Restoration of Lowland Raised Bogs Damaged By Peat Extraction - With Particular Emphasis On *Sphagnum* Regeneration

By

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Summary

1. Revegetation trends in abandoned peat workings indicate that peat cuttings are generally too dry for spontaneous re-establishment of raised bog vegetation. The latter was restricted to small flooded peat pits which had recolonised 'hydroserally' to support floating rafts of bog vegetation.

2. The water storage capacity of cut-over bog surfaces is low compared with undisturbed bog and blocking drains in a peat field at Thorne Moors, S. Yorks, was insufficient to prevent water-table instability. Experiments suggest this may severely inhibit *Sphagnum* growth. Lagoons may increase water storage on a bog surface and facilitate development of raised bog vegetation as floating rafts. This 'hydroseral' approach may be necessary to restore raised bog vegetation to some areas.

3. Hydrochemical conditions of cut-over sites may differ significantly from undisturbed bogs with implications for *Sphagnum* growth. Water samples from a peat field at Thorne Moors were comparatively acidic and contained comparatively high concentrations of most major ions (particularly NH_4 and SO_4), except phosphorus. Moderate nutrient enrichment is unlikely to adversely affect *Sphagnum* and additions of phosphorus to flooded peat pits significantly increased its growth. In solution culture, low pH (3.0-3.5) was sub-optimal for *Sphagnum* growth, but the use of $CaCO_3$ to reduce acidity in the field had a toxic effect.

4. *Sphagnum* recolonisation may be limited by availability of propagules in cut-over areas. Experiments indicate that deliberate re-introduction encourages *Sphagnum* raft development, which is pioneered by aquatic species that regenerate more prolifically from fragments than intact gametophytes. *Sphagnum* rafts are encouraged in shallow water (< 50cm) and pools of small area. Numerous management options exist physically and chemically assisting raft development.

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Chapter 1

Introduction

1. 1 *Raised bogs : their origins and development*

Raised bogs are peatland ecosystems which develop primarily (but not exclusively) in lowland areas such as basins, the head of estuaries and along river flood plains. In such locations drainage may be impeded by a high groundwater table or by low-permeability substrata, such as certain types of bedrock or layers of estuarine, glacial or lacustrine clays. Waterlogging provides anaerobic conditions which retards decomposition of dead plant material and facilitates the accumulation of peat. Continued accrual of peat elevates the bog surface above regional groundwater levels forming a shallow dome from which the term 'raised bog' is derived. As the height of the peat dome increases, drainage continues to be impeded by low permeability of the accumulating peat. The bog surface becomes separated from the influence of groundwater water leading to a surface irrigated almost exclusively by precipitation, a condition referred to as 'ombrotrophic'.

The 'classic' developmental sequence for a raised bog is given by Weber (1908). In this scheme, initiation of ombrotrophic peat occurs from within a minerotrophic fen which has developed over a pool as part of a terrestrialisation process. A distinct cupola of ombrotrophic peat eventually forms occupying a discrete lowland site. In fact, in Britain this type of raised bog is relatively uncommon. Many raised bogs are thought not to have developed from hydroseral infilling of water bodies but from paludification of land (Hesselmån, 1910). This includes the once extensive raised bogs of the Humberhead Levels (Smart, Wheeler & Willis, 1986). Thus starting points for development of raised bog include such diverse habitats as reedswamp, woodland, herbaceous fen and saltmarsh.

Most raised bogs have developed from a preceding phase of fen vegetation. Examination of the peat stratigraphy often reveals the existence of layers of fen peat at the base of the profile. Studies investigating the developmental sequence of raised bogs in Britain only exist for a small number of sites (Walker, 1966; Dickinson, 1973; Tallis, 1973; Smart *et al*, 1986). However, the occurrence of a preceding fen stage has also been identified for bogs of NW Europe (Casparie, 1972).

1. 2 *Size and shape of raised bogs*

Raised bogs show considerable variation in size and shape. Confined to a small topographic basin, a dome of ombrotrophic peat may reach less than 500m across. Alternatively raised bogs may cover extensive areas. The largest example in NW Europe had an estimated area of 1000 km^2 (Barkman, 1992).

In Germany and the Netherlands, well developed raised bogs occur in areas with a high effective humidity and a relatively high intensity of rainfall (700 to 1500 mm a^{-1}) (Streefkerk & Casparie, 1989). This corresponds with the range suggested by Rodwell (1991) for British bogs (800 to 1200 mm a^{-1}). In North German and Irish bogs Streefkerk & Casparie (1989) found rates of annual evaporative loss in the order of 450 to 550 mm a^{-1} and suggested a critical precipitation limit of 600 to 700 mm a^{-1} below which permanent moisture shortage will occur. Rates of evaporative loss will clearly vary between regions as will other potentially important variables such as frequency of wet days; therefore these limits can not be applied universally.

An important contribution to our understanding of raised bog hydrology and development comes from the Groundwater Mound hypothesis elaborated by Ingram (1982). In this model it is suggested that water accumulates due to impeded drainage of precipitation inputs to form a hemi-elliptical mound supported by a growing mass of peat (which has developed due to its presence). The surface of this mound determines the shape and dimensions of the bog. It is dependent on (i) the size and shape of the basal area (ii) precipitation to evaporation ratio (iii) hydraulic conductivity of the peat. Whilst this model has been shown to generate quite close correspondence between predicted and observed profiles of some raised bogs in Scotland, it does not account adequately for the dimensions of all raised mires. Clymo (1991) points out that the mean height of bogs in Niedersachsen are some 90m below their calculated hydrological limit. He suggests these sites may have had insufficient time to grow to their hydrological limit or alternatively further growth is limited by ongoing peat decay.

The 'classic' raised bog morphology as suggested by Weber (1908) is a hemi-elliptical dome of peat. However, in Britain this shape is relatively uncommon and generally restricted to small sites. In a review of Scottish bogs, Ratcliffe (1964), pointed out that many were not strongly domed but formed extensive plateaus with steep edges, a condition to which many UK sites conform. Streefkerk & Casparie (1989) classified British bogs along with counterparts in the Netherlands, NW Germany and Ireland as 'plateau raised bogs' due to this morphological characteristic. Clymo (1991) suggests that a small basal area enables peat growth to occur to approximate the hydrological half ellipse but where bogs develop over a large area the margins may approach a half ellipse but the centre does not due to 'decay limit'.

In some cases extensive bogs are formed by the fusion of several raised bogs which have expanded beyond their original basins. The extensive bogs of the Netherlands are thought to have developed in this way (Streefkerk & Casparie, 1989) as well as some British sites (Walker, 1966; Taylor, 1983). Raised bogs may develop to encompass significant irregularities in the ground surface, a phenomenon thought to be widespread in the UK, for example at Glasson Moss (Walker, 1966), and possibly at Wedholme Flowe (Bragg, 1992). In some cases the topography of the peat dome may conform to some degree to the shape of the underlying ground, for example at Flanders West Moss (Scottish Peat Surveys, 1965) and Coom Rigg Moss (Taylor, 1983).

1. 3 *Location of raised bogs*

The European distribution of raised bogs is summarised by Moore & Bellamy (1974). Once more widespread than they are today, raised bogs are still frequent in parts of Northern Europe especially in lowland temperate and boreal regions. In Britain, raised bogs are a particular feature of cooler, wetter regions in the north and west, but also occur in some southern and eastern localities - for example Somerset and S. Yorkshire. Although a particular feature of lowland areas they may also occur in upland regions where conditions are suitable e.g. Tarn Moss, Malham (west Yorkshire) (Pigott & Pigott, 1963).

1. 4 *Age of raised bogs*

The date of origin for most raised bogs is not known. Streefkerk & Casparie (1989) point out that conditions in the Netherlands have been suitable for raised bog development for 7000 yrs. In the UK, the age of some bog peat dates back to the Atlantic period. Others, however, are much younger in origin dated at post 3000 yrs BC. For example, most of Thorne Moors (South Yorkshire) appears to be less than 4000 yrs old (Buckland, 1979).

1. 5 *Natural vegetation of raised bogs*

In reality it is quite difficult to specify the 'natural' vegetation of raised bogs in Britain. This is partly due to a lack of any comprehensive surveys. Furthermore, very few sites have remained totally unmodified by the original or combined effects of drainage, burning, grazing or peat cutting. There are rather few historical records in existence that can be used to reconstruct the original character of raised bog sites and few studies have aimed to collate such information. Furthermore, few attempts have been made to reconstruct vegetation history from stratigraphical studies.

It is generally accepted that whilst shrubs (e.g ericoid species and Bog Myrtle - *Myrica gale*) are typical constituents of British raised bogs, trees such as birches and pines are not. Stratigraphical evidence for British sites suggest that trees were never a major component of raised bog vegetation (Godwin & Mitchell, 1938; Moore, 1977; Walker, 1966). This is in contrast to other continental mires and it is not clear whether British raised mires are naturally treeless or if their character has been influenced by some form of low intensity past management. Furthermore, the sloping edges of most raised bogs appear drier than the rest of the ombrotrophic surface, a zone referred to as the 'rand'. Typically it supports less *Sphagnum* and a greater abundance of ericaceous shrubs. It is not always clear if this is a natural state or whether it is a symptom of damage to the periphery of the bog, for example, by domestic peat cutting or reclamation.

The 'natural' vegetation of raised bogs has not remained constant through time. Stratigraphical evidence suggests that peat composition does not remain constant vertically or horizontally but reflects temporal and spatial changes in vegetation type. One of the most conspicuous stratigraphical discontinuities is the *Grenzhorizont* of Weber (1908), found widely throughout European bogs but less clearly defined in British bogs (Godwin, 1946). It represents an abrupt change between consolidated, well humified 'black peat' (in which *Eriophorum vaginatum* and remains of ericoid species are particularly conspicuous) to a less dense, less humified 'white peat' (comprised principally of *Sphagnum* remains). The change from deposition of 'black peat' to 'white peat' is thought to reflect changes in surface conditions i.e. increased wetness, possibly due to changes in climate. Several workers have identified recurrent bands of highly humified peat within 'white peat' suggesting recurrent 'dry' periods during bog development (Granlund, 1932; Godwin & Mitchell, 1938; Nilsson, 1935). These two peat types are sometimes separated by a layer containing abundant *Sphagnum cuspidatum* and *Scheuchzeria palustris* indicative of very wet conditions (Godwin, 1946).

The present day composition of raised bog vegetation is unlikely to be completely stable. Instead it is probably undergoing a constant series of subtle changes, for example shifts in dominance between 'wet' and 'dry' species. Dry phases may lead to the suppression of *Sphagnum* and an increase in the abundance of ericaceous shrubs and even localised tree invasion (Casparie, 1972). Stratigraphical records show that *Sphagnum imbricatum* was once a major peat forming species of raised bogs throughout the UK but around the Middle Ages it became largely replaced by *Sphagnum papillosum* and *Sphagnum magellanicum* (Barber, Dumayne & Stoneman, 1993). A climatic shift towards wetter conditions is one of the proposed explanations.

Clearly there are many unknowns surrounding the 'natural' vegetation of raised bogs and currently too little information exists to answer many of these questions. However, despite these caveats, some broad generalisations can be made about the character of the vegetation on a raised bog.

The central area of many bogs is a complex system of pools which may reach depths of over 1m and are often colonised by aquatic species of *Sphagnum* such as *S. cuspidatum* and *S. recurvum*. These pools are separated by lawns and hummocks or ridges composed largely of other *Sphagnum* species such as *S. magellanicum*, *S. papillosum* and *S. capillifolium*. This central zone may be surrounded by a patterned surface of *Sphagnum* hummocks and hollows in which pools are largely absent. Away from the bog centre the vegetation may remain based on a spongy layer of *Sphagnum* mosses but there is a tendency for the surface to become drier with a loss of *Sphagnum* and an increase in ericaceous shrubs (the 'rand' - see above). Around the edges of the mire, there may exist the minerotrophic lagg often taking the form of poor fen or fen woodland. Frequently, the lagg has been removed by peripheral damage to the mire e.g. peat cutting.

Floristic differences between bog sites are often subtle, leading early studies to refer to ombrotrophic vegetation broadly as *Sphagneta* (Tansley, 1939). Previous studies on the vegetation of British raised bogs are few but recently with the development of the National Vegetation Classification (NVC) (Rodwell, 1991) a systematic attempt has been made to examine and classify the vegetation of raised bog sites. The major bog plant community types outlined by NVC are shown in Table 1-1. It must be considered that in reality these groups are often not clearly distinct.

In an undisturbed bog pool vegetation is typically represented by the *Sphagnum cuspidatum / S. recurvum* community (M2). The rest of the vegetation is broadly defined as *Erica tetralix - Sphagnum papillosum* (M18) which is divided into two subcommunities. *Sphagnum magellanicum - Andromeda polifolia* (M18a) refers to the hummock and lawns of *Sphagnum* occurring in amongst the pool complex. *Empetrum nigrum - Cladonia* sub-community (M18b) refers to a drier vegetation with a greater abundance of ericoid plants such as *Calluna vulgaris* which may occur further from the bog centre. The bog rand may support an M18b community though often it sustains a more heathy vegetation i.e. M15 or even *Molinia* grassland.

Erica tetralix - Sphagnum papillosum (M18) vegetation is considered to be particularly characteristic of raised bogs. It is specific to ombrotrophic conditions and is similar in composition to the underlying peat. Disturbance such as draining has led to the expansion of community types M15, M25 and W4 at the expense of M18. Even *Eriophorum vaginatum* dominated communities (M20) normally associated with blanket bog have become a feature of some lowland sites degraded by factors such as drainage, burning, grazing and atmospheric pollution (Rodwell, 1991).

Table 1-1 Major community-types of bogs identified by the National Vegetation Classification (Rodwell, 1991). The main community-types of little-damaged raised bog are shown in bold type.

COMMUNITY-TYPES LARGELY CONFINED TO OMBROTROPHIC MIRES

- M17 Scirpus cespitosus - Eriophorum vaginatum blanket mire
    - (a) *Drosera rotundifolia-Sphagnum* sub-comm.
    - (b) *Cladonia* sub-comm.
    - (c) *Juncus squarrosus-Rhytidiadelphus loreus* sub-comm
- ***M18 Erica tetralix - Sphagnum papillosum raised and blanket mire***
    - ***(a) Sphagnum magellanicum-Andromeda sub-comm***
    - **(b) *Empetrum nigrum-Cladonia* sub-comm**
- *M19 Calluna vulgaris - Eriophorum vaginatum blanket mire*
    - *(a) Erica tetralix sub-comm*
    - *(b) Empetrum nigrum sub-comm*
    - (c) *Vaccinium vitis-idaea-Hylocomium splendens* sub-comm
- ***M20 Eriophorum vaginatum blanket and raised mire***
    - ***(a) species-poor sub-comm***
    - *(b) Calluna vulgaris-Cladonia sub-comm*

COMMUNITY-TYPES ALSO FOUND CHARACTERISTICALLY IN OTHER HABITATS (MAINLY POOR-FEN AND WET HEATH)

- *M1 Sphagnum auriculatum bog pool community*
- ***M2 Sphagnum cuspidatum / recurvum bog pool community***
    - ***(a) Rhynchospora alba sub-comm***
    - ***(b) Sphagnum recurvum sub-comm***
- ***M3 Eriophorum angustifolium bog pool community***
- ***M15 Scirpus cespitosus - Erica tetralix wet heath***
    - *[(a) Carex panicea sub-comm - not strictly ombrotrophic]*
    - ***(b) typical sub-comm***
    - *(c) Cladonia sub-comm*
    - *(d) Vaccinium myrtillus sub-comm*

COMMUNITY-TYPES CHARACTERISTIC OF NON-OMBROTROPHIC HABITATS BUT PRESENT ON (USUALLY DAMAGED) OMBROTROPHIC BOGS.

These include:

- *M25 Molinia caerulea - Potentilla erecta mire*
    - *(a) Erica tetralix sub-comm*
    - *(b) Anthoxanthum odoratum sub-comm*
- *W4 Betula pubescens - Molinia caerulea woodland*
    - *(a) Dryopteris dilatata sub-comm*
    - (c) *Sphagnum* sub-comm
- H9 *Calluna vulgaris - Deschampsia flexuosa* heath
- *Pteridium aquilinum* stands
- Various fen community-types may occur in laggs

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1. 6 *Habitat conditions of undisturbed raised bog*

1. 6. 1 Water levels and species distribution

The surface of an undisturbed raised mire is characteristically 'spongy' and wet underfoot. The vegetation layer dominated by *Sphagnum* stores large amounts of water and downward seepage is inhibited by low hydraulic conductivity of the underlying peat. In an undamaged raised bog water-level fluctuations are very limited (Beets 1992). Clymo & Hayward (1982) suggest vertical movement of the water table on the order of 20cm and Schouwenaars & Vink (1992) point out that fluctuations are typically confined to less than 30 - 40cm.

The bog surface is often extensively patterned by a complex of hummocks, lawns and pools (1.5) and therefore demonstrates considerable microtopographical variation. It has long been observed that certain bog plant species occupy certain zones in relation to water table proximity. Tansley (1939) proposed a scheme for species distribution within the hummock and hollow complex (Fig 1.1). He saw different zones as seral stages in the hummock - hollow regeneration cycle following the theory of lenticular regeneration first proposed by Osvald (1923). Subsequent stratigraphical studies have provided little evidence that this process is important in raised mire development (Barber, 1981; Moore, 1977) but this does not detract from the value of the observations made on species distribution.

From studies on Silver Flowe in Scotland, Ratcliffe & Walker (1958) also suggest a general sequence of species distribution in relation to water level. This is summarised in Table 1-2 . It is important to recognise that these are only general trends and that field distribution does not necessarily represent the limits of tolerance. Many species can occupy a broad range with respect to water level and as a consequence there is frequently overlap. This is often evident in the extensive *Sphagnum* lawn areas of some raised bogs, where hummock and pool species can be found growing together in an intermediate water regime.

1. 6. 2 Water relations and *Sphagnum* growth

The vegetation of an undisturbed bog is characterised by a luxuriant cover of *Sphagnum* . The growth of *Sphagnum* is in part responsible for creating the bog environment itself. It provides the basis for peat formation, impeded drainage and development towards ombrotrophy, stores large volumes of water at the bog surface and is instrumental in creating strongly acidic conditions (sect 1.6.3). *Sphagnum* growth is also largely responsible for the development of microtopography and gradients in water regime. For these reasons, *Sphagnum* has received more study than other bog species. Re-establishment of *Sphagnum* is considered fundamental to restoration and consequently relationships between species of this genus and water regime are given particular attention here.

The Genus *Sphagnum* is divided into sections. The taxa in these sections share distinctive anatomy and ecology (Clymo & Hayward, 1982):

Sect. Cuspidata and **Subsecunda** are found with capitula at or slightly above or below the free water surface. *Sphagnum cuspidatum* and *S. subsecundum* are found in pools and slowly flowing water in ditches.

Sect. Sphagnum which includes *S. papillosum* and *S. magellanicum* are robust and form carpets or low hummocks.

Sect. Acutifolia includes *S. capillifolium* and *S. fuscum* which grow in hummocks some way above the water table.

Fig 1.1 Diagram of the succession of species forming the peat in a typical "hollow-hummock" cycle
From Tansley (1939)

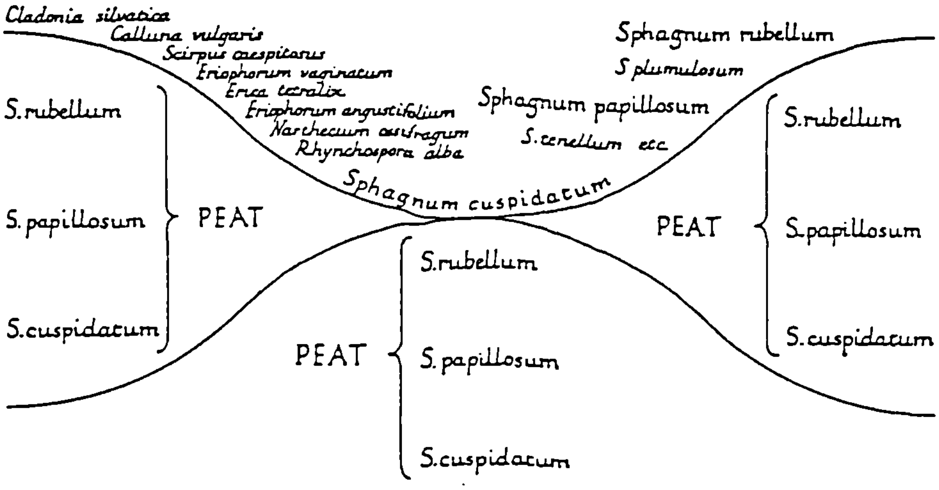


Table 1-2

The approximate vertical range of bog species in relation to the water table
(from Ratcliffe & Walker, 1958, J Ecol, 46 (2), 407-445)

At or below water level

S. cuspidatum,	*S. pulchrum,*	*S. subsecundum,*
Menyanthes trifoliata	*Eriophorum angustifolium*	*Rhynchospora alba*

Low to medium height above water level

S. papillosum	*S. magellanicum,*	*S. plumulosum [subnitens]*
S. tenellum	*Narthecium ossifragum*	*Erica tetralix*
Drosera rotundifolia		

Medium to maximum height above water level

S. rubellum	*Calluna vulgaris*	*Eriophorum vaginatum*
Scirpus cespitosus	*Rhacomitrium lanuginosum*	*Cladonia sylvatica*

There is a vertical distribution of *Sphagnum* species along a hummock-hollow gradient. This has also been documented for North American mires (Vitt, Crum, & Snider, 1975; Andrus, Wagner & Titus, 1983; Luken 1985; Andrus, 1986) and for sites in southern Sweden (Wallén, Falkengren-Grerup & Malmer, 1988).

Water relations are considered important in determining this zonation and have been the subject of detailed research. Early experiments showed this zonation was not simply a product of desiccation tolerance. Clymo & Hayward (1982) found the pool species *S. auriculatum* survived desiccation better than the hummock species *S. capillifolium*. Furthermore, Rydin & McDonald (1985^{a}) found photosynthesis in hollow species was no more sensitive to water stress than in hummock species. However, numerous workers have observed that hummock species are able to maintain a higher tissue moisture content at low water tables than pool species (Clymo, 1973; Clymo & Hayward, 1982; Heikkilä & Löytönen, 1987; Luken, 1985). At low water tables hummock species appear better able to transport water up the stem and maintain capitulum water content. Consequently, capillary water transport capability is generally considered the main factor which differentiates hummock and lawn species (Clymo, 1973; Clymo & Hayward, 1982; Hayward & Clymo 1983; Titus & Wagner, 1984; Rydin & McDonald, 1985^{a}; 1985^{b}; Wagner & Titus, 1984; Wallén *et al*, 1988).

Lawn-forming species occupy an intermediate zone. This is a transitional area in which the dominant producer changes from year to year depending on climatic conditions (Wallén *et al*, 1988). Under dry conditions *S. magellanicum* appears to be a superior competitor for water than *S. papillosum*. It has better water transport ability and maintains greater water content than *S. papillosum*, correlating with greater stem diameter, greater pore number and smaller leaf size (Li, Glime & Liao, 1992). *S.*

papillosum is able to occupy higher elevations when growing in association with *S. magellanicum*. Protocooperation is thought to occur through lateral transport of water along inter-connecting fascicular branches (Li, Glime & Liao, 1992). Most movement of water up the stem occurs in the pendent branches rather like a wick. If an area of damaged stem is encountered water can move sideways to adjacent plants to be returned to the original plant higher up (Clymo & Hayward, 1982). Commensalism has also been observed between *S. fuscum* and *S. balticum* (Rydin, 1985) and between *S. tenellum* and *S. capillifolium* (Heikkilä & Löytönen, 1987).

Luken (1985) observed that a high stem density retards evaporative water loss from *Sphagnum* growing some distance above the water table. Clymo, (1970) also noted that stem dichotomies occurred more often among *Sphagnum* mosses growing in drier habitats, and Lane (1977) found more dichotomous branching in *S. fuscum* and *S. magellanicum* compared with species from wetter habitats. Therefore, in addition to a high water transport capacity, at relatively high elevations hummock formers appear to retain tissue moisture by growing in dense cushions.

Hollow species appear limited physiologically and morphologically at higher elevations. However, conversely, hummock species are not intolerant of waterlogged conditions which exist in pools. *S. capillifolium* grows better in pools than at low water table even though it is a hummock former (Clymo & Reddaway, 1971). Furthermore, measurements of photosynthetic capacity of *Sphagnum* transplants have shown that hummock species can well survive the environmental conditions of hollows (Rydin & McDonald, 1985^{b}). However, where water does abound hollow species grow much faster than hummock species. Clymo & Reddaway (1971) found *S. recurvum* and *S. cuspidatum* in pool habitats greatly out-produced *S. papillosum* and *S. magellanicum*. In fact, numerous workers have observed in the field that pool species consistently out compete hummock species in wet conditions (Andrus, 1986;

Luken, 1985; Pakarinen, 1978; Pedersen, 1975). Therefore hummock species may effectively be excluded from the pool environment by competition. The greater productivity of pool species may be partly due to a longer growing period. At Silver Flowe NNR in south-west Scotland *S. cuspidatum* and *S. auriculatum* were found to have a longer growing season than the lawn / hummock species *S. magellanicum*, *S. papillosum* and *S. capillifolium* (Hulme & Blyth, 1982).

1. 6. 3 Chemical conditions of undisturbed raised bog

Sphagnum bogs are naturally acid systems. This is largely attributable to the physiology of the Genus *Sphagnum* itself (Clymo, 1963; Clymo, 1984; Clymo, 1987; Clymo & Hayward, 1982; Andrus, 1986). Characteristics such as a high cation exchange capacity gives *Sphagnum* the ability to acidify its environment. This is illustrated well where *Sphagnum* has colonised minerotrophic fen systems. Islands of *Sphagnum fuscum* in rich fen have been observed to cause pH shifts from 6.5 to 4.0 (Bellamy & Rieley, 1967). In the minerotrophic peatlands of central Alberta, Canada pH's ranged up to 8.2 but in the *Sphagnum* layer pH was lowered to 3.9 (Karlin & Bliss, 1984). Acidification and cation depletion are also features of *Sphagnum* areas in the fens of the Norfolk Broads (Giller & Wheeler, 1988).

Typically bog water contains low concentrations of dissolved solutes reflecting the fact that raised bogs are almost exclusively irrigated by rainwater. Consequently the chemical constituents of bog water at a particular site tend to reflect local rainwater quality (Proctor, 1992). Numerous published studies include measurements of bog water quality from different sites. Values from a selection of these are collated by Nilsson, Famous & Spencer (1990). Furthermore, an extensive survey of the chemical composition of ombrogenous mire waters is reported for Britain and Ireland by

Proctor (1992). Table 1-3 summarises some chemical conditions reported for little disturbed raised bogs.

Table 1-3: Some chemical conditions in little disturbed raised bogs.
[Concentrations are in mg l $^{-1}$; blank cells indicate no data; SRP = Soluble Reactive Phosphorus]

	Natural waters, U.K.	Natural bog, Ireland	Natural Bog, Finland
Ca	0.2 - 3.0	0.6 - 0.9	2.5
Mg	0.1 - 2.5	0.7 - 1.5	0.82
K	.04 - 2.0	0.5 - 1.4	0.59
Na	2.3 - 23.0	4.0 - 7.6	0.52
Fe	< 1.0		0.26
SO_4	2.4 - 10.0	18.0	
NO_3	0.1 - 0.3		
NH_4-N			3.47
SRP	0.0 - 0.05		0.039
pH	3.7 - 4.4	3.8 - 4.5	3.75
Source	Proctor (1992) Gorham (1956)	Bellamy & Bellamy (1966)	Tolonen & Seppänen (1976)

Low availability of nitrogen and phosphorus provide major constraints to plant growth and bogs are generally considered infertile systems. In an environment characterised by low nutrient availability it is advantageous to be well adapted to scavenge nutrients from dilute solutions and recycle them to avoid loss of a scarce resource. This is a trait clearly seen in *Sphagnum* mosses (Malmer, 1988) and which may also apply to other bog species for example *Eriophorum vaginatum* (Goodman & Perkins, 1959). In a fairly continuous *Sphagnum* carpet productivity is commonly in the range of 100 - 600 g m $^{-2}$ yr $^{-1}$ (Clymo & Hayward, 1982) and on British blanket bog productivity of 150, 500 and 800 g m $^{-2}$ yr $^{-1}$ has been recorded for hummocks, lawns and pools respectively.

Relationships between plant species distribution and chemical conditions are difficult to establish except in gross terms. Bog water chemistry may show considerable inter and intra-site variation (Proctor, 1992) and it is often difficult to relate the localised occurrence of a particular species with a distinctive set of chemical conditions (Gorham, 1956). This may reflect the fact that standard chemical analysis techniques for mire waters bear only a limited relationship to what is actually experienced by the plants. It is also likely that influences other than hydrochemistry determine distribution of bog species.

The species composition of bog vegetation is generally considered to be related to oceanicity. Malmer (1986) observed the tendency for oceanic bogs to support species which in less oceanic situations are restricted to fens. Tansley (1939) reports the occurrence of *Schoenus nigricans* and *Cladium mariscus* in the bogs of western Ireland, species which in eastern Britain are restricted to rich-fen. Bogs in western Scotland may support *Carex panicea*, *Eleocharis multicaulis* and *Sphagnum auriculatum* all of which are restricted to minerotrophic mire in less oceanic parts of Britain. Furthermore, species commonplace in British bogs may be restricted to fens further east in Europe. For example, *Narthecium ossifragum* and *Sphagnum papillosum* are confined to fens in eastern Scandinavia. Similarly *Eriophorum angustifolium* and *Sphagnum imbricatum,* absent from some continental bogs, may grow in adjoining fens (Wheeler, 1993). These trends may be related to generally higher pH and solute concentrations recorded from oceanic bogs reflecting inputs from sea spray (Proctor, 1992) but it is not certain whether this is sufficient explanation (Malmer, 1986).

1. 7 *Exploitation of raised bogs*

1. 7. 1 Background

Until relatively recently, the extent of raised bogs in north-west Europe was much greater than at present. Today peat extraction is generally viewed as the greatest threat to remaining raised bog habitat but historically the greatest losses have come through reclamation for agriculture and forestry. After 200 years of utilisation of bogs in the north German lowlands, Blankenburg & Kuntze (1986) report that natural 'virgin' raised bog in Lower Saxony (which contains most of the raised bogs in the Federal Republic) constitutes only 1% of its original area. Approximately two thirds of raised bog has been reclaimed for agriculture (principally grassland) and a further 11% (approximately 259 Ha) are subject to industrial peat cutting.

Similarly, in the Netherlands bogs have been reclaimed and utilised for centuries as arable land and as a source of fuel. In particular, industrial peat winning followed by cultivation has resulted in only 5% (9000 ha) of original raised bog area remaining, all of which is highly disturbed (Beets, 1992). The largest losses of U.K. bogs have also been to agriculture and forestry (Ratcliffe, 1977; Lindsay, 1993). However, it is difficult to quantify these losses as published historical studies are few. Smart, Wheeler & Willis (1986) recount reclamation of peatland about Thorne Waste, S. Yorks using a process called warping, whereby river sediments were deposited onto peat fields to enhance fertility.

Bather & Miller (1991) suggest that since 1970 peat extraction in the UK has started on just 347 hectares of peatland while losses to forestry were 95000 ha over the same period. However, the umbrella term 'peatland' is misleading as it includes extensive areas (principally upland blanket bog) which are not lowland raised bog. In fact, raised bog is thought to constitute only a small percentage of total peatland area in the UK and whilst expansion of forestry has been primarily on blanket bog (Pyatt, 1993), new peat production has occurred almost exclusively on raised bog.

Raised bogs have traditionally been exploited on a modest scale to provide domestic fuel and this practice is still commonplace in Scotland and Ireland. Cutting of this type is generally restricted to the bog periphery where the dark basal peats (which have a higher calorific value than *Sphagnum* peat) are readily accessible. Consequently, damage is generally only marginal though if cutting is sufficiently intensive, increased drainage may affect the intact bog surface. The nineteenth century onwards saw more elaborate drainage operations and widespread commercial exploitation of raised bog sites for stable litter and fuel. In Ireland, modern peat extraction still occurs principally for fuel to generate electricity in peat fired power stations. It is estimated that peat provides 16% of Ireland's national energy requirements (Bather & Miller, 1991).

In the 1960's the potential use of peat as a medium for growing plants was fully realised. Peat high in *Sphagnum* content has several desirable qualities including: **1.** a high simultaneous water and air storage capacity, **2.** high cation exchange capacity which provides good nutrient storage potential and minimises losses by leaching, and **3.** consistent and predictable hydrochemical behaviour on addition of lime and fertiliser. It may be used in its pure form or as a component part of a medium for growing plants or for improving the organic content of soils. In the UK, horticulture revitalised peat extraction which now produces an estimated 1.76 million m^3 of horticultural grade peat annually, 75% of which is used as a growing medium (Bather & Miller, 1991).

There is a scarcity of information regarding the original extent of raised bog in the U.K. Bather & Miller (1991) suggest a figure of 116000 ha but data subsequently published from the National Peatland Resource Inventory (NPRI) put the figure at nearer 92000 ha (Lindsay & Andrews, 1993; Plantlife, 1992). Further NPRI evidence suggests the total area of raised bog remaining even in a moribund state amounts to no more than 10000 ha in Great Britain and the area of 'intact' bog amounts to just 3.3% of its original area. However, controversy currently surrounds the accuracy of these figures, partly because the distinction between raised bog and blanket bog is often not well defined (Wheeler, *pers comm*). Nevertheless, there is general agreement that only a very small area of raised bog in an intact or semi - intact state remains.

The Peat Producers Association (PPA) which represents 98% of peat production in the U.K. and Ireland currently holds about 5212 ha of raised mire in the U.K. Approximately 987 ha of this area has not been worked and only 513 ha are scheduled for extraction. However, the majority of this latter area retains some 'virgin' component (Bather & Miller, 1991). In Ireland, Cross (1992) suggests that only 11,700 - 19,600 ha of raised bog remains intact from an original area of 310,000 ha. The PPA holds 88472 ha of raised bog in Ireland and of the 9245 ha of 'peatland' (principally raised bog) brought into production between 1981 and 1991, 90% was previously undisturbed (Bather & Miller, 1991). Currently, most peat production in the UK takes place on sites already badly damaged. However, fears that this will eventually extend into areas retaining conservation value has led to controversy surrounding continued peat production.

1. 7. 2 Methods of peat production

There are three main peat extraction techniques operational in the U.K. Common to all three practices are drainage and removal of the vegetation layer to reveal the underlying peat:

1. 7. 2. 1 Block Cutting

Removal of peat turfs by hand is a traditional practice which was once much more widespread (see above). Regeneration was aided by the process of 'shoeing' whereby the surface vegetation is replaced after peat turfs have been removed. However, organised removal even by hand can cause considerable peripheral damage. Machine block cutting generally involves larger scale removal for commercial purposes. Peat is removed in strips to leave a residual topography comprised of a regular system of baulks, flats and trenches. A typical profile is shown in Fig 1-2.

1. 7. 2. 2 Extrusion

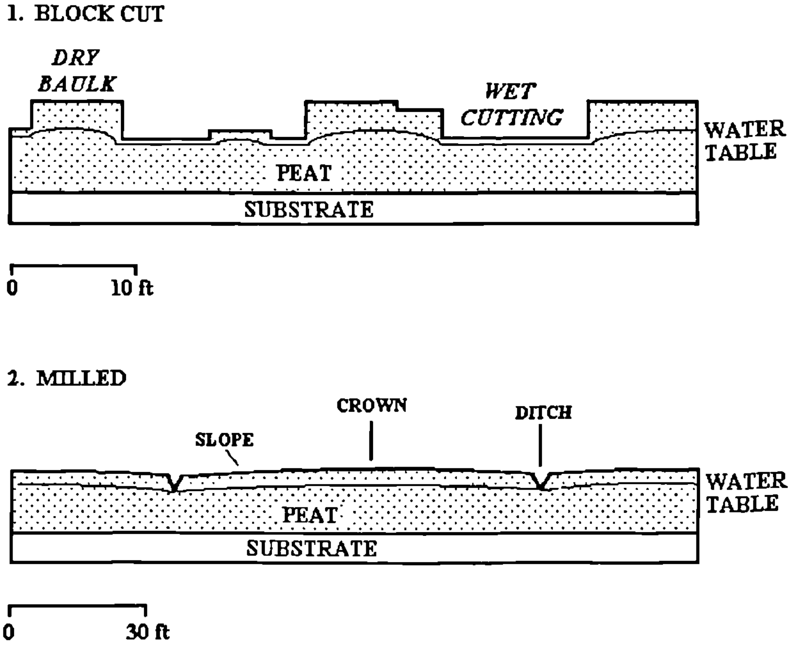
This method is used mostly for extraction of fuel peat both on a small domestic scale and at a larger commercial scale. At Hatfield Moors, S. Yorks extrusion is used on a very large scale for production of horticultural peat (dark basal peats are frequently mixed with lighter *Sphagnum* peat to produce a blend). A rotating blade extracts peat from approximately one metre below the surface before extruding it through nozzles as 'sausages' onto the surface to dry. The vegetation is usually removed to leave a surface similar to milled bog (see below) with additional subsurface drainage channels left by the blade. Even if the vegetation is not removed (as with smaller operations), considerable damage occurs through compaction by machinery and personnel, cutting of roots and deposition of peat onto the surface (Bayfield *et al*, 1991; Meharg, Montgomery & McFerran, 1992).

1. 7. 2. 3 Surface Milling

Milling involves the vacuuming or 'scraping off' of thin layers of peat at a time (15 - 50 mm). The bog surface is prepared by drainage at 15 - 20 m intervals and the vegetation is removed sometimes 5 - 10 years prior to extraction. Deep drains reduce the water content of the surface peat to 85 - 90%, this is further reduced to 55 - 65% by the milling or harrowing operations which occur prior to picking up the peat.

Between 8 and 12 harvests can be made each season and extensive areas must be worked to be economic. A consequence of this production method is the creation of extensive areas of relatively flat or gently crowned bare peat (Fig 1-2). The most modern and widespread method of peat extraction surface milling accounts for 65% of U.K. production and 90% of extraction world-wide (Bather & Miller, 1991). It is estimated that 3000 ha of raised bog in the U.K. is currently being milled and as these areas begin to come out of production attention is increasingly being focused on how to restore them.

Fig 1. 2 : Topographical profile resulting from different methods of peat extraction.



1. 8 *Restoration of cut-over lowland raised mire*

In the UK, the notion of restoring raised bogs damaged by peat extraction is a relatively recent development - a fact reflected by the general scarcity of literature published on the matter. Some general consideration is given to restoration measures by Rowell (1988). Furthermore, restoration efforts at Danes Moss in Cheshire are documented by Meade (1992). Only recently however, has attention been given to restoration of much larger raised bog relics, prompted perhaps by the acquisition by English Nature (statutory conservation organisation for England) of sites such as Fenns and Whixall Mosses, Shropshire and Thorne Moors, S. Yorks.

By contrast, elsewhere in NW Europe, restoration of industrially cut-over peatland has been the subject of investigation for many years. Eggelsmann & Schwaar (1979) give preliminary results for restoration attempts at Lichtenmoor in Lower Saxony (NW Germany). There is a statutory requirement in Germany that on cessation of peat winning, areas must be given over to restoration. Eggelsmann (1987) suggests that in the coming two or three decades in Lower Saxony cut-over raised bog to the sum of 30000 ha will be given back for restoration. Reviews of bog restoration in Germany are given by Eggelsmann (1982) and Kuntze & Eggelsmann (1982).

Restoration of raised bogs is seen by workers on the Continent as a three-phased process. The sequence, as outlined below, follows a scheme proposed by Kuntze & Eggelsmann (1981):

1) Rewetting - establishment of surface wet conditions.
2) Renaturation - development of an ombrotrophic 'raised bog' vegetation.
3) Regeneration - re-establishment of self regulatory, actively growing bog.

In reality no clear boundaries can be drawn between these stages as they are not discrete but exist along a restoration continuum. Most work to date has been aimed at achieving rewetting. This is seen as essential to provide conditions favourable for establishment of an actively-growing *Sphagnum* layer. Rewetting projects have largely entailed engineering measures such as the building of peat dams, blocking of ditches and creation of polders to retain precipitated water. Such 'ecotechnical' aspects of bog restoration are well documented by workers on the continent. Projects conducted in NW Germany are summarised by Eggelsmann (1987), (1988a), (1988b), whilst investigations in the Netherlands are reviewed by Schouwenaars (1982) and Joosten (1992). Furthermore, Wheeler & Shaw (*in press*) review the various options for raised bog 'rehabilitation' in the U.K. based on collated experiences of projects conducted throughout NW Europe.

Restoration is defined by Joosten (1992) as "the complex of human activities aimed at stimulation of bog regeneration" where regeneration is defined as "the process of renewed development towards a bog after natural or cultural disturbance". He also recognises that some key species of the genus *Sphagnum*, like *Sphagnum magellanicum*, *S. papillosum* and *S. rubellum* are obligate for potential bog formation. Eggelsmann (1987) states that the objective of rewetting measures taken in Germany are to provide suitable ecological conditions which in the long term will facilitate development of actively growing raised bog without further human intervention.

W. Fojt of English Nature (*in litt.*, 1992) shares the view that "management should be directed towards achieving ombrotrophic mire vegetation which is part of a net growing ombrotrophic peat bog". Furthermore, the creation of NVC community type *Erica tetralix - Sphagnum papillosum, Andromeda polifolia* sub community (M18a) (1.5) is considered a desirable end point to restoration. This suggestion has substantial rational as M18 vegetation (especially M18a) is believed to be the vegetation type characteristic of British bogs, which due to its vulnerability to damage and the loss of raised bogs, has become very limited in its distribution. Stratigraphical evidence suggests that in many relict bog sites this vegetation was formerly widespread and formed the basis of peat accumulation and bog development.

In practice strategies adopted for restoration will be site specific dependent on extent of damage and conditions prevailing. Several possible scenarios are outlined below:

1. Comparatively intact sites damaged superficially by activities such as drainage, peripheral cutting and burning.

2. Old abandoned peat workings (may be extensive in area) naturally revegetated with communities not resembling an actively growing *Sphagnum* bog. Commercially block cut areas at Thorne Moors, S. Yorks and Fenns and Whixall Mosses, Shropshire are good examples of this.

3. Recently abandoned peat workings characterised by extensive milled peat fields devoid of vegetation.

Most attempts at restoration in the U.K. have been concerned with the second scenario. Remedial measures include: reducing water losses from the bog (e.g. by ditch blocking) to elevate water levels and encourage *Sphagnum* growth, and the physical removal of 'undesirable' species such as *Molinia caerulea* and *Betula* spp. It must be considered that, as a consequence of site specific differences, restoration objectives may also differ between sites. In some situations it may be unrealistic to recreate M18a vegetation and one may have to be satisfied with 'drier' vegetation types such as heathland containing *Erica tetralix*, *Calluna vulgaris* and *Molinia caerulea*. It may not even be conservationally-desirable in some instances to recreate actively growing *Sphagnum* bog where the heathland vegetation which has spontaneously recolonised is of importance in its own right as a habitat for birds and invertebrates.

Increasingly areas are now coming out of production from modern methods of peat production such as surface milling. Sites may consist of numerous large peat fields characteristically well drained, devoid of vegetation and with perhaps 50 - 100 cm of peat remaining above the mineral layer. In the future most cut-over peatland world wide made available for restoration will take this form and, consequently, this study is particularly concerned with restoration of such areas. Unlike sites in scenario 2 (see above) milled surfaces provide a 'clean slate' on which we can attempt to carefully control and direct revegetation to achieve the desired end point.

1. 9 *Objectives of this study*

There seems to be an overall consensus among workers in NW Europe that the aim of bog restoration is to re-establish ombrotrophic bog vegetation typical of undisturbed systems which by definition involves redevelopment of an actively growing *Sphagnum* layer. Therefore, this study was specifically concerned with examining in detail the factors affecting colonisation of milled peat fields by *Sphagnum* mosses. Large amounts of work conducted to date has focused on attempts to rewet cut-over sites but few studies have concentrated on the individual requirements of different species of *Sphagnum*, especially from the point of view of re-establishment.

The aims of this project were as follows :

1. To investigate some of the habitat characteristics of milled peat fields and consider their direct implications for *Sphagnum* recolonisation.
2. To assess the requirements for *Sphagnum* regrowth based on evidence from spontaneously revegetated peat workings.

3. To complement the afore-mentioned objectives with a series of laboratory and field experiments aimed at investigating ways to facilitate and encourage growth of *Sphagnum* in milled peat fields.

Field studies for this project were based at Thorne Moors, S. Yorkshire. It contains examples of old commercial block cuttings which have spontaneously revegetated and extensive areas of milled peat. The site is introduced in more detail below.

1. 10 *Introduction to main study area - Thorne Moors*

1. 10. 1 Background

Thorne Moors (or Thorne Waste) is located at the boundary of South Yorkshire and South Humberside (NGR SE7215). It is an example of a lowland raised bog severely modified and much exploited by man. It has been subject to partial agricultural conversion and massive peat extraction, the latter of which still occurs intensively today. Once part of a much larger wetland complex of bog, fen and saltmarsh which existed at the head of the Humber estuary (an extensive area of flatland referred to as the Humberhead levels), Thorne Moors represents the largest surviving raised bog remnant covering an area of approximately 2630 ha.(Rogers & Bellamy, 1972).

The bog is situated above a bedrock of Bunter sandstone in the west, overlain by Keuper Marl in the east, both capped by drift deposits of clay and silt below the peat (Cory, 1972). The bog is almost completely surrounded by peatland reclaimed for agriculture by the process of warping. The mean annual rainfall is fairly typical for lowland eastern Britain at around 568 mm. Bog formation is thought to have been initiated by the process of paludification. Wood peat (principally *Betula* spp) found at the base of cores probably represents paludified forest which covered the area prior to the main period of peat formation which began 1000 B.C. (Buckland, 1979).

Records of early botanists such as Casson (1869), Peacock (1920, 1921) and Bunker (1898) recount that the natural surface of the bog was covered with several different species of *Sphagnum* and patterned by a mosaic of curiously shaped pools. More specifically, local records complemented by stratigraphical evidence (Smart *et al*, 1986) point to the former abundance of *Sphagnum magellanicum*, *S. imbricatum*, *S. cuspidatum* and other mosses including *Aulacomnium palustre*. Ericaceous plants were common i.e. *Erica tetralix*, *Calluna vulgaris*, *Vaccinium oxycoccos* and *Andromeda polifolia*. *Narthecium ossifragum* was also frequent plus insectivorous plants such as *Drosera anglica*, *D. intermedia*, *D. rotundifolia* and *Pinguicula vulgaris*. Associated with the pools were *Carex limosa*, *Eleocharis palustris*, *Menyanthes trifoliata*, *Rhynchospora alba*, *Scheuchzeria palustris* and *Utricularia minor*. Finally, *Myrica gale* was common near the borders of the bog.

Unfortunately, none of the original bog surface remains undisturbed and peat has been cut from virtually all of the site. Thorne Moors has a long and varied history of exploitation which is relatively well documented and is reviewed by Smart *et al* (1986). Peat extraction has occurred since at least the 18th century but it became much more important in the late Ninteenth century when the site was extensively drained. Records of surveys conducted for commercial purposes suggest in 1871 the bog was still clearly domed with a maximum peat depth of approximately 6.25 m. However, as a result of drainage and cutting the peat depth today varies between 0.5 - 3.5 m (Smart *et al*, 1986).

As a consequence of cutting many of the original bog species have been lost from the site and others have become severely deminished in abundance. The original bog surface has been replaced by an extensive complex of peat cuttings, baulks, drains, dikes, canals and tramways. These nevertheless sustain a rich botanical resource providing a range of habitats that support some of the original bog species plus species not normally associated with ombrotrophic bog i.e. grassland, woodland and fen

(Smart *et al*, 1986). In addition to botanical interest, entomological (Skidmore, Limbert & Eversham, 1985), ornithological (Limbert, Mitchell & Rhodes, 1986) and palaeoecological interests (Buckland, 1979) combine to justify the sites designation as a Site of Special Scientific Interest (SSSI). One series of reflooded, revegetated cuttings (the Southern Dutch Canal System) is of particular importance as it retains the greatest number of former bog species (Smart, Wheeler & Willis, 1989) and is designated as a National Nature Reserve (NNR).

The majority of the northern half of the moors is currently being worked by Fisons plc (Fig 1.3). The peat is won by surface milling which has created large areas of bare peat. The southern half of Thorne consists largely of old block cuttings which have naturally revegetated. Until recently some of these areas were to be reworked, however they are now managed for conservation by English Nature under agreement with Fisons.

1. 10. 2 Location and design of experimental pits

Experimental pits have been dug in two parts of Thorne Moors. The rationale underlying their excavation was to provide a series of experimental microcosms which can be used for introduction of selected bog plant species most notably *Sphagnum* mosses. Two series of experimental pits were excavated in two contrasting sets of conditions:

i. Crowle Moors Pits

These were situated in the triangle of land between the Swinefleet Warping Drain and the Crowle Moors Nature Reserve (Fig 1.3). This is an area of long - abandoned peat workings which has a relatively high water table and a reasonable depth (1.5 m +) of residual peat (including 0.8 - 1.0 m of ombrotrophic peat). The residual topography is one of cuttings separated by upstanding peat baulks. In some locations the cuttings are seasonally wet, but elsewhere many are quite dry all year round, the water table being 30 - 40 cm below the peat surface.

