

UNIVERSITY OF SOUTHAMPTON

**THE PALAEOECOLOGY OF THE FEN/BOG TRANSITION
DURING THE EARLY- TO MID-HOLOCENE IN BRITAIN.**

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ABSTRACT

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THE PALAEOECOLOGY OF THE FEN/BOG TRANSITION DURING THE EARLY- TO MID-HOLOCENE IN BRITAIN.

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The aim of this thesis is to examine the role of autogenic and allogenic forces in determining the development of lowland peatlands, across the fen/bog transition (FBT), by comparing palaeoecological records of mire development from a set of eight paired sites.

One ombrotrophic mire was selected for detailed analyses at the intra-site scale, to provide an assessment of the variability of the early- to mid-Holocene peat stratigraphy associated with the FBT and to establish the degree to which one sample core could represent the main large scale changes in the mire stratigraphy. The remaining seven mires from Cumbria, Wales and Eire were selected to provide comparisons of sites developing in a range of circumstances, including inland and coastal locations and different climatic regimes. One site in Wales was chosen for its proximity to a major river system, to investigate the impact of drainage basin change on a lowland raised mire.

A series of complimentary techniques, including Quadrat and Leaf Count Macrofossil Analysis (QLCMA) of vegetative peat components, Abundance Estimate Macrofossil Analysis (AEMA) of propagules, and field stratigraphy, were employed to provide detailed reconstructions of the pathways of mire development leading to the FBT.

Horizons immediately above and below the FBT were radiocarbon dated to examine the continuity of peat accumulation and Detrended Correspondence Analysis (DCA) was performed to investigate the character of the fen/bog gradient.

The results of the detailed palaeoecological analyses suggest that four models of lowland ombrotrophic bog initiation from fens may be recognized in the group of mires studied. The first is the autogenic model, driven primarily by peat accumulation. The second model proposes that acidification and pseudo-raised mire formation follows a decline in effective precipitation. The third model proposes that a change to dry climatic conditions causes a break in fen peat accumulation. Pseudo-raised mire inception occurs once effective precipitation increases sufficiently to allow peat development. True raised bogs may subsequently displace these 'dry', acidified mires. In model four, improved drainage due to river channel change and the resulting fall in mire groundwaters, provides the trigger for raised mire establishment.

Analyses of the ombrotrophic peat above the FBT indicate a synchronous increase in the surface wetness of all four Cumbrian Mosses at 7850 cal. BP. The inferred climatic wet shift is marked by the first period of dominance of lawn and pool *Sphagna* in the stratigraphy of the mires.

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Notes.

(1) Radiocarbon dates.

Calibrated radiocarbon dates have been quoted as cal. BP (calibrated, Before Present) throughout the thesis.

In a number of cases the discussion refers to diagrams from the literature that are presented in radiocarbon years BP. Where they are referred to in the text, these radiocarbon dates have been converted to cal. BP and the uncalibrated dates are quoted in parentheses.

The conventions used by the original authors have been retained on reproduced diagrams.

(2) Macrofossil diagrams.

The main macrofossil diagrams contain data quantified in two ways. The following conventions have been adopted to distinguish between them:-

(a) Linked histograms denote percentage cover data from Quadrat and Leaf Count Macrofossil Analyses (QLCMA).

(b) Unlinked histograms denote 5 point abundance estimate data (AEMA).

(c) Abundance estimate axes are scaled	5	=	rare
	10	=	occasional
	20	=	frequent
	30	=	very frequent
	40	=	abundant

Some diagrams contain only 5 point abundance estimate data.

(3) DCA biplots.

Diamonds	=	samples scores
Open circles	=	species scores

Chapter 1

Introduction.

1.0 Introduction.

Wetland communities have played a central role in the formulation of theories concerned with change in ecosystems through time (Warming 1895, Weber 1908, Clements 1916, Pearsall 1918, Tansley 1939, Bellamy 1968). Initially ecologists used the clear zonations existing within many peat-forming communities to infer the likely progression of vegetation development (Pearsall 1918, Tallis 1973), coupled with direct observational studies (Clements 1916, Godwin 1936, Godwin *et al.*, 1974). However, the approach of substituting change in space for change in time, termed the 'side-by-side' comparison by Zobel (1988), is not satisfactory as a means for studying previous pathways of ecological change because allogenic factors acting on the system may alter significantly over long time-scales (Gleason 1926). Equally, direct observations of successional pathways are only possible over relatively short time-scales (Backéus 1972, Tallis 1983, Hogg 1993). Studies rarely manage to assemble data for any single site that spans a hundred years, whereas time-scales of five hundred to several thousand years are more commonly relevant to processes of development for a single wetland stage (Walker 1970). These difficulties necessarily lead to a greater interest in the early stages of ecological successions when vegetational changes are more rapid, with ideas concerning later slow successional stages becoming increasingly speculative as the limits of the data are reached (see for example Cowles 1901, Clements 1916, Pearsall 1918, Godwin 1936). However, the anoxic, waterlogged environments occurring in wetlands offer a third methodology for studying ecological change through time, namely the examination of stratified layers of organic debris that accumulate over millennia. The peat body accumulates due to the suppression of organic decomposition to a level below the rate at which plant litter is added to the system (Moore and Bellamy 1973). Preservation of successive levels of local plant material, coupled with the incorporation of pollen deposited from a wider catchment, provides a unique archive of past developmental phases in the peat-forming ecosystem (Barber 1993). Only the macrofossil record provides secure evidence for the sequence of species occupying a mire site, due to the lower probability of their distant transport (Grosse-Brauckmann 1986).

Despite early interest in macrofossil analysis (Gepp 1895, Lewis 1905, quoted in Clements 1916) palaeoecology has been dominated by palynology for much of the twentieth century. Many of the studies that have involved macrofossils have either been archaeobotanical or concerned with lake sediments, peats from previous interglacials and Late-glacial deposits. In most cases sub-fossil fruits and seeds have been the main focus of attention, to the extent that they have become virtually synonymous with the term 'macrofossil'. Birks and Birks (1981) stated in their chapter on the subject, '*macrofossils can consist of*

almost any part of the plant. Most frequently they are fruits and seeds, or megaspores.' (p66).

Consequently many studies have not exploited the full macrofossil record.

Detailed macrofossil diagrams are comparatively rare, with sites in continental Europe and North America accounting for the large majority of diagrams combining vegetative and seed remains. These studies generally focus on one or a few sites (see for example Rybníček and Rybníková 1968, Casparie 1972, 1993, Rybníček 1973, Janssens 1975, Grosse-Brauckmann 1963, 1968, 1976, Griffin 1977, Van Geel 1978, Kuhry 1985, Middelborg 1986, Dupont 1987, Svensson 1988a Green-Winkler 1988, Kuhry *et al.* 1991, Hu and Davis 1994, Almquist-Jacobson and Foster 1995).

In Britain much of the early stratigraphic and macrofossil data available for mire systems have been produced to aid the location of pollen sample cores following the example of Godwin (Walker 1970). The resulting papers are a combination of mire development and wider vegetation history, largely dealing with one or two peatland basins and pollen catchments. Examples include Godwin and Clifford (1938), Pigott and Pigott (1959), Bartley (1960), Smith (1959), Pearson (1960), Chapman (1964), Birks (1965), Thomas (1965), Walker (1966), Bartley (1966). In all of these papers the data presented for the interpretation of mire ontogeny are in the form of field stratigraphies and brief descriptive logs of the macrofossils encountered from a number of borings. The logs were usually compiled using a Hiller corer that provides small samples skimmed from the sides of a borehole. Whilst some verification of sub-fossils may be undertaken in the laboratory, many researchers have only reported a few check levels and have not provided any measures of macrofossil abundance.

Walker (1970), recognized the need to synthesize the wealth of stratigraphic information available for mires into a systematic study of British hydroseral development. Therefore, Walker undertook a literature based study with the aim of testing the long-standing theories concerning the direction, rate and nature of development in mire ecosystems. Walker found that a number of aspects of the theories, formulated before the existence of palaeoecological data, were inaccurate particularly with respect to the later stages of mire development, when ecological change is slow. For example, the study demonstrated that hydrosere could follow a great diversity of pathways, with a significant minority of these being in a reverse direction to the general trend. In addition Walker showed that raised bog rather than mixed oak woodland develops in European oceanic climates.

The historical lack of detailed data available for the study of mire ontogeny is clearly illustrated by the fact that Walker (1970) was unable to draw upon any full macrofossil diagrams from the literature. The review of hydroseral development relied entirely upon data gleaned from field stratigraphy, borehole logs and pollen diagrams. Secondly, few sites were radiocarbon dated, therefore the study of rates of change in wetlands was based upon pollen assemblage zones. The synchronicity of these zones across the British

Isles, and therefore their use as chronological markers has been increasingly questioned. (Smith and Pilcher 1973, Chambers and Price 1985). Consequently, Walker's examination of the original ecological theories for long term wetland change was unable to take full advantage of the information contained within the peat archive.

Since Walker (1970) British pollen studies including stratigraphic information have continued to be published (e.g. Moore 1977, Davis and Turner 1979, Rowel and Turner 1985 and Smith and Goddard 1991). However, a number of British macrofossil analyses have also been completed. These fall into three categories, namely (1) research that focuses upon propagules alone (e.g. Tallis 1973, Smith and Morgan 1989, Wheeler 1992), (2) studies that provide five point abundance estimates of macrofossils, including vegetative as well as propagule subfossils (e.g. Smith 1985, Wimble 1986, Wells 1991-1994), (3) research that provides a fully quantified, Quadrat and Leaf Count Macrofossil Analysis (QLCMA) estimate of the percentage of macrofossils in a sample level (e.g. Stoneman 1993 and Barber *et al.* 1994a, Barber 1995 and 1996, Mauquoy forthcoming). The number of British sites examined at levels 2 and 3 is relatively limited. Many of the level 2 abundance estimate diagrams available for British lowland mires, have been produced by the North West Wetlands Survey (N.W.W.S), for the purpose of determining the environmental context of archaeological finds. Macrofossil diagrams analysed to level 3 have been undertaken to determine past surface wetness in ombrogenous mires, which provides a proxy indicator of past effective precipitation.

Clearly, there is a need to undertake new research into mire ontogeny, building on the work of Walker and combining the techniques of vegetative and propagule macrofossil analyses, pollen analysis (in a supporting role), radiocarbon dating and statistical analyses. However, a detailed re-examination of the whole question of British hydroseral development would be too great a task for one thesis. The review undertaken by Walker (1970) drew data from over thirty research papers published during a fifty year period. Therefore, the aims of this research project will be focused on one major event in the wetland sequence, namely the transition from minerotrophic, groundwater-fed peatlands to ombrotrophic raised mires. This transition represents a profound change in Holocene vegetation history, which remains poorly researched. (Hereafter this transformation will be termed the '**Fen/Bog Transition**' and shortened to **FBT**). Furthermore, the project will concentrate on the first main phase of lowland raised mire development in the early to mid-Holocene.

1.1 Thesis objectives.

The principal objectives of this research project are summarized below.

- (1) To review the literature on peatland development and existing models of raised mire formation.

- (2) To provide detailed reconstructions of the sequence of vegetation change recorded in lowland peatlands, covering the period of the transition from minerotrophic to ombrotrophic conditions, at a suite of sites.
- (3) To examine the nature of the mechanisms creating early Holocene raised bogs, as expressed by the record of past vegetation.
- (4) To evaluate the role of allogenic and autogenic forces in determining the types of mechanisms operating on the early Holocene mires, using a system of paired sites and multiple cores from one mire.
- (5) To formulate new models of raised mire formation, on the basis of new data, where appropriate.

