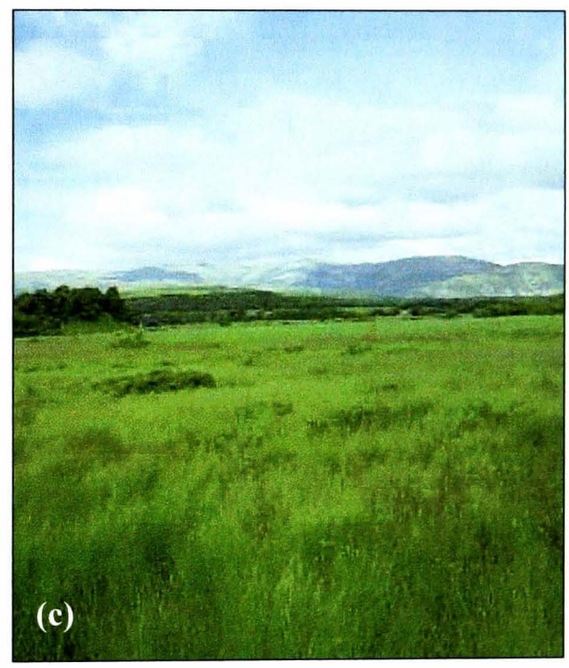


Plate 2.2 Insh marshes. (a) Transect 1 (*Insh Fen*) showing sampling within an area of wet grassland dominated by *Deschampsia cespitosa* and *Juncus effusus*, with a wetter area beyond, dominated by *Carex nigra*, *C. panicea* and *Molinia caerulea*; (b) Transect 2 (*Tromie Fen*) showing an area dominated by *Phragmites australis*, with an undercanopy of *C. lasiocarpa* and *Potentilla palustris*, with standing water visible; (c) A section of transect 2, dominated by *C. panicea* in the foreground, with an area supporting a local population of the nationally rare String Sedge (*C. chordorrhiza*) (see Legg *et al.*, 1995b; Appendix 10).

Plate 2.3 Insh marshes, near to transect 1 (*Insh Fen*), December 1999, showing an area inundated by floodwater.

Plate 2.4 Lochwinnoch (*Aird Meadow*). (a) Transect 1, showing floating-mat vegetation dominated by *Glyceria maxima*, with open water beyond.; (b) Transect 2, with *Phalaris arundinacea* litter in the foreground, and a large stand of *Carex aquatilis* beyond.

Plate 2.5 Nether Whitlaw Moss. (a) View showing mixed nature of vegetation, with *Sphagnum* spp and birch scrub to the foreground; (b) Overall elongated basin shape of the fen (photo courtesy of Sarah Ross).

Plate 2.6 Tarn Moss: view across the basin, showing mixed vegetation with *Deschampsia cespitosa* in the foreground, and sparse scrub.

2.2. Methods and materials

2.2.1. Field data

Permanent transects were set up at each site, with fixed water level monitoring stations being implemented at intervals of approximately 30-50 metres. Stations were set up in order to cover a range of vegetation types, and a range of perceived hydrological variation; as identified from initial site visits, discussion with site managers, and from previous vegetation surveys and site reports, where available. A repeated measure sampling regime, with visits made at approximately monthly intervals (Appendix 1), was implemented at each site. Various measures of the vegetation, and of groundwater and groundwater-related variables were conducted during each visit.

2.2.1.1. Vegetation data

Within a standard radius of 1m around each fixed water level monitoring station (see section 2.2.2.1), sampling was conducted using a $1m^2$ quadrat with twenty-five $20x20cm^2$ sub-divisions. Species lists were drawn up at each visit, and the abundance of each species was noted on the basis of the number of occurrences within the $1m^2$ quadrat; this figure was then multiplied by four to give a percentage abundance estimate. Nomenclature followed Clapham *et al.* (1981), Hubbard (1984), Jermy *et al.* (1982) and Stace (1997) for vascular plants, and Smith (1978) and Watson (1994) for bryophytes. Dominant species were classified as those occurring in 16 or more of the 25 subdivisions, approximating to an abundance of 65%, or more. A maximum of three species was noted as 'dominants' in each case. Following an initial sampling of replicate points around a number of fixed stations, species composition was seen not to vary greatly within the homogeneous mosaics identified (Appendix 2). While the dominant species were generally consistent across replicate station samples, little variation was seen in other species either. Subsequently, single vegetation samples were taken, in order to maximise the total range and number of sites which could be visited. Monthly species lists were drawn up from different areas within a 1m radius of fixed sampling stations, rather than from fixed quadrats, due to the destructive nature of associated sampling (See Chapter 3). This was in order to reduce the impact within a concentrated area the wetland vegetation, which in many cases is generally stress tolerant, but disturbance intolerant (Grime *et al.*, 1988).

2.2.1.2. Groundwater data

Fixed station field sampling

Fixed sampling equipment was installed along the permanent transects established at each field site. Water level range gauges, adapted from the design of Bragg *et al.* (1994) were employed to measure minimum and maximum water levels during the monthly intervals between sampling. Each gauge consisted of a 2 metre length of PVC pipe, with a diameter of 14cm. The top half (1m) frontage of the pipe was removed, to give a 1m length of entire pipe, and a 1m length of half pipe (i.e. semi-circular in cross-section when viewed from above) (see Figure 2.2.1). A 1m scale was fixed to the back of the open top section, and a series of holes of 1cm diameter were drilled into the basal 1m section at intervals of 10cm from the base. Following removal of a substrate core from each of the fixed sample stations using a soil auger, to a diameter of c.14 cm, and to a depth of c.75cm, each piece of prepared pipe was put in place; resulting in 75cm of the tubing being below ground, and 125cm protruding above ground. Each gauge was anchored into the root mat of the vegetation using right-angled brackets, in order to prevent movement of the gauge once operational, and to therefore maximise accuracy of derived water level readings. A ballasted float and markers were fixed to the open top section (see Figure 2.2.2 for basic construction). The ballasted float consisted of a standard 250ml PVC sample bottle half filled with dry sand. The top of each bottle had been drilled, and a 1m length of stainless steel rod inserted and secured using drilled PVC blocks and standard silicone sealant. Each top was placed back onto the respective bottle, and these were made watertight using sealant. At the top end of each rod, a stainless steel eyelet, screwed into a PVC block was secured. A second 1m length of stainless steel rod was inserted through the eyelet, a foam marker was pushed onto the second rod on either side of the eyelet, and the second rod was then secured onto the back of the top half of the gauge casing, between two fixed PVC blocks. This arrangement allowed the ballasted float to move freely within the water column within the lower half of the gauge casing, from where the substrate column had previously been removed. The water column meanwhile, was allowed to move freely in sequence with changing groundwater levels, through the free exchange of water facilitated by the holes drilled in the lower half of the casing. (Figure 2.2.2).

The minimum - maximum water level gauges worked on the principle that the eyelet connected to the ballasted float would shift the two foam markers positioned onto the fixed rod up and down respectively as the groundwater level rose and fell; the reliability of the method had been verified previously by Ross (1999). From dipwell measurements (see below) the groundwater level at the time of sampling could be obtained, and with reference

to the level of the eyelet fixed to the ballasted float, the maximum and minimum groundwater levels since the previous sampling session could be calculated. While such a method gives snapshot information of the minimum and maximum groundwater levels at a single point in time between sampling, repeat sampling throughout the year gives an average measure of minimum and maximum levels, and of overall levels of fluctuation. The study undertaken employed a large number of sites, transects, and individual monitoring stations (Table 2.1.1). The approach taken was considered a reasonable alternative to the installation of continuously-recording data-loggers, due to factors of cost.

At each fixed sample station dipwells were installed within 50cm of the minimum-maximum water level gauges. The dipwells consisted of 75cm (5cm diameter) lengths of PVC pipe, the bottom 50cm of which was perforated every 5cm. The bottom 50cm was buried into the ground following removal of a core of substrate, and PVC bungs were put into the top to prevent direct entry of rainwater. This method, allowed a mixed groundwater sample to be taken from within the rooting zone of the vegetation, whether the vegetation was rooted, or free-floating.

During each sampling visit, the dipwells were evacuated and then allowed to refill with fresh groundwater. Measurements of pH and electrical conductivity (μS/cm) were made using probes connected to pre-calibrated, hand held HANNAH meters. A measure of groundwater level relative to ground surface was also made, using the dipwell when water level was below ground surface. Soil redox potential (mV) was measured using a self-referencing platinum electrode probe, pre-treated for reducing conditions, connected to a hand held meter.

Groundwater samples were taken using a 50ml syringe, to which a length of rubber tubing had been connected. Acid washed 250ml sample bottles were filled at each sample station, and were placed into a freezer box for transport back to the lab for processing. On return to the lab the samples were filtered through 0.5 μm Whatman GF/C glass fibre filters in order to remove suspended materials, for subsequent chemical analysis. Grieve *et al.* (1995) identified no significant lag effects on samples following this protocol, so it is reasonable to assume that dipwell samples would be analogous to the groundwater chemistry of the site at the time of sampling. While Proctor (1993) found variation within the stability of solutes from mire-water samples during storage, refrigeration in the dark was recommended where immediate analysis could not be undertaken, in order to reduce biological activity. All samples were therefore transported back from the field in a cool box, and after filtering, were stored in a freezer until the time of analysis.

In addition to groundwater measurements, the shade cast by nearby trees and/or scrub was assessed on a 0-5 scale; where 0 = no shade, and 5 = heavy shade. Bare ground (%) was also assessed visually.

Groundwater analysis

Groundwater samples were analysed for major anions and cations on the basis of previous hydrochemical studies and associated vegetation characteristics across Insh Marshes (Grieve *et al.*, 1995; Willby *et al.*, 1997). Analyses followed the protocol detailed in Grieve *et al.* (1995) and Ross (1999). Each sample was replicated three times for cation analysis, and three random samples were replicated three times at the beginning of anion analysis in order to ensure precision. Accuracy was also checked by the use of standard solutions and blanks during analysis.

Phosphate (PO_4^{2-}) was determined (during 2000 only) using the Ammonium Molybate/Ascorbic Acid method of Murphy and Riley (1962), with a detection limit of 0.01mg l^{-1}. Chloride (Cl), Fluoride (F), Nitrate (NO_3) Sulphate (SO_4^{2-}) were determined from sub-samples filtered through On-Guard-Ag filters, and using a DIONEX ion chromatograph with a chemical suppressor and an AS4A analytical column. Samples were eluted with a sodium hydroxide ($Na_2CO_3/NaHCO_3$) solution, and conductivity was suppressed with dilute sulphuric acid (H_2SO_4). Detection limits were 0.02 mg l^{-1}. Potassium (K) and Sodium (Na) levels were determined using flame photometry. Calcium (Ca), Magnesium (Mg) and Manganese (Mn) were determined using flame atomic absorption spectrometry (AAS); samples were dosed with strontium nitrate ($Sr(NO3)_2$) solution (0.4%) to suppress interference for Ca and Mg. Iron (Fe) was determined by graphite furnace AAS. Samples were diluted where appropriate. The approximate detection limit for all samples was 0.01 mg l^{-1}.

All groundwater analysis was conducted in the Department of Environmental Science, at the University of Stirling.

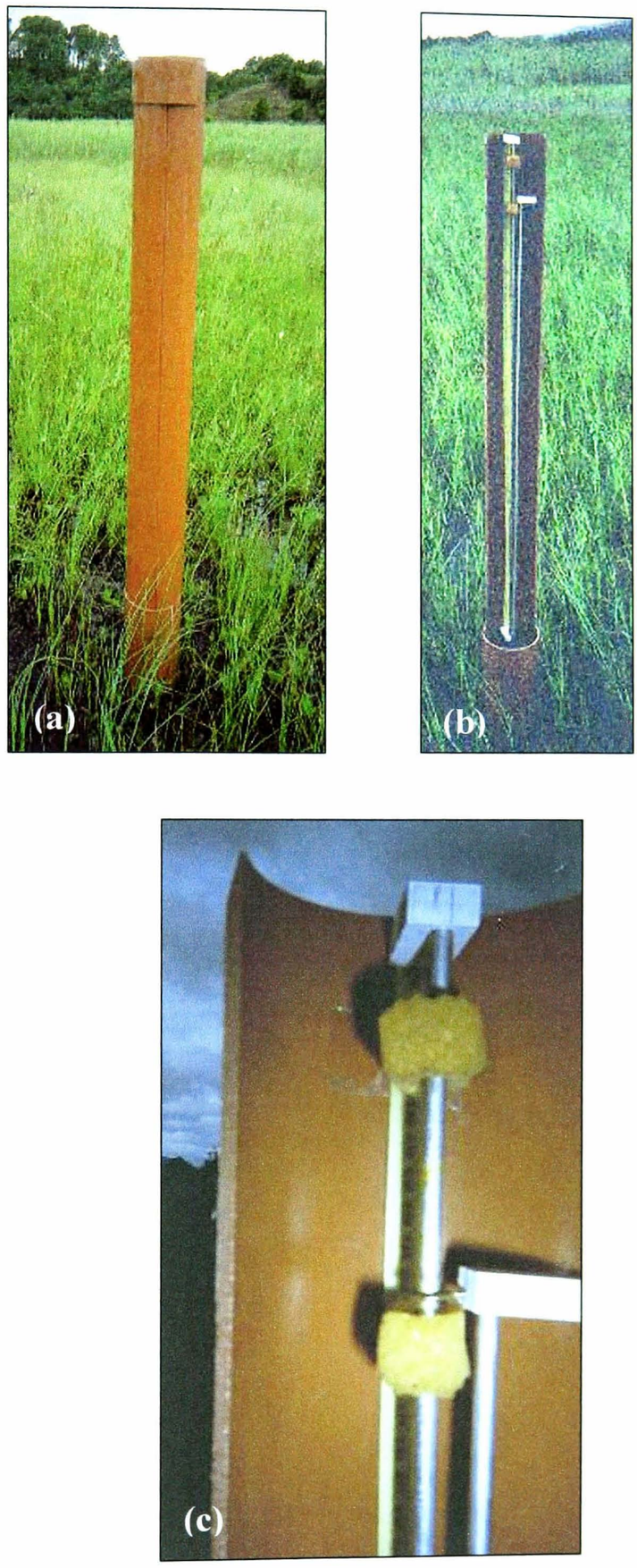


Figure 2.2.1 Minimum-maximum water level range gauge positioned in field at Insh Marshes (*Tromie Fen*). (a) gauge casing with removable front piece clipped in place to act as a weather guard; (b) gauge with front removed, showing internal apparatus; (c) close up of eyelet attached to ballasted float, minimum and maximum water level markers, and measuring scale behind fixed rod.

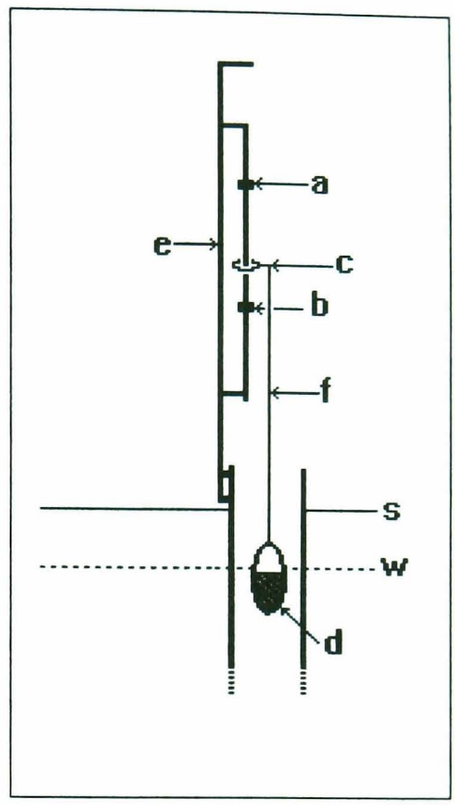


Figure 2.2.2 Minimum-maximum water level range gauge (adapted from the design of Bragg *et al.*, 1994), showing schematic plan of components and mode of operation. (a) Maximum water index marker; (b) Minimum water index marker; (c) eyelet to move water index markers as float moves with varying water level; (d) ballasted float; (e) scale; (f) float stem; S = ground surface; W = Current water level.

2.3. Results

In total 33 field sampling visits were conducted during the three years of research (Appendix 1), in addition to visits for site selection and instrument installation purposes. During 1998 seven sampling visits were made in total, with a full complement of stations sampled over the course of the last visit to each site. A total of 58 species of vascular plants and bryophytes were identified (Table 2.3.3). A more systematic sampling regime was adhered to during the 1999 and 2000 seasons, with a full coverage of all sampling stations during subsequent visits (Appendix 1). A total of 89 and 53 vascular and bryophyte species were identified respectively during 1999 and 2000. In addition, sampling regimes for 1999 and 2000 were more rigorously structured, and were spaced as closely to monthly intervals as all considerations would allow.

An initial attempt to replicate sampling within each station proved time consuming, and did not yield species data which varied greatly between points (Appendix 2). Species were generally consistent across all three replicate points surrounding each station. Some cases of local variation, for example with *Lemna minor* (station 1, Nether Whitlaw Moss), could be explained by the free-floating and motile (mainly by wind action) nature of the species. In others such as *Filipendula ulmaria*, differential canopy spread could be an explanatory variable.

2.3.1. Sample station species composition

A greater number of species were sampled over the course of the 1998 season at Insh Marsh stations (n=47), than at Nether Whitlaw (n=31) (Table 2.3.1). However, the number of stations sampled at Insh Marshes was seventeen, in comparison to just six stations at Nether Whitlaw. Of the fifty-eight species sampled, sixteen were common to stations within both sites, while thirty-one species were exclusive to the Insh Marsh sample stations, with eleven exclusive to Nether Whitlaw moss.

Species exclusive to Nether Whitlaw included a number of bryophytes (*Aulocomnium palustre, Bryum pseudotriquetum, Marchantia polymorpha, Pellia epiphyla, Plagiomnium rostratum and Sphagnum palustre*), and *Lemna minor*, which is indicative of the slow moving waters characteristic of basin fen systems. In contrast, the plant species identified along the transects studied at Insh Marshes are more varied, ranging from those dominated by *Carex* species, through tall herb fen vegetation (dominated by *Phragmites australis* and *Carex lasiocarpa*), and species indicative of wet and acid grassland, such as *Deschampsia cespitosa, Galium palustre, Holcus lanatus, Molinia caerulea and Rumex acetosa*.

For the 1999 season (Table 2.3.2), the intensified sampling regime produced a greater list of species, with some being present across all site stations (e.g. *Angelica sylvestris, Carex echinata, C. lasiocarpa, Menyanthes trifoliata, Sphagnum palustre*). Four species, *Betula pendula, Hydrocotyle vulgaris, Lysmachia vulgaris* and *Poa trivialis*, were unique to the samples from the new Glen Moss site, and 12 species were unique to the samples from Insh Marshes. One species was unique to each of the Nether Whitlaw and Lochwinnoch samples (*Typha latifolia* and *Aulocomnium palustre* respectively). Three species were unique to the samples from Tarn Moss, while a total of thirteen were identified within the Insh Marsh and Tarn Moss samples only. These included a number of calcifuges such as *Molinia caerulea* and *Myrica gale.*

During 2000, only nine species from a total of fifty-three were identified which were common to stations from all three sites sampled in that year. Four species, *L. minor, Lysimachia thyrsiflora, Oenanthe lachenalii* and *T. latifolia* were noted within Endrick Marsh samples only, while eight samples were unique to Insh Marsh samples; again, these were indicative of acid and wet grasslands.

While fewer stations (n=6) were set up at Wood of Cree than at Insh Marshes, eleven species were unique to the samples taken. Two of these species, *Carum verticillatum* and *Eleocharis palustris* had not been recorded in previous years.

For full species lists and their frequencies sampled during 1998-2000 see Appendix 3.

Table 2.3.1 *Total species list for 1998, showing presence (+), and absence (-) at each site: IM = Insh Marshes; NW = Nether Whitlaw Moss.*

	IM	NW		IM	NW
Achillea ptarmica	+	-	*Lemna minor*	-	+
Agrostis stolonifera	+	+	*Marchantia polymorpha*	-	+
Angelica sylvestris	+	-	*Menyanthes trifoliata*	+	+
Aulacomnium palustre	-	+	*Molinia caerulea*	+	-
Betula pendula	-	+	*Myrica gale*	+	-
Bryum pseudotriquetum	-	+	*Oenanthe lachenalii*	-	+
Caltha palustris	+	-	*Pedicularis palustris*	+	-
Campylium stellatum	+	-	*Pellia epiphyla*	-	+
Cardamine pratensis	+	+	*Phalaris arundinacea*	+	-
Carex aquatilis	+	-	*Phragmites australis*	+	-
Carex chordorrhiza	+	-	*Plagiomnium rostratum*	-	+
Carex demissa	+	-	*Poa trivialis*	+	-
Carex echinata	+	-	*Potamogeton polygonifolius*	+	+
Carex lasiocarpa	+	+	*Potentilla palustris*	+	+
Carex nigra	+	-	*Ranunculus lingua*	-	+
Carex panicea	+	-	*Ranunculus flammula*	+	-
Carex rostrata	+	+	*Ranunculus repens*	+	-
Carex vesicaria	+	-	*Rumex acetosa*	+	+
Deschampsia cespitosa	+	-	*Salix cinerea*	+	+
Epilobium palustre	+	+	*Scoropodium scorpioides*	+	-
Equisetum fluviatile	+	+	*Sphagnum palustre*	-	+
Eriophorum angustifolium	+	+	*Sphagnum recurvum*	+	-
Festuca rubra	+	-	*Sphagnum squarrosum*	+	+
Filipendula ulmaria	+	+	*Stellaria alsine*	+	-
Galium palustre	+	+	*Succisa pratensis*	+	-
Holcus lanatus	+	+	*Utricularia vulgaris*	+	-
Juncus articulatus	+	-	*Valeriana officinalis*	+	-
Juncus bufonius	+	-	*Veronica anagallis-aquatica*	-	+
Juncus effusus	+	-	*Viola palustris*	+	-

Table 2.3.2 *Total species list for 1999, showing presence (+), and absence (-) at each site: GM = Glen Moss; IM = Insh Marshes; LW = Lochwinnoch; NW = Nether Whitlaw Moss; TM = Tarn Moss.*

	GM	IM	LW	NM	TM
Achillea ptarmica	-	+	-	-	-
Agrostis capillaris	+	+	-	+	-
Agrostis stolonifera	-	+	-	-	+
Andromeda polifolia	+	+	+	+	+
Angelica sylvestris	+	+	+	+	+
Aulocomnium palustre	-	-	-	+	-
Betula pendula	+	-	-	-	-
Calliergon cuspidatum	-	+	-	-	+
Caltha palustris	-	+	-	-	+
Calluna vulgaris	-	-	-	-	+
Calypogeia muellerana	-	+	-	-	+
Cardamine pratensis	-	+	+	-	-
Carex aquatilis	-	+	+	-	-
Carex chordorrhiza	-	+	-	-	-
Carex diandra	+	+	-	-	+
Carex echinata	+	+	+	+	+
Carex lasiocarpa	+	+	+	+	+
Carex limosa	+	+	-	+	+
Carex nigra	-	+	-	-	+
Carex ovalis	-	+	-	-	-
Carex panicea	+	+	-	+	+
Carex rostrata	+	+	-	+	+
Carex vesicaria	-	+	-	-	-
Cerastium fontanum	-	+	-	-	-
Dactylorhiza majalis	-	+	-	-	+
Deschampsia cespitosa	+	+	-	-	+
Drosera rotundifolia	+	-	+	-	+
Dryopteris dilatata	+	+	+	+	+
Epilobium palustre	+	+	+	+	+
Equisetum fluviatile	+	+	+	+	+
Erica cinerea	-	-	-	-	+
Erica tetralix	+	+	-	+	+
Eriophorum angustifolium	+	+	-	+	+
Eurhynchium praelongum	-	+	-	-	-
Festuca rubra	+	+	+	+	-
Filipendula ulmaria	-	+	+	+	-
Fissidens adianthoides	-	+	-	-	-
Galium aparine	-	+	-	+	+
Galium palustre	+	+	-	+	+
Glyceria maxima	+	+	-	-	+
Holcus lanatus	+	+	-	-	+
Hydrocotyle vulgaris	+	-	-	-	-
Iris pseudacorus	-	+	+	-	+
Juncus acutiflorus	-	-	-	-	+
Juncus articulatus	-	+	-	-	-
Juncus bufonius	+	+	+	-	+
Juncus effusus	+	+	-	+	+
Knautia arvensis	-	+	-	+	+
Lemna minor	-	-	+	+	-
Lysimachia thyrsiflora	+	-	+	-	-
Lysimachia vulgaris	+	-	-	-	-
Lythrum salicaria	+	+	+	+	+
Menyanthes trifoliata	+	+	+	+	+
Molinia caerulea	-	+	-	-	+
Myrica gale	-	+	-	-	+
Mysotis scorpioides	-	+	-	+	-
Oenanthe lachenalii	+	+	-	+	-
Pedicularis palustris	+	+	+	-	-
Phalaris arundinacea	-	+	+	-	+
Phragmites australis	-	+	-	-	+
Poa trivialis	+	-	-	-	-
Polygala serpyllifolia	-	+	-	-	+
Polytrichum commune	-	+	-	+	+
Potamogeton polygonifolius	-	+	-	+	-
Potentilla erecta	+	+	+	+	+
Potentilla palustris	+	+	+	+	+
Pseudoscleropodium purum	-	+	-	+	-
Ranunculus flammula	-	+	-	+	-
Ranunculus lingua	-	+	-	-	-
Ranunculus repens	-	+	-	-	-
Rhytidiadelphus squarrosus	-	+	-	-	+
Rumex acetosa	-	+	-	-	+
Salix cinerea	+	+	-	-	-
Scorpidium scorpioides	+	+	-	-	-
Sphagnum cuspidatum	+	+	+	+	+
Sphagnum palustre	+	+	+	+	+
Sphagnum papillosum	-	+	-	+	-
Sphagnum squarrosum	-	+	-	+	+
Sphagnum teres	-	+	-	-	+
Stellaria holostea	-	+	-	-	+
Succisa pratensis	-	+	-	-	-
Trifolium repens	-	+	+	-	-
Typha latifolia	-	-	+	-	-
Vaccinium myrtillus	+	+	-	-	+
Utricularia vulgaris	+	+	-	-	-
Vaccinium oxycoccus	-	-	+	-	-
Valeriana officionalis	-	+	+	-	-
Veronica officinalis	-	-	-	-	-
Viola palustris	-	+	-	-	-

Table 2.3.3 *Total species list for 2000, showing presence (+), and absence (-) at each site: EM = Endrick Marshes; IM = Insh Marshes; WC = Wood of Cree.*

	EM	IM	WC		EM	IM	WC
Achillea ptarmica	-	+	+	*Lycopus europaeus*	-	-	-
Agrostis stolonifera	-	+	+	*Lysimachia thyrsiflora*	+	-	-
Angelica sylvestis	+	-	+	*Lythrum salicaria*	-	-	+
Caltha palustris	+	+	+	*Lychnis flos-cuculii*	-	+	-
Cardamine pratensis	+	+	+	*Mentha aquatica*	+	-	+
Carex aquatillis	+	+	-	*Menyanthes trifoliata*	+	-	+
Carex diandra	-	+	+	*Molinia caerulea*	-	+	+
Carex echinata	-	+	-	*Myrica gale*	-	+	+
Carex lasiocarpa	-	-	+	*Myosotis scorpioides*	+	+	-
Carex nigra	-	+	+	*Oenanthe lachenalii*	+	-	-
Carex panicea	-	+	+	*Phalaris arundinacea*	+	+	+
Carex rostrata	+	+	+	*Phragmites australis*	-	+	-
Carex vesicaria	+	+	-	*Potentilla palustris*	+	+	+
Carum verticillatum	-	-	+	*Potomogeton polygonifolius*	-	-	+
Eleocharis palustris	-	-	+	*Ranunculus flammula*	-	+	+
Deschampsia cespitosa	-	+	-	*Ranunculus repens*	-	+	-
Epilobium hirsutum	+	-	-	*Rumex acetosa*	-	+	-
Epilobium palustre	+	+	+	*Salix cinerea*	-	+	-
Equisetum fluviatile	+	+	+	*Sphagnum papillosum*	-	+	+
Eriophorum angustifolium	-	+	+	*Succisa pratensis*	-	-	+
Festuca rubra	-	+	-	*Typha latifolia*	+	-	-
Fillipendula ulmaria	+	+	+	*Valeriana officinalis*	+	+	+
Galium palustre	+	+	+	*Veronica officinalis*	-	-	+
Holcus lanatus	-	-	+	*Viola palustris*	-	+	+
Hydrocotyle vulgaris	-	-	+				
Juncus acutiflorus	-	-	+				
Juncus bufonius	-	+	-				
Juncus effusus	-	+	-				
Lemna minor	+	-	-				

2.3.2. Hydrological and hydrochemical ranges measured

Table 2.3.4, contains minimum and maximum values for site and environmental variables measured during August 1998, shows a degree of variability between sites, and within sites. Full data sets can be found in Appendix 4

The highest shade values occurred at Nether Whitlaw, while shade was either low or non-existent across all Insh Marsh stations. Percentage bare ground was also variable; some stations within each site contained no bare ground, while others at Insh Marshes had up to 23% bare ground recorded. A maximum of 4% bare ground was recorded at Nether Whitlaw.

Ground water parameters were also variable. A wider range of pH values (5.20-7.25) were measured at Insh Marsh stations than for Nether Whitlaw, while the maximum conductivity measured at Nether Whitlaw was almost five times higher than any recorded at Insh Marshes. Similarly levels of calcium and sodium, at 72.95 and 74.40 mg l^{-1} respectively, were far higher from Nether Whitlaw than for any of the groundwater samples from Insh Marshes. Previous groundwater sampling at the site by Ross (1999) also revealed high values for these ions at certain points across the site. Iron however, was detected to a maximum of 18.06 mg l^{-1} within Insh Marsh samples, and to 3.56 mg l^{-1} at Nether Whitlaw. Other ions had variable ranges, within sites, but these ranges were more comparable between sites (Table 2.3.4).

For the 1999 season, similar site and environmental measurements were taken during each sampling visit, and the yearly averages are shown in Table 2.3.5. Shading was again variable between sites, and was notably absent from all Insh Marsh stations. Shading was also lower at Nether Whitlaw than in 1998, due to some scrub clearance having been undertaken. Bare ground ranged from 0 at stations within all sites, to a maximum of 34% at Nether Whitlaw. While this value was considerably higher than the maximum for 1998, it represented an average figure as opposed to a single point measurement.

With the exception of Nether Whitlaw, stations within all sites were subject to a variety of groundwater regimes, from negative (below ground surface) to positive (inundated). The greatest groundwater fluctuation occurred at Insh Marsh sites, with average maximum levels of fluctuation reaching 32 cm. In contrast, fairly static situations were found to occur amongst the second transect of stations at Lochwinnoch (floating mat vegetation).

pH ranged from 5.00 to 6.56 across stations, and redox ranged from –72 to 263 mV. The range of redox values were all positive (oxidising) for Tarn Moss stations, and were all negative (reducing) for Lochwinnoch transect 2; all other sites contained stations representative of both oxidising and reducing conditions.

The lowest conductivity value overall was 85 µS/cm, at Tarn Moss, while the lowest range of variation was at Glen Moss (140-329 µS/cm). The largest figure (and largest range) was observed at Nether Whitlaw (146-1334 µS/cm).

Regarding the specific ionic content of the groundwater samples, the highest levels of sodium (59.16 mg l^{-1}) and calcium (90.40 mg l^{-1}) were measured at Nether Whitlaw; these values echoed those from the single measurements taken in August 1998 (see comments above regarding Na and Ca values at this site). Highest levels of iron (mg l^{-1}) were again seen amongst Insh Marsh samples, while the content of other ions was again variable within and between all of the sites. The same situation was true for the major anion content of the groundwater samples, with the exception of the maximum value of 131 mg l^{-1} of chloride measured at Nether Whitlaw, with the next highest value being 28.73 mg l^{-1} from Lochwinnoch. Fluoride was found to be generally variable amongst and between sites, but was found at trace levels only within transect 1, Glen Moss, and for all of the Tarn Moss samples.

The average site and environmental variable values for 2000 (Table 2.3.6) again show variable degrees of shading between sites, with no shading present within the stations at Insh Marshes. Some degree of bare ground was measured at all stations, but overall levels ranged from 2%, to 27% (within Endrick Marsh samples).

All sites contained stations subject to negative and positive water table levels relative to ground surface, with the highest level of water table fluctuation overall (46cm) observed at Insh marshes.

pH ranged from 5.40 at Wood of Cree, to 6.90 at Insh Marshes, with the lowest and the greatest levels of variation being found within these two sites respectively. The same pattern followed for redox, but with all values being positive (oxidising), in contrast to previous years (Table 2.3.4; 2.3.5).

The lowest conductivity was observed at Insh Marshes (51 μS/cm), and the highest at Endrick Marshes (533 μS/cm). Specific ionic contents varied again within sites, and between sites. The highest values for sodium and calcium were measured at Endrick Marshes (22.36 and 24.54 mg l^{-1} respectively), but these figures were considerably lower than the high levels measured previously at Nether Whitlaw (Table 2.3.4; 2.3.5). Phosphate was measured for the first time in 2000 (due to technical difficulties in 1998 and 1999), but only reached moderately high levels within the Insh Marsh samples, with a maximum of 0.35 mg l^{-1}.

Table 2.3.4 Range of site and environmental variable values for August 1998

Variable	*Insh Marshes*				*Nether Whitlaw*	
	T1(n=9)		T2(n=8)		(n=6)	
	Min.	Max.	Min.	Max.	Min.	Max.
Degree of Shading	0	1	0	0	0	4
Water Table Relative to Surface (cm)	-2	24	0	19	0	30
Maximum Water Table Relative to Surface (cm)	8	34	3	34	-	-
Minimum Water Table Relative to Surface (cm)	-34	6	-11	16	-	-
Overall Level of Water Table Fluctuation (cm)	13	54	10	24	2	7
Redox (mV)	-	-	-148	33	-80	165
pH	5.20	5.70	5.70	7.25	5.46	6.74
Conductivity (μS/cm/s^{-1})	56	165	7	136	38	787
Bare ground (%)	0	23	0	8	0	4
Fe (mg l^{-1})*	*trace*	18.06	*trace*	3.56	0.25	2.21
Mn (mg l^{-1})*	*trace*	2.43	*trace*	0.43	*trace*	0.32
Mg (mg l^{-1})*	0.83	2.61	1.12	2.27	0.34	9.25
K (mg l^{-1})*	1.33	4.93	0.49	7.60	0.99	2.56
Ca (mg l^{-1})	2.57	22.48	3.43	6.48	1.19	72.95
Na (mg l-1)*	*trace*	7.72	0.09	16.08	2.52	74.40
Fluoride (F) (mg l^{-1})	-	-	-	-	*trace*	0.41
Chloride (Cl) (mg l^{-1})	-	-	-	-	*trace*	19.18
Nitrate (NO_3^-) (mg l^{-1})	-	-	-	-	0.01	0.26
Sulphate (SO_4^{2-}) (mg l^{-1})	-	-	-	-	0.58	2.23

Trace = undetectable at <0.01mg l^{-1}; *figures based on stations 1-5 only.

Table 2.3.5 Range of mean site and environmental variable values for 1999

Variable	*Glen Moss*				*Lochwinnoch*				*Insh Marshes*						*Nether Whitlaw*		*Tarn Moss*	
	T1(n=3)		T2(n=3)		T1(n=3)		T2(n=3)		T1(n=9)		T2(n=7)		T3(n=4)		(n=6)		(n=5)	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max
Degree of Shading	0.7	0.7	0.3	1	1.0	1.3	0	1	0	0	0	0	0	0	0.0	2.0	0.0	0.7
Water Table Relative to Surface (cm)	-6	17	-1	2	0	1	-10	5	-30	3	-2	13	-16	8	0	23	-6	2
Maximum Water Table Relative to Surface (cm)	-3	17	1	3	1	2	10	21	-16	18	1	18	-2	10	0	26	3	11
Minimum Water Table Relative to Surface (cm)	-17	8	-16	-9	-1	0	-11	3	-35	-1	-7	12	-39	5	0	20	-11	-2
Overall Level of Water Table Fluctuation (cm)	9	14	12	18	2	2	15	22	5	19	3	8	4	32	0	7	6	15
Redox (mV)	-67	69	-43	151	-58	125	-80	-18	-47	263	-72	87	-42	216	-64	89	13	89
pH	5.77	6.30	5.41	5.63	5.0	6.0	6.1	6.5	5.68	6.56	5.67	6.18	5.70	5.95	5.25	6.33	5.17	6.17
Conductivity ($\mu S/cm/s^{-1}$)	168	329	140	198	187	271	638	971	121	666	195	355	234	403	146	1344	85	436
Bare ground (%)	2	3	0	3	0	5	2	7	0	24	0	24	2	26	0	34	0	18
Fe ($mg\ l^{-1}$)	*trace*	0.18	0.03	0.15	0.11	0.21	*trace*	0.05	0.06	1.51	0.03	0.78	0.13	0.87	0.05	0.76	0.01	0.37
Mn ($mg\ l^{-1}$)	*trace*	0.03	*trace*	*trace*	0.04	0.21	*trace*	2.29	*trace*	0.28	0.01	0.38	0.01	0.69	*trace*	0.05	*trace*	0.77
Mg ($mg\ l^{-1}$)	0.85	1.95	0.53	1.09	1.77	2.08	3.47	6.22	0.70	2.31	0.98	2.58	1.30	1.86	0.75	9.33	0.54	1.86
K ($mg\ l^{-1}$)	0.36	0.56	0.19	0.60	2.99	3.00	0.52	1.54	0.27	3.27	0.44	4.09	0.69	2.03	0.47	1.40	0.29	1.38
Ca ($mg\ l^{-1}$)	5.76	22.92	1.92	3.70	4.36	12.75	21.11	38.63	2.82	19.38	3.93	10.33	6.69	12.27	5.42	90.40	2.51	18.49
Na ($mg\ l^{-1}$)	5.69	7.37	5.15	7.26	5.64	6.10	13.33	18.89	3.92	8.09	4.80	7.68	8.33	9.21	5.19	59.16	2.54	5.83
Fluoride (F) ($mg\ l^{-1}$)	*trace*	*trace*	*trace*	0.22	*trace*	*trace*	0.09	0.48	*trace*	0.37	*trace*	0.48	*trace*	0.47	*trace*	0.19	*trace*	*trace*
Chloride (Cl) ($mg\ l^{-1}$)	8.29	13.39	11.66	20.85	9.83	12.64	19.77	28.73	7.91	14.64	6.79	15.73	20.17	24.04	11.73	131	1.61	9.71
Nitrate (NO_3) ($mg\ l^{-1}$)	0.01	0.05	0.03	0.05	0.48	0.77	0.03	0.63	0.05	14.07	0.02	0.24	0.04	0.43	0.02	0.91	0.03	0.36
Sulphate (SO_4^{2-}) ($mg\ l^{-1}$)	0.94	3.36	1.04	7.15	3.43	3.94	0.60	1.98	0.72	3.57	0.41	2.08	0.50	2.66	0.49	2.29	1.49	7.40

Trace = undetectable at < 0.01mg l^{-1}.

Table 2.3.6 Range of mean site and environmental variable values for 2000

Variable	*Endrick Marshes*		*Insh Marshes*		*Wood of Cree*	
	Min.	Max.	Min.	Max.	Min.	Max.
Degree of Shading	0	2	0	0	0	2
Water Table Relative to Surface (cm)	-21	0	-30	-11	-5	1
Maximum Water Table Relative to Surface (cm)	-4	17	-9	40	1	14
Minimum Water Table Relative to Surface (cm)	-31	-1	-37	-14	4	18
Overall Level of Water Table Fluctuation (cm)	5	32	5	46	10	40
Redox (mV)	65	349	95	596	72	192
pH	5.60	6.30	5.50	6.90	5.40	5.60
Conductivity ($\mu S/cm/s^{-1}$)	192	533	51	328	112	205
Bare ground (%)	2	27	2	15	3	13
Fe ($mg\ l^{-1}$)	0.31	3.76	0.04	0.40	0.20	0.98
Mn ($mg\ l^{-1}$)	0.32	3.40	0.05	1.53	0.56	1.04
Mg ($mg\ l^{-1}$)	1.21	2.97	0.43	1.94	1.36	1.61
K ($mg\ l^{-1}$)	0.39	2.30	0.71	5.91	0.34	2.56
Ca ($mg\ l^{-1}$)	9.33	24.54	1.58	31.20	4.91	6.95
Na ($mg\ l^{-1}$)	6.79	23.26	4.24	8.83	7.89	9.79
Fluoride (F) ($mg\ l^{-1}$)	*trace*	0.24	*trace*	0.30	0.33	0.39
Chloride (Cl) ($mg\ l^{-1}$)	14.93	55.95	12.55	30.11	35.13	42.51
Nitrate (NO_3^-) ($mg\ l^{-1}$)	*trace*	9.43	*trace*	6.743	*trace*	0.21
Sulphate (SO_4^{2-}) ($mg\ l^{-1}$)	1.14	74.91	1.15	10.57	5.40	35.47
Phosphate (PO_4^{2-}) ($mg\ l^{-1}$)	0.01	0.01	*trace*	0.35	0.02	0.04

Trace = undetectable at $<0.01 mg\ l^{-1}$.

2.3.3. Water table depths

During the 3 year course of the study, sites with varying groundwater characteristics were sampled (Tables 2.3.4 - 2.3.6). Of the variables measured, average groundwater level was found to vary spatially, both within sites and between sites, and temporally, across the sampling season(s) (Figures 2.3.1 – 2.3.9). In the context of the following descriptions, where the vegetation formed floating mats the term 'ground level' relates to the vegetation into which the water level range gauges were anchored (see Section 2.2.1.2), rather than any underlying substrates.

Endrick Marshes (Aber bog)

Aber bog, which was sampled during 2000, contained stations which had average water table levels below ground surface, and stations where water was consistently around ground surface level (Figure 2.3.1). Fluctuation around the mean levels was relatively low for stations 2-6, while station 1, which had the lowest average water table level, was the most variable.

Glen Moss

Glen moss, which was sampled during 1999, exhibited areas with water table levels below the ground surface, as well as areas with permanently standing waters (Figure 2.3.2). However, the variation in water level between sampling visits was relatively minor, with average levels varying by little more than 1-2 cm. In addition, maximum negative water table depths of approximately 7cm below the ground surface along the first transect (Figure 2.3.2a) represent a site, which was generally waterlogged, if not permanently inundated.

Insh Marshes

Transect 1 (*Insh Fen*) was sampled for the three year duration of the study, with the exception of station number 2, which was abandoned in 2000 due to localised impacts upon the vegetation related to previous sampling. A relatively dynamic system could be seen across the transect during the 1998 season (Figure 2.3.3a), represented by a maximum, average inundation of 10 cm at station number 9 (closest to the main channel of the River Spey). In contrast, an average water table depth in excess of 20 cm below ground level was observed at the neighbouring station, number 8. This difference was due in main to the elevated position of station number 8, but clearly demonstrates the range of water table variation to be found within a single site. The average water table levels of stations 1-7 were less extreme than for stations 8 or 9 in terms of their position relative to the ground surface. A relatively high level of variability was seen over the season, with all stations except 8 and 9 being subject to both positive and negative water table levels.

Sampling continued during 1999 and 2000, and demonstrated the dynamic of the system between years (Figure 2.3.3b and c). Whilst the general pattern of water table levels observed during 1999 were similar to those from 1998, an overall drop in the depth was observed, in addition to a reduction in the overall variability throughout the year. Average water table depths were seen to drop further again during 2000 (Figure 2.3.3c), although seasonal variability was slightly increased upon 1999. The most marked variation between 2000 and the previous two years was a dramatic drop in the average water table depths at stations 7 and 9. From being the wettest location along the transect in 1998, station 9 had become the second driest on average in 2000, although the degree of variation throughout the season remained relatively high. Station 7 also exhibited a lower average water table level in comparison to the previous two years, but this was less extreme than for station 9.

Transect 2 (*Tromie Fen*) contained only one station at which the average water table level was below the ground surface during 1998 (Figure 2.3.4a). This was Station 1, which was dominated by *Sphagnum* species. The rest of the transect comprised areas of floating mat and open water (see Appendix 3 for representative species). Along the length of the transect all stations were inundated during subsequent sampling visits, but the depth of inundation appeared to be lower at the two ends of the transect, and higher on average towards the middle. In addition, seasonal variability appeared greater overall at the end of the transect nearest to the main channel of the River Spey. In contrast to the situation at *Insh fen* the water table levels for 1999 closely mirrored those observed during 1998 (Figure 2.3.4b). It should be noted that station number 17 was abandoned in 1999 due to loss of equipment.

The third transect (*Balavil Fen*) monitored at Insh Marshes (during 1999) sloped down gradually towards the River Spey. The first station (number 18), located amongst wet grassland, was subject to the lowest average water table level (approximately 16cm below ground level) (Figure 2.3.5). Stations 2-4 were more representative of floating mat vegetation, and had water table levels that were more stable and continually inundated.

Lochwinnoch (Aird Meadow)

Transect 1, positioned along an area of floating mat, and anchored only at one edge exhibited very stable water table levels around ground level, with only minor fluctuation through the season (Figure 2.3.6a). Transect 2 dropped away towards the open water of Castle Semple Loch, and was characterised by a steadily increasing average water table level, running from approximately 10 cm below ground surface, to around 5 cm above (Figure 2.3.6b). The level of fluctuation also decreased with proximity to the open water.

Nether Whitlaw Moss

Observations of water table depth during 1998 (Figure 2.3.7a), show a variation in depths over the length of the transect, but relatively little variation between sampling visits. The greatest water depths were observed along the first half of the transect, which comprised mainly of floating mat. Stations 4-6 were amongst areas with greater *Betula* scrub cover (Appendix 3), and were generally closer to the ground surface.

Observations for 1999 (Figure 2.3.7b) followed a similar pattern to 1998, although levels of inundation were slightly lower at stations 1-4, and were more variable between visits. The situation for stations 4-6 was comparable to the previous year, with the low levels of fluctuation indicating that the single point samples for stations 5 and 6 in 1998 were probably fair indications of the water table levels during the main growing season of that year.

Tarn Moss

All of the sample stations were either relatively wet, or were inundated, within a narrow band of fluctuation around ground level (Figure 2.3.8). Station number 1 was most counter to this trend (being slightly elevated above the rest), but was still a relatively wet location, with an average water table depth of 6 cm below ground level, and was the most variable.

Wood of Cree

As with Tarn Moss, all stations were relatively wet, if not inundated. The main difference was however, that the water table at all stations (except number 5) was below ground level on average (Figure 2.3.9). A good degree of variability was seen at most stations, with the exception of number 1, which was fairly constant around ground surface level.

Direct comparisons of the water table depths relative to ground level further demonstrate that variety exists within sites, as well as between sites (Figure 2.3.10). The position of Insh marsh station water tables in 2000 (Figure 2.3.10c) (all negative on average) follow the patterns shown in Figure 2.3.3, of an overall drying of Insh Fen during the three years of the study. A majority of measurements were one-off for 1998. While these may help indicate a general pattern, they may be less accurate. Therefore, in formal modelling exercises in subsequent Chapters, the use of the data sets from 1999 and 2000 will be more appropriate.

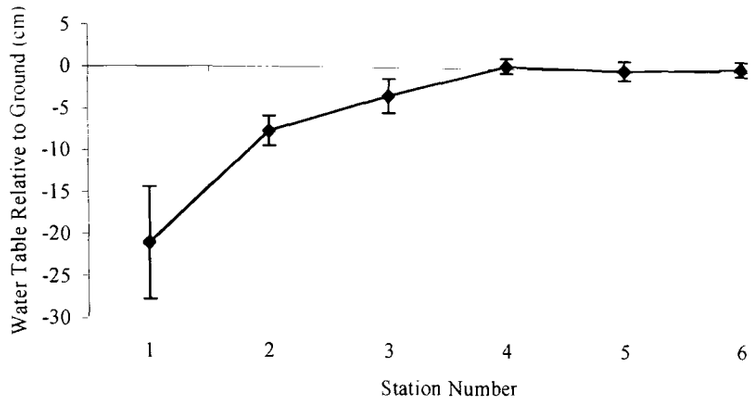
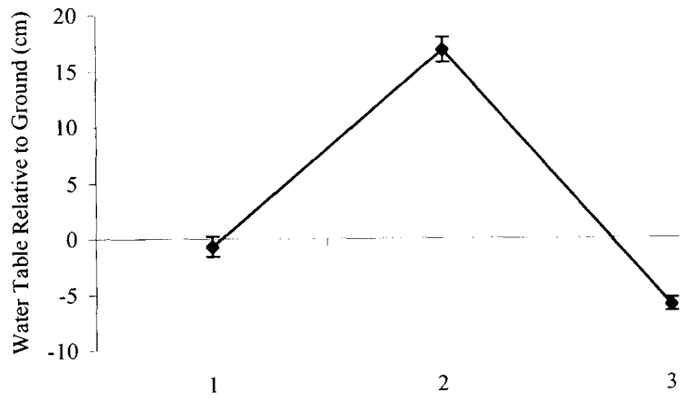


Figure 2.3.1 Average water table levels relative to ground surface (±s.e.) across Endrick Marshes (Aber Bog) sample stations, 2000.

(a)



(b)

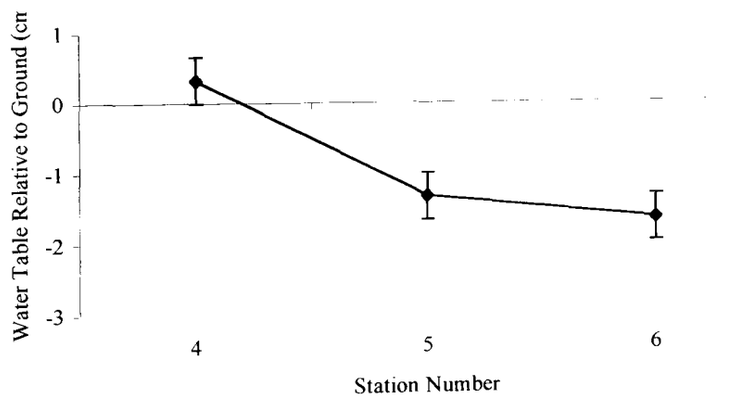
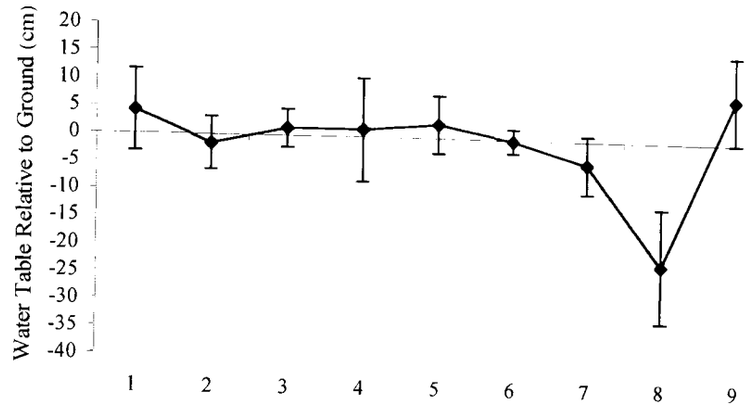
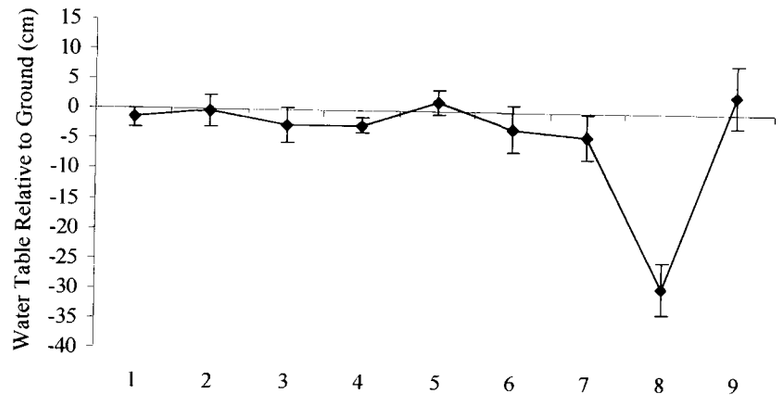


Figure 2.3.2 Average water table levels relative to ground surface (±s.e.) across Glen Moss Transects sample stations. (a) Transect 1; (b) Transect 2.

(a)



(b)



(c)

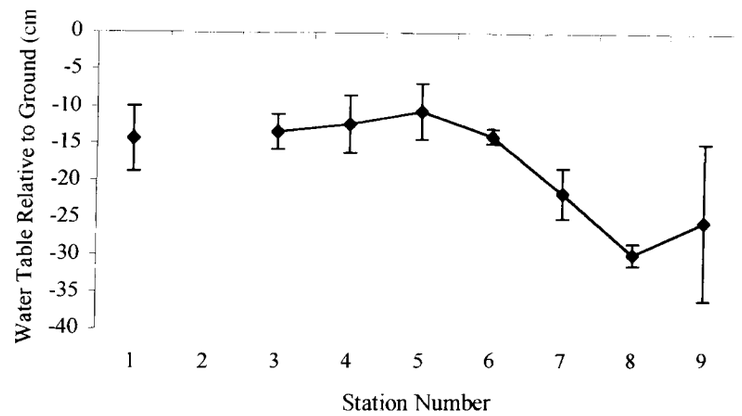
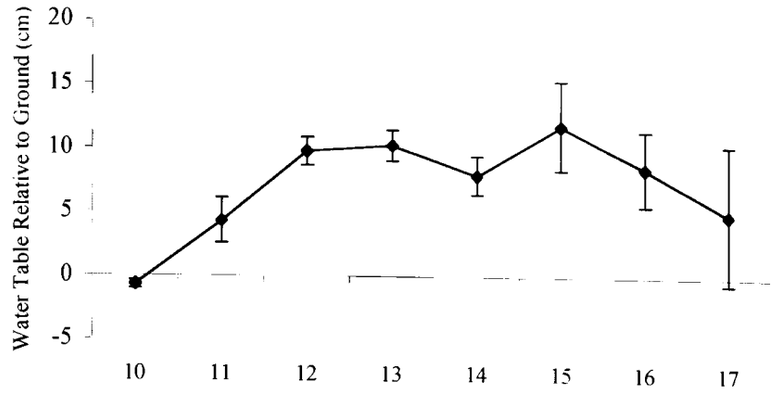


Figure 2.3.3 Average water table levels relative to ground surface (±s.e.) across Insh Marshes Transect 1 (Insh Fen) sample stations. (a) 1998; (b) 1999; (c) 2000.

(a)



(b)

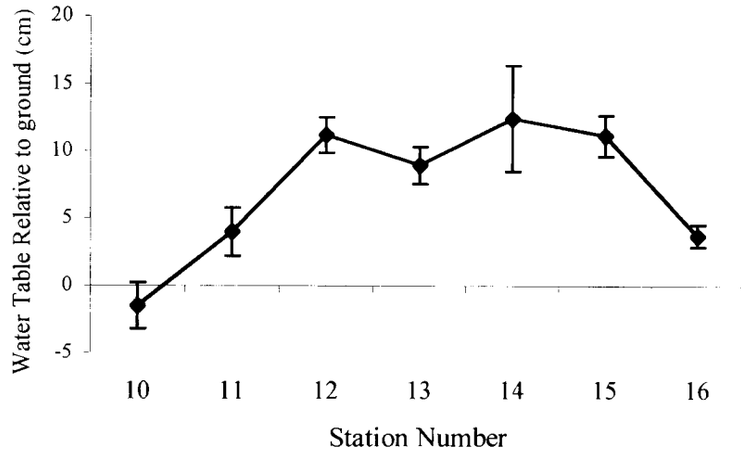


Figure 2.3.4 Average water table levels relative to ground surface (±s.e.) across Insh Marshes Transect 2 (Tromie Fen) sample stations. (a) 1998; (b) 1999.

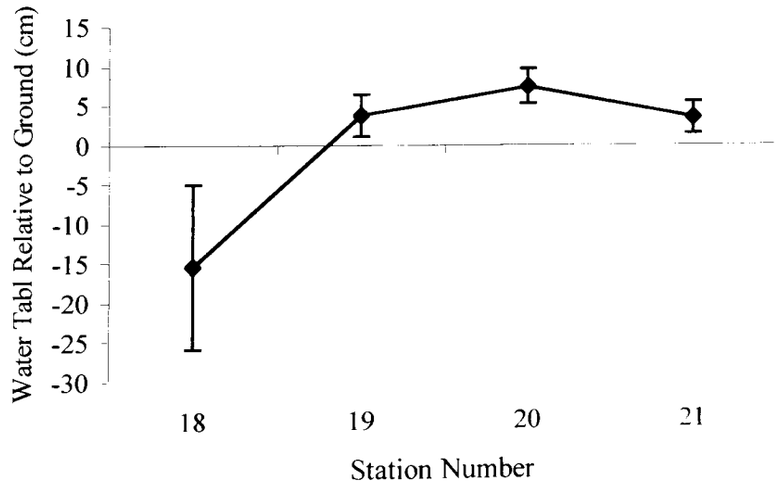
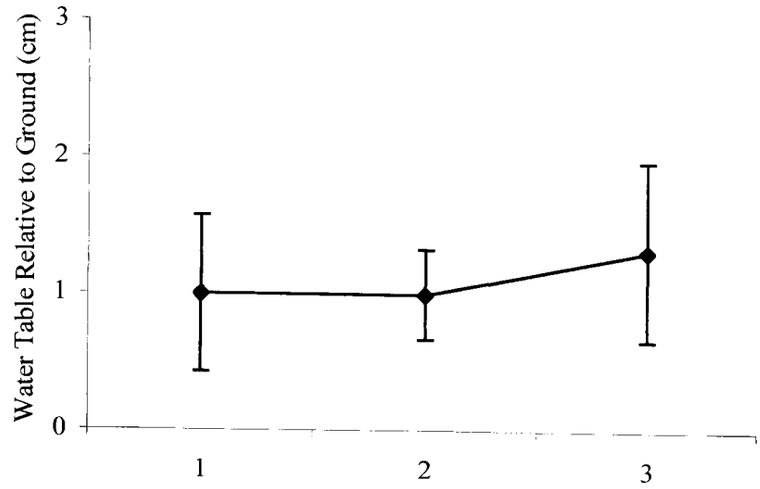


Figure 2.3.5 Average water table levels relative to ground surface (±s.e.) across Insh Marshes Transect 3 (Balavil Fen) sample stations, 1999.

(a)



(b)

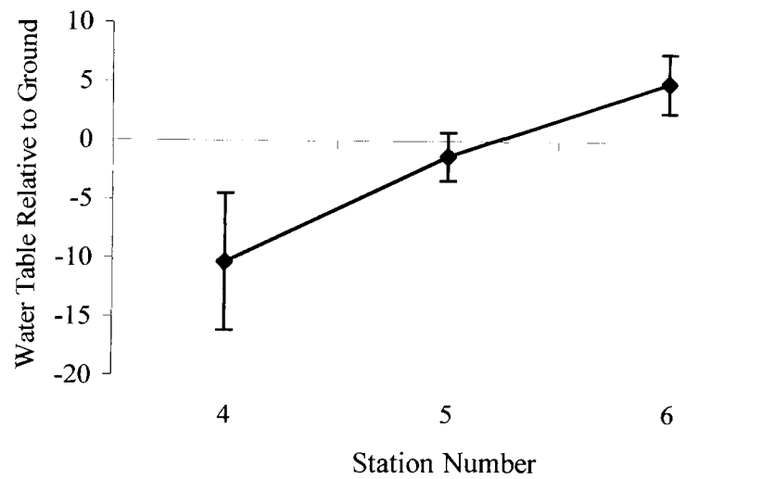
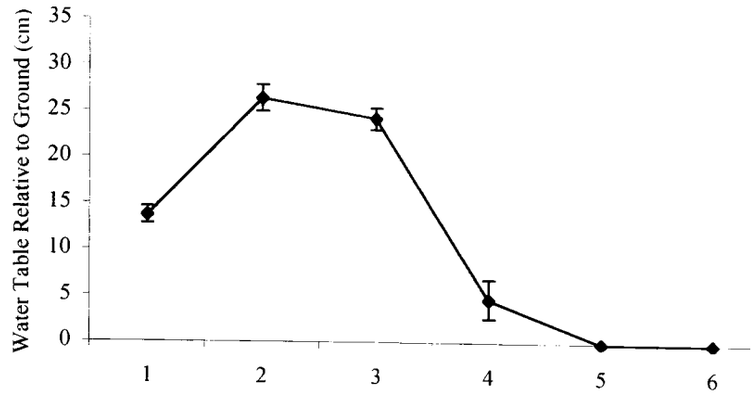


Figure 2.3.6 Average water table levels relative to ground surface (±s.e.) accross Lochwinnoch (Aird Meadow) Transects sample stations, 1999. (a) Transect 1; (b) Transect 2.

(a)



(b)

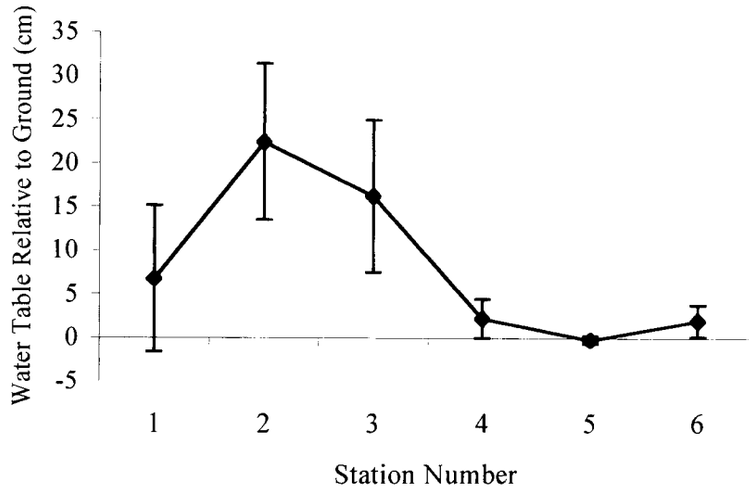


Figure 2.3.7 Average water table levels relative to ground surface (±s.e.) across Nether Whitlaw Moss sample stations. (a) 1998 (Values for stations 5 and 6 based on single samples); (b) 1999.

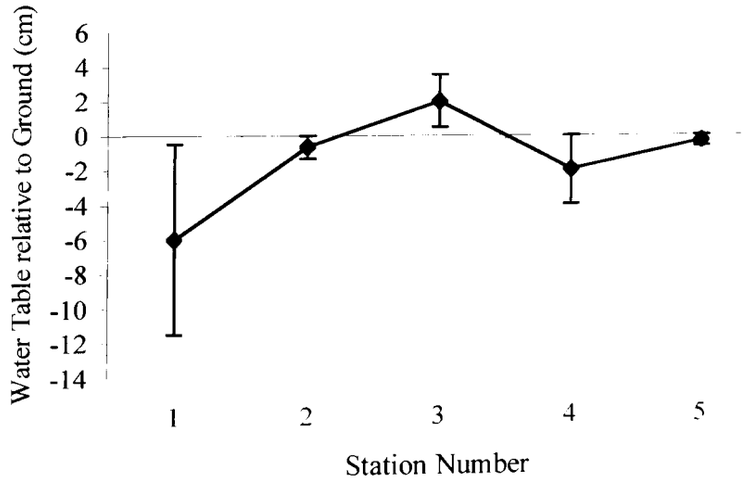


Figure 2.3.8 Average water table levels relative to ground surface (±s.e.) across Tarn Moss sample stations, 1999.

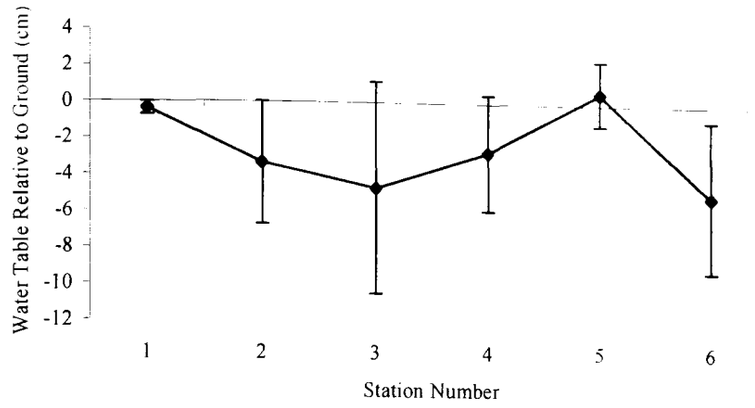
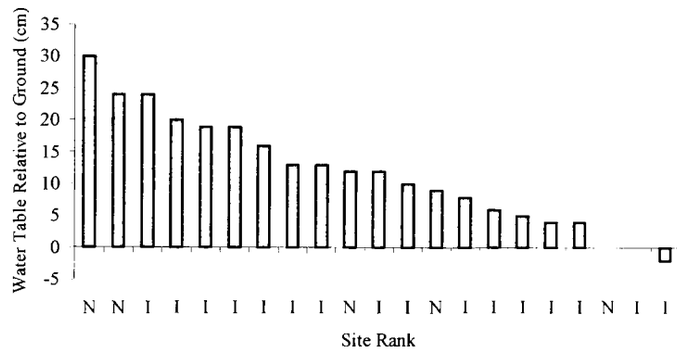
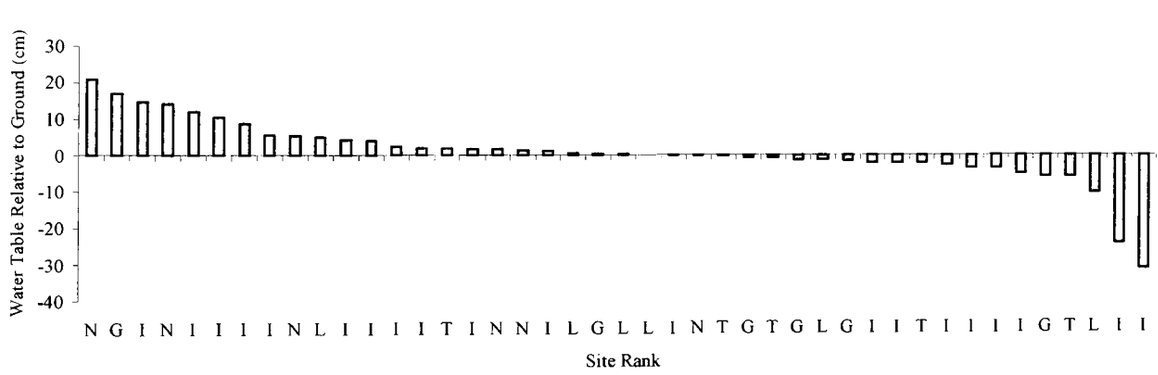


Figure 2.3.9 Average water table levels relative to ground surface (±s.e.) across Wood of Cree sample stations, 1999.

(a)



(b)



(c)

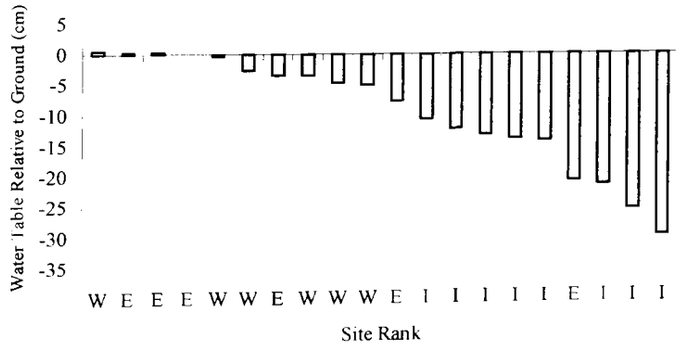


Figure 2.3.10 Ranks of average water table depths relative to ground surface over year for all stations. (a) 1998 (August data only); (b) 1999; (c) 2000. E = *Endrick* Marshes; G = *Glen Moss*; I = *Insh Marshes*; L = *Lochwinnoch*; N = *Nether Whitlaw Moss*; T = *Tarn Moss*; W = *Wood of Cree*.

2.4. Discussion

In terms of vegetation composition, and perceived hydrological regimes, a range of wetland types were studied over the course of the three-year field study. The study sites were subject to a variety of hydrological inputs, and covered a broad transect which ran across Scotland, and into northern England. Variability in the size and position of each site as a parcel within the surrounding landscape was considered.

In a study of the hydrology of Wicken fen, UK, by Godwin and Bharucha, (1932), it was concluded that varying levels of water table 'excess' were probably mainly responsible for controlling the specific communities observed. It appears from the initial results presented in this chapter that the range of water table depths observed are indicative to some degree of the vegetation types present. In addition to average water table levels observed, variation is also apparent within the dynamic of the overall groundwater systems studied. For example, levels of overall fluctuation, ionic content, and the resultant redox systems (see Section 1.1.5, Chapter 1), are variable between and within sites. These relationships will be formally investigated in subsequent Chapters.

A study of the development of the Scottish Border Fens by Tratt (1997) demonstrated that a number of these fen systems had developed through the process of open water being occluded by fringing vegetation over time. Within these basin fens, purely herbaceous mats are more liable to move in relation to underlying water table dynamics, and also become inundated at times. Those in later stages of succession tend to become wooded and stabilised at the margins while less stable areas may still be present towards the centre (also see Rieley and Page, 1990). Thus the groundwater dynamic at *Nether Whitlaw Moss* (one of the Border Fens), exhibits this variation across the length of the transect, with the central stations being more subject to inundation, and higher levels of fluctuation, than those stations towards the edges of the basin. Other sites comprising floating mat vegetation with all round anchorage (i.e. not fringing open water) include *Balavil* and *Tromie Fens* within Insh Marshes. These areas contain little or no scrub vegetation, and as a result, the water table appears to inundate a wider range of stations to some degree (i.e. less stable). In contrast, the section of free-floating mat studied at Lochwinnoch is not anchored along all its margins, and therefore appears to move more freely in relation to the underlying water. As a result, a relatively stable situation dominates, with little or no inundation. The low stress environment is dominated by *Glyceria maxima*, which is a competitive species (Grime *et al.*, 1988). Whilst variation occurs amongst the mat forming vegetation types, the stations

amongst sites with vegetation anchored in mineral and peat substrates appear to have the most extreme water table dynamics, in terms of physical variation.

The sites studied were representative of a range of fen, swamp, and associated mire habitats within northern Britain. Therefore the applicability of predictive methodologies produced from the data sets collected (and presented in subsequent Chapters) is likely to be reasonably good for sites within this biogeographic area.

Chapter 3: Plant communities of seven northern British wetlands: characterisation by groundwater environment and trait variation.

3.1. Introduction

3.1.1. Environmental controls on wetland vegetation composition

Studies of a number of wetlands have produced evidence that the underlying hydrology of such systems is often both complex, and difficult to quantify (e.g. Grieve *et al.*, 1995; Gilvear *et al.*, 1997). However, on a within-site scale, hydrological and hydrochemical regimes of wetlands are major factors driving their vegetation composition and structure, (e.g. Godwin and Bharucha, 1932; Sjors, 1950; Gorham, 1953; Ingram, 1967; Damman, 1978; Malmer, 1986; Mountford and Chapman, 1993). The same factors have also been shown to control the distribution of individual wetland plant species (e.g. Legg *et al.*, 1995b; Brown and Scott, 1997; see also Appendix 10), and sequences of succession within wet grassland species (Schippers *et al.*, 1999). In the same vein, Buttery *et al.* (1965) suggested that the relative uptake capacity of mineral nutrients by *Phalaris arundinacea* was reduced in relation to increasing anaerobic conditions within the substrate, leading to replacement by *Phragmites australis* within an area of Broadland fens, East Anglia, UK.

Basin fen systems are subject to hydrological variation, often largely related to *soligenous* (surface runoff and groundwater discharge) and *topogenous* ('topography made': where drainage is impeded and water collects) inputs (Wheeler, 1999). Floodplain wetlands however are influenced to varying degrees by additional riverine inputs. The flood pulse concept proposed by Junk *et al.* (1989) suggests that low levels of riverine inundation equates to low levels of physical stress (Grime, 1979a; Dickinson and Murphy, 1998), with low inputs of nutrients, sediment, or allochthonous seed material, thereby allowing domination by competitive species. Vegetation assemblages are controlled in such cases by site-specific hydrological variation. Intermediate levels of inundation lead to an increased input of seed and nutrient sources, and in combination with intermediate levels of stress more diverse species assemblages are favoured. High levels of inundation allow little opportunity for deposition of allochthonous loads, or suspended silt and mineral nutrients. In addition, species without considerable stress tolerant components to their strategies (Grime, 1979a; Grime *et al.*, 1988), are unable to establish within regularly flushed, high stress environments, leading to domination by a few species.

In addition to the work of Junk *et al.* (1989), a number of recent studies have investigated the explicit interactions between vegetation and aspects of the underlying hydrology (e.g. Willby

et al., 1997; Ross *et al.*, 1998; Willby *et al.*, 1998), and specifically with regard to processes such as biodiversity maintenance (e.g. Grevilliot *et al.*, 1998). From a global perspective, floodplain wetlands have also been afforded more attention within recent years, from the biodiversity support maintained through flood-pulse mechanisms (Junk, 2000), and the potential impacts upon vegetation and associated biota resulting from the regulation of such systems (Murphy *et al.*, 1999; Agostinho *et al.*, 2000).