This site has been abandoned for several decades and the old cuttings have largely revegetated with a heathy scrub including *Betula pubescens*, *Calluna vulgaris*, *Eriophorum vaginatum*, *E. angustifolium*, *Molinia caerulea*, *Pteridium aquilinum* and *Polytrichum juniperinum*. Some wetter cuttings contain *E. angustifolium*, *Sphagnum recurvum*, *S. fimbriatum* and *Drepanocladus fluitans*. The cuttings in which the experimental pits were dug have subsequently become colonised by prolific *Molinia* and *Betula* spp. Peat baulks are characterised by a mature canopy of *Betula pubescens* and *B. pendula* with an understory of *P. aquilinum*, *C. vulgaris*, *E. vaginatum*, *M. caerulea* and bryophytes such as *Campylopus introflexus*, *P. juniperinum* and lichens, notably *Cladonia* spp.

Three main types of pit were excavated (Fig 1.4):

a) Swinefleet trenches (ST): These were arranged in two rows (A and B). The area of each trench was 16 x 2 m^2 and had a bottom which slopes from 0 - 1 m maximum depth. 31 examples of these trenches were dug separated by 2 m baulks and arranged in two rows (STA 1 - 15, STB 1 - 16).

b) Swinefleet pits (SP): These were small, steep sided pits, area 4 x 2 m^2. 6 of them were 1m depth, 6 were 0.5 m depth (SP 1 - 12).

c) Swinefleet pits (large): Two extensive pits of area 15 x 15 m^2, and 1 m depth (SP 13 - 14).

Fig 1.3: Location and map of main study area, Thorne Moors, South Yorkshire (NGR SE7215). [The site has been reclaimed at its edges to give an irregular boundary and is covered by an intricate network of drains which divide the surface into numerous discrete peat fields.]

Key:
Shading represents areas currently or recently worked by Fisons plc.
A = Location of Crowle experimental pits
B = Location of Creykes experimental pits
NNR = Original area of the National Nature Reserve managed
by English Nature

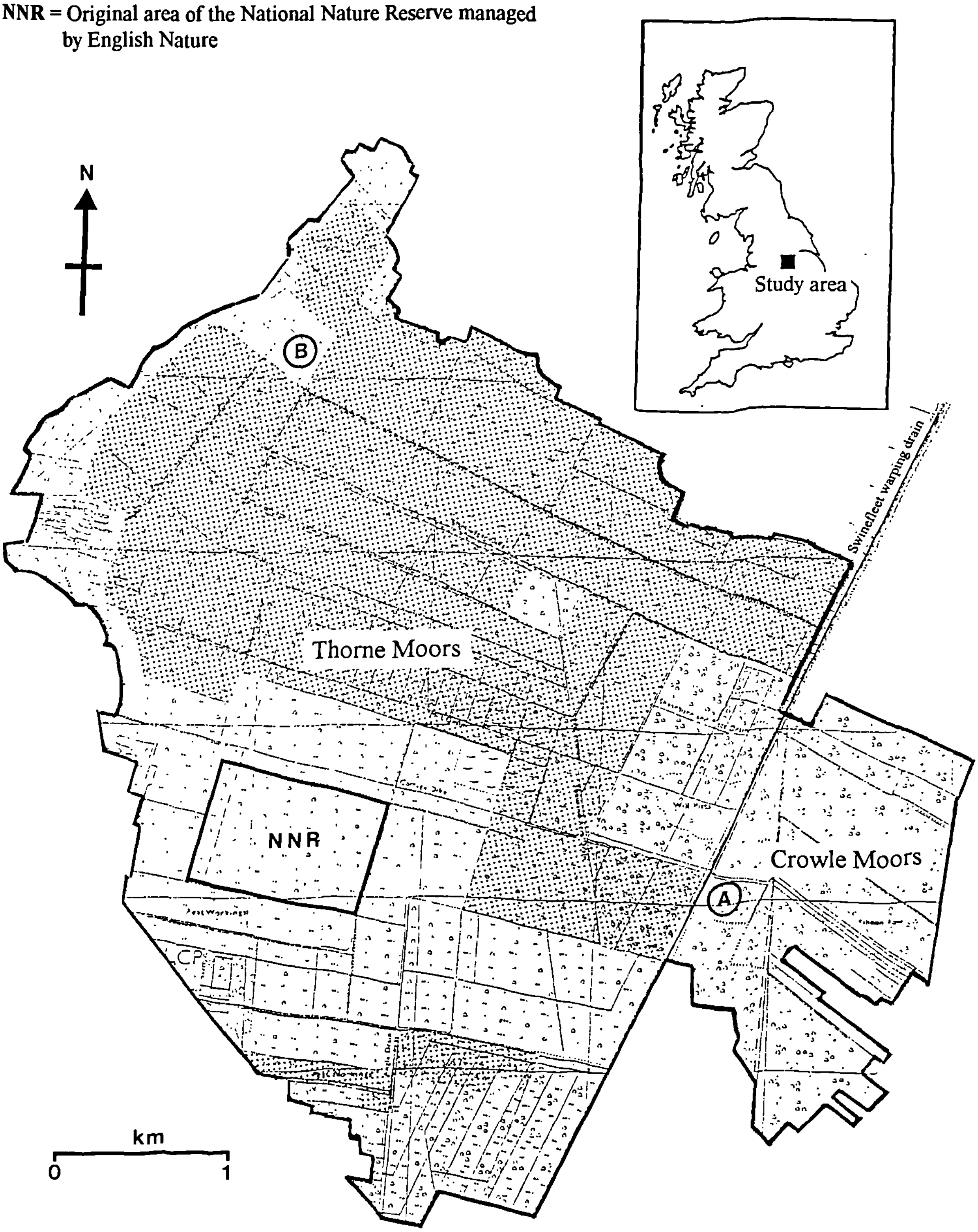
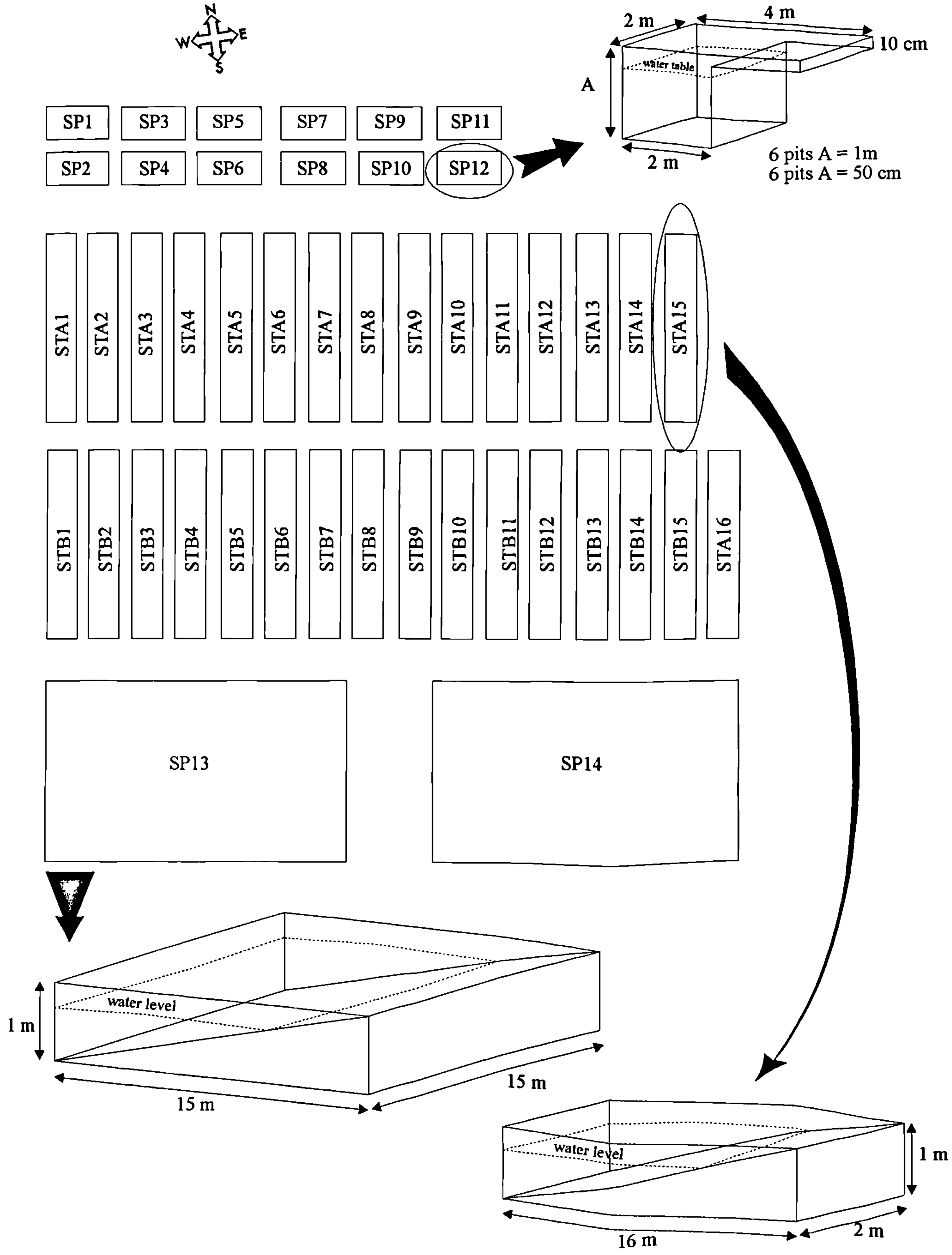


Fig 1-4 : Schematic map showing arrangement and design of pits and trenches in the Crowle experimental area



ii. Creykes Pits.

These were situated in a recently abandoned milled peat field which is considered to be representative of the surface conditions that will prevail over much of the currently worked areas of Thorne when peat extraction ultimately ceases (Fig 1.3). The peat field covered an area of approximately 9.5 ha and had a severely disturbed and completely devegetated surface. There was a relatively shallow depth of residual peat (< 1 m) much of which is brushwood peat, and the area has been intensively drained. In the spring of 1990, around the same time that the pits were excavated, measures were taken to block existing drains with peat dams. The arrangement of excavated pits is shown in Fig 1-5 . They were of three types:

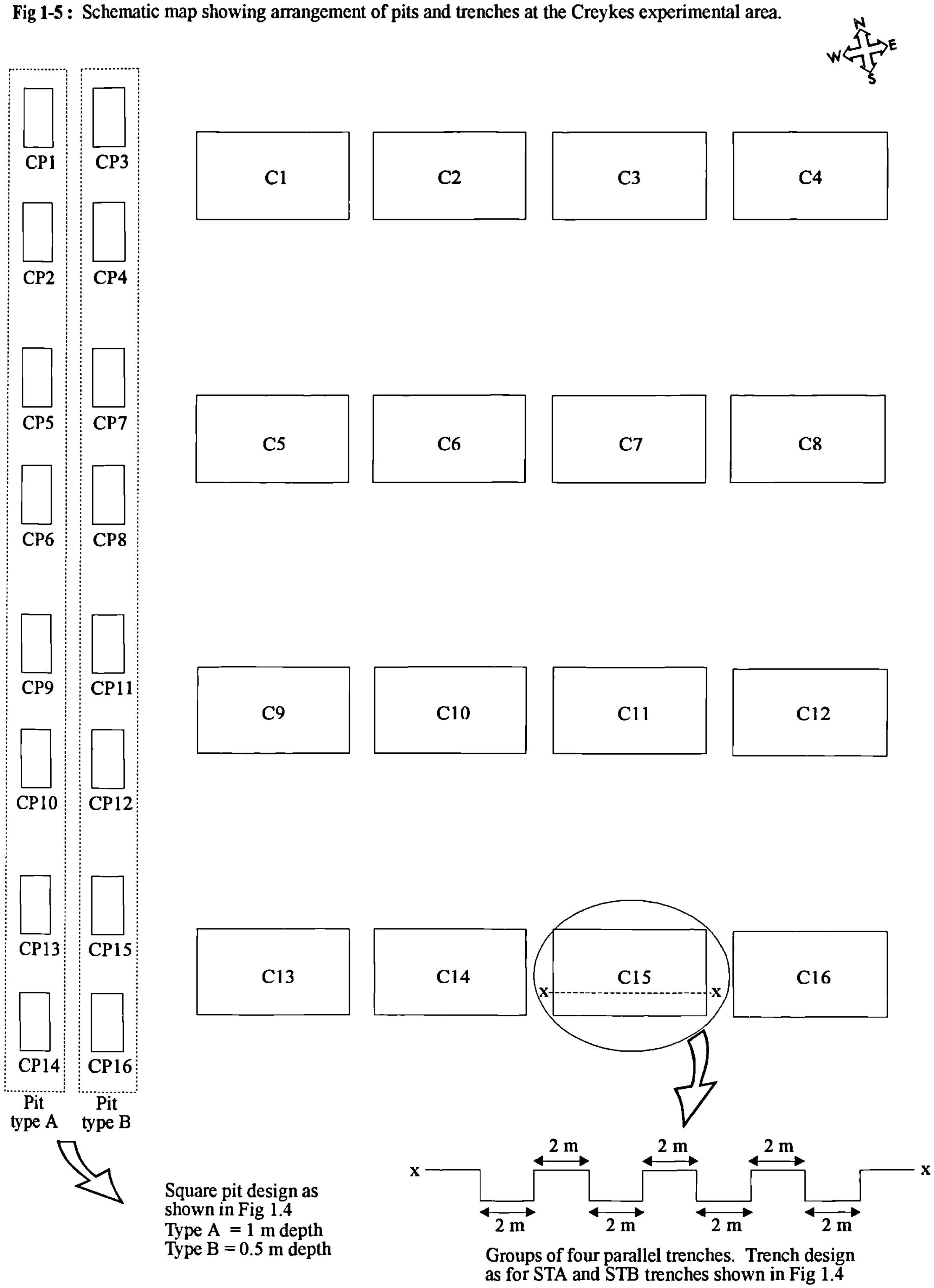
a) Small (2 x 4 m^2) steep sided pits dug down to the level of the underlying clay.

b) Small (2 x 4 m^2) steep sided pits shallower in depth, dug into the underlying fen peat.

c) Groups of 4 trenches with sloping bottoms. Area of each trench approximately 16 x 2 m^2, and maximum depth 0.8 m. There were 16 groups in total.

Unfortunately the pits at Creykes did not retain much water for the first two field seasons of this project's duration (Chapter 3). Consequently, it was not possible to utilise them for *Sphagnum* growth experiments. Such trials had to be restricted to the Crowle site where permanent water could be guaranteed. The Creykes site has however, proved a useful source of data on water quality and water table stability in a severely damaged system.

Fig 1-5 : Schematic map showing arrangement of pits and trenches at the Creykes experimental area.



Square pit design as
shown in Fig 1.4
Type A = 1 m depth
Type B = 0.5 m depth

Groups of four parallel trenches. Trench design as for STA and STB trenches shown in Fig 1.4

1. 10. 3 Sources of *Sphagnum* for experiments

Experiments with *Sphagnum*, conducted during this study, utilised a range of species typical of raised bog and raised bog lagg (1.5). Most of these species can no longer be found growing at Thorne Moors (Chapter 2); therefore material had to be imported from other, mostly damaged bog sites. Permisson was sought from the relevant land-owners and material was collected with care, causing as little disturbence as possible. A list of donor sites is given in Table1-4. *Sphagnum* was transported to Thorne and stored in the Crowle study area in experimental trenches STA 1 - STA 11 (Fig 1.4). Material was then removed when necessary for field and laboratory experiments.

Table 1-4 : Sites visited for collection of *Sphagnum* donor material

Site: Solway Moss GR: NY 3469
Owner: Richardsons Moss Litter Company
Species collected: *S. capillifolium, S. magellanicum, S. recurvum*

Site: Lochar Moss GR: NY 0468
Owner: Forestry Commission
Species collected: *S. capillifolium, S. cuspidatum, S. magellanicum*

Site: Lotus Hill GR: NX 9068
Owner: David Goss, Broomrigg House, Holywood, Dumfries DG2 0RJ
Species collected: *S. auriculatum, S. palustre*

Site: Glen Carron GR: NH 1254
Owner: Not Known
Species collected: *S. cuspidatum, S. capillifolium, S. papillosum*

Site: Thorne Moors GR: SE 7215
Owner: Fisons plc / English Nature
Species collected: *S. fimbriatum*

Chapter 2

Spontaneous recolonisation of cut-over bog

2.1 *Background*

Abandoned peat workings occur widely at bog sites throughout the U.K. and Ireland, ranging from small scale domestic cuttings, through to larger commercial operations. Many of these areas have revegetated naturally and the distribution of bog species, particularly *Sphagnum* mosses, in old peat cuttings may provide valuable information on the conditions required for successful re-establishment of those species to peatland coming out of production today. The vegetation resource of abandoned peat cuttings has not been extensively studied. Detailed investigations are few but some notable exceptions are reviewed briefly below.

Domestic turf cuttings were studied in some detail by White (1930) for the mosses (bogs) of northern county Armagh. He found that depth of cutting determined the type of vegetation that recolonised. When *Calluna* dominated vegetation was cut to depths up to 45cm *Callunetum* became re-established. If depths between 67.5 and 112.5cm were removed *Sphagnetum* became established. An *Eriophoretum* community was also observed as an intermediate. This was one of the earliest documented accounts of factors influencing peatland rehabilitation. White had identified the crucial role of water regime in influencing recolonisation. *Sphagnum* became established only in deeper cuttings which were significantly wetter due to closer proximity to the water table.

A consultant's report for the cut-over area at Fenns and Whixall Mosses on the border of Clwyd and Shropshire (Betts, 1990), concluded the water table was too low to support vigorous growth of *Sphagnum* and prevent invasion by *Molinia*, *Pteridium aquilinum* and *Betula* spp. Drainage ditches and peat diggings were the only places where notable fragments of wet bog communities could be found. Similarly at Danes Moss, east of the Cheshire plain, where peat cutting ceased in the early 1960's, prior to restoration measures the site had revegetated with a dense cover of *Molinia.* Birch had also become widely established and *Sphagnum* was confined to grips bearing water and wet hollows in between them (Meade, 1992). At Thorne Moors, S.Yorks, the NNR comprises a series of cutting bays separated by peat baulks. On abandonment and reflooding in 1920 the cuttings became inundated but peat baulks maintained a strongly subsurface water table. *Sphagnum* re-establishment has been largely confined to the wet cuttings, often floating, while the baulks have revegetated with *Betula* and *P. aquilinum* plus a range of bryophytes normally associated with heathland (Smart, Wheeler & Willis, 1986, 1989).

Most commercial cuttings, except those most recently abandoned, usually consist of block-cut peat fields. This type of cutting complex exists over large areas of Thorne Moors, exhibiting a residual topography of dry ridges and wet trenches (1.7.2). Where there is a high water table, trenches appear to provide a suitable micro-habitat for *Sphagnum*. However, water tables remain far below the baulk surfaces, which support growth of trees and ericaceous shrubs but lack *Sphagnum*.

These trends have also been identified for damaged bog sites in North America (Nilsson, Famous & Spencer, 1990) and elsewhere in NW Europe natural recolonisation by heathland instead of bog is commonplace. In the Lichtenmoor region of NW Germany, Eggelsmann & Schwaar (1979) recount that cut-over bog was dominated by *Calluna vulgaris*, *Erica tetralix* and *Eriophorum* species prior to attempts at rewetting. Notably *Sphagnum* was totally absent. In the Groote Peel area of the Netherlands, cut-over bog is dominated by stands of *Molinia caerulea* and *Betula pubescens* (Joosten & Bakker, 1987). Similar trends were observed by Schouwenaars (1992) for the Engbertsdijksvenen.

Patterns of revegetation for modern milled peat fields are even more poorly documented. Poschlod (1992) observed colonisation of bare peat fields in the foothills of the Alps and concluded these areas would not be readily colonised by peat forming mosses. Frequently water tables were too low and areas became dominated by *Calluna vulgaris.* At Wainfleet bog, Southern Ontario, a vacuum harvested peatland had revegetated after 24 yrs with shrubland and thick bush. Regeneration of *Sphagnum* mosses was extremely limited (Jonsson-Ninnis & Middleton, 1991). Finally, informal observations made during this project suggest that milled surfaces at Thorne Moors become colonised initially by weedy species such as *Rumex acetosella* and *Epilobium angustifolium* which are then superseded by *Eriophorum* spp., *Calluna vulgaris* and *Betula* shrubs with *Sphagnum* remaining absent. Therefore, what limited evidence exists suggests modern cut-over surfaces are also characterised by establishment of dry vegetation lacking *Sphagnum.*

2. 2 *Vegetation survey of abandoned peat workings*

2. 2. 1 Methods

In 1992, an extensive survey was undertaken of revegetated peat workings throughout the UK and Ireland. The aim was to complement existing knowledge of revegetation with a more systematic and comprehensive survey of cut-over sites. A list of sites that were visited is given in Table 2-1. Vegetation was recorded in 4 m^2 quadrats and species abundance quantified using the Domin scale. A record was made of substratum conditions including peat type and water regime, and pH and conductivity of

Table 2 - 1 : Sites of revegetated cuttings visited during survey

England and Wales	
Astley Moss, Lancashire	SJ 692975
Cors Caron (Tregaron Bog), Dyfed	SN 686629
Cors Fochno (Borth Bog), Dyfed	SN 633910
Crowle Moors, Lincolnshire / S. Yorkshire	SE 755150
Danes Moss, Cheshire	SJ 908704
White Moss, Cumbria	SD 225855
Fenns, Whixall and Bettisfield Mosses, Shropshire / Clywd	SJ 43 / 53
Glasson Moss, Cumbria	NY 238603
Risley Moss, Cheshire	SJ 665918
Thorne Waste, S. Yorkshire / Humberside	SE 730160
Wedholme Flowe, Cumbria	NY 220530
Scotland	
Bankhead Moss, Fife	NT 445101
Gardrum Moss, Falkirk	NS 882754
Moss of Achnacree, Argyll	NM 917360
Northern Ireland	
Peatlands Park / Annagarriff / Mullenakill Nature Reserve, Co. Armagh	H 8961
Ballynahone Bog, Co. Londonderry	C 8598
Irish Republic	
Killaun Bog, Co. Offaly	M 210 205

the peat were measured for a sample of quadrats from each site, using a 1:1 volume mix of peat and deionised water. In total, 463 quadrats were recorded. Data were classified using Two Way Indicator Species Analysis (**TWINSPAN**) (Hill, 1979). Nomenclature follows Smith (1978) for mosses, Clapham, Tutin & Warburg (1981) for vascular plants and Purvis *et al* (1992) for lichens.

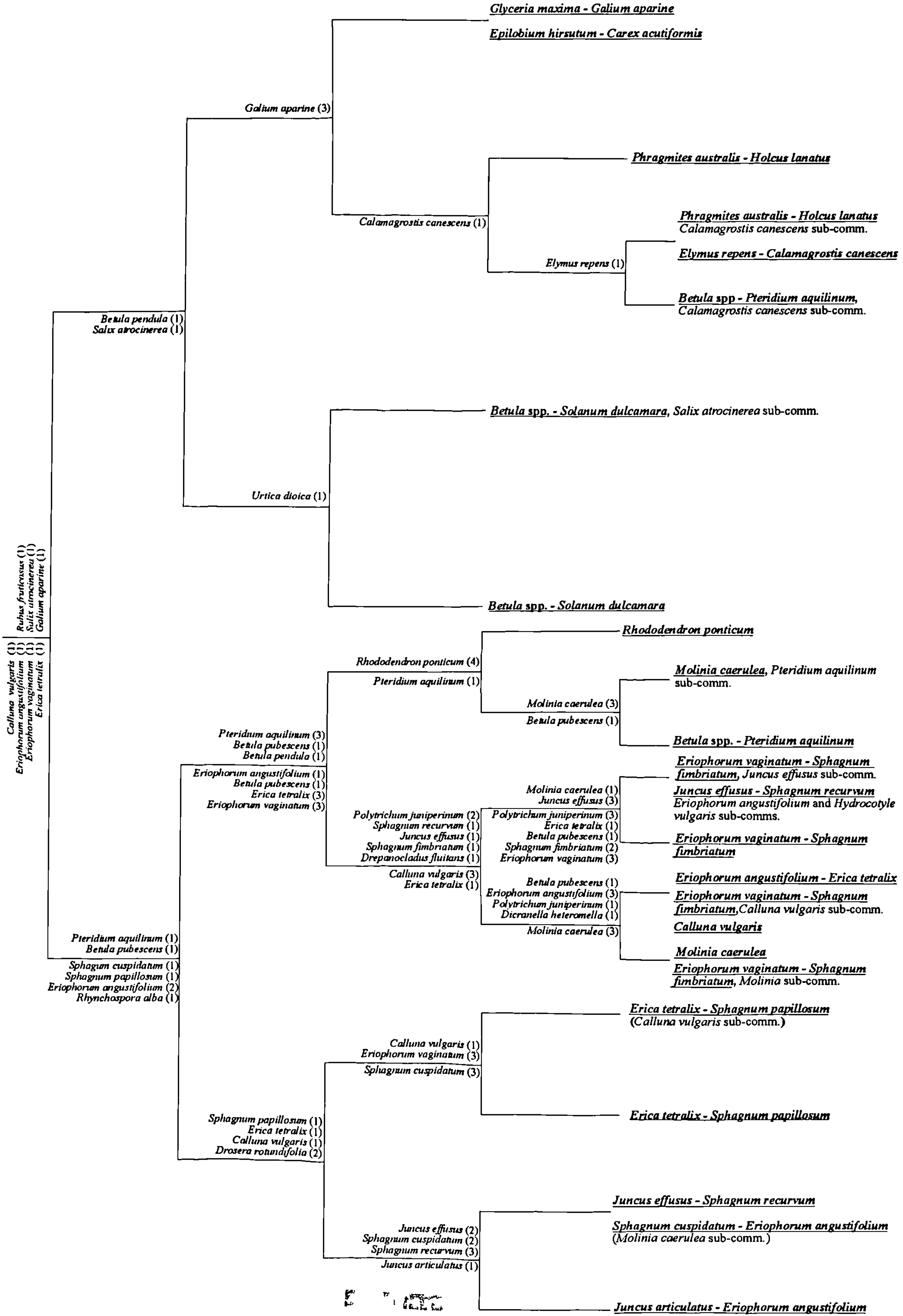
2. 2. 2 Results

Classification of the data using TWINSPAN is illustrated as a dendrogram in Fig 2.1. Major community types derived from this classification are shown on the far right-hand-side of the dendrogram, underlined and written in bold. Several problems were encountered interpreting the TWINSPAN output:

1. After 5 divisions, several end groups contained a disproportionately high number of samples. In these instances there was a tendency for samples to contain many of the same species but in different proportions and TWINSPAN was insufficiently sensitive to differentiate between them. Therefore, the end groups were further divided subjectively from study of the raw data.

2. It was also evident from the raw data, that beyond certain levels of division, some TWINSPAN groups were divided into end groups which did not show any floristic differences. In these instances such divisions were ignored. Consequently, it is evident in Fig. 2.1 that end groups occur at different levels of classification.

Fig 2 - 1 : Dendrogram from classification of vegetation data using TWINSPAN [Indicator species given at each division. Major communites derived are underlined and written in bold. Communities are described in detail in Table 2 - 2]



Despite these problems, TWINSPAN results showed that the abandoned peat cuttings surveyed in this study have been recolonised by a large range of vegetation types. The end groups were given informal names by the author as most did not adequately match recognised NVC groups (Rodwell, 1991). Each of the community types given in Fig 2.1 are described in detail in Table 2-2. Appropriate NVC codes are given in parentheses where a suitable match was obtained. Information is also presented on substratum conditions and sites in which each community type was observed. Conductivity values given are corrected for pH (Golterman, Clymo, & Ohnstad, 1978).

Table 2-3 lists the species recorded in abandoned peat workings during this study. Many species characteristic of undamaged raised bog (1.5) were also recorded in peat cuttings, indicating that peat cuttings are not intrinsically unsuitable for the growth of most, if not all, typical bog species. However, most of the cuttings supporting a rich assemblage of bog species were relatively small excavations which provided a suitable water and chemical regime (refer to Section 2.2.3). Many cuttings supported a range of species atypical of undisturbed raised bog vegetation and typical of fen, heathland and woodland vegetation. This is considered in more detail below.

By far the most widespread communities were those resembling **dry heathland,** represented by the *Calluna vulgaris* and *Molinia caerulea* communities (Table 2-2). These were typical of the very dry peat surfaces which characterised upstanding peat baulks and well drained cuttings, supporting little if any *Sphagnum* regeneration. On damper peat, where growth of *Molinia* was less dense, limited *Sphagnum* regeneration was evident at the base of tussocks (e.g. in the *Molinia caerulea*, - *Calluna vulgaris* sub-community). Even greater *Sphagnum* regeneration was observed on damp peat beneath a *Calluna* canopy (e.g. *Calluna vulgaris* - *Sphagnum capillifolium* sub-community).

Dry heath communities frequently contained an abundance of *Betula* scrub. In some locations, notably at Thorne and Crowle Moors, this vegetation has been succeeded by a mature canopy of birch with an understory consisting of a mixture of heathland and woodland species. The occurrence of **birch woodland** is represented by the *Betula* spp.- *Pteridium aquilinum* community and was restricted almost exclusively to dry peat surfaces notably on peat baulks. At Thorne Moors, it was also observed that dry peat may become vigorously colonised by a dense monoculture of *Rhododendron ponticum*.

Despite the predominance of dry vegetation, spontaneous regeneration by *Sphagnum* had occurred in numerous locations (Table 2-2). It was restricted to where the substrate was at least damp, though more commonly where the peat was wet and soft or inundated. For example, the *Eriophorum vaginatum - Sphagnum fimbriatum* community was a widespread feature of vegetation at Thorne Moors occurring in cuttings and on moist peat baulks. It supported a significant *Sphagnum* cover but as part of a **wet heath** mix i.e. hummocks of *Sphagnum*, predominantly *S. fimbriatum*, were frequently found 'nestling' between 'tussock' forming species such as *Molinia, Eriophorum vaginatum, Polytrichum juniperinum* and *Juncus effusus*. Slightly drier areas supported a greater cover of *Molinia, Betula* and ericaceous shrubs, wetter areas more *Juncus* and *Sphagnum*. It was notable that typical raised bog Sphagna i.e. *S. magellanicum* and *S. papillosum*, were largely absent. Instead, *Sphagnum* cover was dominated by a species not of great importance in the surface vegetation of intact raised bogs i.e. *S. fimbriatum*.

The *Eriophorum angustifolium - Erica tetralix* community was another example of wet heath vegetation that supported *Sphagnum* growth. However, unlike the *Eriophorum vaginatum - Sphagnum fimbriatum* community, it was dominated by an open, low growing lawn of ericaceous species, with only scattered hummocks of *E. vaginatum* and *Molinia*. Total *Sphagnum* cover was less than for the *Eriophorum* *vaginatum - Sphagnum fimbriatum* community but bog species notably *S. magellanicum, S. papillosum, S. tenellum* and *S. capillifolium* were often present. This community was developed generally on damp peat which often showed signs of disturbance. In some locations the vegetation appeared to be recovering from a fire, and other surfaces appeared to be relatively young in age.

Still greater abundance of *Sphagnum* was observed on wet or inundated peat surfaces. For example at Thorne Moors, prolific *Sphagnum* growth was observed in the *Juncus effusus - Sphagnum recurvum* community, almost exclusive to cuttings and ditches. However, once again, raised bog Sphagna were largely absent (except *S. cuspidatum*) and species typical of weakly minerotrophic conditions predominated i.e. *S. recurvum, S. fimbriatum, S. palustre and, S. squarrosum.* Wet peat and inundated cuttings were also frequently colonised by the *Sphagnum cuspidatum - Eriophorum angustifolium* community indicating more ombrotrophic conditions. *Sphagnum cuspidatum* readily colonised open water in flooded cuttings and ditches to form a **floating raft**. *E. angustifolium* did not appear to be a primary raft building species. It often remained rooted in the submerged peat surface with leaves standing proud of the water. In depths over 50 cm it appeared to grow across existing rafts of *Sphagnum* and its presence appeared to provide physical support, giving a more robust structure to the *Sphagnum* raft. In some locations this community was observed growing between tussocks of *Molinia* (*Molinia caerulea* sub-community). This was typical of dry heath areas which had become subsequently flooded as a product of rewetting measures.

Of great significance, *Erica tetralix - Sphagnum papillosum* vegetation was recorded in some locations. Dominated by a thick layer of raised bog Sphagna and supporting a large range of vascular bog species, this community closely resembled that of **undisturbed bog vegetation** and would be considered a desirable endpoint to restoration. It occurred on very wet soft peat but principally as a floating raft in small flooded peat pits up to approximately 100 m^2 in area and up to 5 m deep. A 'drier' version of this community represented by the *Calluna vulgaris* sub-community was also observed, supporting a full range of bog and heath species and occurring on wet peat in cuttings.

Several unusual communities, atypical of raised bog, were recorded exclusively at Thorne Moors, and were suggestive of base-enrichment. Often these occurred as small pockets in *Eriophorum vaginatum - Sphagnum fimbriatum* vegetation, represented by the *Phragmites australis* sub-community, or in the *Juncus effusus - Sphagnum recurvum* vegetation, by the *Hydrocotyle vulgaris* sub-community. The source of this enrichment is not certain. However, these communities occurred in the vicinity of the NNR where an abandoned system of clay lined canals once used for transporting peat off the moors still persist (Smart, Wheeler, & Willis, 1989). It is possible that previous overspill from these canals has caused localised pockets of enrichment.

On other parts of Thorne, the source of enrichment is clearly identifiable. These areas consist of abandoned, drained warpland (refer to sect. 1.7.1), colonised by **fen** and **grassland** and represented by the *Phragmites australis - Holcus lanatus* and *Elymus repens - Calamagrostis canescens* communities. Furthermore, some cuttings adjacent to warped areas exhibited elements of this vegetation, suggesting contamination perhaps from run off. The *Betula spp - Solanum dulcamara* community and its *Salix atrocinerea* sub-community represent **carr woodland** type vegetation developed on abandoned warp. It consisted of a canopy of *Betula* and *Salix* with an understory consisting of a mixture of woodland and fen plants. Clearings in the woodland were characterised by *Glyceria maxima - Galium aparine* and *Epilobium hirsutum - Carex acutiformis* communities.

Table 2 - 2 : Major vegetation communities in abandoned peat cuttings identified from sites listed in Table 2 -1. [Con. = corrected conductivity, p.d. = residual peat depth.] NVC codes given in parenthesis.

Nodum	Description	Substrate / Water Regime	Site
Betula* spp - *Solanum dulcamara (W2, W24, W25)	Mature woodland with a canopy of *Betula pubescens and B. pendula* plus abundant *Salix atrocinerea*. Understory dominated by *Pteridium aquilinum*, *Rubus fruticosus*, *Milium effusum*, *Calamagrostis canescens* and *Eurhynchium praelongum*. Other abundant species include *Holcus lanatus*, *Molinia caerulea*, *Solanum dulcamara*, *Galium aparine*, *Phalaris arundinacea* and *Impatiens glandulifera*. Other associated species: *Galium palustre*, *Lycopus europaeus*, *Cirsium palustre*, *Dryopteris carthusiana*, *Scrophularia auriculata*, *Hieracium maculatum* grp, *Sonchus oleraceus*, *Ranunculus repens*, *Sphagnum recurvum* and *S. squarrosum*. Additional scattered tree species include; *Quercus robur*, *Crataegus monogyna*, *Salix fragilis*, *S. viminalis*, *S. pentandra* and *Sambucus nigra*.	Warped peat / dry and firm. pH 7.8 -8.4 Con. 203 - 442 µS cm^{-1} p.d. ≥ 1.5m	Thorne Moors
Salix atrocinerea sub-community (W1)	Woodland canopy dominated by *Salix atrocinerea*. In addition to the above, understory contains abundant *Agrostis stolonifera* and *Urtica dioica*. Associated species include a range of fen plants i.e. *Phragmites australis*, *Angelica sylvestris*, *Cirsium palustre*, *Epilobium hirsutum*, *Juncus effusus*, *Filipendula ulmaria*, *Valeriana officinalis*.		Thorne Moors
Betula* spp. - *Pteridium aquilinum (W4, W25)	Canopy of *Betula pendula* and *B. pubescens* with a dry heath understory dominated by *Pteridium aquilinum* plus abundant *Calluna vulgaris*, *Eriophorum vaginatum*, *E. angustifolium*, *Molinia caerulea*, *Campylopus introflexus* and bare ground. Associated species : *Erica tetralix*, *Rubus fruticosus*, *Rumex acetosella*, *Salix atrocinerea*, *Epilobium angustifolium*, *Calamagrostis canescens*, *Juncus effusus*, *Dryopteris carthusiana*, *Rhododendron ponticum*, *Quercus robur*, *Festuca rubra*, *Hieracium maculatum*, *Phragmites australis*, *Hypnum cupressiforme*, *Polytrichum juniperinum*, *P. commune*, *Campylopus introflexus*, *C. paradoxus*, *Dicranella heteromella*, *Pohlia nutans*, *Sphagnum fimbriatum*, *Cladonia chlorophaea* and *C. floerkeana*.	*Sphagnum* peat in dry baulks and cuttings. pH 3.2 - 3.3 Con. 342 - 1092 µS cm^{-1} p.d. ≥ 1.5m	Astley Moss Thorne Moors Crowle Moors
- *Calamagrostis canescens* sub-community	Dominated by *C. canescens*, *Rubus fruticosus* and *Pteridium aquilinum* plus abundant *Holcus lanatus* and shrubs of *Betula*. This sub-community is likely to represent an early seral stage in succession towards a *Betula* canopy.		Thorne Moors

Table 2 - 2 : *continued*

Calluna vulgaris	Dry heathland dominated by almost a monoculture of *Calluna* bushes often with abundant bare ground remaining. Associated species: *Eriophorum vaginatum, E. angustifolium, Erica tetralix, Betula* shrubs, *Polytrichum alpestre, Campylopus introflexus* and *Sphagnum tenellum.*	Dry peat baulks. Damp, firm *Sphagnum* peat in drained cuttings (often affected by burning). pH 3.3 - 3.7 Con. 290 - 730 µS cm^{-1} p.d ≥ 1.5m	Wedholme Flowe Glasson Moss White Moss
- *Pteridium aquilinum* sub-community	Dry heathland dominated by *Calluna vulgaris* and *Pteridium aquilinum* plus abundant shrubs of *Betula* spp and bare ground.		Thorne Moors Crowle Moors
- *Sphagnum capillifolium* sub-community (M19 *E. tetralix* sub comm., M15, M20 *C. vulgaris* - *Cladonia* spp. sub comm.)	Wet heath dominated by a canopy of *Calluna* bushes plus abundant *Eriophorum vaginatum, Erica tetralix* and *Hypnum cupressiforme*. Beneath *Calluna* canopy lies an abundance of *Sphagnum capillifolium* hummocks. Associated species: Shrubs of *Betula* spp, *Eriophorum angustifolium, Sphagnum magellanicum* and *Cladonia chlorophaea* agg.	Damp, firm *Sphagnum* peat. pH 3.5 Con. 410 - 534 µS cm^{-1} p.d. ≥ 1.5m	Banks Head Moss Killaun Bog Moss of Achnacree
Molinia caerulea (M25)	Dense virtual monoculture of *Molinia* tussocks. Associated species: *Scirpus cespitosus, Erica tetralix, Calluna vulgaris, Eriophorum vaginatum, E. angustifolium, Betula* spp. shrubs, *Potentilla erecta, Hypnum cupressiforme* and *Cladonia impexa.*	Dry and firm, damp peat in cuttings and baulks Occurring on both light and dark peat. pH 3.2 - 3.7 Con. 311 - 1180 µS cm^{-1} p.d. ≥ 1.5m	Cors Caron Astley Moss Risley Moss Danes Moss Fenns and Whixall moss
- *Pteridium aquilinum* sub-community	Abundant *Pteridium, Betula* spp. and *Campylopus introflexus* plus scattered *Calluna, Eriophorum, Rubus fruticosus, Rumex acetosella, Salix atrocinerea* and *Epilobium angustifolium.*		Thorne Moors Crowle Moors Whixall Moss
- *Calluna vulgaris* sub-community	Abundance of *Calluna* and bare ground. Other frequent species : *Eriophorum vaginatum, E. angustifolium, Erica tetralix, Betula* spp. shrubs and *Campylopus introflexus.* Species recorded less frequently include : *Pteridium aquilinum, Andromeda polifolia, Sphagnum tenellum* and *S. papillosum.*		Astley Moss Thorne Moors Whixall Moss Cors Caron Cors Fochno Wedholme Flowe
Rhododendron ponticum	Dense canopy of *R. ponticum* with scattered *Betula pendula and B. pubescens*. Densly shaded and litter strewn peat surface supports no understory.	Dry *Sphagnum* peat pH 3.2 Con. 435 µS cm^{-1} p.d ≥ 1.5 m	Thorne Moors

Table 2 - 2 : *continued*

Eriophorum vaginatum* - *Sphagnum fimbriatum (M19, M20)	Wet heath vegetation dominated by *Eriophorum vaginatum* and *Sphagnum fimbriatum* plus abundant *E. angustifolium, Polytrichum juniperinum* and *Erica tetralix.* Other associated species: *Calluna vulgaris, Pteridium aquilinum, Molinia caerulea, Calamagrostis canescens, Betula* spp. *shrubs, Vaccinium oxycoccos, Juncus effusus, J. bulbosus, J. articulatus, Salix atrocinerea* shrubs, *Drepanocladus fluitans, Sphagnum recurvum* and *S. squarrosum.*	Soft , damp *Sphagnum* peat. pH 3.8 Con. 350 - 600 μS cm^{-1} p.d. $\geq$ 1.5m	Thorne Moors Crowle Moors
- *Phragmites australis* sub-community	Abundant *Phragmites, Typha latifolia* and *Potentilla palustris* superimposed on the above vegetation. Occurring as discrete pockets.	pH 3.9 p.d. $\geq$ 1.5m	Thorne Moors
- *Molinia caerulea* sub-community	In addition to *Eriophorum vaginatum* an extensive cover of *Molinia* plus abundant shrubs of *Betula pubescens, Calluna vulgaris, Erica tetralix* and *Eriophorum angustifolium*. *Sphagnum fimbriatum* found growing around base of *Eriophorum* and *Molinia* hummocks.	Damp, firm *Sphagnum* and fen peat in cuttings and on damp baulks.	Thorne Moors Crowle Moors Wedholme Flowe
	Associated species: *Vaccinium myrtillus, V. oxycoccos, Empetrum nigrum, Pteridium aquilinum, Potentilla erecta, Dryopteris carthusiana, Andromeda polifolia, Polytrichum alpestre, P. juniperinum, Sphagnum recurvum, S. subnitens, S. palustre, S. papillosum, S. magellanicum* and *Pleurozium schreberi.*	pH 3.6 - 4.0 Con. 450 - 715 μS cm^{-1} p.d. $\geq$ 0.9m	
- *Juncus effusus* sub-community	Similar to *Molinia* sub-community but differentiated by abundance of *Juncus effusus* and reduced occurrence of ericaceous species. Other abundant species include : *Molinia caerulea*, shrubs of *Betula pubescens* and *Sphagnum fimbriatum* in between *E. vaginatum* and *Molinia* tussocks. Associated species: *Pteridium aquilinum, Calluna vulgaris, Eriophorum angustifolium, shrubs of Betula pendula, Polytrichum juniperinum, Sphagnum recurvum, S. squarrosum* and *S. cuspidatum*	Soft, wet *Sphagnum* peat pH 3.7 Con. 385 - 750 μS cm^{-1} p.d. $\geq$ 1.5m	Thorne Moors
- *Calluna vulgaris* sub-community (M20 *C. vulgaris* - *Cladonia* spp. sub-comm.)	Drier version of *Eriophorum vaginatum* - *Sphagnum fimbriatum* community characterised by an abundance of *Calluna vulgaris*. Shrubs of *Betula pubescens, Erica tetralix* and *E. angustifolium* also abundant.	Damp, firm peat (light and dark) in cuttings.	Thorne Moors
	Associated species: *Betula pendula, Molinia caerulea, Rubus fruticosus, Vaccinium oxycoccos, Deschampsia cespitosa, Holcus lanatus, Rhododendron ponticum, Calamagrostis canescens, Salix atrocinerea, Juncus effusus, Drosera rotundifolia, Pohlia nutans, Campylopus introflexus, C. paradoxus, Dicranella heteromella, Polytrichum commune, P. juniperinum, Drepanocladus fluitans, Sphagnum recurvum* and *Cladonia chlorophaea.*	pH 3.4 - 3.7 Con. 310 - 690 μS cm^{-1} p.d. $\geq$ 1.2m	

Table 2 - 2 : *continued*

Juncus effusus - Sphagnum recurvum (M6 *J. effusus* sub comm.)	Sward dominated by *Juncus effusus* with an extensive cover of *Sphagnum* around the base. Principal *Sphagnum* species were *S. recurvum, S. fimbriatum* and *S. cuspidatum*. Additional species include; *S. subsecundum, S. palustre, S. squarrosum* and *S. subnitens.* Associated species: *Eriophorum angustifolium, E. vaginatum, Molinia caerulea, Utricularia minor* and *Drepanocladus fluitans.*	Wet, soft *Sphagnum* peat. Shallow flooded cuttings into dark peat. Deep flooded ditches and cuttings reaching down into mineral layer. pH 3.5 - 4.3 Con. 491- 872 $\mu S\ cm^{-1}$ p.d. ≥ 0	Thorne Moors Crowle Moors Danes Moss Ballynahone More Risley Moss
- *Eriophorum angustifolium* sub-community	Significant cover of *E. angustifolium* in addition to *J. effusus* and *S. recurvum.* Abundant species also include; *S. fimbriatum, Eriophorum vaginatum, Molinia caerulea, Drepanocladus fluitans* and *D. revolvens.* Associated species: *Juncus articulatus, J. bulbosus, Calamagrostis canescens, Salix atrocinerea, Betula pubescens, B. pendula, Calluna vulgaris, Rumex acetosella, Polytrichum juniperinum, Dicranella heteromella, Sphagnum cuspidatum, S. palustre* and *S. squarrosum.*	Wet, soft *Sphagnum* peat in cuttings. pH 3.8 p.d. ≥ 1.5m	Thorne Moors Crowle Moors
- *Hydrocotyle vulgaris* sub-community	An unusual 'fen heath' community dominated by *Eriophorum angustifolium* and *Hydrocotyle vulgaris* plus an abundance of other fen species including; *Juncus effusus, J. articulatus, Potentilla palustris, Galium palustre, Calamagrostis canescens,* shrubs *of Salix atrocinerea* and *Sphagnum squarrosum.* Associated species: *Polytrichum juniperinum, Erica tetralix, Holcus lanatus, Molinia caerulea, Pteridium aquilinum, Typha latifolia, Drosera rotundifolia, Dicranella heteromella, Drepanocladus revolvens* and *Sphagnum recurvum.*	Firm, damp *Sphagnum* peat (possibly contaminated by minerals from old clay lined canals) pH 3.9 Con. 610 $\mu S\ cm^{-1}$ p.d. ≥ 1.5m	Thorne Moors

Table 2 - 2 : *continued*

Eriophorum angustifolium* - *Erica tetralix (M16)	Wet ericaceous heath characterised by a lawn of *Erica tetralix* and *Eriophorum angustifolium* plus abundant *Calluna vulgaris* and *Polytrichum juniperinum.* Associated species: *Eriophorum vaginatum, Juncus effusus, Betula pubescens shrubs, Pteridium aquilinum, Rhododendron ponticum, Molinia caerulea, Drosera rotundifolia, Andromeda polifolia, Sphagnum tenellum, S. papillosum, S. magellanicum, S. capillifolium, Hypnum cupressiforme* and *Cladonia chlorophaea.*	Damp firm *Sphagnum* peat in cuttings and on baulks. pH 3.8 - 4.2 con. 354 - 720 p.d. ≥ 1.5m µS cm^{-1}	ThorneMoors Whixall Moss Peatlands Park Ballynahone More Killaun Bog
Sphagnum cuspidatum* - *Eriophorum angustifolium (M2, M3)	Species-poor community dominated by *S. cuspidatum* and *E. angustifolium.* Associated species: *Rhynchospora alba, Juncus bulbosus, J. effusus, Drosera rotundifolia, Drepanocladus fluitans* and *Sphagnum recurvum.* Generally occurs as a raft in flooded cuttings, pits and ditches. Represents an early seral stage in terrestrialisation. In shallow water *E. angustifolium* is generally rooted.	Soft wet *Sphagnum* peat in cuttings. Shallow inundated (30cm) cuttings and ditches. Deeply inundated (≤ 5m) peat pits of limited area. pH 3.4 - 4.5 Con. 288 - 704 µS cm^{-1} p.d. ≥ 1.0m	ThorneMoors Crowle Moors Danes Moss Whixall Moss Cors Caron Banks Head Moss Ballynahone More Killaun Bog Peatlands Park
- *Molinia caerulea* sub-community	Characterised by frequently-inundated tussocks of *Molinia* and *Eriophorum vaginatum* plus abundant *E. angustifolium. Sphagnum cuspidatum* grows prolifically in shallow water between tussocks. Associated species: *Polytrichum alpestre, Sphagnum recurvum* and *S. tenellum. Vaccinium oxycoccos* and *Andromeda polifolia* also recorded but very rare.	Soft wet *Sphagnum* peat or shallow (≤ 50cm) water in cuttings or ditches. pH 4.5 Con. 590 - 940 µS cm^{-1} p.d. ≥ 1.0m	Whixall Moss Wedholme Flowe Peatlands Park