1.2 Thesis structure.

The thesis is organized into 8 chapters. Having presented the background and general aims of the project in the present chapter, Chapter 2 examines the theories and models of mire development proposed in the literature. More specific research questions are presented in the introductions to Chapters 5 and 6. These have been formulated in the light of the literature presented in Chapter 2. In Chapter 3 the design of the sampling strategy is considered, with respect to site selection. More specific sampling issues are considered in the introductions to sections dealing with the data from individual sites. Chapter 3 also provides an overview of the methods and problems involved in macrofossil and pollen analyses. The fourth chapter provides an introduction to the mires selected for analysis, including maps showing the location of core sites. In Chapter 5 the FBT is studied at the intra-site scale using detailed field stratigraphy and multiple macrofossil cores. Statistical and radiocarbon dating techniques are introduced at this point. The information concerning within-site variability and the degree to which one borehole may represent changes in the wider peatland complex, is used to refine the sampling strategy for analyses presented in the following chapter. Chapter 6 presents an inter-site study of the FBT at eight paired sites stretching from Cumbria to Galway Bay. The remaining two chapters contain the discussion (Chapter 7), conclusions and ideas for further research (Chapter 8).

1.3 Mire classification.

The basic feature that defines mires from other ecosystems is that they are 'peat-forming' or 'accumulative' (Moore 1984). These unbalanced systems, produced by waterlogging and the consequent excess of production over decomposition (Clymo 1965) are diverse in terms of their form, hydro-chemistry and constituent vegetation (Gore 1983). Consequently, attempts at mire classification are similarly varied. Moore (1984) groups the array of classifications into seven basic types, based on floristics, vegetation structure and physiognomy, morphology, hydrology, stratigraphy, chemistry and peat characteristics. In

practice many simplified classifications in common usage combine a number of these features. At the most basic level mires may be split into fens and bogs. Fens are maintained by ground-water, whilst bogs are fed by precipitation alone (Tansley 1939). The bog category was split further by Tansley into raised bogs, which are isolated from groundwater due to doming of the peat body, and blanket mires, which clothe slopes receiving very high levels of precipitation. The inception of blanket peat has been studied elsewhere (e.g. Moore 1973, 1975, 1993, Tallis and Livett 1994) and this subject does not form a part of the present thesis.

Many other researchers have elaborated on the basic division of wetlands. For example Weber (1908) presented a threefold classification of mires as part of the terrestrialization (*Verlandungs*) hypothesis, namely '*niedermoore*', '*ubergangsmoore*' and '*hochmoore*'. The first and last of these terms are approximately equivalent to Tansley's 'fen' and 'bog' respectively. The third term, *ubergangsmoore* is used to describe a transition type, possessing a mix of fen and bog characteristics. Kulczynski (1949) also distinguishes three basic mire types, rheophilous, transition and ombrophilous, based on the mobility of the water supply. Rheophilous mires form where groundwaters are mobile, ombrophilous mires occur in areas of water immobility that are dominated by meteoric water. Transition mires bridge the other two categories. Kulczynski's classification differs from Weber (1908) in that rheophilous peat formation may result from paludification, the formation of peat directly onto a mineral substratum, as well as through deposition in water. In this respect Kulczynski's classification is similar to the pedogenic peat of Taylor and Smith (1972 and 1980).

Fens, poor fens and ombrotrophic bogs may be distinguished on basis of species composition (e.g. Wheeler 1980 a, b and c, Rodwell 1991). The distinction between different mire types is often arbitrary and the variation in peatland vegetation may be considered as a continuous gradient from rich fen, through to raised bog (Sjors 1950), although the division between fen and raised bog may be sharply defined (Sjors 1950). Examinations of the ionic composition of mire peats and free mire waters, have demonstrated that vegetation types closely reflect the ionic composition of mire peats and waters (Kivinen 1935, Du Rietz 1949, Gorham 1950, 1953, Sjors 1950). The large volume of literature describing the chemical gradients in freshwater mires and the accompanying vegetation responses, precludes a comprehensive review of the relevant studies, however, the general findings for the 'rich fen/poor fen/raised bog' gradient may be summarized as follows:

Rich fens tend to have the highest concentrations of bases and a high pH (Sjors 1950, Proctor 1992), as a result of the continuous supply of nutrients and flushing of hydrogen ions by groundwater. Waughman (1980) found that concentrations of calcium (Ca), magnesium (Mg) and potassium (K), in particular were high in fens and low in raised bogs. Damman (1979) and Malmer *et al.* (1992) amongst others, have reported similar findings. However, Malmer *et al.* (1992) noted that hydrochemically, the limit between

poor and rich fen sites is often more decisive than between ombrotrophic bog and poor fen. Some ions appear to be more abundant in raised bogs than in fen. For example, Waughman (1980) found the highest concentrations of ammonium (NH_4^+), zinc (Zn), copper (Cu) and easily soluble forms of phosphorous (P) in ombrotrophic mires. However, these measurements depend to a high degree upon the quality of the rainwater, since ombrotrophic mires by definition receive all of their nutrition from meteoric water and dry atmospheric deposition. Proctor (1992) found that the average proportions of most major ions in ombrogenous mire waters were similar to those of local rainwater samples, although concentrations of ions were slightly higher in ombrotrophic mire waters due to evaporation. Damman (1979) reported similar results from Canada. In addition to generally low concentrations of plant nutrients ombrogenous mire waters have the lowest pH values to be found on the fen/bog gradient. This has been clearly illustrated by Sjors (1950) and many others.

Although the characteristics of mire communities occurring along the fen/bog gradient are highly varied, those within the rich fen category generally have a high species diversity (Wheeler 1980 a, b and c, Wheeler and Giller 1982) and a high level of productivity (Malmer 1986). By contrast the base poor, acidic mires have a low species diversity and lower production. A wide spectrum of intermediate states exist.

Therefore, the central theme of this project is concerned with the mechanisms and circumstances surrounding the removal of the groundwater effect from lowland peatlands and the consequent establishment of base poor, ombrotrophic mire communities on former fens.

Detailed reviews of peatland classification are provided by Moore and Bellamy (1973), Taylor and Smith (1980), Wheeler (1980a, b and c), Gore (1983), Moore (1984) and Rodwell (1991).

1.4 Terminology and nomenclature.

Clear use of terminology is vital for a project of this nature, therefore the following conventions will be used:

The threefold classification of fen, poor fen and raised bog will be adopted as the basis for mire classification. (Tansley 1939, Godwin 1975). Descriptions of vegetation sequences will necessitate further refinement and the inclusion of additional categories.

'Mire' is a general term (Godwin 1941) which will be used interchangeably with 'peatland', whereas 'wetland' will be used to refer to peatlands and open water bodies collectively.

Mires dominated by reeds with permanent standing freshwater will be called 'swamp' or 'reedswamp'.

'Swamp carr' will be used where the community also includes trees and shrubs. All other uses of the word 'swamp' (Gore 1983) will be avoided.

The term 'fen' will be used to describe fresh groundwater-fed wetland communities that are unwooded and not perennially inundated (Godwin 1936).

'Fen carr' and 'carr woodland' may be distinguished from 'fen' on the basis of the proportion of wet woodland tree species present in the community and the character of the field layer.

'Raised bog', 'raised mire/bog' and 'ombrotrophic mire/bog' will be used interchangeably, to refer to domed rain fed mires. N.B. The terms 'raised bog' and 'ombrotrophic bog' have been shortened to 'bog' for use in terms such as 'fen/bog transition'. In such cases 'bog' refers only to ombrotrophic, lowland, raised mires.

It may also be useful to separate dry, 'heath-like oligotrophic bog' dominated by *Calluna vulgaris*, *Pinus sylvestris* and *Eriophorum vaginatum* from 'wet raised bog' dominated by *Sphagnum* mosses.

Nomenclature follows Stace (1991) for vascular plants, Daniels and Eddy (1990) for *Sphagna* and Smith (1978) for non-*Sphagnum* mosses.

Chapter 2

The fen / bog transition: previous research.

2.0 Introduction.

The first section of this chapter deals with the concept of vegetation succession. The aim is to present the development of the opposing ideas concerning sequential development of vegetation through time and to clarify the current position of succession within ecological theory. The discussion is considered to be necessary because succession is one of the central concepts in the study of peatland development and despite the considerable attention given to it over the last 90 years, it is still surrounded by confusion within the ecological literature (Miles 1979, 1987, Finegan 1984, Connel *et al.* 1987, Walker and Chapin 1987). General concepts of vegetation change will be dealt with first, followed by those specific to peatlands. In discussing peatland development, the author aims to demonstrate the gap in knowledge that will be addressed in the present thesis. The second section of the review aims to provide a synthesis of literature, representing the current understanding of processes that shape and direct ongoing development in peatlands

2.1 The study of vegetation change before 1916.

The ancient Greek, Theophrastus (300 BC) is believed to be the first person to have produced a study of vegetation change in time (Clements 1916, Gray *et al.* 1987), whilst King (1685) is credited with the initiation of scientific research into vegetation change, for his work on Irish peat bogs (cited in Golley 1977). However, Golley regards King's paper as no more than the expression of common knowledge, which extends back at least as far as the Neolithic farming communities, that practised shifting agriculture (Golley 1977, Miles 1987). Studies of vegetation succession really began in the nineteenth century. The French biologist, Dureau de la Malle (1825) is recognized as the first person to have used the term succession, in the sense of an ordered sequence of vegetation replacement, in a paper subtitled:

'La succession alternative dans la reproduction des espèces végétales vivant en société, est-elle une loi générale de la nature?' (cited by Cowles 1911).

During the early nineteenth century the concept of succession developed slowly. By the middle of the century increasing numbers of personal observations of sequential vegetation change were being noted in the literature. However, the synthesis of ideas into ecological theories did not occur until 1899 (Cowles 1899). Of the numerous late nineteenth century authors writing on the subject of vegetation change perhaps two are worthy of special note. Kerner (1863, in Clements 1916) acknowledged that change is one of the basic characteristics of a vegetation community. Warming (1895) travelled one step further, stating that dynamism in the structure of vegetation is ubiquitous and importantly, that change is an ongoing process.

2.2 Succession theory.

2.2.1 The contribution of H. C. Cowles to the study of vegetation change.

The work of Cowles on the sand dunes of Lake Michigan substantially aided the crystallization of many observations and half-formed ideas concerning the nature of succession, into a theory of vegetation change (Cowles 1899, 1901, 1911):

'There are cycles of vegetation, which are comparable precisely to cycles of erosion; in each there is a period of youth, which is characterized by vigour of development and rapidity of change; in each there is a period of maturity, and finally one of old age, which is characterized by slowness of transformation and by approach to stability or at least to equilibrium..... the final vegetative aspect varies with climate and hence is called a climatic formation.....It has been ascertained that the original plant formations in any habitat give way in a somewhat definite fashion to those that come after.' (Cowles 1911, p12)

This cyclic theory of vegetation change is evidently influenced to a large degree by the theory of 'The Cycle of Erosion' proposed by W. M. Davis (1909). However, Cowles has stated that his ideas and those of other researchers working in the area of vegetation change could not have predated the work of Lyell, on the Principles of Dynamic Geology and Darwin who pioneered the concept of organic evolution by natural selection. Despite obvious similarities with the succession theory popularized by Clements (1916), for which both researchers can be criticized (see later discussion), Cowles' ideas are quite distinct. His work acknowledges several principles vital to the study of long term vegetation change that are not emphasized by Clements. The first is the idea that shifting climatic conditions are an important factor in the observed sequence of species replacements over long time periods:

'The first vegetation of the hills is xerophytic, and the first vegetation of the hollows, hydrophytic.....These plant formations gave way step by step to the climatic tundra and as the climate became ameliorated, this in turn gave way to climatic coniferous forests, and then to climatic deciduous forests as they exist today.' (Cowles 1911, p15)

Secondly, Cowles realized that pathways of development could differ significantly under the same climatic conditions:

'thus we may speak of alternative or substitute stages, when different plant formations occupy equivalent places in a successional series.....(and)....one may speak here of the elimination of stages.' (Cowles 1911, p15).