3.1.2. Wetland plant communities

Ross (1995) asserts that wetlands can be broadly classified by their nutritional status and modes of chemical input (e.g. ombrotrophic, mesotrophic, and eutrophic; acidic and neutral), which alludes to the fact that these factors are important controls on floristic composition. However, Ross (1995) also indicates that most classifications are in practice based primarily upon floristic composition.

Within studies of wetlands in Britain, a majority of the attention has been paid to the plant communities of fen systems, and particularly to rich-fen systems. For example the descriptions of freshwater systems by Spence (1964) included a number relating to Scottish fens. Studies undertaken by Wheeler (e.g. 1980a,b and c) produced descriptive accounts of such vegetation in other areas of Britain, and particularly East Anglia. The intrinsic interest of these generally species-rich fen communities is without doubt, but in comparison, species-poorer wetlands such as marshes have been somewhat neglected (Rodwell, 1995). However, as Spence (1964) noted, the distinction between fens and swamps is often blurred, and the classification is in effect somewhat arbitrary where one grades into the other.

The NVC (National Vegetation Classification) (Rodwell, 1991 *et seq.*) is today generally accepted as the standard for British plant community descriptions, to the extent that *"it is employed as the main classification for terrestrial habitats in Guidelines for the Selection of Biological SSSIs and has been used to interpret Annex I of the EC Habitats Directive where relevant"* (http://www.jncc.gov.uk/species/default.htm). However, the limitations of the NVC in standing freshwaters and some bog communities are also recognised.

The NVC British Plant Communities *Volume 2, 'Mires and heaths'* (Rodwell, 1991) identifies six communities of bog vegetation, and a number of poor fen and sedge dominated rich fen communities. *Volume 4*, concerning *'Aquatic communities, swamps and tall herb fens'* (Rodwell, 1995) lists twenty-one swamp communities, and five tall-herb fen communities. Despite a greater number of swamp communities being described, Rodwell (1995) states that data on swamps and fens from studies previous to the NVC were few in

number; with swamps particularly so, due to what the author considers the 'unrewarding nature' of such systems (i.e. often large mono-specific stands). It is also often the case with the NVC descriptions of wetland habitats (Rodwell, 1995), that characterisation of environmental variables such as water depth was often based on a single measurement. A small number of studies have helped advance the understanding of the response of wetland vegetation to physical water table characteristics (e.g. Mountford and Sheail, 1989; Blanch and Brock, 1994; Brownlow *et al.*, 1994; Rea and Ganf, 1994; Newbold and Mountford, 1997). However, synthesis of these findings with community descriptions, to give more explicit characterisations of the communities has rarely been attempted (e.g. Gowing *et al.*, 1998). The indicator values defined by Ellenberg (1988) including scales for a number of vascular plants of central Europe, and based on their realised niche have recently been subject to renewed interest (e.g. Mountford and Chapman, 1993; Hill and Carey, 1997). These values, including the 12-point scale for moisture, have recently been revised by Hill *et al.* (1999) to be more applicable to British vegetation.

3.1.3. Measuring variation in defined plant communities

Within wetland systems there is strong evidence that the hydrological processes operating at discrete points within a site, and the vegetation assemblages present are inextricably linked. In order to begin to understand the processes underlying a particular ecosystem or habitat, a survey of the plant species that occur therein is a useful first step. In this Chapter the study sites used during 1998-2000 are described in terms of plant community composition and groundwater characteristics measured. In addition, much evidence points to the value of measuring 'traits' or 'attributes' within plant populations and communities to gauge the influence of underlying environmental gradients (see Chapter 1). A more formal analysis of the specific eco-hydrological interrelations of these variables is provided in Chapter 4. The chapter ends with a formal discussion section, but due to the nature of community descriptions and comparisons, some of the results sub-sections are discursive by necessity.

In summary, this Chapter:

- Groups sample sites with floristic similarities, and classifies these groupings as recognised wetland community types within the British flora.
- Examines temporal variation in the floristics of a number of sites which were studied for more than one year.
- Characterises the various community groupings in terms of average hydrological and hydrochemical values, and average vegetation variable values using a multivariate approach.

3.2. Methods and Materials

3.2.1. Data collection and structure

Species and environmental data for all sites were collected as detailed in section 2.2. The specific environmental variables, collective vegetation variables, and dominant population traits measured are detailed in Tables 3.2.1-3.2.3 respectively. All data were tested for normality using a Ryan-Joiner test in Minitab v.11.21. Where data were not normally distributed, appropriate transformations were made. Where transformation failed to resolve homogeneity of variance amongst residuals, non-parametric tests were subsequently employed. Data were collated into species by sample arrays for subsequent analysis.

3.2.2. Data analysis

A complementary multivariate approach was taken, employing ordination analysis in conjunction with cluster analysis of species data. Gauch (1982) concluded that two specific methods, namely DCA and TWINSPAN (see below), were appropriate for analysing complex sample by species data arrays. Indirect ordination makes no prior assumption about the relationship between the sites, but allows relative similarities and differences to be observed (Manly, 1994). This procedure was followed by a characterisation of groups produced on the basis of underlying groundwater and environmental variables, dominant population traits, and collective vegetation variables. Initial analyses were conducted on repeat data for sites across the year in order to identify potential outliers. Following verification of repeated site representation in comparable ordination space for the total yearly data set, matrices were constructed representing yearly average species by sample arrays.

3.2.2.1. Ordination of species data

Combined species data for all of the study sites was investigated using Detrended Correspondence Analysis (DCA: Hill and Gauch, 1980), within the CANOCO for windows package (ter Braak and Šmilauer, 1998). DCA is an unconstrained ordination technique whose application is favoured where species data exhibit a Gaussian (i.e. unimodal) response curve (Figure 3.2.1: Jongman *et al.*, 1995). This situation is indicated where a gradient length of >c.3.0 standard deviations (S.D.) is obtained for the spread of the data along the first axis of the ordination. A length of >4 S.D. indicates a strong unimodal response (ter Braak and Šmilauer, 1998). DCA represents an improvement upon earlier ordination methods of ordination such as Reciprocal Averaging (RA: Hill, 1973). It also reduces the 'arch effect' seen in the forerunner, Correspondence Analysis (CA), and is therefore regarded as superior in displaying relationships in ecological data (Hill and Gauch Jr., 1980). The default setting for detrending by segments was selected, as it has been shown to perform

consistently better than the alternative method of detrending by polynomials in DCA (ter Braak & Šmilauer 1998).

3.2.2.2. Cluster analysis, group characterisation and community classification

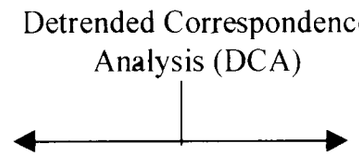
TWINSPAN (Hill, 1979), within the VESPAN III package (Malloch, 1997) was used in the classification of data into groups. TWINSPAN is a polythetic divisive method, which uses species abundance rather than presence or absence, and uses the concept of '*pseudospecies*', to set the presence of a relative species at pre-determined levels of abundance (Kent and Coker, 1995). As percentage data were used, cut levels for pseudospecies scores were set at 1%, 5%, 10%, and 20%. Final group membership for sites was decided by taking into account the relative eigenvalue at each cut level, within the second and third level of the final table (Hill, 1979). An eigenvalue of 0 indicates total homogeneity of data, with no patterns based on pseudospecies abundance, while an eigenvalue of 1 indicates a strong pattern to the data, with clearly defined groups. Therefore, any division with an eigenvalue of greater than c.0.4 was considered for the basis of two groups, although the two groups might not be very well defined. The process is inherently subjective (Kent and Coker, 1995), and therefore, groups were re-amalgamated where divisions were not considered to be ecologically sensible: for example, where no distinct indicator species was apparent in defining the group(s).

The species data for each site were compared to existing National Vegetation Classification (NVC: Rodwell, 1991 *et seq.*) community classifications using the MATCH computer programme (Malloch, 1999). Samples were matched individually, and then as component sites within their defined TWINSPAN groups, following production of constancy tables.

Following allocation of sites to respective groups for each of the yearly average species data sets by TWINSPAN, significant differences were determined between average group values for environmental variables, dominant population traits, and collective vegetation variables, in order to characterise the respective groups. Where data were normally distributed, a one-way Analysis of Variance was applied to investigate potential significant differences between group variable means. Tukey pairwise comparisons were then applied to identify which groups were significantly different from each other. As a relatively large number of comparisons were involved, the relatively conservative Tukey pairwise test was less likely to lead to a Type I error, and rejection of the null hypothesis (H_0) than other post-hoc tests (Zar, 1999). Where data were not normally distributed, and could not be normalised via transformation, non-parametric tests were used. Where group sizes were n = <5, Mann-Whitney pairwise comparisons were made between each pair of groups individually. Where

all group sizes were n = ≥5, the Kruskal-Wallace tests were used, and these were followed by non-parametric post-hoc tests in order to determine which groups, if any, differed significantly from each other (Zar, 1999).

Figure 3.2.1 Selection of ordination technique, following initial application of Detrended Correspondence Analysis (DCA) to determine length of gradient (LG) (Standard Deviation) (adapted from ter Braak and Prentice, 1988).



	LG ≤ 1.5 SD	LG ≥ 3.0 SD
	Linear Response Model	*Unimodal Response Model*
Indirect Gradient Analysis	Principle Component Analysis (PCA)	Detrended Correspondence Analysis (DCA)
Direct Gradient Analysis	Redundancy Analysis (RA)	Canonical Correspondence Analysis (CCA)

Table 3.2.1 Environmental variables measured within vegetation assemblages during sampling. See chapter 2 for full description of methodologies.

Variable	Code	Method	1998	1999	2000
Shade index	SHA	Assessed visually: 0= no shade to 5= heavy shade	✓	✓	✓
Ground water level (cm)	WAT	Measured from fixed dipwells (below surface) or from standing water (above)	✓	✓	✓
Minimum ground water level (cm)†	MIN	Measurement taken from minimum-maximum water level gauge	-	✓	✓
Maximum ground water level (cm)†	MAX	Measurement taken from minimum-maximum water level gauge	-	✓	✓
Degree of groundwater fluctuation (cm)†	FLU	Measurement taken from minimum-maximum water level gauge	✓	✓	✓
pH†	pH	Measured with hand held meter from fixed dipwell	✓	✓	✓
Conductivity (μS/cm)	CON	Measured with hand held meter from fixed dipwell	✓	✓	✓
Redox (mV)	RED	Measured from soil using hand held meter with platinum electrode	-	✓	✓
Fe ($mg\ l^{-1}$)	Fe	Analysed in laboratory	✓	✓	✓
Mg ($mg\ l^{-1}$)	Mg	Analysed in laboratory	✓	✓	✓
Mn ($mg\ l^{-1}$)	Mn	Analysed in laboratory	✓	✓	✓
Ca ($mg\ l^{-1}$)	Ca	Analysed in laboratory	✓	✓	✓
Na ($mg\ l^{-1}$)	Na	Analysed in laboratory	✓	✓	✓
Cl ($mg\ l^{-1}$)	Cl	Analysed in laboratory	-	✓	✓
K ($mg\ l^{-1}$)	K	Analysed in laboratory	-	✓	✓
SO_4^{2-} ($mg\ l^{-1}$)	SO	Analysed in laboratory	-	✓	✓
NO_3^- ($mg\ l^{-1}$)	NO	Analysed in laboratory	-	✓	✓
PO_4^{2-} ($mg\ l^{-1}$)	P	Analysed in laboratory	-	-	✓

Table 3.2.2 Collective vegetation variables measured within vegetation assemblages during sampling.

Variable (calculated 1m x 1m quadrat)	Code	Method	1998	1999	2000
Species richness (S) (m^{-2})	NOSP	Number of species counted	✓	✓	✓
Canopy height (cm)	CAHT	Three random measurements of vegetation	✓	✓	✓
Litter cover (%)	LITT	Estimated by eye	✓	-	✓
Stem density (m^{-2})	STDE	Three random counts within a 10cm x 10cm quadrat	✓	✓	✓
Stem diameter (mm)	STDI	Three random measurements (of any species) at ground level using callipers	✓	✓	✓
Nearest neighbour distance	NENE	Three random measurements taken between three pairs of stems, and then scored 1-5. 1= 0-2cm; 2= 2.1-4cm; 3= 4.1-6cm; 4= 6.1-8cm; 5= >8cm	-	✓	✓
Reproductive structures (n/m^2)	REPR	Three random counts within a 10cm x 10cm quadrat			
Biomass (g/m^2)		Harvested, separated from dead material (necromass), cleaned, and dried at 60^0C for 1 week			
0-10cm	B1	Clipped from within a 10cm x 10cm quadrat from ground level to 10cm above ground level	-	✓	✓
10-20cm	B2	As above, between 10cm and 20cm above ground level	-	✓	✓
>20cm	B3	As above, over 20cm above ground level	-	✓	✓
Total	Bt	All above values combined	-	✓	✓
Necromass (g/m^2)		Harvested, separated from live material (biomass), cleaned, and dried at 60^0C for 1 week			
0-10cm	N1	As for B1	-	✓	✓
10-20cm	N2	As for B2	-	✓	✓
>20cm	N3	As for B3	-	✓	✓
Total	Nt	As for Bt	-	✓	✓
Standing crop (g/m^2)					
0-10cm	BN1	B1+N1	✓	✓	✓
10-20cm	BN2	B2+N2	✓	✓	✓
>20cm	BN3	B3+N3	✓	✓	✓
Total	BNt	Bt+Nt	✓	✓	✓

Table 3.2.3 Dominant population traits measured from whole ramets within vegetation assemblages during sampling.

Variable (per ramet)	Code	Method	1998	1999	2000
Height (cm)	RamHt	Three random measurements taken per quadrat	✓	✓	✓
Number of leaves	RamLv	Three random counts made per quadrat	✓	✓	✓
Canopy area (%)	Can	Using a clear 10cm x 10cm quadrat with 1cm divisions held directly above canopy; plant counted where the intersection of two divisions projected down onto the vegetation (i.e. as with a pin frame), up to a maximum of 100. Three random counts per quadrat.	-	✓	✓
Total leaf area (cm^2)	RamTLA	Scanned using Deskscan software on flat-bed scanner; analysed using customised Delta-TScan software.	✓	✓	✓
Total leaf length (cm)	RamTLL	As for RamTLA	✓	✓	✓
Stem biomass (g)	RamSB	Separated from rest of ramet, cleaned and dried at 60^0C for 1 week	✓	✓	✓
Leaf biomass (g)	RamLB	As for RamSB	✓	✓	✓
Reproductive structure biomass (g)	RamRB	As for RamSB	✓	✓	✓
Total Biomass (g)	RamTB	RamSB, RamLB and RamRB added together	✓	✓	✓
Average seed biomass (mg)	SeedB	An average weight taken for 10 seeds (or all seeds if <10) from randomly selected seed heads	✓	✓	✓
Specific leaf area (cm^2/mg)	SLA	RamTLA divided by RamLB (converted to mg values)	✓	✓	✓

3.3. Results

3.3.1. Community classifications

3.3.1.1. Multivariate classification of the species data

1998 data

A DCA ordination of the 1998 species abundance and site data (August only, due to incomplete data sets for previous months) is shown in Figure 3.3.1. A gradient length of 4.69 s.d. along axis 1 indicates a complete turnover of species across all sites. This is also true of axis 2, with a gradient length of 5.31 s.d.. A greater level of variation in species represented is apparent for the Insh Marsh stations, with the Nether Whitlaw stations clustered to the centre of the ordination space (Figure 3.3.1). A TWINSPAN classification of the August 1998 data (Figure 3.3.2; Table 3.3.1) indicates that groupings can be made on the basis of station characteristics (ie. indicator species), rather than by geographical location, with stations from Insh Marshes being placed into all three groups. Although seasonal variation was not taken into account, differing group characteristics can be inferred on the basis of the indicator species present. Group 1 was characterised by *Molinia caerulea*, suggesting waterlogged, acid soils. Group 2 was characterised by *Deschampsia cespitosa* and *Filipendula ulmaria*, suggesting slightly drier (though still periodically inundated) soils. Group 3 was characterised by a dominance of *Carex rostrata* and *Menyanthes trifoliata*, indicating more permanently inundated conditions

1999 data

In order to assess the validity of mulivariate analysis based on yearly average data, an initial DCA analysis was conduted on the total 1999 data set (Figure 3.3.3). An axis 1 gradient length of 6.59 standard deviations (s.d.) illustrates a complete turnover of species across sample stations. However, two outliers can be seen within the ordination, these being the samples from Lochwinnoch station 3 (L3; July and August), which rapidly became dominated by shoots of *Glyceria maxima* as the growing season progressed. Due to the high level of dissimilarity of this station to all others, it was removed from the data set for subsequent analyses. Following the removal of L3 samples, there was still clearly a complete turnover of species represented when the average site and species data for 1999 was ordinated, suggesting a good range of wetland vegetation types sampled (Figure 3.3.4). The first axis had a gradient length of 5.15 s.d., and the second a length of 4.04 s.d., representing complete turnover of species across samples. The use of averaged data from 3 subsequent vegetation samples over the season was validated by a TWINSPAN analysis of

all the 126 samples (excluding L3) taken over the year. Only four samples (Glen Moss 5, Insh Marshes 10 and 11, and Tarn Moss 2) were not consistently classified into the same group (Appendix 5a). However, these samples were generally classified in the same group for two subsequent months out of the three, suggesting subtle changes in relative species abundances within the assemblages present over the growing season.

Six distinct TWINSPAN groups were produced for the 1999 species data (Figure 3.3.5; Table 3.3.4), with group sizes ranging from n=3 (group 5) to n=11 (group 4). The indicator species for group 1 was *Carex lasiocarpa*. Other species of the genus were indicator species for groups 3 and 4 (*C. panicea* and *C. rostrata* respectively) suggesting differences in water table levels and relative base and nutrient staus between these three groups. Group 2 was characterised by *Galium palustre*, perhaps indicating drier conditions. Group 5 was characterised by a dominance of *Potamogeton polygonifolius*, indicating more permanently inundated conditions within this group. Group 6 was generally characterised by a larger proportion of bryophyte-dominated samples, with dominant species representative of mire communities.

2000 data

A gradient length of 3.80 s.d. for axis 1 represents a complete species turnover across sites (Figure 3.3.5). The gradient length of axis 2 is somewhat shorter at 2.42 s.d.. All station samples except one (Insh Marshes, 1) were consistently re-classified within the same TWINSPAN group (Appendix 5b), verifying the use of averaged data from over the year. Numbers of samples within the four TWINSPAN groups produced from the 2000 data ranged from n=4 to n=6 (Table 3.3.3). Whilst group 2 did not appear to be distinct from group 1, this was mainly due to the presence of just one site, visible on the far right of the ordination (Figure 3.3.5). In addition, the eigenvalue for the division was 0.41, suggesting a degree of difference between the two sites, and the indicator species differed between the groups. Therefore groups 1 and 2 were maintained for subsequent analyses. The dominant species within group 1 were *Deschampsia cespitosa* and *Molinia caerulea*, suggesting waterlogged and acid soils. Group 2 was characterised by a dominance of *Hydrocotyle vulgaris* and *Menyanthes trifoliata*, suggesting slightly more inundated conditions. *Carex aquatilis* was dominant within group 3, suggesting regularly inundated conditions, whilst group 4 had a number of co-dominant species, indicative of swamp communities. Group 2 contained samples unique to Wood of Cree, and group 4 samples unique to Endrick Marshes. However, a number of Endrick samples were also placed into group 3, and Insh samples were split between groups 1 and 3. This shows that as with previous years, groupings were based upon species composition rather than geographical location.

It should be noted that certain sites were placed into different groups between 1998 and 1999. For example, during 1998, all six Nether Whitlaw stations were placed into group 2, while during 1999, the sites were split between groups 1, 4 and 5. Insh Marsh sites 2 and 3 meanwhile formed a separate group during 1998, but were grouped in with other Insh Marsh sites during 1999. Rather than being due to major mis-identifications, which is unlikely, this situation might be explained by two factors. Firstly, a general average drawdown of the water table level during the growing season was observed for a number of repeat sites (see Chapter 2). Secondly, the TWINSPAN groups for 1998 were based solely on data recorded in August, while those for 1999 were based on monthly May-August averages.

Validation of clustering using TWINSPAN

Some criticism has been leveled at TWINSPAN (eg. McCracken, 1994) where it is argued that the algorithms used force hard partitions upon datasets where variation is continuous, and that the use of fuzzy clustering techniques (e.g. see Equihua, 1990) might be more appropriate. Simple comparisons were therefore made between the use of fuzzy clustering (Bezdek, 1981) and TWINSPAN. Ordination diagrams and group membership for classifications undertaken using fuzzy clustering can be found in appendices 6 (a-f). It can be seen that the highest fuzzy partition coefficient was 0.65 (on a scale of 0-100) for the August 1998 data, and that the coefficients were lower at 0.52 and 0.56 for average 1999 and 2000 data respectively. In each case the maximum partition coefficient produced only three groups, and for all of these there was some degree of overlap, and as with the classifications determined by TWINSPAN, not all sites were reclassified within the same groups for subsequent months. In addition, certain samples were placed together which were not floristically similar. For example, Nether Whitlaw samples 2-5 and Tarn Moss samples 3-5 were placed into the same group for the 1999 data classification (see Appendix 6). Whilst those for Nether Whitlaw were generally visually recognisable as fen habitats (e.g. *Menyanthes trifoliata* and/or *Carex* spp. dominated), some of those from Tarn Moss were evidently mire vegetation.

3.3.1.2. Species composition of the defined communities

Tables 3.3.4-3.3.6 show the floristic composition of each of the TWINSPAN groups defined for the August 1998 data, and the site average data for 1999 and 2000 (full, unordered data sets can be seen in Appendix 3). The tables are sorted to aid comparison between groups, on the basis of constant species (categories V and IV), followed by associates (categories I-III) (Rodwell, 1991 *et seq.*). The relative frequency of each species, indicating the proportion of

quadrats within which it was recorded for the defined group(s), and the range of abundances at which the species was recorded at within the relative quadrats are given in each table.

Table 3.3.4 highlights some major differences in floristic composition between the three TWINSPAN groups defined for the August 1998 data. *Equisetum fluviatile* was the only species recorded in all three groups, although the abundance overall was generally very variable. Both groups 1 and 3 are difficult to characterise, due to the small number of sample sites for each. Of the two species recorded within both samples for group 1, *Molinia caerulea* had by far the highest abundance at 100%. *Eriophorum angustifolium* is less abundant within the samples. A number of species of *Carex*, amongst others recorded, are more indicative of waterlogged rather than inundated soils. *Filipendula ulmaria* was the only species recorded within all sites placed into TWINSPAN group 3, however abundance was highly variable, running from 8 to 80%. A number of other species were found in two of the four sites placed within group 3. Some such as *Rumex acetosa* were at a low abundance (4-8%), as were a number of species indicative of waterlogged acid grasslands, such as *Deschampsia cespitosa* and *Carex nigra*. *Succisa pratensis* was the only species recorded in three of the four sites comprising group 3. This is a species with a relatively wide pH and moisture tolerance range. Group 2 was by far the largest for the 1998 data, with seventeen sites. Two species only (from n=46) were constant within the group (*Equisetum fluviatile* and *Potentilla palustris*), but the freqency of both was highly variable. Associates within the group, with frequencies in the range of 41-60% (III) were *Galium palustre*, *Carex rostrata* and *Menyanthes trifoliata*. The latter two species perhaps indicate overall wetter characteristics for the constituent sites. A further division, with an eigenvalue of 0.48 was considered for the individuals of group 2. This division would have placed Insh Marsh sites 10 and 11, and Nether Whitlaw sites 1, 4 and 6 in a separate group. However, there were no indicator species which could be used to define this group separately, but differences lay in the presence of occasional bryophytes, perhaps indicating slightly less inundated conditions. As this division would not produce what was considered to be distinct groups, the larger (n=17) group was maintained for subsequent analyses. The value of the TWINSPAN groupings for the 1998 data was perhaps reduced due to the use of species lists from the end of the growing season (August) only. However, it helped provide a baseline for comparrison to following years findings.

The floristic characteristics of the TWINSPAN groups produced for the average 1999 species data can be seen in Table 3.3.5. Six groups were defined, the smallest of which contained average data for the year for three sites (Group 6), and the largest of which represented eleven sites (Group 4). The ubiquitous nature of *Equisetum fluviatile* within a

number of wetland habitats was again illustrated by its presence in five of the six groups. The frequency of the species was high in all groups where it was recorded, except for group 4, where it was recorded as an associate. However, the abundance of the species within the relative groups where it did form a constant component of the assemblage was highly variable. In groups 2 and 3, for example, abundance was recorded at a maximum of 52%, while it was recorded at a maximum of 99% and 83% for groups 1 and 5 respectively. *E. fluviatile* was the only constant species within group 1. A number of associated species were indicative of waterlogged, if not inundated conditions. *E. fluviatile* was also the most frequent species within group 2 (although not highly abundant), but *Carex aquatilis, Galium palustre, Potentilla erecta* and *Potentilla palustris* were also present as constant species. Group 3 had the highest number of constant species (n=13) of all the 6 groups defined, with the greatest levels of frequency being recorded amongst *Carex nigra, Molinia caerulea* and *Eriophorum angustifolium.* Generally inundated conditions were indicated within the samples comprising group 4, with *Carex rostrata* and *Menyanthes trifoliata* recorded as constants. In addition, a number of *Sphagnum* species were also recorded as associates. *C. rostrata* and *M. trifoliata* were also recorded as constant species within group 5, but the group was differentiated from the rest by the presence of *Potamogeton polygonifolius* (as a constant). Group 6 contained only 3 sites, and the most frequent species recorded as a constant was *Eriophorum angustifolium.* A number of ericaceous species were unique to this site.

For the 2000 data (Table 3.3.6), *Equisetum fluviatile* was once again recorded within all the (four) TWINSPAN groups defined. Some of the groups contained repeat sample sites, and some comprised entirely new sites. The species was recorded as a constant for groups 1-3, and in three out of the four sites representing group 4. *Galium palustre* was also recorded as a constant species throughout all four groups. Five additional species were recorded as constants within group 1 sites, but only *Carex nigra* was recorded at a high level of abundance (95%). A number of associates were unique to this group, with the most frequent of these being *Carex echinata* and *Deschampsia cespitosa.* Group 2 contained by far the greatest proportion of constant species (twenty in total). None of these were recorded at an abundance greater than 76%, with the majority being recorded at levels of abundance less than 50%. Of these constant species, seven were unique to group 2. In addition to *E. fluviatile* and *G. palustre,* group 3 contained *Carex aquatilis* and *Phalaris arundinacea* as constant species. *C. aquatilis* was the only species unique to group 3, and was recorded with levels of abundance of up to 100%, and as low as 27%. The abundance of *P. arundinacea* did not exceed 35%. In contrast, *P. arundinacea* was much more abundant within group 4, and was recorded in three out of the four sites. *Angelica sylvestris, Epilobium palustre* and

Galium palustre were the only three species to be recorded in all four of the sites constituting group 4. However, the recorded abundance of *G. palustre* only just exceeded 50%, while the abundance of the other two species was much lower. Four species were unique to group 4.

3.3.1.3. Comparison to existing community classifications

1998

The Match coefficients for individual stations for all year scan be found in Appendix 7. A range of matches to NVC community types are displayed, but with few exceptions the coefficients are low, indicating poor fits with existing classifications. This was not surprising whilst attempting to match single samples, and therefore the combined data comprising the defined TWINSPAN groups was also matched (Tables 3.3.7a-c). For the August 1998 data match coefficients were again generally low. For group 1 the highest match (34.7) was to an M9 *Carex rostrata-Calliergon cuspidatum/giganteum* mire (Table 3.3.7a). Eight of the eleven species in group 1 were listed within the NVC tables. Whilst the samples appear to fit most conveniently into this community, it is difficulty to classify the group with any degree of certainty, due to the small sample size.

Group 2 was most closely matched to the S27a *Carex rostrata-Potentilla palustris* tall herb fen community, *Carex rostrata-Equisetum fluviatile* sub-community, with a coefficient of 55.7. Twenty two of the fourty seven species recorded in group 2 were listed in the NVC tables for this sub-community type. A majority of those species which were not common to both group 2 and the NVC tables were occasionals rather than constants. The frequency and abundance of both *Equisetum fluviatile* and *Potentilla palustris* in group 2 was comparable to the described S27a community (Rodwell 1995). *Carex rostrata, Galium palustre* and *Menyanthes trifoliata* were all present within group 2, but were recorded at generally lower frequencies than for the described S27a NVC community.

Group 3 for the August 1998 data gave a relatively good match to the M27 *Filipendula ulmaria-Angelica sylvestris* mire, with a match coefficient of 49.5, despite only comprising four samples. Of a total of twenty-five species recorded, fifteen were listed within the community description. *Filipendula ulmaria* was the only species be recorded in all four samples, and is the only species listed as a constant within the M27 community description (Rodwell, 1991). All species recorded in group 3, but not listed in the NVC tables were occasionals with a frequency of 1, with the exception of *Holcus lanatus*, which had a frequency of 2. All of these species were recorded at low levels of abundance.

1999

Group 1 for the mean 1999 data contained stations 7 and 11 from Insh Marshes, which had been placed in groups 1 and 3 respectively for the August 1998 data (Tables 3.3.1 and 3.3.2); all other members were from new sites. The highest match (49.1) was to a S27a *Carex rostrata-Potentilla palustris* tall herb fen, with a *Carex rostrata-Equisetum fluviatile* sub-community (Table 3.3.7b). *Carex rostrata* was in fact absent from the group, but *Carex aquatilis* was present as an occasional, with an abundance of up to 100%. As Rodwell (1995) states, *C. aquatilis*, or *C. vesicaria* can dominate the S27a community. *C. vesicaria* was also present, again as an occasional, but with a high abundance. *Equisetum fluviatile* was the only constant species recorded within the group, with *Galium palustre*, *Menyanthes trifoliata* and *Potentilla palustris* all being recorded as occasionals. Once again, this is a situation which can be representative of the S27a community. Within the group eighteen species from a total of thirty were listed within the NVC community tables. Those which were not had all been recorded as occasionals.

Group 2 gave the highest match (50.3) to a M23b *Juncus effusus/acutiflorus-Galium palustre* rush pasture with a *Juncus effusus* sub-community. As with group 1, some stations which had been grouped together in the previous year were once again grouped together (Insh Marsh 4 and 9; Tables 3.3.1 and 3.3.2), but several were not. *Equisetum fluviatile* was recorded as a constant species, but in the community listings it is recorded as an occasional (Rodwell 1991). In addition, *Carex aquatilis* was also recorded as a constant, but is not present in the community listings. However, both *Galium palustre* and *Potentilla palustris* were recorded as constant species. Of a total of forty-one species recorded, twenty-five were present within the M23b community listings. With the exception of *Carex aquatilis*, all those not listed were recorded as occasional species.

Group 3 contained some stations which had previously been grouped together for the August 1998 data, and some which had not (Tables 3.3.1 and 3.3.2). The group was most closely matched (52.5) to a M9b *Carex rostrata-Calliergon cuspidatum/giganteum* mire with a *Carex diandra-Calliergon giganteum* sub-community. Although *Calliergon giganteum* was not recorded, *Carex diandra* was, albeit as an occasional species, and with a relatively low abundance. *Cardamine pratensis*, *Eriophorum angustifolium* and *Epilobium palustre* were recorded as constant species. This, along with the general levels of abundance of these three species was consistent with the listings for the M9b description. A number of species were recorded as constants in addition to those listed in the community description: notably *Calliergon cuspidatum*, but also *Carex panicea*, *Carex nigra*, *Molinia caerulea*, *Potentilla erecta* and *Ranunculus lingua*. *Carex rostrata* and *Menyanthes trifoliata* on the other hand

were recorded as occasionals. The additional presence of *Equisetum fluviatile* as a constant species may indicate a zonation of the community to a state where this species would begin to become dominant (Rodwell, 1991). Of a total of fourty-nine species, twenty-two were listed within the M9b tables. All of those not listed were recorded as occasionals. However, it should be noted that the M9b community description is based on only twenty-four samples (Table 3.3.7b), and therefore there was greater scope for picking up previously undescribed variations.

Group 4 was most closely matched to a S27a *Carex rostrata-Potentilla palustris* tall-herb fen with a *Carex rostrata-Equisetum fluviatile* sub-community (coefficient: 50.5). All stations witin the group were new, with the exception of Nether Whitlaw 4, 5, and 6, which had previously been grouped together during 1998. Unlike Group 1, *Carex rostrata* was present, and was recorded as a constant species with up to 100% frequency in some cases. *Potentilla palustris* and *Menyanthes trifoliata* were also recorded as constant species, which was consistent with the community listings. *Angelica sylvestris* and *Galium palustre* however were only recorded as occasionals. Of the forty-two species recorded for the group, twenty-two were consistent with the S27 community listings, and those that were not were all recorded as occasional species. A notable example of one of these extra species was *Lysimachia vulgaris,* which comprises a constant component of the S27b sub-community (to which the species also lends its name). However, within group 4 this species was only recorded as an occasional.

Group 5 was most closely matched (53.2) to a S9b *Carex rostrata* swamp with a *Menyanthes trifoliata-Equisetum fluviatile* sub-community, and the group comprised stations which had all been grouped together during 1998 (Tables 3.3.1 and 3.3.2). The presence of *Carex rostrata* and *Menyanthes trifoliata* as constant species was consistent with the S9b community listings. *Carex nigra, Potamegeton polygonifolius* and *Potentilla palustris* were also recorded as constant species rather than occasionals, whilst *Potentilla erecta,* which is not present within the S9b listings was also recorded as a constant species. The presence of *Equisetum fluviatile* as a constant species rather than an occasional within this group may be linked to two factors: firstly, the S9 community is seen to to grade into the S27 community, within which the species is a constant, and secondly, it is often difficult to separate the S9 community from the S10 *Equisetum fluviatile* swamp community (Rodwell, 1995). In addition, this community was also based upon relatively few samples (n=31). The group comprised twenty-one species in total, of which nine were listed within the S9b community description. All those species not present in the listings were recorded as occasionals with relatively low abundance scores, with the exception of *Potentilla erecta,* and also

Calypogeia meullerana and *Carex chordorrhiza*, which were recorded as occasionals, but with 100% abundance.

Group 6 comprised only three samples, but gave a best match (50.0) to a M2 *Sphagnum cuspidatum/recurvum* bog pool community, which itself was based upon only 14 samples. All three stations from which the samples were taken were new during 1999 (Table 3.3.2). Neither *Sphagnum cuspidatum* nor *Sphagnum recurvum* were recorded in the samples taken. Two other species, *Sphagnum palustre* and *Sphagnum teres* were present, and were listed within the M2 community description. *Eriophorum angustifolium* was also present within all three samples, which was consistent with its status as a constant species within the community description (Rodwell 1991). As with other small groups, difficulty arose in definate matches to existing community descriptions. However, ten of the total of twenty-one species recorded were listed within the community description, and those not were again generally (though not exclusively) of low frequency and abundance.

2000

Group 1 for the mean 2000 vegetation data (Table 3.3.7c) comprised samples from Insh Marsh stations which had been placed into the same group in the previous year, with the exception of station 8 (Tables 3.3.2 and 3.3.3). The group had the highest match to a M5 *Carex rostrata-Sphagnum squarrosum* mire (coefficient: 45.0). As with previous examples, this community itself was based on only a small number of samples (n=22). *Carex rostrata* was recorded as an occasional only, with an intermediate abundance, and *Sphagnum squarrosum* was not recorded. However, characteristic of this community, *Carex nigra* and *Eriophorum angustifolium* were recorded as constant species. *Caltha palustris, Equisetum fluviatile, Galium palustre, Ranunculus flammula* and *Viola palustris* were also recorded as constants within the group, but are only represented as occasional species in the M5 community description. Conversely, *Potentilla palustris* was recorded as an occasional species rather than a constant. The presence of *Equisetum fluviatile* as a constant component of the assemblage may be due to the fact that the M5 community is often fronted by the S10 *Equisetum fluviatile* community (Rodwell, 1991). Of the thirty species recorded in total for the group, seventeen were listed within the community description. Those species recorded but not listed in the community descriptions were all recorded as occasionals, and with the exception of *Deschampsia cespitosa*, had low levels of abundance within the samples.

Group 2 had the second highest match to a S27a *Carex rostrata-Potentilla palustris* tall herb fen with a *Carex rostrata-Equisetum fluviatile* sub-community (coefficient: 50.4). Whilst a match to an M9 community was slightly higher at 50.6, the habitat was considered more

reresentative of a fen, with a gradual gradation from *Salix* woodland to open water. Previous surveys have also described the site as a good example of a transitional fen system (Paul Collin, R.S.P.B., pers. com. 2000). All of the stations were newly sampled during 2000 (Table 3.3.3). The presence of *Carex panicea, Equisetum fluviatile, Galium palustre, Mentha aquatica, Menyanthes trifoliata* and *Potentilla palustris* as constant components of the group assemblage was consistent with the S27a community description. However, *Agrostis stolonifera, Angelica sylvestris, Caltha palustris, Carum verticillatum, Hydrocotyle vulgaris, Filipendula ulmaria, Ranunculus flammula* and *Viola palustris* were also recorded as constants rather than occasional species. In addition, *Achillea ptarmica, Juncus acutiflorus, Sphagnum papillosum* and *Succisa pratensis* were all recorded as constant species, but do not appear in the listed species for the community description. Rodwell (1995) states that *Filipendula ulmaria* might be locally dominant within the community where it grows on alluvial banks deposited alongside moving water (the Wood of Cree stations comprising this group are periodically inundated by the River Cree). Of the thirty-five species total recorded for the group, twenty-two were listed within the S27a community description. The presence of additional species recorded as dominants may either represent new samples, or be due to the fact that the S27 community is considered difficult to define (Rodwell, 1995).

Groups 3 and 4 both gave highest matches to a S11 *Carex vesicaria* swamp community, with coefficients of 58.7 and 53.8 respectively. Group 3 comprised two stations which had been grouped together in the previous year, along with stations from sites new in 2000, while group 4 comprised exclusively new sites. Floristic differences between the groups led to them being kept separate rather than re-amalgamated in order to investigate potential differences between underlying environmental variables. In addition, the S11 community description was based upon only 18 samples. The possibility of the samples comprising new records therefore needed to be considered.

Group 3 contained *Carex aquatilis, Equisetum fluviatile, Galium palustre* and *Phalaris arundinacea* as dominant species, which was consistent with the community description listings. The absence of *Carex rostrata* and presence of *Carex aquatilis* appeared to represent an intermediate state between the two defined sub-communities rather than typifying one or the other. Whilst *Carex aquatilis* was absent from group 4 (the species can dominate locally: Rodwell, 1995), *Carex rostrata* was present in three of the four samples taken. *Angelica sylvestris* was also present within all the samples comprising group 4, but absent from group 3. Apart from these floristic dissimilarities and the presence or absence of a few occasional species recorded with low levels of abundance, the two groups were

otherwise comparable. For group 3, eleven of the seventeen species recorded were listed within the community description, and in group 4 this was the case for thirteen species from a total of twenty. As with the case for the groups described previously, the species not listed were generally, but not exclusively, recorded as occasionals, with low abundance values.

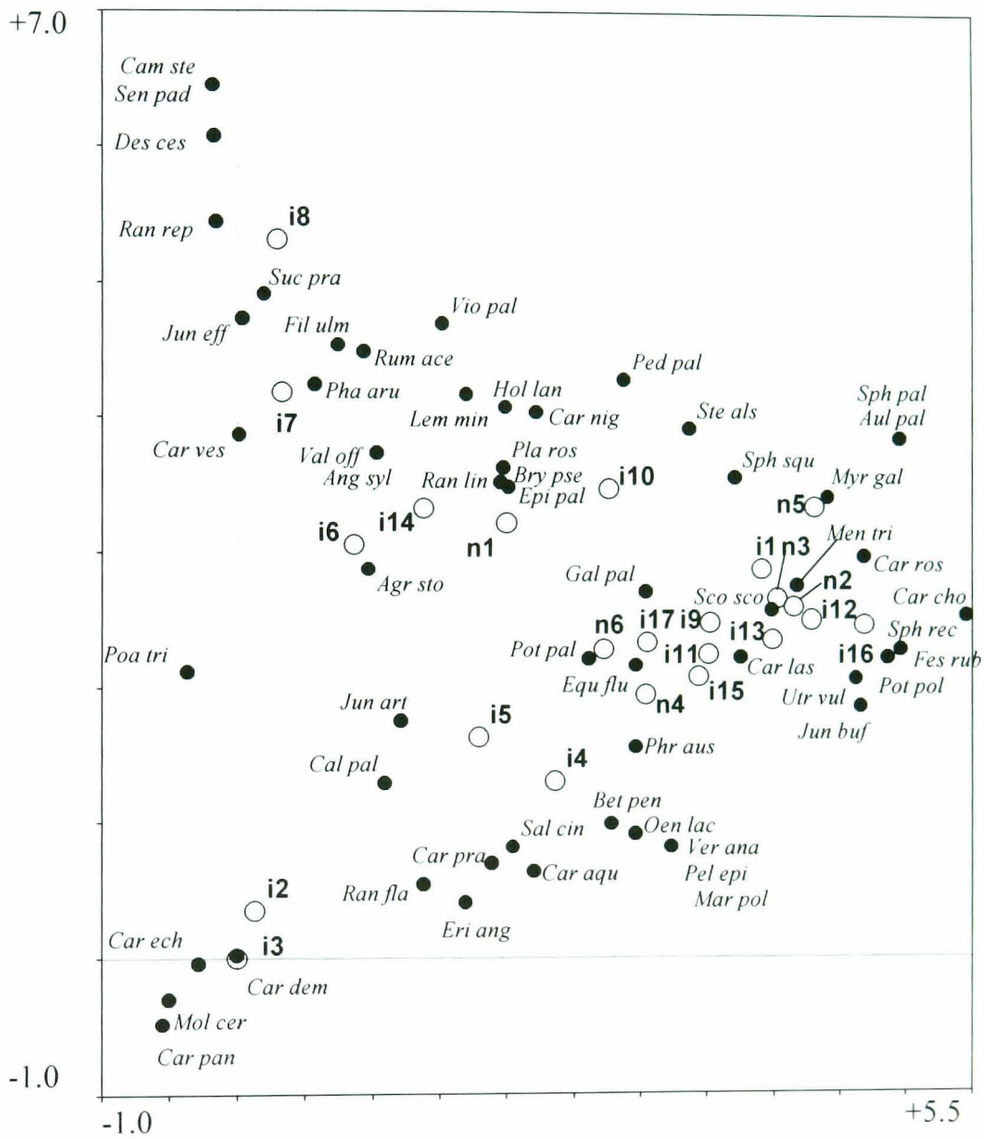


Figure 3.3.1 DCA ordination diagram of August 1998 vegetation data, showing positions of individual sample stations (i= Insh Marshes; n= Nether WhitlawMoss), and of representative species (six letter abbreviations represent species listed in Table 2.3.1). The gradients are 4.69 sd for axis 1, and 5.31 sd for axis 2; total inertia = 6.33, eigenvalues of axes 1-4 are 0.74, 0.46, 0.29, 0.17 respectively. Cumulative percentage variance of species data is 11.7 for axis 1, 7.3 for axis 2 (26.3 for all 4 axes).

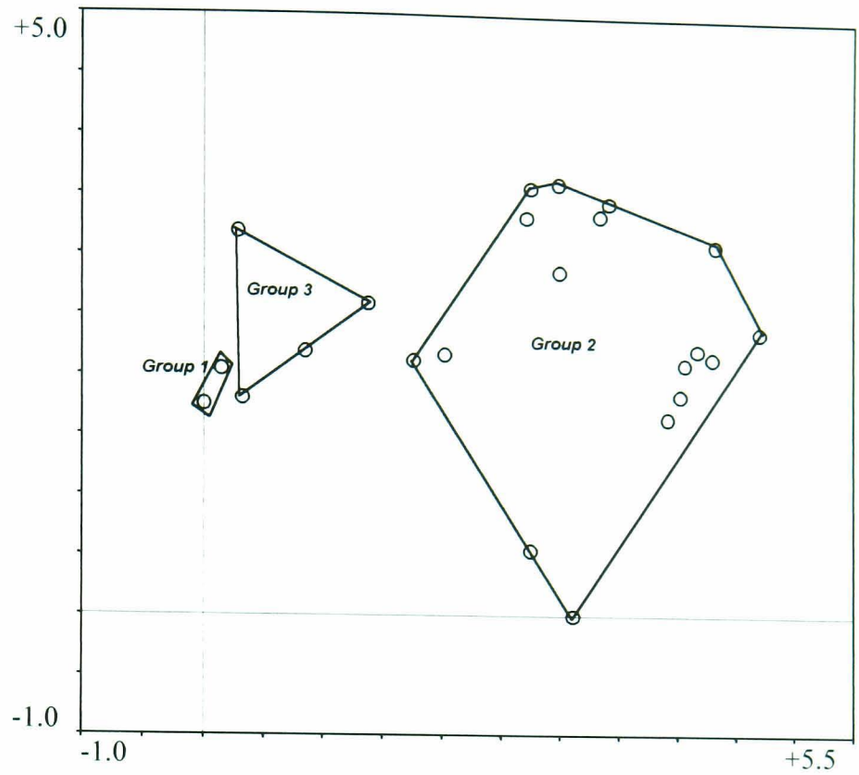


Figure 3.3.2 DCA ordination diagram of vegetation data for the 23 sites sampled in August 1998. The gradients are 4.69 sd for axis 1, and 5.31 sd for axis 2; total inertia = 6.33, eigenvalues of axes 1-4 are 0.74, 0.46, 0.29, 0.17 respectively. Cumulative percentage variance of species data is 11.7 for axis 1, 7.3 for axis 2 (26.3 for all 4 axes). TWINSPAN groups are shown. For site representation within groups see Table 3.3.1.

Table 3.3.1 Site representation within relative TWINSPAN groups for August 1998 vegetation data showing indicator species (dominant within group. If present within other groups, infrequent, and with lower pseudospecies score); I = Insh marshes; N = Nether Whitlaw moss.

TWINSPAN group	Membership	Dominant/indicator species
1 (n=2)	I: 2, 3	*Molinia caerulea*
2 (n= 16)	I: 1, 5, 9, 10, 11, 12, 13, 15, 16, 17, N: 1-6	*Carex rostrata* *Menyanthes trifoliata*
3 (n= 4)	I: 6, 7, 8, 14	*Filipendula ulmaria* *Deschampsia cespitosa*

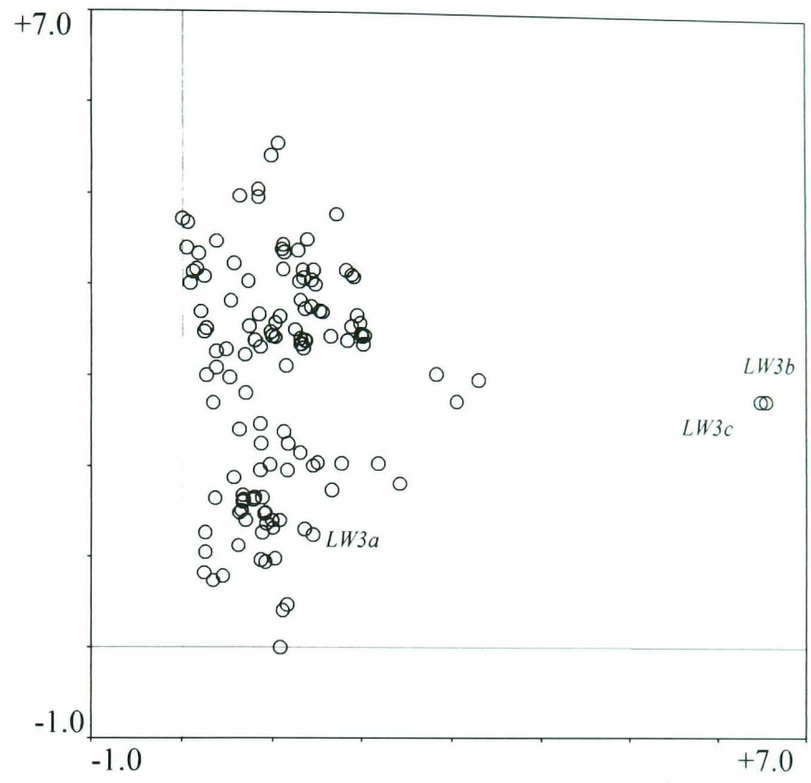


Figure 3.3.3 DCA ordination diagram of vegetation data for the 43 sites sampled in June, July and August 1999 (129 data points in total), showing the relative position of Lochwinnoch site no.3; a-c = June-August. The gradients are 6.59 sd for axis 1, and 5.55 sd for axis 2; total inertia = 11.00, eigenvalues of axes 1-4 are 0.83, 0.64, 0.50, 0.40 respectively. Cumulative percentage variance of species data is 7.5 for axis 1, 5.9 for axis 2 (21.5 for all 4 axes).

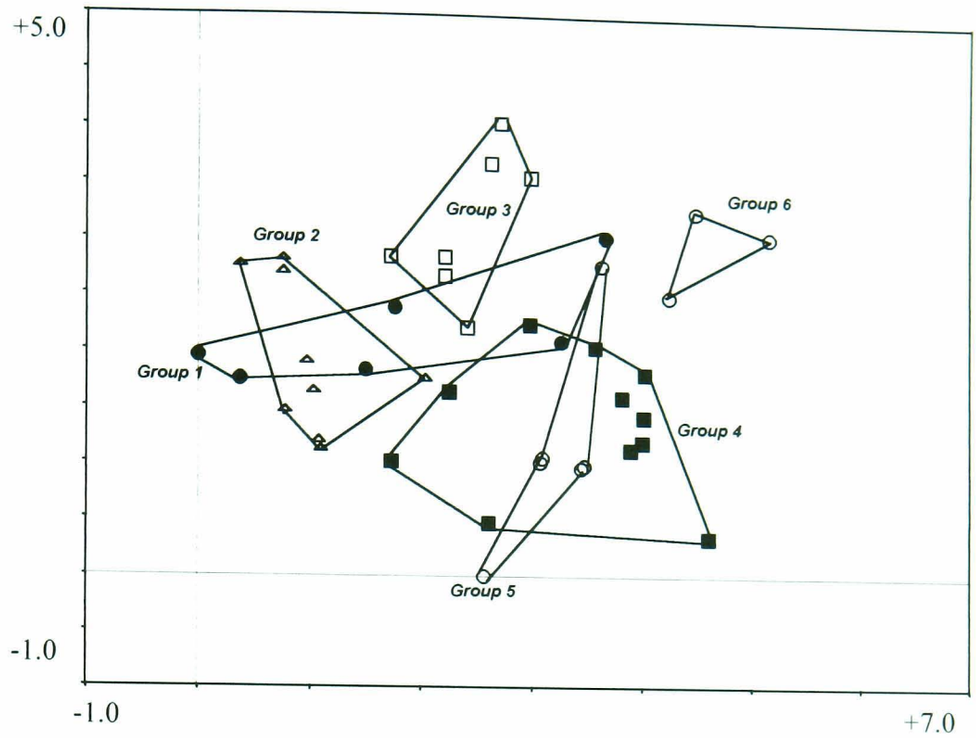


Figure 3.3.4 DCA ordination diagram of vegetation data for 42 sites sampled in June, July and August 1999 (Lochwinnoch site no.3 removed); The gradients are 5.15 sd for axis 1, and 4.04 sd for axis 2; total inertia = 7.91, eigenvalues of axes 1-4 are 0.67, 0.48, 0.36, 0.27 respectively. Cumulative percentage variance of species data is 8.6 for axis 1, 6.1 for axis 2 (22.8 for all 4 axes). TWINSPAN groups are shown. For site representation within groups see Table 3.3.2.

Table 3.3.2 Site representation within relative TWINSPAN groups for average 1999 vegetation data showing indicator species; G = Glen moss; I = Insh marshes; L = Lochwinnoch; N = Nether Whitlaw moss; T = Tarn moss.

TWINSPAN group	Membership	Dominant/indicator species
1 (n=6)	I: 7, 11 L: 1, 2, 4 N:1	*Carex lasiocarpa*
2 (n=9)	I: 4, 8, 9, 18, 19 L: 5, 6 T: 1, 2	*Galium palustre*
3 (n=7)	I: 1, 2, 3, 5, 6, 10, 14	*Carex panicea*
4 (n=11)	G: 1, 2, 3, 5, 6 I: 20, 21 N: 4, 5, 6 T: 3	*Carex rostrata*
5 (n= 6)	I: 12, 13, 15, 16 N: 2, 3	*Potamogeton polygonifolious*
6 (n=3)	G: 4 T: 4, 5	*Vaccinium oxycoccus* *Eriophorum angustifolium* *Calluna vulgaris* *Erica tetralix*

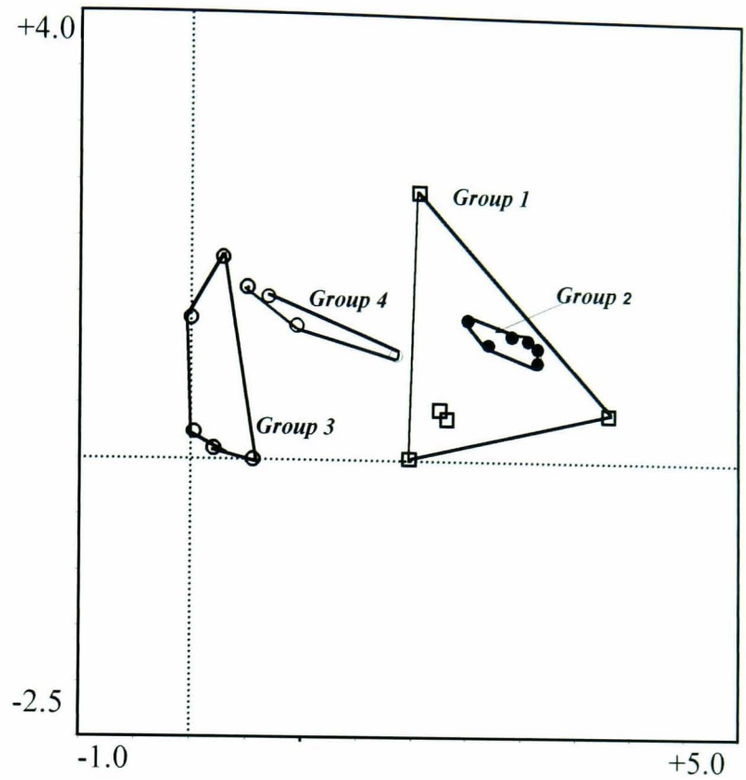


Figure 3.3.5 DCA ordination diagram of vegetation data for 20 sites sampled in May, June and August 2000. The gradients are 3.80 sd for axis 1, and 2.42 sd for axis 2; total inertia = 3.30, eigenvalues of axes 1-4 are 0.58, 0.32, 0.13, 0.06 respectively. Cumulative percentage variance of species data is 17.7 for axis 1, 9.5 for axis 2 (33.2 for all 4 axes). TWINSPAN groups are shown. For site representation within groups see Table 3.3.3.

Table 3.3.3 Site representation within relative TWINSPAN groups for average 2000 vegetation data showing indicator species; I = Insh marshes; W = Wood of Cree fen; E = Endrick marshes.

TWINSPAN group	Membership	Dominant/indicator species
1	I: 1, 3, 5, 6, 8	*Deschampsia cespitosa*
(n=5)		*Molinia caerulea*
2	W: 1-6	*Angelica sylvestris*
(n=6)		*Equisetum fluviatile*
		Hydrocotyle vulgaris
		Menyanthes trifoliata
3	I: 4, 7, 9	*Carex aquatilis*
(n=5)	E: 2, 3	
4	E: 1, 4, 5, 6	*Carex rostrata*
(n=4)		*Epilobium palustre*
		Equisetum fluviatile
		Galium palustre
		Phalaris arundinacea

Table 3.3.4 Floristic table showing the frequency (and abundance) of plant species occurring within the relative groups (G) delimited by TWINSPAN for August 1998 data. I = 0-20%; II = 21-41%; III = 41-60%; IV = 61-80%; V = 81-100%. (S)= sapling

	G1	G2	G3
	(n=2)	(n=17)	(n=4)
Equisetum fluviatile	I (16)	IV (8-100)	2 (12-36)
Potentilla palustris	I (8)	IV (4-76)	2 (16-36)
Galium palustre		III (4-80)	2 (4)
Carex rostrata		III (4-100)	
Menyanthes trifoliata		III (4-100)	
Sphagnum squarrosum		II (8-100)	
Agrostis stolonifera		II (4-64)	2 (80-100)
Cardamine pratensis	I (4)	II (4-24)	
Epilobium palustre		II (4-24)	I (4)
Carex lasiocarpa		II (4-100)	
Carex nigra		II (4-100)	2 (12-20)
Potamogeton polygonifolius		II (4-100)	
Ranunculus flammula	I (12)	I (8-52)	I (16)
Carex demissa	I (60)	I (8-48)	I (8)
Phragmites australis		I (84-100)	
Caltha palustris	I (4)	I (8-18)	2 (4-20)
Bryum pseudotriquetum		I (8-16)	
Plagiomnium rostratum		I (8-16)	
Oenanthe lachenalii		I (8-12)	
Ranunculus lingua		I (8-12)	
Lemna minor		I (8)	
Pellia epiphylla		I (8)	
Phalaris arundinacea		I (8)	I (16)
Filipendula ulmaria		I (72)	4 (8-80)
Succisa pratensis			3 (4-12)
Holcus lanatus		I (4-76)	2 (8-32)
Viola palustris		I (72)	2 (8-28)
Carex vesicaria	I (12)	I (4-8)	2 (60-100)
Rumex acetosa		I (4)	2 (4-8)
Juncus effusus			2 (20-32)
Deschampsia cespitosa			2 (20-100)
Ranunculus repens			2 (16-20)
Carex echinata	I (12)		I (8)
Achilea ptarmica			I (8)
Eriophorum angustifolium	2 (8-28)	I (4-92)	I (4)
Molinia caerulea	2 (100)		
Poa trivialis	I (8)		I (4)
Carex panicea	I (52)		
Campylium stellatum			I (4)
Valeriana officinalis			I (20)

Table 3.3.4 continued

	G1	G2	G3
Juncus articulatus		I (12)	I (12)
Angelica sylvestris			I (12)
Aulocomnium palustre		I (6-8)	
Betula pendula (S)		I (6-16)	
Carex chordorrhiza		I (6-100)	
Myrica gale		I (56)	
Salix cinerea (S)		I (4-8)	
Utricularia vulgaris		I (4-8)	
Juncus bufonius		I (4-16)	
Stellaria alsine		I (4-12)	
Festuca rubra		I (4)	
Marchantia polymorpha		I (4)	
Scorpidium scorpioides		I (4)	
Veronica anagallis-aquatica		I (4)	
Sphagnum palustre		I (32)	
Pedicularis palustris		I (20)	
Sphagnum recurvum		I (16)	
Carex aquatilis		I (12-100)	

Table 3.3.5 Floristic table showing the frequency of plant species occurring within the relative groups (G) delimited by TWINSPAN for mean 1999 data. I = 0-20%; II = 21-41%; III = 41-60%; IV = 61-80%; V = 81-100%. (S)= sapling.

	G1	G2	G3	G4	G5	G6
	(n=6)	(n=9)	(n=7)	(n=11)	(n=6)	(n=3)
Equisetum fluviatile	V (11-99)	V (1-49)	V (3-52)	II (3-49)	V (1-83)	
Angelica sylvestris	III (1-5)	II (4-24)	I (15)	I (4)		
Carex aquatilis	III (9-100)	IV (3-100)		I (83)		
Galium palustre	III (4-37)	IV (15-61)	IV (1-13)	II (1-12)	I (8)	
Potentilla palustris	I (5)	IV (8-67)	IV (5-35)	IV (1-100)	IV (5-37)	1 (3)
Potentilla erecta		IV (1-33)	V (1-24)	III (1-12)	IV (3-13)	
Carex nigra	II (4-8)	III (5-11)	V (3-95)	I (3)	IV (1-33)	
Caltha palustris	I (5)	II (1-8)	V (1-24)	I (1)		
Molinia caerulea		II (5-7)	V (8-87)	I (11)		2 (3-24)
Carex panicea		I (4)	V (8-44)	I (20)	II (1-7)	
Ranunculus lingua		I (39)	V (1-29)			
Eriophorum angustifolium			V (3-80)	III (1-92)	II (1-9)	3 (24-99)
Epilobium palustre	III (1-48)	II (4-28)	IV (1-9)	II (3-11)		
Cardamine pratensis	II (1-3)	I (12)	IV (1-12)			
Carex echinata			IV (4-31)	I (3-4)	I (5)	
Carex rostrata		II (3-99)	III (1-27)	V (11-100)	V (3-100)	1 (29)
Menyanthes trifoliata	III (7-93)	I (1)	I (25)	V (12-100)	V (5-100)	1 (72)
Potamogeton polygonifolius					V (11-83)	
Sphagnum palustre	I (95)			III (11-100)		2 (51-95)
Drosera rotundifolia				I (36)		2 (3)
Vaccinium oxycoccus				I (5)		2 (64-72)
Polytrichum commune			I (25)		III (15-27)	2 (11-13)
Dactylorhiza majalis		II (4-7)				2 (1-7)
Calluna vulgaris						2 (7-31)
Erica tetralix						2 (4-24)
Carex diandra			III (1-29)	II (11-15)		1 (3)
Juncus effusus		III (3-68)	I (11)	I (4-91)		1 (7)
Calypogeia muellerana			I (3)	I (3-8)		1 (7)
Phragmites australis	I (89)	I (3)	I (88)		I (100)	1 (67)
Juncus articulatus			I (1)			1 (3)
Andromeda polifolia						1 (27)
Erica cinerea						1 (17)
Sphagnum teres						1 (97)
Vaccinium myrtillus						1 (3)
Lysimachia vulgaris				II (3-24)		
Agrostis stolonifera	I (4)	I (3)	III (4-28)	I (7)		
Holcus lanatus		II (35-39)	II (15)	I (32)		
Festuca rubra		I (13)	II (3)	I (4)		
Salix cinerea (S)		I (1)	I (1)	I (1)		
Stellaria holostia		I (5)	I (4)	I (1)		
Pedicularis palustris			I (9)	I (4)	II (4)	
Sphagnum squarrosum			I (83)	I (25)		
Galium aparine		I (3)		I (1)	I (7)	
Carex lasiocarpa	III (13-95)			I (44)	I (49)	
Aulocomnium palustre	I (7)			I (1)		
Lemna minor	I (27)			I (31)		
Ranunculus flammula	I (12)			I (12)		
Utricularia vulgaris	I (11)			I (11)	III (19-29)	

Table 3.3.5 continued.

	G1	G2	G3	G4	G5	G6
Betula pendula (S)				I (3)		
Carex limosa				I (29-95)		
Hydrocotyle vulgaris				I (51)		
Lythrum salicaria				I (7)		
Oenanthe lachenalii				I (5-13)		
Poa trivialis				I (3)	III (16-27)	
Scorpidium scorpioides				I (96)		
Viola palustre		II (13-19)	III (5-33)			
Filipendula ulmaria	III (5-57)	I (40)	III (1-63)			
Knautia arvensis		II (3-4)	II (1-11)			
Valeriana officionalis	II (28-36)		II (3-15)			
Calliergon cuspidatum			II (1-3)			
Myrica gale			II (1-45)			
Phalaris arundinacea	II (20-37)	II (7-29)	I (3)			
Rumex acetosa		II (8-29)	I (11)			
Juncus bufonius		I (13)	I (1)		II (1-12)	
Sphagnum cuspidatum					II (20-28)	
Agrostis capillaris			I (3)			
Carex chordorrhiza			I (15)		I (100)	
Carex ovalis			I (3)			
Eurynchium praelongum			I (3)			
Fissidens adianthoides			I (3)			
Deschampsia cespitosa	I (8)	II (12-81)				
Ranunculus repens	I (29)	II (5-31)				
Juncus acutiflorus		II (12-100)				
Achillea ptarmica		I (5)				
Myosotis scorpioides		I (1)				
Polygala serpyllifolia		I (3)				
Pseudoscleropodium purum		I (5)				
Rhytidiadelphus squarrosus		I (7)				
Trifolium repens		I (8)				
Veronica officinalis		I (1)				
Cerastium fontanum		I (3)				
Iris pseudacorus	II (4-9)					
Carex vesicaria	I (99)					
Dryopteris dilatata	I (33)					
Lysimachia thyrsiflora	I (15)					
Sphagnum papillosum	I (8)					
Succisa pratensis	I (1)					
Typha latifolia	I (32)					

Table 3.3.6 Floristic table showing the frequency of plant species occurring within the relative groups delimited by TWINSPAN for mean 2000 data. I = 0-20%; II = 21-41%; III = 41-60%; IV = 61-80%; V = 81-100%. (S)= sapling.

	G1 (n=5)	G2 (n=6)	G3 (n=5)	G4 (n=4)
Galium palustre	V (3-25)	V (3-13)	IV (3-47)	4 (27-52)
Equisetum fluviatile	IV (1-12)	V (21-76)	V (4-13)	3 (57-100)
Caltha palustris	IV (3-25)	V (3-5)	III (4-33)	1 (8)
Carex nigra	V (12-95)	II (1)	III (4-5)	
Eriophorum angustifolium	IV (1-20)	III (4-12)		
Ranunculus flammula	IV (1-12)	IV (4-12)	I (37)	
Viola palustris	IV (5-23)	V (4-13)		
Cardamine pratensis	III (1-7)	III (1)	I (5)	1 (1)
Carex echinata	III (3-27)			
Carex panicea	III (1-19)	V (16-44)		
Filipendula ulmaria	III (5-65)	V (4-43)	I (23)	1 (1)
Molinia caerulea	III (3-25)	V (3-27)		
Potentilla palustris	III (15-29)	V (16-45)	II (8-31)	2 (4-32)
Agrostis stolonifera	I (3)	V (1-4)		
Angelica sylvestris		V (5-16)		4 (4-16)
Carum verticillatum		V (7-23)		
Hydrocotyle vulgaris		V (21-59)		
Mentha aquatica		V (8-21)		1 (33)
Menyanthes trifoliata		V (29-75)		1 (67)
Succisa pratensis		V (3-13)		
Sphagnum papillosum	III (1-8)	IV (5-19)		
Achillea ptarmica	II (1)	IV (3-8)		
Juncus acutiflorus		IV (4-29)		
Potamogeton polygonifolius		IV (3-23)		
Carex aquatilis			V (27-100)	
Epilobium palustre		III (1)	III (1-9)	4 (8-33)
Phalaris arundinacea	II (3-33)	III (1-43)	IV (3-35)	3 (47-100)
Lysimachia thyrsiflora			I (1)	3 (13-23)
Carex rostrata	I (40)	III (1-13)		3 (40-69)
Oenanthe lachenalii				3 (1-4)
Carex vesicaria			III (3-75)	3 (33-49)
Valeriana officinalis	I (3)	III (1)		1 (1)
Epilobium hirsutum				1 (3)
Typha latifolia				1 (16)
Myosotis scorpiodes			I (9)	1 (3)
Lemna minor				1 (27)
Ranunculus repens	II (8-12)		II (1-24)	
Juncus effusus	II (1-44)		I (5)	
Festuca rubra	I (13)		I (8)	
Carex diandra	I (5)	II (11-16)		
Carex lasiocarpa		II (12-33)		
Lythrum salicaria		II (1-3)		
Myrica gale	I (13)	I (21)		
Eleocharis palustris		I (1)		
Holcus lanatus		I (1)		
Lycopus europaeus		I (1)		
Veronica officinalis		I (1)		
Deschampsia cespitosa	III (19-87)			

Table 3.3.6 continued

	G1	G2	G3	G4
Juncus bufonious	I (1)			
Lychnis flos-cuculi	I (5)			
Phragmites australis	I (65)			
Rumex acetosa	I (1)			
Salix cinerea (S)	I (1)			

Table 3.3.7 Summary of National Vegetation Classes designated for defined TWINSPAN groups for (a) August 1998 vegetation data; (b) mean 1999 vegetation data; (c) mean 2000 vegetation data.†Coefficient range 0-100; higher coefficient score = closer match

(a)

Group	Community		MATCH Coefficient†	Sub-community	MATCH Coefficient†	Number of Samples in NVC description
1	M9	*Carex rostrata-Calliergon cuspidatum/giganteum* Mire	34.7	-	-	40
2	S27	*Carex rostrata-Potentilla palustris* Tall-herb fen	51.2	S27a	55.7	197
3	M27	*Filipendula ulmaria-Angelica sylvestris* Mire	49.5	-	-	88

(b)

Group	Community		MATCH Coefficient†	Sub-community	MATCH Coefficient†	Number of Samples in NVC description
1	S27	*Carex rostrata-Potentilla palustris* Tall-herb fen	47.3	S27a	49.1	197
2	M23	*Juncus effusus/acutiflorus-Galium palustre* Rush-pasture	50.2	M23b	50.3	62
3	M9	*Carex rostrata-Calliergon cuspidatum/giganteum* Mire	50.2	M9b	52.5	24
4	S27	*Carex rostrata-Potentilla palustris* Tall-herb fen	50.1	S27a	50.5	197
5	S9	*Carex rostrata* Swamp	45.3	S9b	53.2	31
6	M2	*Sphagnum cuspidatum/recurvum* Bog pool community	50.0	-	-	14

(c)

Group	Community		MATCH Coefficient†	Sub-community	MATCH Coefficient†	Number of Samples in NVC description
1	M5	*Carex rostrata-Sphagnum squarrosum* Mire	45.0	-	-	22
2	S27	*Carex rostrata-Potentilla palustris* Tall-herb fen	49.4	S27a	50.4	197
3	S11	*Carex vesicaria* Swamp	58.7	-	-	18
4	S11	*Carex vesicaria* Swamp	53.8	-	-	18

3.3.2. Temporal and spatial comparatibility between groups and their assigned communities

3.3.2.1. A classification of the three year combined data

A DCA ordination of the combined average vegetation data for 1998, 1999 and 2000 which includes repeat sites is presented in Figure 3.3.6. A gradient length of 4.92 s.d. along axis 1 represents a complete turnover of species. Axis 2 is also relatively long at 3.86 s.d.. Figure 3.3.6a, represents a good mix of sites studied throughout the three years. The 1999 data, with the largest number of samples represents the greatest spread across the ordination space. A TWINSPAN classification of the vegetation data for the three years combined produced nine main groups (Figure 3.3.6; Table 3.3.8) which contained n=5 to n=14 samples. Some of these groups could be clearly defined within the ordination space (Figure 3.3.6b). With group 3, domianted by *Juncus effusus* and *Rumex acetosa*, and group 9, dominated by *Erica tetralix* and *Sphagnum palustre* separated along the first axis a potential gradient relating to mode of groundwater input and pH is inferred. The separation of group 3 from group 1, dominated by *Carex aquatilis* and *Cardamine pratensis* along the second axis suggest a groundwater depth gradient. Specific variations between defined groups, and in relation to specific gradients are investigated further in section 3.3.3 and Chapter 4.

Group 2 was most closely matched to a S11 *Carex vesicaria* swamp community, and group 1 to a S11c with a *Carex rostrata* sub-community. The coefficients were 52.4 and 51.4 respectively. Group 3 had a highest match (50.8) to a M23b *Juncus effusus/acutiflorus-Galium palustre* rush meadow with a *Juncus effusus* sub-community. Groups 4 had a highest match (55.3) to a M9 *Carex rostrata-Calliergon cuspidatum/gigantium* mire, and group 5 to a M9b with a *Carex diandra-Calliergon giganteum* sub-community, with a coefficient of 55.9. Group 6 had a highest match (54.5) to a S9b *Carex rostrata* swamp with a *Menyanthes trifoliata-Equisetum fluviatile* sub-community, and group 7 to a M9 community, with a coefficient of 46.6. Group 9 had a highest match (46.2) to a S27 *Carex rostrata-Potentilla palustris* tall-herb fen, and group 8 to a S27a with a *Carex rostrata-Equisetum fluviatile* sub-community, with a coefficient of 50.7.

Whilst all of the groups were not classified as unique community types relative to each other, a good degree of variation was seen between them, with differing indicator species identified (Table 3.3.8). Where the same community type was assigned, differences in sub-community types were generally identified between groups (Table 3.3.9). Where they were not, for example with the M9 classification of groups 4 and 7, variation within the community types, or new sub-communities may not have prevously been described, due to small sample

numbers (Table 3.3.9). In addition, some community types which had been assigned to groups for individual years, such as an M5 (Table 3.3.7c), were not then assigned to any groups for the total combined data. This may be explained by the low coefficients, whereby individual samples may be assigned equally to different communities, depending on the samples they are combined with. This in turn could be a function of the low sample numbers mentioned previously.

