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THE ECOLOGY OF POOR FEN & WILLOW CARR ON GOSS MOOR NNR, CORNWALL

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THE ECOLOGY OF POOR FEN & WILLOW CARR ON GOSS MOOR NNR, CORNWALL.

by

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THE ECOLOGY OF POOR FEN AND WILLOW CARR ON GOSS MOOR NNR, CORNWALL.

ABSTRACT

Goss Moor NNR is a unique, rare and nationally-important wetland habitat in Mid-Cornwall. The majority of the habitats were created as a result of a long history of tin-stream mining, which ceased in the early 1900s. Phytosociological surveys of poor-fen and willow carr communities provide the first formal descriptions of the vegetation at this site. The poor-fen survey revealed twelve poor-fen vegetation types, which were distributed along a primary environmental gradient of organic matter depth, surface water height and bare substrate. Separation of the poor-fen communities by a moisture gradient was considered as spatial evidence for hydroseral succession, which begins with the colonisation of open-water pools created by tin excavations. The *Salix cinerea* ssp. *oleifolia* willow carr was divided by eight understorey communities, according to age, defined by reference to five sets of aerial photographs of Goss Moor taken over the last six decades. The average number of poor-fen species per unit area in the understorey generally decreased with age. This relationship was related to the increase in canopy cover and, therefore, shade. Willow was found to invade areas with the greatest amounts of accumulated organic material and a low water table. In the oldest and driest willow, oak saplings were found, indicating the beginning of secondary woodland. An architectural analysis of willow showed that useful age descriptors were the height of the first fork, the number of live secondary shoots, tree height and dbh, all of which generally increased with age.

Spatial successional patterns were characterised using the lattice-wombling technique in three large rectangles or 'tranomes'. Plant communities were associated with either abrupt or diffuse boundary types. Abrupt boundaries or ecotones were found between heath communities and densely vegetated tall-herb fen and species-poor willow carr wetland vegetation. Diffuse or ecocline transitions occurred between communities with subtle differences in their composition. Spatial relationships between swamp and poor-fen communities were taken as evidence for space-for-time successions, these patterns varied according to location and microtopography.

Investigations into the water regime showed water depth was governed by substrate heterogeneity. Homogeneous microtopography was associated with deep inundations and greatest amplitude in water depth, and most closely resembled rainfall fluctuations. The most complex microtopography resulted from the most intense tin-streaming activity. Therefore the anthropogenic history of Goss Moor plays an important role in governing the contemporary water regime and vegetation distribution. Of the wetland communities, rush pasture was the driest and poor-fen the wettest. The communities of open habitats were wetter than the willow communities. The youngest willow community was drier in the summer than the other five vegetation types studied, which was indicative of the conditions necessary for willow scrub colonisation to take place.

The N:P ratio revealed that nitrogen was the limiting nutrient in all of the wetland vegetation types suggesting an early stage of successional development. High water levels were thought to be responsible for the prevalence of N-limitation on Goss Moor, creating deoxygenated substrates and leading to the demise of nitrifying bacteria and thus a reduction in the rate of soil N mineralisation. Plant strategies were used to classify the species from a number of wetland communities ranging from open-water pools to willow carr, in order to apply them to Grime's triangular model. The ten communities were ordered into a logical successional sequence. However, the model needs to be modified to account for succession in the aquatic environment.

Based on the findings of this thesis, a number of suggestions were made for the effective management of the wetland habitats on Goss Moor. These include: evaluation of willow scrub before removal so those areas of vegetation subsequently opened-up can be monitored; and the creation of new ponds to encourage the growth of certain poor-fen communities, which are species-rich, but only account for a small area of the whole resource.

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ACKNOWLEDGEMENTS

AUTHOR'S DECLARATION

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

A program of advanced study was undertaken, which included the attendance of an EU Advanced Study Course on the 'Functional Analysis of Wetlands' at the University of Ghent, June, 1998.

Presentation of work at the British Ecological Society annual conference at the University of Leeds in December 1999, entitled 'Analysis and description of the poor-fen communities of Goss Moor NNR, Cornwall'.

Signed...................................

Date...17th August 2001.....

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Chapter One:
General introduction

1.1 INTRODUCTION

Goss Moor National Nature Reserve (NNR) was designated a Site of Special Scientific Interest (SSSI) in 1988, and is of great importance in Britain. The significance of the reserve becomes obvious after considering the criteria used to determine the conservation value of semi-natural habitats in Britain. The criteria take into account mainly the size, diversity, rarity, naturalness and typicalness of a site (Ratcliffe, 1977). Goss Moor NNR is the largest lowland heathland and wetland complex in the south-west of Britain. The site is considered rare due to the recentness of the habitats, which were created as a result of past anthropogenic activities, primarily tin-streaming. These activities were extensive and ceased less than a century ago, leaving a legacy of gravel banks and clay-lined pools. This unusual microtopography has provided a wealth of habitats that make an important contribution to the diversity of the vegetation. The majority of the site is dominated by mosaics of wetland habitats, which, although prevalent in the south-west, are unusual in Britain as a whole. The wetland vegetation communities include open water swamp, fen, bog and wet woodland and are currently undergoing hydroseral succession.

There is no detailed, formal description of the wetland vegetation communities that occur on Goss Moor NNR partly because the biological value of the site has only recently been recognised and, also because many areas are inaccessible due to the preponderance of fully and semi-vegetated deep pools and the extremely difficult topography.

Presently, management on the Moor is directed towards removing *Salix* spp. scrub and woodland, which has invaded the site over the last five decades, and most dramatically over the last two decades. On a countrywide scale, the colonisation of open herbaceous

wetland habitats by woodland is often actively discouraged, based on the assumption that scrub encroachment leads to loss of diversity and conservation value and changes the floristic composition of the site. As a consequence, the conservation value of these wet woodlands has frequently been overlooked (Latham *et al.*, 1999). The literature displays a dearth of information regarding wet woodland ecology, especially in comparison with that of dry woodland types. The contemporary nature and the relatively well recorded history of Goss Moor NNR offers an opportunity to examine some of the questions regarding scrub encroachment by studying the ecology and dynamics of chronosequences of *Salix* spp. invasion. In order to understand vegetation succession and the possible implications for management, the apparent association of scrub invasion in areas of particular seasonal water table changes requires investigation.

The character of Goss Moor NNR, complete with intricate mosaicing and unusual microtopography, provides a unique situation to study the ecology of wetland vegetation communities. Adoption of the ergodic hypothesis enables space-for-time successions to be characterised using the hydroseral habitats that range from open water to wet woodland. In the same areas, a number of novel techniques will be tested for their use and value in successional studies.

1.2 AIMS

The aims of this research are to:

- characterise the wetland vegetation communities and define the environmental conditions associated with them;

- elucidate the triggers to willow encroachment and determine the historic rates and locations of invasion;

- critically appraise the biological/conservation impact of willow;

- identify the community sequences occurring through hydroseral successions, the rates at which they occur and the geographic location of those seres;

- investigate lattice-wombling as a tool to ascertain small-scale space for time successions and community boundary descriptions;

- test the effectiveness of the 'N:P tool' and plant strategies in describing the seral stages of wetland successions;

- tackle some topical questions in wetland conservation management: i.e., identify areas of low diversity and conservation value which are appropriate for scrub removal; ascertain the effects of water drawdown on different vegetation communities; predict future vegetation development.

1.3 OUTLINE OF THE THESIS

This report begins with a description of the site itself, followed by a literature review of wetland ecology and vegetation succession. A summary of the objectives and outcomes can be seen overleaf in Figure 1.1.

Chapter One
'General introduction'

Chapter Two
'An introduction to the natural environment of Goss Moor NNR, wetland ecology and succession'

Goss Moor site description — *A detailed review of wetlands* — *Plant succession*

Chapter Three
'A preliminary survey of the poor-fen communities on Goss Moor'

Classification of the poor-fen communities through detailed phytosociological survey and environmental factors

Chapter Four
'A baseline survey of the willow carr communities on Goss Moor'

Determine chronosequences of willow from image analysis of 50 years of aerial photographs *Describe plant communities and their associated environmental variables*

Selection of habitats suitable for further investigation of the ecological processes on Goss Moor

Creation of three large rectangles or 'tranomes' with distinct substrate heterogeneities for detailed investigations of ecological processes

Chapter Five
'Spatial dynamics of the vegetation communities on Goss Moor NNR.'

Use of the lattice-wombling technique within three selected tranomes of different substrate heterogeneity to identify patterns of hydroseral succession

Chapter Six
'Water regimes associated with the main wetland vegetation types on Goss Moor'

Installation of Water Monitoring Devices to monitor water movements within the three main open wetland habitats and three ages of willow carr

Chapter Seven
'An exploratory investigation of the use of the N:P tool & plant strategies to identify the successional patterns of wetland communities on Goss Moor'

Establish which nutrient limits the wetland vegetation *C-S-R strategies*

Chapter Eight
'General Discussion'

Synthesis of thesis findings *Implications of thesis findings for effective management and conservation of the wetland habitats on Goss Moor*

Figure 1.1 Outline of the thesis.

Chapter Two: An introduction to the natural environment of Goss Moor NNR, wetland ecology and succession

2.1 GOSS MOOR SITE DESCRIPTION

2.1.1 INTRODUCTION

Goss Moor National Nature Reserve (NNR) contains the largest lowland heath and wetland composite in the south-west of England. On the basis of this unique assemblage of plant communities, the site is of national importance (W. Fojt, pers. comm.). The spatial variation of plant communities is testimony to the different substrates, water regimes and hydrochemistry of the Moor, which play a crucial role in maintaining the diversity of vegetation (Dale *et al.*, 1997). The great majority of this heterogeneity arose as a result of the human activity on Goss Moor. Sporadic excavations for tin-bearing deposits and gravel aggregate have occurred extensively in the past, leaving raised banks of gravel waste, which support gorse and heath communities amidst the matrix of poor-fen vegetation in waterlogged hollows between. To understand the vegetation dynamics occurring on Goss Moor, it is necessary to elucidate the factors that both created these plant communities and still maintain them today. This section provides an introduction to the Goss Moor site and reviews the landscape history in order to provide insight into how the landscape and vegetation have been affected by hundreds of years of human activity.

2.1.2 GOSS MOOR SITE DETAILS

2.1.2.1 Location

Goss Moor NNR is situated in mid-Cornwall (NGR SW 950600), between St Austell and Newquay, approximately 25 km south-west of Bodmin Moor (Figure 2.1). The site is positioned immediately south of the A30 trunk road and covers an area of 481 hectares (Figure 2.2). Goss Moor and the adjacent Tregoss Moor, which lies to the east of the site, are part of the Tregothnan estate owned by Lord Falmouth. The Moors have been managed or nature conservation by English Nature since 1992. Prior to this, formalised management as almost non-existent.

Figure 2.1 The location of Goss Moor, NNR in Mid-Cornwall in the south-west of Britain

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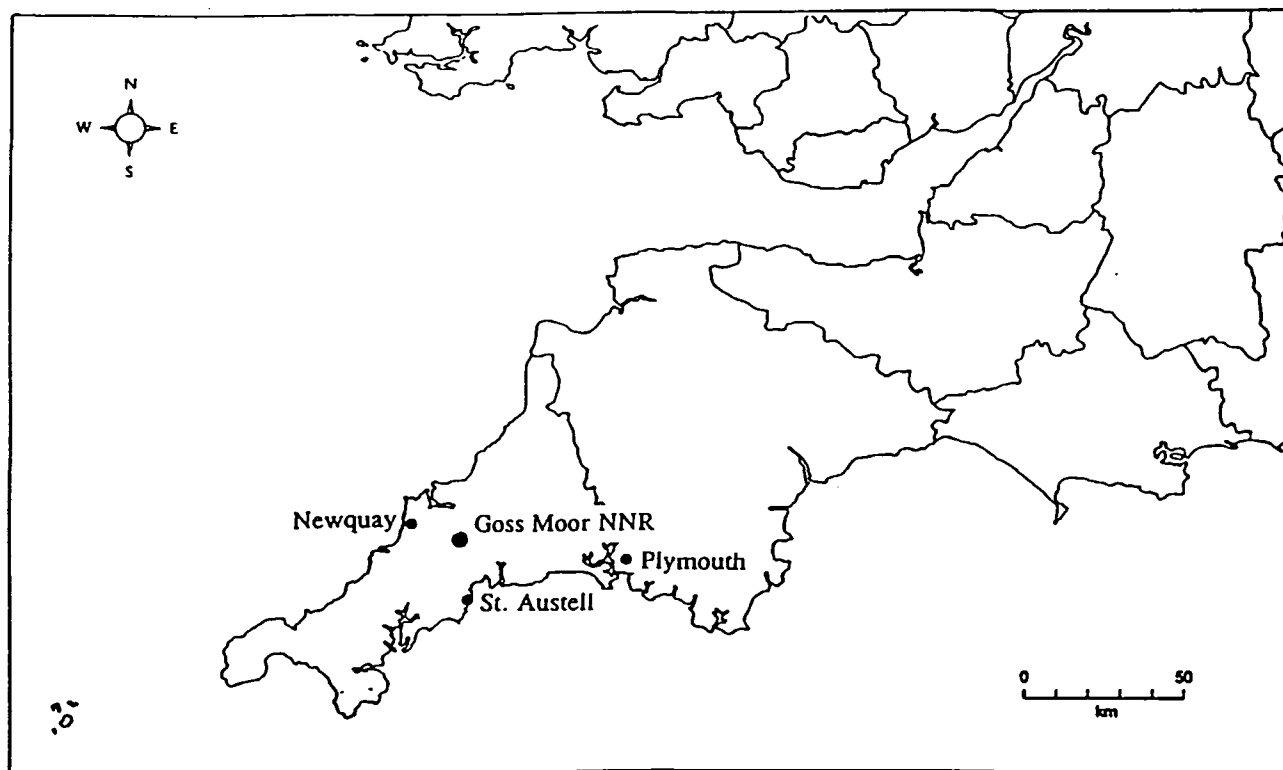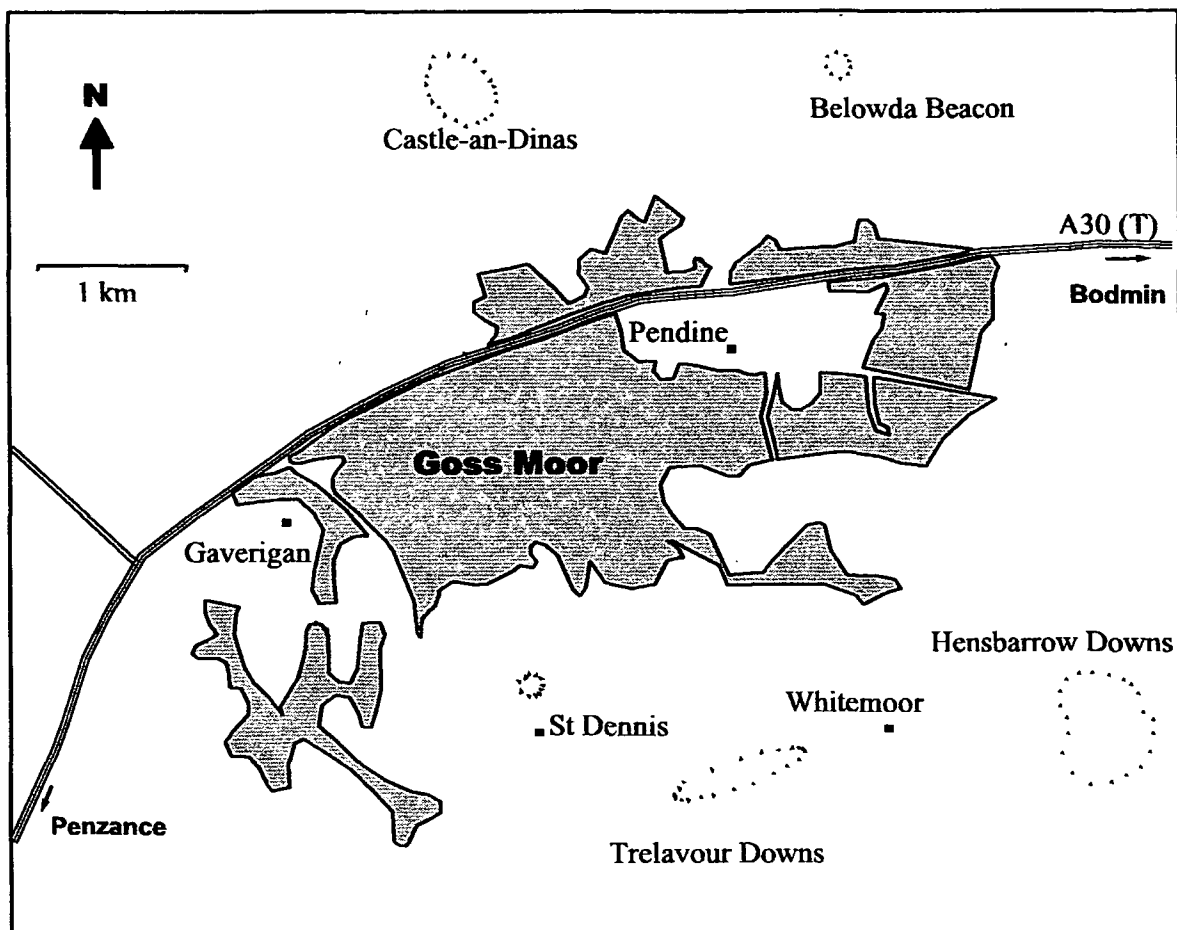
Figure 2.2 A map showing Goss Moor NNR in relation to the other areas incorporated into the SSSI boundary (shaded grey), the A30 trunk road (double line) and the main hills in the vicinity (dotted lines).

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A small number of buildings stand on the Moor (Figure 2.3), which are relics of human activities. The blockhouse building in the centre of the Moor (Figure 2.4) was used to grade the sand and gravel removed for road aggregate around the time of the second World War. The map showing Goss Moor in 1900 (Figure 2.5) shows there was a small engine mill at Wheal Penrose in the south of the moor. West of the moor at Gaverigan lies Indian Queens Power Ltd, an oil-fired power station (Figure 2.2).

2.1.2.2 The geology of Goss Moor

Goss Moor is a broad flat, basin shaped valley situated between the 122 m and 133 m topographical contours within the partly uncapped St Austell granite. South of the moor the exposed granite rises steeply to 312 m at Hensbarrow Downs, while the northern granite is exposed as two prominent cusps; Belowda Beacon, 227 m and Castle-An-Dinas, 205 m (Figure 2.2.). Goss Moor and its catchment lie in the north-west corner of Late Carboniferous St. Austell granite, which dips below the surface of the Moor, 600-700 m at its deepest (Camm, 1981). The St Austell granite displays evidence of extensive metamorphisms from the original adamellitic composition of quartz, perthitic, orthoclase, plagioclase and biotite assemblage (Penhallurick, 1986). The granite ridges are infilled with metasediments of Lower Devonian age. The metasediments are of the Meadfoot Series, which are a rhythmic sequence of slates and inter-laminated silt stones, sandstones and rare but persistent limestones (Barton, 1969). Boase (1832) described this bedrock as grey slate traversed by small quartz and tourmaline veins and often with decomposed clay. The fluvials overly the pelite (clay-like) bedrock or more often a disturbed kaolinised pelite (china-clay), a Pleistocene periglacial form (Camm, 1981).

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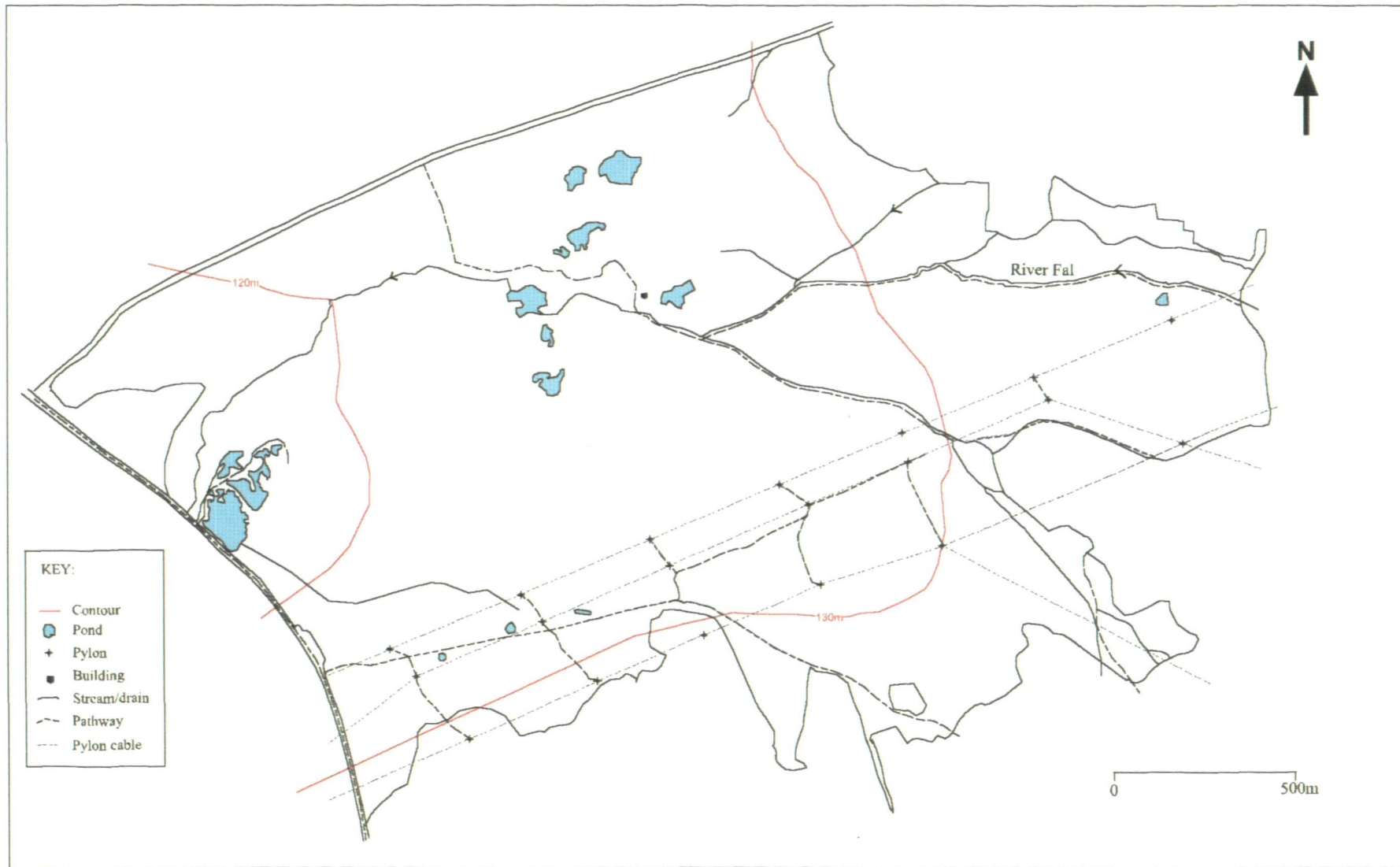
Figure 2.3. Map showing the main physical and landscape features on Goss Moor NNR in 1999.

KEY:

— Contour
⬤ Pond
+ Pylon
▪ Building
— Stream/drain
--- Pathway
--- Pylon cable

River Fal

120m
130m

N

0   500m
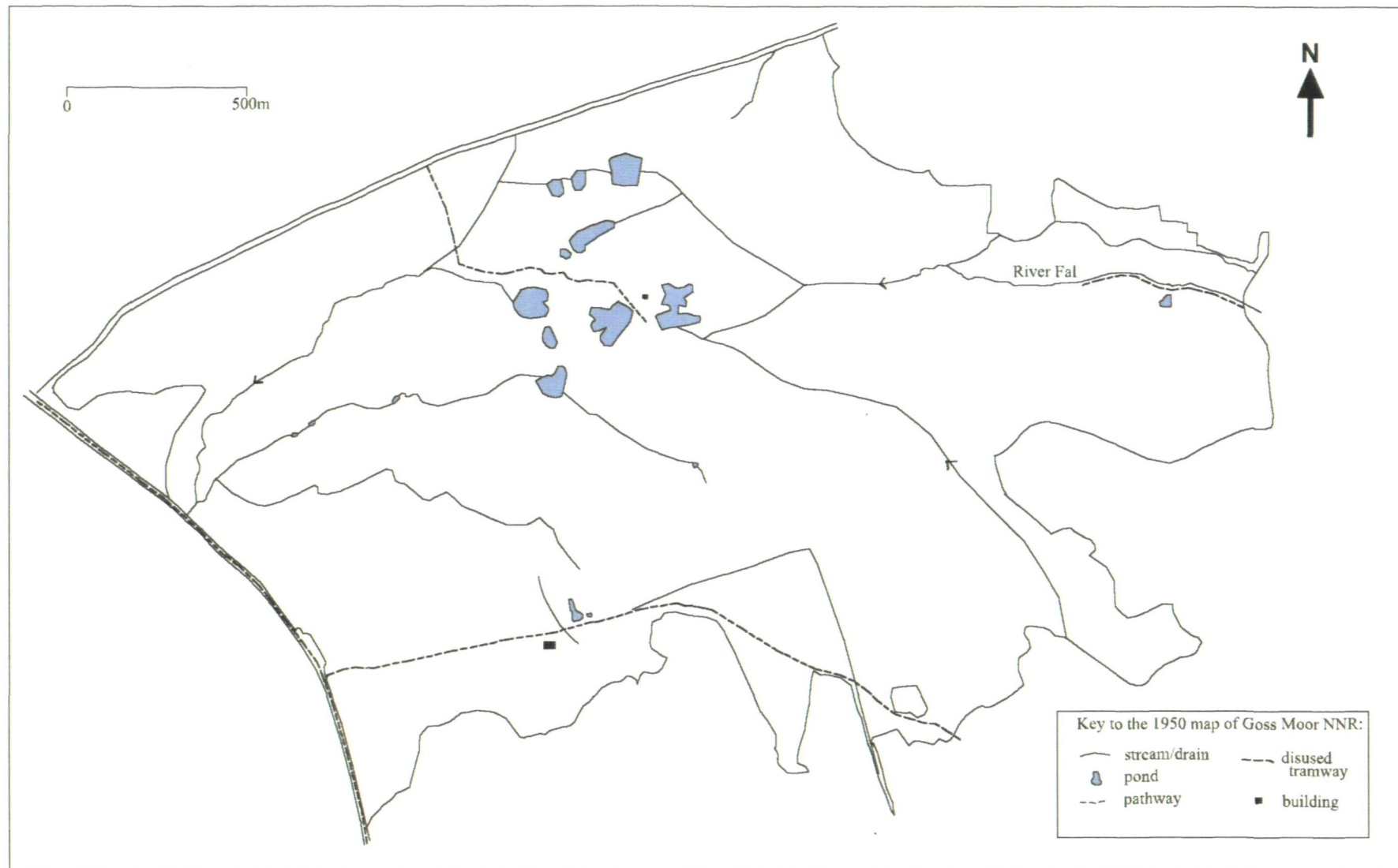
Figure 2.4. Map showing the main physical and landscape features on Goss Moor NNR in 1950.

N

0   500m

River Fal

Key to the 1950 map of Goss Moor NNR:

—— stream/drain   - - - disused
                              tramway
△ pond

- - - pathway   ■ building

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Key to streamworks ⁂
1. Hopewell
2. Lower Three Johns
3. Rock Work
4. Britton
5. Gazen
6. Chance
7. True and Honest
8. Marsh Work
9. Fair Play
10. Bold Venture
11. Good Luck
12. Virgin
13. Gun Deep
14. Quibble
15. Penrose
16. Wheal Penrose tin mine
17. Glasson Pool

River Fal

Tramway

Key to the 1900 map of Goss Moor NNR:

—— stream/drain	—— railway
🝙 pond	▪ building
- - - pathway	⁂ streamworks

Figure 2.5 Map showing the main physical and landscape features on Goss Moor NNR in 1900.

Tin and the landscape history of Goss Moor

The St Austell granite forms part of a large body of granite or 'batholith' 200 km long, emplaced between 270 and 290 million years ago into intensely folded 'killas' (mostly clay slates) of Devonian and Carboniferous age (Collins, 1887). All granites were formerly covered in killas (Penhallurick, 1986). When the granite was formed, the slow cooling upper crust of granite and killas were faulted and fissured, allowing the passage of mineral-rich fluids to fill the fissures, thus forming swarms of mineral veins. Each of these minerals crystallised or solidify within certain limits of temperature and pressure, and those which solidified at the highest temperature, notably tin and wolfram, crystallised first in the veins, which is why tin and wolfram are found close to granite (Penhallurick, 1986). This explanation is somewhat oversimplified, as mineralisation took place over a long period with several important resurgences of activity up to 230 million years ago. Previously mineralised lodes often reopened to receive a suite of minerals to suit those conditions. For this reason, a lode (vein) may contain tin and copper at the same level (Penhallurick, 1986).

Like many moorlands in south-west England, Goss Moor contains wave cut platform relics formed during the 137-m marine incursion of the Tertiary, Pliocene and late Miocene sea (Camm, 1981). Consequently, shallow stanniferous fluvial sections cover approximately 17 % of the Moor. These fluvials are complex intercalations of sand, gravel, silt, clay and peat that shred natural deposits of tin enrichment (Camm, 1981). The unusual grains of orange and red cassiterites found at Gaverigan, at the west of the site (Figure 2.2), can only be accounted for by longshore drift during the Pliocene submergence. Such longshore drift would also account for the very rounded cassiterite pebbles found throughout the Moor, although others on the site are not rounded, indicating the non-marine Pleistocene period

Cross-section:

surface erosion

debris

tin lode

eluvial

material is mechanically
worn and transported by gravity

alluvial

material is transported
and worn by water

Plan:

flow

erosion

deposition

erosion

15
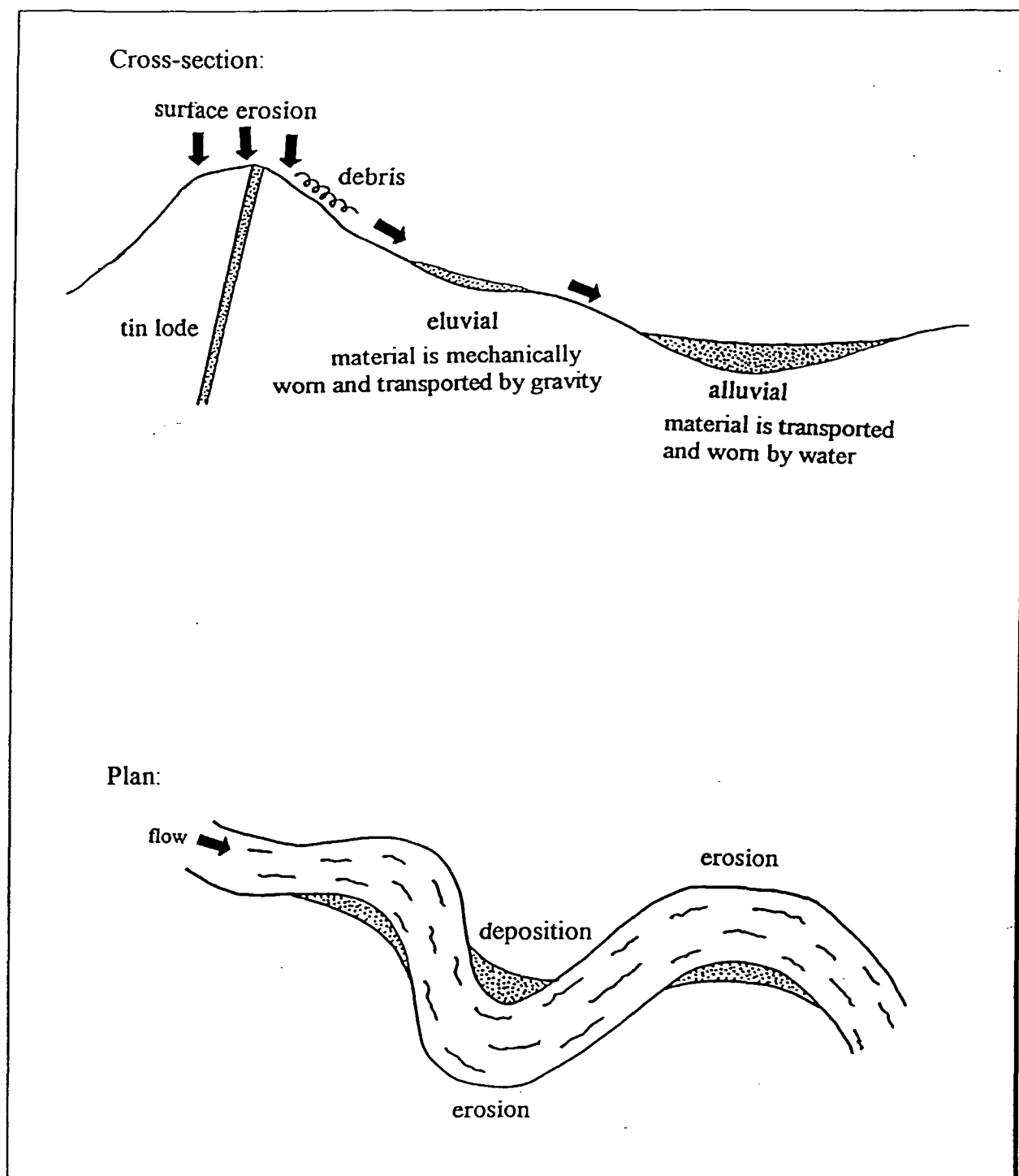
(Penhallurick, 1986). The Pleistocene environment scoured out huge depths of lighter material allowing heavy metals, including cassiterite to later accumulate above the bedrock.

The alluvial tin deposits or tin ground formed principally during the last period of glaciation (100,000-130,000 years BP), although there are indications of older 'palaeo-cassiterite placers' from periods of less intense erosion (Penhallurick, 1986). In the process of surface erosion, any exposed lode of tin contained in the granite will also be eroded (Figure 2.6). In the glacial period, the ice sheets reached their maximum extent at the Bristol Channel and the northern tip of the Isles of Scilly. Under these arctic conditions, deep permafrost predominated and glaciers scoured the underlying rock. The arrival of the summer thaws produced cascading melt-waters, rich with erosional debris, which flooded into the valleys to a sea level estimated to have been several hundred metres higher than it is today. Only the heaviest material, including tinstone, could resist the force of the water enough to allow it to come to rest on the shallow valley floor of Goss Moor.

During the Allerød interstatial 12,000 to 10,800 BP, in the Late Palaeolithic period, oak *Quercus* and alder *Alnus* are thought to have grown on top of the tin ground in the valleys (Penhallurick, 1986). If this is correct, the upper incomplete tin bed, which is of little economic value, may have formed during the succeeding cold 'snap', which lasted for less than a millennium. From 10,000 BP, the climate warmed rapidly with a simultaneous rise in sea level (the Flandrian transgression), which caused the drowning of river valleys and the deposition of thick sediments, both marine and fluvial. The major period of deposition is considered to have been between 9,000 and 6,000 BP (Penhallurick, 1986). As the climate ameliorated, extensive peat covered the alluvium. Pollen dating has shown counts

of tree species such as *Alnus*, *Betula*, *Pinus*, *Quercus* and *Fraxinus*, and also *Calluna* and *Sphagnum* around 5,000-7,000 BP (Camm, 1981). This productive stage was followed by a second stronger fluvial stage of the Atlantic Period, which caused massive run-off and large quantities of weakly stanniferous alluvium to develop over most of the Moor (Camm, 1981). The majority of the alluvium accumulated in the Flandrian III wet Atlantic Stage.

Present sea level was attained during the Neolithic period between 6,000 and 4,000 BP (Penhallurick, 1986). This meant the sediments that accumulated in the lower parts of the Goss Moor valley would have reached their present depth by the beginning of the Bronze Age and the earliest activities of tin streamers. According to Taylor (1980; cited in Penhallurick, 1986), there was further deposition by rivers during the Neolithic period, especially following extensive forest clearance, resulting in greater erosion and run-off. The Bronze Age tinners (2,750 to 4,400 BP) thus found the tin ground was buried to a considerable depth. Finally, an added layer of detritus was deposited rapidly in recent centuries as a result of mining and china-clay extraction (Penhallurick, 1986).

Alluvial tin mining on Goss Moor

Cassiterite is a stable oxide unaffected in the lode or vein of metal ore by secondary chemical weathering. The most valuable metal is found in many lodes above the water table, even though it may be accompanied by ubiquitous iron oxides. Iron sulphide (pyrite) and iron-rich sulphides such as arsenopyrite and chalcopyrite oxidise to produce an iron-rich 'capping' known to the Cornish miner as 'iron hat' (Penhallurick, 1986). The presence of these minerals can be seen as a rusty orange colouring in water running in streams across the Moor and in pools undergoing surface water infiltration (C.V. Smale, pers. comm.).

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Three types of tinstone were identified on Goss Moor (Collins, 1909): fine grains, which are clean and of high quality; small pebbles of equal or higher quality; and fragments of ore and veinstone that requires crushing to obtain the tin. The thickness of the tin deposits ranged from 0.5 m to 10 m. The gravely deposits contain little tin, the bulk being in the shelf depressions (Dines, 1956).

Tin-streaming was very widespread in Cornwall, due to the prominence of granite. The large alluvial tract of Goss and Tregoss Moor is an area formally rich in alluvial cassiterite, for which it was streamed for many centuries (Dines, 1956). The first mining on Goss Moor was documented in 1490, but tin dealing records trace back to 1197, in Roche two kilometres east of the reserve (Dines, 1956). In prehistory, surviving evidence suggests that Goss and Tregoss Moors contained the most important moorland tin streams in the country (Penhallurick, 1986). For this reason, most of the alluvium was turned over at least once if not several times by the 18th century, later operations sometimes revealing these remnants. Tin streaming and mining activities occurred over most of the Moor as is evident from the 1900 map in Figure 2.5.

Evidence from the valley alluvials indicates that prehistoric workings must have been unsystematic by recent standards of working, probably due to technical reasons such as inaccessibility caused by large marshy tracts and the highly variable shape of the landscape (Penhallurick, 1986). However, many small tin streamworks were industriously wrought by speculative workmen, either on ancient detritus or on material imperfectly gleaned by their predecessors. The works were drained either by open cuttings, by hand pumps or by small lifts worked by water wheels, which were often less than two metres in diameter (Henwood, 1873).

Streamworks are the working areas and waste dumps of deposits in tin-bearing material. Streaming refers to the washing of the ore to remove impurities following extraction from the ground. The word 'stream' derives from Cornish dialect meaning 'to wash' (Penhallurick, 1986). Alluvial streamworks remove the ore from the alluvium using water from a nearby river. For optimum tin exploitation, the gradient of the water source was of paramount importance. If the natural topography of the area was unable to provide an adequate gradient, as on Goss Moor, it was created by the construction of a complex system of leats and reservoirs (Austin et al., 1989).

Leats are water channels less than one metre wide with a downslope bank, forming miniature waterfalls, often hundreds of metres long. These contributed to the extensive alteration of the stream tributaries and drainage patterns on Goss Moor. The excess impurities and overburden consisted of clay, sand and stent (the waste of former workings) (Collins, 1909), which when dumped also modified the hydrology and microtopography. These resultant earthworks have been classified into four types, two of which are found on Goss Moor: cuestaworks and parallelworks (Austin et al., 1989).

Cuestaworks are a series of mounds each with a 'cuesta' shape cross section, with steepside (scarp) facing downstream and a more gentle side upstream. A shallow channel usually separates the banks. Several short series of cuestaworks are evident on Goss Moor, but about 25 can be seen in Minzies Downs, Bodmin Moor, suggesting that a more systematic approach was adopted here. The cuestaworks are created by wheelbarrows, the gentle slope allows the wheelbarrow to be pushed up to the top of the dump. The end is the highest point, where the waste is deposited (Austin et al., 1989).

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Parallelworks are sharp sided banks of spoil with a symmetrical profile laid out in parallel lines to a height of 0.2-3 m. The shape of these earthworks is created by the use of a 'Cornish shovel'. The extraction technique is similar to that of the cuesta, and is also systematic, involving washing and dressing upstream followed by dumping the waste downstream onto the recently worked areas. Parallelworks are thought to be the resultant shape for finer, shallower overburden, whereas the wheelbarrows would have proved necessary for dumping the coarse material left over when stripping down to 'tin ground', thus creating cuestaworks (Austin et al., 1989).

Tin mining on Goss Moor

Wheal Penrose was the only underground tin mine on Goss Moor (Figure 2.5). The mine opened in 1846 and employed 14 men who directed the mine eastwards along Carne's Lode and southwards to cross-cut a counter lode (Collins, 1909). Miners dug 9 m in depth and 185 m in width to collect 100,000 sacks of tin material (Jenkin, 1964). The stamping mill at the Penrose tin mine contained a small engine mill to crush the tin ore (Dines, 1956), the building of which remained on the Moor until 1975. The mine was abandoned after a great accession of water drowned one of the workers in 1877 (Dines, 1956).

Mechanised alluvial mining

In the early 1900s, tin streaming ceased to be an economic proposition (Penhallurick, 1986). To overcome this, modern and more efficient methods of tin removal were adopted. Goss Moor Tin Alluvials Ltd, a reconstruction of Goss Moor Ltd, took over the property of the Goss Moor Alluvial Syndicate (Dines, 1956) around the great Glasson Pool (Figure 2.5). The new plant was erected on a barge. A 'Tasmanian suction dredge' washed the

working face and the detritus was collected with a pump located in a sump. Between 1910 and 1913, the company recovered 115 tonnes of black tin from Goss Moor (Dines, 1956). However, this was not enough to profit and the plant was closed in 1914. In 1925, another tin dredge was erected but by March 1926 operations were suspended permanently due to a low recovery rate (Dines, 1956). In 1930, all tinworks on Goss Moor had ceased production (Jenkin, 1964). Nevertheless, intrigue was once again raised in 1978 as Goss Moor was still recognised as a potential tin target. All speculation was finally put to rest following a thorough report from Billiton Exploration (U.K.) Ltd, written by Camm (1981), who concluded that tin extraction was no longer a viable concern, as past operations had liberated the majority of cassiterite.

2.1.2.3 Goss Moor soils

The soils of Goss Moor are of the Laployd association (Edmunds *et al.*, 1969), which are permeable, gritty, coarse loamy upland soils, derived from acidic igneous rocks and some slates. Much of the soil on Goss Moor is waterlogged for most of the year (Findlay *et al.*, 1984). The top soil is humose or peaty, over mottled sandy silt loam, which becomes very stony at a shallow depth (Findlay *et al.*, 1984). There is occasional bare rock (Edmunds *et al.*, 1969).

2.1.2.4 Climate

The south-west of England is characterised by high rainfall and strong, predominately westerly winds with local variations imposed by altitude and exposure. Maritime conditions prevail throughout Cornwall and the region therefore exhibits milder winters and cooler summers compared to the rest of the British Isles. Goss Moor lies equidistant (11 km) from the north and south coasts and the annual rainfall at Goss Moor for the last 5

years between 1995 and 2000 can be seen in Table 2.1. The westerly winds are mostly responsible for the average annual rainfall of 4.03 mm. The mean annual temperature range is between 8 and 10 °C and annual windspeeds are high and between 5-7 m/sec. The driest months are May to July (daily average 2.5 mm) and the wettest months November to April (daily average 4.9 mm).

Table 2.1: Rainfall Data derived from Roche Weather Station between 1995-2000, supplied by the Environmental Agency.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC	annual daily mean
Mean daily Rainfall (mm)	5.46	4.65	2.93	3.52	2.33	3.26	1.86	3.4	3.24	4.66	7.31	5.78	4.03
Highest Figure (mm)	38.7	59.4	30.0	24.6	28.6	23.1	30.8	35.3	34.8	32.4	45.0	53.1	36.32
Total number of dry days in 5 years	49	36	45	51	63	53	62	63	53	42	26	33	

2.1.2.5 Hydrology

The hydrology of the site is very complex. The dendritic drainage pattern of the reserve has altered dramatically due to centuries of tin streaming, as is apparent from Figures 2.3-2.5. The whole Moor valley represents a marked flattening in hydraulic gradient and is therefore an ideal site for fluvial debouchment (Camm, 1981). Water enters Goss Moor NNR via a number of possible routes:

(i)   flood water from the Fal which seeps laterally during autumn and winter, then recedes during late spring and summer;

(ii)   rain water entering directly;

(iii)   water from the catchment to the south, a small amount of which drains through the mire and enters the Fal in the western section of the reserve;

(iv)   groundwater, which rises through the substrate where permeability permits (Dale *et al.*, 1997).

A recent study on the hydrology by the Geographical Sciences Department of the University of Plymouth emphasised the importance of surface water rather than groundwater in terms of water table fluctuation (Ishemo, 2000). Large proportions of the Moor remain partly or wholly submerged for the majority of the year, and drying out only in the summer months, if at all. During heavy rain, most of the Moor becomes totally inaccessible on foot.

The headwaters of the river Fal run from the eastern tip of the Moor at Tregoss Bridge westwards through the northern sector of Goss Moor, to the western outlet (Figure 2.3). Due to drainage problems in fields at Pendine (Figure 2.2), the original meandering course of the river was straightened in the early 1970s at the eastern end of the reserve. However, this canalisation is believed to be drawing water away from the surrounding SSSI, with detrimental effects on the composition of the vegetation. In an attempt to reverse these changes, a series of weirs were constructed in 1996 as part of a rehabilitation scheme.

The access track and public footpath (Figure 2.3) that is situated to the south of the Moor effectively acts as a dyke. The track is raised on an aggregate bank, as are the 18 pylons which elevate three lines of power cables. These banks impede the drainage at the south-east of the site from where water flows to the centre of the Moor. Water movement is stifled south of the track and in the wettest periods water seeps on to the adjacent farmland, flooding the fields.

Goss Moor contains a number of deep-sided ponds (Figure 2.3). These occur at the western side of the Moor, where the River Fal exits the site (Plate 2.1), and in the centre (Plate 2.2).

Plate 2.1 One of the ponds west of the moor, adjacent to the main access path. This pond was also present on the 1900 map in Figure 2.5.

Plate 2.2 One of the ponds in the centre of Goss Moor, created in the 1920s as a result of gravel removal.

The central ponds are water-filled pits, which remain after gravel and sand was extracted over a period of 20 years until 1960. Figures 2.3-2.5 show how the ponds have altered dramatically in size and shape over the last century.

2.1.2.6 Vegetation on Goss Moor NNR

The vegetation on Goss Moor is composed of a mosaic of different habitats, which are mostly derived from previous tin-streaming and mining activities. Tin-streaming has produced a landscape of small dry hummocks interspersed between flat, often extensive wet areas: 'dry hummock and wet hollows' (Penhallurick, 1986) (Plate 2.3). During the peak period of tin-streaming on Goss Moor, between 1820 and 1840, there were some accounts of the appearance of the Moor. In an 1840 description in Henwood (1873), the area was said to be:

'...exhibiting an almost countless succession of low stony hillocks and deep weedy pools; the abandoned scenes of earlier exploitation'.

This statement is reinforced by an unnamed source in 1858 (Dines, 1956):

'...a once fine plain of 3,000 acres (of which) the overburden had not been restored for agricultural purposes...and only a horrid waste of refuse pools of stagnant water, dangerous holes and swamps inhabited only by a few wild horses, goats and flocks of geese'.

More recent streaming and dredging has produced considerably deeper workings, which are evident as ponds of enormous size and depth at the western edge and south of the Moor (Figure 2.3 and 2.4). The deep, relatively recent pools north of the track and south of the great Glasson pool are approximately 7 m in depth and fringed by *Phragmites australis* (Cav.) Trin. Ex Steud. reeds. This species must have been prevalent in early times, as the word Goss is local dialect for this reed (Penhallurick, 1986).

Plate 2.3 View of Goss Moor showing the 'dry hummock and wet hollow' microtopography and Indian Queen Power Station at St Dennis in the background.

Plate 2.4 Mosaics of poor-fen, willow carr and heath, with the St Dennis peak power facility in the background.

In 1883, Martin described the landscape of Goss Moor as a series of scarcely vegetated mounds that varied in height from 1-5 m with corresponding pits. Some mounds were in chains and some isolated. Today, these more freely draining mounds and the higher ground surrounding the valley of Goss Moor are vegetated by *Ulex gallii-Agrostis curtisii* dry heath communities (NVC type H4, Rodwell, 1991b), and patches of *Calluna vulgaris*.

In the north of the reserve above the A30, the wetter ground displays a series of wet heath (*Schoenus nigricans-Narthecium ossifragum* M14) and mire communities of *Molinia caerulea* (M25), which grade into *Iris filipendula-Juncus acutiflorus* (M28) poor-fen communities, intermixed with extensive M23 *Juncus acutiflorus-Galium palustre* rush pasture (Rodwell, 1991b).

The research in this thesis concentrates mostly on the vegetation mosaics south of the A30 in the wettest areas of Goss Moor (Plate 2.4), which are inhabited by variants of S27 *Carex rostrata-Potentilla palustris* swamp (Rodwell, 1995) and dominated by a patchwork of *Salix cinerea-Galium palustre* fen carr (NVC type W1, Rodwell, 1991a), which has invaded the wetland over the past 50 years. The swamp vegetation occupies the lowest point of the valley basin growing in depressions created by tin-streaming. The shallow or more aged depressions, which are isolated from lateral water flow become increasingly acidic, allowing *Sphagnum* to grow and accumulate, which eventually become ombrotrophic and form peat. At present, there is very little peat on Goss Moor.

2.1.3 MANAGEMENT

Throughout the mining periods and up until English Nature took over the management of Goss Moor in 1992, the accessible areas were treated as common land. The common land was over run by wild ponies, goats and flocks of geese less than a century ago (Dines,

1956). Up until 20 years ago, local farmers grazed their bullocks on the site in spring and summer. However, today, only a small herd from Pendine frequents the eastern side of the Moor during the summer. Since 1996 English Nature have been involved in an extensive program of willow scrub removal.

In order to understand the wetland ecology of Goss Moor in the context of British wetlands as a whole, the following section provides a review of the literature regarding this subject.

2.2 INTRODUCTION TO WETLAND ECOLOGY

2.2.1 INTRODUCTION TO WETLANDS

Wetlands are defined as areas of land permanently waterlogged with a water table close to the ground surface for much of the year, or a substrate that is inundated periodically (Wheeler, 1995); they occupy the transitional zone between deep aquatic and dry land ecosystems (Maltby, 1991). Globally, wetlands cover 4 to 6 % of the earth's land surface, or approximately 5.6 million km^2 (Mitsch *et al.*, 1994). Wetlands are found in every climate except the Antarctic (Mitsch *et al.*, 1994) and in a number of different situations: (i) in humid cool regions as bogs, fens and tundra; (ii) along rivers and streams as riparian wetlands; (iii) as seasonally flooded forests and backswamps; (iv) in river deltas; (v) along temperate subtropical, and tropical coastlines as salt marshes, mudflats, and mangrove swamps; and (vi) in arid regions as inland saltflats, seasonal playas and vernal pools (Mitsch *et al.*, 1994).

Wetlands support distinctive and characteristic vegetation types such as marsh grass, rushes, sedges, reeds and willow. In the past, wetlands were perceived as valueless and as a result, have been extensively exploited. Today their intrinsic value is increasingly

recognised: wetlands provide society with valuable environmental and ecological benefits such as flood control, water quality improvement, food chain support, wildlife habitat, a natural carbon sink, nutrient and toxicant retention, and places of recreation (Mitsch et al., 1994). In comparison with other ecosystems, wetlands have numerous functions (Whittaker & Likens, 1973), exhibiting relatively high metabolic activity and productivity. This is illustrated by the vast standing stock rates of animals that wetlands can support and indicates an important landscape role in nutrient recycling and storage, plant and animal harvest, and species conservation (Mitsch et al., 1994).

The global ecological importance of wetlands is exemplified by peatlands, which occupy a mere 3 % of the world's land surface and yet store almost 20 % of the globe's total soil carbon pool (Maltby, 1991). Modifications to this carbon sink could dramatically alter concentrations of carbon dioxide in the atmosphere (Gorham, 1991; Mitsch & Wu, 1994). Wetlands also release hydrogen sulphide, methane (Cicerone & Oremland, 1988) and dinitrogen oxide under naturally waterlogged conditions. Methane and dinitrogen oxide are important greenhouse gases that absorb infrared energy. Research by Devol et al. (1994) estimated that the Amazon floodplain, a tropical wetland system, may be contributing 5 to 10 % of the total global methane emissions. If these atmospheric gases were to alter in concentration, the earth's radiation balance and the global climate may be influenced. There is concern that the area of wetlands drained for agriculture will affect the balance of carbon movement between wetlands and the atmosphere. Oxidation of previously accumulated organic carbon is also accelerated by peat extraction for fuel and horticultural use. These global-scale phenomena have highlighted the importance of understanding the dynamics of the wetland resource.

To quantify and understand the global wetland ecosystem function, ecologists are seeking a universally applicable and scientifically defensible procedure (Mitsch *et al.*, 1994). Verhoeven *et al.* (1994) initiated the process with a multi-year study in The Netherlands and the USA in search of measurable and comparable parameters. They found that the data from both countries displayed remarkable similarities in the nitrogen (N) cycle and established the value of easily measured variables such as N/P (phosphorus) ratios and pH for the prediction of wetland functions. Other indicators have been identified to estimate processes such as plant production, nutrient uptake, and nutrient mineralisation (Van Oorschot, 1994). Maltby *et al.* (1994) also used a functional approach to evaluate European river margin wetlands, based on the characterisation of distinctive ecosystem/landscape complexes or hydrogeomorphic units (HGMUs). The functional assessment of HGMUs evaluates key wetland processes such as groundwater recharge and discharge, surface water generation and plants survival strategies. The ultimate aim behind the development of functional assessment procedures is to establish functional analysis thresholds to predict factors such as resilience to disturbance using dynamic models and empirical investigations (Maltby *et al.*, 1996).

Of the various types of wetland vegetation that occur globally, this work concentrates on fens and bogs in Britain. Further discussion of wetland classification can be found in section 2.2.5.

2.2.2 THE STATUS OF BRITISH FENS AND BOGS

Goss Moor NNR represents an important wetland resource, which covers an area of 481 hectares (ha) and it is the largest wetland poor-fen and bog complex in the south-west of England. Both fen and bog vegetation types show a marked distribution pattern within the U.K. To understand the value of Goss Moor, it is necessary to consider the biogeography

of these two wetland types and the dramatic change in status that they have suffered in contemporary times.

In general, fens are common in Britain although they are usually small, isolated systems (Wheeler & Shaw, 1995), either by virtue of their intrinsic character or because of partial reclamation (Fojt, 1995). Nevertheless, there are some important exceptions such as the rich-fens of Broadland, England, which cover more than 3000 ha and the poor-fens of the Irish Marshes, Scotland, which cover approximately 1177 ha (Fojt, 1995). Rich-fens are mainly analogous to areas of base-rich substrata such as the chalk landscapes of southern and eastern England and the limestones of northern England and North Wales. Poor-fens are found more frequently in the north and west of Britain. Basin fens are also more frequently found in the north and west of Britain, although often small at less than 10 ha in size (Fojt, 1995). All fen types are uncommon in the south-west of Britain (Wheeler, 1984) due to the geology.

The distribution of bog vegetation is also disjunct. Raised bogs are scattered throughout Britain, although rare in the south-west. The majority of raised bogs are found in the north-west of England, mid-Wales and the Forth Valley in Scotland. Thorne Moors in Yorkshire is the largest raised bog in Britain, covering an area of 1900 ha (Heathwaite, 1995). Blanket bogs can also cover immense areas, as illustrated by the Flow Country of Caithness and Sutherland in Scotland, the last so-called 'pristine' wetland in Europe. The Flow Country covers an area of 401,375 ha (Lindsay et al., 1988). Other substantial areas of blanket mires can be found amidst the uplands of England and Wales.

2.2.3 LOSSES OF FENS AND BOGS

The value of the wetland vegetation on Goss Moor NNR is heightened by the significant losses of wetland throughout Britain. The destruction of fens and bogs can be caused by either qualitative and/or quantitative losses. The loss of fen habitat is most dramatically illustrated in the East Anglian 'Fens', a region once covering an area of 3000 km^2 (300,000 ha) (Darby, 1983) between Cambridgeshire and Lincolnshire. A long history of drainage dating back to Roman times has resulted in the loss of fens to arable land, except for a few small scattered areas. The two largest remaining areas are Wicken Fen NNR and Woodwalton Fen in Cambridgeshire, with a combined area of just 500 ha. (Fojt, 1995). These Fens have only survived through careful control of their water table by bunding and pumping (Fojt, 1995). The loss of lowland raised bogs and blanket mires has been equally dramatic, due mainly to agricultural reclamation and afforestation, which has lead to 30 % losses or damage (Nature Conservancy Council, 1985). In the Flow Country, 17 % of the original area of peatland had been afforested or programmed for planting (Lindsay *et al.*, 1988). In contrast, the blanket bogs, which are an integral and important part of upland landscapes, have largely been undamaged (Tallis, 1995).

Qualitative losses of the nature conservation value of wetlands are also widespread, as illustrated by the fens of Broadland, where nearly half of the semi-natural fen habitat is now covered in carr, which has expanded as management has declined (Fuller, 1986). Succession has also occurred at Wicken Fen, where the proportion of scrub was found to double between 1936 and 1956, whilst the area of sedge declined by more than half (Rowell & Harvey, 1988). Of particular importance is the loss of conservation value due to changes in the water regime. Harding (1993) showed how groundwater abstraction gradually caused the floristic diversity of fen vegetation to decline, which in turn degraded

the diversity of invertebrates. Also, nutrient runoff from surrounding agricultural land can alter the fen species composition by increasing the nutrient availability, and in severe cases cause eutrophication (Verhoeven *et al.*, 1993; Koerselman & Verhoeven, 1995).

2.2.4 CONSERVATION VALUE OF FENS AND BOGS

In order to appreciate the unique species assemblages that occur on Goss Moor, it is essential to consider the conservation value and importance of fens and bogs in the U.K.

Generally, fens have high biodiversities (Wheeler & Shaw, 1995), with a large number of plant species organised into a wide range of plant communities reflecting variations in environmental conditions, natural processes of development and the degree of human influence. Wheeler (1993) reported a total of 193 species found within the bog habitat as opposed to 653 for fens. Of the fen species, about 294 were regarded as being particularly characteristic of fens. This floristic diversity is coupled with considerable entomological and ornithological richness (Foster & Procter, 1995). A large number of nationally rare and scarce vascular plant and bryophyte species are associated with fen and carr. For example, *Saxifraga hirculus* L. is protected within the European Union (European Habitats and Species Directive) and another, *Lysimachia thyrsiflora* L., is a nationally scarce species found in carr and M4 fen communities (Rodwell, 1991a; 1991b). Bogs support far fewer plant and rare plant species than fens. In Britain, raised bogs with high conservation value are uncommon. It has been estimated that from a total extent of some 67,000 ha of raised bog in Britain, there is now less than 4000 ha of 'natural, undamaged, primary raised bog' (Plantlife, 1992).

2.2.5 WETLAND CLASSIFICATION

To ensure effective and consistent communication of terms, categories and concepts used to describe wetlands, it is essential to appraise the plethora of different classifications and terminology that have developed in the field (Gore, 1983).

The classification of wetlands is controversial due partly to their enormous variety and highly dynamic character, and also because of difficulties in defining ecosystem boundaries. In addition, successional changes cause some wetlands to progress through various stages to become terrestrial ecosystems. Difficulties of definition are also illustrated by considering the periodicity of inundation and the period of time an area has to be flooded or saturated with water in order to be classified as a wetland (Maltby, 1991).

In Britain, the term *mire* has been widely adopted to describe wetlands that encompass types such as swamp, fen, moor, muskeg and peatland (Gore, 1983). In general terms, mire is used to describe peat-forming wetlands. However, the definition can also include muds evolved from still-water deposition (Heathwaite *et al.*, 1992). The definition of mire is somewhat complex and should not be confused with Rodwell's floristic definition (1991b). The complexity of mire terminology is displayed in Table 2.2 indicating some of the differences in terminology and classification applied to North American and European mires. The table displays a clear consensus for the description of bog, which is vegetated by mosses, ombrotrophic and acidic in nature (Proctor & Maltby, 1998). In North America the term marsh encompasses the swamp, marsh and fen wetlands of Europe.

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Table 2.2 Comparisons of mire terminology in Europe and North America, adapted from Heathwaite et al.(1993).

Terminology				
North America	marsh			bog
European	swamp	marsh	fen	bog
Characteristics				
Vegetation	reeds	grasses and sedges		mosses
Hydrology	rheotropic			ombrotrophic
Soil	mineral			peat
pH	neutral			acid
Trophic state	eutrophic	mesotrophic		oligotrophic

Various wetland classifications exist (e.g. Gore, 1983; Mitsch & Gosselink, 1986; 1993; Succow, 1988). The main divisions between wetland types depend largely on the scale of investigation. Differences in the extent and duration of climatic, geomorphological and hydrological conditions affect the scale of peat accumulation and, therefore, mire formation. The classification of British mires proposed by Moore & Bellamy (1974) was based on these physiographical grounds (Table 2.3) and divided according to general hydrotopography, peat formation and vegetation conditions. The upper four categories could be classified as fens and divided further according to base-status and the vegetation types present.

	Hydrotopography	Peat formation	Vegetation and conditions
Soligenous mires	associated with moving water springs or flushes	slow rates of peat formation due to the oxygenated moving water supply	*Sphagnum recurvum, Molinia caerulea*, sedges and rushes.
Basin mires	often associated with glacially deepened hollows and minimal groundwater oscillation	deep peat formation possible	vegetation surface may be floating
Valley mires	direction of water flow along the valley axis	deep peat formation possible	wide base-status range of vegetation recorded from *Sphagnum* to carr
Floodplain mires	developed on alluvium susceptible to flooding	peat formation possible	commonly base-rich with the sequence open water to swamp to carr. *Sphagnum* common with low nutrient status and reed and sedge communities prevalent with high nutrient supply.
Raised mires or bogs	mire surface is isolated from the groundwater table or ombrotrophic, dependent on water and nutrients derived from atmospheric precipitation.	raised mires usually with characteristic dome shape (Ingram, 1982), growth rate and morphometry are controlled by groundwater flow within the peat mass.	usually relatively species-poor common species include dwarf shrubs, heather (*Calluna vulgaris* or *Erica tetralix*), cranberry (*Vaccinium oxycoccus*) and narrow-leaved sedges
Blanket bogs or mires	generally require both high rainfall and a high number of rain-days together with cold temperatures and minimum evaporation for formation.	usually develop over impermeable soils or bedrock, although podsolisation, and the resultant formation of impermeable horizons within the mineral soil may cause development	wide range of types from *Juncus, Sphagnum* hummocks, *Eriophorum angustifolium* hollows

Table 2.3 The six fundamental types of British mire based on physiographic features, from Moore & Bellamy (1974).

Other wetland classifications are based on features such as site size, shape or hummock and hollow surface patterns but these have been criticised for being too general (Heathwaite *et al.*, 1993). Alternatively, the source of water or the hydrological balance may seem a more appropriate basis for distinguishing mire types, as *all* mire development depends on it (Hollis & Thompson, 1998). Von Post & Granlund (1926; cited in Wheeler, 1995) subdivided mires into three main types according to their water source:

(i)   *ombrogenous* mires develop almost exclusively under the influence of precipitation;

(ii)   *topogenous* mires are irrigated horizontally by mineral soil water;

(iii) *soligenous* mires develop on sloping sites, where laterally mobile mineral soil water maintains the wet conditions (Sjörs, 1950).

Many workers are in agreement with these divisions. Work by Du Rietz (1949; 1954) in Sweden showed the primary divisions of mires to be between those areas fed almost exclusively by precipitation, the ombrotrophic (rain-fed) or ombrogenous (rain-made) mires, and those supplemented by telluric water, the minerotrophic or rock-fed topogenous and soligenous mires. These important categories correspond broadly with major habitat and biological differences within mires and have been widely accepted (Wheeler, 1995). Using these categories many wetland ecologists have come to use the words fen and bog as a synonym for minerotrophic and ombrotrophic mires, respectively (Wheeler, 1995). However, hydrological criteria may require more detailed information to describe mire type, such as the topographical parameters of valleys and basins (Wheeler, 1995). This has led many ecologists to consider the hydrotopography of wetlands (*i.e.* their situation, shape and water supply) to be a particularly characteristic feature and important for classification (Sjörs, 1950). However, the topography of wetlands is often not readily characterised or

quantified and their hydrological mechanisms cannot always be assessed by casual inspection (Wheeler, 1995). Nevertheless, various workers have attempted to generate a plethora of rather different hydrotopographical classifications. Some of these (e.g. Succow & Lange, 1984; Succow, 1988) have been based upon empirical means whilst others have been more subjective (e.g. Goode, 1972). A limitation of many hydrotopographical classifications is that they do not distinguish clearly between the topography of the landscape within which wetlands occur, and the characteristics of the wetlands themselves. For example, British ecologists have distinguished flood-plain mires, basin mires, open-water transition mires and raised mires as hydrotopographical types (Ratcliffe, 1977). However, raised mires, or water bodies with their associated hydroseres, often occur *within* flood plains or basins, raising doubt to which category they should be placed (Wheeler, 1995).

Table 2.4 shows some of the terms used to describe wetland types on the basis of the distinctive cause of surface wetness. The terms correspond broadly to the categories of topogenous and soligenous fen. In reality, specific water sources can be difficult to identify, even in crude terms, and mixtures of sources often occur.

Table 2.4 Some terms often used to describe hydrotopographical components of wetland sites in relation to features of gross topography and distinctive causes of surface-wet conditions. Adapted from Wheeler (1992).

Distinctive cause of surface wetness	Topogenous sites (or parts of sites)
Open water of lakes and pools	Waterfringe wetland; open water transition mires; fringing fen; limnogenous mire
Overbank flooding from rivers and streams	Alluvial wetland; transgression mire; fluviogenous mire
Confined groundwater (strong point-source discharge)	Spring-fed wetland; spring fen; tufa mound
Groundwater flow (from margins or diffuse upwelling)	Percolating mire; headwater fen and seepage fens on sloping sites
Run-off local groundwater	Sump wetland; swamp(ing) mire; kettlehole mire; telmatogenous mire
Precipitation	Topogenous bog; raised bog; blanket bog
Discrete zones of water flow	Soakways and water tracks

On a smaller scale, criteria such as plant cover and water chemistry are thought to provide a more detailed evaluation of the mire and mire forming processes. Water chemistry is evidently governed by the water source (van Wirdum, 1991; Bootsma & Wassen, 1996). For example, exclusively rain-fed mires would contain nutrient-poor water, while groundwater, which has been enriched by agricultural inputs (Verhoeven et al., 1993), would be high in nutrients. Water chemistry can be classified into four types (Heathwaite et al., 1993):

(i)   eutrophic with high nutrient content;

(ii)   mesotrophic of medium nutrient and calcium content;

(iii) oligotrophic of low nutrient and low calcium content; and

(iv)   dystrophic with high humic acid content.

However, the water chemistry of mire types displays much variation, on both regional and local scales (Proctor, 1992) and even seasonally (Proctor, 1994). As well as the external factors of water source, internal factors are important (Koerselman et al., 1993), such as soil temperature, aeration and redox status, which are controlled by soil moisture. These

three factors directly control the rates of decomposition and mineralisation of organic matter and, therefore, the cycling of N and P (Verhoeven *et al.*, 1993).

The water chemistry at different sites can be characterised according to the ionic ratio of calcium and chloride (IR = 2[Ca]/(2[Ca] + [Cl]), molecular concentrations) and the electric conductivity (EC) (van Wirdum, 1991). Using IR-EC diagrams, water originating from different sources were characterised as:

- Atmotrophic: rainwater-fed sites display a low IR and EC

- Lithotrophic: groundwater-fed sites have a high IR and EC.

- Surface water-fed sites show intermediate IR in combination with high EC values (Verhoeven *et al.*, 1993).

Whilst there is a clear conceptual distinction between bog and fen, it is less easy to specify how this can be recognised in the field. Du Rietz (1949; 1954) suggested a floristic approach, based on the 'fen plant limit', which is the absence of species thought to indicate groundwater influence. Ecologists commonly use floristic criteria (e.g. vegetation composition) to identify areas of bog, rather than some independent hydrological measure (Wheeler, 1995). Different types of wetlands are often named by the dominant plant (e.g. *Sphagnum* bog, willow carr), signifying the recognition of distinctive plant associations, which are generally termed a community. In wetlands, it has been suggested that plant associations are more clearly identifiable due to their assemblages upon sharp and sometimes abrupt environmental boundaries such as surface wetness. These environmental boundaries cause distinctive zones in the vegetation (Mitsch & Gosselink, 1993). Although wetland communities were historically identified qualitatively, the application of objective clustering techniques supports the community concept in a number of instances. Rodwell (1991a; 1991b; 1995) produced complete classifications of British plant communities in

the National Vegetation Classification (NVC) along with data tables and location maps, displaying wetland diversity in terms of size, situation and character. Rodwell chronicles 28 swamp and tall-herb fen communities, 37 mire communities, two wet heath communities and six fen woodland communities (Rodwell, 1991a; 1991b; 1995). However these should not be regarded as absolute categories but as identifiable reference points within a field of variation. The capacity for most bog species to grow in poor-fens, coupled with the ability of some fen species to grow in ombrotrophic environments, in at least the more oceanic parts of their range, precludes a universal floristic separation of fen from bog. Also hydrochemical measures cannot be used as universal indicators of ombrotrophy, as any simple specification of chemical thresholds is complicated by regional variation in rainwater composition (Proctor, 1992; 1994).

The most sensible distinction between fen and bog was proposed recently by Wheeler & Proctor (2000) who recommend that bog and fen should be redefined and separated on the basis of pH and subdivided by substratum fertility. Using these distinctions the authors suggest that the infertile, base-poor communities dominated by *Molinia, Juncus* spp. or *Carex* spp. and varying amounts of *Sphagnum*, like those found on Goss Moor are referred to as mesotrophic bog and not poor-fen. Also, vegetation occurring in the hydrosere between swamp and fen carr should be referred to as herbaceous fen and not fen (Wheeler & Proctor, 2000). Although these new classifications are welcomed, more traditional terminology is used for the purposes of this research, the descriptions of which are covered in the next section.

In summary, it is clear that the physical, chemical and biotic characteristics of mires show much variation and there is often a continuum from one mire type to the next. Hence, any

classification, whether based entirely on shape, topography, chemistry, plant species composition or hydrology is somewhat arbitrary.

2.2.6 WETLAND VEGETATION TYPES ON GOSS MOOR NNR

The main wetland community types identified in the site description of Goss Moor NNR are fen, bog and wet woodland, each of which will be considered in more detail in the following sections.

2.2.6.1 The concept of bog

The term 'bog' has been used inconsistently by ecologists. For example, Tansley (1939) used it to include ombrogenous mires together with acidic minerotrophic examples (poor-fens *sensu* Du Rietz, 1949). Today, however, many wetland ecologists restrict the word 'bog' specifically to ombrotrophic sites (Proctor, 1995). In this narrow sense, the concept of bog is generally more clear than that of fen, in that it essentially refers to peat-based mires that are directly and exclusively flushed by precipitation (Clymo, 1991). References to bog in this report will follow this definition. Such sites have a much narrower range of environmental and biological variation than minerotrophic wetlands and it is easier to specify their limits. Ombrotrophic mires or bogs are subdivided into raised and blanket bogs, which are both peat-forming, the former developing in basins and often displaying a raised dome (Table 2.3). The raised dome of living and non-living vegetation is termed the 'cupola' (Tallis, 1983) and the surrounding peat is the 'lagg', where water is guided away from the centre and mixes with runoff from surrounding mineral soil. The upper 'active' growing layer of the peat is termed the acrotelm and the inert dead lower layer is the catotelm (Ingram, 1978; 1982). Blanket bogs form on upland valley sides or any area sufficiently wet to enable mire plant production to exceed the rate of plant decomposition (Tallis, 1983).

2.2.6.2 The concept of fen

There is confusion over use of the term 'fen' (Wheeler, 1995). For example, in Britain fens have been regarded as being:

(i)   topographic features of the landscape (e.g. The Fens of East Anglia);

(ii)   wetlands with a particular range of habitat conditions (Tansley, 1939);

(iii)   wetlands containing a specific range of vegetation-types (Wheeler, 1980);

(iv)   a particular herbaceous phase of the hydrosere interpolated between swamp and mire woodland (fen carr) (Tansley, 1939).

The breadth of the meaning is thought to originate from the Anglo-Saxon word 'Fenn', a generic term used to describe all types of waterlogged habitats including those which would now be called bog (Bosworth & Toller, 1882 cited in Wheeler, 1995). Today, ecologists (e.g. Tansley, 1939) have truncated its meaning to a contradistinction of 'bog' and a synonym for minerotrophic mires (Sjörs, 1950). Hence, the term fen defines a wide variety of environmental conditions and biological features. It is this meaning that has been adopted throughout this thesis. The concept is broader than that of peatland, as it may also encompass sites on mineral soils, although some workers (e.g. Mörnsjö, 1969) consider true fens to be those which have developed exclusively upon peat. Tansley (1939) consigned the term 'marsh' to wet sites developing on mineral soils.

Fens can be classified into rich- and poor-fens on floristic and chemical grounds (Wheeler, 1984). The floristic units were recognised by Du Rietz (1949; 1954) as either species-rich or species-poor-fens. The presence or absence of plants that are thought to indicate basiphilous conditions was also used as a defining factor in fen classification (indicating either base-rich or base-poor). However, the recorded pH 'preferences' of many wetland plants are not always clearly established and may show considerable regional and site

variation (e.g. Sjörs, 1950). Ultimately the classification of fens according to their base-richness range may be arbitrary (Wheeler, 1995).

The range of water regimes appropriate to the concept of fen have not been closely examined (Wheeler, 1995). Often, fens are regarded informally as wetlands that are not swamp, but are wetter than wet heath or wet grassland. The exact water level limits are difficult to specify, as are those sites subjected to strong seasonal water-level fluxes. Likewise, many wetland sites which support what is called 'fen vegetation' have themselves been partly drained, so their natural properties are uncertain. In undisturbed fens, the peat is often waterlogged and the surface may be flooded for a considerable part of the year. The water balance of fens is not directly dependent on rainwater, which means that fens occur in areas of low rainfall where bogs cannot form initially (Heathwaite *et al.*, 1993). Topographically, the fen surface is frequently flat or slightly concave due to the lack of cushion forming mosses, allowing lateral water movement (Heathwaite *et al.*, 1993).

Controls on the composition of fen vegetation

The vegetation of fens is generally a vigorous mixture of broad-leaved grasses and herbs (Heathwaite *et al.*, 1993). On the edge of ponds, fen plants such as reed *Phragmites australis*, bulrush *Typha latifolia* L. and various sedges (*Carex* spp.) are found, whereas alder *Alnus glutinosa* L. (Heathwaite *et al.*, 1993) and willow (*Salix* spp.) are found in forested fens. The composition of fen vegetation varies considerably with altitude, latitude and longitude. This is illustrated by the range of vegetation-types found throughout Britain. All species have a phytogeographical boundary governed by climate, but in general the precise controls of fen plant species distribution is unknown (Wheeler & Shaw, 1995). Nevertheless, there is a wealth of data containing species composition with accompanying

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hydrochemical variables. Complex vegetation-environment relationships (e.g. Wassen *et al.*, 1990) have been studied using Canonical Correspondence Analysis (CCA) (Ter Braak, 1987), although many studies are site specific. However, the distribution of species or vegetation at one site may be applicable to others (Sjörs, 1950). Various experiments have studied the relationship between the performance of fen plants and hydrochemical variables (e.g. Snowden & Wheeler, 1993), but they are far from comprehensive. Moreover, the difficulties of relating the results of single species experiments to field distributions is well known (Wheeler & Shaw, 1995).

To elucidate some of the uncertainties highlighted above, Wheeler *et al.* (1992) examined vegetation-environment relationships in an extensive overview of British fens. Water samples were analysed for pH, conductivity and alkalinity values and soil extracts were analysed for metal cation concentrations, pH, N and P. An innovative feature of their study was the use of a 'phytometer' species, which was used to provide simple and reliable estimates of soil fertility from a large number of sites (Wheeler *et al.*, 1992). CCA analysis revealed that the three independent features of base richness, soil fertility and water level were strongly correlated with the vegetation type. These three factors will be discussed below in further detail.

Base-richness

Base-richness corresponds with increase in water pH, conductivity and extracted concentrations of Ca and Magnesium (Mg) (Wheeler *et al.*, 1992). Base-richness also corresponds negatively to increased concentrations of soil extracted iron (Fe) and manganese (Mn) and aluminium (Al) (Wheeler *et al.*, 1992). High concentrations of soil-extracted Fe and Mn are most typically associated with base-poor conditions, high

concentrations of both elements can also occur in some rich fen soils (e.g. Wheeler *et al.*, 1985). In contrast, high concentrations of extracted Al were invariably associated with fen soils of low pH (<5.0-5.5). The importance of base-richness as a primary determinant of the composition of mire vegetation has long been recognised and is reflected in the gradient of bog → poor-fen → rich-fen (e.g. Du Rietz, 1949; Sjörs, 1950). The reasons for floristic change along the base-richness gradient are not fully understood. For many plant species, variation in pH *per se* is probably of less direct importance, at least within the range of pH 4.0-7.5 (Wheeler & Shaw, 1995). Adaptation to growth in the lower pH of mires may partly depend upon tolerance to toxic metals such as Al, Fe and Mn (Clymo, 1962; Snowden & Wheeler, 1993), although not all base-poor fens are necessarily abundant in these elements. Moreover, in some base-rich fens, both Fe and Mn may reach concentrations that are toxic to some typical fen species. Various calcifuge genera, especially *Sphagnum*, are typically absent from base-rich fens.

As in dry habitats, base-rich fens tend to contain considerably more species than base-poor examples (Wheeler & Shaw, 1995) and are therefore considered to have higher conservation value. Some base-rich sites may show progressive acidification on account of artificial changes such as reduction of inputs of base-rich groundwater (Grootjans & van Diggelen, 1995) or of spontaneous successional changes (van Wirdum, 1995). In both these situations, an increase in acidity is often regarded as undesirable, initiating remedial restoration to a more base-rich condition (Beltman *et al.*, 1995).

<u>Fertility</u>

Fertility is almost independent of base-richness. Consequently it would be inappropriate to classify the trophic status of fens by reference to pH (e.g. Ratcliffe, 1977). However, the trophic status gradient is slightly skewed towards base-rich conditions due to the scarcity of very fertile soils in base-poor fens rather than the absence of low fertility soils from base-rich sites (Wheeler *et al.*, 1992). The availability of nutrients such as nitrogen (N), phosphorus (P), and potassium (K) is undoubtedly of key importance to plant growth and vegetation composition in fens, but general relationships are difficult to demonstrate (e.g. Vermeer & Berendse, 1983; Verhoeven *et al.*, 1988; Wheeler *et al.*, 1992). This may be because simple measurements of N and P concentrations in fen waters or peat do not adequately represent the availability of these nutrients, or because different nutrients are limiting in different situations. Soil N does not adequately represent plant-available N *in situ.*(Wheeler & Shaw, 1995). To overcome this problem fertilisation has been used to detect whether N, P or K are limiting, and as a result control the growth and development of the vegetation. The communities are exposed to each of the nutrients individually and respond to the limiting nutrient with an increase in total primary production (Chapin *et al.*, 1986). However, such experiments are somewhat time-consuming and laborious. Thus, the introduction of the 'N:P tool', which establishes the nature of nutrient limitation by using the amount of total N and total P present in plant tissue to establish the N:P ratio (Koerselman & Meuleman, 1996). The concept of the 'N:P tool' will be discussed further in Chapter Seven and evaluated as a device for characterising nutrient limitation on Goss Moor.

<u>Water level</u>

Low summer water table levels are inversely proportional to redox potential and accelerate nutrient cycling (Verhoeven *et al.*, 1993). However, the hydroperiod of fens can be complex (Wheeler, 1999). It is apparent that certain plant types show distinctive tolerances to summer water table, even though fluctuations can be very small. Understanding the effects of water regime on fen vegetation is critical. Greater knowledge is needed about the following:

(i)   the physiological nature of the tolerance of wetland species to wet conditions;

(ii)   the range of water conditions that particular species can tolerate;

(iii) the importance of species interactions in determining the field response of species to specific water conditions;

(iv)   the importance of different phases of hydroperiod upon species survival i.e. summer *versus* winter drying (Godwin & Bharucha, 1932; Johnson, 1994);

(v)   the importance of the amplitude of water level flux *versus* mean values;

(vi)   the possibility that community distributions are a legacy of former hydrological environments (van Diggelen *et al.*, 1991); and

(vii) the problem that other environmental conditions are primary influences upon vegetation distribution, or modify the direct effects of water regime (Wheeler & Shaw, 1995).

Changes in the water table are thought to be prompting vegetation changes on Goss Moor, particularly the encroachment of willow carr, which is introduced in the following sub-section. The dynamics of the hydroperiod for a number of different community types will be investigated in Chapter Six.

2.2.6.3 The concept of wet woodland

Wet woodland or fen carr is currently a dominant feature of the vegetation on Goss Moor. Wet woodlands occur widely on waterlogged or seasonally wet soils (Latham *et al.*, 1999). The term 'carr' is used today and in this report in the extended form to encompass all kinds of wet scrub and fen woodland (Kelly & Iremonger, 1997). In the past, the term carr was used to describe wet woodland that has developed specifically on peat (Pallis, 1911). However, other sources (e.g. Rackham, 1980) maintain that carr was originally used in reference to alder-woods. In Britain the dominant wet woodland species include *Salix cinerea* L. (grey willow), *Alnus glutinosa* (alder) and *Betula pubescens* Ehrh. (downy birch). Often these are successional habitats on bogs, fens, wet grasslands or lake peripheries. In flooded conditions, trees and other higher plants are particularly affected by anoxia (devoid of oxygen) (Armstrong, 1978) which is an important limiting factor to growth and survival (ap Rees *et al.*, 1987). In comparison to the other wetland tree species *Salix* spp. display a significantly greater tolerance of soil saturation and hypoxia (oxygen deficiency) (Iremonger & Kelly, 1988). From the other wetland tree species *Alnus glutinosa* is not as tolerant to severe or prolonged flooding as one would expect for a flood-plain tree (Rackham, 1980; Wheeler, 1980) and *Betula pubescens* finds winter flooding intolerable, even though it displays a relatively wide ecological range (Iremonger & Kelly, 1988).

Wet woodland plant communities have received rather little attention in studies of wetlands or woodlands (Latham *et al.*, 1999). Klötzli (1970, cited in Kelly & Iremonger, 1997) provided an overview of British wet woodlands and Iremonger (1990; Kelly & Iremonger, 1997) did the same for the Republic of Ireland. In Wales, the Countryside Council for Wales are presently undertaking studies to survey and inventory wet

woodlands in order to develop strategies for conservation (Latham *et al.*, 1999).

Fen carr communities are generally a more stable climax state in comparison to the intrinsically unstable state of open fen systems (Wheeler & Shaw, 1995). As well as the fen carr climax, other climaxes occur including bog and occasionally other types of herbaceous vegetation that may self-sustain for long periods of time (Wheeler & Shaw, 1995). Vegetation change towards a stable state usually occurs either because of on-going, progressive successional development or because of the relaxation of some previously arresting influence, such as vegetation management. From a management perspective the succession from fen to fen carr is undesirable, although few studies in Britain have carefully documented the replacement of herbaceous fen by fen carr (Godwin *et al.*, 1974; Pigott & Wilson, 1978). Nevertheless, the importance of preventing scrub invasion is well known and may be particularly important in order to deter the possibility of terrestrialisation. There is no doubt that as succession proceeds and the substrate dries out, fen carr may give way to oak woodland (Tansley, 1935). This was illustrated by Godwin & Turner (1933) who found reedswamp to be succeeded by carr and eventually an oak-wood climax.

In order to understand and manage the successional processes occurring on Goss Moor it is necessary to consider succession in more detail. The next section reviews the extensive literature covering this subject.

2.3 INTRODUCTION TO PLANT SUCCESSION

2.3.1 INTRODUCTION

Like the vegetation of many fen ecosystems, Goss Moor is intrinsically unstable and liable to change spontaneously towards a more stable, climax state (Wheeler & Shaw, 1995).

Presently, the management on Goss Moor is concentrating on the maintenance of plagioclimax communities, via willow scrub removal. In order to understand these vegetation changes, it is necessary to introduce the concept of vegetation and specifically wetland succession. It is important to highlight the different mechanisms that occur during succession and review some of the methods and models used to predict successional pathways.

Successional theory has dominated the field of ecology for over a century, since the pioneering work of Cowles (1899) and Warming (1895). The significance of these successional processes is reflected in the magnitude of literature and data on the subject, and the concept has generated much philosophical controversy and confusion. There have been various explanations for the pattern and causality of succession but, as yet, a universal theory is lacking (McIntosh, 1980; McCook, 1994). This is not surprising, as an all-encompassing definition to describe a wide range of changes in real-life environments seems intuitively to be an impossible task. This need to provide a universal definition of succession was described by Miles (1987) as an emotional need rather than a logical one. Nevertheless, for the purpose of this research, the theories proposed can be evaluated and used as a learning vehicle to increase understanding of the subject.

2.3.2 DEFINITIONS OF SUCCESSION

2.3.2.1 What is Succession?

Definitions of succession are abundant. Examples include 'the directional change with time of the species composition and vegetation physiognomy of a single site' (Finegan, 1984) or a succinct description by Whittaker (1975) as 'an ecocline in time'. Clements (1916), the most influential earlier worker in the field, defined succession as 'a sequence of plant communities marked by the change from lower to higher life forms' (progression) and

stated emphatically that the reverse of this process was impossible. It is now widely known that this is not always the case (e.g. Walker, 1970). Gleason's 1927 definition was very broad: 'The successional phenomena of vegetation include all types of change in time, whether they are merely fluctuating or produce a fundamental change in the association'. Miles (1979) claimed that this definition was too broad as, traditionally, succession is used as a site level description, rather than one to include geological time scales.

Over the years, definitions have become increasingly varied to exclude stochastic (seasonal, fluctuational and cyclical) changes from the full range of recognised vegetation changes (Miles, 1987; Gibson & Brown, 1985). The essence of succession is the occurrence of entire, directional changes in species composition through time (Drury & Nisbet, 1973). However, successional changes also occur spatially (Anderson, 1986; Botkin, 1992). Also, in secondary succession and the later stages of primary succession, these vegetational changes may simply reflect shifts in dominance between species that remain present throughout the successional period rather than particular stages or seres (Miles, 1987). This major theoretical dichotomy of primary and secondary succession will now be described in more detail.

2.3.2.2 Primary and secondary succession

Primary succession is defined as vegetation development beginning on a newly created or exposed substrate, rather than a developed or modified soil (Glenn-Lewin & van der Maarel, 1992). Primary succession is divided into two concepts, xerarch and hydrarch succession. The former term refers to succession beginning anywhere on dry land (Cooper, 1913) and the latter occurs in wetlands (Colinvaux, 1993) and is discussed at the end of this section. As these terms describe successions beginning at opposite extremes of a

wetness gradient, a third intermediate 'mesic' type is recognised. Currently, only a small proportion of the earth's surface is undergoing primary succession. However, as the present Quaternary climate is unstable and undergoing constant fluctuations both naturally and due to human intervention, exposed substrates are continuously produced, enabling the initiation of primary successions to be infinitely possible (Miles, 1987).

Xerarch succession

In dry conditions, primary sites are usually nitrogen deficient (Gorham et al., 1979), with no organic material or seed bank. For colonisation to occur, propagules must arrive via immigration. An example of primary succession can be seen on the glacial moraines of Alaska. The moraine areas are first colonised by algae and cyanobacteria, then herbaceous plants, followed by spruce forests, which are in turn succeeded by willow and alder thickets (Finegan, 1984). Other examples occur following volcanic eruption (e.g. Aplet et al., 1998; Chadwick et al., 1999), landslides (e.g. Myster & Walker, 1997), sand dune formation (e.g. Cowles, 1899; van Aarde et al., 1998) and, mine and quarry waste (e.g. Booth et al., 1999; Ursic et al., 1997; Wheater & Cullen, 1997).

Hydrarch succession

In the classical view of succession, wetlands are considered transient stages in the hydrarch development of a terrestrial forested climax community from a shallow lake (Figure 2.7). The hydroseral stages begin with a lake, which gradually in-fills with organic material as plants die and accumulate, along with mineral inputs that originate from higher ground. As the lake becomes increasingly shallow, rooted aquatic plants are able to colonise accelerating the rate of organic deposition (Mitsch & Gosselink, 1993). Eventually, the environment can support emergent species, which continue to increase the peat mat.

Shrubs and small trees appear and gradually transform the site to a terrestrial one, not only by adding organic matter to the soil but also by drying it out through enhanced evapotranspiration (Moore & Bellamy, 1974). The occurrence of forests on former lake sites is well documented (Burrows, 1990).

Secondary successions occur following a disturbance or perturbation that causes new species to replace the pre-existing vegetation, whilst some previous biological legacy is present. The majority of the work on secondary successions has taken place on agricultural land that has been subsequently abandoned and allowed to revegetate naturally, so called 'old-fields' (e.g. Burton & Bazzaz, 1995; Guariguata *et al.*, 1997; Franklin *et al.*, 1999). Other areas to receive attention include the study of vegetation development following fire perturbation (e.g. Gitay & Wilson, 1995; Thomas *et al.*, 1994) and the effects of dead plant deposition (mars of wrack) in coastal salt marshes (Pennings & Richards, 1998).

Of the two types, primary succession appears to be the easiest to identify, leaving all other successions *de facto* to be secondary. Primary and secondary successions form a continuum, depending on the attributes and duration of the disturbance and the location of the site in the landscape (Walker & Chapin, 1987). For example, salt marshes are thought to be examples of primary succession but they may receive propagules and organic matter from upstream. This poses the question of whether this is just another form of dispersal into primary sites or does the fact that this organic matter is continually arriving as the salt marsh deposits form, mean that it is secondary succession (Glenn-Lewin & van der Maarel, 1992). Thus, although it is important to have these organisational terms, not all observations in nature will fit neatly into these categories.