Table 2 - 2 : *continued*

Sphagnum papillosum* - *Erica tetralix (M18, *Sphagnum magellanicum* - *Andromeda polifolia* sub comm.)	Characterised by a thick 'spongy' layer of *Sphagnum* mosses. Dominant species were *S. papillosum*, *S. magellanicum* and *S. cuspidatum*. Principal vascular plant species included *Erica tetralix, Rhynchospora alba, Narthecium ossifragum* and *Eriophorum angustifolium.* Other bryophytes recorded in association with this community: *Sphagnum palustre, S. auriculatum, S. subsecundum, S. recurvum, S. capillifolium, S. subnitens, S. pulchrum, S. tenellum* and *Mylia spp.* Associated vascular species: *Drosera rotundifolia, D. intermedia, D. anglica, Andromeda polifolia, Calluna vulgaris, Eriophorum vaginatum, Vaccinium oxycoccos, Molinia caerulea, Eleocharis multicaulis, Myrica gale, Potamogeton polygonifolius, Hypericum elodes, Menyanthes trifoliata, Rhynchospora fusca* and *Dactylorhiza purpurella.* This community includes a range of *Sphagnum* species and vascular plants typical of undisturbed raised bog. It might therefore be considered a desirable end point to restoration.	Floating mats grown over shallow or deeply inundated cuttings, ditches and pits up to 5m. deep. Developed over cuttings with either a *Sphagnum* or fen peat base. Also developed on very wet, soft *Sphagnum* peat surface. pH 3.6 - 4.8 (generally above pH 4.0). Con. 280 - 944 µS cm^{-1}	Cors Caron Cors Fochno Ballynahone More Killaun Bog Peatlands Park Glasson Moss Banks Head Moss Moss of Acnnacree
- *Calluna vulgaris* sub-community (M18, *Empetrum nigrum* ssp. *nigrum* - *Cladonia* spp. sub comm.)	Most raised bog species represented including an abundance of *Sphagnum* principally; *S. magellanicum, S. papillosum, S. capillifolium, S. tenellum* and *S. cuspidatum.* However dominance by *Sphagnum* is shared with a range of species indicative of less saturated conditions i.e. *Calluna vulgaris, Eriophorum vaginatum, Molinia caerulea* and *Polytrichum alpestre.* Associated species: *Narthecium ossifragum, Rhynchospora alba, Andromeda polifolia, Erica tetralix, Myrica gale, Empetrum nigrum, Drosera rotundifolia, D. anglica, Betula* spp. shrubs, *Vaccinium myrtillus, V. oxycoccos, Potentilla erecta, Scirpus cespitosus, Sphagnum subnitens, S. recurvum, S. fimbriatum, S. pulchrum, S. compactum, Aulacomnium palustre, Pleurozium schreberi, Hypnum cupressiforme, Campylopus introflexus* and *Cladonia chlorophaea* agg.	Soft wet *Sphagnum* peat surface in cuttings and ditches pH 3.7 - 4.7 Con. 292 - 585 µS cm^{-1} p.d. $\geq$ 1.5m	Glasson Moss White Moss Whixall Moss Cors Fochno Cors Caron Ballynahone More Killaun Bog

Table 2 - 2 : *continued*

Phragmites australis - Holcus lanatus	'Dry fen' community dominated by *Phragmites* and *Holcus* plus abundant *Glyceria maxima, Phalaris arundinacea, Rubus fruticosus* and *Cirsium palustre.* Associated species: Shrubs of *Salix atrocinerea, Epilobium angustifolium, Elymus repens, Angelica sylvestris, Lycopus europaeus, Ranunculus repens, Hieracium maculatum* grp and *Juncus effusus.*	Abandoned warp pH 7.8 - 8.5 Con. 229 - 485µS cm^{-1} p.d. ≥ 1.5m	Thorne Moors
- *Juncus effusus* sub-community	Similar to above but characterised by abundance of *Juncus effusus* plus associated species *J. articulatus* and *Alisma plantago-aquatica.*	Dark, damp peat surface in cutting pH 3.8 p.d. ≤ 0.5m	Thorne Moors
- *Calamagrostis canescens* sub-community	Dominated by *Phragmites* and *Calamagrostis* plus abundant *Elymus repens, Epilobium angustifolium, Urtica dioica* and *Dipsacus fullonum.* Associated species: *Cirsium arvense, Epilobium hirsutum, Juncus effusus, Pteridium aquilinum, Rubus fruticosus, Scrophularia aquatica, Rumex acetosa* and shrubs of *Salix atrocinerea.*	Dry abandoned warp pH 7.9 - 8.3 Con. 280 - 411µS cm^{-1} p.d. ≥ 1.5m	Thorne Moors
Glyceria maxima - Galium aperine	Dominated by these two species plus abundant *Cirsium arvense, Epilobium hirsutum* and *Polygonum persicaria.*	Dry abandoned warp. Clearing in woodland.	Thorne Moors
Epilobium hirsutum - Carex acutiformis	*Epilobium* and *Carex* dominate plus abundant *Cirsium arvense, Galium aparine, Angelica sylvestris* and *Scrophularia aquatica.* Associated species: *Dipsacus fullonum, Epilobium angustifolium* and *Urtica dioica.*	Damp abandoned warp. Clearing in woodland. pH 7.8 Con. 280 µS cm^{-1} p.d. ≥ 1.5m	Thorne Moors
Elymus repens - Calamagrostis canescens	Species-poor sward completely dominated by these two species. Associated species: Scattered plants of *Cirsium arvense, C. palustre, Heracleum sphondylium, Dipsacus fullonum, Phragmites australis, Rumex acetosa* and *Pohlia nutans.*	Dry abandoned warp at bog periphery. pH 8.0 Con. 310µS cm^{-1} p.d. ≥ 1.5m	Thorne Moors

Table 2-3: Species list of plants recorded growing in abandoned peat cuttings at sites listed in Table 2-1 [List includes species recorded in 'warped' areas of Thorne Moors]

Vascular Plants

Agrostis stolonifera
Alisma plantago aquatica
Andromeda polifolia
Angelica sylvestris
Betula pendula
Betula pubescens
Calamagrostis canescens
Calluna vulgaris
Carex acutiformis
Carex curta
Carex hirta
Carex otrubae
Cirsium arvense
Cirsium palustre
Crataegus monogyna
Dactylorhiza purpurella
Deschampsia cespitosa
Deschampsia flexuosa
Deschampsia setacea
Dipsacus fullonum
Drosera anglica
Drosera intermedia
Drosera rotundifolia
Dryopteris carthusiana
Eleocharis multiflora
Elymus repens
Empetrum nigrum
Epilobium angustifolium
Epilobium hirsutum
Erica tetralix
Eriophorum angustifolium
Eriophorum vaginatum
Festuca rubra
Filipendula ulmaria
Galium aparine
Galium palustre
Glyceria maxima
Heracleum sphondylium
Hieracium maculatum
Holcus lanatus
Hydrocotyle vulgaris
Hypericum elodes
Impatiens glandulifera
Juncus articulatus
Juncus bulbosus
Juncus effusus
Juncus subnodulosus
Lycopus europaeus
Menyanthes trifoliata
Milium effusum
Molinia caerulea
Myrica gale
Narthecium ossifragum
Phalaris arundinacea
Phragmites australis
Polygala serpyllifolia
Polygonum persicaria
Potamogeton polygonifolius
Potentilla erecta
Potentilla palustris
Pteridium aquilinum
Quercus robur
Ranunculus repens
Rhododendron ponticum
Rhynchospora alba
Rhynchospora fusca

Table 2-3: *continued*

Rubus fruticosus
Rumex acetosa
Rumex acetosella
Rumex sanguineus
Salix atrocinerea
Salix caprea
Salix fragilis
Salix pentandra
Salix viminalis
Sambucus nigra
Scirpus cespitosus
Scrophularia auriculata
Scutellaria minor
Solanum dulcamara
Sonchus oleraceus
Sorbus aucuparia
Typha latifolia
Ulex europaeus
Urtica dioica
Utricularia minor
Vaccinium myrtillus
Vaccinium oxycoccos
Valeriana officinalis

Bryophytes and Lichens

Aulacomnium palustre
Campylopus paradoxus
Campylopus introflexus
Campylopus pyriformis
Cladonia bacillaris .
Cladonia chlorophaea
Cladonia floerkeana
Cladonia portentosa
Cladonia uncialis
Dicranella heteromalla
Drepanocladus fluitans
Drepanocladus revolvens
Eurhynchium praelongum
Hypnum cupressiforme
Leptobryum pyriforme
Leucobryum glaucum
Mylia spp.
Pleurozium schreberi
Pohlia nutans
Polytrichum alpestre
Polytrichum commune
Polytrichum formosum
Polytrichum juniperinum
Sphagnum capillifolium
Sphagnum compactum
Sphagnum cuspidatum
Sphagnum fimbriatum
Sphagnum magellanicum
Sphagnum palustre
Sphagnum papillosum
Sphagnum pulchrum
Sphagnum recurvum
Sphagnum squarrosum
Sphagnum subnitens
Sphagnum subsecundum
Sphagnum tenellum

2. 2. 3 Discussion - factors influencing *Sphagnum* recolonisation

2. 2. 3. 1 Water Regime

Water regime appeared to be the factor most frequently limiting *Sphagnum* recolonisation in the sites visited. *Sphagnum* growth was restricted to damp, wet and inundated peat occurring generally in ditches and cuttings. At many sites conditions are too dry on both baulks and in cuttings, leading to growth of *Molinia/Calluna* heathland and ultimately *Betula* woodland. The most luxuriant growth of *Sphagnum* occurred in the form of floating rafts in flooded peat pits and ditches, represented by the *Erica tetralix - Sphagnum papillosum* community (Table 2-2). A similar pattern of revegetation has been observed elsewhere in NW Europe. Eggelsmann (1988a) reports that turf cuttings (dug for domestic fuel during both world wars) have become overgrown over several decades by floating vegetation (referred to as 'schwingmoor') which today provide valuable refugia for raised bog flora and fauna. Adjacent peat baulks, however, remained dry and carried birches and conifers. In the Netherlands, the Groote Peel exhibits typical examples of intensively drained and mined bog remnants. Cut surfaces are dominated by stands of *Molinia* and *Betula* but bog plant communities may be found occurring as floating mats in old flooded peat pits (Joosten & Bakker, 1987). A raft of bog vegetation is able to move vertically with the water table so that the two are never separated and permanent saturation of the *Sphagnum* layer is guaranteed. This provides conditions suitable for the continued growth of bog species but which limit growth of heathland species such as *Calluna, Molinia, Eriophorum vaginatum* and shrubs of *Betula*.

Although the best *Sphagnum* vegetation occurred as floating rafts, results suggest *Sphagnum* will readily colonise solid peat where the surface is persistently damp. However, growth frequently occurred in combination with an abundance of heathland plants, for example in the *Eriophorum vaginatum -Sphagnum fimbriatum* community (see above), and the vegetation did not resemble that of undisturbed raised bog. Tussocks of *E. vaginatum* and *Molinia* may actually help growth of *Sphagnum* in these situations by providing a more conducive microclimate than exposed peat (3.3). In the *Calluna vulgaris*, *Sphagnum capillifolium* sub-community, improved microclimate beneath the *Calluna* canopy may have also have facilitated *Sphagnum* growth. However, dense growth of *Molinia* did not appear to facilitate *Sphagnum* growth on peat. High evapotranspirative losses associated with *Molinia* may exacerbate water table fluctuation, further limiting *Sphagnum* regeneration (Schouwenaars & Vink, 1992). *Sphagnum* growth between tussocks may also be inhibited due to smothering by the large amounts of litter produced by *Molinia*.

It is interesting to note that *Molinia* monocultures and wet heath vegetation supporting *Sphagnum* were both recorded on damp ombrotrophic peat. Why the vegetation should develop differently is not known. It is possible that subtle differences in water regime exist on average over the course of a year, a fact not detectable on a single site visit, for example growth of *Molinia* is often considered to be favoured by fluctuating water tables. Furthermore, the present conditions may not exactly reflect those in which vegetation previously developed. *Molinia* is thought to be favoured at sites in oceanic climates which receive more nutrients in the form of sea spray (1.6.3). Growth of *Molinia* may also be encouraged by increased N-deposition from anthropogenic sources such as fossil fuel combustion and animal husbandry. In the Netherlands, studies suggest that N-enrichment may favour growth of *Molinia* in wet heathlands at the expense of *Erica tetralix* (Aerts & Berendse,1988).

Greatest cover of *Sphagnum* on peat was observed where the peat substratum was wettest, for example in the *Juncus effusus - Sphagnum recurvum* community and the *Erica tetralix - Sphagnum papillosum*, *Calluna vulgaris* sub-community. The latter represents the 'most desirable' bog vegetation observed to have recolonised solid peat as abundant raised bog Sphagna occurred in combination with a range of vascular bog species typical of both undisturbed bog and heathland. This community was observed rarely, requiring a wetter peat surface than the vegetation previously described. Although it cannot be determined from a single site visit, it is probable the peat surface supporting this community remained perennially saturated (rather like a floating raft) limiting the growth of heath species. Such precise conditions were uncommon, particularly in severely disturbed bogs, and were restricted to discrete, fortuitous areas such as the shoulder of flooded cuttings, where the water table was level or fractionally above the peat surface.

2. 2. 3. 2 Peat Depth

An important effect of peat depth is to alter water regime. In block-cut peat fields, wet conditions suitable for *Sphagnum* growth generally occurred in cuttings where the lower residual peat depth brought the peat surface closer to the water table.

Depth of cutting may also determine the type of peat exposed, which may influence recolonisation. Peat composition does not remain constant with depth (1.5). Frequently, lower peats are more humified and compact than upper layers. Schouwenaars (1992) and Poschlod (1988) both observed that *Sphagnum* recolonisation, directly on peat, occurred exclusively on less humified peat layers. Similarly, Buttler, Grosvernier & Matthey (*in prep*) suggest that surface peat is better for *Sphagnum* regeneration. The reason for this is not clear. It is often considered that dark peats have a lower water storage capacity and are consequently more prone to drought, however, consistent evidence for this is lacking (refer to sect. 3.1.4). Most cuttings surveyed in this study retained a depth of light *Sphagnum* peat so it was not possible to make such comparisons. The relevance of this to modern peat fields is anyway limited, as only the very basal peat is left remaining.

Finally, where extraction leaves only a thin layer of bog peat or where the fen peat or mineral subsoil is directly exposed, there is a greater chance of nutrient and base-enrichment. This is considered in more detail below.

2. 2. 3. 3 Enrichment

Communities developed on 'warped' peat at Thorne Moors clearly demonstrate how mineral contamination may influence revegetation. Vegetation was characterised by grassland, and fen and carr woodland, in stark contrast to the acid heathland recorded elsewhere on Thorne (Table 2-2). Conductivity of warped peat was not greater than non-warped peat but pH was markedly higher in the former at around pH 8 (Table 2-2). Therefore, the growth of fen vegetation at Thorne appeared to be an effect of base-enrichment rather than nutrient-enrichment.

The warping process involves application of alluvial silts to the bog surface. However, enrichment may also come from the base of the peat. Many raised bogs are characterised by an underlying layer of fen peat. Where peat cutting exposes the fen peat conditions may exhibit higher pH and elevated concentrations of base elements. The chemical environment will then be more conducive to the development of fen rather than bog vegetation. In Somerset, inundated cuttings are typically colonised by species as *Typha latifolia, Phragmites australis, Alisma plantago-aquatica, Carex pseudocyperus* and *Juncus effusus.* White (1930) also observed that deep cuttings which penetrated fen peat were recolonised by *Menyanthes trifoliata, Iris pseudacorus* and *Lysimachia vulgaris.*

Where peat cutting exposes the mineral subsoil, if it is a base-rich marl or clay then recolonisation will be similar to that outlined above for fen peat. This is hard to predict for peat cutting sites in the UK as the base status of underlying substrata is little documented. Nilsson *et al* (1990) found sites in North America, mined down to the clay substrate, were colonised by *Typha latifolia, Scirpus, Carex* spp, *Eleocharis* spp., and *Sparganium* spp. In the Somerset levels deep flooding of such substrata has lead to colonisation by T*ypha latifolia, Phragmites australis, Alisma plantago aquatica, Carex pseudocyperus* and *Glyceria maxima.* However, in some cases the base status of underlying mineral soils may not differ significantly from overlying peats. For example at Hatfield Moors, S. Yorkshire, the subsoil is an impoverished sand with pH values < 4.5. In these situations *Sphagnum* may directly recolonise base-poor sands and gravels quite readily (Andreas & Host, 1983; B.D. Wheeler, *unpubl.*).

Survey results show that cuttings were frequently characterised by the growth of poor-fen species such as *Juncus effusus, Sphagnum fimbriatum, S. recurvum, S. squarrosum* and *S. palustre.* In some cases occurrence of these species could be related to exposure of the mineral subsoil or of fen peat. In peat from uncut parts of Killaun, Cors Fochno and Cors Caron conductivity values ranged from 395 to 650 µS cm^{-1}. Conductivity values recorded for communities in which poor-fen species occurred, often exceeded this range suggesting mild basal enrichment. This is evident when comparing the *Juncus effusus - Sphagnum recurvum* community with the *Eriophorum angustifolium - Sphagnum cuspidatum* community in Table 2-2.

However, growth of poor fen species also occurred on seemingly ombrotrophic peat with low conductivity and no obvious source of mineral contamination (Table 2-2). This was a particular feature of the vegetation at Thorne Moors, and has been reported by other workers (Smart *et al*, 1989). The *Juncus effusus - Sphagnum recurvum* community was occasionally observed under these conditions but most widespread was the *Eriophorum vaginatum - Sphagnum fimbriatum* community. This suggests that any enrichment must be very subtle. Despite this, the vegetation contrasts strongly with communities developed elsewhere on damp ombrotrophic peat which lacked the growth of *Juncus* and minerotrophic Sphagna. The source of contamination is not known. Possible explanations include wind-throw from old limestone tow paths and the main limestone road that cross the site, anthropogenic nitrogen inputs and mineralisation of the peat substrate. These are considered in more detail in Chapter 4.

The highest conductivity values were recorded for the 'dry' communities; *Betula* spp. - *Pteridium aquilinum*, and *Molinia caerulea*. This vegetation is unlikely to have developed in response to the nutrient regime but rather the dry conditions. High conductivity is probably a by-product of the low water table causing mineralisation of the peat. However, if this was the sole cause then higher conductivity values would have been expected in the dry *Calluna vulgaris* and *Rhododendron ponticum* communities. It is possible that conductivity values were highest in peat from the *Betula* spp. - *Pteridium aquilinum*, and *Molinia caerulea* communities because they produce large amounts of leaf-litter thus returning more nutrients to the peat. However, for reasons that are not clear, high conductivity was not always recorded in peat from these communities and furthermore, *Rhododendron ponticum* also produces large amounts of litter but was not characterised by such high conductivity (Table 2-2). The source of this apparent enrichment is therefore unclear.

Communities resembling undisturbed bog i.e. *Sphagnum papillosum - Erica tetralix* and *Sphagnum cuspidatum - Eriophorum angustifolium*, occurred across a large range of conductivity values sometimes significantly exceeding those recorded for intact bog (Table 2-2). This suggests that whilst mild enrichment appeared to encourage the growth of poor-fen species, if conditions are suitably wet then it does not directly prevent development of a raised bog flora.

2. 2. 3. 4 Availability of propagules

Cuttings recolonised with M18-type vegetation (1.5), and supporting a full range of bog species, occurred at sites where a local source of propagules persisted (Table 2-2). Generally, an area of bog with at least a semi-intact surface, existed in the vicinity. At highly exploited sites such as Thorne Moors, there is no remaining local reservoir of some raised bog plants. Evidence that this limits recolonisation is circumstantial. However, it is interesting, for example at Thorne, that raised bog Sphagna were not observed to have recolonised in cuttings where the substrate was suitably wet. This has also been observed by other workers for the original National Nature Reserve (NNR) area of Thorne (Smart, Wheeler & Willis, 1989). Wet conditions have prevailed in cuttings there for decades, but numerous raised bog Sphagna (notably *S. magellanicum, S. papillosum* and *S. capillifolium*) have not recolonised. Evidence considered above suggests that mild enrichment recorded in the NNR by Smart *et al* (1989) and recorded in cuttings elsewhere on Thorne by this study, is unlikely to have been directly toxic to raised bog Sphagna. Therefore, it it is not clear why species such as *S. papillosum* and *S. magellanicum* have not recolonised alongside *S. recurvum* or *S. fimbriatum.* However, factors other than propagule availability may also be important in explaining the absence of these species at Thorne. This is considered in more detail in section 6.6.

Chapter 3

Water regime in a milled peat field and its influence on *Sphagnum* growth

3. 1 *Water-table fluctuations*

Patterns of spontaneous recolonisation in peat cuttings described in Chapter 2, highlight the importance of water regime in influencing vegetation development. The hydrological conditions in a recently abandoned milled peat field on Thorne Moors were investigated to assess the moisture conditions that are likely to be prevalent over extensive areas of the moor upon the ultimate cessation of surface milling, and the implications for revegetation.

3. 1. 1 Method

In the Spring of 1990, 7 piezometer tubes were placed equidistantly along an east - west transect which stretched approximately 250m across the width of an abandoned peat field in the Creykes study area (1.10.2). Tubes were inserted to the base of the peat, approximately 1 m deep. Water-table depth was recorded by measuring the distance between the peat surface and the top of the water column in the tube. Measurements were taken from each tube, bimonthly, over three years from September 1990 to July 1993. For each recording event, measurements from all the tubes were combined to give a mean water-table depth for the transect.

3. 1. 2 Results

Water-table fluctuations recorded over three years are shown in Fig 3.1. Large variations in water-table depth were recorded during the study period. An overall temporal cycle was observed, the water-table being highest during the winter and spring months, and falling dramatically during the summer. In January 1991 and 1993 the water-table reached, and inundated the peat surface. However, in January 1992 the water-table, although higher than summer levels, did not match the height of adjacent winters. Throughout the study period, the water-table was consistently lowest in July, falling to between 60 and 100 cm below the peat surface. The water-table remained sub-surface for most of the study period, except for periods of winter saturation. However, data recorded in January 1992 suggests that even winter saturation is not guaranteed. The peat surface remained unsaturated and prone to drought for many months at a time, and typically in the summer, conditions at the surface became particularly dry and dusty.

Fig 3.1 : Water-table fluctuations in a milled peat field at Thorne Moors, S. Yorks [Each bar represents the mean value from a series of piezometer tubes. Error bars = 95 % conf. limits. Refer to Sect 3.1 for details]

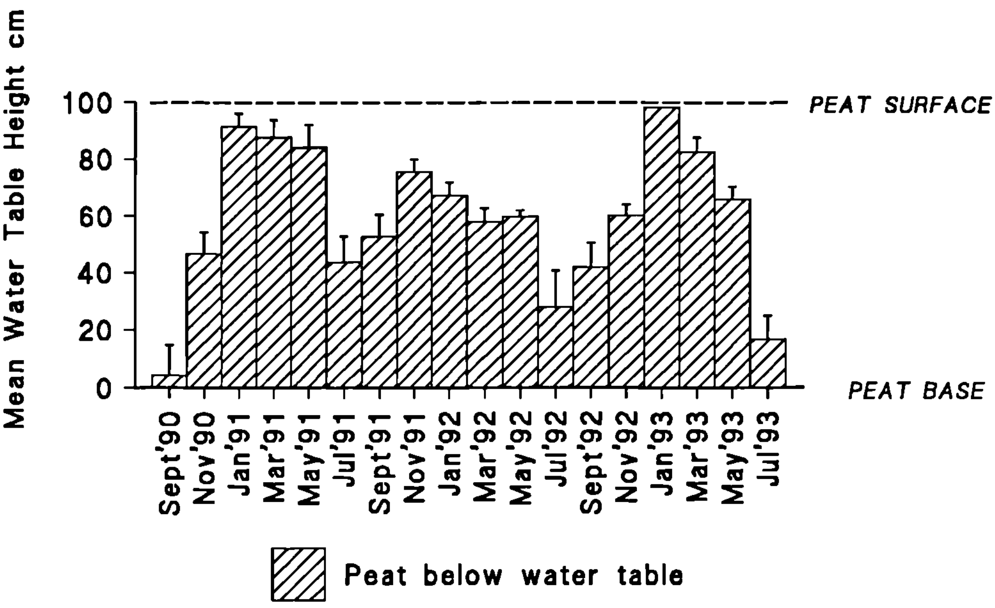
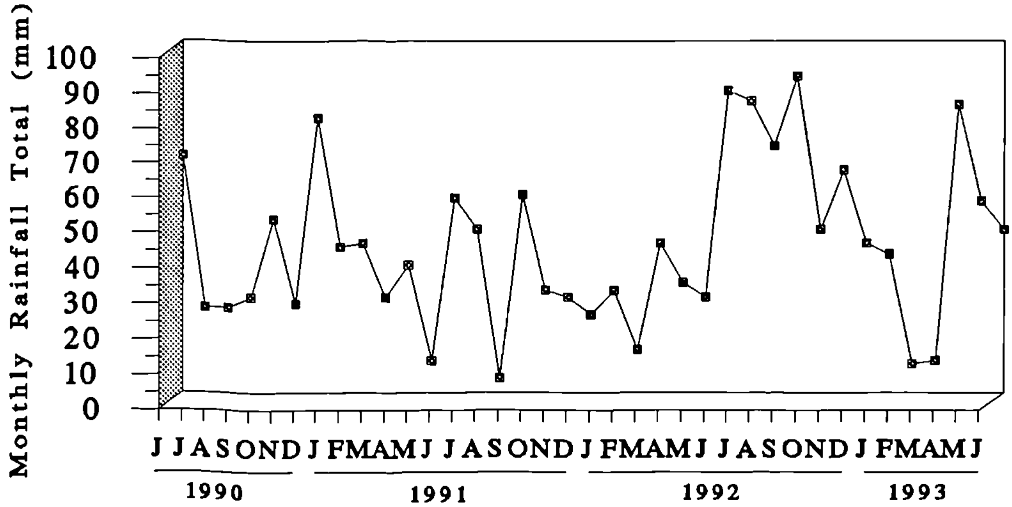


Fig 3.2: Monthly rainfall totals recorded at Finningley Meteorological Office, (nr Thorne Moors), between June 1990 and April 1992.



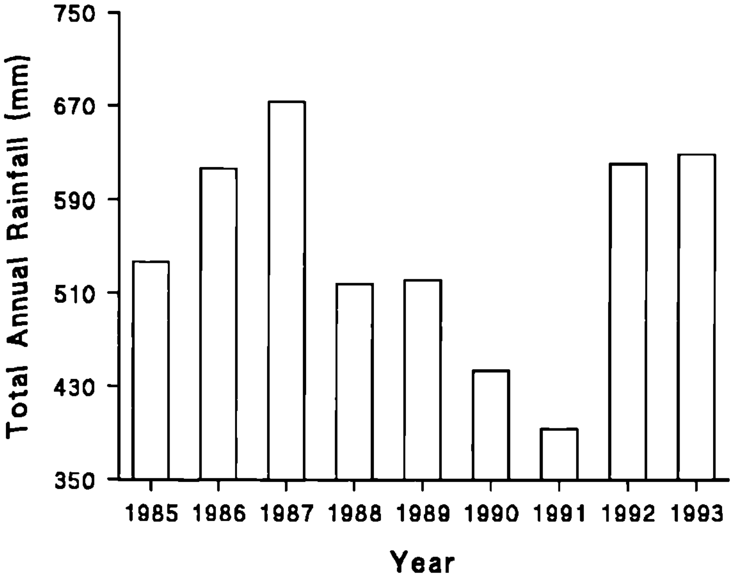
3. 1. 3 Discussion

The seasonality of water-table fluctuations recorded in the Creykes study area (Fig 3.1) suggests that results are closely influenced by temporal changes in the precipitation to evaporation ratio. Monthly rainfall totals from the Meteorological Office at R.A.F. Finningley (NGR: SK 659989), a few miles south of Thorne Moors, are presented in Fig 3.2. No clear seasonal trends were apparent in the rainfall data, with months of high and low rainfall occurring in both the summer and winter. Therefore, water-table fluctuations in the Creykes study area could not simply be related to changes in rainfall. Low summer water-tables may have been due primarily to other factors such as higher air temperature and greater rates of evaporative loss. Furthermore, summer rainfall may be more episodic than winter rainfall, so that rainfall totals may not appear to differ consistently over the year but the frequency of 'dry' days may be greater in the summer leading to increased evaporative losses. Low precipitation may however account for the low water-table recorded in the winter of 1991-1992 (Fig 3.1) compared with adjacent winters. There is the suggestion in Fig 3.2, that rainfall was lower on average in the winter of 1991-1992 compared with the winter of 1990-1991.

Ditches draining the site were not blocked until the Spring of 1990. Consequently much of the water precipitated in the 1989/90 winter may have been lost to drainage and not stored on site. This might explain the very low water-table recorded in September 1990. Water levels did not fall quite as low in following summers after the drains were blocked, suggesting drainage did influence this result. However, the water-table still fell significantly in July 1991, 1992 and 1993 despite periods of winter recharge and blocked drains. In the winter of 1991 and 1993, the water-table was particularly high but it still fell significantly the following summer. This suggests that the residual peat layers, even when saturated, will not store sufficient water to protect the system against summer drought. Therefore, at this site, ditch blocking alone may not be sufficient to restore surface wet conditions.

It is possible that peat dams blocking the ditches may have leaked so that some drainage of the site continued. On inspection there were no obvious signs of leakage but the possibility of chronic, inconspicuous leakage cannot be ruled out. Nevertheless, it is debatable whether such seepage would sufficiently account for the large water-table fluctuations observed. It is probable that water-table fluctuation is exacerbated at Thorne as it is a relatively low rainfall site, receiving 550 - 600 mm a^{-1} compared with over 1000 mm a^{-1} received by sites further north and west in the UK. Furthermore, data from Finningley Meteorological Office shows that annual rainfall totals for Thorne Moors during 1990 and 1991 were low compared with the preceding five years (Fig 3.3), suggesting that the water-table at the Creykes study area was monitored during an unusually 'dry' phase.

Fig 3.3: Annual rainfall totals recorded at Finningley Meteorological Office, (nr Thorne Moors)



Therefore, it might be argued that this study was conducted under exceptional circumstances with lower-than-average rainfall and leaking dams. However, the phenomenon appears to be more widespread as similar water-table fluctuations have been recorded for cut-over bog in higher rainfall locations elsewhere in NW Europe (Eggelsmann, 1982; Schouwenaars, 1988, 1992; Schouwenaars & Vink, 1992; Streefkerk & Casparie, 1989; Beets, 1992).

3. 1. 4 Factors contributing to water-table instability

3. 1. 4. 1 From diplotelmic to haplotelmic mire

Undamaged bogs are dual layered systems (diplotelmic) comprised of an uppermost 'acrotelm' and a lower 'catotelm' layer (Ingram & Bragg, 1984). The acrotelm consists of an actively growing layer of plants (principally *Sphagnum* mosses) up to 50cm thick which covers the bog surface extending downwards into fresh peat. The underlying catotelm comprises the bulk of peat in a raised bog. Typically well consolidated and well humified, it consists of acrotelm-derived material which accumulates as the bog grows upwards. Commercial peat extraction completely removes the acrotelm layer to reveal the catotelm peat which is then harvested, and after peat winning, the base of the catotelm peat is left behind to form the new bog surface.

In an undisturbed system the acrotelm layer has an important regulatory function, preventing drying out of the bog surface during the summer. Its loose and spongy structure stores large volumes of water which buffers the system during periods of low rainfall (Beets, 1992; Ingram & Bragg, 1984; Schouwenaars & Vink, 1992; Bragg, 1989). Water-table fluctuations are correspondingly limited and are contained within the acrotelm (1.6.1), and surface conditions are kept optimal for growth and survival of bog species (Bragg, 1989). The water storage capacity of catotelm peat is much lower. Boelter (1964, 1965) found water storage capacity in undecomposed

Sphagnum peat to be much higher compared with lower catotelm peat and that a rapid gradient of decreasing water storage occurred over the upper 45cm of a living bog. Loose *Sphagnum* peat in an acrotelm can contain some 85 % of 'free' water whilst in strongly humified peat it is only 8% (Streefkerk & Casparie, 1989). The total porosity of catotelm peat is actually high at around 80-97% (Reynolds *et al*, 1992), but it exhibits a greater frequency of micropores over macropores (> 50 μm) which is considered important in explaining its lower water storage capacity (Schouwenaars, 1982; Blankenburg & Kuntze, 1986).

After peat extraction, the bog surface lacks an acrotelm to buffer the system against periods of dry weather and the water storage capacity of residual catotelm peat may be too low to carry out this function. Consequently, no mechanism exists to regulate the water-table which may become highly unstable, and the peat surface become prone both to drought and periodic flooding (Beets, 1992; Joosten, 1992; Schouwenaars, 1988; Schouwenaars, 1992; Schouwenaars & Vink, 1992; Streefkerk & Casparie, 1989)

3. 1. 4. 2 Peat Type

The physical properties of the catotelm are not constant with depth. Lower peats are older and generally more strongly humified. Furthermore, deeper peat becomes compressed beneath overlying layers. Hobbs (1986), suggests that drainage and aeration of upper layers may further compress the underlying water-logged peat, expelling water and lowering porosity. Consequently, lower peats may exhibit even lower water storage capacities than catotelm peat higher in the profile. Schouwenaars (1992), found extraction of a known volume of water from strongly humified peat caused a greater fall in water-table than if less humified peat was used. This he attributed to lower water storage capacity in the former. Streefkerk & Casparie

(1989), also suggest that water storage capacity decreases with increasing degree of humification.

This is of significance to restoration as it suggests water-table fluctuations will be exacerbated where only deep peat is left remaining. However, the evidence supporting the influence of peat type is scarce and conflicting. Whilst deeper peats are considered more compact, profiles of bulk density over several metres are scarce and those that exist do not show consistent patterns of change. Tolonen (1979) described a profile which showed a consistent increase in bulk density with depth, but one reported by Tolonen (1977) did not. Porosity and bulk density may vary both between and within peat types so that 'light' and 'dark' peat cannot always be separated on the basis of water storage capacity (Schouwenaars & Vink, 1992). Streefkerk & Casparie (1989) suggest that some 'white' (less humified) peats may exhibit a water storage capacity as low as 'black' peat. Consequently, whilst there are undoubtedly gross differences in the water storage capacity of acrotelm and catotelm layers, the importance of peat type to water table fluctuations in cut-over areas remains poorly understood.

3. 1. 4. 3 Peat thickness and vertical water loss

A feature of intensively cut-over bogs is a low residual peat depth, often in the region of 1 m or less. In these situations, water-table fluctuations may be compounded by vertical losses of water through the bottom of the bog into the underlying mineral substratum. However, the water-table in raised bogs is generally considered to be independent of regional groundwater-tables. For example the Groundwater Mound Theory (Ingram 1982) assumes an impermeable base to the mound such that vertical water losses feature very little in the water balance equation.

Despite this, it is widely recognised by workers in NW Germany and the Netherlands that bogs can occur on a permeable sandy subsoil, where impermeability is provided by a high water-table in the underlying sandstone aquifer (Joosten & Bakker, 1987; Kuntze & Eggelsmann, 1981). In this situation, the lowering of regional groundwater levels (for example due to water abstraction for agriculture) may cause an unsaturated layer to develop under the bog thus influencing attempts to rewet bog remnants.

Intact bogs might be protected by thickness of the catotelm, but where this layer has been reduced by peat extraction, downward seepage may become an important element in the water budget. However, evidence for this very scarce. Schouwennars, Amerongen & Bootlink (1992) and Schouwenaars (1992) provide some data suggesting downward losses in the Netherlands are inversely related to residual peat depth. In NW Germany, Blankenburg & Kuntze (1987) suggest 50cm of residual peat is required to keep seepage losses to an acceptable level of 60 mm a^{-1}. A thicker layer did not significantly reduce seepage but a thinner layer may be breached by cracking.

Despite a general lack of evidence, downward seepage is considered by workers on the continent as a potentially important variable affecting bog restoration. It is difficult to assess the importance of downward seepage to UK bogs as the nature of the underlying substratum is frequently unknown. Stratigraphical studies are few, but those that exist indicate a layer of clay beneath the peat (Birks, 1965; Godwin & Mitchell, 1938; Gorham, 1949; Pigott & Pigott, 1963; Thomas, 1965; Walker, 1966). This suggests that downward seepage may be relatively unimportant but the possibility that 'permeable windows' may exist in clay layers cannot be discounted. The extent to which other bog sites may be influenced by downward seepage is not known.

3. 1. 4. 4 Vegetation cover

Abandoned peat fields may become colonised by dense swards of *Molinia caerulea* and be invaded by tree species, notably *Betula* spp (Chapter 2). High evapotranspirative losses associated with these species may then serve to exacerbate water-table fluctuations. This was not an important factor affecting the water-table at the Creykes study area as the peat remained only sparsely recolonised. However, at sites where *Molinia* is established, it is considered an important influence on water regime (Schouwenaars, 1990; Schouwenaars, 1992; Schouwenaars & Vink, 1992).

3.2 *The effect of water-table fluctuation on* Sphagnum *regeneration (Experiment 1)*

Periodic reductions in water-table height leave the peat surface prone to drought. The aim of this field experiment was to investigate the significance of this to *Sphagnum* regeneration.

3.2.1 Method

The 'Swinefleet pits' in the Crowle Study area of Thorne Moors were used for this experiment. They consisted of flooded, square pits 4 m^2 in area and 1 m deep, with an adjacent shelf of the same area cut 10 cm below the surrounding peat surface (1.10.2). Two sets of contrasting surface conditions were created:

1. **Periodic drought** - These conditions were provided on the peat shelf. Water-table depth below the surface of the peat shelf was recorded bimonthly for the duration of the experiment. Results are shown in Fig 3.4. Water level in the pits was prone to fluctuation and frequently in the summer the water-table fell below the surface leaving it dry.

2. **Permanently wet** - This was provided by a raft, floated in the flooded part of the pits. The raft was constructed from a bamboo cane framework, plastic (netlon) fence material (mesh size - 1 cm^2) and polystyrene floats all held together by plastic garden ties. Although the water level in the pits fluctuated, the raft remained in contact with it, providing a permanently wet surface.

Eight species of *Sphagnum* were used in this experiment: *S. magellanicum*, *S. papillosum*, *S. capillifolium*, *S. palustre*, *S. fimbriatum*, *S. recurvum*, *S. auriculatum and S. cuspidatum*. The peat shelf was divided into a grid of 16, 0.25 m^2

squares. Two squares were chosen randomly for each species. Twenty five plants, cut to 5cm length, were then placed prostrate into each square. This treatment was repeated exactly on the floating raft. The experiment was set up in May 1991. Results presented represent growth after 30 months. The area covered and capitulum density for each species were recorded using a 4 m^2 quadrat divided into 400, 100 cm^2 squares.

3. 2. 2 Results

This experiment was originally designed so that changes in capitulum density within each square, and any growth beyond the limits of each square, could be recorded for each species. However, such precise measurement was prevented for two main reasons. Firstly on the peat shelf, plants of all species became severely displaced by rain splash. Secondly on the raft, the 'sprawling' growth of some species displaced other plants and merged squares. Consequently, species no longer occupied their original discrete areas. A simpler measure of growth was therefore used. Total area covered and average capitulum density were recorded for each species on the raft and on the peat shelf. The results are presented in Table 3-1 below.

Table 3-1 : Expt.1: *Sphagnum* regeneration from whole plants placed on a persistently wet artificial raft and on a solid peat surface prone to periodic drought. Results represent growth after 30 mths. [Starting density for each species = 1 capitulum per 100 cm^2 over 0.5 m^2]

	PEAT SHELF		**FLOATING RAFT**	
	Area covered m^2	**Mean N^o capitula per 100 cm^2**	**Area covered m^2**	**Mean N^o capitula per 100 cm^2**
S. auriculatum	0	0	0.9	38
S. capillifolium	0	0	0	0
S. cuspidatum	0.25	20	1.9	29
S. fimbriatum	0	0	0	0
S. magellanicum	0	0	0.5	1
S. palustre	0	0	0.5	1
S. papillosum	0	0	0.5	1
S. recurvum	0	0	0.4	25

By multiplying area covered by capitulum density, an estimate of total capitulum number was derived for each species. As the starting number for all species was equal i.e. 50 plants, differences in capitulum number at the end of the experiment provide a crude measure of relative growth, shown in Fig 3.5.

On the peat shelf all species except *S. cuspidatum* failed to regenerate and only dead remains of the original inoculum could be found. On the raft, *S. magellanicum*, *S. papillosum*, *S. capillifolium*, *S. palustre* and *S. fimbriatum* also failed to regenerate. No trace was found of the original *S. capillifolium* and *S. fimbriatum* plants. However, unlike on the peat shelf, living plants of *S. magellanicum*, *S. papillosum* and *S. palustre* did remain. Regeneration of these latter species was very limited as they had become smothered by the growth of other Sphagna. Furthermore, the area covered was difficult to measure as the plants had become displaced from their original squares. Consequently in Table 3-1, *S. magellanicum*, *S. papillosum* and *S. palustre* are listed as retaining their starting density and area on the raft, to indicate that the original plants were not lost but had grown very little.

Prolific growth was observed on the raft for *S. cuspidatum*, *S. recurvum* and *S. auriculatum*. All three showed dramatic increases in capitulum density (Table 3-1). *S. auriculatum* and *S. cuspidatum* also expanded spatially although the cover of *S. recurvum* was slightly reduced. *S. cuspidatum* grew the most prolifically (far exceeding its growth on the peat shelf) to cover eight times its original area of 0.5 m^2 and at a capitulum density over an order of magnitude higher. Consequently, the *total* capitulum number can be estimated at two orders of magnitude above the original 50 used (Fig 3.5). *S. auriculatum* grew at a higher capitulum density than *S. cuspidatum* but expanded to cover only four times its original area. Growth of *S. recurvum* was lowest of the three species. Capitulum density matched that of *S. cuspidatum* but its lower area suggests it is a less competitive species under these conditions (Table 3-1).

Fig 3.4 : Experiment 1- Water regime on the peat shelf. [Water table fluctuations are shown relative to the peat surface. Water level was recorded bimonthly - dates are given for each value]

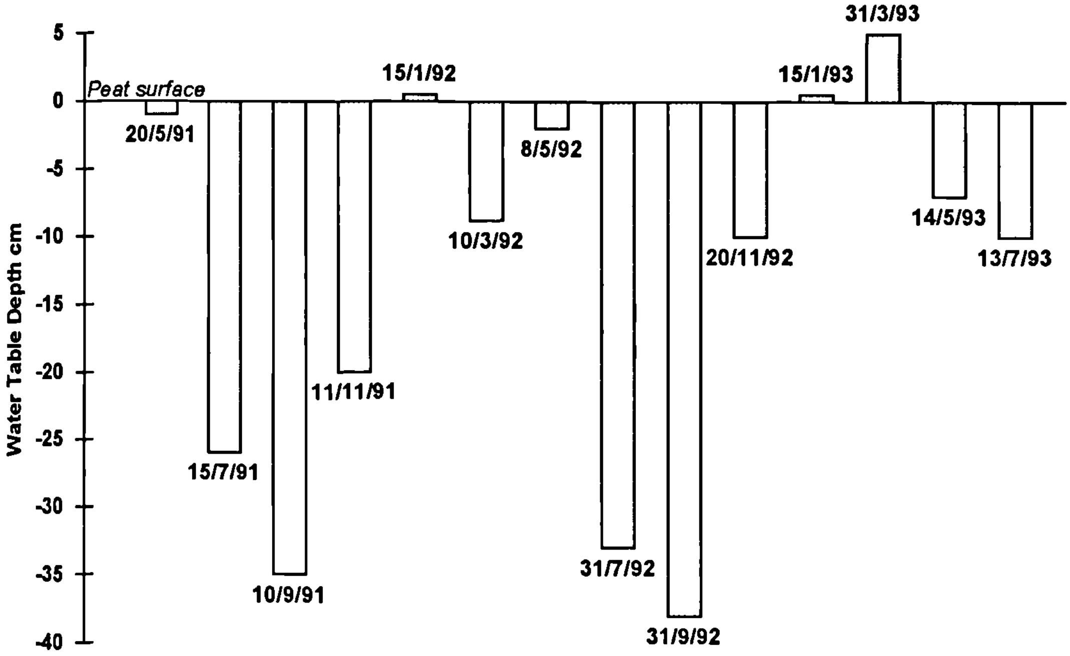
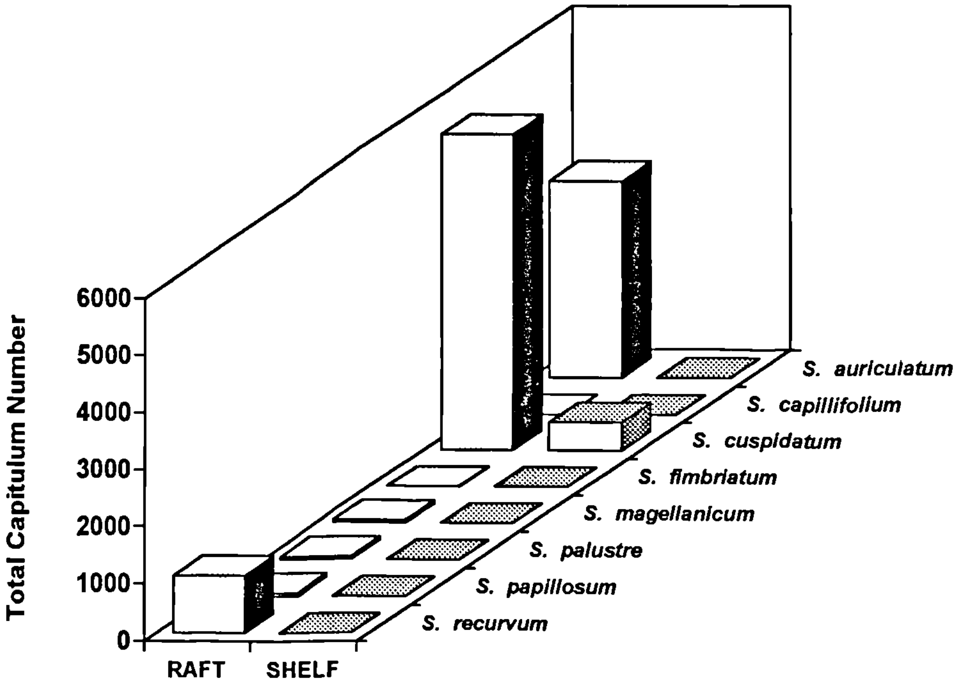


Fig 3.5: Results of experiment 1 - Comparative regeneration of *Sphagnum* applied to a permanently wet raft and a periodically dry peat shelf [For experimental details refer to section 3.2.1]



3.2.3 Discussion

Results suggest that water-table fluctuations severely limited growth of *S. cuspidatum, S. recurvum* and *S. auriculatum* on bare peat. Furthermore, desiccation of the peat surface was probably responsible for the failed regeneration and death of all *Sphagnum* material placed on the peat shelf. It may be argued that failure of *S. magellanicum*, *S. papillosum*, *S. capillifolium*, *S. palustre* and *S. fimbriatum* to regenerate on the raft indicates that water-table was not the primary factor limiting growth of these species on the peat shelf. However, failure of these species to regenerate on the raft may be otherwise explained. It was notable that *S. magellanicum*, *S. papillosum* and *S. palustre* plants did not die on the raft as they did on the peat shelf, but their growth was effectively checked as they became smothered, particularly by growth of *S. cuspidatum* and *S. auriculatum*. However, original plants of *S. capillifolium* and *S. fimbriatum* remained unaccounted for. It is possible that they were lost through the holes in the mesh due to rain splash as individual gametophytes of *S. capillifolium* and *S. fimbriatum* are very delicate and insubstantial compared to other species used.

Plants that regenerated well on the raft were all species known to grow in aquatic habitats (1.6.2). Therefore it is possible that growth of the other species was limited by conditions that were too wet. The raft generally remained a centimetre below the water level so that its surface was just submerged. However, evidence discussed in Section 1.6.2 suggests that hummock-forming species are not intolerant of water-logged conditions but growth of pool species is much more prolific under these conditions. Hence, failure of hummock species to regenerate on the raft was probably due to competitive exclusion and not water-logging.

Despite periods of drought the peat shelf did support some growth of *S. cuspidatum*. It was interesting that a species typical of the wettest situations should be the one most able to survive the 'dry' conditions of the peat shelf. Growth was confined to periods when the water-table was at or above the peat surface. When the water-table was low, plants became desiccated and brown. In abandoned peat fields in the Netherlands, similar desiccation tolerance in *S. cuspidatum* has been observed (B. D. Wheeler, *pers comm*). Furthermore, Clymo & Hayward (1982) found *Sphagnum auriculatum* survived desiccation better than the hummock forming *S. capillifolium*. It would appear pool species can exhibit desiccation tolerance greater than hummock species, which may go some way towards explaining the regeneration of *S. cuspidatum* on the peat shelf.