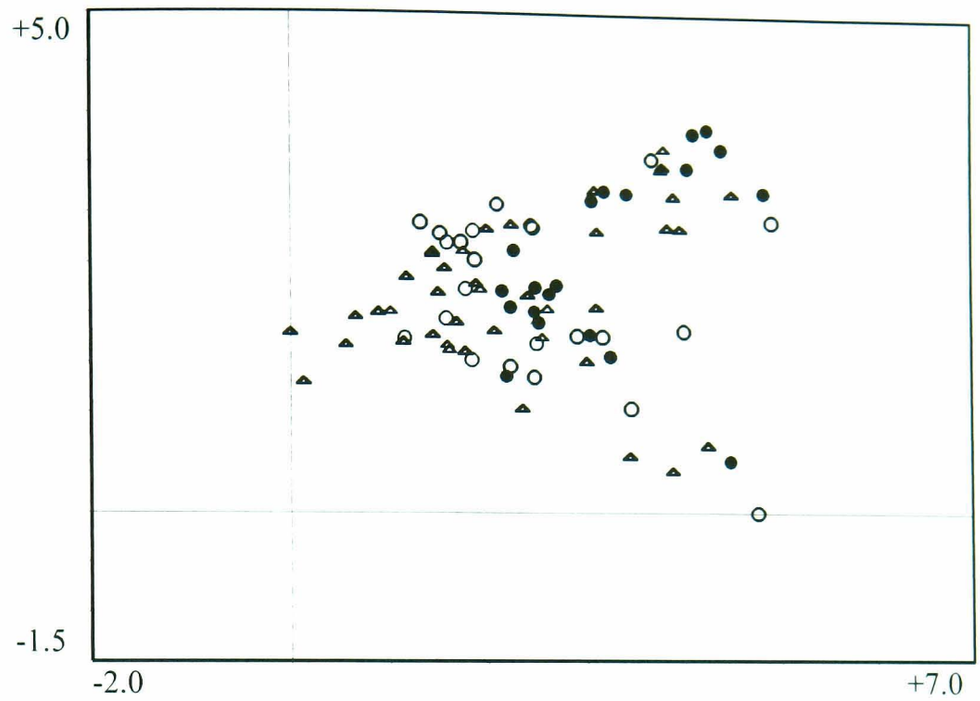
3.3.2.2. Consistency within repeat sample stations

The majority of sites sampled during the course of the study were consistently reclassified within the same TWINSPAN groups. Eight sites, Insh Marshes (IM) 1, 2, 3, 11, 12, 14 and Nether Whitlaw (NW) 4 and 6, were not consistently re-classified (Table 3.3.8). Of these sites, only IM 1 and 3 were sampled during each of the three years and were consistently reclassified during 1999 and 2000, where yearly average data was used. This suggests that yearly averaged data better took into account changes over the growing season. IM 2 saw a shift from an M9 classification in 1998 to an S27 in 1999, and most notably a reduction in the cover of *Molinia caerulea* recorded, and also a reduction in *Carex rostrata* (Appendix 3a and b). The classification for IM 11 saw a shift in the opposite direction, from a S27 to an M9. This was characterised by a reduction in the recorded abundance of a number of species, including *Carex lasiocarpa, Equisetum fluviatile, Menyanthes trifoliata* and *Phragmites australis* (Appendix 3a and b). Changes in floristic composition over the year, and hence comparisons of single point data and yearly average data may once again have been linked to this apparent shift in community type. At IM 12 there was an apparent shift from a S9b to a M9 community. As Rodwell (1995) states however, the former of these two communities often fronts the latter, and the two can grade into one another. Each of stations IM 14 and NW 4 and 6 were placed into different groupings during 1998 and 1999, but these groupings were classified into the same broader community classifications (M9 and S27 respectively). Some differences which may help explain this situation are apparent, such as the lower abundance of *Agrostis stolonifera* at station IM 14 during 1999.

The variability of these sites, but also of a number of others are represented in Figures 3.3.7 and 3.3.8. However, a number of sites which were placed into the same groups (Figure 3.3.6; Table 3.3.8) have a relatively high degree of variation (>0.5 s.d.) within the ordination space. With the exception of station 14, the greatest degree of variation was amongst stations along transect 1 at Insh Marshes. Some variation may be attributable to the use of single point data and average yearly data over successive seasons, it should also be noted that transect 1 stations were subject to the greatest degree of drawdown over successive years, of any of the stations surveyed (see Section 2.3.3). However, on balance, the species

compositions of only two of the stations (IM 5 and 8) varied noticeably (>0.5 s.d.) between the second and the third years of the study (Figure 3.3.8). Meanwhile, the drop in average water table levels was far more pronounced between the same two years (Figure 2.3.3, Chapter 2). Despite potential concerns relating to the comparability of the 1998 vegetation data to that from subsequent years, DCA axis 1 site scores for 1998 were highly correlated to DCA axis 1 sites scores for 1999 ($r = 0.942$). Axis 2 site scores for 1998 and 1999 were also highly correlated ($r = 0.950$) for repeat sample stations (Table 3.3.10). Correlations between axis site scores were also highly significant for stations surveyed over three years along transect 1 (Table 3.3.11). Correlations ranged from $r = 0.879$ between axis 2 1998 and 1999 site scores, and $r = 0.989$ between axis 2 1999 and 2000 site scores.

(a)



(b)

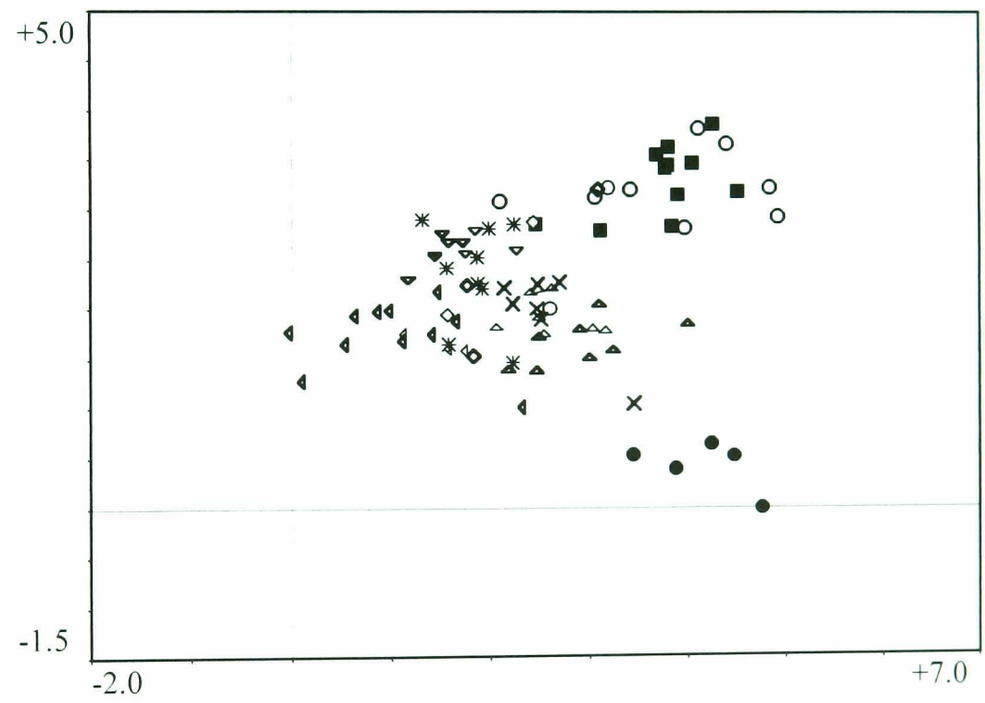


Figure 3.3.6 DCA ordination diagram of combined average 1998, 1999 and 2000 vegetation data The gradients are 4.92 sd for axis 1, and 3.86 sd for axis 2; total inertia = 8.14, eigenvalues of axes 1-4 are 0.57, 0.43, 0.35, 0.31 respectively. Cumulative percentage variance of species data is 7.0 for axis 1, 5.3 for axis 2 (20.3 for all 4 axes). (a) Three years outlined. Open circle = 1998; open triangle = 1999; closed circle = 2000. (b) Defined TWINSPAN groups. Black square = Group 1; open circle = Group2; closed circle = group 3; upwards triangle = group 4; X = Group 5; downwards triangle = group 6; star = group 7; diamond = group 8; left-hand triangle = group 9.

Table 3.3.8 Site representation within relative TWINSPAN groups for average 1998, 1999 and 2000 vegetation data showing indicator species; E = Endrick marsh; G = Glen moss; I = Insh marshes; L = Lochwinnoch; N = Nether Whitlaw moss; T = Tarn moss; W = Wood of Cree fen

TWINSPAN group	Membership			Dominant/indicator species
	1998	1999	2000	
1 (n=11)	I: 4, 9, 17	I: 4, 9, 19 L: 2, 4, 5, 6	I: 4, 9	*Carex aquatilis* *Cardamine pratensis*
2 (n=10)	I: 1*, 7	I: 7 T: 1	E: 1, 2, 3, 4, 5 I:7	*Phalaris arundinacea*
3 (n=5)	I: 8	I: 8, 18 T: 2	I: 8	*Juncus effusus* *Rumex acetosa*
4 (n=15)	I: 2*, 5, 6, 10 N: 1	I: 1*, 5, 6, 10, 14* N: 1	I: 1*, 3*, 5, 6	*Carex nigra*
5 (n= 7)	I: 14*		W: 1-6	*Angelica sylvestris* *Hydrocotyle vulgaris* *Succisa pratensis*
6 (n=9)	I: 12*, 13 N: 2, 3	G: 2 I: 13 N: 2, 3	E: 6	*Carex rostrata* *Equisetum fluviatile*
7 (n=9)	I: 3*, 15, 16	G: 1 I: 11*, 12*, 15, 16, 20		*Carex echinata* *Potentilla erecta* *Potentilla palustris*
8 (n=5)	I: 11* N: 4*, 6*	I: 21		*Carex lasiocarpa* *Galium palustre*
9 (n=14)	N: 5	G: 3, 4, 5, 6 I: 2*, 3* L: 1 N: 4*, 5, 6* T: 3, 4, 5		*Erica tetralix* *Sphagnum palustre*

Table 3.3.9 Summary of National Vegetation Classes designated for defined TWINSPAN groups for average 1998, 1999 and 2000 data combined. †Coefficient range 0-100; higher coefficient score = closer match

(a)

Group	Community		MATCH Coefficient†	Sub-community	MATCH Coefficient†	Number of Samples in NVC description
1	S11	*Carex vesicaria* Swamp	46.0	S11c	51.4	4
2	S11	*Carex vesicaria* Swamp	52.4	-	-	18
3	M23	*Juncus effusus/acutiflorus-Galium palustre* Rush meadow	49.9	M23b	50.8	62
4	M9	*Carex rostrata-Calliergon cuspidatum/gigantium* Mire	55.3	-	-	40
5	M9	*Carex rostrata-Calliergon cuspidatum/gigantium* Mire	53.0	M9b	55.9	24
6	S9	*Carex rostrata* Swamp	50.8	S9b	54.5	31
7	M9	*Carex rostrata-Caliergon cuspidatum/gigantium* Mire	46.6	-	-	40
8	S27	*Carex rostrata-Potentilla palustris* Tall-herb fen	50.1	S27a	50.7	197
9	S27	*Carex rostrata-Potentilla palustris* Tall-herb fen	46.2	-	-	220

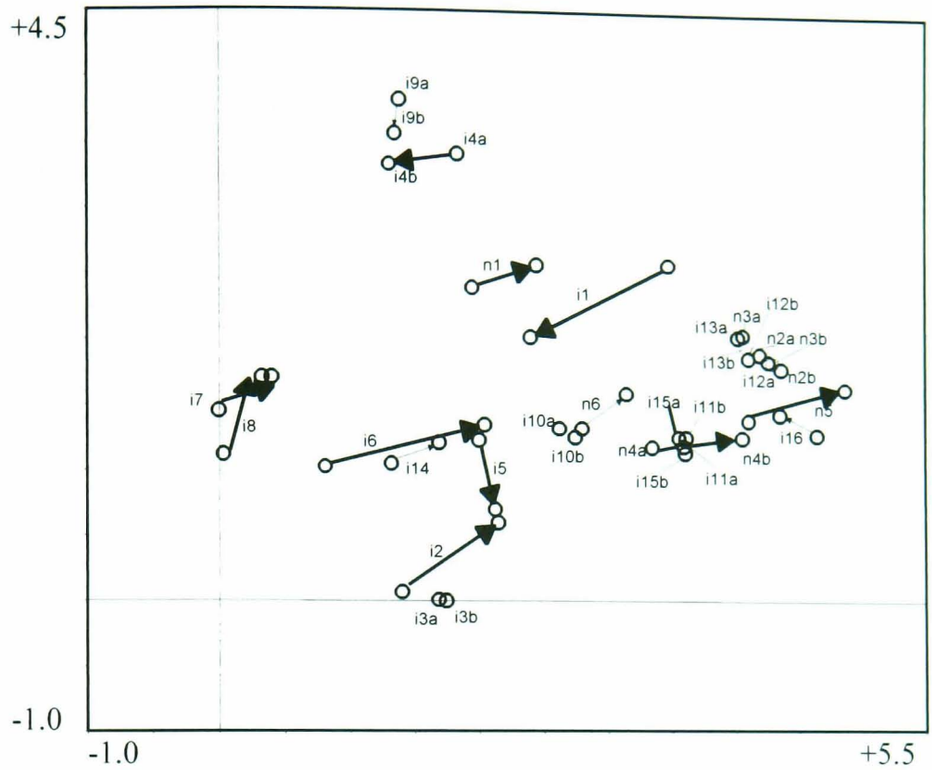


Figure 3.3.7 DCA ordination diagram of vegetation data for Insh Marshes transect 1 and 2, and Nether Whitlaw 1998 and 1999 vegetation data. The gradients are 4.90 sd for axis 1, and 3.83 sd for axis 2; total inertia = 6.50, eigenvalues of axes 1-4 are 0.69, 0.47, 0.32, 0.21 respectively. Cumulative percentage variance of species data is 10.7 for axis 1, 7.1 for axis 2 (26.0 for all 4 axes). Direction of vectors represents differences between years; vectors in bold represent a movement $\geq$ 0.5 s.d. in the ordination space.

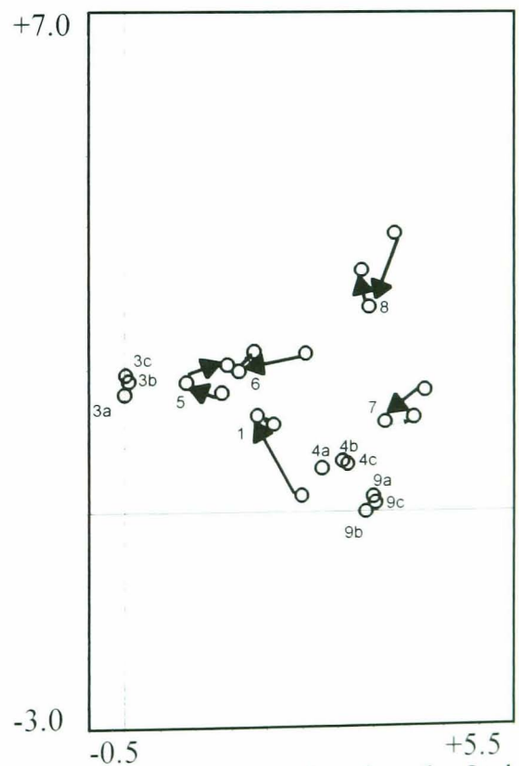


Figure 3.3.8 DCA ordination diagram of vegetation data for Insh Marshes transect 1 1998, 1999 and 2000 vegetation data. The gradients are 4.22 sd for axis 1, and 3.89 sd for axis 2; total inertia = 3.85, eigenvalues of axes 1-4 are 0.67, 0.48, 0.24, 0.10 respectively. Cumulative percentage variance of species data is 17.3 for axis 1, 12.5 for axis 2 (38.8 for all 4 axes). See Figure 3.3.7 for further explanations.

Table 3.3.10 Correlation (r) between DCA axes 1 and 2 scores for 1998 and 1999 resampled sites (df=20). ** $P<0.01$

	Axis 1, 1998	Axis 2, 1998
Axis 1, 1999	0.942**	
Axis 2, 1999		0.950**

Table 3.3.11 Correlation (r) between DCA axes 1 and 2 scores for 1998, 1999 and 2000 resampled sites (df=6). (a) 1998 and 1999, (b) 1999 and 2000, (c) 1998 and 2000.
** $P<0.01$

(a)

	Axis 1, 1998	Axis 2, 1998
Axis 1, 1999	0.956**	
Axis 2, 1999		0.879**

(b)

	Axis 1, 1999	Axis 2, 1999
Axis 1, 2000	0.986**	
Axis 2, 2000		0.989**

(c)

	Axis 1, 1998	Axis 2, 1998
Axis 1, 2000	0.967**	
Axis 2, 2000		0.927**

3.3.3. Multivariate modelling: group characteristics

3.3.3.1. August 1998 data

A number of environmental and site variables, and vegetation variables were measured during 1998 (Tables 3.2.1-3.2.3). Due to inconsistencies in sampling over the season, formal analyses were carried out on only the final August data set.

Environmental and site variables

Groundwater level relative to ground surface was the only environmental variable found to vary significantly (p=0.04) between the three defined TWINSPAN groups for August 1998, following comparison of non-parametric variables by Mann-Whitney confidence tests (Table 3.3.12). Average water table level was highest within group 2 (S27a community: see Table 3.3.7) sample stations, and values were significantly higher than those for group 3 (M27), and group 1 (M9) was intermediate. Whilst not statistically significant, overall, the level of water table fluctuation was highest within the stations comprising group 3 (M27), as were Fe

and Mn concentrations. Conductivity however was lowest within group 3, and highest within group 2 (S27a).

A one way analysis of variance was conducted upon the remaining environmental variable values (Table 3.3.12b), but all results were non significant. Certain trends were obvious however, with Mg, Ca, K, and Na all being highest within group 2 stations.

Vegetation variables

The majority of collective vegetation variables and dominant population traits measured during August 1999 were non-significant between defined TWINSPAN groups when subjected to appropriate tests (Tables 3.3.13 and 3.3.14). Stem density was the only variable to differ significantly between groups (p= 0.04). Stem density was significantly higher within group 3 (M27) stations than within group 2 (S27a), whilst group 1 (M9) was intermediate. Mean canopy height was greatest within group 3, as was litter cover, and total standing crop (combined necromass and biomass).

None of the measured traits for the various dominant populations differed significantly between groups, but once again, certain trends could be seen. The mean height of the individual ramets of the dominant populations was highest within group 3 (M27), although these values were highly variable (Table 3.3.14). Values for leaf area and total length per ramet were highest amongst the dominant populations of group 2 (S27a), as were the leaf dry weights, stem dry weights, and total ramet dry weights. The average dry weight of reproductive structures, and of constituent seeds were highest however in group 3 (M27). Specific Leaf Area was lowest within group 2 (S27a).

3.3.3.2. Mean 1999 data

Environmental and site variables

Normally distributed data were tested using a one way analysis of variance (Figure 3.3.9; Table 3.3.15a), and non-parametric data which could not be normalised by transformation by Kruskal-Wallace tests (3.3.15b). Due to the small sample size, group 6 (M2) was excluded from formal Kruskal-Wallace tests, but the values for this group, along with those for the single Lochwinnoch station 3 (L3: labelled here as Group 7), are included for comparative purposes.

Results of a one-way analysis of variance for the six TWINSPAN groups defined for the 1999 data show significant differences between the mean relative group values for shade

index (p= 0.002) and average level of groundwater fluctuation (p= 0.033) (Figure 3.3.9). For shade, group 4 (S27a) sites were significantly higher than groups 2 (M23b), 3 (M9b) and 5 (S9b). Groups 1 (S27a) and 6 (M2) were intermediate. The single station group 7 had the highest level of shade overall. While average water table level was shown to differ significantly between groups by a one-way analysis of variance, no mean separation was detected by a Tukey test (even where an analysis of variance has rejected a null hypothesis, multiple comparison means separation tests may sometimes yield results which do not indicate a difference between any of the group means. This is due to the fact that analysis of variance is a more powerful test, and therefore Type II errors are more likely to occur in post-hoc multiple comparisons, especially where small sample sizes are involved (Zar, 1999)). A general inference however can be made, whereby the generally drier sites of group 2 (M23b) exhibit the highest levels of groundwater fluctuation, while the overall wetter sites of group 5 (S9b) exhibit lower levels of fluctuation. Bare ground was highest on average in group 5 (S9b), and the hydrosoil redox most anoxic within this same group. Hydrosoil redox conditions indicative of the most oxidising status were found within group 2 (M23b). Of the non-parametric environmental variables measured, groundwater parameters exhibiting significant differences between groups were average water table level (p=0.01), and average minimum (p=0.009), and maximum (p=0.044) water table levels (Table3.3.15b). Group 5 (S9b) sites were significantly wetter than groups 2 (M23b) and 3 (M9b) with an average standing water table level of c.11cm, and continual levels of above-ground inundation.

The average level of groundwater magnesium (Mg) differed significantly between groups (p=0.025), with the highest levels measured in the sites comprising group 5 (S9b), which differ significantly from those of group 4 (S27a). The levels of Mg were lowest in group 6 (M2) samples. Other variables which differed significantly between groups were Mn (p= 0.05) and NO_3 (p= 0.01). For those groups which were formally analysed, the levels of both these nutrients were lowest in group 4 (S27a). NO_3^- was significantly higher in groups 1 (S27a) and 3 (M9b), whilst Mn was significantly higher in groups 1 (S27a), 2 (M23b) and 3 (M9b). No further significant variation was identified between group environmental variables. However, pH values were lowest within group 6 (M2), and highest in group 1 (S27a). Values for both conductivity, and Ca were lowest (amongst the groups formally analysed) within group 3 (M9b) and were highest within group 2 (M23b). Notably, for groups 6 (M2) and 7, not formally analysed, Ca values were amongst the lowest and highest respectively. Cl and K were also recorded at relatively high levels for the sample in group 7, and SO_4^{2-} was highest within this sample, and in group 6 also. Overall, Cl was highest in group 5 (S9b), and lowest in group 3 (M9b).

Vegetation variables

Species richness (S) varied significantly (p= 0.036) between groups (Figure 3.3.10). At an average of around 11.5, the species richness of group 3 (M9b) was significantly higher than both groups 4 (S9b) and 5 (M2) for the equivalent unit area, and other groups were intermediate. Group 7 had the lowest species richness overall, at 3 per m^2. Stem density (p<0.001), nearest neighbour (p<0.001), canopy height overall (p<0.001), number of reproductive structures (p= 0.008), stem diameter (p= 0.003), biomass between 10-20cm above ground level (p= 0.011), necromass above 20cm above ground level (p= 0.016), standing crop between 10-20cm above ground level (p= 0.014) were other collective vegetation variables which differed significantly between groups (Figure 3.3.10). Stem density was lowest amongst groups 4 (S27a), 5 (S9b) and 6 (M2), and was significantly higer within group 3 (M9b). A reverse pattern was observed for nearest neighbour index, with group 2 significantly lower than groups 4, 5 and 6. Average canopy height was significantly higher (c.70 cm) for group 1 (S27a) than for groups 3-6 (M9b, S27a, S9b, and M2 respectively). Canopy height for group 2 (M23b) was also significantly higher than groups 3, 4 and 6. Number of reproductive structures (m^{-2}) was significantly higher for group 3 (M9b) than for group 4 (27a), and all other groups were intermediate. Significantly larger stems were recorded for groups 1 and 4 (both S27a), than for group 3 (M9b), and all other groups were intermediate. The various biomass and necromass values observed per group tended to follow a similar pattern to each other, with the highest dry weights being observed for group 1 (S27a), and gradually decreasing through to the lowest values for group 6 (M2). This general pattern did vary slightly between the specific variables measured, and levels of significance between specific groups also varied (see Figure 3.3.10). Whilst the pattern held true for total dry biomass per m^2, no means separation was obtained following a Tukey test (Figure 3.3.10h). Total standing crop (m^{-2}) at 0 cm to 10 cm above ground level followed this same general pattern, although differences between mean values were not significant (Table 3.3.16a). Mean values for overall percentage litter cover, biomass between ground level and 10 cm above, necromass between 10 and 20 cm above ground level, and necromass at greater than 20 cm above ground level all showed no significant variation between groups. For all of the values for the single sample constituting group 7, levels were either higher or lower than all others, with the exception of ground level to 10 cm biomass. Patterns of variation for non-parametric biomass and necromass variables were similar. Biomass values higher than 20 cm above ground level were significantly higher (p=0.001) for group 1 (S27a), than for all other groups (Table 3.3.16b). Group 2 (M23b) values were also significantly greater than group 3 (M9b), 4 (S27a) and 5 (S9b) values. Values for group 5 were in turn significantly greater than those for groups 3 and 4. An equivalent pattern was observed for standing crop values at the same strata, and were similar for the total standing

crop (Table 3.3.16b). Once again, all values for the single group 7 sample were much higher than all others.

In addition to collective vegetation variables, a number of average dominant population trait values were observed to vary significantly between groups (Figure 3.3.11). The number of leaves observed per ramet was significantly higher (p= 0.031) for group 2 (M23b) than for group 3 (M9b), and values for all other groups were intermediate. Canopy area for the dominant populations was significantly higher (p<0.001) for group 1 (S27a) than for groups 3-6 (M9b, S27a, S9b, and M2 respectively). Group 2 (M23b) values were in turn significantly greater than those for groups 3-6. Values for group 1 (S27a) were also highest for average total leaf area per ramet (p= 0.004), average total leaf length per ramet (p= 0.003), average stem weight per ramet (p= 0.017), and total average leaf weight per ramet (p= 0.016). Values were significantly higher in this group for all of these variables than for group 3 (M9b), and were also significantly greater than the values for group 5 (S9b) for leaf length (Figure 3.3.11). Total ramet dry weight was significantly higher (p= 0.045) amongst group 4 (S27a) dominant populations, than for group 3 (M9b), with the values for other variables being intermediate (Figure 3.3.11i). The opposite trend was observed for Specific Leaf Area (Figure 3.3.11j), with significantly thinner leaves (p= 0.024) amongst the dominant populations of group 3 (M9b), and thicker leaves amongst group 4 (S27a) populations. Average weight of reproductive structures per ramet of the dominant populations was significantly higher (p= 0.004) within groups 2 (M23b) and 4 (S27a) than in group 3 (M9b), and all other groups were intermediate. Whilst number of reproductive structures per ramet was found to vary significantly between groups (p= 0.036), no group mean separation was detected by a Tukey test (Figure 3.3.11c). Average ramet height did not vary significantly between groups (Table 3.3.17). Tallest plants amongst groups 1-6 however were observed for group 1 (S27a), and shortest for group 5 (S9b). The tallest plants were observed in the single sample for group 7. Greatest seed weight (g per individual) was within group 2 (M23b), and lowest within group 3 (M9b) (for groups 1-5, included within a Kruskal-Wallace test: Table 3.3.17).

3.3.3.3. Mean 2000 data

Environmental and site variables

From the variables measured during 2000 whose values were normally distributed, average groundwater level relative to the ground surface was significantly lower (p= 0.028) for group 1 (M5) than for group 2 (S27a). All stations however were subject to water table levels just below ground surface on average during the growing season (Figure 3.3.12a). Average

minimum groundwater levels over the growing season also differed significantly (p= 0.025) between groups, following the same pattern. Groups 2 (S27a), 3 (S11) and 4 (S11) were all subject to some inundation over the growing season (Figure 3.3.12a), as shown by the maximum groundwater levels relative to the ground surface. Whilst the values for these three groups did not significantly differ from one another, the values for group 2 (S27a) were significantly higher (p= 0.021) than those for group 1 (M5). Group 1 had generally waterlogged soils, with the water level approximately 5 cm below the surface on average, and no inundation recorded.

A number of additional variables whose values exhibited a normal distribution were found not to differ significantly between groups (Table 3.3.18a). In contrast to samples from 1998 (Section 3.3.2) all group hydrosoil redox values were positive. Percentage of bare ground was relatively low amongst all groups, and both conductivity and SO_4^{2-} were highest within group 4 (S11). The wettest group, 2 (S27a), also had the greatest average level of groundwater fluctuation.

A further nine environmental variables were measured, whose values were not normally distributed (Table 3.3.18b). Due to relatively small sample sizes, Mann-Whitney confidence tests were conducted between each group in turn. Three of the variables, Mn, Na and NO_3^- were found not to differ significantly between groups, and no extreme values were measured between groups. An average pH of 5.5 within group 2 (S27a) was significantly lower (p= 0.02) than in the other three groups, all of which were circumneutral. Fe levels were significantly higher (p= 0.037) within group 4 (S11) than in group 1 (M5), and groups 2 (S27a) and 3 (S11) were intermediate. Mg (p= 0.02) and Ca (p= 0.037) levels were also highest in group 4 (S11), and significantly higher than all other other groups. P was also highest in group 4 (S11), but significantly higher (p= 0.011) than group 2 (S27a) alone, with groups 1 (M5) and 3 (S11) being intermediate. This overall pattern did not follow for Cl however, with the median value for group 2 (S27a: 41.77 mg l^{-1}) being more than one and a half times higher than the next highest value for group 4 (S11: 25.83 mg l^{-1}). Group 2 however was significantly higher than group 1 (M5) alone, with groups 3 and 4 (both S11) being intermediate (Table 3.3.18b).

Vegetation variables

The values for a number of collective vegetation variables measured during 2000 differed significantly between the TWINSPAN groups defined (Figure 3.3.13). As in 1999, species number (S) varied significantly between groups, and at around 14 species per m^2 for group 2 (S27a) was significantly higher (p< 0.001) than the other three defined groups. Stem density

was significantly higher (p= 0.018) in group 1 (M5) than group 4 (S11) with groups 2 (S27a) and 3 (S11) being intermediate. Canopy height overall was highest in groups 3 and 4 (both S11), but only for group 3 was it significantly higher (p= 0.02) than group 2 (S27a). Average stem diameter within group 1 (M5) was 2.5 mm, and this was significantly lower (p= 0.018) than both groups 2 (S27a) and 3 (S11). Biomass between ground level and 10 cm was lowest within group 3 (S11), and was significantly higher in groups 2 (S27a) and 4 (S11). However, the opposite was true for biomass above 20 cm, total biomass, and total standing crop at 20 cm or more above ground level per m^2, with values for group 3 being the highest, or amongst the highest. Group 3 (S11) values were consistently significantly higher than group 1 (M5) values (at p= 0.019, p= 0.011, and p< 0.001 for these three variables respectively). The same pattern followed for estimates of standing crop, with values for group 3 (S11) being the highest. No group separation however was apparent following a Tukey test (Figure 3.3.13i). A number of other collective variables were found not to differ significantly between groups (Table 3.3.19a). Whilst values for most of these variables did not tend to differ between groups 1 (M5), 2 (S27a) and 4 (S11), they were generally higher within group 3 (S11). Median values for numbers of reproductive structures per m^2 were also roughly equivalent between groups 1, 2 and 3 at 289, but were around half this level for group 4.

Several dominant population traits were found to differ significantly between groups during 2000, with all variables generally being higher amongst the two S11 communities defined for groups 3 and 4 (Figure 3.3.14; Table 3.3.20). Ramets were significantly taller (p= 0.002) for these two groups than for groups 1 (M5) and 2 (S27a). The dominant species of group 3 also had significantly more leaves per ramet (p= 0.047), and canopy area (p= 0.039) than group 2 (S27a). Number of reproductive structures was significantly higher (p< 0.001) amongst groups 1 (M5) and 3 (S11), than for groups 2 (S27a) and 4 (S11). Group 4 had significantly higher values for dominant populations for either group 1 (M5) or group 2 (S27a) for average total leaf area (p= 0.008), leaf length (p= 0.029), leaf weight (p= 0.049), and total weight per ramet (p= 0.044). Group 3 (S11) had the highest average value for reproductive structure weight, and this was significantly higher than for group 1 (M5). Specific Leaf Area did not differ significantly between the dominant populations of the respective groups (Table 3.3.20b).

Table 3.3.12 Environmental variable values per TWINSPAN group for August 1998 data. Different superscript letters show significant differences between groups. (a) Mann-Whitney confidence tests between groups, showing median values. (b) One-way analysis of variance, showing mean values (± standard error (s.e.)) per group (tests based on $\log_e$ transformed values, except *Arcsine tranformed). ns = not significant. For explanation of variables see Tables 3.2.1 – 3.2.3).

(a)

Variable	TWINSPAN Group			*p*
	1 (n=2)	2 (n=17)	3 (n=4)	
WAT (cm)	6^{ab}	13^{b}	5^{a}	0.04
FLU (cm)	9.5	10.3	14.4	ns
pH	5.4	5.8	5.6	ns
CON (µS/cm)	70	104	64	ns
Fe (mg/l)	1.94	1.78	6.95	ns
Mn (mg/l)†	0	0	0.002	ns

†0 = trace; undetectable at < 0.001 mg l^{-1}.

(b)

Variable	TWINSPAN Group			*p*
	1 (n=2)	2 (n=17)	3 (n=4)	
BARE (%)*	3 (±1.7)	4 (±1.6)	1 (±0.5)	ns
Mg (mg/l)	1.71 (±0.53)	2.39 (±0.58)	1.54 (±0.38)	ns
K (mg/l)	3.23 (±0.14)	6.63 (±0.44)	2.43 (±0.94)	ns
Ca (mg/l)	3.54 (±0.97)	14.25 (±5.06)	8.78 (±4.60)	ns
Na (mg/l)	0.97 (±0.97)	13.70 (±5.11)	4.93 (±1.66)	ns

Table 3.3.13 Collective vegetation variable values per TWINSPAN group for August 1998 data. Different superscript letters show significant differences between groups. (a) Mann-Whitney confidence tests, showing median values. (b) One-way analysis of variance, showing mean values (±s.e.) per group (tests based on $\log_e$ transformed values). ns = not significant.

(a)

Variable	TWINSPAN Group			*p*
	1 (n=2)	2 (n=17)	3 (n=4)	
STDE (m^{-2})	1533^{ab}	1033^{a}	1783^{b}	0.04

(b)

Variable	TWINSPAN Group			*p*
	1 (n=2)	2 (n=17)	3 (n=4)	
CAHT (cm)	25 (±0.7)	38 (±4.2)	52 (±16.3)	ns
LITT (%)	6 (±0.8)	12 (±2.7)	13 (±7.2)	ns
BN1 (g)	88 (±6.8)	148 (±17.4)	222 (±101.7)	ns
BN2 (g)	162 (±132.5)	53 (±13.3)	185 (±165.4)	ns
BN3 (g)	16 (±2.9)	58 (±18.5)	163 (±103.4)	ns
BNT (g)	267 (±122.9)	259 (±38.7)	570 (±367.4)	ns

Table 3.3.14 Dominant population trait values per TWINSPAN group August 1998 data by One-way analysis of variance, showing mean values (±s.e.) per group (tests based on $\log_e$ transformed values). ns = not significant.

Variable	TWINSPAN Group			*p*
	1 (n=2)	2 (n=17)	3 (n=4)	
RamHt (cm)	37 (±1.17)	49 (±5.11)	58 (±20.45)	ns
RamLv (cm)	4 (±0.17)	5 (±0.63)	5 (±1.41)	ns
RamTLA (cm^2)	41 (±0.99)	81 (±12.85)	58 (±13.25)	ns
RamTLL (cm)	130 (±5.12)	234 (±39.08)	150 (±26.26)	ns
RamDWS (g)	73 (±20.06)	452 (±138.29)	258 (±139.09)	ns
RamDWL (g)	190 (±15.04)	478 (±74.91)	286 (±50.33)	ns
RamDWR (g)	15 (±2.01)	65 (±19.06)	84 (±46.81)	ns
RamDWT (g)	278 (±37.11)	995 (±182.17)	655 (±167.90)	ns
SeeADW (mg)	0	0.18 (±0.08)	0.50 (±0.50)	ns
SLA (cm^2/mg)	0.21 (±0.02)	0.19 (±0.02)	0.24 (±0.05)	ns

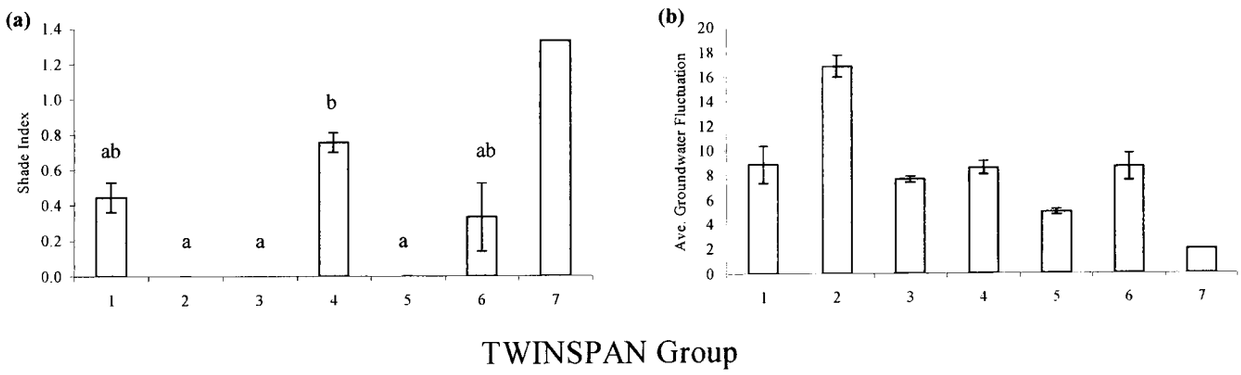


Figure 3.3.9 Mean (±s.e.) environmental variable values per TWINSPAN group for 1999 season by one-way ANOVA. (a) Shade index; (b) Average level of groundwater fluctuation ($\log_e$ transformed data). Different letters at head of graphs represents significant differences between group means (Tukey test). Group seven values are from the single Lochwinnoch (L3) site.

Table 3.3.15 Environmental variable values per TWINSPAN group for average 1999 data. (a) by One-way analysis of variance, showing mean values (±s.e.). (b) by Kruskal-Wallace tests followed by non-parametric multiple comparisons, showing median values per group. Different superscript letters show significant differences between groups. ns = non-significant.

(a)

Variable	TWINSPAN Groups							*p*
	1 (n=6)	2 (n=9)	3 (n=7)	4 (n=11)	5 (n=6)	6 (n=3)	7 (n=1)	
BARE (%)	5 (±1.9)	9 (±2.6)	12 (±2.5)	8 (±2.4)	9 (±3.1)	1 (±1.1)	5	ns
RED (mV)	0 (±25.8)	47 (±37.2)	-1 (±28.2)	24 (±19.9)	-27 (±25.3)	20 (±38.5)	0	ns
F (mg/l)	0.1 (±0.08)	0.1 (±0.04)	0.0	0.0	0.1 (±0.07)	0.1 (±0.07)	0.1	ns

(b)

Variable	TWINSPAN Groups							*p*
	1 (n=6)	2 (n=9)	3 (n=7)	4 (n=11)	5 (n=6)	6 (n=3)	7 (n=1)	
WAT (cm)	0.2^{ab}	-1.3^{a}	-2^{a}	1.3^{ab}	11.2^{b}	-0.3	1	=0.01
MIN (cm)	-0.2^{ab}	-3.3^{a}	-4.3^{a}	-0.3^{a}	10.8^{b}	-4.5	0	=0.009
MAX (cm)	8.0	6.0	2.7	2.7	14.7	2.7	2	=0.044
pH	6.1	6.0	6.1	5.8	6.0	5.3	5.9	ns
CON (µS/cm)	274	394	244	251	361	124	187	ns
Fe (mg/l)	0.14	0.01	0.09	0.13	0.00	0.17	0.11	ns
Mg (mg/l)	2.24^{ab}	1.57^{ab}	1.34^{ab}	1.43^{a}	2.45^{b}	0.91	2.08	=0.025
Mn (mg/l)	0.14^{b}	0.23^{b}	0.23^{b}	0.00^{a}	0.08^{ab}	0.13	0.10	=0.002
Ca (mg/l)	9.36	12.50	5.66	9.70	10.10	3.22	12.75	ns
Na (mg/l)	6.48	5.77	5.49	5.69	7.31	5.83	6.10	ns
Cl (mg/l)	9.38	10.09	8.97	11.66	13.68	9.71	12.64	ns
K (mg/l)	1.29	0.71	0.85	0.56	1.06	0.45	3.00	ns
SO_4^{2-} (mg/l)	0.78	1.98	1.34	1.04	1.07	2.10	3.43	ns
NO_3 (mg/l)	0.56^{b}	0.16^{ab}	0.15^{ab}	0.03^{a}	0.06^{ab}	0.12	0.10	=0.01

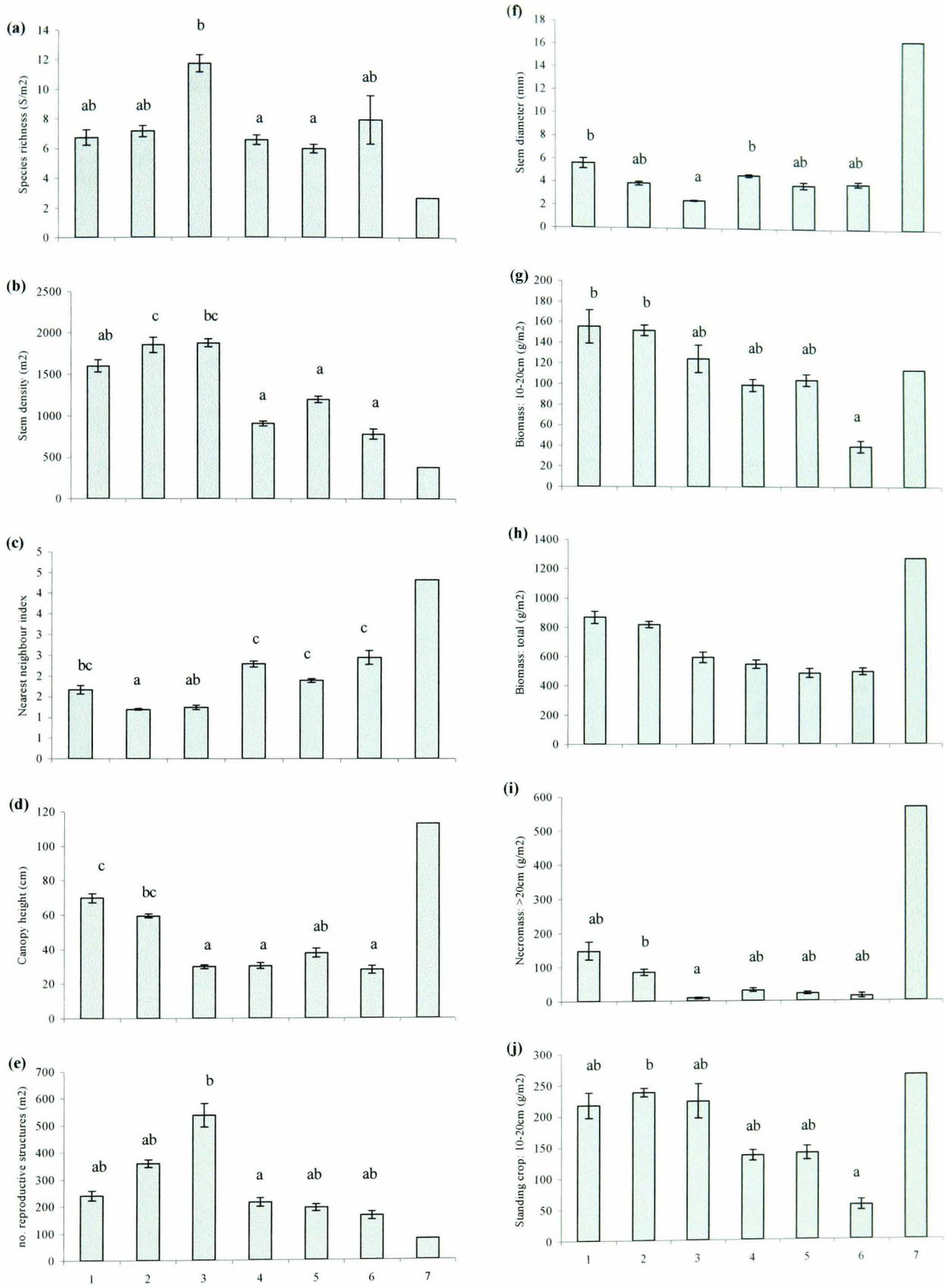


Figure 3.3.10 Mean (±s.e.) collective vegetation variables per TWINSPAN group for 1999 season; different letters at head of graphs represents significant differences between group means (Tukey test). Tests based on $\log_e$ transformed data for variables b, d-g, i and j. Group seven values are from the single Lochwinnoch (L3) site.

Table 3.3.16 Collective vegetation variable values for 1999 (a) by One-way analysis of variance, showing mean values (±s.e.). (b) by Kruskal-Wallace tests followed by non-parametric multiple comparisons, showing median values per group. Different superscript letters show significant differences between groups. ns= non-significant.

(a)

Variable	TWINSPAN Groups							*p*
	1 (n=6)	2 (n=9)	3 (n=7)	4 (n=11)	5 (n=6)	6 (n=3)	7 (n=1)	
Litt (%)	12 (±2)	12 (±2)	11 (±4)	12 (±2)	8 (±2)	14 (±1)	25	ns
B1 (g/m^2)	172 (±56)	261 (±59)	314 (±112)	307 (±71)	213 (±45)	368 (±67)	236	ns
N2 (g/m^2)	62 (±20)	86 (±19)	99 (±64)	36 (±10)	35 (±14)	16 (±7)	150	ns
N3 (g/m^2)	148 (±65)	85 (±30)	9 (±5)	31 (±19)	22 (±9)	14 (±12)	570	ns
BN1 (g/m^2)	423 (±47)	573 (±49)	561 (±48)	499 (±42)	440 (±36)	471 (±73)	993	ns

(b)

Variable	TWINSPAN Group							*p*
	1 (n=6)	2 (n=9)	3 (n=7)	4 (n=11)	5 (n=6)	6 (n=3)	7 (n=1)	
B3 (g/m^2)	403^{d}	379^{c}	81^{a}	83^{a}	151^{b}	103	932	=0.001
N1 (g/m^2)	242	304	129	155	208	96	756	ns
NT (g/m^2)	497	592	216	262	254	134	1477	ns
BN3 (g/m^2)	510^{d}	438^{c}	87^{a}	89^{a}	164^{b}	106	1493	=0.001
BNT (g/m^2)	1373^{e}	1352^{d}	800^{c}	753^{b}	683^{a}	647	2750	=0.025

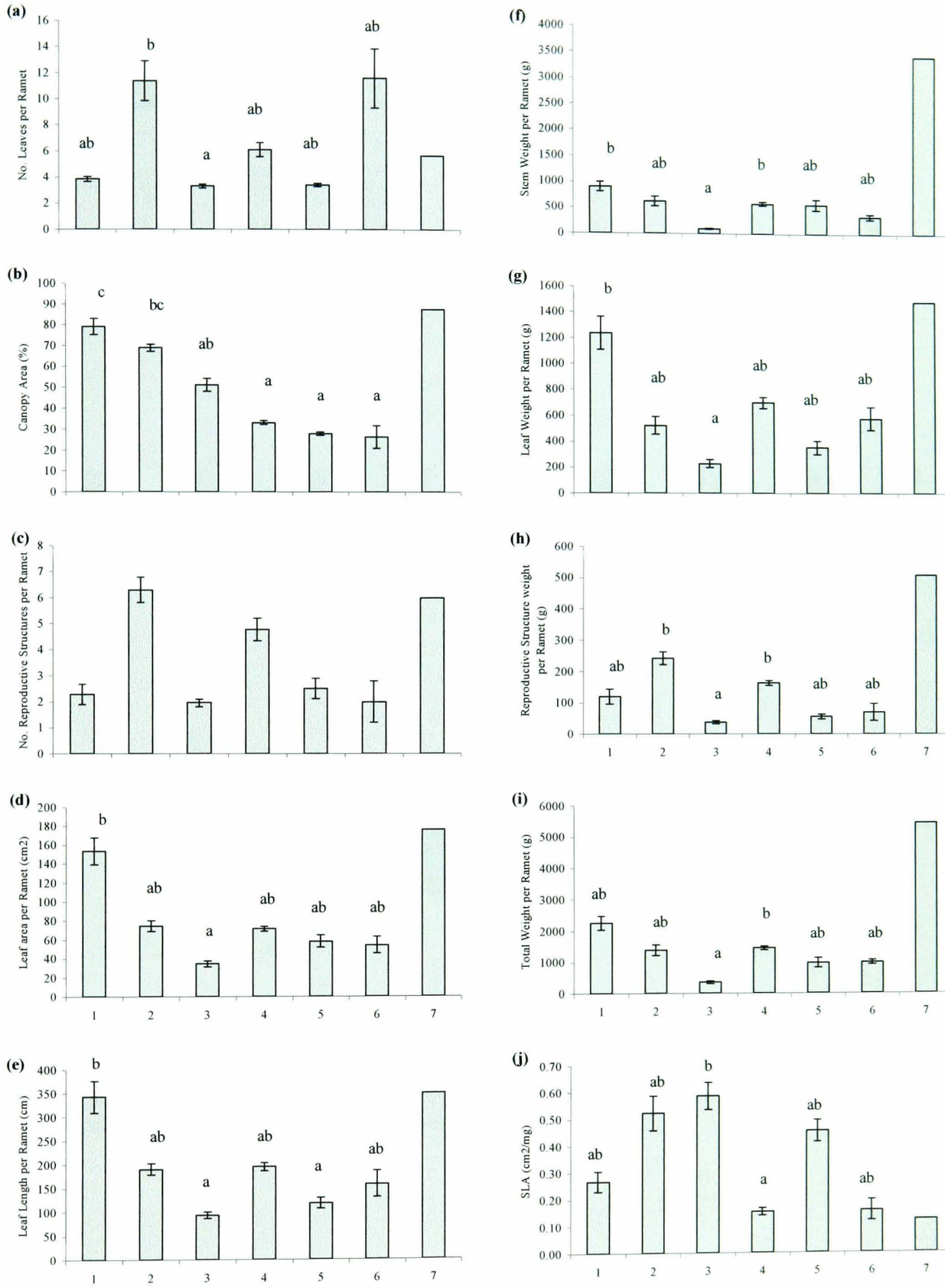


Figure 3.3.11 Mean (±s.e.) dominant population(s) trait data per TWINSPAN group for 1999 season; different letters at head of graphs represents significant differences between group means (Tukey test). Tests based on $\log_e$ transformed data for all variables except b. Group seven values are from the single Lochwinnoch (L3) site.

Table 3.3.17 Non-significant dominant population trait values for 1999 data by Kruskal-Wallace tests followed by non-parametric multiple comparisons, showing median values per group.

Variable	TWINSPAN Group							*p*
	1 (n=6)	2 (n=9)	3 (n=7)	4 (n=11)	5 (n=6)	6 (n=3)	7 (n=1)	
RAMht (cm)	80	73	39	44	30	49	149	ns
SeedWt (g)	0.54	0.61	0.36	0.45	0.51	0.22	0	ns

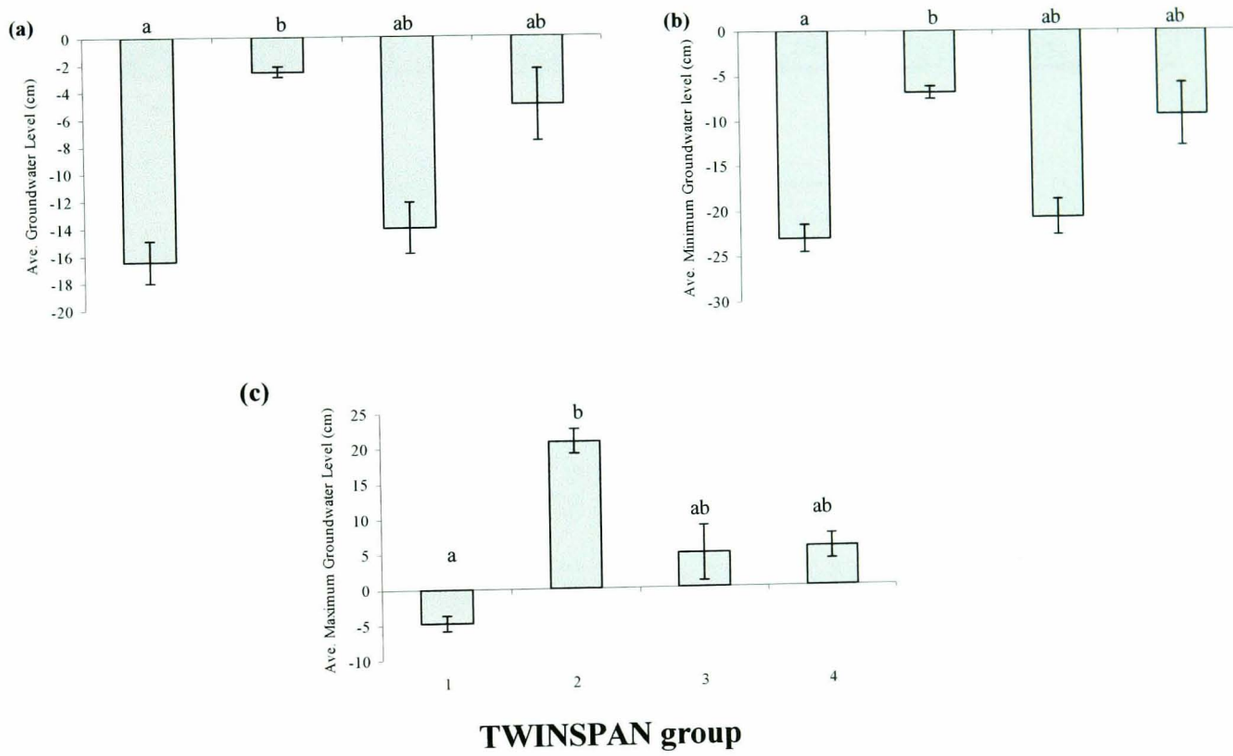


Figure 3.3.12 Mean (±s.e.) groundwater variable values per TWINSPAN group for 2000 season; different letters at head of graphs represents significant differences between group means (Tukey test). All variables untransformed.

Table 3.3.18 Environmental variable values for 2000 (a) by one-way Anova (tests based on $\log_e$ transformed values, except *(Arcsin tranformed)) showing mean values (±s.e.); (b) by Mann-Whitney confidence tests for non-parametric values, showing median values. Different superscript letters show significant differences between groups. ns = non significant.

(a)

Variable	TWINSPAN Group				*p*
	1 (n=5)	2 (n=6)	3 (n=5)	4 (n=4)	
Flu (cm)	18 (±4.2)	28 (±5)	17 (±7.1)	15 (±6.3)	ns
Red (mV)	248 (±92)	124 (±16)	228 (±55)	166 (±64)	ns
Con (µS/cm)	179 (±48)	147 (±16)	198 (±29)	304 (±78)	ns
Bare* (%)	8 (±2)	8 (±1)	7 (±2)	13 (±5)	ns
K (mg/l)	2.82 (±1.07)	1.15 (±0.43)	1.44 (±0.46)	1.29 (±0.36)	ns
F (mg/l)	0.09 (±0.05)	0.15 (±0.05)	0.06 (±0.03)	0.07 (±0.06)	ns
SO_4^{2-} (mg/l)	5.74 (±1.86)	14.13 (±4.68)	9.28 (3.34)	20.31 (±18.21)	ns

(b)

Variable	TWINSPAN Group				*p*
	1 (n=5)	2 (n=6)	3 (n=5)	4 (n=4)	
pH	5.9^{b}	5.5^{a}	5.9^{b}	5.7^{b}	=0.02
Fe (mg/l)	0.25^{a}	0.31^{ab}	0.40^{ab}	0.87^{b}	=0.037
Mg (mg/l)	0.77^{a}	1.40^{a}	1.21^{a}	2.52^{b}	<0.02
Mn (mg/l)	0.14	0.76	0.6	0.78	ns
Ca (mg/l)	1.93^{a}	6.10^{a}	12.36^{a}	16.89^{b}	=0.037
Na (mg/l)	7.19	8.52	7.14	9.12	ns
Cl (mg/l)	22.01^{a}	41.77^{b}	22.55^{ab}	25.83^{ab}	=0.008
NO_3 (mg/l)	0.07	0	0	0	ns
P (mg/l)	0.006^{ab}	0.002^{a}	0.005^{ab}	0.010^{b}	<0.011

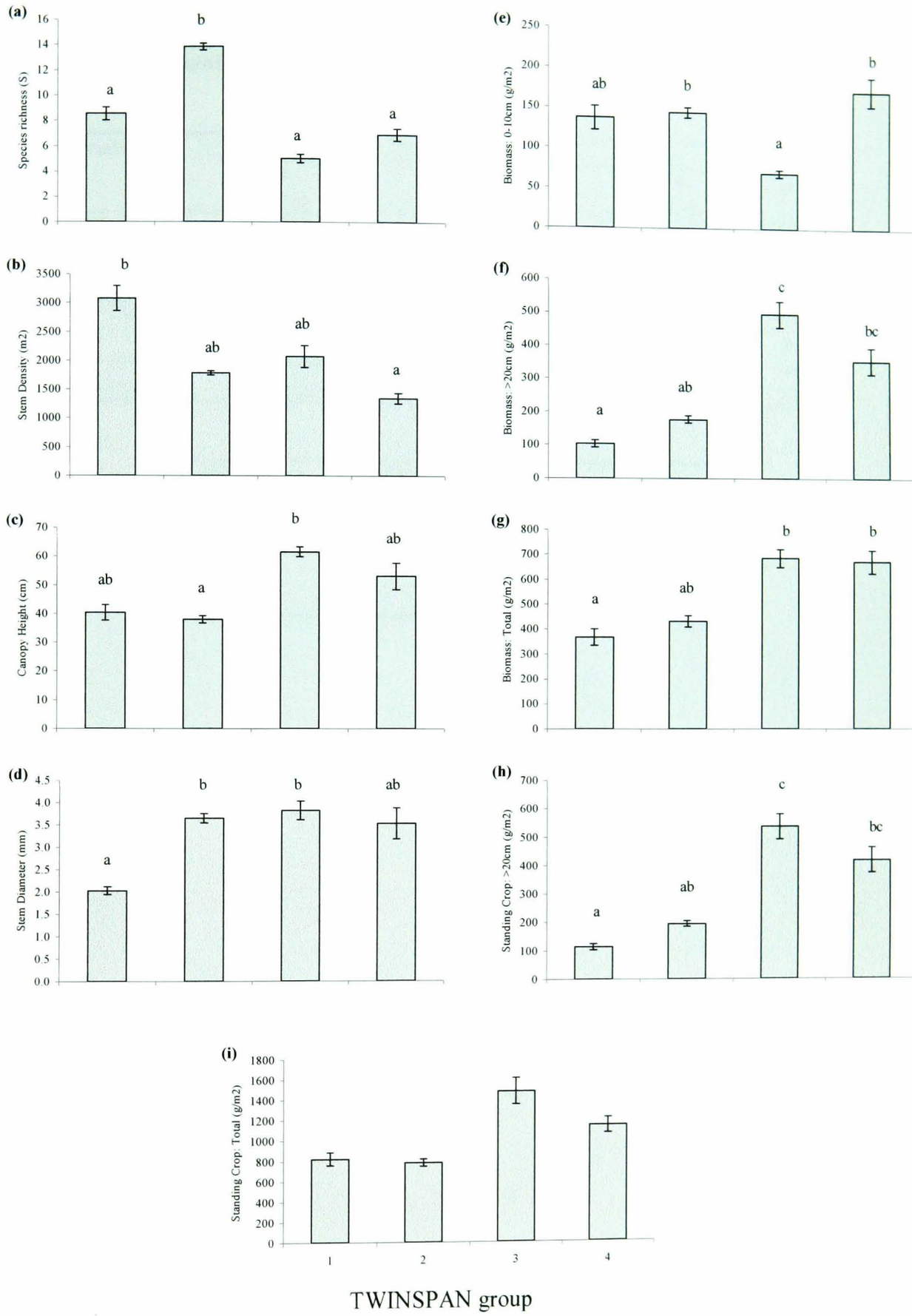


Figure 3.3.13 Mean (±s.e.) collective vegetation variables per TWINSPAN group for 2000 season; different letters at head of graphs represents significant differences between group means (Tukey test). Tests based on $\log_e$ transformed data for variables b and e-i.

Table 3.3.19 Non-significant collective vegetation variables for 2000. (a) by one way analysis of variance, showing mean (±s.e.) values per group; (b) by Mann-Whitney confidence tests, showing median values.

(a)

Variable	TWINSPAN Group				*p*
	1 (n=5)	2 (n=6)	3 (n=5)	4 (n=4)	
LITT (%)	16 (±3.6)	10 (±1.3)	24 (±7.0)	14 (±6.2)	ns
BIO2 (g/m^2)	127 (±19)	110 (±18)	119 (±16)	141 (±18)	ns
NEC1 (g/m^2)	397 (±76)	276 (±41)	520 (±73)	381 (±83)	ns
NEC2 (g/m^2)	47 (±14)	57 (±15)	239 (±165)	33 (±13)	ns
NECT (g/m^2)	454 (±84)	350 (±56)	799 (±207)	476 (±126)	ns
BN1 (g/m^2)	534 (±102)	421 (±48)	590 (±64)	554 (±76)	ns
BN2 (g/m^2)	174 (±28)	167 (±26)	358 (±161)	174 (±13)	ns

(b)

Variable	TWINSPAN Group				*p*
	1 (n=5)	2 (n=6)	3 (n=5)	4 (n=4)	
NENE (m^{-2})	1.0	1.5	1.3	1.8	ns
REPR (m^{-2})	289	289	289	134	ns
NEC3 (m^{-2})	11	14	30	39	ns

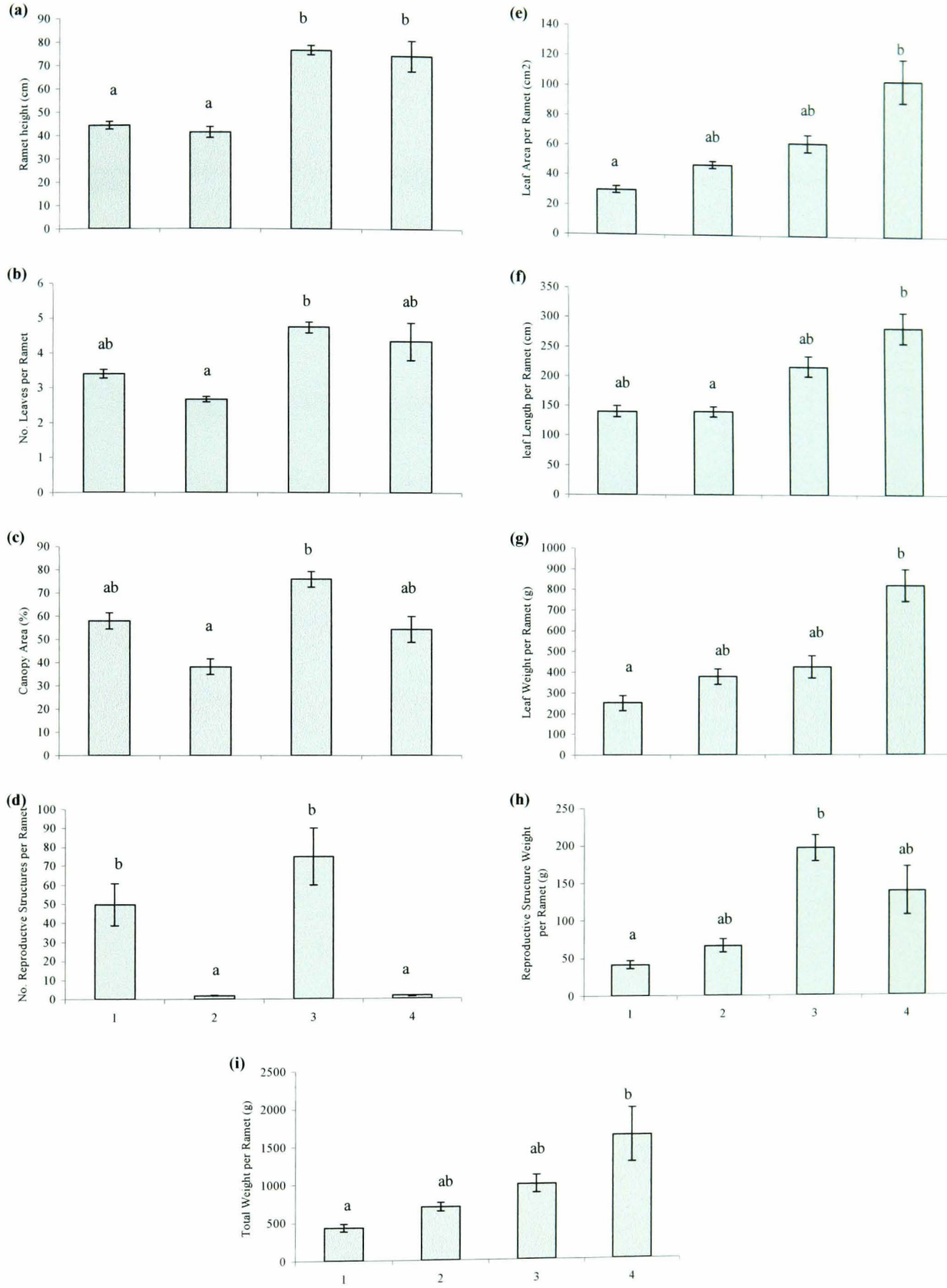


Figure 3.3.14 Mean (±SE) dominant population(s) trait variable data per TWINSPAN group for 2000 season; different letters at head of graphs represents significant differences between group means (Tukey test). Tests based on $\log_e$ transformed data for variables b and e-i.

Table 3.3.20 Non-significant dominant population traits for 2000. (a) by one way analysis of variance, showing mean (±s.e.) values per group; (b) by Mann-Whitney confidence tests, showing median values.

(a)

Variable	TWINSPAN Group				*p*
	1 (n=5)	2 (n=6)	3 (n=5)	4 (n=4)	
DWS (g)	141 (±62)	261 (±65)	372 (±108)	677 (±516)	ns
SeedWt (g)	0.18 (±0.07)	0.27 (±0.13)	0.31 (±0.08)	0.35 (±0.17)	ns

(b)

Variable	TWINSPAN Group				*p*
	1 (n=5)	2 (n=6)	3 (n=5)	4 (n=4)	
SLA (mg/cm^2)	0.19	0.17	0.16	0.15	ns

3.4. Discussion

3.4.1. Species composition between sites and between years

Any study over a timescale of three years can only offer an extended 'snapshot' of the processes occurring within the sites in question, and their effects on species composition. van der Valk *et al.* (1994) consider succession to be one of the main factors which can confound studies of the impacts [of forms] of disturbance upon the composition and structure of vegetation.

Many of the studies cited in section 3.1 are based upon single point measurements of environmental variables. This is a problem mentioned by de Mars *et al.* (1997), who argue that certain events such as extreme flooding or drawdown are important in influencing and maintaining species composition. The authors therefore consider that long term monitoring is important. However, it is often the case that studies are short term due to restrictions upon a number of resources (e.g. manpower; money). The approach taken in this study has been to combine some longer term (three seasons) studies with shorter term (one season) studies of a greater number of sites. This approach has proven useful in elucidating some of the differences in environmental 'drivers' underlying different defined communities, and can help to explain some of the differences in species composition between these communities. Using an approach such as this helps inform management for the maintenance of defined community types, especially where existing classifications such as the NVC are described with only limited reference to underlying environmental parameters, and are not designed for long term monitoring (Rodwell *et seq.* 1991).

Within the lifespan of this study a good deal of consistency was observed in the species composition of sites where repeated sampling was conducted. This adds weight to the case for conducting sampling over a single season in order to attempt to characterise site conditions.

3.4.2. The success and value of fitting data to existing community classifications

The matching of the newly collected data to existing classifications had variable levels of success. However, in almost all cases at least half of the species listed for the new groups were in common with those listed for the NVC classifications, and a good proportion of characteristic dominant species were recorded.

Two factors which are discussed by Rodwell (1991 *et seq.*) offer possible explanations to the intermediate levels of success obtained with fitting the data to pre-defined communities. (1).

many swamp communities have been systematically understudied, and the NVC categories are often based on relatively small group sizes, and (2) low matches may reflect previously un-described associations, or sub-community types of existing communities

When comparing year upon year classifications to those for the combined 3 year dataset the end groupings appear partially dependent upon the scale of the overall data pool. Based upon a TWINSPAN output for the combined data for the three years, less community types are recognised then when all three years are taken independently. However, as with the previous point, this is potentially a function of the poor matching to existing classifications, as outlined above.

Fuzzy clustering is often successfully applied where land use is well defined and species composition is driven by just one or two major gradients related to land management, as shown by Cole *et al.* (2001). TWINSPAN is successful and preferential in the context of this study, where definite indicator species define groups, but where a number of gradients (often surrogates for stress) are important in determining vegetation composition. In this study, fuzzy partition coefficients were therefore low, and groups contained disparate sites.

3.4.3. Characterisation of communities

In a review paper by Wheeler and Proctor (2000) which discusses and aims to clarify the minefield that is wetland nomenclature, the authors indicate that the S27 NVC swamp community type has a trophic status which is variable (in common with a number of swamp communities). For the 1999 community classifications, two S27 communities were defined (groups 1 and 4). Average manganese levels were found to be significantly higher in group 4 than group 1, and in general the measured variables relating to groundwater environment tended to indicate a slightly higher trophic status within group 1. This higher trophic status was perhaps reflected in turn in generally higher values for a number of measured vegetation variables, with average canopy height being significantly higher for the group 1 S27 community. Perhaps as a function of this increased canopy height, various biomass measures were also significantly higher in group 1, as was canopy area. This helps clarify the differences between two sets of samples with the same community classification.

Similarly, examples of the S11 tall sedge fen can have a trophic status ranging from oligotrophic through mesotrophic. The S11 groups defined in 2000 were differentiated by significant differences in the average levels of both calcium and magnesium in the groundwater samples. Significantly higher levels of both were observed in group 4.

As with the S27 community groupings for 1999, the S27 group with the higher tropic status was again characterised by significantly higher average biomass and stem density values. In addition, ramet height, reproductive structure weight of the dominant populations was also significantly higher in the Group 4 S11 community grouping.

Differentiation between mire community types defined within 1998 and 1999 (only one mire community type was classified for 2000) was possible by reference to chemical composition of groundwater. Those mire communities with predominant bryophyte presence (M9 *Carex rostrata-Calliergon cuspidatum* mire; M2 *Sphagnum cuspidatum/recurvum* bog pool community) tended to be characterised by more ombrotrophic groundwater conditions than those with a greater vascular plant presence (M27 *Filipendula ulmaria-Angelica sylvestris* mire; M23 *Juncus effusus/acutiflorus-Galium palustre* rush pasture). This appears relatively consistent with the findings of Daniels (1978), who made a division between such mire types on the basis of chemical and physical properties of groundwater. In mires with more geotrophic groundwater conditions, vascular plants predominated, while ombrotrophic sites tended to contain more bryophytes.

Some of the differences observed between the various groupings bear good relation to the thermodynamic sequences which occur in waterlogged soils, as outlined in Chapter 1. These differences can further be related to the groundwater dynamic of the various groups. For the 1999 dataset, NO_3^- was highest in group 1 (S27a), whilst SO_4^{2-} was lowest in this group. Of the groups formally compared, the water table depth was highest (i.e. inundated) in group 1, but the level of fluctuation of the water table was the second highest, perhaps indicating a dynamic water table underlying this community type. This observation can be related to those of Patrick and Mahapatra (1968), who noted that in wetland soils nitrogen is usually lost too quickly for denitrification to be of value in rice crops, and furthermore mineralization cannot proceed past the ammonium stage because of lack of oxygen necessary for microbial conversion to nitrate. However, frequent fluctuations in the flooding and draining of soils produces ideal conditions for denitrification. Nitrate can then be lost and yields decreased through flooding in agricultural soils where there is excess nitrogen. However, on nitrogen deficient soils nitrate can be increased locally under these condition and yields increased. Amongst the groups formally compared, the average total standing crop values were highest in group 1. In contrast, overall levels of water table fluctuation were lowest in group 5 (S9b, *Carex rostrata* swamp). Nitrate levels were also low in this group, and the average standing crop values were lowest in this group (of those formally compared).

In conclusion, it is possible to characterise some of the differences between defined community types in terms of the environmental variables underlying and them, and the vegetation characteristics which occur as a result. These groupings do have particular floristic compositions which are comparable to recognised community types. From this baseline, there is the potential to look at differences between communities and perhaps predict changes between them, but this is an area which requires further research.

In addition various traits of dominant species and of the collective community assemblages vary in relation to differing environmental drivers. Such traits therefore have potential to act as predictors of environmental regime, and conversely, it may be possible to produce predictions of how vegetation might change if it is subjected to altered hydrological regimes. This is a topic which is considered in more detail in Chapter 4.

Chapter 4: Modelling eco-hydrological relationships within freshwater wetland vegetation

4.1. Introduction

In Chapter 3 vegetation-hydrology relationships were investigated within poor-fen, mire, and swamp communities in a number of northern British wetlands. A multivariate analysis approach was used to examine sets of field data: species assemblage and abundance, trait measures of both individual species and of communities and corresponding underlying environmental variables.

Phytosociological approaches to the classification of vegetation data are obviously important for the understanding and management of a variety of habitats in Britain, and elsewhere (e.g. Denny, 1985). However, Rodwell (1995) notes that clear floristic and structural gradations occur from one extreme to another within fen systems, and that this can lead to difficulties in deciding where to draw boundaries between transitional types of vegetation. Floristic gradations are often varied and complex, making community separation difficult. In addition, Rodwell (1991 *et seq.*) recognises the limitations of these methods in monitoring temporal changes in plant communities. Functional approaches to vegetation classification (e.g. Grime, 1974; Keddy, 1992; Dickinson and Murphy, 1998), have been successfully applied by a number of workers (e.g. Diaz *et al.*, 1998; see also Duckworth *et al.*, 2000 for a recent review of the subject). Examples of successful applications of such techniques exist for wetland and aquatic ecosystems (e.g. Abernethy, 1994; Hills *et al.*, 1994; Murphy *et al.*, 1994; Hills and Murphy, 1996; Daoust and Childers, 1998; Ali *et al.*, 1999). It is apparent from past and present work that functional approaches to vegetation assessment have the potential to be utilised as components of tools for monitoring environmental change, both on a wider habitat and biota basis (e.g. Murphy *et al.*, 1994; Abernethy *et al.*, 1996), and more specifically for wetland vegetation (e.g. Murphy *et al.*, 2001).