WOODLAND STAGE

SHRUB STAGE

SEDGE-GRASS STAGE

SWAMP STAGE

FLOATING STAGE

SUBMERGED STAGE

DEPOSITED MATERIAL

ADVANCE OF SHORELINE INTO POND

ORIGINAL SHORELINE

PRESENT SHORELINE

ORIGINAL BOTTOM

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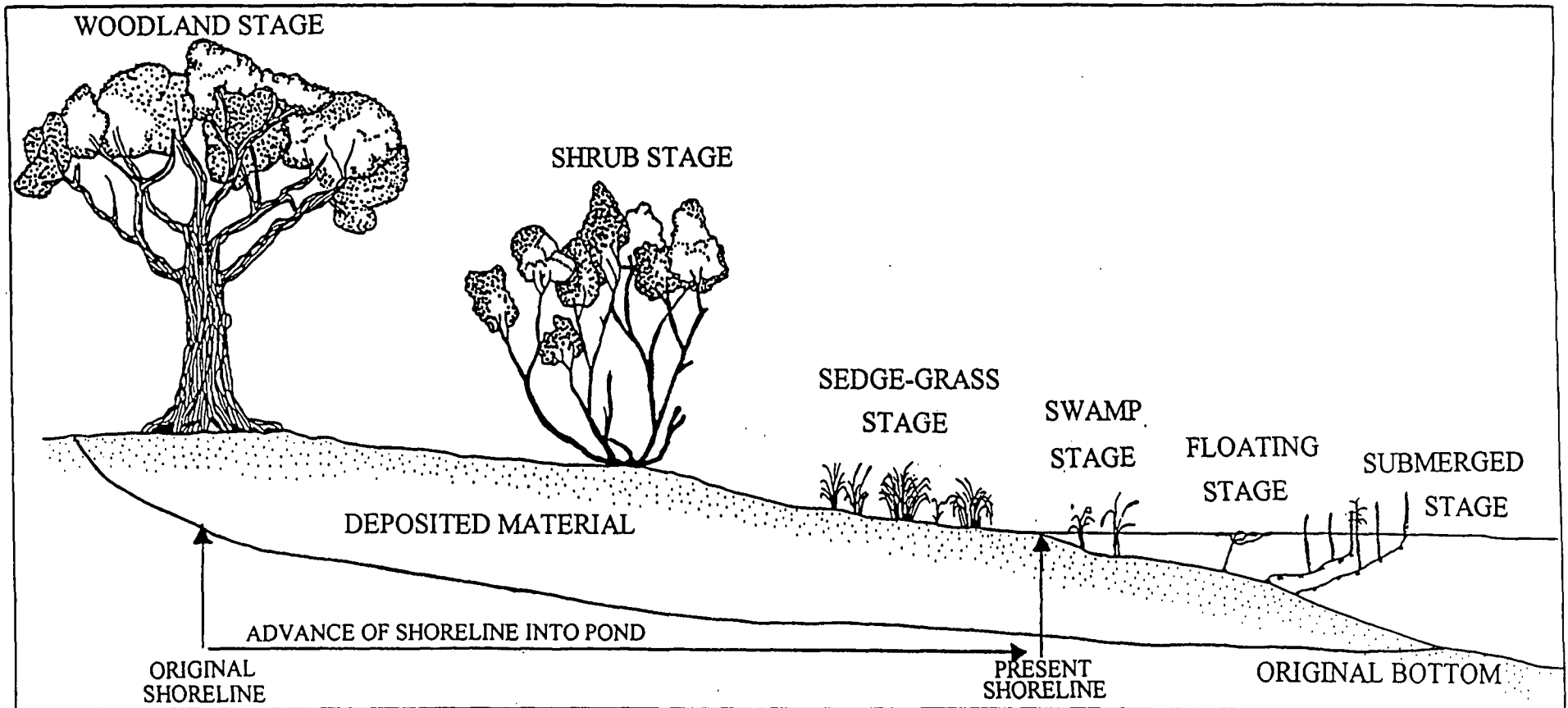
Figure 2.7 Hydroseral succession occurring in zones surrounding a freshwater lake. Modified from Mitsch & Gosselink (1993).

Before a more detailed treatment of succession, two further terms need definition.

2.3.2.3 Autogenic and allogenic succession

Autogenic succession occurs when vegetation change is caused by intrinsic properties of the plants themselves modifying the micro-environment (Tansley, 1935). This implies that succession is community controlled, as Odum (1969) hypothesised, by forces and mechanisms such as competition, shade generation and soil modification.

Allogenic succession results when 'external' abiotic forces cause vegetation change, such as climate change, sea spray or periodic inundations. An example of this can be seen in the mire vegetation of southern Finland, which was dramatically modified following drainage. The populations of dwarf shrubs, tall sedge and Sphagna were depleted as *Pinus* spp. forest gradually developed (Laine *et al.*, 1995). In the Netherlands, prolonged nitrogen enrichment from atmospheric deposition has resulted in drastic changes to the vegetation of *Erica tetralix* L. wet heathlands. The heathland vegetation has almost been replaced by *Molinia caerulea* grassland (Aerts & Berendse, 1988; Berendse *et al.*, 1994). Rare species such as *Gentiana pneumonanthe* L., *Drosera intermedia* Hayne. and *Lycopodium inundatum* L. have also disappeared. In contrast, vegetation change in the Netherlands has also occurred following the removal of environmental stress; the vegetation composition along water courses changed as farmers ceased to fertilise and altered hay making practices (van Duuren *et al.*, 1981).

Sharik *et al.* (1989) questioned the validity of the dichotomy of autogenic and allogenic succession and claimed the distinction to be 'artificial' as both forces are likely to take place in most successions. This was demonstrated by Drury (1956) who found 'late

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successional' bog forests were perched upon a mixed peat composed of mosses and silt. Where the water table had been lowered locally by silt deposition, the forest had grown up and where the water table had risen the forest was replaced by bog. Consequently, it may be more useful to classify individual processes during the succession as being largely either allogenic or autogenic rather than the whole succession (Glenn-Lewin & van der Maarel, 1992).

2.3.3 THE DEVELOPMENT OF SUCCESSIONAL THEORY

Clements (1904; 1916) produced one of the first accounts of the causes of plant succession, although the first person to use the term may have been De Luc (1806, cited in Clements, 1916). This theory dominated the field for the first part of the century, and was based on three assumptions: that vegetation changes were 'deterministic', implying unidirectional, predictable development towards a climax; the climax was inevitable; and succession was driven by reaction. Clements also considered the life histories of plant communities to have organism-like attributes, meaning the formation arises, grows, matures then dies, just like a living being. The scheme of driving processes that Clements (1904; 1916) developed for succession are as follows:

(i)   *nudation,* initiates succession due to creation of a bare area or partially bare area by the disturbance which initiates succession;

(ii)   *migration,* the arrival of organisms to the open site;

(iii) *ecesis,* the establishment of the organisms at the site;

(iv)   *competition,* the interaction of organisms at a site;

(v)   *reaction,* the modification of the site by the organisms thereby changing the relative abilities of species to establish and survive; and

(vi)   *stabilisation,* the development of a stable climax.

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Clements introduced the term 'sere' to describe the complete successional sequence from the first pioneers to the final climax state, and the developing stages or the intermediates were termed the 'seral stages'. Pickett *et al.* (1987a) criticised the final process of stabilisation and stated that it should be viewed more appropriately as a consequence of the first five processes rather than a process itself.

Clements' theories in describing succession were widely criticised (Gleason, 1927; Drury & Nisbet, 1973; Colinvaux, 1993) due to the rigidity of his schemes and lack of scientific rigor (Burrows, 1990). Gleason (1927) dismissed the 'deterministic' theory on the grounds that no two vegetation samples were exactly alike in quantitative or even qualitative composition, because the vegetation properties depended entirely on the properties of the individual plants within it. This 'individualistic' hypothesis was shared by other workers (e.g. Egler, 1954; Glenn-Lewin, 1980), although it was widely appreciated, as Gleason himself emphasised, that similar histories of migration and environmental development tended to produce samples of vegetation with close species correspondence. Gleason considered plant communities as a consequence of the incidental overlap of species distributions with similar environmental tolerances, therefore introducing the emphasis of stochastic processes into successional theory.

2.3.3.1 Organismic hypothesis

The organism analogy that Clements assigned to plant communities was unsupported in the literature or by reality. The palynological record clearly shows that vegetation is not persistent, so plants were unlikely to ever develop to the level of integration needed to behave as a unit (West, 1964). Contemporary communities have no long history in the

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Quaternary, but are merely temporary aggregates under given conditions of climate, other

environmental factors and historical factors (West, 1964).

2.3.3.2 Climax theory

Clements' climax theory has been widely challenged and criticised. Braun-Blanquet (1932)

labelled the climax a 'flight of imagination'. Nevertheless, there are plenty of examples

where succession does terminate in vegetation of a relatively stable and predictable type,

such as the *Fagus sylvatica* L. forests of Central Europe, that have been self reproducing

for hundreds of years (Drury & Nisbet, 1973). Tansley (1935) strongly criticised Clements'

assumption that all vegetation change in a particular region would converge towards the

same type of 'climatic' climax predominantly dependant upon climate. He argued that

local factors, such as rock type and topographic position, may result in climax vegetation

types that differ from that associated with the regional climate. Various assemblages also

form mosaics according to substrate heterogeneity. This was moving away from the

monoclimax, where all community development converges to one vegetation type in

equilibrium with climate, towards the polyclimax theory, which encompasses the many

persistent climaxes that arise in response to other forces in addition to climate. Succession

not only appears to display different end points, but it has also been observed to take many

different pathways (e.g. Fastie, 1995).

2.3.3.3 Multiple pathways

Cooper (1926) described succession as a many braided stream, meaning that succession

could take one of many pathways. Olson (1958) confirmed this when he re-examined

Cowles' (1899) work on sand dune succession. Further evidence in accordance with

multiple pathways was offered by Walker (1970) and Fastie (1995) for hydroseral and

glacial moraine, respectively. Fastie found that a range of different single species chronosequences arose following glacier recession at Glacier Bay, Alaska. These communities included black cottonwood *Populus trichocarpa* L., Sitka spruce *Picea sitchensis* Carr. and Sitka alder *Alnus sinuata* L. and their occurrence was attributed to parent soil and species life history traits, thus highlighting both the inadequacy of much of the evidence accumulated to support putative successional sequences and the seemingly intellectual need of the ecological community to embrace a simple and unifying model of the successional process.

Walker (1970) examined published accounts of stratigraphic sequences at over forty British sites and recorded the occurrence of changes from the frequencies of one particular sediment type to another. The sediments were organised into twelve types, each corresponding to a present-day wetland community. Within the twelve, these sediments included: (i) lake mud, with floating-leaf and submerged macrophytes;. (ii) swamp mud below reed swamp communities; (iii) fen peat, accumulating under low sedge tussocks and herbaceous fen communities; (iv) wood peat, formed below swamp and fen carr; (v) bog peat, largely composed of *Sphagnum*. These five categories correspond to the successive stages of a terrestrialisation scheme. Walker found that certain pathways of change occurred more frequently than others, and were progressive towards terrestrialisation. But, generally, there was no single preferred pathway of development as some were regressive and skipped stages, (Figure 2.8), with bog being the most common end point. Walker remarked that 'variety is the keynote of hydroseral succession'.

Multiple pathways also occur in secondary succession, as evidenced by the work of Miles (1987) on upland successions following fire and grazing. The successional pathways

described by Botkin (1992) for forest systems were extremely varied, stochastic and dependent upon local conditions and chance, leading ecologists (e.g. Glenn-Lewin, 1980) to embrace Gleason's (1927) 'individualistic' theory of vegetation dynamics.

Figure 2.8 A flow diagram displaying the twelve most common transitions of hydroseral change. After Walker (1970).
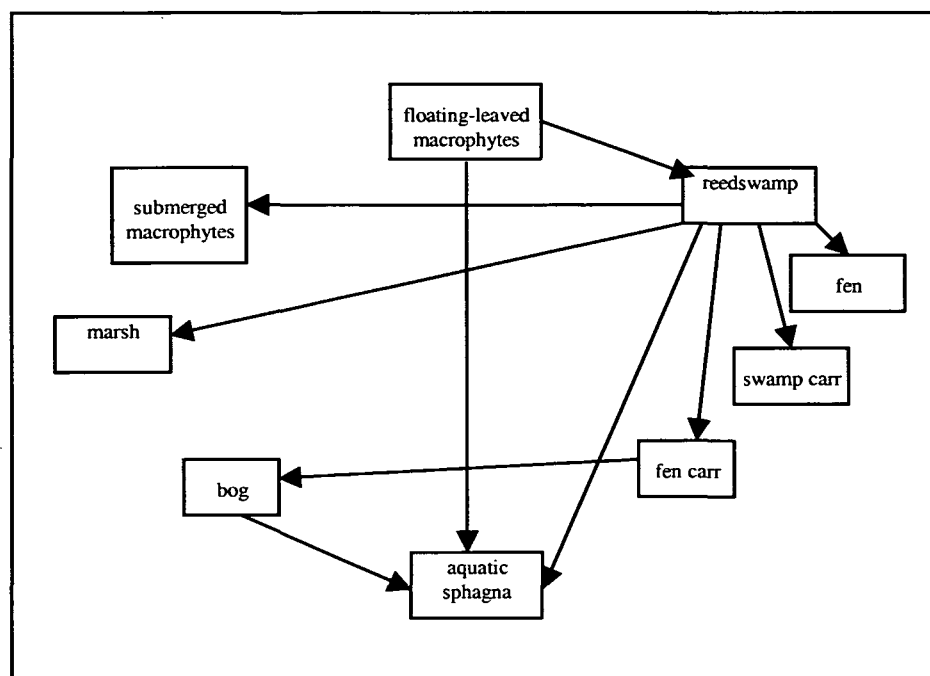
2.3.3.4 Cyclical succession

Species replacement can also occur in cycles. These cycles can repeat a previous stage(s) of the vegetation development, and/or the whole sequence of species replacement. The best examples come from dwarf heathland studies (e.g. Gimingham, 1988), although not all heathlands show cycles (Gimingham, 1988). Cycles can also occur on a community scale, where whole communities rather than individual species are replaced. This was described for bogs by Drury (1956). Watt (1955) showed how *Pteridium aquilinum* (L.) Kuhn., which dominated on the Brecklands of England, would degenerate and die allowing the grass *Festuca ovina* L. to thrive until the bracken would recolonise and eventually shade

out the grass again. Olff *et al.*(1999) used large grazers to manipulate the cyclical relationship of various woodland species, which displayed various grades of palatability, in order to maintain spatial diversity of successional seres.

2.3.4 MECHANISMS DRIVING SUCCESSION

The mechanisms that drive species replacement during succession have generated much interest since their conceptual introduction by Egler (1954). Since there is no unifying theory that can explain all successional patterns and interactions, it seems a logical approach to compile and review the mechanisms that predominate in the range of different models and theories proposed in the literature. The causes of succession proposed by Clements act as a useful basis for this work (Miles, 1979).

2.3.4.1 Disturbance

The term disturbance has been defined in a number of different ways. Grime (1979) defined it as 'the mechanisms that limit the plant biomass by causing its partial or total destruction'. Van Andel & van den Bergh (1987) offered their 'consensus' definition as 'a change in conditions which interferes with the normal functioning of a given biological system...disturbance is a cause (a change in condition) measured by its effects (change in normal functioning of a system)'. However, Glenn-Lewin & van der Maarel (1992) ask the question: 'What constitutes a 'normal' pattern or functioning in an ecological system?' Another approach is to identify disturbance as a process which causes increased resource availability to which plants respond, those being either survivors of the disturbance or new immigrants (e.g. Tilman, 1985). One such response is the increased growth as competition is removed. Other responses are induced by the creation of bare ground, loose soil, and light gaps. Grubb (1988) found examples where local and regional species abundance were

coupled to disturbance, and examples when they were not, highlighting the variability of vegetation dynamics. Disturbance underlies the process that Clements called nudation.

Disturbance can occur both naturally and by anthropogenic intervention and may vary in three dimensions, namely space, time and magnitude (Glenn-Lewin & van der Maarel, 1992). The spatial dimension is the extent of the disturbance according to the area, volume and location, especially in relation to environmental gradients. Different patch sizes and shapes allow plants with different life histories to colonise and create different edge effects. The temporal dimension depends on frequency and predictability. The duration of the intervals between disturbances, such as fire, affects the type of vegetation a site can support. An example of this can be seen in the swamps of New Jersey, USA. Fire intervals have changed from 20 to 65 years over the last century and during this period tree dominance has shifted from white cedar to hardwoods (Forman & Boerner, 1981). Magnitude is described by the effects disturbance has on the vegetation, or by the intensity of the disturbance (Pickett & White, 1985). The extent of the disturbance determines whether vegetation or sexual propagules survive the disturbance and can contribute to the succession of the community (Noble & Slatyer, 1980). Often, disturbance intensity is measured using parameters including grazing pressure, fire temperature or shore wave intensity (Glenn-Lewin & van der Maarel, 1992).

2.3.4.2 Colonisation

Colonisation is the product of interaction between the presence or immigration of propagules, the spatial patterns of the environment and existing vegetation, and the morphology and physiology of the propagules (Glenn-Lewin & van der Maarel, 1992). The presence or absence of these propagules will reflect relative contributions from the seed

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and seedling bank and differential seed dispersal. Other determinants of the outcome of succession are seed source distance (Cooper, 1926; van der Valk, 1981), seed source spatial distribution, neighbourhood influences on establishment (Lippe *et al.*, 1985) and the movement of seeds from productive to unproductive sites (Shmida & Whittaker, 1981).

Spatial discontinuities or interruptions in a homogenous landscape also affect the colonisation of different species. For example, burrowing rodents on grasslands can create topographic heterogeneity (Grubb, 1986), or vertical structures (e.g. an electricity pylon) that can facilitate seed dispersal by birds (Holl, 1998). On a larger scale, landscape elements like streams, banks or roads would affect the spatial arrangement of successional species (Halpern & Harmon, 1983).

The ability of an organism to colonise an area depends on its morphological, physiological and reproductive characteristics. Effective initial colonists or pioneers have adapted to produce a large number of propagules, have good dispersal powers (usually windblown) and are, or able, to survive in a dormant state (Connell & Slatyer, 1977). Colonising species are generally not adapted to germinate, grow or survive in occupied sites with heavy shade and deep litter.

In wetlands, seed recruitment is principally influenced by environmental factors such as flooding, temperature, soil chemistry, soil organic content, pathogens, nutrients (Mitsch & Gosselink, 1993) and allelopathy. Water, in particular, is a critical variable as most seeds require moist but not flooded conditions for germination and early seedling growth. As a result of this restrictive moisture requirement, it is common to find even-aged stands of

trees at low elevations in riparian wetlands, reflecting seed germination when water levels were unusually low during spring and summer (Mitsch & Gosselink, 1993).

2.3.4.3 Initial floristics and pre-emption

Pre-emption occurs when potential invaders are prevented from colonising by a species, a group of species or an undesirable environment created by the vegetation. Egler (1954) first reported pre-emption, which lead to his 'initial floristic composition' model. Egler found that successional changes in vegetation were the outcome of the differential appearance, growth, reproduction and survival of species already at the site and in the seed bank. In view of succession, the changing composition of vegetation is generated by probabilism rather than determinism. The 'initial floristic composition' model is most likely to apply in secondary successions, initiated by small disturbances in a large area of climax vegetation (Gibson & Brown, 1985), or under large scale disturbances, where most species are well adapted to the disturbance and can persist as seeds or other propagules (Purdie & Slatyer, 1976).

2.3.4.4 Competition

Competition describes interactions between the same species or different species, which are termed intraspecific and interspecific, respectively. MacArthur (1972) based his theory of succession solely on competition, using K and r strategies. Species with r strategies are those with attributes suiting reproductive success and the capacity for dispersal and rapid population growth in uncrowded environments (Burrows, 1990). The K species are tolerant of competition in crowded conditions, are relatively slow growing and often large and/or woody. All K species proliferate vegetatively or regenerate by means of a relatively few, locally dispersed seeds (Burrows, 1990).

The 'competitive hierarchy' model proposed by Horn (1981) showed late succession plants to be increasingly dominant by virtue of their competitive success over early species, but a late successional species can also invade in the earlier stages of succession. Patterns of replacement are determined by the outcome of competition among different species. However, in a changing or non-constant environment, the competitive relationships of the species are likely to change; the outcome of succession by this mechanism cannot be predicted (Pickett, 1980; Walker & Chapin, 1987; Bazzaz, 1996). The 'competitive hierarchy' could be seen as the primary—secondary continuum, where complete, non-invasible initial floristics represents one extreme, and initial composition with few species that are rapidly replaced is the other extreme (Glenn-Lewin & van der Maarel, 1992).

Tilman (1985; 1990) recognised the role of competition in succession to be operational and argued the importance of environmental resources such as nitrogen and light. He postulated that species experience trade-offs in resource requirements, meaning that any particular species would be more successful in competition over some particular range of ratios of environmental resources. If resource ratios changed temporally, then the series of species reaching competitive dominance as the resource ratios change would produce the observed succession. Tilman's resource-ratio hypothesis was successful in describing succession on sandy soils and newly exposed sites, but not for nutrient-poor soils as Tilman himself discovered (Gleeson & Tilman, 1990), or in wetland habitats (Shipley & Peters, 1990).

2.3.4.5 Life histories and 'vital attributes'

Understanding the life histories of plants is essential in order to decipher the properties that determine their success at different stages of succession (Drury & Nisbet, 1973; Pickett, 1980). For example, useful attributes for the initial colonising species include a short life cycle, high growth rate, high reproductive resource allocation, continuous, early seed production and small seed size (Whitmore, 1990).

Using life history properties, Noble & Slatyer (1980) predicted succession according to their 'vital attributes'. This conceptual and basically qualitative approach identified those attributes of a species that are fundamental to its active role in successional sequences during regeneration after fire. The 'vital attributes' are grouped into three parts: -

(i)   the method of arrival or persistence of a species at a site during and after disturbance;

(ii)   the ability of a species to establish and grow to maturity in a developing community; and

(iii)   the time taken for a species to reach 'critical life stages', which include time to reach reproductive maturity, lifespan in an undisturbed community and the time period for all propagules to become locally extinct.

This results in a number of transition diagrams for various species 'types', showing those that can dominate a particular disturbance phase and the sequence of life stages that a species will pass through as a result of a particular disturbance regime.

The Noble & Slatyer model was adequate in re-creating successional sequences of relative abundances in *Calluna vulgaris* (L.) Hull. heath in north-east Scotland (Hobbs *et al.*, 1984) but in its original, qualitative form the model failed to reproduce satisfactorily the multi-

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dominant cycling phase complex of *Betula-Acer-Fagus* hardwood forest as described by Forcier (1975). The inability of this model to perform quantitative predictions is unfortunate, as its accuracy cannot be tested statistically (McCook, 1994). Moreover, the outcome of the model is effectively dependent on the species present at the outset of succession in whatever life stage (Miles, 1987). Consequentially, new invaders cannot be predicted, nor can the inevitable phenomenon of site modification. On a more optimistic note, the model proved successful in predicting multiple pathways and post-fire regeneration (Cattelino *et al.*, 1979).

Van der Valk (1981) used a similar qualitative Gleasonian model for freshwater wetlands. His model was based on the presence and abundance of species according to life history and adaptation to allogenic forces. All plant species were classified into life history types based on potential lifespan, propagule longevity, and propagule establishment requirements. Each life history type had a unique set of characteristics and thus potential behaviour in response to controlling environmental factors such as water-level changes. The model uses these environmental factors to create the 'environmental sieve'. As the environment changes, so does the sieve and hence the species present. However, the sieve model does not explicitly recognise autogenic processes, a problem that could easily be ameliorated with the addition of a feedback loop (Mitsch & Gosselink, 1993).

To date, the forest simulation models created by Huston & Smith (1987) have provided the most convincing evidence for the importance of life history correlations, the essence of which is their testability (McCook, 1994). In summary, the simulations follow individual trees through their life cycles, modelling birth, growth and demise as life history traits regulated by competition for light. These are in turn explicitly and individually regulated

by neighbouring plants. Huston & Smith base their ideas categorically, firstly on the JABOWA model created by Botkin *et al.* (1972) and secondly on the FORET model (e.g. Shugart, 1984), although these models are more applicable for prediction and management purposes (McCook, 1994). The simulation models of Huston & Smith are based on an individualistic rather than a population basis and incorporate causal biological concepts. These are: competition for light and nutrients, based on growth and mortality; recruitment and mortality with stochastic and physiological components; growth based on estimated photosynthetic rates for the particular species at particular light levels; and changes in resource levels in the immediate environment. As the simulations are mathematically based, the output is quantitative and testable (McCook, 1994).

Using two species with varying combinations of life history traits, the simulations indicated five possible patterns of species abundance during regrowth (Figure 2.9): replacement succession (sequential); divergence; convergence; total suppression; and pseudo-cyclic replacements.

Figure 2.9 Five different patterns of abundances for two species during succession, as described by Huston & Smith (1987). In simulated succession the authors found the different combinations of life history traits for the two species generated different patterns of species abundances. After Huston & Smith (1987).

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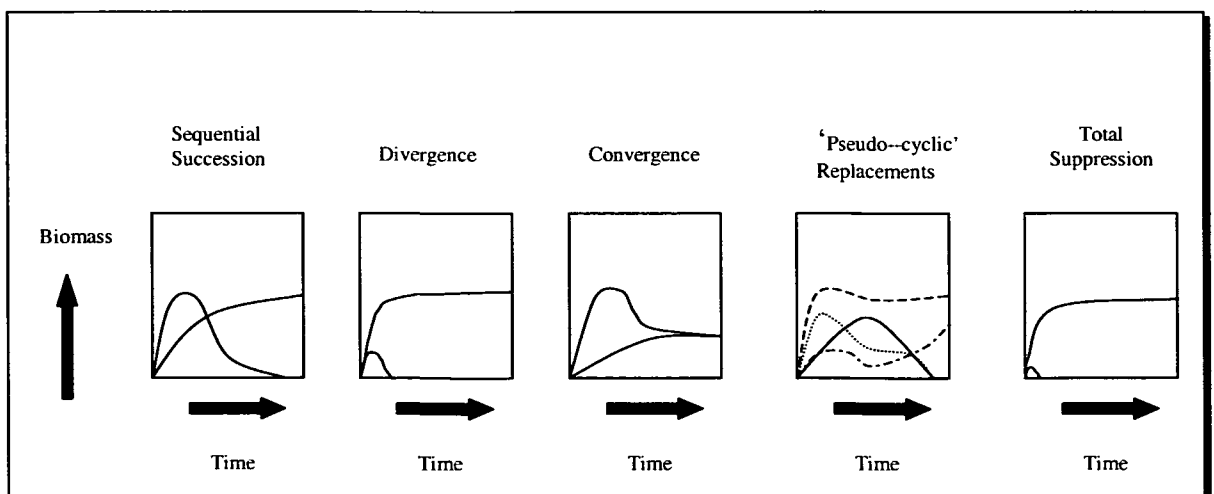
Interestingly, Huston & Smith found that the life history characteristics that confer competitive success for the early- and late-successional species were inversely correlated, producing the sequential replacement pattern, displayed in Figure 2.9. This means that successional replacements occur when species attributes such as wide dispersal, rapid growth and high rates of sapling establishment are exclusive of traits such as high shade tolerance or high maximum size. If these traits are not inversely related, the other patterns of species abundances occur (Huston & Smith, 1987). The model was expanded to include more species and still produced similar sequential successional patterns. The model is not an exclusive explanation of succession but rather a simplest case, which demonstrates that complex, facilitative interactions between species are not necessary to generate sequences of species dominance (McCook, 1994).

2.3.4.6 Changes due to species interactions

Changes in vegetation as a result of the effects of particular species on other species, either directly or via environmental modification, has long been a central theme of succession (Glenn-Lewin & van der Maarel, 1992). As McCormick (1968, page 349) said:

'There is no question that reactions do occur. A single plant, whether lichen or redwood, casts shade, changes the pattern of air movements, produces organic material that may become humus, and affects the site in other ways. The importance of such effects in succession, however, has not been tested adequately and certainly the generalisation that these effects constitute the driving force of succession is not substantiated.'

In an attempt to explain this subject, Connell & Slatyer (1977) expanded the ideas of Drury & Nisbet (1973) and Egler (1954) and proposed a post-colonisation model containing three alternative pathways for autogenic processes which can operate simultaneously for individual species and at different phases of the same vegetation sequence. The processes are termed facilitation, inhibition and tolerance.

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Facilitation

Facilitation describes a situation in which one or more species enable the establishment, growth or development of another species or, simply, they 'prepare the way'. Facilitation may be caused by autogenic changes that are desirable to future species, which is the same as the reaction or relay floristics model Clements (1916; 1928) viewed as the driving force of succession. This facilitation model was essentially deterministic, in that it supposed that perturbation of any stage in the sequence would result in a steady rebuilding of that stage and a return to the trajectory leading to the regional monoclimax. An example of facilitation can be seen in the nitrogen-fixing species that control primary successions after glacial recessions. These plants ameliorate the harsh conditions, paving the way for non-nitrogen fixing plants and eventually spruce forest (Crocker & Major, 1955; Lawrence *et al.*, 1967). These plants are often termed nurse plants. Work by Russell & Vitousek (1997) on the volcanic island of Mauna Loa, Hawaii, showed the mat-forming fern *Dicranopteris linearis* (N.L. Burm.) Underw. has an important influence on soil genesis. As a result of slow decomposition rates, the fern is a major contributor to soil detrital pools where nutrients are accrued, so facilitating 'later' species.

In the case of secondary succession, the extent of the role of reaction is uncertain. Several studies of old-field succession have refuted the theory by finding soil-stored seeds of species also found in the later stages of succession (Egler,1954; Drury & Nisbet, 1973; Niering & Goodwin, 1974). These authors maintained that most species appearing in successions developed on abandoned fields were present at the beginning as soil-stored seeds, rhizomes and regenerating roots. However another example of secondary succession reported by Miles (1987), showed that later colonisers on *Calluna*-dominated heath could

not grow even in the absence of competition, unless previous species had modified the soil. In reality, many soil properties alter during secondary succession, in particular pH and nutrient cycling (Miles, 1987).

Inhibition

Inhibition is the prevention of plant maturation or growth, or especially the prevention of plant establishment, by existing plants. When the first colonists are good competitors it is only their short life span that gives way to other species. Inhibition generally results from environmental changes that are detrimental to potential future species. A good example of inhibition was illustrated by Niering & Egler (1955) and Niering & Goodwin (1974) where the invasion of 'next successional' trees at a site was prevented for 25 years by low light levels created by a dense *Viburnum* shrub canopy. On moorlands, the presence of bracken *Pteridium aquilinum* is seen to prevent the establishment of *Calluna vulgaris* (Miles, 1987).

Tolerance

Tolerance describes the situation where the recruitment and growth of one species will neither inhibit or enable the presence of other species during succession. Tolerance was noted in forest succession where each progressive species can tolerate deeper shade that its predecessor. As the forest advances the canopy becomes denser. In this deeper shade other species become successful (Connell & Slatyer, 1977).

Tolerance certainly operates to some extent in primary succession, but because the soil at the beginning of secondary succession is never devoid of propagules, changes will never occur without a degree of the 'initial floristic composition' model (Miles, 1987).

The three processes proposed by Connell & Slatyer have improved and reshaped thinking on succession and the relative behaviour of species, encouraging new research into successional mechanisms. Connell & Slatyer have been criticised, however, because facilitation, inhibition and tolerance are not mechanisms at the level of species by species replacement (Peet & Christensen, 1980; Walker & Chapin, 1987; Pickett *et al.*, 1987a). Each of the processes groups a number of elements and interactions, the importance of which alters during succession (Walker & Chapin, 1987). Connell *et al.* (1987) responded by explaining that the mechanisms were never designed to describe successional change, but supposed to model one aspect— the *net effect* of an earlier species on a later one. Furthermore, facilitation, inhibition and tolerance address species interactions and were not intended to cover other successional processes such as those that result from life history differences, colonisation or herbivory (Connell *et al.*, 1987). Perhaps most significantly, Connell & Slatyer assert that, while they recognise some examples of the facilitation model, there exists little evidence in support of the tolerance model, a statement in stark contrast to Grime's (Grime, 1979) emphasis on stress-tolerance, as a major component of his model.

Grime's C-S-R model

Grime's (1979) C-S-R model was developed in order to 'analyse in simple terms the processes which control the structure and composition of the vegetation'(Grime, 1979). The essence of Grime's work is that all plants have evolved three broad strategies in response to habitat 'stress' (low levels of resources), habitat 'disturbance' and competition which were originally orientated at the tips of his triangular model (Grime, 1974). The extreme C-S-R strategies that Grime proposed are (Table 2.5) competitor, stress-tolerator

and ruderal, which are strategies for the following environments: low disturbance-low stress; low disturbance-high stress; and high disturbance-low stress, respectively.

Table 2.5 The C-S-R strategies proposed by Grime (1979).

Intensity of disturbance	Intensity of stress	
	Low	High
Low	Competitors	Stress-tolerators
High	Ruderals	(No viable strategy)

Ruderal plants are suited to an environment with frequent disturbance, but not competition. Their powers of escape to uncontested habitats is an important strategy (Colinvaux, 1993). The competitors adapt to low disturbance and low stress and will always replace the ruderals in succession by replacement. The third strategy, the stress-tolerator lives amongst the competitors, which in itself is a powerful stress. Stress-tolerators are suited to conditions of low disturbance with high stress (Colinvaux, 1993). Thus Grime's model has three patterns of resource allocation:

(i) Most resources to competition = C (competitor) species

(ii) Resources divided between stress resistance and competition = S (stress-tolerant) species

(iii) Most resources to fecundity and dispersal = R (ruderal) species

According to Grime, understanding the potential productivity of a site makes it possible to recognise the probable sequence of life form during succession. In a most productive habitat, succession is characterised by a middle phase of intense competition in which competitive herbs, followed by competitive, shade-intolerant shrubs and eventually trees come to dominate the vegetation. The climax phase is one in which stress-tolerance becomes more important as shading and nutrient stress, induced by large, long-lived forest

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trees, which cast deep shade and sequester nutrients, come to dominate the vegetation. In less productive habitats, the appearance of highly competitive species is inhibited by the earlier onset of resource depletion and the stress-tolerant phase. Thus the predictive power of Grime's model is based on an appreciation of the inherent productivity of particular seral habitats. The predictability of this model was questioned by McCook (1994) based on this assumption that plants have fixed strategies on the two dimensions of stress and disturbance, and that these dimensions predict constant successional relationships between any two species. However, according to Huston & Smith (1987) the relative adaptive suitability of two species may vary, depending on the particular circumstances. Also, Grime's approach has not been widely applied to successional studies, so the power of this sort of analysis to decipher the mechanisms of succession remains to be seen (Bazzaz, 1996). One reason why this approach has not been readily adopted may be due to the non-empirical nature of the model. An investigation into the explanatory power of plant strategies and Grime's triangular model for successional processes on Goss Moor can be found in Chapter Seven.

Third party effects

Grubb (1986) defined a 'third party' as a species plant, animal or micro-organism that may change the relative establishment success of two species. In the absence of a third party, one species will always be more successful than the second, but in the presence of the third party the second will be a more successful coloniser. Such a third party may for example be important in the process of establishment. *Calluna vulgaris* suppresses the establishment of the non-native *Picea sitchensis* but not the native *Larix leptolepis* L. in the Scottish uplands. In Sweden, eruptions in the local populations of vole (*Clethrionomys rufocanus* Sundevall.) can destroy the dense *Empetrum hermaphroditum* (Hagerup.) Böcher. and

Vaccinium spp. heath, allowing establishment of *Betula* seedlings. It seems without these gaps, birch would not regenerate, illustrating third party facilitation (Grubb, 1986).

2.3.5 SPATIAL ASPECTS OF SUCCESSION

Community succession can be viewed as a changing mosaic of patches of different sizes, ages, structures and composition (Watt, 1947; Glenn-Lewin & van der Maarel, 1992). Thus, spatial patterns are important for understanding community change and cannot be ignored as random noise (Austin, 1981; Austin & Belbin, 1981; Glenn-Lewin & van der Maarel, 1992). Even in an apparently uniform terrain, most vegetation samples include a complex mosaic of microhabitats, arising from factors such as edaphic variation; interactions in microtopography and climate; selective predation; and local distribution of soil and plant activities themselves—nutrient availability, water, shade, litter accumulation and toxins (Grime, 1979). The scale or scales at which ecologists perceive spatial patterning and recognise boundaries, whether discontinuities or transitions, is a legacy of the geological history and processes that moulded and modified the landscape (Anderson, 1986).

Spatial aspects of succession can be studied using a number of different methods, such as direct historical evidence or experimental manipulation (Glenn-Lewin & van der Maarel, 1992). Spatial models can be used to explain succession, as Botkin (1992) showed using gap processes to describe forest succession. Van Tongeren & Prentice (1986) and Prentice *et al.* (1987) used changes in the spatial coordinates of individual species to describe heathland dynamics. Other workers have equated spatial mosaics on adjacent sites to temporal sequence of phases in the same succession.

Chronosequences have been widely used (e.g. Pickett, 1989; Bakker *et al.*, 1996) to observe vegetation of different ages in areas of similar land form and substrate. To use the 'space for time' theory or ergodic hypothesis (Alexandrov & Logofet, 1994), the assumption is that each site has undergone the same sequences (Colinvaux, 1993). However, this method has received criticism. Dale & Blundon (1991) showed how spatial patterns themselves can change with succession, as seen on glacial moraines where single species and multi-species change, as well as the scales of pattern, but the number of scales at which these patterns occur stay the same. To overcome this problem Miles (1979) emphasised the use of uniform sites and suggested that researchers should be circumspect of the inevitability of allogenic effects.

The continuum concept strongly opposes the hypothesis that zonation indicates succession. Zoning is thought to be produced by groups of species with similar tolerances that tend to aggregate along the different environmental gradients. In wetlands, the moisture gradient is frequently ecologically steep, producing sharp vegetation boundaries (Mitsch & Gosselink, 1993).

Recently, authors have conducted simulations of spatial succession and other vegetation processes using cellular automata (Wolfram, 1984; Inghe, 1989). The cellular automaton consists of an area subdivided into a grid of small cells, in which individual plants grow. Each cell contains discrete ecological conditions which may change with time due to the influence of neighbouring cells and the history of the cell itself (Jeltsch *et al.*, 1996). Colasanti & Grime (1993) used the rules derived from the plant strategy C-S-R theory (Grime, 1979) to construct a cellular automaton model. Using these rules, the fundamental differences in the resource dynamics of founder populations produced familiar successional

patterns, where there are patterns of dominance and decline. These patterns are consistent with Egler's (1954) initial floristic composition hypothesis, Odum's (1969) theory of ecosystem maturation and Connell & Slatyer's (1977) inhibition model of secondary succession.

2.3.6 PREDICTION OF SUCCESSIONAL PATHWAYS

Examination of the literature reveals that descriptive methods are most prevalent for studying succession. These methods can explain what has happened or what is happening, based on investigating the history of the community from sources including old journals, photographs, pollen records, macrofossils, or observing permanent plots (Peet & Christensen, 1980). However, good description is essential as the accuracy and sensibility of both experimental interpretation and modelling depends on it (Glenn-Lewin & van der Maarel, 1992).

Multivariate methods can be used to analyse successional data, to sort out temporal trends from environmental patterns and randomness, and to develop successional vectors of both communities and species (van der Maarel, 1969; Austin, 1977). Analytical methods include multiple regressions, canonical correspondence analysis and detrended correspondence analysis ordination.

Succession experiments have been employed to study species composition changes, changes in ecosystem properties, the importance of resource competition, successional mechanisms and applied management questions. The treatments used in this work involve plant removal or addition (Armesto & Pickett, 1986), resource supplementation (Tilman, 1987) and controlled disturbance regime such as gap creation, fire treatments (Hobbs *et al.*,

1984) and grazing enclosures. However, 'indirect effects of other interacting species may confound interpretation' of the experimental results (Connell *et al.*, 1987).

Modelling in succession expresses the processes of vegetation dynamics in the form of symbolic logic and mathematics (Glenn-Lewin & van der Maarel, 1992). Modelling is becoming increasingly important, as is evident in this review, due largely to the need for ecological forecasting and management. Models can be classified into:

(i) analytical models which are theoretical, explanatory expressions derived from observed characteristics and behaviour of ecological systems (e.g. Finegan, 1984). These models are ideal for heuristic exploration of assumptions and their consequences (Glenn-Lewin & van der Maarel, 1992);

(ii) simulation models such as those proposed by Huston & Smith (1987), which attempt to duplicate processes or phenomenon (Glenn-Lewin & van der Maarel, 1992); and

(iii) statistical models which are determined by a random distribution of probabilities of events that are often replacements or transitions of species to species or state (community) to state. Markov models represent a good example of this type (Usher, 1987).

Huston & Smith (1987) showed that life history traits can predict the various patterns of species occupancy. This is due to trade-offs between traits that favour species early in revegetation of a site, and those that favour long-term dominance. When these traits are inversely correlated, successional replacement will result. These species life history strategy trade-offs have considerable potential for understanding community dynamics (Keddy, 1989; Austin, 1990; Tilman, 1990). Tilman (1990) maintains that these ideas will

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provide a unifying and simplifying theme for vegetation competition theory. In future work the simulation models could be modified to synthesise numerous factors including species availability, the history of disturbances and especially the effects of different species on each other (McCook, 1994). For management purposes, McCook (1994) identified the need to expand the models to include allogenic changes, patchiness and disturbance, so that the outcome of adverse or future perturbations could be predicted (Smith & Huston, 1989).

Horn (1976) used Markovian replacement models to indicate the probability that each tree species will be replaced by one of its kin or by an individual of another species within a specified time period. The composition prediction is made by arranging tree by tree probabilities into a projection matrix and multiplying by a vector of the initial species composition. Horn (1976) used sapling density to predict the replacement probabilities of mature trees.

Markov model predictions are useful for examining largely unknown systems (Miles, 1987) and applied management cases, but their weakness is that the replacement prediction is probability (empirical) based, and they therefore lack explanations as to why species replacements are occurring. Also, the model predicts temporal and not spatial replacements and cannot be tested of falsified (McCook, 1994).

The main problem with Markov models is that the system always converges to a constant outcome, independent of the initial species composition, because the species probabilities are non-changing, thus predicting a single 'climax' whatever the circumstances. Horn (1981) argues that the convergence is entirely statistical and requires no biological cause.

Markov models are a gross oversimplification, as in real life replacement probabilities are affected by recruitment variations. These variations may change according to other factors like seasonal and annual fluctuations, herbivory and other disturbances resulting in several different climaxes (Drury & Nisbet, 1973). Horn's theory that juvenile trees would eventually replace the adult trees was disproved by McIntosh (1980), who discovered that most juveniles died before they even reached adulthood.

It has become evident from the literature that no type of community succession, whether primary or secondary, can ever be explained exclusively by any one of the models mentioned throughout this literature review. The models relate to succession of particular species in particular situations and not vegetation types (Miles, 1987). This is not surprising as it is the individual species and their populations that change, rather than the vegetation type. In order to make generalisations at a community level, the species would have to comprise of a very closely related genetic network. In reality no vegetation properties have ever been found that can not be demonstrated by the effects of species interactions (Burrows, 1990).

Ecesis	Competition	Stabilisation	

Migration

Reaction

THE CLEMENTSIAN VIEW

DISTURBANCE THAT CREATES A BARE PATCH

Mixed propagule bank is present

All species establish → Early-colonists assume dominance. Late successional species remain but are suppressed → Early colonists perish, late-successional species assume dominance

INITIAL FLORISTICS (Egler, 1954)

Species dominance changes as each species responds to changing resource ability

CHANGING RESOURCES (Drury & Nisbet, 1983)

Early-successional species establish

Early-successional species perish → Late-successional species perish → Late-successional species persist

RELAY FLORISTICS

Initial colonists modify the environment so it is more conducive to late-successional species → Late-successional species invade and assume dominance

FACILITATION MODEL (Connell & Slatyer, 1977)

Initial colonists modify the environment so that late-successional species cannot establish → Later species establish only when early-successional species die

INHIBITION MODEL (Connell & Slatyer, 1977)

Early-and late-successional species establish

Early-successional species modify the environment to exclude other species → Late-successional species tolerate competition and assume dominance

TOLERANCE MODEL (Connell & Slatyer, 1977)

TIME

Figure 2.10 Synthesis of the successional models (adapted from Luken, 1990).

2.3.7 A SUCCESSIONAL FRAMEWORK

This review has shown that a great number of interacting mechanisms operate during succession, a summary of which can be found in Figure 2.10. Despite the substantial body of literature on mechanisms, the need for further studies has become evident. Current speculations and hypotheses need to be tested, and new hypotheses developed. One area of interest for resource management may be to review succession when mechanisms are modified, such as changes in grazing regimes and the thinning of woodlands to allow light to reach the ground flora.

To describe the ultimate causes of vegetation change Pickett *et al.*, (1987a; 1987b) summarised the successional mechanisms in an hierarchical manner to span all levels of inquiry. The causes of succession are arranged in a three-level hierarchy (Table 2.6). The highest level in the hierarchy defines the general and universal conditions under which succession occurs: (i) availability of open sites; (ii) differential availability of species; and (iii) differential performance of species at the site. To provide a more detailed understanding of succession, each of these causes is subdivided into ecological processes. A further division results in the third level of hierarchy, which is required to elucidate the mechanisms of succession at particular sites and to make detailed predictions.

The hierarchical layout enables the appropriate causes to be chosen to tackle questions about succession at the desired level of generality or level of organisation. In order to successfully explain succession, design experiments and construct models it is vital to identify which level in the hierarchy is to be investigated (Pickett *et al.*, 1987a; 1987b).

The authors suggest, quite appropriately, that the hierarchy arrangement will enhance insight into the relationship of different causes to one another and lead to increased precision when making predictions to be tested experimentally.

Table 2.6 A hierarchical summary of the causes, processes and factors of succession (after Pickett *et al.*, 1987a; 1987b).

General causes of succession	Contributing processes or conditions	Modifying factors
Site availability	Coarse-scale disturbance	Size, severity, time, dispersion
Differential species availability	Dispersal	Landscape configuration, dispersal agents
	Propagule pool	Time since last disturbance, land use treatment
	Resource availability	Soil condition, topography, microclimate, site history
Differential species performance	Ecophysiology	Germination requirements, assimilation rates, growth rates, population differentiation
	Life history	Allocation pattern, reproductive timing, reproductive mode
	Environmental stress	Climate cycles, site history, prior occupants
	Competition	Hierarchy, presence of competitors, identity of competitors, within community disturbance, predators, herbivores, resource base
	Allelopathy	Soil chemistry, soil structure, microbes, neighbouring species
	Herbivory, predation and disease	Climate cycles, predator cycles, plant vigour, plant defences, community composition, patchiness

2.3.8. SUCCESSION: THE NEXT GENERATION!

In the past, the intellectual need for a generalised community succession theory was evidenced in the literature. Today it seems that this quest has been abandoned and efforts are concentrating on models, mechanisms and understanding the processes that determine the structure and composition of vegetation. Despite much progress in modelling succession the tension between the simplicity of models for prediction and complexity to include all relevant parameters remains unsolved. Because errors in models can interact non-additively (Rastetter *et al.*, 1992) model complexity may overwhelm biological reality (Bazzaz, 1996). However, there are a number of tools available to identify the processes most important to the problems and goals at hand (Gibson & Brown, 1985).

Perhaps one of the most surprising points of the 'model' succession literature is that practical resource managers have not embraced the models or the terminology of 'professional' ecological theory (Anderson, 1986; Miles, 1987). This accentuates the need for improved understanding of the processes that are transferable to real community successions. As one aim of succession research should be to predict changes in vegetation when or if the management changes, the need for improved communication and information transfer is apparent.

In order to understand the ecological and successional processes occurring on Goss Moor it is necessary to first describe the main wetland vegetation communities. This research begins with a preliminary survey of the poor-fen vegetation on Goss Moor.

Chapter Three: A preliminary survey of the poor-fen communities on Goss Moor

3.1 INTRODUCTION

As evidenced in Chapters One and Two, Goss Moor NNR is an internationally important wetland site. Despite this, the vegetation assemblages have not been described in detail. To ensure the wetland is understood in both a scientific and management context, this chapter provides the first formal description of the range of poor-fen communities present on Goss Moor.

The dearth of phytosociological information for the site is mainly due to the age and character of the reserve. Interest in the vegetation was generated following the SSSI designation in 1988. However, the logistics of surveying the site were hampered by the vegetation itself, which encompasses dense tussocks of purple moor grass *Molinia caerulea* (L.) Moench., scattered gorse *Ulex gallii* Planch. and *U. europaeus* L. on raised banks, extensive willow *Salix cinerea* carr and floating-mat poor-fen communities. All of these vegetation communities are relatively recent and a legacy of the past tin streaming operations that were discussed in Chapter Two. The discussion therein revealed how the different types of excavations and waste dumps have produced a range of micro-topographies. The pools produced from excavations are various in size and depth, and have influenced the type of vegetation and the nature of their boundaries. The boundaries between communities can be described as 'transitional areas', which are zones of floristic and ecological change (Kent *et al.*, 1997). These transitional areas between communities can be described as either ecotones or ecoclines. Ecotones describe vegetation zones displaying rapid change or sharp boundaries, which are largely caused by anthropogenic activities. Ecoclines describe plant communities separated with a more gradual gradient of change, corresponding to progressive spatial change in one or more underlying environmental factors (Kent *et al.*, 1997).

Two reports provide the phytosociological information presently available for the site, namely the SSSI designation description and the preliminary report of a long-term monitoring programme commissioned by Indian Queens Power Limited (Dale *et al.*, 1997). The latter report revealed the presence of an interesting array of wetland vegetation types, which were mostly poor-fen among carr. The term poor-fen was discussed in detail in Chapter Two, and is used to describe mire communities that are both species-poor and base-poor (Wheeler, 1984). In terms of both attributes, poor-fen communities can be thought of as intermediates on a gradient from species-rich fen to bog (Du Rietz, 1949). The poor-fen on Goss Moor is most similar to NVC type S27 (Rodwell, 1995). The vegetation is typified by floating-mats of *Potentilla palustris* (L.) Scop. and *Menyanthes trifoliata* L., which are subject to winter flooding (Dale *et al.*, 1997). However, this community occurs along a number of complex transitions, including: gradation into oligotrophic mire (NVC types M5, M29, Rodwell, 1991b); vegetation similar to NVC type M9 (Rodwell, 1991b) *Carex rostrata* Stokes.-*Calliergon giganteum* (Schimp.) Kindb. mire; *Molinia caerulea* mire (NVC type M25, Rodwell, 1991b); rush pasture (NVC type M23, Rodwell, 1991b) open water and willow carr (NVC type W1, Rodwell, 1991b) (Dale *et al.*, 1997). These complex transitional communities also display many intermediates between them, thus highlighting the need for a detailed poor-fen survey. Some of the transitions are undoubtedly successional, originating from the open water pools created by mining excavations. Others are presumably indicative of discrete differences in environmental conditions such as water regime and substrate type. The research described in this chapter intends to:

(i)   provide a classification of the range of poor-fen communities;

(ii)   describe the distribution of these; and

(iii)   identify possible pathways of succession occurring on Goss Moor.

Due to the relatively recent nature of the vegetation communities on Goss Moor, and the absence of peat or long-established ponds, studying succession by methods such as peat stratigraphic investigations (e.g. Webb & Moore, 1982; Moore & Evans, 1991) was not possible. However, to study vegetation change, the ergodic hypothesis was considered. Substituting a spatial ecological series for a time-based successional one is a traditional way of reasoning in studies of ecological succession (Alexandrov & Logofet, 1994). The validity of this ergodic hypothesis is disputed, as spatial ecological series are often very stable and peat stratigraphic studies by Walter (1979) found no real evidence for significant directional boundary shifts. However, Spence (1964) found fen vegetation to be particularly unstable and more susceptible to change than other terrestrial vegetation types. These changes were attributed to variations in water table depth, for which even subtle annual differences can affect the overall structure of the vegetation community. Also, the gradual accumulation of organic material and peat causes water flow patterns in the community to be diverted and modified (Proctor, 1974). This, inevitably, has an autogenic effect on the vegetation composition.

The nutrient dynamics of wetlands are known to behave in a very complex manner (Proctor, 1974; Shaw & Wheeler, 1990), as was discussed in Chapter Two. Previous work has shown that 'snap-shot' chemical surveys, or even quite detailed monitoring has no clear relationship to the composition of the vegetation (Shaw & Wheeler, 1990). This was also true in the baseline survey of Goss Moor (Dale *et al.*, 1997) and for this reason it was decided that variables such substrate and water chemistry would be omitted from the poor-fen survey. In the case of substrate pH, Dale *et al.* (1997) found no significant differences in pH between the range of plant communities recognised qualitatively. In situations when it is impractical or not possible to collect environmental data, the potential ability of plant species to indicate the quality of the environment can be considered (Diekmann & Dupré, 1997; Hawkes *et al.*, 1997). The work of Ellenberg provides a comprehensive set of

numbers for six principal environmental variables (Ellenberg *et al.*, 1991), reflecting the preferences exhibited by individual plants in the field and derived for a large number of Central European species. Although the Ellenberg values were originally applicable to Central Europe they are also thought to be viable for use in Britain. Work by Thompson *et al.* (1993) found that Ellenberg numbers correlated significantly with the results of extensive empirical screening experiments (e.g. Grime *et al.*, 1988). However, recently, the British equivalent to Ellenberg numbers have been produced (Hill *et al.*, 1999). The Ellenberg indicator values are subjective and based on detailed ecological observations, which follow the coding system presented in Table 3.1 for the four variables relevant to wetland plants in Britain. British Ellenberg indicator values have been repredicted from the Ellenberg indicator values by a simple algorithm, which consists of a two-way weighted averaging followed by local regression (Hill *et al.*, 2000). British Ellenberg indicator values follow the same coding system as the Ellenberg indicator values.

Environmental variable	Symbol used for both the Ellenberg and British Ellenberg Indicator value	An explanation of the minimum and maximum values for each environmental variable	
		minimum	maximum
Moisture	F	1=indicates extremely dry condition (e.g. bare rock)	12= depicts plants growing underwater
Reaction	R	1=depicts very acid soils	9=neutral or basic soils
Nitrogen	N	1=plants growing in poor mineral N situations	9=very rich N conditions that indicate pollution
Light	L	1=species showing a preference for full shadow in less than 1% light	9=species showing a preference for full light

Table 3.1 A summary of the definitions of the minimum and maximum Ellenberg and British Ellenberg numbers for the four environmental variables

Previous studies have shown that the unique species assemblages comprising different communities can be used effectively to indicate differences in the environmental conditions favouring each, via Ellenberg numbers (Diekmann & Dupré, 1997; Hawkes *et al.*, 1997).

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This chapter aims to evaluate the viability of both Ellenberg and British Ellenberg indicator numbers in distinguishing environmental variation between the poor-fen communities on Goss Moor.

Knowledge of the range of poor-fen vegetation and an understanding of the environmental factors that govern such communities is an essential basis for effective management. Present management on Goss Moor does not directly consider the poor-fen vegetation. However, this work intends to prioritise vegetation types according to their conservation value. To evaluate sites for conservation, Ratcliffe (1977) provided ten criteria. Of these, the most commonly considered are area, diversity, rarity, naturalness and threat of human disturbance (Usher, 1980). The main goal of conservation is to maximise the biodiversity and representation of notable and rare species present at a site. However, as poor-fens are, by definition, species-poor using this strategy for prioritisation would appear to be somewhat arbitrary. In order to effectively evaluate and prioritise poor-fen community types, other desirable qualities need to be defined. Wheeler (1988; 1996) has provided species scores specifically for evaluating fen sites, based on the numbers of rich-fen species (RFS), poor-fen species (PFS), bog species (BGS) and rare fen species (RARE). The Fenbase database (Wheeler, 1997) calculates a 'biodiversity score' and a 'target species score', which can also be used to evaluate the conservation value of sites.

Another technique is to derive rarity scores based on the distribution records of a given species. Eyre & Rushton (1989) assessed the rarity of water beetles by calculating the total number of tetrad records for a given area to produce a rarity value. The size and distribution of the poor-fen communities also contributes to the conservation value of poor-fen community types. Small, discrete patches are considered more vulnerable and have a higher conservation value than larger common patches of the same community. These methods of

site assessment are used to evaluate and prioritise poor-fen communities for conservation in relation to other fen sites and place them in a regional and national context.

This survey aimed to:

- provide a classification of the poor-fen plant communities;

- reveal the patch size and diversity of each vegetation type;

- assess the relative frequency and spatial distribution of each poor-fen vegetation type;

- look at relationships between the plant communities and their boundaries, as a means of understanding community development;

- investigate the value of Ellenberg and British Ellenberg numbers in distinguishing environmental variation between poor-fen communities; and

- identify possible patterns of hydroseral succession.

3.2 METHODS

3.2.1 SAMPLING STRATEGY

An extensive reconnaissance of the poor-fen vegetation was conducted in July and August 1997 in order to describe the range of the wetland communities that occurs across the whole site. The survey used a stratified random design, which was based on the initial identification of poor-fen vegetation by the presence of the key poor-fen species *Potentilla palustris* and *Menyanthes trifoliata* (Dale *et al.*, 1997). One sample or quadrat was recorded randomly in each patch of poor-fen identified.

3.2.1.1 Vegetation description

A 2 x 2 m quadrat was used to sample the vegetation in accordance with the NVC methodology for surveying 'mire' and 'swamp' communities (Rodwell, 1991b; 1995). All species of higher plants, mosses and liverworts were recorded. Plant taxonomic

nomenclature followed Stace (1997) for higher plants, Daniels & Eddy (1990) for *Sphagna* and Smith (1978) for other bryophytes. Abundance data within each quadrat were based on the percentage cover of each species, assessed by eye. Percentage cover values were also recorded for non-vegetated substrate. This was considered to be the most suitable recording method as percentage cover estimations are rapid, repeatable and cause minimal damage to the vegetation (Kent & Coker, 1992). On occasions when the vegetation patch was smaller than the quadrat, it was recorded in its entirety. In such cases, close consideration was made to ensure that the vegetation on the boundary was not sampled.

3.2.1.2. Collection of environmental data

At each sampling location, data were collected on the depth of the organic layer and standing water depth. The depth of the organic layer was determined using an auger, which was calibrated in mm using a measuring tape. The depth of standing water from the solid substrate to the surface was found using a 2 m long, calibrated metal rod.

3.2.1.3 Collection of mosaic and boundary data

At each sampling point, data were collected on the location, patch size and the type of boundary. To identify the spatial distribution of the poor-fen types, the location of each vegetation patch was recorded using a compass to take bearings from visible landscape features. In order to identify possible relationships between floristic composition and possible transitions that may indicate spatial succession, the surrounding vegetation boundary types, whether abrupt or gradual, were recorded. This was determined by dividing the perimeter of the community patch into quarters according to north-south and east-west bearings. Each quarter was considered in turn and decision was made as to whether the majority of the boundary was gradual or abrupt (Figure 3.1). If that quarter of the boundary was gradual it was counted as 25 %. If all four quarters of the boundary were gradual, the boundary score for that vegetation patch was 100 %.

The total area of each patch of vegetation was found using a 40 m measuring tape to determine the length and width (Figure 3.2). These were then multiplied to give the total area. For vegetation that occurred in different or unusual shapes, their areas were found by dividing them up and measuring more manageable shapes.

3.2.2 ANALYSIS OF VEGETATION AND ENVIRONMENTAL DATA

The aims of the data analysis were to describe the range of poor-fen plant communities and to elucidate the relationship between these communities and selected abiotic factors. To achieve these aims, a number of analyses were carried out.

3.2.2.1 Definition and classification of plant community types

In the first analysis, the main wetland plant communities present on Goss Moor were defined and classified using two-way indicator analysis (TWINSPAN) (Hill, 1979a; Kent & Coker, 1992). TWINSPAN is a polythetic (uses all the species data), divisive classification system, which has the advantage of being both robust and widely-used (Kent & Coker, 1992) and forms the basis for NVC classifications (Rodwell, 1991a; 1991b; 1995). It uses the presence and relative abundances of plant species to split data into successively smaller sub-groups. There is an expectation that differences in species composition between quadrats reflects the response of vegetation to environmental gradients, such as water availability and water chemistry in the case of Goss Moor. Thus these groups of quadrats represent different plant communities and are formed according to the presence of assemblages of species.

North

Sampler

West   East

South

⟋⟍⟍ Gradual boundary

▰▰ Sharp boundary
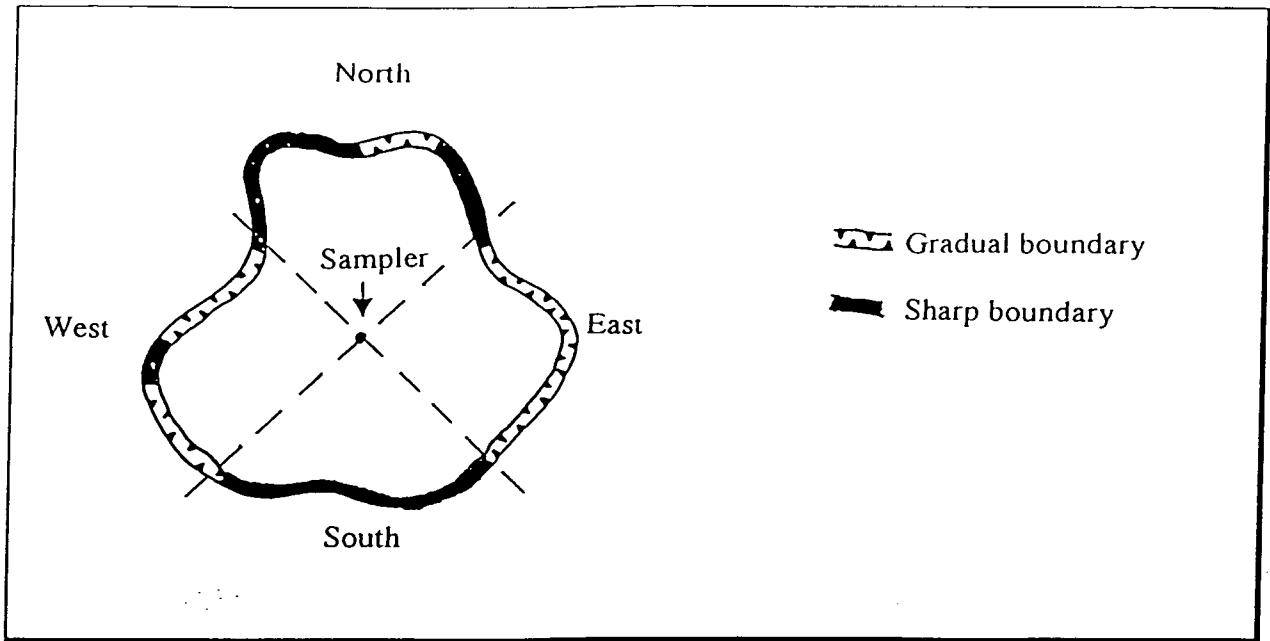
Figure 3.1 Shows how the boundary type was recorded for each patch. For example, to the north of the sampler the boundary is mostly abrupt, therefore this was recorded as 25 %. The total value for the whole of the patch would be 50 % abrupt and 50 % gradual. In this report this was recorded as 50 % ecocline.

Length

A

Width

B
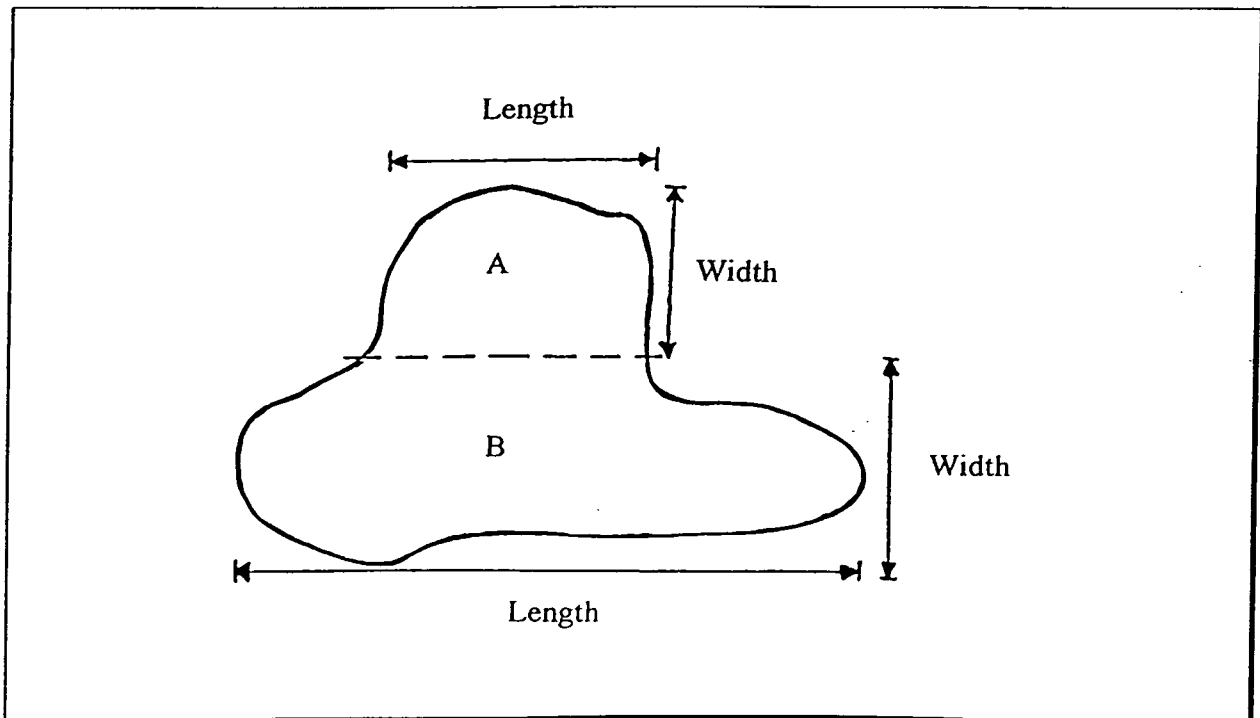
Width

Length

Figure 3.2 Shows how the area of each patch was found. In this example, the patch has been divided into two more manageable parts. The length and width of each segment was used to find the areas. These were added to find the total area

Oksanen & Minchin (1997) and Podani (1997) have illustrated that the TWINSPAN classification computer program is sensitive to the input order of the species data. For this work, classification of the data was achieved using the updated version of the TWINSPAN program, which encompasses stricter convergence criterion (Oksanen & Minchin, 1997). Default cut levels for defining pseudospecies were applied to the analysis (Kent & Coker, 1992). In terms of interpretation of the final output table, the eight groups of quadrats at the third hierarchical level were taken as the starting point for the derivation of TWINSPAN groups. For each group of quadrats in the third and subsequent hierarchical levels, the percentage constancy by group of each species was calculated. Constancy by group was defined as the number of quadrats in which the species was present, expressed as a percentage of the total number of quadrats in that group (Kent & Coker, 1992). Table 3.2 summarises how the TWINSPAN groupings were classified.

Table 3.2 Summary of the TWINSPAN groups used to classify the species present in the communities.

Roman numeral classes	Percentage number of quadrats the species occurs in	Occurrence of the species in the community	Species
V	81-100	constants	dominants
IV	61-80	constants	dominants
III	41-60	common or frequent	companion
II	21-40	occasional	general associates
I	1-20	scarce	general associates

TWINSPAN groups were then characterised by combinations of the most dominant species (*i.e.* those with the highest constancies), companion species and general associated species. Summary tables of the poor-fen community types were constructed. Those groups with the qualitative and quantitative species compositions that made the most ecological sense and which, in addition, related well to previously recognised communities such as those recognised by the NVC (Rodwell, 1991b; 1995) were taken as the final set of TWINSPAN

groups. The final TWINSPAN groups were therefore not all taken from the same hierarchical level.

3.2.2.2 Ordination of floristic and environmental data

In order to further examine the species assemblages, the vegetation data were analysed using the detrended correspondence analysis (DCA) and the associated computer software DECORANA (Hill, 1979b). This method was considered to be the most suitable ordination method for considering vegetation data alone (Kent & Coker, 1992). Once again, the updated version of DECORANA was used (Oksanen & Minchin, 1997), as the original version (Hill, 1979b) is sensitive to the input-order of the data (Podani, 1997; Oksanen & Minchin, 1997).

In order to assess the floristic and environmental relationships occurring across the site, canonical correspondence analysis (CCA) (Ter Braak, 1987) and the associated CANOCO computer software (Ter Braak, 1988) was used. CCA is a direct method of ordination, which incorporates correlation and multiple regression to produce an integrated ordination relating species and environmental factors (Ter Braak, 1987; Kent & Coker, 1992; Waite, 2000). The CCA method of ordination is considered more powerful than other ordination techniques in detecting species-environment relationships and is most suitable where the number of environmental variables is small compared to the number of quadrats (Ter Braak & Prentice, 1988).

3.2.2.3 Ellenberg and British Indicator values

Further environmental differences between the poor-fen community types defined by TWINSPAN were found using weighted Ellenberg indicator (EI) values and British Ellenberg indicator (BEI) values to calculate indicator values for acidity (R), moisture (F), nitrogen (N) and light (L). To estimate the composite value of an environmental variable

for each poor-fen community type, the weighted average of all indicator values for that variable, for those species present was calculated according to the following equation:

$$WA_{jk} = \overline{X}\left(\sum_{i=1}^{n} \left(\left(\frac{CAVij}{\sum_{i=1}^{n} CAVij} \right) * IV_{ik} \right) \right)$$

Where WA_{jk} is the weighted average for poor-fen community (j) and variable (k), CAV_{ij} the cover-abundance value of species (i) in that community, and IV_{ik} the indicator value of the species for that variable. In some cases, the Ellenberg figure for a particular species was uncertain due to the lack of information or the wide-range of environmental conditions it occurs in. In these cases, the species was excluded for that factor (Hawkes *et al.*, 1997). Examples of missing data include the light value for *Sphagnum capillifolium* Brid. and the reaction figure for *Molinia caerulea*. The lack of nitrogen values for bryophytes was dealt with in two ways: by taking the value as zero, or by removing the species from the data set altogether (Ertsen *et al.*, 1998). Both approaches are presented in the results.

Differences among the poor-fen groups for each of the variables were investigated by parametric single factor ANOVA and a Tukey multiple comparisons test, using the SPSS (version 9.0) statistical analysis computer program. When variances were significantly heterogeneous, the data were analysed using the Kruskal-Wallis with the test tied ranks method, followed by multiple comparisons test (Zar, 1996). Differences between the British and Central European Ellenberg indicator numbers were found using a two factor ANOVA (Minitab version 6.0).

3.2.2.4 Determination of differences in conservation value

Once the vegetation types had been identified by TWINSPAN, other community-level characteristics were determined. The species richness or total number of species present in

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a community was found. Differences in species richness among the groups were analysed by single factor analysis of variance (ANOVA) using the SPSS statistical analysis computer program (version 9.0 SPSS Inc., U.S.A), followed by a Tukey multiple comparison test.

To gain further information on the poor-fen communities and to evaluate them in the context of Cornwall, the communities were weighted according to their occurrence in Cornwall as a whole. Using the Flora of Cornwall Database on CD-ROM (French, 2000), the number of tetrads (2 km x 2 km square) out of 1024, the total number of tetrads in Cornwall were attained for each species found. Mean weighted values for each community were found using the same equation as section 3.2.2.3 where the I.V. value was replaced by the number of tetrads within which each species occurred.

3.3 RESULTS

A total of 98 species were found in the 150 quadrats. TWINSPAN was used to identify twelve community types, which are shown in Table 3.3. The complete species assemblages for each poor-fen group are arranged according to NVC standard notation and tabulation and are found in Tables 3.4-3.16. All species are arranged in blocks based on their frequency, which is explained in Table 3.2. To clarify the species abundance range, median and mean abundances are given. The median is used to provide a single Domin value to further differentiate between the groups. To simplify the general content of the twelve poor-fen types pie charts were constructed on the basis of the main functional groups and are displayed in Figure 3.3.

Table 3.3 Summary of the twelve poor-fen community groups identified by TWINSPAN.

Poor-fen community type	Total number of species per group	Number of quadrats
pf-A. *Potentilla palustris- Carex nigra- Menyanthes trifoliata*	32	17
pf-B. *Potentilla palustris- Juncus acutiflorus- Menyanthes trifoliata*	35	20
pf-C. *Potentilla palustris- Equisetum fluviatile- Juncus effusus*	49	17
pf-D. *Potentilla palustris- Juncus acutiflorus- Equisetum fluviatile*	34	13
pf-E. *Potentilla palustris- Sphagnum recurvum- Eriophorum angustifolium*	52	15
pf-F. *Potentilla palustris- Menyanthes trifoliata- Equisetum fluviatile*	27	7
pf-G. *Potentilla palustris - Eriophorum angustifolium- Carex nigra*	33	14
pf-H. *Potentilla palustris- Aulacomnium palustre- Viola palustris ssp. juressi*	40	10
pf-I. *Calluna vulgaris- Sphagnum recurvum- Juncus acutiflorus*	37	10
pf-J. *Molinia caerulea- Rhytidiadelphus squarrosus*	52	11
pf-K. *Eriophorum angustifolium- Sphagnum papillosum- Molinia caerulea*	27	8
pf-L. *Molinia caerulea -Juncus effusus*	20	8

Table 3.4 The mean and median species abundance and frequency for Group pf-A in relation to the standard NVC classification tabulation

GROUP pf-A		Total number of quadrats = 17			
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Potentilla palustris	15	V (2-8)	6	32	25
Carex nigra	14	V (2-5)	5	8	8
Menyanthes trifoliata	13	IV (4-9)	5	19	18
Equisetum fluviatile	12	IV (2-5)	3	9	3
Eriophorum angustifolium	10	III (2-5)	4	12	10
Hypericum elodes	9	III (2-7)	4	7	5
Carex rostrata	9	III (1-8)	4	16	8
Agrostis stolonifera	8	III (1-4)	2	6	2
Juncus bulbosus	7	III (1-4)	1	4	1
Juncus acutiflorus	7	III (2-4)	4	5	5
Ranunculus flammula	7	III (2-4)	3	2	3
Molinia caerulea	4	II (1-9)	4	26	10
Carex echinata	6	II (1-4)	4	6	5
Galium palustre	4	II (1-2)	1	1	1
Erica tetralix	2	I (4-5)	4	15	5
Hydrocotyle vulgaris	3	I (1-4)	4	5	5
Juncus effusus	3	I (1-4)	3	3	3
Hypericum pulchrum	2	I (1-3)	2	2	1
Holcus lanatus	2	I (1-2)	2	2	1
Trichophorum cespitosum	2	I (4)	4	5	5
Carex curta	1	I (3)	3	2	2
Calliergon stramineum	1	I (3)	3	3	3
Eurhynchium praelongum	2	I (3)	3	2	2
Pedicularis palustre	1	I (1)	1	1	1
Caltha palustris	1	I (2)	2	1	1
Dactylorhiza praetermissa	1	I (1)	1	1	1
Sphagnum auriculatum	1	I (2)	2	1	1
Lotus pedunculatus	1	I (2)	2	1	1
Succisa pratensis	1	I (2)	2	1	1
Rhytidiadelphus squarrosus	1	I (1)	1	1	1
Valeriana officinalis	1	I (2)	2	1	1
Salix cinerea ssp. *cinerea*	1	I (2)	2	1	1

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Table 3.5 The mean and median species abundance and frequency for Group pf-B in relation to the standard NVC classification tabulation

GROUP pf-B				Total number of quadrats = 20	
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Juncus acutiflorus	19	V (2-7)	4	11	10
Potentilla palustris	17	V (2-8)	8	40	60
Menyanthes trifoliata	16	V (2-8)	4	18	8
Equisetum fluviatile	14	IV (2-7)	4	8	5
Mentha aquatica	9	III (1-6)	2	5	2
Eriophorum angustifolium	9	III (2-5)	4	5	5
Epilobium palustre	9	III (1-4)	2	2	2
Carex nigra	5	II (2-5)	4	9	5
Ranunculus flammula	7	II (1-2)	1	1	1
Hydrocotyle vulgaris	1	I (4)	4	5	5
Hypericum elodes	3	I (2-5)	4	8	8
Oenanthe crocata	2	I (2-6)	3	16	2
Calliergon cuspidatum	2	I (2)	3	2	2
Aulacomnium palustre	2	I (1-5)	2	11	1
Lotus pedunculatus	3	I (2-4)	3	3	3
Holcus lanatus	4	I (2)	2	1	1
Galium palustre	4	I (1-4)	2	3	1
Salix cinerea ssp. cinerea	2	I (2-3)	2	2	1
Luzula multiflora	3	I (2-4)	3	4	2
Juncus effusus	3	I (2-4)	4	4	5
Calliergon giganteum	2	I (2-4)	2	3	1
Hypericum undulatum	4	I (2-4)	3	2	2
Potamogeton polygonifolius	2	I (2-3)	2	2	1
Agrostis stolonifera	2	I (2)	2	1	1
Hypericum tetrapterum	3	I (1-2)	2	1	1
Calliergon stramineum	1	I (1)	1	1	1
Caltha palustris	3	I (1-2)	1	2	1
Eurhynchium praelongum	2	I (1-2)	1	2	1
Typha latifolia	1	I (8)	8	60	60
Equisetum palustre	1	I (1)	4	4	5
Juncus bulbosus	1	I (7)	7	50	50
Iris pseudacorus	1	I (2)	2	1	1
Dactylorhiza praetermissa	2	I (2)	2	1	1
Angelica sylvestris	1	I (2)	2	1	1
Deschampsia flexuosa	1	I (1)	2	1	1

Table 3.6 The mean and median species abundance and frequency for Group pf-C in relation to the standard NVC classification tabulation

GROUP pf-C		Total number of quadrats = 17			
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Potentilla palustris	13	IV (2-7)	6	29	30
Equisetum fluviatile	13	IV (2-6)	4	10	5
Juncus effusus	12	IV (2-9)	4	26	10
Juncus acutiflorus	9	III (2-9)	5	20	11
Agrostis stolonifera	9	III (1-8)	4	11	5
Eriophorum angustifolium	9	III (2-5)	5	17	20
Valeriana officinalis	9	III (2-5)	4	11	5
Lotus pedunculatus	7	III (1-5)	4	7	4
Hydrocotyle vulgaris	9	III (1-4)	3	2	2
Galium palustre	8	III (1-4)	3	4	2
Mentha aquatica	5	II (4)	4	8	8
Sphagnum squarrosum	4	II (3-7)	6	19	30
Molinia caerulea	5	II (1-5)	3	5	2
Rumex acetosa	6	II (2-4)	3	2	2
Juncus bulbosus	4	II (2-7)	2	16	1
Eurhynchium praelongum	4	II (1-4)	3	4	2
Epilobium palustre	4	II (1-4)	2	5	1
Holcus lanatus	4	II (1-3)	3	2	2
Calliergon cuspidatum	4	II (1-2)	3	2	2
Succisa pratensis	4	II (2)	2	1	1
Carex nigra	2	I (4-5)	4	18	10
Carex rostrata	2	I (4-5)	4	11	10
Calliergon giganteum	2	I (2-5)	3	4	2
Caltha palustris	2	I (2-4)	3	6	2
Lycopus europaeus	3	I (1-4)	3	3	2
Menyanthes trifoliata	2	I (1-4)	2	6	1
Viola palustris ssp. juressi	3	I (1-3)	2	2	1
Ranunculus repens	3	I (1-2)	1	1	1
Carex echinata	2	I (1-2)	2	2	1
Eupatorium cannabinum	2	I (1-2)	2	2	1
Calliergon cordifolium	1	I (3)	3	2	2
Calliergon stramineum	1	I (4)	4	5	5
Agrostis canina	1	I (4)	4	5	5
Sphagnum auriculatum	1	I (3)	3	2	2
Oenanthe crocata	1	I (3)	3	2	2
Angelica sylvestris	3	I (2-5)	2	14	1
Salix aurita	1	I (2)	2	1	1
Hypericum undulatum	1	I (2)	2	1	1
Prunella vulgaris	1	I (2)	2	1	1
Hypericum tetrapterum	1	I (1)	2	1	1
Ranunculus flammula	1	I (2)	1	1	1
Polygala vulgaris	1	I (1)	1	1	1
Aulacomnium palustre	1	I (2)	1	1	1
Lychnis flos-cuculi	1	I (1)	1	1	1
Luzula multiflora	1	I (1)	1	1	1
Carex demissa	1	I (1)	1	1	1
Juncus bufonius	3	I (2)	1	1	1
Calluna vulgaris	1	I (1)	1	1	1
Eleocharis palustris	1	I (1)	1	1	1

Table 3.7 The mean and median species abundance and frequency for Group pf-D in relation to the standard NVC classification tabulation

GROUP pf-D		Total number of quadrats = 13			
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Potentilla palustris	13	V (2-8)	5	27	25
Juncus acutiflorus	9	IV (2-5)	4	10	5
Equisetum fluviatile	9	IV (2-5)	4	9	5
Menyanthes trifoliata	3	II (4-5)	4	12	5
Sphagnum recurvum	3	II (3-7)	5	21	20
Mentha aquatica	3	II (3-5)	3	3	3
Hydrocotyle vulgaris	4	II (3-5)	5	19	20
Carex rostrata	3	II (2-7)	4	17	4
Carex echinata	4	II (1-5)	2	5	1
Eriophorum angustifolium	4	II (1-4)	4	3	5
Salix cinerea ssp. *cinerea*	4	II (2-4)	2	2	1
Carex nigra	2	I (4-5)	4	13	10
Calliergon giganteum	2	I (3-5)	3	9	2
Calliergon cuspidatum	2	I (3-4)	4	7	4
Holcus lanatus	2	I (2-4)	2	4	1
Agrostis stolonifera	3	I (1-2)	2	1	1
Epilobium palustre	2	I (2)	2	2	1
Calliergon stramineum	3	I (2-3)	2	1	1
Trichophorum cespitosum	2	I (8)	8	55	52
Deschampsia flexuosa	1	I (4)	4	5	5
Blechnum spicant	1	I (4)	4	10	10
Hypericum undulatum	1	I (4)	4	5	5
Valeriana officinalis	1	I (5)	5	15	15
Juncus bufonius	1	I (4)	4	5	5
Hypericum elodes	1	I (2)	2	2	2
Pedicularis palustre	1	I (3)	3	3	3
Juncus effusus	1	I (3)	3	2	2
Equisetum palustre	1	I (2)	2	1	1
Ranunculus flammula	2	I (2)	2	1	1
Sphagnum subsecundum	2	I (2)	2	1	1
Galium palustre	1	I (2)	2	1	1
Viola palustris ssp. *juressi*	1	I (1)	1	1	1
Carex curta	1	I (2)	1	1	1
Salix aurita	2	I (1-2)	1	1	1

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Table 3.8 The mean and median species abundance and frequency for Group pf-E in relation to the standard NVC classification tabulation					
GROUP pf-E		**Total number of quadrats = 15**			
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Potentilla palustris	15	V (4-8)	7	35	40
Sphagnum recurvum	13	V (2-6)	5	17	20
Eriophorum angustifolium	13	V (2-5)	3	8	2
Agrostis stolonifera	11	III (1-5)	3	3	2
Sphagnum squarrosum	10	III (2-7)	4	15	8
Equisetum fluviatile	9	III (1-6)	2	6	1
Juncus acutiflorus	9	III (2-6)	3	5	2
Viola palustris ssp. juressi	8	III (1-5)	3	3	2
Lotus pedunculatus	8	III (1-4)	2	2	1
Sphagnum fimbriatum	6	II (2-4)	4	3	4
Dicranum scoparium	5	II (1-7)	5	23	20
Molinia caerulea	6	II (1-5)	3	3	2
Sphagnum capillifolium	6	II (2-5)	4	5	4
Drosera rotundifolia	4	II (1-5)	4	7	5
Aulacomnium palustre	4	II (1-4)	2	3	1
Sphagnum auriculatum	6	II (2-4)	3	4	2
Succisa pratensis	4	II (1-4)	4	4	4
Luzula multiflora	6	II (2-3)	2	1	1
Holcus lanatus	4	II (2)	2	1	1
Epilobium palustre	5	II (2)	2	1	1
Galium palustre	4	II (2)	2	1	1
Menyanthes trifoliata	4	I (3-6)	5	16	20
Calliergon giganteum	2	I (3-4)	4	10	4
Salix cinerea ssp. cinerea	1	I (3)	2	2	2
Carex nigra	3	I (2-5)	1	6	2
Polytrichum commune	2	I (2-4)	1	3	1
Calliergon cuspidatum	3	I (1-3)	1	1	1
Carex rostrata	1	I (5)	5	20	20
Hypericum elodes	3	I (4)	1	4	1
Pseudoscleropodium purum	1	I (2)	1	1	1
Myrica gale	1	I (2)	1	1	1
Narthecium ossifragum	1	I (2)	1	1	1
Deschampsia flexuosa	1	I (1)	1	1	1
Sphagnum subsecundum ssp.. indundatum	1	I (4)	4	8	8
Pedicularis palustre	1	I (3)	3	3	3
Lophocolea cuspidata	1	I (3)	3	2	2
Centaurea nigra	1	I (3)	3	2	2
Hydrocotyle vulgaris	1	I (3)	3	2	2
Valeriana officinalis	1	I (2)	2	1	1
Juncus effusus	2	I (2)	2	1	1
Scutellaria minor	2	I (1-2)	2	1	1
Potentilla erecta	1	I (2)	2	1	1
Salix aurita	1	I (2)	2	1	1
Hypericum undulatum	1	I (2)	2	1	1
Potamogeton polygonifolius	1	I (2)	2	1	1
Hylocomnium splendens	1	I (2)	2	1	1
Rumex acetosa	1	I (2)	2	1	1
Carex echinata	2	I (1-2)	2	1	1
Lychnis flos-cuculi	1	I (2)	2	1	1
Cirsium dissectum	1	I (2)	2	1	1
Anthoxanthum odoratum	1	I (2)	2	1	1
Carex curta	1	I (2)	2	1	1

Table 3.9 The mean and median species abundance and frequency for Group pf-F in relation to the standard NVC classification tabulation

GROUP pf-F	Total number of quadrats = 7				
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Potentilla palustris	7	V (4-7)	5	20	20
Menyanthes trifoliata	6	V (3-7)	5	25	20
Equisetum fluviatile	6	V (2-4)	2	2	1
Sphagnum squarrosum	5	IV (2-10)	5	34	15
Eriophorum angustifolium	3	III (2-4)	3	6	2
Agrostis stolonifera	3	III (1-4)	3	3	2
Sphagnum capillifolium	2	II (5-8)	5	48	20
Sphagnum auriculatum	2	II (1-6)	2	16	1
Hypericum elodes	3	II (2-4)	2	2	1
Carex echinata	2	II (2-3)	2	2	1
Polytrichum commune	2	II (2-3)	2	2	1
Drosera rotundifolia	2	II (2-3)	2	2	1
Calliergon cuspidatum	2	II (2)	2	1	1
Juncus bulbosus	2	II (2)	2	1	1
Aulacomnium palustre	1	I (6)	4	10	10
Salix aurita	1	I (3)	3	3	3
Epilobium palustre	1	I (2)	2	1	1
Hypericum pulchrum	1	I (2)	2	1	1
Calliergon giganteum	1	I (2)	2	1	1
Holcus lanatus	1	I (2)	2	1	1
Juncus acutiflorus	1	I (2)	2	1	1
Polygala vulgaris	1	I (1)	1	1	1
Dactylorhiza praetermissa	1	I (2)	2	1	1
Viola palustris ssp. juressi	1	I (1)	1	1	1
Molinia caerulea	1	I (2)	2	1	1
Succisa pratensis	1	I (1)	1	1	1
Pseudoscleropodium purum	1	I (2)	2	1	1

Table 3.10 The mean and median species abundance and frequency for Group pf-G in relation to the standard NVC classification tabulation

GROUP pf-G		Total number of quadrats = 14			
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Potentilla palustris	12	V (2-9)	6	25	30
Eriophorum angustifolium	12	V (3-9)	5	18	15
Carex nigra	10	IV (4-5)	5	12	12
Sphagnum auriculatum	8	III (4-7)	5	19	20
Sphagnum recurvum	6	III (2-7)	4	15	10
Carex echinata	4	II (4-5)	4	12	10
Sphagnum papillosum	4	II (3-4)	4	5	5
Juncus acutiflorus	5	II (2-6)	4	15	10
Juncus effusus	4	II (2-5)	3	7	2
Lophocolea cuspidata	4	II (2-4)	3	5	3
Sphagnum fimbriatum	3	II (2-4)	4	4	4
Equisetum fluviatile	3	II (2-3)	3	2	3
Luzula multiflora	3	II (2)	2	1	1
Sphagnum subsecundum spp. *inundatum*	2	I (4-8)	4	35	10
Carex curta	2	I (4-5)	4	10	5
Sphagnum palustre	2	I (3-7)	3	26	2
Agrostis stolonifera	2	I (3-4)	3	4	2
Molinia caerulea	2	I (3-3)	3	2	2
Sphagnum squarrosum	2	I (3-7)	2	21	1
Agrostis canina	1	I (1-3)	2	3	1
Hypericum elodes	1	I (7)	7	50	50
Carex rostrata	1	I (5)	5	16	16
Calliergon stramineum	1	I (5)	5	15	15
Dactylorhiza praetermissa	1	I (5)	5	20	20
Juncus bulbosus	1	I (4)	4	10	10
Rhytidiadelphus squarrosus	1	I (4)	4	5	5
Aulacomnium palustre	1	I (4)	4	5	5
Sphagnum cuspidatum	1	I (4)	4	5	5
Drepanocladus fluitans	1	I (4)	4	5	5
Potamogeton polygonifolius	1	I (2)	2	1	1
Succisa pratensis	1	I (2)	2	1	1
Ulex gallii	1	I (2)	2	1	1
Calluna vulgaris	1	I (2)	2	1	1

Table 3.11 The mean and median species abundance and frequency for Group pf-H in relation to the standard NVC classification tabulation

GROUP pf-H			Total number of quadrats = 10		
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Potentilla palustris	9	V (3-8)	5	16	20
Aulacomnium palustre	9	V (3-7)	4	13	10
Viola palustris ssp. juressi	9	V (2-6)	4	9	5
Lotus pedunculatus	7	IV (2-4)	4	4	4
Sphagnum recurvum	6	III (4-6)	5	22	20
Sphagnum capillifolium	4	III (3-5)	5	12	20
Juncus acutiflorus	6	III (2-6)	4	6	5
Molinia caerulea	4	II (3-5)	5	22	25
Agrostis stolonifera	3	II (3-5)	4	6	5
Eriophorum angustifolium	4	II (3-5)	3	6	2
Equisetum fluviatile	3	II (2-4)	3	3	2
Salix cinerea ssp. cinerea	3	II (2-7)	3	18	2
Sphagnum fimbriatum	4	II (2-7)	4	15	10
Juncus effusus	3	II (2-4)	3	3	2
Hydrocotyle vulgaris	3	II (1-3)	2	2	1
Valeriana officinalis	3	II (2)	3	2	2
Luzula multiflora	4	II (2)	2	1	1
Sphagnum palustre	1	I (6)	6	30	30
Sphagnum cuspidatum	2	I (3-5)	2	14	2
Sphagnum auriculatum	2	I (3-4)	2	4	2
Sphagnum papillosum	2	I (3-4)	2	4	2
Calluna vulgaris	2	I (3-4)	4	5	4
Carex nigra	2	I (3-5)	2	6	1
Succisa pratensis	2	I (2-4)	2	6	1
Polytrichum commune	2	I (2)	2	2	1
Scutellaria minor	2	I (2-3)	2	2	1
Potentilla erecta	2	I (2)	2	1	1
Angelica sylvestris	1	I (2)	2	1	1
Calliergon giganteum	1	I (5)	5	15	15
Eurhynchium praelongum	1	I (2)	2	1	1
Drosera rotundifolia	1	I (3)	3	3	3
Centaurea nigra	1	I (1)	2	1	1
Salix aurita	1	I (2)	3	2	2
Rumex acetosa	1	I (2)	2	1	1
Carex echinata	1	I (2)	2	1	1
Cirsium palustre	1	I (2)	2	1	1
Ulex gallii	1	I (2)	2	1	1
Galium palustre	1	I (1)	1	1	1
Holcus lanatus	2	I (1-2)	1	1	1
Epilobium palustre	1	I (1)	1	1	1

Table 3.12 The mean and median species abundance and frequency for Group pf-I in relation to the standard NVC classification tabulation

GROUP pf-I		Total number of quadrats = 10			
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Calluna vulgaris	8	V (2-6)	4	12	10
Sphagnum recurvum	7	IV (4-6)	4	14	10
Sphagnum capillifolium	7	II (2-6)	5	15	15
Juncus acutiflorus	7	IV (2-5)	3	5	3
Aulacomnium palustre	7	IV (2-4)	4	5	5
Molinia caerulea	6	III (3-10)	7	23	35
Agrostis stolonifera	5	III (3-7)	4	16	5
Erica tetralix	5	III (2-7)	4	11	4
Equisetum fluviatile	5	III (2-3)	2	1	1
Eriophorum angustifolium	3	II (2-6)	5	27	20
Dicranum scoparium	3	II (2-5)	4	9	5
Menyanthes trifoliata	3	II (2-4)	3	5	2
Myrica gale	3	II (2-4)	3	3	2
Luzula multiflora	3	II (1-4)	2	2	1
Viola palustris ssp. juressi	4	II (2-3)	3	2	2
Drosera rotundifolia	3	II (2-3)	2	1	1
Potentilla erecta	3	II (2-3)	4	1	10
Sphagnum subnitens	3	II (2-5)	3	10	2
Potentilla palustris	3	II (1-4)	4	6	6
Ulex gallii	2	I (4-7)	4	25	10
Sphagnum auriculatum	2	I (4-5)	4	15	10
Sphagnum papillosum	2	I (3-5)	4	8	5
Sphagnum palustre	2	I (3-4)	3	4	2
Sphagnum squarrosum	2	I (3-4)	3	4	2
Sphagnum cuspidatum	2	I (2-4)	2	3	1
Salix cinerea ssp cinerea	3	I (5)	5	12	11
Pseudoscleropodium purum	1	I (4)	4	6	6
Lotus pedunculatus	1	I (3)	3	2	2
Carex rostrata	1	I (3)	3	2	2
Hypericum elodes	1	I (3)	3	3	3
Rubus fruticosus var.	1	I (3)	3	2	2
Anthoxanthum odoratum	1	I (2)	2	1	1
Galium palustre	2	I (2)	2	1	1
Calliergon giganteum	1	I (2)	2	1	1
Polygala vulgaris	1	I (2)	2	1	1
Sphagnum fimbriatum	1	I (2)	2	1	1
Rhytidiadelphus squarrosus	1	I (1)	1	1	1

Table 3.13 The mean and median species abundance and frequency for Group pf-J in relation to the standard NVC classification tabulation

GROUP pf-J				Total number of quadrats = 11	
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Molinia caerulea	10	V (3-10)	5	40	20
Rhytidiadelphus squarrosus	11	V (2-5)	4	6	5
Pseudoscleropodium purum	8	IV (2-8)	4	15	10
Juncus acutiflorus	8	IV (2-6)	4	8	5
Potentilla erecta	8	IV (2-5)	3	6	3
Lotus pedunculatus	7	IV (2-5)	3	8	3
Luzula multiflora	8	IV (2-4)	5	4	5
Holcus lanatus	4	III (2-3)	3	3	3
Succisa pratensis	5	III (2-5)	4	10	10
Aulacomnium palustre	6	III (2-4)	4	4	5
Thuidium tamariscinum	6	III (2-3)	2	2	1
Agrostis canina	3	II (4-5)	5	18	15
Carex nigra	4	II (3-5)	5	21	11
Potentilla palustris	4	II (3-7)	5	8	20
Agrostis stolonifera	3	II (2-6)	6	21	30
Eriophorum angustifolium	3	II (2-5)	4	6	5
Sphagnum papillosum	4	II (3-4)	4	6	10
Sphagnum squarrosum	3	II (2-4)	4	2	5
Juncus effusus	3	II (2-4)	4	4	5
Lychnis flos-cuculi	3	II (2-3)	2	1	1
Equisetum fluviatile	3	II (2-3)	2	2	1
Cirsium palustre	3	II (2)	2	1	1
Rumex acetosa	3	II (2)	2	1	1
Dicranum scoparium	2	I (3-4)	4	5	4
Eurhynchium praelongum	2	I (2-7)	5	26	13
Sphagnum palustre	2	I (1-5)	4	11	5
Juncus bufonius	2	I (1-4)	4	6	4
Valeriana officinalis	2	I (1-4)	3	3	3
Sphagnum recurvum	1	I (6)	6	30	30
Carex echinata	1	I (4)	5	14	14
Sphagnum capillifolium	1	I (4)	4	10	10
Sphagnum fimbriatum	1	I (4)	4	5	5
Sphagnum subsecundum	1	I (4)	4	8	8
Cirsium dissectum	1	I (3)	3	2	2
Anthoxanthum odoratum	1	I (3)	3	2	2
Erica tetralix	1	I (4)	4	4	4
Myrica gale	1	I (3)	3	2	2
Sphagnum contortum	1	I (3)	3	3	3
Carex hostiana	1	I (2)	3	2	2
Sphagnum subnitens	1	I (4)	4	4	4
Drosera rotundifolia	2	I (2)	2	1	1
Polytrichum commune	1	I (2)	2	1	1
Sphagnum auriculatum	1	I (2)	2	1	1
Narthecium ossifragum	1	I (2)	2	1	1
Mentha aquatica	1	I (2)	2	1	1
Menyanthes trifoliata	1	I (2)	2	1	1
Typha latifolia	1	I (2)	2	1	1
Hydrocotyle vulgaris	1	I (1)	1	1	1
Galium palustre	1	I (1)	1	1	1
Calliergon cuspidatum	1	I (2)	2	1	1
Viola palustris ssp. juressi	1	I (1)	1	1	1
Platanthera bifolia	1	I (2)	2	1	1

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Table 3.14 The mean and median species abundance and frequency for Group pf-K in relation to the standard NVC classification tabulation

GROUP pf-K		Total number of quadrats = 8			
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Eriophorum angustifolium	7	V (3-6)	4	19	10
Sphagnum papillosum	6	IV (4-9)	7	40	40
Molinia caerulea	6	IV (3-10)	8	60	60
Erica tetralix	6	IV (2-7)	4	8	10
Narthecium ossifragum	5	III (2-4)	4	7	10
			2		
Aulacomnium palustre	2	II (2-4)		3	1
Carex echinata	3	II (2-4)	4	3	4
Sphagnum palustre	2	II (2-3)	2	2	1
Juncus acutiflorus	2	II (2-3)	2	2	1
Potentilla erecta	2	II (2-3)	2	2	1
Agrostis stolonifera	2	II (2)	2	1	1
Sphagnum recurvum	2	II (2)	2	1	1
Potentilla palustris	3	II (2)	4	10	5
Drosera rotundifolia	1	I (4)	4	5	5
Sphagnum subsecundum ssp. *inundatum*	1	I (4)	4	5	5
Carex hostiana	1	I (4)	4	5	5
Sphagnum squarrosum	2	I (2-3)	2	2	1
Menyanthes trifoliata	1	I (3)	3	2	2
Equisetum fluviatile	1	I (2)	2	1	1
Dicranum scoparium	1	I (2)	2	1	1
Luzula multiflora	1	I (2)	2	1	1
Viola palustris ssp. juressi	1	I (2)	2	1	1
Sphagnum auriculatum	1	I (2)	2	1	1
Sphagnum cuspidatum	1	I (2)	2	1	1
Rhytidiadelphus squarrosus	1	I (2)	2	1	1
Deschampsia flexuosa	1	I (2)	2	1	1
Epilobium palustre	1	I (2)	2	1	1

Table 3.15 The mean and median species abundance and frequency for Group pf-L in relation to the standard NVC classification tabulation

GROUP pf-L		Total number of quadrats = 8			
	No. of quadrats	NVC coding Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Molinia caerulea	7	V (3-10)	9	80	90
Juncus effusus	6	IV (2-7)	6	20	20
Luzula multiflora	4	III (2-7)	2	13	1
Juncus acutiflorus	3	II (4-5)	4	8	5
Agrostis stolonifera	3	II (2-6)	3	5	3
Potentilla erecta	3	II (2-5)	2	1	1
Sphagnum capillifolium	3	II (2-5)	2	9	1
Carex nigra	2	II (2-5)	2	6	1
Sphagnum papillosum	2	I (5)	4	28	6
Ulex europeaus	1	I (4)	4	10	10
Carex demissa	2	I (1-2)	2	2	1
Cirsium palustre	1	I (2)	2	2	1
Rumex acetosa	1	I (3)	3	3	3
Valeriana officinalis	1	I (3)	3	2	2
Carex echinata	1	I (2)	2	1	1
Erica cinerea	1	I (3)	3	2	2
Calliergon giganteum	1	I (2)	2	1	1
Menyanthes trifoliata	2	I (2)	2	1	1
Caltha palustris	1	I (2)	2	1	1
Rhytidiadelphus squarrosus	1	I (3)	3	3	3

3.3.1 INTERPRETATION OF THE TWINSPAN OUTPUT

Of the twelve poor-fen communities and sub-communities that were identified, Groups pf-A to pf-H (Tables 3.4-3.9) were dominated by *Potentilla palustris* and would be ascribed to the S27 *Carex rostrata-Potentilla palustris* community (Rodwell, 1995). Groups pf-A to pf-D are characterised by aquatic macrophytes and contained very small amounts of bryophytes, the majority being *Calliergon* species. Groups pf-A and pf-B were very similar in their overall structure, although *Juncus acutiflorus* Ehrh. Ex Hoffm. was a constant in Group pf-B alone, with a mean cover of 11 %. *Molinia caerulea* was also a general associate of Group pf-A, sometimes present in high abundances (Domin range 1-9).