Thirdly, Cowles made the very important observation that different successional processes could operate at different rates and in different directions concurrently and that some of these processes could be very slow and of considerable duration:

'To summarize on regional successions, it would seem that secular changes in climate, that is changes which are too slow to be attested in a human lifetime, and

which perhaps are too slow to be attested in a dozen or a hundred lifetimes, are the dominating factors. It is possible that these changes sometimes are more rapid than at other times.....(with the).....complex of cycle within cycle, each moving independently of the others and at times in different directions.' (Cowles 1911, p22)

Finally, Cowles's version of succession theory explicitly distinguishes between succession caused by the biotic processes within the community (autogenic factors) and environmental factors that act upon the community from the outside (allogenic factors), to cause species replacement.

2.2.2 The general theory of plant succession.

At about the time that Cowles was researching on the Lake Michigan sand dunes, Clements was constructing his general theory of plant succession. Apparently neither researcher knew of the work of the other, initially. In 1916 Clements published '*Plant Succession: An analysis of the development of vegetation.*' This work popularized the concept of succession as a rigid, general theory and it has held a great influence over numerous studies of vegetation change during the twentieth century. Unfortunately many of the assumptions that underlie the theory are seriously flawed, leading to increasing criticism of the Clementsian succession concept (Gleason 1917, 1926, 1927, 1975, Whittaker 1953, Egler 1954, McCormick 1968, Walker 1970, Drury and Nisbet 1973, Connell and Slatyer 1977, Miles 1979 and 1987, Colinvaux 1986, Finegan 1984, Mortimer 1987, Van Breeman 1995, Klinger 1996) and also to a considerable degree of confusion in the ecological literature. The main principles of the 'organismic' theory are summarized in table 2.1.

Table 2.1 Summary of the Theory of Succession, after Clements (1916).

(1) The unit of vegetation, the formation, is an organic entity. Like an individual organism, it arises, grows, matures and dies.
(2) The formation develops along an ordered pathway, or <i>sere</i> to a stable end point (<i>climax</i>), the character of the end point vegetation being determined by the prevailing climate and therefore it is called the ' <i>climatic climax formation</i> '.
(3) The occurrence of succession is universal and it is the process of formation development.
(4) Succession is unidirectional and therefore can not occur in reverse order.
(5) Primary successions can be distinguished from secondary successions. The former occurs on a new or greatly disturbed land surface that has no soil. The later initiates on lesser disturbed sites with a pre-existing soil cover.
(6) Seral pathways will differ depending on the initial substrate, but given a particular climate the same stable climax vegetation will dominate the final stage of succession. Clements called this the ' <i>monoclimax</i> '. In temperate latitudes this vegetation is mixed oak forest. The climax vegetation is envisaged as having the same character
(7) Disturbances external to the formation or community are built into the theory as point perturbations. The process acts to damage the vegetation at one point in time and then ceases to operate. The development of the vegetation is retarded and then recommences. If point disturbances reoccur at a shorter return period than the length of time the vegetation takes to return to the climatic climax state, a sub-sere is maintained.
(8) The mechanism of sequential species replacement is envisaged as a facilitation process. Pioneer species colonize an area. Their habitation alters the physical conditions of the environment in such a way as to facilitate the establishment of more demanding species. The second wave of species begin to dominate the community and eventually oust the pioneers. The sequence continues with the new species facilitating the arrival of a third wave of immigrants. Change ceases once the formation develops to the climax state.

2.2.3 Criticism of the Clementsian concept of succession.

2.2.3.1 The nature of the community.

Clements emphasized the similarity of communities growing under similar conditions with similar histories of development. Clearly definable types of community may be recognized and they have been rigorously classified into vegetation types for some time. In Britain the great works of Tansley (1911 and 1939) are of particular note. In Europe Braun-Blanquet (1928) and Tüxen (1937) produced detailed vegetation classifications. More recently the work of Wheeler (1980 a, b and c) on fen vegetation, Birse 1980 and 1984 on upland vegetation, and many others has provided the basis for the National Vegetation Classification project (N.V.C.), Rodwell (1991). However, the ideas of Clements went several steps beyond

this recognition of similarity in vegetation types, to suggest that the community is analogous to an organism. This view is clearly mistaken. A community is an amalgamation of many species with different evolutionary histories. *'It cannot be traced along a distinct ancestral phenogenetic line and so is fundamentally different from an organism.'* (Miles 1979). The work of Godwin (1975) in *'The History of the British Flora'*, clearly demonstrated that throughout the Quaternary period the appearance or lack of a species within the flora may be a result of glaciations, sea level responses, and many other chance factors.

The opposing view, emphasized by Gleason (1917, 1926 1927, and 1975) is the individualistic concept of the community. This view states that no two patches of vegetation are ever identical in composition and that the characteristics of the vegetation are entirely dependent on the properties of the individual constituent plants. Van der Valk (1981) subscribed to this view, presenting a 'Gleasonian' model of mire development, based on the life history traits of individual species. Three key traits have been recognized: lifespan, propagule longevity and propagule establishment requirements. These were combined to give twelve basic life history types. Van der Valk suggested that the future development of a wetland could be predicted, if conditions changed, by studying the composition of the seed bank.

However, the individualistic view has not been universally accepted. Odum (1969), for example, regarded the ecosystem as having emergent properties that could not be explained by examining the sum of the individual component parts. In particular, Odum described the ecosystem as capable of having a strategy to maintain or recover stability if disturbed. Klinger *et al.* (1990) regarded the Gleasonian approach as being inadequate to explain long term successional pathways found in peatlands. For example, Van der Valk's model has difficulty predicting the occurrence of raised bogs from life history information.

Whilst an ecosystem cannot be regarded as a pseudo-organism, it does show properties that are characteristic of the assemblage as a whole (Miles 1987). Some of these characteristics include, structural organization, species and food chain diversity and vegetation stability. However these properties are still essentially functions of the individual species. (Miles 1979).

2.2.3.2 The sere and progression.

The pathways of successional change envisaged by Clements were simple unidirectional sequences, leading in an ordered manner inexorably towards the climax state and equilibrium. This view has been restated by many researchers since 1916 including MacArthur and Connell (1966) who stressed the predictability of succeeding communities. Finegan (1984) provided a succinct summary of this Clementsian view:

'Successional change is usually held to be orderly, predictable and therefore deterministic, converging to forest from various different starting points.'

The analysis of the direction of development of Holocene hydrosereal sequences from Britain, by Walker (1970) has done much to discredit the concept of simple, predictable pathways of change in wetlands and

the idea of convergence of pathways towards forest communities (see later discussion.) In concluding his paper, *Direction and Rate in some British Post-glacial Hydroseres*, Walker stated:

'.....the range of vegetation types in a single locality at any one time does not necessarily reflect the sequence which has led to the current pattern at that site, nor does it alone predict the future of the vegetation there even if allogenic influences can be excluded. The course of a particular hydrosere in the past or in the future can only be hypothesized in a probabilistic manner from a consideration of all possible transitions to and from existing vegetation types weighted for environmental site conditions and species availability.....Variety is the keynote of hydrosereal change for so long as local processes exclude Sphagnum spp.....' (Walker 1970, p123).

More recently Sjørs (1990) reported a similar scale of complexity in wetland transitions, in a paper entitled *'Divergent successions in wetlands'*. However, the recognition of the lack of applicability of Clements' original concept must go to Gleason (1927):

'The point to which I wish to draw objection is the fact that we are led to consider that there is in any region a limited and usually a small number of kinds of seres, that the sequences of successional stages in each sere is fixed and definite, and that different representatives of the same kind of sere, although now in different time-phases have had and will have essentially similar time-phases in the past and future.' (Gleason 1927, p20) .

The lack of predictability and the degree of complexity in successions does not preclude the operation of non-random processes. Lawton (1987) examined the question: 'Are there assembly rules for successional communities?' After a detailed examination of a number of communities and processes including the relations of insects, herbivores and vegetation within ecosystems, Lawton concluded that the broad answer to the question was clearly 'yes'. However the details are considerably more blurred.

Finally, Clements's assertion that seral development is unidirectional has been disproved time and time again by the reporting of retrogressive successions (e.g., Iversen 1964, Walker 1970, Moore 1977, Wheeler 1992). These successions are commonly, but not exclusively, driven by external factors.

2.2.3.3 The monoclimax and stabilization.

Species replacement is traditionally supposed to continue along converging pathways until a community that is stable and in equilibrium with the prevailing climate is produced, almost regardless of the initial substrate. (Clements 1916, Oosting 1948, Braun 1950,). However Gleason (1926) and Cooper (1926) both regarded the development of a long-lived communities to be due to a lack of new species to replace the existing ones. Du Rietz (1924) specifically criticized the idea of diverse pioneer communities converging on a single climax plant assemblage. This view was also held by other Scandinavian researchers such as Faegri (1937), however Du Rietz (1930, cited in Whittaker (1953) supported the idea that dominant

communities can establish, which do not exhibit convergence. In Britain Tansley also recognized that the monoclimax was a flawed concept and advanced the idea of the Polyclimax (Tansley 1939). Objections were also raised by Whittaker (1953) who quoted the use of thirty five different 'Climax' terms by 23 researchers in the first half of the twentieth century:

'Such a multiplicity of terms, many of them clearly exceptions to the concept as originally formulated, may imply that the concept is being stretched this way and that to cover evidence for which it is not actually adequate. If an ideal, the climax, must be so modified in application, it may be suspected that the ideal is at fault.' (Whittaker 1953, p52).

The central assumption of monoclimax theory is convergence of communities growing at different sites, towards the same type of vegetation. In some cases and on a limited scale this may be observed. However, the assumption rapidly breaks down, when applied to large tracts of land, due to the great variety of local edaphic, climatic and topographic conditions. Therefore, it may be reasonable to assume that community convergence can occur under certain conditions in lakes and fens for example (Klinger 1996), however, the phenomenon cannot be universally applied to terrestrial ecosystems.

Succession theory also assumes that a vegetation community will attain a compositionally and structurally stable form termed the 'climax', in the absence of environmental disturbance. A number of commentators have raised the problem of what happens at the hypothesized end of succession (Gleason 1927, Drury and Nisbet 1973 and Williamson 1987). Continuing the analogy of the organism Clements assumed that after a period of stability the community would die. Gleason (1927) argued that climax associations are changing now and must change in the future, but the rate of change and the new community is unknown. He stated that 'If it were known, no one but Clements would call the periods of very slow community change, the climax. (Gleason 1927). Sjors (1980) also questioned the concept of the climax stating that: *'even very old ecosystems such as coral reefs and tropical rain forests undergo short-term changes. There is no proof that they return to exactly the same composition in the long run.'* However, such short term changes do not preclude the possibility that stability or dynamic equilibrium could be reached. A community can change continually under constant conditions and still be stable. *'Change of itself does not indicate instability.'* (Williamson 1987).

2.2.3.4 Successional trends caused by allogenic processes.

Cowles (1911), Gleason (1917, 1927) and Tansley (1939) all recognized that allogenic perturbations acting on successional sequences need not be point disturbances and that they may determine the rate and the direction of a sequence operating over protracted periods of time. For example, in the coastal context there is an host of research reporting progressive and retrogressive successions in response to fluctuations in relative sea level and coastal freshwater-tables, during the Holocene (Smith and Morgan 1989, Shennan 1989, 1994a, 1994b, Waller 1994). However, the relationship between climate change, sea level change or

human impact and the observed sequences of vegetation change may be confounded by other factors such as the rate of soil development and, of course, ongoing autogenic change.