4.1.1. Wetland gradients

In the established phase of their life cycle, higher plants are generally relatively non-motile, and they must therefore be adapted to the conditions prevalent within their habitat. The commonly observed phenomenon of wetland vegetation zonation is closely linked to the level of the groundwater relative to the ground surface (e.g. Etherington, 1983; Denny, 1985; Holland et al., 1990; Risser, 1990), although de Mars *et al.* (1997) argue that more extreme drawdown and flood events are equally as important in characterising certain floodplain fen

communities; for example, the *Glycerietum maximae* is reliant upon spring flooding followed by a degree of drawdown during the summer months.

The study of wetland vegetation has been of particular interest to researchers due to the constricted nature of underlying environmental gradients. This is a phenomenon not generally encountered in systems that are either fully terrestrial or fully aquatic. Begon *et al.* (1996) describe the relationship within a number of land-water ecotones. For example, within rocky shores, exposure strongly dictates the distribution of inter-tidal algae. Meanwhile, fringing coastal ecosystems such as mangroves within the tropics contain species adapted to saline conditions, but with a requirement to have leaves and pneumatophores projecting above the water level. Also, salt marshes contain assemblages of plant species, which become progressively more saline tolerant towards open water. Studies by Marshall and Park (1976) within the North San Francisco Bay salt marshes, showed that *Salicorna virginica* occupied a habitat with higher soil salinity during the growing season than *Spartina foliosa,* which was relatively less effective at excluding ions. While not an aquatic ecotone in the literal sense, a study of cliff-top vegetation within southern England by Malloch (1971, 1972), uncovered salinity gradients running inland, and related to exposure to sea spray, which had a bearing on plant species composition.

4.1.2. Trait based assessments in ecology

Noble and Slatyer (1980) used predominant 'vital attributes' to describe constituent species of communities subjected to recurrent disturbance, based upon (1) methods of persistence during a disturbance, (2) ability to establish and grow to maturity following a disturbance, and, (3) time taken to reach critical stages in their life history. The scheme they propose deals mainly with terrestrial communities, but as they state, could provide a framework for general applications in community biology and ecosystem management.

Following up this concept, Keddy (1992a) stated that 'assembly rules provide one possible unifying framework for community ecology', and that with the environment acting as a filter for certain traits, or combinations of traits, principles should be generally applicable to systems with differing taxonomic compositions. In a further review Keddy (1992b), states that 'the need for general predictive models grows' as 'ecology matures, and the world's environmental problems continue to multiply'. He suggests that the science of functional ecology should have three basic components: (1) construction of trait matrices through screening; (2) exploring empirical relationships among these traits; (3) determining the relationships between traits and environments.

The use of trait-based assessments in plant ecology has potential weaknesses, as identified by Keddy (1992b), and Duckworth *et al.* (2000) amongst others, but these are mainly concerned with the usefulness of what is being measured. Willby *et al.* (2000) also point out that in many cases it is still difficult to assign any specific function to an attribute type. One notable exception to this rule is the isoetid life form found within the shorelines of oligotrophic freshwater lakes (Dickinson and Murphy 1998). The life-form grouping consists of a number of species which are phylogenetically unrelated, but which share a compact rosette form able to withstand disturbance from wave action, in addition to substantial root systems which aid anchorage and nutrient (and CO_2) uptake from gravely sediments. Stress-tolerance is also an important feature of the survival strategy of this group, due to light limitation in the deep water habit occupied by these plants (and which may be compounded where epiphytic algae overgrow their leaves), and due also to nutrient and C shortage in low pH, oligotrophic conditions prevailing in the lakes in which they occur. In this case it is relatively easy to identify the functional significance of both morphological and physiological traits exhibited by isoetid plants.

A special edition of Freshwater Biology (Volume 31, 1994) focussed upon trait-based approaches to habitat assessments (Resh *et al.*, 1994), and how habitats provide the template upon which characteristic species traits evolve within river systems (Townsend, 1994). Multidisciplinary studies were undertaken relating to the Rhône River and its floodplains, which studied trait representation from a general perspective (Cellot *et al.*, 1994; Doledec and Statzner, 1994), and within both floodplain vegetation (Pautou and Arens, 1994), and aquatic macrophytes (Bornette *et al.*, 1994) more specifically. The approach was also extended to a range of animal taxa, including oligochaetes (Juget and Lafont, 1994), Crustacea (Marmonier *et al.*, 1994), Plecoptera and Ephemoptera (Usseglio-Polatera and Tachet, 1994), aquatic Coleoptera (Richoux, 1994), Trichoptera (Tachet *et al.*, 1994), aquatic insects (Usseglio-Polatera, 1994), fish (Persat *et al.*, 1994), amphibians (Joly, 1994), and birds (Bournaud, 1994).

Murphy *et al.* (1994) undertook a study of the analysis of wetland functioning based upon the use of vascular plants and invertebrates, and work by Hills *et al.* (1994) focused on wetland vegetation. For this work information relating to specific strategies was gleaned from Grime *et al.* (1988). From this the authors were able to delimit hydrological units (with differing levels of stress) on the basis of functional groupings of plants, using linear and multiple discriminant analyses.

Willby *et al.* (2000) acknowledge that over the last 20 years much valuable progress has been made towards the assemblage of species into non-taxonomic groupings, providing an appealing framework which synthesises large and complex data sets into smaller and more easily interpreted sets of attributes. As such, they are more accessible to non-specialists. The authors produced a classification of 120 hydrophyte species native or naturalised in Northern Europe, in relation to habitat utilisation following a systematic literature review of the biological characteristics of the species. The study used the habitat template of (Southwood, 1977, 1988) as a framework for the study, with trait development linked to contrasting spatial and temporal variability. From the systematic literature review, the authors composed a species-by-traits matrix (alternatively termed an attribute matrix), which, using discriminant analysis, explained 72% of the variation in physical habitat use.

An approach taken by (Ali *et al.*, 1999) utilised field-measured variables of both the physical and biotic environment to assess the use of macrophyte functional variables as predictors of trophic status in flowing waters. In addition, information relating to morphology, physiology, and life history attributes was gleaned from extensive literature searches (following the methodology developed by Abernethy (1994)). This information was then used as the basis for a non-hierarchical classification of river plant functional groups, which could be compared and contrasted to existing assemblage based classifications (i.e. the Macrophyte Trophic Ranking scheme (MTR)) to predict trophic status. A combination of the models produced (termed River Trophic Status Indicator (RTSI) models), had a high predictive capacity (r=0.72; p<0.001), and explained over half of the variability in P.

Duckworth *et al.* (2000) consider that various approaches using plant functional types in community descriptions and biogeography have great potential, but that trade-offs exist between the time taken to measure traits, and the meaningfulness of the results gained. They also consider that the replacement of traditional taxonomic approaches by functional classifications purported by certain authors is neither imminent nor desirable, and that rather, the two approaches are complementary. One of the main future directions of research which is suggested by the authors relates to the use of plant functional types (PFT's) in the prediction of vegetation response to environmental change, and involving applications to remote sensing and GIS. The development and use of traits and attribute types in vegetation descriptions are further reviewed in Chapter 1 (sections 1.3.3, and 1.3.4).

4.1.3. Predictive modelling in ecology

Murphy and Hootsmans (2001) considers that the use of models in aquatic ecology currently emphasises three general approaches; (1) Simulation models; (2) Minimal linear models; (3) Spatial modelling:

1. Simulation models mathematically link sets of sub-model routines, aiming to provide outputs for one or more biological or ecological response variables for a defined system. Examples include phytoplankton biomass change with time in response to changing catchment nutrient inputs (Frisk *et al.*, 1999); and models of trophic relationships in aquatic ecosystems (e.g. the software package ECOPATH: Christensen and Pauly, 1992). Examples exist for the application of such models in a wetland plant community context (e.g. Ellison and Bedford, 1995). However, it seems that the popularity of larger-scale whole-ecosystem approaches to modelling has waned somewhat since the general failure of ecosystem-scale modelling attempts during the 1970 – 80s (Park *et al.*, 1974).
2. Minimal linear models are usually multiple-regression based procedures, and are restricted to a given envelope of applicability defined by the input values used in their construction and calibration (Scheffer and Beets, 1994). These models may form individual sub-routines within larger simulation models, may be used in stand-alone form to undertake particular tasks (e.g. Ali *et al.*, 1999), or may be used as part of spatial modelling procedures (see below), with model outputs being applied via an appropriate platform.
3. Spatial modelling platforms are usually based on the use of Geographical Information Systems (GIS: e.g. Jensen *et al.*, 1992; Lehmann *et al.*, 1997; Janauer, 1997), and are particularly well-suited for the depiction of "what-if" scenarios of spatial and temporal change in target response variables at landscape level. (Duckworth *et al.*, 2000) consider that the synthesis of trait-based approaches to assessing vegetation response to environmental change is an area of research which has potential to be developed further.

The aim of all of these approaches is the prediction of community performance in terms of one or more measurable attribute(s). Two commonly used attributes are biomass (or some other measure of abundance), and biodiversity. Sometimes the assemblage of organisms present is used, which is inherently more difficult to predict (Murphy and Hootsmans, 2001).

Further developments in the application of modelling approaches have been largely driven by legislative pressures. New environmental laws in Europe (e.g. the EC Water Framework Directive, due to be implemented in 2003; see section 1.2.2) have led to an increased interest in biomonitoring methods for assessment of the biointegrity ("health") of freshwater

ecosystems (Parsons and Norris, 1996). Such assessment methodologies are based around the use of predictive models (or, alternatively, multimetric systems) using aquatic organisms (or their attributes) to assess the ecosystem state of a given type of system (e.g. rivers) within a pre-defined area: the so-called ecoregion concept (Hughes and Larsen, 1988). A review of modelling applications in aquatic ecology is outlined by Murphy and Hootsmans (2001); these include:

- *Catchment models, for modelling nutrient-water relationships for catchment management*: These concern the modelling of nutrient fluxes derived from both point and non-point (diffuse) sources (e.g. Dillon and Rigler, 1974; Bevan and Kirby, 1979; Grieve and Gilvear, 1994). Such models typically simulate the physical and biogeochemical processes, which govern transport of pollutants (usually nutrients) in a catchment, and have been widely applied.
- *Modelling the performance of individual populations or species*: A good deal of work centres around aquatic macrophytes, for which much is known regarding survival and growth, and their relationship to environmental conditions influencing growth, and with other aquatic organisms in a wide range of aquatic habitats (recent studies include: Ali *et al.*, 1995; Sabbatini and Murphy, 1996; Spink and Murphy, 1997; Weisner *et al.*, 1997; Sabbatini *et al.*, 1998; Sidorkewicj *et al.*, 1998; Bini *et al.*, 1999; Ferreira and Moreira, 1999; Dawson *et al.*, 1999; O'Hare and Murphy, 1999; Murphy *et al.*, 2000; Murphy *et al.*, 2001). Despite this it appears that few specific models have been published for macrophytes.
- *Biodiversity modelling*: Attempts have focused on predicting either change in the richness of a target biota, or some measure of diversity incorporating equitability (e.g. diversity indices such as the Simpson index), or have attempted to predict change in assemblage. For example, recent work In Brazilian freshwater lagoon systems has successfully modelled patterns of β-diversity for aquatic macrophytes (Souza *et al.*, 2001 in press; Bini *et al.*, 2001 in press).
- *Modelling spatial distribution using GIS*: Geographical Information Systems (GIS), provide a tool to generate maps describing changes predicted by models over time in space, and are increasingly used as the platform for depicting model outputs in aquatic ecological studies (see above).
- *Changed State Models*: The changed state concept (and its allied concept of the use of "reference sites") is the basis of much current thinking in designing assessment approaches for monitoring aquatic ecosystem health. In Europe, the Water Framework Directive (see section 1.2.2) requires EU member-states to implement, from 2003,

improved techniques, which incorporate biomonitoring methodologies to assess the ecosystem health of freshwater systems. The new techniques largely utilise the changed state concept. Macroinvertebrate community structure (invertebrate-based models) have been the basis for numerous water quality assessment methodologies world-wide (e.g. Metcalf, 1989). A good example of a biomonitoring system adopted in the UK to assess river ecosystem health using invertebrate-based predictive models is RIVPACS (Wright, 1995), and equivalents exist abroad. These changed-state predictive modelling systems are based on data collected from reference sites (unimpaired or minimally impaired) representing the range of natural conditions across the target regions covered by the models.

Much predictive modelling is still based upon assemblage data only (especially for changed state models), with little or no measures of the functional attributes of the target organisms included. However, growing evidence exists for the predictability of functional, or attribute responses of organisms, in a range of aquatic and other systems (e.g. Hills *et al.*, 1994; Murphy *et al.*, 1994; Hills and Murphy, 1996; Willby *et al.*, 2000).

Murphy and Hootsmans (2001) suggest that current minimal modelling techniques are somewhat limited by the fact that they employ linear algorithms, while biological systems are naturally non-linear and inherently noisy. It is suggested that non-linear modelling (based on chaos theory) may offer a promising approach for the future to meet the demands of generality of model application, and improved precision. However, the important role which linear modelling has played in our understanding of processes in biological systems should not be played-down. Murphy and Hootsmans (2001) argue that there is still a need for more generalised models, covering a greater range of issues and systems. Better use should be made of Geographical Information Systems, as an excellent platform for presenting model outcomes and applying them to real systems, in a way which is readily understood by practical users (Duckworth *et al.*, 2000; Murphy and Hootsmans, 2001). In addition, model outputs should be easily accessible to those who can make use of them (e.g. environmental managers, decision-makers and legislators), through the use of media such as Graphic User Interfaces (GUIs), which can show the outcome of modelled scenarios in user-friendly formats (Murphy and Hootsmans, 2001).

4.1.3.1. Basic principles of regression analysis

Regression analysis is regarded by Manly (1994) as one of the most important and frequently used tools available for data analysis. The assumption of a simple linear regression is that there is a relationship between two variables X and Y, and that X is in some way thought to

determine Y. As such, the Y variable is usually termed the 'dependent' variable, and X the 'independent', or 'predictor' variable. The relationship between the two variables therefore takes the form:

$$Y = \alpha + \beta X + \varepsilon$$

Where α and β are constants and ε is random 'error', with mean 0 and standard deviation σ. α, β and σ can therefore be estimated, and used to quantify the relationship between X and Y using regression.

Multiple regression is the generalisation of a simple linear regression where a Y variable is related to more than one X variable(s). As such, Y can be regressed against several X variables, and the relationship takes the form:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + ,\ldots\ldots, + \beta_n X_n + \varepsilon$$

From this basis, the 'best' model can be achieved by restricting the independent (predictor) variables in the model to those with a regression coefficient (β) significant at $P = <0.05$, which produces a substantial increase in the predictive power (R^2) of the model and which justifies the overall increase in the degrees of freedom (Zar, 1999), to obtain the most 'parsimonious' model. Therefore, all modelling procedures will have a level of subjectivity involved.

4.1.3.2. The application of minimal models in ecology

ter Braak and Looman (1995) consider that in ecology, regression analysis has been mainly used for:

- Estimating parameters of ecological interest, such as the optimum and ecological amplitude of a species.
- Assessing which environmental variables contribute most to a species' response, through tests of statistical significance.
- Predicting a species' responses (abundance; presence-absence) at sites from the observed values of one or more environmental variables.

van der Valk *et al.* (1994) assert that many factors can confuse, confound and sometimes invalidate studies of the impact of a form of disturbance upon the structure and composition

of vegetation. These may include site characteristics such as soil type, the number and complexity of environmental gradients, or succession. However, progress has been made in modelling broad scale response of vegetation in relation to environmental parameters. Wheeler and Giller (1982) described predictive relationships between species richness and aspects of above-ground plant material in fen systems within the Norfolk Broads, England. Their findings generally support those of other researchers that increases in biomass are often associated with a reduction of species density. Later work by Wheeler and Shaw (1991) applied this principle over a wider geographical area (lowland England and Wales) and again showed generally negative relationships between species richness and species density.

Willby *et al.* (1998) developed a minimal linear model incorporating attribute measures of the plant community, to predict plant α-diversity in Scottish riverine floodplain wetlands. The model has a high predictive power (R^2>0.9), but due to the relatively large number of predictor variables employed, this is within a strictly limited envelope of applicability.

The Scottish floodplain model for plant species richness (S) is:

$$S = -5.016 + 5.5(\log_{10}\mathbf{STEM}) + 0.43(\sqrt{\mathbf{Eh7}}) + 3.7(\mathbf{CUT}) + 2.21(\log_{10}\mathbf{REPR}) - 1.04(\mathbf{DEEP}) - 1.63\,(\log_{10}\mathbf{Mn}) - 13.4(\arcsin\mathbf{BARE})$$

Where STEM =stem density (m^{-2}); Eh7 =soil redox; CUT =intensity of cutting for hay-making purposes; REPR =density of reproductive structures within the vegetation; DEEP =water depth; Mn =soil manganese content; BARE =percentage of bare ground. As such, the model is driven by two field measured attributes of the wetland vegetation (STEM and REPR), one management variable (CUT), and four environmental variables (BARE, DEEP, EH7, and Mn)

Using a similar approach, recent work by Murphy *et al.* (2001) sought to find environmental predictors of three primary aquatic vegetation parameters (assemblage, α-diversity, and abundance) in the plant communities of a Brazilian sub-tropical riverine floodplain wetland (the *varzea* of the Upper Rio Paraná, Brazil), and to determine whether functional attributes of the vegetation itself might act either as qualitative markers, or quantitative predictors of these parameters for modelling purposes. Previous work (Souza *et al.*, 2001 in press; Bini *et al.*, 2001 in press) has assessed species richness and β-diversity patterns for aquatic vegetation in some of the aquatic habitats (lagoons) of this system.

A minimal linear modelling approach was adopted, with an envelope of applicability limited to varzea waterbodies of the Upper Rio Paraná. During 1999 the aquatic vegetation was sampled at 45 sites within a stretch of the Rio Paraná (and its tributary the Rio Ivinheima), including main and secondary river channels, backwaters, lagoons and distributaries. Macrophyte diversity ($\log_e SPP/100m^2$) and macrophyte biomass (BIOM) were both modelled:

1. $\log_e SPP = 4.75 - 0.237(\log_e \mathbf{Fe_{sed}}) - 0.0148(\mathbf{P_{wat}}) + 0.0045(\log_e \mathbf{TOTW}) - 0.000026(\mathbf{Ca_{sed}})$

   ($R^2 = 63.1\%$; $p<0.001$)

2. $BIOM = 753.0 + 381.0(\mathbf{\log_e k}) + 260.0\ (\log_e \mathbf{TOTW}) - 138(\log_e \mathbf{Fe_{sed}})$

   ($R^2 = 27.2\%$; $p=0.004$)

Where Fe_{sed} =sediment concentration of iron; P_{wat} =water concentration of phosphate; Ca_{sed} =sediment concentration of calcium; K =underwater light extinction coefficient; TOTW =dry weight of individual ramets of dominant species present.

The minimal modelling approach adopted showed that the aquatic vegetation of waterbodies within the Upper Rio Paraná *varzea* exhibits predictable variation in its community attributes (size and shape of dominant species; diversity of plant assemblage present; biomass of plant community), along gradients of water and hydrosoil physico-chemistry occurring across the floodplain.

4.1.4. Chapter overview

In this Chapter a series of multiple regression models are proposed which vary both in terms of the dependent variables which they predict, and also in their generality (as determined by the overall number, and the nature of the independent predictor variables). In terms of the vegetation component of the models, the following are utilised: (1) General measured vegetation traits which exist irrespective of the species complement, and which may therefore vary either as (i) a function of the environment, or (ii) as a function of differing species composition; (2) Attributes recognised within specific species, and gleaned from references within the literature, which may vary between species, and may, or may not be present within a species. The proportion of the overall attributes within a given site, based upon the percentage of each species within the given site being the end product (i.e. an

attribute-by-site matrix, produced from a cross multiplication of a species-by-site matrix and a species-by-attribute matrix). This work attempts to build upon an approach which uses information gleaned from the literature to produce broad classifications relating to attribute types, and morphology etc. (e.g. Abernethy, 1994; Ali *et al.*, 1999; Willby *et al.*, 2000), which allows site by attribute matrix construction, with the inclusion of directly measured environmental variables, and which may act as predictors of attribute assemblage. As such the work represents a pilot study of this approach in the context of emergent northern British wetland vegetation. The various models may be summarised as:

1a. Prediction of collective vegetation variables, and dominant population traits:

- From a combination of groundwater and associated environmental variables, in conjunction with other vegetation variables (specific models: smaller 'envelope of applicability').
- From groundwater and associated environmental variables alone (general minimal models: larger 'envelope of applicability')

1b. Prediction of groundwater variables from measured vegetation variables:

- From both collective vegetation variables, and traits of dominant populations (specific models).
- From collective vegetation variables alone (general minimal models)

2a. Prediction of proportions of attribute types within species combinations at independent sites from groundwater and other environmental variables.

2b. Prediction of measured groundwater and other environmental variables from the proportion of attribute types present at each independent site.

In summary, this Chapter:

- Identifies the environmental gradients that appear to be acting as the primary drivers of species composition in the wetland sites studied.
- Describes sites in terms of trait variations measured within the vegetation.
- Provides a series of general and specific predictive equations describing eco-hydrological relationships within the wetland vegetation studied.
- Tests the predictive capacity of these models using test data from independent and repeat sample stations.
- Assess the use of wetland attribute types as components of predictive equations of eco-hydrological relationships.

4.2. Methods and Materials

4.2.1. Field sampling

Vegetation and groundwater data were collected as detailed in section 2.2.1. On return to the lab water samples were processed as outlined in Table 3.2.1. In addition, above-ground parts of individuals (whole plant or ramet) of each dominant population, from each fixed sample station were sectioned into stem, reproductive structures (where present), and leaves. These were then processed as outlined in Tables 3.2.2 and 3.2.3.

4.2.2. Data analysis

All data were tested for normality and transformed where appropriate. Data were normalised using a $\log_e (X \times 100 + 1)$ transformation (Sokal and Rohlf, 1981).

4.2.2.1. Identification of main environmental gradients

The influence of groundwater and other environmental variables on relative species assemblages was examined using canonical correspondence analysis (CCA: ter Braak & Šmilauer 1998). Following an initial ordination, those environmental variables which were strongly correlated with other environmental variables, and which therefore offered no unique contribution to the analysis were omitted; these variables were identified as those with a variance inflation factor (VIF) >20. By limiting the number of environmental variables for subsequent analyses, the problem of the 'arch effect' was also avoided (ter Braak & Šmilauer 1998). During the analyses the default option of automatic forward selection of environmental variables was selected, as this gives lower type II error, and the reduced model method only better maintains type I error with small data sets (ter Braak & Šmilauer 1998). Monte-Carlo permutations were conducted to determine the variables which significantly influenced the ordination (p <0.05; although all variables $p \leq 0.1$ were included in Tables and Figures for illustrative purposes). The full model permutation option was selected for the same reasons that automatic forward selection was selected, namely to give lower type II error. ter Braak & Šmilauer (1998) however, point out that recent research shows that the selection of either a reduced model or a full model has limited effect on the outcome. In addition, the data had been collected from stations positioned along fixed transects, but the design was semi-randomised, and all stations from several transects were being ordinated together (rather than comparisons being made within single transects). Therefore randomised permutations were used as this approach was valid for a randomised design (ter Braak & Šmilauer 1998).

Further constrained analyses were conducted using the same species matrix, but the environmental variable matrix was substituted variously by two alternative matrices: one consisting of dominant population trait values, and one consisting of collective vegetation variable values (see Appendix 4 for average raw data). This was in order to characterise species and stations by differentiation in these variables.

4.2.2.2. Modelling of field data

Models based upon field measured traits were constructed from the 1999 dataset alone, with the 2000 dataset being retained for model testing purposes. This was due to the fact that whilst species may vary between sites, the traits measured were common to all species and may be expected to vary as a function of the underlying environmental gradients.

The constrained ordinations conducted (see sections 4.2.2.1 and 4.3.1) gave information relating to species composition in relation to environmental gradients and also allowed the characterisation of stations by differentiation in dominant population traits, and in collective variables. However, these were primarily concerned with aspects of the species assemblage within the sample stations, and their relationship to the external measured variables. In addition the number of variables measured was relatively large (see Tables 3.2.1-3.2.3), and therefore attempting to elucidate patterns between them using a method such as Pearsons time-moment correlation was not considered appropriate (Zar, 1999). Therefore, for the construction of the models each variable was tested individually against each of the other variables using the linear regression curve-fit function in SPSS 9.0. This was in order to determine the potential for each variable for use as a predictor variable, and also the response curve (if any) of the predictor variable (i.e. linear, cubic, quadratic) in relation to the independent variable.

Stepwise regressions were then conducted, starting off with full models, where all potential predictor variables were included. Variables were then culled from the predictive equation where they offered no unique contribution to the model (i.e. the increase in degrees of freedom (d.f.) was not justified by the low increase in the R^2). Scores predicted by the regression models were compared with the observed values by calculation of the product-moment correlation coefficient, and residuals for the analyses were checked for normality by the construction of normal probability plots.

Specific models whose envelope of applicability would generally be restricted to those sites where the data were collected were constructed employing a range of predictor variables. In

addition, general minimal models were constructed employing fewer predictor variables, and the envelope of applicability of these would therefore be expected to be wider.

Models were tested using the datasets collected in 2000, which consisted of data from independent sites and repeat sites. This was in order to assess the precision of the models in repeat sites where environmental variables might differ between years (e.g. average water table level; see Chapter 2), and their precision using data collected from entirely new sites. Observed values were plotted against the values predicted by each of the models for the entire test data set, and for various sub-sets of the test data (for example, if some test data values for a certain variable were outwith the parameters of that variable when used to construct the model, the appropriate samples were removed from the analysis for comparison).

4.2.2.3. Modelling attribute data

The second major set of models constructed was more sensitive to species composition as the attributes gleaned from literature-based sources may, in theory, have been unique to just one of the species (e.g. semi-rosette form, rather than rosette or leafy form; see Table 4.2.1). In this instance the combined data (from independent, non repeat sites alone) collected during 1999 and 2000 was used to construct the models. This took into account the fact that a range of sites containing a variety of species was sampled during the course of the study (see Tables 2.3.1– 2.3.3). Attribute types were based on those listed in Grime *et al.* (1988), but were selected on the basis that relevant information could be gleaned from other sources (e.g. Jermy *et al.*, 1982; Stace, 1997; biological floras (*Journal of Ecology*)) if no information appeared for a certain species in the first reference work (Grime *et al.*, 1988)

A standard matrix comprising a species by sample array was constructed. In addition, a second matrix comprising a species by attribute array was constructed. Therefore, where the attribute was present for a species, a score of 1 was assigned, and where absent, a score of 0 was assigned. In cases where a species might exhibit either one of two alternative attributes, a score of 0.5 was assigned to each attribute (0.3 was assigned in the case of three potential attributes being exhibited, and so on). Each row of the species by sample matrix was then cross-multiplied by each column of the species by attribute matrix, in order to produce each individual cell of a new attribute by sample matrix. This matrix therefore contained information relating to the proportion (%) of each attribute within each sample.

A constrained ordination of the attribute data in relation to the environmental data was conducted using CCA. Although the number of attributes was large, it was less than the

overall number of samples, and therefore the approach was valid (ter Braak and Smilauer. 1998). Model construction followed the procedure detailed in section 4.2.2.2.

Table 4.2.1 Attributes present for vegetation within independent sites sampled during 1999 and 2000; based on Grime *et al.* (1988), Jermy *et al.* (1982), Stace (1997) and various biological flora records (*Journal of Ecology*). †Based on mean yearly species lists. ††Attributes significant ($p<0.05$) under Monte-Carlo permutation for CCA ordination (ter Braak and Smilauer, 1998); see Tables 4.3.7 and 4.3.8 for further details.

Attribute Grouping	Attribute type	Attribute present in vegetation sampled†	Attribute used as predictor variable††
Life history (LH)			
1	Summer annual	✓	-
2	Summer or winter annual	-	-
3	Biennial	✓	-
4	Monocarpic perennial	✓	✓
5	Perennial/annual	-	-
6	Polycarpic perennial	✓	✓
7	Monocarpic or polycarpic perennial	-	-
Life form (LF)†††			
1	Phanerophyte (woody; buds >250mm above soil)	✓	-
2	Chamaephyte (woody/herbaceous; buds <250mm but above soil)	✓	-
3	Hemicryptophyte (Herb; buds at soil level)	✓	✓
4	Geophyte (Herb; buds below soil level)	✓	✓
5	Helophyte (Marsh plant)	✓	✓
6	Hydrophyte (Aquatic plant)	✓	✓
7	Therophyte (Perennating as seeds)	✓	-
8	Wetland species (facultatively 5 or 6)	✓	-
Canopy structure (CS)			
1	Rosette (leaves confined to basal rosette, or a prostrate stem)	✓	✓
2	Semi-rosette (stems leafy, but largest leaves towards base)	✓	✓
3	Leafy (no basal rosette or size differentiation)	✓	✓
Canopy height (CH)			
1	<100 mm	✓	-
2	101-299 mm	✓	-
3	300-599 mm	✓	✓
4	600-999 mm	✓	✓
5	1.0-3.0 m	✓	✓
6	3.1-6.0 m	-	-
7	6.1-15.0 m	✓	-
8	>15.0 m	✓	-
Lateral spread (LS)			
1	Limited in extent and duration (therophytes)	✓	✓
2	<100 mm diameter (perennial with compact, unbranched tussocks)	✓	✓
3	100-250 mm (perennial with rhizomes and tussocks)	✓	-
4	251-1000 mm (perennial)	✓	-
5	>1000 mm (perennial)	✓	✓
Dispersule and germinule form (DG)			
1	Fruit (or part of, e.g. nutlet or mericarp)	✓	✓
2	Seed	✓	✓
3	Spore	✓	-
4	Dispersule a fruit, germinule a seed (e.g. Berries)	✓	-
5	Germinule a seed, dispersed within fruit or as a seed	✓	-
6	Bulbils	-	-
7	Bulbils or seeds not produced	✓	-

4.3. Results

4.3.1. Environmental gradients driving species composition, and associated vegetation attributes

4.3.1.1. Field data

Ordination by environmental variables 1999

For the forty-two 1999 wetland samples analysed using a constrained CCA ordination (Lochwinnoch site L3 excluded), 5 environmental variables were shown to be significant drivers of species assemblage within the sites ($p<0.05$ under Monte-Carlo permutation; Table 4.3.1). These variables were: pH ($p=0.005$), redox potential of the substrate (RED: $p=0.005$), percentage shade (SHA: $p=0.03$), maximum average water table level (MAX: $p=0.045$), and groundwater potassium content ($\log_e$K: $p=0.040$). This followed the removal of variables (from the initial 19) which had a VIF>20 (Table 4.3.1a). Water level fluctuation ($\log_e$FLU) was not significant at $p\leq0.05$ ($p=0.10$), but is included for illustrative purposes.

The first axis of the ordination was significant ($p=0.01$), as were all axes combined ($p=0.005$) (Table 4.3.2b). The first two axes combined explained 47.2% of the species-environment relationship alone, whilst all four axes explained 80.1% of this relationship (Table 4.3.2a).

The arrangement of sites and of the community types they represent (as defined in Chapter 3) can be seen in Figure 4.3.1. Shade is closely correlated to the first axis of the ordination, and the G6 (NVC community, M2) mire sites, with relatively high levels of shade, are most clearly differentiated from the G2 (M23) rush pasture sites along this gradient. G5 (S9b) sites are characterised by higher pH values (circumneutral to basic), and also increasing levels of groundwater potassium. In contrast, the G6 (M2) bog pool community types are associated with more acidic, and potassium-poor groundwater conditions.

The swamp associations of G1 (S27a) and G5 (S9b) are generally associated with a higher average level of maximum inundation, and more reducing substrate conditions. However, the sites classified within G4 (S27a) are more variable in relation to these two gradients. One feature which does characterise this group is generally more acidic substrate conditions.

A number of the rush-pasture samples (M23b) of G2 are associated with relatively high levels of groundwater fluctuation (suggesting intermittent flooding and drawdown), while

the G5 (S9b), and G1 (S27a) samples are associated with generally more stable levels of inundation.

Ordination by collective vegetation variables 1999

Five collective vegetation variables were found to significantly influence the ordination of the site and species data collected for the 42 sites during 1999, under a Monte-Carlo permutation (Table 4.3.3b), from an original pool of 19 variables permuted. These were stem density (STDE: p=0.005), canopy height (CAHT: p=0.005), nearest neighbour distance (NENE: p=0.005), species richness/m^2 (NOSP: p=0.005), and biomass at 0-10cm (B1: p=0.02). Two further variables which were not significant at p<0.05, but which have been included for illustrative purposes were, average stem diameter (STDI: p=0.095), and percentage litter cover (LITT: p=0.055).

The first axis of the ordination was significant (p=0.005), as were all axes combined (p=0.005) (Table 4.3.4b). The first two axes combined explained 43.7% of the species-environment relationship alone, whilst all four axes explained 73.2% of this relationship (Table 4.3.4a).

The ordination diagram in Figure 4.3.2 shows that stem density is closely correlated with axis 1 of the ordination, and that the G2 (M23b) *Juncus* pasture and G3 (M9b) *Carex* mire samples are characterised by relatively high stem density values per m^2. The opposite of this trend is generally true for the G4 (S27a) *Carex* fen, G5 (S9b) swamp, and G6 (M2) bog pool samples. Nearest neighbour distance follows the same pattern, being greatest where stem density is lowest; however, the two variables were not autocorrelated (represented in the low VIF: see Table 4.3.3a), suggesting that they may pick up different aspects of the structure of the vegetation (e.g. between tussock and non-tussock forming vegetation). In addition, average stem diameter also follows a similar pattern across the ordination, with larger stems present where stem density is lower (G4, G5, and G6: see Figure 4.3.2).

Canopy height tends to be greatest in G1 (S27a) fen samples, and lowest in G3 (M9b) mire, G4 (S27a) fen and G6 (M2) bog pool samples. Biomass in the lower strata of the canopy (0-10cm) is conversely greatest amongst the latter three community types, and highest amongst samples of the first type.

Ordination by dominant population traits 1999

Five dominant population traits were found to significantly influence the ordination of the site and species data collected for the 42 sites during 1999, under a Monte-Carlo permutation (Table 4.3.5b), from an original pool of 11 variables permuted. These were canopy area (CA: p=0.005), total leaf area per ramet (RamTLA: p=0.005), total number of leaves per ramet (RamLV: p=0.005), total number of reproductive structures per ramet (RamRE: p=0.02), and ramet height (RamHT: p=0.005). Two further variables which were not significant at $p \leq 0.05$, but which have been included for illustrative purposes were dry weight of reproductive structures per ramet (RamDWR: p=0.09), and specific leaf area (SLA: p=0.105).

The first axis of the ordination was significant (p=0.005), as were all axes combined (p=0.005) (Table 4.3.6b). The first two axes combined explained 41.5% of the species-environment relationship alone, whilst all four axes explained 71.5% of this relationship (Table 4.3.6a).

The ordination diagram in Figure 4.3.3 shows that all variables are relatively closely associated with axis 1 of the ordination, with the exception of number of leaves per ramet, and total leaf area per ramet. Therefore, G1 (S27a) *Carex* fen and G2 (M23b) rush pasture samples are generally characterised by dominant populations having a greater percentage canopy cover, greater ramet height, greater specific leaf area (i.e. thinner leaves), and a greater number of reproductive structures, and reproductive structure dry weight overall. In contrast, the values of these variables tend to be lower amongst the samples of the other four groups (Figure 4.3.3). An increase in total leaf area appears to coincide quite strongly with a decrease in the number of leaves per ramet for the dominant populations. However, any relationship between these variables and the ordination of any particular group is less clear, suggesting more variety between groups for these measured variables than for the others.

Table 4.3.1 CCA Variable Conditional Effects for all environmental data, 1999. (a) All environmental variables; (b) Significant environmental variables ($p<0.05$) following Monte-Carlo permutation. See table 3.2.1 for explanation of codes.

(a)

Variable	Variance Inflation Factor
Min	30.5
pH	**3.5**
Sha	**1.9**
Red	**3.0**
log_eK	**2.8**
log_eCl	**13.4**
log_eMg	**11.5**
$log_eSO_4^{2-}$	**1.6**
Cur	22.2
Max	**10.9**
$log_eNO_3^-$	**2.3**
log_eFlu	**4.6**
log_eMn	**2.1**
leNa	21.2
Bare	**1.5**
log_eCa	**8.0**
log_eF	**2.3**
log_eCon	**6.3**
log_eFe	**1.7**

(b)

Variable	LambdaA	*P*	F
pH	**0.39**	**0.005**	**2.05**
Red	**0.37**	**0.005**	**2.05**
Sha	**0.30**	**0.030**	**1.64**
Max	**0.26**	**0.045**	**1.49**
log_eK	**0.27**	**0.040**	**1.50**
$log_eSO_4^{2-}$	0.21	0.200	1.24
log_eFlu	0.23	0.100	1.34
log_eMn	0.21	0.270	1.17
log_eCl	0.18	0.400	1.07
log_eMg	0.19	0.305	1.12
log_eNO_3	0.18	0.460	1.02
Bare	0.15	0.590	0.89
log_eF	0.14	0.675	0.80
log_eCon	0.13	0.820	0.79
log_eCa	0.15	0.720	0.84
log_eFe	0.12	0.835	0.68

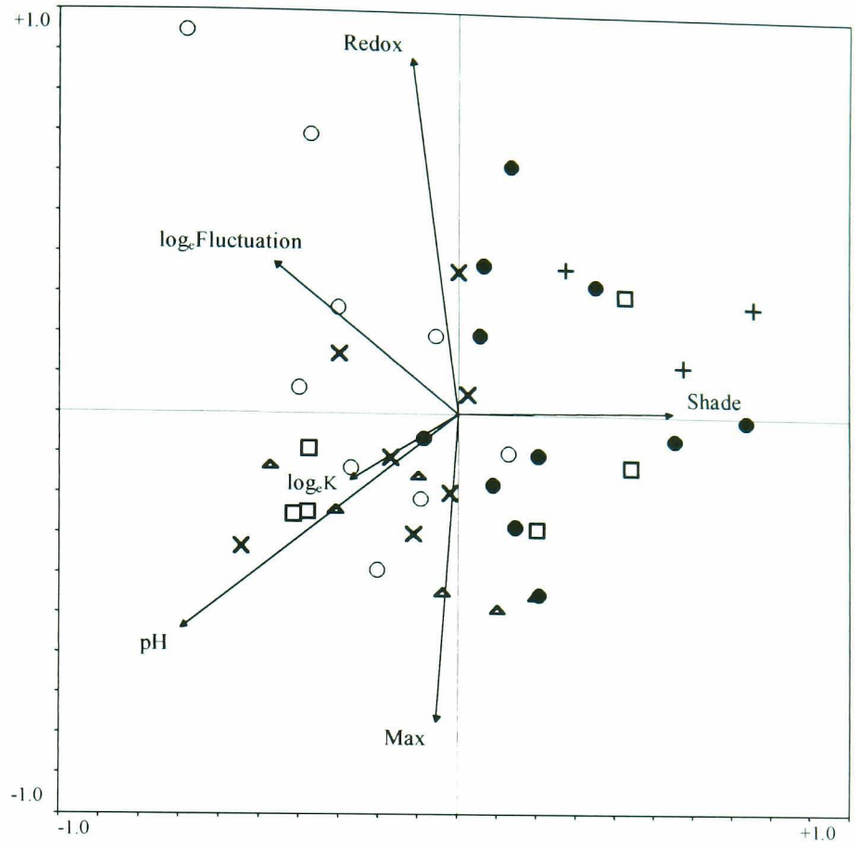


Figure 4.3.1 CCA ordination of site and species data constrained upon environmental variables, 1999. □ = G1 (S27a); O = G2 (M23b); × = G3 (M9b); ● = G4 (S27a); △ = G5 (S9b); + = G6 (M2).

Table 4.3.2 Summary of CCA output with site data constrained upon environmental variable data, 1999. (a) CCA axis scores for first four axes; (b) significance of axes under Monte-Carlo permutation.

(a)

Axes	1	2	3	4	Total inertia
Eigenvalues	.449	.392	.340	.247	7.912
Species-environment correlations	.873	.897	.853	.789	
Cumulative percentage variance					
of species data	5.7	10.6	14.9	18.1	
of species-environment relation	25.2	47.2	66.2	80.1	
Sum of all unconstrained eigenvalues					7.912
Sum of all canonical eigenvalues					1.783

(b)

Test of significance of first canonical axis: eigenvalue =	0.449
F-ratio = 2.105	
P-value = 0.010	
Test of significance of all canonical axes: Trace =	1.783
F-ratio = 1.697	
P-value = 0.005	

Table 4.3.3 CCA Variable Conditional Effects for collective vegetation variables, 1999. (a) All collective vegetation variables; (b) significant environmental variables ($p<0.05$) following Monte-Carlo permutation. See table 3.2.2 for explanation of codes.

(a)

Variable	**Variance Inflation Factor**
log_eSTDE	**6.4**
log_eCAHT	**12.3**
NENE	**4.6**
NOSP	**2.5**
log_eB2	31.6
BT	27.5
log_eSTDI	**3.87**
asinLITT	**2.4**
log_eNT	199.4
log_eBNT	73.8
log_eN3	**12.9**
log_eN1	160.9
log_eBN2	78.3
log_eN2	29.1
log_eBN3	1594
log_eB3	1317
BN1	**17.7**
log_eB1	**6.1**
log_eREPR	**3.1**

(b)

Variable	LambdaA	*P*	F
log_eSTDE	**0.50**	**0.005**	**2.68**
log_eCAHT	**0.38**	**0.005**	**2.11**
NENE	**0.33**	**0.005**	**1.87**
NOSP	**0.28**	**0.005**	**1.62**
log_eB1	**0.26**	**0.020**	**1.51**
log_eSTDI	0.23	0.095	1.40
asinLITT	0.24	0.055	1.39
log_eREPR	0.17	0.510	1.02
BN1	0.17	0.420	1.02
log_eN3	0.16	0.465	0.99

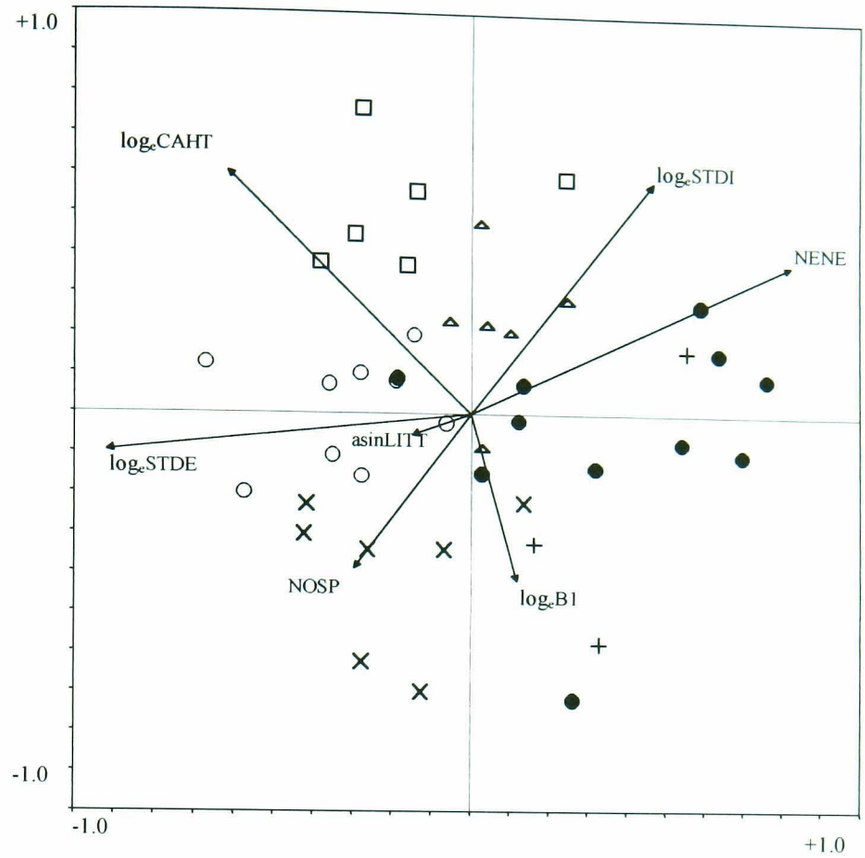


Figure 4.3.2 CCA ordination of site and species data constrained upon collective vegetation variables, 1999. □ = G1 (S27a); O = G2 (M23b); × = G3 (M9b); ● = G4 (S27a); △ = G5 (S9b); + = G6 (M2).

Table 4.3.4 Summary of CCA output with site data constrained upon collective vegetation variable data, 1999. (a) CCA axis scores for first four axes; (b) significance of axes under Monte-Carlo permutation.

(a)

Axes	1	2	3	4	Total inertia
Eigenvalues	.542	.428	.371	.281	7.912
Species-environment correlations	.946	.943	.882	.808	
Cumulative percentage variance					
of species data	6.9	12.3	17.0	20.5	
of species-environment relation	24.4	43.7	60.6	73.2	
Sum of all unconstrained eigenvalues					7.912
Sum of all canonical eigenvalues					2.218

(b)

Test of significance of first canonical axis: eigenvalue =	0.542
F-ratio = 2.105	
P-value = 0.005	
Test of significance of all canonical axes: Trace =	2.218
F-ratio = 1.892	
P-value = 0.005	

Table 4.3.5 CCA Variable Conditional Effects for Dominant population(s) traits. 1999 (a) all dominant population traits; (b) significant dominant population traits ($p<0.05$) following Monte-Carlo permutation. See table 3.2.3 for explanation of codes.

(a)

Variable	Variance Inflation Factor
RamCA	**1.6**
log_eRamTLA	**10.8**
log_eRamLV	**1.9**
log_eRamRE	**2.2**
log_eRamHT	**2.6**
log_eRamDWR	**3.0**
log_eSLA	**2.6**
log_eRamDWS	4.4
log_eRamDWT	9.7
log_eRamTLL	7.4
log_eRamDWL	6.1

(b)

Variable	LambdaA	*P*	F
RamCA	**0.47**	**0.005**	**2.50**
log_eRamTLA	**0.33**	**0.005**	**1.82**
log_eRamLV	**0.32**	**0.010**	**1.83**
log_eRamRE	**0.30**	**0.015**	**1.69**
log_eRamHT	**0.28**	**0.010**	**1.65**
log_eRamDWR	0.24	0.095	1.37
log_eSLA	0.23	0.105	1.37

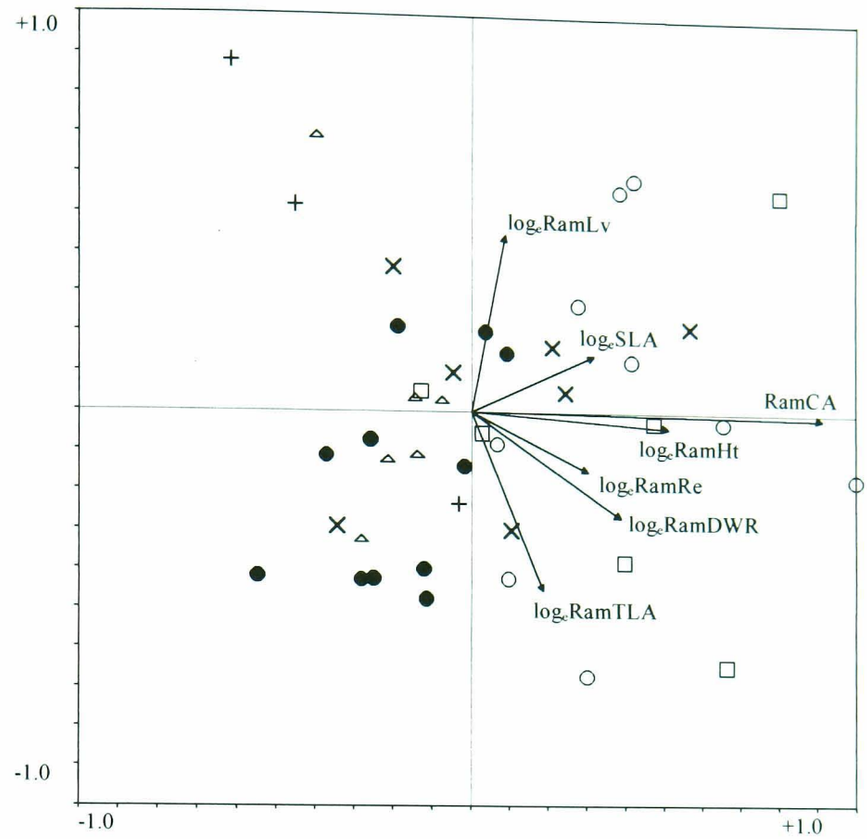


Figure 4.3.3 CCA ordination of site and species data constrained upon dominant population trait variables, 1999. □ = G1 (S27a); O = G2 (M23b); × = G3 (M9b); ● = G4 (S27a); △ = G5 (S9b); + = G6 (M2).

Table 4.3.6 Summary of CCA output with site data constrained upon dominant population trait data, 1999. (a) CCA axis scores for first four axes; (b) significance of axes under Monte-Carlo permutation.

(a)

Axes	1	2	3	4	Total inertia
Eigenvalues	.515	.386	.337	.313	7.912
Species-environment correlations	.907	.890	.894	.893	
Cumulative percentage variance					
of species data	6.5	11.4	15.6	19.6	
of species-environment relation	23.7	41.5	57.1	71.5	
Sum of all unconstrained eigenvalues					7.912
Sum of all canonical eigenvalues					2.169

(b)

Test of significance of first canonical axis: eigenvalue =	0.515
F-ratio = 2.366	
P-value = 0.005	
Test of significance of all canonical axes: Trace =	2.169
F-ratio = 1.834	
P-value = 0.0050	

Table 4.3.7 Variable Conditional Effects for species attribute percentage representation per sample station for combined independent 1999 and 2000 sites, showing attributes significant ($p<0.05$) under Monte-Carlo permutation. See Table 4.2.1 for explanation of codes

Variable	LambdaA	*P*	F	Variance Inflation Factor
Bryo	0.49	0.005	3.82	4.6
LF3	0.39	0.005	3.08	14.6
LS2	0.33	0.005	2.75	3.7
CS1	0.33	0.005	2.81	18.9
CS3	0.25	0.005	2.26	17.6
leLF4	0.27	0.005	2.46	2.1
leLS5	0.27	0.005	2.49	2.6
LH6	0.25	0.005	2.41	12.6
LF5	0.25	0.005	2.52	9.1
LH4	0.21	0.005	2.18	1.9
DG2	0.22	0.005	2.30	13.2
CS2	0.19	0.005	2.02	18.0
DG1	0.21	0.005	2.35	22.8
LF6	0.17	0.015	1.97	1.8
CH5	0.16	0.005	1.93	5.6
CH4	0.17	0.010	2.01	3.8
CH3	0.17	0.010	2.14	5.7
$\log_e$LS1	0.15	0.005	1.93	2.1

Table 4.3.8 Summary of CCA output axis scores for first four axes for site data constrained upon species attribute percentage representation per sample station for combined independent 1999 and 2000 sites

Axes	1	2	3	4	Total inertia
Eigenvalues	.573	.446	.407	.373	7.234
Species-environment correlations	.969	.979	.945	.947	
Cumulative percentage variance					
of species data	7.9	14.1	19.7	24.9	
of species-environment relation	12.8	22.7	31.8	40.1	
Sum of all unconstrained eigenvalues					7.234
Sum of all canonical eigenvalues					4.485

4.3.1.2. Literature derived attribute data

All of the original 17 attributes permuted in a CCA ordination (see Table 4.2.1), plus percentage bryophyte cover (Bryo), were found to significantly influence the ordination of the 54 independent sites sampled during 1999 and 2000 (see Table 4.3.7). The VIF exceeded 20 for one attribute type alone (DG1: dispersule and germinule form = a fruit, or part of), but at only 22.8 was retained within the analysis.

Due to the large number of variables found to be significant ($p\leq0.05$), the production of a CCA biplot was not considered appropriate. However, the first two axes combined

explained 22.7% of the species-environment (attribute) relationship, while the cumulative total explained for all four axes combined was 40.1% (Table 4.3.8).

4.3.2. Predicting eco-hydrological relationships in wetland vegetation from field-derived variables

4.3.2.1. Predicting vegetation variables

A total of eighteen models were produced for the predication of vegetation variables with environmental variables alone, or in combination with other vegetation variables acting as predictors (Tables 4.3.9 and 4.3.10). The models explained from 15% of the variation in the dependent variables (R^2=0.15; p=0.049) for the prediction of number of leaves per ramet of the dominant population(s) ($\log_e$RamLV) (see Table 4.3.9b), to 67% (R^2=0.67; p<0.001) for the predication of stem density ($\log_e$STDE: Table 4.3.9a). The model predicting stem density ($\log_e$STDE) contained 5 independent predictor variables, but the response of pH alone was linear, making the model relatively complex.

The predictive power of the models exceeded 50% ($R^2 \geq$ 0.5) for six of the vegetation variables being predicted (Tables 4.3.12 and 4.3.13). Species richness (S) was strongly predicted (R^2=0.64; p<0.001: Table 4.3.12; equation 1). The equation contained five predictor variables in total. Two environmental variable predictors were redox potential (RED), and Cl content of the groundwater (CL). The suggestion from the cubic function of both of these variables was that they increased initially in relation to increasing species richness, decreased, and then increased again. One collective vegetation variable, stem density (STDE) appeared to increase in a linear fashion in relation to increased species richness, while the dominant population trait of dry weight of reproductive structures per ramet ($\log_e$RamDWR) appeared to decrease linearly. A further dominant population(s) predictor was number of leaves per ramet ($\log_e$RamLV), with a quadratic function in the equation suggesting an initial decrease followed by an increase in the values of the variable relative to increasing species richness.

Using test data from 2000, the model had some success in predicting species richness from the new values, although the limits were noisy (Figure 4.3.4). The model for predicting species richness was relatively specific (due to the relatively large number of predictor variables employed the model would be expected to have a limited envelope of applicability). However, on using the entire test data set (which contained new sites outwith those from which data was collected to build the models), two values predicted from test

data from repeat sites (Insh marshes 7 and 8) were poorly predicted (Figure 4.3.4a); the correlation between predicted and observed values was low (r=0.08) as a result.

The application of the model predicting species richness was further investigated on two sub-sets of the test data. Firstly, due to a general drying of the Insh Marsh transect 1 stations (see sections 2.3.2 and 2.3.3, chapter 2), several highly oxidising redox values were recorded. Therefore, samples with redox values falling outwith the parameters of the model construction data were removed from the analysis. The correlation between observed and predicted values was slightly increased (r=0.19), and it can be seen from Figure 4.3.4b that of the sixteen predicted values remaining, nine were within approximately two units of the corresponding observed values. Values for the independent Endrick Marsh sites are particularly well predicted, suggesting a more general applicability of the model within a poor fen wetland type. However, with the exception of station 6 at Wood of Cree, the values are generally under-predicted for this site. This may be due to the generally species rich nature of the site (see section 2.3.1, Chapter 2), coupled with other variable values which are generally more comparable to the other sites sampled. The removal of these samples (Figure 4.3.4c) increased the correlation between predicted and observed values (r=0.49).

For the models predicting stem density ($\log_e$STDE) both the specific model, and a more general model (with fewer predictor variables) had a predictive power of greater than 50% (R^2= 0.67; p<0.001 and R^2 = 0.55; p<0.001 respectively: see Table 4.3.12, equation 2). The more specific model contained a relatively large number of environmental variables acting as predictors. The NO_3^- content of the groundwater ($\log_e NO_3$) had a cubic function within the equation, suggestive of an initial increase, followed by a decrease and subsequent increase of the variable in relation to increasing stem density. Average water level had quadratic response expressed relative to increasing stem density, with an initial decrease followed by an increase (i.e. greatest stem density in wetter sites). Both level of water table fluctuation and minimum water level were expressed as the opposite of this (with an initial increase relative to increasing stem density). The relationship between pH and stem density appeared more linear, with an increased stem density as groundwater samples became less acidic.

The use of test data from 2000 showed once again that the limits of the prediction were relatively noisy (Figure 4.3.5), with eleven of the total of twenty predicted values being within approximately one unit (on a logarithmic scale) of their corresponding observed values (r=0.41). The removal of samples with extreme NO_3 values (Figure 4.3.5b), outwith those of the original model parameters, led to a reduction in the correlation between observed and predicted values (r=0.37), as did the use of Insh marsh sites alone as test data

(r=0.16). Once again, a number of values were well predicted for the independent Endrick Marsh samples (with the exception of E1), and a number of repeat sample Insh Marsh station values were not predicted well (Figure 4.3.5a). As with the models for species richness, this may have been due in part to relatively dramatic changes in average water table levels between years. However, in contrast, the values predicted for most of the Wood of Cree sites were relatively good.

The more general model for prediction of stem density ($\log_e$STDE) (Table 4.3.12, equation 2b) which utilised equivalent quadratic functions for both average water table level and level of water table fluctuation, and a linear function for pH alone, still gave a relatively good prediction (R^2 =0.55; p <0.001). When tested using all of the 2000 test data, this model gave a slightly higher correlation (r=0.44) between predicted and observed values for stem density, than had the more specific model (Figure 4.3.6a). In this instance, sixteen of the twenty predicted values were within half to one unit of the observed values. This including several samples from Insh Marsh stations (I3, 9, 7 and 8) which had been poorly predicted for the more specific model (Table 4.3.12, equation 2a). In general, the values predicted for the Wood of Cree samples were unimproved by the use of a more general model, although the removal of samples with extreme NO_3 values once again improved the correlation overall (r= 0.48) between observed and predicted values.

Four trait variables measured within the dominant populations of the wetland vegetation were strongly predicted ($R^2 \geq 0.5$) from a number of environmental variables alone (Table 4.3.13). All four models constructed were general, in that the number of variables used was relatively small (three or four only).

Number of leaves per ramet ($\log_e$RamLV) was relatively well predicted (R^2= 0.58; p <0.001) from four groundwater and substrate environment predictor variables (Table 4.3.13, equation 1). Average water table level (WAT) was expressed by a cubic response, suggesting an initial decrease in this variable in relation to an increase in number of leaves per ramet, followed by a decrease. The response suggested in relation to increasing minimum water table levels (MIN) (i.e. samples with less drawdown) was the opposite of this. A decrease in redox potential (RED) followed by an increase in relation to increasing number of leaves per ramet was suggested by the quadratic function of this predictor, and an increased number of leaves appeared to be linked to a linear decrease in pH value (i.e. progressively more acid samples).

When the model was tested with the total complement of data form 2000 (Figure 4.3.7a), the correlation between predicted and observed values was relatively low (r =0.10), and values for three of the samples (I7, I8 and E1) were greatly over-predicted. The removal of these three samples, plus sample I6, due to redox values outwith the parameters of the original model data, increased the correlation between observed and predicted values only slightly (r =0.16). However predicted values for thirteen of the remaining sixteen samples were within approximately one unit of their corresponding observed values (Figure 4.3.7b). The correlation between predicted values and observed values for Insh Marsh samples alone (minus those removed due to excessive redox values: Figure 4.3.7c) was slightly higher again (r= 0.34). Predicted values for two of the samples (E3, and E4) almost exactly corresponded to observed values.

Canopy area (%) was relatively well predicted (R^2 =0.59; p <0.001) from four groundwater variables (Table 4.3.13, equation 2) Average water table level had a cubic function relative to increasing canopy area., with the suggestion that an initial decrease in water table level was linked to increasing canopy area (followed by an increase, and an eventual decrease). A quadratic function for degree of water level fluctuation (logeFLU) suggested that an increase, followed by a decrease in fluctuation was linked to an overall increase in canopy area. A linear increase in both minimum water table level (MIN), and pH suggested a link between an increase in these variables and an increase in canopy area.

There was no correlation between the observed values for the test data and the values predicted from these by the model, and in addition an number of values were greatly over-estimated (i.e. predictions for E1, I6-9, and W4-6 all exceeded 100%). However, across the range of sites, eight of the predicted canopy area values were within 10% of the observed values (Figure 4.3.8a). Predicted values for Insh Marsh sites alone (Figure 4.3.8b) gave a low correlation to observed values (Figure 4.3.8c), with this again possibly due to the dryer nature of a number of sites over subsequent years.

Total leaf area ($\log_e$RamLV) was well predicted (R^2 =0.54; p <0.001) from three groundwater variables alone. (Table 4.3.13, equation 3) Average level of groundwater fluctuation ($\log_e$FLU) followed the same pattern as when predicting canopy area (above). Cl content of the groundwater (CL) was characterised by a quadratic function, with total leaf area appearing to continue to increase as Cl content increased, and then fell once again conductivity (CON) exhibited a positive linear increase relative to increasing leaf area. Once again, a number of sites had values which were greatly over-predicted by the model, but these were sites where conductivity levels were outwith the range of those used to produce

the original model (Wood of Cree sites), or were repeat sites which were dryer than in previous years (e.g. I6 and I9). However, eleven of the twenty predicted values closely corresponded to the observed values from which they were derived, and a further three predicted values (E1, I8, and W3) were within approximately two units of their corresponding observed values. From Figure 4.3.9b, it can be seen that a number of the predicted values for Insh Marsh sites almost exactly corresponded to the observed values from which they were predicted.

The ratio of the dry weight of stems to the dry weight of leaves (DWS:DWL) was significantly predicted (R^2 =0.53; p =0.002), from three groundwater variables (Table 4.3.13, equation 4). An increase in the biomass of stem in relation to the biomass of leaves (i.e. less 'leafy' individuals) was characterised by cubic functions for average water level (WAT), minimum water table level (MIN), and average level of water table fluctuation ($\log_e$FLU). While it appeared that decreasing 'leafiness' was linked to an initial increase in both water level and degree of water table fluctuation, an initial decrease in minimum water table level appeared to be a good predictor (i.e. more drawdown, in association with a greater degree of fluctuation overall).

Predicted values showed a negative correlation with the observed values when the model was applied to the entire set of test data (r =-0.10), and to a sub-set of Insh Marsh sites alone (r =-0.23: see Figure 4.3.10). However, only one value (for Insh Marshes station 8), was greatly over-estimated, and half of the values predicted were within half a unit of their corresponding observed values.

In addition total average dry weight of reproductive structures per ramet ($\log_e$RamDWR) was relatively well predicted (R^2 =0.31; p =0.003) from one groundwater variable alone (average level of groundwater fluctuation: $\log_e$FLU), which took a cubic function within the model (Table 4.3.10; Appendix 8b). An initial decrease in level of fluctuation, followed by an increase and subsequent decrease appeared to characterise increasing reproductive structure dry weight.

4.3.2.2. Predicting hydrological and groundwater-related environmental variables

A total of nineteen models were produced for the prediction of groundwater and associated variables from various vegetation variables (Table 4.3.11). Eight of these were specific models, using a relatively large number of combined collective vegetation variables and dominant population traits to act as predictors (Table 4.3.11a), and their predictive power ranged from R^2 =0.40 (p =0.010) for the prediction of conductivity, to R^2 = 0.79 (p <0.001)

for the prediction of minimum average water table level (MIN). An additional four of the eight models, predicting average water table level (WAT), average level of water table fluctuation ($\log_e$FLU), redox potential (RED), and pH (PH), predicted over 50% of the variation (R^2 >0.5) for the given variable.

General models also were produced for each of these same eight dependent variables (Table 4.3.11b), and also for three additional variables ($\log_e$Cl, $\log_e NO_3$, and $\log_e SO_4^{2-}$). The predictors for these minimal models were reduced to a maximum of three in each case, and consisted only of collective vegetation variables (i.e. variables which could easily be measured in the field, or be quickly derived from field measurements, and required minimal specialised knowledge of the species assemblage). Once again the form taken by the predictor variables was not always a simple linear one, and predictive equations contained quadratic and/or cubic functions in some instances.

The predictive power of the various models ranged from R^2 =0.14 (p =0.013) for the prediction of groundwater sulphate ($\log_e SO_4^{2-}$), to R^2 =0.55 (p <0.001) for the prediction of minimum average water table level (MIN). This was the only general model for which the predictive power exceeded 50% ($R^2 \geq 0.5$).

Average water table level relative to ground surface level (WAT) was strongly predicted (R^2 =0.77; p <0.001) from five basic measures of the dominant population(s) (Table 4.3.14, equation 1), hence the model was relatively specific. An increase in water table level was predicted by a quadratic response in the number of leaves per ramet ($\log_e$RamLV), characterised by an initial decrease in number of leaves. Canopy area (RamCA), and ratio of dry weight of stems to dry weight of leaves (DWS:DWL) also characterised an increase in number of leaves via a cubic function, but this time with an initial increase in the variables. Dry weight of reproductive structures per ramet (RamDWR) and number of reproductive structures per ramet ($\log_e$RamRE) were both characterised by an increase followed by a decrease (quadratic function) in their values, relative to increasing water table level.

The predicted values correlated well with the observed values (r =0.72: see Figure 4.3.11). In the case of some observed values which were negative (i.e. average water level below ground surface), the predictions were not particularly good. However, these tended to be the same sites which were predicted poorly for other variables previously mentioned (i.e. E1, I7, I9), and probably for the same reasons of exceptionally low water table levels in the year that the test data was collected within some of the systems. Overall, from a total observed range of average water table levels of approximately 35cm (c.-30cm to c.5cm), eleven of the sites

had predicted values which were within 5cm of their corresponding observed values. Probably due to the factors discussed earlier (i.e. progressive drawdown between years) some of the Insh Marsh sites were not very well predicted (Figure 4.3.11b).

A specific model and a more general model predicting minimum water table level (MIN) was produced (Table 4.3.14, equation 2a and b). The specific model (R^2 =0.77; p <0.001) utilised one collective vegetation variable, species richness (S: cubic function, with an initial increase in relation to less drawdown), and three dominant population traits as predictor variables. The dominant population traits were, canopy area (RamCA: again with a cubic function with an initial increase), number of reproductive structures per ramet ($\log_e$RamRE: quadratic function, increasing, and then decreasing in relation to more permanently inundated conditions), and ratio of dry weight of stems to dry weight of leaves (DWS:DWL). This final variable exhibited a cubic relationship, with an initial decrease in 'leafiness' of individuals in relation to wetter conditions. The more general model (R^2 =0.55; p <0.001) utilised three collective variables alone: species richness (S) took the same form as for the specific model. Stem density (STDE) characterised increased minimum water table levels by increasing, and then decreasing. Total biomass per m^2 (BT) predicted decreased drawdown as its values decreased linearly.

The values predicted by the specific model for the full test data set were well correlated with the observed values (r =0.65: see Figure 4.3.12a). As with the predictions for average water table levels (Figure 4.3.11), values were poorly predicted for the same sites. However, thirteen of the predicted values were within approximately 5cm of the observed values (over a total observed range running from c.-40cm to c.20cm). Once again, some of the Insh marsh sites with extreme values measured during the collection of test data were poorly predicted (Figure 4.3.12b).

The figures predicted by the general model for the complete test data set were less well correlated with the observed values (r =0.39: see Figure 4.3.13), and the Insh marsh sites with extreme values were again poorly predicted. However, eight of the values predicted were close to those observed (i.e. within 5cm).

Average level of water table fluctuation ($\log_e$FLU) was relatively well predicted (R^2 =0.63; p < 0.001) from three collective vegetation variables: nearest neighbour (NENE), total biomass per m^2 (BT) and number of reproductive structures per m^2 ($\log_e$REPR), and two dominant population variables: dry weight of reproductive structures per ramet ($\log_e$RamDWR) and ratio of dry weight of stems to dry weight of leaves (DWS:DWL). Both nearest neighbour

distance and dry weight of reproductive structures per ramet exhibited a quadratic response, with an initial decrease, and then an increase in values relative to increasing fluctuation (Table 4.3.11). Biomass exhibited a cubic response, suggesting an initial increase in relation to increasing fluctuation, followed by a decrease, and finally increasing again. The number of reproductive structures overall increased relative to an increase in water level fluctuation, while the amount of dry weight of stems to leaves decreased (i.e. the plants comprising the dominant populations became relatively less 'leafy').

Average level of water table fluctuation was well predicted from the observed values for a number of samples. Twelve of the predicted values were within approximately one unit of their corresponding observed values, with seven of these predicted values being very close to the observed (Figure 4.3.14a). The sites with values not well predicted included the Insh Marsh sites (Figure 4.3.14b) which had been subject to drying, and some of the Wood of Cree samples. This may have been due to the relatively general low biomass encountered for the samples comprising this site (see Chapter 3, Figure 3.3.10), leading to under-prediction of groundwater fluctuation values.

Redox potential (RED) was strongly predicted (R^2 =0.68; p <0.001) from three dominant population traits (Table 4.3.14). The number of reproductive structures per ramet ($\log_e$RamRE) exhibited a quadratic response in relation to increasing redox values (i.e. more aerobic substrate conditions), suggesting an initial decrease followed by an increase in values for the variable. The ratio of dry weight of stems to shoots followed the same pattern, suggesting that the dominant populations became progressively less 'leafy', and then increasing in 'leafiness' once again as substrate redox values became more aerobic. The response of the third predictor variable, species richness (S) followed the opposite pattern, with a suggested increase followed by a decrease as redox values increased.

Although there was a visible correlation (r =0.44) between predicted and observed redox values when the predictive equation was applied to the full complement of test data (Figure 4.3.15a), the precision of the predictions was relatively poor in some cases. Seven of the predicted values were within approximately 50mV of the corresponding observed values. Once again, the values which were least-well predicted included repeat sites which had dried from the subsequent year (Figure 4.3.15b), plus a number of Endrick Marsh sites. Under-prediction of values for Wood of Cree sites was possibly due again to the use of species richness as a predictor variables, and samples from this site having relatively higher species richness values than those from other sites.

The model produced for the prediction of pH values (Table 4.3.14, equation 5) explained over 60% of the variation in the samples (R^2 =0.62; p <0.001), from three collective vegetation variables, and three dominant population traits. Average stem diameter ($\log_e$STDI) exhibited a negative relationship in the equation, suggesting a decrease as pH values increased (i.e. stems became narrower as groundwater samples became more circumneutral to alkaline), as did the ratio of biomass present at 0-10cm to that at 10-20cm ($\log_e$B1:B2) (i.e. less biomass in the lower strata of the vegetation relative to the amount higher up in the canopy). Number of reproductive structures ($\log_e$REPR) in the vegetation as a whole had a positive linear function, suggesting an increase as pH values increased. Linear functions suggested that number of leaves per ramet ($\log_e$RamLV) decreased as pH values increased, while canopy area increased. The final predictor variable (number of reproductive structures per ramet of the dominant population(s): $\log_e$RamRE) was the only variable with a non-linear response function. An initial linear increase was indicated relative to increased pH values, followed by a decrease in number of reproductive structures overall.

Although the values predicted from the entire set of test data by the model were negatively correlated to the observed values (r =-0.56), many of the values were well predicted (Figure 4.3.16). Values ranged from approximately pH 5.5 to 7.2, and fourteen of the total predicted values were within 0.2 units of their corresponding observed value. The least-well predicted values were for the Insh Marsh sites which had seen drying from the previous years, and a number of Wood of Cree samples (Figure 4.3.16b), possibly due to the more strongly acidic conditions encountered within this site (see Table 2.3.6, Chapter 2).

The equations for models with R^2 <0.50 are given in full in Appendix 8.

Table 4.3.9 Summary of multiple regression models for the prediction of Collective Vegetation Variables, *showing direction of initial linear phase of response. See Tables 3.2.1-3.2.3 for explanation of codes and units of measurement. (a) specific models with several environmental and vegetation trait predictors; (b) general minimal models with restricted environmental predictor variables.

(a)

Dependent Variable (y)	Independent Predictor Variables (b)	Response*	Regression R^2	p
Species Richness (S)	RED	Cubic+	0.64	=<0.001
	$\log_e$Cl	Cubic+		
	$\log_e$STDE	Linear+		
	$\log_e$RamLV	Quadratic-		
	$\log_e$RamDWR	Linear-		
$\log_e$ Stem Density	$\log_e NO_3$	Cubic+	0.67	=<0.001
	WAT	Quadratic-		
	MIN	Quadratic-		
	$\log_e$FLU	Quadratic+		
	PH	Linear+		

(b)

Dependent Variable (y)	Independent Predictor Variables (b)	Response	Regression R^2	p
Species Richness (S)	RED	Cubic+	0.41	=0.003
	$\log_e$Cl	Cubic+		
$\log_e$ Stem Density	WAT	Quadratic-	0.55	=<0.001
	$\log_e$FLU	Quadratic+		
	PH	Linear+		
Nearest Neighbour	$\log_e$FLU	Quadratic-	0.43	=<0.001
	PH	Linear-		
$\log_e$ Canopy Height	$\log_e$CON	Linear+	0.11	=0.035
$\log_e$ Stem Diameter	$\log_e$Cl	Linear+	0.30	=<0.001
	PH	Linear-		
$\log_e$ Biomass, 10-20cm	$\log_e$FLU	Cubic+	0.37	0.004
	RED	Quadratic-		
Biomass, total	$\log_e$FLU	Cubic+	0.45	=0.006
	RED	Quadratic-		
	$\log_e$K	Cubic-		
$\log_e$ 0-10cm:10-20cm Biomass ratio ($\log_e$ B1:B2)	PH	Linear–	0.27	=0.007
	$\log_e$CON	Quadratic+		
$\log_e$ Number of Reproductive structures	PH	Linear+	0.15	=0.049
	$\log_e NO_3$	Linear+		

Table 4.3.10 Summary of multiple regression models for the prediction of dominant population traits from environmental predictor variables; see Table 4.3.13 for further explanation.