Molinia caerulea does not occur in Group pf-B. *Carex nigra* (L.) Reichard. is co-dominant with *Potentilla palustris* in Group pf-A. Group pf-A contains more associated species than Group pf-B, such as *Juncus bulbosus* L. and *Hypericum elodes* L. that are indicative of very wet conditions. Examples of Groups pf-A and pf-B can be found in Plates 3.1 and 3.2. Like Group pf-B, Group pf-C was also a transitional community between rush pasture and *Potentilla palustris* poor-fen. However, this community was co-dominated by *Potentilla palustris* and *Juncus effusus* L. Unlike Group pf-B, Group pf-C contained only two quadrats with *Menyanthes trifoliata*, whereas this species occurred in 80 % of the samples in Group pf-B. *Menyanthes trifoliata* was substituted in Group pf-C by other common species such as *Agrostis stolonifera* L. and *Valeriana officinalis* L. Unlike Groups pf-A to pf-C, Group pf-D contains *Potentilla palustris* (Table 3.7) in all quadrats with a mean percentage cover of 27 %. Group pf-D was dominated by a sparse covering of *Potentilla palustris* and mostly bare substrate. *Juncus acutiflorus* and *Equisetum fluviatile* L. were the only two frequently occurring species and the remaining 30 species are only associates and occur in four or less of the 13 quadrats.

The pie charts in Figure 3.3 show clearly the prominence of bryophytes in Groups pf-E to pf-K. Groups pf-E to pf-I also show a progressive decrease in amounts of *Potentilla palustris*. In Group pf-E, *Potentilla palustris* was co-dominant with *Sphagnum recurvum* Klinggr. and *Eriophorum angustifolium* Honck. Also, as well as there being many associated species, *Sphagnum squarrosum* Crome. was found in two thirds of the quadrats. In contrast to this large group (15 quadrats), Group pf-F (Table 3.9) was relatively small (7 quadrats). Group pf-F (Plate 3.3) was co-dominated by *Potentilla palustris*, *Menyanthes trifoliata* and *Sphagnum squarrosum*, the latter species being the most abundant in this group, with a mean cover of 34 %. Group pf-G was co-dominated by *Potentilla palustris*, *Sphagnum auriculatum* Schimp. and *Eriophorum angustifolium*, and bears some similarity

Plate 3.1 *Carex rostrata, Eriophorum angustifolium* and *Equisetum fluviatile* in Group pf-A swamp.

Plate 3.2 The community on the left is a typical example of Group pf-B swamp. The community on the right has been terrestrialised by cushion-forming mosses.

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Plate 3.3 *Sphagnum squarrosum, Menyanthes trifoliata* and *Potentilla palustris* within poor-fen Group pf-F.

Plate 3.4 *Drosera rotundifolia* and *Lotus pedunculatus* growing on a cushion of *Sphagnum fimbriatum, Aulacomnium palustre* and *Sphagnum capillifolium* within Group pf-H.

to Group pf-E. However, Group pf-G contains fewer species in total (33) and *Carex nigra* is frequent rather than rare, as in Group pf-F.

Figure 3.3 shows that in comparison with the other poor-fen groups, Group pf-H (Plate 3.4) contains the highest proportion of mosses with a total value of 41 %. *Aulacomnium palustre* (Hedw.) Schwaegr. was constant with a mean of 13 % cover, and *Sphagnum recurvum* and *Sphagnum capillifolium* were common, occurring in approximately half of the samples.
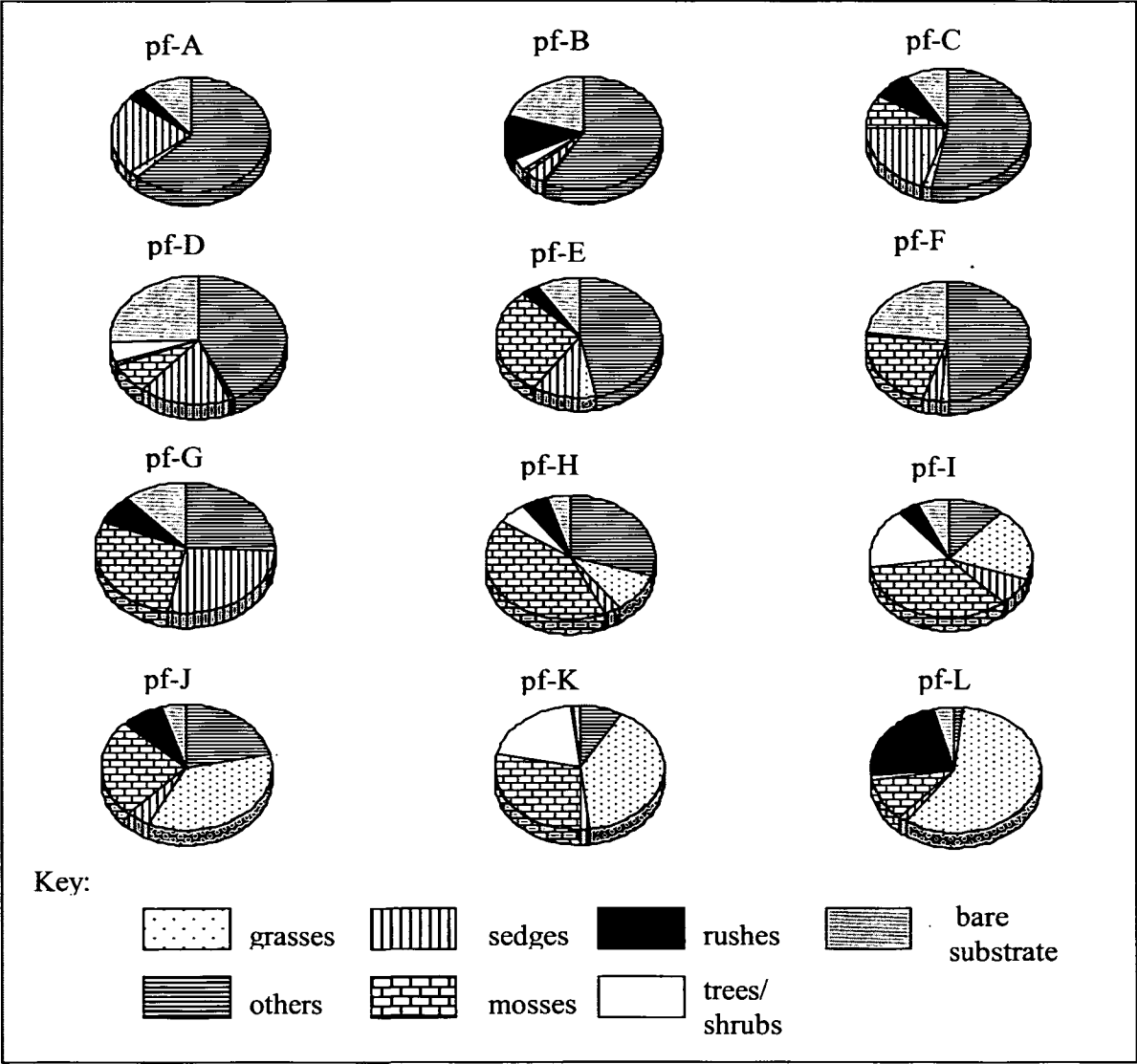
Figure 3.3 Pie charts to display the composition of the main vegetation types for each of the poor-fen types.

Group pf-I was typified by ericaceous dwarf shrubs and was dominated by *Calluna vulgaris*. Although *Calluna* was common in acidic habitats, it is not a typical wetland

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species (Grime *et al.*, 1988). However, the prominence of cushion-forming bryophytes such as *Aulacomnium palustre* and *Sphagnum recurvum* ameliorate wet conditions and provide a suitable substrate for *Calluna vulgaris* to grow. *Erica tetralix* was also common, occurring in 50 % of the samples in Group pf-I.

Groups pf-J, pf-K and pf-L (Tables 3.13-3.15) were dominated by the tussock grass *Molinia caerulea*. Group pf-J was co-dominated by *Molinia caerulea* and *Rhytidiadelphus squarrosus* (Hedw.) Warnst., while *Juncus acutiflorus* was frequent. This community is transitional between rush pasture and *Molinia* mire and contains 41 associated species. Groups pf-K and pf-L were represented by only eight quadrats. Group pf-K was dominated by *Eriophorum angustifolium* and was most similar to *Narthecium ossifragum* (L.) Huds.-*Sphagnum papillosum* Lindb. mire according to Rodwell (1991b). This group contains *Erica tetralix*, which was frequent, and nine bryophyte species occur occasionally. Group pf-L was co-dominated by *Molinia caerulea* and *Juncus effusus* to form a rush pasture and *Molinia caerulea* mire transitional community. This community differs from pf-J in having both double the mean percentage cover of *Molinia caerulea* and *Juncus* and the total number of species present in the community.

3.3.2 INTERPRETATION OF THE DCA ORDINATION

The DCA ordination diagram is presented in Figure 3.4. Poor-fen groups were ordinated linearly across the diagram, which means that most of the variation is explained on the first axis and much less on the second. The eigenvalues for the first two axes were 0.71 and 0.55, respectively. Poor-fen groups associated with wetter habitats were largely situated right-of-centre. The *Molinia* dominant groups were situated left-of-centre. Floristically, axis 1 clearly represents a wetness gradient. The large amount of overlap between the communities shows that there were many species in common and subtle differences in

patterns of abundance exist between the communities, which was reflected in the previous section.
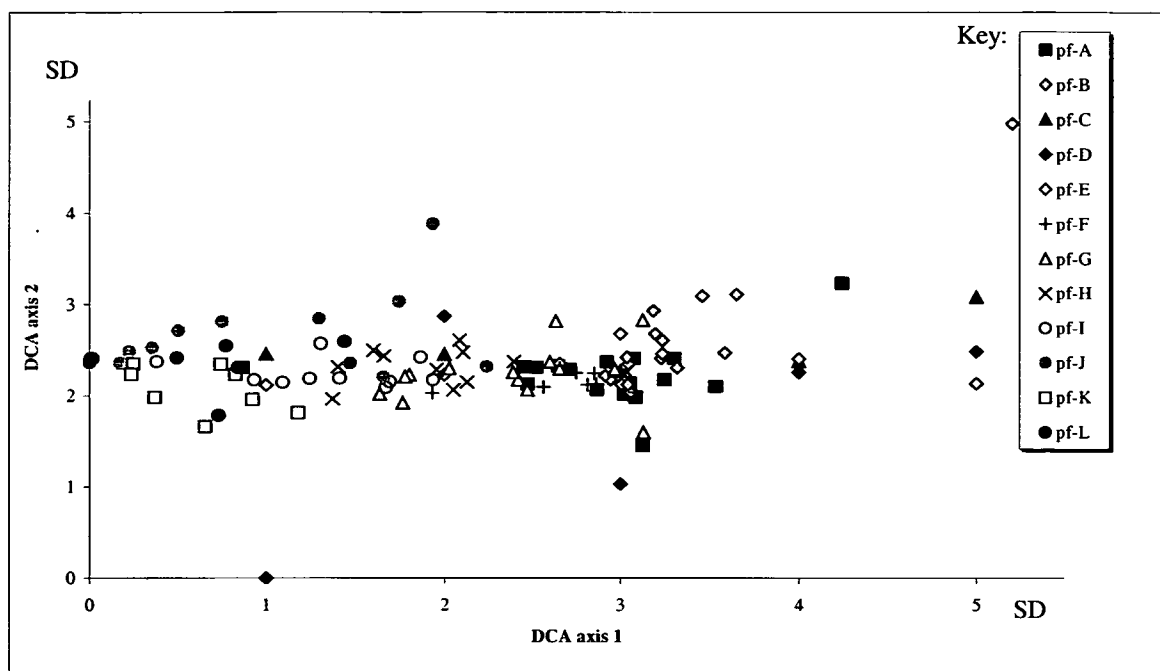
Figure 3.4 Sample ordination diagram derived from detrended correspondence analysis of the 150 quadrats taken from Goss Moor in 1997. Groups pf-A to pf-L are those identified by TWINSPAN. Eigenvalues: Axis 1 = 0. 7055, Axis 2 = 0.5522

3.3.3 RELATIONSHIPS BETWEEN THE VEGETATION & ENVIRONMENTAL VARIABLES

The joint biplot of the poor-fen types and environmental variables produced by CCA is presented in Figure 3.5. The near linear relationship between the 12 groups on the DCA ordination diagram was barely evident on the CCA joint biplot. This may be attributed to the poor explanatory power of the environmental variables recorded. To simplify the CCA ordination, the means or centroids of the points for each of the 12 TWINSPAN groups were taken and are illustrated in Figure 3.6. The eigenvalues for the first and second axes of the species and environmental variables biplot are 0.23 and 0.15, respectively. The species and environmental data account for 38.7 % and 25.9 % of the total variance. Thus the total

variance explained by the first two axes of the joint species/environmental biplot was 64.6%.
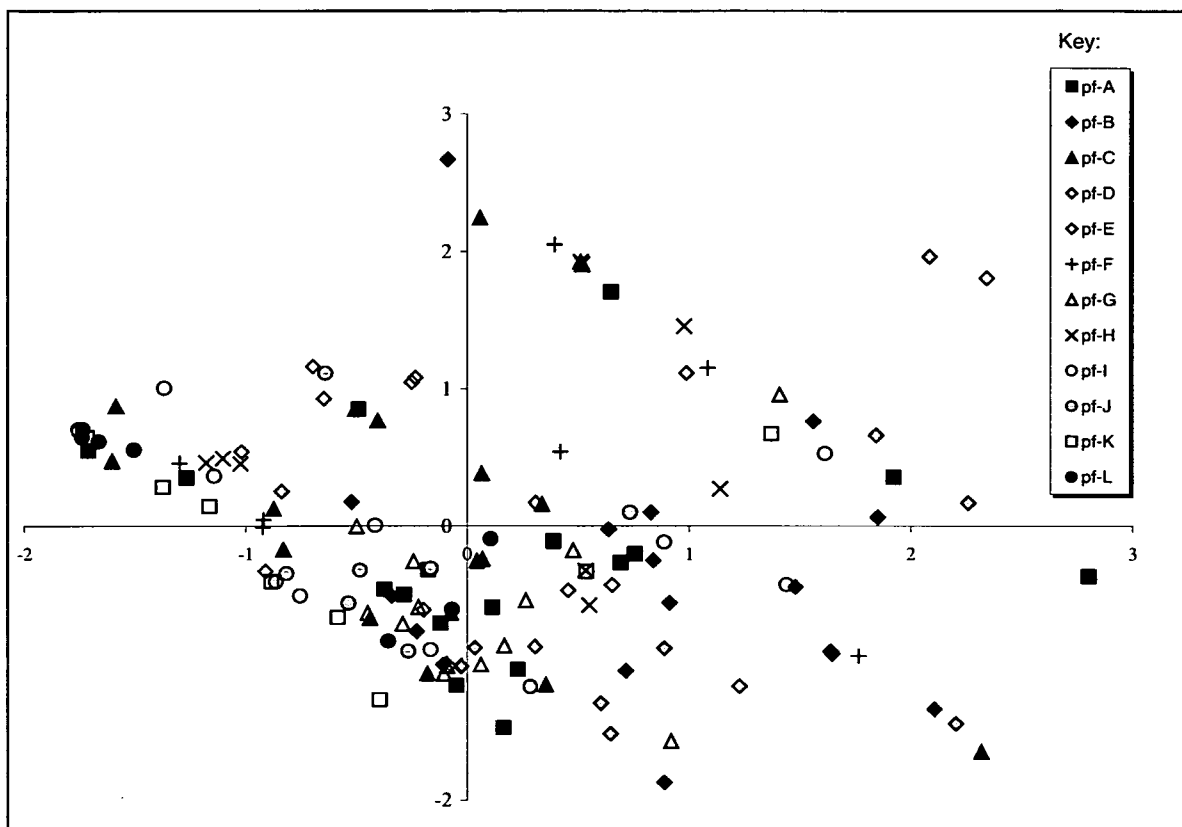
Figure 3.5 The ordination of the poor-fen groups on the joint biplot, before the environmental variables produced by canonical correspondence analysis of the 149 quadrats have been superimposed for the final analysis. TWINSPAN groups pf-A to pf-L are superimposed. Eigenvalues: Axis 1 = 0.23, Axis 2 = 0.15 (Monte Carlo test on the first axis was significant P=0.05).

Analysis of vegetation and environmental data from the 150 quadrats recorded resulted in a clustering of points around the centre of the ordination. In order to gain a better understanding of the distribution of the quadrats along the ordination axes, and produce a less clustered diagram, the CCA was re-run after the outlying quadrat number 148 was removed (Kent & Coker, 1992). The final CCA analysis was run with 149 quadrats and 98 species.
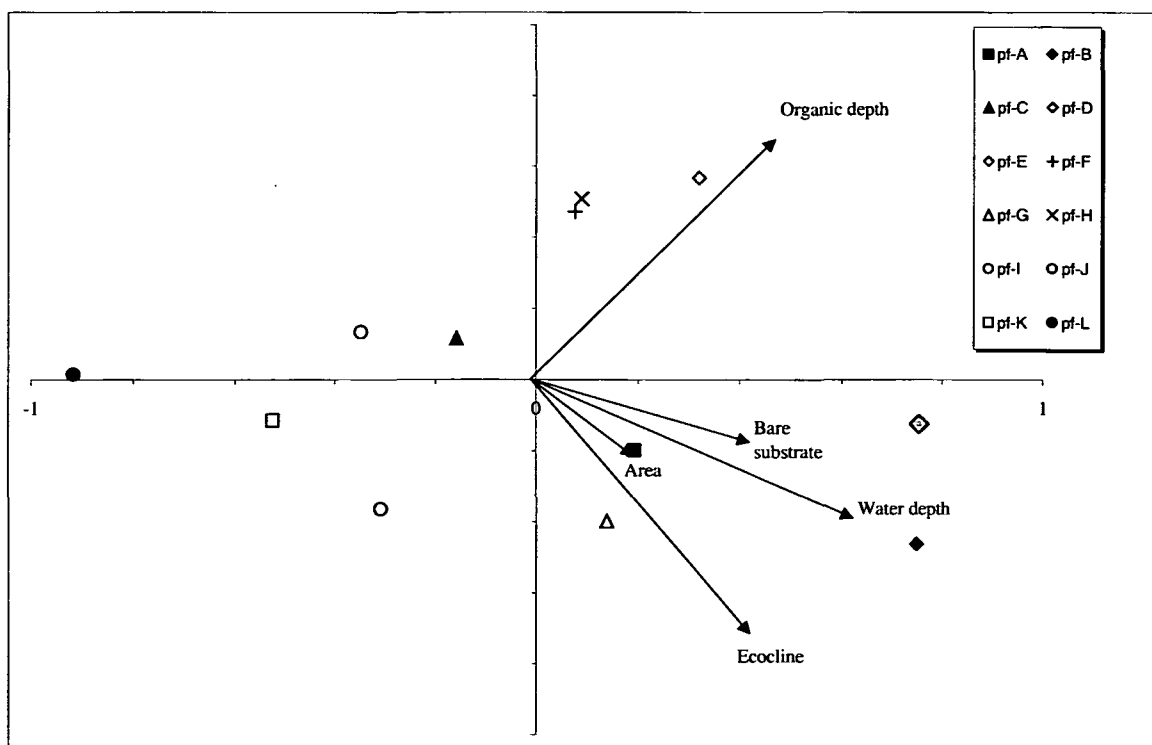
Figure 3.6 A joint biplot showing centroid points of the poor-fen groups defined by TWINSPAN and environmental variables produced by CANOCO of the 149 quadrats used in the final analysis (Monte Carlo test on the first axis was significant P=0.05).

The correlation between organic depth and the first axis was 0.45. Groups pf-E, pf-F and pf-H were associated with greater organic depth, which was not surprising as these groups were dominated by peat forming bryophytes like *Aulacomnium palustre*, *S. recurvum* and *S. squarrosum*. Groups pf-E and pf-F, contained considerable amounts of *S. squarrosum* and *Sphagnum fimbriatum*, which occur in 68 and 27 % of the quadrats, respectively, with an average cover abundance of 25 and 3 %. The second axis accounts for 25.9 % of the total floristic variation and Table 3.16 shows organic depth is correlated to Axis 2 with a value of 0.41.

The correlation between standing water and Axis 1 was 0.34. Samples associated with increased water depth are located in the bottom right hand corner. Groups pf-A, pf-B and pf-D were wetter communities containing *Carex nigra* and *Carex rostrata* and were almost devoid of mosses, besides the occasional appearance of *Calliergon* species.

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As well as being wetter, pf-A, pf-B and pf-D had higher proportions of bare substrate, which was especially notable for pf-D. The poor-fen pf-C, which incorporates elements of both *Juncus* and *Potentilla palustris* communities, was not so highly correlated with the watertable height.

Groups pf-J, pf-K and pf-L were isolated from the other groups on the ordination. Of the three, *Molinia* transitional pf-J is most correlated to the wetter conditions. These *Molinia* transitions are associated with the least organic matter, which is most likely to be related to the species inhabiting well-oxygenated substrates, with better drainage and faster rates of decomposition (Rodwell, 1991b).

	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4	AREA S(M)	ORGA DEPT	WAHT (MM)	ECOC LINE	BARE SUBS
SPEC AX1	1.0000												
SPEC AX2	-.0455	1.0000											
SPEC AX3	.0039	-.0094	1.0000										
SPEC AX4	.0641	-.0381	.0511	1.0000									
ENVI AX1	.6469	.0000	.0000	.0000	1.0000								
ENVI AX2	.0000	.6038	.0000	.0000	.0000	1.0000							
ENVI AX3	.0000	.0000	.4669	.0000	.0000	.0000	1.0000						
ENVI AX4	.0000	.0000	.0000	.4960	.0000	.0000	.0000	1.0000					
AREAS(M)	.1247	-.1191	-.1516	.0253	.1928	-.1973	-.3246	.0510	1.000				
ORGADEPT	.4510	.4117	.0019	.0203	.6971	.6819	.0040	.0410	.1972	1.000			
WAHT(MM)	.3395	-.0645	.3371	.2171	.5248	-.1068	.7221	.4376	-.0781	.3167	1.000		
ECOCLINE	.3062	-.3027	-.0801	-.3173	.4733	-.5013	-.1717	-.6398	-.0515	-.1026	-.1059	1.000	
BARESUBS	.2731	-.0634	-.2649	.2845	.4222	-.1050	-.5673	.5736	-.0457	.1569	.0690	.1000	1.000

Table 3.16 Weighted correlation matrix between ordination axes and environmental variables. The abbreviations are as follows: SPEC AX1 (Axis 1); SPEC AX2 (Axis 2); SPEC AX3 (Axis 3); SPEC AX4 (Axis 4); ENVI AX1 (Environmental Axis 1); ENVI AX2 (Environmental Axis 2); ENVI AX3 (Environmental Axis 3); ENVI AX4 (Environmental Axis 4); AREAS(M) (Size of the patch); ORGADEPT (Depth of the organic matter in mm); WAHT(MM) (Depth of the standing water in mm); ECOCLINE (Percentage of the patch perimeter with a gradual boundary); BARE SUBS (Percentage cover of bare substrate).

Gradual edge or ecocline was correlated to Axis 1 with a value of 0.31. The groups associated with gradual edge were pf-A, pf-B and pf-D, which were communities dominated by aquatic macrophytes rather than bryophytes (Groups pf-E, pf-F, pf-H and pf-I). The correlation between Axis 1 and area (m) or the patch size was 0.12, indicating no obvious associations between poor-fen community type and the individual patch area it occurred in. Results for the total area in relation to species richness and community type are presented in section 3.3.6.

3.3.4 SPATIAL DISTRIBUTION OF THE POOR-FEN COMMUNITIES

The spatial distribution of the 12 poor-fen groups (Figure 3.7) showed that most associations were widespread across the site and are in close juxtaposition. However, *Molinia* pf-L was only found on the east side of Goss Moor, which was drier in character as it is 10 m higher than the west of the site (Figure 2.2) and therefore positioned above the water table (Ishemo, 2000). Groups pf-B and pf-E were only found in the west and centre of the site. The occurrence of pf-E the *Potentilla palustris-Sphagnum recurvum*, species-rich group appeared to coincide with the presence of drainage channels shown on Figure 2.5. Water in these channels originates from the surrounding catchment, which is predominantly farmland (Figure 2.2).

3.3.5 SPECIES RICHNESS OF THE TWELVE POOR-FEN TYPES

Table 3.17 shows the mean species richness, per quadrat of the 12 poor-fen groups, ranked from lowest to highest. Table 3.17 shows that Group pf-J was the most diverse, containing 14 species on average. This group was dominated by *Molinia* and contained many associated species. *Molinia* was also constant in pf-K and pf-L both of which are transitional between *Narthecium ossifragum-Sphagnum papillosum* mire and *Juncus* communities, respectively. However, these communities are far less diverse as their mean number of species per quadrat is 8 and 5, respectively.
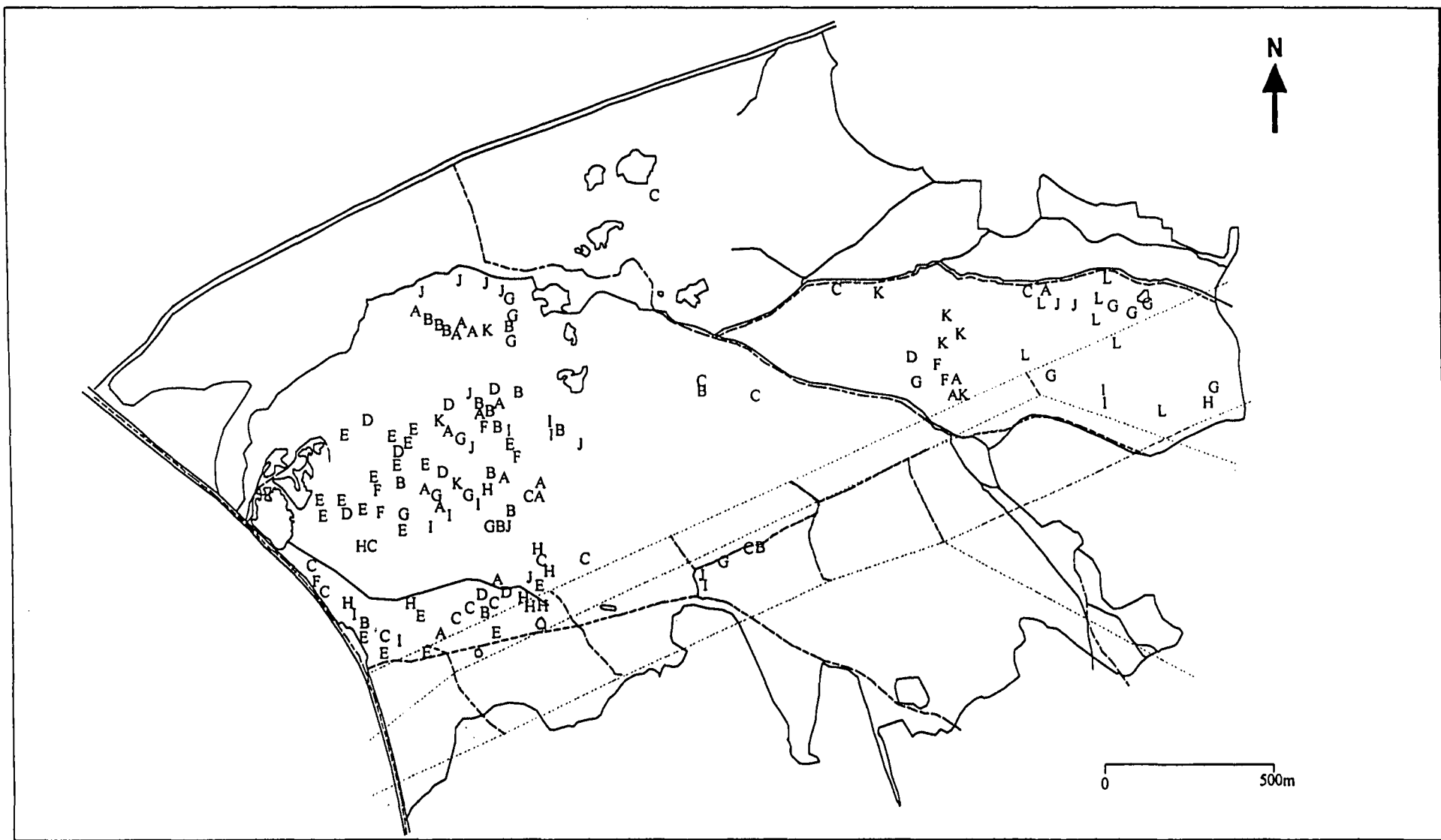
Figure 3.7 The spatial distribution of the 12 TWINSPAN poor-fen groups found on Goss Moor

Table 3.17 Mean number of species occurring in Groups pf-A to pf-L. The groups are ranked from lowest to highest. Significant differences between the groups are graded as shown

	Mean number of species per quadrat											
	5.35	7.32	7.29	7.88	8.15	8.43	9.0	10.6	11.7	11.71	13.2	14.18
Group	pf-L	pf-D	pf-G	pf-K	pf-B	pf-F	pf-A	pf-I	pf-H	pf-C	pf-E	pf-J
pf-L								*	***	***	***	***
pf-D										*	***	***
pf-G										*	***	***
pf-K											*	***
pf-B											***	***
pf-F												*
pf-A											*	***
pf-I												
pf-H												
pf-C												
pf-E												
pf-J												

* = P<0.05
** = P<0.01
*** = P<0.005

The other species-rich groups are pf-H, pf-C and pf-E. In comparison to pf-A, pf-B and pf-D, the other hydrophyte-rich groups, pf-C occupies a drier niche and appears to be transitional between rush pasture and poor-fen, as the main dominants were *Potentilla palustris* and *Juncus effusus*. Together, these two species only made up a third of the cover in the whole group. Groups pf-E and pf-H were moss-rich communities associated with increased organic depth. Group pf-D is species-poor because it contains large amounts of bare substrate and standing water.

3.3.6 DIVERSITY AND COMMUNITY AREAS

Table 3.18 summarises the diversity and area data for the twelve poor-fen types. Within TWINSPAN groupings, sample patch sizes were summed to produce the total area of each poor-fen community. The total area of each community was also summed to give an overall poor-fen area of 1464.2 m² surveyed during the extensive reconnaissance. Of this, pf-B, the *Potentilla palustris-Juncus acutiflorus-Menyanthes trifoliata* community has the greatest proportion and was found in 20 % of the area. Five other groups pf-A, pf-C, pf-D, pf-E and

pf-J make a further 50 % of the total poor-fen area. Four groups, pf-F, pf-I, pf-H and pf-L, have the smallest community areas and together make up only 10 % of the total area of poor-fen.

Table 3.18 The size range and median area for the different poor-fen types and the proportions of each group that make up a total poor-fen area of 1464.2 m^2. Also, a summary of the range, mean and standard deviation of the number of species per quadrat.

Poor-fen Group	Total area of each community type (m^2)	Percentage of each poor-fen type in relation to the whole poor-fen resource	Size range (m^2) of each community	Median Area of each poor-fen type (m^2)	Range of species in 4 m^2	Rounded mean number of species ± 1 s.d. in 4 m^2.
pf-A	161.5	11	1 – 24	10	5-15	9 ± 2.92
pf-B	292.5	20	2 – 100	8	2-15	8 ± 3.72
pf-C	142.4	10	0.5 – 30	5	4-17	12 ± 3.57
pf-D	168.5	11.5	3 – 32	13	1-15	7 ± 4.46
pf-E	162	11	3 – 25	7	9-18	13 ± 2.93
pf-F	45	3	4 – 10	5	5-13	8 ± 2.99
pf-G	111.5	7.5	1 – 18	6	3-10	7 ± 2.09
pf-H	36.8	2.5	1 – 10	2.5	6-16	12 ± 2.87
pf-I	46.5	3	2 – 15	3.5	1-14	11 ± 4.20
pf-J	155.5	10.5	2 – 70	5	9-18	14 ± 2.86
pf-K	112.5	7.5	3 – 40	5	5-13	8 ± 3.23
pf-L	29.5	2	2 - 5	3.5	2-10	5 ± 2.97

The linear regression plot in Figure 3.8 shows that there is no significant relationship between the community size and their associated species richness.

The patch size ranges for each of the poor-fen communities showed that the majority of the communities occurred in both very small patches and also in large patches. Group pf-L the *Molinia caerulea-Juncus effusus* community was the only community that was found solely in small patches. The *Potentilla palustris-Juncus acutiflorus-Menyanthes trifoliata* community in pf-B had the largest range of 2 to 100 m^2 and was most frequent and

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abundant on the site. Of the total poor-fen resource on Goss Moor, the hydrophyte-rich communities in Groups pf-A to pf-D occupy 52 %, the bryophyte-rich communities in Groups pf-E to pf-I cover 2 7% and the *Molinia* transitional communities in Groups pf-J to pf-L cover 20 %.
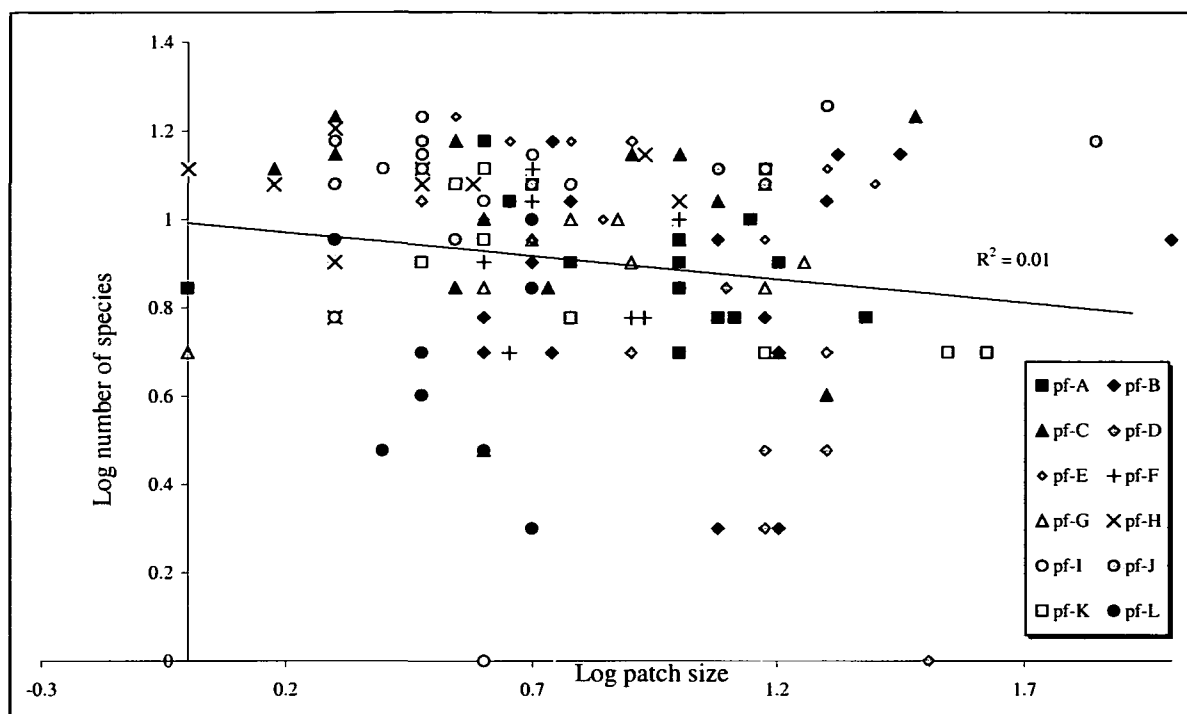
Figure 3.8 The relationship between the log of the number of species per quadrat and the log of the community patch size. 1 % of the variation in axis 1 was explained by the linear regression. (P=0.1 and is not significant).

In order to envisage the patches of poor-fen vegetation, Figure 3.9 shows three sketch maps of three of the areas that were sampled in 1997. Maps *I* and *II* show areas of wetland where terrestrialisation has begun in the centre of the pool. In map *III*, terrestrialisation has been initiated in a more traditional manner, around the edge of the pool.

I

5 m

N

Juncus acutiflorus

Sphagnum recurvum | Molinia caerulea

Potentilla palustris

Sphagnum species

Viola palustris

Aulocomnium palustre

Eriophorum angustifolium

Salix. scrub

II

Ulex gallii

(U.g.)

Menyanthes trifoliata

Molinia caerulea

Calluna vulgaris

Sphagnum species

Potentilla palustris

Juncus acutiflorus

Salix. scrub

5 m

III

Molinia caerulea

Juncus acutiflorus

Equisetum fluviatile

Sphagnum species

Eriophorum angustifolium

Lotus pedunculatus

Ulex gallii

Aulocomnium palustre

5 m

Figure 3.9 Three examples of sketch maps drawn as part of the 1997 poor-fen survey.

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3.3.7 THE IMPORTANCE OF THE COMMUNITIES IN THE CONTEXT OF CORNWALL

The weighted rarity results that were derived from the tetrad data for Cornwall showed

large standard deviations among the mean (Table 3.19). However, for pf-F the smallest

mean value also had the smallest standard deviation. The smaller the mean value the more

important the community would be considered in a Cornish context, as rare species that

occur in few tetrads weight the overall mean towards a lower value.

Table 3.19 Mean weighted rarity scores for each of the 12 poor-fen communities identified on Goss Moor. The lower the score the higher the importance of the community in a Cornish context. The total number of tetrads is 1024.

Poor-fen community type	Mean weighted rarity values ± 1 s.d.
pf-A	142.8 ± 69.2
pf-B	167.6 ± 93.5
pf-C	402.8 ± 208.1
pf-D	155.3 ± 107.2
pf-E	141.5 ± 51.0
pf-F	99.3 ± 43.6
pf-G	153.8 ± 63.8
pf-H	339.3 ± 205.8
pf-I	392.3 ± 138.9
pf-J	359.2 ± 86.4
pf-K	256.1 ± 86.6
pf-L	521.8 ± 164.7

Group pf-L the smallest poor-fen community on Goss Moor had the greatest rarity value of

521.8, and was therefore the least important in terms of rarity in Cornwall. This was mainly

attributed to the large amount of *Molinia caerulea* in this community.

3.3.8 ANALYSIS OF THE ELLENBERG AND BRITISH ELLENBERG INDICATOR VALUE RESULTS

3.3.8.1 Comparisons between the EI and BEI values

The results of the two factor ANOVA, comparing the EI and BEI values of the 12 poor-fen groups are presented in Table 3.20. There were significant interactions between the EI and BEI values for and poor-fen group nitrogen, reaction and moisture, but not light.

Source of variation	df	Nitrogen (N)	Light (L)	Reaction (R)	Moisture (F)
Group	11	0.0020***	0.0009***	0.0009***	0.0009***
Ellenberg (EI vs BEI)	1	0.0009***	0.1500	0.0009***	0.0009***
Group * Ellenberg	11	0.0010***	1.0000	0.0480*	0.0060**

Table 3.20 Significant differences between EI and BEI values given by the two factor ANOVA for nitrogen, light, reaction and moisture. * = P<0.05, ** = P<0.01, and *** = P<0.005

For N, the BEI values were generally higher than the EI values. However Figure 3.10 shows that the values of each community follow the same pattern. The differences were evidently between the groups in which bryophytes prominently feature. The differences between bryophyte-rich and bryophyte-poor communities can be attributed to the fact that the EI values contain no nitrogen numbers for bryophytes and the BEI values do not incorporate mosses. The lack of nitrogen numbers meant that bryophyte-rich Groups pf-E to pf-I were down-weighted. In order to find unbiased nitrogen values, revised BEI and EI values were found by completely omitting the mosses. Proportions were taken from the vascular plants alone. This method appeared to be the most sensible as taking the values as zero, as suggested by Hawkes et al. (1997), would be inappropriate for such a large group of absent species.

The reaction values displayed in Figure 3.12 clearly show that BEI and EI reaction values have the same distribution pattern. This means the general differences lie between the actual indicator values themselves. BEI values were generally one or two values higher

than the EI values (e.g. the reaction EI values was 3 and BEI values was 5, for the majority of species found on Goss Moor). Similarly the original moisture indicator values controlled the community value. All of the community BEI values for moisture were higher than the EI values, by approximately 0.5.

For the purpose of this research, it was decided to only use the Ellenberg indicator values to identify differences between the twelve poor-fen communities. This decision was based on the completeness of the Ellenberg indicator values data set. The BEI values did not incorporate data for bryophytes and the Ellenberg indicator values were used to find these values. As bryophytes are a integral part of poor-fen communities, it seemed logical to use EI values to analyse the whole data set. The following sections contain the results of the single factor ANOVAs which were conducted on the Ellenberg indicator values for the four environmental parameters. To show the similarities between the two sets of indicator values, mean BEI values were included. To aid interpretation, the mean indicator values of the twelve poor-fen communities are joined by a line for each the four variables (Figures 3.10-3.13), and does not imply a sequential relationship.

3.3.8.2 Indicated nitrogen values

Figure 3.10 shows the differences among the mean N or fertility EI values of each community. Using the revised method mentioned above, the nitrogen values for the bryophyte-rich groups were increased. Only pf-K was significantly different, being the lowest or least fertile with a value of 1.5. Group pf-C was the most fertile, with a EI value of 3.24. Although this value was the highest compared to the other poor-fen groups, the value is indicative of low fertility sites with a poor mineral nitrogen supply. The fertility status of pf-C is mostly attributed to the frequent presence of *Agrostis stolonifera*, which has an N-value of 6, whereas the average N-value for pf-C was 3.5. Setting aside pf-C, the overall trend of the revised N-values generally decreased from Group pf-A to pf-L.

Figure 3.10 Mean BEI and EI values for nitrogen for the 12 poor-fen groups. The unrevised EI values are found following the method of Hawkes *et al.* (1997). The horizontal line ---- refers to the significant differences between the revised EI values. Those groups below the line are statistically different (P<0.05) from those above the line.
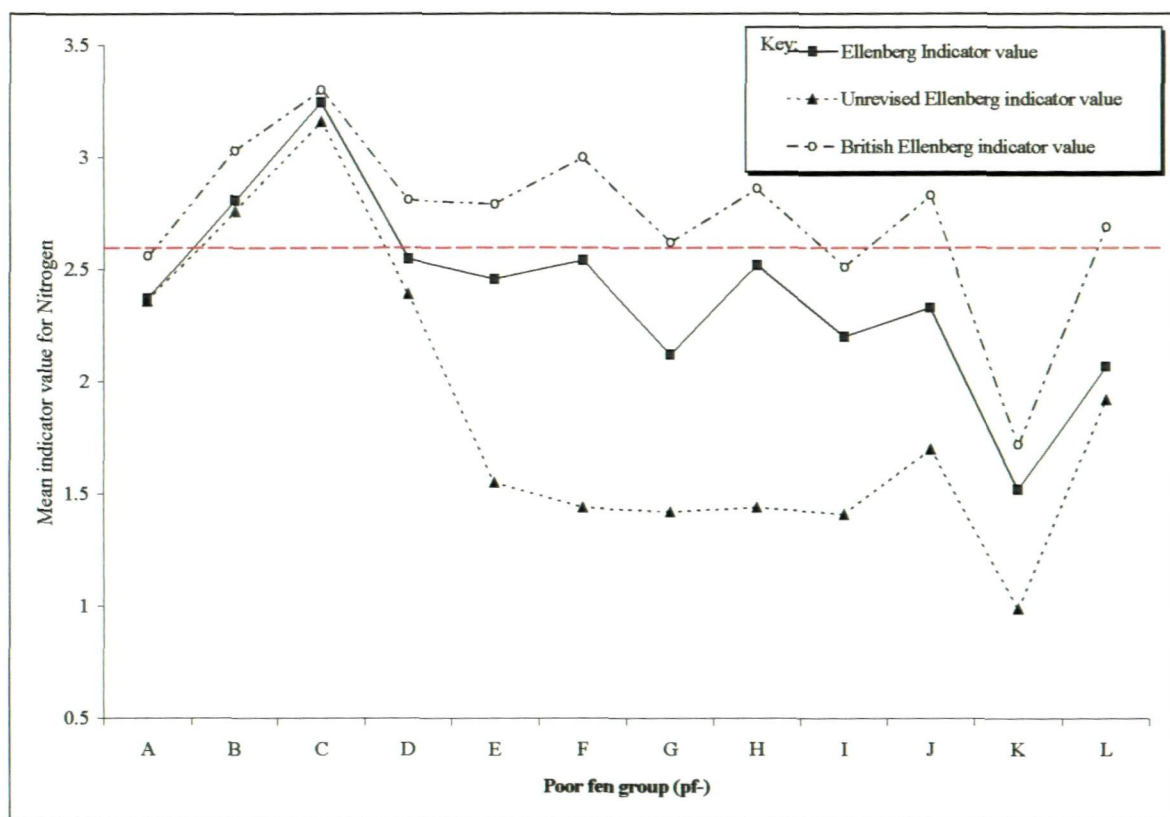
3.3.8.3 Indicated light (L) values

The single factor ANOVA for the EI showed there were differences between the groups with the poor-fen communities were split into two homogenous groups (Figure 3.11). Groups pf-F, pf-H, pf-I and pf-J appear to inhabit shadier habitats as they have lower L values. However, following an examination of the raw quadrat data, it appeared that the differences in all these communities were due to the omission of an EI value for *Sphagnum capillifolium*. This species occurs in high enough amounts to affect the overall community EI values. Therefore, it would be reasonable to conclude that the light values are not significantly different among the poor-fen groups.

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Figure 3.11 Mean BEI and EI values for light for the 12 poor-fen groups. The horizontal line -----
refers to the significant differences between the EI values. Those groups below the line are
statistically different (P<0.05) from those above the line.
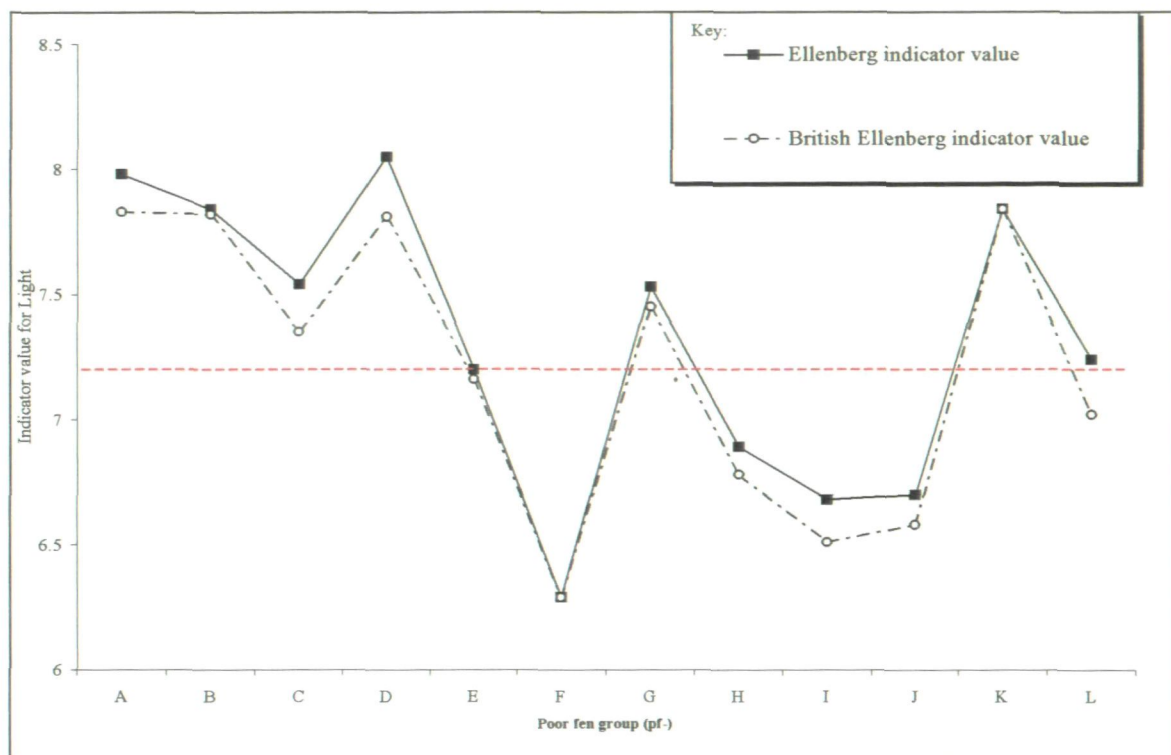
3.3.8.4 Indicated reaction or acidity values

Significant differences among the EI values of the poor-fen communities are shown in
Figure 3.12. Groups pf-A and pf-I to pf-L displayed the lowest EI values for reaction. The
values for these groups ranged from 1.07-2.18, indicating very acid conditions. All other
groups were less acidic with values ranging from 2.27-3.18.

Figure 3.12 Mean BEI and EI values for reaction for the 12 poor-fen groups. The horizontal line ---- refers to the significant differences between the EI values. Those groups below the line are statistically different (P<0.05) from those above the line.
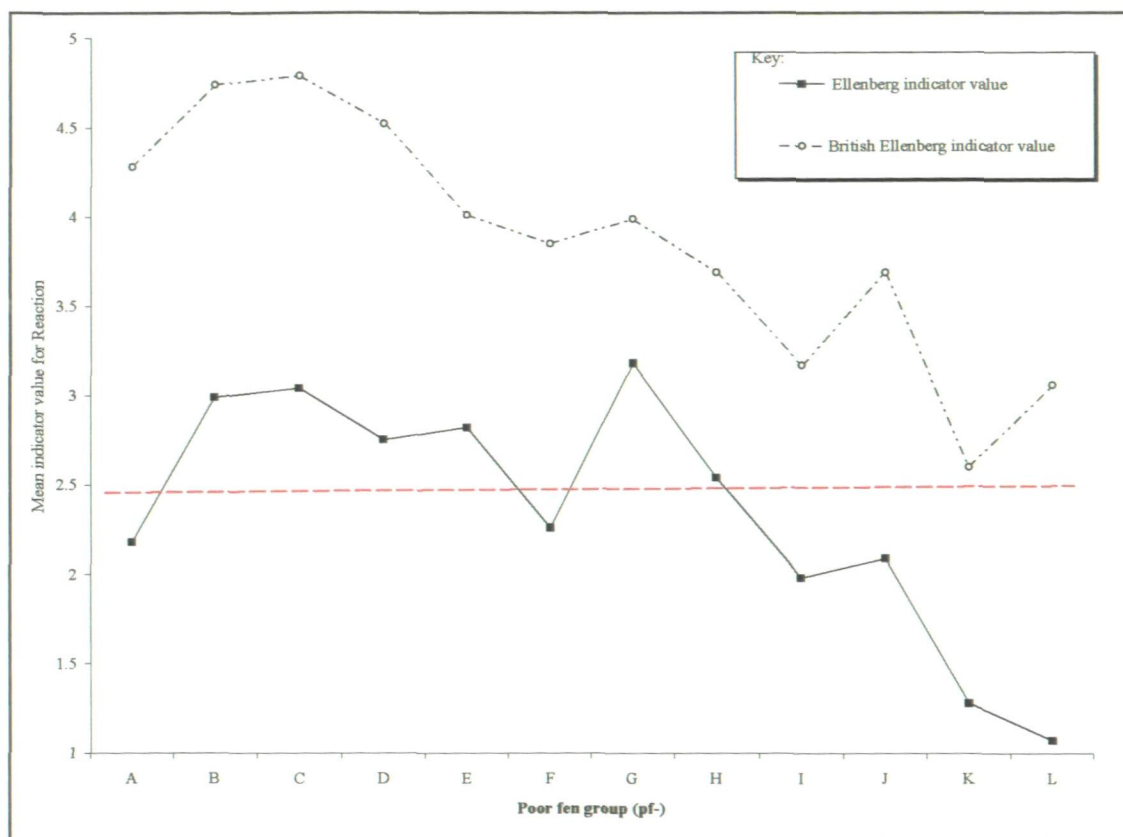
The lower EI values for pf-A appears to be caused by the omission of a reaction value for *Menyanthes trifoliata* in the EI values. This, in turn, down-weighted the overall community Ellenberg number, even though the majority of the species in this group represented a high reaction value (e.g. *Potentilla palustris* and *Carex nigra* both have a EI value of 3). The lack of EI reaction figure for *Molinia caerulea* in Groups pf-K to pf-L did not seem to have an effect on their overall community EI values.

3.3.8.5 Indicated moisture values

Groups pf-A, pf-B and pf-D had the highest EI values, which ranged from 8.64 to 8.71. These values indicate wet, mostly anaerobic conditions. Groups pf-I to pf-L were the driest, with values ranging from 5.99 to 7.19, indicating moist and damp conditions. The

relationship between the moisture values for the 12 poor-fen community types is displayed in Figure 3.13. Groups pf-A to pf-H are significantly different from Groups pf-I to pf-L.
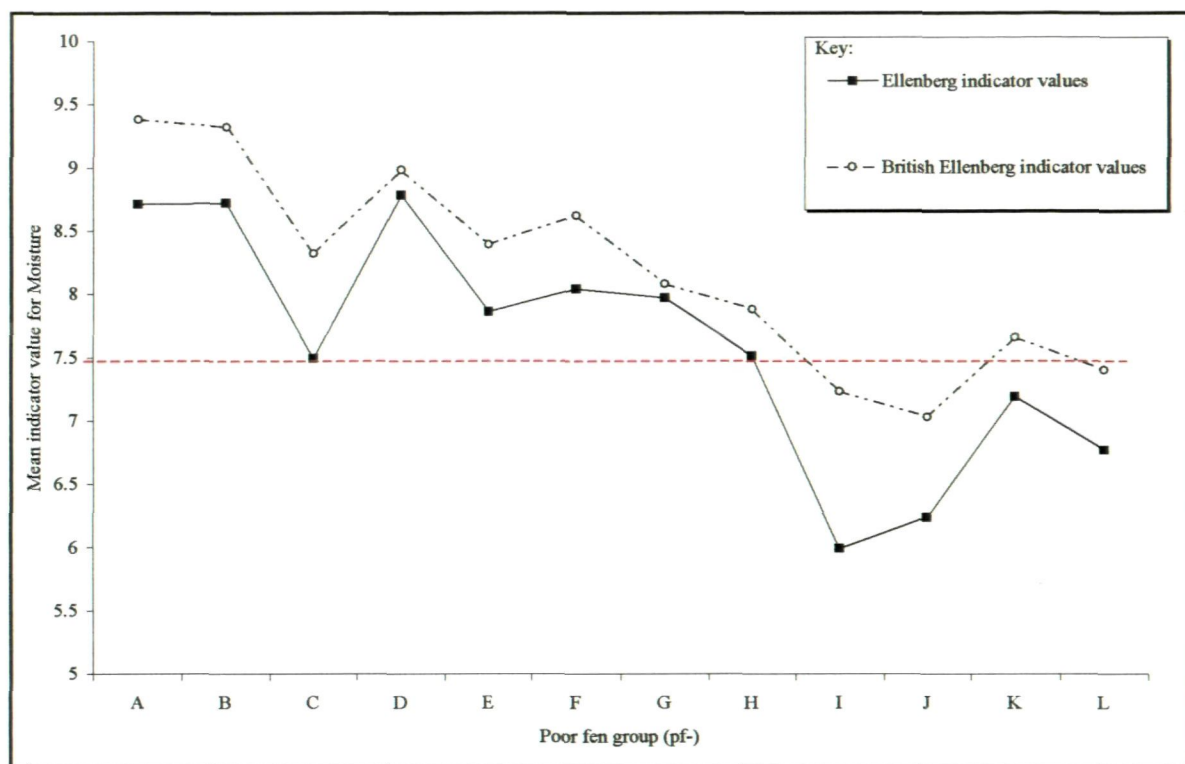
Figure 3.13 Mean BEI and EI values for moisture for the 12 poor-fen groups. The horizontal line ---- refers to the significant differences between the EI values. Those groups below the line are statistically different (P<0.05) from those above the line.

3.4 DISCUSSION

The primary aims of this chapter were to describe the range of poor-fen communities on Goss Moor and characterise them according to a number of environmental factors that were either collected *in situ* or indicated by the different species assemblages.

3.4.1 VEGETATION DESCRIPTION AND ENVIRONMENTAL RELATIONSHIPS

The results from the initial poor-fen survey of Goss Moor have identified twelve community types. This classification provides the first formal description of poor-fen communities on Goss Moor. The species composition of these communities exhibited

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considerable overlap, which was clearly shown by the detrended correspondence analysis. The order of groups on the DCA ordination also corresponded to the depth of the surface water, which was confirmed by correlation produced by the canonical correspondence analysis. This means that communities became increasingly drier from pf-A through to pf-L. This was reflected by the types of species present in the communities at the two extremes of the wetness gradient. *Potentilla palustris*, *Menyanthes trifoliata* and *Carex nigra* are typical poor-fen hydrophytes of open water pools and areas of high water table (Moore & Evans, 1991). These species were found in groups pf-A, pf-B, pf-C and pf-D. The communities of groups pf-E, pf-F, pf-G, pf-H and pf-I, situated at the centre of the ordination/gradient, were rich in bryophytes and strongly correlated with organic depth on the CCA biplot. The drier communities of groups pf-J, pf-K and pf-L were typified by *Molinia caerulea* and are more commonly associated with aerated substrates (Rodwell, 1991b).

This classification of poor-fen communities provides a valuable insight into the range of poor-fen vegetation present on Goss Moor and will undoubtedly be a useful basis for the planning and fulfilment of future management procedures.

3.4.2 THE CONSERVATION VALUE OF THE POOR-FEN COMMUNITIES

The species richness of all the poor-fen communities found on Goss Moor were considerably lower than those found in the national poor-fen survey (Shaw & Wheeler, 1990). This may be attributed to factors such as the recentness of the site or geographical location, which affects species distribution, climate and isolation. Although Shaw & Wheeler's (1990) poor-fen survey did encompass 19 sites from the south-west, Goss Moor was not included. There was no significant relationship between the total number of species in a community and area occupied by the community. Therefore, the relationship between area and species richness cannot be simply explained by the tendency of large areas to

support more niches and hence more species (Usher, 1980). The relationship between area and species richness on Goss Moor is hence a property of the different vegetation types and their associated conditions.

The species richness data for the 12 community types are useful for future management strategies, such as targeting priority areas for conservation. One way of prioritising may be to consider the ecological distribution of species, as indicated by Ratcliffe (1977). The geographical distribution of some of the species found on Goss Moor may be of particular importance. *Cirsium dissectum* (L.) Hill. and *Lycopus europaeus* L. are only prevalent in the south of Britain. *Scutellaria minor* L., *Myrica gale* L., *Oenanthe crocata* L., *Hypericum elodes* and *H. undulatum* Schousb. Ex Willd. are oceanic and associated with the coast, the latter species being confined only to the south-west of England. *Potamogeton polygonifolius* Pourr. is a locally widespread mire species. The tetrad data for Cornwall (French, 2000) showed that some of the key poor-fen species were not very common on a county scale. Table 3.21 summarises the occurrence of some of Cornwall's most common and most rare species that are found on Goss Moor. *Potentilla palustris* is of particular importance as it only occurs in 3 % of total area of Cornwall and is a principal species of the Goss Moor poor-fen communities.

Table 3.21 Some examples to show the number of tetrads (2 km x 2 km squares) out of the 1024 that make up the county of Cornwall, that each species occurs in.

Species	The number of tetrads out of 1024, each species occurs in
Carex curta	9
Potentilla palustris	35
Menyanthes trifoliata	76
Angelica sylvestris	807
Juncus effusus	928
Salix cinerea ssp. *oleifolia*	952

In Cornwall, the occurrence of *Carex curta* Good. has become increasing rare throughout the last century. Today, only 9 out of the 1024 tetrads that encompass Cornwall contain *Carex curta*, with only 13 records since 1980 (French, 2000). The more common species like *Juncus effusus* and *Salix cinerea* ssp. *oleifolia* Macreight. are able to colonise a wider range of habitats including wet meadows, river edges and spoil (Grime *et al.*, 1988).

Placed in a Cornish context, the most valuable poor-fen community on Goss Moor is pf-F-the *Potentilla palustris-Menyanthes trifoliata- Equisetum fluviatile* community. In comparison to other poor-fen communities, this community had intermediate species richness. However, the community was not relatively widespread and only found in 45 m^2 of the area surveyed.

To establish the importance of the poor-fen communities in a national context, it would be useful to utilise the Fenbase data base (Wheeler, 1997) and obtain biodiversity and the target species scores for range of poor-fen communities found on Goss Moor.

3.4.3 ELLENBERG NUMBERS AS INDICATORS OF COMMUNITY CONDITIONS

The results produced by the EI and BEI values were very interesting. The lack of significance between the light values for both Ellenberg methods was anticipated because all of the poor-fen types surveyed were from open habitats, and therefore living in similar light conditions. The community BEI for nitrogen, reaction and moisture were all significantly different from the community EI values and greater in value.

The significant differences found between the twelve poor-fen communities for reaction, moisture and nitrogen, show that even subtle differences in species composition and relative abundance can reflect differences in underlying environmental variables. The community EI values for moisture mirrored the standing water results produced by the

CCA biplot and those indicated by the DCA ordination. The moisture values of Groups pf-A, pf-B and pf-D were notably higher than the other groups, indicating the wettest conditions. Common species in these groups such as *Carex rostrata*, *Carex nigra* and *Menyanthes trifoliata* and the lack of *Sphagnum* species in these areas may also indicate high levels of water fluctuation (Wheeler, 1980).

The results of the pilot study by Dale *et al.* (1997) were also consistent with the EI data, as communities dominated by *Potentilla palustris*, *Eriophorum angustifolium* and *Carex nigra* were significantly wetter than the other communities on Goss Moor. In recent studies, Ellenberg moisture values have been criticised for being too coarse to provide a sensitive indicator of differences within the wetland habitat (Wheeler & Shaw, 1995; Wheeler, 1999). However, in the context of this research, the overall combinations of suites of species have produced results that make good ecological sense. The plants growing on the site may also be able to indicate the overall fluxes of water movement occurring on a site. Work by Ertsen *et al.*(1998) found that the indicator values were best described by mean groundwater levels.

The community BEI values for reaction were also notably higher than the EI values, indicating less acidic conditions. This was a general observation by Hill *et al.* (2000) who found that, in general, BEI values were one point higher than the EI values, representing the different conditions in which species grow according to their location in Europe. The general trend of increased acidity shown from Groups pf-A to pf-L was expected. The hydrophyte-rich groups (pf-A to pf-D) would be expected to be less acidic due to the influx of telmatic waters, which is assisted by the presence of the gradual boundaries. These groups with higher proportions of *Potentilla palustris* and *Calliergon* species, usually indicate slightly more base-rich conditions (Proctor, 1974). Kooijman & Bakker (1995) found *Calliergon cuspidatum* preferred mineral-rich ground water and would not tolerate

mineral-poor rain water alone. The increase of acidifying bryophytes such as *Aulacomnium palustre* and *Sphagnum* species in Groups pf-E to pf-I are well known to be associated with decreases in pH (Clymo, 1991; Moore & Evans, 1991). The lack of EI reaction figure for *Molinia caerulea* in Groups pf-K to pf-L did not seem to have an effect on their overall community EI values. There was no EI value for *Molinia* because it inhabits both acidic and calcareous substrates and therefore shows a bimodal distribution in relation to pH (B.H. Wheeler pers. comm. cited in Grime *et al.*, 1988). It was expected that the communities dominated by *Molinia caerulea* would be more acidic, as pf-L is predominantly rain-fed, as evidenced by the height of the water table. This bimodal distribution explains why the overall community EI value represented the Ellenberg values for the other species in these groups. Group pf-K the *Narthecium ossifragum-Sphagnum papillosum* community predominantly grows in acidic mire or bog conditions (Rodwell, 1991b). Fortunately, these results are similar to those found in the initial field work on Goss Moor (Dale *et al.*, 1997), where the substrate pH was lowest for *Potentilla palustris* communities (3.92) and slightly more base-rich for *Juncus* and *Molinia* communities, being 4.03 and 4.12 respectively (Dale *et al.*, 1997).

BEI and EI values for nitrogen also differ markedly between the species growing in Britain and Central Europe. Both sets of revised community indicator values show the same general pattern and are probably more representative than the unrevised EI values, which were biased towards the bryophyte-rich communities. For further use of the N-values, it is recommended that the method proposed by Ertsen *et al.* (1998), *i.e.* to remove the species from the data set, is more representative than taking the value as zero (Hawkes *et al.*, 1997). The general trend of the N-values made good ecological sense; the *Calluna vulgaris* community in pf-I had the lowest N-value after the *Molinia* dominant communities and *Calluna* is a shrub characteristic of unproductive sites (Grime *et al.*, 1988). The low fertility of the *Narthecium ossifragum-Sphagnum papillosum* community represented in pf-K was

consistent with the results of the extensive poor-fen survey conducted by Shaw & Wheeler (1990). Recently, the definition of Ellenberg's (1991) N scale has been criticised for being too vague (Hill *et al.*, 2000). Diekmann & Falkengren-Grerup (1998) linked the scale to the annual mineralisation of nitrogen. However, Hill & Carey (1997) and Ertsen *et al.* (1998) found EI values were general indicators of nutrient availability rather than nitrogen in particular. N-values may therefore indicate a combination of the availability of N, P and K. More research is needed to decide which dynamic source of N, P or K can be best related to the N-value and, thus, be related to the integrated values of the poor-fen communities. The findings from this research would be valuable as in different stages of succession the relative availability of N, P and K is thought to shift (Verhoeven *et al.*,1993).

3.4.4 PROPOSED PATTERNS OF HYDROSERAL SUCCESSION ON GOSS MOOR

In broad terms, the presence of the different communities along the moisture gradient can be considered as spatial evidence for hydroseral succession, which begins with the colonisation of open water. In the case of Goss Moor, the source of open water was the tin excavations. On the basis of the evidence discussed, the twelve poor-fen groups can be suggested as showing different stages of hydroseral succession. An attempt to display these patterns has been made in Figure 3.14. The poor-fen communities have been ordered according to increased terrestrialisation, which is represented by the abundance of bryophytes, increasing the structural complexity as the community develops. The conceived patterns of succession for the poor-fen groups are reminiscent of the sequences of mire succession proposed by Sjörs (1950) and Alexandrov & Logofet (1994).

The sequence for poor-fen communities on Goss Moor, at present, begins with floating hydrophytic communities in pools and suggests that there are three or four possible starting points of hydroseral succession. Groups pf-A to pf-D represent the initial stages, which are dominated by aquatic macrophytes such as *Menyanthes trifoliata, Potentilla palustris,*

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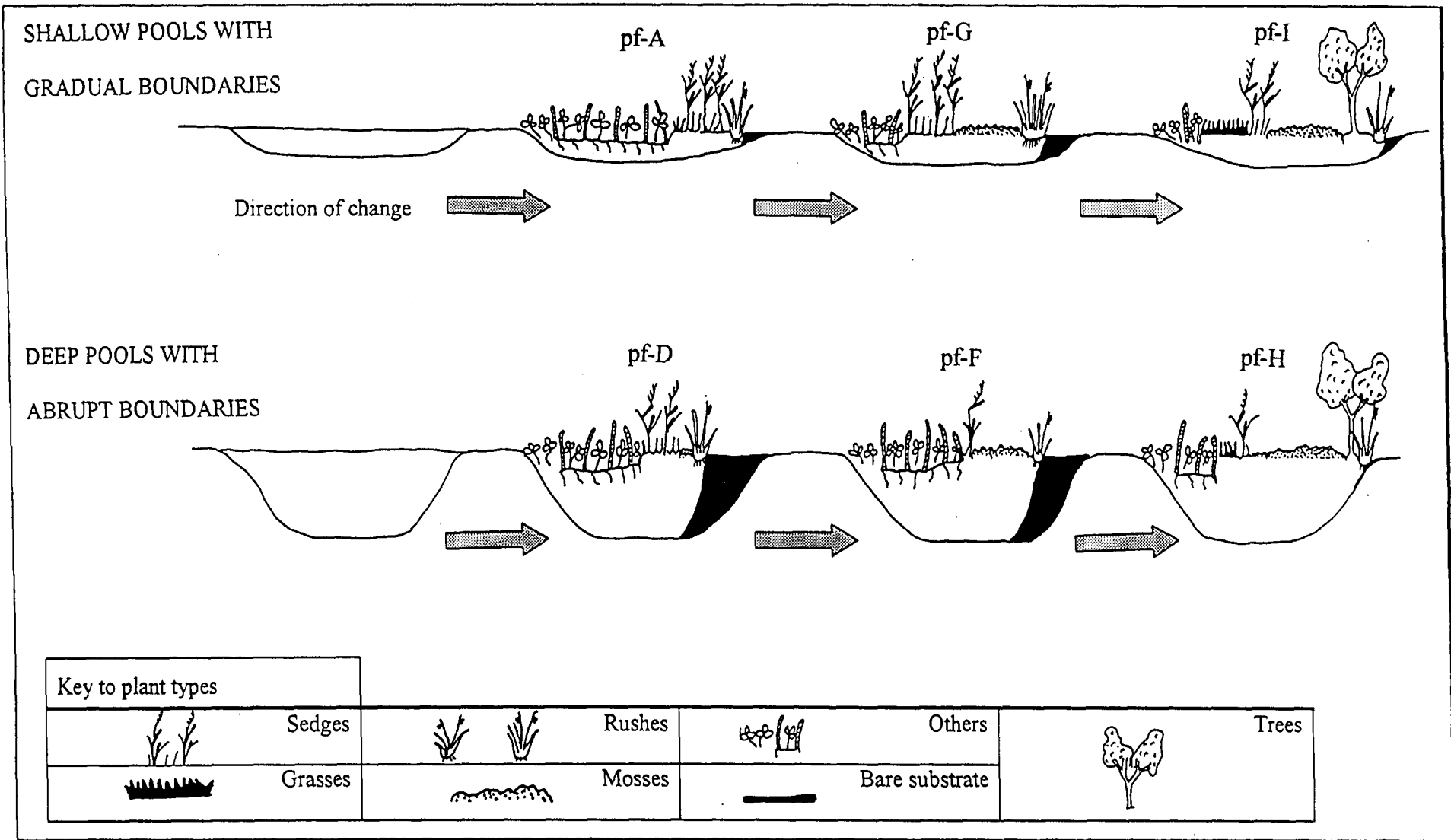
Figure 3.14 Some of the poor-fen communities on Goss Moor, ordered according to the proposed direction of hydroseral succession or vegetation change. Each community type is divided into proportions along the length of each pond to represent each vegetation type. The proportions correspond to the pie-charts in Figure 3.3.

Equisetum fluviatile, Carex nigra and *Carex rostrata. Carex rostrata*, in particular, has a vigorous root system, which allows the colonisation of open water up to 30 cm in depth (Proctor, 1974).

The conditions at this seral stage are inherently soligenous and wet with negligible amounts of organic material. The lack of dead, decomposing plant material may be due to the contemporary nature of the communities, because the vegetation receives telluric water of a higher base status (Dale *et al.*, 1997), and/or high water table fluctuation inhibiting the establishment of bryophytes.

The next stage of terrestrialisation involves gradual invasion by mat-forming bryophytes, which generally grow immediately above the water table to form a raft (pf-E to pf-G). Their appearance may be aided by species such as *Sphagnum squarrosum*, which can withstand a certain amount of water fluctuation (Wheeler, 1980; Giller & Wheeler, 1988) and base-rich inputs (Clymo, 1974; Kooijman & Bakker, 1995). Giller & Wheeler (1988) found that *Sphagnum* species may be precursors for other mosses such as *Aulacomnium* and *S. recurvum*, as the mineral-rich inundations become less significant and *Sphagnum* species coalesce. Over time, the lawn communities become more isolated from the water table and, therefore, increasingly more base-poor (Clymo, 1991), until rainwater is the predominant water source and the vegetation is ombrotrophic. The water availability controls the development of organic matter, which in turn regulates the pH of the substrate (Dale *et al.*, 1997). Once water fluctuations have reduced sufficiently trees and shrubs such as *Salix cinerea, S. aurita* L. and *Calluna vulgaris* are able to invade. This marks the initiation of the next successional sere and is represented in pf-H and pf-I.

Inevitably, there are various patterns and rates of successional change depending on combinations of water regime, substrate, micro-topography and species interactions such as

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competition. The situation or position on the Moor can also decide the type of successional pathway a community will undergo. The spatial distribution of pf-B, pf-E and pf-L show these communities to be restricted to specific regions of the moor (Figure 3.7). The presence of high proportions of *Sphagnum squarrosum* in pf-E may indicate nutrient-rich water (Kooijman & Bakker, 1995) arriving directly from the surrounding catchment. Group pf-B is also found in the vicinity of these drainage channels. However, the bryophyte component is not as developed and this community is comparatively less species-rich than pf-E. Soro *et al.* (1999) found that species diversity in mire vegetation increased over time and attributed this to a greater frequency of non-random species associations, thus emphasising the importance of random events for colonisation and the early successional stages. Differences between the species richness of pf-B and pf-E may indicate the presence of a successional pathway. Group pf-E may be a more developed version of pf-B. Whether there is a temporal relationship between them or not, the spatial distribution of pf-B and pf-E suggests they may be undergoing separate successions at this point in time in comparison to the other poor-fen groups.

The communities that have a better developed bryophyte layer and are therefore more advanced in the terrestrialisation process may indicate communities that are older than the groups which are rich in hydrophytes. This is possible, as the main period of tin excavations on the moor occurred for over 100 years, during the 19th century and up until the late 1920s. This means that the wetland habitats age between 80 years and 200 years old. Other factors that may govern the type of vegetation are factors such as high water table, moving water or fluctuation that reduce the speed of development. Further evidence for different patterns of succession can be ascribed to substrate heterogeneity, which are signified by the presence of *Molinia* and *Juncus* communities. *Juncus* communities indicate transitional areas where the substrate is predominantly mineral rather than organic (Proctor, 1974). These communities occur in various proportions as transitions between *Molinia* and

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poor-fen communities and indicate considerable substrate heterogeneity on Goss Moor. *Molinia* communities often occupy areas between abrupt wet and dry transitions (Grime *et al.*, 1988). The substrate is often aerated and lacking in significant amounts of organic material. In wetter conditions, *Molinia* can be replaced by *Juncus effusus* and *Eriophorum angustifolium* (Jefferies, 1916). So, depending on the water regime, species assemblages in pf-J, pf-K and pf-L may be susceptible to change.

The micro-topography of Goss Moor affects the types of community that occur. Small, deep pools with abrupt boundaries are dominated by community types pf-F, pf-H and pf-I. Of these, pf-H and pf-I are dominated by cushion-forming bryophytes such as *Aulacomnium palustre* and *Sphagnum recurvum*, which usually grow above the water table. As these mosses grow and die, the water column is gradually infilled with organic matter which reduces the surface water height. Group pf-F may represent an earlier seral stage to the communities of pf-H and pf-I due to the greater prominence of early stage aquatic macrophytes such as *Potentilla palustris* and *Menyanthes trifoliata* and, most importantly, *Sphagnum squarrosum*. In contrast, large shallow pools with less defined boundaries are occupied by the early seral communities pf-A, pf-B, pf-C and pf-D. The rate of succession in these larger pools is probably slow due to lateral water movement that maintains the conditions required by the aquatic macrophytes and simultaneously prevents the colonisation of significant quantities of bryophytes.

In classical hydroseral succession, vegetation usually encroaches an open-water pool as a raft growing centripetally from the edge towards the centre of the pool (Tansley 1939; Walker, 1966; Tallis, 1973). Therefore, terrestrialisation of the pool is most advanced at the edges. On Goss Moor this type of hydroseral development is common. However, in some pools the thickest most developed raft appears to be in the centre of the pool. It is not unusual to observe miniature willow trees growing on a thick raft of bryophytes in the

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centre of a pool. This phenomenon has also been reported in the Scottish Border Fens (Tratt, 1997). One possible explanation for this type of raft development has been proposed by Tratt (1997) and may be attributed to the small size and isolation of some of the pools. This would enable the colonising network of species such as *Equisetum fluviatile* and *Carex rostrata* to spread quickly and fairly uniformly across the pool. It is expected that central areas would suffer smaller surface water fluctuation due to buffering of the vegetation attached to the pool edge. Decomposition rates would therefore be faster at the edges due to the impacts of water fluctuations. Hence the central areas of the pools, buffered from the decomposition processes experienced by the edges, would become relatively thicker.

3.5 SUMMARY

- Hydroseral succession can explain the variation among the twelve poor-fen communities found on Goss Moor.

- The Ellenberg Indicator values were more useful than the British Ellenberg Indicator values for detecting environmental differences between poor-fen communities due to the presence of the comprehensive data on bryophytes.

- Weighted Community Ellenberg Indicator values for N, light, reaction and moisture are recommended as an effective tool for indicating differences between plant communities

- Of the environmental variables measured, high water levels were associated with the swamp communities (pf-A, pf-B, pf-D), increased organic depth was associated with poor-fen pf-E, pf-F, pf-G, pf-H and pf-I, and the type of boundary affects the resulting community composition. The spatial pattern and water regime of the wetland communities will be investigated further in Chapters Five and Six, respectively.

The next chapter provides a detailed description of the willow carr communities in relation to their age and understorey composition.

Chapter Four: A baseline survey of the willow carr communities on Goss Moor

4.1 INTRODUCTION

Throughout the last fifty years, willow scrub has become increasingly prevalent on Goss

Moor. The invasion of scrub on nature reserves is generally perceived to be an undesirable

feature, as total domination can lead to extinctions of more valuable animal and plant

species. Habitat management guidelines recommend that the proportion of scrub on fens

and wetlands should not exceed 15-20% (Sutherland & Hill, 1995). When limited to these

amounts, scrub can add to the diversity of the site as it can often support many birds and

invertebrates that are not found in open fen communities, such as Cetti's warbler *Cettia*

cetti Temm. (Sutherland & Hill, 1995), craneflies and the netted carpet moth *Eustromia*

reticulata Schiff. (Joint Nature Conservation Committee, 1998). The amount of willow

scrub on Goss Moor has by far exceeded the English Nature protocol of 16 %, prompting

the largest scale of scrub removal in the whole of the British Isles to date (I. Davies pers.

comm.). Previous attempts to remove the willow have proved ineffective due to re-growth

from stumps, so new removal strategies are presently being contemplated. In the face of

such extreme measures, it is surprising that the dynamics of willow carr invasion on Goss

Moor remains undescribed, as does the understorey composition. The research in this

chapter intends to evaluate the willow resource by providing a phytosociological

description of the willow carr communities and characterising them according to a number

of physical factors, which are described herein. These findings will be used to help

formulate management strategies for prioritising areas for future conservation and scrub

removal.

Wet woodlands frequently occur as successional habitats on fens, mires and bogs, often

forming a complex mosaic. Willow invasion is thought to represent the first stage of

woodland or fen carr development (Tansley, 1953), which has traditionally been thought to

invade the drier locations on wetlands (Tansley, 1939; Walker, 1970). However, the

thresholds for tree colonisation are determined by a variety of interacting hydrological and

environmental variables, which definitely vary amongst sites and tree species and may change with time. So far, identification of simple or exact hydrological thresholds for tree establishment has proved elusive (Wheeler, 1999). Some research on tree establishment has revealed the importance of flood timing and amplitude, a more detailed account of which will be covered in Chapter Six.

The conservation value of wet woodlands has only recently been recognised. The U.K. Habitat Action Plan for Wet Woodlands has been published as part of its commitment to the Rio Convention (Earth Summit Convention on Biological Diversity, Rio de Janeiro, 1992), and this includes targets for wet woodland conservation, restoration and re-establishment across the UK. As well as gaining data on the general nature of wet woodlands, one of the key areas of research identified was to investigate the dynamics of this habitat in relation to other priority habitats such as fens and mires. Despite this interest, the main difficulty in evaluating the importance and potential of wet woodlands in contributing to the species resource of the wetland is that although they may be (sub-) climax systems, they are not thought to be 'natural' (Wheeler *et al.*, 1999). This is because the distribution and character of wet woodlands is often a result of human intervention or disruption of former natural processes. These include:

- changes or cessation of management regimes that formerly favoured herbaceous vegetation, such as grazing, thus enabling the initiation of wet woodlands;

- the modification of natural hydrological processes, which once controlled the distribution of woody and herbaceous vegetation in wetlands (e.g. the extent, amplitude and duration of river flooding);

- direct, partial drainage or indirect drainage of adjacent agricultural land altering the hydrodynamics of wet woodlands;

- coppicing of mature wet woodlands that often results in a rather uniform 'even-aged' canopy.

These considerations make it difficult to assess the potential importance and character of 'natural' wet woodlands, especially as the amount to which existing wet woodlands have been modified is difficult to evaluate. It is possible to gain some insights by considering less modified landscapes, such as those in the sparsely populated regions of Poland and Scandinavia. However the differences in climate pose obvious constraints upon comparability (Wheeler *et al.*, 1999).

It is evident from investigations in less modified environments than the U.K. that natural, boreal wet woodlands are often more species-rich than herbaceous vegetation growing in close proximity, in slightly wetter locations. There are a number of factors which help explain this (Wheeler *et al.*, 1999): many plants, including a number of characteristic 'wetland' species, are intolerant of very wet conditions, all year round; high water tables and amplitude are often associated with species reduction (Weiher & Keddy, 1995); substrate heterogeneity permits the survival of plants with a range of water tolerances; tree falls create glades allowing species of open habitats to survive (Wheeler *et al.*, 1999).

Wet woodlands are often botanically richer than open herbaceous vegetation in 'natural' mires, because they are able to support species from the open herbaceous habitats and adjoining other habitats as was found for the fen woodlands in Sweden and tamarack swamps of North America (Wheeler *et al.*, 1999). In contrast, the understorey composition of British fen woodlands generally contains an impoverished subset of species that occur in herbaceous conditions, and rather few notable species that are exclusive to fen woodlands (Wheeler *et al.*, 1999). In order to identify factors associated with valuable communities, this study intends to distinguish the environmental conditions that are associated with increased understorey diversity of the willow carr communities and compare them with the species richness data of the poor-fen communities identified in the previous chapter.

The willow scrub on Goss Moor is mostly dominated by trees and shrubs of *Salix cinerea* ssp. *oleifolia*, and bushy shrubs of *Salix aurita*. Like all willow species, *Salix cinerea* and *Salix aurita* are deciduous, catkin bearing and much-branched (Meikle, 1984). *Salix cinerea* grows to a height of up to 10 m and is widely distributed in the fens of south and east England (Meikle, 1984). *Salix aurita* is a small shrub reaching 2.5 m in height and is found throughout Britain, although it is uncommon in the Midlands (Meikle, 1984). The average lifespan of *Salix caprea* L., a similar willow species, has been reported to be between 50 to 60 years and a maximum of 76 in Poland (Faliński, 1997). *Salix cinerea* is associated with field layer species such as *Galium palustre* L., *Mentha aquatica* L. and *Juncus effusus*. This community is assigned to NVC type W1 *Salix cinerea-Galium palustre* community, the composition of which is known to show considerable heterogeneity (Rodwell, 1991a).