2.2.3.5 Mechanisms of succession.

The original mechanism proposed for the operation of succession was the facilitation model in which pioneer species had a net positive effect on later colonists and were themselves ousted by competition with the new arrivals (Clements 1916). Dissatisfaction with this model was expressed by Eglar (1954), who proposed the concept that the 'Initial Floristic Composition' of the community determined the direction of development, and McCormack (1968, cited in Drury and Nisbet 1973) who noted from experimental removals in old fields that facilitation did not occur. Consequently, Connell and Slatyer (1977) proposed a threefold scheme of mechanisms. These models included facilitation but also mechanisms of tolerance and inhibition. Their paper provided a framework for field experiments to test these models. Many recent papers have taken up the challenge with experiments involving pruning, simulated grazing, artificial introduction and removal of species (see Armesto and Pickett 1986, Schmidt 1988, Hester *et al.* 1991a, Hester *et al.* 1991b). Two main points of interest to the present thesis arise from all the recent research on mechanisms of succession. The first is that Connell and Slatyer's three mechanisms are points of reference on a continuum of overlapping processes. Both Walker and Chapin (1987) and Finegan (1984) regarded Connell and Slatyer's work as another attempt to artificially pigeonhole the attributes of succession. Walker and Chapin (1987) pointed out that two mechanisms can operate concurrently and that no one mechanism can individually explain succession. Connell, Noble and Slatyer (1987) countered the criticism by stating that their classification was meant to represent the two extremes and the mid point of the spectrum and, whilst their original paper did not foresee the simultaneous operation of contrasting mechanisms, the net effect must still be either positive, negative or zero.

The second point of interest is that the pioneer stages, particularly of wetland environments are one of the few examples where the original facilitation model is most applicable, due to the dominant effect of water-level and the fact that many species cannot physically tolerate the early successional environment. In later stages of wetland succession, however, processes may become more blurred, as with other environments.

2.2.4 The implications of the present state of succession theory for wetlands research.

Recent literature on vegetation succession recognizes the bewildering variety of forms and processes covered by the scope of the term (Gray *et al.* 1987, Miles 1987, Walker and Chapin 1987). Succession is considerably more complex than the original conceptualization would suggest. One of the principal problems with the theory is that the record of its operation is the outcome of numerous interacting processes. There is now a full appreciation that no general law or structure has been successfully imposed upon succession. Finegan (1984) has argued that to seek a unified theory is wholly unrealistic. This should be expected since succession is not one but many phenomena. Furthermore these processes may be

operating on time-scales ranging from days and weeks to millennia. Therefore, the significance of allogenic forces will vary widely depending upon the time-scale under consideration. The only sensible general usage of the word succession is therefore, as a descriptive term for the sequential replacement of species. The concept as applied to all ecosystems, should imply no individual mechanism or process.

The problems concerning some of the original ideas and the mechanisms suggested for the operation of succession, are not quite so great when ecological change in just one system, namely wetlands, is considered. As Lawton (1987) noted, there are some assembly rules governing change in distinct ecosystems such as a wetland: For example, the rule of gradual infilling and removal of the groundwater supply from the growing surface seems to be generally applicable to lakes in the absence of external forcing. Acidification appears to be inevitable once the groundwater effect has been removed from peat. Facilitation, is the dominant mechanism of succession in the pioneer stages of lake infilling. Klinger (1996) has expressed a similar view stating that *'The organismic theory of succession, though not without deficiencies, is more consistent with observed successional patterns in peatlands than other successional viewpoints.'* However, there is still a considerable degree of complexity, as demonstrated by Walker (1970). For example, there are numerous possible pathways of development. Reversal of trends may occur at any point due to allogenic processes and once the fen stage is reached the mechanism of succession becomes a complex spectrum of interactions, in which facilitation, tolerance and inhibition are points of reference.

2.3 Peatland development.

2.3.1 The template for peat formation.

Peat accumulation occurs when the rate of plant production exceeds the rate of organic decomposition at a site. The imbalance is usually caused by low rates of decomposition, due to soil saturation. Water at the water-table is oxygenated, allowing aerobic decay. However the diffusion of oxygen through water is very slow, therefore continued decomposition in the zone of saturation uses oxygen faster than it is replaced (Clymo 1992b). This creates anaerobic conditions unfavourable to soil decomposers such as fungi, bacteria and invertebrate grazers (Ovenden 1990). Low sediment temperatures may contribute to the imbalance by further reducing or even preventing soil respiration (Fenton 1980), whilst the penetration of roots into deeper peat layers will also add to the accumulation rate of a peat body (Wallen 1992).

The extent of peat forming communities is directly related to the local eccentricities of the water budget, whose parameters include, precipitation, evaporation and efflux (Ivanov 1981). The competence of the natural drainage network, topography, vegetation cover and permeability of the underlying geology, will also be significant in influencing where waterlogging and peat growth can occur. The specific combination of these factors may be regarded as a template for mire formation (Bellamy 1972).

Clymo (1992/3) has recognized three principal mechanisms that maintain soil saturation. First, groundwater seepage (e.g. Casparie 1972) or overland flow may be channelled into an area, having an effect similar to a localized increase in precipitation. Local geology determines the solute load and the trophic status of mires supplied in this manner.

Second, enclosed or semi enclosed basins may retain water as lakes because they lie in an area of impermeable parent material. Even in permeable geology, water may stand permanently at the surface because the topography dips below the level of the water-table arc, connecting interfluvies (Ivanov 1981). Enclosed basin mires tend to be particularly prone to fluctuating water-levels in response to periods of rainfall or drought because water replenishment is largely from the local catchment (Clymo 1992/3).

The third mechanism causing waterlogging relates to the retention of water within a peat body that has accumulated above the general groundwater-level. The development of catotelmic peat (anoxic, waterlogged peat, Ingram 1978) greatly reduces the rate at which water can move laterally in the peatland. Consequently, in humid climates, precipitation may equal or exceed the rate of discharge, enabling ombrotrophic mires to be maintained in a state of dynamic equilibrium (Ingram 1982). Where precipitation is greatly in excess of evaporation, waterlogged conditions may be maintained on sloping sites, resulting in the formation of blanket mire.

Given that wetland development is so closely connected to water relations in the drainage basin, it follows that any changes in the input, output and retention parameters of the water balance equation (Bellamy 1972) will have a profound effect upon mires. Peat inception itself is an expression of hydrological change (Moore 1986, Korhola 1995). Although many factors direct change in wetlands, each one may be classified as either allogenic or autogenic. Allogenic processes originate from beyond the limits of the peatland system (e.g. climate change, human disturbance), whilst autogenic processes operate as a result of internal peatland development. Since the present thesis is concerned with one of the most profound wetland changes, namely the fen/bog transition (FBT), the following sections will examine the main autogenic and allogenic models and processes that have been proposed in the literature to account for wetland change with particular reference to the fen/bog transition.

2.3.2 Autogenic models of mire development.

2.3.2.1 General models of mire community change concerned with vertical groundwater movement.

Early attempts to produce qualitative models for peatland development tended to concentrate upon autogenic mechanisms of vegetation succession and peat accumulation. In 1908 Weber presented the terrestrialization hypothesis (*Verlandungshypothese*) which proposed that wetlands would develop through a number of distinct stages from open water to raised bog. The main mechanism driving community change was considered to be the accrual of peat and inorganic sediment trapped by plants. Minerogenic inwash and organic deposition from aquatic plants would shallow the water body to the point that rooted phanerogams could survive on the lake bed. Further accumulation of debris from the resulting reedswamp would accelerate the rate of basin infilling. As the peat surface reached the water-table, fen communities could replace reedswamp. Ultimately the peat body would accumulate above the level of the water-table, in a humid climate. This would result in isolation of the fen surface from the influence of mineral-rich groundwater and facilitate the development of acidic poor fen. Weber suggested that continued peat accumulation would lead to ombrotrophic raised bog, with the waterlogged surface being maintained by a humid atmosphere combined, with capillary rise in the peat mass. The development of a relatively impermeable wood peat layer causing flooding of the mire surface was proposed as an alternative mechanism to explain the formation of wet raised bog. Although Weber (1908) stressed the autogenic nature of the sequence he also recognized that allogenic processes might influence peat accumulation. For example he invoked climate change as the factor responsible for the major humification change in ombrotrophic peat that he termed the Grenzhorizont.

In America, Clements (1916) established a similar autogenic model of wetland succession called the hydrosere, as part of a wider theory of vegetation succession. This theory differed from the Terrestrialization Hypothesis in that it postulated that mixed *Quercus* forest would form the climax community in temperate climates. Clements placed tight constraints upon his model stating that sequences of vegetation development would be unidirectional and irreversible (see section 2.2) Tansley (1939) adapted the hydrosere by presenting a scheme of multiple climax communities. The unaltered hydrosere (*sensu* Clements 1916) was accepted as representative of wetland development in the drier eastern counties of the British Isles,

'.....'eventually the surface layers of the soil become dry enough for the growth of mesophytic trees which cannot tolerate waterlogged soil, and this hydrosere, as it is called, beginning in water, culminates, like the xerosere, in the establishment of mixed forest.' (Tansley 1939,).

Raised bog was considered to be the climax community in more oceanic western areas. Acceptance of the Clementsian hydrosere in Britain was based on slim evidence of *Quercus* establishment in carr

communities at sites in East Anglia such as Wicken Fen (Godwin 1936). However, at Calthorpe Broad, although Godwin and Turner (1933) suggested that *Quercus* woodland might be a self maintaining successional phase, they acknowledged that there was more evidence for acidification of the fen. Indications of bog development at Woodwalton Fen were even stronger (Godwin and Clifford 1938), with remnant *Sphagnum-Calluna-Eriophorum* communities surviving, despite a prolonged phase of peat extraction.

Resurveying at Wicken Fen (Godwin *et al.* 1974) found little or no development in the *Quercus* community and considerable colonization of the fen by *Betula* and *Sphagnum*, in response to a drop in average water-levels. This led Godwin *et al.* to suggest that bog communities may be recolonizing the site having been completely removed by previous peat working. However, Rowell and Harvey (1988) found no evidence to suggest the existence of former bog vegetation at Wicken Fen. Acidification of the fen appears to be a new development in response to artificially altered hydrological conditions. Similar changes in hydrology at Esthwaite Water have complicated the interpretation of long-term observations of hydrosereal change (Pearsall 1918, Tansley 1939, Pigott and Wilson 1978 and Tallis 1983).

The early discussion and speculation about the true 'end-point' of hydrosereal change in lowland Britain was heavily influenced by the theories of Cowles and Clements and clearly illustrates the problems involved with drawing inferences about longterm community change from vegetation zonation studies. Gleason (1926) has warned against the use of vegetation zonations in this manner. Whilst vegetation zonation studies may have supported succession theory, the belief '*that the hydrosere must culminate in the climax forest of the region was simply a logical outcome of successional theory of the time,the notion that bogs may be climax was simply not considered because it was not expected*' (Klinger 1996, pg. 2).

The benchmark paper by Walker (1970) redefined many of the concepts relating to the direction and rate of development in hydroseres. Walker's literature review of over forty papers containing stratigraphic information from mire sequences revealed the great diversity of developmental pathways in peatlands. To aid interpretation of the main community changes, Walker classified the spectrum of wetland communities involved in mire succession into a simplified twelve point scheme (see table 2.1). These units may be considered as points of reference on a continuum of vegetation change.

Table 2.2 Classification of wetland stages, after Walker (1970).

Unit	Vegetation unit description.
1	Biologically unproductive water.
2	Micro-organisms in open water.
3	Totally submerged (or only flower emerged) macrophytes.
4	Floating-leaved macrophytes, usually with some intervening open water.
5	Reedswamp, rooted in the substratum and standing in perennial water with aerial leaves.
6	Sedge tussock rooted in the substratum and standing in perennial water.
7	Fen dominated by sedges with a variety of acid tolerant herbs, rooted in waterlogged peat.
8	Swamp carr formed by trees growing on unstable sedge tussocks with some fen herbs and intervening pools containing thin reedswamp of floating leafed macrophytes.
9	Fen carr dominated by trees with an undergrowth rich in fen herbs and ferns all rooted in stable peat.
10	Aquatic Sphagna, floating just below or at the water surface.
11	Acid raised bog, usually distinguished by a variety of Sphagnum species and acid tolerant phanerogams.
12	Marsh composed of fen species.