Dependent Variable (y)	Independent Predictor Variables (b)	Response	Regression R^2	p
$\log_e$ RamHT	$\log_e$K	Cubic-	0.29	=0.004
$\log_e$ RamLV	WAT MIN RED PH	Cubic- Cubic+ Quadratic- Linear-	0.58	=<0.001
RamCA	WAT MIN $\log_e$FLU PH	Cubic- Linear+ Cubic+ Linear+	0.60	=<0.001
$\log_e$ RamRE	MIN $\log_e$FLU	Quadratic+ Quadratic-	0.30	=0.009
$\log_e$ RamTLA	CON $\log_e$FLU $\log_e$CL	Linear+ Cubic+ Quadratic+	0.54	=<0.001
$\log_e$ RamDWR	$\log_e$FLU	Cubic-	0.31	=0.003
Stem:Leaf biomass ratio per Ramet (DWS:DWL)	WAT MIN $\log_e$FLU	Cubic- Cubic+ Cubic-	0.53	=0.002

Table 4.3.11 Summary of multiple regression models for the prediction of groundwater variables; see Table 4.3.13 for further explanation.. (a) specific models with several collective vegetation and dominant population trait predictors; (b) general minimal models with restricted collective vegetation predictor variables only.

(a)

Dependent Variable (y)	Independent Predictor Variables (b)	Response	Regression R^2	p
WAT	$\log_e$RamLV	Cubic-	0.77	=<0.001
	RamCA	Cubic+		
	$\log_e$RamRE	Quadratic+		
	$\log_e$RamDWR	Quadratic+		
	DWS:DWL	Cubic+		
MAX	S	Linear-	0.43	=0.018
	$\log_e$STDE	Quadratic+		
	$\log_e$RamLV	Cubic+		
	DWS:DWL	Cubic-		
MIN	S	Cubic+	0.79	=<0.001
	RamCA	Cubic+		
	$\log_e$RamRE	Quadratic+		
	DWS:DWL	Cubic-		
$\log_e$ FLU	NENE	Quadratic-	0.63	=<0.001
	BT	Cubic+		
	$\log_e$RamDWR	Quadratic-		
	$\log_e$REPR	Linear+		
	DWS:DWL	Linear-		
RED	$\log_e$RamRE	Quadratic-	0.68	=<0.001
	DWS:DWL	Quadratic-		
	S	Quadratic+		
PH	$\log_e$STDI	Linear-	0.62	=<0.001
	$\log_e$B1:B2	Linear-		
	$\log_e$RamLV	Linear-		
	RamCA	Linear+		
	$\log_e$RamRE	Quadratic+		
	$\log_e$REPR	Linear+		
$\log_e$ K	$\log_e$STDI	Quadratic-	0.43	=<0.001
	$\log_e$RamTLA	Quadratic-		
	DWS:DWL	Linear+		
$\log_e$ CON	$\log_e$RamLV	Cubic+	0.40	=0.010
	$\log_e$RamTLA	Linear+		
	$\log_e$B1:B2	Cubic+		

Table 4.3.11 (b)

Dependent Variable (*y*)	Independent Predictor Variables (*b*)	Response	Regression R^2	*p*
WAT	log_eSTDE NENE	Quadratic+ Quadratic+	0.34	=0.003
MAX	S log_eSTDE	Linear- Quadratic+	0.23	=0.019
MIN	S log_eSTDE BT	Cubic+ Quadratic+ Linear-	0.55	=<0.001
log_e FLU	NENE BT log_eREPR	Quadratic- Cubic+ Linear+	0.44	=0.002
RED	S	Cubic+	0.31	=0.002
PH	log_eSTDE NENE leB1:B2	Linear- Linear- Linear-	0.38	=<0.001
log_e K	log_eSTDI	Linear+	0.27	=0.001
log_e CL	S log_eSTDI	Quadratic- Linear+	0.27	=0.007
log_e CON	log_eCAHT log_eB2 log_eB1:B2	Quadratic+ Quadratic+ Cubic+	0.34	=0.036
log_e NO_3	S NENE log_eREPR	Linear+ Quadratic- Linear+	0.31	=0.008
log_e SO_4^{2-}	asinLITT	Quadratic+	0.14	=0.048

Table 4.3.12 Multiple regression equations (specific and minimal models) predicting collective vegetation dependent variables for $R^2 > 0.50$.

S = -13.871 +0.01991(**RED**) +11.466(log$_e$**CL**) +2.940(log$_e$**STDE**) –3.498(log$_e$**RamLV**) +0.0001887(**RED**^{2}) –0.00000128(**RED**^{3}) –5.014(log$_e$**CL**^{2}) +0.594(log$_e$**CL**^{3}) +0.816(log$_e$**RamLV**^{2}) –0.7381(log$_e$**RamDWR**)

(F = 5.489; d.f. = 10; R^2 = 0.64; p = <0.001)

(1)

log$_e$**STDE** = 4.054 –0.0462(**WAT**) –0.03722(**MIN**) +0.997(log$_e$**FLU**) +0.363(**PH**) –0.00126(**WAT**^{2}) +0.001489(**MIN**^{2}) –0.241(log$_e$**FLU**^{2}) +0.639(log$_e$**NO$_3$**) –0.405(log$_e$**NO$_3$**^{2}) +0.08018(log$_e$**NO$_3$**^{3})

(F = 6.14; d.f. = 10; R^2 = 0.67; p = <0.001)

(2a)

log$_e$**STDE** = 3.352 –0.0278(**WAT**) +0.0003852(**WAT**^{2}) +0.469(**PH**) –1.072(log$_e$**FLU**) 0.282(log$_e$**FLU**^{2})

(F = 8.930; d.f. = 5; R^2 = 0.55; p = <0.001)

(2b)

Table 4.3.13 Multiple regression equations predicting dominant population dependent variables for $R^2 > 0.50$.

---

log$_e$**RamLV** = 7.014 –0.0457(**WAT**) +0.009462(**MIN**) –0.00493(**RED**) –0.893(**PH**) +0.00003844(**RED**^{2}) +0.0005531(**WAT**^{2}) +0.00006788(**WAT**^{3}) –0.000153(**MIN**^{2}) – 0.0000264(**MIN**^{3})

(F = 4.877; d.f. = 9; R^2 = 0.58; p = <0.001)

(1)

RamCA = -153.647 –4.105(**WAT**) +1.823(**MIN**) +94.657(log$_e$**FLU**) +30.275(**PH**) +0.030(**WAT**^{2}) +0.003032(**WAT**^{3}) –71.738(log$_e$**FLU**^{2}) +14.946(log$_e$**FLU**^{3})

(F = 5.329; d.f. = 9; R^2 = 0.60; p = <0.001)

(2)

log$_e$**RamTLA** = 1.314 +4.064(log$_e$**FLU**) –3.429(log$_e$**FLU**^{2}) +0.726(log$_e$**FLU**^{3}) +0.136(log$_e$**CON**) +0.639(log$_e$**CL**) –0.0395(log$_e$**CL**^{2})

(F = 6.773; d.f. = 6; R^2 = 0.54; p = <0.001)

(3)

DWS:DWL = 2.5 –0.0116(**WAT**) +0.001598(**WAT**^{2}) –0.0000927(**WAT**^{3}) +0.02969(**MIN**) – 0.00196(**MIN**^{2}) –0.0000109(**MIN**^{3}) –1.482(log$_e$**FLU**) +0.38(log$_e$**FLU**^{2}) –0.0147(log$_e$**FLU**^{3})

(F = 3.931 d.f. = 9; R^2 = 0.53; p = 0.002)

(4)

Table 4.3.14 Multiple regression equations (specific and minimal models) predicting groundwater variables from collective vegetation and dominant population variables for $R^2 > 0.50$.

WAT = -20.838 –23.368(log$_e$**RamLV**) +1.372(**RamCA**) +6.732(log$_e$**RamRE**) +6.605(log$_e$**RamDWR**) –11.491(log$_e$**RamLV**^{2}) –0.0284(**RamCA**^{2}) +0.001287(**RamCA**^{3}) – 4.0(log$_e$**RamRE**^{2}) –0.849(log$_e$**RamDWR**^{2}) –0.845(**log$_e$RamLV**^{3}) –18.266(**DWS:DWL**) +19.305(**DWS:DWL**^{2}) –5.106(**DWS:DWL**^{3})

(F = 6.504 d.f. = 13; $R^2 = 0.77$; $p = <0.001$)

(1)

MIN = -33.154 + 5.344(**S**) +1.531(**RamCA**) +13.274(log$_e$**RamRE**) –0.856(**S**^{2}) +0.03442(**S**^{3}) – 0.0295(**RamCA**^{2}) +0.0001534(**RamCA**^{3}) –6.535(log$_e$**RamRE**^{2}) –1.864(**DWS:DWL**) +9.391(**DWS:DWL**^{2}) –3.398(**DWS:DWL**^{3})

(F = 10.08; d.f. = 11; $R^2 = 0.79$; $p = <0.001$)

(2a)

MIN = -567.438 +5.543(**S**) –1.031(**S**^{2}) +0.04672(**S**^{3}) +122.854(log$_e$**STDE**) –0.844(log$_e$**STDE**^{2}) – 0.00979(**BT**)

(F = 6.99; d.f. = 6; $R^2 = 0.55$; $p = <0.001$)

(2b)

log$_e$**FLU** = 0.160 –1.753(**NENE**) +0.407(**NENE**^{2}) +0.01581(**BT**) –0.0000234(**BT**^{2}) +0.00000001025(**BT**^{3}) –0.924(log$_e$**RamDWR**) +0.149(log$_e$**RamDWR**^{2}) +0.321(log$_e$**REPR**) – 0.283(**DWS:DWL**)

(F = 5.95; d.f. = 9; $R^2 = 0.63$; $p = <0.001$)

(3)

RED = -5.237 –125.762(log$_e$**RamRE**) +48.743(log$_e$**RamRE**^{2}) –107.299(**DWS:DWL**) +45.315(**DWS:DWL**^{2}) +24.323(**S**) –1.002(**S**^{2})

(F = 12.48; d.f. = 6; $R^2 = 0.68$; $p < 0.001$)

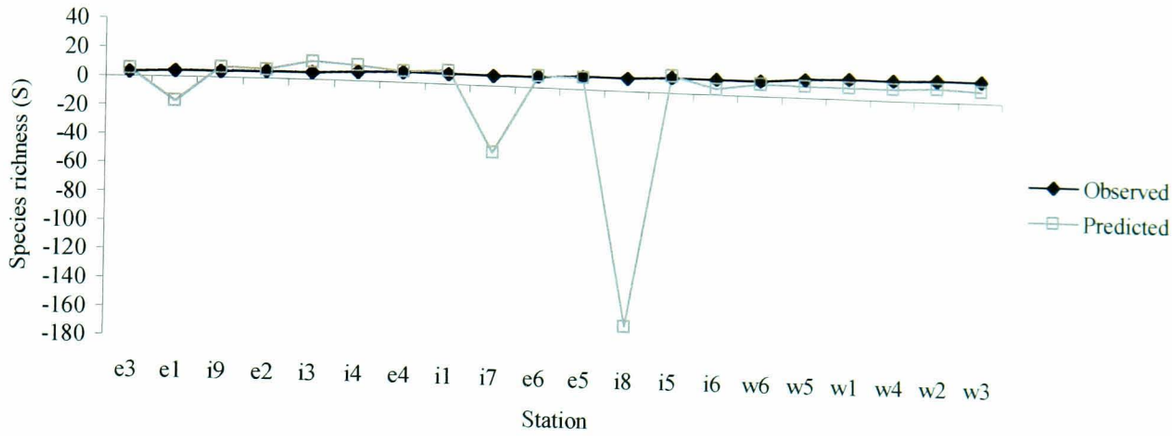
(4)

PH = 5.866 –0.296(log$_e$**STDI**) –0.11(log$_e$**B1:B2**) –0.172(log$_e$**RamLV**) +0.004367(**RamCA**) +0.519(log$_e$**RamRE**) –0.153(log$_e$**RamRE**^{2}) +0.0747(log$_e$**REPR**)

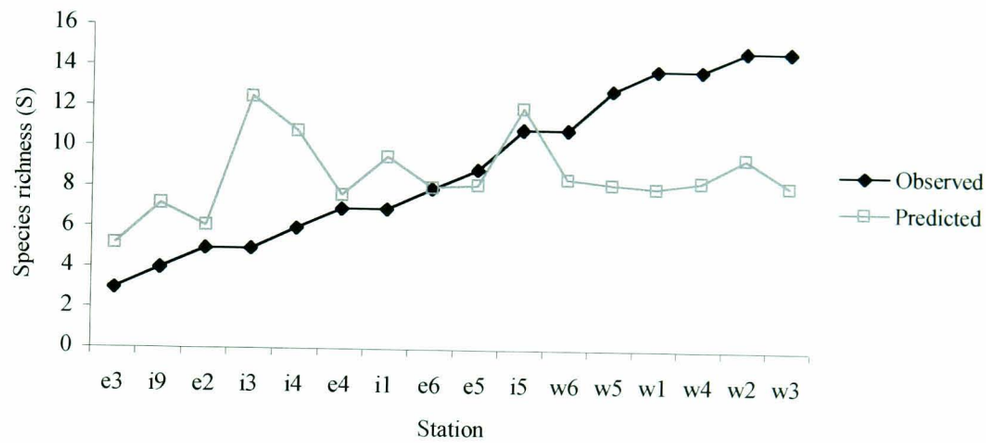
(F = 7.57; d.f. = 7; $R^2 = 0.62$; $p = <0.001$)

(5)

(a)



(b)



(c)

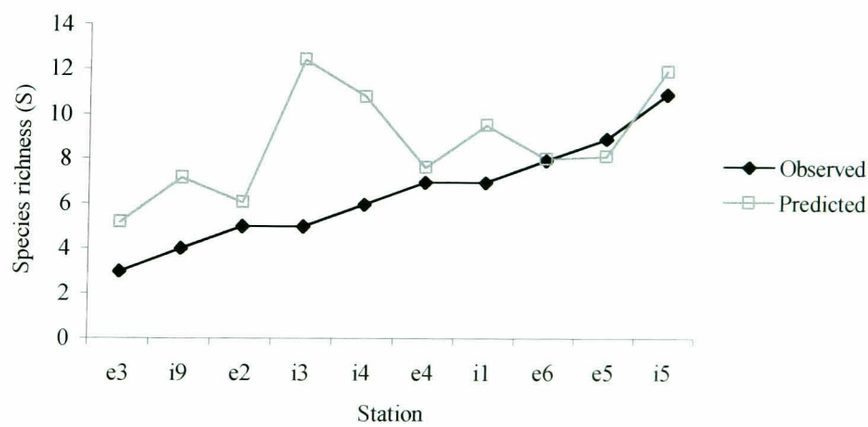
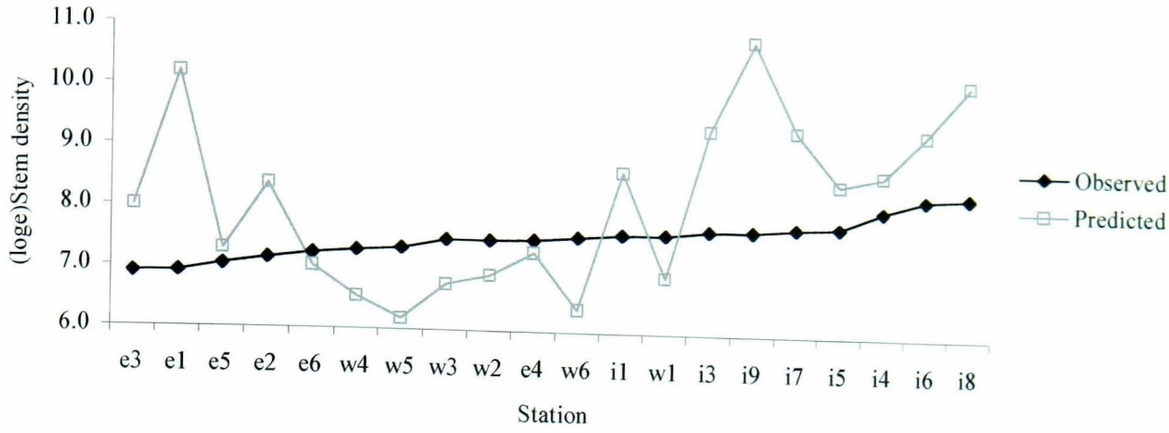
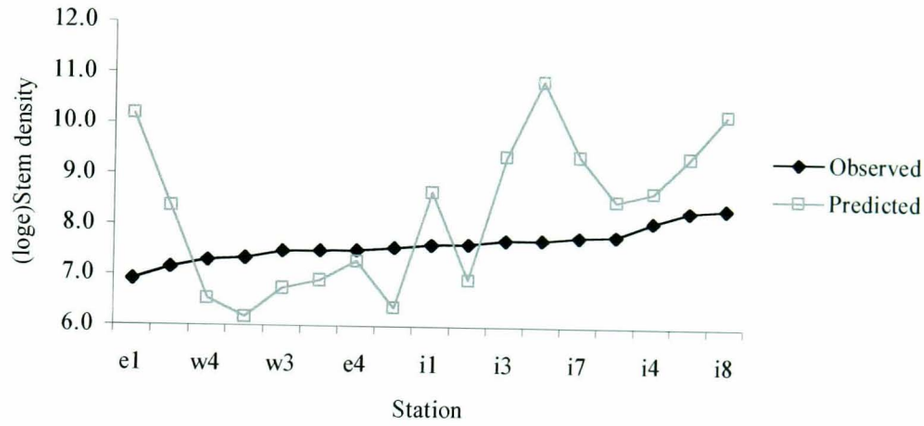


Figure 4.3.4 Rank scores of observed species number plotted against values predicted from specific model (See Table 4.3.12, equation 1). (a) all test data (r =0.08); (b) sites with extreme redox values removed (stations E1 and I6-8) (r =0.19); (c) sites with extreme redox values, and *Wood of Cree* sites removed (r =0.49).

(a)



(b)



(c)

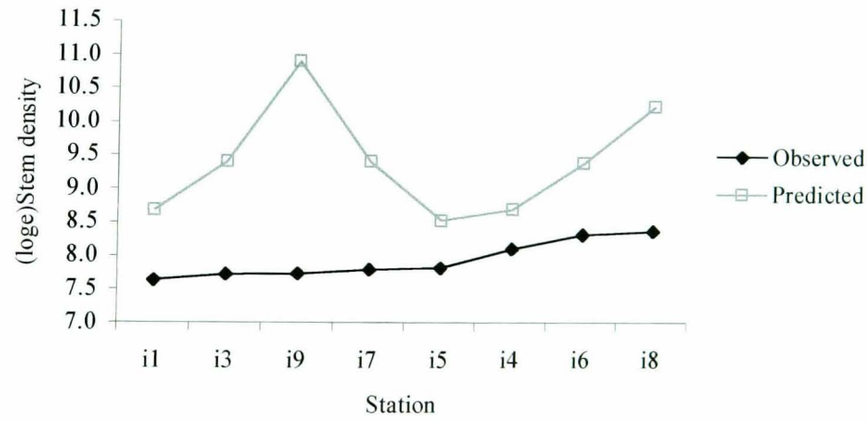
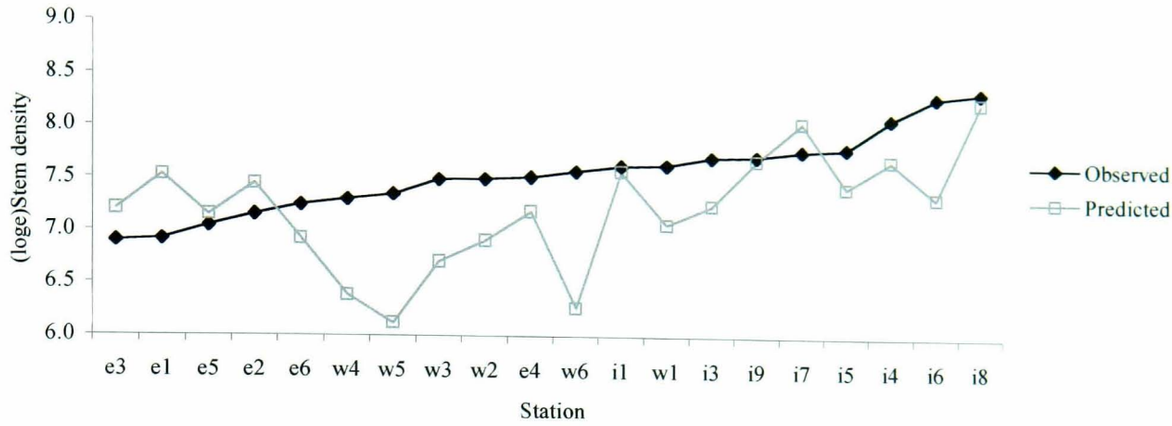


Figure 4.3.5 Rank scores of observed ($\log_e$) stem density values (m^{-2}) plotted against values predicted from specific model (See Table 4.3.12, equation 2a). (a) all test data (r =0.41); (b) sites with extreme NO_3^- values removed (stations E3, E5b and E6) (r =0.37); (c) Insh marsh sites alone (r =0.16).

(a)



(b)

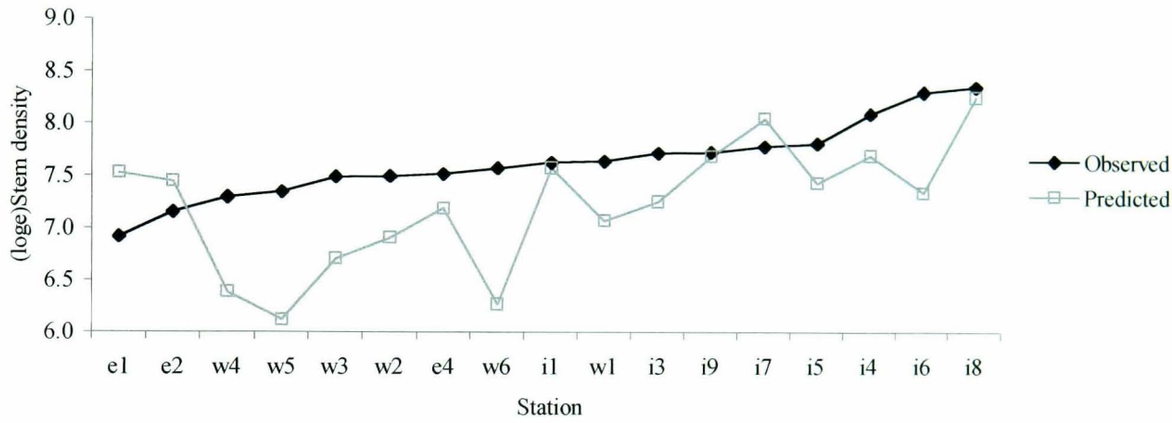
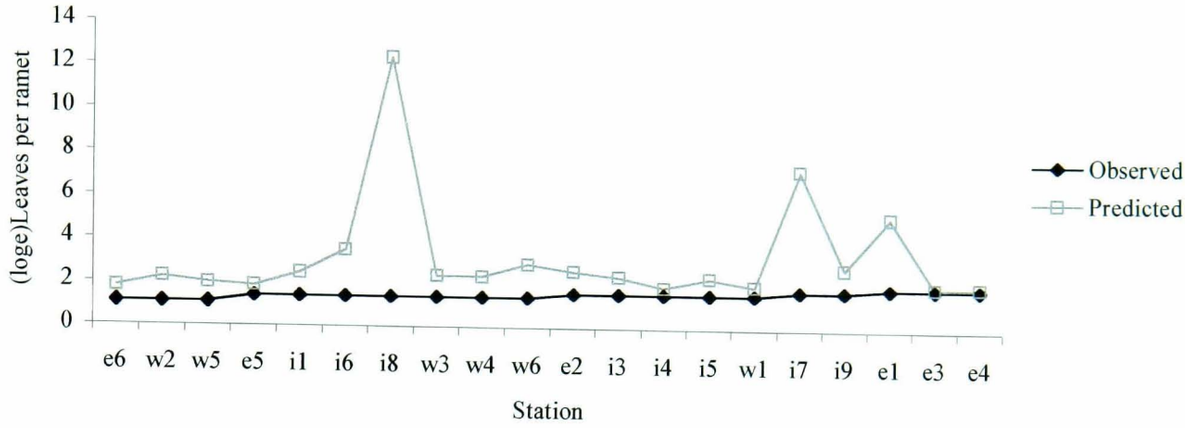
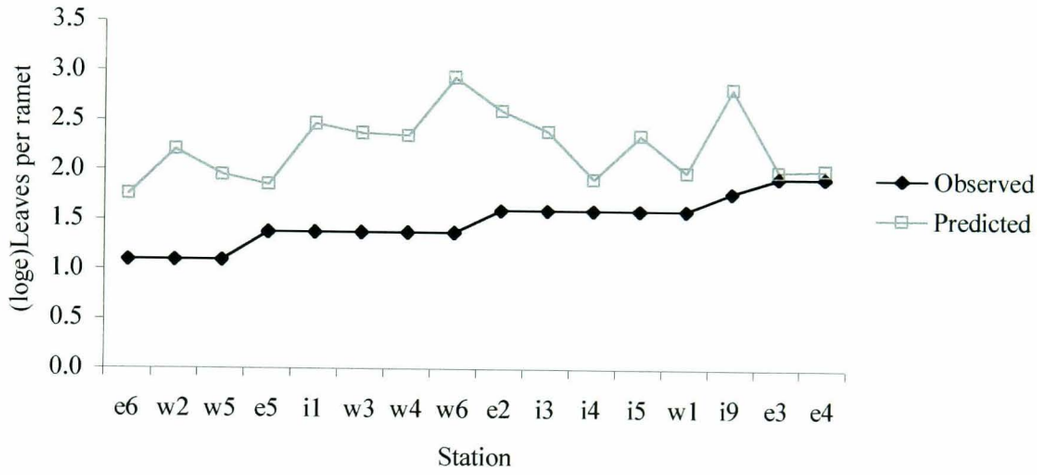


Figure 4.3.6 Rank scores of observed (log_e)stem density values plotted against values predicted from General model (See Table 4.3.12, equation 2b). (a) all test data (r =0.44); (b) sites with extreme NO_3^- values removed (stations E3, E5 and E6) (r =0.48).

(a)



(b)



(c)

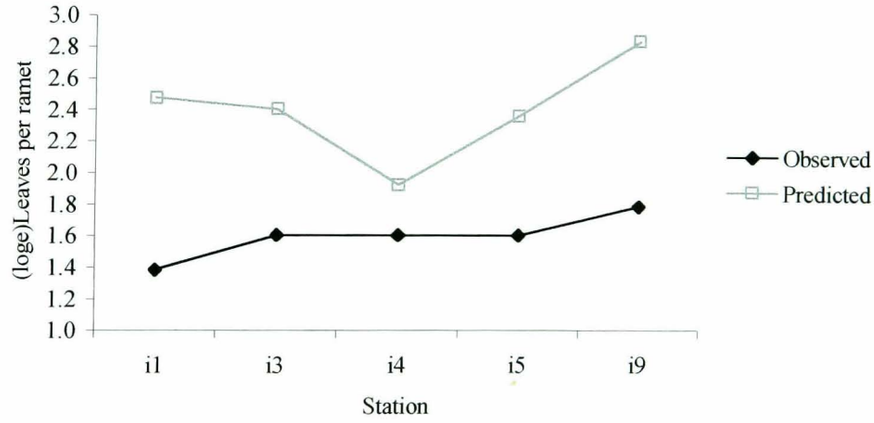
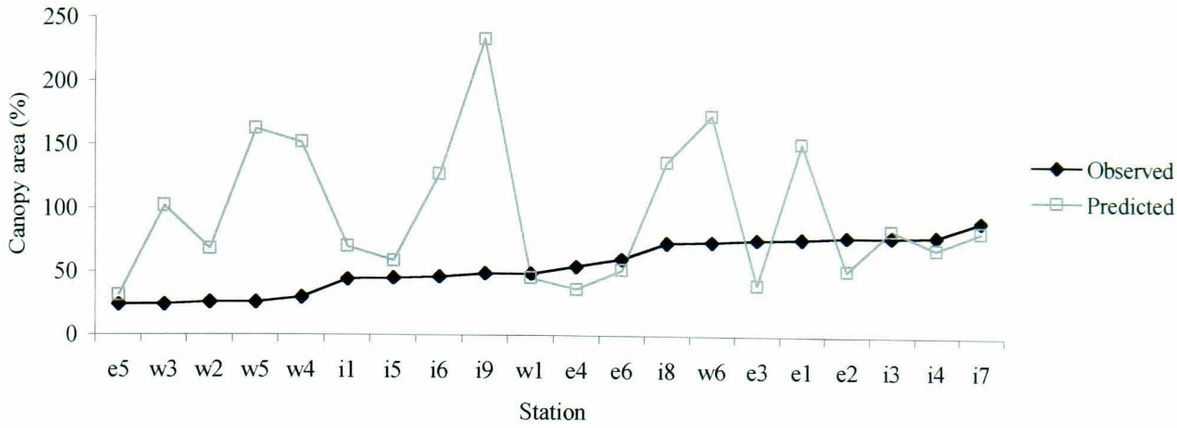


Figure 4.3.7 Rank scores of observed ($\log_e$)number of leaves per ramet of dominant population(s) plotted against values predicted from specific model (See Table 4.3.13, equation 1). (a) all test data stations (r =0.10); (b) sites with extreme redox values removed (stations E1, I6-8) (r =0.16); (c) Insh marsh sites alone (r =0.34).

(a)



(b)

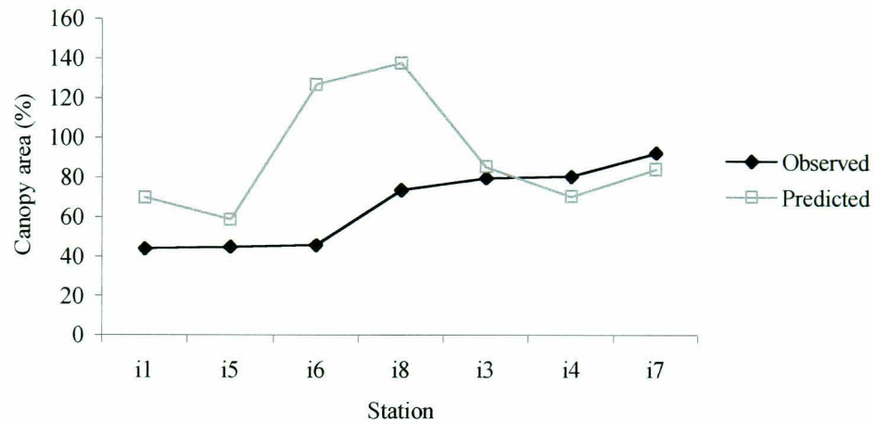
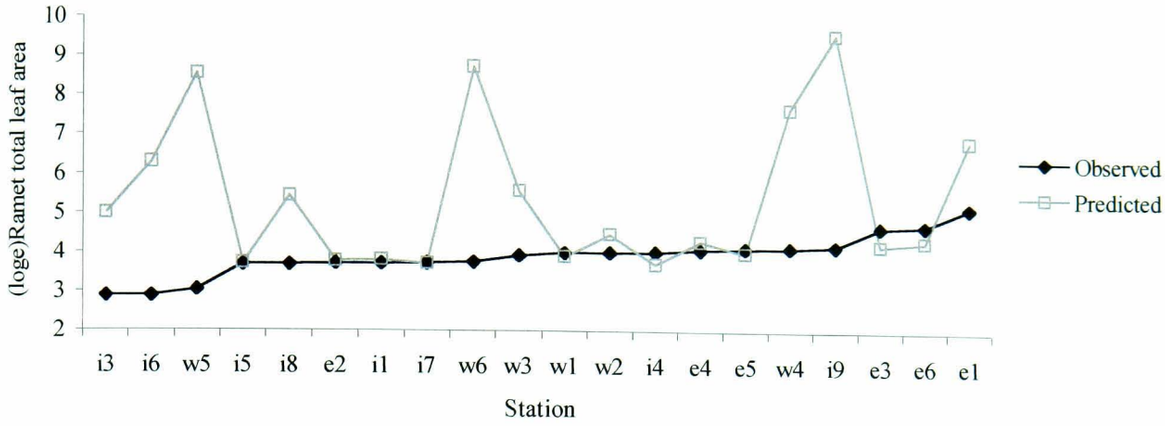


Figure 4.3.8 Rank scores of observed canopy area (%) of dominant population(s) plotted against values predicted from specific model (See Table 4.3.13, equation 2). (a) all test data (r =0); (b) Insh marsh sites alone (with I9 removed due to extreme low average water table levels) (r =0.10).

(a)



(b)

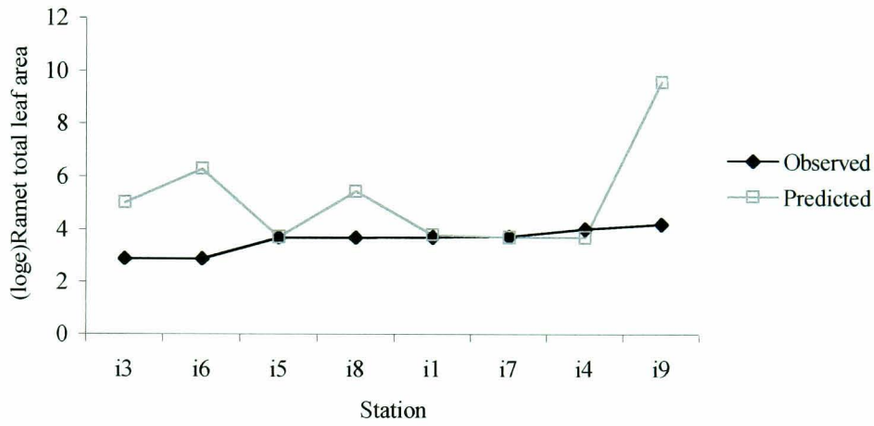
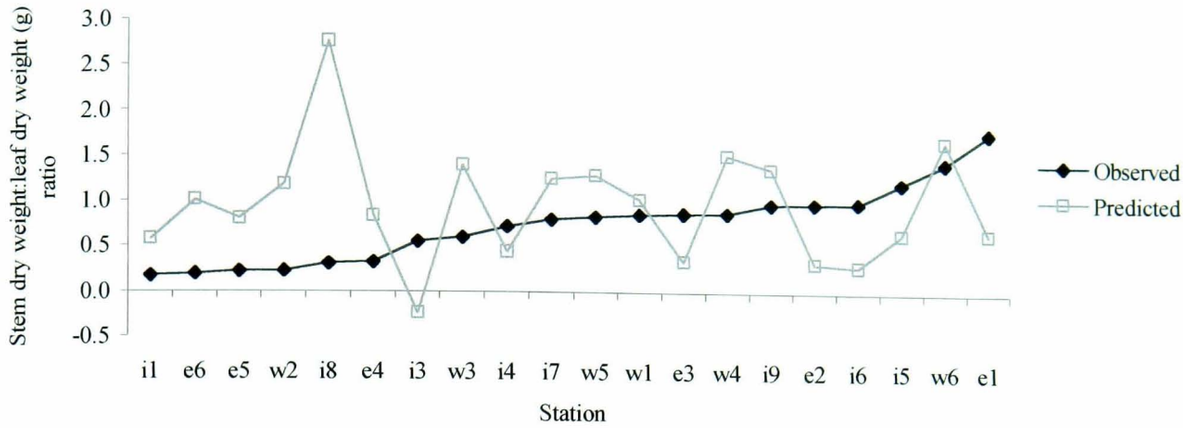


Figure 4.3.9 Rank scores of observed ($\log_e$)average total leaf area per ramet of dominant population(s) plotted against values predicted from specific model (See Table 4.3.13, equation 3). (a) all test data (r =-0.06); (b) Insh marsh sites alone (r =0.15).

(a)



(b)

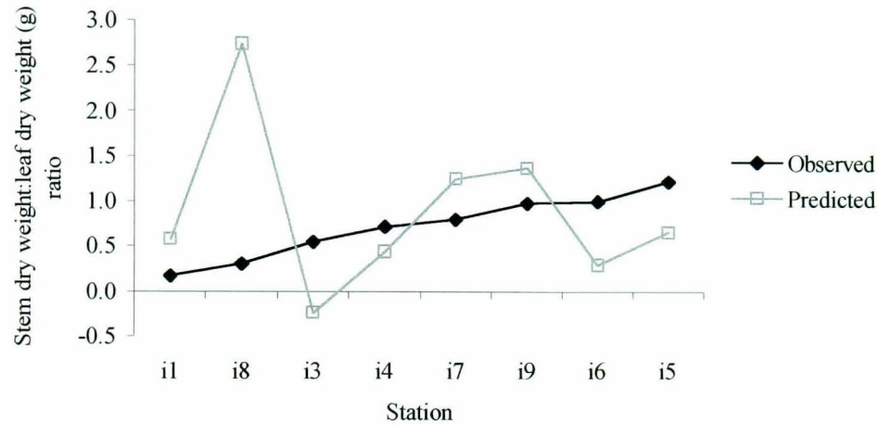
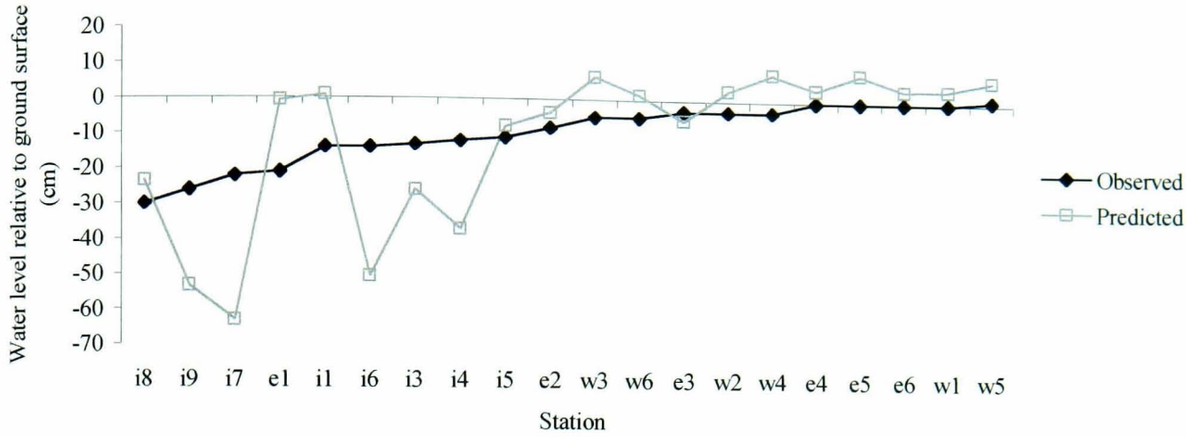


Figure 4.3.10 Rank scores of observed stem dry weight:leaf dry weight ratio (DWS:DWL) per ramet of dominant population(s) plotted against values predicted from specific model (See Table 4.3.13, equation 4). (a) all test data (r =-0.10); (b) Insh marsh sites alone (r =-0.23).

(a)



(b)

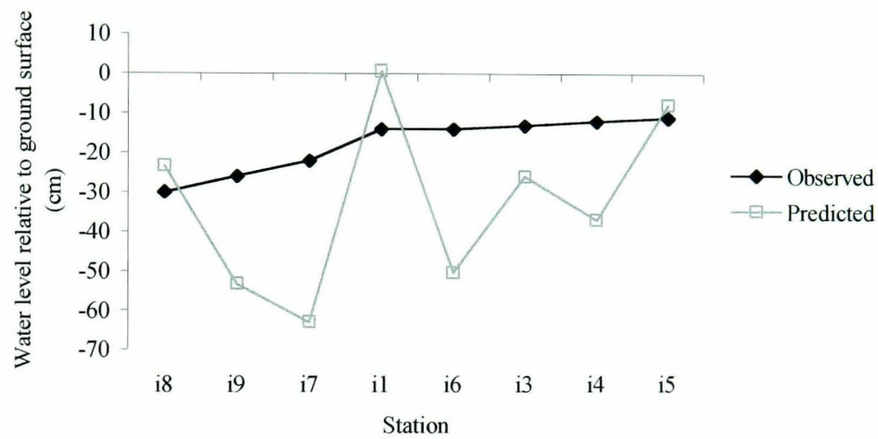
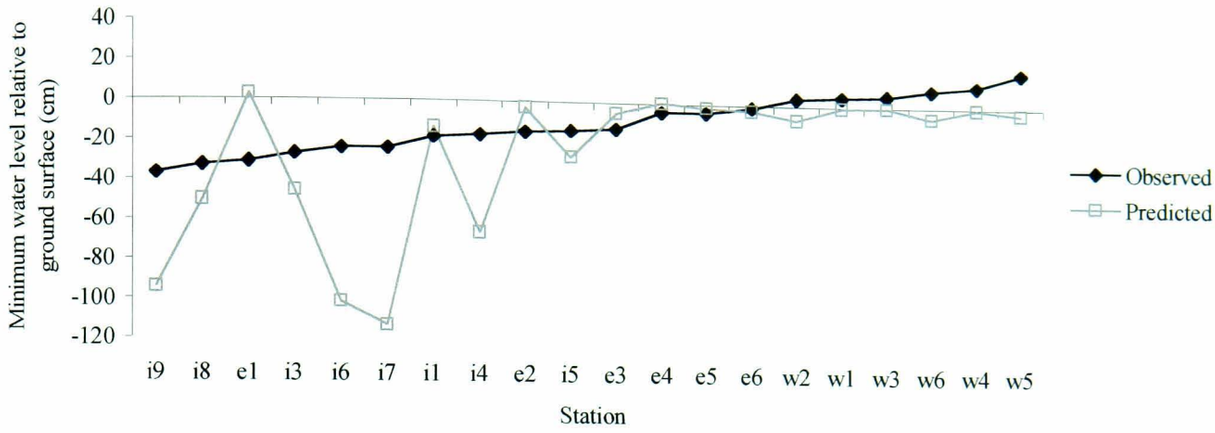


Figure 4.3.11 Rank scores of observed average water level relative to ground surface level plotted against values predicted from specific model (See Table 4.3.14, equation 1). (a) all test data (r =0.72); (b) Insh marsh sites alone (r =0.37).

(a)



(b)

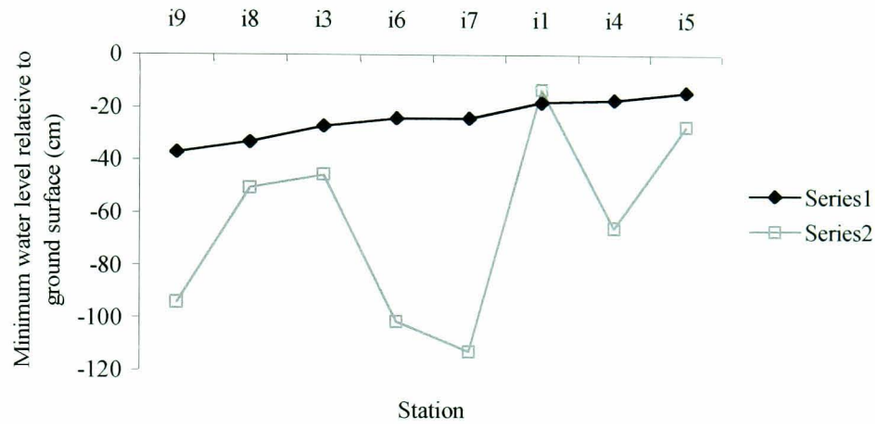


Figure 4.3.12 Rank scores of observed average minimum water level relative to ground surface level plotted against values predicted from specific model (See Table 4.3.14, equation 2a); (a) all test data (r =0.65); (b) Insh marsh sites alone (r =0.43).

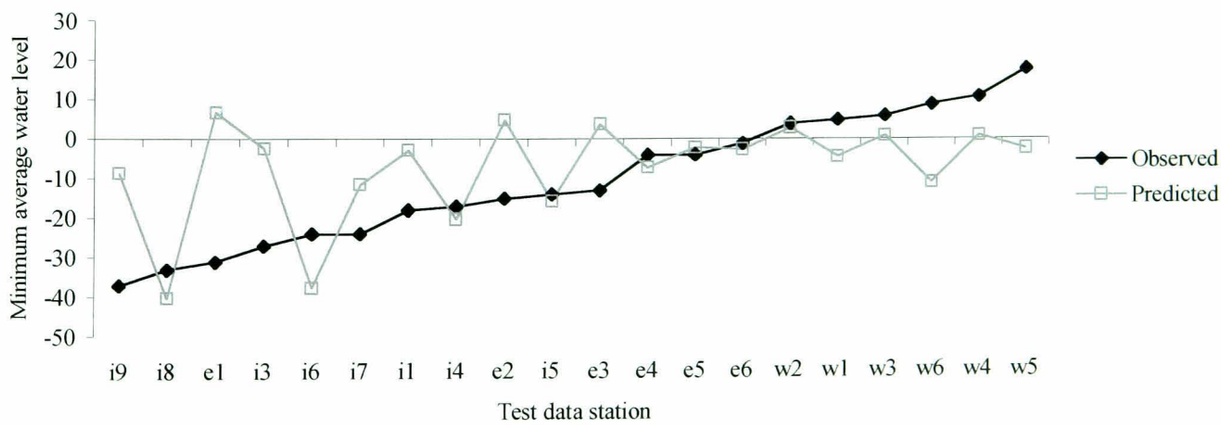
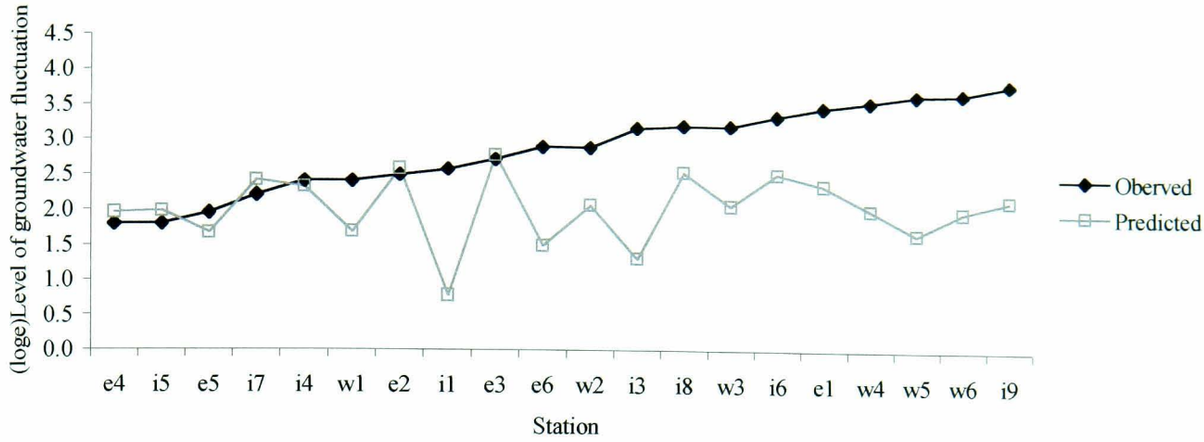


Figure 4.3.13 Rank scores of observed average minimum water level relative to ground surface level predicted from general model (See Table 4.3.14, equation 2b); predicted from all test data (r =0.39).

(a)



(b)

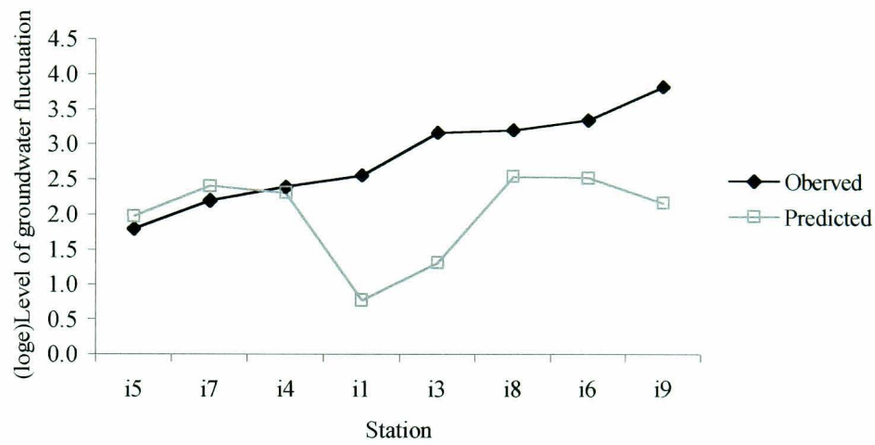
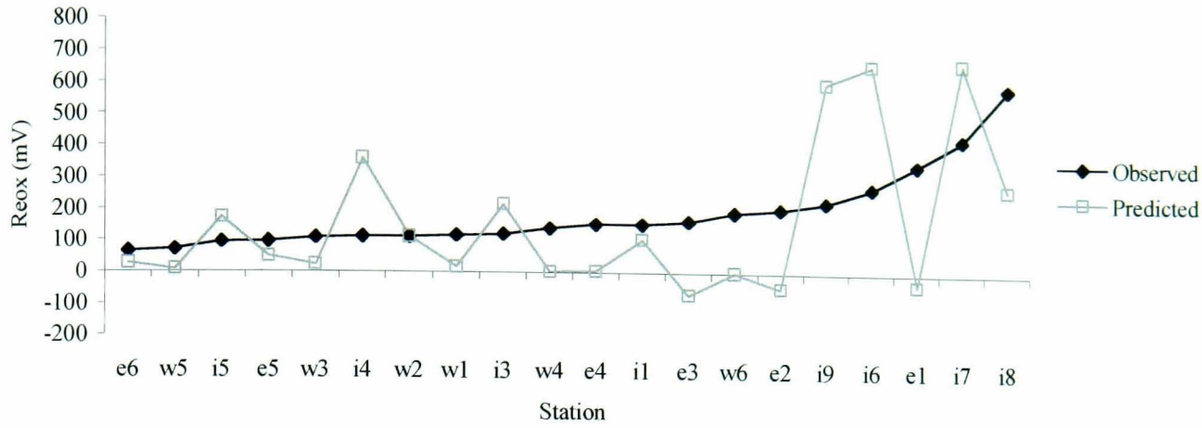


Figure 4.3.14 Rank scores of observed average level of groundwater fluctuation plotted against values predicted from specific model (See Table 4.3.14, equation 3); (a) all test data (r =0.10); (b) Insh marsh sites alone (r =0.13).

(a)



(b)

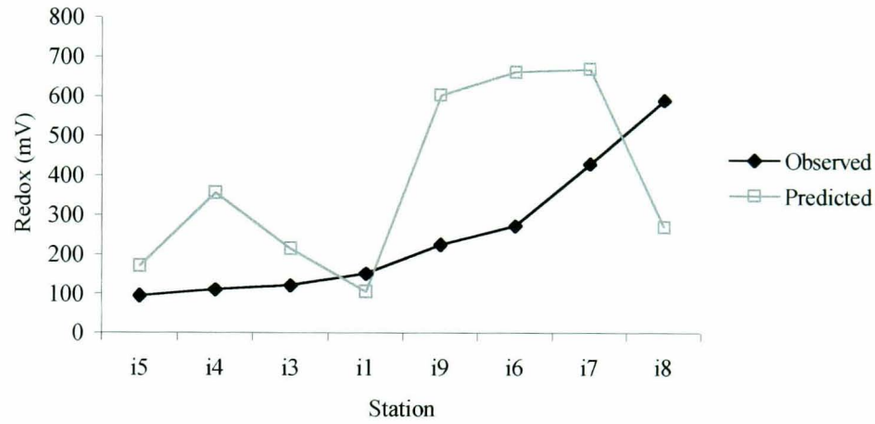
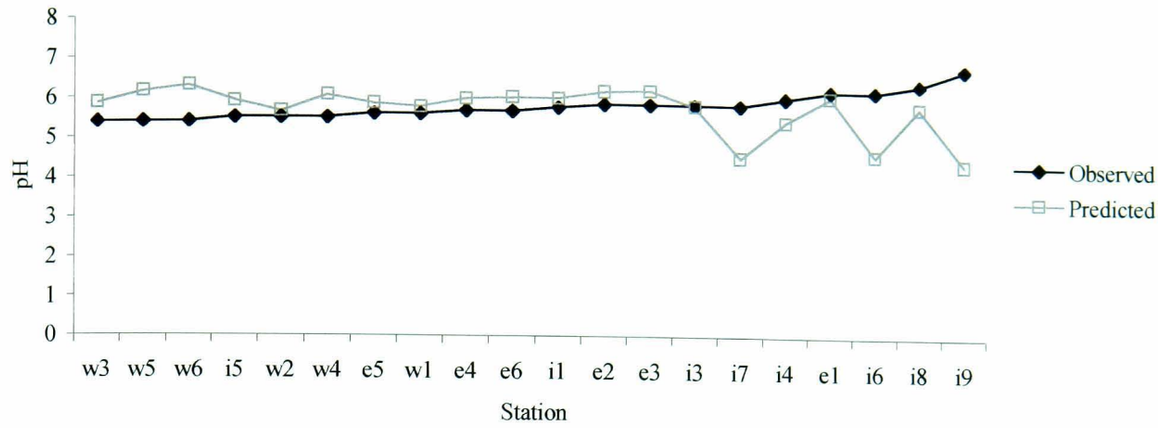


Figure 4.3.15 Rank scores of observed redox potential (mV) plotted against values predicted from specific model (See Table 4.3.14, equation 4); (a) all test data (r =0.44); (b) Insh marsh sites alone (r =0.40).

(a)



(b)

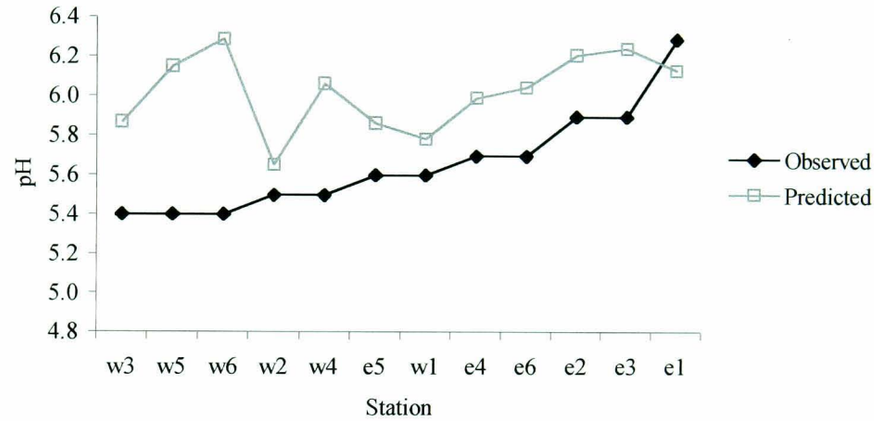


Figure 4.3.16 Rank scores of observed pH values plotted against values predicted from specific model (See Table 4.3.14, equation 5); (a) all test data (r =-0.56); (b) sites with extreme values for number of reproductive structures per ramet of dominant population(s) ((loge)RamRE) removed (stations I3-9) (r =0.32).

4.3.3. Predicting relationships between wetland attribute types and environmental variables

A total of eleven (mostly relatively specific) predictive models were produced which utilised a combination of hydrological and other environmental variables to predict the percentage presence of various attribute types amongst the wetland vegetation sampled during 1999 and 2000 (Table 4.3.15). Although the predictive power of none of the models was greater than 50%, the results were relatively promising. The predictive power of the models ranged from R^2 =0.23 (p =0.046) for the prediction of the percentage of dispersules and germinules present as seeds (from three environmental variables), up to R^2 =0.45 for both bryophyte cover (p <0.001), and percentage of species with lateral spread >1000mm (p =0.022). While five variables were used as predictors in the model for lateral spread, only two were involved in the prediction of bryophyte cover (conductivity: $\log_e$CON, and bare ground: BARE). In addition, two variables which featured as predictors in a majority of the models, and which are easily measured in the field were redox potential of the substrate (RED), and minimum average water table level (MIN).

A further six relatively specific models were generated which predicted characteristics of the groundwater and substrate environment, using the same range of attribute values present per sample as predictors (Table 4.3.16). The predictive power of these models ranged from R^2 =0.20 (p =0.004) for the prediction of groundwater conductivity ($\log_e$CON), to R^2 =0.59 (p <0.001) for the prediction of minimum water table level (MIN). While the first model contained only two predictor variables with negative linear relationships relative to increasing conductivity, the second was somewhat more complex, with a number of quadratic and cubic functions for the predictor variables (Table 4.3.17).

In relation to an increasing minimum water table level (i.e. a more permanently inundated substrate, or presence of standing water), the amount of species with the potential to produce dispersules in the form of fruits appears to increase linearly, as does the amount of plants with the potential to form a taller (1-3m) canopy. The amount of polycarpic perennials present appears to decrease initially in relation to wetter conditions, while the opposite is true for species forming rosette-type canopies. Having a quadratic function within the equation, the amount of rosette forming species then appears to decrease as minimum water table rises (i.e. less drawdown). The influence of this apparent reduction in drawdown has a more complex (cubic) interaction with the degree of potential lateral spread present amongst the representative species. As species with a larger degree of potential later spread (>1000mm) initially increase relative to decreased levels of drawdown, those with a limited capacity to

spread laterally appear to decrease. The relationship between these two variables changes direction twice more relative to decreasing drawdown, and within the confines of the model. The amount of hemicryptophyte presence (plants with buds at ground level) also has a cubic function within the equation, with an initial decrease characterising wetter conditions.

Table 4.3.15 Summary of multiple regression models for the prediction of percentage attribute type representation per sample station from measured groundwater variables; see Table 4.2.1 for descriptions of attribute types. *Indicates direction of initial linear phase of response

% Dependent Attribute type per station (y)	Independent Predictor Variables (b)	Response*	Regression R^2	p
Polycarpic Perennial	MIN RED	Quadratic+ Cubic+	0.28	=0.006
Hemicryptophyte	logeFLU MIN WAT RED	Linear+ Cubic+ Linear- Quadratic+	0.34	=0.006
Helophyte	logeFLU MIN WAT RED	Quadratic- Quadratic- Quadratic+ Quadratic+	0.35	=0.009
Rosette Canopy	BRYO MIN $\log_e$PH	Linear+ Quadratic+ Quadratic+	0.41	=<0.001
Semi-rosette Canopy	BARE $\log_e$PH	Quadratic+ Quadratic-	0.24	=0.008
Canopy Height 1-3m.	BRYO $\log_e$CON $\log_e$FLU WAT	Linear- Quadratic- Linear- Linear+	0.37	=0.006
$\log_e$ Lateral Spread 1 (limited)	BRYO MIN $\log_e$PH	Quadratic+ Cubic+ Linear-	0.42	=<0.001
$\log_e$ Lateral Spread 5 (perennials > 1000mm)	BARE MIN RED WAT $\log_e$FLU	Quadratic- Cubic+ Cubic+ Cubic+ Cubic+	0.45	=0.022
Dispersule/Germinule 1 (fruit, or part of)	BARE BRYO $\log_e$PH MIN	Cubic+ Quadratic- Quadratic+ Linear +	0.34	=0.011
Dispersule/Germinule 2 (seed)	$\log_e$CON $\log_e$PH RED	Linear- Quadratic+ Cubic-	0.23	=0.046
Bryophyte Cover	$\log_e$CON BARE	Quadratic- Cubic-	0.45	=<0.001

Table 4.3.16 Summary of multiple regression models for the prediction of measured groundwater variables from percentage attribute type representation per sample station: see Table 4.3.20 for further explanation. (a) specific models with several attribute predictors; (b) general minimal models with restricted attribute predictor variables.

(a)

% Dependent Groundwater Variable per station (y)	Independent Predictor Variables (% per sample station) (b)	Response	Regression R^2	p
$\log_e$FLU	Hemicryptophyte Hydrophyte Leafy Canopy	Linear+ Cubic+ Cubic+	0.28	=0.028
WAT	Hemicryptophyte Helophyte Hydrophyte Canopy Height 1-3m $\log_e$Lateral Spread 5 (perennials > 1000mm)	Linear- Linear+ Linear+ Linear+ Cubic+	0.37	=0.002
MIN	Polycarpic Perennial Hemicryptophyte Rosette Canopy Canopy Height 1-3m $\log_e$ Lateral Spread 1 (limited) $\log_e$ Lateral Spread 5 (perennials > 1000mm) Dispersule/Germinule 1 (fruit, or part of)	Quadratic- Cubic- Quadratic+ Linear+ Cubic- Cubic+ Linear+	0.59	=0.001
RED	Polycarpic Perennial Hemicryptophyte	Cubic- Cubic+	0.36	=0.001
$\log_e$PH	$\log_e$ Lateral Spread 1 (limited) Lateral Spread 2 (compact perennial < 100mm)	Quadratic- Quadratic-	0.31	=0.001
$\log_e$CON	BRYO Dispersule/Germinule 2 (seed)	Linear- Linear-	0.20	=0.004

(b)

% Dependent Groundwater Variable per station (y)	Independent Predictor Variables (% per sample station) (b)	Response	Regression R^2	p
WAT	Helophyte	Linear+	0.28	=<0.001
MIN	Helophyte $\log_e$ Lateral Spread 5 (perennials > 1000mm)	Linear+ Cubic+	0.32	=0.001

Table 4.3.17 Multiple regression equations (specific model) predicting groundwater variables from percentage attribute type per sample station for $R^2 > 0.50$.

MIN = -15.785 –0.0706(**LH6**) –0.235(**LF3**) +0.183(**CS1**) –10.909($\log_e$**LS1**) +5.703($\log_e$**LS5**) +0.113(**DG1**) +0.00002875(**LH6**^{2}) +0.002298(**LF3**^{2}) –0.00000615(**LF3**^{3}) –2.680($\log_e$**LS5**^{2}) +0.002298(**LS5**^{3}) +5.819($\log_e$**LS1**^{2}) –0.794 –0794($\log_e$**LS1**^{3}) –0.000474(**CS1**^{2}) +0.0576(**CH5**)

(F = 3.655 d.f. = 15; $R^2 = 0.59$; $p = 0.001$)

(1)

4.4. Discussion

4.4.1. Defining environmental drivers of wetland vegetation composition

Reinforcing the findings of Chapter 3, the wetlands sampled can be clearly defined in terms of a number of major environmental pressures on plant survival, forming gradients which drive wetland vegetation assemblage and structure. Along with this, there are clear variations in a number of traits which are common between species, and variations in collective state variables of the vegetation. As van der Valk (1981) and Gaudet and Keddy (1988) have previously shown, simple traits (i.e. the ability to germinate under flooded conditions, or the degree of rhizome production) can act as useful predictors of the underlying environment. The work undertaken here has shown that major gradients such as maximum level of inundation, level of water table fluctuation, and associated hydrosoil redox and pH status are major drivers of wetland vegetation composition, and that broad vegetation groupings along these gradients may be conveniently classified into community types. In addition, a number of collective state variables of the vegetation can also be used to differentiate between these same groupings (e.g. stem density, species richness, canopy height, and biomass values). Traits more specific to the dominant populations, which, by definition, are most successful in relation to the prevailing environment (e.g. canopy area, biomass values, reproductive capacity etc.) can also be seen to vary between equivalent community types.

Variability in trophic status was clearly noted between pairs of both S27 *Carex rostrata-Potentilla palustris* fens, and S11 *Carex vesicaria* swamps. Wide trophic ranges have also been noted for these community types by Wheeler and Proctor (2000). In addition, the growth responses of species are seen to vary in relation to water level, and their specific water level requirements (e.g. Newbold and Mountford, 1997; Vretare *et al.*, 2001). Relative herb height meanwhile, has been shown to be significant in predicting the competitive ability of a species (Keddy and Shipley, 1989), and in characterising hydrochemical parameters (Willby *et al.*, 1997). In agreement with these findings, significant differences relating to canopy height were observed between equivalent community groupings, with a shorter canopy height related to lower nutritional status of the groundwater.

Whilst the species comprising the various associations will inevitably change between sites, the variables mentioned above will generally always be present. Various trait-based measures (which may be used to indicate function: e.g. Vretare *et al.*, 2001) have the potential to override the limitations of floristic approaches in a context of characterising and predicting vegetation-environment interactions; floristic approaches to predicting broad-scale

vegetation-environment interactions (in this case, eco-hydrological interactions specifically), are amplified as spatial scales increase due to variation in constituent species (Duckworth *et al.*, 2000; Keddy, 1992a and b). Further evidence exists for the consistency of such methodologies at larger geographical scales (e.g. Hills *et al.*, 1994; Hills and Murphy, 1996; Ali *et al.*, 1999).

4.4.2. Predicting eco-hydrological relationships in wetland vegetation, using field-measured traits and attributes

The methodologies adopted have been relatively successful in the context of predicting eco-hydrological relationships within the wetlands sampled. The predictive power of the various models formally tested using an independent data set ranged from around R^2 =0.5 to 0.78, which equates to around fifty to almost eighty percent of the variation in the dependent variable(s) being explained by the various equations. Therefore the fact that generally over half of the values predicted by the various models were close to their observed values (more for some of the models), indicates a relatively good level of accuracy. There is also evidence for a wider applicability of the outputs of the work to equivalent systems (i.e. predicted values were often good for data collected from entirely independent sites).

In terms of specific predictions from the models produced, the results can be compared to the findings of other workers. Biomass appears to increase as disturbance, in the form of water table fluctuation, increases. Whilst this prediction appears to counter the findings of Wilson and Keddy (1986), which illustrated a predictive relationship between low levels of disturbance and increased biomass along a lake shore, this may be explained by considering the relative level of disturbance, which is likely to be lower (and less frequent) in most wetland systems than in vegetation fringing open water. In Chapter 5, *Phalaris arundinacae* is seen to be susceptible to treatments which could be approximated to conditions of stress within the field (e.g. summer drawdown, or rapidly fluctuating water levels). Other species with a strong competitive component to their strategies, such as *Agrostis stolonifera*, when found at the extremes of their ecological limits (e.g. level of water table tolerance) have a reduced competitive ability, and are therefore less likely to suppress more stress tolerant species such as *Deschampsia cespitosa*. This is a species which can form large plants, with dense tossocks (Grime, 1988).

The suggestion by Hills (1994) that relationships between biomass and other state variables remain largely untested has now been countered to a degree. In this study, various measures of biomass did not prove to be good predictors of other state variables, nor other state variables particularly good predictors of biomass. However, various biomass measures (of

both collective units of vegetation, and dominant populations) were important for the construction of models predicting level of drawdown, level of water table fluctuation, pH, and electrical conductivity. In common with the findings of Murphy *et al.* (2001), potassium content of the water was important in the prediction of total biomass values. Also in common with the findings of Willby *et al.*, (1998), redox potential of the substrate proved to be a good indicator of species diversity, as did stem density. Murphy *et al.*, (2001) also used redox potential as a predictor of diversity, but the predictive power of the model was relatively low. This suggests that the value of using substrate redox potential as a predictor of species diversity (and other variables) may be limited to wetland habitats with rooted vegetation, where substrate redox values have a direct influence on the plants present (the work described by Murphy *et al.* (2001) included assessments of floating vegetation in addition to rooted species in construction of the predictive models). However, it also appears that redox may be of most use in stable wetland systems where substrates are anoxic. Where drawdown occurred for a number of stations, resulting in more aerobic substrate conditions, redox values were not well predicted.

Another factor confounding the ability to predict species richness may be the history of the sites. The Wood of Cree samples used as test data were relatively more species rich than those for all the other fen habitats sampled (including those from which data was collected for model construction), despite comparable substrate and groundwater conditions. A number of comparable systems (e.g. Endrick Marshes, Glen Moss, and Nether Whitlaw Moss) have been subject to activities including major landscaping, controlled winter flooding, and marl digging (see Chapter 2, section 2.1.2), all of which may have impacted upon diversity (due to lack of detailed records previous to these workings, and of limited peat deposits which might yield pollen evidence, this is a hypothesis which may remain untested). In addition, Wood of Cree fen is groundwater fed, but is also subject to periodic inundation from the main channel of the river Cree (Paul Collin, RSPB., pers. com. 1999). In cases where flooding is intermediate, nutrients and hydrophyte seed sources are maintained at favourable levels (Junk *et al.*, 1989; Abernethy and Willby, 1999). In addition to their past management the other sites mentioned do not have a direct link to a source of such inputs, and this may help explain the lower diversity. Over-prediction of values for these samples may therefore have occurred as a result of the initial higher species richness within some of the samples.

A number of intuitively likely eco-hydrological relationships have also been described. For example, stem density appears to initially increase in relation to increasing level of water table fluctuation, and then fall off again as fluctuations become more extreme. As discussed

in Chapter 3, frequent fluctuations may allow mineralization of nitrogen to nitrates, and increase their availability in generally nutrient-poor wetland soils (Patrick and Mahapatra, 1968). However, higher levels of fluctuation will cause a stressful environment (Grime *et al.*, 1988), and therefore may preclude many species from establishment. Higher levels of fluctuation still may favour stress tolerators, and competition and stem density may be reduced as a result.

4.4.2.1. Model criticism

Predictions derived from models can only ever be as good as the underlying statistical and ecological components used to construct the fitted model (Nicholls, 1989), and as there is never a 'perfect' model, the 'best' model can never be known with certainty (Crawley, 1993). The fact that biological systems are inherently noisy, means that general minimal models will often have 'noisy limits' (Murphy and Hootsmans, 2001).

Wetlands are dynamic systems, and are therefore no exception to this rule. This can confound the construction of models based upon data collected over one or two years only (in addition to factors of succession over time, which van der Valk *et al.* (1994) consider to be major confounding factors). Within this study a number of stations at Insh Marshes were seen to be subject to a relatively large level of drawdown (for wetland vegetation) over a period of three seasons, from 1998 to 2000. Some of the models constructed appeared to be sensitive to this phenomenon, and although they included data from a number of such sites in their predictive equations, the models failed to predict values well for repeat sample data (from the following year) for these sites. Whilst criticism could be levelled at some of the models for this weakness, a prolonged drawdown in any wetland system would undoubtedly lead eventually to conversion of the vegetation away from a wetland community, and towards a more terrestrial community type. However, these same models, which could be regarded as relatively specific due to the use of several predictor variables, consistently predicted values well for samples from independent test data sites (e.g. for Endrick Marsh stations, which were sampled in the third year of the study only). In addition, a number of stations from Insh Marshes remained relatively stable over the three years in terms of their average water table levels, and predicted values for these stations were also generally good. Grieve *et al.* (1995) identified areas of the marshes away from the main channel of the River Spey which were less reliant upon riverine input, and were largely maintained by groundwater (telluric) inputs. It therefore seems that a number of the models produced may be better applied to freshwater wetland systems with major groundwater inputs. In this instance, variables such as hydrosoil redox potential, which proved to act as a good predictor of variation in several state variables, would remain stable. While the models may be

applicable to less stable riverine-influenced systems, this will undoubtedly be within 'noisy' limits.

Where certain species are concerned, extreme morphological plasticity needs to be considered. Low correlations were seen between observed and predicted values for some models. Some, such as those predicting the number of leaves per ramet of dominant populations may be less accurate for a number of wetland grasses, for example, due to high plasticity (Spedding and Diekmahns, 1972). Cooling *et al.* (2001) present evidence of rapid plastic responses in the dicotyledonous running marshflower, *Villarsia reniformis* R.Rr. (Menyanthaceae), in relation to rising water levels. Plastic responses have also been noted in *Phragmites australis* specifically in relation to increasing water level (Vretare *et al.*, 2001). However, the benefit of using an approach which measures variables such as leaf area, and leaf number etc., is that their values can be related to the environment, and are a direct function of the environment, irrespective of degree of morphological plasticity.

4.4.3. Use of attributes in modelling

Willby *et al.* (2000) explained a large percentage of habitat utilisation by reference to hydrophyte attributes. However, the use of life-forms and attribute types appear limited in scope in the context of this study, which covers a relatively small geographical range. In addition, Raunkaier (1937) originally produced his classifications to delimit broad differences between vegetation types, and these were in turn linked to broad environmental categories, running from open water to terrestrial. Therefore, such an approach may have limited sensitivity in the scope of considering wetlands alone. In addition, in the initial consideration of choosing attributes for which information could be obtained, it may be that the most useful attributes were not selected. For example, an increase in the complement of species with a potential lateral spread of >1000mm does not necessarily mean they will spread that far, or the potential to produce a certain type of reproductive structure does not necessarily mean that any will be produced. As an example, *Menyanthes trifoliata* has aquatic and terrestrial forms, and the latter form, which may be found in upland sites, tends to be far smaller and almost never produces flowers or reproductive structures (Hewett, 1964).

As a pilot study the approach may have some potential. For example, the presence of hemicryptophyes is informative if the species require certain water table levels; a reduction in hemicryptophyte presence may be useful to predict water level variation. However, this approach still requires the use of fieldwork, plus identification skills, and given the

predictive power of the models produced, is not preferred to the measurement of easily identifiable traits which are common across species.

4.4.4. Applications and future directions

A number of the eco-hydrological relationships described, and the predictions made between various vegetation variables and hydrological and other environmental variables are interesting, but nonetheless intuitive. However, some of the relationships have the potential for development as 'monitoring tools' in eco-hydrology.