3. 2. 4 Stabilising water-tables

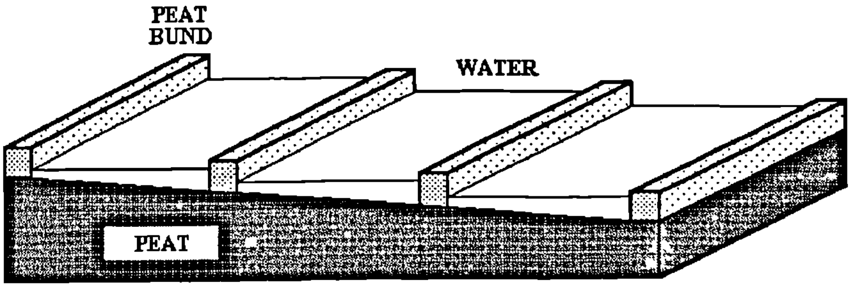
Results from Experiment 1 suggest that water table fluctuations, such as those recorded in a milled peat field at Thorne (3.1), may severely restrict *Sphagnum* recolonisation. Beets (1992) suggests the water storage capacity of abandoned peat fields will be increased by creating open water across the bog surface. In water balance studies for bog relics in the Netherlands, Schouwenaars (1992) also points out that the storage coefficient of open water is 100% and areas characterised by a high proportion of permanently inundated surface show limited water-table fluctuations when compared with areas where the open water is absent.

Creation of open water will require reconfiguration of the peat surface. In Germany, a system of lagoons, resembling paddy fields, has been utilised widely and is considered a particularly important method for creating open water on sloping surfaces (Eggelsmann, 1987, 1988a, 1988b). Fig 3.6 gives an example of suggested lagoon construction for a slightly inclined slope. Once the lagoons are constructed, the surface is further reconfigured by 'ploughing' a series of longitudinal hummocks and hollows. The aim is to produce a fine network of open water instead of extensive lagoons which may produce problems of wave action.

On flatter surfaces a mosaic of pools could be constructed by building an interstitial network of bunds. Alternatively open water could be created by excavating pools. Beets (1992) suggests distance between pools should be minimised to reduce water-table fluctuations in the bunds. The depth of pools required to ensure perennially wet conditions will depend on the severity of water-table fluctuations at a particular site. Experience in the Netherlands suggests depths of 0.5 - 0.6m should be sufficient (Beets, 1992).

Such constructs serve to reduce lateral water losses and retain precipitated water on site. Their exact design will vary depending on site specific factors such as climate. For example, areas characterised by a relatively high annual evaporation to precipitation ratio may require larger, deeper pools to maintain surface water.

Fig 3.6 : System of lagoons for allowing storage of water on sloping surfaces



3. 2. 5 Implications for *Sphagnum* regeneration

Creation of open water areas may stabilise water-tables, but consideration must be given to how this will influence *Sphagnum* recolonisation. Regeneration of *Sphagnum* deliberately introduced to open water is considered in detail in Chapter 5. Evidence presented in Chapter 2 suggests that open water was the starting point for some of the most 'desirable' bog plant assemblages observed to have recolonised old peat workings. These had developed as floating rafts over flooded peat pits. Rafting refers to the growth of plants floating in or on supra-surface water and therefore requires (by definition) some degree of inundation. Plants may be free floating or attached to the margins of pools, from which they expand centripetally. Development of rafts produces a 'skin' permitting subsequent colonisation by species that would not normally colonise open water. For example *Sphagnum* rafts were observed to support species such as *Narthecium ossifragum, Erica tetralix, Andromeda polifolia* and three species of *Drosera.*

In undisturbed bogs, rafts are not a major component of the surface being restricted to the vicinity of pools but rafts are often very important in the initiation and early development of ombrotrophic bog. Stratigraphical studies suggest that development of *Sphagnum* vegetation within some basin mires in NW England occurred by colonisation of floating fen rafts i.e. a hydroseral succession from open water to bog (Walker, 1970). Development of *Sphagnum* bog on fen rafts has also been recorded for basin mires in the Scottish Borders (R. Tratt *pers comm.*), in peat cuttings in the Norfolk Broads (Giller & Wheeler, 1986, 1988) and in the Dutch mires of NW Overijsel (Segal, 1966; van Wirdum, 1991).

Where conditions are not base-rich, *Sphagnum* rafts may directly colonise open water without the need for a pre-existing raft of fen vegetation. Stratigraphical evidence indicates that deposits of *Sphagnum* peat at Flaxmere, in north Cheshire, originated as a floating raft of *Sphagnum cuspidatum.* Furthermore, the present day vegetation of other small basin mires in the region consists of floating rafts of *S. cuspidatum* and *S. recurvum* overlying open water (Tallis, 1973). Floating bog mats are also reported to have developed in kettle-hole mires in south west Ontario (Hanf & Warner, 1992).

Rafts appear to be favourable environments for the development of *Sphagnum* bog vegetation. They have the critical advantage of being able to move with the water-table if it fluctuates. Therefore, relative to the vegetation layer the water-table remains stable and the *Sphagnum* mosses are never subject to drought. Furthermore, growth of undesirable 'dry' species such as *Molinia*, *Betula* and *Pteridium aquilinum* is suppressed in permanently saturated conditions.

3.3 *Effect of surface humidity on* Sphagnum *growth (Experiment 2)*

3. 3. 1 Introduction

In an abandoned milling field, physical conditions at the peat surface may be highly unstable. In addition to the direct effects of low water table on *Sphagnum* growth (see above), colonisation must contend with a substrate prone to considerable temperature fluctuations, frost heave, rain-splash, surface crusting and wind erosion (Nilsson *et al*, 1990). Cut-over bog may remain substantially bare for many years and consequently, wind resistance at the bog surface is probably low. Without a layer of relatively still air, analogous to the boundary layer surrounding a leaf, it is quite conceivable that humidity at the bog surface is very low. The significance of plant cover to surface microclimate was demonstrated by Salonen (1992). In a novel experiment he planted plastic plants on a bare peat surface to simulate a cover of *Vaccinium vitis-idaea* and found that it significantly increased peat water content and reduced temperature at the peat surface.

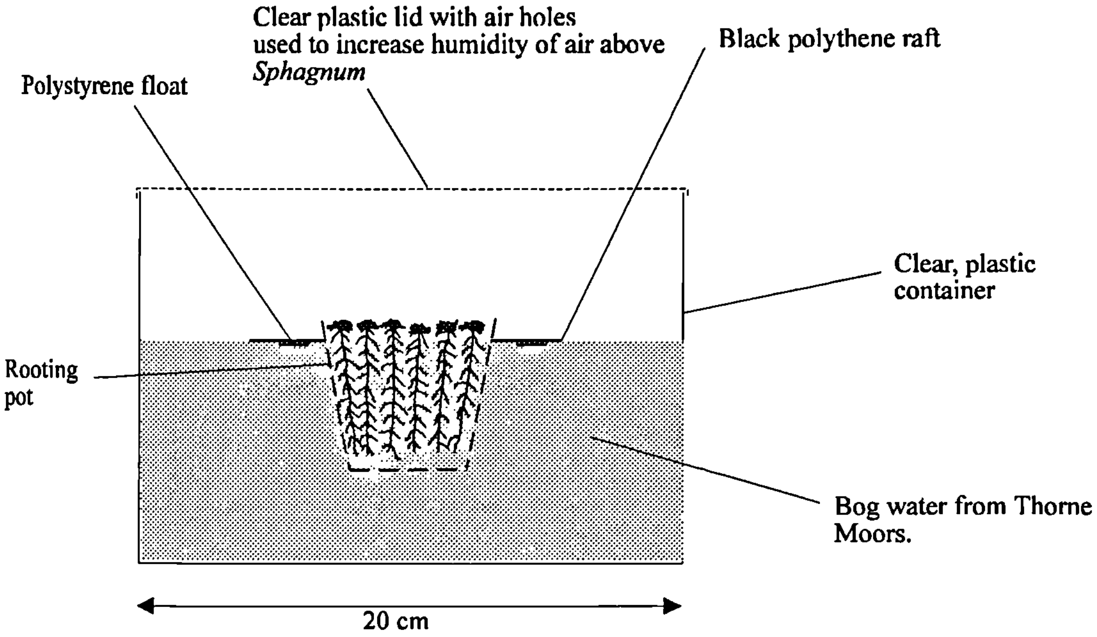
In undisturbed systems, *Sphagnum* species growing some distance from the water table generally occur in dense hummocks, suggesting some importance to *Sphagnum* growth of sustaining a humid microclimate around the plants (1.6.2). The importance of humidity was also alluded to in Chapter 2, as revegetation trends suggest that *Sphagnum* growth on peat is favoured by the shelter provided by a cover of vascular plants (2.2.3.1). There has been little detailed research on the effects of surface microclimate on *Sphagnum* growth; however, very recent studies by Buttler, Grosvernier & Matthey (*in prep*) show that under the cover of *E. vaginatum* and *Polytrichum* spp., *Sphagnum* does find better growing conditions, with higher humidity and less extreme temperatures.

The aim of this investigation was to conduct a simple laboratory experiment to examine the effect of humidity on growth and morphology of *Sphagnum.*

3. 3. 2 Method

S. cuspidatum plants cut to 5 cm in length, were placed in batches of ten, into rooting pots, which were then placed in clear plastic containers filled with water collected from the Crowle study area of Thorne Moors (1.10.2). The rooting pots were floated by small polystyrene rafts so that the *Sphagnum* was submerged up to 1 cm below the capitula at the start of the experiment (Fig 3.7). Some containers were covered by a clear plastic lid (with air holes) to increase humidity and other '*control*' containers were left uncovered. The containers were placed in a greenhouse for eight weeks, exposed to natural light and a maximum temperature range of 15 - 22 ^{o}C. There were three replicates per treatment. As the plants grew, so the capitula became more distant from the water level. No attempt was made to keep the water level 1 cm below the capitula as this would have defeated the object of the experiment. By floating the pots, the original water level of 4cm above the base of the plants was kept constant in both treatments. Humidity was not measured, but it was evident from condensation in the covered containers that the atmosphere was saturated for the duration of the experiment. The chemical condition of water used in this experiment is considered in detail in Chapter 4. Growth in weight was measured using the Capitulum Correction Method (Clymo, 1970) and was expressed as Relative Growth Rate, where RGR = (nL final plant dry weight - nL original plant dry weight) / time. Increase in shoot length and the number of innovations produced were also recorded. Innovations are the product of vegetative reproduction in *Sphagnum,* and consist of new shoots resembling the parent plant, which branch from the parent stem.

Fig 3.7: Cross section showing design used for growing *Sphagnum* at different humidities (Experiment 2)



3. 3. 3 Results

Difference in RGR, shoot length and innovation number between the treatments were tested for using the Student-t test assuming equal variances. For RGR data, normal distribution and equal variance was assumed as the data were in log form. Frequency distribution suggested that shoot length data were also normally distributed, and F_{max} results (F_{max} = 1.58, d.f. 2,29, p>0.05) showed that variance between the two treatments did not differ significantly. Data for innovation number, being in the form of small, whole numbered counts were transformed by the equation $\sqrt{(x + 0.5)}$.

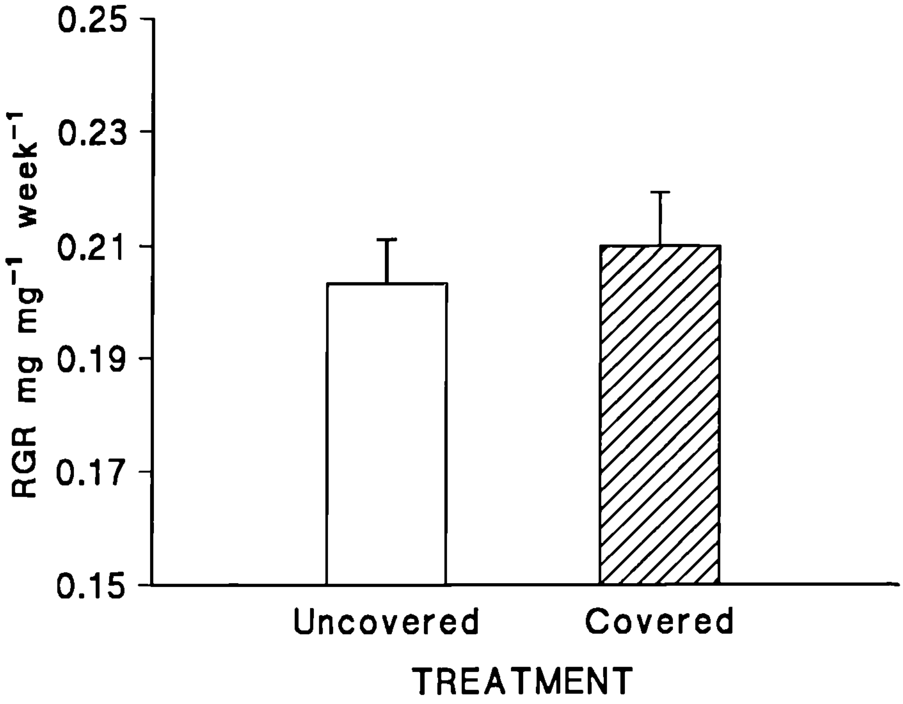
Growth in weight did not differ significantly between the control and the covered *Sphagnum* (p = 0.267), (Table 3-2, Fig 3.8i). However, growth in length was significantly greater in plants growing under covered conditions (p= 0.0001)(Table 3-2, Fig 3.8ii). Furthermore, innovation production was also on average, significantly greater in *Sphagnum* growing under covered conditions (p = 0.0001)(Table 3-2, Fig 3.8iii).

Table 3-2 Growth of *S. cuspidatum* under different microclimatical regimes (Expt. 2).
[Mean values are given with standard errors in parentheses. RGR = Relative growth rate (mg mg^{-1} $week^{-1}$ dry wt.)]

	RGR	**Shoot Length (mm)**	**N° Innovations per original shoot**
Uncovered (Control)	0.203 (0.004)	93.7 (2.126)	0.73 (0.082)
Covered	0.210 (0.005)	168.83 (2.671)	2.267 (0.158)
Student-t test results (2- tail)	d.f. = 58 t = -1.1204 p = 0.2672	d.f. = 58 t = -22.005 p = 0.0001	d.f. = 58 t = -8.5867 p = 0.0001

Fig 3.8: Expt 2: Growth of *Sphagnum cuspidatum* in pots (shown in Fig 3.7) at different humidities for 8 weeks. [Covered pots provided a more humid microclimate. Uncovered pots = Control. Error bars = 95 % confidence limits]

i. Relative Growth Rate (RGR)



ii. Shoot Length

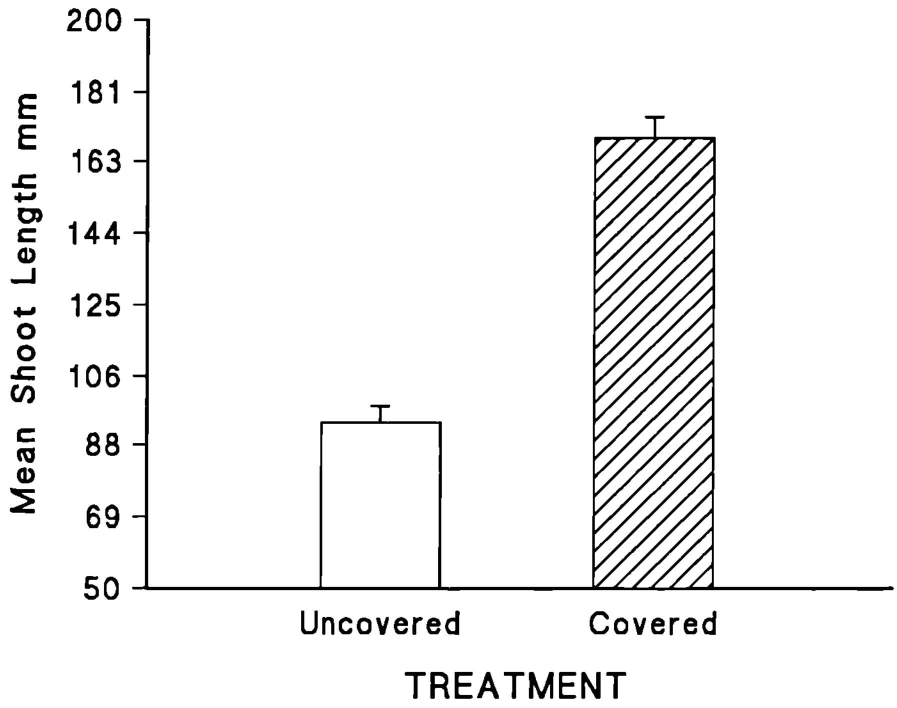
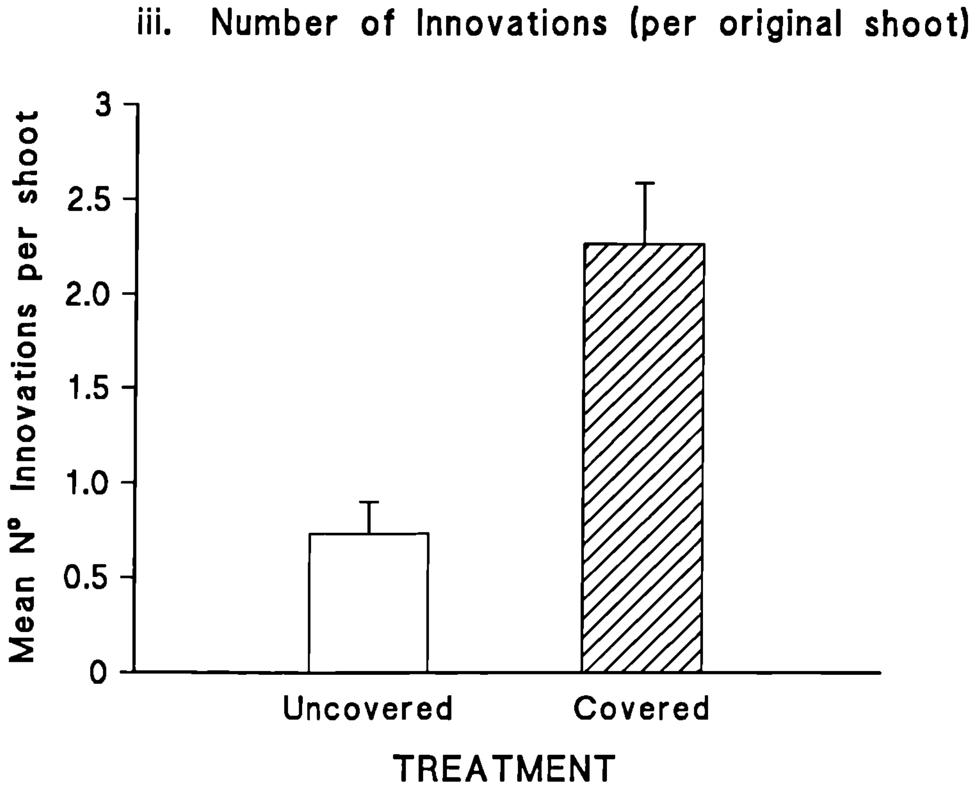


Fig 3.8: *Continued*



3. 3. 4. Discussion

The results of this experiment suggest that surface humidity may have an important influence on *Sphagnum* growth. Conditions provided by the covered containers facilitated growth of *Sphagnum* to much greater lengths compared with the control. This is probably because evapotranspirative stresses were much lower in the covered containers and *Sphagnum* shoots were able to sustain capitulum moisture content at significantly greater distances from the water table. It is likely that growth of *Sphagnum* observed beneath a canopy of vascular plants (see above) is also facilitated in this way.

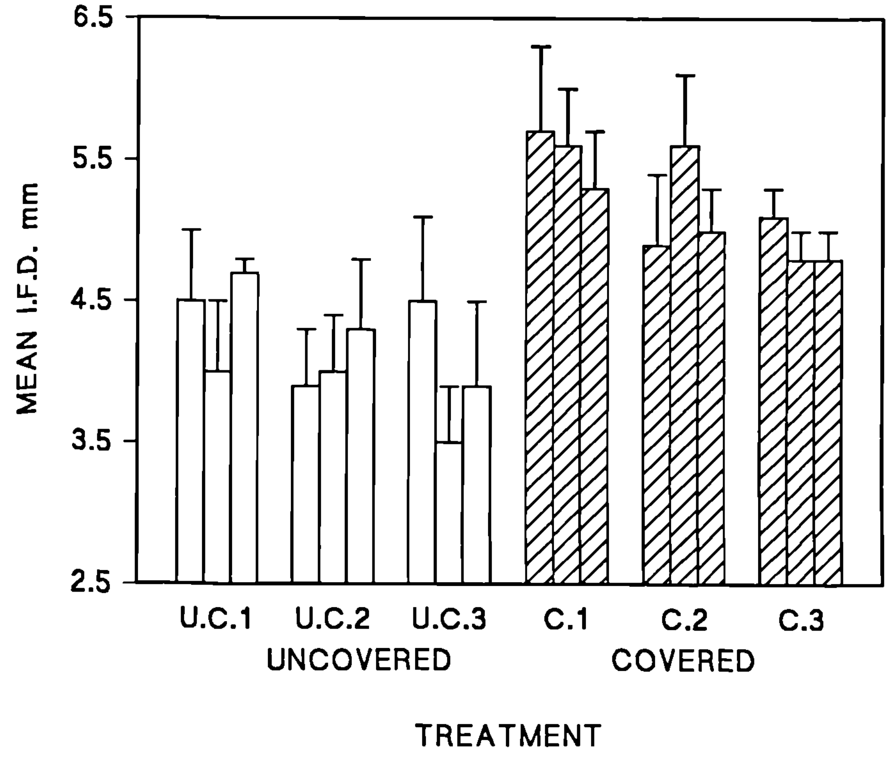
The average distance between groups of branches (or fascicles) on a stem was recorded for a sample of three plants from each replicate (Fig 3.9). The results suggest that this 'inter-fascicular distance' was, on average, greater in longer plants from the covered containers. Therefore, growth in length appears to have occurred primarily by stretching or elongation of the stem between fascicles.

It could be argued that increased humidity has served to modify growth form but has not increased growth as RGR did not differ from the control (Fig. 3.5i). However, it is possible that growth in mass was limited by other factors, particularly phosphorus concentration in the bog water used. This is considered in more detail in Chapter 4.

Modification of growth form in this way without an increase in overall mass may nevertheless be significant for *Sphagnum* recolonisation. Greater extensional growth and greater innovation production, would conceivably encourage the vertical development of *Sphagnum* cushions. Once established, the microclimate within such cushions would be more regulated enabling *Sphagnum* to be more resistant to periodic drought. Experiments have shown that *S. magellanicum* and *S. fuscum* are less sensitive to low water tables when in dense hummocks or lawns (Buttler *et al*, in prep).

This would be of particular significance to growth of *Sphagnum* around the periphery of pools, considered in section 3.2.3. However, this is completely conjectural and requires further study.

Fig 3.9: Mean Inter Fascicular Distance (I.F.D.) in *S. cuspidatum* grown under different humidities [Covered pots provided a more humid microclimate. Uncovered pots = Control. Error bars = 95 % confidence limits. Each bar represents mean IFD for an individual plant. Three plants were measured from each replicate U.C.1 - U.C.3 & C.1 - C.3]



Chapter 4

Some hydrochemical characteristics of cut-over bogs

4. 1 *Field survey of cut-over peatland*

There has been little detailed study on the effect of peat extraction on bog hydrochemistry. However, changes in water quality would be of particular significance to the development of floating raft vegetation. The aim of this study was to investigate whether the chemical environment of a milled peat field differed significantly from an undamaged bog and consider the implications of any differences to *Sphagnum* regeneration.

4. 1. 1 Method

Water samples were collected from two contrasting types of cuttings on Thorne Moors. The Creykes study area was representative of a recently abandoned milled peat field and the Crowle study area consisted of long abandoned block cuttings retaining a reasonable depth of ombrotrophic peat (1.10.2). Water samples were collected in triplicate from the following pits:

Creykes CP1, C1, C3, CP5, C5, C7, CP9, C9, C11, CP13, C13, C15 (Fig 1.4)

Crowle SP1, SP5, SP9, STA1, STA5, STA9, STA13, STB1, STB5, STB9, STB13, SP13, SP14 (Fig 1.5)

Between June 1990 and July 1991, samples were collected bimonthly, filtered and measured for pH, conductivity and the ionic concentration of calcium, potassium, iron, soluble reactive phosphorus, ammonium, sulphate and nitrate. Methods of analysis are outlined in Table 4 -1. Measurement of pH and conductivity continued bimonthly until July 1993. Conductivity values were corrected for pH (Golterman, Clymo, and Ohnstad, 1978).

Table 4-1: Methods used in analysis of water samples

pH	Jenway 3030 Portable pH Meter
Conductivity	Jenway 4070 Portable Conductivity Meter
Calcium, Iron	Atomic Absorption Spectrophotometry. Perkin - Elmer 2100 AAS
Potassium	Atomic Emission Spectrophotometry Corning Flame Photometer 410
Nitrate, Sulphate	High Performance Liquid Chromatography Dionex 2000i HPLC
Ammonium-N	Colorimetric (Indophenol) method modified from Scheiner (1976). Absorbance measured on Cary 1 UV-Visible Spectrophotometer (Varian)
Soluble Reactive Phosphorus	Colorimetric. Acid Molybdate Antimony/L -ascorbic acid method modified from John (1970). Absorbance measured as for Ammonium.

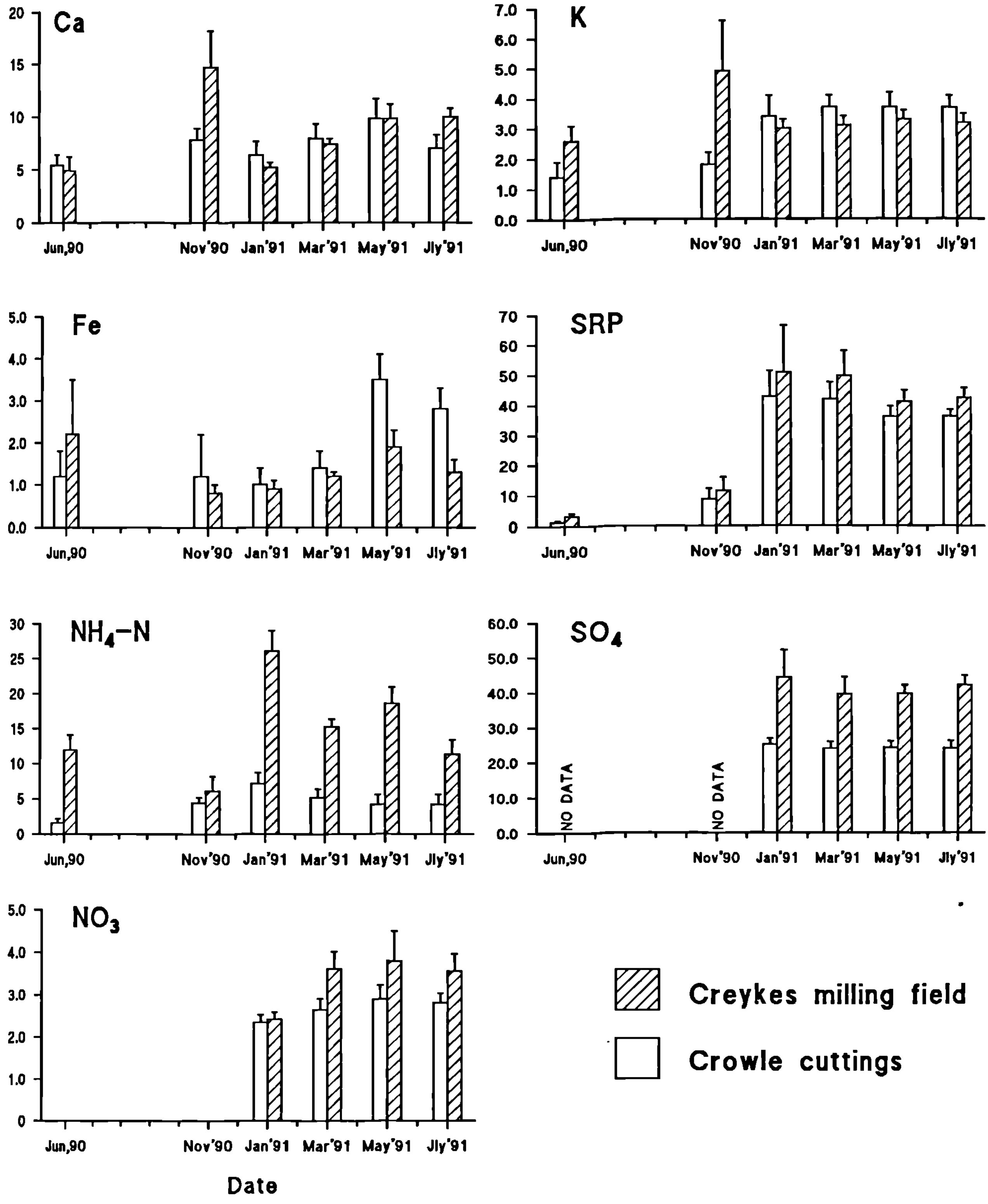
4. 1. 2 Results

Fig 4.1 shows the mean concentrations of major ions recorded for Creykes and Crowle at each sampling event. Mean values were derived by combining data from all the pits sampled at each study area. Furthermore, data from all the sampling events were combined to give overall annual means for pits at the Creykes and Crowle study areas which were then compared using the Student t-test. In all cases the data approximated a normal distribution. Data were analysed using the F_{max} to test for homogeneity of variance so that the appropriate t-test (assuming equal or unequal variances) could be used. Mean concentrations and t-test results are presented in Table 4 -2.

Table 4-2: Mean pH, conductivity and solute concentration in water from peat cuttings.
[SRP = Soluble reactive phosphorus. All concentrations in mg l^{-1} except where stated. Standard Errors in parentheses]

	pH	Cond. µS cm^{-1}	Ca	K	Fe	SRP µg l^{-1}	NH_4-N	SO_4	NO_3
Creykes	3.4 (0.01)	425.0 (15.4)	8.6 (0.5)	3.3 (0.16)	1.44 (0.15)	31.1 (2.7)	14.9 (0.81)	41.3 (1.25)	3.4 (0.14)
Crowle	3.44 (0.02)	158.1 (3.6)	7.4 (0.28)	3.0 (0.15)	1.83 (0.16)	27.7 (2.11)	4.4 (0.81)	24.2 (0.5)	2.7 (0.07)
t - value df prob.	-1.73 507 0.08	16.9 262 < 0.001	-2.06 120 0.056	-1.6 152 0.11	1.85 154 0.067	0.98 145 0.33	-12.21 96 < 0.001	12.73 61 < 0.001	4.35 71 < 0.001

Fig 4.1 Mean concentration of major ions recorded in water samples from the Creykes and Crowle study areas of Thorne Moors (4.1). [Error Bars = 95% confidence limits. All measurements in mg l^{-1} except SRP which = $\mu g\ l^{-1}$. SRP = Soluble Reactive Phosphorus]



Concentrations of Ca, K, Fe and SRP in water from pits in the Creykes and Crowle study areas, remained similar throughout the study period (Fig 4.1). In November 1990, concentrations of Ca and K were temporarily elevated at the Creykes study area, but overall, means did not differ significantly ($p > 0.05$) (Table 4-2). The reason for this apparent 'pulse' of Ca and K in November is not clear. It may be a brief episodic occurrence following a recent precipitation event or represent a general 'flushing' effect as the peat field became recharged with water after the summer dry period (Section 3.1). Concentrations of NH_4-N, SO_4 and NO_3 were higher at the Creykes study area throughout the year (Fig 4.1) and were found, overall, to differ significantly from the Crowle area ($p < 0.001$) (Table 4-1). There was some evidence of a flushing effect with NH_4-N, as concentrations greater than 20 mg l^{-1} occurred only in January 1991, and levels around 10 - 20 mg l^{-1} were more usual (Fig 4.1).

The range of values recorded at the Creykes study area were compared against those recorded by other workers for undisturbed sites (Fig 4.2). Concentrations of SRP were similarly small but concentrations of Ca, K, Fe, NH_4-N, SO_4 and NO_3 were all much higher at Creykes. Ca, SO_4 and NH_4-N concentrations were the most markedly elevated. At the Creykes study area, Ca occurred at between 5 - 18 mg l^{-1} compared to < 3 mg l^{-1} in undisturbed bogs. However, Fig 4.1 suggests that 5 - 10 mg l^{-1} Ca was more normal at Creykes, values above 10 mg l^{-1} occurred exceptionally in November 1990 (see above).

Conductivity measurements recorded over three years suggest that conductivity at the Creykes study area was significantly higher than at the Crowle area ($p < 0.001$) with a mean of 425µS cm^{-1} compared with 158µS cm^{-1} respectively (Table 4-2). It is evident from Fig 4.3 that conductivity at the Creykes study area, whilst generally higher than at the Crowle area, was also much less stable during the study period. Levels are strongly peaked around November 1990 and July - October 1992, falling sharply afterwards both times. It is tempting to suggest that these peaks represent a 'flushing' effect of late autumn and winter rainfall, the subsequent fall in conductivity being due to a dilution effect, but monthly rainfall totals between June 1990 and April 1992 show no clear seasonal pattern (Fig 3.2). 'Flushing' of the peat may nevertheless have occurred in response to a general increase in water levels in the peat, which did show some seasonal trend, for example water table data (Fig 3.1) suggest that high conductivity recorded in November 1990 corresponded with a period of increasing 'wetness'. Similarly, water levels rose around November - January in 1992 though not to as high a level. This corresponds with just a small increase in conductivity around that time (Fig 4.3). However, in July 1992, conductivity was greatest despite the water table being low, suggesting a winter flushing effect was not responsible. It is possible that sampling took place after a recent precipitation event which caused a pulse of solutes to be released from the peat or, alternatively, it may represent a concentration effect due to high evaporative losses during the summer. It was notable that a high conductivity persisted in the autumn but was subsequently lowered during the winter possibly due to a dilution effect. Therefore, some degree of seasonality may have influenced the conductivity values recorded.

Overall, no significant difference was found between the pH of water at the Creykes and Crowle study areas, both sites recording a mean of pH 3.4 (Table 4-2). However, in Fig 4.4 it is evident that during the second half of the study period there was a trend towards a greater frequency of lower pH values at Creykes. A regression line can be fitted to data from the Creykes area which shows a linear trend of decreasing pH with time ($p = 0.0002$). No significant relationship was found for the Crowle area ($p = 0.1461$) (Fig 4.5). This suggests that since ditches were blocked at Creykes there has been a trend of increasing acidification during the study period. If the site had been monitored for longer then a significant difference in mean pH between the Creykes and Crowle study areas may have been detected. The range of pH values recorded at the Creykes area were compared to those recorded at undisturbed sites (Fig 4.2). Water at Creykes was generally of comparatively low pH. It is evident from Fig 4.4 that very low pH values of 3.0 - 3.2 persisted in flooded pits at the Creykes study area for several months at a time.

Fig 4.2 Water quality of cut-over bogs compared with undisturbed sites.
[Bars represent the range of pH and solute concentrations recorded in water samples from the Creykes milling field (4.1), compared with values recorded by other workers for undisturbed bog]

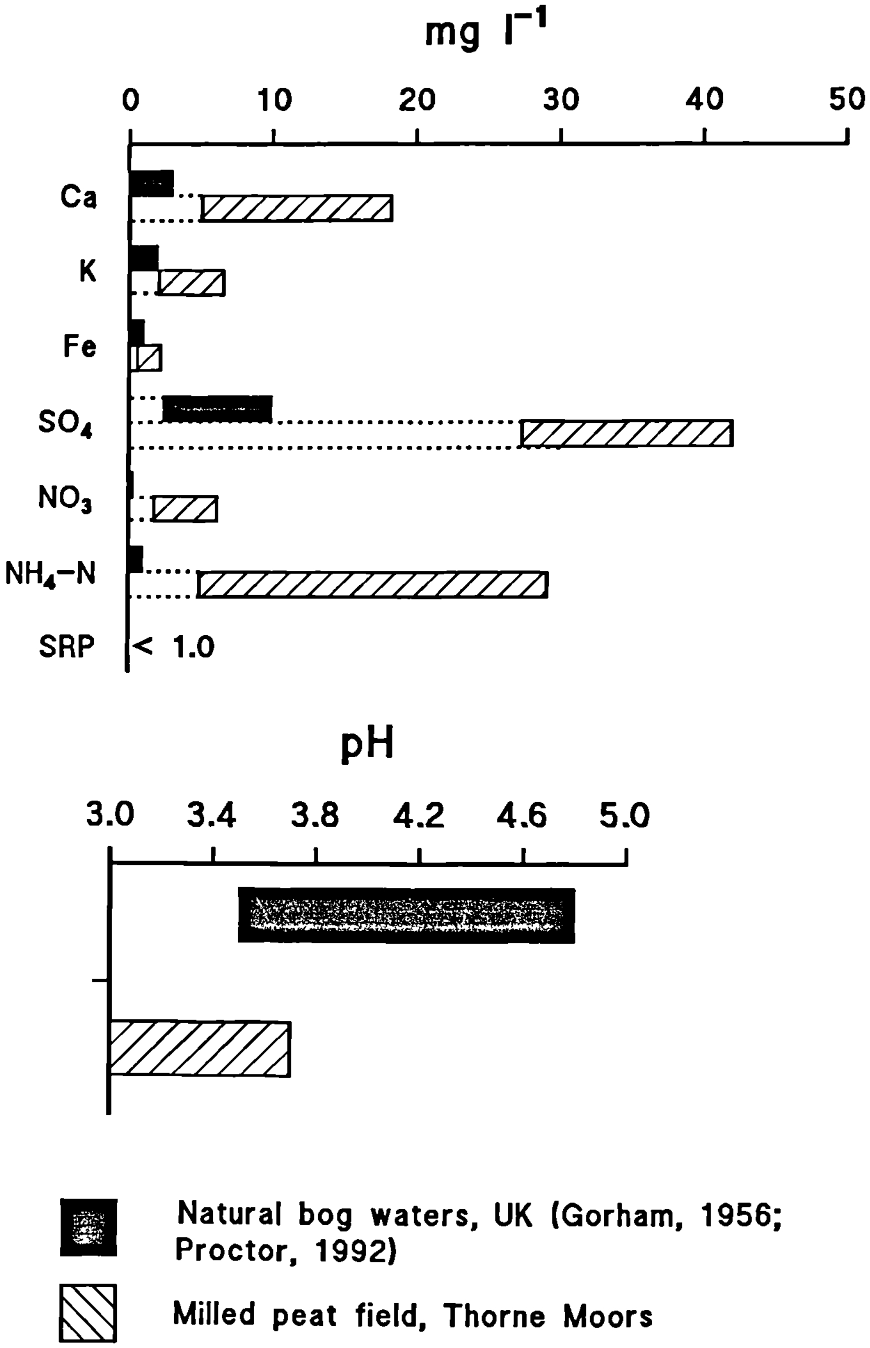


Fig. 4.3 Mean Conductivity of water samples taken from the Creykes and Crowle study areas during the study period. [Values given are corrected for pH. Error bars = 95% confidence limits]

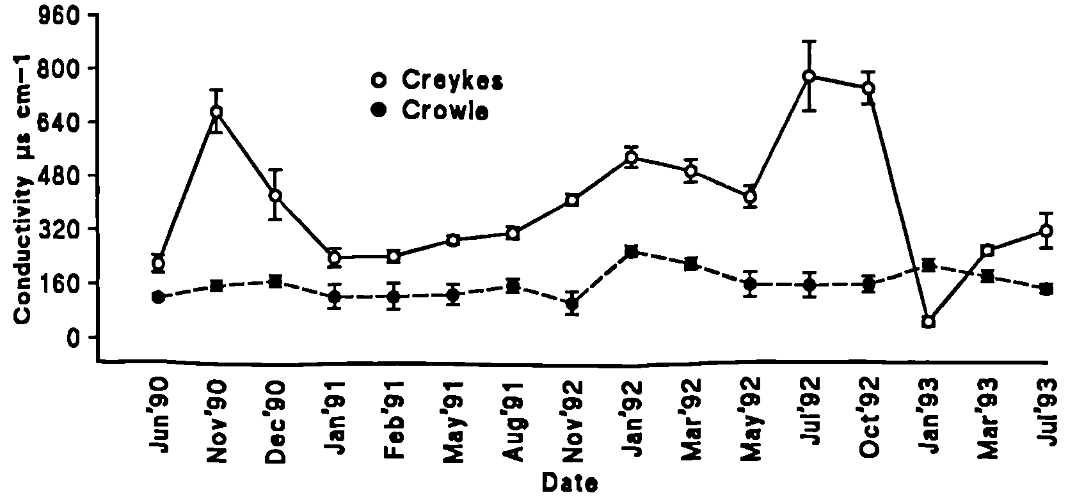


Fig. 4.4 Mean pH of water samples taken from the Creykes and Crowle study areas during the study period. [Error bars = 95% confidence limits]

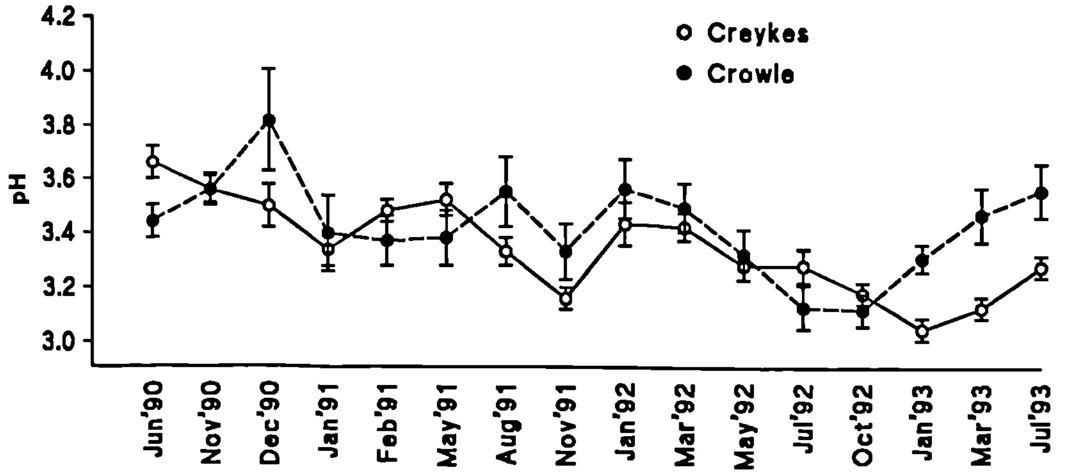
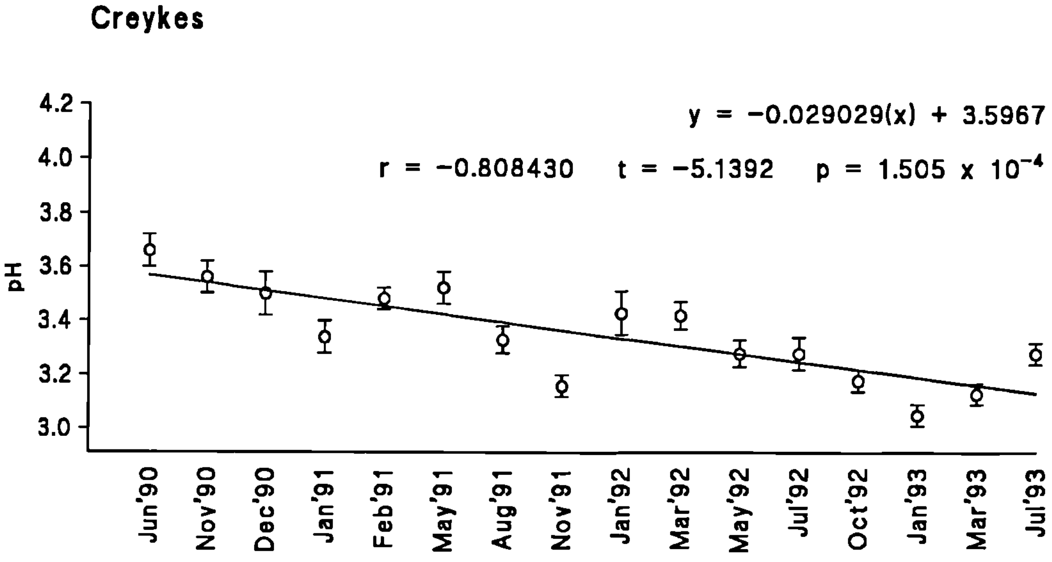
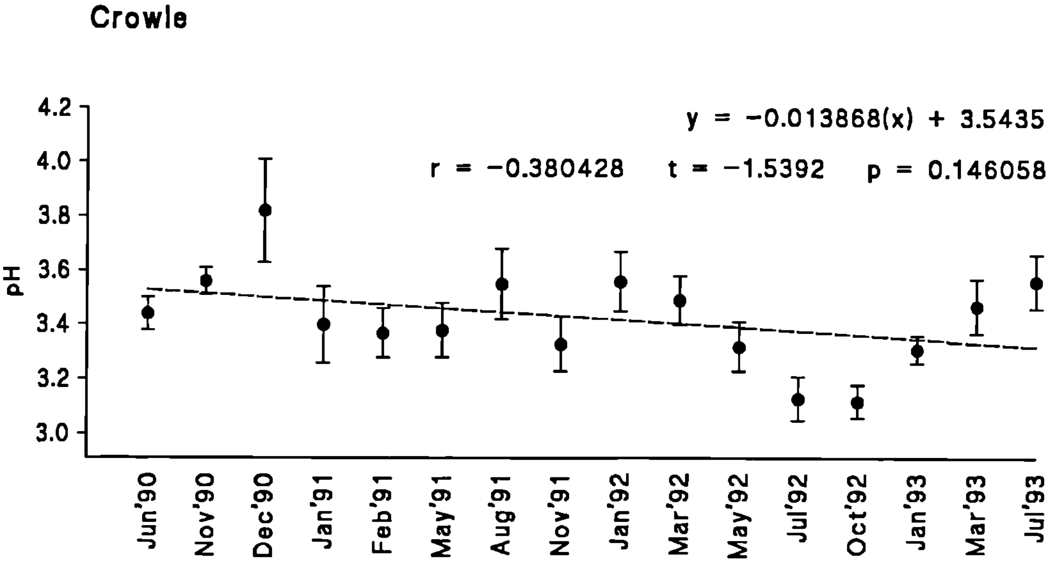


Fig. 4.5 Overall trends observed in the pH of water samples taken from the Creykes and Crowle study areas during the study period [Error bars = 95% confidence limits]





4. 1. 3 Discussion

4. 1. 3. 1 Sources of enrichment

Results provide some suggestion for chemical enrichment at both the Creykes and Crowle study areas compared with undisturbed bog. Furthermore, at the Creykes area, concentrations of SO_4, NH_4-N and NO_3 were significantly greater than at the Crowle area. The source of this enrichment is not known, however, several possibilities are considered below:

4. 1. 3. 1. 1 Basal contamination

Exposure of the mineral substratum may lead to base enrichment of cuttings (2.2.3.3). The bottom of pits at the Creykes study area frequently made contact with, or remained very close to, the mineral substratum. However, it is unlikely the mineral layer was a major source of contamination as concentrations of Ca, Fe and K were not significantly greater at the Creykes area than at the Crowle area, the latter of which retained at least a meter of peat below the pits. This supports observations made by Wheeler (*unpublished data*) that in parts of Thorne and Hatfield Moors, underlying sands and gravels are of low pH and base status.

4. 1. 3. 1. 2 Drainage

Drying of peat may cause biochemical oxidation, mineralisation and release of nutrients (Streefkerk & Casparie, 1989). On an intact bog, Breakke (1981) observed that the process of N - mineralisation may show seasonal variation due to the effect of climate on peat saturation and microbial activity. A seasonally-low water table may lead to nutrient release on rewetting. Drying-out of peat has also been observed to cause a four-fold increase in total amounts of soluble N due to increased aerobic microbial activity (Piispanen & Lähdesmäki, 1983). At the Moor House Nature Reserve (N. Pennines) concentrations of SO_4^{2-} in bog pools were observed to increase four-fold during periods of dry weather, accompanied by a fall in pH below 4.0 (Gorham, 1956). This was attributed to sulphide oxidation and release of protons. Note in this study, high conductivity and low pH values were generally recorded where the peat substrate was dry (Table 2-2).

Peat drainage during harvesting may lead to extensive sulphide oxidation and N - mineralisation which may explain the enriched conditions and low pH recorded at Thorne Moors. Furthermore, these processes remain important after peat cutting where sites remain drained or where drains have been blocked but the water-table remains unstable (Chapter 3). The Creykes area had suffered much more intensive and more recent disturbance than Crowle. It was also prone to much more severe water table fluctuation (Chapter 3). This may explain why higher concentrations of NH_4-N, SO_4 and NO_3 and greater conductivity were recorded there. It may also explain the trend observed at Creykes towards more acidic conditions. A lack of vegetation could also explain, at least in part, the higher N- values recorded at the Creykes study area as no plants were present there to assimilate excess N, however this is purely conjectural.

4. 1. 3. 1. 3 Anthropogenic inputs

1) Run off from surrounding agricultural land - This is most likely to occur where the bog has developed in a basin, especially where ditches have been deliberately introduced into the bog to drain adjoining fields for example at Danes Moss in Cheshire (Meade, 1992). This is unlikely to be of significance at Thorne Moors as, unlike Danes Moss, it is not surrounded by higher ground and drainage occurs primarily away from the bog.