Willow species such as *Salix cinerea* are able to establish in a wide range of habitats along a moisture gradient. However, in comparison to other wetland tree species, *Salix cinerea* shows a marked tolerance to waterlogging (Iremonger & Kelly, 1988). The main problem for plants growing in waterlogged conditions is the lack of oxygen available to the root (Kawase, 1981). Water-filled pores diffuse oxygen 100,000 times slower than when the same pores are air-filled (Armstrong, 1982). *Salix cinerea* and other wetland vascular plants have a diffusive internal oxygenation system (Talbot & Etherington, 1987), which both supplies root respiration and also, by leakage of oxygen to the root surface, detoxifies ions such as Fe^{2+} and Mn^{2+} carried within the incoming transpiration stream (Armstrong, 1982). This research intends to identify the range of watertable conditions that willow trees inhabit on Goss Moor and to characterise the type of conditions that willow invades.

One of the most common methods used to describe succession is to order vegetation data taken from sites of similar environments but different ages, an approach termed the spatial chronosequence (Glenn-Lewin & van der Maarel, 1992), which was discussed in detail in

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section 2.3.5. Chronosequences of forest development are commonly utilised for studying ecosystem dynamics (Marques & Ranger, 1997; Yanai *et al.*, 1999) and gaining some broad indications of the rate of succession. Bakker *et al.* (1997) used different ages of aerial photographs to define chronosequences of vegetation change and to quantify the amount of vegetation change from open water to swamp forest in the Netherlands. Aerial photographs have also been effectively used to describe the development of *Salix cinerea* woodland in North Wales (Alliende & Harper, 1989). The aerial photographs available for the Goss Moor area were used to quantify the amount of change in the vegetation of Goss Moor.

As well as examining the phytosociological aspects of the different ages of willow carr community, it is also useful to investigate the structural aspects and tree population dynamics. The architectural attributes of tree structure can be used to characterise the growth of the trees present in the chronosequence of willow carr development. There· are also a number of measurable architectural parameters that can be used to provide a broad account of the conditions experienced by the trees.

The architectural approach has been used extensively in the tropics (Hallé *et al.*, 1978) and continental Europe (Walter, 1982) and the only published data of this kind from wet woodlands is provided by Iremonger (1990) for Irish woods. This approach to forest dynamics analysis was developed by Hallé *et al.* (1978) and focuses on an abstracted reproduction of a sample plot in a profile diagram and the collection of numerical information at each sampling location. The analysis concentrates on the growth of the individual tree in relation to its immediate environment (Oosterhuis *et al.*, 1982). An indicator of the general vigour of the tree is the position of the lowest living branch or reiterated trunk on the main trunk. The height of the lowest branch can be related to a reference line that indicates half the total height of each tree and is used to judge the maturity and degree of architectural homogeneity in a forest plot (Oldeman, 1978). When

the lowest living branch is below the middle reference line, the predominance of positive morphogenesis and an ecological situation of increasing energy availability is indicated. When this point lies in the upper half of the trunk, negative morphogenesis or branch shredding predominates, indicating either a diminishing environmental energy supply or stress. The point of insertion of the lowest major branch or fork of the tree is called the 'morphological inversion point' (Oldeman, 1978; Hallé *et al.*, 1978).

The development of different tree communities can be assessed using the relationship between the diameter at breast height (D) and the total height (H) or the H/D relation (Iremonger, 1990). To this end, Cusset (1980) and Rich *et al.* (1986) used the equation H = AD, where A was a constant for a particular stand of trees. In model-conforming trees it has been empirically shown that H = 100.D. In cases of excess energy when reiteration or the production of new branches has taken place as an energetic adjustment mechanism, H<100.D (Oldeman, 1978). Reiteration utilises the excess energy as it complicates the network of energetic pathways within the tree and increases the number of points among which the total energy from the roots must be divided and from which photosynthates must be exported (Oldeman, 1978). However, Ogawa & Kira (1977) showed that the relationship could be best approximated by a hyperbolic equation:

$$\frac{1}{H} = \frac{1}{AD^{h}} + \frac{1}{H^{*}}$$

Where H, A and D are used as in the first equation, H* represents the theoretical maximum tree height, and *h* is an allometric constant (McMahon, 1975).

The aims of this section of the willow study were to examine the architectural characteristics of trees from the spatial chronosequence of willow growth, to establish a growth curve and make some broad statements on the general condition of the willow stands on Goss Moor.

4.1.1 SOIL CATION ANALYSIS

Many studies of factors determining species distributions and community composition in wetlands have concentrated on differences in water and substrate chemistry (Sjörs, 1950; Proctor, 1995). A number of correlations have been identified between the availability of soil calcium and magnesium cations and certain habitat conditions. Proctor (1974) found the Ca^{2+} content of peat waters was highest in fen carr and lowest in poor-fen, which may indicate that Ca^{2+} increases over time and may thus be used to indicate a successional relationship. In the same study, the availability of Mg^{2+} was found to behave in an opposite manner to Ca^{2+}. Other observations related to changes over time include the gradual decrease of soil Mg and Ca, which occurs as a natural feature of weathering and pedogenesis (Brady, 1990; Richter *et al.*, 1994).

High concentrations of calcium and magnesium in peat waters have been associated with the close proximity to drainage inputs, often originating from agricultural land (Wheeler & Giller, 1982a). On Goss Moor, there is a large amount of spatial heterogeneity regarding water chemistry, thought in part to be related to drainage channels (Dale *et al.*, 1997). This part of the research intends to ascertain whether the concentrations of soil nutrients are associated with various ages of willow due to soil development as a successional process or whether the spatial variation is a governing factor.

The aims of this chapter were to:

- describe the variation among the understorey willow carr communities and relate to age and spatial variation;

- assess the effectiveness of the British NVC (Rodwell, 1991a) for accommodating variation in the species composition of understorey communities

- use aerial photographs to quantify the rates of willow invasion of different ages and location;

- from a management perspective, discover whether the conditions associated with increased understorey richness are related to age;

- examine whether there is a successional relationship between the concentrations of exchangeable cations in the soil associated with willow carr communities of different ages;

- describe the process of sylvigenesis for *Salix cinerea* on Goss Moor and assess the architectural characteristics in relation to age and growth conditions.

4.2 METHODOLOGY

4.2.1 AERIAL PHOTOGRAPHS

Aerial photographs were used to identify a chronosequence of areas to be used to study the ecology and dynamics of willow carr on Goss Moor. Photographs taken in 1946, 1963, 1976, 1988 and 1994 were available, the details of which are presented in Table 4.1. The aerial photographs were used to identify major scrub cover in the following age ranges: pre-1946; 1946-1962; 1963-1975; 1976-1987; and 1988-1994.

Table 4.1 Information on the size, reference number and producers of the five aerial photographs used for the image analysis and vegetation survey of Goss Moor.

Date	Scale	Reference number	Contact
05/05/1946	1:10,000	B32 4127-8	NMRC, Wilts
25/05/1963	1:10,000	HSL UK 63 38 1510-1	Aerofilms, Herts
26/08/1976	1:10,000	HSL UK 76 39 1194-5	Aerofilms, Herts
21/05/1988	1:10,000	52 88 046-048	JAS AIR, Surrey
18/04/1994	1:13, 333	Site No: 93/23	NERC

4.2.2 ANALYSIS OF WILLOW COVER

The rate and pattern of spread of willow scrub across the Moor was determined by image analysis of the five different ages of aerial photographs. Prior to analysis, Goss Moor was

divided into 13 500 m x 500 m blocks (Figure 4.1). Each 250, 000 m^2 square was then further divided into 25 100 m x 100 m squares and numbered 0-24.

The image analysis was performed using the Leica Quantimet 570, which incorporates grey scale image processing software based on mathematical morphological techniques. First the image was captured by placing the aerial photograph under the video camera and digitising it to a 512 x 512 pixel image of 256 grey values. Colour images were captured using an Hitachi HV-OC20 colour camera and the black and white images with an Hitachi VK-C150ED. For colour images, the red green & blue were used for grey scale values. Each pixel represented 1m^2. The 'offset' and 'gain' settings were used to give high contrast and the best possible detection. Once the image was obtained the grey image was detected by thresholding the grey values, which are transformed to produce a binary image. The measure field function provided a measurement of the total area of willow found in each 100 x 100 m square.

4.2.3 WILLOW CARR SAMPLING STRATEGY

Sampling areas for the 1998 willow survey were determined using the five ages of aerial photographs, discussed above. From each of the age ranges, five willow stands were chosen randomly for analysis.

In June and July 1998, the vegetation growing beneath the willow of each age was surveyed using a 2 x 2 m quadrat, and employing the same nomenclature stated in section 3.2.1.1. Sampling points in each stand were located using a stratified random design and, depending on the size of the stand, between four and ten quadrats were recorded per stand. Willow that was not part of the main canopy was also included in the quadrats.
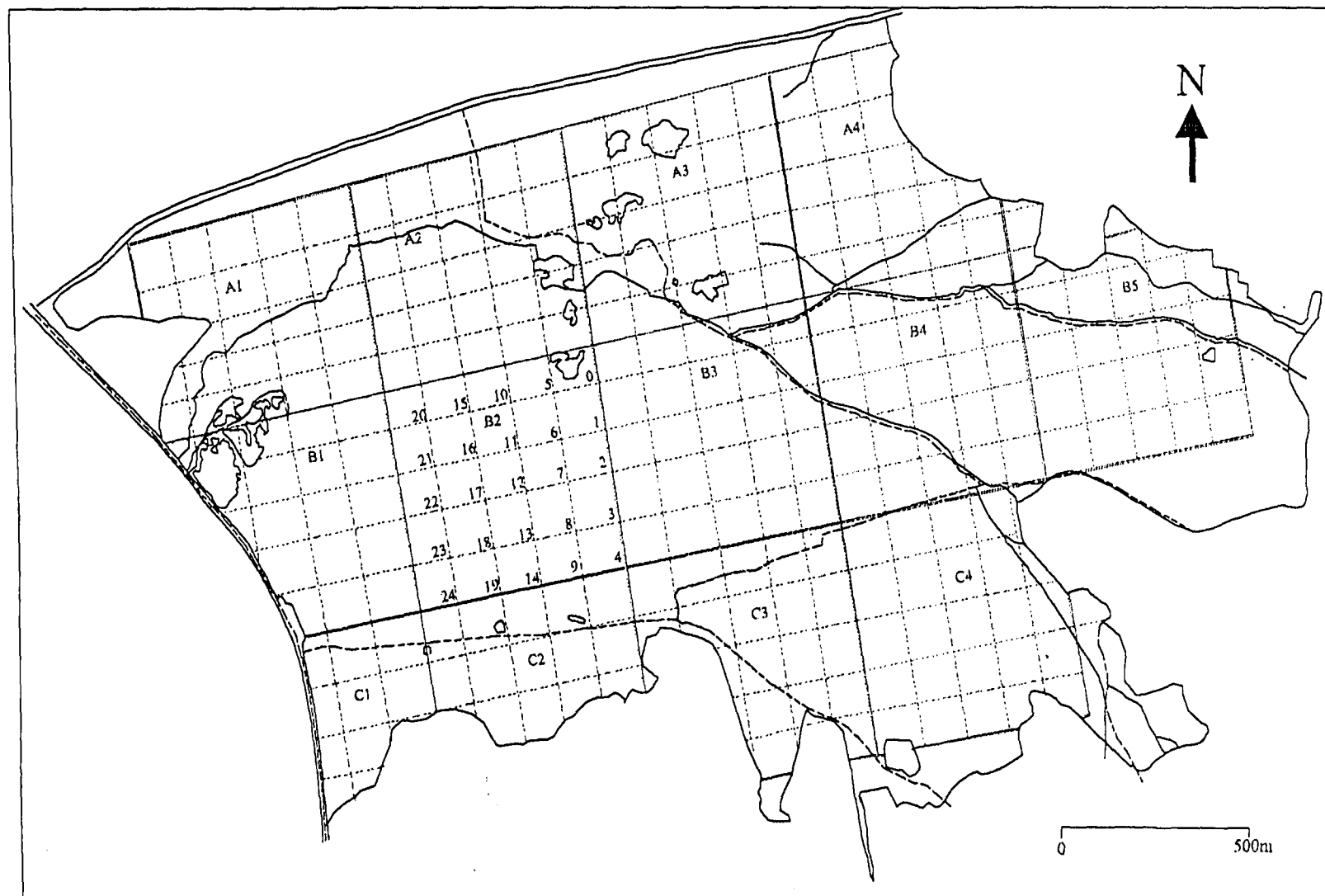
Figure 4.1 Divisions of Goss Moor used for the image analysis. Each 500 x 500 m square was further divided according to the grid shown in B2.

4.2.4 COLLECTION OF ENVIRONMENTAL DATA

The height of standing water and organic depth were recorded in each quadrat, following the methodology described in section 3.2.1.2. Percentage cover of willow canopy was determined using a 'Moosehorn', which enables the sampler to view and quantify the reflected image of the canopy with the aid of a 100 x 100 square grid.

4.2.4.1 Soil analysis

Two random soil samples were taken from the top 5 cm of the 'A' horizon from each quadrat. Consistency in the sampling strategy was essential as soil cation concentrations commonly reduce with depth (Wheeler & Giller, 1982a). On collection, each sample was stored in a polythene bag and frozen at -26 °C on the same day. Samples remained frozen for 6 months until the day of analysis when they were laid out on trays to defrost. A range of pedological analyses were undertaken in an attempt to establish broad correlation between soil, stand age or vegetation type.

Soil pH

The pH of the soil is considered to be an indication of its overall chemicals status and, thus, provides a useful basis for comparison (Smith & Atkinson, 1975). Soil pH is generally affected by air drying (Allen, 1989). Approximately 10 g of air –dried soil was placed in a 100 ml beaker, followed by 25 ml of distilled water and agitated for 30 seconds then left for 10 minutes. If the soil was quite dry, 2 ml of 0.125 M Calcium Chloride was also added to free up any H^+ that may have adhered to clay particles. The pH was measured using a calibrated Metler Toledo MP220 glass-electrode pH meter.

Exchangeable calcium and magnesium

The fractions of soil Ca and Mg available to plants are cations weakly held on exchange sites (Lanyon & Heald, 1982). Exchangeable calcium and magnesium were determined

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following extraction from 1 M ammonium acetate (Allen, 1989; Smith & Atkinson, 1975). This method relies on an excess of ammonium ions displacing the calcium and magnesium cations from the soil exchange sites. Soil samples were air dried and sieved. Following this preparation, 5 g of the soil was mixed in 50 ml of 1 M Ammonium acetate for 30 mins on a 100 rpm orbital shaker. The mixture was left to stand for 10 mins and was filtered using 41 Whatman filter paper and transferred to a 50 ml volumetric, where the volume was made up with 1 M Ammonium acetate. Concentrations of available magnesium (Mg^{2+}) and calcium (Ca^{2+}) were determined using VARIAN SpectrAA-600 flame atomic absorption spectrophotometer (AAS) with automatic 'sip' dilution facility.

4.2.5 ARCHITECTURE

In order to gain some information on the structural aspects of the willow carr growing on Goss Moor, thirty *Salix cinerea* spp. *oleifolia* trees were randomly chosen from each age range and a number of architectural features were measured. These included: tree height (m); the number of base poles; height of first fork greater than 10 cm in diameter (m); diameter at breast height (dbh) of the largest pole (cm); the number of poles at 1.5 m greater than 5 cm diameter. The height of the trees was determined by attaching the measuring tape to a 3 m long cane, which was aligned with the highest point of the tree canopy. Trees greater than 5 m were measured using a clinometer. Each tree was drawn to scale in a two-dimensional format, from a southerly position. Tree density was found by counting the number of individuals in a 10 x 10 m square, to give the number of trees per 100 m^2. For comparison, the mean distance between four randomly chosen trees was found at each sampling location.

4.2.6 ANALYSIS OF VEGETATION AND ENVIRONMENTAL DATA

The broad aims of the data analysis were to describe the range of plant communities that occur in association with the different aged stands of willow carr and to elucidate the

relationship between these communities and selected abiotic factors. To achieve these aims, a number of separate analyses were carried out.

4.2.6.1 Definition and classification of the main species assemblages associated with willow carr

The principal plant communities associated with the different areas of willow surveyed were defined and classified using the revised version of the TWINSPAN program (Hill, 1979a; Oksanen & Minchin, 1997). The interpretation of the final output table followed the method described in section 3.2.2.1.

4.2.6.2 Ordination of floristic and environmental data

As in section 3.2.2.2, the vegetation quadrat data were analysed using the DCA and the updated version of the associated software DECORANA (Hill, 1979b). Floristic and environmental relationships between the different ages of willow and TWINSPAN groups were assessed using CCA (Ter Braak, 1987) and the associated CANOCO computer software (Ter Braak, 1988).

4.2.6.3 Determination of differences in stand diversity

The average number of species per quadrat, or species richness, for each of the species assemblages identified by TWINSPAN and those associated with the different ages of willow carr were determined. Differences in the number of species among the age groups and the communities identified were analysed using single factor analysis of variance (ANOVA) on the SPSS statistical analysis computer program (version 9.0 SPSS Inc., USA), followed by a Tukey multiple comparison test.

4.2.6.4 Analysis of the tree architecture data

In order to identify any relationships between the architecture data collected from the 30 trees sampled for each age range, a multivariate test was conducted. To test differences between the age classes discriminant function analysis on the Minitab (version 6.0, U.S.A) computer software was used. This method utilises a set of weightings to distinguish the different age groups by providing a probability of the accuracy of assigning an unassigned individual to a group according to its architectural attributes. If the probability is high then the unknown can be confidently assigned to a group (Dytham, 1999).

To describe the process of willow carr sylvigenesis, the hyperbolic equation given in the introduction to this chapter was modelled using the non-linear regression feature in the Statgraphics (version 4.0, U.S.A.) computer program.

4.3 RESULTS

4.3.1 FIVE DECADES OF WILLOW CARR GROWTH ON GOSS MOOR

Table 4.2. shows the total amount of willow that was present in each of the three blocks A, B and C, for each of the given years. Table 4.3 summarises these amounts as a percentage cover of willow on Goss Moor for each of the five years. In 1994, block B contained the least amount of willow carr, covering 33 % of the total area. The majority of the wetland resource was found in Block B. Figures 4.2–4.6 show the vigour of willow scrub growth that occurred between each year of study, in each 100 x 100 m square.

Table 4.2. Amount of *Salix* spp. cover (m^2) in each 250, 000 m^2 on Goss Moor NNR, labelled A1-A4, B1-5 and C1-4,. taken from the five aerial photographs for 1946, 1963, 1976, 1988 and 1994. The total area sampled was 2,740,000 m^2.

Date Block	1946	1963	1976	1988	1994
A1	11000.0	60946.4	110064.5	142911.7	164881.5
A2	0	72622.1	103001.5	136374.5	132259.8
A3	11000.0	72804.3	114727.5	159578.2	176733.0
A4	0	30397.9	47646.2	75257.5	94841.0
B1	0	4.0	3332.4	17045.8	26370.3
B2	3600.0	40234.2	58445.4	72817.6	94247.4
B3	12300.0	44959.0	79120.2	133636.9	145539.2
B4	0	8923.4	23815.0	81194.4	91968.6
B5	3100.0	16500.0	25735.2	30655.1	36914.8
C1	0	0	6846.6	22226.1	26801.4
C2	0	0	16166.8	33662.4	42807.1
C3	6480.0	25623.8	48387.7	83680.3	92379.8
C4	30.0	41774.9	92971.0	117405.7	132790.3
Total	**47510**	**414790**	**730260.8**	**1106445.9**	**1258534.2**

The results clearly show that willow spread was more prominent in some areas than others. In 1946 the willow carr present or dense enough to be detected by the image analysis and eye amounted to only 1.7 %. In this year the majority of the willow was found at the north and centre of the site in squares A1, A3 and B3.

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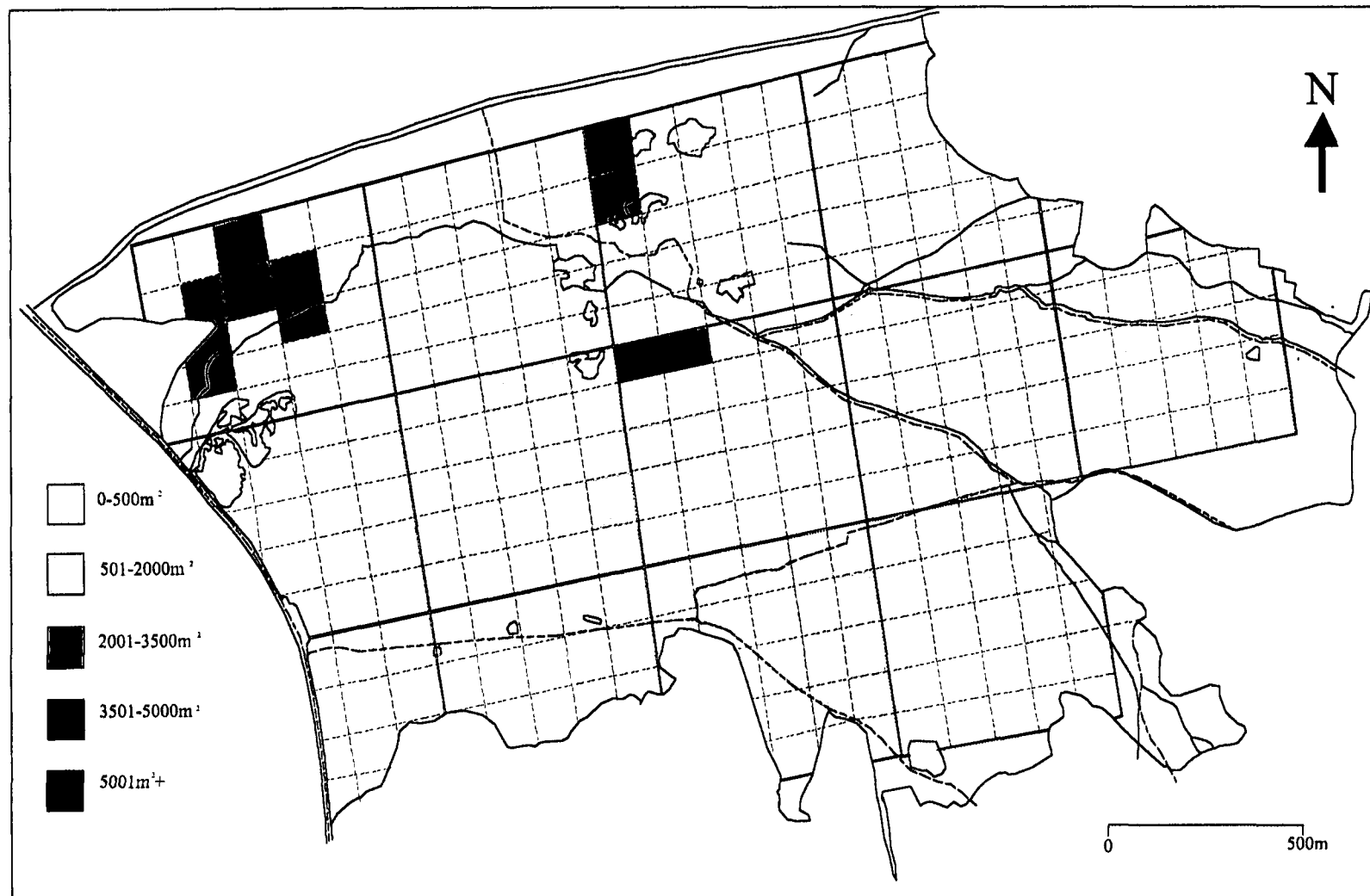
Figure 4.2 The amount of willow in m² present in each 100 m x 100 m square in 1946.

Figure 4.3 Change in willow density, expressed as cover in m^2, between 1946 and 1962.

Legend:
- 0-500m^2
- 501-2000m^2
- 2001-3500m^2
- 3501-5000m^2
- 5001m^2+

0 — 500m
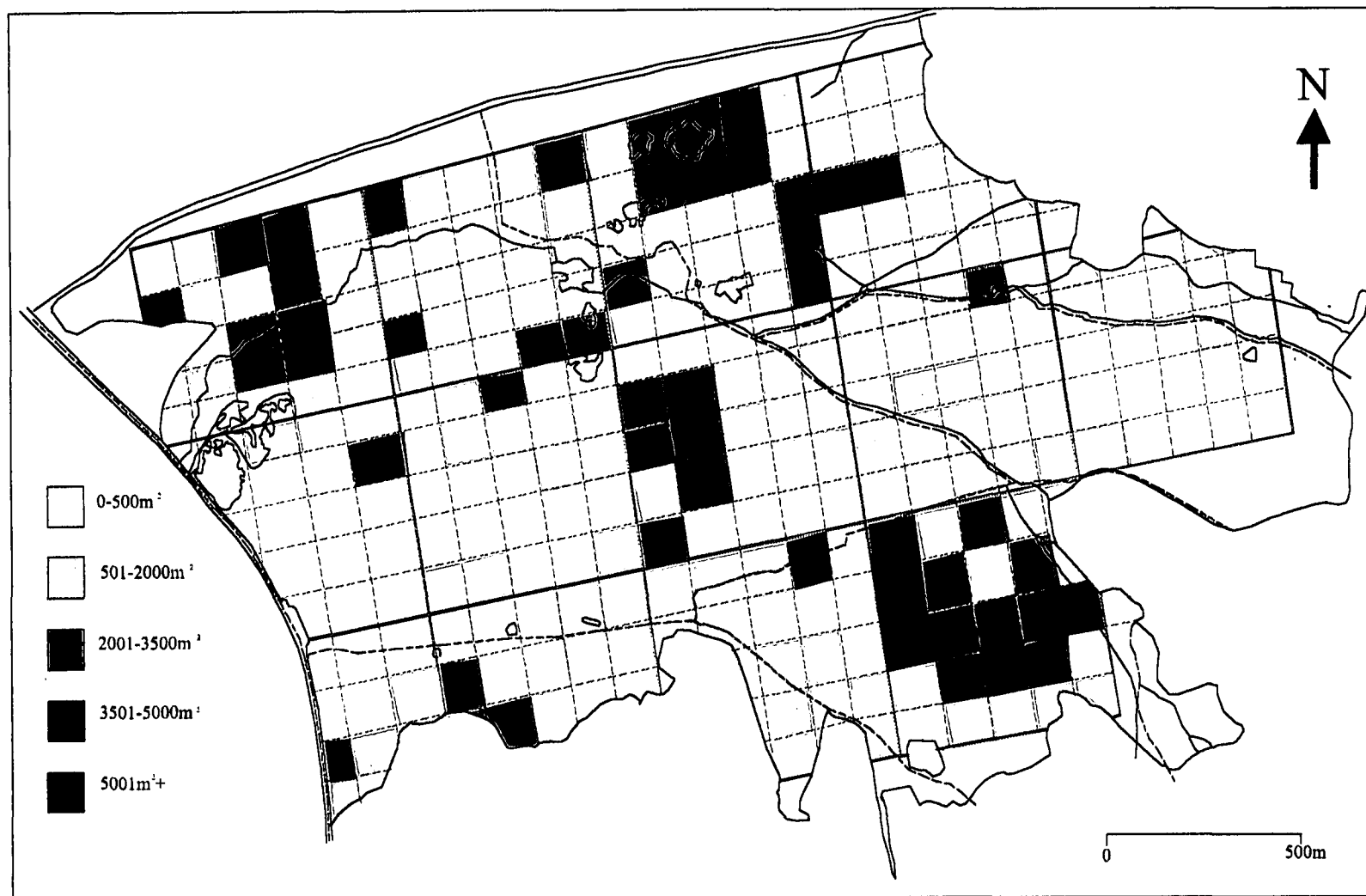
Figure 4.4 Change in willow density, expressed as cover in m², between 1963 and 1975.
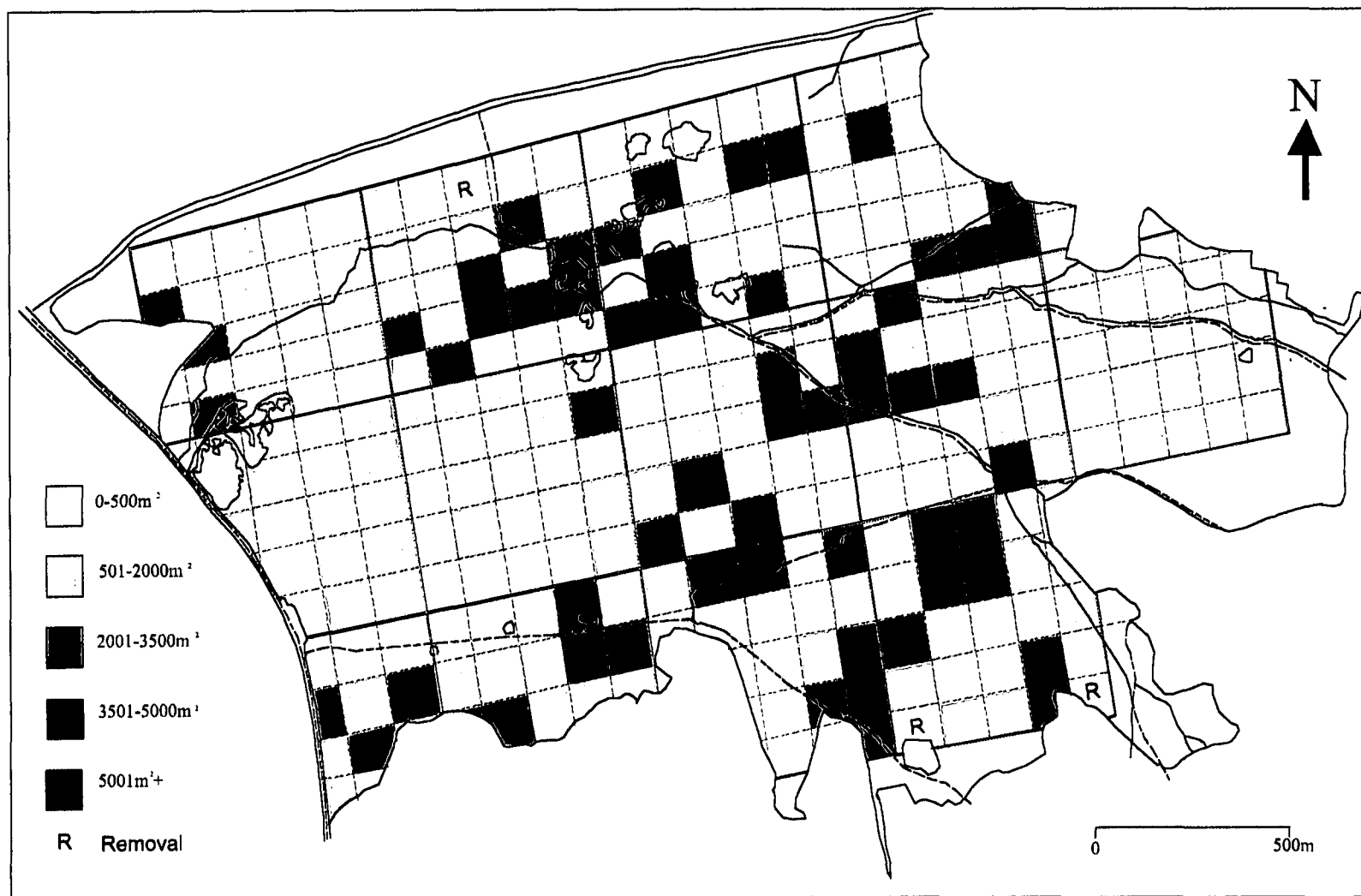
Figure 4.5 Change in willow density, expressed as cover in m², between 1976 and 1987.

Legend:
- 0-500m²
- 501-2000m²
- 2001-3500m²
- 3501-5000m²
- 5001m²+
- R Removal

N

0 500m
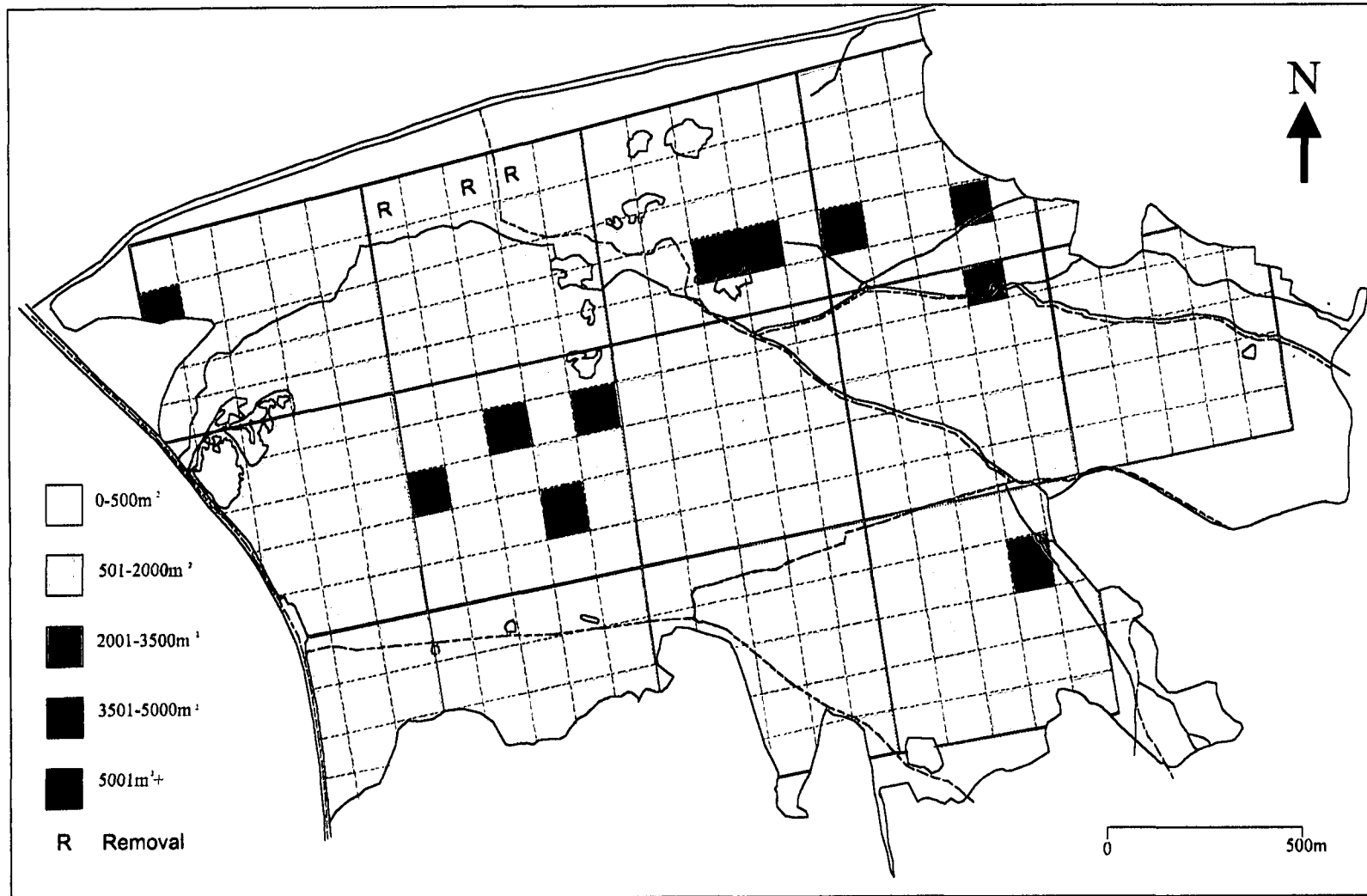
Figure 4.6 Change in willow density, expressed as cover in m^2, between 1988 and 1994.

Legend:
- 0-500m^2
- 501-2000m^2
- 2001-3500m^2
- 3501-5000m^2
- 5001m^2+

R   Removal

Between 1946 and 1962 the majority of the growth occurred in squares A2 and B2. Compared with the other 12 squares, A2 contained the fifth highest amount of willow coverage at 132, 219.8 m^2 in 1994, despite the willow removal that occurred between 1976 and 1994. The spread of willow in B2 has been intermediate and at a constant rate (Figure 4.7) with an average of 2081 m^2 per year. Between 1963 and 1975, the most willow growth occurred in square C4, in the south-east of the Moor and A1, in the north-west, when A1 increased by 4912 m^2 and C4 by 51196 m^2.

Table 4.3 Percentage cover of willow out of the total area in each of the blocks A, B and C and the total percentage cover of the whole site in the five ages determined by the dates of the aerial photographs.

Date	1946	1963	1976	1988	1994
A	2.4	25.3	40.2	55.0	60.8
B	1.6	9.2	15.9	27.7	32.9
C	1.1	11.1	27.2	42.5	48.7
Site total	**1.7**	**15.1**	**26.7**	**40.4**	**45.9**

Although no willow was detected in C1 and C2 until 1976, today these squares contain 38% and 33 % of willow carr, respectively, and most of this appeared between 1976 and 1987. Willow growth across the whole site was most noticeable between these years and increased by 14.5 % in 12 years. This is despite the removal of 10,849 m^2 of willow at the north of the site in squares A2 and A3 and 3540 m^2 in C4. Between 1988 and 1994, more willow was removed from A2 and C4. Squares A1 and A3 contained the most willow, with amounts of 161, 882 m^2 and 175, 703 m^2 or 67 % and 70 %, respectively. In 1994, the total amount of willow carr in the sample squares amounted to 1, 247,465 m^2 or 46 % of the sample area. Areas on the moor containing the least amount of willow carr are B1, B5, C1 and C2. However, the amount of willow carr in these areas is gradually increasing; between 1988 and 1994, and coverage in B1 increased from 17046 m^2 to 26370 m^2.
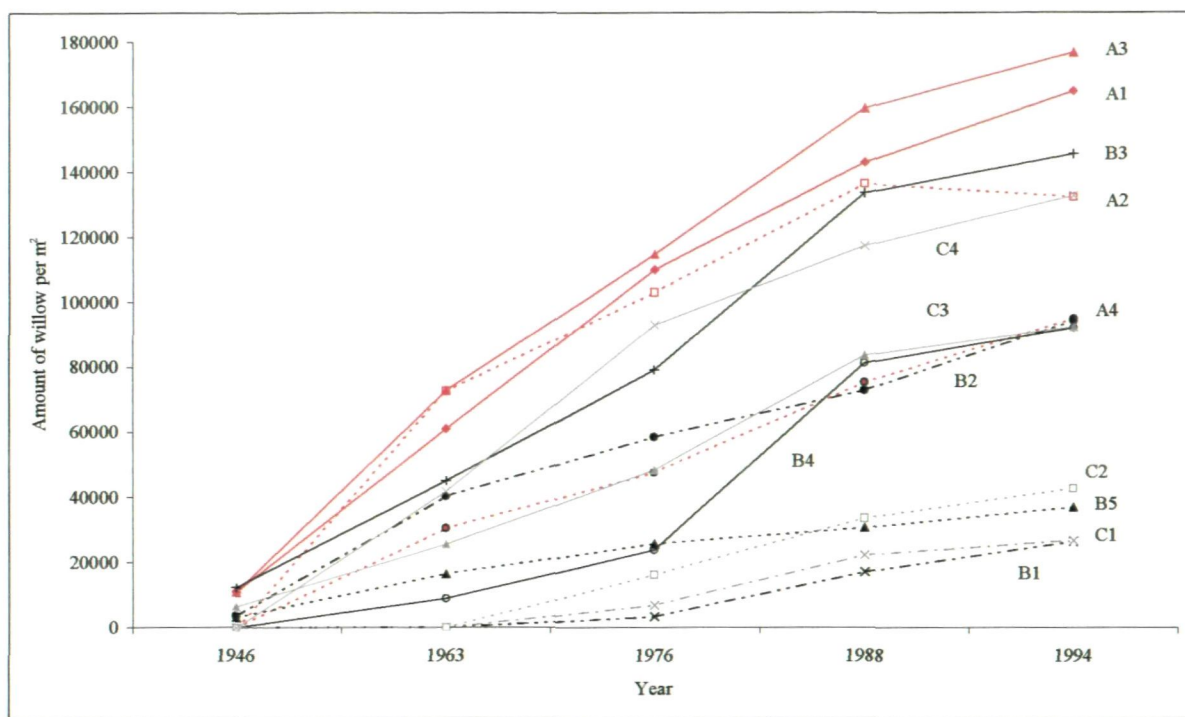
Figure 4.7 Change in the total amount of willow between 1946 and 1994, found in each 250, 000 m^2 block, which were defined in order to use image analysis to analyse the growth of willow on the aerial photographs (Figure 4.1)

On Goss Moor the average rate of willow spread was 22850 m^2 per year (Table 4.4). The expansion of willow across the whole site was most prominent between 1963 and 1975 where the rate of invasion was 52983 m^2 per year.

Table 4.4 The rate of willow spread occurring between 1946 and 1994, found on Goss Moor in the 2,740,000 m^2 sample area, which was defined in order to use image analysis to analyse the growth of willow on the aerial photographs (Figure 4.1).

	Age range			
	1946-1962	1963-1975	1976-1987	1988-1994
Amount of willow spread (m^2) in each age range	367280	688782	376185	152088
Willow spread (m^2) per year in age range	21605	52983	28937	21727
Mean spread (m^2) per year	22849.5			

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4.3.2 CLASSIFICATION OF THE WILLOW COMMUNIITIES

A total of 98 species were found in 251 quadrats. TWINSPAN identified eight willow understorey community types, a summary of which is provided in Table 4.5. The complete species assemblages for each of the eight understorey community are found in Tables 4.6-4.13, the explanation of which can be found in section 3.3.

Table 4.5. Willow understorey communities, as revealed by TWINSPAN.

Understorey community descriptor and type	Number of quadrats
wc-M. *Juncus effusus- Molinia caerulea*	19
wc-N. *Holcus lanatus- Agrostis stolonifera*	49
wc-O. *Agrostis stolonifera- Juncus effusus*	46
wc-P. *Juncus effusus- Galium palustre*	30
wc-Q. *Equisetum fluviatile- Menyanthes trifoliata*	36
wc-R. *Equisetum fluviatile- Potentilla palustris*	31
wc-S. *Potentilla palustris- Mentha aquatica*	17
wc-T. *Molinia caerulea-Viola palustris*	23

Table 4.6 Mean and median species abundance and frequency for the willow understorey community of Group wc-M, in relation to the standard NVC classification tabulation

Group wc-M		Total number of quadrats = 19			
	No. of quadrats	NVC coding: Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Standing water	16	V (1-6)	6	39	33
Juncus effusus	14	IV (3-7)	5	19	14
Molinia caerulea	10	III (4-8)	5	27	25
Galium palustre	10	III (1-6)	3	5	2
Agrostis stolonifera	9	III (2-9)	5	24	20
Holcus lanatus	9	III (1-8)	4	18	5
Mentha aquatica	7	II (1-5)	3	6	2
Potentilla palustris	7	II (1-5)	3	5	2
Equisetum fluviatile	6	II (3-8)	4	15	4
Valeriana officinalis	5	II (3-5)	4	7	4
Angelica sylvestris	5	II (2-5)	3	4	2
Salix cinerea ssp. *oleifolia*	5	II (1-4)	3	2	2
Viola palustris	4	II (3-7)	5	19	11
Agrostis canina	4	II (1-6)	5	15	15
Lotus pedunculatus	4	II (1-3)	3	2	2
Hydrocotyle vulgaris	3	I (1-5)	3	5	2
Menyanthes trifoliata	2	I (4-5)	5	18	18
Petasites hybridus	2	I (2-5)	4	10	10
Carex echinata	2	I (1-5)	4	8	8
Salix aurita	2	I (1-4)	3	3	3
Oenanthe crocata	2	I (1-2)	2	1	1
Rhytidiadelphus squarrosus	1	I (5)	5	20	20
Sphagnum recurvum	1	I (5)	5	13	13
Hypericum elodes	1	I (4)	4	5	5
Thuidium tamariscinum	1	I (2)	3	2	2
Ranunculus flammula	1	I (2)	3	2	2
Iris pseudacorus	1	I (2)	3	2	2
Pseudoscleropodium purum	1	I (1)	1	1	1
Epilobium palustre	1	I (1)	1	1	1
Rubus fruticosus agg.	1	I (1)	1	1	1
Cirsium palustre	1	I (1)	1	1	1
Galium aparine	1	I (1)	1	1	1
Bare substrate	1	I (1)	1	1	1

Table 4.7 Mean and median species abundance and frequency for the willow understorey community of Group wc-N, in relation to the standard NVC classification tabulation

Group wc-N	Total number of quadrats = 49				
	No. of quadrats	NVC coding: Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Holcus lanatus	40	V (3-10)	6	38	30
Agrostis stolonifera	36	IV (1-9)	6	36	30
Juncus effusus	32	IV (2-8)	4	15	9
Valeriana officinalis	27	III (2-5)	4	12	7
Galium palustre	19	III (1-7)	3	4	2
Rubus fruticosus agg.	19	II (1-5)	3	2	2
Bare substrate	18	II (2-50)	4	8	5
Calliergon cuspidatum	14	II (3-5)	5	20	13
Angelica sylvestris	15	II (3-5)	4	5	5
Equisetum fluviatile	12	II (2-3)	2	2	1
Lychnis flos-cuculi	10	II (1-3)	2	2	1
Carex nigra	8	I (2-7)	4	10	4
Ranunculus repens	9	I (2-5)	3	5	3
Potentilla palustris	8	I (2-5)	4	6	4
Oenanthe crocata	8	I (2-4)	3	4	3
Rhytidiadelphus squarrosus	8	I (2-5)	5	17	20
Viola palustris	7	I (2-5)	4	10	10
Carex echinata	6	I (1-6)	4	8	4
Cirsium palustre	7	I (2-5)	3	4	3
Mentha aquatica	6	I (3-5)	4	9	8
Rumex acetosa	5	I (1-9)	3	21	2
Petasites hybridus	5	I (2-4)	4	4	4
Lotus pedunculatus	5	I (2-4)	3	3	2
Lonicera periclymenum	5	I (2-3)	2	2	1
Hedera helix	4	I (4)	4	8	8
Dryopteris dilatata	4	I (2-4)	3	4	2
Ranunculus flammula	4	I (1-3)	2	1	1
Hydrocotyle vulgaris	3	I (4-5)	5	14	16
Thuidium tamariscinum	2	I (4-5)	5	13	13
Carex rostrata	3	I (3-4)	4	7	10
Calliergon giganteum	3	I (3-4)	4	4	5
Prunella vulgaris	3	I (2-3)	3	2	2
Iris pseudacorus	3	I (2-3)	3	3	3
Menyanthes trifoliata	2	I (2-4)	4	6	6
Scorpidium scorpoides	2	I (2-4)	4	4	4
Crataegus monogyna	2	I (2-3)	3	2	2
Standing water	2	I (3-4)	4	4	4
Lysimachia nummularia	1	I (2)	2	1	1
Juncus acutiflorus	1	I (7)	7	40	40
Lycopus europaeus	1	I (4)	4	10	10
Osmunda regalis	1	I (4)	4	7	7
Plagiomnium undulatum	1	I (4)	4	6	6
Dryopteris filix-mas	1	I (3)	3	3	3
Filipendula ulmaria	1	I (3)	3	2	2
Myosotis caespitosa	1	I (2)	2	1	1
Senecio aquatica	1	I (2)	2	1	1
Polytrichum commune	1	I (2)	2	1	1
Geranium robertianum	1	I (2)	2	1	1
Epilobium palustre	1	I (2)	2	1	1
Rumex hydrolapathum	1	I (2)	2	1	1
Scrophularia aquatica	1	I (2)	2	1	1
Salix cinerea ssp. *oleifolia*	1	I (2)	2	1	1
Hylocomium splendens	1	I (2)	2	1	1

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Table 4.8 Mean and median species abundance and frequency for the willow understorey community of Group wc-O, in relation to the standard NVC classification tabulation

Group wc-O		Total number of quadrats = 46			
	No. of quadrats	NVC coding: Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Agrostis stolonifera	37	V (3-9)	7	42	40
Juncus effusus	36	IV (2-8)	5	21	12
Mentha aquatica	28	IV (2-7)	4	10	5
Galium palustre	27	III (1-5)	3	3	2
Oenanthe crocata	21	III (2-8)	4	17	10
Potentilla palustris	20	III (2-5)	3	6	3
Equisetum fluviatile	18	III (1-5)	3	9	3
Valeriana officinalis	19	II (2-4)	4	4	4
Rubus fruticosus agg.	15	II (3-7)	3	7	2
Lonicera periclymenum	15	II (3-7)	3	13	3
Holcus lanatus	14	II (2-5)	4	18	10
Calliergon cuspidatum	14	II (2-5)	3	3	2
Ranunculus repens	11	II (2-6)	3	6	2
Rhytidiadelphus squarrosus	9	II (2-5)	4	9	10
Dryopteris dilatata	9	I (2-4)	3	4	3
Standing water	8	I (1-5)	4	7	4
Agrostis canina	7	I (2-8)	3	16	2
Ranunculus flammula	7	I (2-4)	3	2	2
Iris pseudacorus	7	I (3-5)	4	8	6
Angelica sylvestris	6	I (3-4)	3	3	3
Lotus pedunculatus	5	I (2-7)	4	12	10
Cirsium palustre	5	I (3-5)	3	6	3
Calliergon giganteum	5	I (1-5)	2	6	1
Petasites hybridus	5	I (2)	2	1	1
Sphagnum squarrosum	5	I (5-9)	7	35	43
Polytrichum commune	4	I (3-9)	5	26	12
Lychnis flos-cuculi	3	I (2-3)	3	2	2
Hedera helix	3	I (3-7)	5	22	20
Menyanthes trifoliata	3	I (2-5)	4	8	10
Senecio aquatica	3	I (2-3)	3	3	2
Bare substrate	3	I (3-4)	4	4	4
Juncus acutiflorus	3	I (1-4)	2	2	1
Carex nigra	2	I (4-5)	4	8	8
Sphagnum recurvum	2	I (3-4)	4	4	4
Epilobium hirsutum	2	I (3-4)	4	4	4
Dryopteris filix-mas	2	I (2-5)	4	9	9
Molinia caerulea	2	I (3)	3	2	2
Lycopus europaeus	2	I (3)	3	3	3
Rumex acetosa	2	I (2-3)	3	2	2
Quercus robur	2	I (1-3)	3	3	3
Viola palustris	2	I (2-3)	3	2	2
Prunella vulgaris	2	I (2)	2	1	1
Pseudoscleropodium purum	1	I (6)	6	30	30
Osmunda regalis	1	I (5)	5	25	25
Blechnum spicant	1	I (5)	5	20	20
Eriophorum angustifolium	1	I (3)	3	4	4
Carex rostrata	1	I (3)	3	4	4
Vaccinium myrtillis	1	I (3)	3	2	2
Crataegus monogyna	1	I (3)	3	3	3
Thuidium tamariscinum	1	I (3)	3	3	3
Myosotis caespitosa	1	I (3)	2	1	1
Scorpidium scorpoides	1	I (3)	2	1	1
Rumex hydrolapathum	1	I (3)	2	1	1
Polypodium vulgaris	1	I (3)	2	1	1
Salix cinerea ssp. *oleifolia*	1	I (3)	2	1	1

Table 4.9 Mean and median species abundance and frequency for the willow understorey community of Group wc-P, in relation to the standard NVC classification tabulation

Group wc-P	Total number of quadrats = 30				
	No. of quadrats	NVC coding: Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Bare substrate	26	V (4-9)	4	27	10
Juncus effusus	21	IV (2-7)	4	14	10
Galium palustre	20	IV (2-6)	3	8	2
Potentilla palustris	19	IV (3-5)	4	7	6
Valeriana officinalis	15	III (2-4)	3	3	2
Equisetum fluviatile	15	III (2-6)	3	11	2
Holcus lanatus	15	III (2-5)	4	8	10
Petasites hybridus	14	III (1-4)	2	2	1
Carex nigra	12	II (2-5)	4	9	5
Agrostis stolonifera	12	II (2-5)	3	4	2
Mentha aquatica	12	II (3)	3	2	2
Calliergon cuspidatum	11	II (2-5)	3	6	2
Angelica sylvestris	8	II (2-7)	5	18	16
Hydrocotyle vulgaris	8	II (2-6)	4	8	4
Molinia caerulea	6	I (4-9)	7	41	38
Carex echinata	6	I (3-4)	4	6	4
Ranunculus flammula	6	I (1-3)	2	2	1
Lychnis flos-cuculi	5	I (1-3)	2	1	1
Sphagnum squarrosum	4	I (5-10)	7	46	38
Cardamine amara	4	I (1-3)	3	2	2
Menyanthes trifoliata	3	I (4-8)	7	38	45
Viola palustris	3	I (3-8)	5	26	15
Cirsium palustre	3	I (2-3)	3	2	2
Ranunculus repens	3	I (1-3)	2	1	1
Lotus pedunculatus	3	I (2)	2	1	1
Juncus acutiflorus	2	I (4-6)	5	18	18
Hypochaeris radicata	2	I (2-3)	3	2	2
Calliergon giganteum	2	I (2-3)	3	2	2
Geranium robertianum	2	I (2)	2	1	1
Caltha palustris	2	I (2)	2	1	1
Salix cinerea ssp. *oleifolia*	2	I (2)	2	1	1
Oenanthe crocata	2	I (2-3)	3	2	2
Potamogeton polygonifolius	1	I (9)	9	90	90
Standing water	1	I (8)	8	60	60
Agrostis canina	1	I (5)	5	20	20
Dead wood	1	I (5)	5	20	20
Thuidium tamariscinum	1	I (4)	4	5	5
Epilobium palustre	1	I (4)	4	5	5
Sphagnum recurvum	1	I (3)	3	2	2
Mnium hornum	1	I (3)	3	3	3
Hylocomium splendens	1	I (3)	3	3	3
Hypericum elodes	1	I (3)	3	2	2
Hedera helix	1	I (2)	2	1	1
Lonicera periclymenum	1	I (2)	2	1	1
Rhytidiadelphus squarrosus	1	I (2)	2	1	1
Polygala vulgaris	1	I (2)	2	1	1
Carex rostrata	1	I (2)	2	1	1
Potentilla erecta	1	I (2)	2	1	1

Table 4.10 Mean and median species abundance and frequency for the willow understorey community of Group wc-Q, in relation to the standard NVC classification tabulation

Group wc-Q	Total number of quadrats = 36				
	No. of quadrats	NVC coding: Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Equisetum fluviatile	34	V (3-8)	5	23	20
Menyanthes trifoliata	27	IV (3-8)	8	30	40
Carex nigra	25	IV (2-8)	5	27	15
Bare substrate	23	IV (2-8)	4	15	10
Potentilla palustris	24	IV (2-5)	5	16	20
Galium palustre	21	IV (1-5)	2	2	1
Carex rostrata	16	III (2-4)	3	4	3
Valeriana officinalis	13	II (2-5)	4	6	4
Juncus effusus	10	II (2-7)	3	4	2
Agrostis stolonifera	9	II (2-7)	4	15	5
Mentha aquatica	6	I (2-3)	3	2	2
Holcus lanatus	4	I (2-4)	3	2	2
Hydrocotyle vulgaris	3	I (3-6)	3	12	3
Petasites hybridus	5	I (1-3)	2	1	1
Salix cinerea ssp. *oleifolia*	2	I (2-3)	3	2	2
Calliergon giganteum	2	I (2-5)	5	13	13
Calliergon cuspidatum	2	I (2-5)	5	10	11
Lycopus europaeus	3	I (3)	3	2	2
Cirsium palustre	2	I (2-3)	3	2	2
Dryopteris dilatata	2	I (2)	2	1	1
Angelica sylvestris	2	I (2-3)	3	2	2
Viola palustris	1	I (2)	2	1	1
Carex echinata	1	I (4)	4	7	7
Ranunculus repens	1	I (2)	2	1	1
Cardamine amara	1	I (3)	3	2	2
Lonicera periclymenum	1	I (3)	3	2	2
Ranunculus repens	1	I (3)	3	2	2
Scorpidium scorpoides	1	I (3)	3	2	2
Myosotis caespitosa	1	I (2)	2	1	1
Juncus acutiflorus	1	I (2)	2	1	1
Lotus pedunculatus	1	I (1)	1	1	1

Table 4.11 Mean and median species abundance and frequency for the willow understorey community of Group wc-R, in relation to the standard NVC classification tabulation

Group wc-R	Total number of quadrats = 31				
	No. of quadrats	NVC coding: Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Equisetum fluviatile	28	V (2-5)	4	17	5
Potentilla palustris	22	IV (2-6)	5	13	14
Mentha aquatica	19	IV (2-7)	4	5	5
Menyanthes trifoliata	18	III (3-8)	4	23	10
Juncus effusus	18	III (2-7)	5	22	13
Carex nigra	15	III (3-6)	4	16	7
Galium palustre	20	III (2-4)	3	3	2
Valeriana officinalis	14	III (2-4)	3	2	2
Agrostis stolonifera	13	III (3-7)	5	19	11
Calliergon cuspidatum	10	II (2-5)	4	9	5
Standing water	10	II (3-9)	7	41	40
Angelica sylvestris	8	II (2-4)	3	4	3
Carex rostrata	7	II (2-4)	3	2	2
Petasites hybridus	7	II (1-3)	2	1	1
Cirsium palustre	6	I (2-3)	3	2	2
Lychnis flos-cuculi	5	I (2-5)	4	6	5
Carex echinata	5	I (3-6)	4	9	5
Holcus lanatus	5	I (1-5)	2	4	1
Lotus pedunculatus	4	I (1-4)	3	3	2
Ranunculus flammula	4	I (2)	2	1	1
Juncus acutiflorus	3	I (2-3)	2	1	1
Viola palustris	2	I (2-3)	3	4	2
Calliergon giganteum	2	I (3-5)	5	11	11
Dryopteris filix-mas	2	I (2-3)	3	2	2
Hydrocotyle vulgaris	2	I (2)	2	1	1
Bare substrate	2	I (2)	2	1	1
Sphagnum squarrosum	1	I (9)	9	80	80
Molinia caerulea	1	I (4)	4	40	40
Dicranium scoparium	1	I (4)	4	10	10
Rhytidiadelphus squarrosus	1	I (4)	4	10	10
Eriophorum angustifolium	1	I (4)	4	10	10
Hedera helix	1	I (3)	3	2	2
Senecio aquatica	1	I (3)	3	2	2

Table 4.12 Mean and median species abundance and frequency for the willow understorey community of Group wc-S, in relation to the standard NVC classification tabulation

Group wc-S		Total number of quadrats = 17			
	No. of quadrats	NVC coding: Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Potentilla palustris	16	V (3-8)	7	41	50
Mentha aquatica	16	V (2-5)	4	13	10
Equisetum fluviatile	14	V (1-3)	3	2	2
Eriophorum angustifolium	14	V (1-5)	3	8	5
Lotus pedunculatus	13	IV (2-4)	3	3	3
Hydrocotyle vulgaris	13	IV (2-4)	4	4	4
Juncus acutiflorus	9	III (3-5)	5	12	16
Angelica sylvestris	9	III (3-4)	3	4	2
Salix aurita	9	III (1-5)	4	11	10
Juncus effusus	8	III (2-7)	4	11	6
Galium palustre	8	III (1-4)	2	2	1
Valeriana officinalis	7	III (2-5)	3	4	3
Calliergon cuspidatum	7	III (1-4)	4	7	10
Bare substrate	7	III (2-7)	4	14	10
Succisa pratensis	7	III (1-4)	3	2	2
Ranunculus flammula	6	II (1-4)	3	3	2
Salix cinerea ssp. *oleifolia*	6	II (1-4)	3	3	3
Hypericum undulatum	6	II (1-4)	3	2	2
Molinia caerulea	5	II (4-7)	7	52	40
Hypericum elodes	4	II (3-5)	4	9	7
Viola palustris	4	II (3)	3	3	2
Sphagnum quinquefarium	3	I (3)	4	4	4
Carex nigra	3	I (3)	3	3	3
Menyanthes trifoliata	3	I (3)	3	2	2
Hypericum tetrapterum	3	I (2-3)	3	2	2
Aulacomnium palustre	3	I (3)	3	3	3
Rhytidiadelphus squarrosus	3	I (2-4)	3	3	3
Epilobium palustre	4	I (1-2)	2	1	1
Lychnis flos-cuculi	2	I (1-2)	3	2	2
Rubus fruticosus agg.	2	I (4)	4	7	7
Pseudoscleropodium purum	2	I (2-3)	3	2	2
Calliergon stramineum	2	I (2-3)	3	2	2
Calliergon giganteum	2	I (2)	2	1	1
Lophocolea cuspidata	2	I (2-3)	3	3	3
Sphagnum fimbriatum	1	I (3)	3	1	1
Potentilla erecta	2	I (2)	2	1	1
Sphagnum squarrosum	1	I (5)	5	16	16
Holcus lanatus	1	I (4)	4	10	10
Cirsium palustre	1	I (3)	3	2	2
Drepanocladus fluitans	1	I (3)	3	2	2
Sphagnum subnitens	1	I (3)	3	3	3
Sphagnum teres	1	I (3)	3	3	3
Petasites hybridus	1	I (2)	2	1	1
Rumex acetosa	2	I (1)	1	1	1

Table 4.13 Mean and median species abundance and frequency for the willow understorey community of Group wc-T, in relation to the standard NVC classification tabulation

Group wc-T	Total number of quadrats = 23				
	No. of quadrats	NVC coding: Frequency and Domin cover range	Median Domin value	Mean percentage cover	Median percentage cover
Molinia caerulea	22	V (5-10)	8	66	70
Potentilla erecta	11	III (1-7)	3	9	2
Viola palustris	9	II (2-5)	3	4	2
Carex nigra	7	II (3-4)	4	5	4
Potentilla palustris	7	II (3-7)	5	17	12
Hydrocotyle vulgaris	6	II (1-4)	3	3	3
Juncus acutiflorus	5	II (3-7)	4	17	10
Juncus effusus	6	II (3-7)	4	14	10
Calluna vulgaris	6	II (2-6)	5	14	11
Eriophorum angustifolium	5	II (2-5)	3	7	3
Myrica gale	6	II (2-5)	3	6	3
Ulex europaeus	6	II (2-4)	3	3	2
Agrostis canina	6	II (3-4)	4	4	4
Salix aurita	4	II (3-5)	4	8	4
Agrostis stolonifera	5	II (3-4)	4	4	4
Lotus pedunculatus	4	II (3-7)	3	11	2
Valeriana officinalis	4	II (3-4)	3	3	3
Sphagnum recurvum	5	II (3-4)	4	12	4
Succisa pratensis	4	II (1-3)	3	2	2
Erica tetralix	4	I (3)	3	3	2
Rubus fruticosus agg.	4	I (3)	3	2	2
Calliergon cuspidatum	4	I (1-3)	3	2	2
Sphagnum auriculatum	3	I (1-3)	3	2	2
Sphagnum palustre	3	I (2-5)	3	6	5
Carex echinata	3	I (3)	3	3	2
Standing water	2	I (7)	7	40	40
Erica cinerea	2	I (3-5)	4	9	9
Angelica sylvestris	2	I (3-5)	4	7	7
Centaurea nigra	2	I (3-4)	4	4	4
Cirsium palustre	2	I (1-4)	3	3	3
Hypericum elodes	2	I (3)	3	3	3
Mentha aquatica	1	I (1-2)	3	2	2
Aulacomnium palustre	1	I (5)	5	10	10
Blechnum spicant	1	I (4)	4	6	6
Galium palustre	1	I (4)	4	5	5
Thuidium tamariscinum	1	I (3)	3	2	2
Salix cinerea ssp. *oleifolia*	1	I (3)	3	2	2
Luzula multiflora	1	I (3)	3	2	2
Sambucus nigra	1	I (3)	3	2	2
Sphagnum inundatum	1	I (3)	3	2	2
Juncus bulbosus	1	I (3)	3	2	2
Narthecium ossifragum	1	I (2)	2	1	1
Galium aparine	1	I (2)	2	1	1
Hylocomium splendens	1	I (2)	2	1	1
Mnium hornum	1	I (2)	2	1	1
Bare substrate	1	I (5)	5	20	20
Cardamine amara	1	I (1)	1	1	1
Equisetum fluviatile	1	I (1)	1	1	1
Lychnis flos-cuculi	1	I (1)	1	1	1

Of the eight understorey communities that were growing beneath willow carr, within Groups wc-M to wc-P *Juncus effusus* was constant and co-dominant with *Galium palustre*, *Potentilla palustris* and graminoid species. Typical examples of the willow carr communities can be found in Plates 4.1 and 4.2.

In wc-M, standing water was the most prominent feature and *Juncus effusus* was the most abundant species. *Molinia caerulea* and *Agrostis stolonifera* occurred frequently in moderate amounts with a mean cover of 27 % and 24 %, respectively, and *Holcus lanatus* L. in small amounts with a median of 5 % (medians are reported when the species frequency was less than ten). The occasional occurrence of *Potentilla palustris* and tall-herbs like *Valeriana officinalis* and *Angelica sylvestris* L. represent elements of poor-fen vegetation. A third of the quadrats in this group contain regenerated *Salix cinerea* and *Salix aurita*. Although the community grows beneath willow of all ages, it is mostly found beneath willow established between 1946 and 1975 (Table 4.14).

Group wc-N was the largest understorey community with 49 quadrats and 51 species. *Juncus effusus*, *Agrostis stolonifera* and *Holcus lanatus* were constant. Compared to wc-M, wc-N contains more Poaceae and *Valeriana officinalis*. This community grows mostly under willow established between 1946 and 1962 and 90% of the species were either occasional or scarce. This large group of general associates contain various common poor-fen species, eight bryophyte species including *Calliergon cuspidatum* and a number of pteridophytes, including the impressive *Osmunda regalis* L. Group wc-N does not contain *Molinia caerulea*.

Group wc-O, the *Agrostis stolonifera-Juncus effusus* community, is co-dominated by *Mentha aquatica* and is very similar to wc-N. However, poor-fen species such as *Potentilla palustris* and *Equisetum fluviatile* are more common in wc-O. Poor-fen bryophytes are

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Plate 4.1 A typical example of willow established between 1946 and 1962 on Goss Moor.

Plate 4.2 A typical example of willow established between 1963 and 1975 on Goss Moor.

also present, such as *Calliergon cuspidatum* and *Sphagnum squarrosum*, which can sometimes form large carpets. This community is found in all ages of willow carr on Goss Moor, but mostly beneath the oldest willow established before 1946. *Quercus robur* L. seedlings were recorded on two occasions in this community.

Bare substrate is the most prominent feature of wc-P. *Potentilla palustris*, *Juncus effusus* and *Galium palustre* are the common plant species. This community is widespread under all ages of willow on Goss Moor and, unlike the other field layer types, areas of dead wood were found.

Table 4.14 Number of quadrats in each of the eight communities found in the different age ranges willow carr appears to have been initiated, as identified by the aerial photographs.

Willow carr understorey community group	Pre-1946	1946-1962	1963-1975	1976-1987	1988-present	Total number of quadrats per group
wc-M	1	6	9	2	1	**19**
wc-N	12	24	6	7	0	**49**
wc-O	31	9	2	3	1	**46**
wc-P	7	9	3	8	3	**30**
wc-Q	1	0	7	22	6	**36**
wc-R	7	4	9	6	5	**31**
wc-S	0	0	0	2	15	**17**
wc-T	0	2	1	3	17	**23**

Group wc-Q contains the smallest total number of species and poor-fen/swamp species such as *Equisetum fluviatile*, *Menyanthes trifoliata*, *Potentilla palustris* and the sedge *Carex nigra*; *Carex rostrata* is also common. This community is mostly found under willow established between 1976 and 1987. The species composition of Groups wc-Q and wc-R are almost identical. However, wc-R, the *Equisetum fluviatile-Potentilla palustris* community, contains less bare substrate and one third of the quadrats contain 40 % standing water. Importantly, wc-R occurs fairly constantly beneath all ages of willow.

Group wc-S was the smallest group with 17 quadrats and contains the largest number of dominant species, all of which were frequent in poor-fen. *Juncus acutiflorus* and *Eriophorum angustifolium* are more common in this community than Groups wc-M to wc-R, where they are either rare or not present. Also, the regionally rare species *Hypericum undulatum* was a general associate of this group. Almost 90 % of the quadrats were recorded in areas of recent willow invasion. This *Potentilla palustris-Mentha aquatica* community contains the largest number of bryophytes species, including *Sphagnum quinquefarium* (Braithw.) Warnst., *Aulacomnium palustre* and *Sphagnum fimbriatum* Wils.

Group wc-T, the *Molinia caerulea-Potentilla erecta* understorey, is mostly found in the youngest willow. Almost 96 % of the species present in this group are general associates, which are commonly found in a range of different poor-fen community types. These include a number of shrubs such as *Calluna vulgaris*, *Myrica gale*, *Erica cinerea* L. and *Erica tetralix*.

4.3.3 SPATIAL DISTRIBUTION OF THE WILLOW UNDERSTOREY COMMUNITIES

The locations of the willow understorey communities are displayed in Figure 4.8. The understorey communities in groups wc-N, wc-O and wc-P were found under willow growing throughout the whole site. Groups wc-Q and wc-R were only found in the centre of the moor and not in the west or east. Group wc-M was only found in the east of the site, Group wc-S was only found in the west and Group wc-T was not found in the centre.
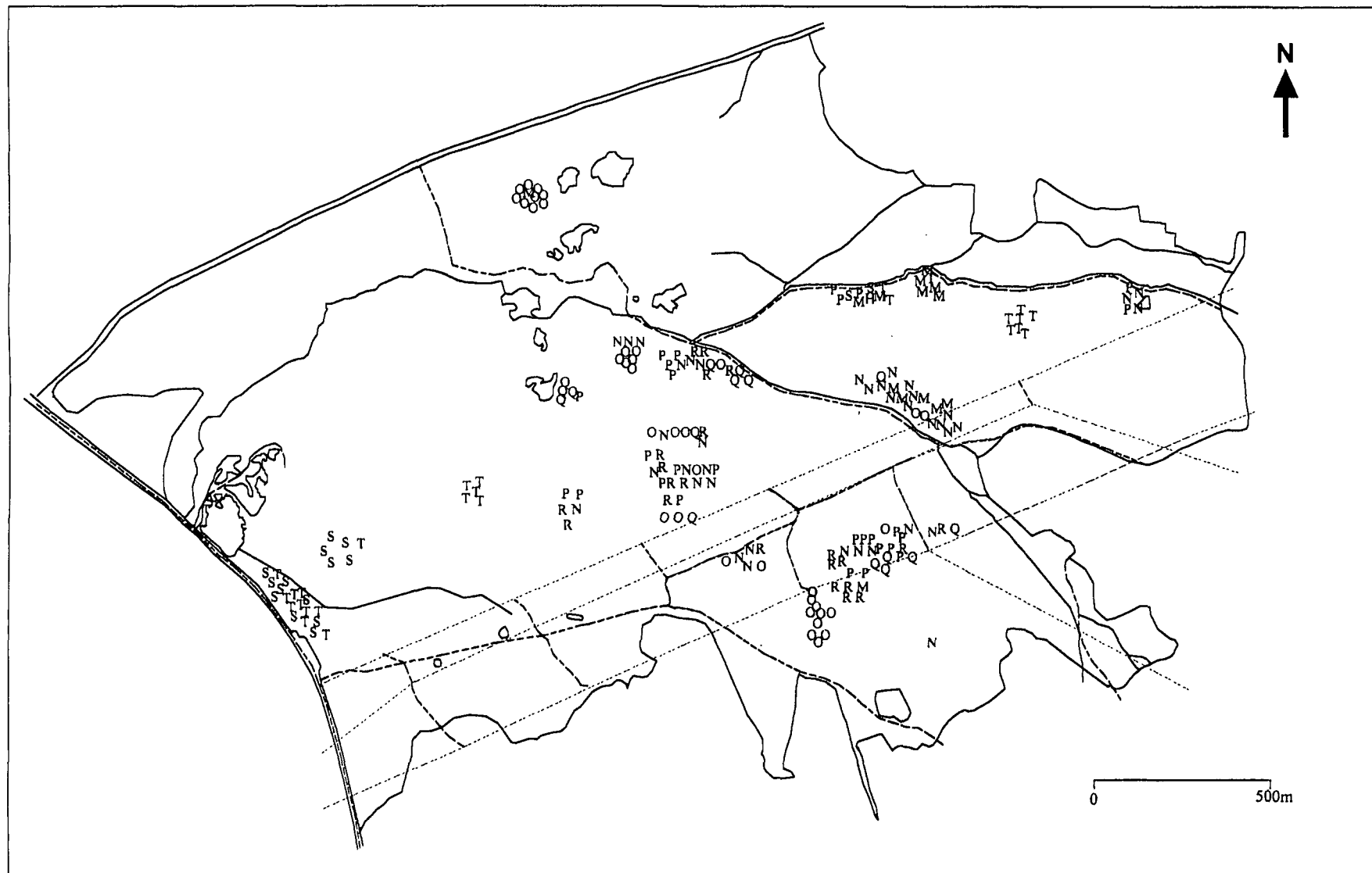
Figure 4.8 The spatial distribution of the willow carr understorey communities of wc-M to wc-T identified on Goss Moor NNR in the 1998 survey.

4.3.4 DCA ORDINATION OF THE WILLOW UNDERSTOREY DATA

The DCA ordination of the willow understorey data in Figure 4.9 shows the different ages of willow superimposed. The most recent willow occurs on the left hand side of the ordination. Willow age increases from the left hand-side of the ordination to the right side of the diagram. There was little overlap between the points of the oldest and youngest willow indicating the extent of floristic change during willow community development. The eigenvalues for the first two axes are 0.79 and 0.52, respectively, showing that the majority of the variation was explained by the first axis. Axis 1 clearly represents an age gradient.

Figure 4.9 Sample ordination diagram derived from detrended correspondence analysis of the 251 quadrats of the willow carr study conducted in 1998. The five age ranges are those identified by image analysis of the aerial photographs. Eigen values: Axis 1 = 0.789, Axis 2 = 0.521.
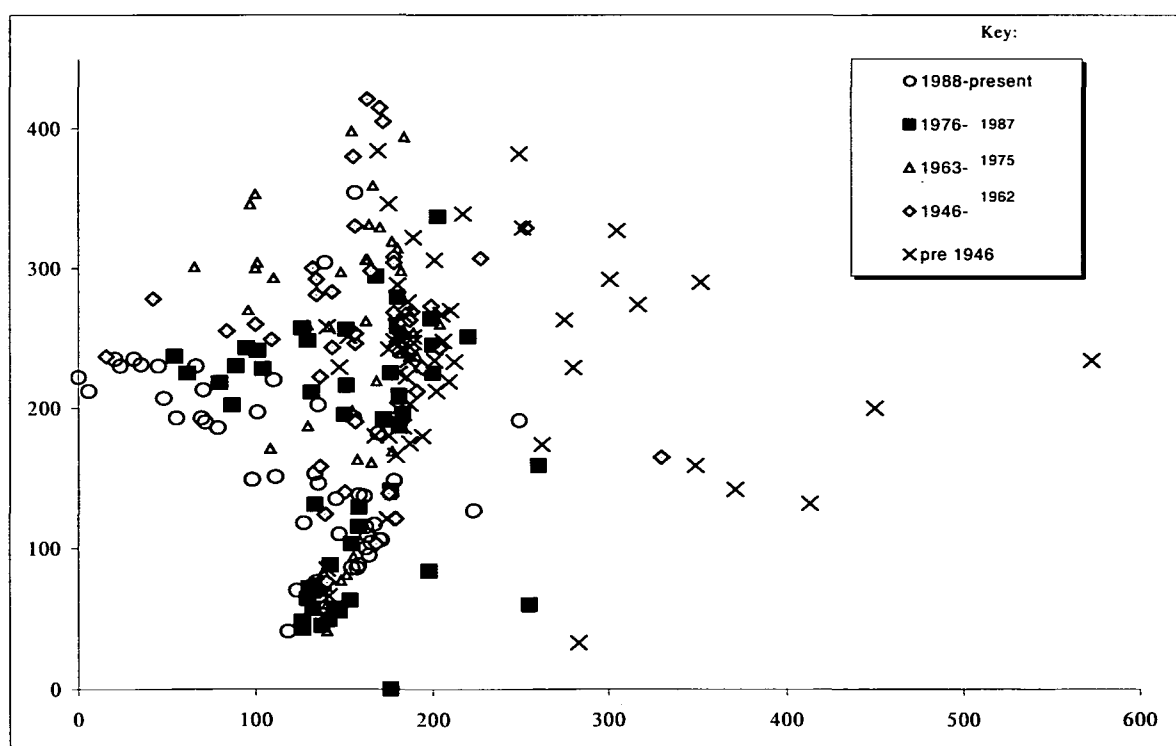
4.3.5 CCA BIPLOT OF THE WILLOW DATA

The joint biplot of the willow carr understorey communities and the environmental variables produced by the CCA is presented in Figures 4.10-4.13. In order to identify any relationships, the points were grouped according to the age of the willow sampled (Figure

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4.10) or TWINSPAN understorey groups (Figure 4.12). To simplify the CCA ordinations, the means or centroids of the points for each of the age groupings (Figure 4.11) and the eight TWINSPAN groups (Figure 4.13) were found. The eigenvalues for axes 1 and 2 are 0.45 and 0.32, respectively. The species and environmental data account for 32.9 % and 56.7 % of the variance, thus, the total variance explained was 89.6 %.

The correlation between tree height and Axis 1 is –0.76. The ordination diagram shows that, as expected, the tree height increases with age. The understorey communities associated with the tallest trees were wc-N and wc-O.
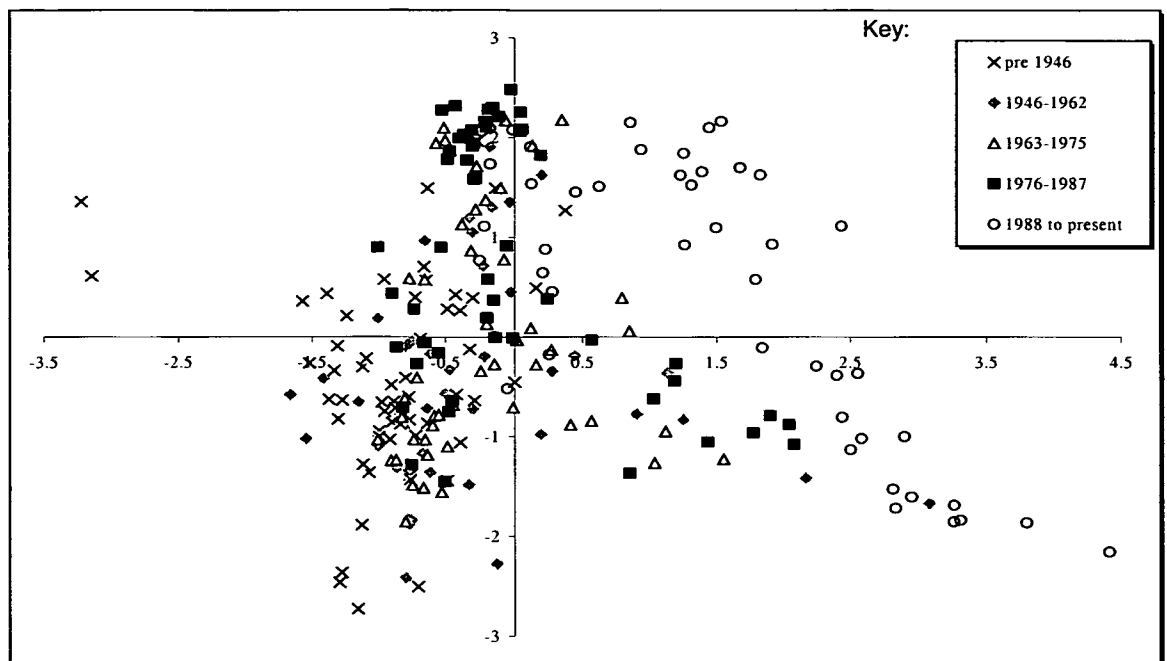
Figure 4.10 Ordination of the willow carr understorey communities on the joint biplot, before the environmental vectors produced by canonical correspondence analysis of the 251 quadrats have been superimposed for the final analysis. The five age ranges of willow carr are superimposed. Eigenvalues: Axis 1 = 0.445, Axis 2 = 0.322 (Monte Carlo test on the first axis significant P=0.005)

The mean distance between individual trees was smallest between trees that had established between 1988 and the present. Naturally, this corresponded to the number of trees per 100 m^2, for which the least dense willow occurred in the two oldest age classes of pre-1946 and 1946-1962, respectively; these classes contained 15.5 and 13.7 trees per 100 m^2. These age classes were associated with the communities in groups wc-N and wc-O. The youngest

willow contained an average of 39.1 trees per 100 m^2. The correlation between inter-tree distance and Axis 1 is –0.22 and quite weak.

The correlation between canopy cover and Axis 1 was –0.48. The majority of the understorey groups are associated with a dense canopy cover. Groups wc-S and wc-T, and wc-M to a lesser extent occur under willow with less canopy cover. Groups wc-S and wc-T occur predominantly in the youngest willow. When the centroid points of the different age classes were considered the oldest willow had the most dense canopy cover and the youngest was least dense. The strongest second axis correlation was –0.68, for organic depth, and was associated with groups wc-Q, wc-R and wc-S. Groups wc-Q and wc-S occur under recently established willow carr and wc-R is found beneath willow of all ages. All three groups are dominated by poor-fen species. Standing water depth and Axis 1 are correlated by –0.20, showing that increased water depth is weakly associated with the Groups wc-M, wc-N and wc-O, and the older willow carr.
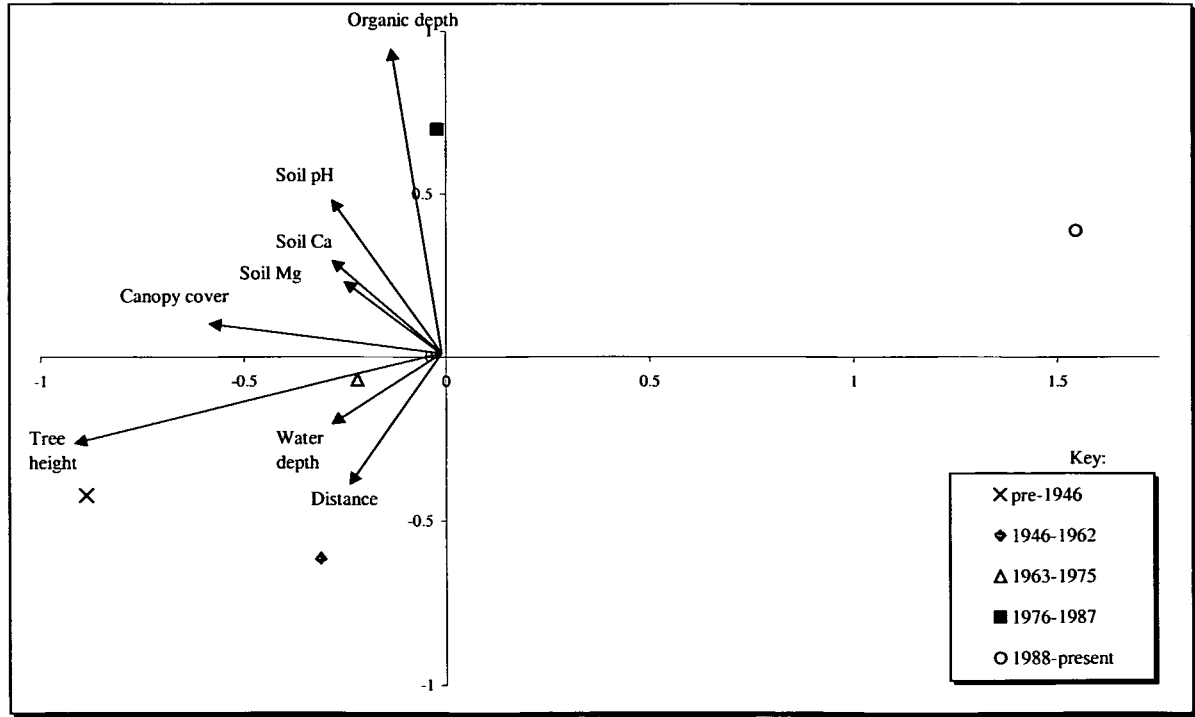
Figure 4.11 Joint biplot showing centroid points of the willow carr understorey data and environmental vectors produced by canonical correspondence analysis of the 251 quadrats. The five age ranges of willow carr are superimposed. Eigenvalues: Axis 1 = 0.445, Axis 2 = 0.322 (Monte Carlo test on the first axis significant P=0.005)
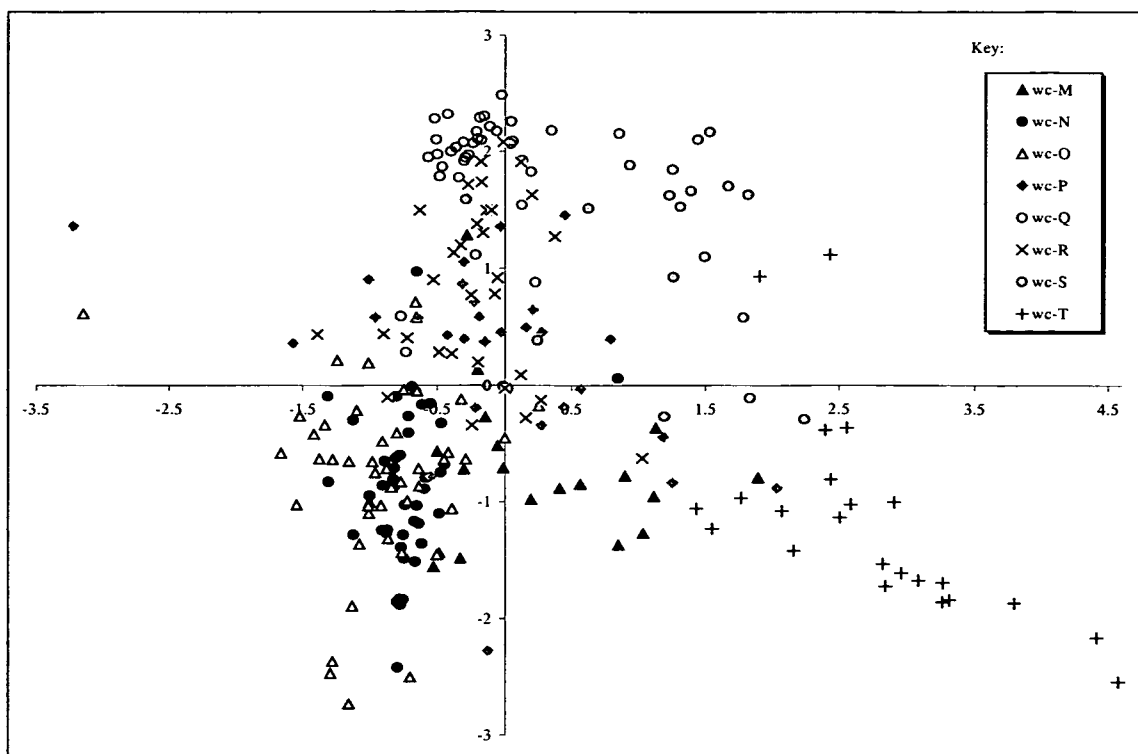
Figure 4.12 Ordination of the willow carr understorey communities on the joint biplot, before the environmental vectors produced by canonical correspondence analysis of the 251 quadrats have been superimposed for the final analysis. TWINSPAN groups wc-M to wc-T are superimposed. Eigenvalues: Axis 1 = 0.445, Axis 2 = 0.322 (Monte Carlo test on the first axis significant P=0.005)
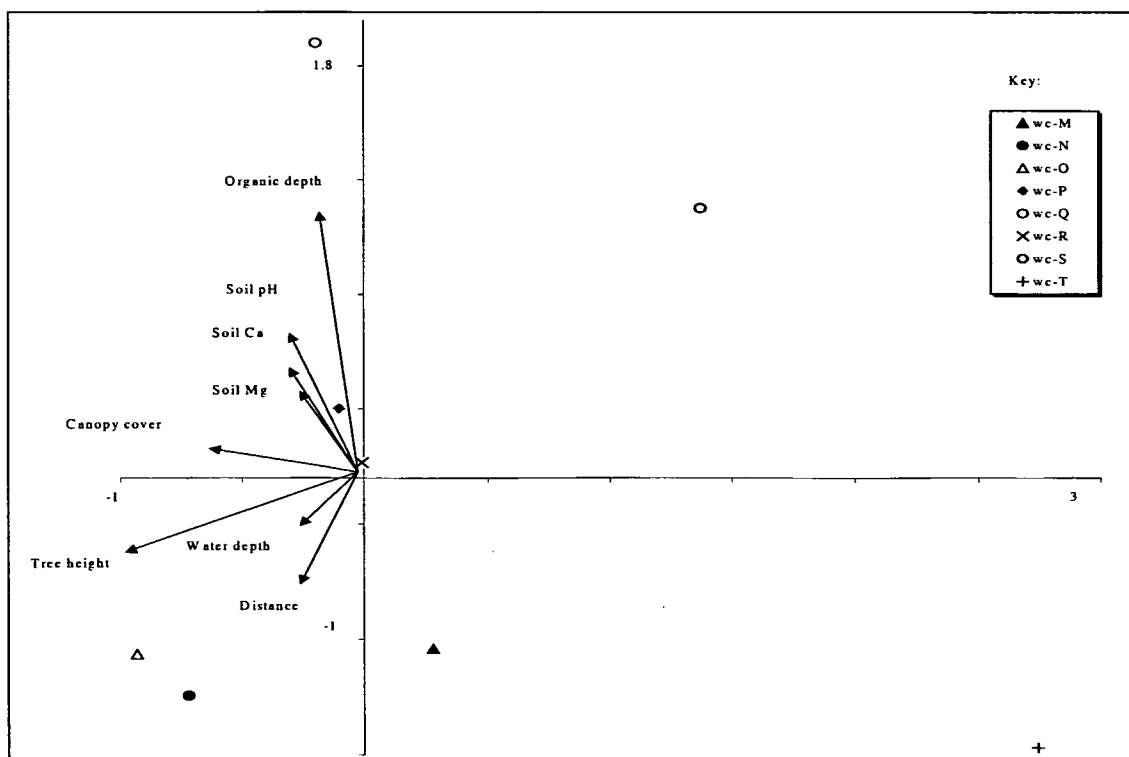
Figure 4.13 Joint biplot showing centroid points of the willow carr understorey data and environmental vectors produced by canonical correspondence analysis of the 251 quadrats. TWINSPAN groups wc-M to wc-T are superimposed. Eigenvalues: Axis 1 = 0.445, Axis 2 = 0.322 (Monte Carlo test on the first axis was significant P=0.005)

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Soil pH, available calcium and magnesium were correlated significantly with Axis 1 (–0.25, -0.24 and –0.13, respectively). The soil factors are covered in more detail in the next sub-section. The full range of correlations between the ordination axes and the environmental variables can be found in Table 4.15.

	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4	TREE SHTM	DIST ANCE M	ORG ADEP T	WAH T(CM)	CAN OPY* %	SOIL* PH*	SOIL* CA*	SOIL* MG*
SPEC AX1	1.000															
SPEC AX2	-0.045	1.000														
SPEC AX3	0.036	-0.015	1.000													
SPEC AX4	0.091	0.068	-0.026	1.000												
ENVI AX1	0.826	0	0	0	1.000											
ENVI AX2	0	0.757	0	0	0	1.000										
ENVI AX3	0	0	0.576	0	0	0	1.000									
ENVI AX4	0	0	0	0.631	0	0	0	1.000								
TREESHTM	-0.762	-0.205	-0.127	0.035	-0.922	-0.271	-0.220	0.055	1.000							
DISTANCEM	-0.224	-0.309	-0.078	-0.161	-0.27	-0.408	-0.135	-0.254	0.389	1.000						
ORGADEPT	-0.100	0.677	-0.036	-0.237	-0.121	0.895	-0.062	-0.375	-0.120	-0.162	1.000					
WAHT(MM)	-0.200	-0.130	0.410	-0.201	-0.243	-0.172	0.711	-0.318	0.056	0.108	0.142	1.000				
CANOPY*%	-0.479	0.049	0.192	0.427	-0.580	0.065	0.334	0.676	0.444	-0.048	-0.146	0.142	1.000			
SOIL*PH*	-0.252	0.367	-0.293	0.226	-0.305	0.485	-0.508	0.358	0.259	-0.058	0.300	-0.232	0.233	1.000		
SOIL*CA*	-0.243	0.2385	-0.059	0.202	-0.295	0.315	-0.102	0.321	0.297	0.096	0.286	0.016	0.241	0.536	1.000	
SOIL*MG*	-0.132	0.232	0.108	0.329	-0.160	0.306	0.188	0.522	0.148	-0.109	0.100	-0.057	0.316	0.425	0.625	1.000

Table 4.15 Weighted correlation matrix between ordination axes and environmental variables. The abbreviation are as follows: SPEC AX (Axis 1); SPEC AX2 (Axis 2); SPEC AX3 (Axis 3); SPEC AX4 (Axis 4); ENVI AXI (Environmental Axis 1); ENVI AX2 (Environmental Axis 2); ENVI AX3 (Environmental Axis 3); ENVI AX4 (Environmental Axis 4); TREESHTM (Height of the trees in m); DISTANCEM (The average distance between individual trees in a stand); ORGADEPT (Depth of the organic layer in mm); WAHT(MM) (Depth of standing water in mm); CANOPY% (Percentage canopy cover); SOIL*PH* (The pH of the A horizon); SOIL*CA* (The amount of available calcium in the soil); SOIL*MG* (The amount of available calcium in the soil).