Wheeler and Shaw (1995), consider that a clearer understanding of the relationships between wetland vegetation and hydrology is needed to aid the use of vegetation as a conservation and management tool. While Wassen and Grootjans (1996) consider ecohydrology as an application-driven discipline, Murphy and Hootsmans (2001) considers that the production of general minimal models is an important key to understanding freshwater ecology. To this end, predictive relationships have been formulated between average level of drawdown within a representative sample of northern British wetlands, and easily identifiable and measurable components of the vegetation. The predictions provided by the model are more reliable when applied to more stable groundwater fed wetland systems; however, these are perhaps some of the more vulnerable wetland types (see Section 1.1.4). Further testing of the models to refine them and test their applicability is probably desirable. However, the work described in this thesis goes some way to answering some of the long standing questions in wetland vegetation management. For example, much previous work stemmed from the desire to predict the effects of drawdown on wetland species (Newbold and Mountford, 1997). If relationships between water level drawdown and vegetation variables such as stem density and biomass per unit area can be broadly modelled for wetlands, then some progress has been made in the use of vegetation as a hydrological monitoring tool (Wheeler and Shaw, 1995), as has progress towards the identification of 'useful' traits (Duckworth *et al.*, 2000).

In conclusion, the use of simple traits measured within wetland vegetation can act as useful predictors of the interaction of vegetation and the major groundwater hydrological and hydrochemical gradients. As such, predictive relationships have been formulated between factors of the vegetation, and the underlying environmental regime which agree with, and build upon previous studies. Conversely, a good deal can be said about certain characteristics of the hydrology from factors of the vegetation.

Such knowledge may facilitate the application of simple measurements from the vegetation as rapid assessment tools in the eco-hydrological management of wetland reserves. In association with initial scoping studies of major hydrological inputs and balances in wetlands (i.e. riverine or telluric), the use of a number of 'useful' trait measurements may be utilised as part of an informative and coherent assessment of potential water level change impacts upon wetland vegetation. In the same way, this approach can inform us of current hydrological regimes (e.g. how dynamic the water table is, average level of inundation etc.) The need to make such broad-scale predictions in wetland vegetation management is one which is undeniable, and essential.

Chapter 5: The response of selected wetland plant species to ground-water stress, and competitive interaction.

5.1. Introduction

There are a number of reasons why wetland managers may wish to understand the relationship between a single plant species and water level regime; for example, in order to:

- protect and conserve a rare species whose response to potential water level change is not necessarily known (e.g. String sedge; *Carex chordorrhiza* L.fil.: Legg *et al.*, 1995a; Legg *et al.*, 1995b; also see Appendix 10).
- promote growth of a particular species which is regarded as 'desirable' to feeding and nesting waterfowl (e.g. Tickner and Evans, 1991).
- to reduce dominance of a single invasive species, and increase site specific diversity through active wetland water level management (e.g. Bhatia, 1999)

Therefore, underlying the need for broad-scale forecasts of how perturbations of ecosystems, anthropogenic or otherwise, may affect community structure, is the need to gain an insight into individual species responses to environmental gradients. The concept of individual species response curves was formulated relatively early last century (Cain, 1938), but it was not until more recently that screening of individual species response was begun by Grime and co-workers (Grime, 1974). This work resulted in a volume of autecological accounts of a number of species of British higher plants (Grime *et al.*, 1988), and has recently been expanded upon (Hodgson *et al.*, 1999) to enable a trait-based prediction of strategies to be made for a number of British species. This increased understanding of individual species responses, along with more recent studies looking at specific water level requirements (Newbold and Mountford, 1997), may help provide the basis of a clearer understanding of the impact of natural or anthropogenic disturbances on more complex wetland vegetation assemblages.

5.1.1. Water level requirements

A number of descriptions of the effects of natural groundwater variation (e.g. Summer drawdown) on individual wetland plant species exist in the literature (Van der Valk, 1980; Rea and Ganf, 1994; Brown and Scott, 1997; Hicks *et al.*, 1998;). Examples also exist for specific responses such as seed yield in relation to groundwater levels in agriculture (e.g. Hamdi *et al.*, 1992), or where lake water-level variation may control potentially invasive species (Poovey and Kay, 1998). More recently however, experimental studies have aimed

to address and quantify the influence that water level variation within such systems may have on wetland species (Mountford and Chapman, 1993; Newbold and Mountford, 1997). From this work 'preference ranges' have been proposed for a number of wetland species (including plants), in addition to 'tolerance ranges' (i.e. the limits under which a species can survive, at least experimentally).

For example, potential water level change threats to *C. chordorrhiza*, classified as 'rare' within the British Red Data Book for Vascular Plants (Perring and Farrell, 1983), lead to both field and pond-based experiments of the species response to water level change being carried out (Legg *et al.*, 1995a). It was concluded that the species would not survive prolonged inundation, and that any prolonged drawdown leading to drier conditions would lead to retardation of growth; these conclusions being based on various trait measurements amongst others. It was also concluded that variations in inter-specific competitive interactions would need to be assessed in relation to water level changes.

5.1.2. Plant response to water level variation

Given the premise that plant species have 'preference ranges' in terms of groundwater regime, and that differentiation in growth parameters measured vary in relation to these regimes (section 5.1.1), the measurement of morphological traits in relation to such gradients is a practical and desirable tool for assessing plant response to factors of stress.

Differences in the general morphology of plants from differing habitats, subject to varying environmental gradients, has long been recognised; a famous early example being the 'life forms' proposed by Raunkaier (1937). It is apparent though that within these broader categories, intra-specific variation occurs in relation to the overall spectrum of the underlying gradients. Within wetland vegetation, as resource allocation varies in relation to hydrological regime, so therefore will the overall measurable traits of a given species. In addition to the morphological differences observed by Legg *et al.* (1995a) for *C. chordorrhiza* in relation to relative water level, Rea and Ganf (1994) found that under experimental conditions, *Baumea arthrophylla* (Nees. Boeckler) was able to withstand short periods of relatively minor inundation (50cm) by allocating significantly more biomass to above ground parts than to rhizomes, and still maintain growth; a higher inundation level (100cm) however lead to critical root loss. *Triglochin procerum* R. Br. (Water Ribbons) on the other hand, maintained growth under similar conditions via a rapid turnover of spongy leaves; differing abilities to maintain growth under varying levels of inundation were partly attributed to differences in nutrient uptake strategies. Similar reductions in below-ground resource allocations have been observed in waterlogging-tolerant grasses (Rubio and

Lavado, 1999). While the life history classification of differing species are regarded as important factors for survival in wetlands (timing of important life cycle events around flooding), the degree of morphological plasticity, and associated metabolic adaptations are also important (Blom and Voesenek, 1996). Such adaptations may include aerenchyma production in roots, or the contrasting strategies of shoot growth cessation, or shoot elongation for example. *Glyceria fluitans* (L.) R. Br. (Flote-grass) has also been shown to suffer where hydrological restoration of degraded wetland meadows, in which the species often dominates, has been attempted; raised water tables facilitate the reduction of insoluble Fe(III) oxides to Fe(II), causing iron toxicity (Lucassen *et al.*, 2000).

5.1.3. Competitive interactions within wetland vegetation

The work of Newbold and Mountford (1997) represents possibly the first serious attempt at assessing how a wide range of wetland species respond to groundwater level regimes, and what changes in such regimes individual species may be able to tolerate. The work briefly considers 'competitive' interactions, which undoubtedly occur within mixed communities. Such interactions are viewed as an important component of vegetation zonation in wetlands, along with water regime (Holland *et al.*, 1990; Risser, 1990), but are understandably difficult to assess for a wide range of species.

Competition is defined by Keddy (1989 pp. 2) as:

> "*the negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability*"

Similarly, Grime (1974) states that:

> "*competition may be defined as the attempt by neighbouring plants to utilise the same units of light, water, mineral nutrients or space*"

These are but two definitions, and while Milne (1961) asserted that competition should have only one "*...clear, precise and unambiguous...*" meaning, within plant community ecology, the precise meaning of competition is still under debate (Thompson, 1987; Tilman, 1987; Thompson and Grime, 1988: see section, 1.3.4.1). Whatever the precise definition of competition, abiotic factors may be limiting in a stressed environment, leading to competition between species; the emphasis is shifted in more moderate environments to competition between biotic factors (e.g. competition for space). Several authors have described relationships within vegetation associated with various environmental gradients. For example, Wilson and Keddy (1986) found that competitive ability, based upon a measure

of relative yield of dry mass per plant, was significantly correlated with mean position on an exposure gradient: species found on sheltered, nutrient-rich shores around Axe Lake, Ontario, Canada, had higher competitive abilities than those found on exposed, nutrient-poor shores. This relationship was also observed by Day *et al.* (1988) from studies across a number of Canadian marshland sites. Keddy *et al.* (1994) also found evidence of characteristics linked to competitive traits (rhizomatous) associated with relatively fertile, high biomass shorelines. This was consistent with the findings of Gaudet and Keddy (1988) that larger species were better competitors.

5.1.4. Background to experimental work on ground-water stress and competition

The ability to detect intra-specific trait differentiation along various environmental gradients has been illustrated in the previous sub-sections of this chapter, and competitive interactions between wetland species have been briefly outlined. The concept of survival strategies within species (Grime *et al.*, 1988) is covered in Chapter 1. Traits measured in the field can be used to determine where a species may fit into Grime's strategy theory (Hodgson *et al.*, 1999), and the use of such an approach provided a basis for the prediction of Plant Functional Groups (PFG's) within European riverine wetland vegetation (Hills, 1994; Hills *et al.*, 1994; Hills and Murphy, 1996;). Conversely, it was considered that manipulations might also be applied to species of a known strategy within an experimental framework, to infer possible impacts of environmental change within the field. Three grass species, *Agrostis stolonifera* L. (Creeping Bent), *Deschampsia cespitosa* (L.) Beauv. (Tufted Hair-Grass), and *Phalaris arundinacea* L. (Reed Canary-Grass) were chosen out of a pool of species observed in the field (Table 5.1.1), for experimentation; these species were selected due to availability, and ease of cultivation. The overall aim was to assess the relative impacts of inter-specific competition, and/or duration and magnitude of water level fluctuations, in terms of morphological variation within the test species.

Agrostis stolonifera

This is a morphologically variable species which forms a relatively low canopy, but is fast growing and stoloniferous, and is found within a wide range of habitats. Associated floristic diversity is often low to intermediate (Grime *et al.*, 1988). It is common in the British Isles and is often regarded as a weed in cultivated land, being able to successfully invade swards of other species of sown grass (Spedding and Diekmahns, 1972), either via vegetative means (stolons) or within persistent seed banks (Grime *et al.*, 1988). Studies undertaken by Bradshaw and co-workers. (1964) have shown that the yield of *A. stolonifera* is much higher than for other species of *Agrostis* (*A. canina; A. tenuis*) and other species of unimproved pasture, such as *Festuca ovina* (Sheep's fescue). The species was found to be more

comparable to *Lolium perenne* (Perennial rye-grass) in terms of its yield (up to 8170 kg/ha/yr: Spedding and Diekmahns, 1972) along a fertility gradient, but while shoot:root biomass ratio exhibited very marked variation along such a gradient in *Agrostis*, this phenomenon was not observed in Lolium. *A. stolonifera* has a pan-global distribution, having been introduced into Australia and South America (Hubbard, 1984).

Deschampsia cespitosa

This species is variable in terms of its size, and is often ubiquitous within wet grasslands, with associated floristic diversity ranging from intermediate to low. The species forms dense tussocks with often persistent leaf litter (Grime *et al.*, 1988), and the potential of the species for regenerative lateral growth is limited; daughter ramets have however been observed to form, through fragmentation of tussocks. *Deschampsia* has also been observed to form relatively persistent seed banks, and this appears to be its main mode of reproduction within areas of open ground (Grime *et al.*, 1988). Studies conducted by Roberts (1986) have shown seeds of *Deschampsia* to persist and emerge into the third year after sowing. While morphological variability is mainly expressed in terms of overall size, a good degree of physiological variability exists, leading to the species being found across a number of substrates and habitats. The species however is generally considered to be characteristic of habitats providing refugia from intense competition (i.e. direct stress such as seasonal flooding, which in turn reduces competition from other species) (Davy, 1980). *Deschampsia* has a global distribution within temperate and arctic regions.

Phalaris arundinacea

This is the largest and most robust of the three species studied here. It is found along river banks, which it can help to protect from erosion, and also marshes and wet valley bottoms (Grime *et al.*, 1988). While sometimes used as a source of herbage for grazing, *Phalaris* can contain alkaloids which are harmful to sheep (Sculthorpe, 1967). The species can become invasive and dominate large areas via high levels of rhizome production (Hubbard, 1984); seed production also occurs, with water bodies acting as vectors for their distribution. Field observations in the Insh Marshes, Scotland, have associated the species with a groundwater hydrology characterised by summer inundation, and increased concentrations of K, Cl, NO_3^- and SO_4^{2-} above that of the surrounding fen (Willby *et al.*, 1997). The ability of *Phalaris* to tolerate inundation has been investigated by Smirnoff and Crawford (1983), who observed a significant increase in root aerenchyma production for individuals grown under flooded conditions. *Phalaris* also has a global distribution.

It can be seen from Table 5.1.1 that each of the three species has a competitive component to its established phase strategy, but that only *Phalaris* is a true competitor. While *Agrostis* is intermediate between a competitor and ruderal in its classification, *Deschampsia* is more of a generalist, with elements of stress tolerance. The three species span a water level 'preference' range of –40cm to +5cm. With this pre-existing knowledge of varying characteristics, experimental investigations of response to water level stress, and competitive interaction are of potential interest.

Experiment 1 consisted of mixtures of *A. stolonifera* and *D. cespitosa* grown under various replacement series (de Wit, 1960) and fixed water level treatments. While Connoly (1983) gives an overview of various criticisms of the replacement series, he goes on to point out that no better alternative has yet been found to this approach in the experimental assessment of competitive interaction in plants. Experiments 2 and 3 consisted of individuals of both *D. cespitosa* and *P. arundinacea* grown under varying combinations of magnitude and duration of water level fluctuation.

Table 5.1.1. Species screened for consideration in experimental assessment of effects of competitive interaction, and ground-water level manipulation experiments; C = competitor; S = stress tolerator; R = ruderal (disturbance tolerator). For further explanation see Chapter 1. - = no information available. 'water level preference' figures in parentheses indicate 'tolerance range'. Source: †Grime *et al.* (1988); ††Newbold and Mountford (1997); positive values represent inundation.

Species	Established Phase Strategy†	Water Level depth Preference relative to surface (Cm) ††
Agrostis stolonifera	CR	-10 to +5
Carex aquatilis	-	-40 to +10 (-100 to +30)
C. rostrata	-	0 to +30 (-15 to +60)
C. vesicaria	-	-30 to 0 (-30 to +25)
Deschampsia cespitosa	CSR-CS intermediate	-20 to –10 (-50 to +5)
Equisetum fluviatile	CR	+60 (-10 to +100)
Eriophorum angustifolium	S	-30 to 0 (-50 to +10)
Menyanthes trifoliata	-	+10 to +75 (-10 to +100)
Molinia caerulea	CS	-50 to –25 (-100 to 0)
Phalaris arundinacea	C	-40 to 0 (-60 to +30)
Phragmites australis	C	-20 to 0 (-100 to +50)

In summary, this Chapter describes the use of an experimental approach to:

- Examine the response of two wetland grass species with differing established phase strategies to fixed groundwater stress and competitive interaction.
- Examine the response of two wetland grass species with differing established phase strategies to groundwater stress in the form of varying magnitude and duration of groundwater level fluctuation.

5.2. Methods and Materials

5.2.1. The response of two wetland grass species to ground-water stress and competitive interaction (Experiment 1)

5.2.1.1. Experimental design

Seeds of *A. stolonifera* and *D. cespitosa* were sown onto standard seed compost, and after germination were grown onto the 3-4 leaf stage. Seedlings were transplanted into 4 litre plastic tubs, into which a 3:1:1 ratio mix of general purpose potting compost, topsoil and horticultural grade grit-sand had been filled to a standard level; the plants were allowed to establish for one week. Planting regimes giving two levels of competition treatment were employed, and after the establishment period fixed water level treatments were imposed. Responses were measured in terms of final height, above and below-ground biomass, number of leaves and tillers per individual, average number of leaves per tiller, and SLA (specific leaf area; formerly defined by Evans (1972) (see Table 5.2.1.). Measures of variation in relative leaf thickness/leaf weight in relation to environmental controls include terrestrial (Evans and Hughes, 1961), and freshwater examples (Spence, 1972; Spence and Chrystal, 1970).

Each experimental unit consisted of four individuals of *D. cespitosa,* four individuals of *A. stolonifera*, or two individuals of each species in a replacement series design (de Wit, 1960). Three replicates of each treatment unit were arranged in a completely randomised design.

Fixed water level treatments were imposed via holes drilled in the sides of the plastic tanks, thereby allowing water to drain out of the respective tanks at three different set levels. The three set levels were 7cm below soil surface level (-7cm), at soil surface level (0cm), or at 7cm above surface level (7cm); these levels were intended to represent conditions of dryness, saturation and inundation of the soil environment respectively. For the duration of the experiment water levels were maintained by daily watering.

The experiment was carried out in heated (23°C) glasshouses at the University of Glasgow for a period of 13 weeks, from 17-12-1999 to 21-03-2000. Measurements were taken at 0, 24, 46, and 94 days, with the plants being harvested on day 94. For the duration of the experiment a sixteen-hour day regime was imposed, supplemented by 400-Watt sodium lamps.

5.2.1.2. Processing procedure

Post-harvest, the above-ground part of each individual plant per treatment unit was separated from its roots. The leaves were separated from the stems for each of the excised individuals; one of the lowest leaves still containing photosynthetic tissue, along with one of the post-terminal leaves from a randomly selected tiller were kept aside for each individual. These two leaves were scanned using DESKSCAN software on a flat bed scanner, and the images were saved as monochrome tagged image format (*.TIF) files. The images were analysed using customised Delta-T-SCAN image analysis software in order to obtain the leaf area for the two sub-sample leaves. All leaves and stems were placed into a drying oven at 60°C for 7 days, with the two scanned leaves per individual being separated from the rest of the leaves. Following drying, the stems, leaves and scanned leaves were then weighed separately; estimates of SLA (cm^2/mg) per individual were then calculated on the basis of the weight of the scanned sub-sample leaves. The use of two leaves from the extremes of the plants was employed in an attempt to reduce any between-sample variation in SLA which may be linked to leaf age (Gunn *et al.*, 1999). Average biomass per individual was calculated for each treatment unit, with these values being based upon total species complement per treatment unit (i.e. an average of 2 individuals for those in a 1:1 species replacement ratio, and an average of four individuals for those in a single species unit).

Roots were washed clean of any soil residues and were oven-dried at 60°C; these were left as a treatment unit total, as separation of individual plant roots was impractical. Following drying, roots were weighed to give a dry biomass value per treatment unit.

Average biomass values per treatment level were calculated for both the individual above-ground components and the total below-ground components (root and rhizome complement) for each treatment factor at each replacement level.

Table 5.2.1. Morphological traits measured per individual plant for ground-water stress and competitive interaction experiment (Exp. 1), and for ground-water stress: magnitude and duration experiments; for *Phalaris arundinacea* (Exp. 2), and *Deschampsia cespitosa* (Exp. 3) respectively.

Trait Measured	Trait Code	Exp.1	Exp. 2	Exp. 3
Above-ground biomass (g)[†]	A-B	✓	✓	✓
Plant height (cm)	PH	✓	✓	✓
Number of leaves	LN	✓	✓	✓
Total leaf biomass (g)	LB	n/a[†]	✓	n/a[†]
Number of tillers	TN	✓	✓	✓
Number of leaves per tiller	LNT	✓	✓	✓
Specific leaf area (cm^2/mg)	SLA	✓	✓	✓
Specific root length (cm/mg)	SRL	-	✓	✓
Below-ground biomass (g)	B-B	-	✓	✓
Stem biomass (g)	StB	n/a	✓	n/a
Total biomass (g)	TB	-	✓	✓
Root length (cm)	RL	-	✓	✓
Above-ground root length (cm)	A-RL	n/a	✓	n/a
Rhizome length (cm)	RhL	-	✓	✓
Reproductive structure biomass (g)	RB	n/a	✓	n/a
Average seed biomass (mg)	SdB	n/a	✓	n/a

✓ = trait measured; - = trait not measured; n/a = trait not present/measurable.
[†]Stems not discernible from leaf bases in non-flowering individuals: A-B used for comparative purposes between Exp. 2 and Exp. 3.

5.2.2. Effects of ground-water stress on two wetland species with differing strategies: magnitude and duration of fluctuation (Experiments 2 and 3)

5.2.2.1. Experimental design

Stock plants of *Phalaris arundinacea* (from an artificial wetland within the University of Glasgow glasshouse facility) whose basal stem diameter fell between 8-10mm were harvested at ground level. Dead and senescing leaves were removed, and the stems were trimmed to a length of approximately 5cm, with one internode being left per stem section; all obvious buds were removed from the internodal joint. Stem sections were then planted out into 12 cm plastic plant pots with basal drainage holes, into which a compost mixture (see section 5.2.1.1) had been filled to a standard level. Stem sections were allowed to establish for one week, and the soil surface in each pot was covered with equal volumes of washed horticultural grade pea-gravel to avoid soil loss with subsequent flooding. Fixed, and fluctuating water levels, varying in both magnitude and duration were then imposed (See Table 5.2.2). Responses were measured as per section 5.2.1.1, with the addition of Specific Root Length (SRL: cm/mg) (see Table 5.2.1). Three replicates of each treatment unit were arranged in a completely randomised design.

In order to manipulate water table levels, the plant pots were placed into 32 litre plastic tanks, which had a series of holes drilled into the side at set levels relative to the substrate surface. Water levels were maintained, or manipulated by application, and/or removal of waterproof tape at either weekly or fortnightly intervals (See Table 5.2.2), thus allowing water to drain down, or to be topped up to the 'new' level. The relative water levels were maintained by regular watering.

Tillers of *Deschampsia cespitosa* (L.) Beauv. collected from an area of wet grassland within the Insh Marshes reserve (see Chapter 2) were prepared in the same manner, and were subjected to the same treatments as for *P. arundinacea.*

Both experiments were carried out in the University of Glasgow glasshouses for a period of 8 weeks, with measurements taken at approximately weekly intervals. Treatments for *P. arundinacea* ran from 31-03-2000 to 28-05-2000, and those for *D. cespitosa* from 11-07-2000 to 06-09-2000; plants were harvested on the 56^{th} and 57^{th} days respectively. Natural summer daylight was used with no supplementary lighting.

5.2.2.2. Processing procedure

Post-harvest, a number of morphological measurements were made for individuals of *P. arundinacea* and *D. cespitosa* (see Table 5.2.1). The individual plants were processed as per section 5.2.1.2. However, the roots of each individual could be treated separately, and therefore, three random root sections were also taken from each individual, and these were scanned and processed in addition. Digitally scanned sub-samples of roots and leaves were again kept separate during drying, and estimates of SLA and SRL derived. Average biomass values per treatment level were also calculated.

5.2.3. Data analysis

All data sets from the experiments were tested for normality using a Ryan-Joiner test in MINITAB.11. Where data were not distributed randomly within the residual plots, they were transformed accordingly. Data were normalised using a $\log_e (X \times 100 + 1)$ transformation (Sokal and Rohlf, 1981).

Experiment 1

Average values for all traits per treatment unit were calculated separately for each of *A. stolonifera* and *D. cespitosa* grown in single species stands, and for the two species grown in replacement series. For each set of data per treatment level a balanced analysis of variance was carried out: for each of the two species in turn, with and without competition factors. As

the experimental design was orthogonal Fischers LSD (Least Significant Difference) multiple comparison tests (Little and Jackson Hills, 1978) were applied where significant differences occurred between treatment level means (derived from the variance ratio statistic, F). In all cases, original rather than transformed data have been plotted to give an improved understanding of the results. Where LSD scores were calculated from these transformed data, these are shown on the plots (as back transformation is not possible). Significant differences between treatment means are indicated by graph notation, but as the graphs show untransformed data only, these differences may not always be visually apparent from the plots when they are derived from transformed values. The word 'significant' is only used where a statistical test has been applied to the treatment means.

In order to assess the relative competitive interaction of either of the two species on the other, 'agressivity' scores were calculated for each of the two species, based on yield data from the reciprocal mixes (see below). Relative Yield (RYT) totals were also calculated, in order to assess any combined variation in biomass under different water level treatments. Both of these scores related to the above ground portion of the plants only, as roots could not be separated into respective species from the mixed treatment units (section 5.2.1.2); the relative scores were calculated as per Martin and Snaydon (1982):

$$RYT = \tfrac{1}{2}(Yij/Yii + Yji/Yjj)$$

$$\text{Aggressivity} = \tfrac{1}{2}(Yij/Yii - Yji/Yjj)$$

Where Yij = yield per plant of species i grown in mixture with species j; Yji = yield per plant of species j grown in mixture with species i; Yii and Yjj = pure stand yields per plant of species i and j respectively.

Experiments 2 and 3

One way analyses of variance were carried out for all trait values between treatment levels for both *P. arundinacea* and *D. cespitosa*. Once again, treatments which resulted in significant variation between the treatment level means of the measured variables were determined by LSD multiple comparison tests; the same protocol applied as described for *Experiment 1*.

Table 5.2.2. Magnitude and duration of water level fluctuation treatments applied to *Phalaris arundinacea* and *Deschampsia cespitosa* (see section 5.2.2.1).

Treatment Number	Water Level(s) Relative To Surface (Cm)	Duration Of Each Treatment Component (Weeks)
1	-12	8
2	-6	8
3	0	8
4	+6	8
5	+12	8
6	0 and –6	1(x4)
7	0 and –6	2(x2)
8	0 and –12	1(x4)
9	0 and –12	2(x2)
10	0 and +6	1(x4)
11	0 and +6	2(x2)
12	0 and +12	1(x4)
13	0 and +12	2(x2)

5.3. Results

5.3.1. Ground-water stress and competitive interaction

The results of the competition and ground-water level variation experiment show a number of significant relationships between these two factors, which apparently have differing impacts upon the two species under investigation. It can be seen from Table 5.3.1 that the above-ground biomass of *Agrostis* differs significantly in relation to water level relative to the surface ($p<0.001$), but competition had no significant effect. The equivalent portion of biomass for *Deschampsia* varies significantly in relation to both water level variation ($p<0.001$) and competitive interaction ($p=0.006$) with *Agrostis*; there is also a combined water level and competition effect ($p=0.05$) (Figure 5.3.1). For both *Agrostis* and *Deschampsia*, above-ground biomass is generally higher for the treatments with water levels at soil surface (0cm). However, while *Agrostis* grown in a single species stand does not differ significantly from treatments at a higher water level treatment (+7), the biomass is significantly higher for individuals grown in replacement series with *Deschampsia*. The opposite of this situation is observed for *Deschampsia* (Figure 5.3.1), suggesting a possible competitive advantage of *Agrostis*>*Deschampsia*, at at least one water treatment level (0cm).

Further investigation of the interaction between the two species at various treatment levels reveals that in all cases, *Agrostis* produces a greater above-ground biomass than does *Deschampsia* (Figures 5.3.1; 5.3.2), both in single species stands, and in competition. However, the apparent dominance of *Agrostis* over *Deschampsia* is successively reduced as water level rises relative the surface. This is illustrated in Figure 5.3.2, where the theoretical crossover point at which both species would contribute evenly to the total stand (above-ground) biomass is closest to being reached where water inundation is +7cm. While relative yield is maintained at a similar level between 0cm and +7cm water level treatments (and reduced from a slightly higher level at –7cm) (Table 5.3.2), the dominance of *Agrostis* over *Deschampsia*, in terms of 'aggressivity', is greatly reduced at the highest level of inundation (Table 5.3.3).

Inferences from competitive interaction and water level treatment effects on the root (below-ground) portions of each treatment are restricted to treatment level totals (Figure 5.3.7), as they were not sorted into separate species for the mixed treatment units. However, it can be seen that relative to water level treatment, biomass only differs significantly between single *Deschampsia* stands and both the mixed species and single *Agrostis* stands ($p<0.001$), with a generally consistent decrease in biomass as water level increases. While no significant differences are apparent for the root biomass of *Deschampsia* across water level treatments,

for *Agrostis*, the trend is of a significant decrease in relation to increased inundation. This situation is also true of the mixed treatments, suggesting a reduced dominance of *Agrostis* in relation to level of inundation. With significant differences between replacement series (p=0.014) and water level (Table 5.3.4), the findings are generally consistent with those for the above-ground biomass.

Further significant trait-based variation can be seen in relation to factors of competition and relative water level. Once again, these factors are not equal across the two species investigated (Table 5.3.1). For *Agrostis*, all variation in measured traits is due to water level variation alone, with none attributable to competitive interactions. For *Deschampsia*, while most variation is attributable to relative water level, significant competition factors are also defined. It should be noted that a significant water level x competition interaction was identified for above-ground biomass alone (p=0.05).

Plant height (Figure 5.3.3) is significantly lower where water level is below soil surface (-7cm), than at the other two treatment levels for both *Agrostis* (p<0.002) and *Deschampsia* (p<0.001); at this same level, overall height in *Deschampsia* is further reduced with competition (p=0.024). A similar trend is seen for both the number of leaves (p<0.001) (Figure 5.3.4), and number of tillers (p<0.001) (Figure 5.3.5) in *Agrostis* (i.e. significantly less overall for the –7cm water level treatment). In *Deschampsia* however, while the same trend holds for number of leaves (p<0.001), competitive interactions only occur at the 0cm and +7cm water levels, with these plants in wetter conditions producing significantly less leaves where competitive interaction occurs (p=0.002). The production of tillers by *Deschampsia* appears less well defined in relation to relative water level (Table 5.3.1); the highest level of tiller production, although not significantly higher than all other treatment level means, appears to be at the highest quantity of inundation, in single species stands (p<0.04) (Figure 5.3.5b).

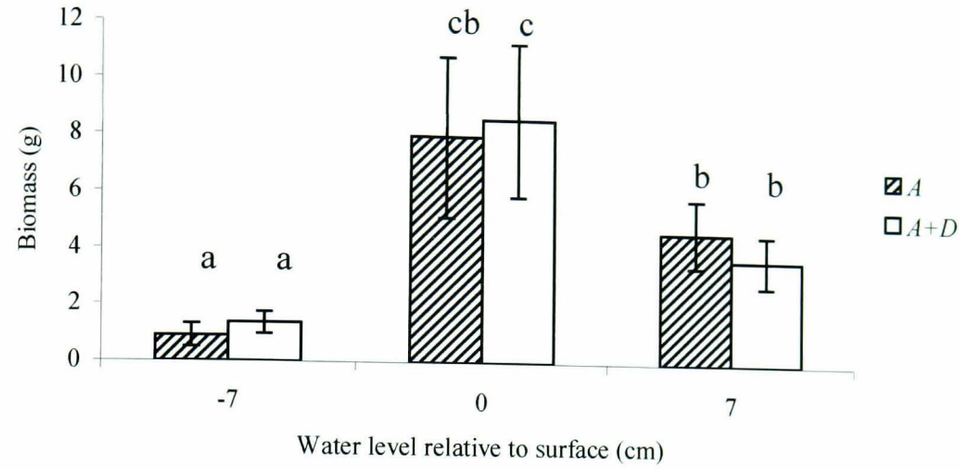
No significant variation was observed in the overall production of leaves per tiller for *Agrostis* (Figure 5.3.6), while in *Deschampsia*, significantly more 'leafy' tillers were observed for individuals at the two higher levels of inundation (p<0.001), than those at –7cm. A further index, SLA, which was calculated from directly measured traits exhibited no significant variation between treatments for either species (Table 5.3.1).

Table 5.3.1. Significant differences between plant attributes in relation to water level treatment relative to soil surface, competition between species, and water level*competition interaction shown by balanced analysis of variance; ns=not significant; *=$P<0.05$; **= $P<0.01$; ***= $P<0.001$.

	A. stolonifera	*D. cespitosa*
Above-ground biomass (g)		
Water level	***	***
Competition	ns	**
Water level*Competition	ns	*
Plant height (cm)		
Water level	**	***
Competition	ns	*
Water level*Competition	ns	ns
Number of leaves		
Water level	***	***
Competition	ns	*
Water level*Competition	ns	ns
Number of tillers		
Water level	***	*
Competition	ns	*
Water level*Competition	ns	ns
Number of leaves per tiller		
Water level	ns	***
Competition	ns	ns
Water level*Competition	ns	ns
Specific leaf area (cm^2/mg)		
Water level	ns	ns
Competition	ns	ns
Water level*Competition	ns	ns

Values for all variables natural log (log_e) transformed.

(a)



(b)

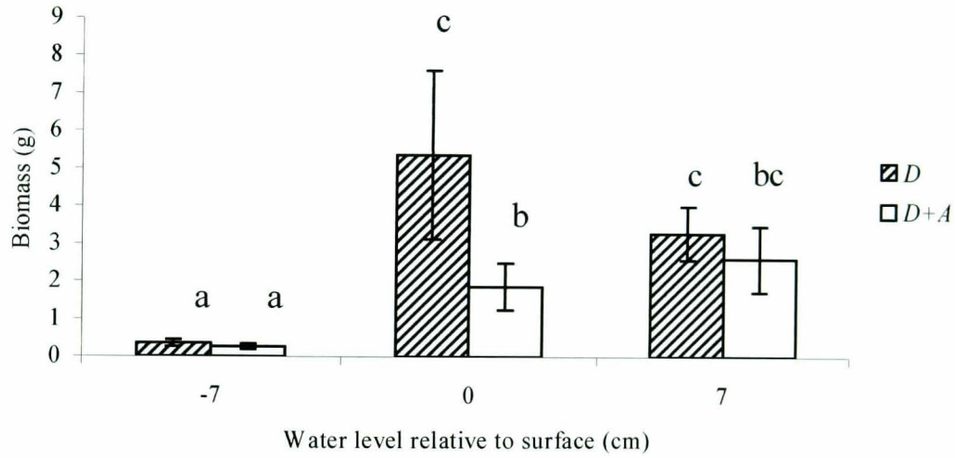
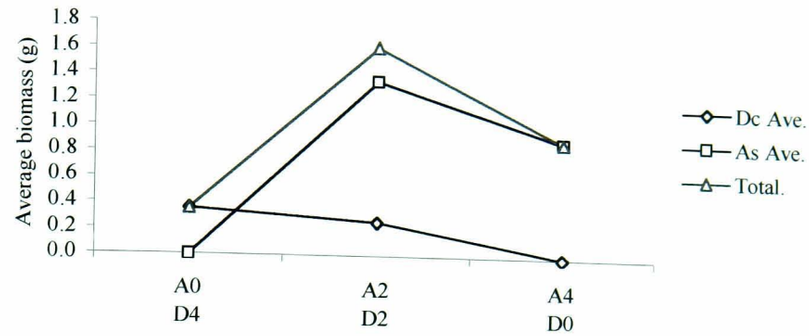


Figure 5.3.1. Mean (±s.e.) above ground biomass for replacement experiments under three fixed water level regimes. (a) *Agrostis* grown in single species stands (*A*), and in 1:1 replacement series with *Deschampsia* (*A+D*); (b) *Deschampsia* grown in single species stands (*D*), and in 1:1 replacement series with *Agrostis* (*D+A*). Same letters at head of graph represent no significant difference between group means (LSD=0.47 and 0.40 ($\log_e$ transformed data), $p<0.05$ respectively).

(a)



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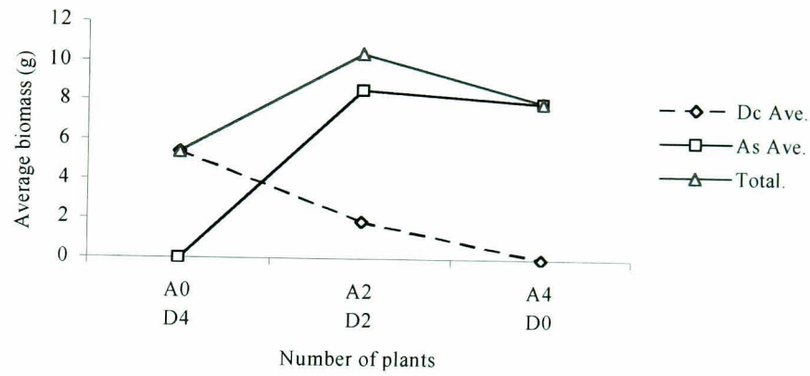


(c)

(c)

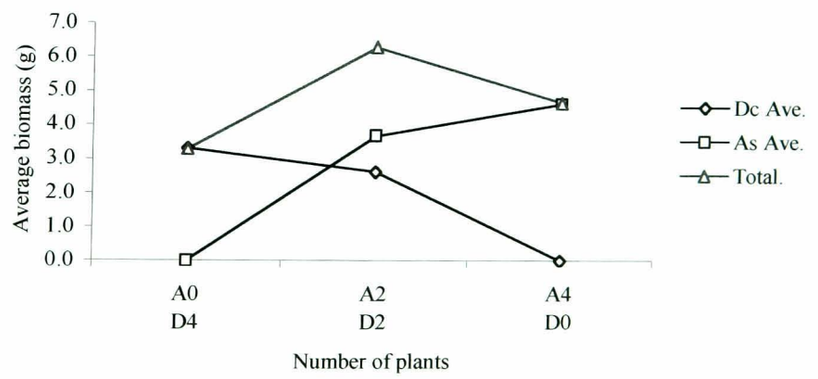


Figure 5.3.2. Mean (±s.e.) above ground biomass per individual for replacement experiments under three fixed water level regimes; (a) water level –7cm relative to soil surface, (b) 0cm, (c) 7cm. Dashed line represents significant difference between replacement series means; Dc= *Deschampsia;* As= *Agrostis*. (LSD=0.4 ($\log_e$ transformed data), $p<0.05$).

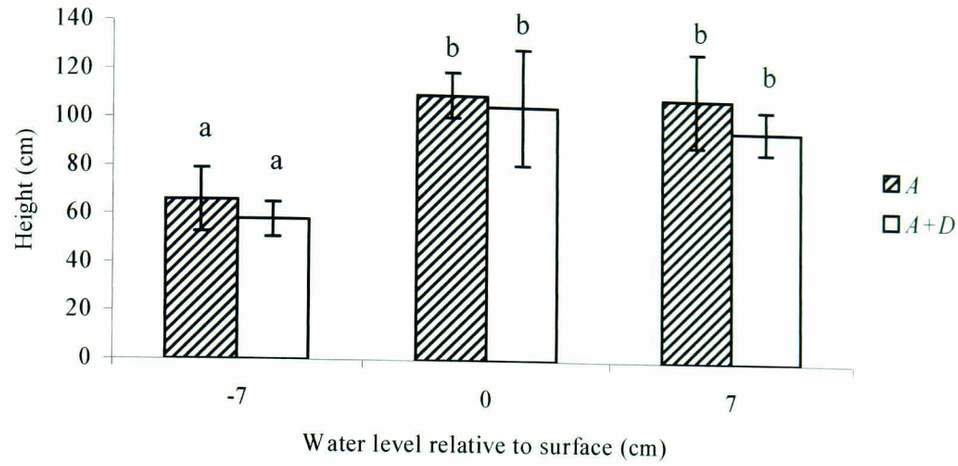
Table 5.3.2 Performance of mixtures of *Agrostis* and *Deschampsia* grown under different fixed water level regimes expressed as Relative Yield Total, for above-ground biomass (log_e transformed values).

Water Level Relative to Surface (cm)	Relative Yield Total
-7	1.09
0	0.82
7	0.87

Table 5.3.3 'Aggresivity' *A. stolonifera* relative to *D. cespitosa*, and *vice versa*, for the two species grown in mixtures, and under different fixed water level regimes; based on figures for above-ground biomass (log_e transformed values).

	'Aggressivity' of species relative to each other	
Water Level Relative to Surface (cm)	*A. stolonifera*	*D. cespitosa*
-7	0.32	-0.32
0	0.25	-0.25
7	0.02	-0.02

(a)



(b)

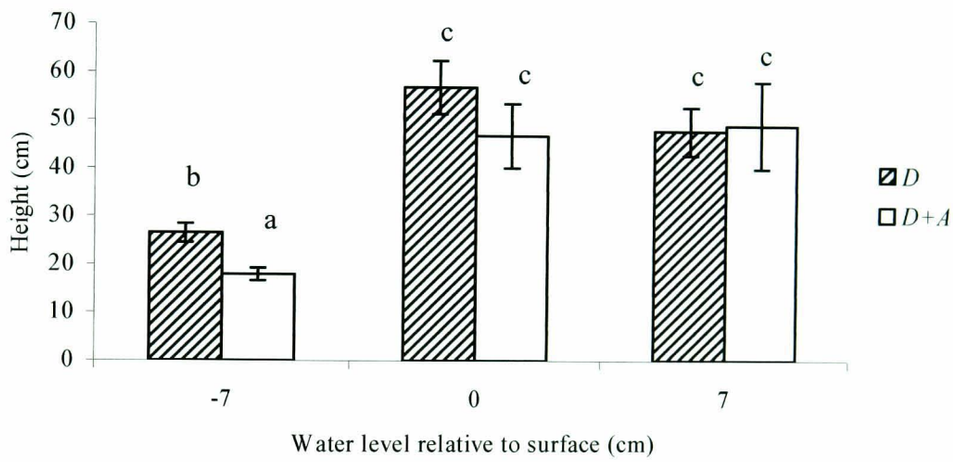
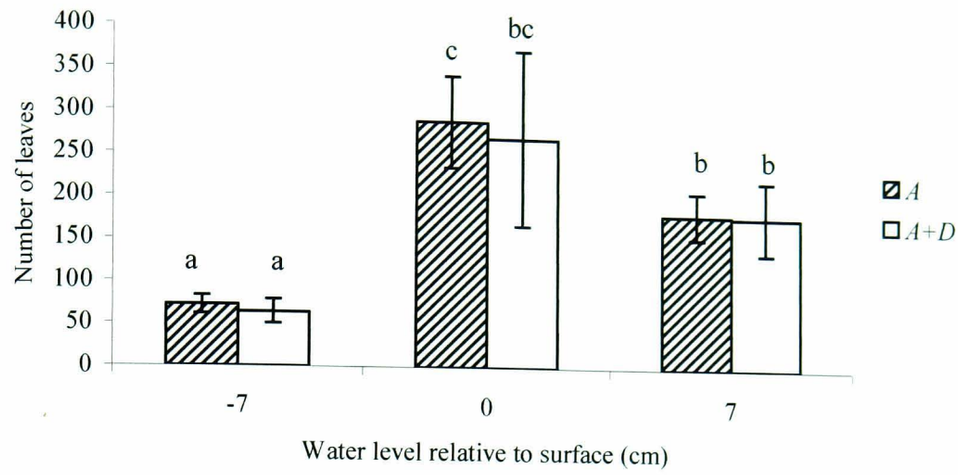


Figure 5.3.3. Mean (±s.e.) plant height for replacement experiments under three fixed water level regimes. (a) *Agrostis* grown in single species stands (*A*), and in 1:1 replacement series with *Deschampsia* (*A+D*); (b) *Deschampsia* grown in single species stands (*D*), and in 1:1 replacement series with *Agrostis* (*D+A*). Same letters at head of graph represent no significant difference between group means (LSD=0.41 and 0.27 ($\log_e$ transformed data), $p<0.05$ respectively).

(a)



(b)

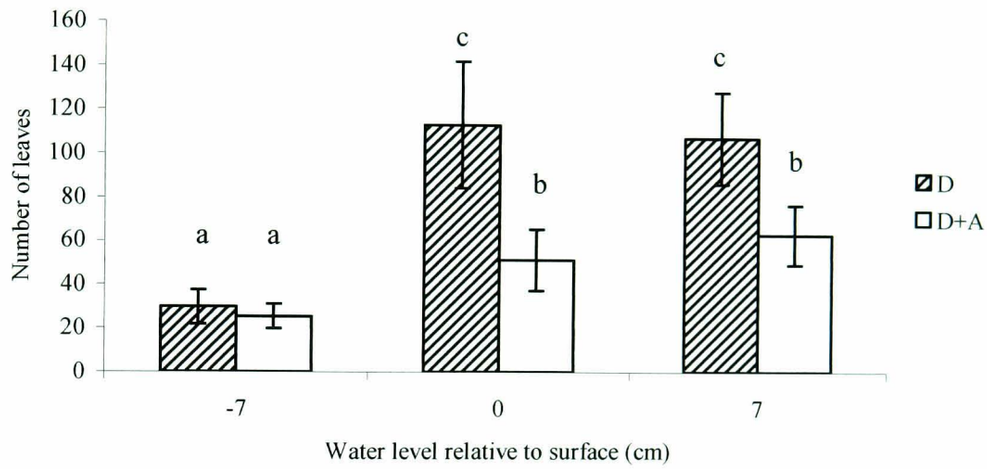
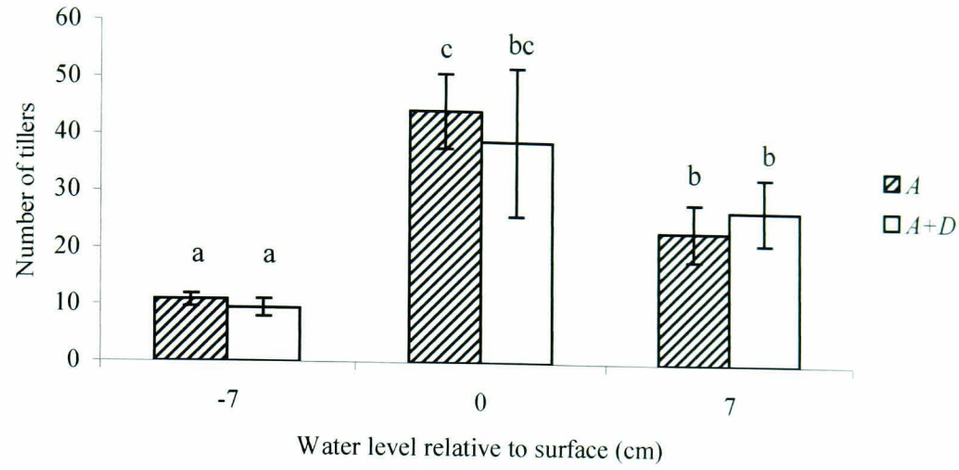


Figure 5.3.4. Mean (±s.e.) number of leaves per plant for replacement experiments under three fixed water level regimes. (a) *Agrostis* grown in single species stands (*A*), and in 1:1 replacement series with *Deschampsia* (*A+D*); (b) *Deschampsia* grown in single species stands (*D*), and in 1:1 replacement series with *Agrostis* (*D+A*). Same letters at head of graph represent no significant difference between group means (LSD=0.39 and 0.48 ($\log_e$ transformed data), $p<0.05$ respectively).

(a)



(b)

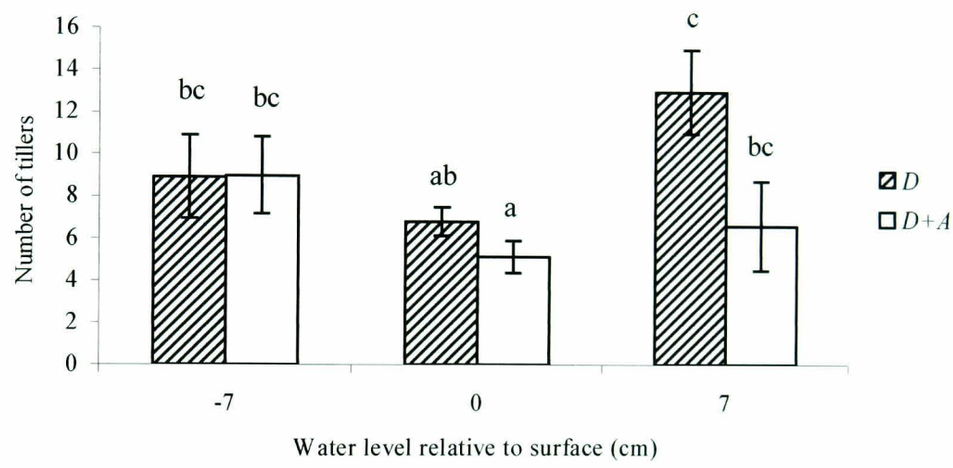
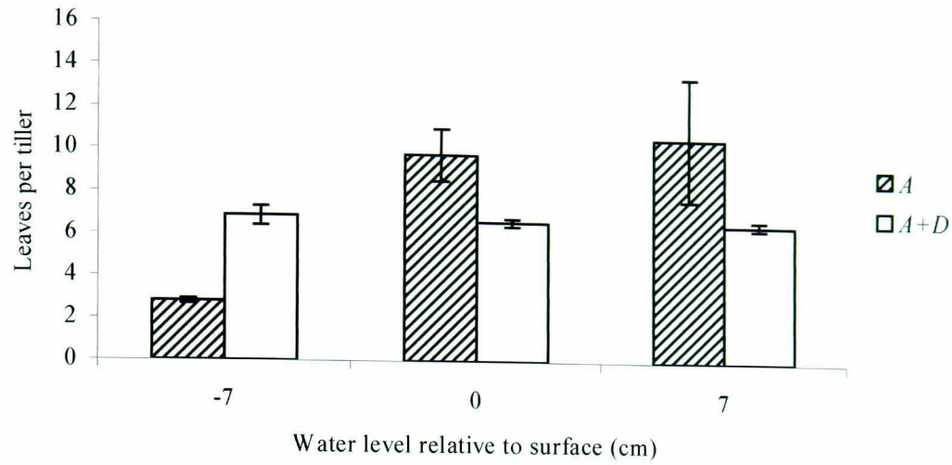


Figure 5.3.5. Mean (±s.e.) number of tillers per plant for replacement experiments under three fixed water level regimes. (a) *Agrostis* grown in single species stands (*A*), and in 1:1 replacement series with *Deschampsia* (*A+D*); (b) *Deschampsia* grown in single species stands (*D*), and in 1:1 replacement series with *Agrostis* (*D+A*). Same letters at head of graph represent no significant difference between group means (LSD=0.41 and 0.42 ($\log_e$ transformed data), $p<0.05$ respectively).

(a)



(b)

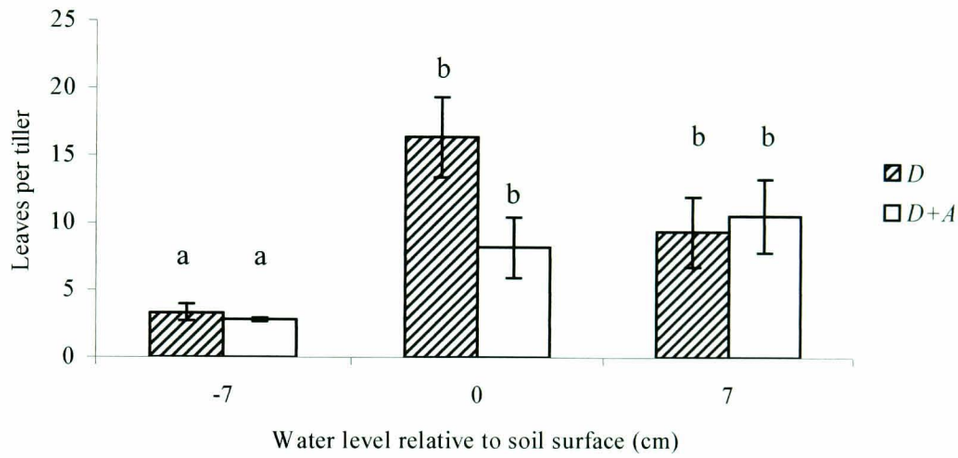


Figure 5.3.6. Mean (±s.e.) number of leaves per tiller for replacement experiments under three fixed water level regimes. (a) *Agrostis* grown in single species stands (A), and in 1:1 replacement series with *Deschampsia* (*A+D*); (b) *Deschampsia* grown in single species stands (*D*), and in 1:1 replacement series with *Agrostis* (*D+A*). Same letters at head of graph represent no significant difference between group means (LSD= not significant and 0.42 ($\log_e$ transformed data), $p<0.05$ respectively).

Table 5.3.4. Results of balanced analysis of variance for average total root biomass per treatment unit (Experiment 1).

Source of variation	d.f.	s.s.	m.s.	f	*p*
Replacement series	2	0.58	0.29	5.46	=0.014
Water level	2	3.63	1.82	34.38	<0.001
Replacement series* Water level	4	0.54	0.13	2.55	ns
Error	18	0.95	0.05		
Total	26	5.70			

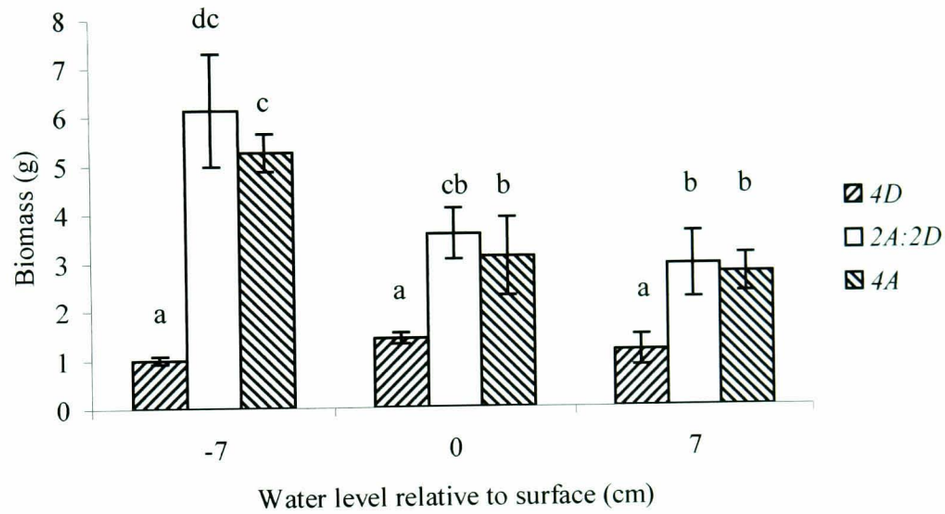


Figure 5.3.7. Mean (±s.e.) root biomass per treatment for replacement experiments under three fixed water level regimes (Replacement series: *4D*= 4 *Deschampsia; 4A*= 4 *Agrostis; 2D:2A*= 2 each of *Deschampsia* and *Agrostis*). Same letters at head of graph represent no significant difference between group means (LSD=0.39 ($\log_e$ transformed data), $p<0.05$)

5.3.2. *Ground-water stress: magnitude and duration of fluctuation*

From a range of variables measured (Table 5.2.1), those found to vary significantly in relation to water table fluctuation were above-ground biomass (p=0.01), total plant biomass (p=0.022), stem biomass (p=0.014), above-soil root length (p<0.001), and rhizome length (p=0.043) for *Phalaris*, and root length alone (p=0.011) for *Deschampsia* (Table 5.3.5).

Similar trends were observed in the response to treatments imposed on *Phalaris* in terms of total above-ground biomass (Figure 5.3.8), total whole plant biomass (Figure 5.3.9), and stem biomass (Figure 5.3.10). The lowest biomass production was amongst treatments involving:

- those whose water levels were at a fixed low inundation (-12cm and -6cm; treatments 1 and 2).
- those whose water table fluctuated between the surface (0cm) and –12cm on a fortnightly basis (treatment 9).
- those, which were subject to periods of inundation (+6cm and +12cm), interspersed with periods at the surface over shorter (weekly) periods (treatments 10 and 12).

High biomass production was seen amongst treatments involving:

- fixed water levels above and including the water table at the surface (0-+12cm; treatments 3, 4 and 5).
- those whose water table fluctuated between surface (0cm) and –6cm on a fortnightly basis (treatment 7).
- those, which were subject to periods of inundation (+6cm and +12cm), interspersed with periods at soil surface over extended (fortnightly) periods (treatments 11 and 13).

Non-significant differences between root biomass, leaf number, or leaf biomass means between treatments (Table 5.3.5) would suggest that most of the overall variation in biomass was apportionable to variation within the stem of *Phalaris*.

Rhizome production varied significantly between treatment level (Figure 5.3.12), with the lowest production being under conditions of fluctuation between soil level and +12cm over a fortnightly cycle. Various other levels of higher and lower rhizome production corresponded roughly to the treatment levels which produced higher and lower biomass levels respectively; exceptions however, were treatments 10 and 13 (fluctuation between soil level,

and either +6cm or +12cm over a fortnightly cycle), which resulted in a relatively high level of rhizome production. The significance of these variations however, was not as marked as for biomass.

Production of roots above soil surface level was seen in fixed level treatments, only under the two highest levels of inundation, with the highest level of production being under an inundation level of +12cm; this treatment mean being significantly higher than all others (Figure 5.3.11). In relation to fluctuating water tables, above-soil root production was mainly seen under treatments where fluctuations rose above soil level; with the exception of treatment 9, which had a drawdown to –12cm over a fortnightly cycle.

The only measured trait found to differ significantly between treatments in *Deschampsia* was overall root length (Figure 5.3.13). Longer roots were produced where water tables were at a fixed level below the soil, or where a degree of drawdown below soil level constituted a part of the fluctuation cycle.

Raw data for all experiments can be found in Appendix 9.

Table 5.3.5. Significant differences between measured traits in relation to water level treatment relative to soil surface for **(a)** *Phalaris arundinacea* and **(b)** *Deschampsia cespitosa*; ns=non significant; *=$p<0.05$; ***=$p<0.001$; - = information not available. For definitions of codes see Table 5.2.1

(a)

A-B[†]	B-B[†]	TB	PH[†]	LN[†]	LB[†]	TN[†]	LNT	StB	RL	A-RL[†]	RhL	RB	SdB	SLA	SRL
*	ns	*	ns	ns	ns	ns	ns	*	ns	***	*	ns	ns	ns	ns

(b)[††]

A-B[†]	B-B[†]	TB	PH	LN[†]	LB[†]	TN[†]	LNT	StB	RL	A-RL	RhL	RB	SdB	SLA	SRL[†]
ns	ns	ns	ns	ns	-	ns	ns	-	*	-	ns	-	-	ns	ns

[†] $\log_e$ transformed values; [††] treatment units –6cm fixed, and –6/1week removed from analysis

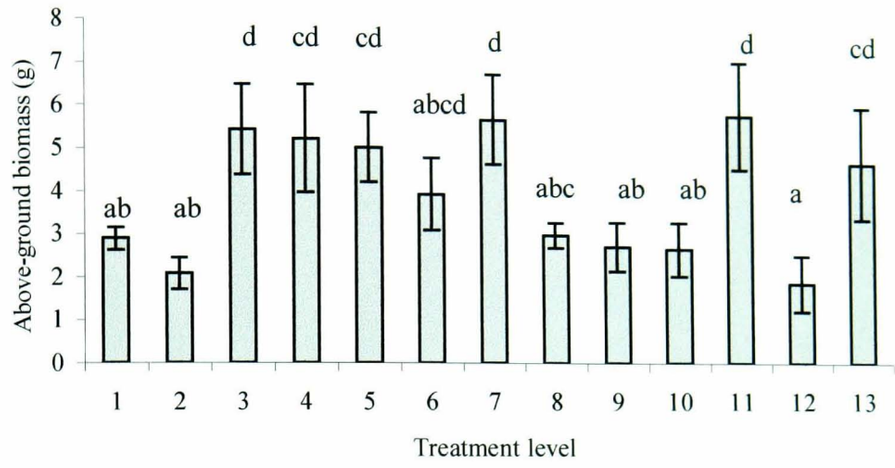


Figure 5.3.8 Mean (±s.e.) total above-ground biomass for *Phalaris* under differing water level treatments (Experiment 2). See Table 5.2.2 for treatment levels. Same letters at head of graph represent no significant difference between group means (LSD=0.51 (log_e transformed data), $p<0.05$).

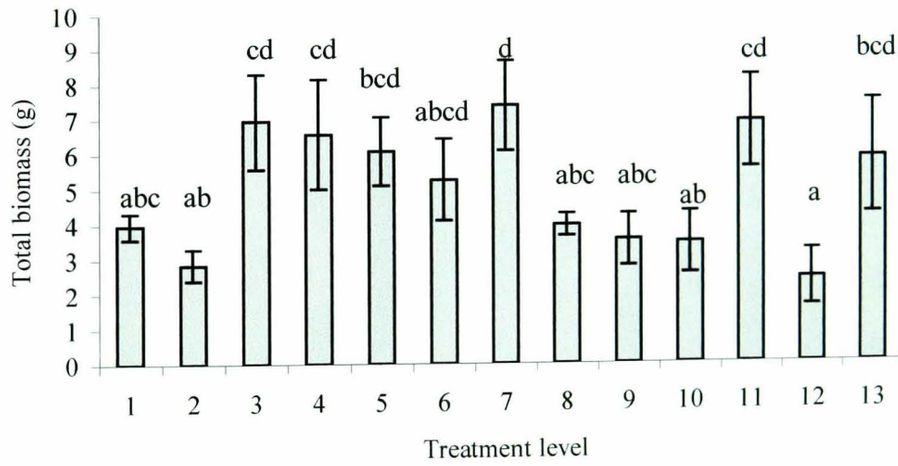


Figure 5.3.9 Mean (±s.e.) total plant biomass *Phalaris* under differing water level treatments (Experiment 2). See Table 5.2.2 for treatment levels. Same letters at head of graph represent no significant difference between group means (LSD=3.16, $p<0.05$).

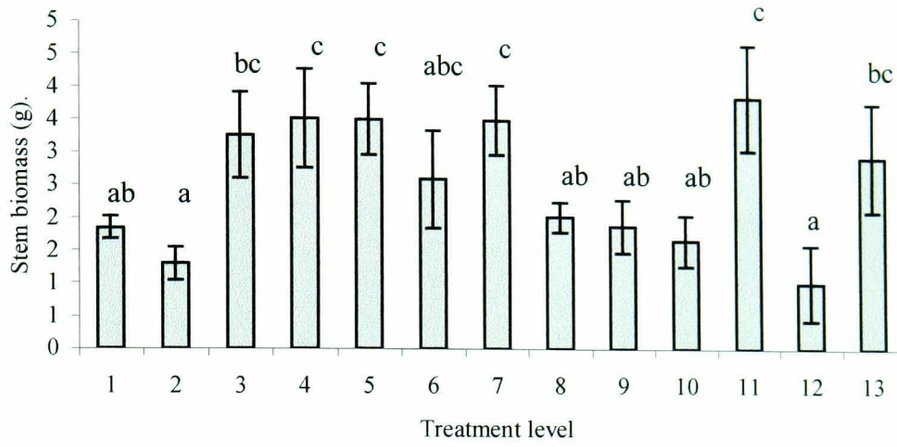


Figure 5.3.10 Mean (±s.e.) stem biomass per plant for *Phalaris* under differing water level treatments (Experiment 2). See Table 5.2.2 for treatment levels. Same letters at head of graph represent no significant difference between group means (LSD=1.68, $p<0.05$).

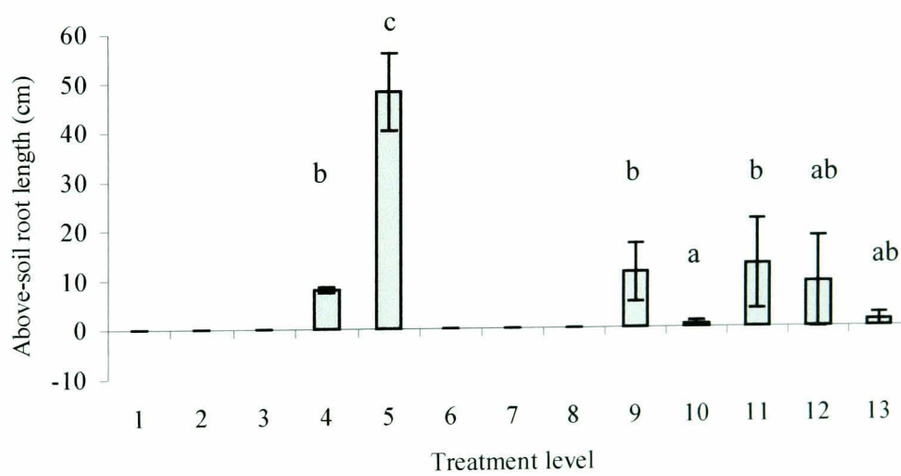


Figure 5.3.11 Mean (±s.e.) above-soil root length for *Phalaris* under differing water level treatments (Experiment 2). See Table 5.2.2 for treatment levels. Same letters at head of graph represent no significant difference between group means (LSD=1.54 ($\log_e$ transformed data), $p<0.05$).

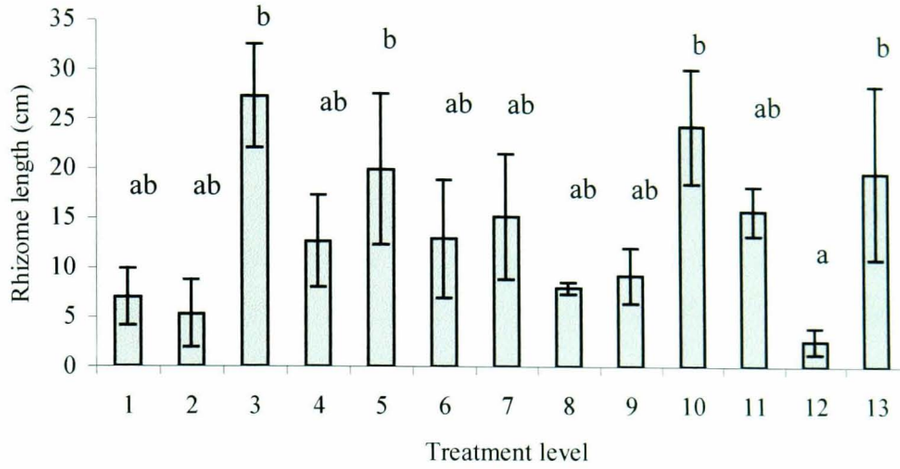


Figure 5.3.12 Mean (±s.e.) rhizome length for *Phalaris* under differing water level treatments (Experiment 2). See Table 5.2.2 for treatment levels. Same letters at head of graph represent no significant difference between group means (LSD=14.72, $p<0.05$).

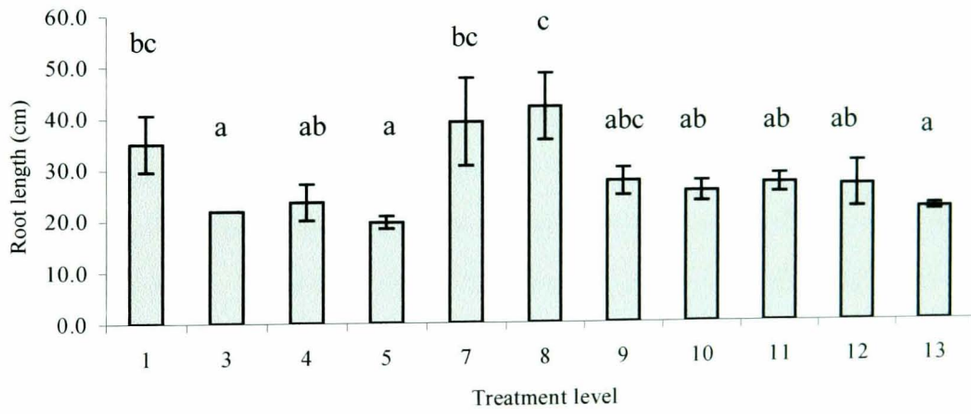


Figure 5.3.13 Mean (±s.e.) root length for *Deschampsia* under differing water level treatments (Experiment 3). See Table 5.2.2 for treatment levels. Same letters at head of graph represent no significant difference between group means (LSD=0.38 ($\log_e$ transformed data), $p<0.05$).

5.4. Discussion

5.4.1. Variation in species traits in relation to factors of stress

Spedding and Diekmahns (1972) state that grasses exhibit properties of extreme plasticity, and a very varied range of responses in size and form in relation to their environment. The results of the experiments detailed within section 5.3 have shown this to be the case amongst the three species of wetland inhabiting grasses investigated (*Agrostis stolonifera, Deschampsia cespitosa* and *Phalaris arundinacea*), under experimental conditions. This response is represented within a number of measurable traits of the species in question, which exhibited significant levels of variation between a number of treatments relating to factors of both water table regime, and competition.

Traits have been shown to act successfully as indicators of plant strategies (Grime, 1974; Grime *et al.*, 1988). Specifically, for the three species under investigation, these traits have been shown to vary in relation to one parameter for which they have known tolerance ranges, namely water table depth (Newbold and Mountford, 1997). In addition, factors of competition have been shown to contribute to variation in measurable traits, and both are known to contribute to zonation in wetlands (Hodgson *et al.*, 1999).

5.4.2. The relationship between ground-water stress and competitive interaction

Within the conditions of the experiments undertaken, *Agrostis* appears to be a superior competitor to *Deschampsia*, consistently producing significantly higher quantities of above ground biomass, and contributing more to the root biomass of mixed stands. The response of *Deschampsia* to competition from *Agrostis,* in the form of reduced biomass and reduced production of leaves is consistent with the species having a less extreme competitive component within its strategy (Grime *et al.*, 1988). The results also appear to show however, that the competitive advantage of *Agrostis* is reduced as level of inundation increases. While the maximum level of inundation which *Deschampsia* has been shown to tolerate is no higher than that for *Agrostis* (Newbold and Mountford, 1997), the finding is consistent with *Deschampsia* generally being associated with habitats where factors of stress reduce the competitive advantage of other species (Davy, 1980). Thereby, acquisition of nutrients from soil, for example, may be reduced in *Agrostis* under increased levels of inundation, while *Deschampsia* gains advantage in this instance by its greater stress tolerant capacity.

The findings here reflect field observations, where *Deschampsia* is often ubiquitous within infertile wet grasslands, and help demonstrate the mechanisms involved in the phenomenon of zonation in wetland vegetation. *Deschampsia* is able to reach high abundance under

conditions which are limiting to a competitive species such as *Agrostis*. In addition, biomass is significantly reduced in *Agrostis* where inundation increases from soil surface level to a flooded level, and specifically, where competition is a factor. While a slight decrease is observed in mean biomass for single species stands of *Deschampsia* under equivalent conditions, it is not significant. Tillering also decreased significantly in *Agrostis*, following the same pattern (decreased tillering has also been noted by Spedding and Diekmahns (1972), under situations where competition for resources is greater). In the case of *Deschampsia*, tillering is increased by factors of both water level, and of competition at the two higher levels of inundation, suggesting once again a reduced advantage of *Agrostis* under situations where the environment is more stressful. These high levels of variation in traits within *Agrostis* relate well to the observations of Spedding and Diekmahns (1972), whereby the relative shoot:root biomass allocation is very variable along fertility gradients.

5.4.3. The influence of duration and magnitude of ground-water fluctuation

The results of the groundwater manipulation experiments carried out on individuals of *D. cespitosa* and *Phalaris arundinacea* further represent the variation of traits within species in relation to environment, and also how the relative plasticity of these traits varies between species with different established phase strategies.

Deschampsia showed little variation in relation to treatment. Roots of greater overall length were produced in relation to situations where the water was below ground level; this was the only measured factor which differed significantly between treatments. While this situation may not appear immediately consistent with the findings of experiment 1, it should be noted that the factor of competition was absent in the water level manipulation experiment, whereas intra-specific competition was a factor for the first experiment, within the single species treatment units. In established plants of *Deschampsia*, the dense nature of the tussocks has been linked to factors of self-shading (Davy, 1980), and is a factor which should be considered where plants reaching 50cm in height are growing in close proximity to one another (Figure 5.3.3).

Phalaris shows a much wider range of morphological variation in relation to the various treatments applied. Many of the potential inferences from the results of the effect of water level manipulation upon *Phalaris*, are consistent with the expected responses of a species with a strong competitive component to its strategy. Wilson and Keddy (1986) found larger, more competitive species in sheltered, fertile positions along such gradients. From the results, overall biomass accumulation can be related to treatments which were fixed at surface, or above surface situations, or where levels fluctuated between the surface and

inundation; namely, those treatments which pose the lowest levels of stress to a competitive species, which is adapted to inundation during its growing period. This adaptability is strongly associated to the ability to produce aerenchyma relatively rapidly (Smirnoff and Crawford, 1983). Conversely, treatments resulting in lowest biomass could be likened to conditions which simulated stress for such a species; i.e. drought, and consistent fluctuation cycles of water level variation over short time-scales (e.g. weekly).

Inferences can also be made from the results about the potential lateral spread and establishment via rhizome production. As with biomass, rhizome production was greatest under conditions of lowest stress in relation to the overall tolerance range of *Phalaris* (fixed, inundated levels, and fluctuation of water levels over longer time periods; i.e. fortnightly). Therefore under equivalent low stress situations within the field, it may be that *Phalaris* comes to dominates large areas via rhizome production; some form of control may therefore be afforded by greater variation within groundwater levels. The production of above-soil roots is less clear in relation to treatment level, but appears to be higher under conditions which are subject to inundation, with the highest production being under the highest fixed level of inundation.

5.4.4. General comments on stress and competition treatments, and potential applications.

In section 5.1.3 it was commented that single species experiments cannot take full account of competitive interactions within mixed communities (or indeed, within single species swards) in the field. Such experiments have the potential to indicate the likely results of changes in water table levels within wetlands. In conjunction with field observations, where a wider range of variables co-differ, such experiments can be highly informative. From these results alone, different modes of response can be seen within species with contrasting strategies, in terms of morphological response. For example, *Phalaris* was more susceptible to treatments which could be approximated to conditions of stress within the field (e.g. summer drawdown, or rapidly fluctuating water levels). In addition, species with a highly competitive component to their strategy, such as *Agrostis stolonifera*, when found at the extremes of their ecological limits (in this case, in terms of water table tolerance) have a reduced competitive ability, and are therefore less likely to supress more stress tolerant species such as *Deschampsia*.