2) Limestone dust - Windblown dust from limestone trackways at Thorne may have contributed to the elevated calcium concentrations recorded. However, Smart *et al* (1989) recorded elevated calcium concentrations in the original National Nature Reserve at Thorne Moors prior to construction of the main limestone road. Alternatively, it is possible that liming of surrounding agricultural land may have had an influence on calcium concentrations in the bog but this is only speculation and its true origin remains unclear.

3) Atmospheric pollution - In ombrotrophic systems the chemical environment is particularly susceptible to atmospheric inputs. The principal contaminants are likely to be those associated with 'acid rain' i.e. SO_2 and its derivatives, especially bisulphite and sulphate, and nitrogen oxides (NO_x) and derivatives, especially nitrate and ammonia. Emissions of SO_2 and NO_x originate from fossil fuel combustion, with motor vehicle exhaust making a major contribution to the latter. The distribution of major emissions generally reflects the distribution of power stations, industry and major centres of population. (Gillham, Leech & Eggleston, 1992). This is of potential importance to Thorne Moor as numerous major power stations operate in the area of the Humberhead levels. By contrast, the major source of ammonia emissions is animal husbandry. Agriculture adjacent to Thorne is largely arable, though a number of 'factory' farms exist in the region. The major pathways by which these pollutants may enter the bog is by wet and dry deposition. However, no records exist for inputs to Thorne and no attempt was made to measure them in this study. Consequently, whilst atmospheric inputs may have contributed to the high SO_4 and NH_4-N concentrations and low pH values recorded at Thorne, their actual importance remains unknown. If atmospheric pollution was solely responsible, then it is not obvious why concentrations of some ions would be greater at the Creykes study area compared with the Crowle area unless other factors are causing this this discontinuity (see above). In the future, it would be useful to investigate whether high N is a characteristic of other milled peat fields on Thorne Moors, when they eventually come out of production.

Data on the water quality of cut-over bogs are scarce. However, the results from a number of studies are presented in Table 4 -3, alongside data recorded for undisturbed bog. High SO_4 concentrations were also observed at Danes Moss, Cheshire and in NW Germany, Blankenburg (*unpubl.*) recorded high NH_4-N concentrations for a milled peat field in the Leegmoor region. In North America, Clausen & Brooks (1983) compared run-off water from 5 'mined' bogs in Minnesota with that of 66 natural 'control' bogs. Run-off from mined bogs contained significantly greater concentrations of ammonia-N. Therefore the enriched conditions observed at Thorne appear not to be unique but part of a general trend of enrichment in cut-over areas. Solute concentrations recorded in the Creykes study area, were significantly greater than those recorded by Smart, *et al* (1989) for the National Nature Reserve area of Thorne. The reason for this is not clear but it may again reflect the fact that Creykes was much more severely, and more recently disturbed and that it supports little vegetation for assimilating the nutrients. It is interesting to note that despite a general level of enrichment, concentrations of SRP at Creykes remained comparable to those of undisturbed bog, i.e. negligible.

Table 4-3 : Some chemical conditions in peat cutting sites (compared with little-disturbed mires) [Concentrations in mg l^{-1}; blank cells indicate no data]

	Natural waters, UK	Danes Moss, Cheshire	Thorne Waste, Vegetated cuttings	Thorne Waste, Milling Field	Leegmoor Milling Field
Ca	0.2 - 3.0	3.2 - 11.4	3.8 - 6.2	5.1 - 18.2	
Mg	0.1 - 2.5	1.7 - 2.9	1.8 - 4.5		
K	0.04 - 2.0	0.5 - 0.8	0.6 - 2.1	2.1 - 6.6	
Na	2.3 - 23.0		4.6 - 6.3		
Fe	< 1.0			0.6 - 2.2	
SO_4	2.4 - 10.0	18.6-32.9	6.2 - 13.8	27 - 42.0	
NO_3	0.1 - 0.3	1.3 - 2.2	0.04 - 0.2	1.8 - 6.2	0.6 - 2.5
NH_4-N		0.4 - 0.7	0.0 - 0.3	5.5 - 29.0	7.0 - 13.5
SRP	0.0 - 0.05	0.0 - 0.3	0.0 - 0.08	0.0 - 0.06	0.0 - 0.05
pH	3.5 - 4.7	3.0 - 3.8	3.8	3.0 - 3.7	
Source	Clausen & Brooks (1980) Proctor (1992)	Meade (1992)	Smart Wheeler & Willis (1989)	Money (*this study)*	Blankenburg (*unpub.*)

4. 1. 3. 2 Implications of hydrochemical changes to *Sphagnum* regeneration

4. 1. 3. 2. 1 Sulphur

Sulphur pollutants have long been considered important in explaining loss of *Sphagnum* from south Pennine blanket mires which occurred proximate to industrialisation (Tallis, 1964). Numerous fumigation experiments with SO_2 and irrigation experiments with bisulphite and sulphate have demonstrated that *Sphagnum* species are differentially sensitive to S pollution (Ferguson, Lee & Bell, 1978). Ferguson & Lee (1980) showed that irrigation of an unpolluted bog surface in Snowdonia with approximately 1 mg l^{-1} HSO_3^-, reduced growth of *Sphagnum magellanicum* and *S. papillosum*. In laboratory experiments growth of *S. cuspidatum* was significantly reduced when irrigated with 9.6 mg l^{-1} HSO_3^- (Baxter, Emes & Lee, 1989). The concentration of HSO_3^- in rainfall at Thorne Moors was not measured in this study, but Smart (1983) measured the concentration between March and December 1981 at 5.8 mg l^{-1}. Therefore inputs of HSO_3^- at Thorne may well be sufficient to inhibit growth of some *Sphagnum* species.

Bisulphite is rapidly oxidised to sulphate having a half life of around 5.5 hours (Ferguson *et al*, 1978). Consequently, for plants growing in pools exposure to HSO_3^- will be acute and episodic but exposure to SO_4^{2-} will be more long term. Application of an artificial rain solution containing 14.4 mg l^{-1} SO_4^{2-} has been shown to reduce the growth of *S. recurvum*, *S. papillosum*, *S. magellanicum*, *S. capillifolium* and *S. tenellum* (Ferguson & Lee, 1983). This suggests that SO_4^{2-} concentration recorded at the Creykes study area may be toxic to *Sphagnum* growth. However, by contrast to this, Bayley, Rochefort & Vitt (1990) found that spraying a poor fen once a month with lake water modified to contain 26.9 mg l^{-1} SO_4^{2-} did not reduce *Sphagnum* growth. It is possible in the latter case that exposure time was not sufficient to produce a toxic effect. Austin & Wieder, (1987) found growth of *Sphagnum* in solution culture was significantly reduced at 422 μmol/l^{-1} (40.5 mg l^{-1}) SO_4^{2-}. However, in contrast, immersion experiments with *S. cuspidatum*, have shown that chronic exposure to concentrations as high as 96 mg l^{-1} SO_4^{2-} may only reduce stem elongation slightly (Ferguson *et al*, 1978). It is therefore uncertain whether SO_4^{2-} concentrations at Thorne may limit *Sphagnum* regeneration. Furthermore, deposition rates of S pollutants have fallen dramatically in the last few decades and are no longer considered high enough to explain the paucity of *Sphagnum* in the S. Pennines (J. Lee *pers comm*). Ferguson & Lee (1983) suggest that deposition rates in the S. Pennines may remain super optimal for *Sphagnum* but cannot entirely account for the failure of transplants. Similarly, at Thorne Moors it is unlikely that the high SO_4^{2-} concentrations recorded will alone prevent *Sphagnum* regeneration, but the possibility that growth is constrained cannot be dismissed.

4. 1. 3. 2. 2 Nitrogen

The effect of high atmospheric nitrogen on *Sphagnum* growth has been the subject of quite intensive study. Whilst atmospheric sulphur deposition has decreased, N deposition has increased markedly over the last century. Moreover, NO_x deposition has significantly increased in recent decades in response to increased use of the motor car. Consequently, nitrogen pollution is now considered by some workers as an important factor limiting *Sphagnum* regeneration in the south Pennines (Press & Lee, 1982; Woodin, Press & Lee, 1985; Press, Woodin & Lee, 1986).

Press *et al* (1986) found *Sphagnum cuspidatum* collected in North Wales and grown in solution culture, showed reduced growth in response to small increases in N, i.e. 0.01mM NO_3^- (0.62 mg l^{-1}) and 0.01mM NH_4^+ (0.18 mg l^{-1}), the latter having the most toxic effect. Furthermore, growth of *S. cuspidatum* in pools at Holme Moss in the S. Pennines was considerably less than at the unpolluted Berwyn Mountains in N.

Wales and this was associated with a larger increase in tissue N content. Clymo (1987) reported that addition of < 2 mg l^{-1} NO_3^- and < 1mg l^{-1} NH_4^+ to a distilled water medium depressed growth of *S. papillosum*. He also pointed out that these concentrations were similar to those recorded in UK rainfall. Concentrations of NH_4^+ exceeding 4 mg l^{-1} have also been shown to reduce growth of *S. magellanicum*, with a strong depression occurring at around 10 mg l^{-1}(Rudolf & Voigt, 1986).

Nitrogen toxicity appears to show some species specificity. This was demonstrated by Twenhöven, (1992) in field experiments on *S. recurvum* and *S. magellanicum* on an ombrotrophic mire near Kiel, Germany. Unmodified rain contained 1.5 mg l^{-1} NH_4^+ and 4.2 mg l^{-1} NO_3^-. These concentrations were then elevated independently to 6.7 mg l^{-1} and 18.6 mg l^{-1} respectively. On the hummocks NO_3^- and NH_4^+ reduced growth of both species while in the lower part of the hummock-hollow gradient growth of *S. recurvum* was promoted. There was also some evidence of reduced growth in *S. magellanicum* and under increased N deposition, in the hollows and lawns *S. recurvum* was able to out-compete *S. magellanicum.*

Evidence considered so far suggests the high concentrations of NH_4^+ and NO_3^- recorded in the Creykes area of Thorne may be inhibitory to *Sphagnum* regeneration. However, there is also considerable experimental evidence to suggest that modest N enrichment may stimulate *Sphagnum* growth. In laboratory culture, Rudolf & Voigt (1986) found that NO_3^- concentrations of up to 322 μM (20 mg l^{-1}) were favourable to the growth of *S. magellanicum* (though 100 μM was recommended as an upper limit due to accumulation of green algae). Baker & Boatman (1990) found that reducing NO_3^- from 12 mg l^{-1} to 0.2 mg l^{-1} while keeping other nutrient ions in culture solution constant caused a significant reduction in growth of *S. cuspidatum*. Furthermore, concentrations of 20 mg l^{-1} NO_3^- have been found to be favourable to the growth of *S. cuspidatum* and several other *Sphagnum* species in culture solution

(Baker & Macklon, 1987 *unpublished;* Baker & Boatman, 1990). Li & Glime (1990) found that 3.4 mg l^{-1} $NH_4^+$and 12.4 mg $l^{-1}NO_3^-$ in culture solution had no adverse effect on the growth of *S. magellanicum* and increased growth in length of *S. papillosum*. Bayley *et al* (1990) found that spraying lake water modified to contain 6.8 mg $l^{-1}NO_3^-$ on to poor fen once a month increased *Sphagnum* productivity over 2-3 years and although growth declined beyond this time span, it was not reduced below the control. Aerts, Wallén & Malmer (1992) applied nitrogen as NH_4NO_3 at rates similar to total N deposition in polluted parts of Britain and recorded a four fold increase in *Sphagnum* productivity in a relatively unpolluted bog in Swedish Lapland. In a more polluted southern Swedish bog, added N did not increase *Sphagnum* growth but neither was it detrimental. Similarly, Austin & Weider (1987) observed in laboratory studies lasting 40 - 50 days that moderate additions of NH_4^+ and NO_3^- did not adversely affect *Sphagnum* growth.

Experimental results show considerable inconsistency, probably due to variations in experimental conditions. Nitrogen toxicity may be partly dependent on the balance of other nutrients. For example concentrations of NH_4^+ up to 18 mg l^{-1} have been shown not to affect the growth of *S. cuspidatum* in submerged culture when a high CO_2 concentration (1000 μM CO_2/l^{-1}) was simultaneously applied (Paffen and Roelofs, 1991). Furthermore, plants of the same species collected from geographically different locations may show variations in sensitivity (Press *et al*, 1986). Therefore, it remains difficult to assess the potential importance of high N to *Sphagnum* regeneration at Thorne.

4. 1. 3. 2. 3 Potassium

Concentrations of K at Thorne Moors were measured in the range 2.1 - 6.6 mg l^{-1} (Fig 4.2) with a mean of 3.3 mg l^{-1} (Table 4 -2). This compares to values of < 2 mg l^{-1} recorded in undisturbed sites (Table 1-3, Fig 4.2). In laboratory experiments, Baker &

Boatman (1990) found that 7.8 mg l^{-1}K in culture solution was favourable to growth of *S. cuspidatum* and that reducing the concentration depressed growth. Critical evidence for the importance of K in the field is lacking but Tallis (1973) suggests that high K concentrations (5-10 mg l^{-1}) may be important in the development of floating *Sphagnum* communities in north Cheshire basin mires. Therefore, although there has been little detailed study on the influence of K on *Sphagnum* growth, the evidence that does exist indicates that concentrations of K recorded at Thorne Moors are likely to be beneficial rather than detrimental to *Sphagnum* growth.

4. 1. 3. 2. 4 Iron

At Thorne Moors Fe concentrations in the range 0.6 to 2.2 mg l^{-1} were measured compared to < 1 mg l^{-1} recorded for undisturbed sites (Table 1-3, Fig 4.2). The effect of Fe concentration on *Sphagnum* growth has not been studied in any detail. Ferguson, Robinson, Press & Lee (1984) showed that Fe concentration in plants transplanted from unpolluted sites to polluted sites increased four fold in 18 months. Consequently, Aerts *et al* (1992) suggest that poor growth of *Sphagnum* in the South Pennines may be due not only to high loads of atmospheric nitrogen but also to iron toxicity. Therefore, increased Fe concentration may inhibit *Sphagnum* regeneration at Thorne but critical evidence for this is lacking,

The importance of elevated calcium concentration, low pH and low SRP concentration on *Sphagnum* growth were investigated experimentally in this study. They are considered independently in more detail below.

4.2 *The effect of calcium concentration on the growth of* Sphagnum *(Experiment 3)*

The concentration of calcium in water collected from the Creykes study area ranged from 5.1 - 18.2 mg l^{-1} (see above). The aim of this laboratory investigation was to determine whether calcium concentration in this range influenced *Sphagnum* growth.

4.2.1 Method

Three species of *Sphagnum* of contrasting habitat were used:

S. cuspidatum	- a species of pools and wet hollows generally in ombrotrophic bogs though occasionally in weakly minerotrophic sites.
S. magellanicum	- a species forming lawns and hummocks, typically in ombrotrophic conditions
S. recurvum	- may form hummocks or occur in pools, generally in minerotrophic fens, though sometimes in ombrotrophic bogs.

Individual gametophytes, cut to 5cm in length, were washed in distilled water and then grown in solution culture in pots as shown in Fig 4.6. The culture solution was a modification of the medium used by Boatman & Lark (1971) and is outlined in Table 4-4. Unlike their experiments, the plants used in this investigation were not cultivated in sterile conditions but were collected from the field (1.11). Consequently, the concentration of nitrate was reduced from 20 mg l^{-1} in the original formulation to 4 mg l^{-1}. This latter figure is the upper limit suggested by Rudolph & Voigt (1986) to prevent prolific growth of algae.

The *Sphagnum* material used in this study was collected from a number of sites (Table1-4). However, the material was stored for several months in experimental trenches at the Crowle study area (1.11) prior to any experimentation. Therefore, all species used would have had a chance to acclimatise to similar conditions prior to their use in experiments.

Table 4-4 : Composition of culture solution used in Experiments 3 and 4.

Stock solution (S)

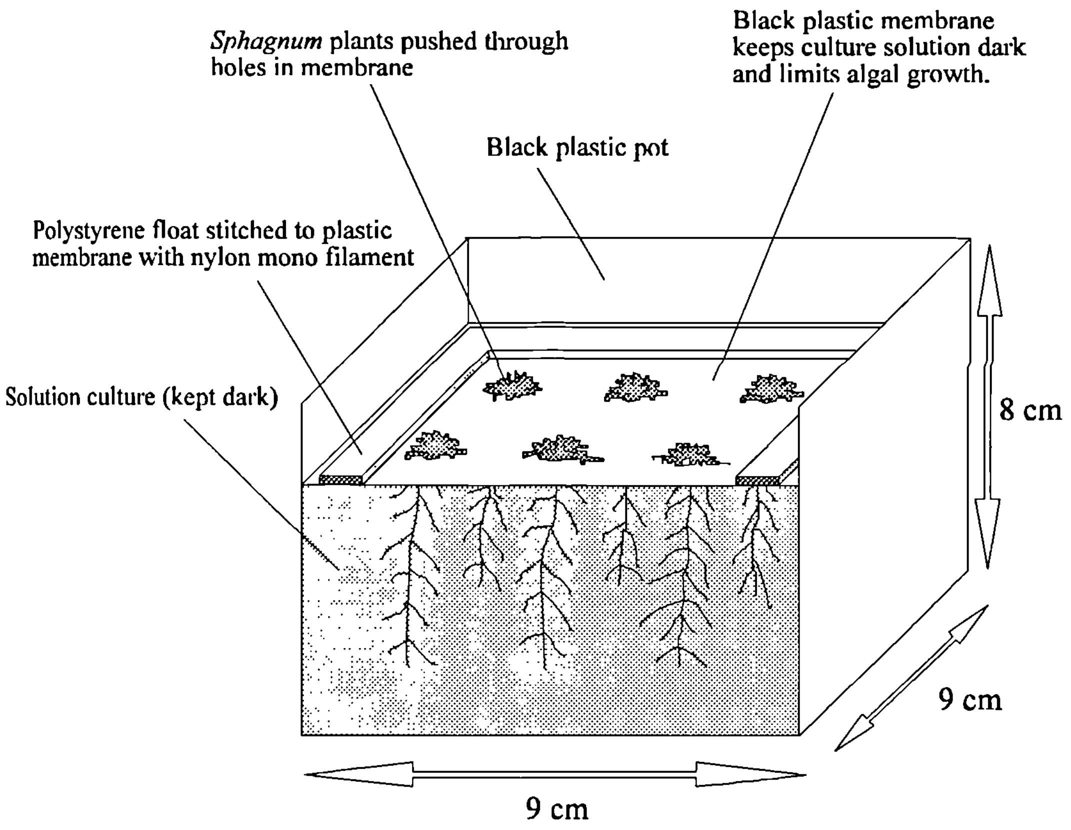
Compound	*Quantity (mg l^{-1})*
$NaH_2PO_4 2H_2O$	208.0
$Ca(NO_3)_2 4H_2O$	72.7
$CaCl_2 6H_2O$	206.0
KNO_3	77.6
$MgSO_4 7H_2O$	225.0
Na Cl	5.6
$MnSO_4 H_2O$	2.85
$CuSO_4 5H_2O$	0.24
$ZnSO_4 7H2O$	0.29
H_3BO_3	1.86
$(NH4)_6Mo_7O_{24} 4H_20$	0.035
$(NH4)_2SO_4$	62.245
FeEDTA	5.0

Concentration of major ions in 0.1 (S) (mg l^{-1})

Ca^{2+}	5.0
Mg^{2+}	2.4
K^+	3.0
Na^+	2.9
NH_4^+	1.7
NO_3^-	4.0
SO_4^{2-}	14.1
$H_2PO_4^-$	12.6

Calcium concentration in the standard culture solution was 5.0 mg l^{-1}. *Sphagnum* was also grown at three higher concentrations i.e. 10, 15 and 20 mg l^{-1}. Calcium was added to the culture solution as $CaCl_2$ $6H_2O$. The pH of all solutions was adjusted to pH 4 using 0.5 M HCl. Nine plants were grown in each pot, with three replicate pots per treatment for each species. The experiment was conducted in a greenhouse under natural light for 9 weeks. During this period the maximum temperature range was between 18 - 25 °C. The culture solution was changed every 3 days to maintain water quality and prevent algal growth. The position of the pots was rotated at each solution change. As the plants grew upwards they were pushed down through the polythene to maintain the water level just below the capitulum throughout the duration of the experiment.

Fig 4.6 : Pot design for solution culture experiments.



Plants were harvested and measured according to the Capitulum Correction Method (Clymo, 1970) and the results expressed as relative growth rate i.e. RGR = (nL final plant dry weight - nL original plant dry weight) / time. Any significant effect of treatment was tested for using ANOVA. As RGR data were already in log form, it was considered unnecessary to test for normality within the data sets or to test for homogeneity of variance.

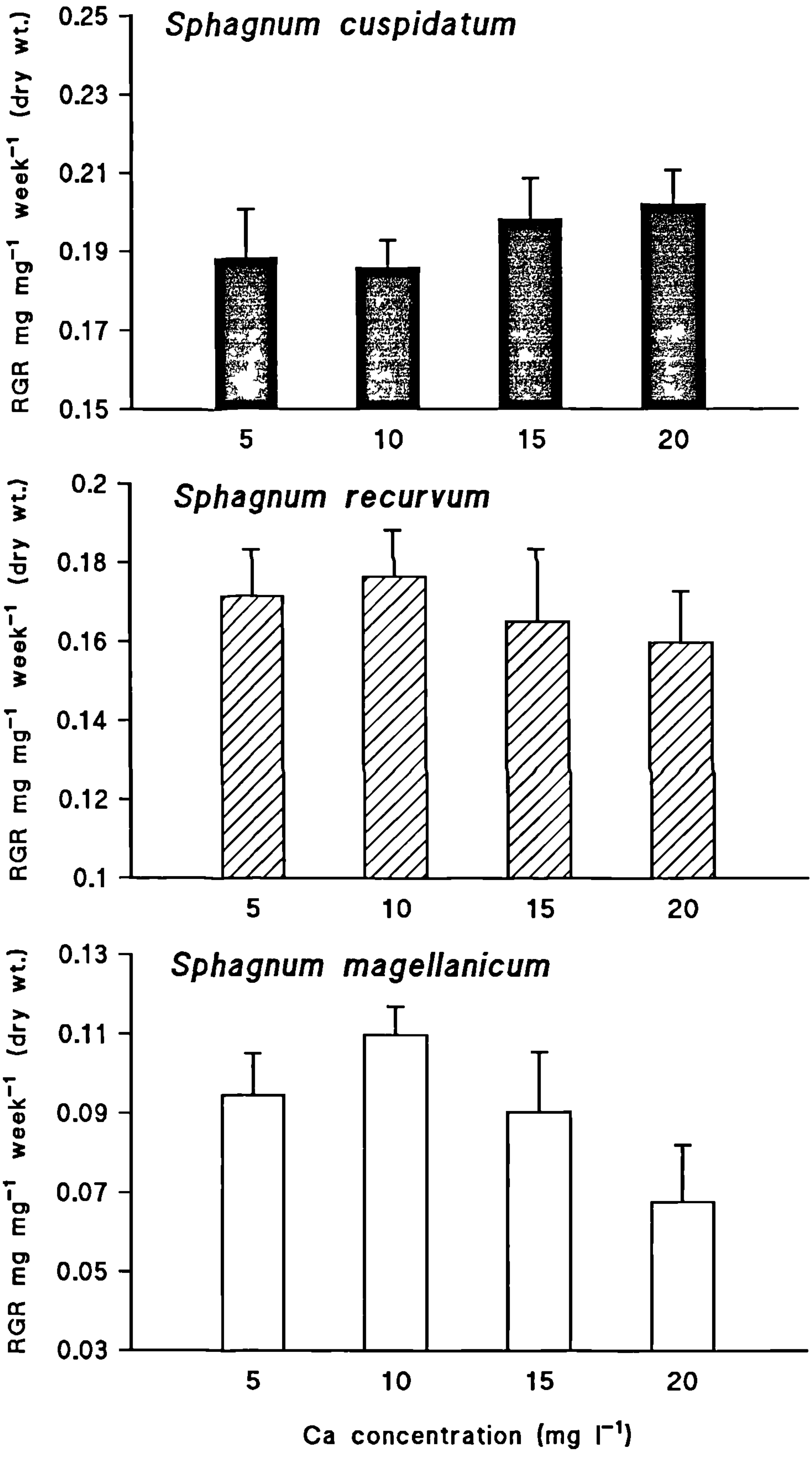
4. 2. 2 Results

Mean values for RGR are given in Table 4-5 along with probability values derived from ANOVA and results are shown graphically in Fig 4.7. Increased calcium concentration up to 20 mg l^{-1} had no effect on the growth of *S. cuspidatum* and *S. recurvum*. However, growth of *S. magellanicum* was significantly reduced at 20 mg l^{-1} (p= 0.0001).

Table 4.5 : **Expt. 3 - Mean Relative Growth Rate (RGR) of *Sphagnum* grown at different Ca^{2+} concentration.** [Standard Errors given in parentheses. RGR in mg^{-1} mg^{-1} $week^{-1}$ dry wt]

	Calcium concentration mg l^{-1}				
	5 (control)	**10**	**15**	**20**	**ANOVA results**
S. cuspitatum	0.188 (0.006)	0.186 (0.004)	0.198 (0.005)	0.202 (0.004)	d.f. = 3 F = 2.673 p = 0.0513
S. magellanicum	0.095 (0.005)	0.110 (0.004)	0.090 (0.007)	0.068 (0.007)	d.f. = 3 F = 8.647 p = 0.0001
S. recurvum	0.171 (0.006)	0.176 (0.006)	0.165 (0.009)	0.160 (0.006)	d.f. = 3 F = 1.126 p = 0.342

Fig 4.7 Mean Relative Growth Rate of *Sphagnum* grown in laboratory culture for nine weeks at different calcium concentrations (Experiment 3)(4.2). [Error bars = 95 % confidence limits].



4.2.3 Discussion

Results suggest that calcium concentration in the upper range of those recorded at the Creykes milling field (5 - 18.2 mg l^{-1}) may inhibit growth of some *Sphagnum* species. However, concentrations above 15 mg l^{-1} were only recorded temporarily and concentrations of 5 - 10 mg l^{-1} occurred on average (4.1.2). Consequently, results from this experiment suggest that overall yearly growth of *Sphagnum magellanicum* is unlikely to be too adversely influenced by calcium concentrations recorded on average at Thorne.

Clymo (1973) grew twelve *Sphagnum* species at calcium concentrations of approximately 1, 10 and 100 mg l^{-1}. He found a trend towards reduced growth in response to increased calcium but this pattern was not significant. He concluded that calcium had little influence independently on growth of *Sphagnum* but significantly reduced growth in combination with a pH elevated above 3.5. However, in Experiment 3 outlined above, pH of the culture solution was relatively low at pH 4.0. Therefore, in contrast to Clymo's observations, results from this experiment suggest that growth of *S. magellanicum* (and possibly other species) may be significantly reduced by moderate increases in calcium concentration whilst maintaining a low pH. Low pH of the culture solution may however, explain why no toxic effect of calcium was observed in *S. magellanicum* at lower concentrations or at all in *S. cuspidatum* and *S. recurvum*. The pH of water samples taken from the Creykes study area were generally below pH 4.0 (4.1.2). Therefore, any toxic effect of calcium enrichment in cut-over areas may be negated to some extent by the low pH which also appears to characterise such area.

4.3 *The effect of pH on* Sphagnum *growth (Experiment 4)*

4.3.1 Introduction

Evidence from Thorne Moor suggests that commercially cut-over areas are more acidic environments than undisturbed bogs. A mean pH of 3.4 was recorded for the Creykes milled peat field with values frequently measured as low as pH 3.0 (4.1.2). The aim of this experiment was to determine whether such low pH values adversely influence the growth of *Sphagnum*. Andrus (1986) studied the distribution of *Sphagnum* species with pH in 49 New York State mires. The pH ranges of four raised bog species are summarised below. The figures in brackets represents the pH value at which plants were most frequent:

	pH
Sphagnum papillosum	3.6 - 6.4 (4.0 - 4.5)
Sphagnum magellanicum	3.5 - 6.3 (4.0 - 5.0)
Sphagnum cuspidatum	3.5 - 5.9 (4.0)
Sphagnum rubellum	3.5 - 5.4 (3.8)

Similar trends have been identified for a plateau bog on the southern coast of Finland (Heikkila & Löytönen, 1987) and for *Sphagnum* communities colonising floating mats of fen vegetation in the Norfolk Broads (Wheeler & Shaw, 1992 *Unpubl.*). It is also notable in Chapter 2, that floating *Sphagnum* communities developed in old turf cuttings rarely occurred at pH values below 4.0 (Table 2-2).

Sphagnum bogs are naturally acid systems and the ability of *Sphagnum* to acidify its own environment is widely accepted (refer to sect. 1.6.3). Therefore, it may seem unusual to suggest that low pH may limit *Sphagnum* growth. However, as pH is a logarithmic scale, pH 3.0 represents a H^+ concentration an order of magnitude higher than pH 4.0. Therefore pH values recorded at Thorne represent conditions significantly more acidic than those outlined above for natural *Sphagnum* communities.

There has been little detailed study on the effects of pH on *Sphagnum* growth. Clymo (1973) observed that there was a trend for several species to grow better at pH 5.5 than at pH 3.5, but this was not significant. At pH 3.0 it is possible a significant effect would have been seen. This investigation considered in more detail the effect of pH within the range recorded for cut-over and undisturbed raised bogs.

4. 3. 2 Method

Experimental design closely followed that of Experiment 3 (see above). Plants were grown in culture solution at four different pH values i.e. 4.7 , 4.0, 3.5 and 3.0. The control culture solution used (Table 4-4) had a natural pH of 4.7. This was acidified using 0.5 M HCl to produce the three other pH treatments. The experiment lasted for sixty days in conditions as outlined in Experiment 3 (see above). The culture solution was changed every three days. At each change the solution pH was measured. After three days all treatments remained at their designated pH except the 4.7 treatment which was consistently reduced to pH 4.3. Therefore, pH 4.3 is always given in parentheses when this treatment is referred to. Growth was measured as outlined in Experiment 3 (see above) and the data analysed using ANOVA.

4. 3. 3 Results

S. recurvum **:** pH significantly influenced the growth of S. recurvum ($p = 0.0001$)(Table 4-6). There was a trend of increased growth with increasing pH (Fig 4.8). The treatments which showed significant differences were determined by partitioning the sum of squares (PSS) (Table 4-7). Growth at pH 3.0 was significantly lower than growth at pH 3.5, 4.0 and 4.7$_{(4.3)}$ ($p < 0.001$). Growth at pH 3.5 was not significantly lower than pH 4.0 but was significantly less than at pH $4.7_{(4.3)}$ ($p = 0.01$).

***S. cuspidatum* :** ANOVA results show that pH significantly influenced growth of this species ($p = 0.0001$)(Table 4-6). Fig 4.8 suggests an optimum curve whereby growth increased from pH 3.0 to 4.0 and then declined at pH $4.7_{(4.3)}$. Results from PSS (Table 4-7) show that growth at pH 3.0 was significantly lower than at pH 3.5, 4.0 and $4.7_{(4.3)}$ ($p < 0.001$). Growth at pH 4.0 was optimal, being significantly greater than at pH 3.5 and $4.7_{(4.3)}$ ($p < 0.001$). Growth at pH $4.7_{(4.3)}$ did not differ significantly from growth at pH 3.5 ($p > 0.05$).

***S. magellanicum* :** Fig 4.8 suggests a trend towards reduced growth at pH 3.0. However results from ANOVA suggest this difference is not significant ($p = 0.1886$) (Table 4-6). Therefore, pH treatment in the range used had no significant effect on growth of this species under these experimental conditions.

4. 3. 4 Discussion

Results showed that below pH $4.7_{(4.3)}$ conditions were sub-optimal for the growth of *Sphagnum recurvum*. This is perhaps unsurprising as *S. recurvum* is a typical species of poor-fen environments. Nevertheless, it is an important coloniser of cuttings at Thorne Moors and in other raised bogs, possibly in response to factors such as nutrient enrichment (2.2.3.3) The evidence presented above suggests that pH values in the range recorded at Thorne (4.1.2) are sub-optimal for its growth.

Similarly, the results suggest that pH values below 4.0 are sub-optimal for growth of *S. cuspidatum*. Therefore, highly acidic conditions measured at Thorne may also limit growth of this species. Unlike *S. recurvum*, above pH 4.0 growth of *S. cuspidatum* declined, possibly reflecting its less base tolerant nature.

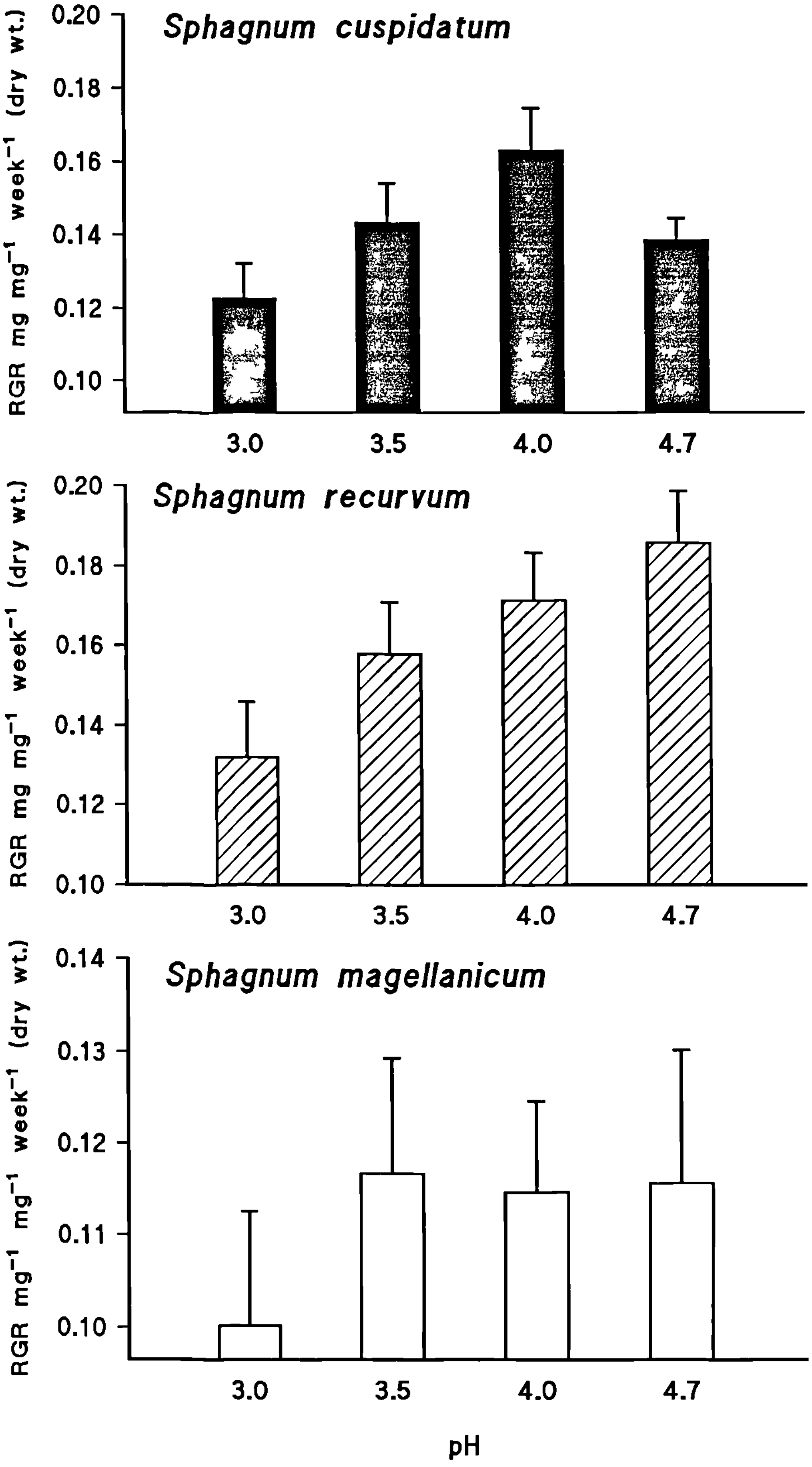
Table 4.6 : Expt. 4 - Mean Relative Growth Rate (RGR) of *Sphagnum* grown at different pH.
[Standard Errors given in parentheses. RGR in mg mg^{-1} $week^{-1}$ dry wt]

	pH				
	3.0	**3.5**	**4.0**	**$4.7_{(4.3)}$**	**ANOVA results**
S. cuspidatum	0.123 (0.005)	0.143 (0.006)	0.163 (0.006)	0.139 (0.003)	d.f. = 3, 107 F = 11.815 p = 0.0001
S. magellanicum	0.100 (0.006)	0.117 (0.006)	0.115 (0.005)	0.116 (0.007)	d.f. = 3, 107 F = 1.623 p = 0.1886
S. recurvum	0.132 (0.007)	0.158 (0.006)	0.171 (0.006)	0.186 (0.006)	d.f. = 3, 107 F = 13.034 p = 0.0001

Table 4.7 : Expt. 4 - Effect of pH on growth of *Sphagnum* - results from partitioning the sum of squares

S. recurvum		***S. cuspidatum***	
pH 3.0 vs (3.5, 4.0, $4.7_{(4.3)}$)	d.f. = 1, 107 F = 34 P = 0.001	**pH 3.0 vs (3.5, 4.0, $4.7_{(4.3)}$)**	d.f = 1, 107 F = 24.2 p = 0.001
pH 3.5 vs 4.0	d.f. = 1, 53 F = 1.848 p > 0.05	**pH 4.0 vs (3.5, $4.7_{(4.3)}$)**	d.f. = 1, 80 F = 14.24 p = 0.001
pH 3.5 vs $4.7_{(4.3)}$	d.f. = 1, 53 F = 9.524 p = 0.01	**pH 3.5 vs $4.7_{(4.3)}$**	d.f. = 1, 53 F = 1.424 p > 0.05

Fig 4.8 Mean Relative Growth Rate of *Sphagnum* grown in laboratory culture for nine weeks at different pH (Experiment 4)(4.3). [Error bars = 95 % confidence limits].



These results are in broad agreement with observations made by Austin & Weider (1987). In experiments lasting 50 days, they found that three other species of *Sphagnum* grew markedly less in culture solution at pH 3.0 compared with 4.0.

Clymo (1987) found that changing culture solution pH by 2 units either side of pH 5.5, caused only a small change (0.1 - 0.2 units) in the cytoplasm pH of *Sphagnum* plants. Therefore, he suggests that shifts in pH of that order are unlikely to adversely affect *Sphagnum* growth. However, his experiments lasted only a few days and longer exposure may have produced a different result. Similarly Bayley *et al*, (1990) found spraying lake water modified to pH 3.0 onto a poor fen did not adversely affect growth of *Sphagnum*. However, water was only sprayed once a month so exposure was very short and episodic. Evidence from sect. 4.1.2, suggests that plants growing in pools at Thorne may be chronically exposed to pH below 3.5. Therefore, Experiment 4 represents more realistic exposure conditions. Furthermore, it is possible if the experiment had lasted longer than nine weeks a response to low pH may also have been observed in *S. magellanicum*.

4.4 *The effect of phosphorus and lime on the submerged growth of* Sphagnum *in the field (Experiment 5)*

4.4.1 Introduction

The concentration of phosphorus in ombrotrophic bog waters is generally very small (1.6.3). Based on empirical evidence, some workers have suggested that low phosphorus may limit *Sphagnum* productivity. McVean (1959) observed that when ground rock phosphate was applied to a bog surface in preparation for forestry, the growth rate of *Sphagnum compactum*, *S. auriculatum*, *S. cuspidatum* and *S. tenellum* appeared to increase. Baker & Boatman (1990) noted that *Sphagnum* plants collected from ombrotrophic sites on the Silver Flowe in 1983 and 1984 showed higher innovation frequency from sites at the southern end of the reserve. Coniferous forests surrounded or were adjacent to these sites and in September 1982 these forests were fertilised from the air with rock phosphate and potassium chloride. Therefore, the higher innovation frequency observed may have been a consequence of fertiliser drift.

More recently laboratory studies have provided further evidence of the importance of phosphorus to *Sphagnum*. Clymo & Hayward (1982) observed that *S. papillosum* was able to take up phosphate rapidly from solution and suggested that growth rate of *Sphagnum* may be limited in the field by the supply of phosphate. However, in further experiments on *S. papillosum*, Clymo (1987) found that addition of a dilute solution of orthophosphate to plants growing in a distilled water medium reduced growth at concentrations less than 1 mg l^{-1}. The balance of other ions in solution appears important in determining the response of *Sphagnum* to phosphorus. In distilled water, dilute solutions of inorganic P may kill *Sphagnum* (Clymo, 1987), however, in the presence of other nutrient ions numerous workers have observed a fertilising effect. For example, in solution culture, Baker & Boatman (1990) observed a reduction in growth of *S. cuspidatum* at concentrations of H_2PO_4 below 7.6 mg l^{-1}. When the concentration of this element was enhanced, other elements, particularly N, became limiting. They concluded that in ombrotrophic conditions innovation production in *Sphagnum* is limited by the concentration of P in the water. Similarly, Li & Glime (*in prep.*, cited Li & Glime, 1990) found that growth in length and dry weight of *Sphagnum papillosum* and *S. magellanicum* increased as phosphorus concentrations in culture solution increased within less than a 0.1 mM (9.7 mg l^{-1}) $H_2PO_4^{2-}$ range.

Evidence presented in Section 4.1 suggests that whilst peat extraction may lead to some degree of chemical enrichment, concentrations of phosphorus remain negligible, similar to undisturbed systems. Water quality measurements made for Thorne Moors suggest that phosphorus is the one nutrient most likely to be limiting (Table 4-2). This experiment had two main aims :

1. To determine whether growth of *Sphagnum* in the field may be enhanced by elevating phosphorus concentration in bog water.

2. To determine whether increasing the pH of pool water at Thorne will encourage *Sphagnum* growth (Evidence from Experiment 4 suggests that the pH of pool water at Thorne is sub-optimal for *Sphagnum* growth)

4.4.2 Method

The square experimental pits in the Crowle study area of Thorne were utilised for this investigation (1.10.2). *Sphagnum* was grown under four different chemical conditions:

1. CONTROL - no treatment
2. + LIME (to elevate pH)
3. + PHOSPHORUS (+P)
4. + LIME +P - both treatments

The experimental pits each contained approximately 4000 litres of water. Water quality of pits in the Crowle study area is considered in Section 4.1. It was calculated that 30 g of NaH_2PO_4 would be required to raise the concentration of soluble reactive phosphorus in the pit water from 0.05 mg l^{-1} to 2 mg l^{-1}. It was estimated from simple laboratory trials, in which lime was added to small, known volumes of pit water, that 160 g of laboratory standard $CaCO_3$ was required to raise the pH of 4000 litres of pit water from around pH 3.0 - 3.2 up to pH 4.0. The toxic effect of lime on *Sphagnum* is well recognised (Mackenzie, 1992). However, this generally applies to direct dusting of *Sphagnum* with limestone powder whereas in this experiment the lime was to be added in relatively small quantities to solution around the plants. Chemicals were added to the pits in March 1992, two weeks after *Sphagnum* had been placed in the pits. *Sphagnum* was removed and placed in control pits while the chemicals were applied and then returned 6 hours later to avoid acute exposure.

Sphagnum cuspidatum and *S. recurvum* were used in this experiment. The rationale behind this choice of species was that they are both species which have been observed to grow in bog pools and form floating rafts. Therefore, they are potentially important species for pioneering raft development (6.6) and their growth is likely to be strongly influenced by water quality. Furthermore, *S. recurvum* is most frequently a species of poor-fen environments and its growth response in this experiment would provide an interesting comparison with the response of *S. cuspidatum* which is more typical of ombrotrophic bog.

Sphagnum plants were cut to a standard length (5cm) and placed into bunches of 10, secured by nylon monofilament. Bunches of both species were grown in each of the four treatments. There was three replicates for each treatment. The *Sphagnum* 'bunches' were suspended by nylon monofilament from bamboo canes lying horizontally across the pits. A plasticine weight was used to keep the *Sphagnum* bunches suspended 30cm below the water surface. Conditions below the water surface are sub optimal for growth with regard to light and gaseous exchange. However, this design was chosen as it represents realistic starting conditions for plants deliberately added to shallow pools on cut-over surfaces as part of a restoration strategy. This is considered in more detail in Section 6.6.

pH of water in the pits was measured fortnightly for the duration of the experiment. Water samples were collected fortnightly and analysed to determine concentrations of soluble reactive phosphorus (SRP) and calcium. Methods of analysis are described in Table 4 -1. The experiment lasted for 20 weeks after which the plants were removed and growth was measured using the capitulum correction method (Clymo, 1970). Results were expressed as relative growth rates i.e. RGR = (nL final plant dry weight - nL original plant dry weight) / time. A sample of ten plants of each species from each treatment was analysed for tissue phosphorus and calcium concentration. Tissue was digested using a sulphuric acid - hydrogen peroxide procedure (Allen, 1974). Samples were then analysed for calcium and phosphorus as for water samples (see above). The technique for phosphorus analysis was slightly modified to adjust for low pH of the samples.

Any significant effect of treatment was tested for using ANOVA. As RGR data were already in log form, it was considered unnecessary to test for normality within the data sets or to test for homogeneity of variance. Data for tissue calcium and tissue phosphorus concentration were tested for homogeneity of variance using the F_{max} test. In both cases treatment variances were found to be significantly different, therefore the data were transformed using natural logs prior to applying ANOVA (Table 4 -10, Table 4 -12).

4.4.3 Results

4.4.3.1 Water quality

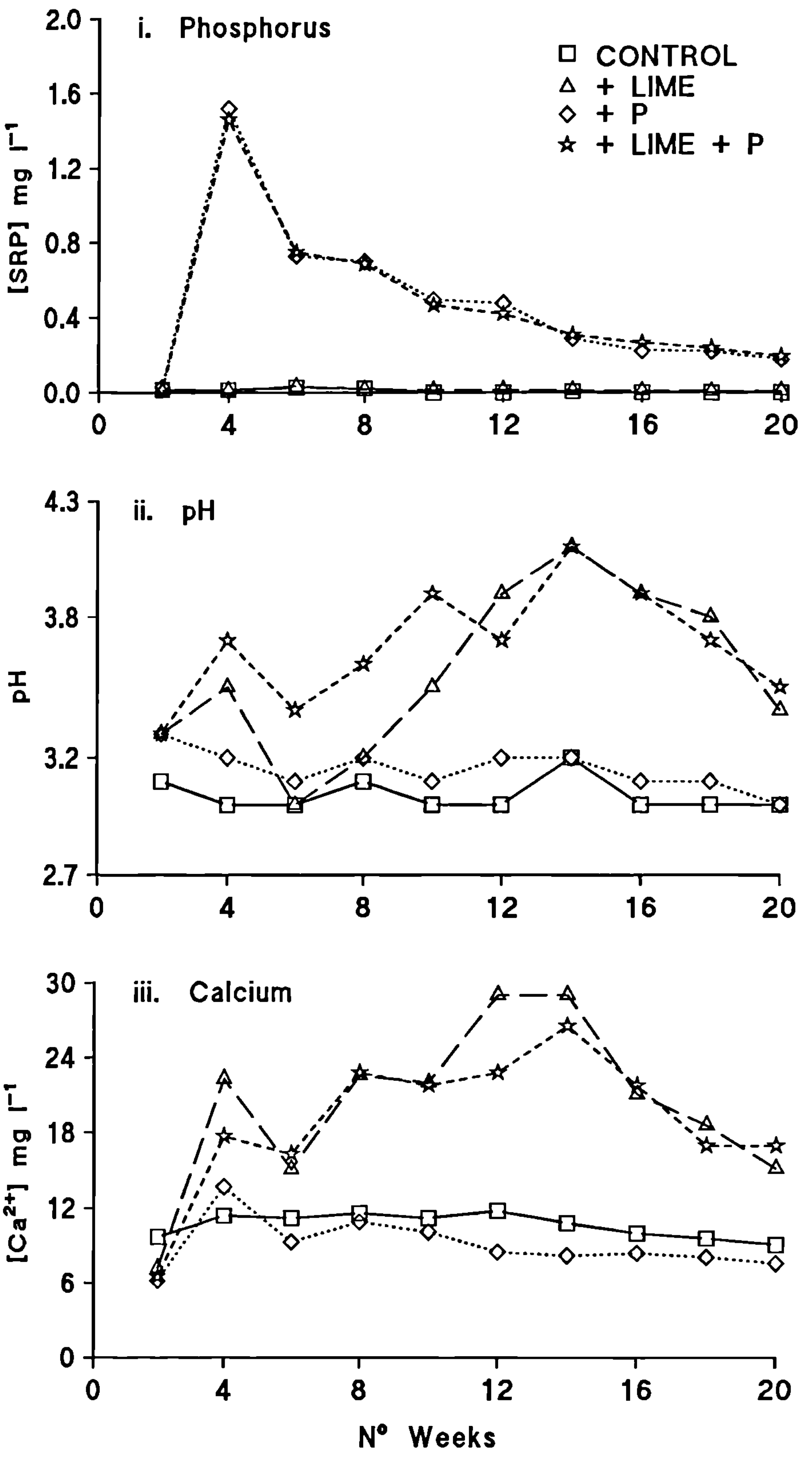
Fig 4.9 shows the concentration of SRP, calcium and the pH of pit water which persisted in each treatment for the duration of the experiment.