4.3.6 SOIL PROPERTIES

Figure 4.14 shows the concentration of available cations found in the air-dried soil associated with the different understorey communities. Soil samples collected from wc-R the *Equisetum fluviatile-Potentilla palustris* understorey community contain the highest mean concentrations of exchangeable Ca^{2+} (347.8 µg of calcium per g of dry soil) and the second highest concentration of exchangeable Mg^{2+} and therefore the lowest Mg:Ca ratio. The lowest concentration of available cations were found in wc-S, the *Potentilla palustris-Mentha aquatica* understorey community: 106.1µg g^{-1} for calcium and 64.6 µg g^{-1} for magnesium.
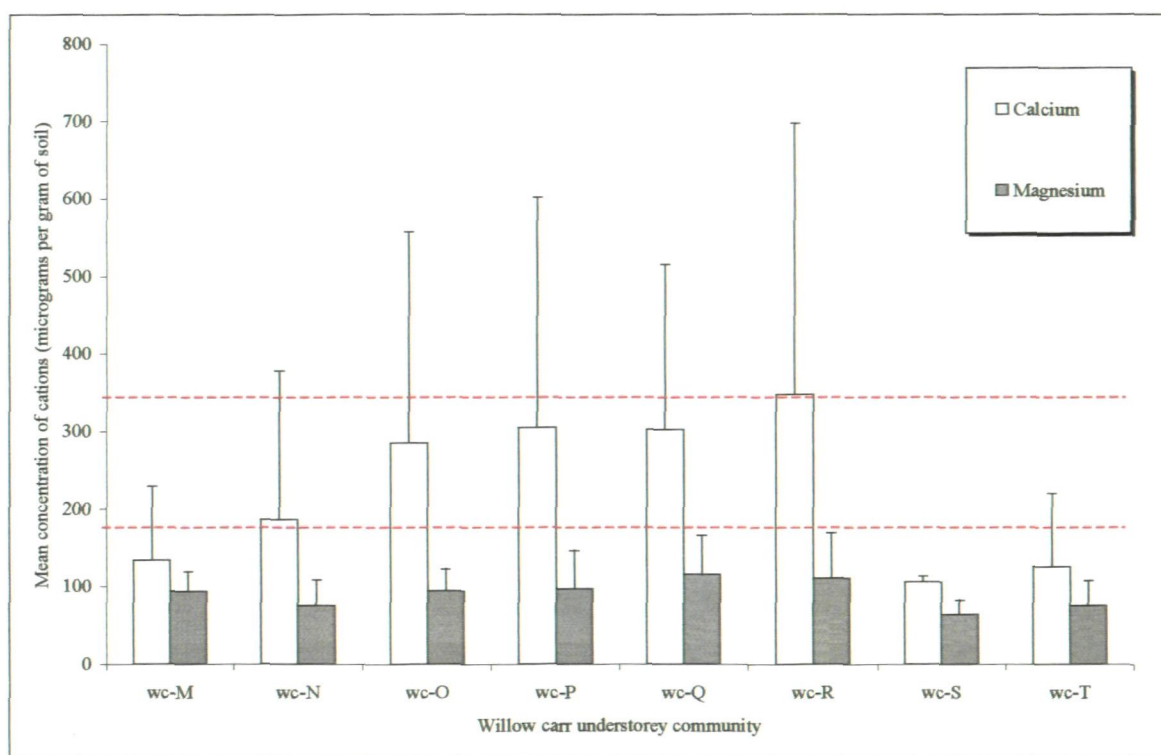
Figure 4.14 Mean concentrations of available calcium and magnesium per gram of dried soil found in the eight willow carr understorey communities, recognised by TWINSPAN. Error bars indicate the standard deviation. The two ----- lines are used to show significant differences among the amounts of available calcium (P<0.05). The bars that reach above the top line are significantly different from those below the bottom line. There were no significant differences among the magnesium concentrations.

Figure 4.15 shows there were no significant differences among the cation data arranged according to age. The oldest willow contains the highest concentrations of available Ca^{2+},

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and these were greater than the soil in the habitats recently invaded by willow. However, soil beneath the youngest willow contains the third highest concentration of available Ca²⁺.
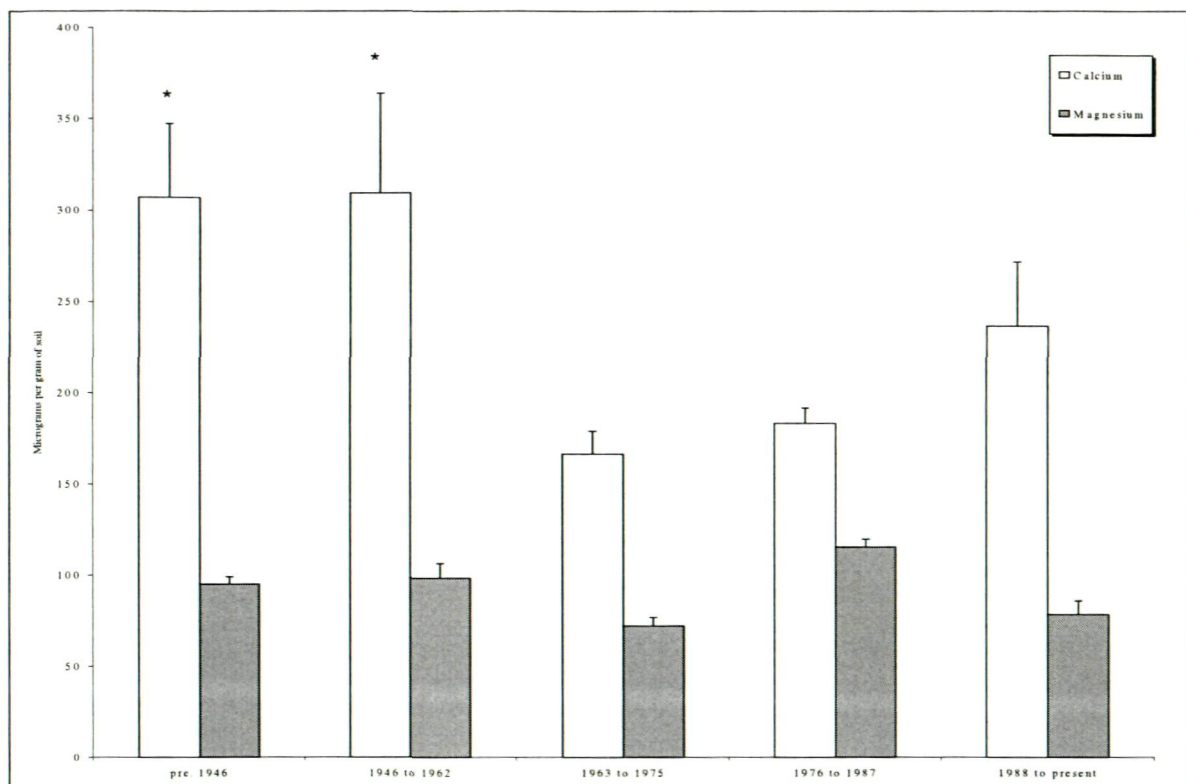
Figure 4.15 Concentrations of available calcium and magnesium per gram of dried soil found in the five age ranges, identified by the aerial photographs. Error bars indicate the standard deviation. Significant differences among the concentrations of available calcium are indicated by * (P<0.05). There were no significant differences among the available magnesium data.

The pH showed a similar pattern to that of the available soil cations. Figure 4.16 shows soil pH associated with the understorey communities identified by TWINSPAN and Figure 4.17 shows soil pH according to age. The mean range of soil pH associated with the willow was 4.75-5.46. The *Juncus effusus-Galium palustre* understorey community of wc-P was the most alkaline and the *Molinia caerulea-Viola palustris* was the most acid. Willow established before 1946 and between 1976 and 1987 have the highest pH at 5.34 and 5.32, respectively.
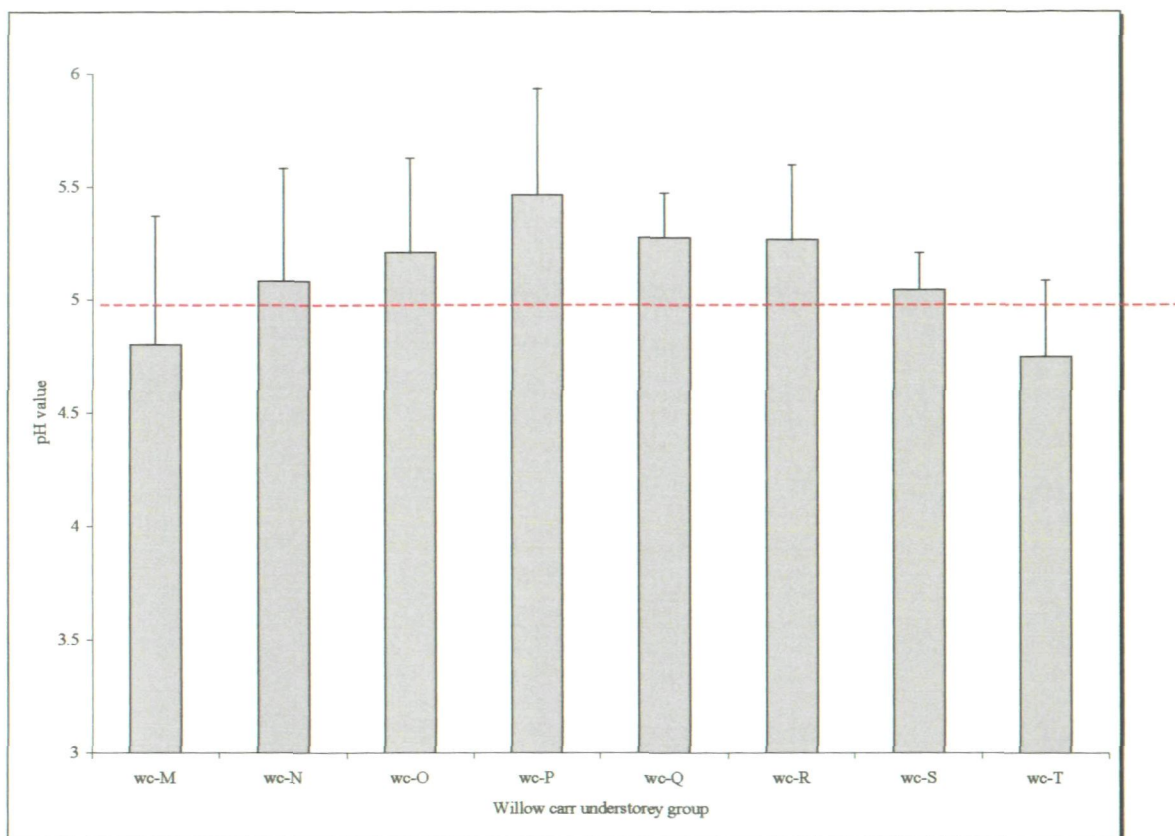
Figure 4.16 Dried soil pH of the eight willow carr understorey communities, recognised by TWINSPAN. Error bars indicate the standard deviation. ----- indicates significant differences among the year ranges that were identified by a single factor parametric ANOVA and a multiple comparisons Tukey test. Those below the line are significantly different to those above the line.
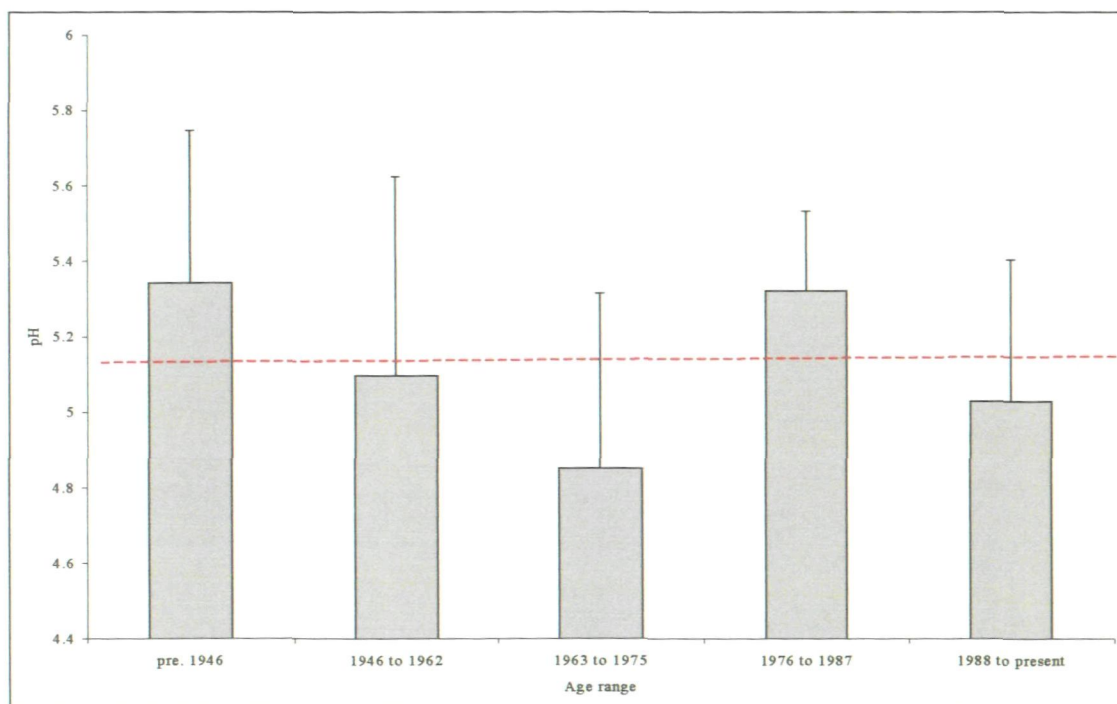
Figure 4.17 The pH of dried soil found in the five age ranges, identified by the aerial photographs. Error bars indicate the standard deviation. ----- indicates significant differences among the year ranges that were identified by a single factor parametric ANOVA and a multiple comparisons Tukey test. Those below the line are significantly different to those above the line.

4.3.7 DIVERSITY

Figure 4.18 shows the mean number of species per quadrat for each of the eight willow carr understorey communities. Although there were no significant differences among the groups, wc-S, the *Potentilla palustris-Mentha aquatica*, was the most species-rich with an average of 13.4 species per quadrat. Groups wc-M and wc-Q were both species-poor, both with a mean of 6.4 species per quadrat.
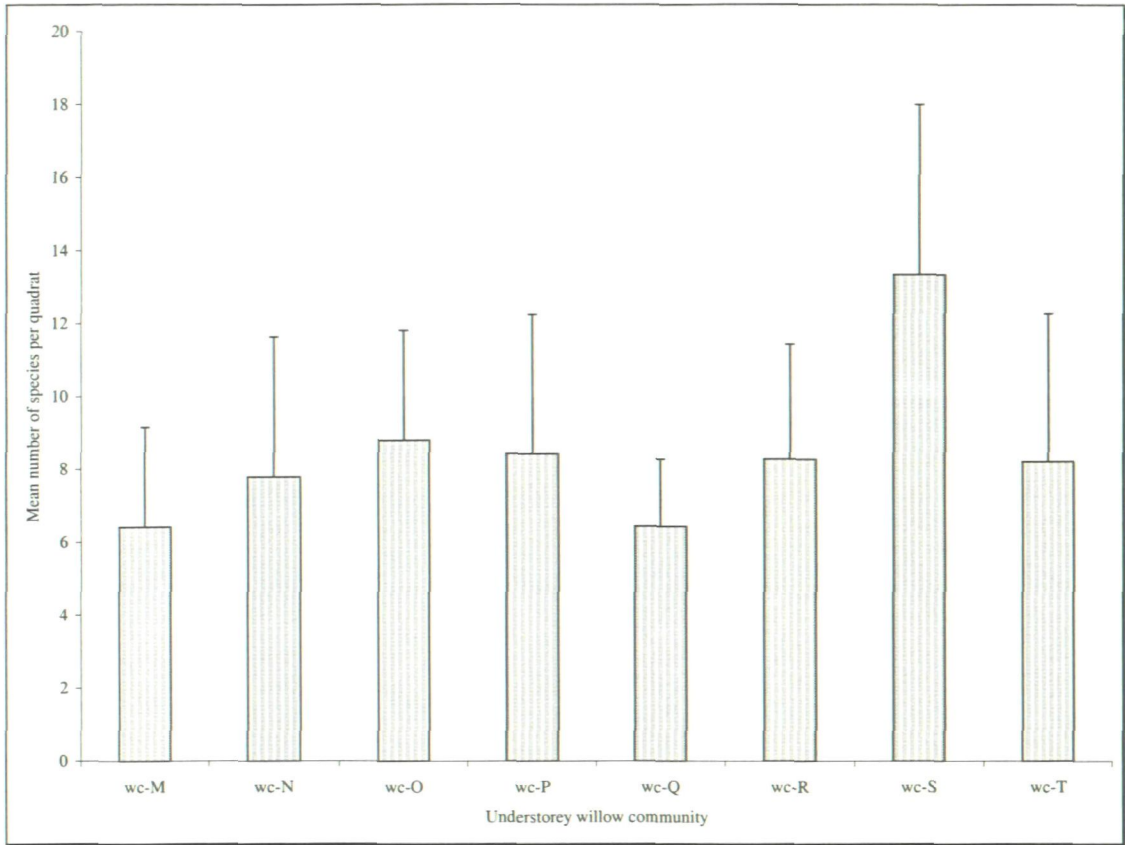
Figure 4.18 Mean number of species per quadrat or species richness occurring in Groups wc-M to wc-T. Error bars indicate the standard deviation. The single factor ANOVA showed there were no significant differences between the willow community groups.

Table 4.16 summarises the main differences in diversity among the five age ranges. The most recent willow was the most diverse with 10.3 species per quadrat. While, the least diverse was 1963-1975. All of the year classes show quite a large standard deviation, indicating a lot of heterogeneity between the stands.

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Age range	Pre- 1946	1946-1962	1963-1975	1976-1987	1988 to present
Mean number of species per quadrat	9.6 ± 3.1	7.8 ± 3.2	6.5 ± 2.3	7.9 ± 4.2	10.3 ± 4.2
Pre- 1946			*		
1946-1962					***
1963-1975					***
1976-1987					*
1988 to present					

Table 4.16 Mean and standard deviation of the number of species growing beneath willow of different ages. Significant differences between the ages are graded using the following star system: * = P<0.05; ** = P<0.01; and *** = P<0.005.

4.3.7 TREE ARCHITECTURE

The discriminant analysis showed that all of the trees sampled from the willow that established prior to 1946 were classified into the correct category. This analysis is displayed in Table 4.17, where the 'true group' and the group that individuals were placed into can be compared and indicates that a tree chosen at random would have a 75 % chance of being classified into the correct age range. Trees sampled that had established between 1976 and 1987 were most variable and displayed similarities with all ages of tree except those established prior to 1946.

	True group				
Placed into group	Pre-1946	1946-1962	1963-1975	1976-1987	1988-present
Pre-1946	30	0	0	0	0
1946-1962	0	23	7	2	0
1963-1975	0	6	18	8	1
1976-1987	0	1	5	16	4
1988-present	0	0	0	4	25
Proportion correct in each group	**1.00**	**0.77**	**0.60**	**0.53**	**0.83**
Total proportion correct = 0.75					

Table 4.17 Findings of the discriminant function analysis, which weighted the willow architecture data to assign a tree of unknown origin into the correct age group. Based on assigning 30 trees.

The box and whisker plots in Figures 4.19–4.24 summarise the tree architecture data of the five age ranges. Tree height and the dbh of the largest pole show an increase in size over time, which was expected. The height of the first fork and the number of live secondary shoots also appear to show a simple relationship with age. However, the trees established before 1946 have a lower first fork height, indicating structures akin to coppiced trees. All ages of willow possessed the same number of base poles, with a median of one. The number of poles at 1.5 m are very similar for each age class, but 1963-1975 shows the least variation. To help visualise the structure and design of the individual trees, to-scale diagrams are displayed in Figures 4.25–4.30. It is evident from these diagrams that many of the trees that established between 1946 and 1975 are situated above the water table on a plinth or mound.
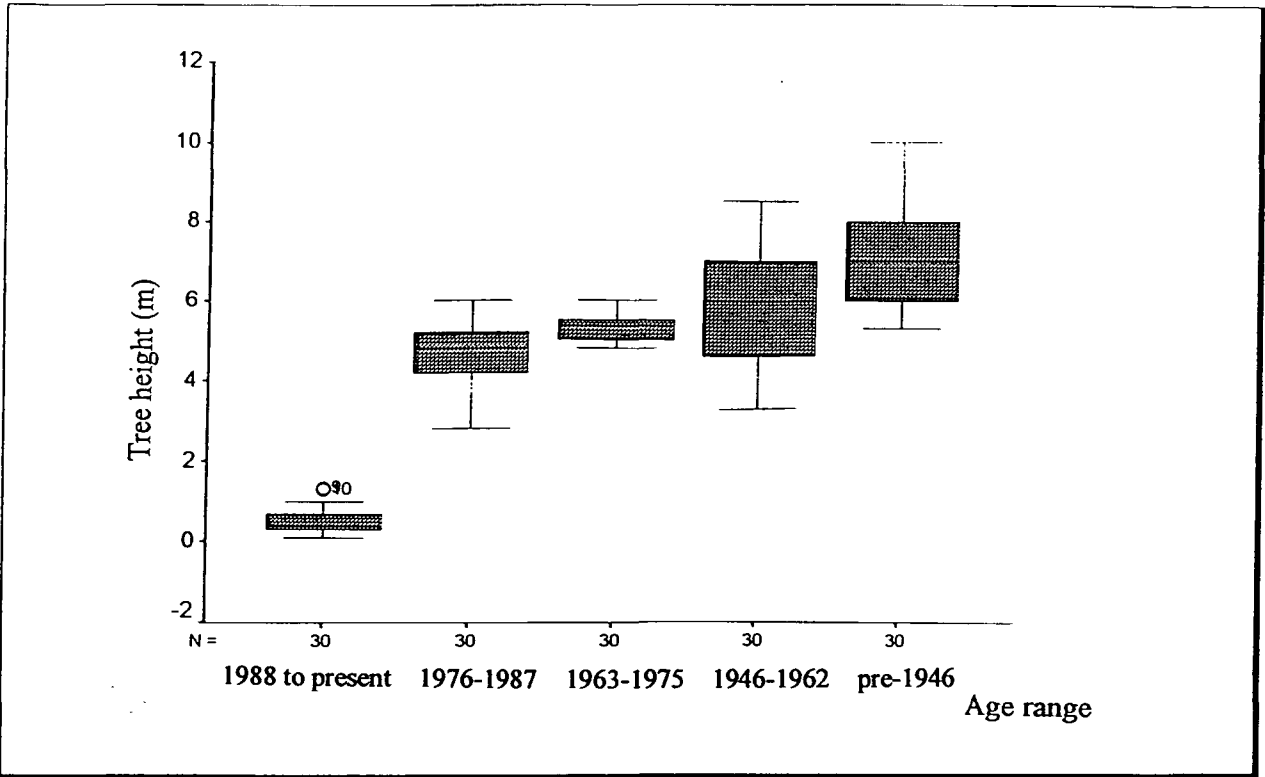
Figure 4.19 Box and whisker plots to summarise differences in height among 5 age groups of willow on Goss Moor NNR. The box is divided at the median and the top and bottom represent the upper and lower quartiles. The line or whisker at the top of the box shows the largest value within a 1.5 inter-quartile range.
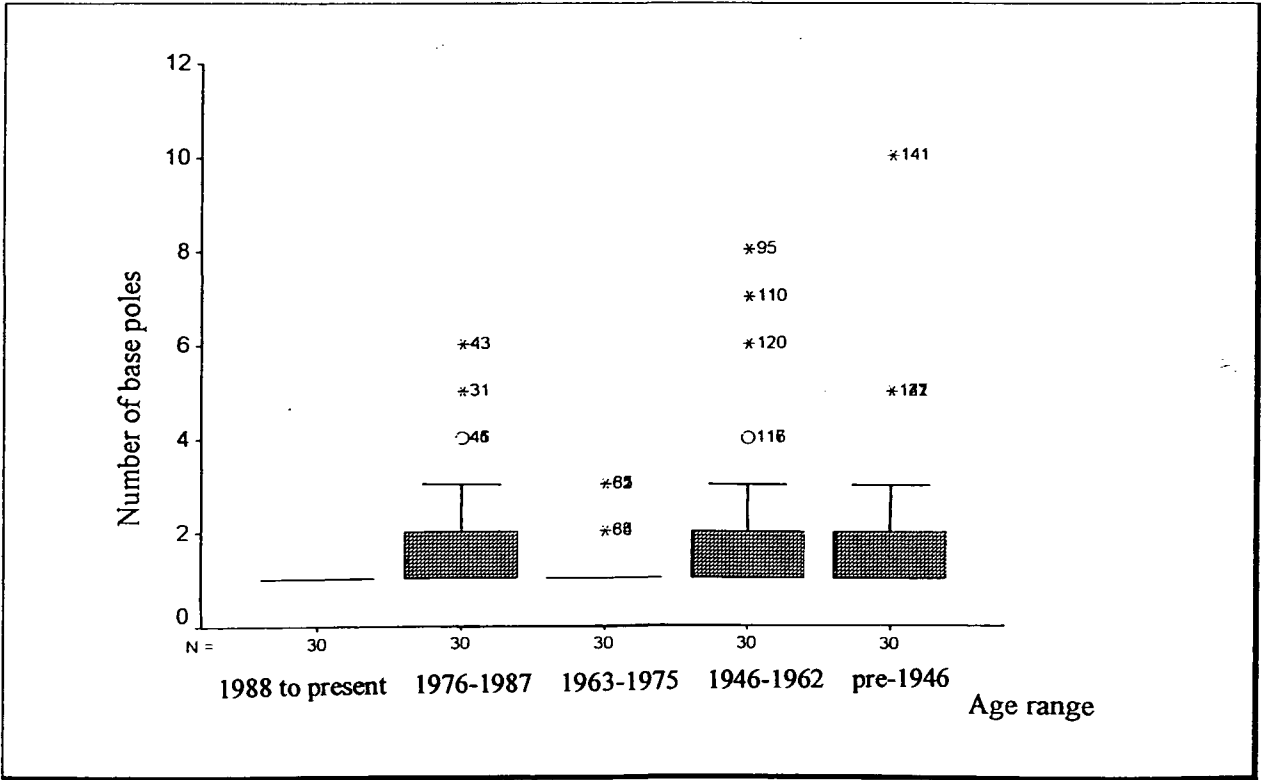
Figure 4.20 Box and whisker plots to summarise differences in the number of base poles among 5 age groups of willow on Goss Moor NNR. The box is divided at the median and the top and bottom represent the upper and lower quartiles. The line or whisker at the top of the box shows the largest value within a 1.5 inter-quartile range. Outliers are shown.

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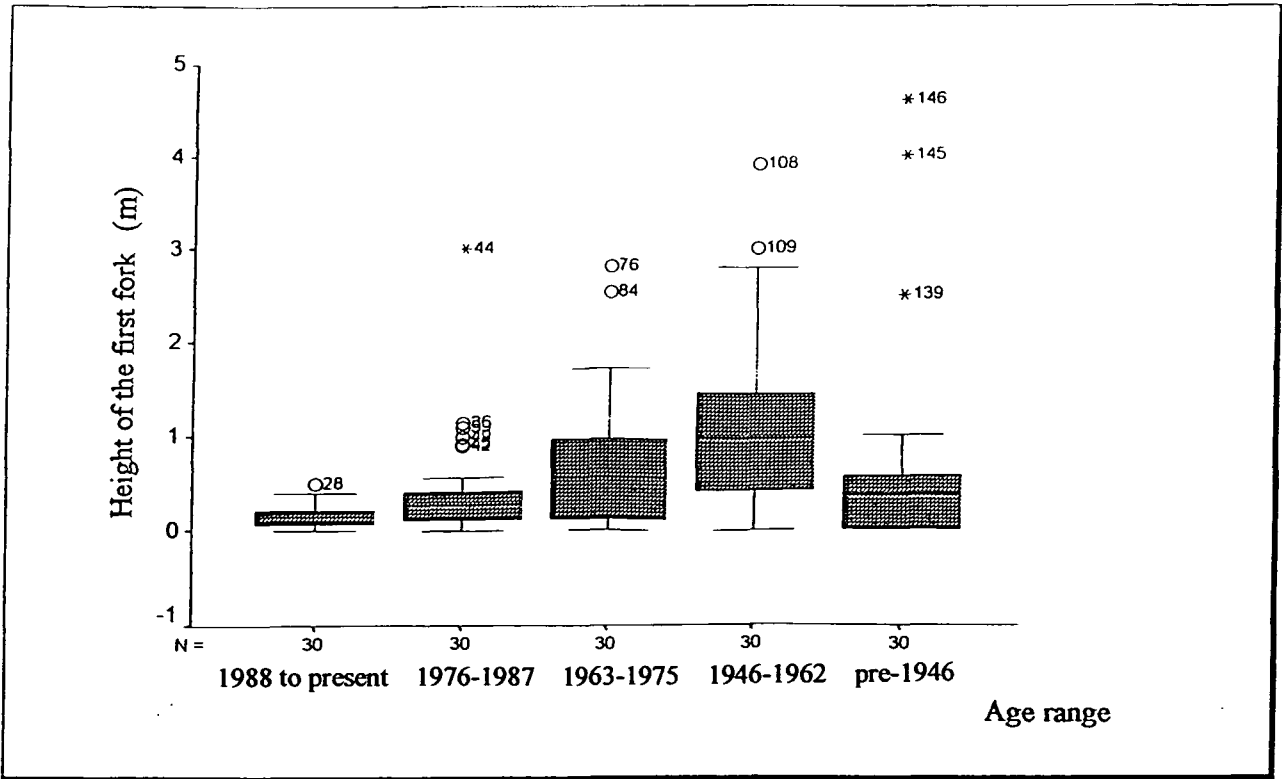
Figure 4.21 Box and whisker plots to summarise differences in the height of the first fork among 5 age groups of willow on Goss Moor NNR. The box is divided at the median and the top and bottom represent the upper and lower quartiles. The line or whisker at the top of the box shows the largest value within a 1.5 inter-quartile range. Outliers are shown.
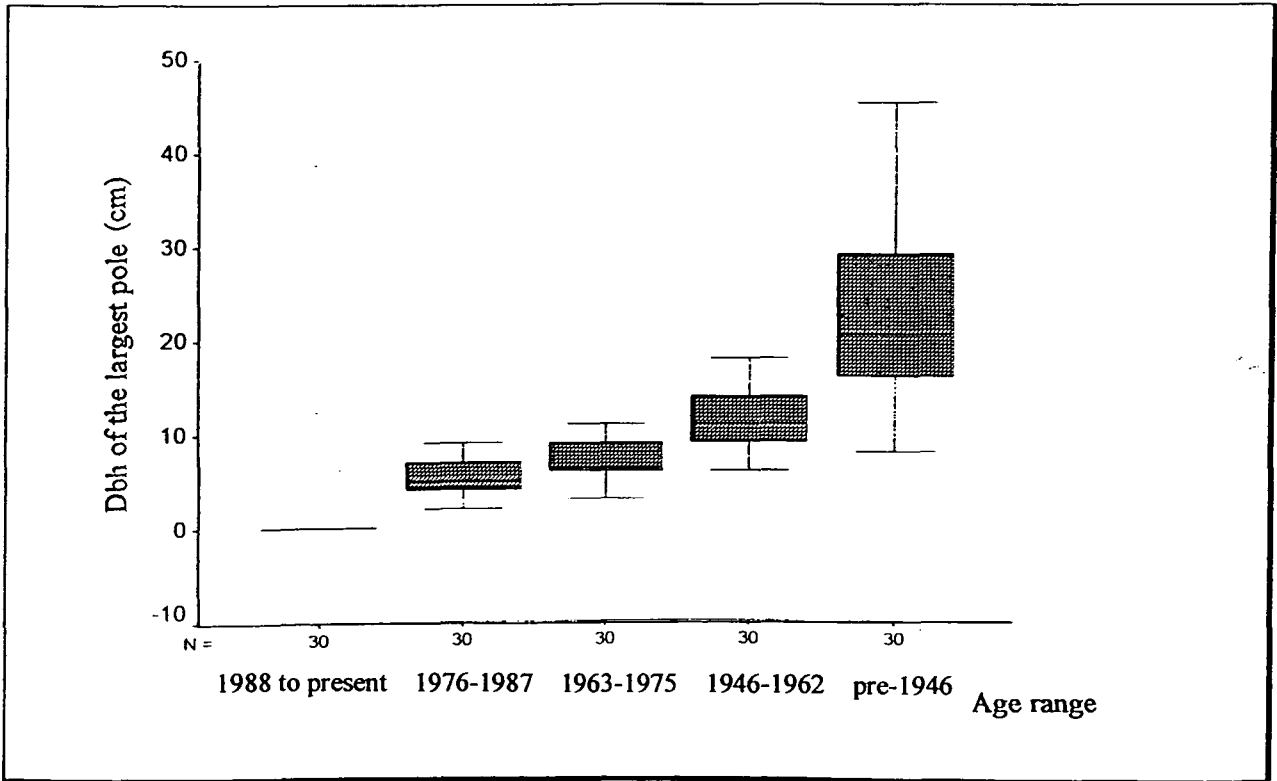
Figure 4.22 Box and whisker plots to summarise differences in the dbh of the largest pole among 5 age groups of willow on Goss Moor NNR. The box is divided at the median and the top and bottom represent the upper and lower quartiles. The line or whisker at the top of the box shows the largest value within a 1.5 inter-quartile range.
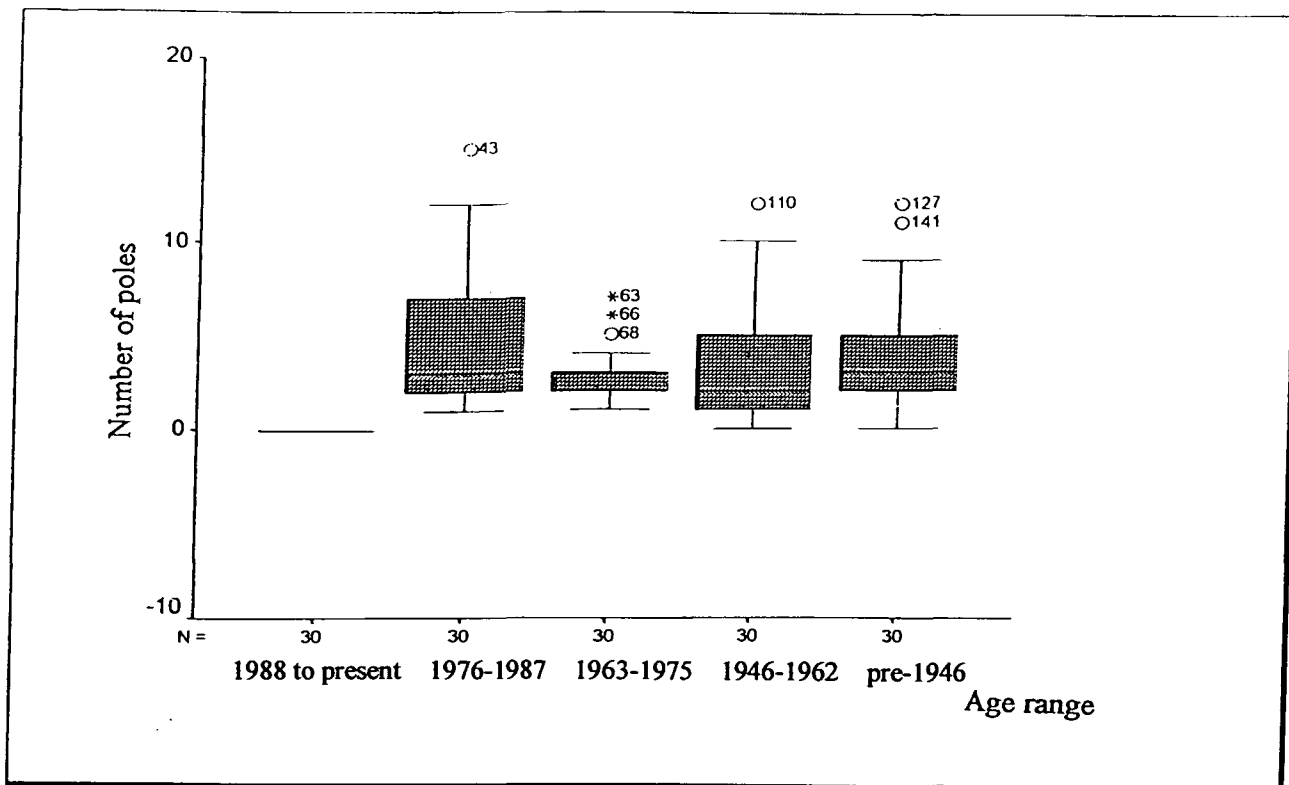
Figure 4.23 Box and whisker plots to summarise differences in the number of poles at 1.5 m among 5 age groups of willow on Goss Moor NNR. The box is divided at the median and the top and bottom represent the upper and lower quartiles. The line or whisker at the top of the box shows the largest value within a 1.5 inter-quartile range. Outliers are shown.
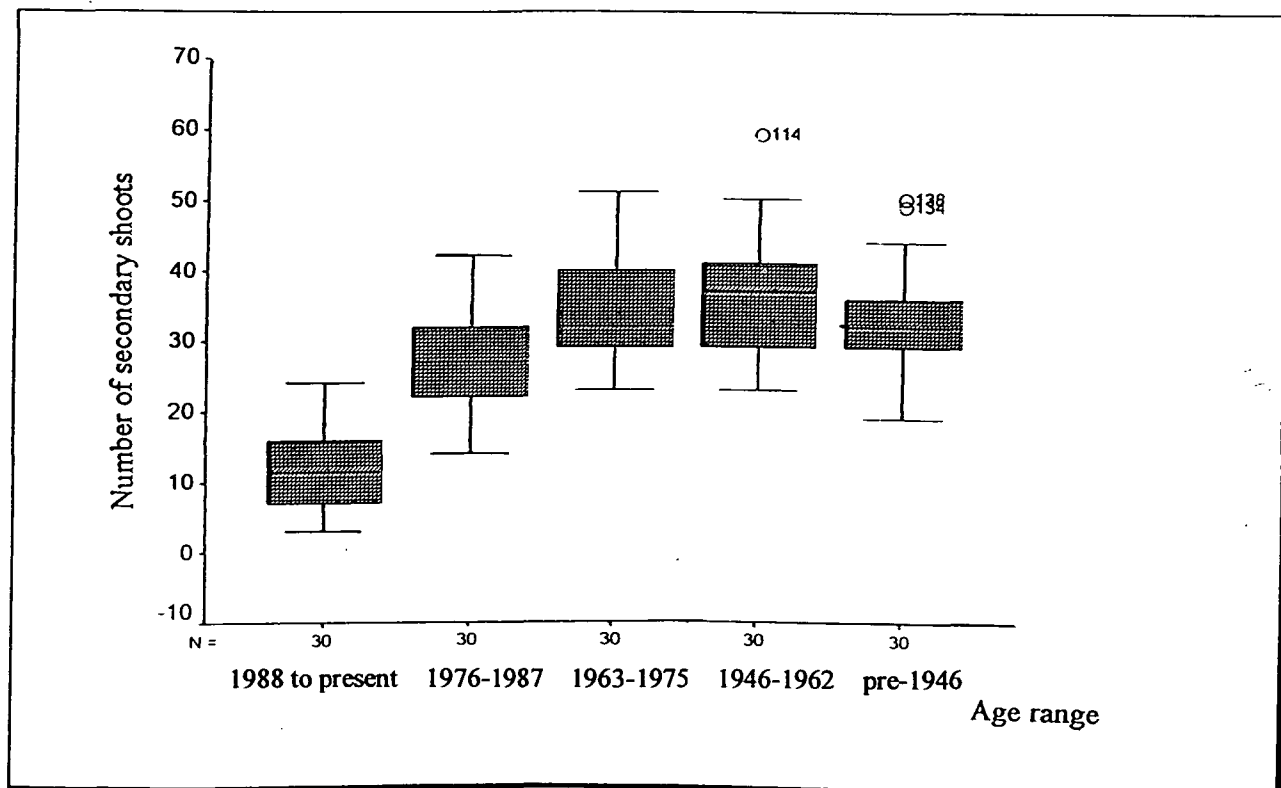
Figure 4.24 Box and whisker plots to summarise differences in the number of secondary shoots among 5 age groups of willow on Goss Moor NNR. The box is divided at the median and the top and bottom represent the upper and lower quartiles. The line or whisker at the top of the box shows the largest value within a 1.5 inter-quartile range. Outliers are shown.

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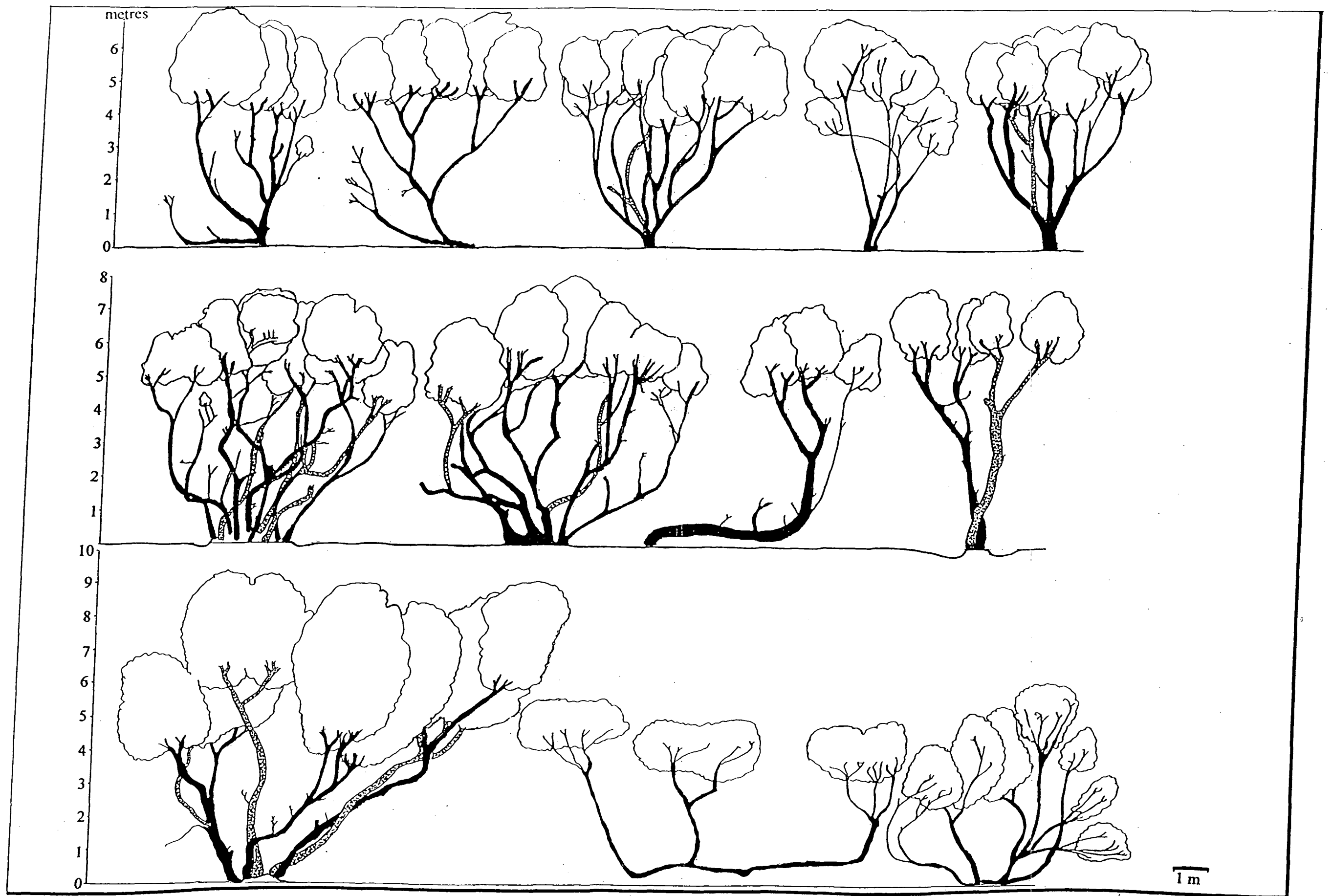
Figure 4.25 Profile diagrams of the south side of 12 of the 30 trees randomly chosen from woodland that appeared previous to the 1946 aerial photographs
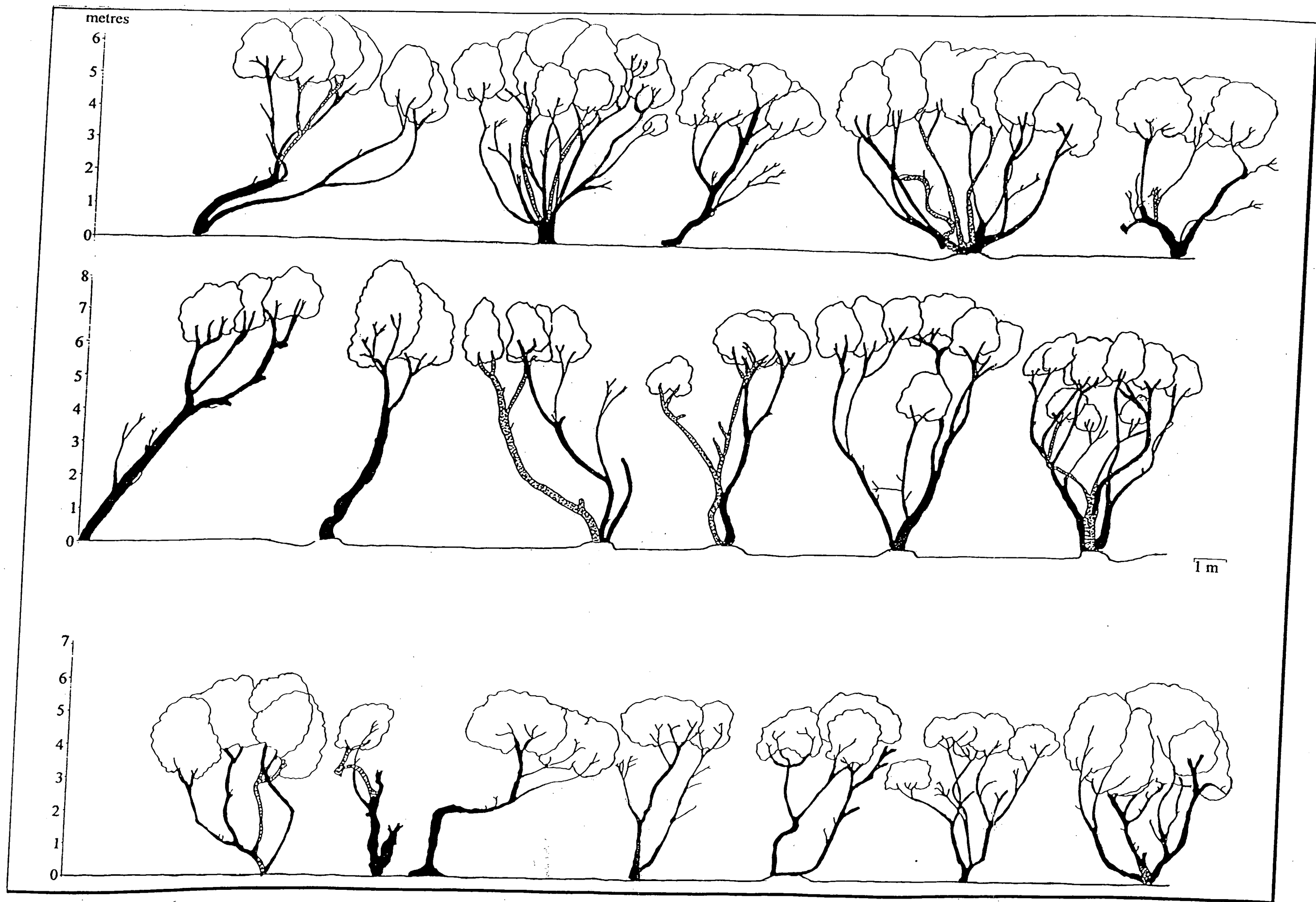
Figure 4.26 Profile diagrams of the south side of 18 of the 30 trees randomly chosen from woodland that appeared previous to the 1946 aerial photographs
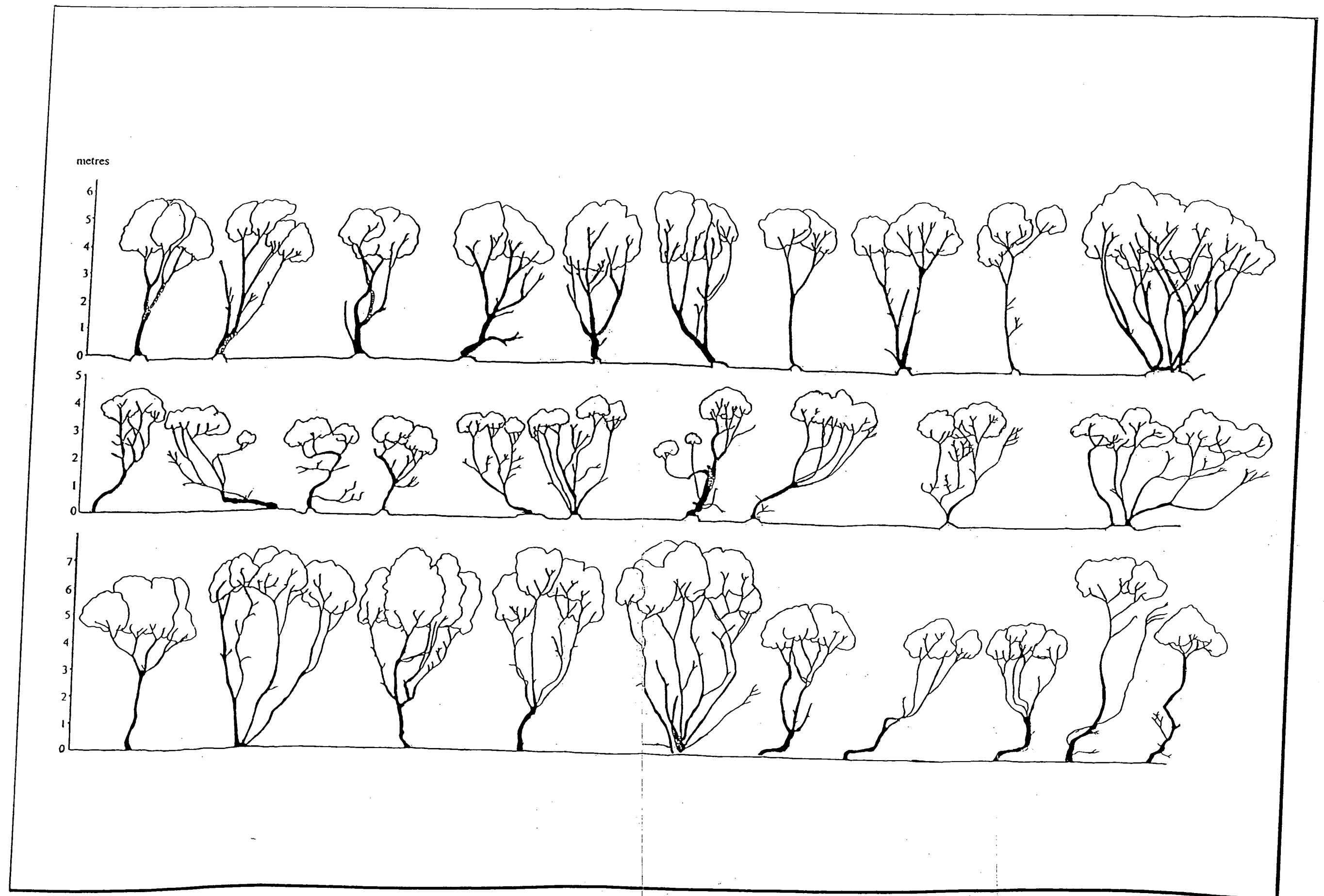
Figure 4.27 Profile diagrams of the south side of 30 trees randomly chosen from woodland that appeared on the aerial photographs between 1946 and 1962.

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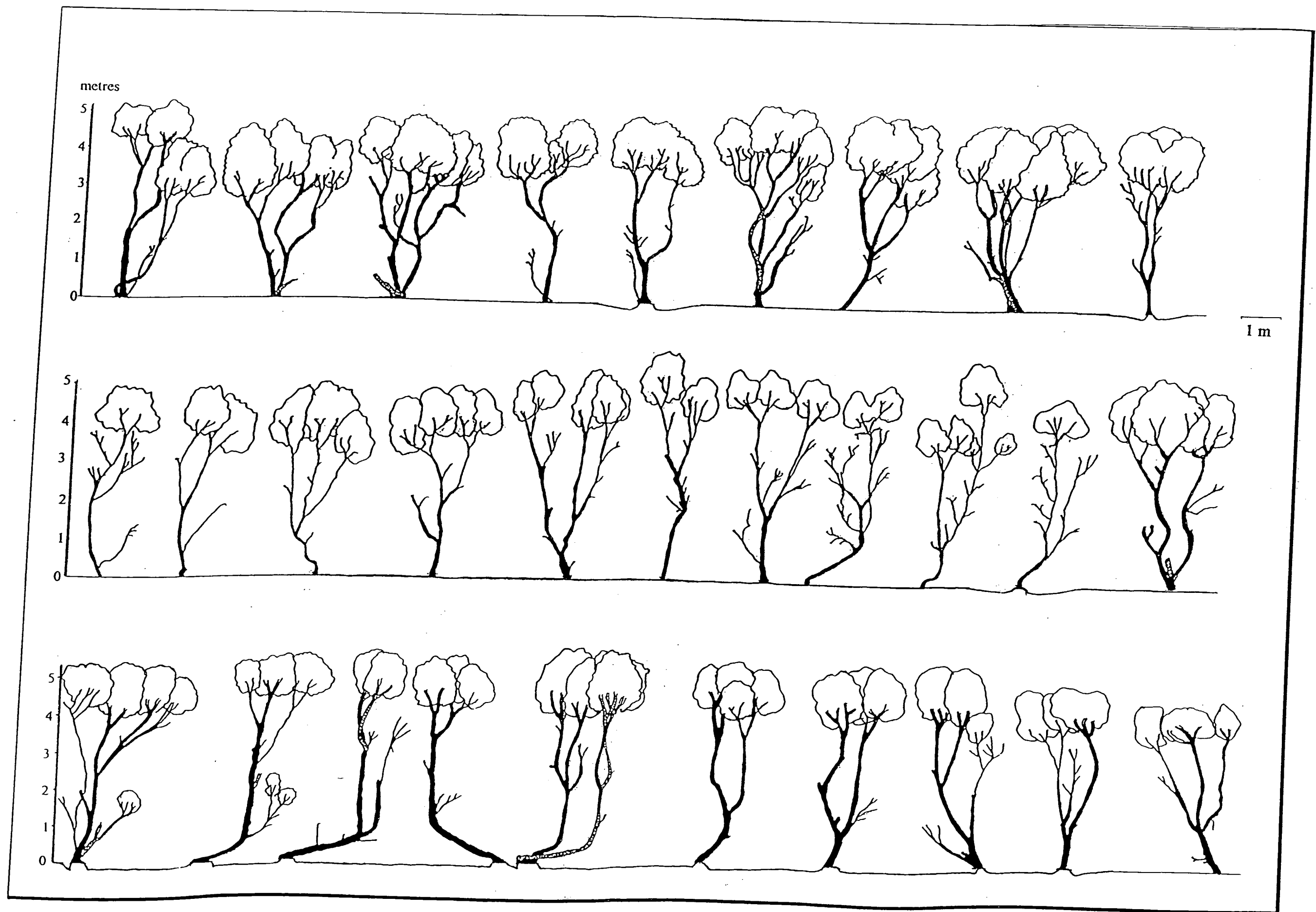
Figure 4.28 Profile diagrams of the south side of 30 trees randomly chosen from woodland that appeared on the aerial photographs between 1963 and 1975.
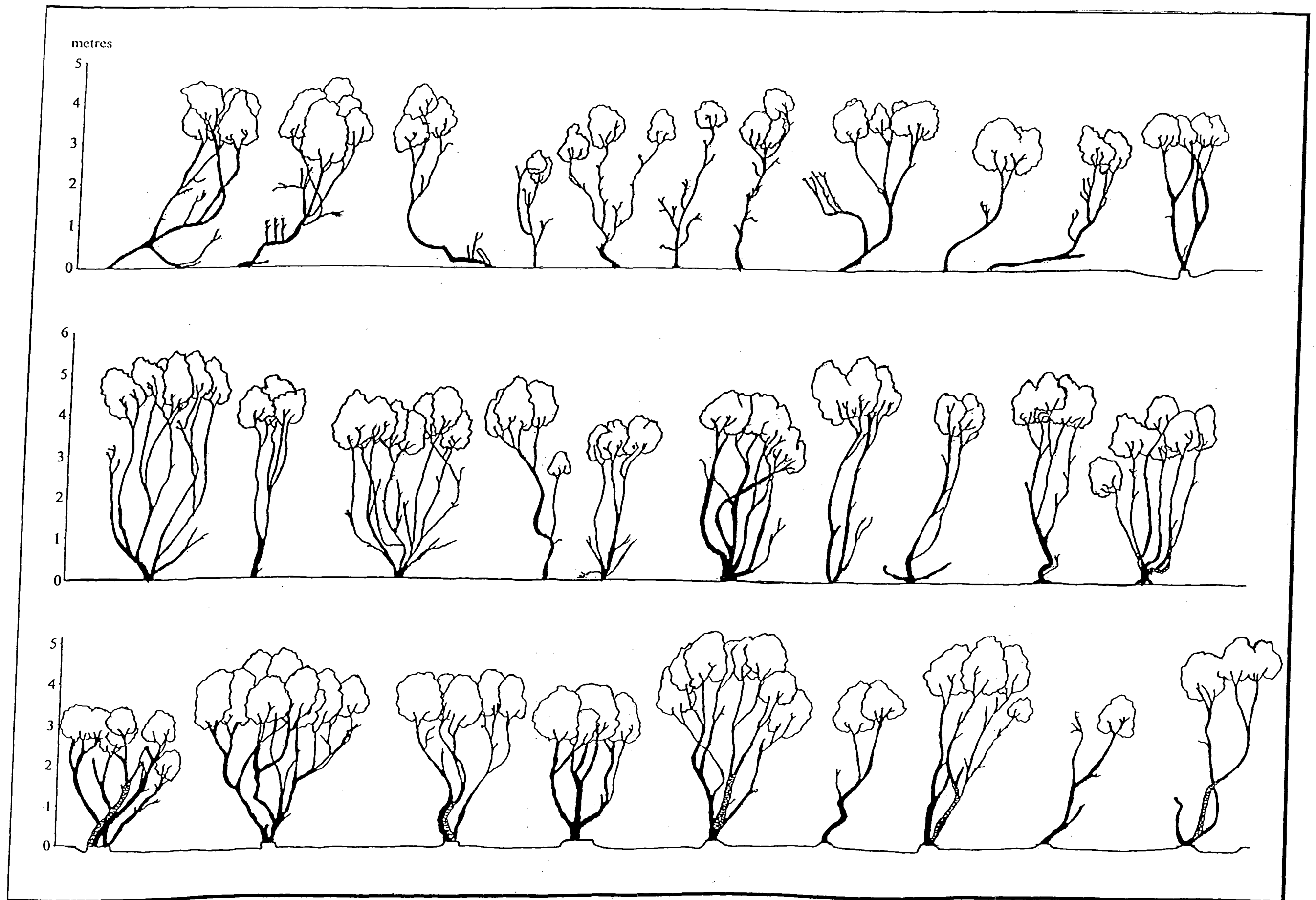
Figure 4.29 Profile diagrams of the south side of 30 trees randomly chosen from woodland that appeared on the aerial photographs between 1976 and 1987.
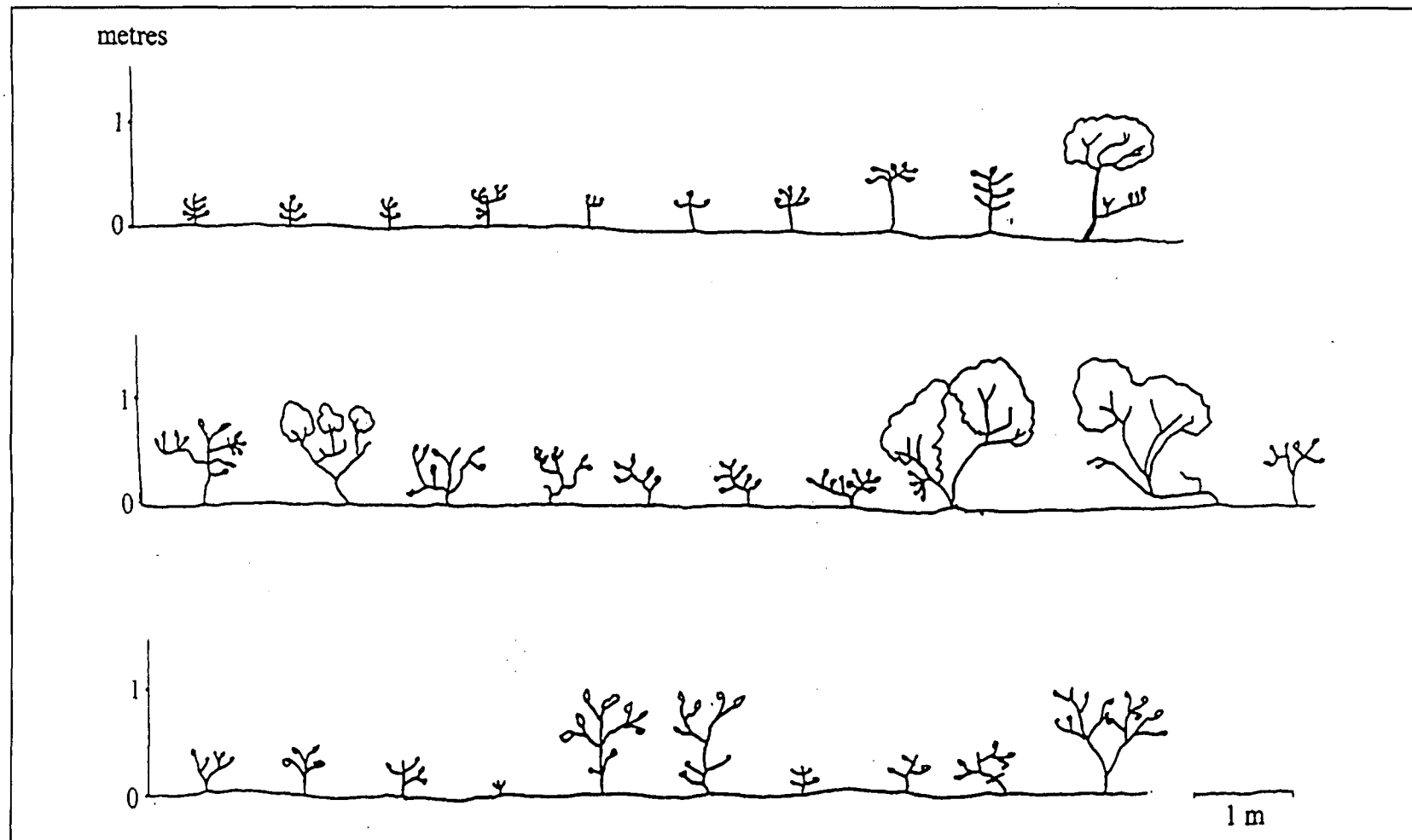
Figure4.30 Profile diagrams of the south side of thirty trees randomly chosen from woodland that appeared on the aerial photographs between 1988 and 1999

4.3.7.1 A comparative analysis of stand dynamics

The development of willow carr (sylvigenesis) on Goss Moor was examined using the hyperbolic growth equation based on the height:dbh relationship (Ogawa & Kira, 1977).
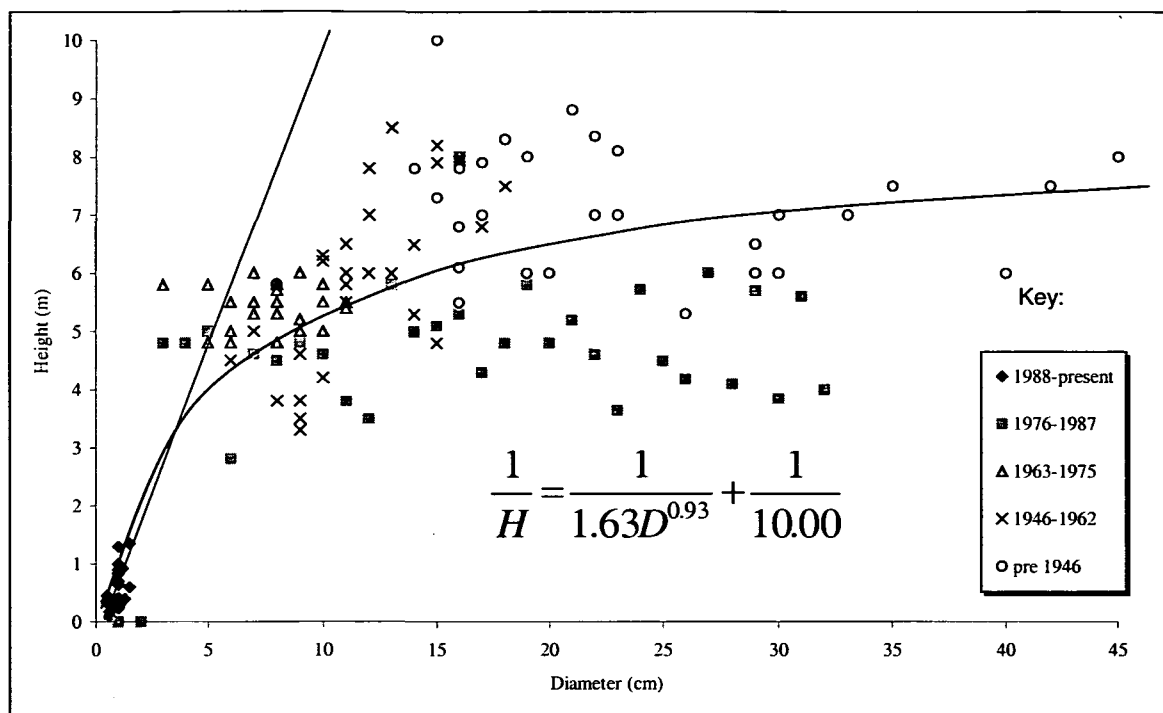
Figure 4.31 Tree height : dbh scatter plots for the five ages of willow, identified by the aerial photographs. The dbh was taken from the largest pole. The straight line indicates H=100 x dbh (D). The regression coefficient $R^2 = 0.821$. (ANOVA; $F_{0.05\,(2),\,2,\,148}= 3.78$, F = 1905.65, P<0.001).

Figure 4.31 shows the growth relationship of the dbh and height of the willow at different ages. The regression line fitted to the data (i.e. the hyperbolic model with fitted parameters) and explains 82 % of the variation in the y axis. This indicates the predicted model fits the observed data. The hyperbolic shape of the data shows that after a certain height dbh increases, while height is limited. The ANOVA shows that the fitted model is a significantly good fit of the observed data. Therefore, the growth of willow can be predicted well by using the fitted model. The fitted model shows that the allometric constant *h* was 0.93 and the tree constant A was 1.63. The tallest tree recorded was 10 m and the largest dbh was 45 cm. The position of the data in relation to the straight line

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(H=100.D) shows that willow carr is equivalent to H<100.D. This value indicates that reiteration has taken place as an energetic adjustment mechanism. This reiteration complicates the network of energetic pathways within the tree and increases the number of points among which the total energy from the roots must be divided and from which photosynthates must be exported (Oldeman, 1978).
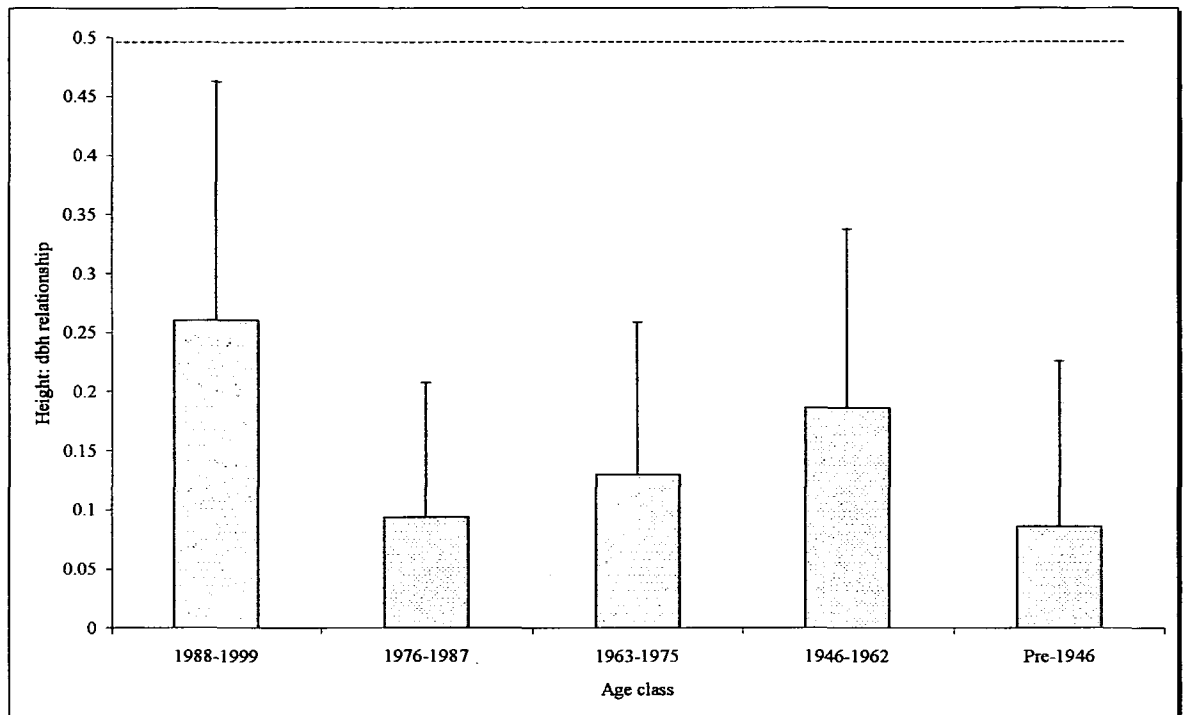
Figure 4.32 Mean height : height of the first fork ratio of the thirty trees sampled from each age of trees on Goss Moor. ------ indicates the threshold between positive and negative morphogenesis. Mean values below the line indicate positive morphogenesis.

Figure 4.32 shows the mean height of first fork : total height ratio. The majority of the trees had a ratio less than 0.5 and therefore displayed positive morphogenesis, which indicates an increase in the energy availability. There was one tree in each age class with a ratio greater than 0.5.

4.4 DISCUSSION

The main objectives of this chapter were to characterise the willow carr communities on Goss Moor and evaluate them according to their ecology and age.

4.4.1 VEGETATION DESCRIPTION

Eight understorey communities were found to be associated with the willow carr on Goss Moor. As evidenced by the DCA ordination, there was some overlap between the species composition of these communities. However, there was a definite pattern of distribution related to the age of the willow carr. The oldest willow on Goss Moor, established before 1946 is mostly associated with Group wc-O, the *Agrostis stolonifera-Juncus effusus* community. Another similar community, Group wc-N, was found mostly underneath willow established between 1946 and 1962. Group wc-Q contains large amounts of poor-fen/swamp species such as *Equisetum fluviatile, Menyanthes trifoliata, Potentilla palustris, Carex nigra* and *Carex rostrata* and was mostly found beneath willow that appeared between 1976 and 1987. The composition of Group wc-Q corresponds greatly with Group pf-A the poor-fen/swamp community, identified in Chapter Three. The understorey community containing the most poor-fen species was wc-S, the *Potentilla palustris-Mentha aquatica* vegetation, which contained *Juncus acutiflorus* and *Eriophorum angustifolium* and a large number of cushion-forming bryophytes species. This community was found in areas of most recent willow invasion and is comparable with the poor-fen Group pf-G, recognised in Chapter Three. Group wc-T the *Molinia caerulea-Potentilla erecta* understorey associated with shrubs such as *Calluna vulgaris, Myrica gale, Erica cinerea* and *Erica tetralix* was also found beneath the youngest willow.

On the whole, the number of poor-fen species in the understorey communities of willow carr decreased with age. However, there were occasions when the poor-fen understorey community persisted. The poor-fen communities that grow under willow of all ages were:

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Group wc-R the *Equisetum fluviatile-Potentilla palustris*, which contains large areas of standing water; Group wc-M, a community dominated by standing water and *Juncus effusus*; and wc-P the community co-dominated by *Potentilla palustris*, *Juncus effusus*, *Galium palustre* and bare substrate.

The correspondence between the communities identified on Goss Moor and the NVC community description of W1 *Salix cinerea-Galium palustre* woodland (Rodwell, 1991a) was poor. The main differences between the NVC description and the Goss Moor data appeared to be related to the greater frequency of the most dominant species found on the site: many of the general associates in the NVC description, such as *Potentilla palustris*, *Agrostis stolonifera* and *Molinia caerulea*, are found to be dominant components of the willow understorey communities on Goss Moor. This classification of the understorey communities shows the range of variation that occurs within the W1 community type on Goss Moor and the ability of poor-fen species to maintain their standing beneath *Salix cinerea*. In many cases the willow understorey communities contain an impoverished version of the poor-fen vegetation described in Chapter Three with greater proportions of bare substrate. However, there were no areas of understorey vegetation similar to the valley mire community *Narthecium ossifragum-Sphagnum papillosum*, or cushion-forming bryophyte communities beneath willow greater than 10 years old. This classification of the willow carr communities according to age and understorey composition provides the first comprehensive description of willow carr on Goss Moor. This information will provide a valuable basis for effective future management strategies, a more detailed discussion of which can be found in Chapter Eight.

4.4.2 DIVERSITY OF THE WILLOW

Out of the seven wet woodland NVC communities identified by Rodwell (1991a), W1 was one of the least diverse (Wheeler *et al.*, 1999), containing a mean of 17 species per sample.

Salix cinerea woodland, like poor-fen communities, is therefore intrinsically species-poor. Group wc-S, the *Potentilla palustris-Mentha aquatica* understorey community was the most species-rich with an average of 13.4 species per quadrat. This was similar to the two most species-rich poor-fen communities, which contained 13 and 14 species.

A relationship was found between willow age and understorey species diversity. The most recent willow was associated with the most diverse understorey communities. Diversity declined gradually to be lowest between 1963 to 1975. After this, diversity gradually increased to peak in the pre-1946 willow. The increase in diversity with age represents a general decline in poor-fen species and an increase in Poaceae and woodland species. However, there was a large amount of heterogeneity between the stands, reflected in the large standard deviation of the mean number of species per quadrat for each age. Some species-rich poor-fen understorey communities such as groups wc-P and wc-R were found in all ages of willow.

In poor-fen and fen carr communities the species assemblages and their diversity often reflect tolerances to water fluctuation or shade, or both (Wheeler *et al.*, 1999). This research has identified a definite correlation between the broad shifts in species composition and the amount of shade, which increases with the age of the stand. Poor-fen species that appear to persist under older willow, and are considered shade tolerant, include *Valeriana officinalis*, *Mentha aquatica* and *Equisetum fluviatile* (Ellenberg *et al.*, 1991, Hill *et al.*, 1999). Hydrological factors are reportedly one of the most important factors affecting the floristic composition and succession of wetland vegetation, especially water table height, movement and fluctuation (Wheeler *et al.*, 1999). Although surface water depth increased with the age of the willow carr on Goss Moor, other factors such as organic depth and tree height were more highly correlated with stand age.

This knowledge of the age and environmental conditions associated with the diversity or species richness of willow carr on Goss Moor can be used as a management tool to prioritise areas for conservation. A further discussion of the implications of these findings for management and conservation can be found in the final chapter.

4.4.3 SOIL PROPERTIES

There was no direct relationship between the mean concentration of exchangeable Ca^{2+} and the age of the stand. However, the two oldest stands (pre-1946 and 1946-1962) had the highest concentration of available Ca^{2+}. These results were contradictory to the findings of Richter *et al.* (1994), who reported that concentrations of exchangeable calcium and magnesium were depleted over time in forested old-fields. In their study, the accumulation of exchangeable Ca was of the same order of magnitude as Ca lost via soil leaching. The higher concentration of Ca^{2+} in the older willow on Goss Moor may be attributed to the movement of surface water transporting cations from the surrounding catchment (Wheeler & Giller, 1982b; Likens & Bormann, 1995). Unfortunately, there was no direct relationship between the presence of drainage channels and the positions of willow stands with high cation concentrations. This may be attributed to the inaccuracy of the maps, as it was evident from field observations that the number of channels had been under-estimated. One explanation for this may be the constant change the vegetation is undergoing. For example, colonisation by willow carr would obstruct previous patterns of surface water by their intrusive presence and eventually divert water flow as the trees mature. These changes may be intensified by periods of high rainfall, which would dramatically increase the amount of water arriving from the surrounding catchment and may therefore erode the original drainage channels and create new ones. Another source of cations in older willow may be wash-off from tree surfaces (Marques & Ranger, 1997). The build-up of cations from dry deposition and rainfall would be greater in the older trees. In broad terms, the soil analysis results were concordant with peat water analysis data produced by Proctor (1974) who

showed available Ca^{2+} concentrations to be higher in fen carr than in poor-fen recently colonised by willow, indicating the possibility of a successional relationship whereby Ca^{2+} increases over time. However, conversely to Proctor's findings the concentrations of available Mg^{2+} were in proportion to concentrations of available Ca^{2+}.

The inverse relationship between soil pH and available soil cations also corresponded to work by Richter *et al.* (1994). This is not surprising, as pH is closely correlated with base-saturation and, since calcium is reportedly the most abundant metallic cation in fen systems (Proctor, 1974), pH is closely related to calcium concentration.

Although the soil analysis was useful and interesting, in future studies it may be more beneficial to collect samples on more than one occasion. Snap-shot measurements may not represent nutrient availability throughout the year, as the chemical composition of fen soils show a large amount of seasonal variation (Wheeler, 1983; Verhoeven *et al.*, 1988; Proctor, 1994). Spatial variation is also a problem as replicate soil samples from apparently uniform stands may show large differences in the chemical environment (Wheeler *et al.*, 1992). Also, there is some doubt over the accuracy of using dried samples. It has been suggested that the analysis of fresh samples may be more meaningful (Wheeler *et al.*, 1992).

4.4.4 THE STATUS OF WILLOW CARR ON GOSS MOOR

The vegetation structure of Goss Moor has altered quite significantly since 1946 and by 1994 willow coverage had certainly exceeded the English Nature scrub protocol of 16 %. Using the aerial photographs and image analysis, the average rate of willow expansion was found to be 22850 m^2 per year. Willow invasion on Goss Moor was most prominent between 1963 and 1975 where the rate of spread averaged at 52983 m^2 per year. Between these years the majority of the willow increase occurred in the north of the site away from

the principal wetland habitats. However, in the centre of Goss Moor in block B, where most of the wetland habitats were found, willow carr covered 33 % of the total block area.

The accuracy of using aerial photographs to identify age classes of willow was validated by the discriminant analysis of the architecture data, which verifies that tree age can be assessed in the field. Using all of the factors measured there was a 75 % chance of accurately ageing a randomly chosen tree of unknown age. The most useful determinants were height of the first fork and the number of live secondary shoots, tree height and dbh. Tree height and dbh were used to model of willow growth on Goss Moor. The increase of tree height and dbh of the largest pole over time was in agreement with the relationship between dbh and growth shown by Henry & Swan (1974). The trees established prior to 1946 have a low first fork height, and have a structure akin to coppiced trees. As trees become older and mature, the reiterations become smaller in stature (Bell, 1993) indicating that the coppiced structure of the oldest trees occurred at an early stage of development. The reiteration of these trees is most similar to adaptive reiteration, which is caused by favourable conditions (Bell, 1993). Another factor indicating favourable conditions for willow growth on Goss Moor is the mean height of the first fork : total height ratio, which was less than 0.5 for the majority of the trees. This value is indicative of positive morphogenesis and the availability of a more than ample energy supply for growth. More evidence to substantiate reiteration was provided by the H=100.D relationship claimed by Oldeman (1978). The Goss Moor data equated to H<100D, strongly indicating the occurrence of reiteration as an adjustment mechanism to an increase in energy availability (Oldeman, 1978). It can therefore be concluded that the conditions provided by Goss Moor for willow carr colonisation and growth are more than adequate. These ideal conditions were illustrated by the speed of willow invasion across the Moor.

The growth curve of the willow carr, derived from the height:dbh relationship showed a very good fit (R^2 = 0.82) to the data collected on Goss Moor. The h constant for Goss Moor willow was 0.93, which was much lower than that recorded in Irish woodlands for *Salix cinerea* (2.07) (Iremonger, 1990). The allometric constant h has been found to approach unity in stabilised stands of shade tolerant species, whereas in stands of 'sun-trees' it tends to be greater than 1 (Ogawa & Kira, 1977). The tree stands in Ireland were taller and thinner than those on Goss Moor, which would account for the differences in h constant. The stand densities in the present study ranged between 3 and 100 individuals per 100 m^2 and a mean of 26.3 individuals per 100 m^2, which falls within the range of those recorded for wet woodlands in Ireland (16-54 individuals per 100 m^2). The densities on Goss Moor are generally higher than those recorded for Europe, i.e. 13.6 per 100 m^2 (Walter, 1982) and 4.7 to 11.6 per 100 m^2 (Oosterhuis *et al.*, 1982).

It was evident from the diagrams of the individual trees that many of them were situated upon a mound composed of soil and organic matter trapped between the root ball of the tree. From field observations, it is evident that these trees are raised above the surface water level. Water movement between these mounds is often quite substantial and may contribute to low understorey diversity experienced beneath the willow. The constant washing through of water would dislodge soil and organic material, thus impeding the germination and stabilisation of new colonisers.

4.4.4 PATTERNS OF SUCCESSIONAL CHANGE IN WILLOW CARR ON GOSS MOOR

The evidence gained on the present state of willow that has established at different times on Goss Moor can be used to speculate on and construct a process of events that occur during willow carr development. These findings are concordant with the few studies in Britain that have carefully documented the replacement of herbaceous fen by fen carr (Godwin *et al.*, 1974; Pigott & Wilson, 1978).

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Willow invades areas of Goss Moor where there are the greatest amounts of accumulated organic material and a low water table. It is the build-up of organic material that may reduce vertical water fluctuation in the immediate vicinity. The type of vegetation the willow invades strongly influences the composition and structure of the field layer of the future woodland (Wheeler *et al.*, 1999). In a wetland context, the types of vegetation that are subject to invasion contain cushion-forming bryophytes such as *Aulacomnium palustre* and *Sphagnum recurvum*. These species grow above the water table where conditions are less reduced and may provide improved conditions for germination. Of course the success of the invasion is governed by factors such as seed availability, which may be reliant on stochastic events such as mast years (Wheeler *et al.*, 1999). Between 10 and 25 years old, willow is still associated with a large amount of organic matter and has an understorey community mostly dominated by declining numbers of poor-fen species such as *Equisetum fluviatile* and *Menyanthes trifoliata*. Bare substrate becomes an increasingly prominent feature. Between 25 and 40 years old the community is still dominated by species that are largely classified as poor-fen. However, standing water becomes a significant feature. The movement of surface water dislodges and washes the substrate between the tree bases, leaving only the substrate protected by the tree bases and root mass. For this reason many of the trees become raised above the water level and trees appear to be positioned on a mound. Species richness is lowest in this age class. Between 40 and 55 years, poor-fen species such as *Potentilla palustris*, *Calliergon cuspidatum* and *Carex nigra* are further reduced and bare ground dominates, along with graminoid species like *Holcus lanatus* and *Agrostis stolonifera*. Nevertheless, there are still a large number of plant species associated with both this age group and the oldest willow. Willow greater than 55 years old is more species-rich than the 10 to 55 year old willow, even though canopy cover is denser than for other age classes. This understorey community contains a number of different pteridophytes and species associated with dry woodlands such as *Lonicera periclymenum* L. and *Hedera*

helix L. (Grime *et al.*, 1988). Apart from *Potentilla palustris*, poor-fen species occur only occasionally.

Due to the relatively short time-scale of the colonisation of Goss Moor, it is difficult to detect any major progression from willow carr to woodland climax. However, the presence of oak saplings in the oldest and driest willow may suggest that some move towards secondary woodland is taking place. In the next chapter, further evidence for hydroseral succession will be sought through the spatial analysis of the main wetland plant communities found on Goss Moor.

4.5 SUMMARY:

- The NVC type W1 on Goss Moor was found to encompass eight different understorey community types.

- A definite relationship exists between the age of the willow carr and the type of understorey community that persists. In general, there was a progressive decrease in poor-fen species and a concomitant increase in woodland species, which appeared to be related to an increase in canopy cover, and therefore shade.

- The most diverse community was found with the most recent willow and was dominated by poor-fen species. The oldest willow was the second most diverse and was associated with a reduction in poor-fen species and an increase in woodland species.

- Tree height and dbh were identified as useful parameters to accurately assess willow age in the field.

Chapter Five: Spatial dynamics of the vegetation communities on Goss Moor NNR.

5.1 INTRODUCTION

The vegetation on Goss Moor exhibits patchiness. When the patchiness has a certain amount of predictability so that it can be described quantitatively, it is called spatial pattern (Dale, 1999). The poor-fen survey of Goss Moor presented in Chapter Three described 12 different poor-fen community types occurring as a series of mosaics. As in many habitats, these mosaics are repeated throughout the wetland (Dale, 1999). Some of the poor-fen community types appeared to represent stages of a successional sequence, culminating in willow carr and ombrotrophic bog. The presence of spatial patterns on Goss Moor is yet to be proven formally. In Chapter Three, it was proposed that some poor-fen types represent transitional communities between *Molinia*, rush pasture and other poor-fen community types. As transitional areas sometimes correspond with boundaries between successional stages (Kent *et al.*, 1997), it will be advantageous to identify the type of vegetation occurring in juxtaposition, and compare associations with the successional patterns proposed in Chapter Three. From observation, some poor-fen community types were associated with abrupt or gradual transitions. Abrupt or ecotone boundaries (Kent *et al.*, 1997) were associated with ponds created during tin-stream mining activities. Gradual or ecocline boundaries (Kent *et al.*, 1997) were associated with swamp and poor-fen communities dominated by aquatic macrophytes. The importance of understanding the origin of boundaries and the spatial dynamics of mosaics on Goss Moor is paramount, especially in the knowledge that mosaics account for a significant proportion of the total area of the site. This chapter aims to describe the scale, spatial pattern and boundaries of the plant communities on Goss Moor in relation to former anthropogenic activities and identify any sequences of hydroseral succession that occur spatially.

Surprisingly, there is a dearth of information in the literature relating to the description and analysis of floristic data across vegetation boundaries (Margalef, 1994; Dale, 1999). However, most of the general literature on plant successional concepts has some relevance

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(Miles, 1987; Burrows, 1990; McCook, 1994). Transitional areas are defined as 'zones of interaction and tension' between adjacent communities and these may sometimes correspond with boundaries between successional stages (Kent *et al.*, 1997). Thus different types of transitional area may be recognised in relation to the degree of successional advancement in the communities on either side. In this case the ergodic hypothesis is invoked, whereby variation in space is substituted for variation in time (Chorley & Kennedy, 1971; Bennett & Chorley, 1978; Alexandrov & Logofet, 1994). Patches of vegetation present in different areas at one time are taken to represent distinct successional stages. Evidence for these patterns or chronosequences can be demonstrated in long-term studies of an area, or palaeoecologically from soil profiles where the relicts of vegetation remains represent a temporal sequence, the oldest being at the bottom (Tallis, 1973; 1983). As the vegetation communities on Goss Moor are of a contemporary nature, pollen or sedimentary analysis is not feasible. On Goss Moor, any chronosequences or patterns of spatial succession shall be identified using to the ecological literature and knowledge of the site.

The design and application of spatial sampling strategies to adequately sample across plant community boundaries in order to characterise transitions or boundaries is important and an area that requires further research (Kent *et al.*, 1997). Most early work on transitions used the one-dimensional transect approach but this has been shown to be inadequate for the accurate description of floristic and environmental variation across transitions (Johnston *et al.*, 1992; Fortin, 1994). Van der Maarel (1976) was the first to indicate the potential relevance and the possible adaptations that could be made to established methods of qualitative plant ecology in order to study variation across transitions. He was also the first author to introduce the idea of edge or boundary detection between plant communities and he describes how a supposed boundary may be studied by laying out a transect at right angles to the boundary or transition zone. Similarity coefficients, such as the percentage

dissimilarity (Bray & Curtis, 1957) and squared Euclidean distance (Kent & Coker, 1992) have been used to describe floristic change between successive quadrats along the transect. However, the method failed to pick up and account for mosaics in the vegetation because:

(i) both the location of the transect and the sample placement along the transect are usually subjective (Johnston *et al.*, 1992);

(ii) transects are usually placed at right angles to the perceived transition, which is often based on a subjective impression, rather than any objective criterion and;

(iii) transect lengths are often variable, making comparison difficult (Kent *et al.*, 1997).

Consequently, two dimensional spatial sampling is preferred by the adoption of a wider, rectangular sampling grid (Johnston *et al.*, 1992; Fortin, 1994). A range of different sampling designs may be adopted within the rectangle, but the key point of its use is the possibility of sampling lateral variation, and particularly mosaic patterns across the transition (Kent *et al.*, 1997). Where the whole rectangular area is sampled using contiguous quadrats, the sampling area may be described as a 'tranome'. This term was derived from the two words 'transect' and 'isonome'. The isonome method consists of laying out a grid of contiguous quadrats over the sample area and in each quadrat recording the abundance of the species of interest (Ashby & Pidgeon, 1942; Kershaw & Looney, 1985). The tranome technique was chosen to investigate the spatial pattern and successional dynamics of the plant communities on Goss Moor.