The potential exists to predict specific strategies from traits measured within the field (Hodgson *et al.*, 1999). Even where the exact identity of a species is not necessarily known, the potential impacts of water level variation upon the survival of this species could still be

predicted using such an approach. While the studies outlined here apply to species from temperate environments, which have similar climatic and environmental controls acting upon them, the approach is likely to have wider applicability.

With specific reference to potentially invasive species such as *Phalaris*, any information which can be used to counter unwanted spread, or to reduce its extent witin a given wetland is desirable; especially where the hydrological inputs of many wetlands are actively managed (as with the examples outlined in section 5.1).

5.4.5. Possible future directions

A short term study such as this can provide useful information in terms of trait differentiation in relation to (i) plant strategy, (ii) underlying environmental gradients, (iii) possible inter-specific and intra-specific interactions within wetland vegetation. A number of logical extensions to such an approach include:

- long term, non-destructive monitoring of similar experiments, involving a wider range of wetland species, with contrasting strategies.
- field observations of localised areas of wetland vegetation, which can be continually monitored, and whose groundwater regime can be manipulated; from which, any variation within the traits of individual species could be directly compared to surrounding, untreated reference stations, and for which competitive interaction can also be taken into account.

In conclusion, the study of traits within vegetation can help inform how species with differing strategies respond to relative treatments. From this basis, it may be possible to infer how comparable water level regimes may influence such species within the field, and therefore, aid prediction of the impact of potential water level change upon wetland vegetation. In terms of either conserving rare species, or of managing invasive species, such an understanding is critical.

Chapter 6: General discussion

6.1. Review of the project

This final chapter brings together the work from previous chapters and reviews and discusses the outputs as components of a coherent piece of applied research. The results of the work are also discussed in the wider context of understanding eco-hydrological relationships in wetland vegetation, and in their potential application to the management of these habitats.

6.1.1. Summary of the aims and objectives

Wetlands provide a wide range of valuable functions including biodiversity support, flood control, and groundwater amelioration, but threats still exist from a number of sources, including urbanisation, dam construction, and groundwater abstraction for agriculture. These are practices which inevitably affect localised hydrology and water table levels within wetlands (see Chapter 1 for a full review). Therefore, there is still an overwhelming need to be able to predict the impacts of such changes on wetland vegetation (Keddy, 1992a and b; Gowing *et al.*, 1998).

The main aim of this project was to determine the main environmental pressures underlying diversity, vegetation structure, and functional characteristics of the dominant plant populations in different assemblages within a number of representative freshwater wetland systems across northern Britain. For this purpose, a number of fen, swamp and mire habitats were identified, and characteristics of the vegetation and groundwater and substrate environment were sampled. This allowed elucidation of eco-hydrological interactions within a defined range of wetland types, and in conjunction with experimental work, permitted identification of traits within the vegetation with the potential to act as predictors of hydrological variation. It also allowed the prediction of what changes, if any, might occur in the vegetation as a result of altered hydrological regimes. Such work was considered important in strengthening the production of broad-scale management tools for these important habitat types. The chapters presented in this thesis each cover different aspects of an applied study of a number freshwater wetland vegetation types.

6.1.2. Review of main findings

A general overview of the study sites sampled during 1998-2000 was provided in Chapter 2. The plant species recorded at each site, along with the values for hydrological and substrate environmental variable ranges measured, were listed. From the initial investigation of the data it was considered that the sites studied represented a good range of fen, swamp, and

associated mire habitats from the target biogeographic area (northern Britain). This provided a good case for the use of the data to characterise, and predict eco-hydrological relationships in wetland vegetation, as presented in subsequent chapters.

In Chapter 3 the study sites used during 1998-2000 were characterised in terms of plant community composition and underlying groundwater characteristics. This approach used a combination of phytosociological and physiognomic assessments of the vegetation. Multivariate analyses allowed characterisation of consistent groupings which could be defined as particular community types (Rodwell, 1991 *et seq.*). In certain cases differences could also be highlighted between groupings given the same community classifications, in terms of their relative trophic status, and in terms of collective vegetation variables (e.g. canopy height). In agreement with Duckworth *et al.* (2000) it was concluded that along with more traditional phytosociological classifications, the use of vegetation traits could serve as useful indicators of environment-vegetation relationships. Once again, this was a good basis from which to approach the subsequent sections of the thesis.

The main environmental gradients driving wetland vegetation composition were determined in Chapter 4 using constrained ordination. Significant variables included maximum levels of inundation, and the pH and redox potential of the substrates. Different samples were also characterised and differentiated in terms of the predominant vegetation characteristics present. A number of multiple regression models were developed which successfully highlighted eco-hydrological relationships between the groundwater environment and variation in collective vegetation variables and dominant population traits. The same approach was extended to the use of attributes gleaned from literature searches, following the construction of an attribute by sample matrix. This approach represented a pilot study which has the potential to be developed further.

Trait measures successfully acted as predictors of the interaction of vegetation and the major groundwater hydrological and hydrochemical gradients. As such, predictive relationships were described between factors of the vegetation, and the underlying environmental regime. A number of the findings complemented and built upon previous studies (e.g. Ross *et al.*, 1998; Willby *et al.*, 1997; Willby *et al.*, 1998). In addition, aspects of the groundwater environment important in the functioning of wetlands were shown to be predictable from the variables measured within the vegetation.

Chapter 5 took an experimental approach to monitoring the growth responses of three wetland species to water level variation and competition. Grime's strategy theory (Grime,

1979) has previously provided a basis for the successful prediction of Plant Functional Groups (PFG's) within European riverine wetland vegetation (Hills, 1994; Hills *et al.*, 1994; Hills and Murphy, 1996). Therefore various water level variation and competition treatments were applied to native species with known strategies *Agrostis stolonifera* L., *Deschampsia caespitosa* (L.) Beauv., and *Phalaris arundinacea* L.. The results provided information relating to the contrasting growth responses of these different species, which may help inform potential impacts of water level change when considered in conjunction with field observations. This is important for effective and sensitive wetland management.

6.1.3. Criticisms of the work

Many of the aspects of the work undertaken can be criticised. While a good deal of these relate to the time limitations imposed by a three-year research period, they should still be mentioned, and their importance assessed. Main criticisms might relate to (i) aspects of the field sampling; (ii) the selection of traits measured; (iii) length of field study period:

(i) *Aspects of field sampling:* One concern might be that only above-ground samples were taken, and that resource ratios between above and below-ground parts of relative species, or general morphology might vary in certain populations as a result of varying hydrological or fertility gradients (Spedding and Diekmahns, 1972; Koncalová, 1990). However, the successful removal of entire (or even a majority of) root systems in the field was virtually impossible. The lack of root data means we might have less information relating to the variability of a community, or population, in relation to its environment. It does not represent a flaw in the data however, as meaningful predictions were still made from the data which could be collected.

In addition, the experimental work undertaken in Chapter 5 has provided some information as to root:shoot allocations in relation to groundwater variation (for example, root length was one of the few variables shown to be significantly reduced in *Deschampsia cespitosa* where water inundated the substrate continuously, or where levels of inundation were deeper, and lasted for longer periods. However, any such short-term glasshouse experiments require care in extrapolating to the field, and the pros and cons of these experiments (i.e. the absence of multiple biotic and abiotic interactions) in relation to informing field observations are discussed in Chapter 5.

(ii) *The selection of traits measured.* All of the traits measured were simple morphological measurements which related to the size or biomass of constituent parts of the vegetation. Keddy (1992) considered that such traits represent only a "very small window into the rich landscape of traits". Indeed traits relating

biochemical and physiological processes may enable the clarification of certain functions within species (Willby *et al.*, 2000). However, such work would undoubtedly require intensive and large-scale screening of a large number of species. For this reason Willby *et al.* (2000) produced an attribute classification of habitat utilisation in northern European hydrophytes, rather than attempting to define any specific functions.

In addition, the aim of this work was not to produce a definitive functional classification (for the reasons outlined above), but rather to produce a useable methodology for predicting broad-scale changes in wetland vegetation in relation to hydrological variation. The value of the results speak for themselves in this context.

(iii) *Length of field study period.* This is an issue raised in Chapter 3, but deserves reiteration here. van der Valk *et al.* (1994) consider long term processes such as succession to be one of the main factors which can confound studies of the impacts of disturbance upon the composition and structure of vegetation. Meanwhile, de Mars *et al.* (1997) consider that long term monitoring of wetlands is important to capture extreme flooding or drawdown events, which are important in influencing and maintaining species composition. This weakness is highlighted in the limited applicability of the predictive models produced to a number of stations at Insh Marshes, which were subject to sustained levels of increased drawdown over the three year study period (however, the models have good potential to be successfully applied to systems with less severe drawdown in their groundwater regimes). However, this is not a problem which can be overcome in the confines of a three-year research period, and not one for which a solution is apparent.

6.1.4. Potential future directions

Some of the criticisms above arise from factors which were outwith the scope of the project (in terms of its remit as an ecological study, and within the limited time period). Considering these factors, ideas for the potential development of the work presented in the thesis have arisen directly from the work, and in conjunction with existing theories and applications. These ideas are discussed in the relevant chapter discussion sections, but are summarised below for reference purposes:

- Directed sampling to increase data for some of the defined habitat types studied (i.e. specifically fen or swamp systems), and refine models utilising some state variables (e.g. biomass). The development of such a dataset might allow:

- Long term monitoring of sites which have seen large drawdown impacts during the study period, in order to assess re-inundation and its implications for the vegetation present.
- Development of methodologies to predict differences between one definable community type to another (e.g. NVC), and therefore potential changes between communities due to perturbation, with the dissemination of outputs via a web or CD-ROM-based GUI, or other appropriate platform.

- The biogeographical coverage of data comprising the work of the CSR strategy theory of Grime (Grime, 1979; Grime *et al.*, 1988) was largely restricted to the flora around the region of Sheffield and Derbyshire in the U.K. The application of the theory to formerly unclassified species is now a possibility (Hodgson *et al.*, 1999). This could allow for the testing of the functional classification methodology devised by Hills *et al.* (1994) to a range of British wetland vegetation types (and with the addition of a few relatively easily measured groundwater-related environmental gradients as identified by the work presented here).
- Measurement of physiological traits so that 'function' can be defined, and perhaps inferred from morphological traits would be a useful development, with outputs which could inform management practices further. Recent work by Vretare *et al.* (2001) shows one potential approach, which combines experimental and field observations. The work links phenotypic responses in *Phragmites australis* to the species ability to regulate gas exchange between aerial and below-ground parts of the plant, and its ability to uptake nutrients. However, this is but one species, and much more screening work is required in this area of research.

6.2. Application of the work to wetland management

6.2.1. Synthesis of the results

A relatively few major hydrological and hydrology-related environmental pressures appear to drive the structure and composition of the vegetation within the fen, mire and swamp communities sampled. In addition, important variables such as pH are largely influenced by source of groundwater input (e.g. telluric, or riverine), while relative redox potential is strongly influenced by physical factors of drawdown, inundation and fluctuation. Variations in these factors are therefore intimately linked to the stable state of redox potential.

It is apparent that relative levels of drawdown, inundation and fluctuation equate to relative levels of stress within the given systems. These factors of stress in turn favour certain species assemblages and certain characteristics within the wetland vegetation via a number

of routes. Both level of drawdown, and levels of inundation will favour certain species, and effectively exclude others with different water level requirements (Newbold and Mountford, 1997), especially if amplitudes of fluctuation are relatively low. Variation of relative water table levels within these prescribed limits will influence the morphology of the constituent species within their parameters of plasticity. More dynamic systems (in terms of fluctuating water levels) however, will provide a different form of stress: intermediate levels of regular fluctuation have been shown to influence relative trophic status of wetland soils via nitrogen and phosphorus mineralization (Patrick and Mahapatra, 1968), but there will undoubtedly be a trade-off in terms of the ability of vegetation to withstand increasingly higher levels of stress. This has been demonstrated in the results presented by predictive relationships between increasing values of stress, and biotic variables such as stem density, and biomass.

A relatively large number of predictor variables were best expressed as quadratic and cubic functions within the predictive models, and this can perhaps be explained by the dynamic nature of the wetland environment, as outlined above. One example is the morphological variation observed in wetland graminoids by Koncalová (1990). More sub-surface roots are produced with increasing water table levels, rather than are deep-penetrating roots, and vice-versa for lower water table levels. Rapid fluctuations between these two states however is likely to represent a hostile environment to even those species adaptable to water level variation, with a trade-off between production of photosynthetic biomass and specialised root biomass likely to be compromised. Therefore, relative to the more stable states of near-continuous inundation or drawdown, a good deal of wetlands probably represent predominantly stress-driven environments, with constricted gradients. Evidence for this has been provided by the eco-hydrological interactions detailed in this work.

6.2.2. Specific applications

The work presented has tangible outputs with the potential to be applied as components of tools to manage wetland ecosystems in an informed manner, and also as tools to monitor wetland health (biointegrity). The work goes some way to fulfilling what Wheeler and Shaw (1995) regarded as a need to be able to understand interrelationships between mire vegetation and hydrology, to enable the prediction of the likely effects of hydrological change upon vegetation. Further work, as discussed above, is however clearly still needed. The specific applications of the work might allow:

- A prediction of the effects of groundwater drawdown, for consideration where proposed abstraction (or other) works might directly affect wetland hydrology.

- An informed management of rare and endangered species, or species with a restricted distribution whose ecological requirements are not known (e.g. see Appendix 10).
- Hydrological management of certain wetlands; for example, the aim of management of certain wetlands may be to produce canopy structures conducive to nesting and over-wintering birds (e.g. Bhatia, 1999). Broad-scale changes to state variables within the vegetation in relation to water-level variation can be predicted using this approach.
- Management of invasive species (often a problem in wetlands whose hydrology is managed: e.g. Bhatia (1999), Mitchell (2000) by appropriate manipulation of water levels.

In conclusion, this study represents a stage of progression in the application of trait-based assessments to the understanding of wetland ecology. As such, a number of predictable relationships between major gradients and aspects of the vegetation have been described. However, as with any aspect of vegetation ecology there is an obvious need to complement the trait-based approach with an assessment of the community assemblage, in order to rationalise the use of broad-scale predictive approaches at finer spatial scales (e.g. within a single site). This thinking perhaps helps to rationalise the general state of views in vegetation ecology at the current moment, somewhere between the extremes of the organismic and individualistic models of vegetation composition proposed by Clements and Gleason (see Chapter 1). On the one hand, a number of traits are shared by species composing the vegetation, and the environment will act as a 'filter' of certain traits, or will at the very least determine the relative values of these traits, irrespective of geographical location. On the other hand, the characteristics and potential 'irregularities' of the individual species also need to be considered if wetland management is to be best informed.

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Appendix 1 Sampling dates at each site during period 1998-2000, showing numbers of stations sampled per visit.

Site	1998					1999				2000			
	May	June	July	Aug.	Sept.	May	June	July	Aug.	May	June	July	Aug.
Endrick Marshes	-	-	-	-	-	-	-	-	-	30th 1-6	28th 1-6	-	2nd 1-6
Glen Moss	-	-	-	-	-	-	14th 1-6	16th 1-6	8th 1-6	-	-	-	-
Insh Marshes	25th 1-2(x3)	-	7th 1-11(x3)	14th 1-17	-	c.20th 1-16; 18-21	22nd 1-16; 18-21	20th 1-16; 18-21	17th 1-16; 18-21	23rd 1-7, 9	27th 1-7, 9	-	3rd 1-7, 9
Lochwinnoch	-	-	-	-	-	-	14th 1-6	16th 1-6	8th 1-6	-	-	-	-
Nether Whitlaw moss	14th 1-3(x3)	25th 1-5(x3)	22nd 1-4(x3)	-	3rd 1-6	18th 1-6	15th 1-6	15th 1-6	11th 1-6	-	-	-	-
Tarn moss	-	-	-	-	-	-	16th 1-5	14th 1-5	12th 1-5	-	-	-	-
Wood of Cree	-	-	-	-	-	-	-	-	-	22nd 1-6	29th 1-6	-	1st 1-6

Appendix 2 Vegetation quadrats sampled at Nether Whitlaw during June 1998

	Station 1			Station 2			Station 3			Station 4			Station 5		
Species	1.1	1.2	1.3	2.1	2.2	2.3	3.1	3.2	3.3	4.1	4.2	4.3	5.1	5.2	5.3
Equisetum fluviatile	100	100	100	100	100	100	88	48	88	0	0	0	0	4	4
Carex lasiocarpa	48	44	4	0	0	0	0	0	0	100	4	52	100	100	100
Galium palustre	64	8	52	0	0	0	0	0	0	16	16	0	0	0	0
Bryum pseudotriquetum	0	0	8	0	0	0	0	0	0	8	32	0	0	0	0
Epilobium palustre	8	4	8	0	0	0	0	0	0	0	0	0	0	0	0
Filipendula ulmaria	0	4	100	0	0	0	0	0	0	0	0	0	0	0	0
Lemna minor	56	100	8	0	0	0	0	0	0	0	0	0	0	0	0
Menyanthes trifoliata	24	0	0	32	100	100	100	100	100	100	100	100	4	0	16
Potamogeton coloratus	0	0	0	68	36	4	0	4	44	0	0	0	0	0	0
Ranunculus flammula	8	8	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentila palustris	8	0	4	0	0	0	0	0	0	8	8	0	0	0	0
Agrostis stolonifera	12	8	0	0	0	0	0	0	0	0	0	0	0	0	0
Veronica anagalis-aquatica	4	0	12	0	0	0	0	0	0	0	0	0	0	0	0
Lychnis flos-cuculi	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiomnium rostratum	0	0	20	0	0	0	0	0	0	8	20	0	0	0	0
Eriophorum angustifolium	0	0	0	0	0	0	0	0	4	60	24	52	0	0	8
Cardamine pratensis	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0
Salix cinerea (s)	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0
Pellia epiphylla	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0
Carex diandra	0	0	0	0	0	0	0	0	0	0	44	0	0	0	0
Oenanthe lachenalii	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0
Holcus lanatus	0	0	0	0	0	0	0	0	0	0	48	0	0	0	0
Carex rostrata	0	0	0	100	100	100	100	100	100	0	0	0	0	0	0
Betula pendula	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0
Juncus effusus	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0
Polytrichum commune	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0
Sphagnum squarrosum	0	0	0	0	0	0	0	0	0	0	0	0	100	100	100

Appendix 3 Species lists and abundance values per sample station.

Appendix 3(a) For August 1998; three letter codes represent species listed in Table 2.3.1. i= Insh Marshes, n=Nether Whitlaw

	i1	i2	i3	i4	i5	i6	i7	i8	i9	i10	i11	i12	i13	i14	i15	i16	i17	n1	n2	n3	n4	n5	n6
Ach pta	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agr sto	0	0	0	0	64	80	0	0	0	4	4	0	0	100	0	0	0	24	0	0	0	0	0
Ang syl	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0
Aul pal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0
Bet pen	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16
Bry pse	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	8	0	0
Cal pal	8	4	0	0	12	20	0	0	0	0	0	0	4	4	0	0	0	0	0	0	0	0	0
Cam ste	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Car pra	0	4	0	4	0	0	0	0	0	4	4	0	0	0	0	0	0	0	0	0	12	0	0
Car aqu	0	0	0	100	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Car cho	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0
Car dem	0	0	60	0	48	0	0	0	0	0	0	0	8	8	0	0	0	0	0	0	0	0	0
Car ech	0	0	12	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Car las	0	0	0	0	0	0	0	0	0	0	100	0	0	0	100	0	100	4	0	0	60	0	0
Car nig	0	0	0	0	0	20	0	0	0	100	4	0	0	12	12	4	8	0	0	0	0	0	0
Car pan	0	0	52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Car ros	100	0	0	0	0	0	0	0	20	0	0	100	100	0	0	0	0	4	100	76	0	100	4
Car ves	0	12	0	0	0	60	100	0	0	0	0	0	0	0	0	4	8	0	0	0	0	0	0
Des ces	0	0	0	0	0	0	20	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epi pal	0	0	0	0	0	0	0	0	0	4	0	0	0	4	0	0	0	12	0	0	8	0	4
Equ flu	8	0	16	100	24	0	12	0	0	44	0	72	100	36	0	8	60	100	76	56	0	0	60
Eri ang	0	28	8	0	0	4	0	0	0	4	0	0	0	0	0	0	0	0	0	0	76	0	92
Fes rub	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
Fil ulm	0	0	0	0	0	8	8	44	0	0	0	0	0	80	0	0	0	72	0	0	0	0	0
Gal pal	4	0	0	0	16	4	4	0	80	8	12	0	0	0	0	0	0	4	0	0	8	0	12
Hol lan	0	0	0	0	0	0	0	8	0	76	0	0	0	32	0	0	0	0	0	0	4	0	44
Jun art	0	0	0	0	12	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0

Appendix 3(a)

Jun buf	0	0	0	0	0	0	0	0	0	0	0	4	16	0	0	0	0	0	0	0	0	0	0
Jun eff	0	0	0	0	0	32	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lem min	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0
Men tri	0	0	0	0	0	0	0	0	0	84	100	76	0	0	4	36	0	0	100	56	96	8	12
Mol cer	0	100	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myr gal	56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oen lac	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	12
Ped pal	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0
Pel epi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0
Pha aru	8	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phr aus	0	0	0	0	84	0	0	0	0	0	100	0	0	0	100	0	0	0	0	0	0	0	0
Pla ros	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	8	0	0
Poa tri	0	8	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pot pol	0	0	0	0	0	0	0	0	0	0	0	100	100	0	44	100	0	0	48	4	0	0	0
Pot pal	20	0	8	24	24	16	0	0	8	56	12	8	16	36	48	16	76	0	0	0	4	0	36
Ran fla	8	12	0	52	32	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ran lin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	8
Ran rep	0	0	0	0	0	0	16	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rum ace	0	0	0	0	0	0	0	4	0	0	0	0	0	8	0	0	0	0	0	0	4	0	0
Sal cin	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
Sco sco	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Sph pal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32	0
Sph rec	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0
Sph squ	0	0	0	0	0	0	0	0	0	96	8	0	0	0	0	0	0	0	0	0	0	100	100
Ste als	0	0	0	0	0	0	0	0	0	12	0	0	4	0	0	0	4	0	0	0	0	0	0
Suc pra	0	0	0	0	0	4	0	12	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0
Utr vul	0	0	0	0	0	0	0	0	0	0	0	8	8	0	4	0	0	0	0	0	0	0	0
Val off	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0
Ver ana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0
Vio pal	0	0	0	0	0	0	0	28	0	72	0	0	0	8	0	0	0	0	0	0	0	0	0

Appendix 3(b) Species lists and average abundance values per station for 1999; three letter codes represent species listed in Table 2.3.2: g= Glen Moss; i= Insh Marshes; l= lochwinnoch; n=Nether Whitlaw; t= Tarn Moss.

	g1	g2	g3	g4	g5	g6	i1	i2	i3	i4	i5	i6	i7	i8	i9	i10	i11	i12	i13	i14	i15	i16	i18	i19	i20	i21	l1	l2	l3	l4	l5	l6	n1	n2	n3	n4	n5	n6	t1	t2	t3	t4	t5
Ach pta	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agr cap	0	0	0	0	0	7	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0
Agr sto	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	4	0	0	0	28	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0
And pol	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	5	0	17	0
Ang syl	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	5	0	0	0	0	0	4	0	0	0	0	1	4	19	0	0	0
Aul pal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
Bet pen	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cal cus	0	0	0	0	0	0	11	1	0	0	12	15	0	0	0	8	3	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Cal pal	0	0	0	0	0	0	15	0	0	1	13	9	0	1	0	15	3	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	5	0
Cal vul	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31	7
Cal mue	0	0	0	0	0	0	9	0	0	0	3	0	0	3	0	4	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1	0
Car pra	0	0	0	0	0	0	3	0	0	33	3	3	3	12	33	5	1	0	0	1	0	0	0	33	0	33	9	33	0	33	32	33	0	0	0	0	0	0	0	0	0	0	0
Car aqu	0	0	0	0	0	0	0	0	0	67	0	0	0	0	67	0	0	0	0	0	0	33	0	61	0	49	0	29	0	67	65	63	0	0	0	0	0	0	0	0	0	0	0
Car cho	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45	0	0	0	5	0	67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Car dia	1	0	0	0	0	0	20	4	3	0	3	7	0	0	0	3	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	3
Car ech	4	0	0	0	0	0	0	0	15	0	17	15	0	0	0	0	33	5	0	28	20	0	0	0	0	0	4	0	0	0	0	0	12	0	0	0	0	0	0	0	12	0	0
Car las	32	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	61	0	0	0	29	0	0	0	0	0	9	0	0	0	0	0	8	0	0	0	0	0	0	0	33	0	0
Car lim	63	0	17	0	0	0	24	3	0	0	16	32	0	0	0	4	4	1	0	3	0	5	7	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	8	0	0	0
Car nig	0	0	0	0	0	0	16	0	4	11	19	63	0	5	0	5	4	0	1	8	33	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
Car ova	0	0	0	0	0	0	0	5	7	0	23	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Car pan	11	33	4	0	33	0	17	29	19	0	21	8	0	0	0	12	0	23	33	27	0	4	4	0	33	3	0	0	0	0	0	0	0	32	33	19	32	15	33	0	53	0	3
Car ros	17	65	7	0	39	12	24	0	0	0	0	0	33	0	16	0	0	67	64	1	0	0	0	11	67	24	0	0	0	0	0	0	0	67	67	36	67	24	65	0	35	0	27
Car ves	0	0	0	0	0	0	0	0	0	0	0	0	65	0	1	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cer fon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Dac mai	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	4	0	1	4
Des ces	13	0	0	0	0	0	0	0	0	0	0	0	8	48	0	0	0	0	0	0	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0
Dro rot	23	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Dry dil	0	0	0	0	0	4	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	28	12	0	0	0	0	0	0	0	0	0	1	12	0	0	0	0

Appendix 3(b)

Epi pal	0	0	4	0	0	0	8	0	1	0	11	16	3	0	13	16	5	19	25	28	1	8	7	9	0	0	29	69	0	0	0	0	49	24	20	0	0	29	17	11	3	0	0
Equ flu	0	0	0	0	0	3	20	3	4	3	9	20	28	0	8	41	15	55	57	25	0	1	9	40	0	0	5	36	0	0	5	4	65	47	44	0	0	29	0	4	3	0	0
Eri cin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	4
Eri tet	0	0	4	33	9	0	7	33	11	0	0	19	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	29	0	0	5	27	23
Eri ang	0	0	11	65	20	0	12	47	16	0	0	24	0	0	0	19	0	4	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	43	1	63	0	0	4	41	1
Eur pra	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fes rub	0	0	0	0	0	4	0	3	0	0	1	3	1	20	0	0	0	0	0	21	0	0	13	0	0	0	0	0	0	33	0	0	23	0	0	0	0	0	0	0	0	0	0
Fil ulm	0	0	0	0	0	0	1	0	0	0	11	0	4	20	0	0	0	0	0	41	0	0	0	0	0	0	0	0	0	13	0	0	35	0	0	0	0	0	0	0	0	0	0
Fis adi	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gal apa	0	0	0	0	0	0	9	0	1	7	0	4	0	17	13	0	5	0	0	4	0	5	8	3	0	4	0	0	0	0	0	0	7	0	0	0	0	0	16	13	0	0	0
Gal pal	0	0	1	0	0	0	4	0	0	15	1	4	4	24	25	0	5	0	0	5	0	3	9	15	0	9	0	0	0	0	0	0	31	0	0	0	0	0	45	23	3	0	0
Gly max	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	13	0	0	0	0	0	96	0	0	0	0	0	0	0	0	0	9	16	0	0	0
Hol lan	0	0	16	0	0	16	0	0	0	0	0	0	0	0	0	15	0	0	0	13	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	21	0	0	0
Hyd vul	0	0	0	0	0	35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iri pse	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	4	24	0	0	0	0	0	0	0	0	0	12	33	0	0	0
Jun art	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	67	0	0	3
Jun buf	0	0	0	0	0	33	1	0	0	0	0	3	0	27	0	0	0	8	0	0	1	0	35	9	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	7
Jun eff	0	0	0	0	0	57	0	0	0	0	0	8	0	23	0	0	0	0	0	0	0	0	47	36	0	0	0	0	0	0	0	0	0	0	0	0	0	4	3	5	0	0	0
Kna arv	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	27	0	0	0	0	9	0	1	0	0	0
Lem min	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	21	0	0	0	0	0
Lys thy	0	0	8	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lys vul	3	0	4	0	21	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lyt sal	29	33	37	0	12	0	0	0	0	0	0	0	0	0	0	0	20	15	0	0	33	5	0	0	0	12	32	0	0	0	0	0	0	33	33	33	13	4	0	1	33	0	12
Men tri	56	65	65	0	15	0	0	0	33	0	21	0	0	0	0	33	57	20	39	0	53	0	7	0	0	0	61	0	0	0	0	0	7	67	67	67	24	9	5	0	69	0	72
Mol cer	0	0	0	0	0	0	15	39	53	0	52	9	0	0	0	0	0	0	0	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	3	12
Myr gal	0	0	0	0	0	0	31	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Mys sco	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Oen lac	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0
Ped pal	0	0	3	0	0	0	0	0	0	4	0	0	3	5	0	9	0	0	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pha aru	0	0	0	0	0	0	3	0	0	25	24	0	17	1	0	0	23	0	0	0	33	0	0	0	0	0	19	0	0	0	0	0	0	0	0	0	0	17	0	0	0	21	

Appendix 3(b)

Phr aus	0	0	0	0	0	0	0	0	0	0	64	0	0	3	0	0	67	27	27	0	67	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
Poa tri	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pol ser	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pol com	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	0	16	15	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	31	19	0	0	0	0	0	0	11	12
Pot pol	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	20	4	11	23	0	0	0	0	0	0	0	0	0	0	0	0	52	49	0	0	0	0	0	0	0	0
Pot ere	20	0	20	0	0	16	13	9	0	17	13	33	0	0	16	24	5	5	8	24	13	27	0	16	33	24	0	0	0	0	67	67	0	0	0	3	0	1	1	8	16	0	1
Pot pal	11	0	4	0	0	5	8	0	0	17	8	17	0	0	17	0	0	4	3	13	19	21	0	0	67	67	0	0	0	0	33	33	0	0	0	0	0	1	0	0	7	0	1
Pse pur	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0	0	0	0
Ran fla	0	0	0	0	0	0	7	5	0	9	3	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	9	0	0	0	0	0
Ran lin	0	0	0	0	0	0	23	12	3	29	3	1	7	8	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ran rep	0	0	0	0	0	0	0	0	0	5	0	0	23	23	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ryt squ	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	4	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Rum ace	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	7	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0
Sal cin	33	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sco sco	63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sph cus	0	0	33	33	33	7	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	12	0	0	0	1	33	0	0	0	0	0	0	0	0	0	33	0	0	0	4	29	0
Sph pal	0	0	65	61	67	59	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	11	61	0	0	0	0	0	0	0	0	0	67	0	0	0	7	21	0
Sph pap	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0
Sph squ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	33	
Sph ter	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	64	
Ste hol	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	
Suc pra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Tri rep	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Typ lat	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	
Vac myr	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0		
Vac vul	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	25	5	0	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	16		
Vac oxy	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	12	8	0	0	0	0	0	0	0	0	0	0	0	5	48	56	
Val off	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	3	0	0	0	0	0	0	24	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Ver off	0	0	0	0	0	0	0	0	0	0	0	0	7	0	12	0	0	0	3	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Vio pal	0	0	0	0	0	0	0	0	0	0	8	0	0	18	0	32	0	0	0	26	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Appendix 3(c) Species lists and average abundance values per station for 2000; three letter codes represent species listed in Table 2.3.3 e= Endrick Marshes; i= Insh Marshes; w= Wood of Cree.

	e1	e2	e3	e4	e5	e6	i1	i3	i4	i5	i6	i7	i8	i9	w1	w2	w3	w4	w5	w6
Ach pta	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	8	8	4	0	3
Agr sto	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	4	1	3	3	4
Ang syl	7	0	0	4	7	16	0	0	0	0	0	0	0	0	16	13	7	8	5	16
Cal pal	0	33	32	0	8	0	3	0	4	24	25	0	4	0	5	4	4	4	3	3
Car pra	1	0	0	0	0	0	0	0	0	1	5	5	7	0	1	0	1	0	1	0
Car aqu	0	27	67	0	0	0	0	0	100	0	0	39	0	93	0	0	0	0	0	0
Car dia	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	16	11	0	0	0
Car ech	0	0	0	0	0	0	0	27	0	3	9	0	0	0	0	0	0	0	0	0
Car las	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	33
Car nig	0	0	0	0	0	0	67	12	5	71	95	0	15	4	0	1	0	1	0	0
Car pan	0	0	0	0	0	0	0	12	0	19	1	0	0	0	44	0	28	24	44	16
Car ros	0	0	0	44	40	69	40	0	0	0	0	0	0	0	0	13	7	0	1	0
Car ves	0	67	0	49	33	0	0	0	0	0	0	75	0	3	0	0	0	0	0	0
Car ver	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	7	23	17	21	9
Des ces	0	0	0	0	0	0	0	0	0	33	19	0	87	0	0	0	0	0	0	0
Ele pal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Epi hir	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epi pal	8	9	1	33	31	24	0	0	0	0	0	0	0	7	0	1	1	0	0	1
Equ flu	0	7	7	57	89	100	12	1	4	12	8	13	0	9	51	55	84	76	28	21
Eri ang	0	0	0	0	0	0	5	20	0	1	8	0	0	0	0	9	4	0	12	0
Fes rub	0	0	0	0	0	0	0	0	8	0	13	0	0	0	0	0	0	0	0	0
Fil ulm	0	0	0	0	0	1	0	0	0	5	21	23	69	0	13	36	24	43	4	15
Gal pal	52	12	0	27	44	44	17	3	47	8	11	3	25	27	4	3	11	9	13	27
Hol lan	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hyd vul	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	21	55	31	59	37
Jun acu	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	20	0	29	4	0
Jun buf	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Jun eff	0	0	0	0	0	0	0	0	5	0	1	0	44	0	0	0	0	0	0	0

Appendix 3(c)

Lem min	0	0	0	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lyc eur	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Lys thy	0	1	0	23	13	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lyt sal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	0
Lyn flo	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0
Men aqu	0	0	0	0	0	33	0	0	0	0	0	0	0	0	12	8	17	21	8	13
Men tri	0	0	0	0	0	67	0	0	0	0	0	0	0	0	71	52	75	63	56	29
Mol cer	0	0	0	0	0	0	0	100	0	51	23	0	0	0	53	47	25	3	12	67
Myr gal	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	21	0
Mys sco	0	0	0	3	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
Oen lac	1	0	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pha aru	100	12	35	47	72	0	0	0	3	33	0	7	3	0	1	0	24	43	0	0
Phr aus	0	0	0	0	0	0	0	0	0	65	0	0	0	0	0	0	0	0	0	0
Pot pol	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	3	0	0	23	13
Pot pal	0	0	0	0	32	4	15	0	31	21	29	0	0	8	20	29	45	29	32	16
Ran fla	0	0	0	0	0	0	4	1	37	12	7	0	0	0	4	0	8	12	0	7
Ran rep	0	0	0	0	0	0	0	0	1	8	0	24	12	0	0	0	0	0	0	0
Rum ace	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Sal cin	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Sph pap	0	0	0	0	0	0	1	0	0	1	8	0	0	0	19	12	0	0	5	1
Suc pra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	13	7	13	3	4
Typ lat	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Val off	1	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	0	1	1
Ver off	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Vio pal	0	0	0	0	0	0	5	0	0	5	7	0	23	0	9	9	4	5	4	13

Appendix 4 Groundwater and related variables, collective vegetation variables, and dominant population(s) trait values per sample station.

Appendix 4(a) Average groundwater and other environmental variable values per station for August 1998. i= Insh Marshes, n=Nether Whitlaw

Station	Degree of shading	Water table level (cm.)	Level of fluctuation (cm.)	pH	Conductivity (µS/cm)	Bare ground (%)	Fe (mg/l)	Mn (mg/l)	Mg (mg/l)	K (mg/l)	Ca (mg/l)	Na (mg/l)
i1	0	19	28	5.4	84	13	0.75	0.00	1.80	4.38	5.32	0.42
i2	0	8	18	5.3	60	5	3.88	0.00	1.18	3.38	4.51	0.00
i3	0	4	13	5.5	81	2	0.00	0.00	2.24	3.09	2.57	1.93
i4	1	20	18	5.5	165	23	1.58	0.00	1.50	1.33	18.17	0.00
i5	0	13	18	5.2	133	10	0.98	0.00	1.15	2.22	4.88	1.84
i6	0	4	14	5.7	56	2	18.06	2.43	2.61	2.66	22.48	3.99
i7	0	6	33	5.3	74	2	12.71	0.00	1.33	1.66	5.51	7.37
i8	0	-2	54	5.4	89	0	1.18	0.00	0.84	4.93	3.12	7.72
i9	0	24	36	5.3	69	2	3.14	0.00	1.06	2.12	3.94	1.81
i10	0	0	10	5.8	136	0	3.56	0.43	1.65	7.60	5.29	4.58
i11	0	5	24	5.7	72	7	0.00	0.00	1.40	2.69	3.98	12.40
i12	0	12	19	5.8	75	0	1.18	0.01	1.12	2.27	3.43	16.08
I13	-	-	-	-	-	-	-	-	-	-	-	-
i14	0	10	17	7.0	7	0	1.19	0.00	1.37	0.49	3.99	0.65
i15	0	19	17	6.8	68	8	0.71	0.00	1.24	1.48	3.89	7.16
i16	0	13	20	7.3	104	0	0.49	0.00	2.27	2.43	5.61	5.89
i17	0	16	22	6.2	97	0	1.20	0.00	2.08	4.27	6.48	0.09
n1	0	12	6	6.7	787	0	0.88	0.32	9.25	1.18	72.95	74.40
n2	0	30	7	6.2	506	0	1.59	0.26	5.41	1.94	43.07	35.66
n3	0	24	6	6.1	280	0	0.25	0.00	3.30	2.56	23.35	26.22
n4	0	9	4	6.2	159	0	2.21	0.00	2.23	0.99	12.27	16.48
n5	2	0	2	5.5	38	0	1.47	0.02	0.34	1.94	1.19	2.52
n6	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 4(b) Average colective vegetation variable values per station for August 1998. i= Insh Marshes, n=Nether Whitlaw.

Station	Stem density (1x1m)	Canopy height overall (cm)	Litter cover (%)	Standing crop 0-10cm (g/m2)	Standing crop 10-20cm (g/m2)	Standing crop >20 cm (g/m2)	Total standing crop (g/m2)
i1	800	30	5	42	7	2	50
i2	1533	24	7	95	30	19	144
i3	1533	25	5	82	295	13	389
i4	1133	39	10	64	21	14	99
i5	1767	35	8	235	146	0	381
i6	1700	27	10	56	13	40	108
i7	1733	44	5	128	30	99	256
i8	3200	99	33	516	681	470	1667
i9	1667	64	8	83	37	75	195
i10	1033	27	50	104	20	16	140
i11	1433	61	13	221	121	272	614
i12	1100	24	25	93	24	11	128
i13	933	24	10	142	8	4	154
i14	1833	37	2	188	16	43	247
i15	633	70	10	101	32	78	211
i16	1367	20	10	149	21	3	173
i17	18	24	5	152	77	26	255
n1	2100	59	5	112	50	157	318
n2	533	48	5	298	54	174	526
n3	600	54	12	165	44	78	287
n4	833	26	12	206	33	46	285
n5	233	22	5	99	8	15	122
n6	1333	24	5	248	205	20	473

Appendix 4(c) Average dominant population(s) trait values per station for August 1998. i= Insh Marshes, n=Nether Whitlaw.

Station	Ramet height (cm)	No. leaves per ramet	Total leaf area per ramet (cm2)	Total leaf length per ramet (cm)	Dry weight of Stem per ramet (g)	Dry weight of leaves per ramet (g)	Dry weight of reproductive structures per ramet (mg)	Total ramet dry weight (g)	Seed average dry weight (mg)	Specific leaf are (g/cm2)
i1	34	6	76	226	0	320	0	320	0.00	0.24
i2	39	3	25	87	130	140	24	294	0.00	0.18
i3	37	4	23	77	90	110	20	220	0.00	0.21
i4	50	3	92	319	0	620	0	620	0.00	0.15
i5	43	5	28	85	111	125	11	247	0.00	0.30
i6	24	4	40	113	55	169	15	239	0.00	0.20
i7	54	3	90	223	110	280	210	600	2.00	0.32
i8	117	9	33	111	670	280	100	1050	0.00	0.12
i9	72	14	72	234	155	435	155	745	0.45	0.26
i10	29	3	61	107	223	245	64	532	0.17	0.29
i11	63	5	92	231	1660	703	37	2400	0.00	0.15
i12	24	4	41	87	115	227	0	341	0.00	0.18
i13	28	2	21	56	60	60	0	120	0.00	0.26
i14	38	3	69	155	305	415	11	731	0.00	0.30
i15	69	4	102	205	1605	675	45	2325	0.00	0.16
i16	20	5	29	67	62	103	35	200	0.35	0.25
i17	34	4	46	153	600	355	0	955	0.00	0.13
n1	90	4	192	497	1405	650	40	2095	0.15	0.15
n2	67	3	185	486	703	797	0	1500	0.00	0.17
n3	78	4	48	190	120	500	140	760	0.90	0.10
n4	38	4	47	101	570	285	140	995	0.00	0.14
n5	35	7	95	382	50	810	210	1070	1.00	0.12
n6	55	5	159	560	250	1210	230	1690	0.00	0.13

Appendix 4(d) Average groundwater and other environmental variable values per station for 1999. g= Glen Moss; i= Insh Marshes; l= lochwinnoch; n=Nether Whitlaw; t= Tarn Moss.

Station	Degree of shading	Water table level (cm.)	Maximum level (cm.)	Minimum level (cm.)	Level of fluctuation (cm)	Redox (mV)	pH	Conductivity (µS/cm)	Bare ground (%)	Fe (mg/l)	Mn (mg/l)	Mg (mg/l)	K (mg/l)	Ca (mg/l)	Na (mg/l)	Flouride (mg/l)	Chloride (mg/l)	Nitrate (mg/l)	Sulphate (mg/l)
g1	1	-1	5	-6	11	-67	6.3	329	2	0.00	0.00	1.95	0.36	22.92	5.87	0.00	10.97	0.03	2.58
g2	1	17	17	8	9	-58	6.0	291	3	0.00	0.03	1.43	0.53	16.82	5.69	0.00	13.39	0.05	3.36
g3	1	-6	-3	-17	14	69	5.8	168	3	0.19	0.00	0.85	0.56	5.76	7.37	0.00	8.29	0.01	0.94
g4	1	0	3	-9	12	-43	5.6	198	3	0.03	0.00	1.09	0.32	3.23	7.26	0.22	20.85	0.05	7.15
g5	1	-1	1	-11	12	42	5.5	140	3	0.15	0.00	0.53	0.60	1.92	5.30	0.00	11.66	0.03	1.59
g6	0	-2	2	-16	18	151	5.4	146	0	0.09	0.00	0.90	0.19	3.70	5.15	0.00	13.02	0.03	1.04
i1	0	-2	3	-4	7	85	6.1	169	22	0.18	0.10	1.08	0.85	3.82	6.43	0.00	11.09	2.12	4.27
i2	0	0	6	-4	10	-57	6.3	223	13	0.17	0.31	1.27	0.69	5.66	5.34	0.00	8.73	0.15	0.84
i3	0	-3	2	-8	10	4	6.1	245	13	0.04	0.23	2.38	0.55	6.37	7.79	0.00	7.50	0.09	0.44
i4	0	-3	5	-7	12	32	6.0	339	5	0.00	0.11	1.23	0.29	24.47	5.77	0.12	10.09	0.06	0.24
i5	0	2	4	-3	7	-85	6.6	666	13	0.11	0.34	1.34	4.07	18.67	5.79	0.00	10.02	16.42	2.75
i6	0	-4	1	-5	5	-54	6.3	451	8	0.09	0.19	1.87	1.91	8.94	4.99	0.00	7.46	11.52	1.96
i7	0	-5	9	-10	19	-20	6.3	277	13	0.30	0.38	1.02	1.20	5.49	4.45	0.00	6.81	0.11	0.86
i8	0	-32	-16	-35	18	226	5.9	195	0	0.00	0.00	0.56	2.23	2.50	3.72	0.00	5.30	1.34	2.36
i9	0	1	18	-1	19	15	6.0	139	18	0.16	0.06	0.86	0.87	2.88	3.49	0.12	6.71	4.23	1.09
i10	0	-2	1	-7	8	113	5.7	234	0	0.06	0.24	0.99	0.70	3.79	3.93	0.00	8.97	0.05	0.34
i11	0	4	7	4	3	-17	5.8	230	7	0.00	0.06	2.71	0.40	8.70	6.93	0.00	5.83	0.02	0.39
i12	0	12	16	12	4	84	6.1	270	8	0.00	0.11	2.02	1.11	9.74	7.44	0.00	12.75	0.07	0.41
i13	0	9	13	8	5	9	6.0	222	10	0.00	0.09	2.37	0.95	8.67	7.19	0.42	14.62	0.25	2.04
i14	0	15	18	11	7	-15	5.9	244	12	0.00	0.05	1.44	1.77	5.08	5.49	0.00	9.20	0.04	1.34

Appendix 4(d)

Station	Degree of shading	Water table level (cm.)	Maximum level (cm.)	Minimum level (cm.)	Level of fluctuation (cm)	Redox	pH	Conductivity	Bare ground (%)	Fe (mg/l)	Mn (mg/l)	Mg (mg/l)	K (mg/l)	Ca (mg/l)	Na (mg/l)	Flouride (mg/l)	Chloride (mg/l)	Nitrate (mg/l)	Sulphate (mg/l)
i16	0	4	8	3	5	-60	6.1	296	22	0.00	0.02	2.32	5.04	9.81	6.44	0.00	8.92	0.31	2.15
i18	0	-24	-2	-39	32	205	5.7	394	3	0.00	0.91	1.87	0.71	8.58	8.43	0.00	20.12	0.05	2.50
i19	0	2	6	2	4	-43	6.0	426	22	0.21	0.61	1.83	0.99	12.35	8.33	0.39	20.83	0.03	0.35
i20	0	6	9	5	4	-49	6.0	372	10	0.13	0.07	1.59	1.17	9.70	8.28	0.00	22.48	0.10	0.60
i21	0	2	10	2	8	13	5.8	269	10	0.27	0.00	1.26	2.21	6.42	8.67	0.00	19.66	0.05	0.62
l1	1	0	1	-1	2	125	5.0	237	0	0.21	0.04	1.22	2.99	4.36	5.64	0.00	8.93	0.48	2.29
l2	1	0	2	0	2	-58	6.0	271	2	0.17	0.21	1.77	2.39	10.01	6.03	0.00	9.83	0.77	3.94
l3	1	1	2	0	2	-64	5.9	187	5	0.11	0.10	2.08	3.00	12.75	6.10	0.00	12.64	0.10	3.43
l4	1	-10	10	-11	22	-18	6.5	971	3	0.02	2.29	6.22	0.52	38.63	18.89	0.48	28.24	0.63	0.60
l5	0	-1	11	-3	15	-80	6.3	793	2	0.00	0.23	3.55	0.59	22.46	13.46	0.25	19.77	0.57	0.76
l6	0	5	21	3	20	-77	6.1	638	7	0.05	0.00	3.47	1.54	21.11	13.33	0.09	28.73	0.03	1.98
n1	0	5	10	4	6	-10	6.4	1528	7	0.11	0.05	9.71	1.38	92.67	56.64	0.04	128.78	0.99	0.70
n2	0	21	26	20	6	-46	5.9	977	0	0.96	0.07	4.75	0.57	44.01	25.02	0.10	72.79	0.06	0.91
n3	0	14	20	13	7	-67	6.0	999	3	0.10	0.02	3.71	1.65	36.50	31.12	0.08	80.55	0.04	1.24
n4	1	1	2	1	1	-2	5.6	364	25	0.05	0.00	1.63	0.96	13.64	8.69	0.00	24.51	0.02	1.51
n5	1	0	0	0	0	83	6.0	173	0	0.29	0.00	0.73	0.39	5.24	4.19	0.00	10.00	0.04	0.35
n6	2	2	3	1	2	41	5.2	250	12	0.26	0.01	2.02	1.31	13.72	5.10	0.00	11.07	0.02	0.93
t1	0	-6	4	-11	15	82	6.1	436	8	0.05	0.23	1.34	0.35	12.50	3.56	0.00	2.13	0.22	3.38
t2	0	-1	11	-2	13	68	6.2	201	17	0.01	0.77	1.57	0.29	18.15	2.54	0.00	1.61	0.16	7.40
t3	0	2	9	-6	15	42	5.7	251	18	0.03	0.00	1.86	0.56	18.49	2.98	0.00	3.94	0.03	1.61
t4	0	-2	4	-5	9	13	5.2	85	0	0.37	0.13	0.91	0.45	3.22	5.83	0.00	8.70	0.12	1.49
t5	0	0	3	-3	6	89	5.3	124	0	0.17	0.16	0.54	1.38	2.51	4.21	0.00	9.71	0.36	2.10

Appendix 4(e) Average collective vegetation variable values per station for 1999. g= Glen Moss; i= Insh Marshes; l= lochwinnoch; n=Nether Whitlaw; t= Tarn Moss.

Station	Species richness (S)	Stem density (1x1m)	Nearest neighbour	Canopy height overall (cm)	Litter cover (%)	No. reproductive structures (m2)	Stem diameter (mm)	Biomass 0-10cm (g/m2)	Biomass 10-20cm (g/m2)	Biomass >20cm (g/m2)	Biomass total (g/m2)	Necromass 0-10cm (g/m2)	Necromass 10-20cm (g/m2)	Necromass >20cm (g/m2)	Necromass total (g/m2)	Standing crop 0-10cm (g/m2)	Standing crop 10-20cm (g/m2)	Standing crop >20 cm (g/m2)	Total standing crop (g/m2)
g1	7	1015	1	14	8	601	3.1	234	55	19	308	29	3	1	33	263	58	20	341
g2	3	478	3	34	15	133	6.9	298	207	229	735	155	80	27	262	453	287	257	997
g3	12	1011	3	14	3	222	4.5	440	73	5	518	65	1	0	66	505	74	5	585
g4	3	579	3	28	13	189	4.7	255	54	103	411	119	12	3	134	374	66	106	545
g5	5	478	3	19	8	178	4.1	357	47	83	487	252	11	6	269	609	58	89	756
g6	7	1255	2	78	20	467	4.1	538	226	576	1340	214	100	213	527	753	326	788	1867
i1	13	1800	1	21	5	244	3.0	147	102	38	287	26	14	2	42	173	116	40	330
i2	6	1633	1	24	25	122	2.0	283	115	84	482	285	29	3	318	568	145	87	800
i3	6	1822	1	34	23	511	2.1	559	109	81	748	359	62	11	433	918	171	92	1181
i4	7	1567	1	56	7	400	2.6	204	148	337	689	154	26	9	189	358	174	346	878
i5	14	2267	1	41	10	1000	2.2	292	328	428	1048	116	100	0	216	409	427	428	1264
i6	12	2011	1	33	10	844	2.8	267	96	69	432	129	12	5	146	396	109	73	578
i7	6	1689	2	42	5	211	2.8	262	127	323	712	59	5	2	67	321	132	326	779
i8	10	3156	1	69	17	433	2.3	179	191	368	739	392	155	69	617	572	346	438	1356
i9	6	1578	1	59	13	189	3.9	147	124	273	545	597	43	11	652	744	168	285	1196
i10	14	1311	2	20	2	511	2.8	369	31	36	436	98	2	0	100	467	33	36	536
i11	8	1278	2	79	15	244	5.0	97	346	314	756	451	98	83	632	548	444	397	1389
i12	8	1144	2	28	5	233	2.8	113	58	50	221	254	5	3	261	366	63	53	482
i13	6	1455	2	27	3	134	3.0	244	93	104	441	215	13	5	233	459	106	109	674
i14	17	2289	1	37	3	522	2.1	280	91	352	724	714	473	41	1227	994	564	393	1951

Appendix 4(e)

Station	Species richness (S)	Stem density (1x1m)	Nearest neighbour	Canopy height overall (cm)	Litter cover (%)	No. reproductive structures (m2)	Stem diameter (mm)	Biomass 0-10cm (g/m2)	Biomass 10-20cm (g/m2)	Biomass >20cm (g/m2)	Biomass total (g/m2)	Necromass 0-10cm (g/m2)	Necromass 10-20cm (g/m2)	Necromass >20cm (g/m2)	Necromass total (g/m2)	Standing crop 0-10cm (g/m2)	Standing crop 10-20cm (g/m2)	Standing crop >20 cm (g/m2)	Total standing crop (g/m2)
i15	6	1000	2	60	13	100	3.5	228	143	387	758	382	67	45	494	611	210	432	1252
i16	7	1433	2	22	5	300	2.0	360	83	26	469	157	15	5	177	517	98	31	646
i18	12	3356	1	51	13	522	2.8	533	248	356	1137	304	54	56	414	837	302	412	1551
i19	6	1755	1	61	23	344	3.4	203	136	420	760	369	124	100	592	572	260	520	1352
i20	2	1045	2	34	7	55	4.0	493	95	75	663	301	23	5	329	794	119	79	992
i21	7	1433	2	35	23	233	3.8	296	106	190	591	577	64	14	655	873	170	204	1246
l1	11	1022	3	68	10	122	10.7	366	159	450	975	147	62	174	383	513	221	623	1357
l2	5	1700	2	88	13	189	4.8	126	138	685	949	337	79	195	611	463	217	880	1560
l3	3	378	4	113	25	78	16.6	236	115	923	1273	757	150	570	1477	993	265	1493	2750
l4	2	1578	1	76	17	233	4.9	66	83	1107	1256	432	124	427	983	499	207	1534	2239
l5	3	1200	1	70	8	211	6.7	278	116	543	937	365	104	199	669	643	220	743	1605
l6	3	800	1	73	7	247	5.9	478	86	432	996	173	186	262	621	651	272	695	1618
n1	8	2322	1	67	10	444	5.5	117	81	356	554	74	2	5	82	191	83	361	636
n2	4	1200	2	52	8	256	5.4	187	149	241	577	152	86	53	291	339	235	294	868
n3	4	955	2	38	10	144	6.4	147	103	197	446	201	23	22	246	348	125	219	692
n4	4	711	3	23	8	67	5.9	226	63	38	327	61	7	1	69	286	70	40	396
n5	3	456	3	19	12	67	4.7	127	19	16	161	19	10	1	31	146	29	17	192
n6	10	878	2	33	22	133	6.3	112	108	124	343	305	58	47	410	417	165	171	753
t1	7	1556	1	43	8	344	3.7	116	142	379	638	162	41	17	221	278	183	397	858
t2	11	1700	1	51	13	544	3.8	210	177	551	938	290	40	41	370	499	217	592	1308
t3	12	1200	2	30	5	200	4.1	262	94	173	529	129	37	30	208	391	143	203	737
t4	9	944	2	21	17	189	4.1	503	20	20	543	96	6	2	104	600	26	22	647
t5	12	822	2	35	12	114	3.3	346	46	143	535	94	30	38	162	441	75	181	697

Appendix 4(f) Average dominant population(s) trait values per station for 1999. g= Glen Moss; i= Insh Marshes; l= lochwinnoch; n=Nether Whitlaw; t= Tarn Moss.

Station	Ramet height (cm)	No. leaves per ramet	Canopy area per ramet (%)RamCA	No. reproductive structures per ramet	Total leaf area per ramet (cm2)	Total leaf length per ramet (cm)	Dry weight of Stem per ramet (g)	Dry weight of leaves per ramet (g)	Dry weight of reproductive structures per ramet (mg)	Total ramet dry weight (g)	Seed average dry weight (mg)	Specific leaf are (g/cm2)
g1	19	4	18	4	49.1	85.8	298	278	65	641	0.50	0.12
g2	53	4	26	6	100.7	250.5	1158	1032	200	2390	0.50	0.06
g3	16	3	48	0	85.6	106.4	823	820	100	1743	0.00	0.11
g4	52	6	45	5	72.9	254.5	173	890	167	1230	0.30	0.09
g5	46	5	15	4	48.2	212.5	277	630	153	1060	0.50	0.09
g6	96	24	40	19	88.2	267.8	20	1840	183	2043	0.00	0.05
i1	28	4	55	2	27.5	95.9	22	124	10	156	0.25	0.20
i2	40	3	53	3	58.8	157.5	152	574	25	752	-	0.56
i3	50	3	85	1	23.5	75.9	73	105	101	278	-	0.42
i4	73	5	98	5	74.5	180.9	40	39	19	98	-	1.91
i5	53	5	58	1	73.6	153.6	242	500	64	806	0.20	0.53
i6	39	3	55	4	12.0	59.7	51	71	50	173	0.65	0.48
i7	61	4	100	3	37.7	113.6	130	211	107	448	2.00	0.63
i8	79	26	68	7	46.2	167.0	586	186	351	1122	0.30	0.27
i9	81	5	83	5	53.7	139.4	246	167	224	637	1.40	0.70
i10	23	2	17	2	22.9	52.7	94	138	1	232	0.00	1.35
i11	75	4	47	1	114.2	245.6	789	710	64	1563	0.25	0.44
i12	34	3	29	2	27.3	85.0	31	173	22	226	0.80	0.79
i13	40	2	23	2	36.7	100.8	106	157	81	344	1.10	0.45
i14	38	3	37	1	23.8	60.0	25	89	15	129	0.68	0.57
i15	50	4	25	1	80.0	128.3	460	358	34	853	0.25	0.65
i16	20	4	31	1	11.7	38.8	110	58	2	170	0.00	0.47

Appendix 4(f)

Station	Ramet height (cm)	No. leaves per ramet	Canopy area per ramet (%)RamCA	No. reproductive structures per ramet	Total leaf area per ramet (cm2)	Total leaf length per ramet (cm)	Dry weight of Stem per ramet (g)	Dry weight of leaves per ramet (g)	Dry weight of reproductive structures per ramet (mg)	Total ramet dry weight (g)	Seed average dry weight (mg)	Specific leaf are (g/cm2)
i17	82	64	-	16	91.7	241.4	0	166	4	170	-	0.55
i18	82	42	60	18	59.3	134.4	52	635	154	841	-	0.69
i19	63	5	62	3	61.2	167.8	138	273	63	473	0.60	0.59
i20	43	4	37	2	57.8	157.7	566	301	168	1035	0.78	0.59
i21	38	4	32	5	104.5	162.1	1098	627	392	2117	0.23	0.16
l1	52	4	58	0	220.5	417.7	1088	1673	5	2767	0.00	0.14
l2	121	4	80	1	245.8	612.9	1657	2383	97	4137	0.00	0.10
l3	149	6	88	6	175.7	350.0	3450	1487	510	5447	0.00	0.12
l4	89	5	100	7	211.2	502.7	1380	1450	398	3228	1.00	0.17
l5	84	6	70	6	190.7	441.4	2477	1950	605	5032	1.00	0.14
l6	80	4	51	5	106.8	250.3	1530	860	340	2730	0.00	0.14
n1	83	2	90	1	91.2	163.2	366	993	44	1403	0.00	0.11
n2	55	4	37	3	114.9	235.1	1284	877	121	2282	0.50	0.18
n3	40	4	25	7	78.7	120.8	1409	497	78	1985	0.42	0.19
n4	32	4	42	2	61.2	244.6	1323	523	93	1940	0.25	0.12
n5	45	6	28	5	26.8	90.3	157	213	117	487	0.90	0.12
n6	55	6	38	4	102.2	404.5	253	1040	189	1482	0.00	0.11
t1	48	6	75	4	39.1	128.4	193	247	277	717	1.00	0.15
t2	64	3	55	3	38.0	105.5	347	347	150	843	0.00	0.11
t3	39	4	44	4	60.1	164.5	440	413	138	992	1.25	0.14
t4	29	19	18	1	24.5	91.3	405	470	25	900	0.37	0.10
t5	35	10	17	0	65.3	130.6	453	382	21	857	0.00	0.29

Appendix 4(g) Average groundwater and other environmental variable values per station for 2000. e= Endrick Marsh, i= Insh Marshes, w= Wood of Cree.

Station	Degree of shading	Water table level (cm.)	Maximum level (cm.)	Minimum level (cm.)	Level of fluctuation (cm.)	Redox (mV)	pH	Conductivity (µS/cm)	Bare ground (%)	Fe (mg/l)	Mn (mg/l)	Mg (mg/l)	K (mg/l)	Ca (mg/l)	Na (mg/l)	Flouride (mg/l)	Chloride (mg/l)	Nitrate (mg/l)	Sulphate (mg/l)	Phosphate (mg/l)
e1	0	-21	2	-31	32	349	6.3	533	3	1.27	1.70	2.61	2.30	24.54	6.79	0.24	14.93	9.43	74.92	0.005
e2	0	-8	-4	-15	11	204	5.9	224	2	0.70	0.60	1.21	0.53	16.42	8.43	0.05	25.48	0.00	20.69	0.009
e3	2	-3	1	-13	14	163	5.9	199	7	2.34	3.40	2.37	0.39	12.36	23.26	0.03	55.92	0.00	10.22	0.005
e4	0	0	2	-4	5	153	5.7	192	5	3.76	1.18	2.97	0.62	9.33	12.43	0.03	42.88	0.00	3.31	0.011
e5	0	0	3	-4	6	97	5.6	265	15	0.31	0.32	1.99	0.98	15.33	8.90	0.00	25.83	0.00	1.87	0.008
e6	1	0	17	-1	17	65	5.7	224	27	0.47	0.38	2.42	1.26	18.45	9.33	0.00	25.83	0.00	1.14	0.011
i1	0	-14	-6	-18	12	153	5.8	113	10	0.38	0.08	0.77	0.71	1.58	8.00	0.08	30.11	0.00	1.37	0.018
i3	0	-13	-5	-27	23	122	5.9	172	10	0.25	0.54	1.94	0.73	7.03	8.83	0.02	12.55	0.00	1.79	0.000
i4	0	-12	-7	-17	10	111	6.1	246	5	0.04	0.40	1.45	1.89	31.20	7.14	0.17	22.55	0.00	1.15	0.000
i5	0	-11	-9	-14	5	95	5.5	51	10	0.08	0.05	0.43	1.33	1.93	4.24	0.02	12.98	4.90	5.92	0.003
i6	0	-14	4	-24	28	274	6.3	328	10	0.20	1.53	1.52	5.91	11.70	7.19	0.30	25.07	6.74	9.12	0.006
i7	0	-22	-6	-24	8	433	5.9	237	7	0.40	1.06	1.09	2.87	5.68	6.35	0.06	20.14	0.07	4.28	0.003
i8	0	-30	-9	-33	24	596	6.5	232	2	0.27	0.14	0.68	4.39	1.76	6.48	0.02	22.01	0.07	10.57	0.353
i9	0	-26	40	-37	46	226	6.9	85	15	0.29	0.21	0.87	1.50	2.91	6.18	0.00	16.27	2.12	10.05	0.021
w1	2	0	3	5	10	117	5.6	205	5	0.39	0.78	1.42	2.56	6.66	8.54	0.15	41.64	0.00	18.56	0.002
w2	0	-3	1	4	17	112	5.5	186	8	0.35	0.99	1.61	2.40	6.81	8.63	0.39	41.89	0.00	5.40	0.002
w3	0	-5	7	6	24	108	5.4	131	8	0.25	0.65	1.36	0.69	5.54	8.50	0.08	42.03	0.00	9.58	0.002
w4	0	-3	8	11	35	141	5.5	120	8	0.26	0.73	1.38	0.39	5.00	8.21	0.11	42.51	0.21	7.26	0.002
w5	0	1	14	18	39	72	5.4	112	13	0.20	0.56	1.38	0.48	4.91	7.89	0.11	38.02	0.00	8.50	0.004
w6	1	-5	4	9	40	192	5.4	125	3	0.98	1.04	1.61	0.35	6.95	9.79	0.03	35.13	0.00	35.47	0.004

Appendix 4(h) Average collective vegetation variable values per station for 1999. e= Endrick Marsh, i= Insh Marshes, w= Wood of Cree.

Station	Species richness (S)	Stem density (1x1m)	Nearest neighbour	Canopy height overall (cm)	Litter cover (%)	No. reproductive structures (m2)	Stem diameter (mm)	Biomass 0-10cm (g/m2)	Biomass 10-20cm (g/m2)	Biomass >20cm (g/m2)	Biomass total (g/m2)	Necromass 0-10cm (g/m2)	Necromass 10-20cm (g/m2)	Necromass >20cm (g/m2)	Necromass total (g/m2)	Standing crop 0-10cm (g/m2)	Standing crop 10-20cm (g/m2)	Standing crop >20 cm (g/m2)	Total standing crop (g/m2)
e1	4	1011	1.7	73	32	145	2	73	87	350	510	515	65	169	749	588	152	519	1259
e2	5	1278	1.3	50	33	178	4	108	113	325	547	330	15	30	375	438	128	355	922
e3	3	989	2.0	69	25	867	5	48	146	592	786	757	107	27	891	805	253	618	1676
e4	7	1845	1.7	63	13	256	5	202	170	556	928	521	42	49	613	723	212	606	1541
e5	9	1145	2.3	32	8	122	3	244	156	169	569	303	18	29	349	547	174	198	918
e6	8	1400	2.0	44	3	89	5	173	150	352	676	183	8	0	191	357	158	352	867
i1	7	2078	2	28	4	78	2	89	74	33	197	159	4	3	166	248	78	36	363
i3	5	2278	1	28	22	167	2	70	122	64	256	441	51	16	507	511	173	80	763
i4	6	3345	1	63	43	189	2	58	72	386	516	541	116	8	664	599	188	394	1181
i5	11	2511	1	47	12	289	2	116	105	130	351	324	57	8	389	440	162	138	740
i6	11	4144	1	39	18	489	2	154	146	127	427	443	87	11	541	597	233	138	968
i7	7	2444	1	56	12	289	4	73	163	387	623	414	59	39	512	486	222	426	1135
i8	9	4378	1	60	23	488	2	257	187	164	608	616	37	13	666	873	223	177	1274
i9	4	2300	3	70	5	422	4	62	100	794	955	560	897	97	1554	622	997	890	2509
w1	14	2100	2	36	10	133	5	131	50	98	279	232	40	23	295	363	90	121	574
w2	15	1811	1	49	13	256	4	100	99	188	388	282	67	14	363	382	166	202	750
w3	15	1800	2	29	15	267	4	205	158	239	602	246	28	4	278	451	186	243	880
w4	14	1478	1	38	8	311	4	120	104	167	391	142	12	14	168	262	116	181	559
w5	13	1556	2	32	7	356	3	143	88	117	348	307	86	37	430	450	173	155	778
w6	11	1955	1	44	8	355	3	169	161	256	586	448	109	9	566	617	270	265	1152

Appendix 4(i) Average dominant population(s) trait values per station for 1999. e= Endrick Marsh, i= Insh Marshes, w= Wood of Cree.

Station	Ramet height (cm)	No. leaves per ramet	Canopy area per ramet (%)RamCA	No. reproductive structures per ramet	Total leaf area per ramet (cm2)	Total leaf length per ramet (cm)	Dry weight of Stem per ramet (g)	Dry weight of leaves per ramet (g)	Dry weight of reproductive structures per ramet (mg)	Total ramet dry weight (g)	Seed average dry weight (mg)	Specific leaf are (g/cm2)
e1	111	6	78	1	185	368	2223	1243	307	3773	0.17	0.15
e2	63	4	80	4	40	129	247	250	200	697	0.30	0.16
e3	78	6	77	5	111	344	767	878	312	1957	0.20	0.14
e4	74	6	55	3	60	188	188	583	173	945	0.83	0.17
e5	55	3	24	1	63	203	130	585	31	746	0.35	0.13
e6	56	2	61	2	115	381	167	873	47	1088	0.05	0.14
i1	35	3	44	13	40	220	43	260	73	377	0.30	0.17
i3	42	4	80	34	17	97	57	103	20	180	0.10	0.16
i4	77	4	81	60	56	224	287	400	103	790	0.20	0.14
i5	51	4	45	23	39	123	373	305	25	703	0.02	0.19
i6	39	3	46	146	17	124	70	70	63	203	0.37	0.25
i7	71	5	93	158	41	148	147	183	120	450	0.63	0.22
i8	53	3	74	34	39	139	160	520	27	707	0.10	0.31
i9	91	5	49	148	67	248	413	423	247	1083	0.20	0.16
w1	40	4	49	1	54	192	238	277	168	683	0.83	0.25
w2	48	2	26	0	55	116	150	665	25	840	0.33	0.12
w3	36	3	24	1	50	119	237	396	81	714	0.33	0.17
w4	51	3	30	4	64	200	540	617	47	1203	0.05	0.13
w5	17	2	26	4	20	63	84	102	27	213	0.00	0.48
w6	56	3	75	2	42	155	315	217	50	582	0.07	0.36

Appendix 5 Site representation within relative TWINSPAN groups

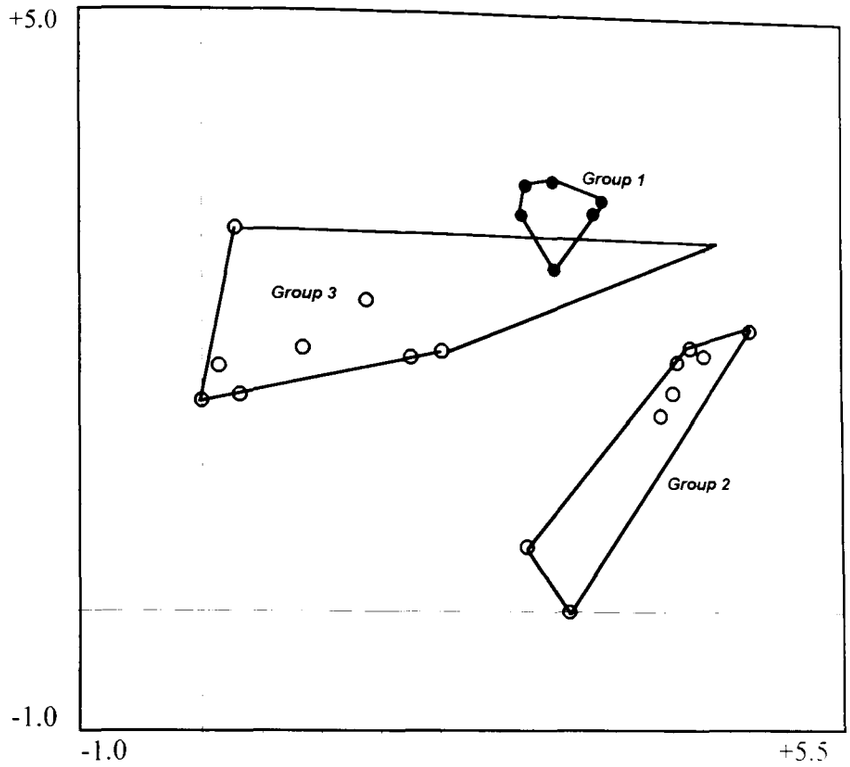
(a) For combined 1999 vegetation data showing indicator species (dominant within group; if present within other groups, infrequent, and with lower pseudospecies score): G = Glen moss; I = Insh marshes; L = Lochwinnoch; N = Nether Whitlaw moss; T = Tarn moss. *Indicates representation within different groups over subsequent sampling periods.

TWINSPAN Group	Membership			Dominant/indicator species
	June	July	August	
I (n=14)	G: 4, 5*, 6 T: 4, 5	G: 4, 5*, 6 T: 4, 5	G: 4, 6 T: 4, 5	*Hydrocotyle vulgaris* *Vaccinium oxycoccus*
II (n=52)	G: 1-3 I: 11*, 12, 13, 15, 16, 20, 21 L: 1 N: 2, 3, 4, 5, 6 T: 3	G: 1-3 I: 10*, 12, 13, 15, 16, 20, 21 L: 1 N: 2, 3, 4, 5, 6 T: 3	G: 1-3, 5* I: 11*, 12, 13, 15, 16, 20, 21 L: 1 N: 2, 3, 4, 5, 6 T: 3	*Carex rostrata* *Menyanthes trifoliata*
III (n=22)	I: 1, 2, 3, 5, 6, 10*, 14 T: 2*	I: 1, 2, 3, 5, 6, 11*, 14	I: 1, 2, 3, 5, 6, 10*, 14	*Carex paniced* *Carex nigra* *Molinia cerulea*
IV (n=17)	I: 7, 8, 18 N: 1 T: 1	I: 7, 8, 18 N: 1 T: 1, 2*	I: 7, 8, 18 N: 1 T: 1, 2*	*Deschampsia cespitosa* *Ranunculus repens*
V (n=21)	I: 4, 9 ,19 L: 2, 4, 5, 6	I: 4, 9 ,19 L: 2, 4, 5, 6	I: 4, 9 ,19 L: 2, 4, 5, 6	*Carex aquatilis*

(b) For combined 2000 vegetation data showing indicator species (dominant within group; if present within other groups, infrequent, and with lower pseudospecies score): I = Insh marshes; W = Wood of Cree fen; E = Endrick marshes. *Indicates representation within different groups over subsequent sampling periods.