SRP - In both treatments to which phosphorus was added, the concentration of SRP remained elevated above the control throughout the experiment (Fig 4.9i). An early peak of 1.6 mg l^{-1} SRP occurred two weeks after treatment was applied after which the concentration gradually declined to 0.2 mg l^{-1} at the end of the experiment. SRP concentration in the control and the '+lime' treatment remained below 0.05 mg l^{-1}. The response of pit water to phosphorus addition was very similar with or without lime.

pH - On average, both treatments to which lime was added showed an increase in pH compared with the control (Fig 4.9ii). However, the original addition of lime proved inadequate to sustainably elevate the pH and a further 400g of lime was added in total, on separate occasions during the first two months in order to approximately produce the desired pH.

Ca - Addition of lime outlined above resulted in the concentration of calcium in pits to which lime was added increasing to very high concentrations i.e. 25-30 mg l^{-1} (Fig 4.9iii).

Fig 4.9 Water quality of experimental pits used in Experiment 5 (4.4), in response to chemical treatment. [For details of treatment refer to section 4.4.1. Measurements are given for pH plus concentration of phosphorus and calcium recorded over the experiment's duration. Results demonstrate the different chemical conditions in which *Sphagnum* was grown]



4.4.3.2 *Sphagnum* growth

Treatment significantly affected the growth of both *Sphagnum* species ($p < 0.0001$) (Table 4 -8).

Fig. 4.10 suggests that addition of phosphorus increased growth in *S. cuspidatum*, but growth was reduced in the presence of lime. More detailed analysis of differences between treatments was conducted by partitioning the sum of squares (Table 4-9). Addition of phosphorus and the addition of phosphorus plus lime significantly increased growth of above the control ($p < 0.001$). Addition of lime on its own significantly reduced growth ($p = 0.01$). Fig 4.10 suggests that growth in the presence of phosphorus and lime was slightly less than in the presence of just phosphorus , but this difference was not statistically significant ($p > 0.05$) (Table 4 -9).

Growth of *S. recurvum* also increased significantly in the presence of added phosphorus ($p < 0.001$)(Table 4-8). Furthermore, like *S. cuspidatum*, growth was significantly depressed in the presence of lime ($p = 0.01$) (Table 4-9), but unlike *S. cuspidatum*, growth rate in the presence of lime plus phosphorus was significantly less than growth in the presence of phosphorus alone. In fact, growth with lime plus phosphorus did not differ significantly from the reduced growth which occurred in the presence of just lime ($p > 0.05$) (Table 4-9).

Results suggest that in control conditions, the growth rate of *S. recurvum* was significantly less than *S. cuspidatum* i.e. 0.076 compared with 0.113 mg mg^{-1} $week^{-1}$ dry wt respectively. However, growth of *S. recurvum* became similar to that of *S. cuspidatum* in the presence of phosphorus (Table 4-8).

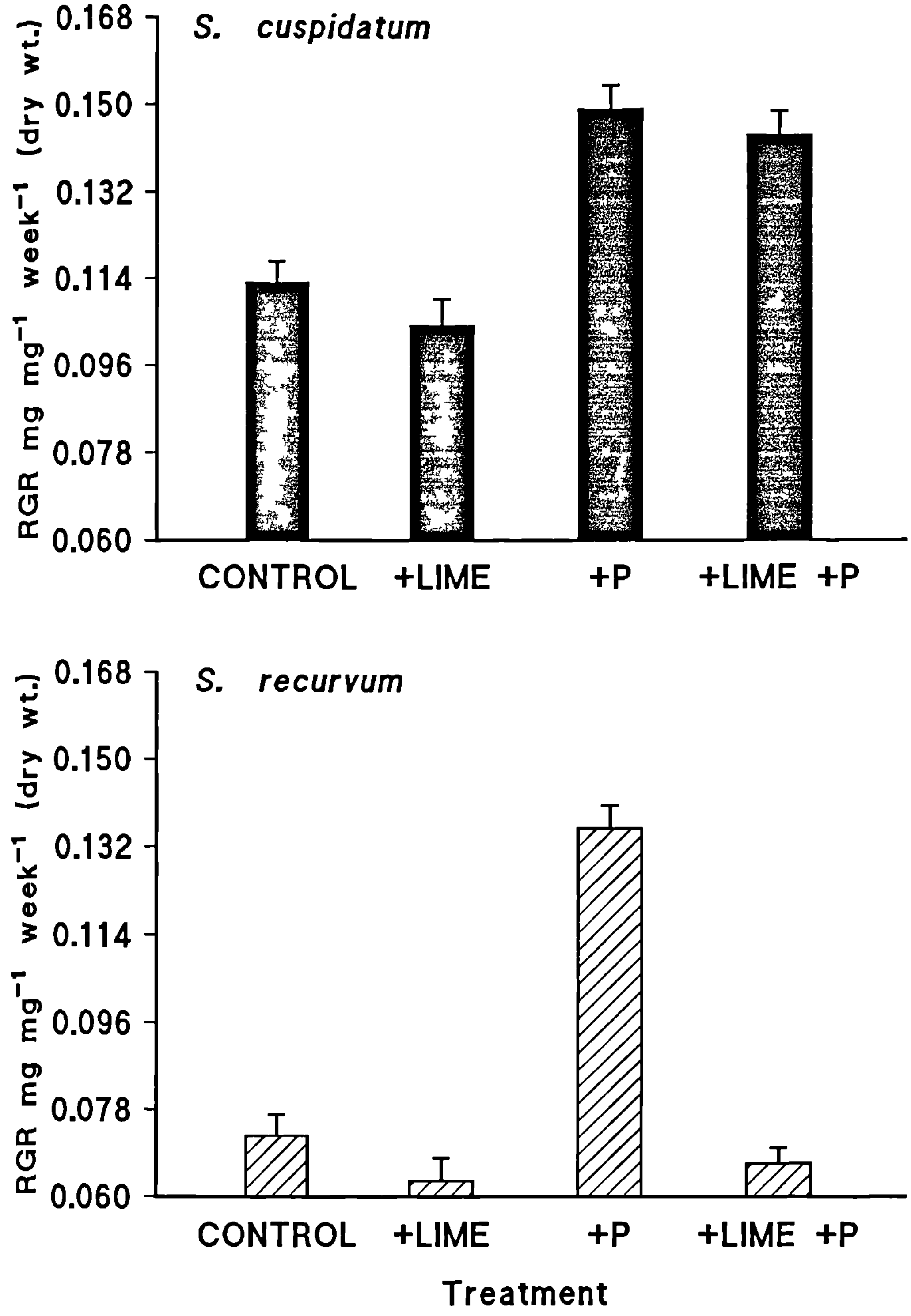
Table 4-8 : **Expt. 5 - Mean Relative Growth Rate of *Sphagnum* in the field on addition of lime and phosphorus.** [Standard Errors given in parentheses. RGR in mg mg^{-1} week^{-1} dry wt]

	Treatment				
	Control	**+ Lime**	**+ P**	**+ Lime + P**	**ANOVA results**
S. cuspidatum	0.113 (0.002)	0.104 (0.003)	0.149 (0.002)	0.144 (0.002)	d.f. = 39, 3 F = 89.924 p = 0.0001
S. recurvum	0.076 (0.002)	0.063 (0.002)	0.136 (0.002)	0.067 (0.002)	d.f. = 39, 3 F = 263.319 p = 0.0001

Table 4-9: **Effect of lime and phosphorus on growth of *Sphagnum*** - results from partitioning the sum of squares.

S. cuspidatum		***S. recurvum***	
Control *vs* (+P, +Lime +P)	d.f. = 1, 89 F = 135.34 P < 0.001	**Control *vs* (+Lime, +Lime +P)**	d.f = 1, 89 F = 8.501 p = 0.01
Control *vs* +Lime	d.f. = 1, 59 F = 8.049 p = 0.01	**+P *vs* (Control, +Lime, +Lime +P)**	d.f. = 1,119 F = 779.82 p < 0.001
+P *vs* +Lime +P	d.f. = 1, 59 F = 2.541 p > 0.05	**+Lime *vs* +Lime +P**	d.f. = 1, 59 F = 1.392 p > 0.05

Fig 4.10 Mean Relative Growth Rate (RGR) of *S. cuspidatum* and *S. recurvum* after 20 weeks immersed in flooded peat pits modified by additions of phosphorus and lime (Experiment 5) (4.4). [For details of treatment refer to section 4.4.1. Error bars = 95 % confidence limits]



4. 4. 3. 3 Tissue phosphorus concentration

Tissue phosphorus concentration (TPC) varied significantly between treatments in both species ($p < 0.0001$) (Table 4-10). Concentration closely mirrored the pattern obtained for RGR (Fig 4.11). Results from partitioning the sums of squares show that in *S. cuspidatum,* TPC was significantly greater in plants from the phosphorus only and the phosphorus plus lime treatments compared with the control ($p < 0.001$) (Table 4-11) . No significant difference existed in TPC ***between*** the two treatments ($p > 0.05$). Despite reduced RGR in the presence of lime (Fig. 4-10), TPC was not significantly less in the lime only treatment compared with the control ($p > 0.05$).

In *S. recurvum,* TPC was conspicuously greatest in the phosphorus only treatment ($p < 0.001$) (Fig 4.11). It was significantly less in the '+ lime' treatment compared with the control ($P < 0.001$). In the lime plus phosphorus treatment, TPC was significantly less than in the phosphorus only treatment but it was significantly greater than the control ($p < 0.001$) (Table 4-11).

In general, TPC was smaller in *S. recurvum* compared with *S. cuspidatum*. This was in keeping with the lower growth rates generally recorded for this species. In the phosphorus treatment, which showed rates of growth similar to *S. cuspidatum* (Fig 4.10*)*, TPC in *S. recurvum* was on average almost double that recorded for S. cuspidatum (Table 4-10, Fig 4.11).

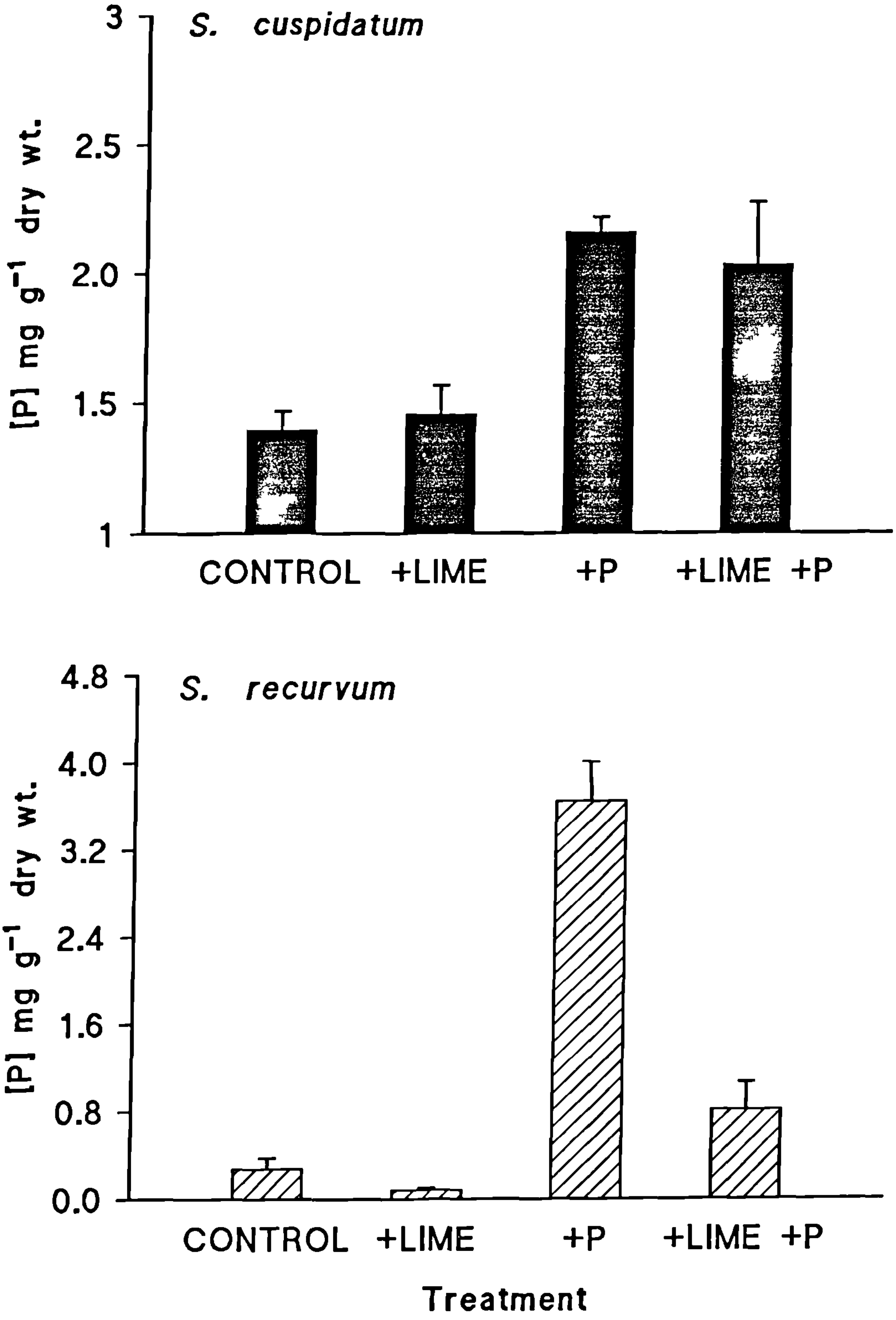
Table 4-10 : **Expt. 5 - Mean tissue concentration of phosphorus in *Sphagnum***
[Standard Errors given in parentheses. Mean values in mg g^{-1} dry wt]

	Treatment					
	Control	**+ Lime**	**+ P**	**+ Lime + P**	**F_{max} results**	**ANOVA results**
S. cuspidatum	1.395 (0.036)	1.456 (0.056)	2.16 (0.032)	2.034 (0.136)	d.f. = 9\\$^{4}$ F = 17.66 p = 0.001	d.f. = 3, 39 F = 28.994 p = 1.03 x10^{-9}
S. recurvum	0.275 (0.05)	0.081 (0.009)	3.638 (0.187)	0.811 (0.127)	d.f. = 9\\$^{4}$ F = 206.22 p = 0.001	d.f. = 3,39 F = 119.284 p = 9.26 x10^{-19}

Table 4-11 : **Expt. 5 - Tissue phosphorus concentration in *Sphagnum*** - results from partitioning the sum of squares.

S. cuspidatum		*S. recurvum*	
(Control, +Lime) *vs* (+P, +Lime +P)	d.f. = 1, 39 F = 84.794 P < 0.001	**+P *vs* (Control, +Lime, +Lime +P)**	d.f = 1, 39 F = 255 p < 0.001
Control *vs* +Lime	d.f. = 1, 19 F = 2.162 p > 0.05	**+Lime +P *vs* (Control , +Lime)**	d.f. = 1, 29 F = 82.278 p < 0.001
+P *vs* +Lime +P	d.f. = 1, 19 F = 1.753 p > 0.05	**Control *vs* +Lime**	d.f. = 1, 19 F = 275.58 p < 0.001

Fig 4.11 Mean tissue phosphorus concentration in *S. cuspidatum* and *S. recurvum* after 20 weeks immersed in flooded peat pits modified by additions of phosphorus and lime (Experiment 5) (4.4). [Error bars = 95 % confidence limits]



4. 4. 3. 4 Tissue calcium concentration

Tissue calcium concentration (TCC) varied significantly between the treatments for both species. ($p < 0.0001$) (Table 4-12). TCC was conspicuously greater for both species in the lime plus phosphorus treatment (Fig 4.12). In both cases TCC was in the order of 4 - 4.5 mg l^{-1}. Results from partitioning the sum of squares confirm that TCC in the lime plus phosphorus treatment was significantly greater than all other treatments for both species ($p = 0.001$). Furthermore, in both Sphagna, there was no significant difference in TCC between the remaining treatments ($p > 0.05$) (Table 4-13).

Table 4-12 : Expt. 5 - Mean tissue concentration of calcium in *Sphagnum*
[Standard Errors given in parentheses. Mean *values in mg g^{-1} dry wt*]

	Treatment					
	Control	**+ Lime**	**+ P**	**+ Lime + P**	**F_{max} results**	**ANOVA results**
S. cuspidatum	2.826 (0.254)	2.614 (0.134)	2.337 (0.091)	4.189 (0.307)	d.f. = $9\backslash^{4}$ F = 11.47 p = 0.001	d.f. = 3, 39 F = 15.142 p = 1.55 x10^{-6}
S. recurvum	2.248 (0.266)	2.343 (0.165)	2.423 (0.144)	3.509 (0.230)	d.f. = $9\backslash^{4}$ F = 3.421 p > 0.05	d.f. = 3, 39 F = 8.123 p = 0.0003

Table 4-13 : Expt. 5 - Tissue calcium concentration in *Sphagnum* - results from partitioning the sum of squares.

S. cuspidatum		***S. recurvum***	
+Lime +P *vs* (Control, +Lime, +P)	d.f. = 1, 39 F = 41.93 P = 0.001	**+Lime+P *vs* (Control, +Lime, +P)**	d.f = 1, 39 F = 22.672 p = 0.001
Control *vs* +Lime *vs* +P	d.f. = 1, 29 F = 3.495 p > 0.05	**Control *vs* +Lime *vs* +P**	d.f. = 1, 29 F = 1.697 p > 0.05

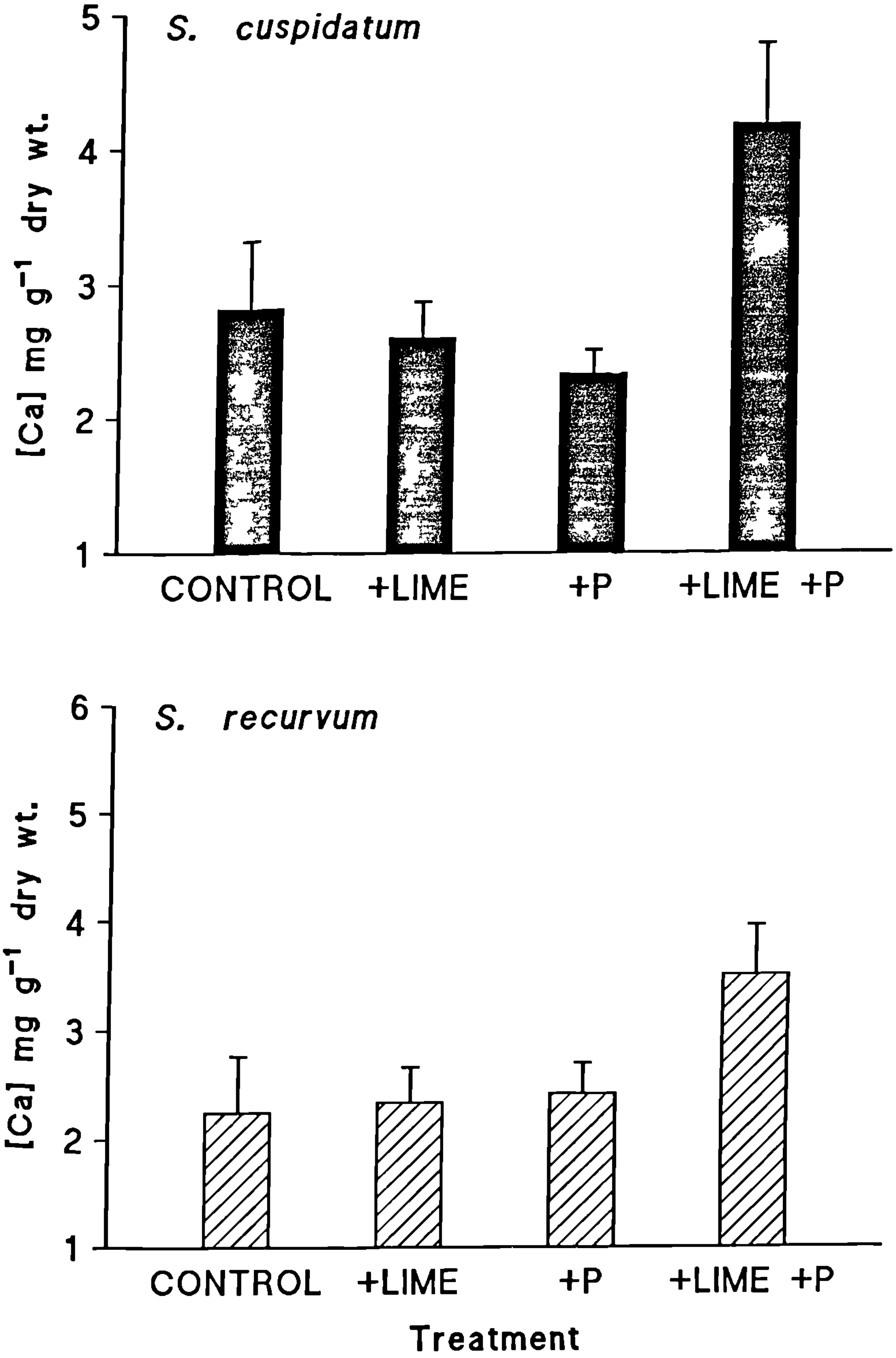


Fig 4.12 Mean tissue calcium concentration in *S. cuspidatum* and *S. recurvum* after 20 weeks immersed in flooded peat pits modified by additions of phosphorus and lime (Experiment 5) (4.4). [Error bars = 95 % confidence limits]

4. 4. 4 Discussion

Addition of inorganic phosphorus significantly increased the growth of *S. cuspidatum* and *S. recurvum* in the field. Both species also showed a capacity for increased phosphorus uptake (Fig 4.11). Thus, despite some degree of nutrient enrichment detected at Thorne Moors (4.1), phosphorus concentrations appear to be sub-optimal for growth of at least two *Sphagnum* species.

Overall, application of lime had an adverse effect on *Sphagnum* growth. One exception to this was the growth of *S. cuspidatum* in presence of both lime and phosphorus. Fig 4.10 shows that its growth was less in the combined treatment compared with the phosphorus only treatment (suggesting lime did have a detrimental effect on growth) but this difference was not significant (Table 4-9). pH was successfully elevated in the pits from pH 3.0 in the control to between pH 3.5 and 4.0 (Fig 4.9) but, in contrast to the results from laboratory experiments (Expt. 4), this increase in pH did not improve *Sphagnum* growth. Results from Experiment 4 suggest that a pH shift in this range would not itself have a detrimental effect on growth, therefore, depressed growth was probably a toxic response to addition of calcium.

Clymo (1973) suggests that a toxic effect of calcium is unlikely in this pH range. Furthermore, results from laboratory experiments conducted in this study (4.2) showed that Ca concentrations up to 20 mg l^{-1} had no toxic effect on *S. cuspidatum* or *S. recurvum* (over nine weeks). However, water calcium concentration in pits to which lime was added exceeded 20 mg l^{-1}, reaching up to 30 mg l^{-1} (Fig 4.9) and exposure to such high concentrations over a longer period of twenty weeks could conceivably have had a toxic effect. The mechanism by which lime exerted a toxic influence is unclear as application of just lime did not increase tissue calcium concentration (TCC) in either species (Fig 4.12) suggesting that calcium was not readily taken up.

Growth of *S. recurvum* under control conditions was less than that of *S. cuspidatum* (Table 4-8, Fig 4.10). There are several possible explanations for this. *Sphagnum cuspidatum* is innately a quite productive species in the bog-pool environment (1.6.2) and whilst *S. recurvum* may be found growing in pools, it is also frequently observed growing in lawns and hummocks. Therefore, the pool environment may be less optimal for growth of *S. recurvum* than *S. cuspidatum,* especially when plants start off submerged 30 cm below the surface as they were in this study. However, *S. recurvum* may be a prolific coloniser of weakly-minerotrophic pools (Tallis, 1973). Therefore, it may have been the chemical environment and not submergence that limited its growth in this experiment. *S. recurvum* is most commonly associated with poor-fen environments and may be less efficient at 'scavenging' nutrients than *S. cuspidatum*. It was notable in this experiment, that *S. recurvum* achieved a similar growth rate to *S. cuspidatum* only in the presence of added phosphorus (Table 4-8, Fig 4.10). Furthermore, at a similar growth rate, TPC in *S. recurvum* averaged at 3.64 mg g^{-1} dry wt. compared with 2.16 mg g^{-1}dry wt in *S. cuspidatum* (Table 4-10, Fig 4.11). This suggests that *S. recurvum* required greater availability and uptake of phosphorus to achieve a similar growth rate to that of *S. cuspidatum*. If this is the case then it is not surprising that *S. recurvum* is much less frequent than *S. cuspidatum* on ombrotrophic bogs.

Comparison between Fig 4.10 and Fig 4.11 suggests that growth rate was closely associated with tissue phosphorus concentration (TPC) and therefore phosphorus uptake. This suggests that adding calcium limited P-acquisition. For example, Fig 4.11 shows that TPC in *S. recurvum* was significantly reduced in the presence of lime, and so, notably, was growth (Fig 4.10). Reduced TPC may be an indirect effect of calcium toxicity or, alternatively, it may be a direct effect of the chemical association between calcium and phosphorus. Boyer & Wheeler (1989) suggest that emerging spring waters saturated with $CaCO_3$ bind phosphorus at the spring head to produce infertile pockets of species-rich fen within stands of more productive, less diverse vegetation. Therefore, adding lime may have limited P-availability and thus limited *Sphagnum* growth. However, P-adsorption requires solid $CaCO_3$, and at pH 3.5-4 most of the added lime was likely to have been dissolved (Wheeler, *pers. comm.*), therefore the real significance of P - $CaCO_3$ interaction in explaining these results remains unclear. Lime application only significantly increased tissue calcium concentration (TCC), when applied in combination with phosphorus (Fig 4.12) suggesting some interaction did occur between the two elements.

In contrast to *S. cuspidatum*, relative growth rate in *S. recurvum* was significantly lower in the combined treatment compared with the phosphorus only treatment (Fig 4.10). A toxic effect of lime seems rather unlikely as *S. recurvum* has been shown to be more base tolerant than *S. cuspidatum* (Clymo, 1973). This may instead be a product of phosphorus acquisition, as low growth in *S. recurvum* was mirrored by significantly lower TPC (Fig 4.11). TPC was significantly higher compared with the control but this did not appear sufficient to produce a positive growth response. This supports a previous suggestion that *S. recurvum* requires greater phosphorus uptake than *S. cuspidatum* to promote growth. This presents an interesting paradox whereby *S. recurvum*, a species which may grow in base rich conditions, has grown less in the presence of lime than the *S. cuspidatum* which is comparatively base-intolerant. Furthermore, the reason for this appears to be that the presence of lime has limited phosphorus uptake in *S. recurvum* but not in *S. cuspidatum*.

There is no obvious explanation for this result. A possible explanation is suggested below but it is based purely on conjecture. It is possible that base-tolerance for which *S. recurvum* is renowned may, to some extent, be a product of its ability to exclude base elements from uptake (essentially a base avoidance strategy). However, in this case because of bonding between phosphorus and lime, avoiding base uptake also reduced uptake of phosphorus. Fig 4.12 suggests that uptake of phosphorus and calcium were linked as TCC was only significantly greater when lime occurred in combination with phosphorus. In *S. cuspidatum* base uptake may not have been restricted (no base avoidance strategy) and consequently neither was phosphorus acquisition. This would explain why *S. cuspidatum* in the combined treatment, exhibited higher TPC, TCC and RGR than *S. recurvum* and any toxic influence of calcium may have been over-ridden by the growth benefits of increased phosphorus. However, in *S. recurvum* phosphorus uptake may have been limited by excluding calcium from uptake; hence a moderate increase in TPC and TCC occurred but the increase in phosphorus uptake was not sufficient to invoke a growth response (see above). If this hypothesis is correct then one would expect TCC to be lower in *S. recurvum* compared with *S. cuspidatum*. Indeed, mean TCC in *S. recurvum* was 3.5 mg g^{-1} dry wt, compared with 4.2 mg g^{-1} dry wt in *S. cuspidatum*. However, this explanation is not entirely satisfactory as this small difference in TCC was not proportional to the large difference in TPC.

Chapter 5

Re-introduction of *Sphagnum* to cut-over bog surfaces

5.1 *Background*

Recolonisation of cut-over bog by *Sphagnum* may be influenced not only by habitat conditions but also by availability of propagules. Clymo & Duckett (1986) observed that new shoots of *S. papillosum* developed on peat discs taken from up to 30cm below the surface of an uncut bog. When the peat discs were exposed to light and saturated air in a cool greenhouse, green shoots developed from brown, apparently dead *Sphagnum* material estimated to be up to 60 years old. This suggests that a persistent vegetative 'seed' bank exists for *Sphagnum* in surface peat layers from which regeneration may take place. However, in most peat cutting situations extraction exposes deeper more humified peats which do not retain viable diaspores (Salonen, 1987; Clymo & Duckett, 1986).

The lack of a persistent diaspore bank in the peat of newly abandoned, cut-over surfaces, means spontaneous recolonisation is dependent upon dispersal of viable diaspores from proximate source areas. There is little information on the rates and methods of propagule dispersal in *Sphagnum*. Poschlod (1992) points to the importance of wind dispersal of bryophyte shoot fragments as a source of propagules for milled bog surfaces in S. Germany. However, bogs extensively damaged by peat extraction, such as Thorne Moors, often retain few refugia for survival of bog species that can act as a source of propagules. It is difficult to estimate to what extent this limits *Sphagnum* recolonisation as the natural propensity for *Sphagnum* to establish in old peat cuttings is frequently obscured by unsuitably dry conditions (Chapter 2 and 3). However, raised bog Sphagna have also failed to colonise suitably wet cuttings, notably at Thorne Moors (2.2.3), suggesting recolonisation may be hindered by the absence of a local propagule source.

Therefore, it may be necessary to consider deliberately reintroducing *Sphagnum* to accelerate (if not initiate) the revegetation process. For relatively small operations, plants could be collected under careful guidelines from donor sites considered least 'sensitive' to disturbance. Recently, concern has been voiced over inter-site transplants as disturbance of regional gene pools is considered undesirable (B. Johnson, English Nature, *pers comm*). Furthermore, the possibility exists of introducing plant or animal species previously alien to a site. However, whilst intra-site transplants would be preferable, there may be insufficient material for this to be possible. For larger scale restoration, removal of *Sphagnum* from donor sites would be unsatisfactory. In order to obtain the required quantity of inoculum too much damage would be sustained by the donor site. In this situation the possibility of 'farming' *Sphagnum* must be considered. This is considered in Section 6.7.

There is very little published research that considers *Sphagnum* regeneration from inocula applied to cut-over bog surfaces. Occasionally 'ad hoc' trials have been conducted by wardens at nature reserves and employees of peat cutting companies but these initiatives are seldom recorded. The aim of this investigation was to investigate the propensity for a variety of *Sphagnum* species to regenerate from inoculum applied in the field and furthermore, determine the water regime required for optimal re-establishment.

5.2 Sphagnum *regeneration from whole plants (Experiment 6)*

In this experiment *Sphagnum* was applied in the form of intact gametophytes, in contrast to Experiment 7 in which inocula were decapitated into fragments prior to application.

5.2.1 Method

Trenches STB 1 - STB 16 in the Crowle experimental of Thorne were used in this investigation. Details of trench design are given in Section 1.10.2. They were approximately 16m long and 2m wide with a sloping bottom that provided a range of water regimes so that a trench could be crudely divided into sections as follows:

Peat slope	Remains dry for long periods
Peat-water interface	Thin band either side of the water's edge. Consists of moist peat on one side and very shallow water on the other.
Shallow water	Depths up to 50 cm
Deep water	Depths exceeding 50 cm up to approx. 100 cm

Sphagnum was applied to the trenches as shown in Table 5-1. Prior to addition of *Sphagnum*, birch brashings were added to the flooded part of trenches STB 1 - STB 8 to investigate whether physical support would assist colonisation of open water. Between 100 and 150 litres of loosely packed, living *Sphagnum* material was applied to each trench. The material was scattered by hand at an approximately even density along the entire length of the trenches. Inocula were applied during December 1990 and January 1991 with the exception of *S. papillosum* which was added in April 1991 and *S. fimbriatum* which was added in July 1991. Growth was recorded in November 1993. A 1 m^2 quadrat divided into a hundred 10 x 10 cm squares was used to measure the mean number of capitula per 100 cm^2 at 1 m intervals along the length of each trench.

Water levels were not uniform throughout the trenches. Therefore, in each trench the length of peat slope exposed was recorded bimonthly for comparison. Details of water quality were taken from results of the broader survey described in Chapter 4, sect 4.1. Water chemistry of trenches STB 1, STB 5, STB 9 and STB 13 were routinely measured, as part of that survey, between June 1990 and July 1991, and pH and conductivity between June 1990 and July 1993. The data were examined for heterogeneity of water quality across the trenches. Data were tested for homogeneity of variance using the F_{max} test prior to applying ANOVA.

Table 5-1 : Inoculation of trenches with *Sphagnum* (Experiment 6)

Trench	Species	Treatment
STB1	*S. recurvum*	+ Brushwood
STB2	*S. cuspidatum*	+ Brushwood
STB3	*S. palustre*	+ Brushwood
STB4	*S. capillifolium*	+ Brushwood
STB5	*S. auriculatum*	+ Brushwood
STB6	*S. magellanicum*	+ Brushwood
STB7	*S. papillosum*	+ Brushwood
STB8	*S. fimbriatum*	+ Brushwood
STB9	*S. recurvum*	
STB10	*S. palustre*	
STB11	*S. capillifolium*	
STB12	*S. auriculatum*	
STB13	*S. magellanicum*	
STB14	*S. cuspidatum*	
STB15	*S. papillosum*	
STB16	*S. fimbriatum*	

5. 2. 2 Results

5. 2. 2. 1 *Sphagnum* growth

Growth of *Sphagnum* in each of the trenches is recorded in Table 5-2. Successful regeneration was only observed for *S. recurvum, S. cuspidatum* and *S. auriculatum,* though limited regeneration was also observed in *S. fimbriatum*. Results for *S. recurvum, S. cuspidatum* and *S. auriculatum* are illustrated in Fig 5.1. All three species showed similar patterns of regeneration. Growth was confined to the shallower end of the trench where it formed a continuous floating raft extending 3 - 4 m along the trench to a maximum water depth of 50 cm. Some growth was observed in deeper water occurring as small floating 'clumps' anchored to the pool periphery.

Less prolific regeneration of *S. recurvum*, *S. cuspidatum* and *S. auriculatum* also occurred in trenches inoculated with other species. For example *S. cuspidatum* was found growing in STB 6, STB 11, STB 13 and STB 15. Furthermore, *S. recurvum* and *S. auriculatum* were observed growing in STB 3 and STB 10. However, no *Sphagnum* regeneration was observed in the control trench and, this growth almost certainly resulted from contamination in the source material and not from spontaneous recolonisation.

Comparison of results in Fig 5.1 suggests that in the limited number of trenches which showed regeneration, the presence of brushwood had no obvious effect on *Sphagnum* growth.

Table 5-2 : **Regeneration of *Sphagnum* from whole plants applied to trenches STB 1 to STB 16** (Expt. 6) [Results describe *Sphagnum* cover approx. 3 yrs after inoculation. Regeneration of *S. auriculatum*, *S. cuspidatum* and *S. recurvum* illustrated in Fig 5.1]
Cover - distances refer to position along trench. 0 = top of peat slope (refer to Fig 5.1)
Water depth = max. depth of water in which *Sphagnum* regeneration was observed

Trench	Species	Cover	Growth form	Water depth	Notes
STB 1	*S. recurvum*	0 to 3.7 m - Continuous cover. Capitulum density = 40 - 60 per 100 cm^2 (Fig 5.1)	Floating raft	≤ 50 cm	0 to 30 cm - 30% cover of *Eriophorum vaginatum* with interstitial growth of *S. recurvum*. 3.7 to 16 m - Occasional floating 'clumps' of *S. recurvum* anchored to the trench periphery. Prolific growth of green filamentous algae, particularly *Oedogonium* sp., frequently observed to smother *Sphagnum*.
STB 2	*S. cuspidatum*	0 to 2.7 m - Continuous cover. Capitulum density = 40 - 80 per 100 cm^2 (Fig 5.1)	Floating raft	≤ 40 cm	0 to 1.5 m - 30% cover of *Eriophorum vaginatum* with interstitial growth of *S. cuspidatum* Prolific growth of algae (as for STB 1).
STB 3	*S. palustre*	0 to 0.3 m - Sparse cover ≤ 10%	Hummock on peat	≤ 5 cm	0 to 2.7 m - 40% cover of *Eriophorum vaginatum* and *E. angustifolium*. Interstitial water colonised by a floating raft of *S. auriculatum* and *S. recurvum* to a max water depth of 30 cm. Prolific growth of algae (as for STB 1).
STB 4	*S. capillifolium*	No regeneration	N/A	N/A	0 to 1.5 m - 30% cover of *Eriophorum vaginatum*
STB 5	*S. auriculatum*	0 to 3.1 m - Continuous cover. Capitulum density = 40 - 60 per 100 cm^2 (Fig 5.1)	Floating raft	≤ 45 cm	Conspicuously less algae

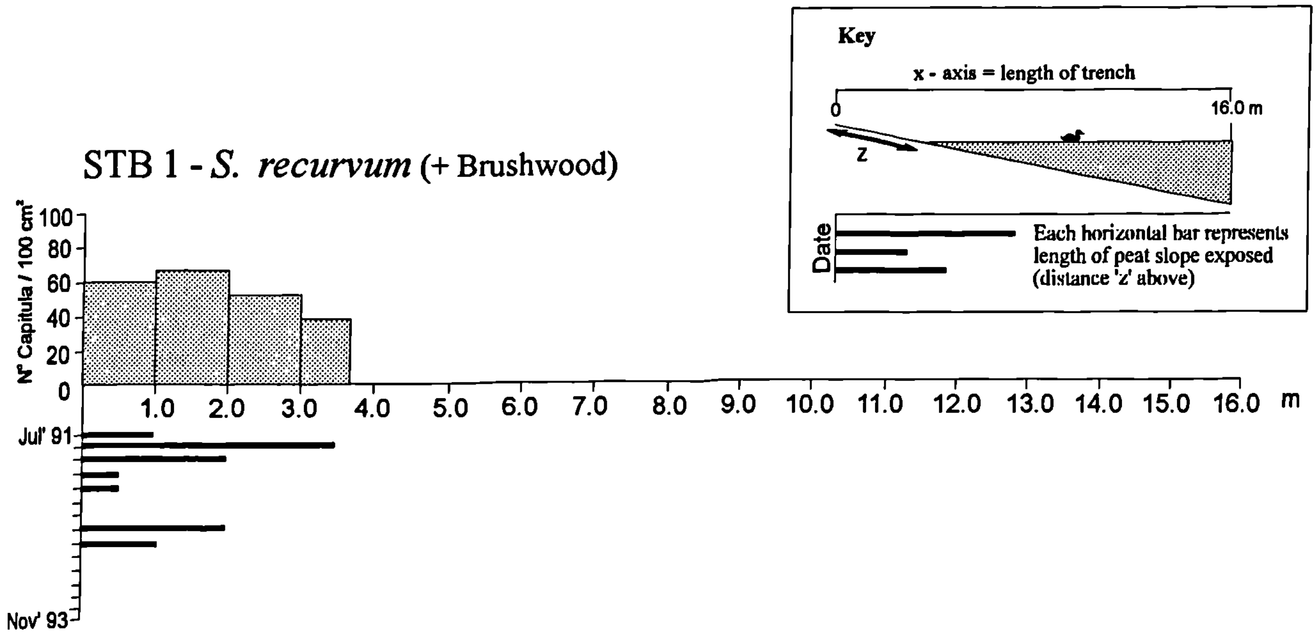
Table 5-2 : *Continued*

Trench	Species	Cover	Growth form	Water depth	Notes
STB 6	*S. magellanicum*	No regeneration	N/A	N/A	0 to 1.5 m - Sparse growth of *S. cuspidatum.* No prolific algal growth.
STB 7	*S. papillosum*	No regeneration	N/A	N/A	0 to 1m - Embryonic green shoots occasionally visible on seemingly dead inoculum. Loose floating raft of *S. cuspidatum* developed to depths of 40 cm. No prolific algal growth.
STB 8	*S. fimbriatum*	0.5 to 3 m - Discontinuous covering ≤ 40% of peat surface.	Submerged 'clumps' composed of a dense mat of spindly shoots (abnormal growth with no definite capitula)	≤ 40 cm	No prolific algal growth.
STB 9	*S. recurvum*	0 to 4 m - Continuous cover. Capitulum density = 60 - 100 per 100 cm^2 (Fig 5.1)	Floating raft	≤ 40 cm	No prolific algal growth.
STB 10	*S. palustre*	No regeneration	N/A	N/A	0 to 1m - Sparse growth of *S. recurvum* and *S. auriculatum.* No prolific algal growth.

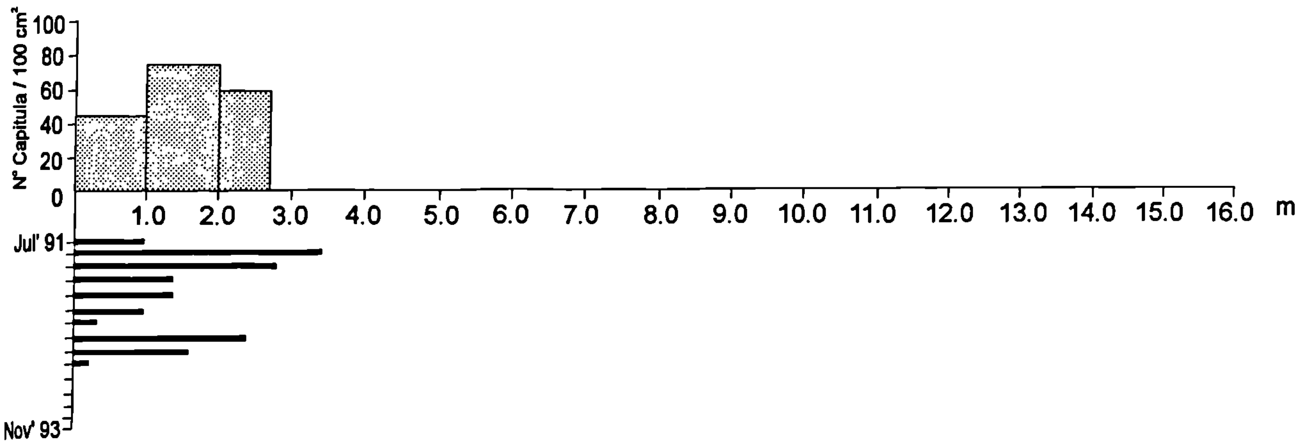
Table 5-2 : *Continued*

Trench	Species	Cover	Growth form	Water depth	Notes
STB 11	*S. capillifolium*	No regeneration	N/A	N/A	0 to 0.5 m - Sparse growth of *S. cuspidatum* No prolific algal growth
STB 12	*S. auriculatum*	0.7 to 3 m - Continuous cover. Capitulum density = 50 - 60 per 100 cm^2 (Fig 5.1)	Floating raft	≤ 30 cm	No prolific algal growth
STB 13	*S. magellanicum*	No regeneration	N/A	N/A	0 to 3 m - Loose, discontinuous floating raft of *S. cuspidatum* up to a max. depth of 40cm. No prolific algal growth
STB 14	*S. cuspidatum*	0 to 3.7 m - Continuous cover. Capitulum density = 40 - 50 per 100 cm^2 (Fig 5.1)	Floating raft	≤ 30 cm	No prolific algal growth
STB 15	*S. papillosum*	No regeneration	N/A	N/A	0 to 0.5 m - Embryonic green shoots occasionally visible on seemingly dead inoculum. 0 - 3 m - Loose floating raft of *S. cuspidatum* developed to depths of 40 cm. No prolific algal growth.
STB 16	*S. fimbriatum*	1.5 to 3.4 m - Discontinuous covering ≤ 50% of peat surface.	Submerged 'clumps' composed of a dense mat of spindly shoots (abnormal growth with no definite capitula)	≤ 35 cm	No prolific algal growth.

Fig 5-1 - Growth of *Sphagnum* added to sloping trenches in Expt. 6. [Trenches were inoculated with *Sphagnum* along their entire length. Results represent distribution of *Sphagnum* in the trenches approximately 3 yrs after inoculation. Records also presented for each trench showing changes in position of the water table between July 1991 and Nov 1993. Results only given for those trenches in which the *Sphagnum* added grew successfully. For further details of these and and other trenches refer to Table 5-2]


STB 1 - *S. recurvum* (+ Brushwood)

STB 2 - *S. cuspidatum* (+ Brushwood)



STB 5 - *S. auriculatum* (+ Brushwood)

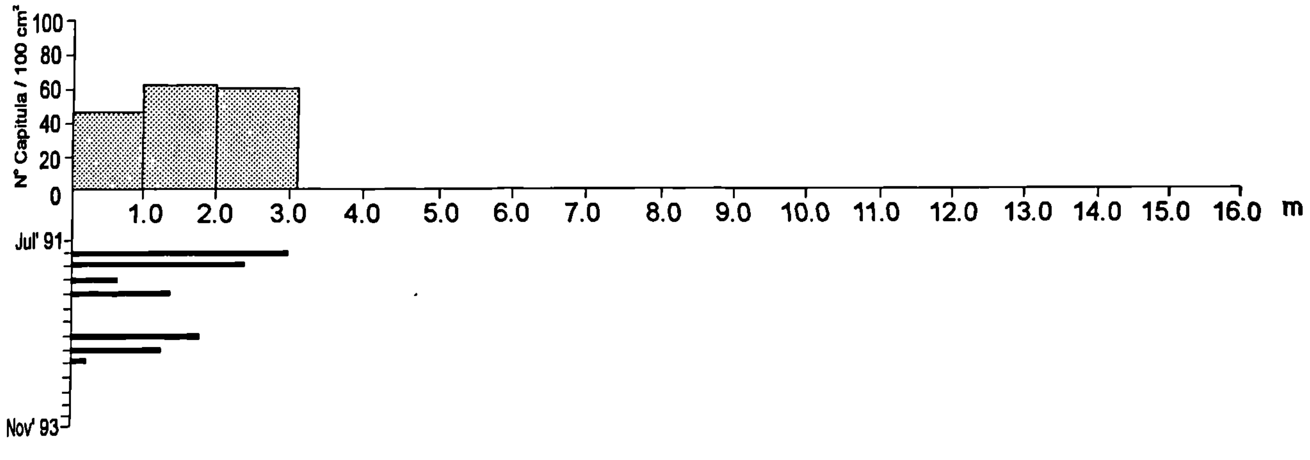
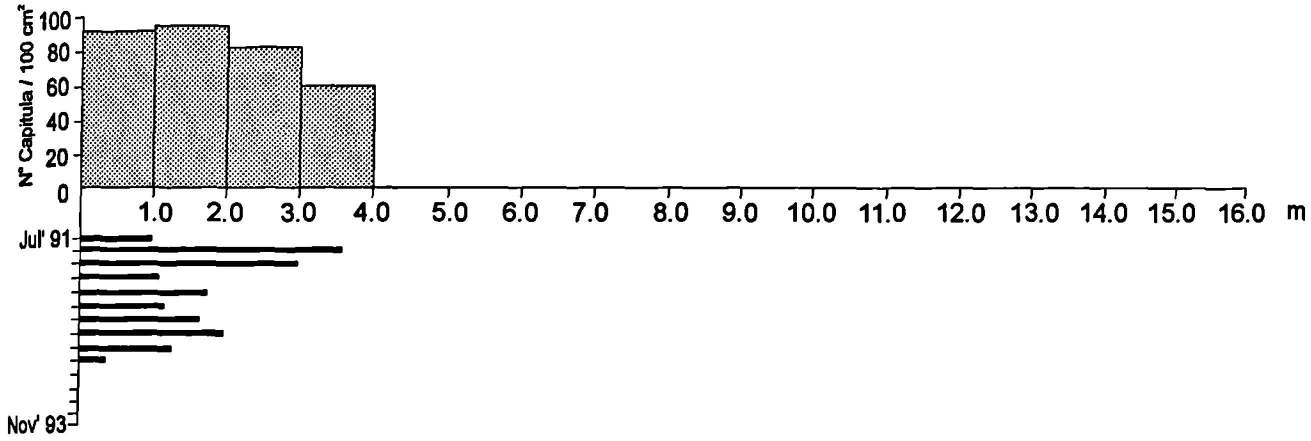
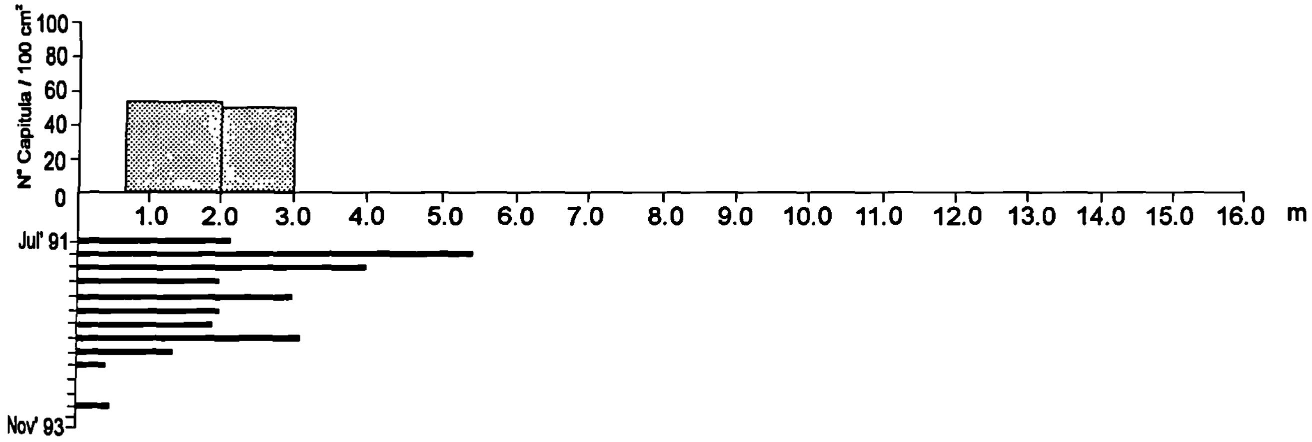


Fig 5.1 - continued.