Techniques used to analyse floristic data across transitional areas in tranomes include the Mantel test, pattern analysis, spectral analysis and moving-window analysis. Of these the moving-window analysis has the greatest potential (Kent *et al.*, 1997). This method comes under the general heading of 'edge detection' which was originally devised to locate discontinuities along ecological gradients (Dale, 1988; Johnston *et al.*, 1992). The moving-window algorithm analyses multivariate floristic data along a one-dimensional transect or

spatial gradient. The rate of change or dissimilarity is calculated for a subset, or 'window' of contiguous data stations. The window is then 'moved' either along or across the data, and the change is recalculated for those data in the window. Based on this idea, Lange & Sparrow (1985) located and quantified transitions in semi-arid heath vegetation in Southern Australia by using a sampling grid or 'tranome', rather than a transect. Interspecific association was used to calculate homogeneity between the sample blocks or 'windows', which were sequentially positioned or 'moved' across the heath and mallee-heath vegetation. The method is not unidirectional, as it uses interspecific association within adjacent blocks, as opposed to a dissimilarity measure between samples, to detect rates of change. The method can therefore be applied to two-dimensional data.

Fortin (1994) has introduced two further methods for edge detection within two-dimensional areas. Regularly sampled quantitative data can be analysed by an edge detection algorithm called lattice-wombling. Wombling was first derived from the work of Womble (1951), who described the variation between a set of continuous or quantitative variables in space by an algorithm which averages the absolute values of their derivatives or gradients (Fortin, 1994). The lattice-wombling algorithm requires that the values of the variable are mapped on the nodes of a rectangular lattice, most often as the result of a systematic sampling design. The wombling algorithm or the magnitude of the rate of change is calculated for each set of four nearby points that form a square within the sampling design as shown in Figure 5.1. When the values in the four quadrats are similar, the magnitude of the rate of change will be close to zero; when the values at the four quadrats change abruptly, the magnitude of the rate of change is high (Fortin *et al.*, 2000). A boundary is identified from the spatially adjacent locations which are characterised by high rates of change.

LATTICE-WOMBLING

Rate of Change
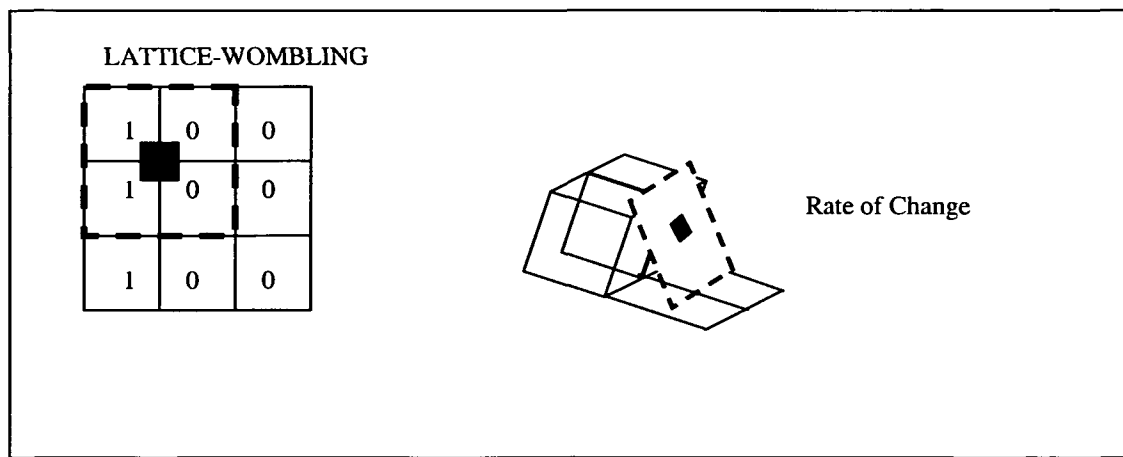
Figure 5.1 Lattice-wombling is computed for the four adjacent quadrats that form a square as indicated by a dashed line. The number (0 or 1) in each quadrat is the quantitative value measure. The black filled square indicates the location of the centroid at which the rate of change is computed. The z-axis is the quantitative value. The slope of the grey plane that fits the quantitative values represents the intensity of the rate of change. Steeper slopes represent greater rates of change (Fortin *et al.*, 2000).

When field data have quantitative but irregularly spaced, a triangulation-wombling detection algorithm is more appropriate (Fortin, 1994). This algorithm also finds first-order derivatives, but rather than using four nearby points that form a square, it uses the three nearest points that form a triangle (Fortin *et al.*, 2000).

Recently the wombling methods of data collection and edge detection were culminated in the production of a computer software package called BoundarySeer (Maruca & Jacquez, 2001). The package includes boundary delineation by moving split window, wombling as well as boundary statistics and significance tests. The spatial pattern of the plant communities on Goss Moor will be analysed using the BoundarySeer package.

The principal aim of this chapter is to find evidence of hydroseral succession from mosaics of vegetation occurring adjacent to each other and secondly to:

• establish the distribution of plant communities within the selected tranomes;

• describe the type of boundary associated with different species assemblages;

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- validate the use of the wombling for identifying different scales of vegetation pattern.

5.2 METHODOLOGY

In order to understand the successional sequences of the poor-fen and willow carr communities on Goss Moor, three tranomes were defined. The location and size of each tranome was chosen primarily to encompass the range of swamp, poor-fen and willow carr vegetation types occurring on the site, which are thought to represent different stages in the hydrosere, and also on the basis of substrate heterogeneity. Secondly, accessibility and time availability were also considered. Previous research on Goss Moor has revealed that particular community types only occur in certain locations (Chapter Three). This is thought to be attributed to the microtopography, which is more heterogeneous where tin-streaming was more intense. On the west side of the Moor, east of the disused railway, the substrate is extremely uneven and considered old, as there were no active tin-streaming mines present on the 1900 map (Figure 2.5). Tranome A was located in this area (Figure 5.2).

Tranome B was positioned in the middle of the Moor in an area considered to be less uneven than Tranome A, and where tin-stream mining was still ongoing in 1900. The vegetation in Tranome B was therefore more recent than the vegetation in Tranome A. The microtopography of Tranome C was relatively homogeneous and there is no evidence of past tin-stream mining in this area. The exact positions of the Tranomes are displayed in Figure 5.2. Tranome A was 70 m x 80 m, Tranome B was 170 x 110 m and Tranome C 150 m x 40 m. Prior to spatial sampling, a detailed vegetation map of each tranome was produced in December, 1998.

Pond
Pylon
Building
Stream/drain
Pathway
Pylon cable

Tranome A

Tranome B

Tranome C

River Fal

N

0   500m
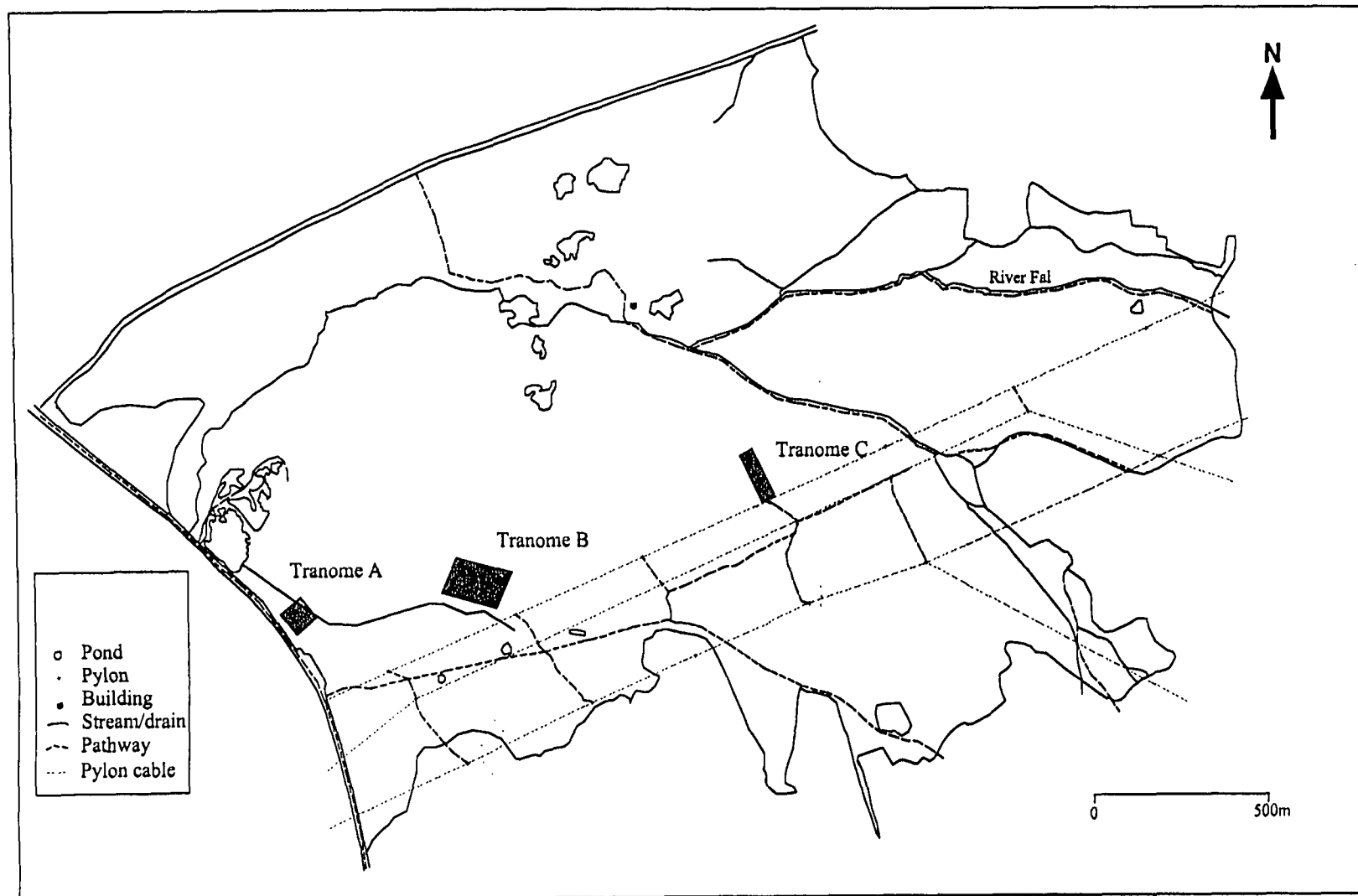
Figure 5.2 Locations of the three tranomes used for the spatial analysis of vegetation on Goss Moor.

Due to the time of year, the vegetation map was based on the presence of dominant perennials and litter.

5.2.1 SAMPLING STRATEGY

Each tranome was surveyed in summer 1999 using the lattice-wombling technique (which is visualised in Plates 5.1 and 5.2). Quadrat samples were recorded every 10 m according to grids shown in Figure 5.3. A 2 x 2 m quadrat was used to record the percentage cover of each plant species present. Individual quadrats are displayed as a small black square in the centre of each grid square on Figure 5.3. Nomenclature and methodology was as described in section 3.2.1.1. For consistent sampling, the centre of the quadrat was positioned directly upon each point on the grid.

Plate 5.1 Mosaics of tall-herb fen and willow carr within Tranome C.

Plate 5.2 Lattice-wombling in Tranome B on Goss Moor.
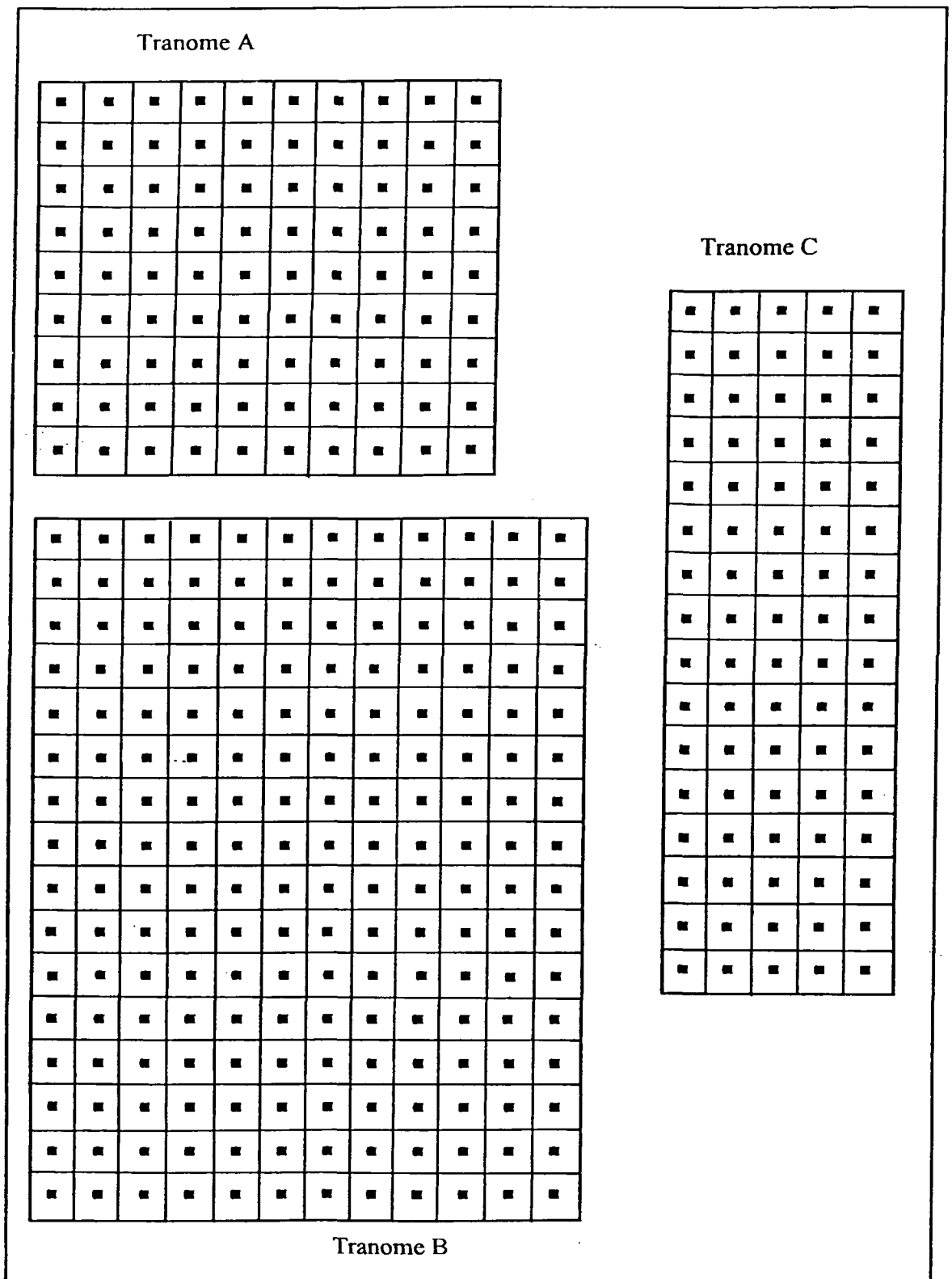
Figure 5.3 Quadrat positions (small black squares) within tranomes A, B and C, which were sampled using the lattice-wombling technique.

5.2.2 STATISTICAL ANALYSIS

The quadrat data from all three tranomes were classified using TWINSPAN (Hill, 1979a; Kent & Coker, 1992), as described in Chapter Three. The grid of ordered quadrats from each tranome was then analysed using the BoundarySeer computer package (Maruca & Jacquez, 2001). For each tranome, the 'Rate of Change Magnitudes' analysis was used to identify the rate of change occurring between each set of four quadrats that form a square, which was defined in Figure 5.1. The computer program grades each boundary within the tranome according to the rate of change in species composition. The boundaries or rates of change in each tranome are then put in descending order allowing them to be graded into one of the following five categories: the top 10 % show the greatest amount of change and are the most important boundaries; then 11-20 %; 21-40 %; 41-70 %; and the bottom 71-100 % contain boundaries of least importance. The most important or the sharpest boundaries were defined as the top 20 % and classified as ecotone boundaries. The remainder were intermediate and ecocline. A summary of the rates of change and their associated boundary types is shown in Table 5.1.

Table 5.1 The magnitude of the rates of change between four adjacent quadrats are graded according to their importance. The largest rates of change occur along the sharpest boundaries or ecotones

Rate of change	Class size	Boundary type	Amount of change
1-10 %	10	Ecotone (sharp transition)	Most change
11-20 %	10	Ecotone (sharp transition)	
21-40 %	20	Intermediate	
41-70 %	30	Ecocline (gradual transition)	
71-100 %	30	Ecocline (gradual transition)	Least change

To identify which vegetation types were associated with the ecotone, ecocline or intermediate boundary types (Table 5.1) tallies were made in each tranome. At each

boundary position the boundary type and community type of each of the four adjacent sampling points was recorded. Contingency tables were produced and the Chi-squared test (Zar, 1996) was used to identify whether associations between community type and boundary type were random or non-random, in each tranome.

Associations between vegetation types classified using TWINSPAN were analysed by recording a tally of the number of occasions a different vegetation type occurred adjacent to each patch of homogenous vegetation. These data were collected using the shaded grids in Figures 5.7-5.9. Each homogenous patch of vegetation was analysed in turn, which resulted in a folded contingency table of data. The coefficient of association (COA) was used to identify which two vegetation types occurred together most frequently.

$$COA = \frac{100 \times 2 N_t}{(N_a + N_b)}$$

Where N_t is the number of occasions in which A and B communities are found together and N_a and N_b are the total number of observations for A and B, respectively. The results range from 1 to 100, 100 indicating the strongest association.

5.3 RESULTS

5.3.1 VEGETATION DESCRIPTION

The communities identified by TWINSPAN analysis within each of the three tranomes are shown in italics in Table 5.2; those which correspond to poor-fen and willow carr communities described in Chapters Three and Four, respectively are also shown, the distribution of the communities among the three tranomes is shown in Table 5.3. It should be noted that

Table 5.2 Summary of the plant community groups identified in the three tranomes sampled in Summer, 1999 and their corresponding poor-fen and willow carr community, described in Chapters Three and Four, respectively.

Community type	Poor-fen (P-F) or willow carr (W-C)	Community description	Tranome group
pf-A	P-F	*Potentilla palustris-Menyanthes trifoliata-Juncus acutiflorus.* *Equisetum fluviatile* and *Carex nigra* constant. Devoid of *Carex rostrata* and bryophytes, except for the occasional *Calliergon* species.	*A*
pf-D	P-F	*Potentilla palustris-Valeriana officinalis-Juncus acutiflorus.* Also, bryophytes such as *Rhytidiadelphus squarrosus, Sphagnum subnitens* and *Sphagnum auriculatum* common.	*B*
pf-H	P-F	*Potentilla palustris-Aulacomnium palustre-Juncus acutiflorus* High frequencies of *Carex echinata, Menyanthes trifoliata, Eriophorum angustifolium* and bryophytes such as *Calliergon* species, *Sphagnum recurvum, Sphagnum subnitens* and *Sphagnum fimbriatum*	*C*
wc-Q	W-C	*Salix cinerea-Equisetum fluviatile-***bare substrate.** Also high frequency of *Potentilla palustris* and *Galium palustre. Valeriana officinalis* and *Juncus acutiflorus* prominent	*D*
wc-P	W-C	*Salix cinerea-Juncus effusus-* **bare substrate.** Also high cover of *Potentilla palustris, Equisetum fluviatile* and *Galium palustre.* Fewer poor-fen species than D	*E*
		Molinia caerulea- Potentilla erecta- Valeriana officinalis	*F*
		Ulex gallii-Rubus fruticosus-Molinia caerulea	*G*
pf-B	P-F	*Potentilla palustris- Equisetum fluviatile- Menyanthes trifoliata.* Also high cover of the common poor-fen species, including: *Carex nigra, Juncus acutiflorus, Mentha aquatica, Lychnis flos-cuculi* and *Lotus pedunculatus.* High frequencies of *Eriophorum angustifolium, Carex echinata* and *Calliergon* species. In Tranome C, this community was dominated by *Menyanthes trifoliata* and *Carex rostrata.*	*H*
pf-C	P-F	*Equisetum fluviatile- Juncus acutiflorus- Potentilla palustris.* Contained large amounts of the common poor-fen species, as in Group H. However, *Molinia caerulea* and *Potentilla erecta* were common. Devoid of *Eriophorum angustifolium, Carex echinata, Menyanthes trifoliata* and *Calliergon* species.	*I*
		Molinia caerulea- Aulacomnium palustre-Sphagnum capillifolium.. Vegetation raised above the water table on floating rafts. Also high frequency of common poor-fen species, as in H.	*J*
		Molinia caerulea-Calluna vulgaris-Drosera rotundifolius. This community was raised above the water table on floating rafts	*K*
		Molinia caerulea. Species-poor containing *Ulex gallii* and *Juncus effusus*	*L*
wc-S	W-C	*Salix cinerea- Equisetum fluviatile- Juncus acutiflorus*	*M*
pf-A	P-F	*Potentilla palustris-Equisetum fluviatile-Carex rostrata.* Unlike the other groups, this group contained small patches of *Calliergon* bryophytes growing on the fen surface, amongst the litter.	*N*
pf-D	P-F	*Valeriana officinalis- Potentilla palustris-Mentha aquatica.* This community is devoid of *Carex rostrata*	*O*
wc-R	W-C	*Salix cinerea- Potentilla palustris-Equisetum fluviatile.* Bare substrate and *Menyanthes trifoliata* were also prominent in this group	*P*
		Salix cinerea- Rubus fruticosus-Dryopteris dilatata Found on a raised gravel bank within the willow carr	*Q*

Tranome	Group	Community description	Number of quadrats
Table 5.3 Summary of the plant community groups identified in the three tranomes sampled in summer, 1999.			
A	*A*	*Potentilla palustris-Menyanthes trifoliata-Juncus acutiflorus*	20
	B	*Potentilla palustris-Valeriana officinalis-Juncus acutiflorus*	20
	C	*Potentilla palustris-Aulacomnium palustre-Juncus acutiflorus*	7
	D	*Salix cinerea-Equisetum fluviatile*-bare substrate	9
	E	*Salix cinerea-Juncus effusus*- bare substrate	12
	F	*Molinia caerulea- Potentilla erecta- Valeriana officinalis*	10
	G	*Ulex gallii-Rubus fruticosus-Molinia caerulea*	12
B	*C*	*Potentilla palustris- Aulacomnium palustre-Juncus acutiflorus*	25
	G	*Ulex gallii-Rubus fruticosus -Molinia caerulea*	18
	H	*Potentilla palustris- Equisetum fluviatile- Menyanthes trifoliata*	55
	I	*Equisetum fluviatile- Juncus acutiflorus- Potentilla palustris*	42
	J	*Molinia caerulea- Aulacomnium palustre-Sphagnum capillifolium*	16
	K	*Molinia caerulea-Calluna vulgaris-Drosera rotundifolius*	8
	L	*Molinia caerulea*	21
	M	*Salix cinerea- Equisetum fluviatile- Juncus acutiflorus*	7
C	*H*	*Potentilla palustris-Equisetum fluviatile- Menyanthes trifoliata*	18
	N	*Potentilla palustris-Equisetum fluviatile-Carex rostrata*	15
	O	*Valeriana officinalis- Potentilla palustris-Mentha aquatica*	10
	P	*Salix cinerea- Potentilla palustris-Equisetum fluviatile*	36
	Q	*Salix cinerea- Rubus fruticosus-Dryopteris dilatata*	1

although the vegetation of the three tranomes was shown to be distinctive, Groups *C* and *G* were found in Tranomes A and B and Group *H* was found in Tranome B and C.

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Tranome A contained seven communities. These included three *Potentilla palustris* poor-fen communities in groups *A* to *C*, two *Salix cinerea* carr communities (*D* and *E*), Group *F* a *Molinia caerulea* and *Valeriana officinalis* community and Group *G* the *Ulex gallii-Rubus fruticosus* community that grows on the dry gravel banks throughout the tranome.

Eight communities were found in Tranome B: Groups *C*, *H* and *I* were dominated by *Potentilla palustris*; *Molinia caerulea* was prominent in groups *J*, *K* and *L*; and Group *M*, the *Salix cinerea* carr community, contained an understorey of *Equisetum fluviatile*, *Juncus acutiflorus* and *Hydrocotyle vulgaris*. As in Tranome A, Group *G* represented a dry bank community dominated by *Ulex gallii* and *Rubus fruticosus*.

Tranome C was divided into five communities. Groups *H*, *N* and *O* were dominated by *Potentilla palustris*, *Equisetum fluviatile*, *Galium palustre* and *Mentha aquatica*. The willow carr (Group *P*) was a homogeneous *Salix cinerea-Potentilla palustris-Equisetum fluviatile* community. Group *Q* the *Salix cinerea- Rubus fruticosus-Dryopteris dilatata* vegetation type, was found on a gravel bank within the willow carr and was only recorded in one quadrat.

5.3.2 VEGETATION DISTRIBUTION WITHIN THE TRANOMES

Figures 5.4 to 5.6 show the maps produced by the initial reconnaissance survey of the three tranomes that took place in December 1998. Each of the tranome maps are overlaid by the distribution of the vegetation types identified by TWINSPAN. Larger grid squares are used to represent the vegetation types which were sampled in the centre of each square (Figure 5.3). For further definition, Figures 5.7 to 5.9 show the distribution of the TWINSPAN vegetation types as shaded grids within each tranome. The reconnaissance maps of the tranomes show considerable resemblance to the wombling vegetation distribution data.
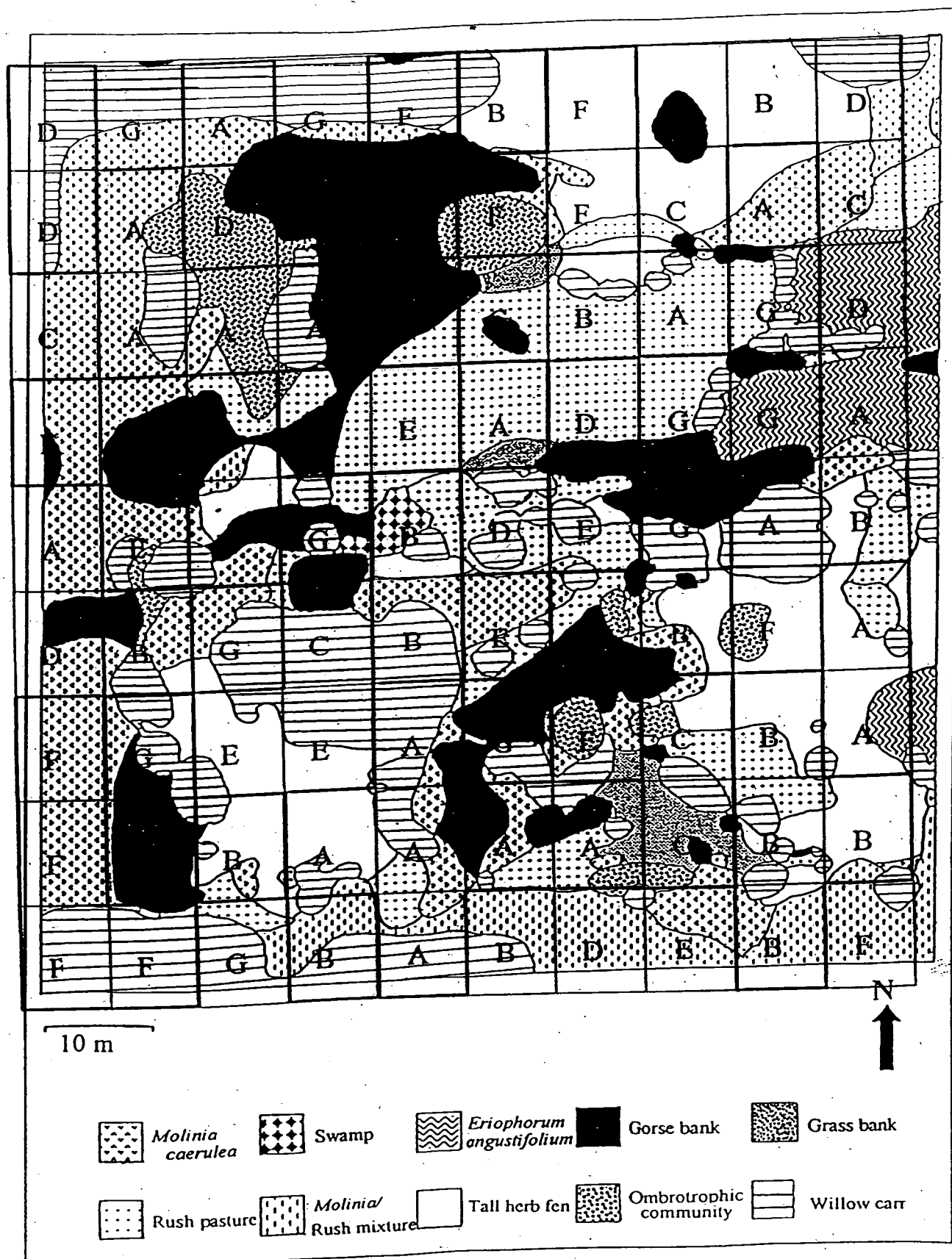
Figure 5.4 Map of the vegetation distributions recorded during the reconnaissance survey of Tranome A in December 1998. Overlaid is the distribution of the community types (*A* to *G*) identified by TWINSPAN (Table 5.2), from quadrat positions collected for the lattice-wombling analysis. Thicker lines on the grid outline homogenous patches.
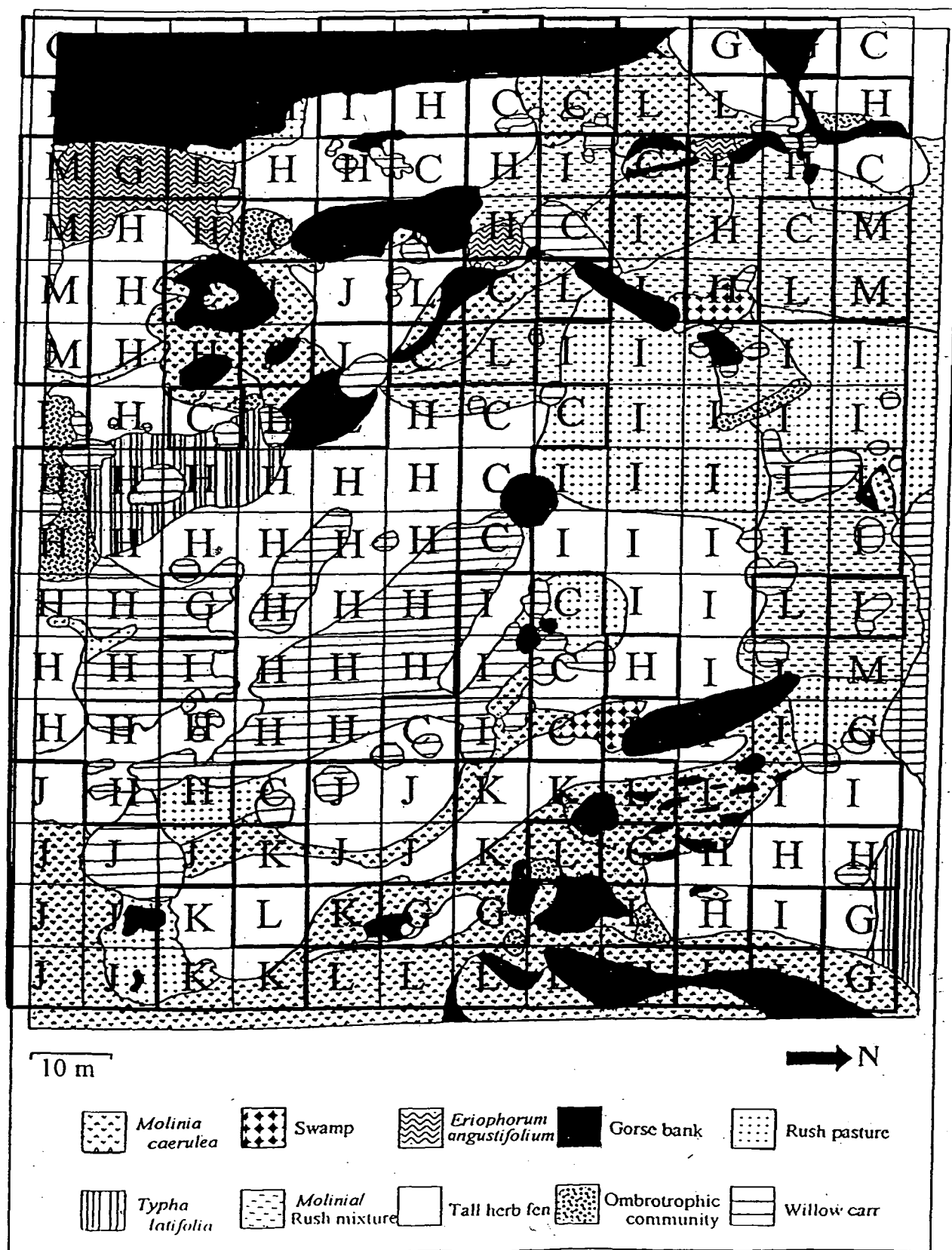
Figure 5.5 Map of the vegetation distributions recorded during the reconnaissance survey of Tranome B in December 1998. Overlaid is the distribution of the community types (*C* and *G* to *M*) identified by TWINSPAN (Table 5.2), from quadrat positions collected for the lattice-wombling analysis. Thicker lines on the grid outline homogenous patches.
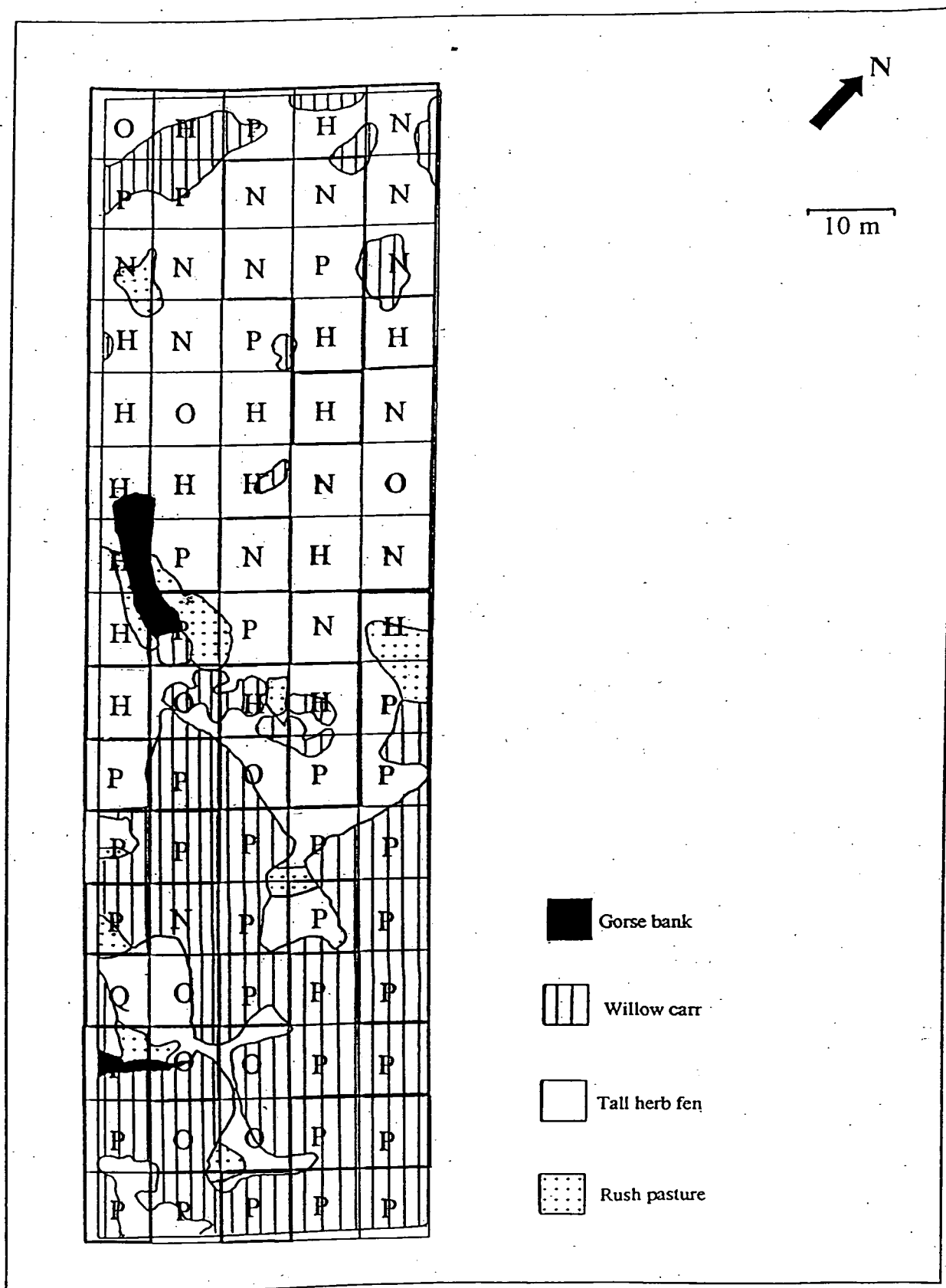
Figure 5.6 Map of the vegetation distributions recorded during the reconnaissance survey of Tranome C in December 1998. Overlaid is the distribution of the community types (*H* and *N* to *Q*) identified by TWINSPAN (Table 5.2), from quadrat positions collected for the lattice-wombling analysis. Thicker lines on the grid outline homogenous patches.
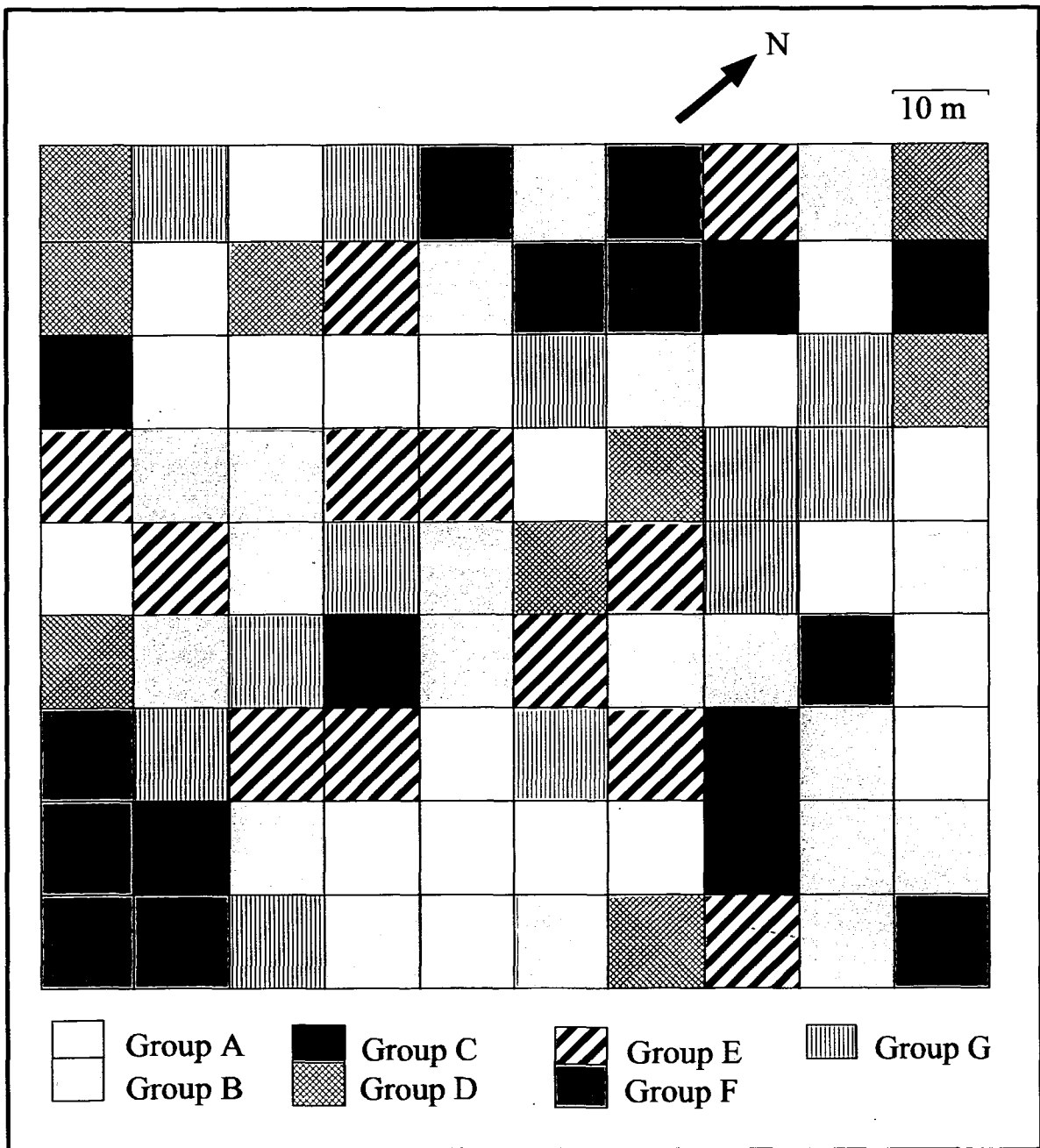
Figure 5.7 Distribution of community types (*A* to *G*) identified by TWINSPAN for Tranome A (Table 5.2), which correspond to quadrats sampled using the lattice-wombling technique.
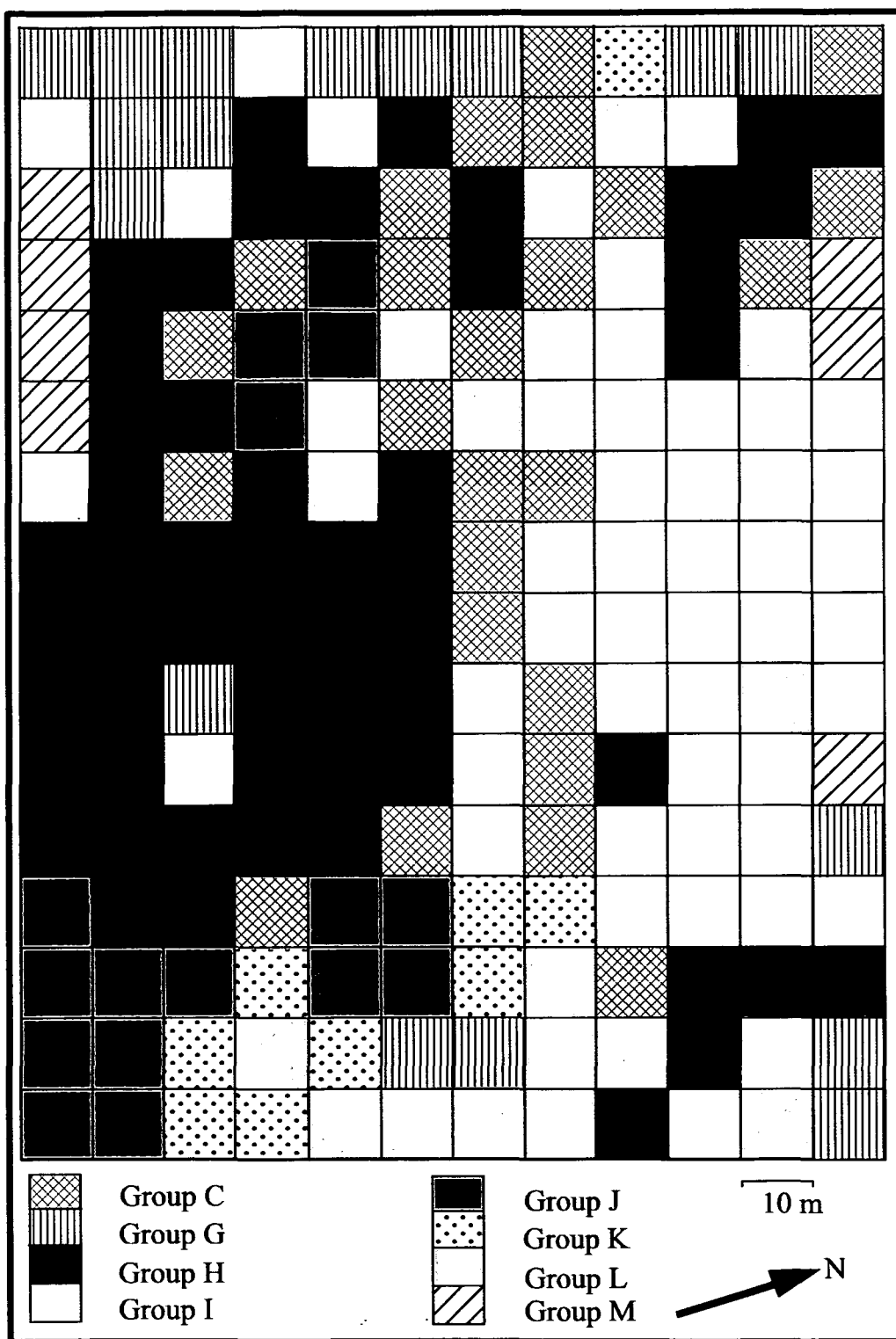
Figure 5.8 Distribution of community types (*C* and *G* to *M*) identified by TWINSPAN for Tranome B (Table 5.2), which correspond to quadrats sampled using the lattice-wombling technique.
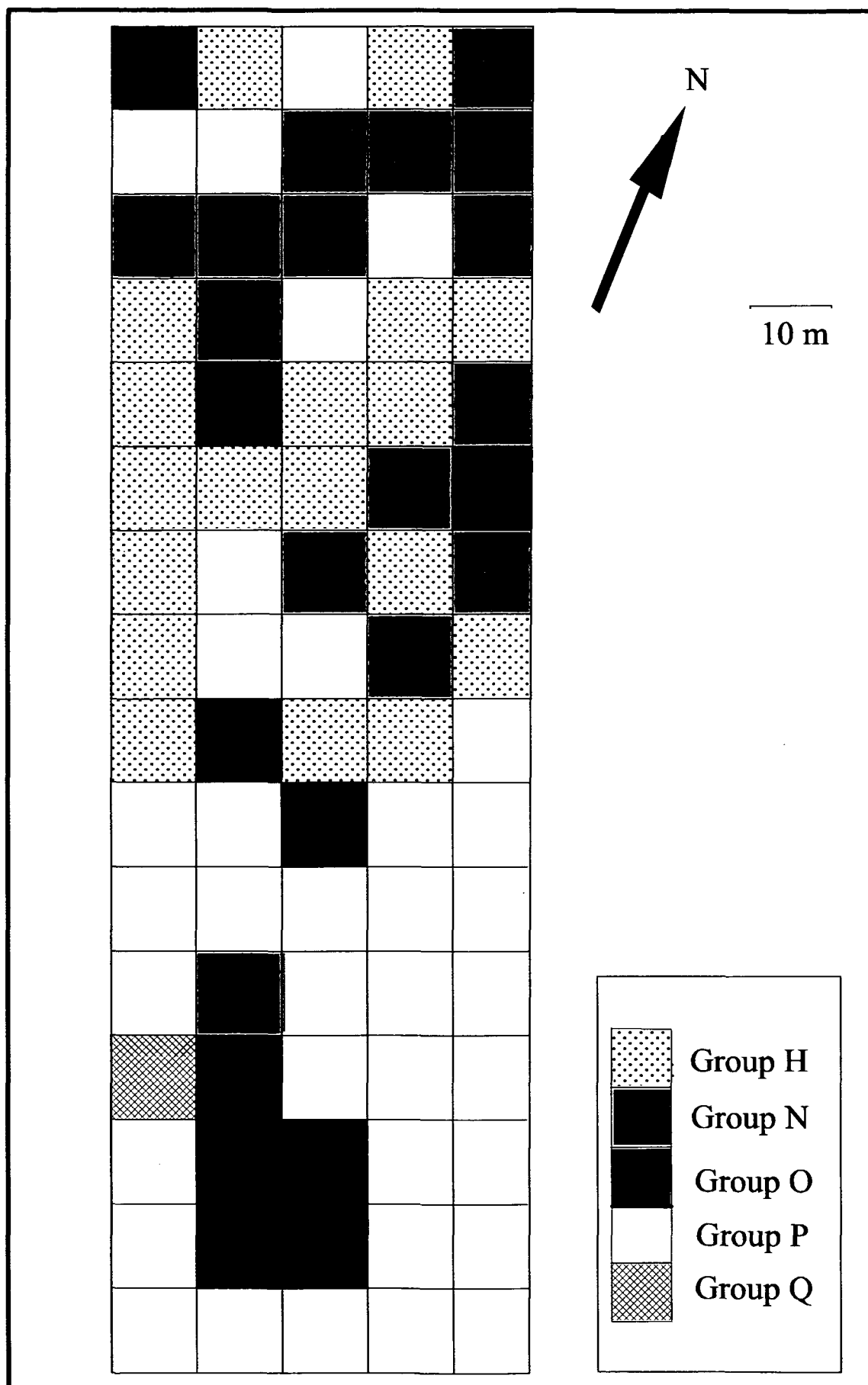
Figure 5.9 Distribution of community types (*H* and *N* to *Q*) identified by TWINSPAN for Tranome C (Table 5.2), which correspond to quadrats sampled using the lattice-wombling technique.

However, there are some important differences. Due to the timing of the initial survey, the proportions of vegetation types dominated by perennials such as *Molinia caerulea* and *Juncus* spp. were over-estimated. In winter, large areas of vegetation dominated by either of these two species appear homogeneous and thus provide a coarser assessment of the vegetation. When these areas were re-examined in the following summer, it revealed that the *Molinia caerulea* and *Juncus* spp. were interspersed as mosaics within poor-fen.

The main inconsistencies between the two mapping techniques were more pronounced in Tranome A, which contained the most heterogeneous vegetation and mosaicing. Many of the patches of vegetation in this tranome were smaller than 10 m^2, which meant that whole patches of vegetation were often missed when using the wombling sampling technique at 10 m intervals. All of the grass banks and some of the ombrotrophic communities identified by the reconnaissance survey were missed by the wombling sampling technique.

5.3.3 BOUNDARYSEER ANALYSIS OF THE THREE TRANOMES

The BoundarySeer analyses of tranomes A, B and C are displayed in Figures 5.10, 5.11 and 5.12, respectively. These figures clearly display the vegetation types and their associated boundary type which correspond to the rate of change categories described in Table 5.1. Ecotones, or boundaries with rates of change of 20 % or greater, were associated with three or four vegetation types.

D	G	A	G	F	B	F	E	B	D
D	A	D	E	B	F	F	C	A	C
C	A	A	A	A	G	B	A	G	D
E	B	B	E	E	A	D	G	G	A
A	E	B	G	B	D	E	G	A	B
D	B	G	C	B	E	B	B	F	A
F	G	E	E	A	G	E	C	B	A
F	C	B	A	A	A	A	C	B	B
F	F	G	B	A	B	D	E	B	F

+ The greatest 10%
+ Between 11 and 20%
+ Between 21 and 40%
+ Between 41 and 70%
Between 71 and 100%
Group A
Group B
Group C
Group D
Group E
Group F
Group G
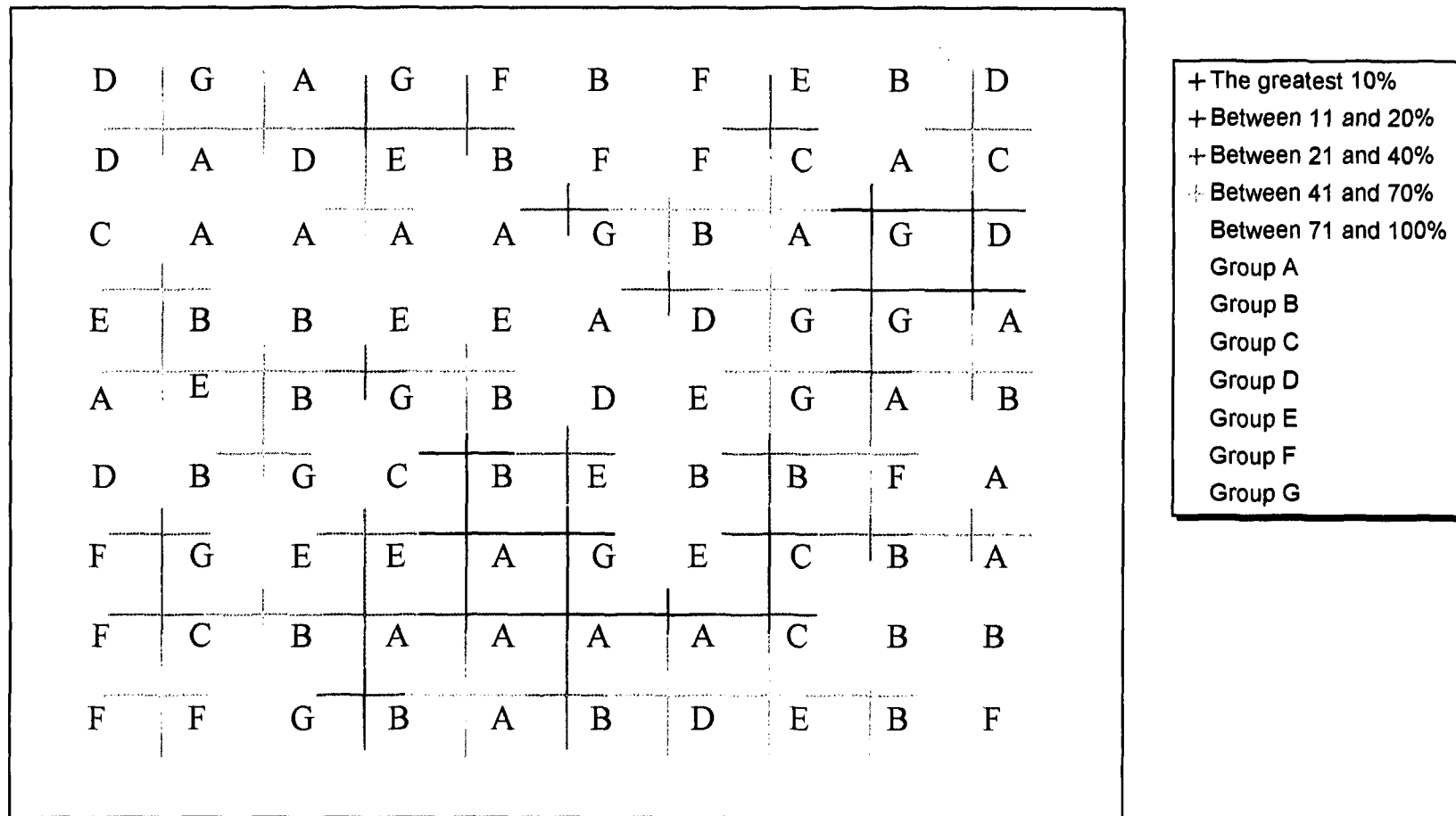
Figure 5.10 Distributions of the seven community types (*A* to *G*) identified by TWINSPAN for Tranome A (Table 5.2), and their associated boundary types. Boundary classifications are based on the Rate of Change Magnitudes. The greatest 10 % Rate of Change show the largest difference between quadrats.

G	G	G	L	G	G	G	C	K	G	G	C
L	G	G	H	I	H	C	C	L	L	H	H
M	G	L	H	H	C	H	I	C	H	H	C
M	H	H	C	J	C	H	C	I	H	C	M
M	H	C	J	J	L	C	L	I	H	L	M
M	H	H	J	I	C	L	I	I	I	I	I
I	H	C	H	L	H	C	C	I	I	I	I
H	H	H	H	H	H	C	I	I	I	I	I
H	H	H	H	H	H	C	I	I	I	I	I
H	H	G	H	H	H	I	C	I	I	L	I
H	H	I	H	H	H	I	C	H	I	I	M
H	H	H	H	H	C	I	C	I	I	I	G
J	H	H	C	J	J	K	K	L	I	I	I
J	J	J	K	J	J	K	L	C	H	H	H
J	J	K	L	K	G	G	L	L	H	I	G
J	J	K	K	L	L	L	L	H	I	L	G

Group G	+ The greatest 10%
Group H	+ Between 11 and 20%
Group I	+ Between 21 and 40%
Group C	··· Between 41 and 70%
Group J	Between 71 and 100%
Group K	Group L
Group M	

Figure 5.11 Distributions of the eight community types (*C* and *G* to *M*) identified by TWINSPAN for Tranome B (Table 5.2), and their associated boundary types. Boundary classifications are based on the Rate of Change Magnitudes. The greatest 10 % Rate of Change show the largest difference between quadrats.

N	N	N	H	N	O	N	H	P	P	P	P	P	P	P	P
H	N	P	H	H	N	H	N	H	P	P	P	P	P	P	P
P	N	N	P	H	H	N	P	H	O	P	P	P	O	O	P
H	P	N	N	O	H	P	P	O	P	P	N	O	O	O	P
O	P	N	H	H	H	H	H	H	P	P	P	Q	P	P	P

+ The greatest 10 %
+ Between 11 and 20%
+ Between 21 and 40%
-+ Between 41 and 70%
  Between 71 and 100%
  Group H
  Group N
  Group O
  Group P
  Group Q

Figure 5.12 Distributions of the five community types (H and N to Q) identified by TWINSPAN for Tranome C (Table 5.2), and their associated boundary types. Boundary classifications are based on the Rate of Change Magnitudes. The greatest 10 % Rate of Change show the largest difference between quadrats.

The folded contingency tables derived from the vegetation associations for Tranomes A, B

and C are displayed in Tables 5.4, 5.5 and 5.6, respectively. These tables also display the

COAs found between each vegetation community type.

Table 5.4 Folded contingency tables of the seven vegetation types and their associated boundary type in Tranome A. The left-hand, unshaded side of the table represents the number of times that any two communities were adjacent. The shaded, grey side of the table shows the coefficient of association for any two communities.

Community type→
↓

	A	B	C	D	E	F	G
A		27.6	12.4	22.9	25.7	7.3	14.9
B	18		18.3	11.6	24.3	19.7	23.0
C	6	9		9.1	14.5	14.7	12.0
D	10	6	4		12.4	4.4	18.6
E	13	16	7	6		5.7	17.1
F	2	11	7	2	3		14.6
G	12	14	6	9	9	5	

Community type→
↓

	C	G	H	I	J	K	L	M
C		5.3	33.9	21.8	16.9	10.4	16.2	3.8
G	4		17.6	10.4	4.7	9.3	22.9	9.3
H	23	17		29.4	13.7	1.5	19.2	7.9
I	16	7	22		5.1	2.8	22.0	9.3
J	12	2	9	4		13.6	7.6	0
K	6	3	1	2	7		15.6	0
L	13	13	14	11	4	8		7.1
M	2	3	5	3	0	0	4	

Table 5.6 Two folded contingency tables of the five vegetation types and their associated boundary type in Tranome C. The left-hand, unshaded side of the table represents the number of times that any two communities were adjacent. The shaded, grey side of the table shows the coefficient of association for any two communities.

Community type→
↓

	H	N	O	P	Q
H		51.2	24.7	36.4	0
N	15		10.4	36.4	4.9
O	5	2		40.5	8.7
P	15	15	23		5.5
Q	0	1	1	1	

The boundary types associated with the different vegetation communities and their associated vegetation communities have been amalgamated for each of the three tranomes and are addressed individually in the following sections.

5.3.3.1 Vegetation and boundary analysis of Tranome A

The Chi-squared analysis (Zar, 1996) of the vegetation and boundary matrix of Tranome A (Figure 5.13) showed that the distribution of the vegetation types between the three boundary types was random. However, the observed associations of Groups A and G with ecotone were considerably greater than the expected values, because the gorse communities in Group G grow on the dry free-draining gravel banks between the low-lying wet areas holding poor-fen (Group A).
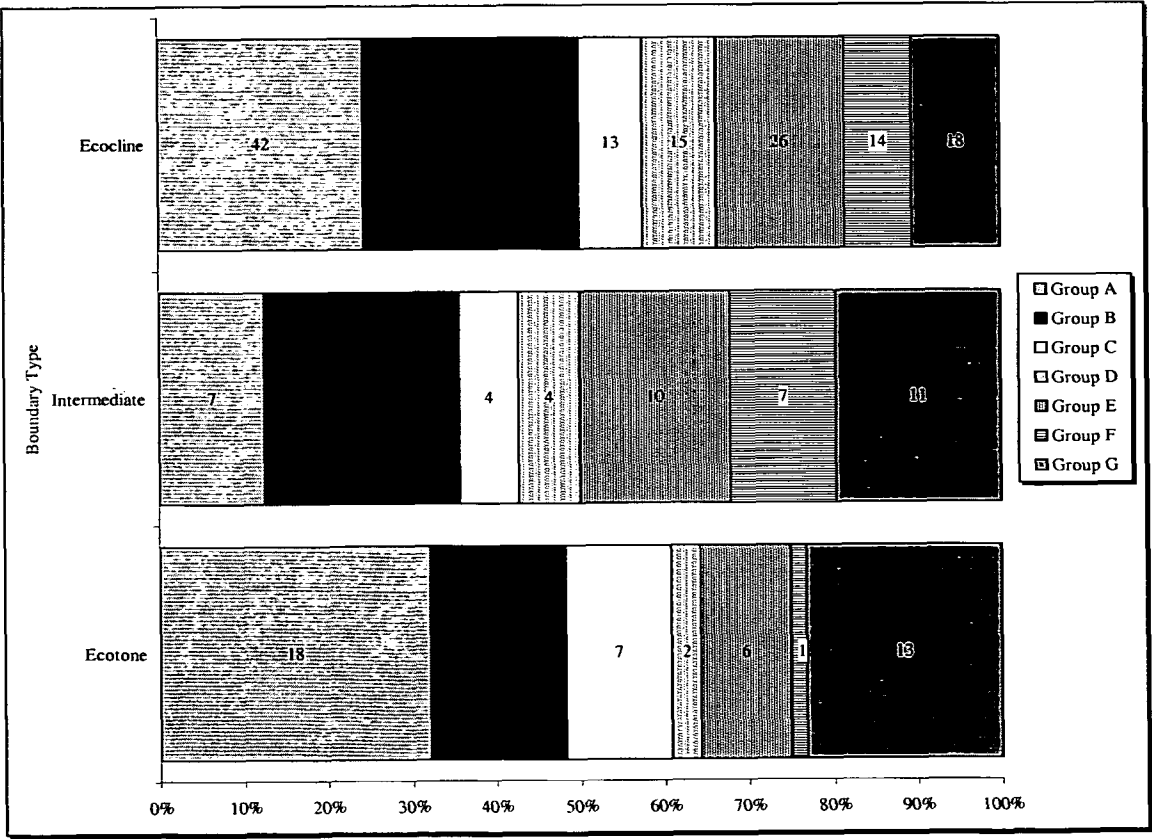
Figure 5.13 Mosaic display (Zar, 1996) for the contingency table of the seven vegetation types A to G and their associated boundary type in Tranome A. $\chi^2 = 19.764$; $\chi^2_{0.05, 12} = 21.026$
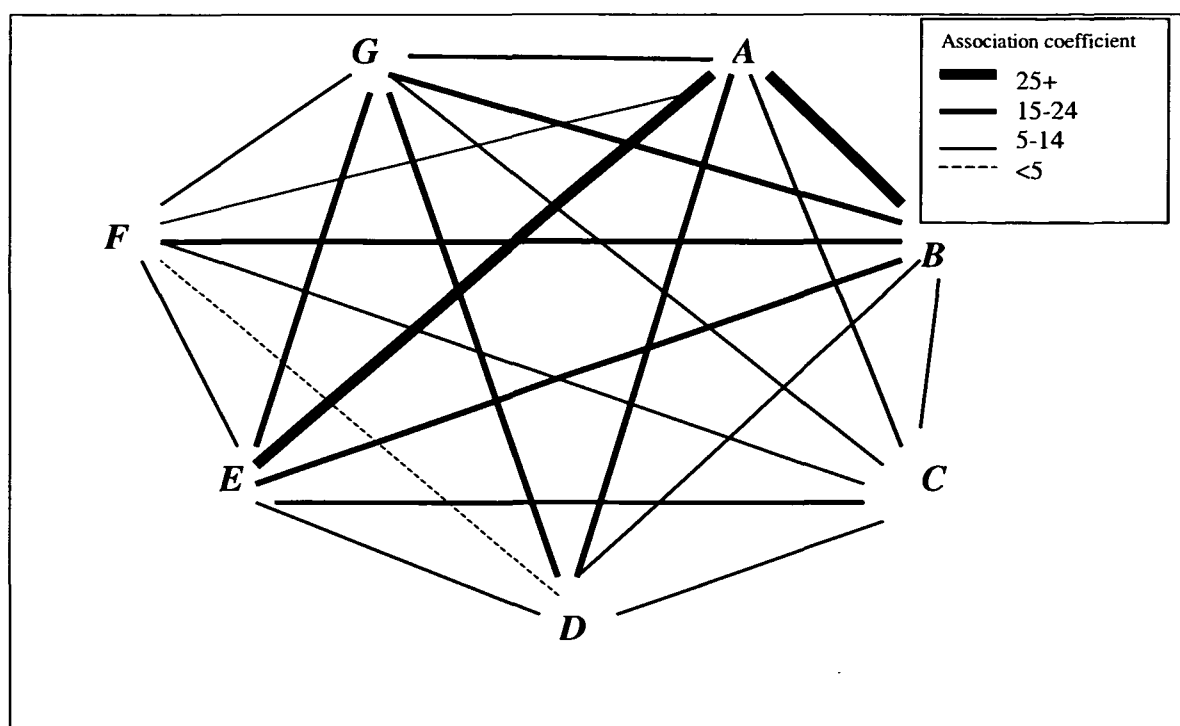
Figure 5.14 Vector diagram showing the relationships between vegetation types *A* to *G* in Tranome A. The thickest lines represent the largest COA and strongest associations.

The COA (Figure 5.14) showed that Group *A*, the *Potentilla palustris–Menyanthes trifoliata* swamp community was associated with Groups *B* and *E*, the tall-herb fen and willow carr community, respectively. Groups *A* and *B* were also greatly associated with ecocline boundaries, which might be expected between two similar swamp and poor-fen communities. Groups *B* and *E* were also associated with each other. Group *C*, which is thought in successional terms to be an intermediate between Groups *A* and *B*, and *D* and *E*, was only weakly associated with all vegetation types.

5.3.3.2 Vegetation and boundary analysis of Tranome B

In the Chi-squared analysis (Zar, 1996) of Tranome B the null hypothesis was rejected (P<0.05) showing the relationship between community and boundary type was not random (Figure 5.15). The *Equisetum fluviatile-Juncus acutiflorus-Potentilla palustris* community of Group *I* was associated with ecotone, as was Group *G*, again. Group *H* the *Potentilla palustris-Equisetum fluviatile-Menyanthes trifoliata* community was associated with ecocline boundary types.

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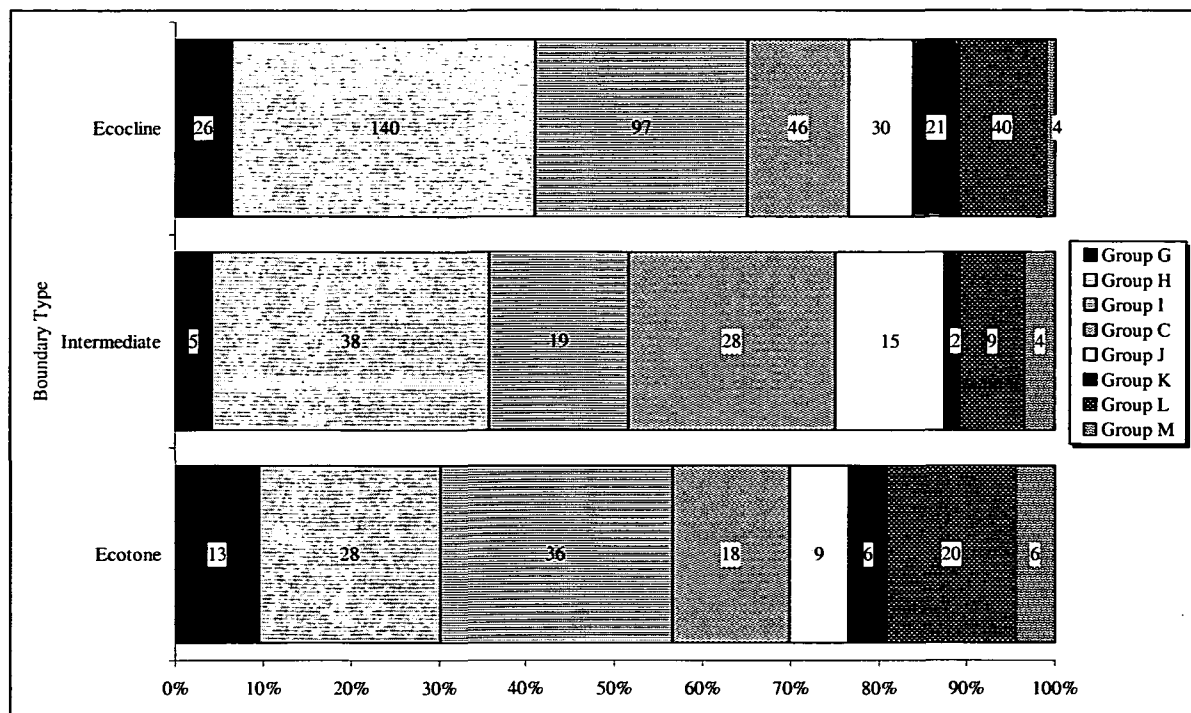
Figure 5.15 Mosaic display (Zar, 1996) for the contingency table of the eight vegetation types C, G to M and their associated boundary type in Tranome B. $\chi^2 = 38.579$; $\chi^2_{0.05, 14} = 23.685$

The COA (Figure 5.16) revealed that Group H was strongly associated with Group C, the bryophyte-rich poor-fen community, which was surrounded by intermediate boundary types in general. This spatial relationship may be evidence for the successional process of terrestrialisation. However, the willow group, M (the next seral stage) was not associated with Group C.
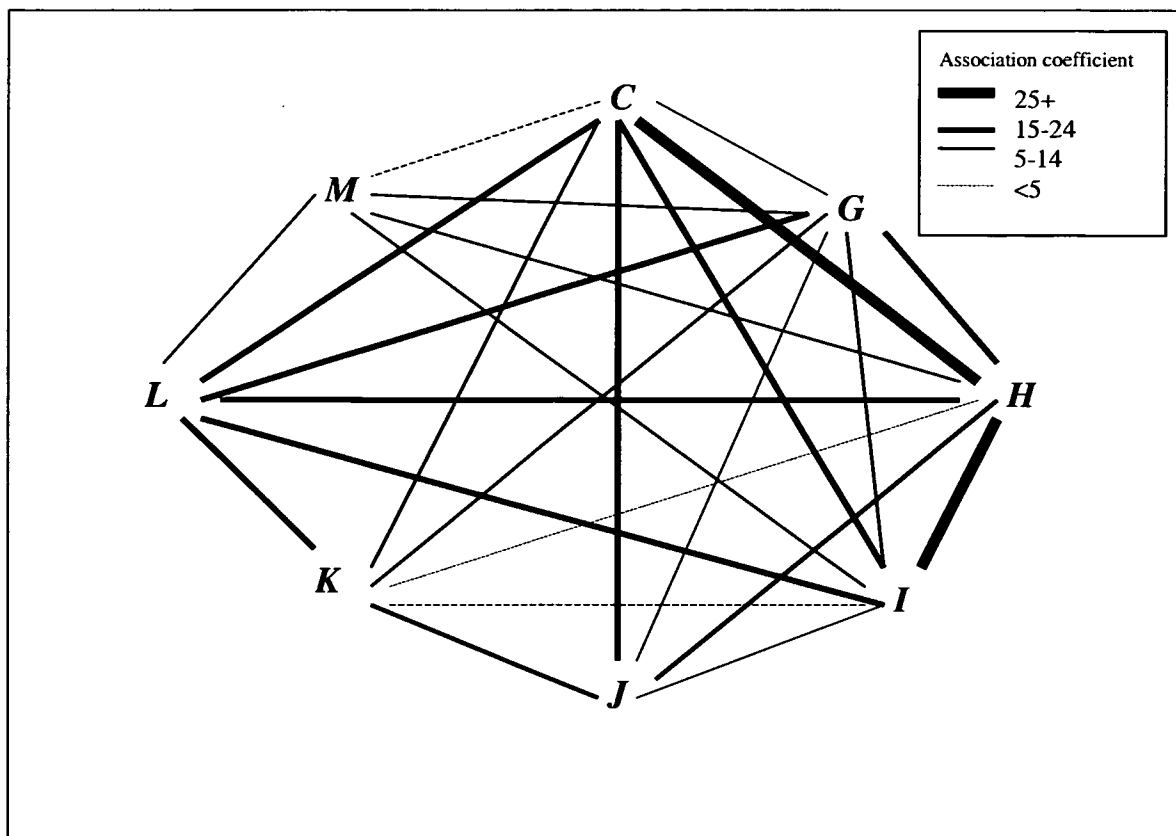
Figure 5.16 Vector diagram showing the relationships between vegetation types *C* and *G* to *M* in Tranome B. The thickest lines represent the largest COA and strongest associations.

Group *M* was most greatly associated with Group *I* and was never found with Groups *J* and *K*, the *Molinia caerulea* communities.

5.3.3.3. Vegetation and boundary analysis of Tranome C.

The Chi-squared analysis (Zar, 1996) of the boundary and vegetation data in Tranome C also showed that different communities were associated with different boundary types (P<0.05) (Figure 5.17).
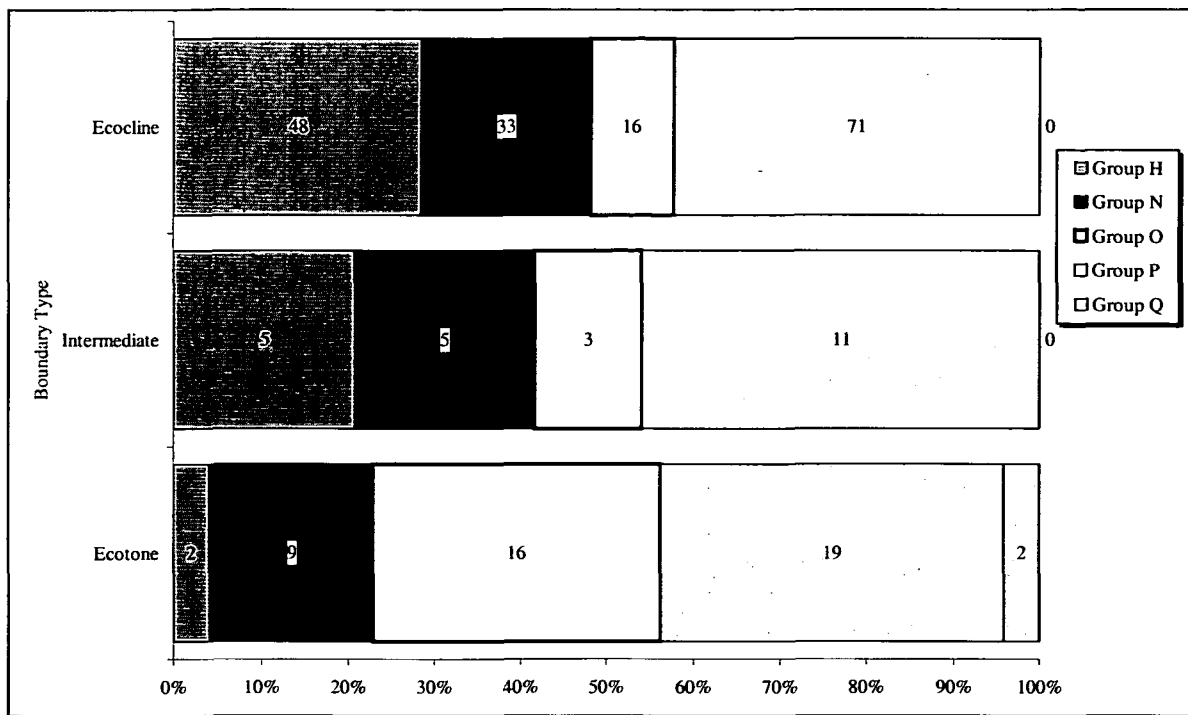
Figure 5.17 Mosaic display (Zar, 1996) for the contingency table of the five vegetation types and their associated boundary type in Tranome C. As n<5 for Group Q only groups H, N, O and P were used for the Chi-squared analysis $\chi^2 = 24.531$; $\chi^2_{0.05,6} = 12.592$.

Groups O and Q were positively associated with ecotones. It was expected that the infrequent *Salix cinerea-Rubus fruticosus* vegetation assemblage of Group Q would have an abrupt boundary. This vegetation was growing on a mound surrounded by inundated vegetation.

The *Valeriana officinalis-Potentilla palustris* vegetation in Group O was associated with Group P the *Salix cinerea* community. Even though the boundary between these vegetation types was usually sharp, the juxtaposition of these communities may represent the hydroseral succession spatially.

Group H, which was associated with the ecocline boundary type was also greatly associated (COA=51.2) with Group N, (Figure 5.18) a similar community to Group H, but

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less swamp-like. Group *N* contained patches of *Calliergon* spp. mosses and was devoid of species such as *Menyanthes trifoliata*. These mosaics of vegetation with subtle differences in their composition growing in juxtaposition may be indicative of spatial succession.
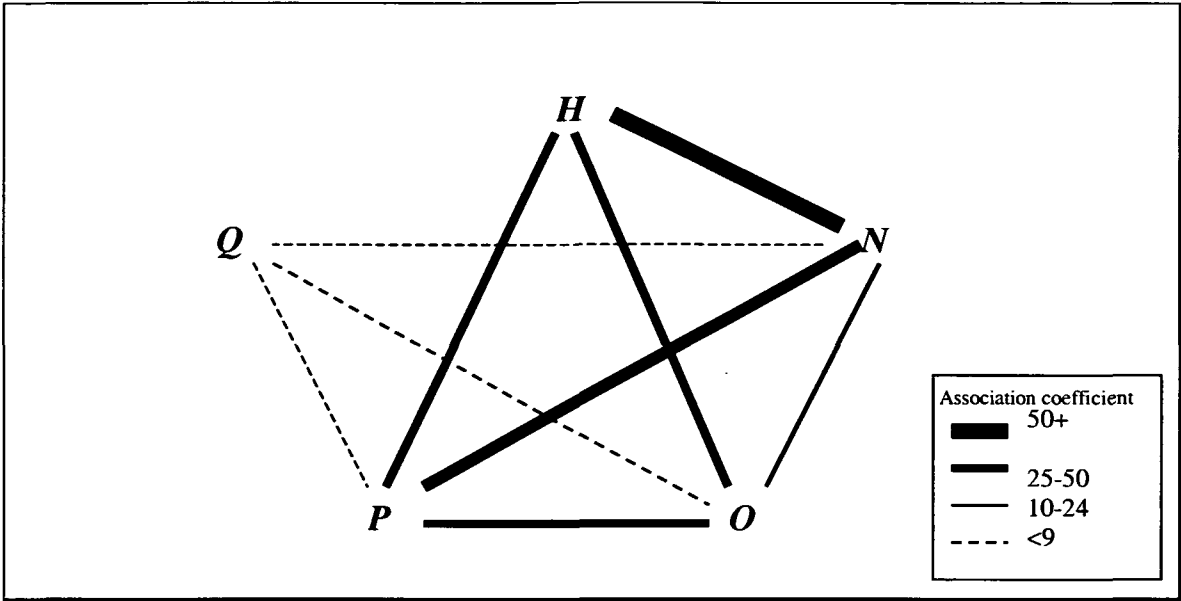
Figure 5.18 Vector diagram showing the relationships between vegetation types *H and N* to *Q* in Tranome C. The thickest lines represent the largest COA and strongest associations.

5.4 DISCUSSION

The main objective of this chapter was to investigate the nature of vegetation mosaics and their boundaries within the three tranome study areas, and to identify possible successional patterns. For consistent comparisons, the classifications of the wetland communities made in this chapter need to be referred back to those identified in Chapters Three and Four. To simplify these classifications Table 5.7 provides a summary of the main findings of this chapter according to the original classification. All vegetation descriptions in this discussion relate to the terminology derived in Chapters Three and Four.

Tranome	Communities associated with ecotone (sharp transitions)	Communities associated with ecocline (gradual transitions)	Community associations
A	Group pf-A *Potentilla palustris–Menyanthes trifoliata* swamp community and the gorse community were greatly associated with ecotone.	Groups pf-A the *Potentilla palustris–Menyanthes trifoliata* swamp community and pf-D the *Valeriana officinalis-Potentilla palustris* poor-fen community	Group pf-A the *Potentilla palustris–Menyanthes trifoliata* swamp community was associated with, the tall-herb fen of Groups pf-D and willow carr community (Group wc-P). Groups pf-D and wc-P were also associated with each other.
B	The *Equisetum fluviatile-Juncus acutiflorus-Potentilla palustris* community of Group pf-C was associated with ecotone, the gorse/heath community, again.	Group pf-B the *Potentilla palustris-Equisetum fluviatile-Menyanthes trifoliata* community	Willow Group wc-S was most greatly associated with poor-fen Group pf-C and was never found with *Molinia caerulea* communities.
C	Group pf-D the *Valeriana officinalis-Potentilla palustris* poor-fen community and the infrequent *Salix cinerea-Rubus fruticosus* were associated with ecotone.	Group pf-B the *Potentilla palustris-Equisetum fluviatile-Menyanthes trifoliata* community.	Poor-fen Group pf-B was greatly associated with Group pf-A, which was floristically similar, but less swamp-like. . The *Valeriana officinalis-Potentilla palustris* vegetation in Group pf-D was associated with Group wc-R the *Salix cinerea* willow community.

Table 5.7 Summary of the boundary analysis findings using the poor-fen and willow carr community terminology established in Chapters Three and Four.

5.4.1 VEGETATION DISTRIBUTION AND BOUNDARY ANALYSIS

Some of the plant communities in tranomes B and C were found to be associated with particular boundaries types. Ecotones or sharp transitions were associated with the heathland, gorse community, and the infrequent *Salix cinerea-Rubus fruticosus* vegetation assemblage. These communities were expected to have abrupt boundaries, as they inhabit dry mounds surrounded by water inundated vegetation. Both have little in common, in terms of vegetation composition, with wetland communities. The dry mounds that these vegetation communities inhabit are undoubtedly relics of the tin-stream mining activities

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that ceased over a century ago. Ecotones between 'wet' and 'dry' communities are therefore attributed to historic land-use and are anthropogenic.

The wetland communities associated with ecotones were the *Equisetum fluviatile-Juncus acutiflorus-Potentilla palustris* poor-fen community (Group pf-C) from Tranome B, and Group wc-R of Tranome C, the *Salix cinerea* willow carr community. The latter was often adjacent to the *Valeriana officinalis-Potentilla palustris* tall-herb fen vegetation (Group pf-D). The vegetation composition of Groups wc-R and pf-D differed greatly and ecotone boundaries were anticipated: the tall-herb fen was densely vegetated and species-rich, and the willow carr overshadowed a swamp understorey of sparsely vegetated *Potentilla palustris*, *Equisetum fluviatile* and *Menyanthes trifoliata*. The ecotones between these wetland communities were not thought to be anthropogenic in origin.

As expected, ecocline boundaries were found between superficially similar plant communities. In Tranomes B and C, the *Potentilla palustris-Equisetum fluviatile-Menyanthes trifoliata* community (Group pf-B) was associated with ecocline. In Tranome B, Group pf-B was greatly associated with Group pf-H, the *Potentilla palustris-Aulacomnium palustre* poor-fen community. Groups pf-B and pf-H were very similar in composition, besides considerable amounts of cushion-forming bryophytes, in the latter indicating ombrotrophic conditions. In Tranome C, Group pf-B was greatly associated with Group pf-A, which was similar phytosociologically. However the vegetation of Group pf-A was better developed, with patches of *Calliergon* spp. mosses and lacked swamp species such as *Menyanthes trifoliata*.

The logical associations found between vegetation types and their boundaries in Tranomes B and C show that the lattice-wombling analysis using Boundaryseer (Maruca & Jacquez, 2001) was an effective means to identify boundaries. Unfortunately, the data collection

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procedure in the field was very rigorous and systematic and demanding to apply, especially in the wet and densely vegetated terrain of Goss Moor. The maps produced by the reconnaissance method were easier and effective in showing the most important community boundaries. However, gradual boundaries were more difficult to identify using the reconnaissance method and the results were purely descriptive. For this reason, the more rigorous statistically based lattice-wombling technique is recommended for spatial analysis of plant community mosaics.

There were no significant relationships between vegetation types and boundary class in Tranome A, although in reality such relationships probably do exist. Compared with the other tranomes, Tranome A was most heterogeneous and many of the vegetation patches were smaller than 10 m². The strategy of sampling tranomes using a regular 10 m grid was therefore unsuitable. This exposes a common problem when using spatial analysis techniques, namely the scale of sampling required to obtain reliable results (Dale, 1999). Thus, vegetation occurring in patches of 10 m² and smaller should be sampled at 5 m intervals by the lattice-wombling method. Alternatively, the triangulation-wombling method could be adopted, which enables irregularly spaced samples to be collected from vegetation mosaics of interest (Fortin, 1994).

5.4.2 SUCCESSIONAL PATTERNS

If the space-for-time or ergodic hypothesis is to be accepted for the communities on Goss Moor evidence can be sought using the patterns of poor-fen succession and increased terrestrialisation proposed in Chapter Three. The patterns hypothesised for each tranome are given in Figure 5.11, using the poor-fen and willow carr community descriptions given in Table 5.2 and 5.7.
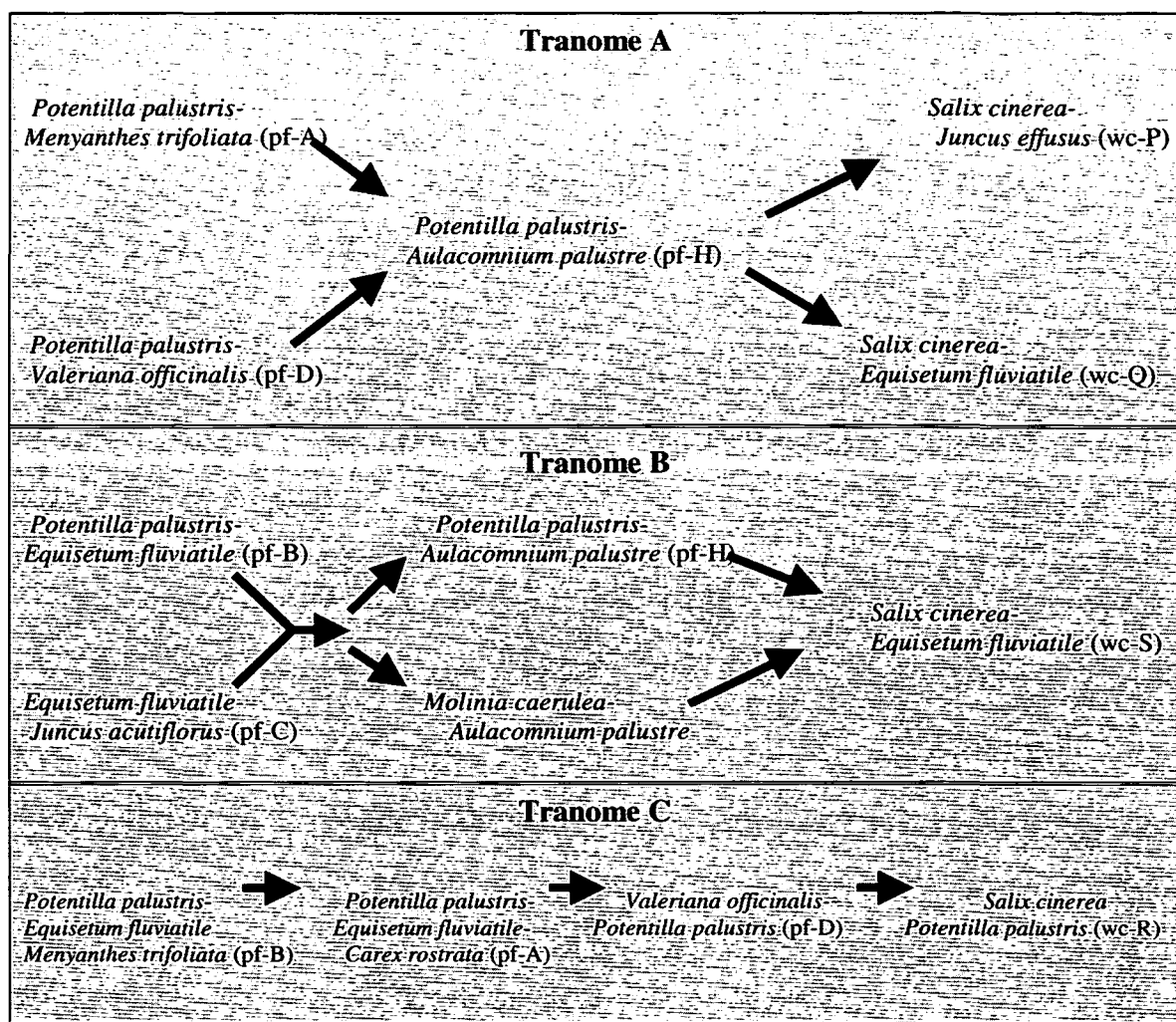
Figure 5.19 Patterns of hydroseral succession, based on the terrestrialisation hypothesis proposed in Chapter Three.

If the ergodic hypothesis of successional pattern can be inferred for the vegetation on Goss Moor, evidence for spatial succession was found. There was evidence to support two of the proposed successional pathways, in two geographically distinct areas on Goss Moor. Both successions began with the *Potentilla palustris-Equisetum fluviatile-Menyanthes trifoliata* Group pf-B swamp, identified in the poor-fen survey (Chapter Three). In Tranome B, increased terrestrialisation was signified by a high cover of *Aulacomnium palustre* and other cushion-forming mosses. In contrast, increased terrestrialisation was distinguished by the occurrence of *Calliergon* spp. in Tranome C. These two successional pathways probably reflect the differences in microtopography, which in turn affects the surface water movement throughout the tranome. The relatively homogenous microtopography of

Tranome C would be expected to have less of an impact on the water movements in this area. In contrast, the heterogeneous microtopography in Tranome B would impede and divert surface water, enabling patches of bryophytes to grow, which are usually inhibited by water inundation. A detailed study of water regimes and their associated vegetation in Tranomes A, B and C is provided in Chapter Six.

The putative successions between poor-fen types were associated with ecocline boundaries. However, the boundaries between Group wc-R the willow carr community, described in Chapter Four, and the *Valeriana officinalis-Potentilla palustris* poor-fen vegetation in Group pf-D were ecotones. If the pf-D/wc-R association is truly indicative of the ergodic hypothesis, it can be concluded that successions are associated with both ecotone and ecocline boundary types. This is not surprising as boundary types were derived from differences between data based on vegetation cover. These phytosociological differences between groups pf-D and wc-R can seemingly be attributed to the low light level conditions cast beneath the willow canopy, abruptly inhibiting the growth of poor-fen species normally associated with open habitats.

Many of the patterns of hydroseral succession found on Goss Moor concur with the patterns proposed for each tranome, based on those described in Chapter Three. However, other associations revealed by the vector diagrams may indicate multiple pathways of succession. Evidence for multiple pathways in wetland succession was presented by Walker (1970) who found that, generally, there was no single, preferred pathway of terrestrialisation in succession and stages were often skipped (Section 2.3.3.3). This occurs because different mosaics of vegetation are produced by 'positive-feedback switches', which magnify small differences between mosaics by the interaction of the plants with their environment (Wilson & Agnew, 1992). A vegetation positive feedback switch is a process by which a community modifies the environment, making it more suitable for that

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community unlike classical autogenic successional processes which act negatively (Dale, 1999). Switches operate by modifying the environment of the patch the community occupies, with four possible outcomes (Wilson & Agnew, 1992):

(i)   a stable vegetational mosaic can develop within a previously uniform environment;

(ii)   a vegetational gradient caused by environmental change can be intensified to give a sharp boundary;

(iii)   succession can be accelerated if the switch is operated by an invading species which makes the environment more suitable for individuals of the next seral stage this then sharpens or displaces temporal boundaries;

(iv)   succession can be delayed.