TWINSPAN Group	Membership			Dominant/indicator species
	June	July	August	
I (n=14)	I: 1*, 3, 5, 6, 8	I: 3, 5, 6, 8	I: 1*, 3, 5, 6, 8	*Carex nigra*
II (n=18)	W: 1-6	W: 1-6	W: 1-6	*Hydrocotyle vulgaris* *Mentha aquatica* *Menyanthes trifoliata*
III (n=28)	E:1-6 I: 4, 7, 9	E:1-6 I: 1*, 4, 7, 9	E:1-6 I: 4, 7, 9	*Carex aquatilis* *Phalaris arundinacea*

Appendix 6 Group memberships determined by fuzzy clustering

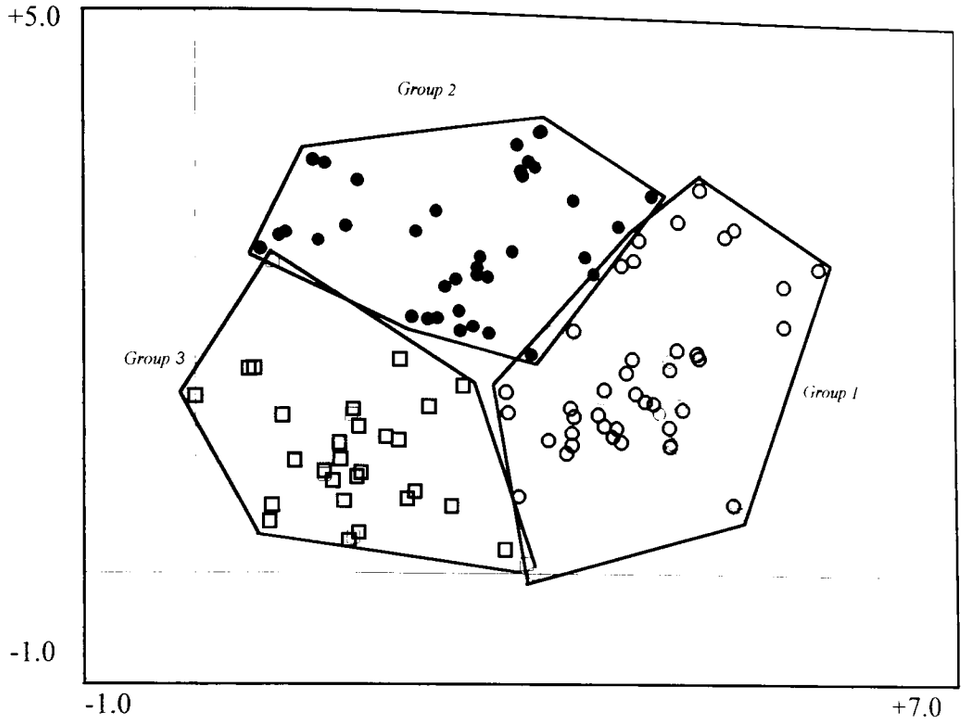


(a) DCA ordination diagram of vegetation data for the 23 sites sampled in August 1998. The gradients are 4.69 for axis 1, and 5.31 for axis 2; total inertia = 6.33, eigenvalues of axes 1-4 are 0.74, 0.46, 0.29, 0.17 respectively. Cumulative percentage variance of species data is 11.7 for axis 1, 7.3 for axis 2 (26.3 for all 4 axes). groups determined by fuzzy clustering. For site representation within groups see Appendix 6b.

(b) Site representation within relative fuzzy clusters for August 1998 vegetation data; I = Insh marshes; N = Nether Whitlaw moss. Fuzzy partition coefficient = 0.65

Cluster	Membership
I	I: 2, 3, 5, 6, 7, 8, 14
(n=9)	N: 1, 5
II	I: 1, 4, 9, 12, 13, 16
(n= 8)	N: 2, 3
III	I: 10, 11, 15, 17
(n= 6)	N: 4, 6

Appendix 6

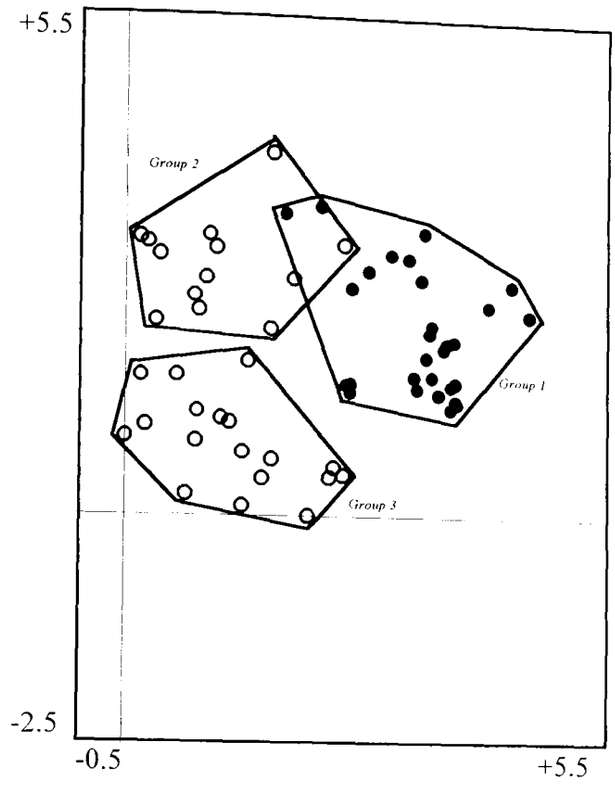


(c) DCA ordination diagram of vegetation data for 42 sites sampled in June, July and August1999 (Lochwinnoch site no.3 removed: 126 data points in total); The gradients are 5.71 for axis 1, and 3.96 for axis 2; total inertia = 10.13, eigenvalues of axes 1-4 are 0.69, 0.53, 0.45, 0.31 respectively. Cumulative percentage variance of species data is 6.8 for axis 1, 5.2 for axis 2 (19.5 for all 4 axes). groups determined by fuzzy clustering. For site representation within groups see Appendix 6d.

(d) Site representation within relative fuzzy clusters for combined 1999 vegetation data; G = Glen moss; I = Insh marshes; L = Lochwinnoch; N = Nether Whitlaw moss; T = Tarn moss. Fuzzy partition coefficient = 0.52. *Indicates representation within different groups over subsequent sampling periods.

Cluster	Membership		
	June	July	August
I (n=54)	G: 1, 2, 3, 4, 5 I: 12, 13, 15*, 20 L: 1 N: 2-5, 6* T: 3-5	G: 1, 2, 3, 5, 6* I: 11*, 12, 13, 20 L: 1 N: 2-5 T: 3-5	G: 1, 2, 3, 5, 6* I: 12, 13, 15*, 16*, 20 L: 1 N: 2-5, 6* T: 3-5
II (n=37)	I: 1, 2, 3, 5, 6, 10, 11*, 14, 18 N: 1 T: 1*, 2	I: 1, 2, 3, 5, 6, 8*, 10, 14, 15*, 18 N: 1, 6* T: 1*, 2	I: 1, 2, 3, 5, 6, 8*, 10, 11*, 14, 18 N: 1 T: 2
III (n=32)	G:6* I: 4, 7, 8*, 9, 16*, 19, 21 L: 2, 4, 5, 6	I: 4, 7, 9, 16*, 19, 21 L: 2, 4, 5, 6	I: 4, 7, 9, 19, 21 L: 2, 4, 5, 6 T: 1

Appendix 6



(e) DCA ordination diagram of vegetation data for 20 sites sampled in May, June and August 2000. The gradients are 4.58 for axis 1, and 4.00 for axis 2; total inertia = 6.05, eigenvalues of axes 1-4 are 0.65, 0.48, 0.4.355, 0.23 respectively. Cumulative percentage variance of species data is 10.8 for axis 1, 7.8 for axis 2 (28.2 for all 4 axes groups determined by fuzzy clustering. For site representation within groups see Appendix 6f.

(f) Site representation within relative fuzzy clusters for combined 2000 vegetation data: E = Endrick marshes; I = Insh marshes; W = Wood of Cree fen. Fuzzy partition coefficient = 0.56. *Indicates representation within different groups over subsequent sampling periods.

Cluster	Membership		
	June	July	August
I (n=18)	E: 1, 2, 4, 5, 6	E: 1, 2, 4, 5, 6 I: 1*, 7*	E: 1, 2, 4, 5, 6 I: 7*
II (n=27)	I: 1*, 3 W: 1-6	I: 3, 5*, 6* W: 1-6	I: 1*, 3, 5*, 6* W: 1-6
III (n=15)	E: 3 I: 4, 5*, 6*, 7*, 8, 9	E: 3 I: 4, 8, 9	E: 3 I: 4, 8, 9

Appendix 7 Summary of National Vegetation Classes defind for individual samples

(a) Classes designated for August 1998 vegetation data for all 23 sites: coefficients shown are from MATCH (Malloch, 1999); I = Insh Marshes; N = Nether Whitlw Moss.

Site	Transect Number	Community		MATCH Coefficient†	Sub-community	MATCH Coefficient†
I1	1	M5	Mire	34.4	-	-
I2	1	M25	Mire	32.1	M25a	35.8
I3	1	M25	Mire	26.7	M25a	28.7
I4	1	S11	Swamp	34.6	S11b	35.6
I5	1	M9	Mire	41.3	M9b	43.9
I6	1	M9	Mire	38.6	M9b	40.5
I7	1	S11	Swamp	44.1	S11b	46.6
I8	1	M23	Rush-pasture	30.4	M23b	35.3
I9	1	S11	Swamp	47.0	S11c	57.1
I10	2	M5	Mire	33.2	-	-
I11	2	S4	Swamp and reed-beds	29.6	S4c	39.2
I12	2	S9	Swamp and reed-beds	34.4	S9b	42.6
I13	2	S9	Swamp	41.6	S9b	50.2
I14	2	S27	Tall-herb fen	41.8	-	-
I15	2	S4	Swamp and reed-beds	31.5	S4c	47.9
I16	2	M4	Mire	35.8	-	-
I17	2					
N1	1	S10	Swamp	33.4	-	-
N2	1	S9	Swamp	62.1	S9b	62.9
N3	1	S9	Swamp	62.1	S9b	62.9
N4	1	S10	Swamp	34.8	S10b	59.6
N5	1	M4	Mire	31.1	-	-
N6	1	M5	Mire	43.4	-	-

†Coefficient range 0-100; higher coefficient score = closer match

(b) Classes designated for average 1999 vegetation data for all 42 sites; G = Glen Moss; I = Insh Marshes; L = Lochwinnoch; N = Nether Whitlw Moss; T = Tarn Moss.

Site	Transect Number	Community		MATCH Coefficient†	Sub-community	MATCH Coefficient†
G1	1	M9	Mire	29.0	M9a	29.5
G2	1	S9	Swamp	52.6	-	-
G3	1	S27	Tall-herb fen	39.8	S27b	40.3
G4	2	M2	Bog pool community	35.0	-	-
G5	2	S9	Swamp	35.4	-	-
G6	2	S9	Swamp	38.3	-	-
I1	1	M5	Mire	34.4	-	-
I2	1	M25	Mire	32.1	M25a	35.8
I3	1	M25	Mire	26.7	M25a	28.7
I4	1	S11	Swamp	34.6	S11b	35.6
I5	1	M9	Mire	41.3	M9b	43.9
I6	1	M9	Mire	38.6	M9b	40.5
I7	1	S11	Swamp	44.1	S11b	46.6
I8	1	M23	Rush-pasture	30.4	M23b	35.3
I9	1	S11	Swamp	47.0	S11c	57.1
I10	2	M5	Mire	33.2	-	-
I11	2	S4	Swamp and reed-beds	29.6	S4c	39.2
I12	2	S9	Swamp and reed-beds	34.4	S9b	42.6
I13	2	S9	Swamp	41.6	S9b	50.2
I14	2	S27	Tall-herb fen	41.8	-	-
I15	2	S4	Swamp and reed-beds	31.5	S4c	47.9
I16	2	M4	Mire	35.8	-	-
I18	3	MG10	Mesotrophic grassland	33.2	MG10a	35.5
I19	3	S11	Swamp	44.7	S11c	58.5
I20	3	S9	Swamp	57.1	-	-
I21	3	S27	Tall-herb fen	31.2	-	-
L1	1	S27	Tall-herb fen	24.7	-	-
L2	1	S27	Tall-herb fen	22.0	-	-
L4	2	M27	Mire	15.8	M27b	20.3
L5	2	S11	Swamp	32.5	S11c	43.6
L6	2	S11	Swamp	24.7	S11c	36.0
N1	1	S10	Swamp	33.4	-	-
N2	1	S9	Swamp	62.1	S9b	62.9
N3	1	S9	Swamp	62.1	S9b	62.9
N4	1	S10	Swamp	34.8	S10b	59.6
N5	1	M4	Mire	31.1	-	-
N6	1	M5	Mire	43.4	-	-
T1	1	M23	Rush-pasture	29.1	-	-
T2	1	M23	Rush-pasture	34.1	M23b	37.1
T3	1	S10	Swamp	29.9	S10b	44.8
T4	1	M21	Valley mire	38.8	M21b	42.3
T5	1	M21	Valley mire	41.3	M21b	42.8

†Coefficient range 0-100; higher coefficient score = closer match

(c) Classes designated for average 2000 vegetation data for all 20 sites: G = Glen Moss; I = Insh Marshes; L = Lochwinnoch; N = Nether Whitlw Moss; T = Tarn Moss.

Site	Community		MATCH Coefficient†	Sub-community	MATCH Coefficient†
E1	S28	Tall-herb fen	28.8	S28a	31.7
E2	S11	Swamp	43.9	S11b	44.1
E3	S28	Tall-herb fen	31.8	S28a	36.1
E4	S11	Swamp	48.5	-	-
E5	S11	Swamp	41.0	-	-
E6	S27	Tall-herb fen	47.4	S27a	53.3
I1	M5	Mire	39.6	-	-
I3	M23	Rush-pasture	28.9	-	-
I4	S11	Swamp	42.8	-	-
I5	M9	Mire	37.9	-	-
I6	M9	Mire	38.6	M9b	39.7
I7	S11	Swamp	51.5	S11b	53.2
I8	M23	Rush-pasture	36.1	M23b	42.3
I9	S11	Swamp	50.3	S11c	55.4
W1	S27(W3)	Tall-herb fen (woodland)	35.4(40.0)	S28a	39.6
W2	S27	Tall-herb fen	45.8	-	-
W3	S27	Tall-herb fen	46.0	-	-
W4	S27	Tall-herb fen	37.8	S27a	41.2
W5	S27	Tall-herb fen	43.4	S27a	44.3
W6	S27	Tall-herb fen	36.6	S27a	39.8

†Coefficient range 0-100; higher coefficient score = closer match

Appendix 8 Equations for predictive models for R^2 <0.50.

(a) Predicition of collective vegetation variable

Species richness (S) = -8.103 +24.364log$_e$**CL** –10.521log$_e$**CL**^{2} +1.275log$_e$**CL**^{3} –0.0179**RED** +0.0002195**RED**^{2} –0.00000107**RED**^{3}

(F = 4.068; d.f. = 6; R^2 = 0.41; p = 0.003)

NENE = 9.045 –1.031log$_e$**FLU** –1.033**PH** +0.199log$_e$**FLU**^{2}

(F = 9.579; d.f. = 3; R^2 = 0.43; p = <0.001)

log$_e$**CAHT** = 2.428 +0.217log**eCON**

(F = 4.758; d.f. = 1; R^2 = 0.11; p = 0.035)

log$_e$**STDI** = 3.220 +0.169log$_e$**CL** –0.350**PH**

(F = 8.527; d.f. = 2; R^2 = 0.30; p = 0.001)

log$_e$**B2** = 3.031 +3.866log$_e$**FLU** –0.00296**RED** +0.00003127**RED**^{2} –2.572log$_e$**FLU**^{2} +0.485log$_e$**FLU**^{3}

(F = 4.304; d.f. = 5; R^2 = 0.37; p = 0.004)

BT = 764.301 +1069.216log$_e$**FLU** –736.947log$_e$**FLU**^{2} +147.880log$_e$**FLU**^{3} –1.334**RED** +0.0117**RED**^{2} –2601.349log$_e$**K** +2921.445log$_e$**K**^{2} –930.428log$_e$**K**^{3}

(F = 3.371; d.f. = 8; R^2 = 0.45; p = 0.006)

log$_e$**B1:B2** = 10.470 –0.330**PH** –2.257log$_e$**CON** + 0.171log$_e$**CON**^{2}

(F = 4.643; d.f. = 3; R^2 = 0.27; p = 0.007)

log$_e$**REPR** = 3.094 +0.392**PH** +0.260log$_e$**NO$_3$**

(F = 3.280; d.f. = 2; R^2 = 0.15; p = 0.049)

(b) Prediction of dominant population traits

log$_e$**RamHT** = 5.292 –6.786log$_e$**K** +8.766log$_e$**K**^{2} –3.165log$_e$**K**^{3}

(F = 5.270; d.f. = 3; R^2 = 0.29; p = 0.004)

log$_e$**RamRE** = 1.748 +0.004877**MIN** –0.974**leFLU** +0.0006065**MIN**^{2} +0.328**leFLU**^{2}

(F = 3.936; d.f. = 4; R^2 = 0.29; p = 0.009)

log$_e$**RamDWR** = 5.0 –6.408log$_e$**FLU** –.717log$_e$**FLU**^{2} +0.292log$_e$**FLU**^{3}

(F = 5.618; d.f. = 3; R^2 = 0.31; p = 0.003)

(c) Prediction of groundwater and related substrate enviornmental variables

WAT = -227.950 +52.011$\log_e$**STDE** –0.4111$\log_e$**STDE**^{3} +12.621**NENE** –3.505**NENE**^{2}

(F = 4.91; d.f. = 4; R^2 = 0.34; p = <0.0010.003)

MAX = -296.810 +65.853$\log_e$**STDE** +0.440$\log_e$**STDE**^{3} –0.575**S**

(F = 3.741; d.f. = 3; R^2 = 0.23; p = 0.019)

$\log_e$**FLU** = -0.528 –2.035**NENE** +0.460**NENE**^{2} +0.01843**BT** –0.0000266**BT**^{2} +0.00000001174**BT**^{3} +0.142**REPR**

(F = 4.397; d.f. = 6; R^2 = 0.44; p = 0.002)

PH = 7.684 –0.145$\log_e$**STDE** –0.303**NENE** –0.151$\log_e$**B1:B2**

(F = 7.767; d.f. = 3; R^2 = 0.38; p = <0.001)

$\log_e$**K** = 6.398 –3.826$\log_e$**STDI** +1.033$\log_e$**STDI**^{2} –1.361$\log_e$**RamTLA** +0.179$\log_e$**RamTLA**^{2} +0.154**DWS:DWL**

(F = 5.496; d.f. = 5; R^2 = 0.43; p = 0.001)

$\log_e$**K** = 4.940 –5.204$\log_e$**STDI** +1.535$\log_e$**STDI**^{2}

(F = 7.369; d.f. = 2; R^2 = 0.27; p = 0.002)

$\log_e$**CL** = 2.763 –0.238**S** +0.01017**S**^{2} +0.576$\log_e$**STDI**

(F = 4.643; d.f. = 3; R^2 = 0.27; p = 0.007)

$\log_e$**CON** = -0.535 +7.832log**RamLV** +0.150log**RamTLA** –3.808log**RamLV**^{2} +0.535log**RamLV**^{3} +3.045log**B1:B2** –2.111 log**B1:B2**^{2} +0.373log**B1:B2**^{3}

(F = 3.205; d.f. = 7; R^2 = 0.40; p = 0.010)

$\log_e$**CON** = -1.338 +2.033$\log_e$**CAHT** +1.145$\log_e$**B2** –0.0423$\log_e$**CAHT**^{3} –0.160$\log_e$**B2**^{2} +0.721$\log_e$**B1:B2** –0.568$\log_e$**B1:B2**^{2} +0.05796$\log_e$**B1:B2**^{3}

(F = 2.486; d.f. = 7; R^2 = 0.34; p = 0.036)

$\log_e$**NO$_3$** = -0.308 +0.04114**S** –0.780**NENE** +0.04535**NENE**^{3} +0.245$\log_e$**REPR**

(F = 4.077; d.f. = 4; R^2 = 0.31; p = 0.008)

$\log_e$**SO$_4^{2-}$** = -0.680+0.185asin**LITT** –0.00493asin**LITT**^{2}

(F = 3.281; d.f. = 2; R^2 = 0.14; p = 0.048)

(d) Predicition of proportion of attribute types per sample

Polycarpic Perennial (LH6) = 217.537 +2.308**MIN** +0.08997**MIN**^{2} +0.08347**RED** –0.002495**RED**^{2} –0.0000121**RED**^{3}

(F = 3.710; d.f. = 5; R^2 = 0.28; p = 0.006)

Hemicryptophyte (LF3) = 50.591 +19.155log$_e$**FLU** +3.738**MIN** –0.0315**MIN**^{2} –0.00446**MIN**^{3} +0.128**RED** –0.00116**RED**^{2} –4.386**WAT**

(F = 3.322; d.f. = 7; R^2 = 0.34; p = 0.006)

Helophyte (LF5) =176.464 –59.764log$_e$**FLU** +15.558log$_e$**FLU**^{2} +3.461**WAT** +0.008842**WAT**^{2} – 0.351**MIN** –0.00854**MIN**^{2} +0.121**RED** –0.000733**RED**^{2}

(F = 2.985; d.f. = 8; R^2 = 0.35; p = 0.009)

Rosette canopy (CS1) = 23.547 +0.433**BRYO** +2.648**MIN** +0.06459**MIN**^{2} +9.473log$_e$**PH** – 0.278log$_e$**PH**^{3}

(F = 6.762; d.f. = 5; R^2 = 0.41; p = <0.001)

Semi-rosette Canopy (CS2) = 198.583 +5.507**BARE** –0.211**BARE**^{2} –78.949log$_e$**PH** +10.686log$_e$**PH**^{2}

(F = 3.859; d.f. = 4; R^2 = 0.24; p = 0.008)

Canopy Height 1-3m (CH5) = 351.594 –0.632**BRYO** –72.065log$_e$**CON** +6.653log$_e$**CON**^{2} – 17.013log$_e$**FLU** +1.106**WAT**

(F = 3.451; d.f. = 5; R^2 = 0.26; p = 0.01)

Log$_e$**Lateral Spread 1; limited (LS1)** = 1.827 +0.05517**BRYO** +0.08086**MIN** –0.224log$_e$**PH** – 0.00125**MIN**^{2} –0.000446**BRYO**^{2} –0.000109**MIN**^{2}

(F = 6.234; d.f. = 6; R^2 = 0.44; p = <0.001)

Log$_e$**Lateral Spread 5; perennials >1000mm (LS5)** = 1.323 –0.00305**BARE** +0.002431**BARE**^{2} +0.104**MIN** +0.001236**MIN**^{2} –0.0000518**MIN**^{3} +0.001302**RED** –0.0000710**RED**^{2} +0.000000791**RED**^{3} +0.002292**WAT** -.0099**WAT**^{2} –0.000222**WAT**^{3} +0.687log$_e$**FLU** +0.647log$_e$**FLU**^{2} –0.197log$_e$**FLU**^{3}

(F = 2.271; d.f. = 14; R^2 = 0.45; p = 0.022)

Dispersule and Germinule 1; fruit, or part of (DG1) = 243.902 +5.387**BARE** –0.138**BARE**^{2} - 0.00276**BARE**^{3} –0.0656**BRYO** –0.00182**BRYO**^{2} –59.477log$_e$**PH** +7.519log$_e$**PH**^{2} +1.074**MIN**

(F = 2.897; d.f. = 8; R^2 = 0.34; p = 0.011)

Dispersule and Germinule 2; seed (DG2) = -54.555 –1.998log$_e$**CON** +79.906log$_e$**PH** – 10.123log$_e$**PH**^{2} –0.04836**RED** +0.002366**RED**^{2} –0.00000851**RED**^{3}

(F = 2.344; d.f. = 6; R^2 = 0.23; p = 0.046)

Bryophyte Cover = 480.604 –140.493log$_e$**CON** –10.353log$_e$**CON**^{2}

(F = 6.116; d.f. = 2; R^2 = 0.19; p = 0.004)

(e) Prediction of groundwater and related substrate enviornmental variables from proportion of attribute types per sample

$\log_e$**FLU** = 1.833 +0.002554**LF3** +0.04008**LF6** –0.0023**LF6**^{2} +0.0000007223**LF6**^{3} +0.001423**CS3** – 0.000116**CS3**^{2} +0.0000001925**CS3**^{3}

(F = 2.515; d.f. = 7; R^2 = 0.28; p = 0.028)

WAT –7.927 –0.0308**LF3** +0.03422**LF5** +0.156**LF6** +0.01873**CH5** +4.184$\log_e$**LS5** –1.031$\log_e$**LS5**^{2} +0.06519$\log_e$**LS5**^{3}

(F = 3.857; d.f. = 7; R^2 = 0.37; p = 0.002)

RED = 955.083 –14.346**LH6** +0.764**LF3** +0.06817**LH6**^{2} –0.000103**LH6**^{3} –0.00424**LF3**^{2} +0.00001252**LF3**^{3}

(F = 4.430; d.f. = 6; R^2 = 0.36; p = 0.001)

$\log_e$**PH** = 6.338 –1.3$\log_e$**LS1** –0.0417**LS2** +0.000262**LS2**^{2} +0.311$\log_e$**LS1**^{2}

(F = 5.409; d.f. = 4; R^2 = 0.31; p = 0.001)

$\log_e$**CON** = 5.955 –0.00686**BRYO** –0.00294**DG2**

(F = 6.218; d.f. = 2; R^2 = 0.20; p = 0.004)

WAT = -9.708 +0.07639**LF5**

(F = 19.708; d.f. = 1; R^2 = 0.28; p = <0.001)

MIN = 18.175 +0.09324**LF5** +3.638$\log_e$**LS5** +0.637$\log_e$**LS5**^{2} +0.02578$\log_e$**LS5**^{3}

(F = 5.645; d.f. = 4; R^2 = 0.32; p = 0.001)

Appendix 9 Raw average data from competiton and water level treatment experiments (Chapter 5)

Appendix 9a Final harvest values for competiton and water level treatment experiments. A = *Agrostis stolonifera*; D=*Deschampsia cespitosa.*

Replicate number	Species mix	Water level relative to surface(cm)	Above ground biomass (g)	Scanned leaf area (cm2)	Scanned leaf weight (mg)	Specific Leaf Area (SLA) (cm2/mg)	Plant height (cm)	No. of leaves.	No. of tillersrs	Ave. no. leaver per tiller
1a	D	-7	0.38	1.35	3.1	0.44	29	41	11	4
1a	D	-7	0.27	4.4	1	4.40	23	32	10	3
1a	D	-7	0.34	2.54	2	1.27	30	28	8	4
1a	D	-7	0.57	2.57	1.6	1.61	30	7	7	1
1b	D	-7	0.48	1.27	1.5	0.85	27	13	4	3
1b	D	-7	0.13	0.97	0.4	2.43	28	30	6	5
1b	D	-7	0.17	4.79	2.3	2.08	20	16	6	3
1b	D	-7	0.2	1.82	2.7	0.67	21	18	7	3
1c	D	-7	0.37	4.06	2.2	1.85	29	43	17	3
1c	D	-7	0.59	4.39	2.5	1.76	26	38	9	4
1c	D	-7	0.35	3.84	2.2	1.75	30	51	11	5
1c	D	-7	0.45	3.99	2.4	1.66	25	38	11	3
1d	D	-7	0.36	4.49	2.2	2.04	20	33	11	3
1d	A	-7	1.03	1.72	0.5	3.44	65	77	12	6
1d	A	-7	2.33	2.91	0.7	4.16	45	101	11	9
1d	D	-7	0.19	3.25	2	1.63	19	24	8	3
1e	D	-7	0.16	2.51	1.7	1.48	20	16	6	3
1e	A	-7	1.43	2.89	1	2.89	63	68	9	8
1e	A	-7	1.94	3.78	1.1	3.44	75	80	12	7
1e	D	-7	0.38	1.82	1.5	1.21	14	38	13	3
1f	D	-7	0.11	2.09	1.9	1.10	18	28	11	3
1f	A	-7	0.61	2.01	0.6	3.35	58	52	8	7
1f	A	-7	0.82	2.71	1	2.71	43	53	13	4
1f	D	-7	0.37	2.81	1.5	1.87	17	13	5	3
1g	A	-7	0.72	1.05	0.3	3.50	98	95	13	7
1g	A	-7	1.25	2.17	0.7	3.10	44	100	14	7
1g	A	-7	1.88	1.53	0.6	2.55	99	65	10	7
1g	A	-7	0.75	1.94	0.6	3.23	53	62	12	5
1h	A	-7	0.35	5.88	0.8	7.35	45	47	6	8
1h	A	-7	2.66	3.02	0.3	10.07	51	44	9	5
1h	A	-7	0.57	1.7	0.7	2.43	60	59	9	7
1h	A	-7	0.5	2.06	0.6	3.43	93	106	9	12
1i	A	-7	0.42	2.67	0.5	5.34	79	40	8	5
1i	A	-7	0.85	2.12	0.7	3.03	32	47	8	6
1i	A	-7	0.46	2.89	0.5	5.78	75	67	10	7
1i	A	-7	0.44	2.53	0.8	3.16	59	37	5	7
2a	D	0	2.35	13.44	10.4	1.29	53	97	7	14
2a	D	0	4.88	8.47	6.6	1.28	43	73	7	10

Appendix 9a

replicate	spp	water level	no. spp	Above ground biomass (g)	Scan leaf area (cm2)	Scan leaf weight (mg)	SLA (cm2/mg)	plant height (cm)	No. Lvs.	No. Tillers	Ave. lvs/til
2a	D	0		15.77	5.98	3.5	1.71	42	93	7	13
2a	D	0		2.35	8.19	1.7	4.82	52	257	9	29
2b	D	0		6.09	19.55	6.8	2.88	57	84	8	11
2b	D	0		4.45	18.59	16.8	1.11	48	122	7	17
2b	D	0		9.17	24.88	27.2	0.91	63	134	8	17
2b	D	0	1	4.2	17.3	14.5	1.19	65	97	7	14
2c	D	0	1	2.97	11.21	6.1	1.84	66	101	6	17
2c	D	0	1	2.4	21.39	8.1	2.64	72	86	5	17
2c	D	0	1	7.2	18.02	7.8	2.31	66	141	6	24
2c	D	0	1	2.99	8.98	3.4	2.64	57	77	5	15
2d	D	0	2	3.15	11.93	7.6	1.57	57	55	6	9
2d	A	0	2	6	3.45	0.9	3.83	53	385	56	7
2d	A	0	2	3.02	5.11	1.3	3.93	82	133	26	5
2d	D	0	2	1.78	8.71	4.9	1.78	61	62	5	12
2e	D	0	2	0.74	6.43	5	1.29	35	22	5	4
2e	A	0	2	10.37	2.92	0.8	3.65	90	259	41	6
2e	A	0	2	10.19	2.39	0.8	2.99	110	277	45	6
2e	D	0	2	2.08	5.23	6.8	0.77	32	72	7	10
2f	D	0	2	0.57	15.31	10.8	1.42	47	77	5	15
2f	A	0	2	5.73	3.42	0.7	4.89	123	298	42	7
2f	A	0	2	16.26	9.02	1.5	6.01	175	381	57	7
2f	D	0	2	2.97	7.4	5.6	1.32	50	21	3	7
2g	A	0	1	4.82	5.38	2.2	2.45	107	355	52	7
2g	A	0	1	11.72	2.28	2.1	1.09	87	147	27	5
2g	A	0	1	6.03	1.33	1	1.33	109	198	32	6
2g	A	0	1	15.98	5.19	1.8	2.88	86	326	46	7
2h	A	0	1	15.17	4.8	1.6	3.00	101	67	14	5
2h	A	0	1	4.63	3.7	1.1	3.36	103	638	73	9
2h	A	0	1	12.77	1.7	0.6	2.83	119	498	82	6
2h	A	0	1	1.45	2.66	0.9	2.96	119	136	21	6
2I	A	0	1	4.54	5.49	1.4	3.92	104	66	15	4
2I	A	0	1	6.9	6.75	1.5	4.50	115	147	17	9
2I	A	0	1	2.42	5.85	1.4	4.18	140	288	40	7
2I	A	0	1	9.27	9.26	2.1	4.41	132	376	50	8
3a	D	7	1	5.34	4.22	2.7	1.56	51	63	14	5
3a	D	7	1	2.3	5.28	4.7	1.12	50	43	10	4
3a	D	7	1	2.08	4.33	6.3	0.69	62	97	17	6
3a	D	7	1	1.9	4.15	3.3	1.26	37	121	20	6
3b	D	7	1	4.17	8.88	5	1.78	40	115	14	8
3b	D	7	1	2.69	12.63	10.4	1.21	51	122	11	11
3b	D	7	1	5.33	6.29	7.6	0.83	56	95	12	8
3b	D	7	1	2.83	3.87	1.9	2.04	41	134	15	9

Appendix 9a

replicate	spp	water level	no. spp	Above ground biomass (g)	Scan leaf area (cm2)	Scan leaf weight (mg)	SLA (cm2/mg)	plant height (cm)	No. Lvs.	No. Tillers	Ave. lvs/til
3c	D	7	1	2.88	11.08	11.4	0.97	44	81	10	8
3c	D	7	1	4.52	6.26	6.6	0.95	35	163	16	10
3c	D	7	1	4.34	4.72	3.8	1.24	59	96	9	11
3c	D	7	1	1.92	5.1	3.2	1.59	51	165	9	18
3d	D	7	2	2.88	5.25	2.1	2.50	53	92	5	18
3d	A	7	2	1.78	3.26	0.7	4.66	122	250	27	9
3d	A	7	2	5.82	5.23	1.3	4.02	91	198	24	8
3d	D	7	2	1.35	5.98	2.6	2.30	51	58	4	15
3e	D	7	2	4.26	7.86	7.2	1.09	49	93	14	7
3e	A	7	2	1.85	2.74	0.8	3.43	98	113	14	8
3e	A	7	2	4.41	3.1	1	3.10	103	154	12	13
3e	D	7	2	4.41	16.41	15	1.09	59	53	7	8
3f	D	7	2	0.64	8.69	7.7	1.13	32	34	5	7
3f	A	7	2	4.12	4.19	1	4.19	75	174	32	5
3f	A	7	2	4.25	1.66	0.7	2.37	93	206	32	6
3f	D	7	2	2.22	3.15	2.6	1.21	52	50	5	10
3g	A	7	1	6.19	3.44	1.1	3.13	126	117	22	5
3g	A	7	1	7.4	2.96	1	2.96	121	326	51	6
3g	A	7	1	7.14	2.02	0.9	2.24	134	179	26	7
3g	A	7	1	4.75	2.84	1.1	2.58	140	199	25	8
3h	A	7	1	2.27	2.97	0.9	3.30	94	134	17	8
3h	A	7	1	2.21	3.14	0.8	3.93	176	146	26	6
3h	A	7	1	3.26	2.59	0.9	2.88	117	149	24	6
3h	A	7	1	5.88	3.53	1	3.53	112	213	27	8
3i	A	7	1	6.85	2.16	1.5	1.44	101	259	29	9
3i	A	7	1	2.07	2.19	1.1	1.99	79	101	22	5
3i	A	7	1	5.31	3.18	1.2	2.65	59	267	44	6
3i	A	7	1	2.55	1.73	0.5	3.46	61	83	16	5

Appendix 9b Harvest values for *Deschampsia cespitosa* flood and drought magnitude and duration experiment

Treatment	Replicate	Plant height (cm)	Root length	Stolon length	Leaf weight (g)	Scan leaf weight (mg)	Scan leaf area (cm2)	Below soil biomass (g)	Scan root weight (mg)	Scan root length (cm)	Total biomass	No. leaves	No. ramets	No. lvs/ramet	SLA (cm2/mg)	SRL (cm/mg)
1	a	80	29	2.5	3.94	193	35.02	0.19	42	143.5	4.14	52	5	10	0.18	3.42
	b	74	46	0	4.28	342	50.27	0.34	62	117.4	4.62	74	7	11	0.15	1.89
	c	60	30	0	1.83	203	44.90	0.20	42	128.6	2.04	44	4	11	0.22	3.06
2	a	97	23	0	3.37	262	78.16	0.26	33	107.7	3.63	47	5	9	0.30	3.26
	b															
	c	80	59	10	4.44	297	52.70	0.30	67	157	4.73	64	7	9	0.18	2.34
3	a	40	16	2	0.61	85	23.04	0.09	9	55	0.69	42	4	11	0.27	6.11
	b	73	21	2	2.09	326	54.42	0.33	26	136.8	2.41	38	5	8	0.17	5.26
	c	48	29	1	5.16	150	36.35	0.15	34	110.8	5.31	199	12	17	0.24	3.26
4	a	36	17	0	0.26	28	8.32	0.03	7	63.3	0.29	26	3	9	0.30	9.04
	b	55	29	9	3.66	165	42.14	0.17	31	128.7	3.82	97	6	16	0.26	4.15
	c	66	25	0	1.88	173	44.90	0.17	30	83.7	2.06	48	3	16	0.26	2.79
5	a	64	19	0	0.85	131	35.01	0.13	20	70	0.98	19	3	6	0.27	3.50
	b	55	22	0	2.16	212	46.90	0.21	38	140.6	2.37	50	5	10	0.22	3.70
	c	56	18	0	0.73	190	43.62	0.19	18	79.5	0.92	12	2	6	0.23	4.42
6	a	74	50	0	2.40	245	50.48	0.25	40	108	2.64	42	3	14	0.21	2.70
	b															
	c	36	19	4	0.37	42	17.75	0.04	13	66.7	0.41	27	2	14	0.42	5.13
7	a	64	35	0	4.09	210	43.00	0.21	29	204.9	4.30	83	7	12	0.20	7.07
	b	58	27	1	2.28	230	46.75	0.23	44	141	2.51	61	5	12	0.20	3.20
	c	70	56	0	2.82	134	33.84	0.13	35	130.4	2.96	38	4	10	0.25	3.73
8	a	72	55	1	3.77	310	53.84	0.31	37	194	4.08	51	5	10	0.17	5.24
	b	65	33	1	2.60	175	25.14	0.18	29	96.1	2.77	55	4	14	0.14	3.31
	c	76	39	2	3.40	330	62.20	0.33	48	126	3.73	41	4	10	0.19	2.63
9	a	56	26	3	2.08	185	42.93	0.19	25	119.9	2.26	46	4	12	0.23	4.80
	b	49	33	2	1.83	149	37.73	0.15	40	126.4	1.98	79	5	16	0.25	3.16
	c	59	24	0	1.02	107	27.80	0.11	39	133	1.12	25	3	8	0.26	3.41
10	a	67	29	2	2.47	190	29.78	0.19	27	136.4	2.66	40	4	10	0.16	5.05
	b	40	22	0	0.67	55	17.97	0.06	19	124.5	0.72	46	5	9	0.33	6.55
	c	50	26	1	1.95	105	29.13	0.11	34	131.9	2.05	65	4	16	0.28	3.88
11	a	66	25	0	2.36	235	47.07	0.24	38	117.6	2.59	42	4	11	0.20	3.09
	b	72	31	3.5	3.08	343	49.00	0.34	36	136.6	3.43	52	6	9	0.14	3.79
	c	67	26	1	4.12	263	39.48	0.26	34	165.7	4.39	61	6	10	0.15	4.87
12	a	52	23	0	0.73	66	24.96	0.07	24	147	0.79	27	4	7	0.38	6.13
	b	46	22	0	1.01	81	26.78	0.08	24	165.7	1.09	45	4	11	0.33	6.90
	c	77	36	4.5	2.35	287	52.13	0.29	45	207	2.63	39	5	8	0.18	4.60
13	a	65	23	0	1.32	204	42.71	0.20	34	148.9	1.53	22	3	7	0.21	4.38
	b	69	23	0	1.57	230	39.41	0.23	31	102	1.80	23	3	8	0.17	3.29
	c	71	21	2.5	1.25	141	44.73	0.14	22	138.1	1.39	30	4	8	0.32	6.28

Appendix 9c Harvest values for *Phalaris arundinacea* hlood and drought magnitude and duration experiment

Treatment	Replicate	Plant height (cm)	Root length	Stolon length	Above soil root length	Stem weight	Leaf weight	Scan leaf weight (mg)	Scan leaf area (cm2)	Repro. Weight (mg)	Ave. seed weight (mg)	Total above-ground weight (g)	Below soil biomass (g)	Total biomass (g)	Scan root weight (mg)	Scan root length (cm)	No. leaves	No. ramets	No. lvs/ramet	SLA (cm2/mg)	SRL (cm/mg)
1	a	65	63	12	0	1.83	1.38	147	34.8	0	0	3.21	1.27	4.47	156	857	35	8	4	0.24	5.5
	b	129	58	7	0	2.15	0.78	133	35.5	155	0.96	3.09	1.05	4.14	68	442	19	5	4	0.27	6.5
	c	87	61	2	0	1.55	0.73	73	20.3	71	0	2.35	0.86	3.22	24	119	24	6	4	0.28	5
2	a	76	46	1	0	0.87	0.62	83	29.3	0	0	1.49	0.54	2.03	46	373	21	5	4	0.35	8.1
	b	69	58	12	0	1.74	1.03	95	28.2	0	0	2.77	0.85	3.62	31	252	28	7	4	0.3	8.1
	c	75	73	3	0	1.29	0.67	82	20	0	0	1.96	0.91	2.87	107	678	20	4	5	0.24	6.3
3	a	91	62	36	0	4.15	2.84	119	39.8	0	0	6.99	2.03	9.02	150	823	55	11	5	0.33	5.5
	b	87	53	18	0	1.97	1.47	60	18.5	0	0	3.44	0.94	4.38	172	998	37	8	5	0.31	5.8
	c	83	59	28	0	3.63	2.19	139	37.9	0	0	5.82	1.65	7.47	72	323	34	7	5	0.27	4.5
4	a	132	50	21	9	4.79	1.89	131	33	338	0.82	7.02	1.78	8.79	76	437	38	8	5	0.25	5.8
	b	79	49	5	8	2.2	0.61	67	22.2	0	0	2.81	0.71	3.52	41	229	37	7	5	0.33	5.6
	c	143	49	12	7	3.55	2.09	90	23.1	167	0.8	5.8	1.66	7.46	76	543	15	4	4	0.26	7.1
5	a	77	34	35	39	2.72	1.17	102	30.5	0	0	3.89	0.76	4.66	24	168	20	4	5	0.3	7
	b	151	57	10	42	3.24	1.04	138	38.7	263	0	4.54	1.14	5.68	61	389	19	6	3	0.28	6.4
	c	126	50	15	64	4.55	1.79	125	33.3	253	1.04	6.6	1.39	7.99	95	533	37	8	5	0.27	5.6
6	a	66	42	6	0	1.23	1.51	35	11.5	0	0	2.74	0.59	3.33	99	781	14	3	5	0.33	7.9
	b	112	57	25	0	3.81	1.66	92	29.1	77	0.34	5.55	1.86	7.41	55	404	46	11	4	0.32	7.3
	c	128	65	8	0	2.74	0.58	68	25.2	180	0	3.5	1.63	5.13	115	555	26	6	4	0.37	4.8
7	a	131	45	8	0	2.81	1.13	98	22.1	86	1.06	4.02	1.26	5.28	105	650	24	6	4	0.23	6.2
	b	126	61	10	0	4.55	2.89	73	18.3	179	0.79	7.62	2.12	9.74	67	583	52	12	4	0.25	8.7
	c	88	64	28	0	3.15	2.27	128	34.6	0	0	5.42	1.85	7.27	128	703	55	13	4	0.27	5.5

Appendix 9c

Treatment	Replicate	Plant height (cm)	Root length	Stolon length	Above soil root length	Stem weight	Leaf weight	Scan leaf weight (mg)	Scan leaf area (cm2)	Repro. Weight (mg)	Ave. seed weight (mg)	Total above-ground weight (g)	Below soil biomass (g)	Total biomass (g)	Scan root weight (mg)	Scan root length (cm)	No. leaves	No. ramets	No. lvs/ramet	SLA (cm2/mg)	SRL (cm/mg)
8	a	117	54	8	0	1.55	0.8	90	27.4	68	1.22	2.42	1.1	3.52	72	596	21	5	4	0.3	8.3
	b	133	38	9	0	2.22	0.84	80	21.2	127	0	3.19	0.68	3.87	34	242	16	3	5	0.27	7.1
	c	134	53	7	0	2.3	0.99	71	25	101	0	3.39	1.21	4.6	62	444	25	5	5	0.35	7.2
9	a	115	44	7	14	1.13	0.46	57	27.4	112	0.82	1.7	0.53	2.23	33	318	14	3	5	0.48	9.6
	b	115	38	6	20	2.01	0.71	71	20.5	108	0.81	2.83	0.83	3.66	73	592	27	7	4	0.29	8.1
	c	77	43	15	0	2.53	1.13	71	30.8	0	0	3.66	1.14	4.81	94	541	28	6	5	0.43	5.8
10	a	64	39	13	0	1.05	0.39	74	25.9	0	0	1.44	0.41	1.85	48	420	17	3	6	0.35	8.7
	b	71	46	31	0	1.57	1.48	761	23.1	0	0	3.05	0.68	3.73	58	293	19	4	5	0.03	5
	c	86	42	30	2	2.39	1.14	123	29.1	0	0	3.53	1.36	4.9	52	337	23	4	6	0.24	6.5
11	a	140	51	13	31	4.56	1.99	125	31.9	233	0.9	6.78	1.41	8.19	221	1457	30	6	5	0.26	6.6
	b	118	50	14	0	2.27	0.92	91	24.3	144	0	3.34	0.99	4.33	44	259	25	6	4	0.27	5.9
	c	90	53	21	8	4.84	2.53	126	28.9	0	0	7.37	1.08	8.45	143	635	43	11	4	0.23	4.4
12	a	147	53	0	0	0.33	1.1	70	25.5	77	0.4	1.51	0.53	2.04	85	317	15	3	5	0.36	3.7
	b	73	37	4	28	2.19	0.89	91	26.5	77	0	3.16	0.87	4.03	61	472	19	4	5	0.29	7.7
	c	55	39	4	0	0.56	0.43	54	22.4	0	0	0.99	0.3	1.29	38	353	13	3	4	0.42	9.3
13	a	112	74	7	0	4.17	1.69	85	27.6	99	0.6	5.95	1.74	7.7	123	805	34	8	4	0.32	6.5
	b	69	40	16	0	1.35	0.74	84	24.5	0	0	2.09	0.58	2.67	38	224	15	3	5	0.29	5.9
	c	86	51	37	4	3.41	2.69	154	44.6	0	0	6.1	1.39	7.49	88	630	38	8	5	0.29	7.2

Appendix 10 Paper with general relevance to the project, submitted to *Aquatic Botany*.

Environmental variables and vegetation characteristics associated with a population of *Carex chordorrhiza* L. fil. (String Sedge).

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ABSTRACT

The hydrological and hydrochemical conditions characterising a riverine wetland habitat supporting a large population of *Carex chordorrhiza* within the Insh Marshes, Scotland, were quantified and related to structural measurements of the species, and the plant assemblages in which it occurred. Environmental factors which produce intermediate levels of stress, such as moderately reducing hydrosoil conditions and near-constant shallow inundation were associated with the occurrence of *C. chordorrhiza* as a dominant species at this site.

KEYWORDS: Groundwater variables, vegetation variables, Insh Marshes, riverine wetlands, Scotland

INTRODUCTION

Carex chordorrhiza L. fil. (String sedge) is a perennial plant, with far-creeping rhizomes and solitary shoots arising from the base of the flowering stems. The species is characterised by an ovoid flowering head, 7-15mm (*Vignea* subgenus), and by pale yellow-brown scales which rapidly decay (Jermy *et al.* 1982). *C. chordorrhiza* has a circumpolar distribution within the boreal and subarctic regions. It is common in Iceland, Scandinavia, Finland and Russia, but has a sporadic distribution in other areas of Europe and in North America (Page and Rieley 1985).

In Britain, the species is considered to be a relict, left behind following the retreat of boreal species at the end of the last glaciation. As such, it constitutes a Northern Montane element of the British flora (Page and Rieley 1985). Populations have been recorded at only two sites in the UK, both in the Highlands of Scotland. In West Sutherland (VC 108) three large and several smaller colonies are present within a 10-km square, at the head of Loch Naver, Altnaharra. The estimated population size is in the order of 100,000's of shoots. A greater number of scattered colonies are present in Easterness and Nairns (VC 96), throughout the Insh Marshes, within three 10-km squares. The estimated shoot population is >1,000,000. The restricted distribution *C. chordorrhiza* in Britain gives it threatened species status. It is included in the British Red Data Book for Vascular Plants (Legg *et al.* 1995b). The species was first recorded in Britain in 1897 by the Rev. E.S. Marshall, and Dr W.A. Shoolbred in West Sutherland (NC5636) (Alex Lockton, BSBI, pers. comm. 2001). The first record of the species within the Insh Marshes (Easterness and Nairns) was by S.E. Page and J.O. Rieley in 1978 (Page and Rieley 1985). More recently a systematic survey of the distribution of the species on the Insh Marshes was carried out by Legg *et al.* (1995b), who reported the area containing *C. chordorrhiza* (c. 15.4 ha) to be five times larger then previously recorded. The authors considered that a rapid vegetative spread of the species may have occurred during the late 20th century, rather than the plant having been routinely under-recorded at this site.

From experimental investigations into the effects of water level change on the survival of *C. chordorrhiza*, based on the measurement of a number of morphological traits, Legg *et al.* (1995a) concluded that the species would not survive prolonged inundation, and that any prolonged drawdown would lead to retardation of growth. We have also found (Kennedy *et al.* 2001) that the magnitude and duration of water level fluctuations can produce predicatble changes in recorded values for a range of morphological traits, related both to survival (e.g. root and leaf production), and to vegetative spread (e.g. rhizome and stolon production) in wetland grasses, sedges and forbs. Previous publishd field observations on the groundwater dynamic influencing populations of *C. chordorrhiza* are, however, limited to single water depth measurements, and associated hydrochemical analyses (pH, Ca, Mg, Na, Fe, Mn and K), conducted by Page and Rieley (1985).

During the course of a wider study into eco-hydrological interactions within northern British poor-fen systems, we collected data on vegetation and environmental variables within two areas where *Carex chordorrhiza* was recorded at Invertromie Fen, within the Insh Marshes. At one location the species formed the dominant component of the assemblage. At the second location it was present at a lower percentage cover. The data provide an insight into hydrological and hydrochemical factors influencing the distribution of the species in Scotland. It also aids a characterisation of the plant communities within which this species is found in the British isles. This may help provide a baseline for the appropriate management of this rare sedge.

MATERIALS AND METHODS

Site description

The Insh Marshes RSPB reserve is a nationally and internationally important site (Gibbons 1993), with a grade 1 SSSI, and RAMSAR designation. The underlying and local geology is predominantly hard, acidic quartz, feldspar and schist of the Dalradian and Moinian series, with some possible enrichment from limestone outcrops upstream of the River Spey (Page and Rieley 1985). Botanical surveys of the wetlands (Fojt 1989; Loizou 1997; Murphy & Hudson 1991; Wood & Evans 1989) have classified the main communities as swamp and poor fen, with scattered and infrequent mire and scrub communities. Work undertaken by Grieve *et al.* (1995) suggests that a complex system of hydrological inputs and balances including valley side runoff, groundwater upwelling, and riverine inundation underpin the functioning of the marshes. Invertromie Fen (NH775001-775003) consists of peat based areas mixed with floating mat vegetation, and contains one of the larger colonies of *C. chordorrhiza* (c. 100m^2) surveyed by Legg *et al.* (1995b). Sampling was conducted along a fixed transect (c 600m long) running at right angles to the south (true right) bank of the River Spey, along a WNW-ESE direction. Trees and shrubs were absent from the transect, giving effectively unshaded conditions. Seven sampling stations were established at regular intervals along the transect.

Vegetation data

Species lists were drawn up for each visit to the site (in August 1998, and monthly, during May-August 1999) using a 1m^2 quadrat with twenty-five 20x20cm^2 sub-divisions, and the percentage abundance of each plant species was noted. The frequency of species was derived from the repeat samples conducted throughout the growing season. Nomenclature followed Jermy *et al.* (1982) and Stace (1997) for vascular plants, and Smith (1978) for bryophytes. Sampling was carried out within different patches each month in order to minimise the impact upon the vegetation, but always within a 1m radius of fixed sampling equipment (see below) to make samples comparable. Measurements were made of specific morphological traits of individual plants from the dominant species present within each quadrat, and the vegetation assemblage as a whole was characterised by measuring a number of collective vegetation variables (CVV's: see Tables 2 and 3).

Groundwater data

Fixed sampling equipment was installed at each station along the transect across Invertromie Fen. Water level range gauges, based on the design of Bragg *et al.* (1994) were employed to measure minimum and maximum water levels during the monthly intervals between sampling. Following removal of a peat/root mat core, each gauge was anchored into the root mat of the vegetation using right-angled brackets, in order to prevent movement of the gauge once operational, and to maximise accuracy of derived water level readings. An eyelet connected to a ballasted float shifted two foam markers up and down a fixed rod as groundwater levels rose and fell. The maximum and minimum water levels reached, indicated by the markers, could then be derived from a fixed scale. Dipwells installed within 50cm of the gauges allowed groundwater levels to be measured at the time of sampling, where the level was below the ground surface. Otherwise, the depth of standing water was measured from ground level. Mixed groundwater samples were taken from the dipwells using a 50ml syringe, to which a length of rubber tubing had been connected, and were placed into acid washed 250ml sample bottles. Measurements of pH and electrical conductivity (µS/cm) were made using probes connected to pre-calibrated, hand held Hanna meters, and soil redox potential (mV) was measured using a self-referencing platinum electrode probe, pre-treated for reducing conditions, connected to a Hanna meter. Shade cast by nearby trees and/or scrub, and percentage bare ground were assessed visually.

On return to the lab groundwater samples were filtered through 0.5 µm Whatman GF/C glass fibre filters in order to remove suspended materials, and analysed for major anions and cations. Chloride (Cl), fluoride (F), nitrate (NO_3), and sulphate (SO_4^{2-}) were determined from sub-samples using a DIONEX ion chromatograph with a chemical suppressor and an AS4A analytical column. Samples were eluted with a sodium hydroxide (Na_2CO_3/$NaHCO_3$) solution, and conductivity was suppressed with dilute sulphuric acid (H_2SO_4). Detection limits were 0.02 mg l^{-1}. Potassium (K) and sodium (Na) levels were determined using flame photometry. Calcium (Ca), magnesium (Mg) and manganese (Mn) were determined using flame atomic absorption spectrometry (AAS); samples were dosed with strontium nitrate ($Sr(NO3)_2$) solution (0.4%) to suppress interference for Ca and Mg. Iron (Fe) was determined by graphite furnace AAS. Samples were diluted where appropriate. The approximate detection limit for these samples was 0.01 mg l^{-1}.

RESULTS

Community assemblage

Within the Invertromie Fen transect, *Carex chordorrhiza* formed the dominant population at station 7 (Table 1). A co-dominant species was the amphibious *Potamogeton polygonifolious* Pourret (Bog Pondweed), which helps to characterise the consistently inundated conditions in which *C. chordorrhiza* is found. Apart from *P. polygonifolious*, all other associated species were occasional. A small-leaved form of *Menyanthes trifoliata* L. (Bogbean) was also recorded, and the presence of this, plus other sedge species (*C. diandra* Schrank, *C. panicea* L.) suggest that the area was waterlogged, but probably not deeply inundated for long periods of time. The highest level of similarity to a recognised National Vegetation Community (NVC) type was to the S9 *Carex rostrata* swamp community (Match coefficient = 44.0; Malloch 1999). In turn, sub-community S9b (*Menyanthes trifoliata-Equisetum fluviatile*) had the highest Match coefficient (48.2). The S9b floristic table does not list *C. chordorrhiza* as a constituent species of this community type (Rodwell 1995), but the associated species were consistent.

At station 1 on the Invertromie Fen transect *C. chordorrhiza* formed a smaller componet of the vegetation, within a predominantly *Sphagnum squarrosum* Crome dominated sward. Three grass species, *Agrostis stolonifera* L. (Creeping Bent), *Holcus lanatus* L. (Yorkshire-fog), and *Molinia caerulea* (L.) Moench (Purple Moor-grass) were also present, indicating slightly drier conditions than for station 7. The highest matched community type was to an M9 *Carex rostrata-Calliergon cuspidatum/giganteum* mire (Coefficient: 44.7). The second highest match (41.3) to a *Carex rostrata-Sphagnum squarrosum* mire community seems more sensible. A number of species recorded from Invertromie are not listed within the NVC tables for this community type, but the description is based on only 22 samples in total, making scope for further records possible.

Vegetation characteristics

The plants of *C. chordorrhiza* from station 7 formed a low canopy, with a discontinuous spread (see Table 2). For the average data for 1999, it appears that the stem component of the ramets studied formed the bulk of the biomass. The low total biomass is indicative of the slight nature of the species. Comparable trait measurements were not taken for the species at station 1, as it was not a dominant species here.

Collective Vegetation Variables (CVVs), which provide an indication of the structural characteristics of the species assemblage as a whole were also measured (Table 3). The results for station 7, where the species dominated, suggest a crowded species assemblage with an intermediate level of diversity and a high density of small stems. An overall canopy height of 19-20cm indicated that *C. chordorrhiza* is rarely overtopped by other species. Much of the standing crop at the end of the growing season (1998 data) consisted of equal proportions of living and dead material. However, over the length of a growing season, the average proportion of living material appears to be much highe than then necromass propotion. Not all species within the assemblage could be assigned an established phase strategy (Grime *et al.* 1988). Of the six which could (Table 1), all had strong elements of stress-tolerance, generally characteristic of plants occurring in low-nutrient European riverine wetland systems (Hills *et al.* 1994; Hills & Murphy 1996).

Vegetation structural characteristics such as stem density were comparable at both stations 1 and 7, but species richness at station 1 was about twice that at station 7. Standing crop was similar between the two sites, but necromass formed a greater part of the standing crop at station 7 (Table 3). In addition, some species recorded at station 1 showed relatively strong competitive elements to their strategies, and the species component also had a more of a ruderal element. Overall a strong stress-tolerant elememt was also still apparent (Table 1).

Environmental data

The data for water table dynamics (Table 4a) show that constant inundation was a factor associated with the population of *C. chordorrhiza* at station 7, although the average depth of inundation was relatively shallow. Drawdown below the soil surface was not evident during the course of the season, and the station was subject to occasional deeper flooding. The redox potential of the substrate at station 7 was consistently negative when measured over the two seasons of the study. However, the conditions appeared to be less reducing during the 1999 season, perhaps reflecting the lower incidence of flooding during the growing season. Measured pH values were variable, but circumneutral, and conductivity was also variable, but never very high. None of the major metals or anions measured were present at conspicuously high, or variable levels. The presence of sulphate in moderate quantities was in line with the hydrosoil redox potentials recorded.

When compared to the stations along the transect in which *C. chordorrhiza* was not found, it can be seen that station 7 differs in some respects. Across the Invertromie transect, sample stations were subject to similar water table fluctuations (Figure 1), apart from those at the extreme ends, which did not support floating mat vegetation. The drop in levels of inundation and fluctuation was more pronounced for station 7 during the 1999 season, than for other stations (Figure 1b). However, other areas of the marshes were subject to greater levels of draw-down during 1999 (information available from author), indicating a relatively stable situation within Invertromie Fen. Significant differences between sample stations were found for 10 of the 18 environmental variables measured (Table 4). Average water table level, maximum and minimum water table levels all varied significantly between stations, as did Mg, Ca, Na, and Cl. At station 7 values recorded for Mg and Ca were amongst the highest found across the Insh Marsh sites. Significant variation was also found between stations for K, NO_3 and SO_4^{2-} (non-normal data analysed using non-parametric statistics). Compared with other sites across the transect, station 7 had the highest value for F, the joint highest value for NO_3, and the second highest value for SO_4^{2-}.

In contrast to station 7, conditions at station 1 were drier on average, with a generally oxidising hydrosoil/*Sphagnum* carpet. Overall levels of water table fluctuation were relatively high during the growing season. Generally across the transect, nutrient levels were amongst the lowest at station 1. Cl levels however were were intermediate within the range for both stations 1 and 7.

DISCUSSION

The community assemblage within which *C. chordorrhiza* was sampled, was comparable to those described previously by Page and Rieley (1985). Within the framework of the NVC, this assemblage fits most closely to the *Carex rostrata* dominated S9b swamp community. Other co-dominants are found within the assemblage, and the relatively high species diversity for this swamp community was evident. However, the presence of *C. chordorrhiza* as a dominant component of the assemblage, plus the increased number of occurrences recorded (Legg *et al.* 1995b) may warrant revision of the community description. The samples taken where *C. chordorrhiza* was recorded as an occasional species were comparable to relevés described by Page and Riely (1985), though slightly more species rich.

The general structure of the vegetation assemblage where *C. chordorrhiza* was dominant suggests that it is experiencing intermediate intensities of environmental stress. Primary productivity estimates for western European wetlands run, for example, from 125 to 2500 $g/m^2/yr$ for wetlands dominated respectively by *Molinia caerulea* (L.) Moench and *Phragmites australis* (Cav.) Trin. Ex Steudel (Gore 1983). Standing crop estimates for the assemblage containing *C. chordorrhiza* are at the lower end of this range, perhaps reflecting the slight nature of the species, its dominance within the vegetation, and the relatively low productivity of poor-fen vegetation generally (Cadbury and Grace 1983). These factors are consistent with the findings of Hills *et al.* (1994) and Hills & Murphy (1996) where

primary established phase strategies relating to stress tolerant capacity were predominant within low nutrient European wetlands. A lower total biomass value for ramets of *C. chordorrhiza* sampled during August 1998, than for the average 1999 values data may relate to the early maturity of the species (Legg *et al.* 1995a). This characteristic, along with the relatively low nutrient levels at station 7 are also indicative of intermediate levels of stress being prevalent driving factors. In addition, more reducing conditions may help explain the dominance of *C. chordorrhiza*, and also the absence of any strongly competitive species such as *A. stolonifera*. A greater overall degree of water table fluctuation and lower nutrient status may explain the restricted nature of species with strong competitive capacities, and also the higher overall species diversity at station 1.

The redox values recorded were generally low enough to suggest anoxic soil conditions, with reduced availability of nitrate, and with the appearance of manganous and ferrous ions, but not low enough for the disappearance of sulphate or appearance of methane in quantity (Laanbroek 1990). A slight variation in these factors across the Invertromie Fen may contribute to limiting the spread of *C. chordorrhiza*. Legg *et al.* (1995b) suggest that the species has the capacity to spread fast via rapid shoot elongation following favourable winter conditions (flooding, which prevents soils from freezing). The observation of such conditions within the Insh Marshes might suggest that the species may have a narrow ecological niche, restricted by subtle water table and redox dynamics, and not by dispersal capacity. However, Legg *et al.* (1995b) also suggest that the species may have spread more rapidly during the last half of the 20th century. Therefore, future assessments of spread and/ or decline relative to this 1995 baseline survey would be sensible. Comparable community assemblages, which differ only by the absence of *C. chordorrhiza*, are detailed by Page and Rieley (1985). They also describe three main phytosociological groups containing the species. One of these groups consists solely of the colonies found at the head of Loch Naver, where *C. chordorrhiza* is generally less abundant. A sensible progression would be to investigate and compare the groundwater regimes between the communities containing *C. chordorrhiza* and those not containing the species. Similar investigations within the main phytosociological groups described could also be informative. In addition Legg *et al.* (1995a) found that morphological variation (and hence potential variability in survival capacity) in *C. chordorrhiza* was related to increased inundation during experiments. It would be of interest to investigate the degree of morphological plasticity, and of measured traits between field populations within the three phytosociological groups defined. As Legg *et al.* (1995b) state, it seems unlikely that *C. chordorrhiza* could survive extended periods of inundation. However, more studies are required to clarify the ecological range of the species, in northern Europe.

The environmental parameters which influence the section of Invertromie Fen where *C. chordorrhiza* is present as the dominant species appear to relate to specific factors of stress, including mildly anoxic hydrosoil and shallow inundation during the growing season, which may also help explain the specific community assemblage. The findings may be used as gauges for future surveys of the distribution of the species. The verification of these inferred controls would benefit from further sampling, and could form a useful tool for the conservation of this rare and restricted species.

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Table 1 Floristic table showing the frequency (F) (and abundance) of plant species associated with the presence of *Carex chordorrhiza* at stations across Invertromie Fen. Figures represent four successive samples taken May-August, 1999. I = 0-20% F; II = 21-40%; III = 41-60%; IV = 61-80%; V = 81-100%. Figures represent single sample, August 1998; and four successive samples taken May-August, 1999. Established phase strategies (*sensu* Grime *et al.* 1988) for species recorded in assemblage with *C. chordorrhiza*; - = description not available. C= competitior; S= stress tolerator; R= ruderal (disturbance tolerator).

Species	Station 1		Station 7		Established phase strategy
	1998*	1999	1998*	1999	
Agrostis stolonifera	I	I (1)	-	-	CR
Angelica sylvestris	-	I (1)	-	-	C/CR
Caltha palustris	-	II (4)	-	-	S/CSR
Calliergon stramineum	-	I (1)	-	-	
Cardamine pratensis	I	I (3)	-	-	R/CSR
Carex chordorrhiza	-	I (2)	V	V (4)	-
Carex diandra	-	II (2)	-	I (1)	-
Carex nigra	V	II (2)	I	I (3)	S/SC
Carex panicea	-	I (2)	I	I (1)	S
Carex rostrata	-	I (1)	-	I (1)	-
Epilobium palustre	I	I (2)	-	-	S/CSR
Equisetum fluviatile	III	III (4)	I	I (2)	SC
Eriophorum angustifolium	I	I (3)	-	-	S
Galium palustre	I	-	-	I (2)	CR/CSR
Holcus lanatus	IV	I (3)	-	-	CSR
Lemna arvensis	-	I (1)	-	-	CSR
Menyanthes trifoliata	V	II (2)	II	I (2)	S/SC
Molinia caerulea	-	I (1)	-	-	SC
Pedicularis palustris	I	I (2)	-	I (1)	-
Potamogeton polygonifolius	-	-	V	IV (4)	-
Potentilla palustris	III	II (2)	I	III (4)	S/SC
Sphagnum cuspidatum	-	-	-	III (2)	-
Sphagnum palustre	-	-	-	II (1)	-
Sphagnum squarrosum	V	V (4)	-	-	-
Valeriana officinialis	-	I (3)	-	-	CSR
Viola palustris	IV	II (4)	-	-	S/CSR

Table 2 Average values (±standard error) for measured traits of *C. chordorrhiza* from a whole ramet. Figures represent single sample, August 1998; and four successive samples taken May-August, 1999.

Measured species trait per ramet	1998	1999
Height of plant (cm.)	32	26 (±2.9)
Number of leaves	7	4 (±0.2)
Canopy area (%)	-	53 (±5.3)
Number of reproductive structures	-	2 (±0.9)
Stem biomass (mg)	80	79 (±35)
Total leaf biomass (mg)	160	34 (±9.4)
Reproductive structure biomass (mg)	35	5 (±1.9)
Total biomass (mg)	310	118 (±42)
Specific leaf area (cm^2/mg)	0.31	0.39 (±0.23)

Table 3 Average values (±standard error) for collective vegetation variables measured for assemblage containing *C. chordorrhiza* population. Figures represent single sample, August 1998; and four successive samples taken May-August, 1999.

Collective vegetation variable	Station 1		Station 7	
	1998	1999	1998	1999
Species richness (S) (m^2)	13	14 (±1.6)	7	7 (±1.3)
Stem density (m^2)	1033	1133 (±354)	1367	1333 (±155)
Canopy height overall (cm)	27	18 (±4.9)	20	19 (±4.4)
Litter cover (%)	50	1 (±1)	10	5 (±2.0)
Density reproductive structures (m^2)	-	425 (±183)	-	425 (±134)
Stem diameter (mm)	-	3.2 (±0.5)	-	2 (±0.4)
Biomass total (g/m^2)	131	403 (±39)	87	417 (±174)
Necromass total (g/m^2)	10	77 (±66)	86	173 (±173)
Standing crop total (g/m^2)	141	480 (±88)	173	590 (±166)

Table 4 (a) One way ANOVA between stations for mean (±se) values across Invertromie Fen transect. Figures represent four successive samples taken May-August, 1999 (1998 figures also shown for station 7, with *C. chordorrhiza*); *$\log_e$ values. Different superscript letters represent significant differences between groups (by Tukey tests). (b) Kruskal-Wallace test between stations for non-parametric variables, showing median values. Figures represent single sample for August 1998 (except †July and August); and four successive samples taken May-August, 1999.

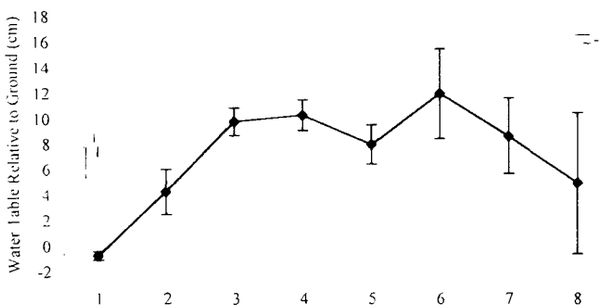
(a)

Variable	1	2	3	4	5	6	7		*P*
							1998	1999	
Water table level (cm)	-2 (±0.9)^{a}	4 (±0.9)^{ab}	11 (±0.7)^{b}	9 (±0.7)^{b}	13 (±2.0)^{b}	11 (±0.8)^{b}	8 (±5.0)†	4 (±0.4)^{ab}	<0.001
Maximum water table level (cm)*	1 (±0.7)^{a}	7 (±0.7)^{ab}	16 (±0)^{b}	13 (±0.4)^{b}	18 (±4.1)^{b}	13 (±0.7)^{b}	21 (±3.3)†	8 (±1.5)^{ab}	<0.002
Minimum water table level (cm)	-7 (±0.4)^{a}	4 (±1.5)^{ab}	12 (±0.8)^{b}	8 (±1.0)^{b}	11 (±4.0)^{b}	10 (±1.0)^{b}	4 (±1.0)†	3 (±0.8)^{ab}	<0.01
Interim fluctuation (cm)	8 (±0.8)	3 (±0.9)	4 (±0.9)	5 (±1.2)	7 (±1.7)	3 (±1.5)	18 (±2.3)†	5 (±0.7)	ns
Redox potential (mV)	-87 (±69)	-6 (±7)	+52 (±23)	-37 (±28)	-4 (±19)	-72 (±27)	-127	-53 (±6.3)	ns
pH	5.7 (±0.1)	5.7 (±0.1)	6.2 (±0.1)	6.1 (±0.1)	5.7 (±0.2)	5.9 (±0.1)	7.3	6.0 (±0.1)	ns
Conductivity (µS/cm)*	205 (±38)	198 (±38)	244 (±43)	195 (±37)	201 (±37)	355 (±74)	104	257 (±46)	ns
Mg (mg l^{-1})	0.98 (±0.90)^{a}	2.58 (±0.06)^{c}	1.95 (±0.04)^{bc}	2.41 (±0.11)^{c}	1.41 (±0.07)^{ab}	2.50 (±0.17)^{c}	2.27	2.44 (±0.16)†	<0.001
Ca (mg l^{-1})	3.93 (±0.14)^{a}	8.47 (±0.17)^{b}	9.46 (±0.17)^{b}	8.74 (±0.47)^{b}	5.13 (±0.15)^{a}	10.33 (±0.75)^{b}	5.61	9.82 (±0.31)^{b}	<0.001
Na (mg l^{-1})	4.80 (±0.44)^{a}	7.06 (±0.09)^{ab}	7.68 (±0.13)^{b}	7.52 (±0.19)^{b}	6.02 (±0.30)^{ab}	7.32 (±0.26)^{ab}	5.89	7.07 (±0.37)^{ab}	<0.02
Chloride (Cl) (mg l^{-1})	10.05 (±0.55)^{ab}	6.79 (±0.51)^{a}	14.45 (±0.85)^{b}	15.73 (±0.67)^{b}	10.89 (±0.93)^{ab}	12.53 (±0.84)^{ab}	-	9.86 (±0.59)^{ab}	<0.008

(b)

	1	2	3	4	5	6	7		*P*
							1998	1999	
Fe (mg l^{-1})	0.09	<0.01	<0.01	<0.01	0.01	<0.01	0.49†	<0.01	ns
Mn (mg l^{-1})	0.17	0.05	0.09	<0.01	0.03	<0.01	<0.01†	<0.01	ns
K (mg l^{-1})	0.73	0.40	1.17	0.98	1.12	0.97	2.43†	3.28	<0.03
Fluoride (F) (mg l^{-1})	<0.02	<0.02	<0.02	<0.02	<0.02	0.63	-	0.68	ns
Nitrate (NO_3) (mg l^{-1})	0.06	0.02	0.05	0.09	0.04	0.02	-	0.09	<0.05
Sulphate (SO_4^{2-}) (mg l^{-1})	0.41	0.42	0.47	2.05	1.07	0.61	-	1.08	<0.008

(a)



(b)

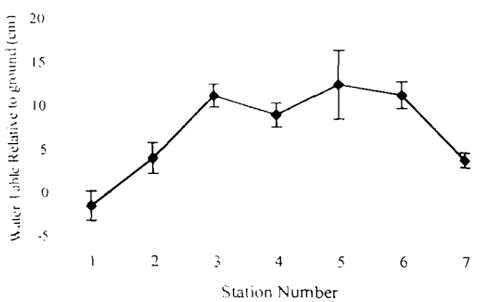


Figure 1 Average water table levels (±se) relative to ground surface across Tromie Fen transect (Insh Marshes) sample stations. (a) 1998 (July and August samples); (b) 1999 (May-August samples).