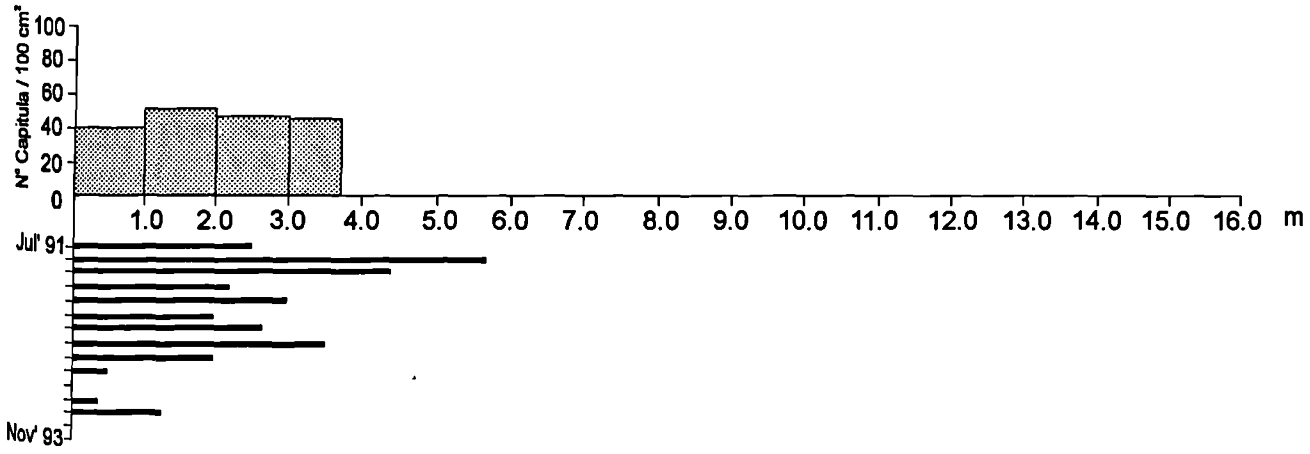
STB 9 - *S. recurvum*



STB 12 - *S. auriculatum*



STB 14 - *S. cuspidatum*

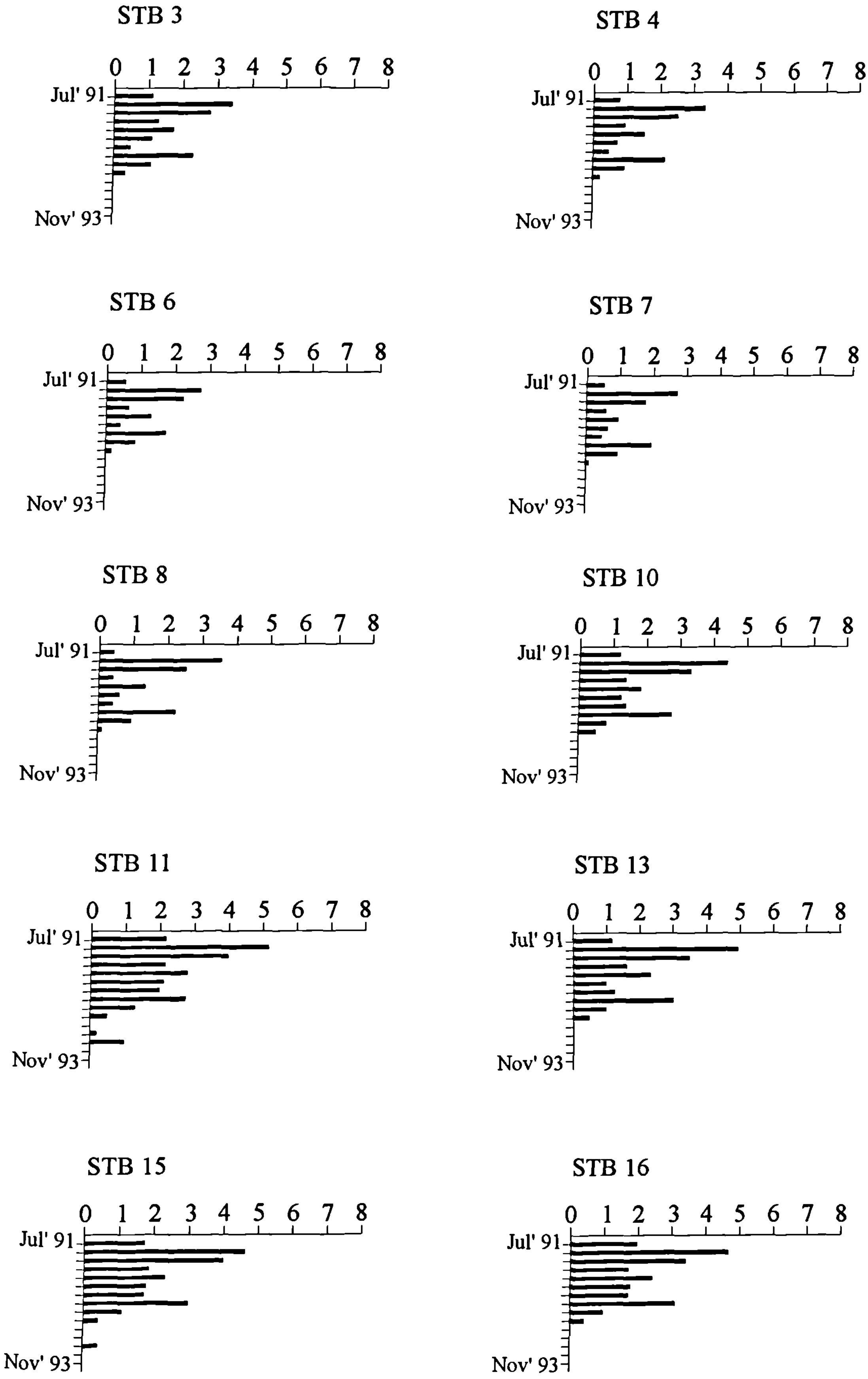


5. 2. 2. 2 Water table

In Fig 5.1 water table fluctuations are shown alongside growth data for those trenches in which *Sphagnum* regeneration was successful. Water table fluctuations in the remaining trenches are shown in Fig 5.2. All trenches showed similar patterns of water table change with fluctuations largely confined to the top 6 m of the peat slope. During at least the first half of the experiment's duration, a significant length of peat slope remained exposed in all trenches. However, from winter 1992/1993 onwards, Thorne Moors received greater amounts of rainfall than in the previous two years and surface conditions became much wetter. Consequently, all the trenches were completely submerged for the duration of 1993.

Overall there was a general trend of increasing wetness across the trenches towards STB 1. In Fig 5.2 it is evident that more peat slope was exposed, on average, in trenches STB 10 - 16 than in STB 3 - 8. The same trend is evident in Fig 5.1 between trenches STB 9 - 14 and STB 1 - 5. In 1993, when all the trenches were full of water, the ground around trenches STB 1 - 3 was also flooded.

Fig 5.2 : Water table fluctuations in trenches in Experiment 6. [x - axis represents first 8 m length of trench within which fluctuations were confined. For details refer to key in Fig 5.1]



5. 2. 2. 3 Water quality

The mean concentration of major ions plus mean pH and conductivity (corrected for pH) are shown for the trenches sampled (Fig 5.3). Mean values and results from analysis of variance are given in Table 5-3. The results indicate no significant trend in pH across the trenches. There is a suggestion of elevated conductivity in STB 1 but this was not significant ($p = 0.217$). Therefore, results indicate that over three years the gross ionic character of water in the trenches did not differ. Results for individual ions show that concentration of SRP and K did not differ significantly between the trenches (Fig 5.3). However, there was a trend of decreasing NO_3, NH_4-N and SO_4 towards STB 1 but differences were only significant for NO_3 and NH_4-N (Table 5-3). Conversely, Ca and Fe showed a significant trend of increasing concentration towards STB 1 ($p = 0.006$ and 0.034 respectively) (Table 5-3).

Fig 5.3 Mean pH, conductivity and concentration of major ions recorded in water samples taken from the 'STB' trenches used in Experiment 6 (5.2) [All units in mg l^{-1} unless otherwise shown. Errorbars = 95% confidence limits]

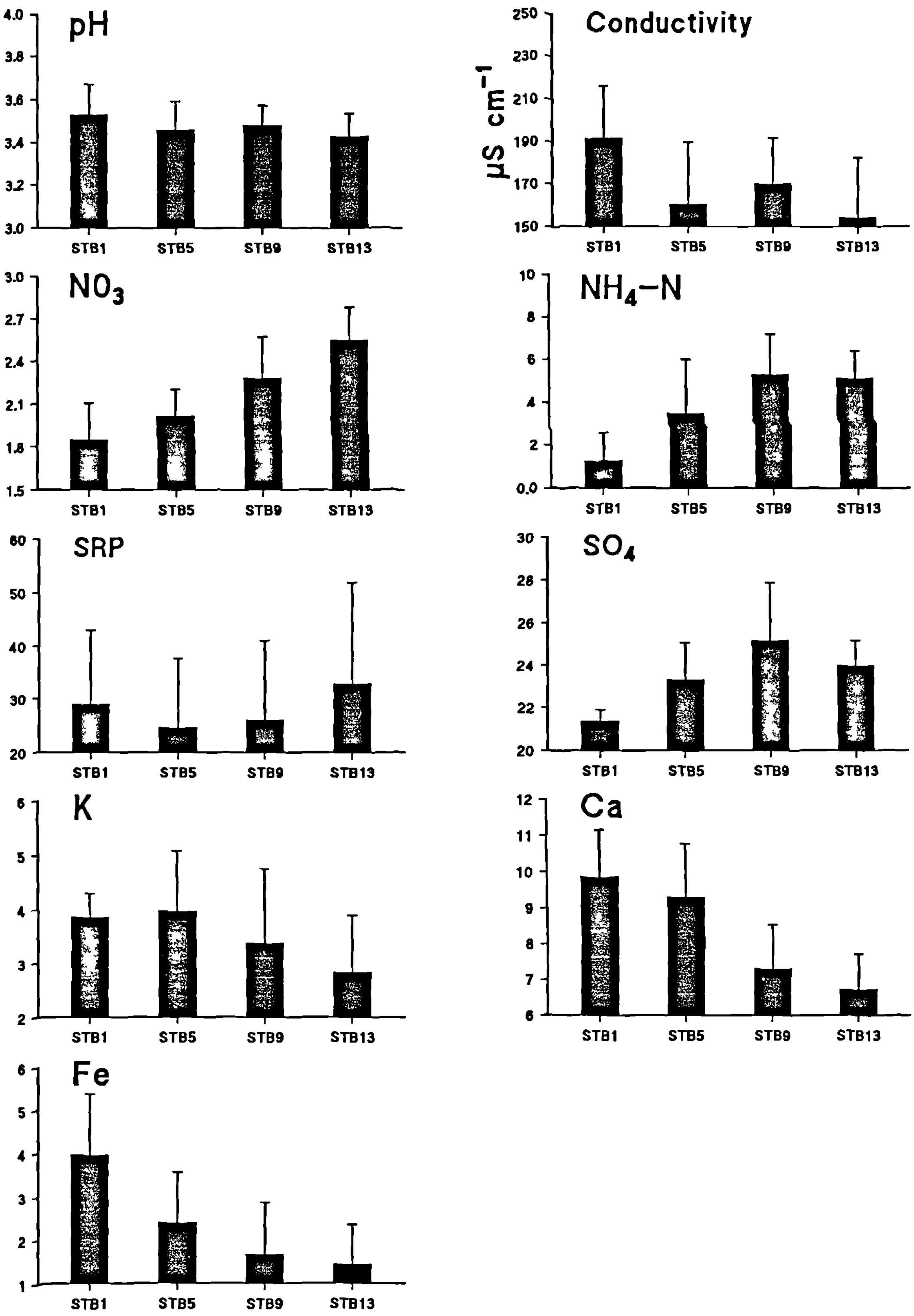


Table 5-3 : Water quality of trenches used in Experiment 6. [Mean values given with standard errors in parenthesis. Units of conductivity = $\mu S\ cm^{-1}$. All other units = $mg\ l^{-1}$ except SRP which = $\mu g\ l^{-1}$]

	STB 1	STB 5	STB 9	STB 13	F_{max} results	ANOVA results
pH	3.5 (0.073)	3.5 (0.068)	3.5 (0.047)	3.4 (0.054)	d.f. = 4, 13 F = 2.4 $p > 0.05$	d.f. = 3, 55 F = 0.474 p = 0.702
Corrected Conductivity	191.44 (12.39)	160.5 (14.83)	170.03 (10.98)	154.15 (14.26)	d.f. = 4, 15 F = 1.824 $p > 0.05$	d.f. = 3, 63 F = 1.525 p = 0.217
NO_3	1.85 (0.132)	2.02 (0.095)	2.28 (0.149)	2.55 (0.119)	d.f. = 4, 3 F = 2.5 $p > 0.05$	d.f. = 3, 15 F = 5.907 p = 0.010
NH_4-N	1.293 (0.648)	3.5 (1.294)	5.3 (0.968)	5.13 (0.660)	d.f. = 4, 5 F = 3.99 $p > 0.05$	d.f. = 3, 23 F = 4.0 p = 0.022
SRP	29.03 (7.160)	24.68 (6.678)	25.98 (7.696)	32.88 (9.718)	d.f. = 4, 5 F = 2.118 $p > 0.05$	d.f. = 3, 23 F = 0.213 p = 0.886
SO_4	21.38 (0.272)	23.32 (0.890)	25.18 (1.382)	24.0 (0.610)	d.f. = 4, 3 F = 25.8 $p > 0.05$	d.f. = 3, 15 F = 3.219 p = 0.061
Ca	9.87 (0.662)	9.317 (0.750)	7.3 (0.629)	6.73 (0.503)	d.f. = 4, 5 F = 2.22 $p > 0.05$	d.f. = 3, 23 F = 5.611 p = 0.006
K	3.87 (0.225)	3.98 (0.569)	3.38 (0.708)	2.83 (0.547)	d.f. = 4, 5 F = 9.93 $p > 0.05$	d.f. = 3, 23 F = 0.937 p = 0.441
Fe	3.97 (0.727)	2.4 (0.6)	1.67 (0.614)	1.43 (0.473)	d.f. = 4, 5 F = 2.4 $p > 0.05$	d.f. = 3, 23 F = 3.51 p = 0.034

5. 2. 3 Discussion

5. 2. 3. 1 Water regime and *Sphagnum* regeneration

Inoculum applied to the exposed peat slope which persisted 2 years prior to 1993, failed to regenerate largely due to desiccation. During this period, growth of *Sphagnum* was restricted to a narrow band at the peat water interface and shallow water zone. During 1993, the previously dry peat slope became permanently inundated by shallow water and *Sphagnum* subsequently grew to cover that part of the trench. This explains why in Fig 5.3, *Sphagnum* was generally recorded to the top of the trench slope. The wind direction was predominantly from the shallow end towards the deeper part of the trench. Therefore, predominance of plants at the shallow end of the trench was not a product of wind blown accumulation.

When initially applied, inoculum of all species floated on the open water. Initially it was thought possible that plants might continue to float and regenerate '*in situ*'. but, results from this experiment suggest this is unlikely to occur. Within 24 hours, all inoculum sank to the trench bottom. Subsequently, regeneration of all species largely failed in the deep water zone. It is likely that at depth, low availability of light and dissolved gases severely limited regeneration. Brown remains of all *Sphagnum* species were retrievable from the bottom of the trenches.

This warns against construction of deep lagoons in cut over areas. However, at Banks Head Moss in Fife (refer to Chapter 2) *Sphagnum* rafts have developed over water 5 m deep. Similarly at Killaun Bog rafts were developed over one metre depth. In these deep water situations, colonisation may occur slowly by centripetal invasion from the pool edges. In this way plants stay supported at the water surface. At Killaun and

Banks Head Moss, colonisation was probably encouraged by the small area of the peat pits. Small pits limit wave action and provide a greater pool edge : area ratio for centripetal invasion. In the experimental trenches, some clumps of plants were observed floating in deeper water anchored to the trench periphery. In the future, it is possible that these 'nuclei' and the existing rafts developed in shallow water, will expand to colonise deeper parts of the trenches.

The only species which successfully regenerated i.e. *S. recurvum, S. cuspidatum* and *S. auriculatum* are all species known to occupy aquatic habitats, often being associated with pools in undisturbed bogs where they may form floating rafts (1.5). Similarly, in this experiment growth of these species occurred in the form of floating rafts to water depths up to 50 cm. Those species which showed poor or no regeneration i.e. *Sphagnum papillosum, S. magellanicum, S. palustre, S. fimbriatum* and *S. capillifolium,* were all species normally associated with lawns and hummocks in undisturbed bogs. The reason these latter species failed to regenerate at the peat-water interface or in the shallow water zone is not clear. One possible explanation would be is a difference in productivity between hummock and pool species in the pool environment. Hummock species are not averse to shallow inundation but growth of pool species is much more prolific (1.6.2). The peat-water interface and shallow water zone was not static in the trenches during the experiment. Fig 5.1 shows how the water table was prone to fluctuation until 1993. During this time, inoculum on the peat slope was prone to periodic drought and inundation. The relatively high productivity of the aquatic species could mean they were more able to compete against the difficult starting conditions and get established whilst the lower productivity of hummock species may have rendered them unable to get a 'foot hold'. Furthermore, a faster growth rate would enable aquatic species to 'escape' smothering by loose peat sediments. Hummock species were frequently observed coated in peat. Rain splash may also have caused further disturbance and loss of inoculum into the soft peat surface.

5. 2. 3. 2 Effect of brushwood

Brushwood added to the flooded part of the trenches temporarily floated and then sank to the trench bottom. Consequently, any potential benefit of brushwood to act as a climbing frame or reduce wave action in deeper water was lost. Therefore, results from this experiment are inconclusive as to whether physical support may or may not assist *Sphagnum* regeneration. The brushwood in the shallow water may eventually exert an influence on *Sphagnum* growth, but this was not sufficient at the time of measurement to demonstrate this.

5. 2. 3. 3 Influence of water quality

Results for water quality must be treated with caution as the data were part of a larger data set for the Crowle study area and results for individual trenches have only a small sample size. Furthermore, the survey period represents only the first year of the experiment duration and may not be representative of water quality over three years. Therefore, these results can only be considered to give a crude indication of water quality. Despite this, the data suggest that over three years there was no significant gradient of pH or conductivity across the STB trenches. However, ion concentrations for the first year suggest significant trends of increasing Ca and Fe and decreasing NO_3 and NH_4-N from STB 16 to STB 1. It is possible that the balance of these two trends explains why overall conductivity did not significantly differ. However, whether these trends persisted beyond the first year is not known. There is no clear evidence that addition of brushwood significantly altered water chemistry. If this were so one would have expected concentration of N, P and K plus overall conductivity to be significantly higher in STB 1 and STB 5 but this was not the case (Fig 5.3).

High calcium and iron concentrations in STB 1 were recorded prior to addition of brushwood (June and December 1990) as well as afterwards, therefore, enrichment by brushwood cannot be considered responsible. Furthermore, the same trend of increasing Ca and Fe concentration towards the western limit of the Crowle trenches was recorded in neighbouring STA trenches in which *Sphagnum* for experiments was stored without any additions of brushwood (Fig 1.4). The reason for this gradient remains unclear. The western edge of the Crowle experimental area appeared to be a zone of water accumulation and ground around trenches STB 1 and STA 1 was frequently inundated (Fig 5.1). The low NO_3 and NH_4-N concentrations recorded in STB 1 may reflect lower mineralisation rates in wetter less aerobic conditions. Alternatively, larger amounts of N may have been incorporated into algal biomass which was particularly prolific in trenches STB 1 and STB 2 (Table 5-2). This is considered in more detail below.

Any variation in trench water quality did not appear to influence *Sphagnum* growth significantly . From Fig 5.1 it might be suggested that growth of *S. recurvum* and *S. cuspidatum* was less in STB 1 and STB 2 compared with STB 9 and 10 respectively but this is more likely to be an effect of interaction with algae (see below). Perhaps most importantly, evidence discussed in Chapter 4 suggests that there was no feature of water quality in the STB trenches that could be considered severely detrimental to *Sphagnum* growth and which would explain the observed failure of lawn and hummock species to regenerate (Chapter 4). However, it is possible that regeneration of these species would have been increased by addition of phosphorus (4.4).

Growth of algae was noticeably greater in trenches STB 1 - STB 8 after addition of brushwood. This suggests that brushwood did have some eutrophicating effect. However, this effect was only temporary except for in trenches STB 1 and STB 2 which remained persistently over-grown by filamentous green algae (*Oedogonium* sp.) throughout the duration of the experiment (Table 5-2). This was unlikely to be an effect of brushwood as a similar trend existed in neighbouring STA trenches which did not contain brushwood. The reason may be related to the high water table recorded around those trenches. Frequently, there was direct contact between water in the trenches and water lying between hummocks of *Molinia* in the surrounding flooded ground. This water appeared to be enriched by decomposition of the *Molinia* litter and was generally infested with algae.

5. 3 Sphagnum *regeneration from fragments (Experiment 7)*

This experiment was designed to complement Experiment 6. The growth of lateral buds (or innovations) in *Sphagnum* can be stimulated by removal of the capitulum (Clymo & Hayward, 1982; Clymo & Duckett, 1986; Jones, 1978). This suggests that suppression of lateral buds in *Sphagnum* is similar to that seen in vascular plants which is controlled by the apex itself and that regeneration of inoculum in the field might also be stimulated by decapitation. The aim of this experiment was to investigate the propensity for *Sphagnum* to regenerate from fragments in the field and compare regeneration from fragments with regeneration from whole plants seen in Experiment 6.

5. 3. 1 Method

Trenches STA 12 - STA 15 were used in this experiment (Fig 1.4). Design of the trenches was exactly the same as neighbouring STB trenches used in Experiment 6. The experiment was conducted using *S. cuspidatum* and *S. recurvum*. The rationale behind this choice of species was that they were both species which showed successful regeneration in Experiment 6 and therefore were most likely to grow successfully in this experiment. It would have been desirable to also use *S. auriculatum* but this was limited by availability of trenches.

Plants of *S. cuspidatum* and *S. recurvum* were shredded in a household food blender and the resultant mulch diluted to form a thin 'slurry' in which capitula remains and fragments of stem up to 0.5 cm long remained visible. The 'slurry' was then dispensed using a watering can (without the rose !) along the length of the trenches which were assigned as shown below:

Trench	**Species**	**Treatment**
STA 12	*S. recurvum*	Fragments
STA 13	*S. recurvum*	Fragments + Brushwood
STA 14	*S. cuspidatum*	Fragments
STA 15	*S. cuspidatum*	Fragments + Brushwood

Each trench was inoculated with approximately 5 kg spun wet weight of fragmented *Sphagnum,* approximately half (maximum) the quantities used in Experiment 6. Brushwood was placed in the flooded part of certain trenches (see above) to investigate whether physical support might assist growth. Inocula were applied in March 1991 and growth was recorded in December 1993 as detailed in Experiment 6. Water table fluctuations were recorded bimonthly in each trench as for Experiment 6. Water chemistry in the trenches was only recorded only after a single sampling event in July 1991. Therefore, results give only a crude indication of water quality and must be treated with caution. Methods of analysis are detailed in Table 4-1.

5. 3. 2 Results

5. 3. 2. 1 Water table

Water table fluctuations in the experimental trenches are shown in Fig 5.4. Overall, shifts in position of the peat water interface were confined to the upper 7m of the peat slope and on average, 2 - 4 m of peat remained exposed. Unlike the STB trenches in Experiment 6 (Fig 5.1 and Fig 5.2), a minimum of 2 m of the peat slope was exposed throughout the duration of the study.

5. 3. 2. 2 Water quality

The mean concentration of major ions and mean values for pH and conductivity are given in Table 5-4. Conductivity values were corrected for pH (Golterman, Clymo & Ohnstad, 1978). Results suggest that water quality amongst the trenches was very similar. Concentrations were similar to those recorded for the neighbouring STB trenches (Table 5-3).

Fig 5-4 : Water quality of trenches used in Experiment 7 [Mean values and standard errors (in parenthesis) are presented based on 5 replicate samples from a single sampling event in July 1991. Units of conductivity = $\mu S\ cm^{-1}$. All other units = $mg\ l^{-1}$ except SRP which = $\mu g\ l^{-1}$]

	STA 12	STA 13	STA 14	STA 15
pH	3.5 (0.055)	3.5 (0.067)	3.6 (0.058)	3.6 (0.071)
Corrected Conductivity	155.8 (15.30)	179.2 (12.93)	159.5 (14.22)	161.4 (11.67)
NO_3	0.87 (0.239)	1.31 (0.624)	.90 (0.299)	0.96 (0.438)
NH_4-N	5.3 (0.221)	5.74 (0.140)	5.32 (0.172)	5.36 (0.140)
SRP	28.0 (3.0)	21.0 (2.0)	26.0 (3.0)	21.0 (2.0)
SO_4	48.12 (0.984)	45.72 (0.373)	45.30 (0.835)	49.52 (0.708)
Ca	5.48 (0.073)	5.7 (0.095)	5.42 (0.08)	5.54 (0.068)
K	1.36 (0.04)	1.36 (0.024)	1.46 (0.147)	1.76 (0.412)
Fe	3.78 (0.037)	3.9 (0.055)	4.08 (0.039)	4.22 (0.049)

5. 3. 2. 3 *Sphagnum* growth

Sphagnum fragments sank to the bottom of the trenches soon after they were applied. Regenerative success of fragments along the length of each trench is recorded in Table 5-5. Results are illustrated in Fig 5-4. Regeneration of ***S. cuspidatum*** (STA 14 and STA 15) was extremely limited over the top 2 - 3 m of the peat slope. This corresponded with the area of peat slope which remained above the peat-water interface throughout the experiment (Fig 5-4). Some regeneration occurred from inoculum lying in cracks in the peat but in general only desiccated remains of inoculum were evident. Growth was most prolific 3 - 4 m along the trench, forming a continuous carpet at the average position of the peat-water interface. As in Experiment 6, this distribution could not be explained by prevailing wind direction.

Below the peat-water interface, prolific regeneration continued forming a continuous floating raft. In STA 15 this extended to 9.5 m along the trench. At this point water depth reached 70 cm. Regeneration was evident up to 13 m along the trench (water depth = 90 cm) but here growth was subsurface and sparse. Trench STA 14 showed a similar pattern of growth. Capitulum density was slightly higher at the peat-water interface but the floating raft only extended to 9 m (water depth = 60 cm). Poorer subsurface regeneration was observed to 11m along the trench and a maximum water depth of 80 cm. In both STA 15 and STA 14 floating rafts had developed at the deepest end of the trench (15.5 - 16 m, water depth 100 cm). This growth came from groups of plants dislodged from the shallow end of the trench and blown to the deep end where they became anchored to the edge of the trench and were thus supported at the water surface.

S. recurvum (STA 13 and STA 12) showed similar patterns of growth to *S. cuspidatum*. Inoculum largely failed to regenerate on the exposed peat slope but prolific regeneration occurred at the peat-water interface. At this point capitulum density in *S. recurvum* was generally higher than that of *S. cuspidatum* but there was no difference in overall cover, so that *S. recurvum* was characterised by a larger number of small capitula and *S. cuspidatum* by a smaller number of larger capitula. Below the peat water interface *S. recurvum* also showed potential for floating raft development. In STA 13 the raft extended to 7m (maximum water depth = 45 cm). In STA 12 the raft extended to 8 m (maximum water depth = 40 cm) and poorer subsurface regeneration was observed to 10 m (maximum water depth = 55 cm). In both trenches some peripheral regeneration was observed in deeper water from plants anchored to the trench periphery.

Table 5-5 : Regeneration of *Sphagnum* from fragments applied to trenches STA 15 to STA 12 (Expt. 7)
[Results describe *Sphagnum* cover 2 yrs 9 mths after inoculation. Results are presented graphically in Fig 5.4] **Water Depth :** ' - ' Below surface, ' + ' Above surface. **Cover** - distances refer to position along trench. 0 = top of peat slope (refer to Fig 5.4)

Trench	Species	Cover	Growth form	Water depth
STA 15	*S. cuspidatum*	0 to 1m - no cover		- 25 to -15 cm
		1 to 2 m - sparse. < 4 Capitula per 100 cm^2	Isolated capitula growing close to the peat surface, particularly from within cracks in the peat .	-15 to 0 cm
		2 - 3 m - Discontinuous at 5 - 10 capitula per 100 cm^2.	Clumps of plants floating in a few cm of water but prone to periodic drought.	0 to + 10 cm
		3 to 9.5 m - Continuous cover steadily decreasing in capitulum density along trench from 35 per 10 cm^2 at 3 m to 5 - 10 per 100 cm^2 at 9.5 m	Floating raft at the water surface	+ 10 to + 70 cm
		9.5 to 13 m - sparse at 5 capitula per 100 cm^2	Clumps of plants suspended subsurface.	+ 70 to + 90 cm
		13 to 15.5 m - No growth		
		15.5 to 16 m - Continuous cover. Capitulum density 15 per 100 cm^2	Floating raft at the water surface	+ 100 cm
STA 14	*S. cuspidatum*	0 to 2 m - very sparse regeneration. < 5 capitula per 0.5 m^2	Isolated capitula growing close to the peat surface, particularly from within cracks in the peat.	- 20 to - 5 cm
		2 to 3 m - sparse. 5 capitula per 100 cm^2	Clumps of plants floating in a few cm of water and on moist peat but prone to periodic drought.	- 5 to + 7 cm
		3 to 9 m - Continuous cover steadily decreasing in capitulum density along trench from 50 per 100 cm^2 at 3 m to 10 per 100 cm^2 at 9 m.	Floating raft at the water surface	+ 5 to + 60 cm
		9 to 11 m - sparse at 5 capitula per 100 cm^2	Clumps of plants suspended subsurface.	+ 60 to + 80 cm
		11 to 15.5 m - No growth		
		15.5 to 16 m - Continuous cover. 15 capitula per 100 cm^2	Floating raft at the water surface	+ 100 cm

Table 5-5 : *Continued*

Trench	Species	Cover	Growth form	Water depth
STA 13	*S. recurvum*	0 to 1 m - No growth		- 20 to - 15 cm
		1 to 3 m - Sparse. < 5 capitula per 100 cm^2	Isolated capitula growing close to the peat surface, particularly from within cracks in the peat.	- 15 to 0 cm
		3 to 7 m - Continuous cover steadily decreasing in capitulum density along trench from 65 per 100 cm^2 at 3 m to 15 per 100 cm^2 at 7 m.	Floating raft at the water surface	0 to + 45 cm
STA 12	*S. recurvum*	0 to 1 m - No growth		- 20 to - 10cm
		1 to 2 m - Sparse. < 5 capitula per 100 cm2	Isolated capitula growing close to the peat surface, particularly from within cracks in the peat.	-10 to 0 cm
		2 to 8 m - Continuous cover steadily decreasing in capitulum density along trench from 70 per 100 cm^2 at 2 m to 15 per 100 cm^2 at 8 m.	Floating raft at the water surface	0 to + 40 cm
		8 to 10 m - Sparse. < 1 capitulum per 100 cm^2	Clumps of plants suspended subsurface.	+ 40 to + 55 cm

Fig 5.4 : Regeneration of *Sphagnum* from fragments applied to trenches in Experiment 7. [Inoculum was applied in March 1991. Results represent growth after 2 yrs 9 mths. Vertical bars show cover of *Sphagnum* along length of trench. Horizontal bars represent water table fluctuations - refer to key. Growth described in detail in Table 5-5]

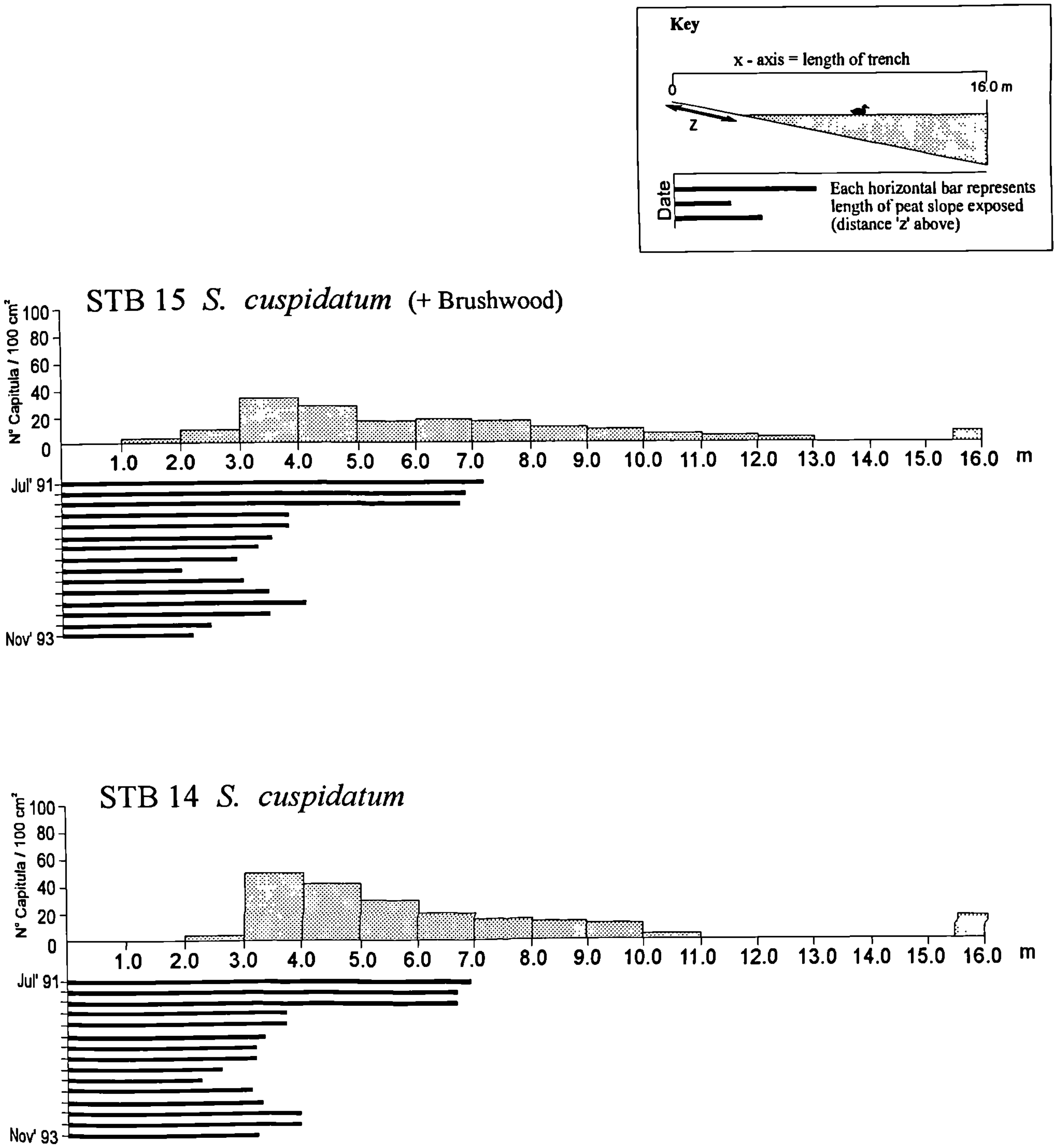
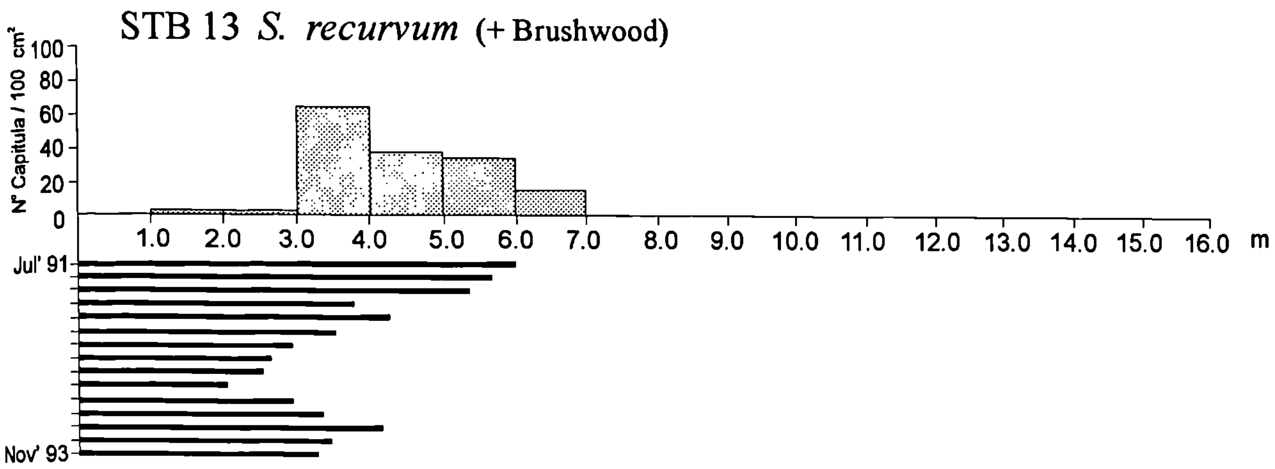
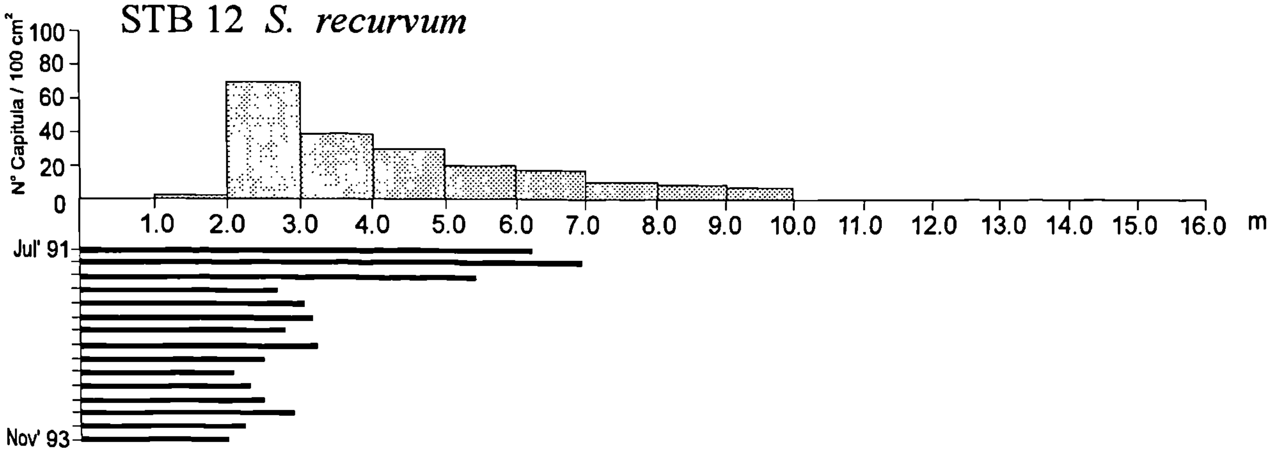


Fig 5.4 : *continued*





5. 3. 3 Discussion

5. 3. 3. 1 Water regime and *Sphagnum* regeneration

The influence of water regime on *Sphagnum* regeneration was much clearer in this experiment than in Experiment 6. The position of the peat water interface was relatively stable for the duration of the experiment and a significant length of the peat slope remained exposed. The dry conditions of the peat slope were clearly unsuitable for regeneration. Growth in all trenches was most prolific at the peat water interface in depths of water less than 10 cm. However, good regeneration was also observed in shallow water conditions (less than 50 cm deep), where floating rafts became established. Results show a clear trend of decreasing capitulum density with increasing depth. These results support evidence from Experiment 6 that deep water conditions (>50 cm deep) limit regeneration from inoculum.

These results represent growth after approximately three years and regeneration is likely to continue into the future. However, there was no evidence of any growth even at the base of the water column in deeper water (> 70 cm) (Table 5-5). It seems reasonable to infer that inoculum applied to these areas completely failed to regenerate and is unlikely to do so in the future. This does not imply that deep water in the trenches will remain uncolonised but that growth is unlikely to come from *in situ* regeneration of inoculum lying at the trench bottom. Instead, deep water is more likely to become colonised by lateral spread of existing *Sphagnum* rafts at the shallow end of the trench. In this way, new growth is supported by neighbouring plants which themselves are supported by the pool edge. Furthermore, it is possible that in an established raft, a build up of entrapped gases helps to provide buoyancy. Natural colonisation of deep abandoned peat pits or drains is frequently observed to occur by centripetal colonisation from the edges. In all trenches (as in Experiment 6), small 'clumps' of *Sphagnum* were observed floating at the trench periphery in deeper water. In the future these may represent the 'nuclei' from which centripetal colonisation takes place. Future monitoring of these trenches would be valuable.

Overall, growth of *S. cuspidatum* was more prolific than *S. recurvum*, with the former colonising deeper conditions (Table 5-5). However, this is not clear in Fig 5.4 when comparing trenches STA 14 and STA 12, as *Sphagnum* cover appears to be similar for both species. This incongruity is due to slight differences in slope of the trenches created during their excavation. In STA 12, a floating raft was observed up to 8m along the trench with further subsurface growth up to 10 m and water depth at these points was only **40** and **55 cm** respectively. However, in STA 14, a floating raft was observed to a similar length along the trench (9m) with further subsurface growth up to 11 m but water depth at these points was greater at **60** and **80 cm** respectively (Table 5-5).

5. 3. 3. 2 Effect of brushwood

By April 1992, 1 year after the experiment was set up, trenches STA 15 and STA 13 showed markedly less regeneration than their counterparts. Furthermore, they were characterised by prolific algal growth, especially the green filamentous *Oedogonium* spp. Numerous workers have observed a detrimental effect of algae on *Sphagnum* growth in both laboratory and field conditions (Boatman, 1983; Baker & Boatman, 1985; Goode, 1970; Jones, 1978; Rudolph & Voigt, 1986; Skene, 1915; Slater, 1986/87). Whether this is an allelopathic effect or just an effect of smothering is not known, but addition of brushwood appeared to have some detrimental effect upon *Sphagnum* regeneration. Water quality data from July 1991 (3 months after the experiment was set up) does not indicate nutrient enrichment in trenches STA 15 and STA 13 (Table 5-5). It is possible there was a delayed or slow release of nutrients or else a release of complex organics that were not detected, or perhaps most importantly, this highlights the difficulty of interpreting data from 'spot' samples of water quality.

By April 1993 a recovery of *Sphagnum* had occurred in trenches STA 15 and STA 13 and the proliferation of algae was not recurrent. These observations agree with those in Experiment 6 that eutrophication from brushwood does not appear to be long term. At the time growth was recorded (December 1993), cover of *S. cuspidatum* was similar to its non-brushwood counterpart STA 14. However, as is evident in Fig 5.4, recovery in *S. recurvum* was not as complete. This is not surprising as *S. recurvum* was notably slower to regenerate than *S. cuspidatum* over the first 2 years of the experiment and appeared to be generally less productive (see above).

As with Experiment 6, brushwood added to deep water sank to the bottom of the trenches, and the intended effect of providing structural support at the water surface was not achieved. Furthermore, in shallow water no effect of brushwood was observed though this may be because of insufficient time for any effect to be realised. It remains possible that brushwood will act as a climbing frame encouraging upward growth of the *Sphagnum* layer in the future, but further monitoring is required. In STA 15 there was some indication that brushwood lying subsurface had encouraged raft development in *S. cuspidatum* over a greater length of the trench than in STA 14 (Fig 5.4). In *S. recurvum* any such benefit to date will have been masked by the earlier effects of algal growth. Clearly, care must be taken in making such comparisons when growth is not markedly different. An effect may become more apparent in the future, therefore, further monitoring is required.

5. 3. 3. 3 *Sphagnum* fragments vs whole plants

Comparison of Fig 5.4 with Fig 5.1 suggests that regeneration from fragments was far more prolific than regeneration from whole plants. Fragments grew to cover a much greater length of the trenches using less than half the volume of starting material. Comparison of water quality data in Table 5-4 and Table 5-1 suggests there were no major differences in water quality that might account for this, which is not surprising as STA and STB trenches were the same design, directly adjacent and dug into the same substrate. It seems reasonable to infer from these results that vegetative growth of *S. cuspidatum and S. recurvum* was stimulated by decapitation under these conditions and inoculating pools with fragments of these species would be a more effective way of encouraging colonisation than using whole plants.

Chapter 6

General Discussion

6. 1. *Spontaneous revegetation of peat cuttings*

Evidence presented in Chapter 2 suggests that an actively growing *Sphagnum* cover will not necessarily return spontaneously to an intensively cut-over peatland without some intervention. In general, re-establishment of *Sphagnum* at cut-over sites in the UK has been poor. Among the sites visited, water regime appeared to be the primary factor limiting *Sphagnum* regrowth and frequently, conditions in cut-over areas were too dry and the most widespread communities to have recolonised them resembled dry heath vegetation characterised by the growth of ericaceous shrubs, *Betula* spp and *Molinia*. Water regime at the surface of cuttings was strongly influenced by the residual topography of the peat. Upstanding peat baulks often remained dry while 'basin-like' cuttings and ditches harboured wetter conditions. However, even cuttings may exhibit conditions similar to baulks where drainage remains effective.

Good-quality raised bog vegetation was observed to have recolonised peat cuttings in some locations, as represented by the *Erica tetralix - Sphagnum papillosum* community (Table 2-2). Generally, this occurred in cuttings at the fringes of less extensively damaged sites where bog vegetation in the form of floating mats had colonised flooded peat pits. Such vegetation closely mirrored that of undisturbed bog and would be considered a very desirable endpoint to restoration (1.5). This observation alone is of significance because it suggests that that it is possible for raised bog vegetation to recolonise cut-over areas if given the right conditions.

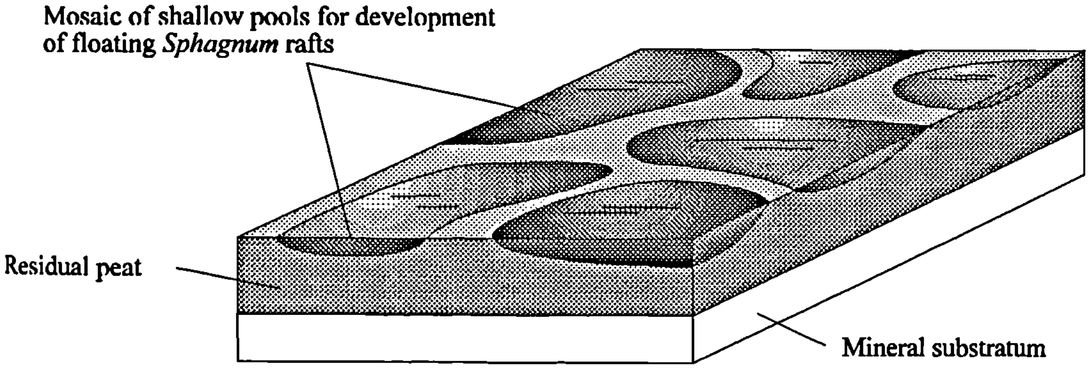
6.2 *Hydrological conditions required for restoration - a case for rafting.*

Among the peat cuttings surveyed, most retained functional drainage ditches which would account to some extent, for the predominantly dry conditions observed. Clearly an early priority for any restoration strategy must be to obstruct such drainage (1.8). However, evidence discussed in Chapter 3 suggests that in intensively cut-over areas, ditch blocking alone may not be sufficient to restore surface wet conditions. Despite blocked ditches the water-table may remain highly unstable leading to long periods of surface drought during the summer months. Fundamental differences exist in the hydrophysical properties of catotelm peat and the living acrotelm layer of an undisturbed bog. Water storage capacity of the catotelm peat surface left after peat winning is much lower than that of an acrotelm; hence the surface of a cut-over system does not retain sufficient water to prevent drought (3.1.4).

Although Thorne Moors is a relatively low rainfall site, evidence exists that water-table fluctuations are a commun characteristic of intensively harvested bogs in a range of climatic regimes (3.1.3). It would be of great value to set up monitoring programs at sites elsewhere in the UK to obtain comparative data. Results from Experiment 1 (3.2) demonstrate that water-table fluctuations less extreme than those recorded for the Creykes milled-peat field at Thorne Moors can severely limit *Sphagnum* regeneration. This raises concern over what real opportunities there are for restoring *Sphagnum* dominated vegetation to milled peat fields under such environmental constraints.