The concept of environmental modification by plant communities moves away from the facilitation theory of Clements (1916) and Watt's theory of cyclical succession (1947), which both suggested that plants change their environment making it less suitable for themselves. The switches concept is closer to Gleason's (1927) 'individualistic' theory of vegetation dynamics. Gleason's theory states that no two vegetation samples are exactly alike in quantitative or even qualitative composition, because the properties of the vegetation depend entirely on the properties of the individual plants within it. According to the individualistic theory, plant communities occur as a consequence of the incidental overlap of species distributions with similar environmental tolerances. However, this concept does not accommodate mechanisms that naturally produce sharp boundaries, even though they occur commonly in the field (Wilson & Agnew, 1992). When the presence of ecotones is not attributed to human influences such as those surrounding mosaics of heathland on Goss Moor, these differences may be due to boundaries between two communities being reinforced or sharpened by a switch (Wilson & Agnew, 1992). Boundaries between willow carr and open poor-fen communities would be reinforced by the shade cast by the willow canopy which limits the growth of poor-fen species beneath the canopy.

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5.5 SUMMARY

- Within the three tranomes 20 plant community types were described;

- Each tranome was microtopographically unique and encompassed distinct patterns of spatial succession;

- There is evidence that specific plant communities were associated with one of three boundaries types;

- Marked ecotones occurred between wetland and heathland habitats with contrasting microtopographical profiles, which were attributed to past tin-streaming activities;

- Ecoclines occurred between poor-fen communities with subtle differences in composition;

- The lattice-wombling technique was adequate for sampling Tranome B and C. However, it is recommended that areas with finer grained patterning such as Tranome A, should be sampled more intensively.

Successional patterns within the three tranomes were seen to reflect the differences in microtopography and the surface water movement. In the next chapter relationships between wetland vegetation and water regime will be investigated within the three tranomes.

Chapter Six: Water regimes associated with the main wetland vegetation types on Goss Moor

6.1 INTRODUCTION

Water regime is one of the most significant ecological factors to affect mire systems (Ingram, 1992), and is especially important in controlling plant community development and patterns of plant zonation (Wheeler, 1999; Casanova & Brock, 2000). On Goss Moor, different wetland vegetation types are presumed to experience and be sustained by their own unique water regimes. Several studies have associated the onset of scrub invasion and, therefore, successional change with specific aspects of the water regime. In Chapters Three and Four, surface water height recorded in 'snap-shot' events during field work conducted in the summers of 1997 and 1998 was identified as an important environmental factor in explaining the vegetation composition. In the literature, water regimes and the character of seasonal water table fluctuations have been described by their depth, duration, frequency, rate of filling and drying, timing and predictability of flooded and dry phases in a wetland (Bunn *et al.*, 1997). This chapter investigates those aspects of the water regime that are associated with the most abundant types of wetland vegetation and in particular the colonisation of willow scrub, which indicates the beginning of the next seral stage of the successional sequence on Goss Moor.

A number of different studies have drawn attention to the importance of distinct components of water table behaviour in regulating plant species distribution and vegetation composition (Wheeler, 1999). However, it is difficult to generalise due to the following reasons:

(i)   there have only been a small number of studies;

(ii)   not all of the investigations consider every component of water table behaviour and some look at different aspects of species distribution;

(iii)   some water variables may behave in a complex manner and may be site specific.

Nevertheless, a short review of these findings is a useful basis for this chapter.

Water regime can be is an important factor affecting the colonisation of herbaceous plant species. The success of seed germination appears to be affected by the nature of the water inundation. The highest germination rates and greatest species richness occur when wetland species are inundated during the spring and autumn, while the lowest germination rates are associated with summer inundations (Britton & Brock, 1994). The duration of the inundation is also thought to have an effect on the occurrence of some plant species, because prolonged flooding eliminates some species and favours others (Noest, 1994). The depth of the inundation is another important factor that can significantly affect the species composition and the biomass of establishing plants (van den Brink *et al.*, 1995).

Water regime has also been associated with scrub invasion and many theories have evolved. At Wicken Fen, Godwin & Bharucha (1932) found the limits of shrub invasion were best correlated with a reduction in winter water levels. On this basis, Rodwell (1991a) ascribed the initiation of W2 *Salix cinerea-Betula pubescens-Phragmites australis* woodland to the accumulation of consolidated litter, which eventually raises the surface of the peat mat above the winter flood water, facilitating scrub invasion. However, this generalisation is flawed, as many examples of W2 woodland are known to experience deep inundations (Wheeler *et al.*, 1999). In fact, summer water levels are thought to be more important in determining the survival of trees in wetlands than are winter water levels. Wetland trees would appear to be more capable of survival during winter flooding rather than flooding during the growing season (Kramer, 1969; Britton & Brock, 1994; Crawford, 1996). Various workers have associated summer flooding with a reduction in the abundance of trees in wetland vegetation (*e.g.* Gill, 1970) and have suggested that woody plants could be excluded if flooding lasted for more than 40 % of the growing season. Johnson (1994) assessed the expansion of marginal *Populus-Salix* woodland into river channels in response to reduced flow. He found that low river-flow in June combined with

summer drought coincided with the peak period of tree germination. Subsequent survival of the seedlings was determined by high winter flows, which correlated with ice-melt. In riparian wetlands, Toner & Keddy (1997) found that an association between the last day of the first flood and the time of the second flood best described the distribution of woody plants. They suggested that the longer the period between the two floods, the greater the chance that trees would recover sufficiently to withstand the second flood and, hence, the more likely the occurrence of wooded vegetation (Wheeler *et al.*, 1999).

The amplitude of water level flux is also important both to vegetation composition and community boundaries in wetlands, especially in situations where it is of sufficient magnitude and duration to cause detrimental modifications to certain components of the established vegetation (Wheeler *et al.*, 1999). With less frequent or lower amplitude, fluctuations a more stable vegetation can develop, with community limits determined partly by the water level range. Hill & Keddy (1992) observed that for some shoreline vegetation, greater amplitude of water levels were associated with less development of woody plants, a wider zone of wet meadow, greater species diversity and more rare species. In such systems, invasion of fen or wet grassland vegetation by woody species may be limited less by average water conditions than by periodic flooding episodes and extreme events. In wetlands experiencing regular or diurnal water level change, such as freshwater tidal wetlands, the lower limits of tree species can be related to both the duration and frequency of inundation, though these effects are difficult to separate (Wheeler *et al.*, 1999).

In the field, water table fluctuations are measured using a number of different types of instrumentation. The commonest and easiest way to measure water levels is to use dipwells (Brooks & Stoneman, 1997). These perforated plastic tubes are usually inserted into the peat so that the neck lies just above the peat surface. Both ends are normally capped: on

the base to prevent peat from upwelling into the dipwell and on the top to prevent snow, mice and insects from entering. As dipwells rarely extend into a firm substrate, measurements of water table depth are often affected by ground movement. If this is the case, the ground rises with the water table and dipwells are likely to underestimate the range of water table fluctuations. To overcome this, the insertion of a datum post next to the dipwell enables the observer to detect any differences. The depth of the water table (DWT) is calculated by measuring from the top of the dipwell to the ground surface and subtracting that from the top of the dipwell to the water level. Measurements are taken using steel measuring tape or specially designed dipsticks, which buzz or light up when the end reaches the water. But, frequent visits are necessary to gain a meaningful data set. To help overcome this, data collection from WALRAGs (WAter Level RAnge Gauge) is recommended. WALRAGs are dipwells which not only provide the current depth of the water table but also show the highest and lowest water table depth that occurred since the previous reading (Bragg et al., 1994).

For the purpose of water monitoring on Goss Moor, the use of intricate instrumentation such as WALRAGs or dipwells was dismissed, as these instruments are primarily used to monitor groundwater fluctuations. Recent research has found that most of the water fluctuation on Goss Moor is governed by surface water flow and local rainfall (Ishemo, 2000), and not by vertical groundwater movements. In support of this, soil samples collected in Chapter Three revealed that many of the vegetation-filled pools were lined with a thick layer of china clay. As well as preventing water from draining out of the pools, this impervious layer of clay acts as a barrier preventing the upward percolation of groundwater. Water Monitoring Devices (WMDs) are suitable for quantifying vertical surface water fluctuation and the amount of substrate drying for a number of different plant community types when frequent access to the site is possible. WMDs are inexpensive to

buy and install, involve low maintenance and are therefore suitable for monitoring a large number of locations over a wide area.

On Goss Moor, the water regime is an integral component of the wetland ecology. The literature indicates that water regime affects vegetation in different ways and there are few generalities possible. For this reason, it is important to characterise and understand the components of water table behaviour that regulate community composition on Goss Moor. Such knowledge will be vital for the future conservation and management of the site.

The aims of this chapter are to:

- characterise the water regime of three geographically distinct wetland habitats on Goss Moor, which differ in their degree of substrate heterogeneity;

- compare and contrast vertical water fluctuations with the mean rainfall data to determine how different substrates and communities respond to their climatic template;

- identify those aspects of the water regime that are principally associated with the different vegetation types on Goss Moor;

- distinguish any differences in the water regime related to the seral stage of the vegetation.

6.2 METHODOLOGY

6.2.1. INSTALLATION AND MONITORING OF THE WMDS

To identify possible differences between the water regimes of the main vegetation types, and especially between the 'early' and 'late' successional communities on Goss Moor, WMDs were installed. The WMDs were positioned within the three tranomes identified in Chapter Five. Of the 60 WMDs, 35 were positioned in non-willow or 'early' communities and 25 in willow or 'late' successional communities, the distributions of which are shown in Table 6.1 and Figures 6.1-6.3.

Table 6.1. The distribution of water recorders in the three tranomes and six different vegetation types

	Vegetation type						
	With willow			Without willow			
	Old	medium	young	poor fen	rush pasture	ombrotrophic	total
Tranome A	3	3	2	6	3	4	21
Tranome B	4	2	2	5	3	4	20
Tranome C	3	4	2	6	4	0	19
Total	10	9	6	17	10	8	60

For the purposes of this research, a simple approach was adopted for comparing the water regimes of the wetland vegetation types. The willow carr communities were divided into old, medium and young stands. These categories were identified by age, which was defined according to height and dbh data collected and described in Chapter Four. A summary of definitions and guidelines for field identification are provided in Table 6.2.

Molinia | Swamp | Eriophorum | Gorse bank | Grass bank
caerulea | | angustifolium | |

Rush pasture | Molinia/ | Tall herb fen | Ombrotrophic | Willow carr
| Rush mixture | | community |
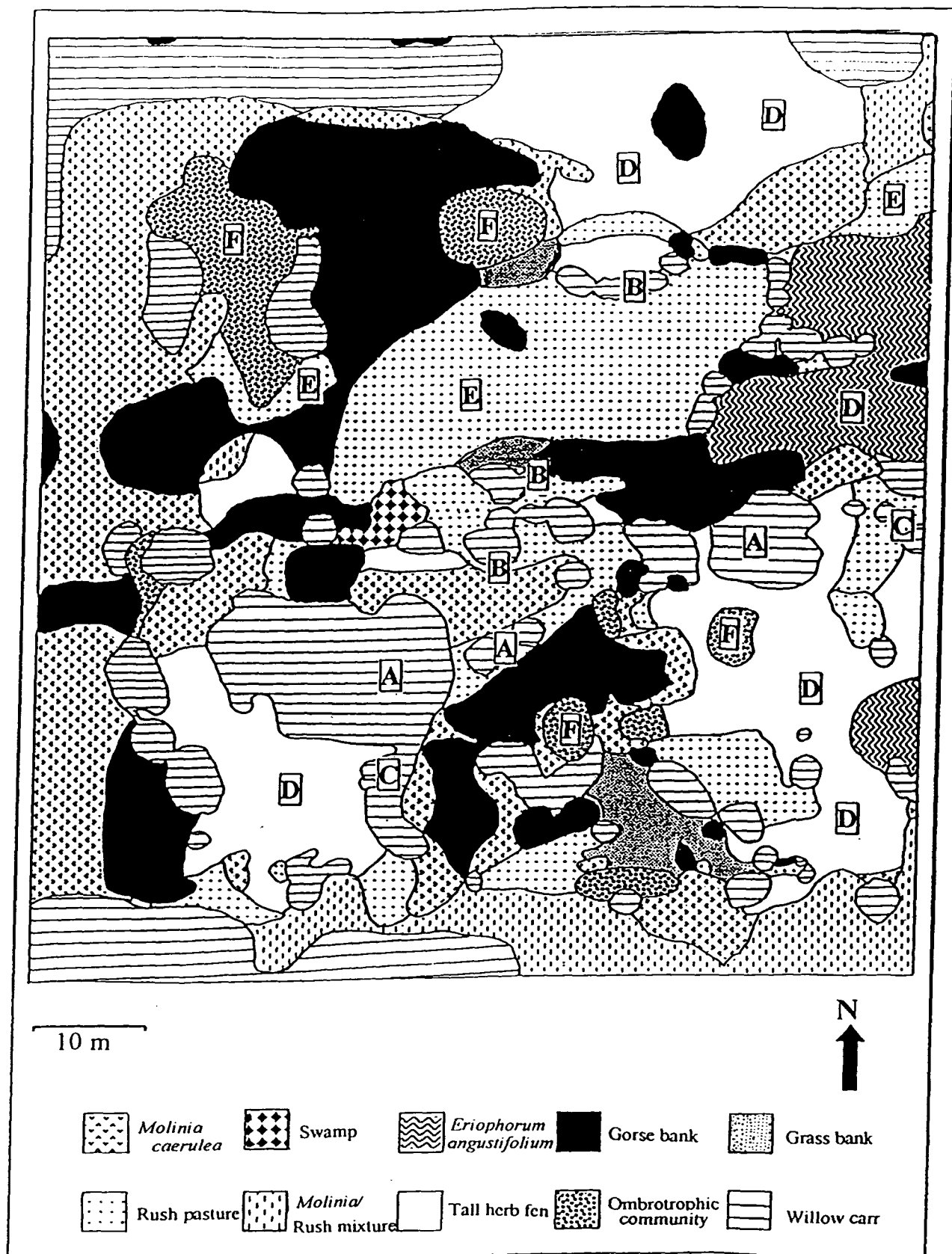
Figure 6.1 Shows the positions of the 21 WMDs in Tranome A. The associated vegetation types are marked with the following letters: A Old Willow; B Medium Willow; C Young Willow; D Poor-fen; E Rush pasture; and F Ombrotrophic communities.

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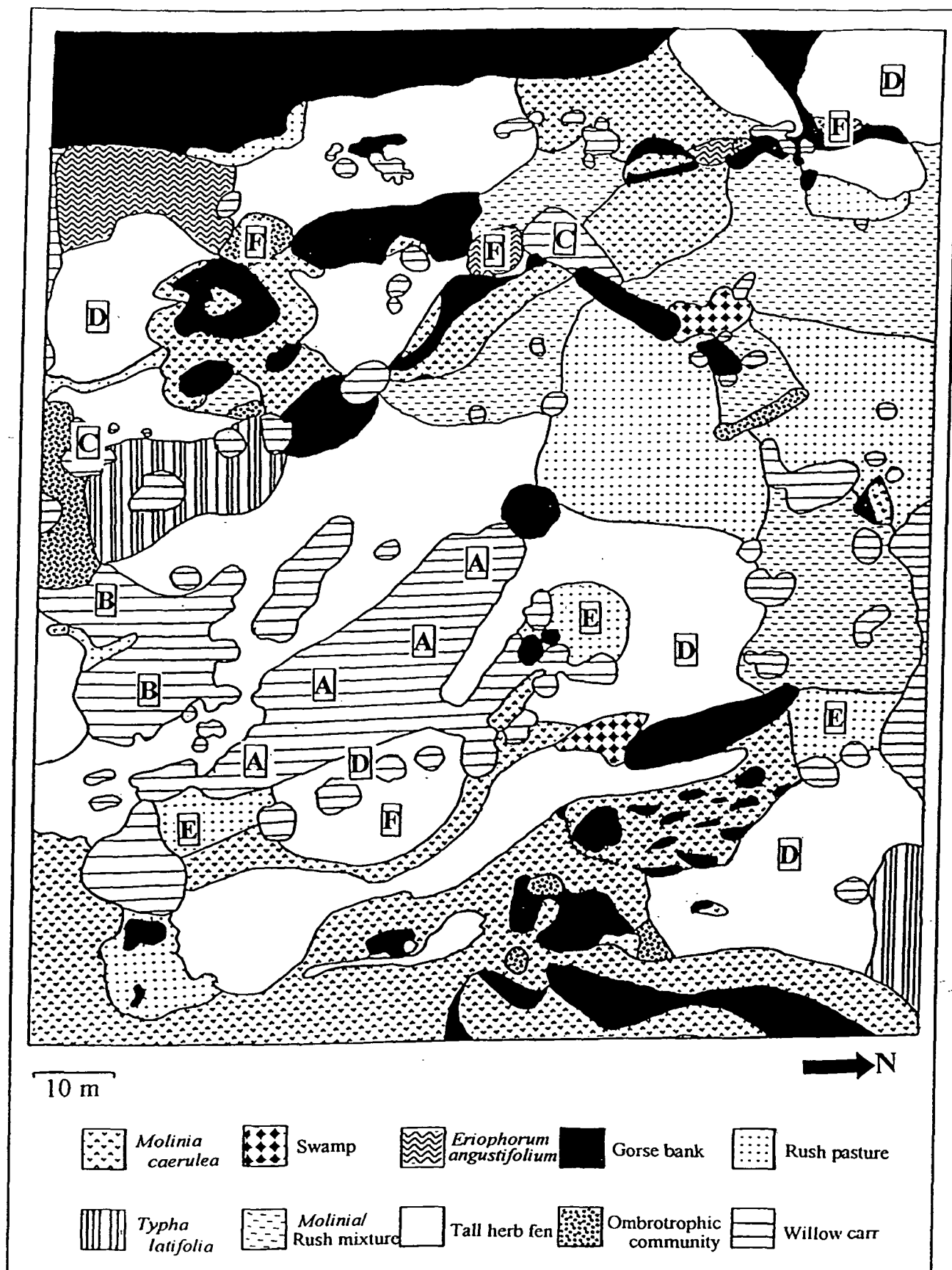
Figure 6.2 Shows the positions of the 20 WMDs in Tranome B. The associated vegetation types are marked with the following letters: A Old Willow; B Medium Willow; C Young Willow; D Poor-fen; E Rush pasture; and F Ombrotrophic communities.
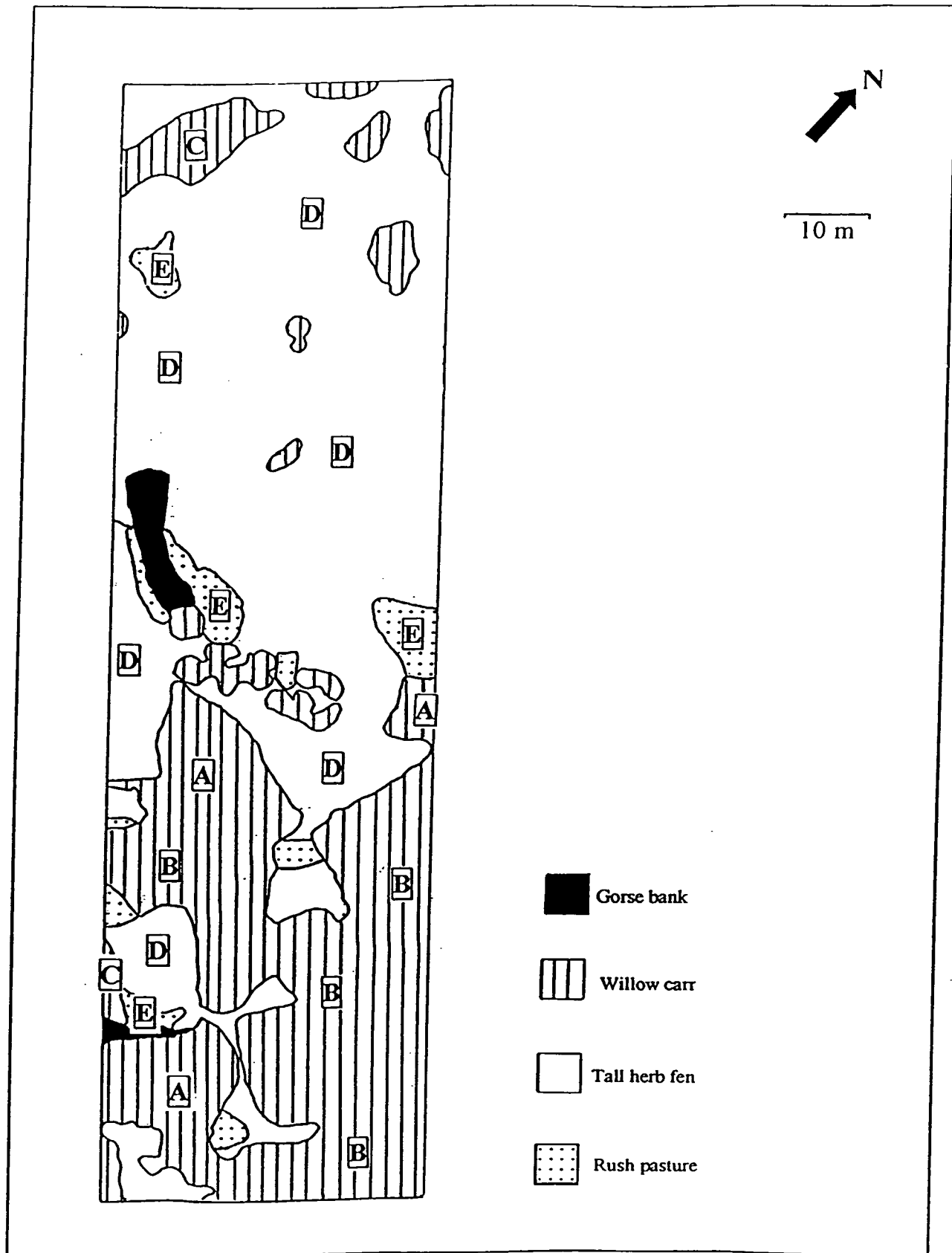
Figure 6.3 Shows the positions of the 19 WMDs in Tranome C. The associated vegetation types are marked with the following letters: A Old Willow; B Medium Willow; C Young Willow; D Poor-fen; and E Rush pasture.

Willow type	Approximate age (years)	Approximate dbh (cm)	Height (m)
Old willow	25+	13+	6 m+
Medium willow	12-25	5-12	1-6 m
Young willow	0-12	<5	Up to 1 m

Table 6.2 Guidelines used to assess the approximate age of willow carr in the field

In the non-willow sites, 35 WMDs were assigned to communities dominated by poor-fen, ombrotrophic or rush pasture. These plant communities were identified in Chapter Three as three of the four key poor-fen types, which also included *Molinia caerulea* communities. All are ubiquitous on Goss Moor and are easy to distinguish visually in the field: definitions are given in Table 6.3. Due to the environment of Tranome C there were no WMDs situated in ombrotrophic vegetation.

Vegetation type	Definition
Poor-fen	Vegetation dominated by a floating mat of *Potentilla palustris*, *Menyanthes trifoliata*, *Carex nigra*, *Carex rostrata* and *Equisetum fluviatile*.
Rush pasture	Vegetation dominated by ≥50 % cover of *Juncus effusus* and *Juncus acutiflorus*
Ombrotrophic	Vegetation dominated by cushion-forming bryophytes such as *Sphagnum squarrosum*, *Sphagnum subnitens* and *Aulacomnium palustre*.

Table 6.3 Guidelines used to distinguish between the three vegetation types on Goss Moor

In January 1999, 60 WMDs were inserted into the solid substrate situated below the organic layer of the allocated vegetation type. Each WMD was randomly situated within the patch of the appropriate vegetation type (Plates 6.1 and 6.2). For consistent sampling, the minimum size of the vegetation patch for non-willow vegetation was 2 x 2 m, and 4 x 4 m for willow communities. The WMD consisted of a 1.5 m length of 2 mm thick polyethylene pipe with a 40 mm diameter. As water levels reach a maximum in the winter, the pipes were inserted until only the top 15-25 cm of pipe was protruding above the surface water level.

Figure 6.4 A diagram showing how measurements were taken from the water monitoring device. Values were rounded up or down to the nearest 0.5 cm.
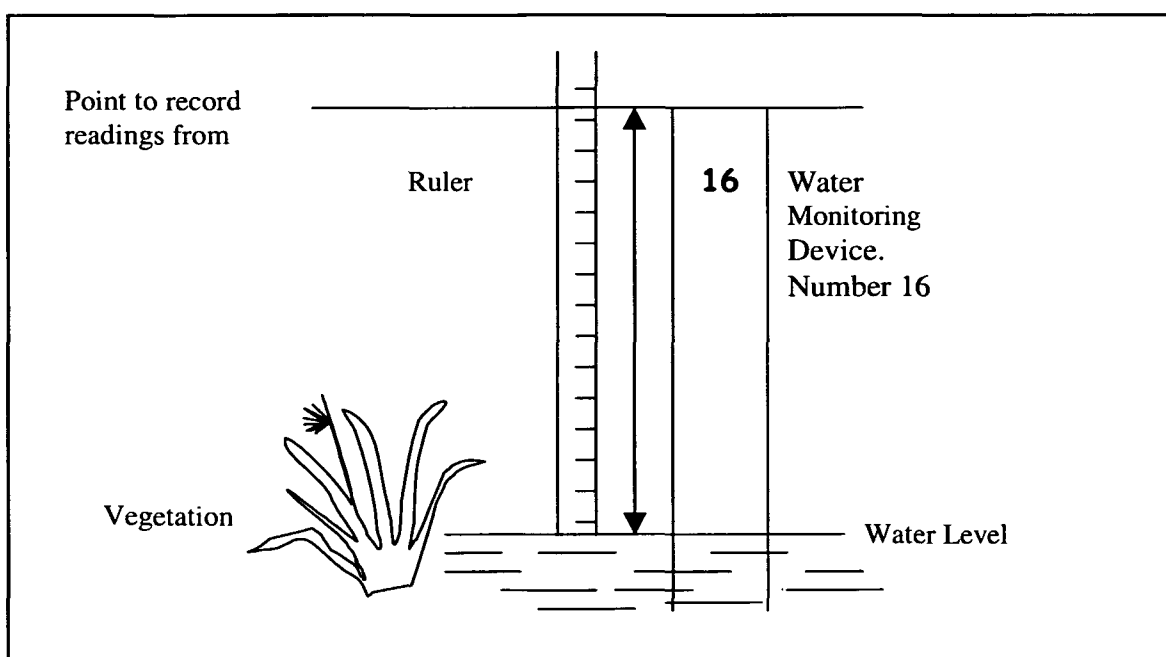
Water measurements were obtained by measuring the distance between the top of polyethylene pipe and the surface water level with a tape measure (Figure 6.4). Measurements were collected fortnightly for 60 weeks and values were rounded up or down to the nearest 0.5 cm. Sampling commenced on 21-01-1999, five days after all WMDs had been installed, and ceased on 03-03-2000, giving 30 sampling events. During the summer months, the surface water associated with the majority of the WMDs dried out and gave readings of zero. Values less than zero were attributed to substrate shrinkage due to desiccation.

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Plate 6.1 Water Monitoring Device number 28 situated in willow carr in Tranome B.

Plate 6.2 Water Monitoring Device number 3 situated in Tranome A.

In July 1999, the area of vegetation surrounding each WMD was sampled to obtain a quantitative assessment of the vegetation. A 2 x 2 m quadrat was used for poor-fen, ombrotrophic, rush pasture and young willow vegetation and a 4 x 4 m quadrat was used for willow carr communities, to collect abundance data following the NVC sampling procedure (Rodwell, 1991a; 1991b; 1995). Data recording and plant taxonomic nomenclature were as described in Chapter Three.

6.2.2 STATISTICAL ANALYSIS

The data collected from each WMD during the sampling period provided seven variables, which are given in Table 6.4. Differences among the vegetation types and tranomes for the seven variables were investigated by a two factor ANOVA (Statgraphics version 4.0, U.S.A.).

Table 6.4 The water variables used to analyse the surface water data.	
Description	**Definition and rationale**
Dry day	This value represents the number of occasions out of the 30 sampling days that the WMD was recorded as zero or less
Mean	The average water level recorded during the sampling period at each WMD.
Lowest	The lowest water level recorded during the sampling period. Once the substrate had dried out the level was recorded as zero. Minus values were recorded as the substrate underwent further drying and shrinkage.
Highest	The highest water level recorded during the sampling period
Amplitude	This value is used to represent the total amplitude. The value is derived from the highest water level minus the lowest water level, for each WMD.
Summer mean	The average summer water height recorded between and including the 13-05-1999 and 14-09-1999. Dates were chosen to include the main summer months of June, July and August, plus one sampling day either side of these months.
Winter mean	The average winter water height recorded between and including the 22-01-1999 to 26-04-1999 and the 25-09-1999 to the 03-03-2000, using the same rationale for defining as for the summer period.

To assess the relationships between the vegetation types and water variables, CCA (Ter Braak, 1987) and the associated CANOCO computer software (Ter Braak, 1988) were used. The use of CCA provided a more objective analysis of the data than the vegetation types recognised by eye, because it uses the data to detect species-environmental relationships using correlation and multiple regression. The precise definitions of the vegetation recognised in the field for the ANOVA analysis provided a discrete dataset, while the quadrat data were continuous and took into account the subtle variations between the vegetation types.

6.2.3 WEATHER CONDITIONS

In studies of water regime, rainfall data were essential as the seasonal input of rainfall affects the climatic template against which wetland development takes place, although in summer the rainfall often exerts less control than evaporation over the behaviour of water levels (Gilman, 1994). Fluctuations in rainfall were quantified using daily rainfall data collected from the Roche Rainfall station (Grid Reference: SW 9895 6063), 2 km from Goss Moor, between January 1999 and March 2000 (Environmental Agency Data). The mean daily rainfall was calculated for the two weeks before sampling began and for the period between each sampling event, beginning with the last sampling day.

6.3 RESULTS

6.3.1 WATER FLUCTUATIONS

The mean daily rainfall that occurred between sampling days throughout the sampling period is displayed in Figure 6.5. These fluctuations were largely reflected in the depth of surface water of the three tranomes (Figures 6.6, 6.7 and 6.8). The main troughs in mean daily rainfall during sampling weeks 6, 9-10, 14-15 and 18 were mirrored clearly in Tranome C and were also recognisable in Tranomes A and B. The peaks in mean daily

rainfall during sampling weeks 8, 11 and 24 were clearly reflected in all three tranomes. The greatest mean rainfall occurred between the 11-12-1999 and 22-12-1999, prior to the 25th fortnightly sampling day. However, this abrupt peak was not reflected in the WMDs positioned in the tranomes. This could be explained by an isolated rain event, which occurred only in the vicinity of the rain gauge and not in the Goss Moor catchment. However, this is unlikely due to the large amount of rain that occurred during the fortnight and the closeness of the weather station to Goss Moor.

Water levels recorded at two of the WMDs on Tranome A were continuously almost 5 cm higher than the other locations. The vegetation types associated with these particular WMDs were old willow carr with an understorey of occasional *Juncus acutiflorus* and a preponderance of standing water, and poor-fen vegetation dominated by *Potentilla palustris*, *Carex echinata* Murr. and *Carex nigra*. In comparison to the other vegetation types, poor-fen had the deepest standing water throughout the sampling period. As expected, the ombrotrophic communities were situated above the water level for the majority of the sampling period.
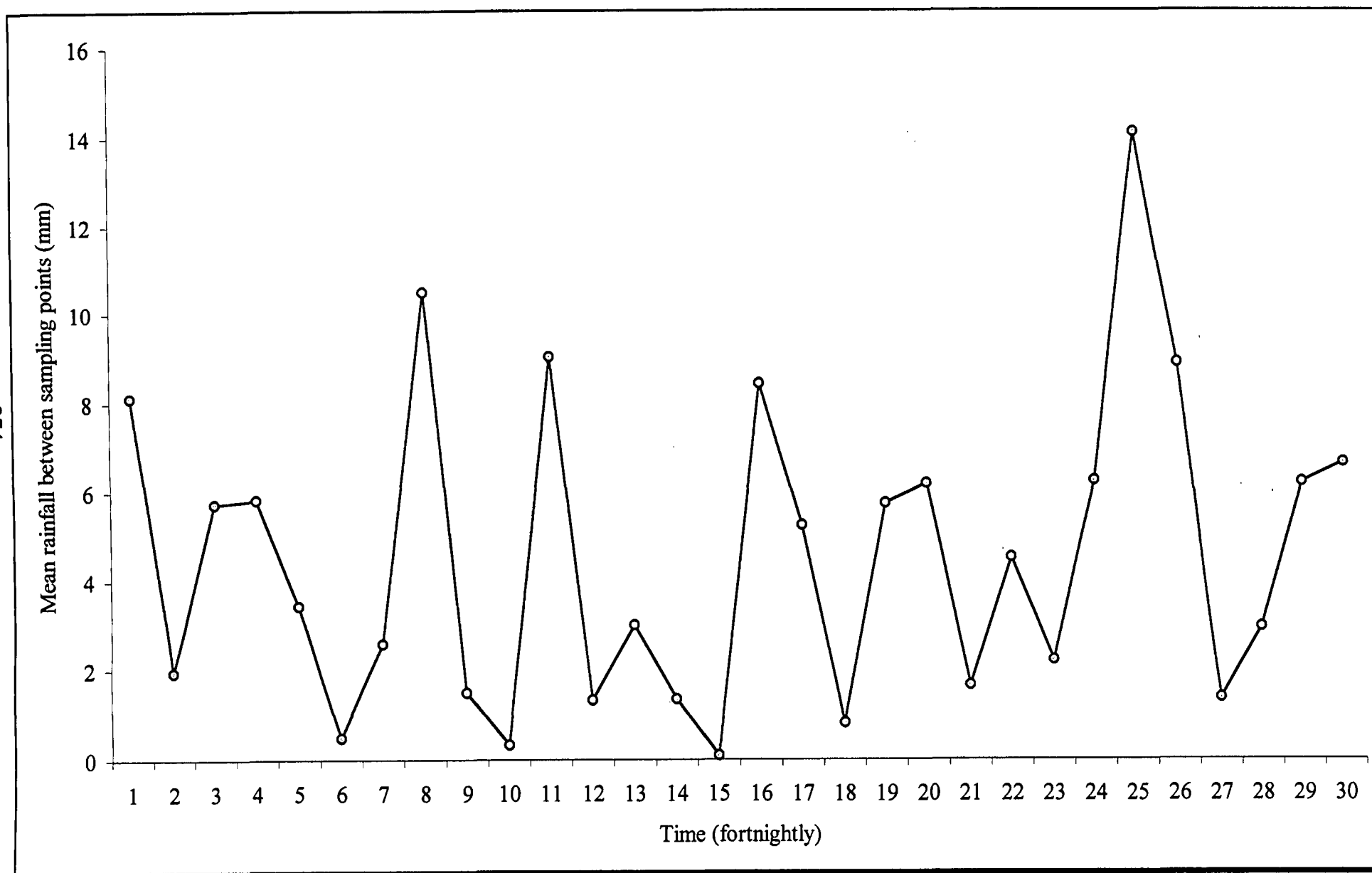
Figure 6.5 Mean daily rainfall (mm) that occurred in the fortnight between each sampling day. There were 30 sampling days over a 60 week period.
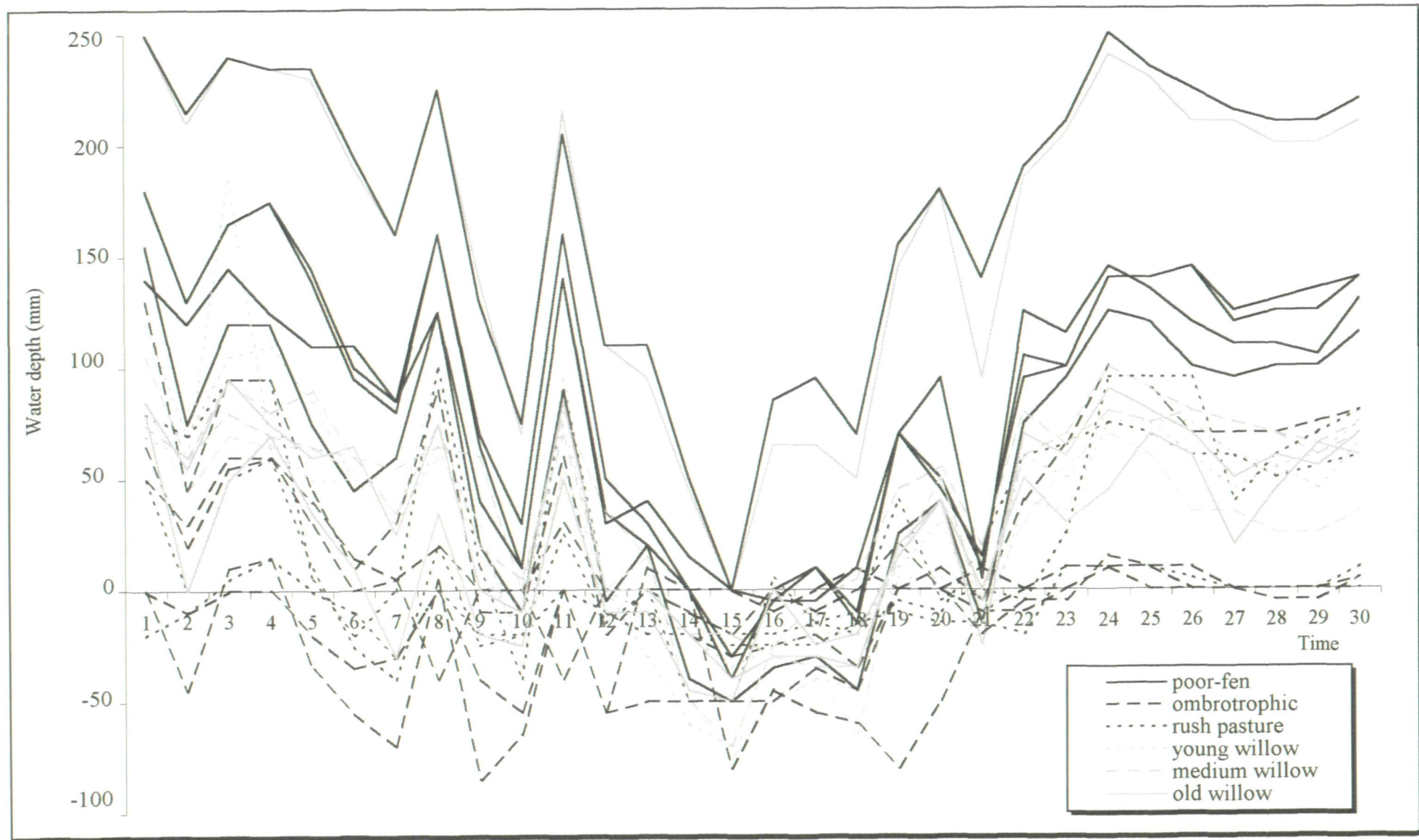
Figure 6.6 Surface water heights of the 21 WMDs placed in the six vegetation types in Tranome A. There were 30 sampling days over a 60 week period.
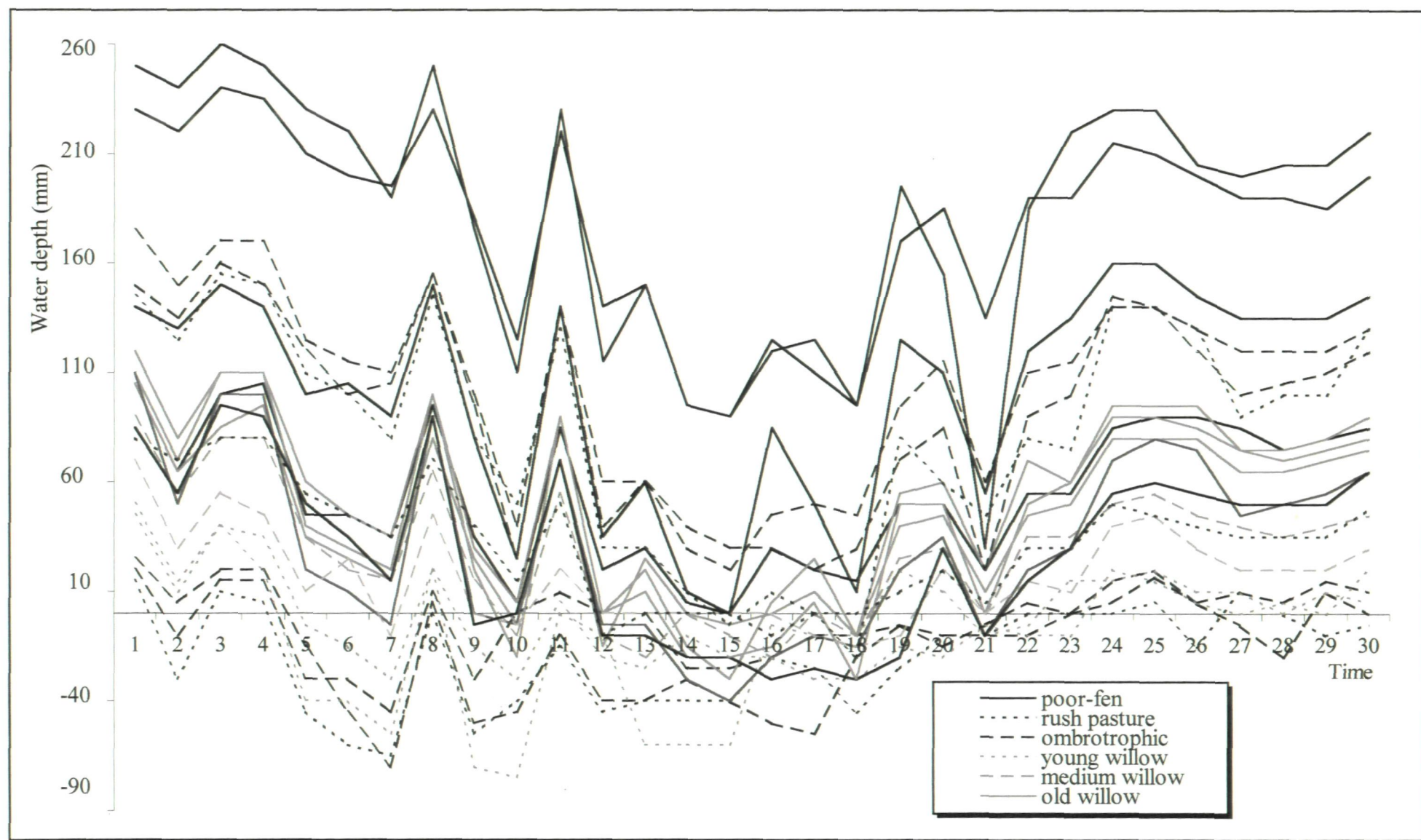
Figure 6.7 Surface water heights of the 20 WMDs placed in the six vegetation types in Tranome B. There were 30 sampling days over a 60 week period.
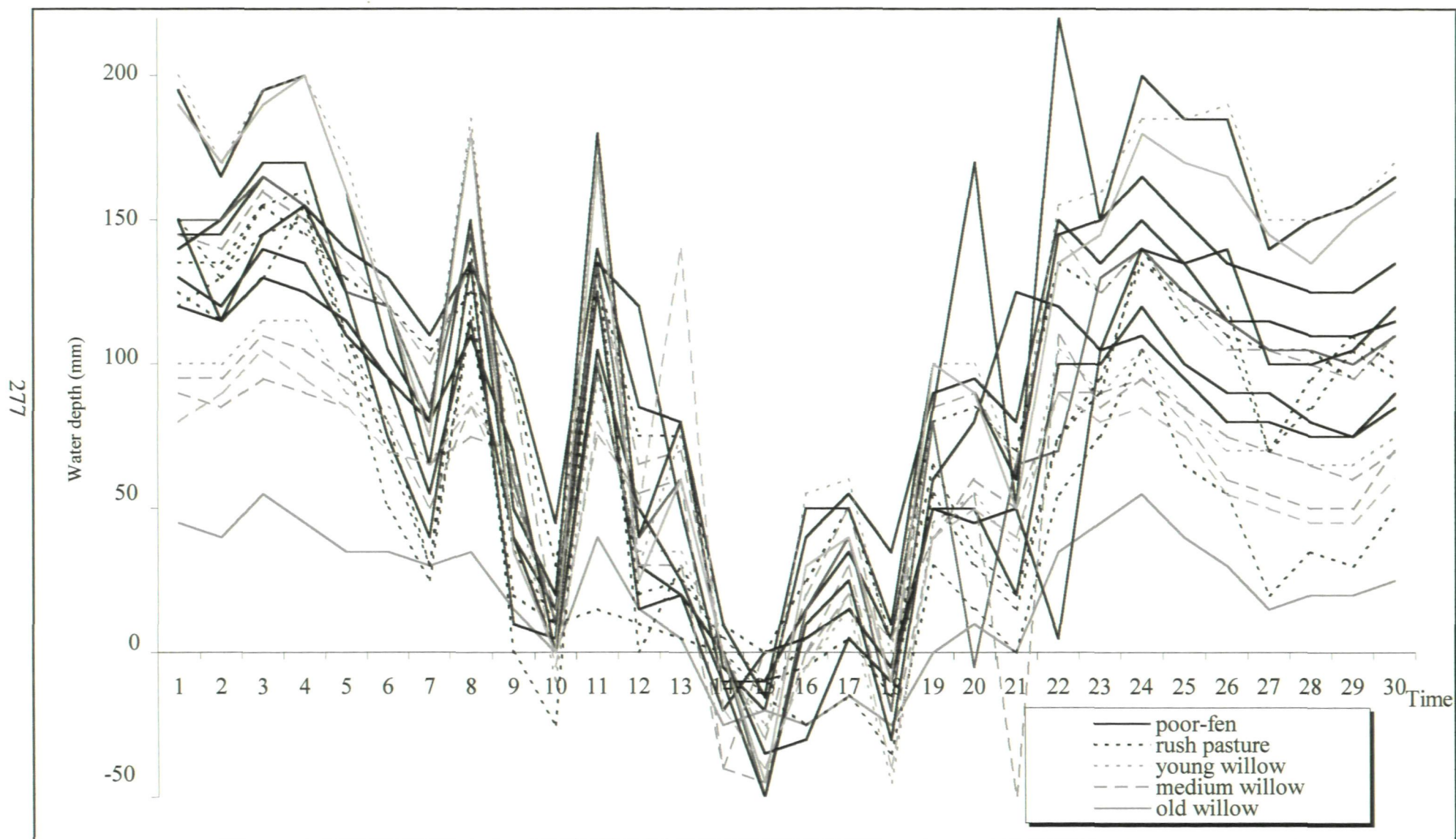
Figure 6.8 Surface water heights of the 19 WMDs placed in the five vegetation types in Tranome C. There were 30 sampling days over a 60 week period.

In Tranome B (Figure 6.7), the vegetation types experienced similar water levels to those in Tranome A, with poor-fen experiencing deeper inundations than the other types. The surface substrate in four of the sampling locations remained inundated even at the driest sampling point in the 15th fortnight (04-08-1999). These WMDs were situated in two poor-fen and two of the ombrotrophic communities. However, the two WMDs positioned in the ombrotrophic communities had been placed randomly in gaps between the bryophyte lawns.

The water fluctuations in Tranome C were least variable among the sampling locations and vegetation types and most closely resembled the rainfall data (Figure 6.8). Although there were fewer differences between the water levels of each of the community types in this tranome, the poor-fen still had the highest. All community types were free from surface water by the 15th sampling day.

Figure 6.9 illustrates the variance for each vegetation type and the overall 'mean variance' for that vegetation type, calculated from those variances. Poor-fen vegetation consistently experienced the greatest amount of variation and therefore water flux, followed by rush pasture. The medium aged willow carr and ombrotrophic vegetation showed the least amount of variation.
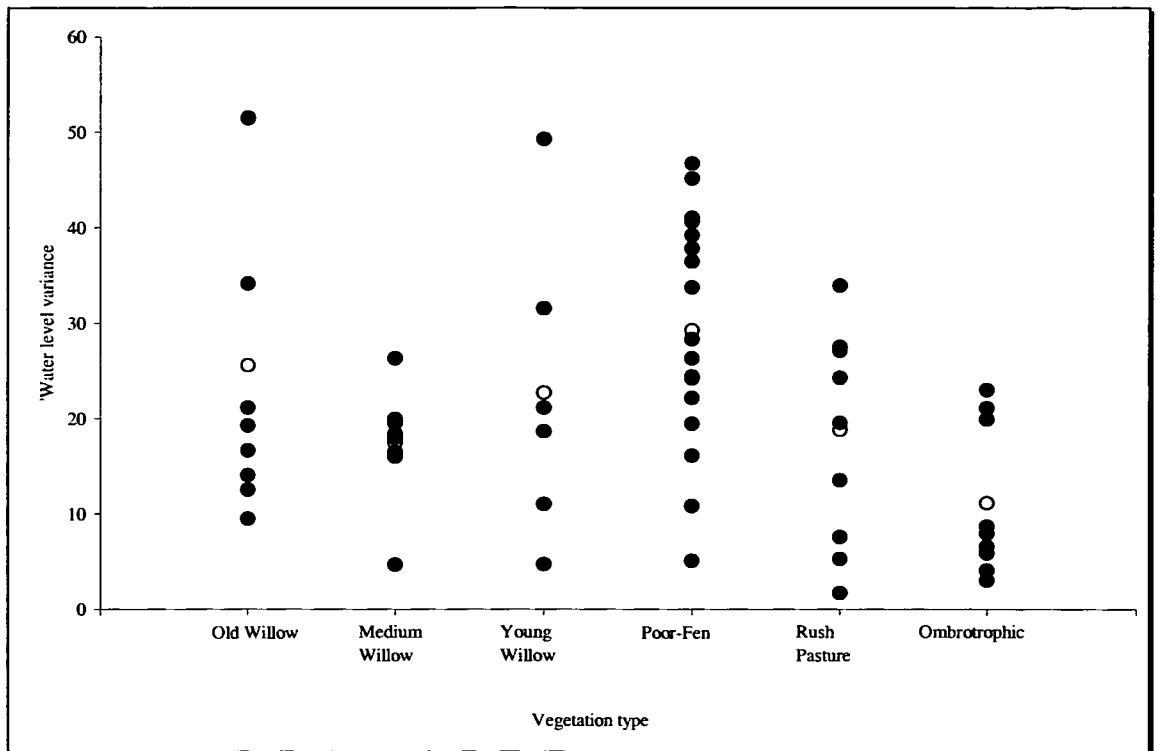
Figure 6.9 Distributions of the sample variance (filled dots) for each vegetation type and the 'mean variance' (unfilled dots) for that vegetation type. From water level data of the six vegetation types

6.3.2 ANALYSIS OF THE SEVEN WATER VARIABLES

6.3.2.1 Comparisons among six vegetation types

The two factor ANOVA distinguishes between the effect of tranome and vegetation type on the water regime. As ombrotrophic vegetation was not present in Tranome C, these data were removed to maintain a balanced two factor ANOVA design.

Table 6.5 shows that the majority of the variation lay among the tranomes rather than the vegetation type. Significant differences between the tranomes were found in all of the water variables, except for the lowest recorded water level. Significant differences between the vegetation types were found for dry days, the mean water level and the winter mean. No interactions were identified between the vegetation type and tranome.

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Table 6.5 Probabilities of the water variables of the six wetland vegetation types given by the two factor ANOVA for Dry days, Amplitude, Mean, Highest, Lowest, Summer mean and Winter mean. * = P<0.05, ** = P<0.01, and *** = P<0.005.

Source of variation	df	Dry days	Amplitude	Mean	Highest	Lowest	Summer mean	Winter mean
Vegetation type	4	0.0244*	0.0965	0.0389*	0.0654	0.0542	0.0610	0.0382*
Tranome	2	0.0004***	0.0014***	0.0050***	0.0055**	0.1790	0.0201*	0.0033***
Vegetation type * Tranome	8	0.2278	0.7659	0.6854	0.5597	0.5812	0.6095	0.7044

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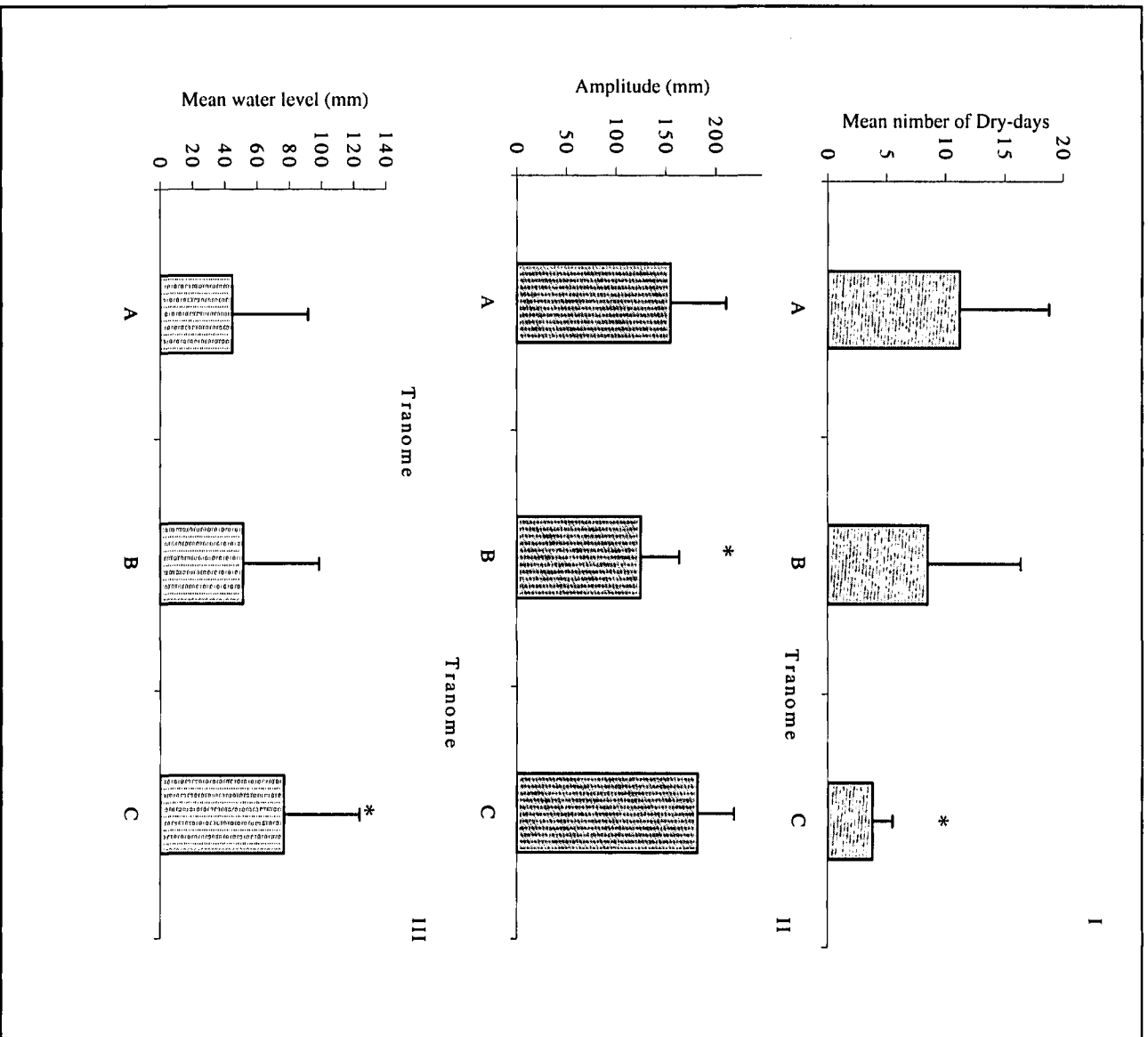
Figure 6.10 Mean and standard deviation of the following water variables: (I) Dry days, (II) Amplitude (III) Mean water level. * indicates a significant difference between the tranomes (P<0.05).

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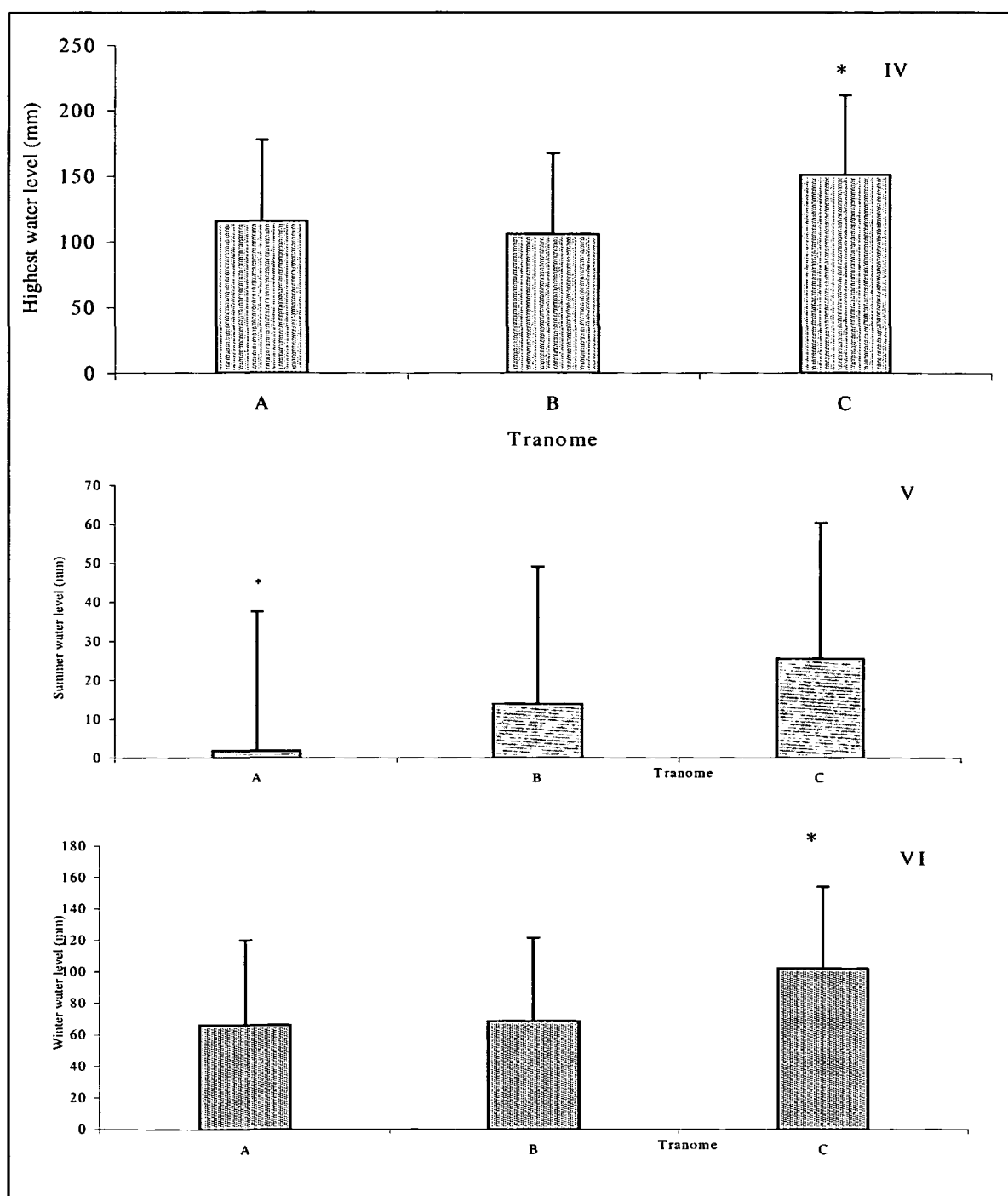
Figure 6.11 Mean and standard deviation of the three water variables: (IV) Highest recorded water level, (V) Summer mean water level and (VI) Winter mean water level. * indicates a significant difference between the tranomes (P<0.05).

Figures 6.10 and 6.11 show the main differences between the number of dry days, amplitude, the mean water level, the highest recorded water level, and the summer and winter means. Tranome A experienced the lowest mean water level, the greatest number of dry days and the lowest summer and winter means. Tranome C experienced the greatest

water amplitude, the fewest dry days and the greatest summer and winter means. Although Tranome B experienced the highest water levels, the water conditions were generally intermediate to tranomes A and C.

Differences among the five vegetation types were tested by the parametric Tukey multiple comparisons analysis, the results of which are shown in Table 6.6. This table also includes the ombrotrophic data to enable qualitative comparisons.

Table 6.6 Mean values for water variables of each of the six vegetation types. Significant differences found in water variables between the different vegetation types by the multiple comparisons analysis are shown by different letter suffixes, which in all cases represents $P<0.05$. There were no significant differences between the Lowest and Highest recorded water levels, Amplitude or Summer mean.

	Vegetation Type					
Water variable	Old Willow	Medium Willow	Young Willow	Poor-fen	Rush Pasture	Ombrotrophic
Dry days (out of 30)	6.5[b]	6.9[b]	10.5[b]	5.2[c]	10.6[a]	11.4
Amplitude (mm)	158[a]	151[a]	167[a]	171[a]	130[a]	136
Mean (mm)	61[b]	46[b]	39[b]	77[a]	37[c]	60
Highest (mm)	127[a]	106[a]	119[a]	149[a]	100[a]	118
Lowest (mm)	-31[a]	-44[a]	-48[a]	-22[a]	-30[a]	-18
Summer Mean (mm)	14[a]	8[a]	-4[a]	28[a]	2[a]	22
Winter Mean (mm)	84[b]	65[b]	61[b]	101[a]	55[c]	78

The significant differences lay mostly between the poor-fen vegetation and the rush pasture. Poor-fen was consistently the wettest vegetation type, experiencing the least dry days, the greatest amount of water level amplitude and the highest mean and winter mean. Rush pasture was the driest vegetation type with the greatest number of dry days, the lowest mean water level and amplitude. The willow communities experienced lower lowest mean water levels than the non-willow communities. In comparison to the other willow communities, young willow experienced more dry days and the lowest mean water

level. The ombrotrophic vegetation was associated with the greatest number of dry days and the lowest recorded water levels.

6.3.3 MULTIVARIATE ANALYSIS OF THE SEVEN WATER VARIANTS

The joint biplot of the seven water variables for each vegetation type and tranome produced by CCA are presented in Figures 6.12 and 6.14, respectively. Figure 6.13 shows the mean or centroid points of the six vegetation types. The eigenvalues for the first and second axes of the species and environmental variables biplot were 0.25 and 0.14, respectively. The species and environmental data account for 40.8% and 22.7% of the variance. Thus the total variance explained by the first two axes of the joint species/environmental biplot is 63.5%.

Analysis of vegetation and the water variables resulted in a clustering of points around the centre of the ordination. In order to gain a better understanding of the distribution of the quadrats along the ordination axes, and produce a less clustered diagram, the CCA was re-run after the outlying quadrat number 18 was removed (Kent & Coker, 1992). This quadrat represented young willow from Tranome A. The final CCA analysis was run with 59 quadrats and 99 species.
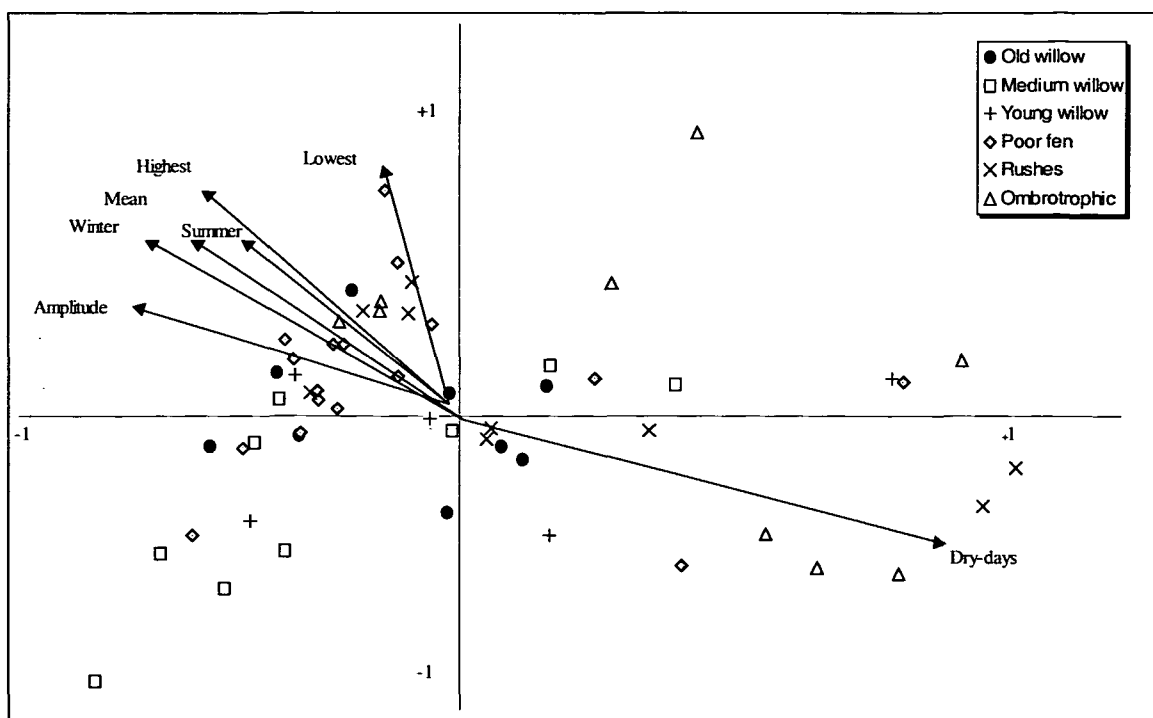
Figure 6.12 Ordination of the vegetation associated with the different WMDs and environmental vectors produced by Canonical Correspondence Analysis of the 59 quadrats. The six vegetation types are superimposed. Eigenvalues: Axis 1 = 0.25 and Axis 2 = 0.14.

A summary of the weighted correlation matrix between ordination axes and the water variables is given in Table 6.13. The number of dry days was the most significant water variable to explain the vegetation data, and was correlated to Axis 1 with a value of 0.87. The vegetation types associated with dry days were the ombrotrophic and to a lesser extent, rush communities. Tranomes A and B were also associated with the number of dry days. This association may be explained by the fact that ombrotrophic vegetation was only found in tranomes A and B.

Water amplitude was correlated to Axis 1 with a value of -0.70. The groups associated with the greatest water fluctuation were poor-fen communities dominated by aquatic macrophytes, and old willow. The ombrotrophic communities were associated with areas experiencing the lowest total water amplitude. The rush pasture communities also experienced low amplitude. However, two outliers appear to be responsible for pulling the vegetation mean or centroids away from the centre of the ordination.
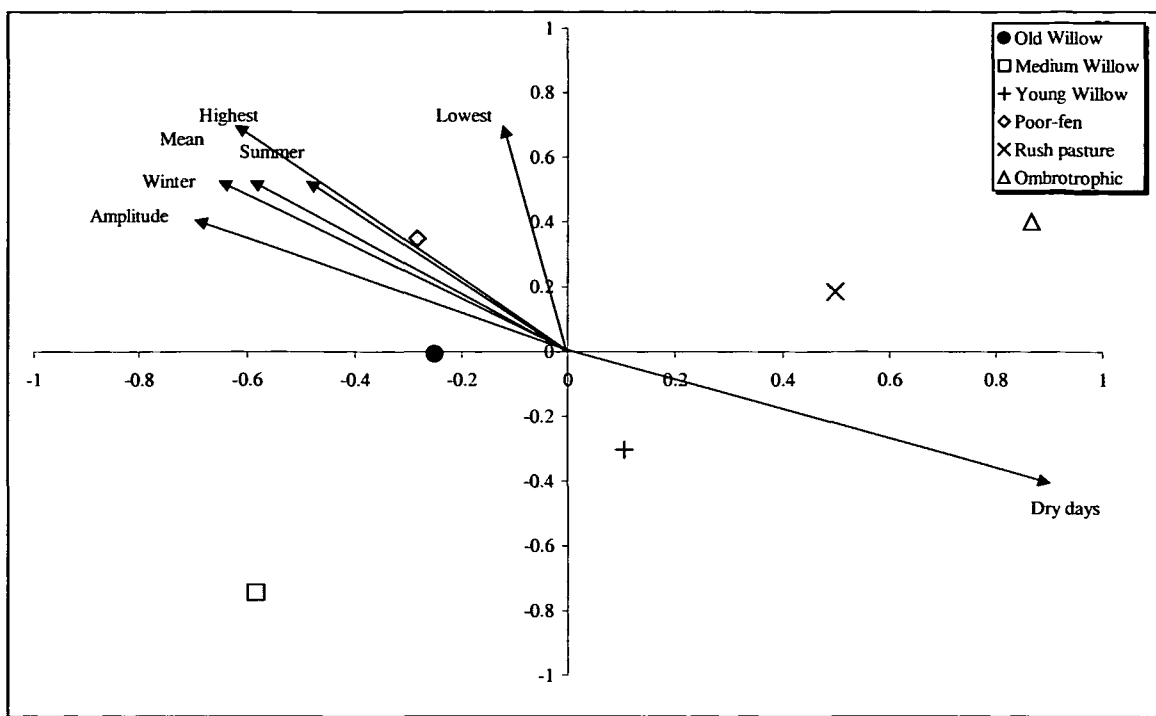
Figure 6.13 Joint biplot showing centroid or mean positions of the quadrat data and the seven water variables produced by CANOCO of the 59 quadrats used in the final analysis (Monte Carlo test on the first axis was significant P=0.05). The six vegetation types are superimposed.

Poor-fen communities were associated with the overall mean water level, which was correlated to Axis 1 and Axis 2 with values of -0.61 and 0.58 respectively, mean summer water depth (Axis 1, -0.50 and Axis 2, 0.57) and winter mean (Axis 1, -0.65 and Axis 2, -0.58).

Although there were obvious relationships between some of the water variables and vegetation types, there was a large amount of variation. The dispersal of the ordination points was especially marked for the poor-fen and ombrotrophic vegetation.

Tranome C was the wettest location surveyed, as it was associated with the highest water levels, Tranomes A and B were associated with a greater number of dry days. This trend was also reflected in the lowest water levels which were recorded in tranomes A and B.

The correlation between the lowest water level and the first two axes was -0.13 and 0.73, respectively.
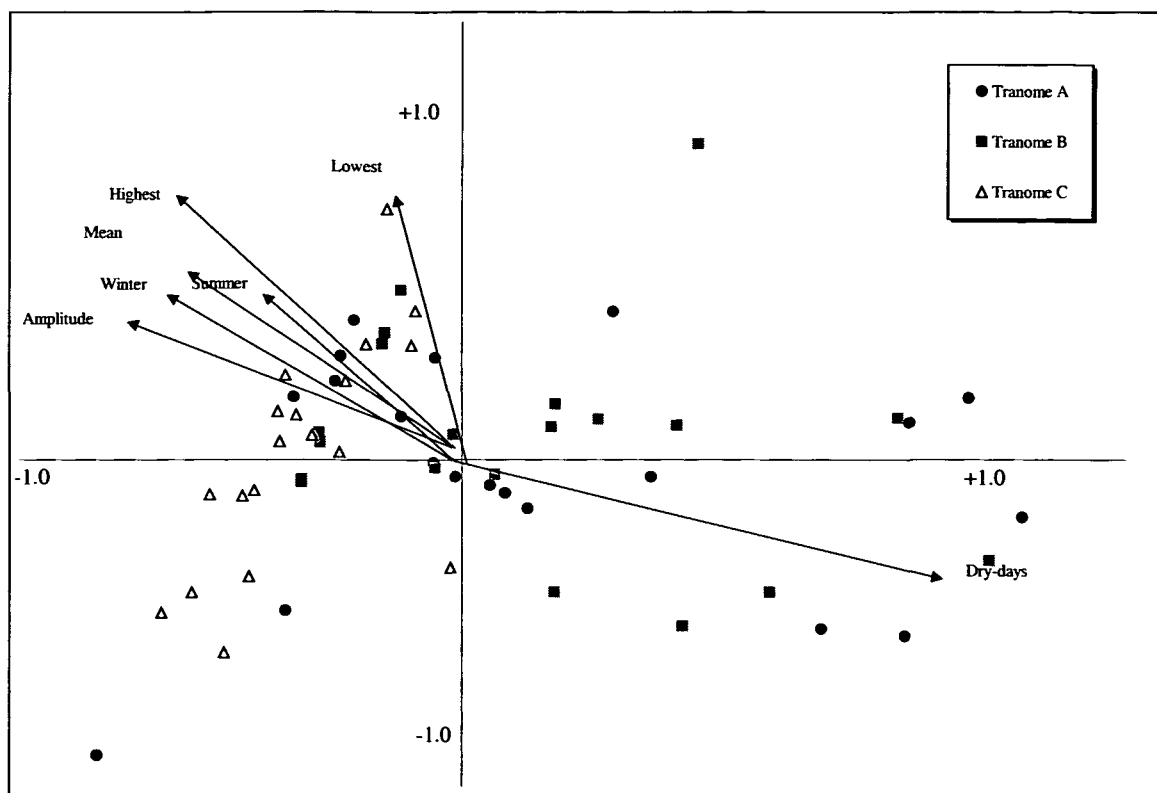
Figure 6.14 Joint biplot of the quadrat data and the five most significant water variables produced by CANOCO of the 59 quadrats used in the final analysis (Monte Carlo test on the first axis was significant P=0.05). The three tranome types are superimposed.

The ordination in Figure 6.14 also reflects the relative substrate heterogeneity of the tranomes. The points associated with Tranome C with the most homogenous substrate show less dispersal than Tranomes A and B.

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	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4	WINTMEAN	SUMMMEAN	AMPLITDE	DRY-DAYS	MEANWATE	HIGHESTW	LOWESTWA
SPEC AX1	1.0000														
SPEC AX2	.2203	1.0000													
SPEC AX3	-.0353	-.2455	1.0000												
SPEC AX4	.0340	.1344	-.1616	1.0000											
ENVI AX1	.8100	.0000	.0000	.0000	1.0000										
ENVI AX2	.0000	.6265	.0000	.0000	.0000	1.0000									
ENVI AX3	.0000	.0000	.6584	.0000	.0000	.0000	1.0000								
ENVI AX4	.0000	.0000	.0000	.6669	.0000	.0000	.0000	1.0000							
WINTMEAN	-.5232	.3616	-.0071	.3277	-.6459	.5772	-.0108	.4914	1.0000						
SUMMEAN	-.4023	.3587	.2116	.3400	-.4966	.5726	.3214	.5098	.9208	1.0000					
AMPLITDE	-.5661	.2737	-.3076	.1669	-.6988	.4370	-.4672	.2502	.8496	.6245	1.0000				
DRY-DAYS	.7059	-.2618	-.1475	-.0733	.8714	-.4179	-.2240	-.1099	.8500	.7847	.7021	1.0000			
MEANWATE	-.5012	.3662	.0464	.3356	-.6187	.5847	.0704	.5032	.9954	.9539	.8070	-.8465	1.0000		
HIGHESTW	-.5062	.4319	-.0655	.2175	-.6250	.6894	-.0995	.3261	.9750	.8728	.8928	.8380	.9644	1.0000	
LOWESTWA	-.1030	.4584	.4017	.1795	-.1272	.7317	.6101	.2691	.6246	.8000	.1786	.5866	.6768	.6027	1.0000

Table 6.7 Weighted correlation matrix between ordination axes and environmental variables for the water variable data. The abbreviations are as follows: SPEC AX1 (Axis 1); SPEC AX2 (Axis 2); SPEC AX3 (Axis 3); SPEC AX4 (Axis 4); ENVI AX1 (Environmental Axis 1); ENVI AX2 (Environmental Axis 2); ENVI AX3 (Environmental Axis 3); ENVI AX4 (Environmental Axis 4); WINTMEAN (Winter mean in mm); SUMMEAN (Summer mean in mm); AMPLITDE (Amplitude: the difference between the minimum and maximum in mm); DRY-DAYS (Number of dry days recorded out of the 30 sampling days); MEANWATE (The average water level in mm); HIGHESTW (Highest level experienced during sampling in mm); LOWESTWA (Lowest level experienced during sampling in mm).

6.4 DISCUSSION

6.4.1 DIFFERENCES AMONG THE THREE TRANOMES

The three tranomes displayed very different patterns of surface water fluctuation. These differences can be attributed to variations in the substrate heterogeneity of each tranome, the complexity of which progressively decreased from A to C. The most homogeneous microtopography experienced the deepest inundation and greatest amplitude, and most closely resembled the rainfall data. Also, there was less differentiation between the water levels of the community types present in this tranome. According to records, there was no tin-streaming or mining activity in Tranome C, which means that this habitat is the most 'natural' and least disturbed out of the three studied. Habitats containing very few raised gravel banks or deep isolated ponds permit surface water to flow throughout the vegetation unimpeded. The high water levels and fluctuation in Tranome C would prevent the colonisation of cushion-forming bryophytes and explain why ombrotrophic communities were not found in this tranome. Ombrotrophic communities were found in tranomes A and B, which both contained heterogeneous substrates. The most complex microtopography in Tranome A was situated west of the site, next to the disused railway. This area is thought to have experienced the most intense tin-streaming activity, which ceased more than 100 years ago. Tranome A was the driest, experiencing the lowest summer mean, winter mean and overall mean, and the most dry days. Due to its complex microtopography, Tranome A was watered directly by rainfall and discrete channels of surface water flow. This contrasts with the unimpeded and widespread surface movement characteristic of Tranome C. The hydrological and microtopographical conditions in Tranome B were intermediate to those in tranomes A and C.

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6.4.2 DIFFERENCES AMONG THE VEGETATION TYPES

Although each of the six vegetation types experienced quite varied water regimes, there was little doubt that different plant communities were associated with distinct aspects of the water regime. Rush pasture was the driest vegetation type experiencing the most dry days, the lowest mean water level and amplitude. Rush pasture communities are usually associated with mineral rather than organic substrates (Proctor, 1974), indicating greater aeration and thus a different type of community to poor-fen. For this reason, rush communities are not thought to be part of the hydroseral succession process, which begins with open-water ponds and ends in willow carr.

Poor-fen can be described as the 'wettest' vegetation type, experiencing fewest dry days, the greatest water level amplitude and the highest mean and winter mean surface water levels. These findings agree with the assumptions made in Chapter Three regarding the character of the poor-fen communities, which are hypothesised as being maintained by consistently high water levels. High water levels are thought to reduce the colonisation rates of lawn-building bryophytes and willow scrub, and thus suspend the process of succession.

The ombrotrophic communities were characterised by very stable water regimes with low amplitude and variation, and they thus remained inundated throughout the summer. This was because the mat-forming bryophytes were situated above the water table in isolated ponds that were chiefly rain-fed. In these communities, the surface layer of bryophytes and the depth of the pools are thought to reduce summer evaporation rates, which would help maintain constant water levels throughout the sampling period.

In comparison to the other willow communities, young willow experienced the most dry days and the lowest water levels. The colonisation of wetlands by woody plants is thought to be promoted in areas that experience reduced water levels during the growing season (Gill, 1970). Colonisation of ombrotrophic communities may only occur once the water levels have reduced sufficiently during the growing season, as the summer water levels for young willow on Goss Moor were lower than the other five vegetation types.

In comparison to the non-willow communities, the willow communities were associated with the lowest water levels and therefore experienced a greater degree of drying. The association between the colonisation of woody plants and drying in wetlands is, however, almost certainly partly dependant upon other environmental variables, although their significance is unknown (Wheeler et al., 1999). One factor that may play a role in reducing water levels is evapo-transpiration, which is considerably greater in trees and shrubs than herbaceous plants. Once willow invasion has taken place, further colonisation of trees would be encouraged by the enhanced drying caused by greater rates of evapo-transpiration. The invasion of willow in a community is thought to represent the initiation of secondary fen carr woodland (Tansley, 1935) and the next successional stage.

In direct contradiction to the above hypotheses, old willow was the wettest of the willow communities, with the fewest dry days the highest mean water height and winter mean. Water inundation during the winter is common in many fen woodlands, although toleration levels are lower during the growing season (Gill, 1970). On Goss Moor, the summer water levels in old willow were reduced by 70 mm on average, however, these habitats were still inundated during the growing season. Many trees, especially those in Tranome C, appear to have overcome the problem of inundation and are situated on a mound above the water. This phenomenon was also described in Chapter Four.

6.4.3 ANALYSIS OF THE WATER REGIME

The seven water variables were an effective tool in distinguishing among the six vegetation types. The number of dry days was the most distinguishing water variable for the vegetation types in the multivariate analysis. The dry days variable was different of the other water variables, as it was not a direct measurement of water level.

Water variables with strong explanatory power in the multivariate analysis were amplitude, and the highest and lowest water levels. Spieksma *et al.* (1995) and Wierda *et al.* (1997) also found that the lowest and highest water levels were important factors governing vegetation composition. Summer mean was another important variable in distinguishing between the three tranomes on Goss Moor, which was also found by Spieksma *et al.* (1995) and Wierda *et al.* (1997) for individual species.

6.4.4 THE GENERAL CRITIQUE

This research has described the water regime on Goss Moor monitored over a period of 60 weeks during 1999 and 2000, in three locations. As this was a relatively short sampling period, the results may not be representative or typical of the water regime on Goss Moor in these areas. This survey has not been comprehensive enough to detect occasional extreme hydrological events, which may have an important effect on the present vegetation structure (Wheeler, 1999). Obviously a longer sampling period would improve the dataset. However, the pattern of water fluctuation in each tranome resembled the mean rainfall data between each sampling event quite consistently. The close correlation between the vertical water fluctuations and the mean rainfall data would also provide a good basis for predicting water fluctuations from future rainfall data. However, the abrupt peak in rainfall that occurred prior

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to the 25th sampling day was not reflected in the WMDs positioned in the tranomes. This abrupt peak may be caused by an isolated rain event that occurred only in Roche where the rain gauge was situated and not on Goss Moor. Another explanation for the lack of response to this rain event may be because the carrying capacity of the substrate had been reached. Peaks in water level were detected on the 8th, 11th and 24th sampling day, for the majority of the WMDs, which reflected the rainfall data. If the water levels on these three dates reflected the maximum amount of water the habitats could retain, any subsequent rain events would not be registered. This means the large amount of rainfall that occurred in the fortnight prior to the 25th sampling day would not be detected.

The associations found between water regime and plant communities were anticipated. However, these associations are more likely to be relics of past water levels, rather than the water levels present at the time of survey (Roberts, 1994). The species distributions are in a state of change: some species may be currently growing in sub-optimal conditions and may decline in future (Wheeler, 1999). All of the relationships found between the vegetation types and aspects of the water regime assume that the wetland is a stable environment. Although it is difficult to assess, the water regime in the area studied on Goss Moor is considered to be quite stable because unlike many fens very little alteration to the water regime has taken place since the original creation of the habitats during the tin-streaming era, which ended almost 100 years ago. The only known attempts to alter the water regime took place in the north-east of the site on the river near Pendine in the 1970s (Figure 2.2). The Lode was canalised as remedial action due to drainage problems in the surrounding farmland, which were thought to be drying out the surrounding SSSI. In the 1990s, the rapid expansion of willow carr across Goss Moor was attributed to a reduction in surface water levels. To remedy this a number of weirs were constructed in 1996 along the eastern side of the River Fal. These dams reduce the speed and

raise the height of the water flow and thus reduce the amount of water drawn from the surrounding wetland.

By investigating the water level data with seven different variables, it was possible to detect whether community structure was determined more by occasional extreme events such as periodic deep flooding, or by average events. It was also advantageous to analyse the water data by two different methods: discrete *versus* continuous. The discrete data were collected subjectively, where the six different discrete vegetation types were recognised in the field. These data enabled statistical differences to be found between the vegetation types. The quadrat data used for multivariate analysis provided a continuous dataset that included actual species abundance data. The ordinations showed that the vegetation types were not clustered in discrete patches and there was a great deal of overlap. However, the average situations, or the centroid values of these vegetation types showed the results of the two data sets to be very similar.

6.5 CONCLUSION

Microtopography was found to be an important factor governing the water regime and vegetation patterns on Goss Moor. The non-willow communities were the wettest and the willow carr communities were, on the whole, driest. This suggests differences between the seral stages. Young and medium-aged willow experienced the lowest water levels in comparison to the other vegetation types, suggesting that reduced water levels encourage the colonisation of woody vegetation.

In this chapter the character of the water regime was found to be related to the type of vegetation and the stage of hydroseral succession it represents. In the next chapter, further

evidence for successional patterns in the wetland habitats on Goss Moor will be sought through an exploratory analysis of nutrient limitation and plant strategies.

Chapter Seven:
An exploratory analysis of the N:P tool & plant strategies to identify the successional patterns of wetland communities on Goss Moor

7.1 INTRODUCTION

7.1.1 NUTRIENT LIMITATION

Resource availability is a driving force in vegetation succession, and nutrients are among the most important plant resources that structure plant communities (Grace & Tilman, 1990; Vitousek & Howarth, 1991). This is because different plant species vary in their ability to tolerate different levels of nutrient limitation, which in turn causes competition (Koerselman & Meuleman, 1996). Nutrients are limiting to plant growth when the demands of the growing plant cannot be fulfilled (Verhoeven *et al.*, 1996b; Boeye *et al.*, 1997). The most common nutrients to limit plant growth are N, P and to a lesser extent, K. During succession, the relative availability of soil N and P shifts from initially being N-limited in early succession to P-limitation during late-succession (Olson, 1958; Vitousek & Reiners, 1975; Tilman, 1987; Berendse, 1990; Vitousek *et al.*, 1993). In the first stages of succession, P is more readily available, as weathering dissolves phosphates from newly exposed rock and N availability is relatively low because of the absence of previously stored organic N. This shift has also been demonstrated for wetlands by Verhoeven *et al.* (1996b), who showed that early-successional rich-fens were generally N-limited while late-successional bogs were P-limited. Recently, it has been proposed that the N:P ratio of the vegetation can be used to identify the nature of nutrient limitation in plant communities (Koerselman & Meuleman, 1996). In this chapter the 'N:P tool' will be used to characterise the nature of nutrient limitation in plant communities on Goss Moor and establish any shift in nutrient limitation in relation to hydroseral stages, ranging from open-water pools to fen carr, as a means of identifying successional pathways.

Nutrient availability was first proposed as a controlling factor of plant growth in the field of agronomy. According to Von Liebig's Law of the Minimum (Von Liebig, 1840) crop growth is always limited by one of the mineral nutrients, and when the limiting nutrient is

supplied in excess, another nutrient becomes limiting (Verhoeven $et\ al.$, 1996b). For mature crops, concentrations found to indicate nutrient limitation were equal to, or lower than, 14 mg g^{-1} for N, 0.69 mg g^{-1} for P and 8 mg g^{-1} for K (De Wit $et\ al.$, 1963). However, in a review of 40 fertilisation studies in natural and semi-natural habitats Koerselman & Meuleman (1996) found the majority of the values for N-limitation were below the critical values determined for crops (De Wit, $et\ al.$, 1963) and there were some N-limited systems with distinctly higher values. The same principal applied for P concentrations, although more P-limited stands have P concentrations above the critical level for crops (Koerselman & Meuleman, 1996; Verhoeven $et\ al.$, 1996b).

Plants absorb N from soils in the two ionic forms of nitrate (NO_3^-) and ammonia (NH_4^+). These forms differ from each other in mobility and in cost of assimilation by the plant. Nitrate is more mobile, easily leached, and must be reduced with the enzyme nitrate reductase before it can be incorporated into plants. In contrast, ammonia is less mobile, less leachable, and can be readily incorporated into nitrogen-containing compounds in the plant. Phosphorus is an essential part of many sugar phosphates involved in photosynthesis, respiration and other metabolic processes, and it is also part of nucleotides, as in RNA and DNA, and of the phospholipids present in membranes (Salisbury & Ross, 1992). P is absorbed by the plant mainly as monovalent phosphate anion $H_2PO_4^-$ and less rapidly as the divalent anion HPO_4^{2-}. Soil pH controls the relative abundance of these two forms. On Goss Moor the substrate pH is less than 7, which means that $H_2PO_4^-$ would be favoured.

Traditionally, community level nutrient limitation was established in a factorial fertiliser experiment, where the major plant nutrients N, P and K were supplied (Chapin $et\ al.$, 1986). However, these experiments are time-consuming, laborious and involve disturbance

to the site. Also, the high supply rates may not have the same effects as the gradual nutrient inputs expected to occur in nature (Boeye et al., 1997). To overcome these drawbacks, the 'N:P tool' provides the same information as the fertilisation experiment but is faster, cheaper and causes less disturbance. The N:P ratio for a given plant community is attained from the mean total N and P contents of the species removed from that community. The use of the N:P tool was validated by work on European lowland fens by Boeye et al. (1997) and by comparisons to numerous fertiliser experiments on rich-fens, poor-fens, litter fens, bogs and dune slacks (Koerselman & Meuleman, 1996). In the review by Koerselman & Meuleman (1996), 85 % of the studies showed that plant growth was limited by either N or P. Co-limitation, defined as an increase in biomass following combined fertilisations, was found only occasionally. Further investigations of the results revealed that a N:P ratio of 15:1 separated N-limited from P-limited situations almost perfectly. When the N:P was lower than 14:1, plant growth was N-limited in 86 % of the cases. If the N:P ratio was higher than 16:1 plant growth was P-limited. At ratios between 14:1 and 16:1, either N or P was limiting or there was N and P co-limitation (Koerselman & Meuleman, 1996; Verhoeven et al., 1996b).

Plant communities respond to the addition of a limiting nutrient with an increase in primary production (Chapin et al., 1986), which is usually controlled by N and P. In a multi-species community, however, plant species may co-exist that are differentially limited by N and P. A site where certain species encounter severe P-deficiency may be P-rich to species that have special adaptations for P uptake (Verhoeven et al., 1993). Plants adapted to low-P sites have different characteristics to plants adapted to low-N sites (Tilman, 1985). Plant species adapted to low P availability have traits that maximise phosphate mobilisation and uptake. For example, exudation of phosphate solubilising substances, development of long thin roots or the presence of mycorrhizae (Verhoeven et

al., 1996b), which have been reported to stimulate the growth of grass species in particular (DiTomasso & Aarsen, 1989). Plant species adapted to low N availability are likely to have traits that optimise the use of N in the photosynthetically active parts of the plant, for example, through high N productivity or a long residence time of N in the leaves (Konings *et al.*, 1989). Plant species that have a symbiosis with N-fixing organisms, such as leguminous species, are capable of nitrogen dinitrogen fixation and are able to exploit the large N store in the atmosphere. Hence, the species composition of N-limited vegetation is expected to be different from that of P- or K-limited vegetation, even if the level of biomass production is similar (Verhoeven *et al.*, 1996b). In fens, plant growth is commonly limited by N (Hayati & Proctor, 1991; Verhoeven & Schmitz, 1991), P (Boyer & Wheeler, 1989; Kooijman, 1993) and occasionally K (DiTomasso & Aarsen, 1989; Koerselman & Verhoeven, 1995), or a combination of these three elements (Verhoeven *et al.*, 1996b).