Having applied the twelve point wetland community classification to each of the stratigraphic records of hydrosere development described in the literature, Walker (1970) found that most sequences ended in acid raised bog formation. The most common pathways were (a) 3-5-7-9-11 (b) 3-5-9-11 and (c) 3-5-11. None of the hydroseres developed into mixed deciduous woodland, as Walker (1970) had suspected. Secondly, Walker found that much of the complexity in the seral pathways occurred in the minerotrophic phases of peatland development with ombrotrophic communities demonstrating less diversity. Finally, reversed successions were by no means infrequent (approximately 19% of all pathways), indeed almost all transitions in the forward direction had a reversed sequence counterpart.

The terrestrialization hypothesis and the hydrosere are substantially similar autogenic models, when the latter is reinterpreted in the light of Walker's (1970) findings. Both concentrate on vertical changes in mire water-levels controlled by peat accumulation. These models have been perhaps too influential (Tallis 1983) because they do not account for the processes that cause floating mat establishment on lakes (Poore and Walker 1959, Tallis 1973), inception of mires on mineral soil (paludification) (Smith 1959, Barber and Clarke 1987, Foster *et al.* 1988, Foster and Wright 1990), the formation of mires in areas affected by flowing water (Kulczynski 1949, Siegel 1983), or the possibility of reversed succession (Iversen 1964, Walker 1970, Sjörs 1990).

2.3.2.2 An autogenic model of acid mire formation incorporating lateral water flow.

Having considered the shortcomings of the terrestrialization hypothesis, Kulczynski (1949) formulated an alternative scheme to explain peatland development, based on water movement in mires. This hypothesis was largely developed from Kulczynski's observations of an extensive area of peatlands on the Russian-Polish border known as the Pripet Marshes.

Water movement was regarded as the fundamental factor in mire differentiation. Bogs developing in absolutely immobile water, such as at the crest of water partings (water flow dividing lines, usually created by relatively higher ground), in completely enclosed lakes or on raised peat mounds would be ombrophilous. Mires developing in areas of mobile groundwater would assume the character of fens. A third peatland category was recognized in this system, namely transition mires which were either rheophilous (groundwater-fed) mires with insufficient water supply or rheophilous mires that had recently converted from fen to ombrotrophic bog.

The Pripet marshes are low-lying with base-poor permeable geology and subdued relief. Under these conditions Kulczynski (1949) found that ombrotrophic bogs rarely had basal fen peats. Water partings appeared to have always supported raised mire alone, whilst fens were only found in the valleys. The transition from fen to bog was observed however, where peat had accumulated above the level of the shallow valley sides enabling a water flow line to establish across a former water parting. The new flow line deprived surface peats of groundwater thus converting the hydrology to an ombrotrophic regime. It is interesting to note that increased mire drainage was proposed as the trigger for acidification. Heinselman (1970) has invoked the same mechanism for raised bog formation in the Lake Agassiz Peatlands of Minnesota.

Kulczynski's (1949) model of mire differentiation, based on lateral water movement may be extended to consider autogenic change taking place in a valley mire, unaffected by the river capture process described in the previous paragraph. In section 1.3 the effect of nutrient supply to the peatland, by ground and surface waters, was identified as of considerable importance to the maintenance of a high base status and pH level.

In sites lacking frequent surface inundation, areas furthest from the source of a nutrient rich groundwater or surface water supply may acidify first (Kulczynski 1949, Giller and Wheeler 1988, Wheeler A.J. 1992). Water flow rate is highly significant for plant nutrition, both in minerotrophic and ombrotrophic peatlands (Damman 1986). High rates of lateral water movement, even in oligotrophic conditions effectively increase the availability of nutrients (Ingram 1967, Damman 1986). Therefore, water movement may be expressed in the spatial zonation of different vegetation types (Ivanov 1981). Accumulation of peat tends to reduce the efflux of water (Kulczynski 1949, Bellamy 1968, Moore 1986, Clarke 1988) due to its property of low hydraulic conductivity (Ingram 1983) and as a consequence, base supply is autogenically

reduced as water flow is redirected around the margins of the mire basin (Bellamy 1968) or via a channel running through the mire. However, bases continue to be lost from the peat surface due to leaching and uptake by plants. Intermittent drying out of the fen surface may also favour acidification due to the release of H^+ ions as a by-product of oxidation processes (Walker 1970, Proctor 1994, Kazda 1995), creating conditions suitable for the colonization of poor fen species such as *S. palustre* and *S. recurvum*. Species within the *Sphagnum* genus are powerful ecosystem engineers, capable of rapidly acidifying the surface peat. The action of *Sphagnum* is discussed in more detail in section 2.3.3.1.

2.3.2.3 The interaction of vertical and horizontal water movements during raised mire formation.

Bellamy (1968) considered the rate of water flow through an infilling lake basin and proposed that high rates of water movement would result in the formation of a dense, slowly accumulating peat deposit with a high proportion of allochthonous (transported) material. Water would therefore flow over the peat surface. Once the peat had emerged from the general water-level, flood events would continue to inundate the peatland. In contrast basins with a very subdued efflux would produce light peat which could float as a mat. Measurements taken in the Louisiana Delta, on floating mats, support this statement (Swarzenski *et al.* 1991). However rates of gas production, species composition (Hogg and Wein 1988) and compaction (Kratz and DeWitt 1986) are also important in determining mat buoyancy. The ability of the peat surface to float, and therefore avoid surface inundation, may enable ombrotrophic communities to develop over a flow line of base-rich groundwater (Wiegers 1990). Siegel and Glaser (1987) demonstrated that as little as 50 cm of peat may be needed to achieve total separation between solute-rich groundwater and oligotrophic vegetation. Where acid geology creates oligotrophic lake waters, a floating *Sphagnum* mat may develop directly in the surface waters (Tallis 1973).

Even if mat floatation does not occur, expansion and contraction of peat may be sufficient to prevent surface inundation and encourage oligotrophy. In the Norfolk Broadlands, Giller and Wheeler (1988) found that fledgling acid *Sphagnum* carpets (<150 years old), which were unrelated to relict ancient raised bog systems, had formed in rich fen sites. All of the oligotrophic patches were sited on peat that was capable of considerable vertical expansion. Thus inundation from the Ca^{2+} rich groundwater was avoided. The evidence from the Norfolk Broadlands shows that the spongy properties of *Sphagnum* augment the ability of the carpet to swell (Giller and Wheeler 1988). However, the expansion properties of the peat are mainly determined by the preceding fen community type. Thus, acid patches only form regularly on flexible *Phragmites* and *Typha* dominated peats and rarely upon more solid *Carex paniculata* peat. In turn, water flow, water chemistry and species availability may determine the preceding fen type (Lambert 1951). Almendinger *et al.* (1986) also demonstrated that the ability of the peat surface to move vertically was vital for the presence of raised bog communities, under conditions of variable groundwater seepage.

In larger peat forming systems such as the Red Lake Peatlands, fens and raised bogs might be abruptly differentiated within the peat expanse, indicating rapid spatial changes in water chemistry (Siegel 1983). Fen vegetation in the region has a pH range of 5.2 to 7.0 and a high Ca^{2+} content, whilst raised bogs lying in close proximity can vary from pH 3.8 to 4.1 and have low Ca^{2+} levels (Glaser *et al.* 1981). Siegel (1983, 1992 and Glaser 1992) have invoked groundwater discharge (artesian flow) as a mechanism to account for the spatial distribution of mire types. Fens are maintained in zones where upwelling of solute loaded water from the underlying geology reaches the mire surface. Bogs are situated in zones of groundwater recharge with their lateral growth being limited by the neutralization of bog waters, by groundwater discharge. However, whilst these hypotheses may explain the current distribution of mire types, Siegel (1983) has not explained the initial process that causes the onset of mire differentiation; since the development of domed water mounds under raised bogs, within the peat expanse, were suggested as the factor driving most groundwater circulation.

2.3.2.4 The Mire climax model.

The Bog Climax Model presented by Klinger (1996), based on the bog climax hypothesis (Klinger 1990, 1991), is an attempt to provide a more comprehensive framework than that offered by the concept of the hydrosere. Klinger (1996) has integrated the processes of terrestrialization and paludification and incorporates the ideas of Walker (1970). The model proposes that bogs and fens initiate from the margins of standing water bodies, spreading outwards into the water via terrestrialization and onto mineral ground via paludification. The sequence of wetland development will attain a climax situation in the ombrotrophic bog phase. The model also proposes that mesophytic (upland) woodland marginal to the wetland expanse is only maintained so long as allogenic factors such as fire (Section 2.3.7.3) hinder the advancing mire front. Klinger's (1996) model is substantially similar to processes described by a number of mire researchers, differing only in the proposed climax status of ombrotrophic bogs.

2.3.3 Mechanisms leading to the formation of a domed water-table in peatlands.

In sections 2.6.2.1 to 2.6.2.3 the factors of peat accumulation and hydrology that lead to the removal of the groundwater influence from the peat surface were examined. This section deals with the immediate mechanisms that create and maintain a raised water-table once the prerequisite isolation from the groundwater has occurred.

Capillarity was considered to be the main mechanism by which raised bogs maintained a perched water-table (Bellamy 1972).

'The peat mass can form a reservoir above the actual level of the groundwater producing what is in fact a perched water-table held within the peat mass by capillarity against gravity. This process could be regarded as vertical paludification' (Bellamy 1972, p15).

Consequently, the mechanism that is frequently cited to account for the transformation from a rheotrophic hydrological system to an ombrotrophic one, is also the drawing up of water within an accumulating peat body, by capillarity (Tallis 1983). However, Ingram (1982) has presented several lines of evidence which suggest that such matric forces are not significant in deep peats. First, the maximum recorded rise in water, through an experimental peat column is 50cm (as recorded by Granlund 1932, cited in Godwin 1954) whilst raised mire water-tables commonly attain altitudes of >5 metres. A rise of this magnitude would require a mean pore radius of <3 μ m. This implies complete humification of the entire depth of peat and does not allow for levels of fresh and poorly humified peat which are frequently found in bogs.

Second, the capillarity hypothesis has no mechanism for generating a dome shaped water-table which is common to all raised mires (Ingram 1982).

Third, sediments that remain waterlogged purely due to matric forces contain water under tension with negative hydraulic potentials. If raised mire water displayed these properties, dip well water-levels would be at the same level as the lagg streams rather than just under the peat surface, which is the observed situation. Therefore, the majority of the peat body displays a positive hydraulic potential.

Ingram (1982) has explained the raised water-table using the mechanism of impeded drainage. Humified peat has a very low hydraulic conductivity (Ingram 1983, Siegel 1983), hindering the lateral movement of water. This effect is great enough to enable a pool to exist for some time, on a peat surface, within a few metres of a cutting. The raised water-table, therefore, represents a '*dynamic equilibrium between recharge and seepage*.' (Ingram 1982). This implies that the general water movement through a raised peatland should be in a downward direction and that the establishment of ombrotrophic conditions requires a certain depth of unsaturated peat.

The passage of water in a saturated permeable material such as a sandy or silty soil obeys Darcy's law. Flow rate is dependent upon the viscosity of the water, the pressure gradient and the saturated conductivity of the soil (Rycroft *et al.* (1975). If Darcy's law is a true reflection of environmental conditions, the permeability of the material should remain constant through time, with differing water pressures and with variations in the thickness of the permeable material. Frequently, however, humified peat does not conform to Darcy's Law, since saturated conductivity may vary with changes in each of these factors Mathur *et al.* (1991). This suggests that further factors affect the conductivity of peat. Mathur and Levesque (1985) first proposed that the production and retention of occluded or supersaturated methane may block pore spaces in the catotelm, rendering the peat impermeable. Even at low temperatures and in acid conditions sufficient anaerobic bacteria exist in the catotelm to produce significant amounts of methane (Brown *et al.* 1989). A proportion of the CH₄ production is lost to the atmosphere, approximately 66 giga tonnes from all northern wetlands (Mathews and Fung 1987). However, Klinger *et al.* (1994)

found that emissions were variable and could be very low, with variance most closely related to changes in water-table and sedge productivity. These findings support Diné *et al.* (1988) and Nilsson and Bohlin (1993) who demonstrated that considerable quantities of methane could be retained in peat and that concentrations increased with depth in ombrotrophic *Sphagnum* bogs.