Evidence from workers on the Continent suggests that water-table fluctuations may be limited by increasing water storage on the cut-over surface. This can be achieved by reconfiguration of the peat surface to produce a series of pools (3.2.4). Evidence from this study suggests that open water does not preclude *Sphagnum* regeneration. In fact the best examples of recolonisation by raised bog vegetation were observed to be floating rafts which remain perennially wet, suppressing the growth of heathland species (see above). Hence, pools created on a milled bog surface can be seen to serve two functions. Firstly, they increase surface water storage and reduced water-table fluctuation (especially low summer water-table). Secondly, pools provide conditions suitable for the hydroseral development of *Sphagnum* vegetation in the form of floating mats. Thus, cut-over surfaces can be engineered to support a mosaic of *Sphagnum* hydroseres (Fig 6.1). It may be expected that, in time, as the pools become in-filled with fresh peat, a series of 'miniature raised bogs' will develop over a site which may grow out beyond the perimeter of their original pools and ultimately coalesce. By this time a sufficient acrotelm layer will have developed for the system to become self regulating and open water will no longer be essential for sustaining surface wet conditions.

Fig 6.1 Pool system for the restoration of bog vegetation to cut-over peat fields.



6.3 *Open Water - an obligate requirement ?*

Despite the potential benefits of rafting, results of the vegetation survey show there were many instances where spontaneous *Sphagnum* regeneration was observed on solid peat (2.2.3). Development of *Sphagnum* dominated vegetation is favoured by perennially wet conditions and although rafts clearly provide this, *Sphagnum* colonisation should be equally successful if a permanently wet peat surface can be provided.

Kuntze & Eggelsmann (1981) indicate that restoration in NW Germany is aimed at establishment of bog vegetation on constantly moist surfaces rather than open water . Great emphasis is placed on the need for a layer of 'top spit' (or 'Bunkerde') to be placed on the peat surface after extraction to improve its hydrophysical characteristics. 'Bunkerde' is a German term for the surface layer of vegetation and peat which is removed prior to peat cutting. Placing a layer of 'Bunkerde' over residual dark peat is thought to improve conditions for recolonisation by bog species. It is able to float during periods of inundation and in periods of drought it is supposed to limit water-table fluctuations by storing large amounts of water (Eggelsmann, 1987) - essentially it acts as an artificial acrotelm. However, clear evidence that 'Bunkerde' actually has a positive effect is generally lacking. Furthermore, in the UK any possible benefits of 'Bunkerde' are largely irrelevant as no measures have been taken to store surface layers.

Communities dominated by *Sphagnum* were very rarely observed growing directly on solid peat. This suggests that cut peat surfaces rarely provide sufficiently wet conditions. More frequently *Sphagnum* growth occurred in combination with an abundance of heathland plants such as *Calluna vulgaris, Molinia caerulea* and *Eriophorum vaginatum,* and the resultant vegetation resembled wet heath rather than undisturbed bog (2.2.3).

There is some evidence that *Sphagnum* growth benefits from the improved microclimate provided by a cover of vascular plants (2.2.3). Buttler, Grosvernier & Matthey (*in prep*) suggest that this provides a mechanism for establishment of *Sphagnum* in cut-over areas which exhibit a low water-table. This would remove the need for a rafting strategy and suggests that cut-over areas are ultimately self restoring. However, critical evidence that this succession takes place is lacking and in many UK situations, the general absence of any such trends indicates it may have limited relevence. Therefore, the fate of wet heath communities in abandoned peat workings remains debatable. Whilst it is possible *Sphagnum* may grow to dominate wet heath it remains equally possible, particularly in drier locations, that vegetation will remain wet heath for the foreseeable future. Evidence from the vegetation survey shows that many examples of dry heath vegetation on peat exist where a cover of *Molinia* or *Calluna* has not facilitated any *Sphagnum* regeneration. Furthermore much of the wet heath vegetation has persisted as such for at least 50 - 100 yrs.

It seems likely that just allowing milled peat fields to recolonise with heath species may result in development of dry heath devoid of *Sphagnum* or wet heath containing some *Sphagnum* (dependent on site specific water regimes). The latter community will be finely balanced and susceptible to temporal changes in climate. For example, a few years of below average rainfall may cause an increase in abundance of 'dry' species, invasion by scrub and increased susceptibility to fire. If a dense cover of *Molinia* becomes established then evapotranspirative losses can exacerbate water-table fluctuations and further dry out the system (3.1.4)

Although conditions may vary amongst sites, evidence from this study suggests that maintenance of wet conditions at the surface of abandoned peat fields will prove extremely difficult without the excavation of pools. Conditions must be kept sufficiently wet all year round to encourage *Sphagnum* regeneration and discriminate against 'undesirable species'. It is possible that surface inundation will be unnecessary in some high rainfall locations but at low rainfall sites such as Thorne Moors it is probable that a hydroseral approach to restoration may be necessary.

6.4 *Problems with rafting*

6. 4. 1 Guanotrophication

For bogs in NW Germany, Blankenburg & Kuntze (1986) warn that the creation of 'free water sheets' must be prevented if possible as they may attract birds with concomitant problems of guanotrophication. It is difficult to evaluate to what extent this is likely be a universal problem. At Cors Caron in Wales, peripheral cuttings dominated by *Molinia* have been inundated by construction of a peat bund. It was evident on visiting the site that the open water attracted large numbers of gulls and the discoloured peat bulks were suggestive of significant faecal inputs! However, many large reflooded cuttings have not proved to be attractive to birds, and workers in the Netherlands, who have created large inundated sites, seem unconcerned about the matter (Wheeler, *pers comm.*). Furthermore, there is some evidence that bog vegetation can develop over stands of *Juncus effusus* which characterise sites of former gull colonies (Baaijens, 1984 *cit* Joosten & Bakker, 1987) so guanotrophication may not ultimately prevent bog regeneration. The precise conditions which may encourage birds have yet to be established.

6. 4. 2 Pool size and wave action

The creation of ponds has also been discouraged on account of the fact that floating vegetation can be significantly disturbed or even prevented by wave action (Egglesmann, 1988a). Joosten (1992) also warns that inundation may lead to the development of lakes of black water in which no floating bog mats come into being. Any problems of wave action can be reduced by creating a large number of small pools

(3.2.4). Small pools also provide a greater length of pool edge per unit area of open water which may encourage recolonisation particularly by centripetal growth from the pool edges. The density of pools will be limited by the practicalities of reconfiguring a mire surface, something which has yet to be determined. Evidence from Experiment 6 and 7 (Chapter 5) suggests that shallow pools are likely to recolonise most rapidly but minimum pool depth will be limited by their susceptibility to drying out.

Therefore, whilst a complex network of small, shallow pools would be the ideal the extent to which it can be realised will depend on site specific conditions (3.2.4). Large sheets of free water do not necessarily preclude formation of *Sphagnum* rafts. Colonisation by floating mats of *Sphagnum cuspidatum* have been observed in large inundated areas such as the flooded peat fields at Amsterdamsche veld in the Bargerveen Reserve, Netherlands (Wheeler *pers comm*). Colonisation may be particularly prolific where conditions remain shallow, for example at Peatlands Park, Belfast, where *S. cuspidatum* was observed to have colonised a shallow pond, 10 ha in area and 30 - 40cm deep.

Despite the possible problems associated with rafting, it offers a strategy for restoring bog vegetation to intensively cut-over areas which have a water regime too unstable to permit recolonisation by *Sphagnum* directly onto the peat surface. There is agreement from some workers in the Netherlands that development of floating rafts may be the only effective way of re-establishing bog vegetation. Schouwenaars & Vink (1992) suggest that for areas which have been colonised by *Molinia*, the only potential for regrowth of *Sphagnum* is by complete inundation. Furthermore, Schouwenaars (1992) concludes that the residual peat surface of most bog relics in the Netherlands is not suited to direct establishment of a *Sphagnum* vegetation. " In these areas the only practical solution seems to be the creation of permanently inundated sites where floating mats of *Sphagnum* spp are able to fluctuate with the water level and permanently water-logging of the *Sphagnum* layer is guaranteed".

6.5 *Hydrochemical conditions and* Sphagnum *growth*

6. 5. 1 pH

Results from Experiment 4 suggest that the low pH values recorded at Thorne, particularly in the milled peat field are sub-optimal for the growth of *Sphagnum* (4.3). However, in Experiment 5, addition of lime to pools in the field was unsuccessful in both sustaining an increase in pH and in increasing *Sphagnum* growth (4.4). In fact, overall, lime could be said to have had a detrimental effect on growth. In simple field trials an attempt was made to elevate the pH of water in experimental pits at Creykes using alternative agents i.e. 1 M NaOH and $NaHCO_3$. They were found to produce similar pH response curves to 80 g of $CaCO_3$ (Appendix 1). Unlike lime, NaOH and $NaHCO_3$ may not be toxic to *Sphagnum*, however, they would be expensive to use. Therefore, unless a suitably cheap and effective method could be found it may simply be unrealistic to attempt to elevate the pH of abandoned peat fields.

6. 5. 2 Nutrient and base-enrichment

Evidence presented in Chapter 4 suggests that significant differences may exist between the hydrochemistry of cut-over and undisturbed bog surfaces. Water samples from cuttings at Thorne Moors were found to contain elevated concentrations of Ca^{2+}, Fe^{2+}, K^{+}, NO_3^{-}, NH_4-N and SO_4^{2-}, and exhibit lower pH. From the limited evidence available from other workers, this appears to be part of a more universal trend towards enrichment in cut-over areas (4.1.3). Such enrichment may explain the growth of-poor fen species such as *S. recurvum*, *S. fimbriatum* and *Juncus effusus* characteristic of cuttings at Thorne (2.2.3).

The source of this enrichment is not clear. Modern methods of peat extraction frequently leave only shallow depths of peat above the mineral ground introducing the possibility of basal enrichment. Whilst basal enrichment may be a feature of some sites, at Thorne Moors evidence suggests it was not an important influence on water quality in the Creykes and Crowle study areas (4.1). Atmospheric pollution may have contributed to the high S and N concentrations recorded but its significance is not known (4.1.3.1). NH_4-N, NO_3 and SO_4 concentrations were significantly higher at the Creykes study area than at Crowle (4.1) suggesting factors other than pollution may also have influenced the results. Firstly, the vegetation cover present may have lowered S and N concentrations at the Crowle area. Secondly, more recent and severe disturbance by peat cutting may have caused higher S and N concentrations (through mineralisation) at the Creykes area. (4.1.3.1).

6. 5. 2. 1 Implications of nutrient enrichment for *Sphagnum* growth.

The fear is often expressed among workers in the field that chemical enrichment will encourage growth of poor fen species. Whilst this may be so, there is considerable evidence to suggests that mild enrichment is not be directly detrimental to plant species typical of raised bog and that it may even stimulate their growth. Boatman (1977) transplanted shoots of *S. cuspidatum* from weakly minerotrophic pools in the lagg zone of a bog to ombrotrophic pools on the bog's surface. He found that, initially, they contained more tissue N, K and Mg than shoots in the bog pools, and they produced more extensional growth and more innovations. In solution culture experiments on *S. cuspidatum,* Baker & Boatman (1990) found greatest innovation frequency and growth (in weight) at concentrations of N, P and K far in excess of those recorded in ombrotrophic bog waters. Similar results were obtained for a range of species by Baker & Macklon (1987). A number of sites in north Cheshire, exhibit overgrowth of open water by *S. recurvum* rafts which support numerous plant species normally associated with ombrotrophic bog. Water samples from these *Sphagnum* rafts differ little in pH from truly ombrogenous sites, but have higher total cation concentration (particularly with respect to K^+) (Tallis, 1973). Finally, conductivity measurements shown in Table 2-2 indicate that mild enrichment occurred in some cuttings which were observed to support a desirable raised bog vegetation (2.2.3). Therefore, modest nutrient enrichment is not necessarily prohibitive to restoration.

6. 5. 2. 2 Nutrient enrichment and *Sphagnum* spore regeneration

Regeneration from spores is potentially an important process for recolonisation of damaged peatland as it would enable long distance inoculation of areas devoid of a local source of propagules. However, the contribution made by sexual reproduction in *Sphagnum* is poorly understood. Boatman & Lark (1971) found that protonemata of *S. papillosum*, *S. magellanicum* and *S. cuspidatum* would not develop in the nutrient regime of oligotrophic mire pools unless concentrations of phosphorus were raised to artificially high levels. *S. palustre* has also been observed to regenerate successfully from spores on agar though growth was much slower than from vegetative reproduction (Sabotka, 1976).

In order to obtain plants free from algal contamination, methods now exist for routinely growing *Sphagnum* from protonemata on mineral enriched agar (Baker & Boatman, 1985). However, under nutrient poor conditions in the field, it would appear regeneration from spores is less important than vegetative reproduction. Despite this, certain species do fruit frequently e.g. *S. fimbriatum*. Clymo & Duckett (1986) suggest that some of the green shoots observed to grow on discs of peat arose from unattached protonemata thought to have originated from spores. If this is the case, then it suggests protonemata can develop given no more than light, air, and whatever inorganic or organic solutes are available in newly formed peat. However, regeneration was not observed in peat from depths greater than 30cm. Therefore, such spontaneous growth cannot necessarily be expected in deeper peats left after extraction.

Long distance dispersal of viable diaspores must take place in order for *Sphagnum* to spontaneously colonise in remote locations. Andreas & Host (1983) recount colonisation of the wet floor of an abandoned sandstone quarry which was excavated between 1911 and the mid 1940's. Since then, an extensive bog mat some 0.75 km in diameter has developed supporting *Sphagnum teres, S. recurvum, S. capillifolium, S. fuscum* and *S. magellanicum*. This suggests that *Sphagnum* is able to disperse over considerable distances, the nearest extant bog being 14 km away.

It is possible that regeneration from diaspores at Andreas & Host's site was encouraged by the weakly minerotrophic conditions in the quarry. *Sphagnum* colonisation is also frequently observed in remote fen systems (6.5). This suggestion would agree with laboratory observations (see above) that regeneration from spores is only possible under mineral enriched conditions. In fact, rarely in nature does *Sphagnum* vegetation *initially* colonise under ombrotrophic conditions. Ombrotrophic conditions are a natural consequence of growth of the *Sphagnum* layer and peat accumulation and as a bog grows upwards and conditions become ombrotrophic, so the environment may become less favourable for regeneration from spores. This may explain why in bog vegetation the primary method of *Sphagnum* regeneration is vegetative.

If this hypothesis is correct, then it would be unreasonable to expect *Sphagnum* regeneration from spores in abandoned peat fields as these represent conditions nearer to ombrotrophy than minerotrophy. Evidence presented in Chapter 4 suggests that cut-over bogs are characteristically nutrient enriched compared to undisturbed bog which would be expected to encourage spore regeneration. However, phosphorus concentration was not enriched, thus spore regeneration may still be limited. Notably, phosphorus was an element suggested by Boatman & Lark (1971) to be critical in spore regeneration (see above).

6.5.2.3. The importance of phosphorus to *Sphagnum* recolonisation

Despite the general level of enrichment recorded at Thorne, concentrations of phosphorus were very small as in undisturbed systems (4.1.2). In Experiment 5, modest additions of phosphorus in the field were found to significantly increase productivity of *S. cuspidatum* and *S. recurvum* in pools, confirming the inferences of other workers that concentrations of P in ombrotrophic waters are sub-optimal for *Sphagnum* growth (4.4). In attempts to restore cut-over areas it may therefore be possible to encourage *Sphagnum* recolonisation by fertilising with phosphorus.

Further work is required to investigate fully the potential growth response of *Sphagnum* in the field to a range of phosphorus concentrations. It would be useful to know how little P is required to increase growth significantly and also to what extent growth can be promoted without promoting a change in species balance. Future investigations must also consider the effect of added phosphorus on growth of a broader range of *Sphagnum* species. Aerts *et al* (1992) found growth of *S. magellanicum* at N rich sites in southern Sweden was limited by P availability. In cut-over areas a similar scenario may exist where N concentrations are enriched, perhaps due to mineralisation (or pollution), but P concentrations remain small. Recently, Rochefort, Gautier & Lequeré (*in prep*) found growth of *S. nemoreum* on peat was increased on addition of bone meal and a slow release chemical fertiliser. Therefore, growth of numerous *Sphagnum* species in cut-over areas may benefit from additions of P. Clearly there is much scope here for further research.

6.5.2.4 Nutrient conditions, bog development and restoration.

Raised bogs are naturally low-nutrient environments (1.6.3) so it may seem inappropriate to suggest that mild enrichment may encourage *Sphagnum* growth. However, stratigraphical evidence suggests that most raised bogs may have originated from fen vegetation (refer to Section 1.1), and within present day areas of fen numerous studies have revealed development of *Sphagnum* dominated bog, ranging from small ombrotrophic nuclei to extensive ombrotrophic surfaces (Giller & Wheeler, 1988; Shaw & Wheeler, 1991; Bellamy & Reiley, 1967; Karlin & Bliss, 1984). The propensity for *Sphagnum* to 'invade' fens is considered by Lindholme & Vasander (1990), who point out that *Sphagnum papillosum* is an important coloniser of poor fen systems in Southern Finland. Furthermore, in Britain and Ireland, it has been suggested that the majority of minerotrophic mire sites have become over-run by the growth of *Sphagnum* (Goodwillie, 1980; Rodwell, 1991). Prolific growth of *Sphagnum* in fens is also documented for sites in the Netherlands, where ironically, it is viewed as a management problem in the conservation of fen vegetation (van Wirdum, 1991).

Therefore, weakly minerotrophic conditions may be the optimum nutrient regime for *Sphagnum* growth and despite the dominance of *Sphagnum* in raised bog vegetation we should not assume that ombrotrophic conditions represent an optimum for its growth. Instead, *Sphagnum* may simply be one of the few plants able to tolerate the acid, ombrotrophic conditions arising from succession from fen to bog (refer to Section 1.6.3).

In base-rich fens, growth of *Sphagnum* is generally pioneered by base-tolerant species such as *S. contortum*, *S. fimbriatum*, *S. recurvum*, *S. squarrosum*, and *S. subnitens* which are not species typical of raised bog. They do however, provide a platform for colonisation by less base-tolerant Sphagna such as *S. magellanicum* and *S. papillosum* but at the stage these latter species colonise, the chemical environment may still be enriched compared to the surface of a raised bog (Shaw & Wheeler, 1991). Base-tolerant species become pooly represented as conditions become ombrotrophic. This suggests that some *Sphagnum* species are less able to grow in ombrotrophic conditions than others. If such a gradient does exist then it may follow that ombrotrophic conditions are sub-optimal even for growth of typical raised bog species - however, this is speculative.

In an intact bog, it is possible that most of the growth-limiting nutrients are concentrated in the living *Sphagnum* layer, due to the effectiveness of *Sphagnum* and other bog species at scavenging and recycling nutrients (1.6.3). Chemical profiles for bogs are few but evidence from Damman (1978) indicates that the concentration of most elements are highest in the surface peat (0 - 35 cm depth). Similarly, chemical profiles from Flaxmere, north Cheshire, revealed that K and P concentrations were highest at the surface of recent *Sphagnum* peat (Tallis, 1973). This is partly because elements do not simply accumulate in ombrotrophic peat and most are translocated or removed to some extent (Damman, 1978) . However, Damman does provide some evidence that essential elements in short supply such as N, P and K are actively conserved by the living *Sphagnum* layer. This suggests a recycling mechanism but further study is required.

If essential nutrients are actively recycled, then, in an intact bog, new *Sphagnum* growth will benefit from nutrients salvaged from old growth. However, vegetation and surface peat is removed by peat extraction and plants colonising an abandoned peat field will not have access to such a resource. Therefore, restoration ecologists may be attempting to restore *Sphagnum* bog vegetation in conditions of lower nutrient status than bog species are naturally exposed to and it may not be inappropriate after all, to suggest that an injection of nutrients (notably P) might be required to encourage revegetation.

At the Creykes milled peat field, concentrations of some ions (notably NH_4-N, SO_4^{2-} and Ca^{2+}), reached very high concentrations. Evidence from Experiment 3 (4.2), suggests that Ca concentration at the upper limit of values recorded at Thorne may inhibit growth of some *Sphagnum* species. However, such high concentrations occurred only temporarily and on average, concentrations of Ca in the range recorded seem unlikely to be damaging (4.2.3). The effects of elevated S and N on *Sphagnum* growth have been the subject of quite intensive study (4.1.3.2), but ambiguous results in the literature make it difficult to infer what effect concentrations in the range recorded at Thorne would have on *Sphagnum* regeneration. Ultimately, the suitability of sites to support *Sphagnum* might be best assessed empirically by simple transplant experiments.

6. 6 *Inoculation of cut-over bogs with* Sphagnum

6. 6. 1 The need for inoculum

During the vegetation survey of abandoned peat cuttings (Chapter 2) it was observed that raised bog Sphagna such as *S. magellanicum*, *S. papillosum* and *S. capillifolium* had failed to recolonise in some locations despite conditions being suitably wet for growth of other Sphagna (2.2.3). This was a particular feature of the vegetation at Thorne Moors and may be due to a lack of a local propagule source (5.1). However, recolonisation at Thorne may also have been influenced by other factors besides propagule availability and these are considered in more detail below.

Very high concentrations of N and S were recorded in water samples taken from the Creykes peat field at Thorne and it is possible that these concentrations have limited *Sphagnum* recolonisation (4.1.3.2). However, whilst such high concentrations were recorded in the milling field, concentrations of S and N in the Crowle study area were not as elevated (4.1). The latter area consisted of long abandoned, revegetated cuttings which typify most of workings in the southern half of the moors. An extensive vegetation survey of the southern area (conducted as part of the broader survey described in Chapter 2) found little evidence of recolonisation by typical raised bog Sphagna. Therefore, whilst it is possible that S and N concentrations in milling fields

Thorne may hinder recolonisation, it is less obvious why recolonisation has not occurred elsewhere.

The general paucity of raised bog *Sphagnum* on Thorne may in part be a legacy of higher sulphur deposition rates in the past (4.1.3.2). In addition to the effects of enrichment, this may also explain why *S. recurvum* is a common species on Thorne as it is regarded as one of the more pollution tolerant species (Ferguson *et al*, 1978). However, *S. cuspidatum* is also a common species on Thorne despite being more sensitive to S pollution than *S. recurvum*, thus the significance of pollution to *Sphagnum* growth at Thorne remains unclear. Overall it seems unsatisfactory in explaining the current absence of some raised bog species from Thorne. This is particularly so as surplus *Sphagnum*, from material transplanted to Thorne for regeneration experiments, has survived in trenches where it has been stored. This suggests that whatever pollution inputs continue at Thorne Moors, they are not lethal.

It is possible that spores of *S. magellanicum*, *S. papillosum* and *S. capillifolium*, dispersed over long distances, reach Thorne Moors but fail to regenerate because of unsuitable chemical conditions (6.5.2.2). It would be interesting to conduct a 'seed rain' study at Thorne Moors to investigate this. *S. recurvum* and *S. cuspidatum* have colonised isolated cuttings and ditches on Thorne Moors but this may have occurred by vegetative growth from fragments dispersed by the wind or by birds and other wildlife. Where a local source of propagules persists, as it does for *S. recurvum* and *S. cuspidatum*, there would be reduced reliance on regeneration from spores.

The absence of a local propagule source is a potentially important factor limiting recolonisation by raised bog Sphagna at Thorne Moors. A milled peat field engineered to form a mosaic of pools for the development of rafts of raised bog vegetation, may take decades to become spontaneously inoculated. Potentially, the process of recolonisation could be accelerated by inoculating cut-over areas with *Sphagnum*.

6. 6. 2 *Sphagnum* regeneration from inoculum applied in the field

Experimental trenches to which *Sphagnum* was added in Experiments 6 and 7, could be seen as representing sections along the radius of a pool created on a cut-over bog surface. Growth was only observed in trenches to which *Sphagnum* was added which suggests that reintroduction significantly increases rates of recolonisation. However, only species which exhibit an aquatic habit successfully regenerated i.e. *S. recurvum, S. cuspidatum* and *S. auriculatum,* and the water regime required for successful regeneration was quite precise. Growth directly on peat above the water-table was limited by desiccation. Growth was most prolific at the peat/water interface and in shallow water up to 50 cm deep, but at depths > 50 cm regeneration largely failed. *Sphagnum* applied to open water floated temporarily but ultimately sank; hence inoculum cannot be expected to float and regenerate *'in situ'* to develop floating rafts. Instead, regeneration must come from submerged plants, and depths > 50 cm appear to severely constrain growth, probably due to low availability of light and CO_2.

Results indicate that the shallower the pool the greater the rate of recolonisation. However, the minimum pool depth that can be maintained without drying out will be dependent on the water budget of specific sites (3.2.4). *Sphagnum* regeneration may occur at depths > 50 cm where colonisation occurs largely by centripetal invasion from the pool edges (5.2.3). In the future it is likely the deeper parts of the experimental trenches will colonise in this way. However, colonisation dependent on centripetal invasion will be slower than colonisation from inoculum applied across the whole area of a pool and will be more affected by wave action, particularly in large pools (5.2.3).

The general failure of non-aquatic Sphagna to regenerate at the peat/water interface and in shallow water was initially of some concern. Conditions at the peat-water interface were highly unstable and *Sphagnum* material thrown prostrate into the trenches was prone to periodic submergence, desiccation, agitation by waves and smothering by peaty sediment. The failure of hummock and lawn forming Sphagna to regenerate may have been due to their low productivity compared with more aquatic species (5.2.3). Consequently, inoculum was unable to transcend its initially vulnerable condition to become established. Furthermore, productivity of these species may have been limited by low P availability (see above). Therefore, it must be considered how hummock and lawn forming species can be effectively introduced to pools in cut-over areas.

Observations from inundated peat pits at various stages of recolonisation suggest that raft formation follows a distinct successional pathway whereby a floating mat of aquatic *Sphagnum*, particularly *S. cuspidatum*, generally precedes colonisation by lawn and hummock forming Sphagna. Therefore, a raft of *S. cuspidatum* appears to provide a favourable template for invasion from the pool edges by species such as *S. papillosum* and *S. magellanicum* and thence by vascular species such as *Narthecium ossifragum* and *Erica tetralix*. Similar hydroseral succession has been observed in reserves of Bargerveen, Deurnse Peel, Engbertsdyksvenen and Fochterloerveen in the Netherlands (Joosten, 1992; Schouwenaars, 1982; Streefkerk & Casparie, 1989). Evidence from Experiment 6 suggests that floating rafts of aquatic Sphagna including *S. cuspidatum* can quite readily be achieved in depths of water up to 50 cm (5.2). Therefore, a viable restoration strategy might be to concentrate on establishing rafts of aquatic Sphagna in order to provide a suitable template for colonisation by lawn and hummock forming Sphagna. Furthermore, in order to assist floating mat development certain measures might be considered to accelerate raft formation:

6. 6. 3 Facilitating rafting

6. 6. 3. 1 Pool size

Experiment 6 suggests that shallow pools will colonise more rapidly but this must be balanced against the tendency for shallow pools to dry out. Furthermore, pools small in area will limit disturbance caused by wave action (refer to Section 6.4).

6. 6. 3. 2 The use of brushwood

Branches of trees such as *Betula* placed in pools may help to break up the open water reducing the effects of wave action and providing a climbing frame for *Sphagnum* growth. At Haaksbergerveen in the Netherlands, inundation of a dry bog relic led to small floating bog mats being lifted from their original pits. Rapid expansion of these mats was favoured by the suppression of wave action by dying and dead birch trees standing in the water (Joosten, 1992). In Experiments 6 and 7 brushwood added to open water sank and consequently results were inconclusive. However, there was some evidence that brushwood had assisted colonisation of deeper water in a different way by forming a layer at the pool bottom effectively reducing pool depth but little affecting water storage. Furthermore, the potential for brushwood to act as a climbing frame in shallower conditions may only become apparent in the future when *Sphagnum* regeneration has proceeded further. Consequently, future monitoring of these experiments is required. Addition of brushwood was observed to increase growth of algae, notably the filamentous *Oedogonium* sp., and inhibit *Sphagnum* growth. However this effect was short term, occurring only in the first year after birch brashings were applied (5.2 & 5.3).

6.6.3.3 'Tussock buffering'

This process requires initial colonisation by species like *Molinia, Eriophorum spp* and *Juncus effusus*. Water levels may then be elevated to inundate the area and the tussocks of vascular plants will help to reduce the effects of wave action (Joosten, 1992). This method depends on sufficient inundation being achievable and maintained to encourage *Sphagnum* growth at the expense of the tussock forming plants (Streefkerk and Casparie, 1989)

6.6.3.4 Artificial rafting

1) Peat debris

This may float to provide a permanently wet surface for *Sphagnum* growth. Peat of low humification generally floats best, as has been observed at the Bargerveen reserve in the Netherlands (Janson & Oosterveld, 1987 *cit.* Streefkerk & Casparie, 1989). However, frequently, no light *Sphagnum* peat remains after industrial peat extraction. Simple trials conducted at Thorne found that 'bricks' of basal catotelm peat failed to remain afloat. Critical evidence for the benefits of peat debris is lacking.

2) Detachment of rooting zone upon inundation

In the Bargerveen reserve floating bog mats were created accidentally (Joosten, 1992). Dry vegetation became inundated as a consequence of rewetting measures where upon the rooted layer lost purchase and rose to the water surface providing a favourable template for establishment of *Sphagnum* mosses. The significance of this process to larger scale restoration requires further study.

3) Other artificial rafts

In the latter part of this project's duration some preliminary trials were conducted in experimental trenches at Thorne Moors to test the floatation of purpose-made mats composed of biodegradable materials (Appendix 2). Early observations suggest that such mats may provide a useful tool to restoration. Mats can provide a permanently wet surface for regeneration of hummock and lawn forming species. They also increase the length of pool edge per unit area of open water for centripetal colonisation by non aquatic Sphagna. Furthermore, mats will help to break up large areas of open water reducing the effects of wave action. The potential use of these mats requires further investigation.

6. 6. 3. 5 Utilising vascular plants

Certain species such as *Menyanthes trifoliata* form skeletal rafts of rhizomes over open water. Such plants may assist *Sphagnum* raft development though their significance requires clarification. *Eriophorum angustifolium* is also frequently found growing in association with rafts of *S. cuspidatum* (2.2.2). However, this species does not appear to be innately a raft former. Simple field trials conducted at Thorne found that tillers of *E. angustifolium* placed into experimental trenches did not float and regenerate unless given the support of a netlon raft. Furthermore, turfs of *E. angustifolium* transplanted to the peat-water interface did not readily grow across open water. Therefore, *E. angustifolium* may colonise *Sphagnum* rafts and not the reverse. Even so, its growth may give more structure to a raft and the tillers may encourage upward growth of *Sphagnum* by providing a climbing frame and possibly, by creating a more conducive microclimate to *Sphagnum* growth at the raft surface (2.2.2.). At pool margins, *E. angustifolium* can colonise some distance into a pool, to water depths in the order of 30cm, remaining firmly rooted and with its leaves emerging above the water surface. Tillers breaking up the water surface may help provide a sheltered environment for *Sphagnum* growth. *E. angustifolium* is a vigorous coloniser of abandoned cuttings (Chapter 2), and may prove to be a useful tool for restoration, however, the overall role of vascular species requires further research.

6. 6. 4. Regeneration from *Sphagnum* fragments

Evidence from Experiment 7 suggests that regeneration of aquatic *Sphagnum* from fragments is far greater than regeneration from intact gametophytes (5.3). Therefore, pioneering *Sphagnum* rafts may be encouraged to develop by inoculating pools with fragments instead of whole plants. Regenerative success from fragments provides a means for using inoculum more economically and efficiently. Furthermore, 'hydro-dispersal' of fragments offers a more practical way of inoculating more extensive areas. In laboratory studies, the ability of *Sphagnum* to regenerate from fragments has been observed by numerous workers. Sabotka (1976) successfully grew *S. palustre* from fragments placed on agar, with green stems and apical branches showing the highest regenerative capability. Poschlod & Pfadenhauer (1989) achieved regeneration from fragments in nine species of *Sphagnum* including most major raised bog species. All parts of the plant were found to regenerate except leaves. More recently, Rochefort *et al* (*in prep*) obtained growth on agar from all fragments including leaves, in *S. magellanicum, S. rubellum, S. recurvum* and *S. papillosum*. Therefore, the potential exists for regenerating hummock and lawn species from fragments in the field as well as aquatic species. However, further research is required to investigate this.

6. 6. 5 Inoculation with hummock and lawn-forming Sphagna

Assuming a raft of aquatic *Sphagnum* can be successfully established, it must then be considered how hummock and lawn forming species would be introduced. Results from Experiment 6 suggest that material scattered at the pool periphery may fail to regenerate due to instability of the peat water interface (5.2.3). However, evidence from trenches at Thorne in which *Sphagnum* was stored for experiments, suggests that hummock and lawn forming species are able to survive and grow at the pool periphery where 'clumps' of material are not disaggregated. Plants in a hummock exist in a more humid, self-regulating microclimate, a property lost when hummocks are disaggregated and the component plants scattered (3.3). Furthermore, hummocks will give the component plants physical support during periods of submergence. Therefore groups of *Sphagnum* plants may be a more appropriate way of introducing species such as *S. magellanicum* and *S. papillosum* to the pool periphery. They could then be allowed to grow centripetally across an existing raft of aquatic *Sphagnum*.

In theory, a raft of aquatic *Sphagnum* should itself provide a perennially wet substrate, favourable for *direct* inoculation with hummock and lawn species. However, at Thorne an attempt was made to inoculate a *S. cuspidatum* raft with whole plants but they became displaced through the raft by heavy rain. A similar result would be expected with fragments. This would not occur if robust artificial mats were used. It would not be realistic to suggest covering inundated areas fully with artificial floating rafts. However, they could be used as nuclei for growth of hummock and lawn species within aquatic *Sphagnum* rafts, in addition to hummocks placed at the pool periphery.

6.7 Sphagnum *'farming'*

Fundamental to any strategy of deliberate re-introduction, is to provide a source of inoculum. Elling & Knighton (1984) report that *Sphagnum* has been harvested sustainably from bogs in the USA and Canada since the 1800's for use primarily as a packing material for transporting plant seedlings. Traditionally, this was done manually by pulling up *Sphagnum* from the bog surface but modern, mechanised methods involve almost complete removal of the *Sphagnum* layer. Despite this, regeneration of the *Sphagnum* layer does occur from fresh, residual peat exposed to the surface in a way similar to that observed by Clymo & Duckett (1986)(5.1). For a Minnesota peatland, they recommend that a 20 year harvest cycle would be needed for 90% recovery of the 72 tonnes per hectare present before harvest.

With extensive areas of *Sphagnum* bog remaining, particularly in Canada, restoration projects in North America could conceivably acquire large quantities of inoculum in this way. However, in the UK, extensive areas of productive, *Sphagnum*-dominated vegetation are comparatively rare and what remains would be considered too precious to consider converting to large-scale *Sphagnum* production. Instead the possibility of 'farming' *Sphagnum* must be considered. Evidence from this investigation suggests that growth of aquatic Sphagna in shallow water can be very prolific especially when regeneration occurs from fragments. Therefore, a series of 'nursery' trenches at cut-over sites could be developed to provide adequate amounts of material. If trenches were harvested on a rotation a constant supply could be maintained. Growth may further be stimulated by manipulating the water quality. Evidence from Experiment 5 suggests that addition of phosphorus may dramatically increase productivity (4.4).

Consideration might also be given to increasing CO_2 availability. Abnormal growth of *Sphagnum cuspidatum* is frequently observed in still water and this may be a consequence of carbon limitation. In acid solutions there is a poor reserve of bicarbonate (HCO_3^-) so shortage of C may be particularly acute. Carbon dioxide (CO_2) is considered more important than HCO_3^- as the inorganic carbon source for submerged vegetation, its source being largely from microbial decomposition and organic compounds (Bain & Proctor, 1980).

On Silver Flowe, Boatman (1983) observed greater innovation production in *S. cuspidatum* in hollows compared with deep pools. Greater production was also observed at the ends of pools. He considered this may be due to increased exposure to the atmosphere as the rate of diffusion of CO_2 through water is extremely slow. Boatman, (1977) observed greater innovation production in transplants of *S. cuspidatum* grown in the swallow hole of a lagg compared with plants in a surface bog pool. He suggested that the importance of CO_2 should not be overlooked as water movement not only increases rate of supply of solutes but also levels of dissolved CO_2.

Spindly growth and poorly developed capitula are a feature of C limitation. In laboratory studies, Baker & Boatman (1985) found growth of *S. cuspidatum* resembling that which occurs naturally, could only be produced when CO_2 was passed through the culture solution. Jones (1978), achieved normal growth of *S. cuspidatum* by addition of simple sugars to the culture solution. Further laboratory studies have shown that at concentrations of N, P and K only slightly higher than those recorded in rain i.e. 2 mg l^{-1} NO_3^-, 0.78 mg l^{-1} K^+, 1.3 mg l^{-1} $H_2PO_4^-$, CO_2 gas bubbled through solution can significantly increase innovation production (Baker & Boatman, 1990).

In the Maria Peel area of the Netherlands luxuriant growth sites of *S. cuspidatum* were observed to correspond with high levels of dissolved CO_2 i.e. 780 µM CO_2 l^{-1} (Roelofs, 1983). Consequently, it was suggested that too low CO_2 levels in the water layer might be responsible for lack of growth of submerged Sphagna in numerous pools of the Groote Peel area (Roelofs, Schuurkes & Smits, 1984). Laboratory experiments on *S. cuspidatum* in submerged culture showed that high CO_2 was necessary for growth. At CO_2 concentrations below 750 µM l^{-1} plants showed reduced growth and were unable to form a floating mat (Paffen & Roelofs, 1991).

Therefore good evidence exists for a beneficial effect of increased concentration of dissolved CO_2 on *Sphagnum* growth. However, whether this knowledge could be utilised on a large scale comes down to a question of logistics and particularly of economics. Bubbling gaseous CO_2 or air through numerous pools across an old milled peat field would be prohibitively expensive. However, it may be more applicable for rapid production of inoculum in special 'nursery' trenches.

Farming of non-aquatic species may be more difficult due to their lower productivity. However, Baker & Macklon (1987) found in laboratory studies that aeration of culture solution with air containing 10% CO_2, dramatically increased submerged growth of several hummock and lawn forming species of *Sphagnum*, with potential for scaling up the operation. In the field, artificial rafts may be of use as they would provide a stable water regime for regeneration. Results from Experiment 3 (3.3) suggest the potential also exists for improving microclimate in nursery trenches, perhaps with plastic sheeting, in order to improve regeneration. Clearly there are many possibilities for facilitating *Sphagnum* farming. However, further research is urgently required to test many of these ideas.

6.8 *Final remarks*

Throughout this thesis, attention has been drawn to the many environmental constraints which act to limit *Sphagnum* recolonisation. However, overall, results from this study are quite encouraging. There is good evidence that desirable bog vegetation can become re-established in abandoned cuttings given certain conditions. If it is possible to reproduce such conditions then it is quite conceivable, assuming *Sphagnum* growth is not constrained by atmospheric pollution, that a raised bog flora can be restored to milled peat fields.

It is thought that rafts of bog vegetation in abandoned peat pits have developed unaided in 50 - 100 yrs and although the area of these individual pits is generally small (< 100 m^2), regeneration had occurred simultaneously in a number of adjacent pits so the total area over which this vegetation had developed is much greater. Tallis (1973) reports that at Scouts Wood in Delamere Forest, north Cheshire, a shallow pool some 100 m in diameter has become completely overgrown by *Sphagnum*; and at Flaxmere, shallow peat excavations have infilled with *Sphagnum* within ten years. Therefore, a mosaic of pools colonising simultaneously across a milled peat field could be expected to show considerable progress in a matter of decades. Furthermore, results of field experiments suggest numerous management options may be considered for actively assisting vegetation development. There is enormous potential for encouraging revegetation. Many suggestions have been made based on empirical evidence, which require further experimental investigation. This reflects the very embryonic nature of the subject and the scope for further research is great.

This project has focused primarily on the need for a hydroseral approach to restoration. This concept has been devised with particular reference to the hydrological conditions that persist at Thorne Moors. At this stage, there is insufficient evidence from abandoned milling fields elsewhere to suggest that this approach would be required universally, particularly in wetter climatic regimes. However, the limited evidence which does exist suggests this may be the case.

Some particularly important questions lead on from this project which need to be considered. Some attempt must be made to actually reconfigure a milled surface to investigate the logistics of creating a mosaic of pools. If this can be achieved then *Sphagnum* regeneration experiments need to be scaled up to attempt establishment of aquatic *Sphagnum* rafts over larger areas as part of an actual restoration procedure. Perhaps the biggest unknown which needs to be addressed, is whether we can successfully establish later successional species. We know this has taken place spontaneously on a small scale but uncertainty surrounds whether this can be replicated over larger areas. Once these questions have been answered we will be in a much better position to suggest whether or not it is possible to return a *Sphagnum*-dominated flora to milled peat fields.

It must be considered that a cut-over bog could never be returned to its *original* condition as thousands of years of palaeoecological record and the archaeological archive cannot be replaced. Therefore, research into restoration can never be considered justification for future peat extraction from conservationally valuable areas. Although a bog cannot be restored to its original condition this does not detract from the value of the research, as a knowledge of the methods required to regenerate raised bog vegetation would enable expansion of a nationally rare habitat into damaged bog sites.

Chapter 7

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Appendix 1

Attempts to reduce pool water acidity in a cut-over bog.

As a consequence of drainage, pools in cut-over bog may be characterised by unusually low pH. In the Creykes study area, flooded peat pits frequently exhibited values as low as pH 3.0 (refer to Chapter 4). Results of Experiment 4 indicate that low pH may be sub-optimal for growth of *Sphagnum*. The aim of this investigation was to test the effectiveness of three chemical agents at reducing acidity of pools in cut-over bogs.

Method

Applications of NaOH, $NaHCO_3$ and $CaCO_3$ were made to water in peat pits in the Creykes study area (refer to Section 1.10.2). Each pit contained approximately 4000 litres of bog water at around pH 3.5. The aim was to increase pH to around pH 4.0. The quantity of each chemical required was estimated from simple laboratory trials in which each chemical was added to a small known volume of bog water. Chemicals were applied to peat pits as shown below:

Pit	**Treatment**
CP2 CP4	1 litre of 1Molar Na OH
CP6 CP8	80g $NaHCO_3$ (in 5 litres of distilled water)
CP10 CP12	80g $CaCO_3$ (in 5 litres of distilled water)
CP14 CP16	Control

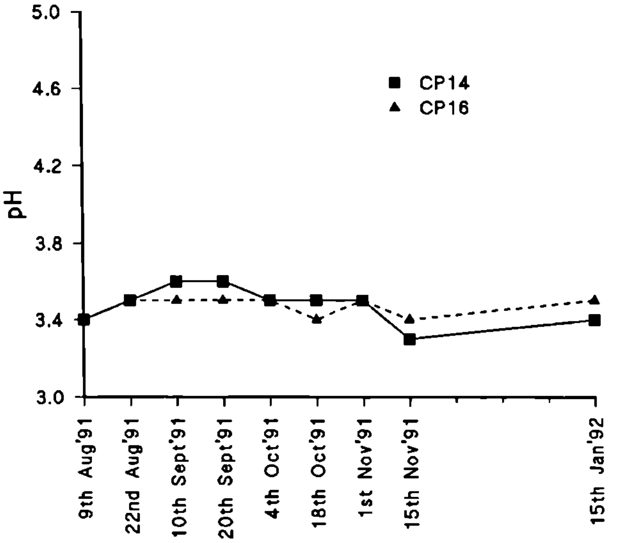
There were two replicate pits for each treatment (see above). The location of these pits in the Creykes study area is shown in Fig 1.5. One application was made on the 9th August 1991 and a further application was made on 22nd August 1991. pH was recorded fortnightly from 9th August 1991 to 15th November 1991 (at which point pH had returned to its original level) and a further measurement was made on 15th January 1992. pH was measured using a Jenway 3030 portable pH meter.

Results

All three treatments were successful in increasing pH to around pH 4.0. However the effect was very short term and pH was higher than the control only for the period 22nd August 1991 - 18th October 1991 (approximately two months). Each of the chemicals used produced a very similar pH effect. Fig A1 shows that there was little difference in pH response to different treatments.

Fig A1: The pH of pit water in the Creykes study area in response to addition of NaOH, $CaCO_3$ and $NaHCO_3$. [There were two replicate pits per treatment - refer to text for details of treatment]

Control



NaOH

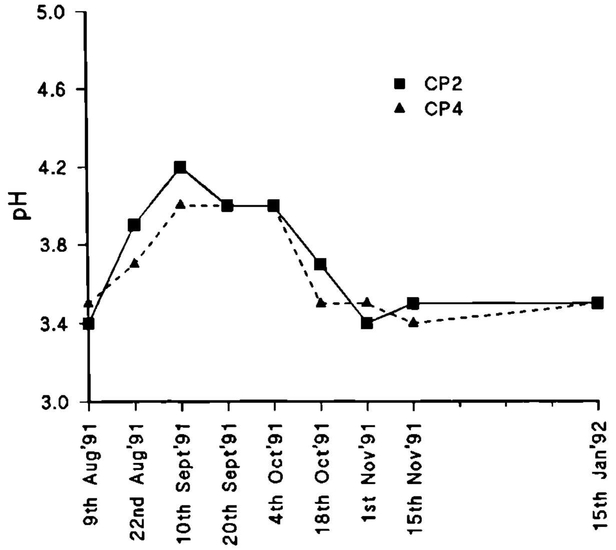
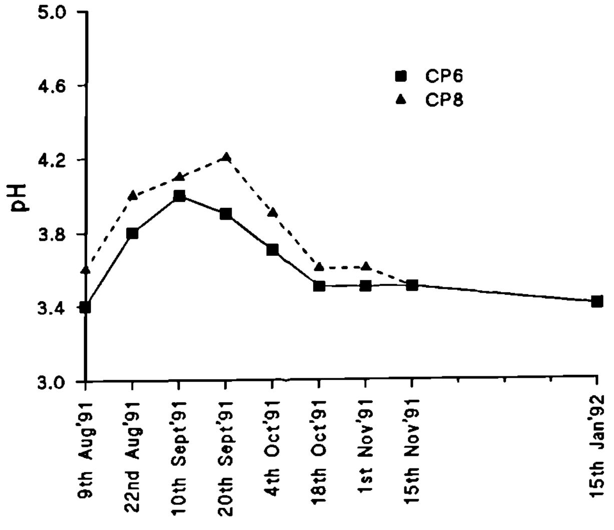
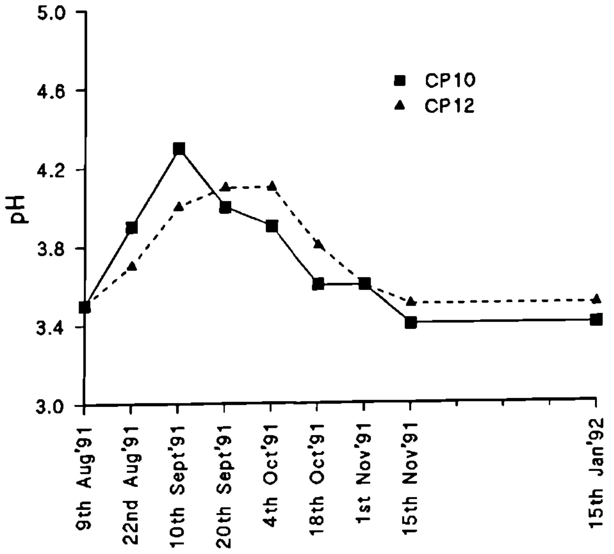


Fig A1: *continued*

$NaHCO_3$



$CaCO_3$



Appendix 2

Floatation trials with artificial rafts

During the course of this study a series of 'ad hoc' trials were conducted at Thorne Moors to investigate the feasibility of using artificial rafts as tools for assisting growth of lawn and hummock forming *Sphagnum* on open water (refer to Section 6.6). In Experiment 1 (Chapter 3) a netlon raft was successfully used for growing *Sphagnum,* however, netlon is prohibitively expensive and is probably inappropriate for large scale restoration. Efforts during this study have concentrated on using mats composed of Jute fibres. Jute material is comparatively cheap and technology exists for 'weaving' it into mats of varying thicknesses. It may be produced in rolls (rather like rolls of carpet) which are easy to administer to the field. The absorbent mat provides a wet surface on which laboratory trials suggest *Sphagnum* will readily grow. Thus, jute matting potentially provides a cheap and effective rafting material.

However, field trials indicate that mats comprised purely of jute only remain afloat for up to 72 hrs, and once fully saturated, they invariably sink. This applied to mats both loosely and tightly woven and to mats of differing thicknesses. Mats were therefore created with strips of cork adhered (using a non-phytotoxic glue), to give buoyancy. However, even mats with over 50% of their area covered by a 5 mm layer of cork failed to stay afloat. Finally, rafts were produced with a thin (2 mm) layer of polystyrene 'stitched' to the underside which was successful in providing buoyancy.
These rafts were inoculated with plants of *Sphagnum papillosum* and *S. magellanicum* and early indications are that the mats are providing a suitable template for growth of these species.

The need for a layer of polystyrene to achieve buoyancy perhaps makes the use of these mats less desirable aesthetically, but they may nevertheless be a useful tool in encouraging recolonisation by providing a permanently wet template suitable not only for growth of *Sphagnum* but also vascular bog species. Aesthetics will be less important in *Sphagnum* 'farming' (refer to Section 6.7) therefore mats with a polystyrene base may still have a function in producing large amounts of inoculum for restoration. In the future, it is possible that an alternative solution to the problem of buoyancy may be achieved. The potential benefits are such that artificial rafts warrant further investigation.