7.1.2 C-S-R PLANT STRATEGIES

In addition to abiotic conditions, plant communities have been described by reference to plant strategies for acquiring resources and for reproduction (Grime, 1974; 1977; 1979). Plant strategies can be defined by the morphological and physiological traits of species, as exemplified by the ideas proposed by Grime and co-workers (1988). The three primary plant strategies Grime proposes are Competitive, Stress-tolerant, and Ruderal (C, S and R), which can each be represented by a separate corner of an equilateral triangle (Figure 7.1). Species which have slow rates of growth, infrequent flowering, and an evergreen habit are considered stress tolerators (Grime, 1979). Species which have rapid rates of growth, and the potential to produce a dense canopy of leaves are considered competitive strategists. Ruderal strategists are annuals with precocious flowering and reproduction. As well as the three primary strategies, four other substrategies are distinguished, which are combinations

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of the primary strategies: C-R, competitive ruderal; S-R, stress-tolerant ruderal; C-S-R, competitive stress-tolerant ruderal; and C-S, competitive stress-tolerant. The strategies of species occupying different communities can be found using strategy theory, without the need for a large amount of autecological data.
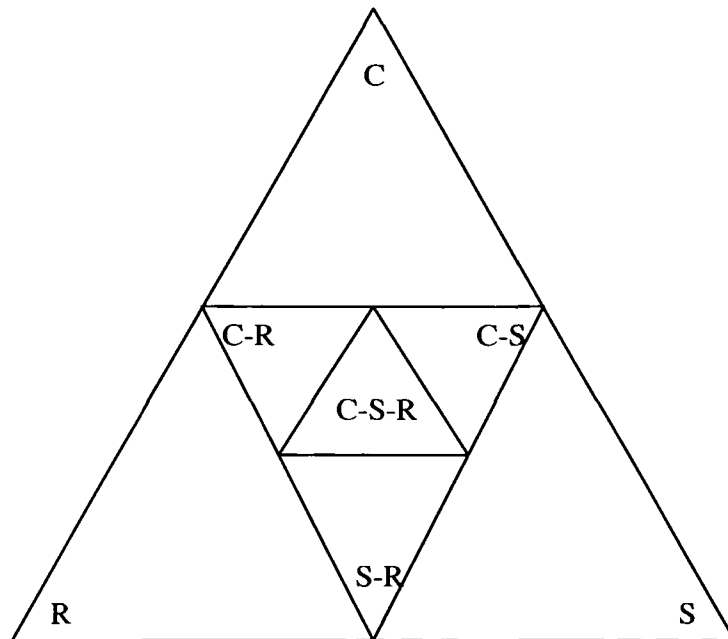
Figure 7.1 Positions of the three primary and four secondary strategies within Grime's (1974) triangular model of plant strategies.

Vascular species are assigned to one of the seven plant strategies by either using the extensive catalogue of British species found in Grime *et al.* (1988) or alternatively by using the simple dichotomous key (Table 7.1) (Grime, 1984). The dichotomous key bases strategy assignment on traits such as plant growth, canopy morphology and longevity.

Table 7.1 Key to plant strategy assignment based on morphological and phenological characters for vascular plant species, adapted from Grime (1984). R = ruderal; C-R = competitive ruderal; S-R = stress-tolerant ruderal; C = competitor; C-S-R = competitive stress-tolerant ruderal; C-S = competitive stress tolerant; S = stress-tolerant.

Annuals and monocarpic perennial	
Annuals	
Fast growing	
Precocious flowering	R
Delayed flowering	C-R
Slow growing	S-R
Monocarpic perennials	
Fast growing	C-R
Slow growing	S-R
Perennials	
Spring flowering	S-R
All other plants	
Rapid leaf turnover	
Rapid shoot proliferation	C-R
Shoots not proliferating rapidly	
Shoots tall and laterally extensive	C
Shorts short or creeping	C-S-R
Slow leaf turnover	
Shoots tall and laterally extensive	C-S
Shoots short or crowded	S

In the literature there is much controversy over the acceptance of Grime's ideas on plant strategies and the triangular model, which will be discussed further in section 7.4.2. However, to counterbalance the negative views many workers have endorsed Grime's ideas. Work by Bonham *et al.* (1991) used plant strategies to compare the life histories of species present in three sagebrush communities which dominate the sagebrush steppe of North America. Similarly, Cottrell (1996) used plant strategy theory in order to find relationships between two woodland habitats dominated by either *Salix planifolia* or *Salix monticola*. With the aid of detrended correspondence analysis, Cottrell defined which plant strategies and abiotic factors, such as pH and summer redox potentials were important to the structure of each willow carr vegetation type. Using this information, it was possible to predict the strategies of species occurring in other similar habitats.

The relative importance of the three primary plant strategies in vegetation communities can be used to identify successional patterns (Grime, 1979). However, the potential productivity of a habitat plays a controlling role. All successional sequences begin with the initial colonisation and decline of the ephemeral ruderal strategists. In the most productive habitats, the course of succession is characterised by a middle phase of intense competition in which competitive herbs, then competitive, shade-tolerant shrubs and finally trees dominate the vegetation (Grime, 1977). In unproductive habitats, plant biomass remains low, the dominant life forms being lichens, bryophytes, small herbs and dwarf shrubs, and the course of succession moves almost directly from the ruderal to the stress-tolerant phase. These successional sequences suggested by Grime (1977) represent those with fixed potential productivity. However, in most natural habitats, productivity either progressively increases or decreases (Grime, 1977). In this chapter, the species of the plant communities on Goss Moor will be characterised according to their plant strategies. These will then be aggregated to give the overall plant strategies for each community and applied to Grime's triangular model to identify any successional pathways.

7.1.3 AIMS

The aims of this chapter are to:

- utilise the N:P tool to establish the nature of nutrient limitation for the various wetland plant communities on Goss Moor as a means of identifying any successional differences;

- use plant strategy theory to distinguish successional sequences and allude to the productivity of the wetland communities on Goss Moor.

7.2 METHODOLOGY

Differences in nutrient limitation between early- and late-successional vegetation were investigated using foliage samples collected from the range of hydroseral communities recognised on Goss Moor. These included poor-fen and willow carr community types identified in Chapters Three and Four, and open-water pools. In previous studies using the N:P tool all species including perennial herbs, Cyperaceae and grasses were sampled to give an average critical N:P ratio for that community. As time was a constraint and to be consistent, the N:P ratio of only one species was chosen from the hydroseral communities for the study on Goss Moor. *Menyanthes trifoliata* was chosen for the destructive samples, as it is common in willow carr, open water and all stages of the hydroseral succession proposed in Chapter Three. In this research, it is assumed that the N:P ratio of *Menyanthes trifoliata* represents the N:P ratio of the whole community.

In late May 1999, 194 above ground biomass samples of *Menyanthes trifoliata* were collected from open-water, poor-fen and willow carr communities. As the N:P analysis was entirely exploratory, samples were collected from across the breadth of the moor, south of the River Fal, to identify any broad trends. The relatively early collection date was chosen to maximise concentrations of N and P in the foliage (Shaver & Melillo, 1984). Two samples were collected at each site to identify any variation occurring at each sampling point. Each sample included three trifoliate leaves, which were removed from the stem approximately 5 mm below the leaves. The samples were dried at 70°C for 48 h on the same day of collection and then milled in an electric blender. To determine total N and total P, the organic N and P was converted to ammonium and phosphate, respectively using the semi-micro Kjeldahl method (Allen, 1989), which is described below.

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Abundance data were collected at each sampling point site following the NVC sampling procedure (Rodwell, 1991a; 1991b; 1995). A 2 x 2 m quadrat was used for open-water pools, poor-fen and ombrotrophic vegetation and a 4 x 4 m quadrat was used for willow carr communities. Data recording and plant taxonomic nomenclature were as described in Chapter Three. Quadrat data were collected in order to classify the vegetation data into TWINSPAN groups, which could then be related to the classifications established in Chapters Three and Four. Abundance data were also necessary for the plant strategy analysis, which is described in section 7.2.2.

7.2.1 THE KJELDAHL METHOD

From each milled vegetation sample two known weights of pseudoreplicate amounting to approximately 0.12 g were each added to a separate digestion tube. Pseudoreplications were used to identify any discrepancies in the colorimetric analysis, which is often temperamental. To each pseudoreplicate 10 ml of salicylic acid and sulphuric acid mixture (Bremner & Mulvaney, 1982) was added and left to stand for at least five hours. After this period, 10 ml of 1M sulphuric acid and a selenium catalyst mixture (a modification of the Kjeldahl method; Bremner & Mulvaney, 1982) was added. The samples were placed on a Tecater digestion block and boiled for 5 hours. After cooling, the digest was carefully mixed with distilled water, filtered using Whatman GFC filter paper and made up to a 250 ml.

The N and P concentration of the digests were quantified colorimetrically. The P concentration was found using molybdic heteropoly acid, the phospho molybdenum blue method. N concentration was found using a similar reaction to the indophenol blue method, but using a nitroprusside catalyst, where ammonium utilises the Berthelot

reaction. The mean value of the two sub-samples was used in the final analysis to reduce variation.

7.2.2 STATISTICAL ANALYSIS

The quadrat data from all sampling locations were classified using TWINSPAN, following the procedure outline in section 3.2.2.1. Differences among the N:P ratios and the N and P concentrations of the pseudoreplicates from each of the wetland vegetation types classified using TWINSPAN were investigated by single factor ANOVA and the Tukey multiple comparisons test (Statgraphics version 4.0, U.S.A.).

7.2.3 TRIANGULAR ORDINATION USING THE GRIME MODEL

An ordination of the plant strategies associated with each of the hydroseral plant communities identified by TWINSPAN was carried out following Bonham *et al.* (1991) and Cottrell (1996). Firstly, all vascular species found in the quadrat survey of sample plots were assigned to one of seven plant strategies. Plant strategies for the majority of species found on Goss Moor were given in Grime *et al.* (1988), plant strategies for the few remaining species were found using the dichotomous key (Table 7.1) and the aid of Stace (1997) to make intelligent classifications.

Although the triangular model has three axes, the plant communities are ordinated using the stress and disturbance coordinates, only, and not the competition axis. The stress and disturbance coordinates corresponding to each of the seven strategies can be found in Table 7.2, which relates to triangular model in Figure 7.2. The coordinates of the four secondary strategies, C-R, C-S-R, C-S and S-R of Grime's (1977) triangular model correspond to the geometric centres of each triangle. The coordinates of the three primary C, S and R strategies are shown in Figure 7.2.

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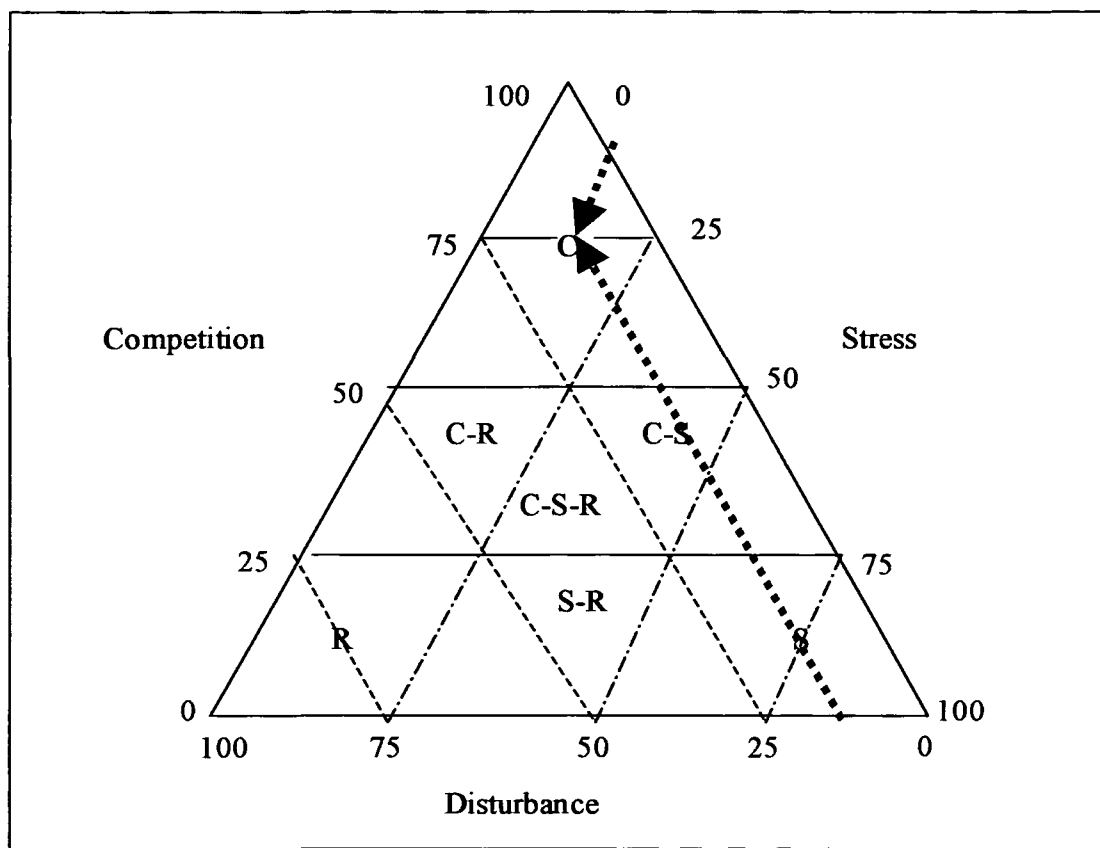
Figure 7.2 Model describing the various equilibria between competition, stress and disturbance in vegetation and the location of the primary and secondary strategies. C; S; R; C-R; S-R; C-S; C-S-R. I_c, relative importance of competition (⎯⎯); I_s relative importance of stress (⎯ ⎯ ⎯); I_d relative importance of disturbance (------). Adapted from Grime (1984). ⎯⎯→ shows how the C value is found using the stress and disturbance axes.

Table 7.2 Coordinates of the seven plant strategies used to ordinate plant communities within Grime's triangular model (1974; 1977; 1979).

Plant strategy	STRESS	DISTURBANCE
C	12.5	12.5
C-S	42	17
C-S-R	34	34
C-R	17	42
R	12.5	75
S-R	42	42
S	75	12.5

The cover value of each species was multiplied by the stress coordinate for its strategy. The products were then summed within each community to yield the stress coordinate for that community. Disturbance coordinates were calculated in the same manner, using the

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disturbance coordinates for each strategy. All communities were then applied to the triangular ordination by their calculated stress and disturbance coordinates for each strategy.

7.3 RESULTS

7.3.1 THE TEN VEGETATION TYPES

Altogether 97 quadrat and 194 biomass samples were collected. The results of the TWINSPAN analysis revealed that there were ten wetland communities represented in the study. This included an open-water community (I), three swamp communities (II, III and IV), a tall-herb fen (V), ombrotrophic poor-fen communities (VI and VII) and three willow carr communities (VIII, IX and X).

Table 7.3 shows summary descriptions of the ten communities and their corresponding poor-fen and willow carr community types, identified in Chapters Three and Four. The locations of the 97 quadrats are shown in Figure 7.3. All of the vegetation types were distributed evenly across the site, except Group I the open water community which was restricted to the south of the moor below the access track. As discussed in section 2.1.2.5, the access track is raised on an aggregate bank which acts as a dyke impeding water movement to the centre of the moor.

Table 7.3 The ten wetland plant communities identified by TWINSPAN and their corresponding poor-fen and willow carr type, as recognised in Chapters Three and Four.

Community type	Community description	Number of quadrats	Corresponding to poor-fen community (P-F) and willow carr (W-C)	
I	Standing water /bare substrate- *Equisetum fluviatile- Juncus bulbosus*	6	-	
II	*Potentilla palustris-* bare substrate- *Menyanthes trifoliata- Carex nigra*	15	P-F	pf-A
III	*Menyanthes trifoliata- Potentilla palustris- Equisetum fluviatile*	5	P-F	pf-B
IV	*Potentilla palustris- Equisetum fluviatile- Juncus acutiflorus- Mentha aquatica*	15	P-F	pf-C
V	*Potentilla palustris- Juncus acutiflorus- Valeriana officinalis- Calliergon cuspidatum*	14	P-F	pf-D
VI	*Potentilla palustris- Juncus acutiflorus- Agrostis canina- Sphagnum* spp.	7	P-F	pf-G
VII	*Aulacomnium palustre- Potentilla palustris- Sphagnum capillifolium-Drosera rotundifolia*	8	P-F	pf-H
VIII	*Salix cinerea* ssp. *oleifolia* - bare substrate/open water- *Equisetum fluviatile- Potentilla palustris*	6	W-C	wc-Q
IX	*Salix cinerea* ssp. *oleifolia – Equisetum fluviatile- Potentilla palustris*	14	W-C	wc-R
X	*Salix cinerea* ssp. *oleifolia- Sphagnum squarrosum - Potentilla palustris*	7	W-C	wc-S
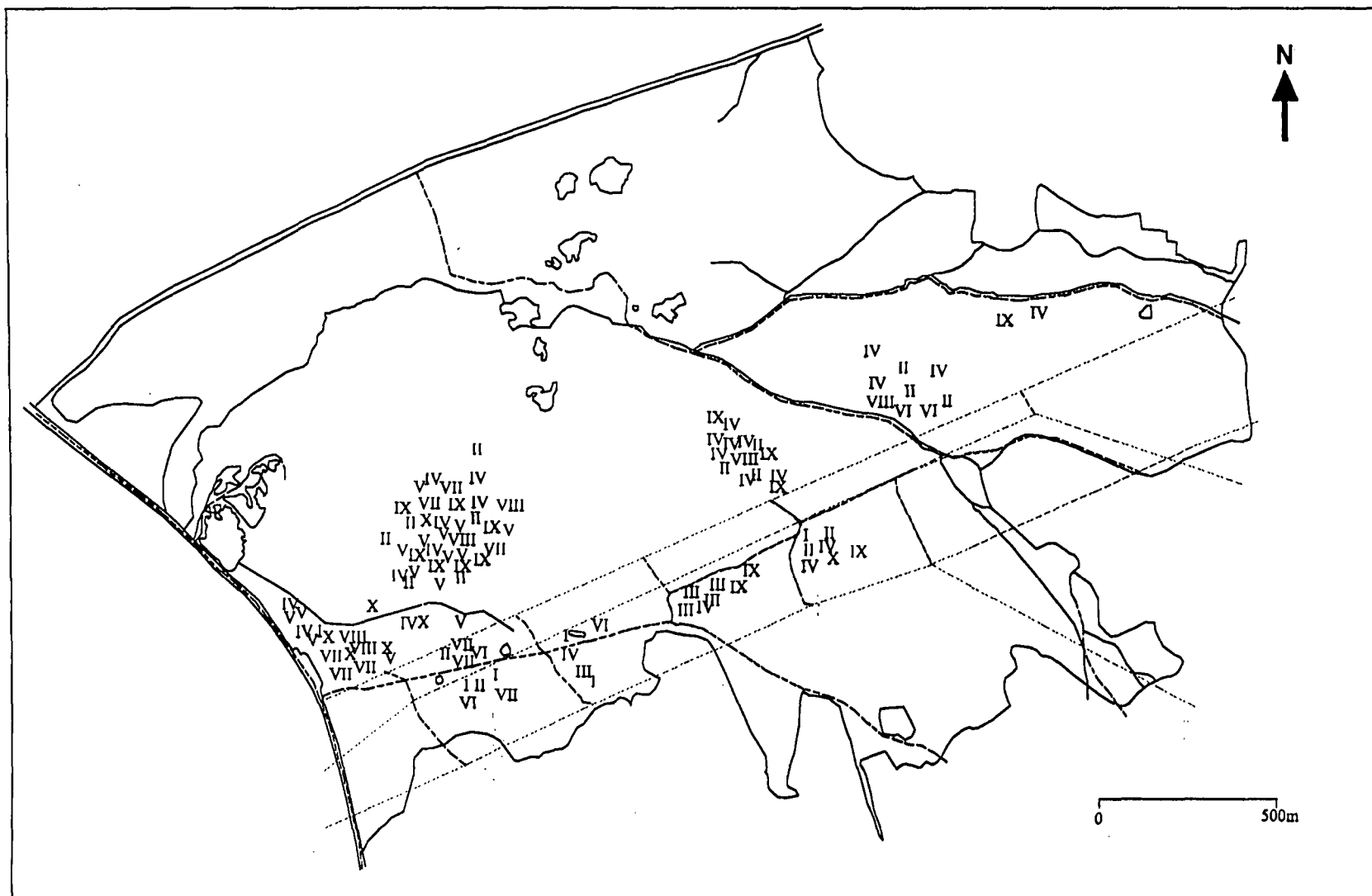
Figure 7.3 Locations of the sites used for the collection of quadrat data and foliage samples of *Menyanthes trifoliata* for Total N and Total P analysis. Groups I to X refer to the vegetation types described in Table 7.3.

7.3 2 THE N:P RATIOS OF *MENYANTHES* IN THE TEN WETLAND COMMUNITIES

Figure 7.4 shows the N and P contents of the *Menyanthes trifoliata* sampled from the ten wetland vegetation types. The N and P concentrations of *Menyanthes trifoliata* collected from each community are extrapolated to represent the N and P concentrations of the whole community. By using the N:P ratio threshold values proposed by Koerselman & Meuleman (1996), the type of nutrient limitation can be identified. When N:P>16 plant growth is thought to governed by P-limitation and when N:P<14, N-limitation is indicated. The majority of the vegetation on Goss Moor was N-limited. Only two samples showed P limitation and these were collected from the same willow carr community in Group X. The vegetation was dominated by *Salix aurita* with an ombrotrophic understorey of *Aulacomnium palustre*, *Sphagnum squarrosum*, *Menyanthes trifoliata* and *Juncus acutiflorus*. A few samples, namely those from Group I, were co-limited by N and P.
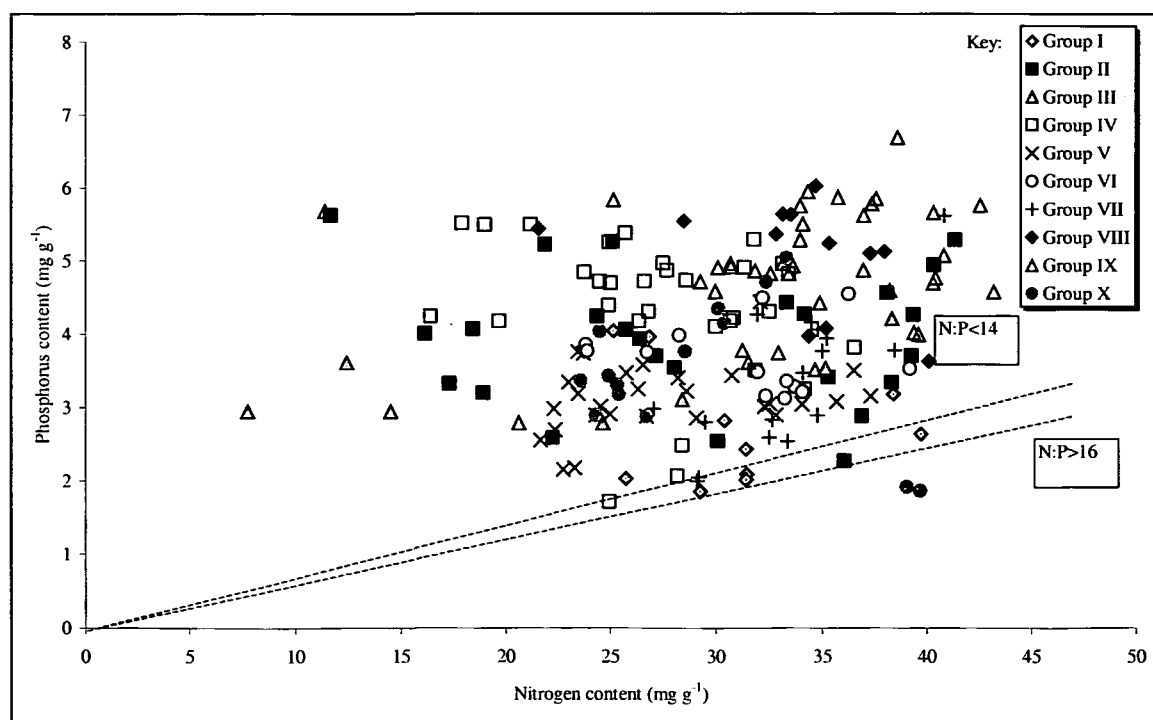
Figure 7.4 The relationship between *Menyanthes trifoliata* N and P and the nature of nutrient limitation of the ten wetland communities on Goss Moor. For clarity each point represents the mean N and P value of the pseudoreplicates taken for each sample. Dashed lines represent N:P ratios of 14 and 16, by mass. When N:P<14 plant growth is N-limited, and when N:P>16 plant growth is P-limited.

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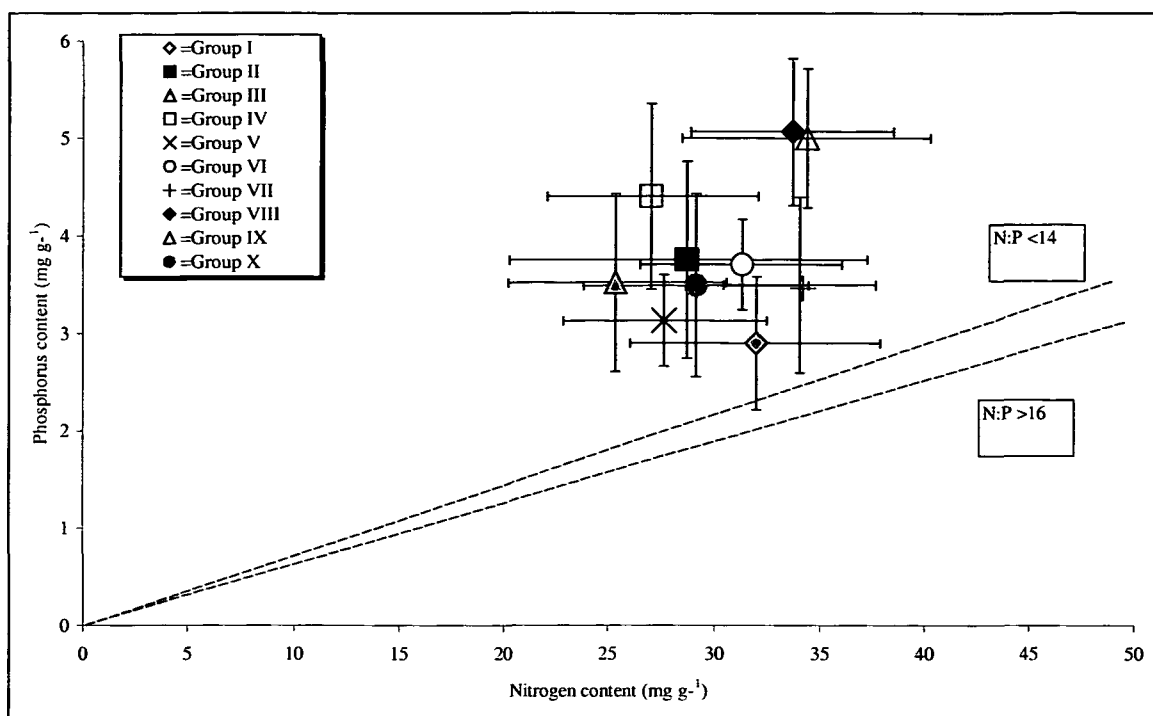
Figure 7.5 The mean and standard deviation of the N:P ratios of *Menyanthes trifoliata* vegetation samples removed from the ten wetland communities on Goss Moor. Dashed lines represent N:P ratios of 14 and 16, by mass.
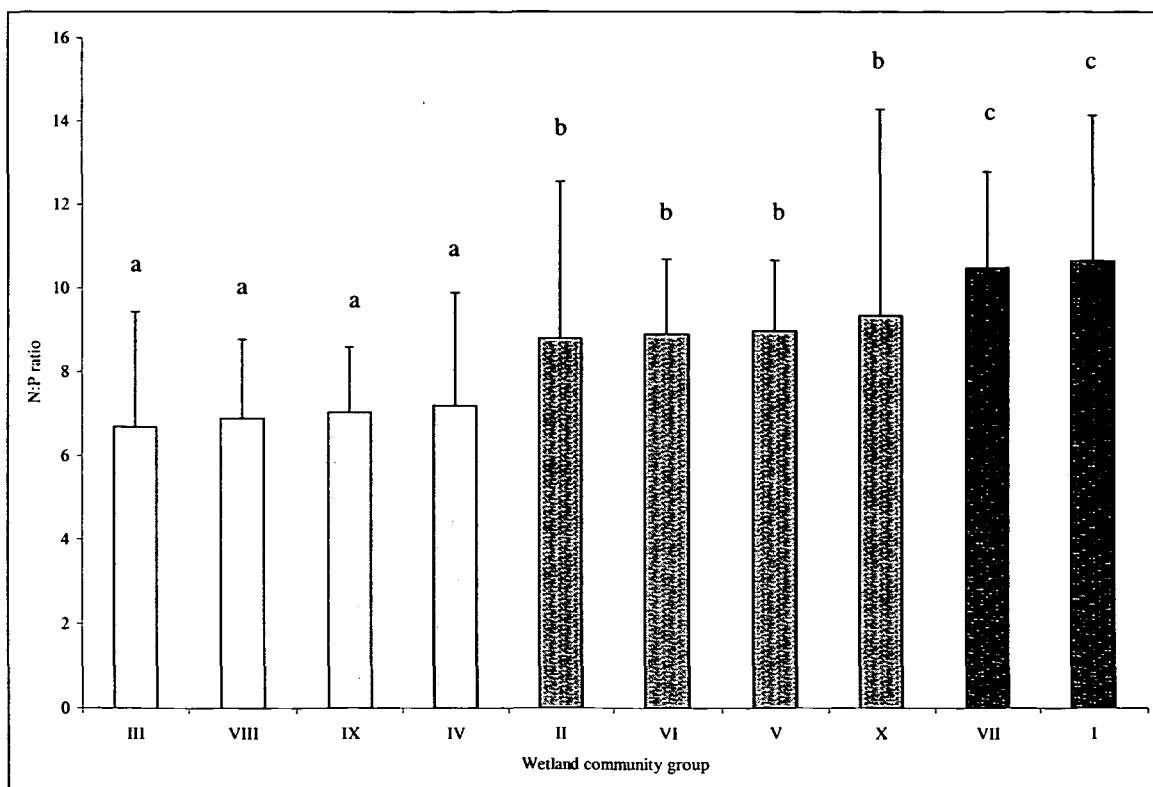
Figure 7.6 The mean and standard deviation of the N:P ratios for the ten communities studied on Goss Moor. Significant differences were found between those communities labelled with 'a' and 'c' P<0.05.

The mean and standard deviations of the N:P ratios from the ten wetland community types, show the communities are divided into two groups (Figure 7.5). The willow carr communities of groups VIII and IX appear to be separated from the other communities and have greater mean N and P contents.

Although the majority of the N:P ratios of the different plant communities were N-limited, significant differences were found among them. Figure 7.6 shows that the barely vegetated open-water pools and the *Aulacomnium palustre* ombrotrophic community, Groups I and VII, respectively, had the greatest N:P ratios ($P<0.05$). Swamp community groups III and IV, and willow carr community groups VIII and IX, were the lowest ($P<0.05$). The general ordering of the community groups from I to X represents possible hydroseral successional patterns, beginning with open-water pools and ending with willow carr communities. Therefore, the mean N:P ratios of the ten wetland communities represent no obvious successional trend. However, there was considerable variation in the N:P ratios of communities representing the same seral stage. Variation between the willow carr communities was reflected in the species compositions of their respective understoreys. Willow carr groups VIII and IX were species-poor with extensive bare substrate and resembled swamp, unlike the luxuriant species-rich ombrotrophic understorey associated with Group X.

There was a large amount of variation in P content ranging from 1.9 to 6.7 mg P g^{-1} dry weight. Even greater variation occurred in N content, which was 7.8 to 43.2 mg N g^{-1} dry weight. This variation was most likely to reflect differences in the supply ratio of N and P rather than differences in absolute N and P availability (Koerselman & Meuleman, 1996). Figure 7.7 shows the amounts of total N and total P associated with the ten vegetation types. Group I had the lowest total P and one of the highest total N ($P<0.05$). This may be

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related to the spatial distribution of the groups, all open water communities were situated south of the dyke and would most likely be affected by water draining from surrounding farmland. As shown in Figure 7.5, Groups VIII and IX were associated with the greatest combined N and P concentrations (P<0.05).
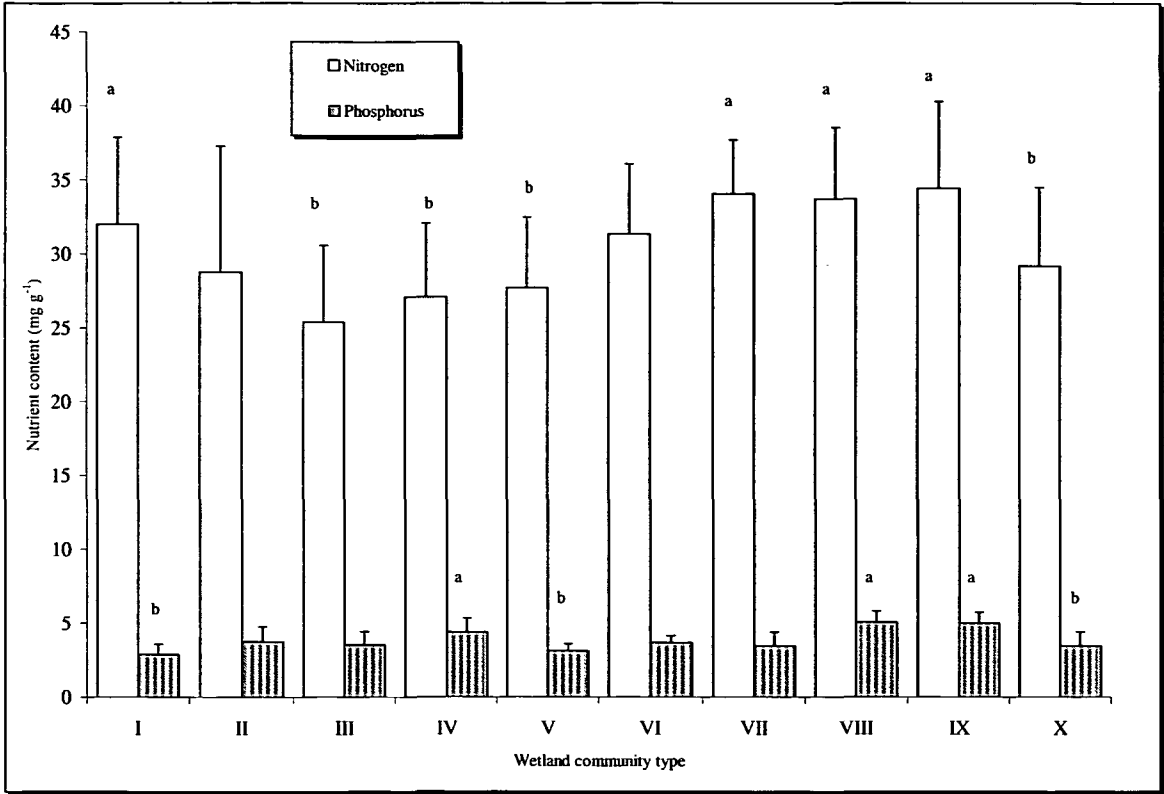
Figure 7.7. The mean and standard deviation of the total N and total P contents of the *Menyanthes trifoliata* vegetation samples taken from the ten wetland community types. Significant differences among N concentrations and P concentrations are labeled with different letters P<0.05 *i.e.* a is significantly different to b.

7.3.3 PLANT STRATEGY ORDINATION

The C-S-R plant strategy ordination (Figure 7.8) showed that all wetland plant communities were situated around the C-S area of the triangle, along the right hand edge of the C-S-R sub-triangle. The communities were situated on the ordination in two clusters, which represents a split between the poor-fen and willow carr. Intermediate to these clusters was Group VII, the ombrotrophic community. The sparsely vegetated open-water habitat was also situated away from the main clusters in the centre of the C-S-R sub-triangle. Communities dominated by *Salix cinerea* and *Salix aurita* were situated towards the top of the ordination, indicating that these were more influenced by competitive strategists than the open canopy communities. The poor-fen and swamp groups represented stress-tolerant communities. Frequent stress tolerators and competitive stress tolerators of these communities include *Carex nigra*, *Carex rostrata*, *Menyanthes trifoliata* and *Potentilla palustris*.

According to the direction of succession proposed by Grime (1974; 1977), all of the communities, except open-water (Group I), are situated at the same successional stage. Nevertheless, there are subtle successional differences, Groups II to V occur left of the green dashed line and Groups VI to X, to the right. Most of the variation is associated with the stress axis. In comparison to the disturbance axis along which scores were little dispersed (from 19.4 to 36.0; Figure 7.8), the stress axis varied from 24.2 to 48.1. Differences in the stress axis are thought to be related to the productivity of the habitat (Grime, 1977). This means that the willow communities are the most productive, followed by the open-water and finally the poor-fen and swamp communities.
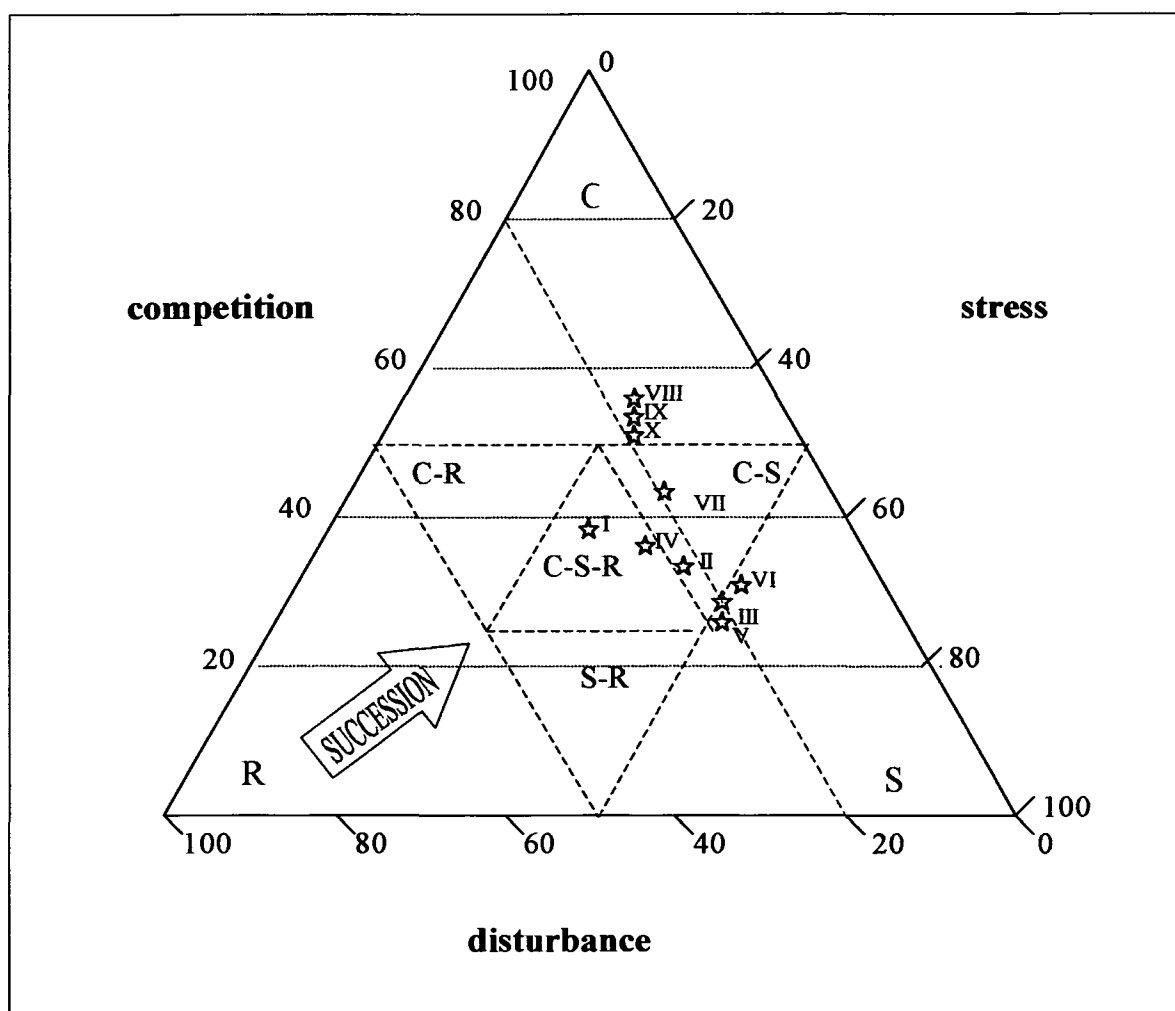
Figure 7.8 Mean plant strategy coordinates for each of the ten wetland communities (I-X). The stars indicate the mean strategy of each community, based on the strategies of member species weighted by their relative cover abundance. The direction of succession is represented by the green arrow. The green dashed line is only a guide to identify the community positions on the ordination.

7.4 DISCUSSION

This chapter has provided an exploratory analysis of the vegetation on Goss Moor using the N:P tool and plant strategies, which have both been used to assist with the description of successional processes (Grime, 1984; Verhoeven & Schmitz, 1991; Verhoeven *et al.*, 1996a).

7.4.1 N:P RATIOS

In this research, the N:P ratio for *Menyanthes trifoliata* was presumed to represent the type of nutrient limitation experienced by the whole community. Use of one species to indicate nutrient limitation in habitats such as wet heath, fen and bog was validated by Hayati & Proctor (1991) using *Molinia caerulea*, and Boyer & Wheeler (1989) and Tamm (1954) using *Juncus subnodulosus* and *Eriophorum vaginatum*, respectively. Using one species is an accepted method to estimate nutrient limitation in communities as any plant growing in certain conditions of nutrient availability is presumably adapted to inhabit that niche.

The nutrient contents of *Menyanthes trifoliata* collected from Goss Moor were comparable to those recorded in mires at Biebrza, Poland (Wassen *et al.*, 1995). In comparison to other wetland species such as *Potentilla palustris*, *Equisetum fluviatile* and the Cyperaceae, *Menyanthes trifoliata* was found to have significantly greater N and P contents (Wassen *et al.*, 1995). Nevertheless, the overall N:P ratio which indicates the nature of the nutrient limitation is comparable to other species in the same community (Shaver & Melillo, 1984; Koerselman & Meuleman, 1996). It should be noted, however, that *Menyanthes trifoliata* is clonal and can therefore grow in extensive patches by means of rhizomal growth. The implications of this trait were not investigated in this study, nonetheless, it is possible that shoots of *Menyanthes trifoliata* could inhabit sub-optimal environments and draw more suitable resources from neighbouring ramets via their rhizomes.

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Nutrient availability is a limiting factor in peat-forming wetlands because substantial amounts of N, P and humic compounds are sequestered (Clymo, 1978; Verhoeven et al., 1988) and stored in the peat. Hence recycling is incomplete and plant growth becomes more strongly limited by the availability of N and P, or both, than in terrestrial systems that accumulate much less organic matter (Verhoeven et al., 1990). On Goss Moor, nitrogen was the limiting nutrient in a range of different wetland vegetation types, which included open-water pools, swamp, poor-fen and willow carr habitats from across the site. Other wetland habitats found to exhibit N-limitation include wet heaths (Hayati & Proctor, 1991), rich-fens (Verhoeven et al., 1996a) and unmanaged poor-fens in the Netherlands, which had developed from open-water pools formed in the 1930s. N-limitation in these poor-fens was only reported in the early successional stages where vegetation was growing amongst floating-mats of organic material (Verhoeven, 1986; Verhoeven et al., 1988). The presence of N-limitation in poor-fen on Goss Moor verifies that the vegetation represents early successional stages. On Goss Moor, P-limitation was only recorded in one low-growing willow carr community dominated by *Salix aurita* and lawn-building bryophytes such as *Aulacomnium palustre* and *Sphagnum subsecundum*. The vegetation in this community was mature and growing above a substantial mass of organic material. The N:P ratio of this well developed ombrotrophic community may provide evidence to suggest a switch to a more advanced successional stage on Goss Moor.

If there was evidence to suggest a switch from N-limitation to P-limitation during succession one might expect those communities representing later successional stages to have greater N:P ratios than those from earlier ones. The mean N:P ratio of the ombrotrophic community Group VII, dominated by *Aulacomnium palustre* and *Sphagnum capillifolium* was significantly greater than the other community groups. However, the

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greatest mean N:P ratio of 10.6 was found in the sparsely vegetated open-water pools of Group I. With the omission of Group I, it seems that the presence of bryophytes were associated with the greatest N:P ratios. The high N and P contents and overall N:P ratio in the open water pools in Group I may be related to the geographic location. All open water pools sampled on Goss Moor were situated south of the dyke which was created to accommodate the tramway built in the 19 th century (Bennett, 1992). Vegetation growing south of the dyke is therefore more likely to be influenced by water draining from the surrounding farmland. Water that has originated from farmland would be expected to have higher concentrations of phosphates and nitrate, which would be reflected in plant tissue.

There was much phytosociological variation between and within the community types representing the same successional stage, as illustrated by the willow carr communities in the scrub phase. The understoreys associated with the willow communities in groups VIII and IX were species-poor swamp, dominated by bare substrate. The understoreys of groups VIII and IX were very different to the luxuriant species-rich ombrotrophic understorey associated with Group X willow carr. In successional terms, the understorey community of Group X was more developed than the understoreys of Groups VIII and IX. For this reason, further investigations into the N:P ratios of different successional stages would need to pay special attention to the understorey structure of the willow carr communities, rather than the dominant species alone.

One reason for the prevalence of N-limitation, even in the scrub dominated areas of Goss Moor, may be due to the preponderance of standing water. Water inundation deoxygenates the substrate, which leads to the demise of nitrifying bacteria and thus a reduction in the rate of soil N mineralisation. Water inundation therefore reduces the amount of N available to plants. As well as water inundation, widespread N-limitation on Goss Moor may be

indicative of low concentrations of soluble phosphates in water inputs from drainage channels and surface flow (Verhoeven *et al.*, 1993). Some plant species show special adaptations for utilising the large store of inorganically bound P that accumulates in fen systems. Such species are able to overcome the P-limitation in their habitat and become N-limited. If, however, the orthophosphate availability in such habitats increases as a result of changes in water chemistry, bringing about dissolution of the inorganic bound P, the 'lithotrophic' species would lose their advantage and be replaced (Verhoeven *et al.*, 1993). Therefore, if N-limitation on Goss Moor is related to low phosphate water inputs, any change to the water source would alter the vegetation composition. Similarly, any changes to the water source increasing the amount of nitrates would affect the N:P balance and, thus, vegetation composition. Changes in water inputs to Goss Moor are conceivable in the future as the catchment is dominated by farmland used for livestock grazing and china clay mining. Both of these industries are in decline.

The N:P tool ratio may not be sufficiently sensitive to distinguish between different successional stages on Goss Moor due to the recentness of the habitats. Tin streaming and other tin deeming activities were most prominent in the 1800s and ended in the 1920s (Chapter Two), which means the youngest communities began development 80 years ago. The age of habitats on Goss Moor therefore ranges between 80 and 200 years old. A successional switch between the N:P ratios of mid- and late-successional mesotrophic fens in habitats similar in age to those on Goss Moor was found by Verhoeven & Schmitz (1991). In these mesotrophic fens the mid-successional ponds were created 100 years previous and the late-successional pond was created at least 180 years before (Verhoeven & Schmitz, 1991). Although the age of the ponds on Goss Moor and Vechtplassen are comparable the 'switch' on Goss Moor may not have yet occurred. This is possible because the rate of succession on nutrient-rich soils is faster than succession on more

nutrient-poor soils, like those on Goss Moor (Prach, 1993). Also, in some ecosystems such as those that have evolved on volcanic islands, the N:P switch takes thousands of years (Chadwick *et al.*, 1999). As well as differences in the speed of successional processes at different sites, there are also important differences regarding their location. In the literature, evidence for the 'switch' has never been reported at the same site. All successional sequences were inferred from different sites with comparable histories displaying similar patterns of terrestrialisation. This investigation on Goss Moor provides the first within site analysis of the N-P switch from vegetation associated with different stages of hydroseral succession.

The 'switch' from N- to P-limitation could be obscured by differences between the N and P cycle, which can maintain or accentuate N-limitation by positive feedback mechanisms, whatever the initial cause (Vitousek *et al.*, 1993). Nitrogen-deficient plants produce tissue and litter that has higher carbon:nitrogen ratios and relatively higher contents of lignin and other recalcitrant compounds than plants with sufficient nitrogen (Vitousek, 1982). Their tissue therefore decomposes relatively slowly, and the microorganisms decomposing it immobilise large quantities of N for long periods of time (Melillo *et al.*, 1982). This immobilisation in turn reduces nitrogen availability in plants and the cycle continues towards greater N-limitation as long as organic nitrogen continues to accumulate. These positive feedback mechanisms can also apply to P, although organic P can be mineralised on demand, thus, completing the feedback cycle (Vitousek & Howarth, 1991). However, in the aquatic environment once *Sphagnum* spp. invades the fen community changes in N availability can occur (Koerselman & Verhoeven, 1992). The bulk of the *Sphagnum* spp. litter is mostly composed of cell walls which are very resistant to decomposition, have a high C:N ratio and contain hardly any N and P but are rich in 'inhibitor' compounds that slow down microbial growth (Clymo, 1983). The cell membranes and protoplasm of

Sphagnum spp. form only a minor component of the dry weight, are rich in N and P with a low C:N ratio and decompose rapidly (Koerselman & Verhoeven, 1992). These low total rates of *Sphagnum* spp decay can nevertheless lead to high rates of nutrient mobilisation and thus N availability, which would in-turn affect the type of nutrient limitation (Koerselman & Verhoeven, 1992).

7.4.2 C-S-R PLANT STRATEGIES

The plant strategies of the different species present in the ten communities were a useful means for identifying successional patterns on Goss Moor. By using the triangular ordination of the ten communities and the direction of terrestrial succession proposed by Grime (1974; 1977), a logical successional sequence was obtained, thus, conforming to Grime's theory. The sequence began with open-water pools, followed by poor-fen and ended with the willow communities. However, Grime's model may need some modification to accommodate for succession in aquatic environments. According to Grime's model succession begins with the colonisation by ruderal strategists, which are either annuals or monocarpic perennials. However, the colonisation of open water pools on Goss Moor appears to begin with *Juncus bulbosus,* *Equisetum fluviatile* and *Menyanthes trifoliata*, which are not ruderal strategists. *Equisetum fluviatile* is a competitive-ruderal strategist, which comes closest to a ruderal strategist although this species is common in all communities on Goss Moor.

The C-S-R plant strategy ordination showed that poor-fen and swamp vegetation represented stress-tolerant communities, while *Salix cinerea* and *Salix aurita* willow communities were dominated by competitive and competitive stress tolerator strategists. The plants of poor-fen and swamp communities are typical stress tolerators (Koerselman &

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Verhoeven, 1992), which means they acquire and store resources for future less favourable conditions (Boeye *et al.*, 1997). Common stress tolerators and competitive stress tolerators on Goss Moor include *Carex nigra*, *Carex rostrata*, *Menyanthes trifoliata* and *Potentilla palustris*. These plants have slow potential growth rates (Grime *et al.*, 1988) and traits which are an evolutionary response to chronically low productivity (Grime *et al.*, 1988). The majority of stress tolerators exploit habitats containing low availability of mineral nutrients like N and P. On Goss Moor the plants are exploiting habitats with low N availability. Figure 7.9 shows the interacting characteristics of plant strategies that are adaptive under conditions of low nutrient availability. The water-logged conditions associated with the poor-fen and swamp communities on Goss Moor means that successful plants either have low respiration rates during part of the growing season, develop morphological traits such as aerenchyma tissue that permit transport of oxygen to the rhizosphere, or tolerate products of anaerobic respiration (Jackson & Drew, 1984).

Competitors such as *Salix cinerea* and *Salix aurita* are characterised by a dense canopy of leaves, and extensive lateral spread above and below ground. Competitors monopolise resource capture in relatively crowded and undisturbed conditions. Rapid response to resource availability is paramount.

The invasion of plants with large stature such as *Salix cinerea* represent a consistent feature of vegetation succession. Species which contribute a large component to the plant biomass (Grime, 1977) represent the existence of an additional dimension to the three main strategies controlling the composition of plant communities. This other dimension is dominance. Large competitive dominants, such as the *Salix* spp. on Goss Moor, remove a large amount of resources from the environment.
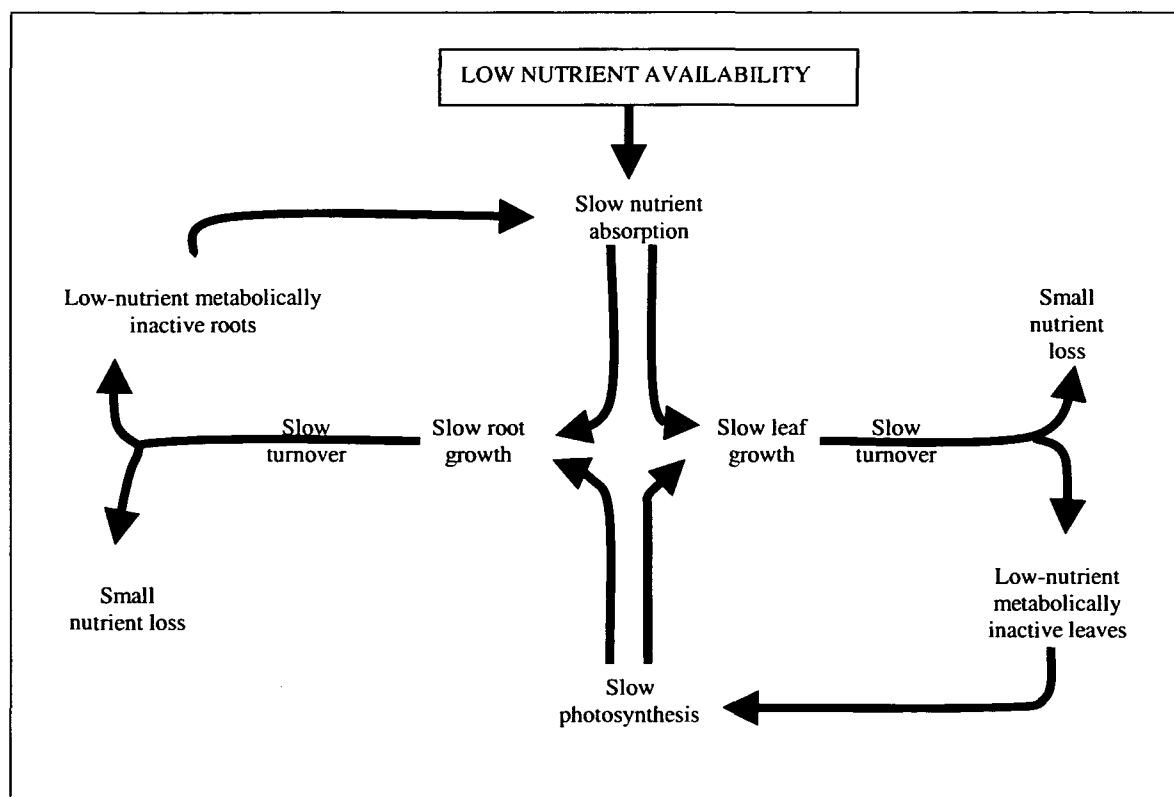
Figure 7.9 Interacting characteristics of plant strategies adapted for conditions of low nutrient availability. Adapted from Chapin (1980).

As well as successional differences, the majority of variation occurred on the stress axis, which is directly related to the productivity of the habitat (Grime, 1977), which means that the willow communities were the most productive habitats, followed by the open-water and finally the poor-fen and swamp communities. The small dispersion of scores on the disturbance axis indicates that this axis was less important in the description of the vegetation than the stress and competition axes.

In general, the different traits of individual species from each community on Goss Moor lead to explainable and logical associations, and thus appears to conform to Grime's theory. This was despite the fact that it was difficult to assign some plant species to their associated strategy, fortunately the majority of plant strategies were found in Grime *et al.*,

(1988) and only five of the species on Goss Moor were found using the key (Table 7.1).

Also the strategies inferred for all U.K. plant species were based on work conducted in the

Sheffield area of England. However, the geographic location of the original research is not

the major drawback (Silvertown *et al.*, 1992).

The most prevalent opposing theory to Grime's plant strategies based on life-histories is

the more reductionist demographic approach (Silvertown *et al.*, 1992). Recently, attempts

were made to reconcile the two opposing theories. This was done by comparing traits used

by Grime (1974; 1979) to superficially similar demographic variables (Silvertown *et al.*,

1992), which can be used to calculate the fitness of a life-history phenotype (Silvertown *et*

al., 1992). The three demographic processes that contribute to the finite rate of population

increase (λ) are fecundity (F), growth (G) and survival (L), which superficially relate to C-

S-R: Competitors maximise growth (C$\approx$G); stress-tolerators must maximise survival

(S$\approx$L); and ruderals, which are essentially fugitive species and rely on maximising

fecundity (R$\approx$F) (Silvertown *et al.*, 1992). The demography of a plant population can be

summarised by the stage specific rates at which individuals develop from one life-history

stage to another by growth, survival, reproduction, fecundity and regeneration. These

stages allowed population projection matrices to be constructed, which classified 18 herb

species using both CSR and demographic theories (Silvertown *et al.*, 1992). The results of

the experiment showed no correspondence between C-S-R and *GLF* even though

correspondence is plausible (Silvertown *et al.*, 1992). The main reason for conflict

between the theories was related to life cycle of plants. Grime bases the C-S-R

classification on the established phase of the mature plant and the projection matrix

summarises the whole life cycle of plants, which seems more realistic.

Grime's use of the established phase of plants to base the C-S-R strategies was the main criticism made by a number of authors (Smith & Huston, 1989; McCook, 1994; Grubb, 1998; Stanton et al., 2000). In many cases, Grubb (1998) found that established, adult plants of dominant species of many nutrient–poor habitats such as heath and bog conformed well to Grime's stress-tolerator strategy. However, there were examples of species that were not wholly concordant (Grubb, 1998), for example adult *Calluna* plants, whose relative growth rate greatly increased within 1-2 years by addition of N, P and K (Aerts, 1993). *Calluna vulgaris* therefore only conforms to Grime's stress-tolerator strategy as a seedling. This behaviour emulates the switching strategy (Grubb, 1998). On this basis, Grubb (1998) recommended that the stress-tolerator strategy of Grime (1977; 1979) should be replaced by three different sub-strategies of the main strategy. These are:

(i)   'low-flexibility strategy', where species are stress-tolerant throughout the whole life of the plant and are characterised by long-lived leaves, low maximum growth rates and inflexibility of form and low gas exchange rates, when resource shortage is relieved throughout the whole life of the plant;

(ii)   'switching strategy', where species display the low-flexibility strategy as young seedlings, but are flexible in form as older plants, and commonly have high relative growth rates then; and

(iii)   'gearing down strategy', which is based on the ability of a species to reduce strongly the respiration rate when resources are in short supply, both as seedling and as adult. Plants showing this strategy have some characteristics which are the opposite of those shown by plants with the low-flexibility strategy: short-lived leaves, and high flexibility in form and in rates of gas exchange.

Also Loehle (1988) found the triangular model distorted the species data, because the three-dimensional space relating to the three axes were crammed into two dimensions of a triangle. The two-dimensional model results in the loss of information, and generated overly restrictive assumptions about strategic or environmental trade-offs. To replace the triangular model Loehle recommended the use of three independent axes and a standard rectilinear two or three dimensional plot, although their graphic representation is difficult (Loehle, 1988). With reference to the demographic variables, distortion of triangle does not occur using the three new variables (*G, L* and *F*) as they sum to unity when measured as proportional contributions to λ (the finite rate of population increase).

Thus the plants of the wetland communities on Goss Moor show traits of stress toleration, which enable the plants to exploit habitats which are N-limited with persistently high water levels.

7.5 SUMMARY

- Nitrogen was the limiting nutrient in a range of different wetland vegetation types on Goss Moor, which included open-water pools, swamp, poor-fen and willow carr habitats across the site.

- The high mean N:P ratio of a well developed ombrotrophic community may provide evidence indicating a switch to a more advanced successional stage on Goss Moor.

- N-limitation was attributed to the prevalence of high water levels or low concentrations of phosphates in water inputs.

- The nutrient content of *Menyanthes trifoliata* collected on Goss Moor was similar to that recorded in mires at Biebrza, Poland.

- The plant strategies of the different species present in the ten communities were a useful means for identifying successional patterns on Goss Moor.

- Grime's triangular model needs modifications to accommodate for succession in aquatic environments.

- Further work is necessary to attempt to reconcile Grime's plant strategies based on life-histories of established plants and the more reductionist demographic approach.

In the next and final chapter the findings of all chapters will be brought together and discussed.

Chapter Eight: General discussion

8.1 INTRODUCTION

This thesis has examined the plant ecology and community dynamics of poor-fen and willow carr on Goss Moor NNR, which together possess great ecological value. Poor-fen and willow carr exist as mosaics formed as a result of past anthropogenic activities, primarily tin-streaming. These activities were extensive, resulting in unusual microtopographies which are fundamental to the diversity of the vegetation. The main aim of the research was to reach a greater understanding of the ecology and community dynamics of poor-fen and willow carr communities, with the ultimate aim of aiding their conservation at this site. To satisfy this aim, the first part of the study focused on the description and spatial distribution of the poor-fen and willow vegetation types. Secondly, lattice-wombling was used to characterise successional spatial patterns, which provide the basis to understanding the community dynamics of the wetland. The third part of the research was to monitor and identify the water regimes associated with selected wetland vegetation types. Finally, an exploratory analysis of the putative successional patterns was conducted using the 'N:P tool' and Grime's C-S-R plant strategies.

8.2 MAIN FINDINGS OF THE THESIS

In Chapter Three, the identification and description of the poor-fen communities on Goss Moor suggested twelve poor-fen vegetation types with a diversity of compositions. The communities described included four swamp communities: *Potentilla palustris-Carex nigra* (pf-A); *Potentilla palustris-Menyanthes trifoliata* (pf-B); *Potentilla palustris-Juncus effusus* (pf-C); *Potentilla palustris-Equisetum fluviatile* (pf-D). Three poor-fen communities: *Potentilla palustris-Sphagnum recurvum* (pf-E); *Potentilla palustris-Sphagnum squarrosum* (pf-F); and *Potentilla palustris-Eriophorum angustifolium* (pf-G). Three bog communities: *Potentilla palustris-Aulacomnium palustre* (pf-H); *Calluna vulgaris-Sphagnum capillifolium* (pf-I); and *Eriophorum angustifolium-Sphagnum*

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papillosum (pf-K) (Figure 8.1 on page 340). The two remaining communities (pf-J and pf-L) were transitional between poor-fen and NVC M25 *Molinia caerulea-Potentilla erecta* mire (Rodwell, 1991b). These descriptions provide the first formal characterisation of poor-fen variation on Goss Moor NNR and serve as a valuable basis for effective future management. The botanical characteristics of these poor-fen communities and their distribution along a primary environmental gradient of organic depth, surface water height and bare substrate was concordant with existing phytosociological literature on poor-fen (Moore & Evans, 1991). Ellenberg Indicator values were used to extrapolate environmental information not collected in the field. Novel weighted community Ellenberg Indicator values for nitrogen, reaction and moisture were an effective tool for indicating subtle differences in the conditions associated with the poor-fen communities.

The separation of the poor-fen communities along a moisture gradient was considered as spatial evidence for hydroseral succession. It was proposed that the successional process begins with the colonisation of open-water pools created by tin excavations by floating hydrophytic communities. Shallow pools were colonised by the *Potentilla palustris-Carex nigra* community (Group pf-A) and deeper pools were dominated by *Potentilla-palustris-Equisetum fluviatile* (Group pf-D). These pools are gradually invaded by mat-forming bryophytes, which generally grow immediately above the water table to form a raft. In the shallow ponds this hydroseral stage was dominated by Group pf-I *Calluna vulgaris-Sphagnum capillifolium*, and Group pf-H *Potentilla palustris-Aulacomnium palustre* dominated in deeper ponds. On Goss Moor, those communities with a well developed bryophyte layer are therefore more terrestrialised and indicate older communities than hydrophyte-rich communities.

The most frequent poor-fen community found on Goss Moor was Group pf-B a *Potentilla palustris-Menyanthes trifoliata* swamp community. Group pf-B was found at 20 locations, covering almost 20 % of the whole poor-fen resource. Group pf-B was restricted to the west and centre of Goss Moor, where the surface water levels were greater and movements were more conspicuous, thus maintaining conditions for the growth of early successional swamp vegetation. In contrast, the rarest poor-fen communities were Groups pf-F and pf-H which together covered less than 6 % of the whole poor-fen resource. In successional terms, these communities were considered more advanced than Group pf-B, and Group pf-H the *Potentilla palustris-Aulacomnium palustre* community was further terrestrialised than Group pf-F *Potentilla palustris-Sphagnum squarrosum*. This trend was a general feature of the poor-fen on Goss Moor: more than 50 % of the resource was early successional or swamp; almost 22 % was poor-fen and 13 % was bog or the most terrestrialised by mat-forming bryophytes.

In Chapter Four, willow carr was classified into eight different understorey communities, representative of the variation occurring within the NVC W1 *Salix cinerea* ssp. *oleifolia* community (Rodwell, 1991a). This research provides the first formal in-depth description of *Salix cinerea* woodland in the south-west of England. The composition of the understorey communities was related to the age of the willow carr, whereby the number of poor-fen species in the understorey communities of willow carr generally decreased with age. This relationship was related to the increase in canopy cover and, therefore, shade.

This thesis has provided the first detailed architectural analysis of willow, not only on Goss Moor but in the U.K. Useful descriptors of the age of willow on Goss Moor were the height of the first fork, the number of live secondary shoots, tree height and dbh, all of which generally increased with age. Indicators of the general vigour and well-being of the

willow trees revealed the prevalence of positive morphogenesis and reiteration, which represent high productivity and the availability of a generous energy supply for growth (Oldeman, 1978).

The study of aerial photographs taken over the last six decades proved a valuable means of defining the spread and growth of willow carr on Goss Moor. From these investigations, it was possible to describe the general pattern of events that occur during the willow scrub stage of wetland succession. Since 1946, willow has invaded Goss Moor at an average rate of 22850 m^2 per year. The most prolific willow spread occurred between 1963 and 1975 when the average rate was 52983 m^2 per year. The areas of the moor experiencing the fastest rates of invasion were in the northern and southern regions, where the wetland habitats were less widespread.

In the wetland habitats willow invades areas with the greatest amounts of accumulated organic material and a low water table. Species that grow above the water table in raised cushions, such as *Aulacomnium palustre* and *Sphagnum recurvum*, provide suitable conditions for willow germination. Following successful colonisation, willow between 10 and 25 years old continued to be associated with a large amounts of organic matter, although the poor-fen species in the understorey were in decline. Between 25 and 40 years old, standing water was a significant component of willow carr and trees were commonly growing on mounds raised above the water level. Between 40 and 55 years, poor-fen species were further reduced and bare ground dominated, along with Graminoids and species of dry woodland such as *Lonicera periclymenum* and *Hedera helix* (Grime *et al.*, 1988). Oak saplings were found in the oldest and driest willow, indicating the beginning of secondary woodland.

The spatial analysis of the three tranome areas by the lattice-wombling method, described in Chapter Five, showed that certain plant communities were associated with either ecotone or ecocline boundary types. Ecotones or abrupt boundaries were found between heath communities and wetland vegetation. Ecotones were also found between densely vegetated tall-herb fen and willow carr with a very diminished understorey composition. Ecoclines or gradual boundaries were found only between communities that displayed subtle differences in their composition. In previously tin-streamed areas with a large amount of substrate heterogeneity, ecocline boundaries were found between *Potentilla palustris-Juncus effusus* (pf-B) and *Potentilla palustris-Aulacomnium palustre* (pf-H) poor-fen communities. In more homogenous habitats, ecoclines were found between *Potentilla palustris-Juncus effusus* (pf-B) and another less swamp-like community (pf-A) without *Menyanthes trifoliata*, but containing patches of *Calliergon* spp. mosses. The spatial relationship between these swamp and poor-fen communities was taken as evidence for space-for-time successions. The two different successional pathways reflect differences in location and microtopography, which in turn affects the water regime of the locale. Successional patterns on Goss Moor were associated with both ecotone and ecocline boundary types. However, various other associations from the COA data were revealed by the vector diagrams, which may indicate multiple pathways of succession. Evidence for multiple pathways in succession was presented by Walker (1970) and Miles (1987), who found that generally there was no single preferred pathway of terrestrialisation in succession and often stages were omitted.

In Chapter Six, the water regime was found to be governed by substrate heterogeneity created by tin stream-mining. The most homogeneous microtopography was associated with the deepest inundation and greatest amplitude in water depth, and most closely resembled the rainfall data. Also, there was less differentiation between the water levels of

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the community types present in this habitat. The most complex microtopography resulted from the most intense tin-streaming activity. Therefore the history of Goss Moor plays an important role in governing the contemporary water regime, vegetation distribution and successional pathways.

In the surface water survey, rush pasture experienced the most dry days, the lowest mean water level and amplitude. In contrast, poor-fen had the fewest dry days, the greatest water level amplitude and the highest overall mean and winter mean surface water levels. The ombrotrophic communities were characterised by very stable water regimes with low amplitude and variation, and remained inundated throughout the summer. Compared to the other willow communities, young willow experienced the greatest number of dry days and the lowest water levels. The hydrological conditions of areas recently colonised by willow are harmonious with studies of wetland invasion by other woody species (Gill, 1970). Although not statistically significant, summer water levels for young willow on Goss Moor were lower than the other five vegetation types studied, which may indicate the amount of drying necessary before colonisation can take place.

In contrast to the non-willow communities, all willow communities were associated with the lowest water levels and therefore experienced a greater degree of drying. The association between the colonisation of woody plants and drying in wetlands (Tansley, 1939; Walker, 1970) is, however, almost certainly partly dependent upon other environmental variables, although their significance is unknown (Wheeler *et al.*, 1999). Once willow has invaded the wetland, further colonisation of trees is encouraged by enhanced drying caused by evapo-transpiration, which is considerably greater in trees and shrubs than herbaceous plants due to the greater leaf area index. The invasion of willow in

a community is thought to represent the initiation of secondary fen carr woodland (Tansley, 1935) and the next successional stage.

Chapter Seven provided an exploratory analysis of the successional patterns of the wetland vegetation on Goss Moor using the N:P ratio and Grime's C-S-R plant strategies. The N:P ratio can be used to identify the nature of nutrient limitation in plant communities (Koerselman & Meuleman, 1996). The N:P ratio of *Menyanthes trifoliata* from plant communities representative of different successional stages was investigated to establish whether there was a switch from N-limitation in early-succession to P-limitation in late-succession (Vitousek & Reiners, 1991). Results showed that nitrogen was the limiting nutrient in a range of different wetland vegetation types on Goss Moor. N-limitation has also been identified in a number of habitats including wet heaths (Hayati & Proctor, 1991), rich-fens (Verhoeven *et al.*, 1996) and in the early successional stages of poor-fen in the Netherlands (Verhoeven, 1986; Verhoeven *et al.*, 1988). N-limitation in poor-fen on Goss Moor suggests the vegetation represents an early successional stage. The only evidence for a switch to P-limitation was recorded in one low-growing willow carr community dominated by *Salix aurita* with a luxuriant lawn of bryophytes including *Aulacomnium palustre* and *Sphagnum subsecundum*. Therefore in this instance the N:P tool is not sufficiently sensitive to distinguish between successive seral stages, but only ones several stages apart.

The prevalence of N-limitation on Goss Moor may be due to the persistence of standing water across the site. Water inundation deoxygenates the substrate, which leads to the demise of nitrifying bacteria and thus a reduction in the rate of soil N mineralisation. Water inundation therefore reduces the amount of N available to plants. An alternative is that there are low concentrations of phosphates in water inputs from drainage channels and

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surface flow. However, the most realistic explanation for N-limitation on Goss Moor is the contemporary nature of the communities. In the early stages of ecosystem development, there is insufficient N in the system to permit P–limitation.

The precedence of N-limitation on Goss Moor corresponded to values on N availability extrapolated from the weighted Ellenberg numbers for N. The N values for poor-fen communities ranged between 2 and 3, indicating infertile sites with poor mineral N conditions. Ellenberg's (1991) N scale has been linked to the annual mineralisation rates of N in a number of habitats (Diekmann & Falkengren-Grerup, 1998).

The strategies of the different plant species present in the ten communities were effective for identifying successional patterns on Goss Moor. The ten communities could be ordered into a logical successional sequence using Grime's triangular ordination (Grime, 1974; 1977). The sequence began with open-water pools, followed by poor-fen and ended with the willow communities. However, Grime's model may need to be modified to account for differences in the plant strategies of the species that initially colonise aquatic environments. None of the species growing in sparsely vegetated open water pools on Goss Moor were ruderal as predicted by the Grime's (1977) model. Plants adapted to invade the open water ponds are largely stress-tolerant.

The C-S-R plant strategy ordination showed that poor-fen and swamp vegetation represented stress-tolerant communities, while *Salix cinerea* and *Salix aurita* willow communities were dominated by competitive and competitive stress tolerator strategists. Although the combinations of species traits from each community lead to explainable and logical associations of the data, use of the C-S-R strategies have been criticised, as some plant species are able to change their life strategy when under stress (Oksanen & Ranta,

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1992; Stanton *et al.*, 2000). Grubb (1998) found examples of species that had different strategies throughout their life cycle, for example *Calluna vulgaris* only conforms to Grime's stress-tolerator strategy as a seedling (Aerts, 1993). On this basis, Grubb (1998) recommended that the stress-tolerator strategy of Grime (1977; 1979) should be replaced by three different sub-strategies of the main strategy.

The most prevalent opposition to Grime's plant strategies theory is related to its incompatibility with demographic variables such as growth, fecundity and survival (Silvertown *et al.*, 1992). The demography of a plant population can be summarised by the stage specific rates at which individuals develop from one life-history stage to another by growth, survival, reproduction, fecundity and regeneration. Further work is necessary to reconcile demographic theories with Grime's plant strategies of established plants.

As well as successional differences, the majority of variation on the triangular ordination occurred on the stress axis, which was directly related to the productivity of the habitat (Grime, 1977). Willow communities were the most productive habitats, followed by the open-water and finally the poor-fen and swamp communities.

8.3 IMPLICATIONS OF THESIS FINDINGS FOR WETLAND MANAGEMENT AND CONSERVATION

Goss Moor NNR is a unique and nationally-important site. The phytosociological surveys detailed in Chapters Three and Four identified a large amount of variation within the semblance of poor-fen and willow carr vegetation. The ecological value of the vegetation on Goss Moor was acknowledged by its status as a National Nature Reserve and Site of Special Scientific Interest (SSSI) in 1988. However, management on the reserve is very

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unfocused, concentrating mainly on scrub removal from areas of easy access. In order to
preserve the quality of the resource on Goss Moor, there is need for more refined, smaller
scale conservation and management measures relating to specific vegetation types. To
accomplish this, the rest of this section uses the main findings of the thesis to prioritise
conservation issues in order to make management recommendations for the wetland
habitats on Goss Moor. The main suggestions are summarised in Figure 8.1.

In a national context, the importance of wet woodlands was recognised by their inclusion
into the UK Biodiversity Action Plans in 1998 (UK Biodiversity Group, 1998), as priority
habitats for immediate conservation action. However, it is evident that there is generally a
dearth of information regarding wet woodlands. The main objective of the Biodiversity
Action Plan was to maintain the current extent of semi-natural wet woodlands by
developing a national framework for management through policy and legislation. Another
objective of the Biodiversity Action Plan was to develop and implement systems for
recording the occurrence, distribution, management and composition of wet woodlands. In
this thesis the data on willow carr provides an important contribution towards the
inventory on Cornish wet woodlands, regarding their composition and extent. This
research provides detailed phytosociological and hydrological documentation of the
sequence of events at different stages of carr development. This ecological information is
valuable for the investigation of ways to assist wet woodland development in relation to
other priority habitats such as fens, a further target of the Action Plan.
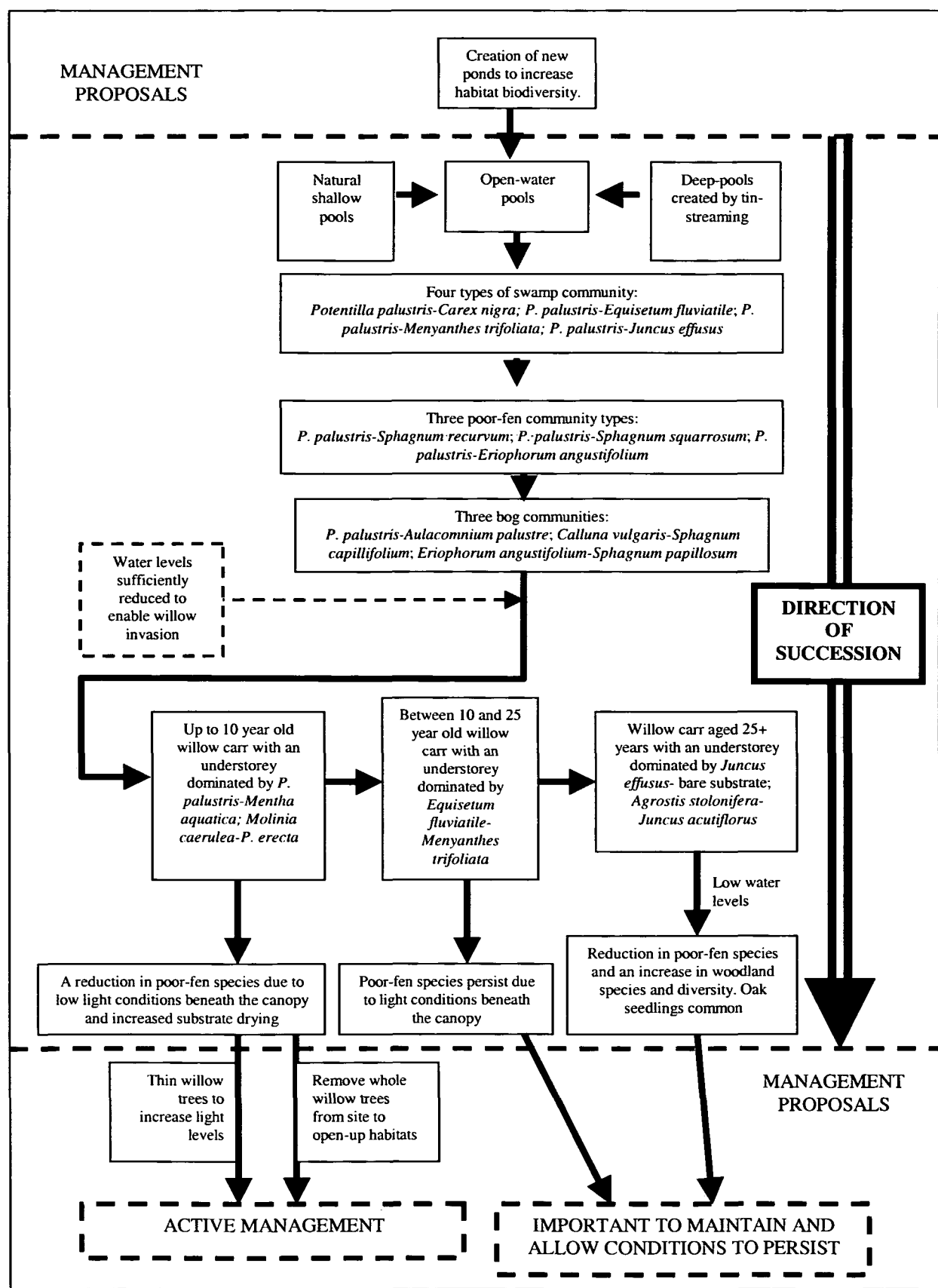
Figure 8.1 Flow diagram summarising the main findings of the thesis and their implications for conservation management of the wetland habitats on Goss Moor NNR.

Presently, management on Goss Moor involves the large scale removal of the willow carr by uprooting and burning on site, in order to reduce the amount of willow to the 16 % protocol recognised by English Nature as a manageable amount of scrub for any site (I. Davies pers. comm.). In Chapter Four, it was found that willow carr covered almost 46 % of the survey area on Goss Moor, exceeding the English Nature scrub protocol by 30 %. Normally, the colonisation of open herbaceous wetland habitats by willow carr is actively discouraged, based on the assumption that scrub encroachment leads to loss of diversity and conservation value. In terms of species richness, willow carr on Goss Moor is species-poor. The most species-rich willow understorey community was *Potentilla palustris-Mentha aquatica* (wc-S) with an average of 13.4 species per quadrat. However, this was similar to the two most species-rich poor-fen communities, which contained 13 and 14 species. In comparison to the seven other wet woodland NVC communities identified by Rodwell (1991a), W1 was one of the least diverse (Wheeler *et al.*, 1999), containing a mean of 17 species per sample. On Goss Moor, *Salix cinerea* ssp. *oleifolia* woodland, like poor-fen communities, appears to be intrinsically species-poor. This can be attributed to the recentness of the site and geographical location.

The species richness of the willow understorey communities was related to the age of the willow trees. The most recent willow was associated with the most diverse understorey communities. Over time, diversity and the number of poor-fen species gradually declined and was lowest when the willow was between 30 and 40 years old. After this, diversity gradually increased to another peak in willow established before 1946. The increase in diversity with age represents a general decline in poor-fen species and an increase in Poaceae and woodland species. *Quercus* spp. seedlings were often found in these older willow communities representing the beginning of the next seral stage. As the habitats on Goss Moor are entirely anthropogenic, without an established history of management, it

would be interesting to adopt a non-traditional approach to management by not removing the majority of the scrub. If the natural development of wetland habitats on Goss Moor is permitted in some areas, it will maintain the habitat diversity of the site. The Goss Moor reserve is large enough to accommodate all stages of the hydrosere from open pools to dry oak woodland.

The number of poor-fen species in the understorey of willow carr generally decreased as canopy cover and the amount of shade increased. It has been suggested that even-aged stands with closed canopies would naturally create gaps in the canopy as trees die and/or fall, leading to an increase in the overall floristic diversity (Wheeler et al., 1999). To enhance the natural process of gap creation within the willow carr, some areas of trees could be thinned to increase the amount of light reaching the understorey. Areas suitable for thinning would be willow carr that is sufficiently wet enough to still support poor-fen species in the understorey, although their abundance has greatly diminished due to reduced light levels. The willow carr that fits these criteria are generally less than 40 years old.

Despite the trends outlined above, there was a large amount of variability between the willow stands, as some species-rich poor-fen understorey communities such as Group wc-R the *Equisetum fluviatile-Potentilla palustris* community were found in all ages of willow. For this reason, priority should be given to conserving these species-rich willow communities over the species-poor communities of the same age. To ensure species-rich willow is conserved, it is recommended that a full vegetation survey is conducted in willow carr nominated for removal. If willow in these nominated areas is then subsequently removed, the vegetation survey will provide a useful reference point to monitor the progress and recovery of habitats undergoing such disturbances. To make certain that willow carr is represented from all of the age classes characterised in this

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thesis, architectural determinants (Chapter Four) such as height of the first fork and the number of live secondary shoots, tree height and dbh can be used in the field.

However, pragmatically, it is easier to remove the recently invaded willow, as the whips can be pulled up with minimum disturbance to the fen surface. The removal of willow from these fen habitats will not only help maintain the integrity of vegetation communities and suspend succession, but, also these areas will probably have better recovery rates because disturbance, and the loss of the poor-fen species would be minimal.

In areas where willow is to be removed, it is recommended that the scrub is felled using a chainsaw and quickly transported from the fen surface. Leaving brash and logs on site can cause localised enrichment and heavy shade, which in particular kills *Sphagnum* spp. (Brooks & Stoneman, 1997). The removal of waste material should be done carefully to reduce damage to the fen surface by trampling and dragging of heavy branches. Fortunately, most of Goss Moor has good access tracks across the site leading to the north, east and south of the reserve. If it is necessary to burn the removed scrub, it should be transported to a dry and safe location away from the fen and burned surrounded by a firebreak. Burning on site damages the fen surface by trampling and ash enrichment.

In comparison with the national poor-fen survey (Shaw & Wheeler, 1990), the species richness of poor-fen communities was low on Goss Moor. As poor-fen is by nature species-poor, species rarity provides a useful means for prioritising areas for conservation (Ratcliffe, 1977). Nationally rare species, which are common on Goss Moor and found only in the south of England are *Cirsium dissectum* and *Lycopus europaeus. Scutellaria minor, Myrica gale, Oenanthe crocata, Hypericum elodes* and *H. undulatum* are oceanic, *H. undulatum* being confined to the south-west of England. *Potamogeton polygonifolius* is

a locally widespread mire species. As all poor-fen communities on Goss Moor contain one or more of these species in small proportions (Chapter Three), special attention should be paid to conserving them. Also, in a Cornish context, some key poor-fen species are uncommon within the county (French, 2000). The principal species of poor-fen communities on Goss Moor, *Potentilla palustris*, is of particular importance as it only occurs in 3 % of the total area of Cornwall. Over the last century, *Carex curta* has become increasing rare throughout Cornwall (French, 2000), yet it occurs sporadically in all wetland habitats on Goss Moor.

Although the poor-fen communities on Goss Moor were species-poor, the communities with the greatest species-richness were the *Potentilla palustris-Juncus effusus*, *Potentilla palustris–Sphagnum recurvum*, *Potentilla palustris-Aulacomnium palustre*, *Calluna vulgaris-Sphagnum capillifolium* and the *Molinia caerulea-Rhytidiadelphus squarrosus* communities, which correspond to groups pf-C, pf-E, pf-H, pf-I and pf-J, respectively. Of these poor-fen groups, pf-H and pf-I are infrequent and together form less than 6 % of the total poor-fen resource of 1464.2 m^2. Both these poor-fen communities have developed in small deep-sided pools between gravel-banks, which are relics of tin-streaming. As these communities are rare on Goss Moor, it would be advantageous to increase their occurrence, by creation (Figure 8.1). Ponds can be dug amongst the gravel banks up to 2 m in depth, which was the deepest recorded depth in the poor-fen survey, although shallower pools will terrestrialise faster. The size of the pools can be based on those already present on the moor: Group pf-H ranged from 1 to 10 m^2 and Group pf-I ranged from 2 to 15 m^2. Once these ponds have been created, it would be interesting to monitor the nature and rates of vegetation development, which will be useful as a reference for management decisions.

The water regime plays an integral role in maintaining the wetland communities on Goss Moor and any disruptions would almost definitely impact the vegetation composition. Likely causes of these changes include the diversion of water courses to or away from the moor or increased rainfall. An increase in water levels would initially affect the composition of rush pasture, the driest community and possibly alter the colonisation rates of willow carr, which prefer reduced water levels during the summer (Gill, 1970). An increase in water inputs may alter the vegetation composition indirectly by altering the N cycle. This may occur because greater water levels reduce N availability by reducing soil N mineralisation rates. In these conditions, stress-tolerators rather than competitive strategists such as *Salix* spp. would be better able to survive (Grime, 1979).

Recent attempts to manage the water regime on Goss Moor were made in 1996. In the eastern section of the River Fal a series of weirs were installed to raise the river height and impede flow and thus increase the residency time of water in the surrounding wetland habitats. These operations were undertaken as an aid to halt the rapid expansion of willow scrub on the site, which was attributed to a reduction in surface water levels. It will be interesting to learn the outcomes of this manipulation.

Land-use changes in the surrounding catchment can also have an effect on the vegetation on Goss Moor. Any modifications in agricultural practice that leach nitrates and increase the quantities of nitrogen reaching the Goss Moor ecosystem are particularly important. Additional nitrogen inputs, together with *in situ* mineralisation, increase the N supply to exceed plant demands. In such cases, the system exports nitrates to adjacent ecosystems or N_2O to the atmosphere or is poisoned by excess nitrogen (Aber *et al.*, 1989). The N economy of both early- and late-successional habitats would change, so that N-limited ecosystems become nitrogen saturated (Vitousek & Reiners, 1975). Changes in nitrogen

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supply are expected to influence the rate of successional changes and may also influence their trajectories (Bazzaz, 1996). An increase of N deposition in the locality of Goss Moor may cause a marked increase in productivity, although shifts to P limitation have not been reported (Verhoeven *et al.*, 1993). Probable sources of increased N deposition may arise from increased use of the A30 trunk road by motor vehicles, north of the moor or from the oil-fired power station (Indian Queens Power Ltd) at Gaverigan (Figure 2.2), west of Goss Moor. Five years of monitoring of the plant communities has however revealed no evidence to suggest N deposition has any influence on the vegetation (Dale *et al.*, 2000).

Finally, it is vital to recognise that vegetation on Goss Moor has evolved and developed under both anthropogenic and natural processes and presently exists in a dynamic equilibrium with them both. Ecological processes are not static and conservation and management policies must, therefore, recognise the need to maintain dynamism inherent to Goss Moor. Any inappropriate developments, which may upset the dynamic balance of the site, such as land-use changes in the surrounding catchment or alterations to the water regime must be avoided.

8.4 FUTURE RESEARCH

To establish the importance of the poor-fen and willow carr communities in a national context and prioritise vegetation for conservation, it would be useful to utilise the Fenbase data base (Wheeler, 1997). The database would enable biodiversity and target species scores to be obtained for the range of poor-fen and willow communities found on Goss Moor.

The large-scale removal of willow carr on Goss Moor aims to restore the poor-fen vegetation and increase the species richness of the site. This relies largely on one or a combination of: fen species being already present in the understorey, persistence of fen species in the seed bank, or the propagules of fen species reaching the site (Wheeler *et al.*, 1999). To establish the success of scrub removal and prioritise areas for future removal, seed-bank surveys of different aged willow carr and understorey would be valuable.

The architectural analysis of willow trees together with the aerial photograph analysis in Chapter Four was an effective and unique way to age trees in the field. However, in future studies, it may be useful to compare these results with tree cores, which allow the precise age of the tree to be found.

The lattice-wombling method was effective for surveying most of the habitats on Goss Moor. However, in areas where the microtopography was most heterogeneous the lattice-wombling sampling strategy was unable to identify any significant relationships between the different vegetation types and their boundary class. It is suggested that vegetation mosaics and patches smaller than 10 m^2 could be sampled by the lattice-wombling method at 5 m intervals, rather than every 10 m. Alternatively, the triangulation-wombling method could be adopted, which enables irregularly spaced samples to be collected from vegetation mosaics of interest (Fortin, 1994).

The use of Water Monitoring Devices to investigate the surface water fluctuation of the different wetland vegetation types on Goss Moor provided valuable results. However, further research is possible. Although 60 weeks of water monitoring data have produced some interesting results, a longer water sampling period would be beneficial.

The exploratory analysis of hydroseral succession using the N:P tool provided an interesting insight into nutrient limitation on Goss Moor. However, investigations were not exhaustive. As illustrated by the willow carr communities, there was a large amount of variation between and within the understorey vegetation of community types representing the same successional stage. For further investigations into the N:P ratios of different successional stages, special attention to the understorey structure of the willow carr communities could be made. The understorey vegetation could be divided according to the degree of terrestrialisation based on amounts of bare substrate, water depth, swamp species and the extent of ombrotrophic bryophytes. Although using the N:P ratios of foliage from one species is a recognised method to identify the type of nutrient limitation for whole communities (e.g. Boyer & Wheeler, 1989; Hayati & Proctor, 1991), the method may not be suitably sensitive to identify differences between similar communities. To identify any subtle differences between communities occurring next to each other in the hydroseral sequence it would be interesting to collect foliage samples from a range of species.

This research has focused on the dynamics of the plant communities on Goss Moor. However, fauna also play an important part in the ecosystem. Wet woodland is an important habitat for many invertebrate and vertebrate taxa, including a number of priority species otter *Lutra lutra* L., craneflies *Lipsothrix ecucullata* Edwards, 1938 and *L. errans* (Walker, 1848) (JNCC, 1998). Open wetland habitats are important for species that include breeding snipe *Gallinago gallinago* L. and the hen harrier *Circus cyaneus* L. (Fuller, 1982). It is therefore important that the requirements of the fauna, as well as flora, should be taken into account in the planning of management for Goss Moor. To this end, a full survey of the animal populations and their associated habitats on Goss Moor is recommended.

8.5 CONCLUSION

The research presented in this thesis represents a significant, positive contribution to knowledge and understanding of the ecology of poor-fen and willow carr communities, and hydroseral succession in habitats created anthropogenically, specifically by tin-stream mining. Hydroseral development from open water ponds, to swamp, poor-fen and finally willow carr has been quantified and described in detail. The results of this thesis have enabled preliminary formulation of practical management measures to effectively conserve the wealth of poor-fen and willow carr communities on Goss Moor.

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