Methane is sparingly soluble in water, unlike carbon dioxide. Therefore, Brown *et al.* (1989) concluded that sufficient CH₄ was present in the catotelmic peat for free occluded gas to exist within pore spaces. Constantz *et al.* (1988, cited in Brown and Overend 1993) have demonstrated experimentally that trapped air in soils dramatically reduces hydraulic conductivity, therefore, it may be reasonable assumed that methane acts in a similar manner in peat. This explanation of the low conductivity of peat has important implications for the mechanisms leading to the fen/bog transition. Clearly, enough time must pass and sufficient overburden of peat must develop before hydrostatic pressure retains significant quantities of methane, resulting in the blockage of pores in the peat matrix. The shallowest record of occluded methane was gained from a peat sample at 45 cm depth (Butler *et al.* in prep., cited in Mathur *et al.* 1991). Records of high methane production at 10 to 15 cm in wetter acid mires have been recorded, but, most of this gas is evolved to the atmosphere (Svensson and Rosswall 1984). Therefore, other mechanisms are needed to initiate the raised water-table.

Granlund's (1932) work established that capillarity can hold water above the general groundwater-level to a height of 50 cm. Thus, rainwater may be held in small peat hummocks, or in a partially drained peat surface, against gravity due to the strength of its surface tension. Studies of the vegetation composition of 'kragge' carr woodlands in the Netherlands, found that rainwater tended to 'pond up' in the surface layers of peat and that incipient ombrogenous conditions could exist on the woodland floor after just 30 to 60 years from the initial invasion of carr species (Wiegers 1986). An accumulation of peat reaching 40 to 45 cm depth under such conditions would then meet the requirements for the retention of methane. Reduced drainage caused by the build up of methane could conceivably take over from matrix forces, enabling the raised water mound to accumulate above 50 cm in height.

2.3.3.1 The influence of individual plants species on fen/bog transition mechanisms.

Phragmites australis, *Typha* spp., *Cladium mariscus* and *Carex paniculata*.

The species composing an antecedent fen have an important influence on the mechanisms of raised bog development due to physical differences in the peat and the topography of the mire surface created by each species. In favourable habitats *Phragmites australis* (Haslam 1972) and *Typha latifolia* may produce large quantities of litter and relatively light peats, forming floating mats. These peat rafts are capable of protecting fledgling oligotrophic communities from flooding events, thus hastening the transition to ombrotrophy (Giller and Wheeler 1988). By contrast *Cladium mariscus* and *Carex paniculata* (Lambert 1951) produce denser peat hindering floating mat formation. However, *Carex paniculata* also produces

large tussocks that enable oligotrophic bryophytes and tree species such as *Alnus*, *Betula* and *Salix* to invade the wetland community, due to the height of the tussocks above the groundwater-level (Lambert 1951, Walker 1970), thus producing a swamp or semi-swamp carr. These oligotrophic hummock communities may subsequently provide the foci for acid mire formation.

***Alnus glutinosa*, *Betula pendula* and *B. pubescens*.**

Alnus glutinosa may invade a range of solid (Den Held *et al.* 1992) and semi-floating base-rich substrates (Wiegiers 1990). Within the base-rich *Alnus* carr several sub-associations can be discerned (Wiegiers 1986). Wiegiers found that each of these communities represents a line of progressive peat formation tending towards more aerated conditions in the surface layers of the peat and lower levels of nutrient availability. *Alnus* spp. fix nitrogen (N) in root nodules producing, peat rich in N compounds. The growth of root boles also tends to elevate the peat mass in close proximity to individual trees. The resulting increase in humification of N rich peat within the raised areas can result in significant acidification since H^+ ions are produced as a by-product of N mineralization (e.g. Kazda 1995). With the trend towards increasing acidity and base depletion, the composition of the woodland trees tends to change towards dominance by *Betula*.

Betula pendula and *B. pubescens* are frequently found in the palaeoecological record at the transition between fen and bog. (e.g. Moore 1977). *B. pubescens*, in particular, may grow on very acid damp, peaty ground with a pH as low as 3.5 (Atkinson 1992). *Betula pendula* is usually considered to be an inhabitant of lighter soils but Atkinson (1992) regards the two species as having little ecological difference. The presence of *Betula* spp. in a transitional carr woodland may result in a degree of soil improvement and de-acidification (Gardiner 1968). However, this effect may be completely off set by the action of *Sphagnum* species in the ground layer. *Betula* and other carr woodland species such as *Alnus glutinosa* may favour the establishment of *Sphagnum* by producing a humid sheltered micro-environment, less susceptible to desiccation.

***Pinus sylvestris*.**

Pinus sylvestris may occur in new oligotrophic communities during the establishment of ombrotrophic mire conditions (Godwin 1975) although individuals are frequently stunted because the growth of the species is limited by high water-tables. The presence of *P. sylvestris* in the mire community may have several important impacts that shape further mire development. Firstly, root uptake of nitrogen (N) compounds may cause substrate acidification so long as the concentration of nitrate accounts for less than 70% of the total available N (Arnold 1992). Secondly, *P. sylvestris* needles contain relatively high concentrations of resin acids (Buratti *et al.* 1990) which produce a strongly acidic litter upon decomposition. Thirdly, sapwood extracts may efficiently inhibit fungal activity (Bruce and Munro 1995). All of these factors favour the accumulation of oligotrophic peat and the invasion of acid mire species such as *Sphagnum*.

Sphagnum.

A profound and virtually irreversible change occurs once *Sphagnum* enters the peatland ecosystem (Walker 1970). *Sphagnum* may invade fen communities at almost any stage, although the genus frequently establishes in the carr phase. A number of *Sphagnum* species commonly inhabit carr woodland eventually forming extensive carpets around the root barks. *Sphagnum squarrosum* is most common in depressions whilst *Sphagnum fimbriatum* occupies the highest hummocks, with *Sphagnum palustre* and *Sphagnum recurvum* found in intermediate areas (Wiegers 1988). Other species associated with the moss community include *Aulacomnium palustre* and *Mnium hornum*, which grows on exposed tree roots. Whilst the appearance of *Sphagnum* signals a major decrease in nutrient availability and pH, all of the above members of the genus are capable of tolerating relatively high nutrient levels and pH compared to true raised bog species.

Sphagnum is capable of out-competing the carr woodland community through the operation of several processes. Firstly the leaves of *Sphagnum* mosses are well adapted to waterlogged conditions having a network of porose hyaline cells capable of storing great quantities of water whether living or dead. (Daniels and Eddy 1990) A carpet of the moss can therefore act as a large sponge inhibiting the dispersal of rainwater, thus creating an elevated reservoir (Ingram 1982). The collection of rainwater on the surface dilutes the concentration of mineral nutrients available to shallow rooted plants. Under waterlogged conditions many of the trees will fall into this category.

Secondly, *Sphagnum* has a well developed capacity to draw cations out of the surrounding environment and replace them with hydrogen ions (H^+). (Clymo 1963, 1964, Daniels and Eddy 1990). This places *Sphagnum* at a competitive advantage where nutrients are a significant limiting factor in the ecosystem, whilst reducing the pH of the peat (Gagnon and Gline 1992). Therefore, *Sphagnum* acidifies the carr woodland actively as well as passively. *Sphagnum* itself is naturally well adapted to tolerate low pH. Rochefort *et al.* (1990) showed that the growth rate of several oligotrophic *Sphagnum* species actually increased when plants were subjected to artificially lowered pH levels.

Thirdly, *Sphagnum* is apparently able to inhibit tree seedling growth, preventing regeneration. Wiegers (1988) reported that seedlings of *Betula* spp. and *Alnus glutinosa* in Dutch Kragge woodland were absent from most *Sphagnum* carpets, being found only on bare wet soil or in loose clumps of *S. squarrosum* and *Mnium*. Ohlson and Zackrisson (1992) reported similar findings. Furthermore, research in the forests of south-eastern Alaska and northern New York suggested that *Sphagnum* growth is correlated with the death of the feeder rootlets of adult trees (Klinger 1990). Klinger regards 'bryophyte-paludification' of mature forest as one of the main mechanisms leading to widespread forest 'die back', which need not be restricted to wetland woodland. This hypothesis is not new having been proposed by Weber (1908) and restated by a number of other researchers including Noble *et al.* (1984).

The ability of *Sphagnum* to grow apically from the tip, leaves its lower branches starved of light. These die and enter the semi-waterlogged zone as the water-table rises with the upward growth of the mosses.

Sphagnum is therefore an important peat former (Daniels and Eddy 1990). Continued accumulation can eventually replace carr woodland with acid raised bog.

2.3.4 Quantitative and simulative models of mire development.

The models discussed in previous sections are relatively simple qualitative explanations of mire processes that may be represented pictorially. At present there is 'no single well defined conceptual model' (i.e. brief telescoped explanation) (Zobel 1988) that satisfactorily accounts for all the major features of mire succession. However, two further basic types of modelling are available for the exploration of mire form and process, namely quantitative models and simulative models Clymo (1992/93). Most quantitative models aim to characterize the nature of peat accumulation and, or decay (Clymo 1978, 1984b, Winston 1994, Almquist-Jacobsen and Foster 1996). Clymo (1983, 1984a and 1992/3) provided a detailed examination of this subject. Attempts have also been made to produce quantitative models of the domed groundwater form of raised bogs (Ivanov 1981, Ingram 1982) and to examine carbon accumulation in mires on the basis of CO₂ and CH₄ budgets (Silvola and Hanski 1979, Aleksandrov and Logofet 1985, in Zobel 1988). All of these models by necessity involve major simplification of the systems being modelled to avoid the loss of all understanding in a maze of complexity (Clymo 1992/3). Frequently the simplifying assumptions dispense with the fen stage of mire development altogether assuming that raised mires form on a flat impermeable plane. Therefore, many qualitative models developed to date have little bearing on the processes causing the fen/bog transition. Neglect of this aspect of mire form may introduce considerable error into some models. The usefulness of models may be further reduced due to difficulties associated with estimating the values of constituent variables, see for example Kneale's examination of the groundwater mound model. (Kneale 1987).

Wildi (1978) represented an ambitious attempt to produce a simulation model of bog development which includes both fen and bog phases. Variables incorporated into the analysis included the amount of water, the quantity of peat, the biomass of fen and bog plants and the amount of dissolved plant nutrients. An array of parameters controlling the processes were specified and differential elevation between mire segments was also modelled. The results of the simulation successfully model some aspects of mire succession such as progressive immobilization of nutrients and increasing acidity with time, for certain slope conditions. However, some versions of the simulation produced outcomes that were not present in field observations indicating that the model required improvements. Clymo (1992/3) concluded that such models may be useful as aids but '*they are no substitute for observation and experiment.*' p135, due to the great complexity of natural systems. Korhola (1992) agreed with this opinion.

Before moving on to consider the allogenic or external factors that could affect the development of the fen/bog transition, such as climate change and human impact, two further autogenic models of raised bog

growth need to be considered because the consequences of their operation would prevent the clear identification of a climate signal in ombrotrophic peat. If proxy climate signals cannot be discerned from autogenic processes and 'ecological noise', then the climatic conditions prevailing when the first ombrotrophic mire community established cannot be investigated and used as evidence for the environmental conditions associated with the transition. The two models in question are those of the 'Cyclic succession of hummocks and hollows' (Von Post and Sernander 1910) and the hypothesis that raised bogs develop through an autogenic sequence of hydrological changes leading to a dry bog surface.

2.3.5 Autogenic cyclic succession of raised bog hummocks and hollows Falsification of a model.

The theory that raised bog vegetation develops through an ongoing successional cycle, producing an alternating lenticular hummock and hollow stratigraphy, was proposed by Von Post and Sernander (1910). The uncritical reviews and reiteration of the cyclic theory of regeneration by Clements (1916), Osvald (1923) and Tansley (1939) were extremely influential in establishing its universal acceptance during the early to mid twentieth century. Such was the influence of the theory that it formed the basis for the interpretation of a number of important papers on the ecology of raised mires, see for example Godwin and Conway (1939) and Kulczynski 1949. However, the proposals made by Von Post and Sernander (1910) were merely based on their interpretation of patterns in the surface vegetation. There is no published stratigraphic work relating to the formulation of the concept. Therefore, Barber (1978, 1981) rigorously tested the theory for the first time using detailed descriptions of peat face sections and numerous macrofossil analyses on monolith samples. The test of the theory provided no evidence to suggest that hummocks and hollows alternate in the stratigraphy in a consistent manner. Barber (1981) therefore concluded that the theory of cyclic regeneration may be falsified. Instead hummocks and hollows appear to expand and contract in response to bog surface wetness. Backéus (1990) has subsequently retrieved Sernander's note books from 1909 and 1910, to discover whether his ideas were based on stratigraphic evidence that was never published. However, he failed to find any such work. Since the publication of Barber (1981) a number of other researchers have reported that data from their sites do not support the theory either. (see for example Smart 1982, Svensson 1988a and b).

2.3.6 Autogenic development of surface dryness in raised bogs.

The concept that raised bogs may develop through an autogenically driven sequence of hydrological change tending towards increased surface dryness was first proposed by Granlund (1932), in order to explain the morphology of recurrence surfaces (cited in Godwin 1954). Granlund suggested that under constant climatic conditions raised bogs would have a maximum height to which they could grow, limited by the steepness or curvature of the dome. Having reached the greatest attainable altitude for the prevailing climatic conditions, the bog would enter a 'standstill phase'. The hypothesis postulates that this halt in the growth of the bog occurs because surface water losses from the peat, due to evaporation and drainage, increasingly counteract the inputs of water to the surface from precipitation and capillary rise from lower

peat levels (Tallis 1983). During periods of wetter climate, the maximum theoretical height of a raised bog would be greater than in dry periods. This part of the hypothesis is endorsed by Wickman (1951):

'A critical study of Granlund's curves shows that his relationship (between climate and bog height) is not coincidental but real and that it is not a consequence of the methods chosen by Granlund when drawing his curves.' (Wickman 1951, p 414).

The fresh, poorly humified peat on the younger side of a recurrence surface would be explained by a change to more Atlantic conditions, freeing the bog to grow towards a new maximum. Multiple recurrence surfaces could result from the operation of several of these cycles. Aaby (1976) has agreed with Granlund's concept., stating that whilst decreasing peat humification may be attributed to higher precipitation and/or lower rainfall, increased humification need not be climatically induced.

'The opposite shift, from light to dark coloured peat does not necessarily depend only on climatic parameters because peat formed under stable climatic conditions will also show the same trend in decompositional behaviour, since the relative distance to the water-table increases as new peat accumulates.' (Aaby 1976)

The concept of the autogenic drying trend could be used to explain the theoretical succession of bog species, from open water pools to mature bog hummocks, which begins with *Sphagnum cuspidatum* and pool algae, proceeds through a succession of lawn dwelling *Sphagnum* species and ends with a *Calluna-Eriophorum* dominated association. (Ratcliffe and Walker 1958).

Godwin (1954) criticized Granlund's hypothesis for two major reasons. Firstly, to explain a sequence of superimposed recurrence surfaces (a feature of many bogs), the hypothesis requires that Holocene climatic conditions have developed, possibly with some halts, towards ever increasing oceanicity. Godwin suggested that climate was much more likely to have fluctuated over the period in question between wet and dry phases. This opinion is supported by the detailed macrofossil work of Barber 1978, Haslam 1987, Blackford 1990 and Stoneman 1993.

Secondly, Godwin (1954) stated that an increased height of 50 or 60 cm in a large bog of several kilometres diameter *'.....could not possibly be held responsible for the entire difference between continued growth and total cessation.'* By contrast Godwin (1954) suggested that fluctuations in rainfall and evaporation, annually and over much greater time periods must be a major influence on bog stratigraphy.

Evidence for great longevity of pools also places doubt on the autogenic drying hypothesis. Foster and Wright (1990) demonstrated that deep and virtually static pools have been in existence on Hammarmossen almost since its initiation. Rochefort *et al.* (1990) described a mechanism which may account for this longevity. They find that hummock top, mid-hummock and hollow species, decay in the ratio 7:9:13. Thus accumulation is highest in hummocks. Johnson *et al.* (1990) and Johnson and Damman (1991) corroborated the finding, showing that *S. cuspidatum* peat may decay up to one and a half times more

rapidly than the hummock species *S. fuscum*, despite the wetter conditions in the hollows, thus deepening the pools. Hummocks may also be very long lived (Walker and Walker 1961), persisting as a 'wall' of hummock peat down through the bog, surrounded by pool peat.

The implication in Granlund's hypothesis is that, under constant climatic conditions the pace of peat development exceeds the rate at which the water-table can rise due to matric forces, whilst greater elevation of the peat surface enables freer drainage. Having established in section 2.6.7.1 that raised bogs are elevated, principally due to impeded drainage, ineffective capillarity may be dismissed as a process causing autogenic drying. This leaves the process of increased drainage, which is unlikely to operate if the bog remains undissected, because the hydraulic conductivity of peat is low (Ingram 1982). In addition, the principal input of water to the surface is from above and not from below. However, Chapman (1965), Ivanov (1981) and Moore (1986) suggested that accentuated drainage may occur due to the creation of erosion channels, by surface flow on a dome that is increasing in gradient. This would lead to a humified surface layer. Many bogs may never reach the stage of developing a dome steep enough for erosion to occur, because there is a height limiting mechanism. Clymo (1983) suggested that a bog will reach its maximum height when the rate of subsidence due to catotelmic decay equals or exceeds the rate of accumulation of new material entering the acrotelm.

Wet and dry phases in the stratigraphy may be interpreted as climatic, as Barber 1981 suggested, provided that there is no evidence for disturbances such as mire dissection, base level change or peat cutting. A humified peat will result from reduced precipitation and/or increased evaporation, whilst lateral drainage continues at much the same rate, thus reducing the water-table. This mechanism has also been suggested by Walker and Walker (1961) along with erosion to explain the observed infilling of shallow pools on a raised bog in Ireland.

2.3.7 Allogenic factors affecting the fen/bog transition.

2.3.7.1 Climate.

Traditional theories of hydrosereal change usually emphasize the role of autogenic processes. Whilst re-evaluating the status of British hydroseres (Walker 1970) stated that *'this essay is concerned almost exclusively with autogenic processes beginning in more or less confined fresh water.'* (pg. 117). Walker went on to describe how sites were selected that were free from significant allogenic disturbances. However, all sites in Britain have experienced considerable environmental change over the duration of the Holocene, not least due to climatic fluctuations (Barber 1978, 1981, Smith 1985, Wimble 1986, Haslam 1987, Blackford 1990, Stoneman 1993, Barber *et al.* 1994). The importance of climate with respect to mire development is also demonstrated in the correlation between climatic gradients and the spatial differentiation of mire types (Damman 1979, Glaser and Janssens 1986). Therefore, climatic fluctuations must be taken into account when considering major changes in mire development such as the fen/bog

transition. A number of recent papers have inferred a significant role for climate change in forcing the rate and sometimes the direction of hydrosere change. Green-Winkler (1988), Korhola (1990, 1992), Kuhry *et al.* (1992) Hu and Davis (1994) and Tipping (1995a) all correlated the emergence of phanerogam dominated peatlands from lakes or pools, with shifts to drier climates. In contrast, fen initiation via paludification (development on a terrestrial surface) has been linked to wet shifts (Davis 1984, Korhola 1994, 1995).

Many researchers have also suggested a link between increased oceanicity and raised peat inception (Weber 1908, Granlund 1932, Godwin 1946, Conway 1948, 1954, Walker and Walker 1961). There appears to be a long-standing opinion in the literature that raised bog formation occurs during wetter periods (see for example Berglund *et al.* 1983, Green-Winkler 1988, Tipping 1995a). Whilst this factor may be important for the onset and continuation of paludification (Korhola 1994, 1995) and the rejuvenation of existing raised bog peats (Aaby 1976, Barber 1978, 1981, Smith 1985, Dupont 1986, Wimble 1986, Haslam 1987, Svensson 1988a, Stoneman 1993, Barber *et al.* 1994) the same may not be universally true for the inception of raised peat on a fen surface. Increased oceanicity will also increase the level of the groundwater. A change to higher groundwater-levels, could operate against the main mechanism of autogenic succession in fens, namely the progressive removal of the groundwater effect (Smith and Morgan 1989, Waller 1994). Therefore, a mature fen may not always respond to a wetter climate by switching directly to more oligotrophic or even ombrotrophic conditions, unless the mire is sited on acidic parent material. By contrast there is limited evidence to suggest that mire acidification can occur during a period of relatively low effective precipitation (Svensson 1988a). At Store Mosse raised bog rejuvenation occurred during periods correlated with higher lake levels and wetter climatic conditions, as expected. However, the stratigraphic transition from fen peat to ombrotrophic peat correlated with a period when lake levels were low. The *Sphagnum* species that established at the transition were hummock dwellers, such as *S. fuscum* and *S. capillifolium* var. *rubellum*, indicating a relatively dry acid bog. During Svensson's concluding remarks he stated;

'It ought to be stressed that the bog formation on the fen with colonization by Sphagnum fuscum happened when dry conditions were prevailing. This is quite contrary to general opinion viz. that bog formation was caused by a climatic change towards more humid conditions.' (Svensson 1988a p57).

Perhaps the important factor is a change towards **relatively drier** conditions. The preceding wetter conditions would serve to build fen levels up to the level of the high water-table. Drier conditions would provide the necessary removal of the groundwater effect. However, the old fen surface still needs to receive sufficient rainfall to maintain a bog. Streefkerk and Casparie (1987) provided minimum climatic values that are supposedly necessary to allow bog development. These were quoted as a mean temperature below 11°C, a mean annual potential evaporation below 600 mm, an excess of rainfall over evaporation of at least 150 mm and a regular distribution of rainfall throughout the year. It is possible that a bog with

vegetation approaching that of heath, could have a raised hydrology, surviving in rather drier conditions than those suggested by the figures quoted above. It is interesting to note that Godwin (1975) also correlated the first main phase of lowland ombrogenous bog growth to a phase of relatively dry climatic conditions.

However, a change to wet conditions could indirectly facilitate raised bog initiation, by bringing a peatland into a climatic zone that is suitable for bog growth, for the first time. The effect would be lagged because the hydrosere would be set back and would have to redevelop to the stage of mature fen, reaching a position just above the level of the new higher water-table. Therefore, such a trigger could not be correlated with other proxy records of climatic change.

Under constantly wet climatic conditions, the fen would mature and develop above the water-table as with any other climatic zone. In these conditions full ombrotrophic wet *Sphagnum* bog might be expected to colonize the mire surface rapidly facilitated by the leaching out of bases from the newly emerged peat surface.

2.3.7.2 The relative importance of climate and autogenic processes in raised mire initiation.

The discussion in Section 2.3.7.1 demonstrates that the relative importance of autogenic processes and climate change during mire development is still a subject of considerable debate in the literature. Foster and Wright (1990) tested three models of raised bog development at Hammarmossen and Nittenmossen, using basal radiocarbon dates in order to evaluate the relative importance of allogenic and autogenic factors. The models are (1) development from a single locus (2) development from multiple loci, and (3) simultaneous peat initiation across the whole site as proposed by Granlund (1932). The basal dates indicated that both bogs had spread centripetally from a single locus at a steady rate. From this Foster and Wright (1990) concluded that autogenic processes dominate mire development. This conclusion was also reached by Tolonen *et al.* (1985). In addition Foster and Wright (1990) suggested that the lateral and vertical growth increments revealed by the radiocarbon dates supported the theoretical models of Clymo (1978, 1984) and Ingram (1982, 1983). However, the basal radiocarbon determinations do not represent raised mire development directly onto an impermeable plane, although this process may be possible (Ingram 1967). The material dated by Foster and Wright (1990) was mainly fen peat, therefore, their dates represent the paludification of the basal fen and not the inception characteristics of a raised bog. A similar study by Korhola (1992) at a wider range of sites found that *'results do not fully corroborate the theoretical models that emphasize the autogenous nature of the development of raised bogs'* p25. In particular Korhola (1992) found that mires could initiate over large areas at one time and that much of this lateral extension occurred in the fen phase. Similar results have been reported from other sites (Svensson 1988b, Tipping 1995a). Additionally, the lateral and vertical rate of peat accumulation could vary significantly even within one site. Some of these fluctuations have been linked to climate change. (Korhola

1992, 1995). Subsequently, Almquist-Jacobson and Foster (1995) have assigned a more prominent role to allogenic forces in their integrated model of raised mire development. Field evidence, collected to evaluate the usefulness of the model, includes some data on the timing of the fen/bog transition at seven sites. Significantly, Almquist-Jacobson and Foster (1995) found that at a number of sites the fen/bog transition coincided with recorded low lake levels in Scandinavia, suggesting a possible link with a change to drier climatic conditions. This conclusion is in accordance with Svensson (1988a). Kubiw (1989) working on the Muskiki Lake peatlands concluded that both autogenic and allogenic processes have been significant in shaping the developmental pathways of the mires with factors such as deglaciation, topography, drainage, moisture conditions, vegetation, fire and climate all interacting, such that the sequence of bog development cannot be determined from knowing the original site conditions. Klinger (1990, 1991, 1996) attempted to define the role of allogenic and autogenic forces more explicitly in the bog climax hypothesis, postulating that early successional pathways are primarily under the control of allogenic factors, and that during the course of succession there is an increase in the importance of autogenic factors, which come to dominate later successional pathways. However, Klinger (1990, 1991, 1996) did not state where the transitional phase between fens and bogs fits into this scheme.

2.3.7.3 Fire.

The role of human induced fires has been recognized as being of importance in the inception of blanket mires (Moore 1973, 1975, 1993) in conjunction with climatic deterioration, podsolization and prevention of tree regeneration (Doyle 1990, Fossitt 1996). In contrast, fires on lowland raised mires are often interpreted as having only short lived effects. Kuhry (1994) observed that the mire vegetation response to fire is generally limited to a few decades after the event. However, a period of very dry conditions would heighten the vulnerability of a mire (Mackay and Tallis 1996), increasing the depth to which the peat would be burnt. Klinger (1996) assigned a more important role to burning events, with respect to lowland mire initiation, suggesting that fires on the margin of a peatland complex enable woodland ecosystems to perpetuate at the expense of mire paludification. The return time for burning episodes could therefore be regarded as one factor controlling the rate of mire paludification.

Tolonen *et al.* (1985) suggested that fires may raise the water-table of a peatland due to the blockage of the peat matrix by fine charcoal particles. If this process occurred in a mature fen which had recently developed above the zone of regular inundation, an impermeable layer could form, suitable for the retention of rainwater on the mire surface, leading to progressively more oligotrophic conditions.

2.3.7.4 Hydrological change in the drainage basin network.

Local hydrological change in the drainage network surrounding a mire complex may significantly affect the process of mire acidification as well as the nature of raised peat. The highly detailed examination of Emmen bog (Casparie 1972, Casparie and Streefker 1992) revealed that the end of fen and seepage, peat formation was very sudden at 5100 radiocarbon years BP. Closer examination of the old fen surface, using

archaeological style excavations showed that the mineral peat surface was crossed by numerous large desiccation cracks. Macrofossil and pollen evidence indicated that *Alnus* woodland was the immediate colonizer of the newly dried out surface, however, the replacement of wood peat by humified *Sphagnum* peat over large areas of the system indicates the rapid spread of ombrogenous bog conditions shortly after the fen peat dried out. Casparie (1972) concluded that the raised peat developed in the Hunze depression, in response to the falling-off of the groundwater and seepage supply, as a consequence of changes in the drainage network external to the peatland system.

2.3.7.5 The effect of sea level change on the freshwater-table and mire development.

The effect of sea level rise triggering the inception of freshwater peats, in the coastal lowlands, is clearly recognized in the literature. (Smith 1985, Pons 1992, Wheeler 1992). Pons (1992) described the formation of a band of fen peat several kilometres wide behind the dune barriers of the Dutch coast. These wetlands were able to develop due to the ponding up of fresh groundwater behind the rising sea waters. In the Fenland of East Anglia, Wheeler (1992) recognized several phases of peat inception, each related to the rise of the groundwater-table in response to changing base level. Successional stages that last rather longer than expected have been attributed to the effects of gradual sea level rise. Kidson and Heyworth (1973) explained the existence of three metres of coastal alder carr peat accumulation, as resulting from this process.

At the other end of the spectrum there are numerous clear examples of rapid sea level rise terminating peat growth. (see for example, Waller 1994, Shennan 1994a and b). However, the response of wetland vegetation to gradual sea level rise is rather more complex. In the Lower Scheldt basin, Denys and Verbruggen (1989) described changes from mesotrophic fen to wet heath and local acid bog formation, with large intervening pools of freshwater. However, Smith and Morgan (1989) found virtually the opposite vegetational response. In the Gwent levels the rising base level appears to have caused a retrogressive succession from *Salix* and *Alnus* carr woodland to reedswamp before stabilization and the onset of the main succession to ombrotrophic bog occurred. This evidence was supported by Wheeler (1992) who also described the replacement of *Alnus* carr by reedswamp under conditions of sea level rise. Wheeler concluded that the advance of marine conditions appeared to have prevented Wood Fen developing into acid bog. Acidification is more likely to occur in susceptible basins that lie above the regional groundwater-table and thus are protected from all but the largest sea level fluctuations. The literature presented above suggests that base level change can cause the retardation or advancement of hydrosere successions in coastal freshwater systems by raising or lowering the level of the regional groundwater-table. This factor could be important in some fen/bog transitions.

2.4 Fen/bog transitions in the literature.

Many of the early stratigraphic studies of raised bogs classified the ombrotrophic peat into two broad units consisting of a lower humified *Sphagnum* peat overlying fen deposits and an upper less humified

Sphagnum peat. (see for example Godwin and Mitchell 1938, Williams, Parry and Parker 1939 in Slater 1972). Humification level H5, on the von Post scale, was often adopted as the classification boundary (e.g. Thomas 1965, Walker 1966). Occasionally, the field stratigraphies include further units such as 'fibrous *Sphagnum* peat' and *Molinia* peat.

However, more detailed stratigraphic and macrofossil work suggests that *Sphagnum* may form a relatively minor proportion of the ombrotrophic deposits immediately superseding many FBTs. The North West Wetlands Survey (N.W.W.S.) has carried out a range of stratigraphic work at sites ranging from Liverpool and Manchester to Cumbria. In the Manchester area Hall *et al.* (1995) studied the deposits of twelve ombrotrophic peatlands producing stratigraphies based on field and laboratory analyses. At Chat Moss the fen levels are directly overlain by humified *Eriophorum/Calluna* peat across the entire expanse of the mire. Similar results have been reported for Ashton Moss, Carrington Moss, Knearsley Moss and other smaller mosses in the study area. The survey for North Lancashire has reported similar findings (Middleton *et al.* 1995 eds.). For example, an abundance estimate macrofossil diagram from Fenton Cottage (Wells in Middleton *et al.* 1995 eds.) shows that *Eriophorum vaginatum*, *Calluna vulgaris* and *Aulacomnium palustre* formed the main components of the lowermost oligotrophic peat, indicating the presence of a relatively dry mire surface.

Detailed stratigraphic studies from the wetlands of Flanders indicated similar findings to the work of the N.W.W.S. At numerous ombrotrophic mire sites (Allemeersch 1991, reprinted in Gullentops ed. 1995) has noted a lower peat unit overlying the fen deposits, containing abundant remains of *Eriophorum vaginatum* and *Calluna vulgaris* with only a minor proportion of *Sphagnum* species indicative of 'hummock-level' environments.

The identification of dry oligotrophic communities at the FBT, during investigations such as those carried out by the N.W.W.S. support the findings of Svensson (1988a) who found that the FBT at Store Mosse occurred during a period of reduced effective precipitation, as indicated by lake level data. Records of communities indicative of dry mire conditions at the FBT may be traced back at least as far as Weber (1909 in Kulczynski 1949) who considered *Pinus sylvestris* to be an important component of many 'Übergangsmoore' (transition mire) communities. Godwin (1975) has also highlighted the importance of *P. sylvestris* in raised mire peats immediately overlying fen levels.

Figure 2.1 and Table 2.3 present a selection of radiocarbon dated FBTs from British mires. Figure 2.1 shows that ombrotrophic mire formation has occurred throughout the early to mid-Holocene. More recent FBTs have also been recorded, however, these have not been included since they lie outside the study period of the present project. The Tröels-Smith symbols plotted in Figure 2.1 show the importance of *Eriophorum vaginatum* in many of the FBTs.

Table 2.3 Key to Figure 2.1: A selection of radiocarbon dated British fen/bog transitions.

Site code	Site name	Date of FBT cal. B.P.	Source
RWM	Rawcliffe Moss	8850	Middleton <i>et al.</i> 1995
SCB	Scaleby Moss	8370	Walker 1966
RDM	Red Moss	8245	Hall <i>et al.</i> 1995
SLB	Suggan Bog	7715	Smith and Goddard 1991
TRG	Tregaron South-East Bog	7300	Hibbert & Switsur 1976
RHM	Rishworth Moss	6535	Bartley 1975
WMM	Winmarleigh Moss	6520	Middleton <i>et al.</i> 1995
GDF	Goldcliff	5910	Smith and Morgan 1989
ABW	Abbots Way	5530	Beckett & Hibbert 1979
FTC	Fenton Cottage	5300	Middleton <i>et al.</i> 1995
HTM	Hatfield Moor	5100	Smith 1985
SWT	Sweet Track	5015	Beckett & Hibbert 1979
CRB	Crymlyn Bog	3990	Hughes 1993

The existence of relatively dry raised bog conditions, with low levels of *Sphagnum*, immediately after the FBT, at the sites mentioned above, suggests that the processes involved in ombrotrophic mire formation are more complicated than those proposed in the autogenic model of ombrotrophic mire formation as stated by Walker (1970).

A number of specific research questions concerning the FBT arise from the study of the literature presented in the previous sections of this chapter. The main questions of interest are outlined below. These are elaborated in the introductions to Chapter 5 and 6 where appropriate.

- (1) Do allogenic factors such as a climate change, drainage basin change, human impact and base level change have a discernible impact upon the character of the FBT?
- (2) Can a change to conditions of lower effective precipitation cause acidification of a fen and oligotrophic mire formation?
- (3) Does the character and rapidity of the FBT differ between mires in wetter and drier parts of the British Isles and between known wet and dry climatic periods?

(4) Does the *Eriophorum vaginatum* / *Calluna vulgaris* mire that forms immediately above many transitions, occur throughout the British Isles? Does this community represent a dry climate at the time of the FBT or is it related to autogenic factors of mire development?

(5) Does *Sphagnum* form an important part of all transitional communities?

(6) Is acidification still possible when there is little or no *Sphagnum*?

Chapter 3

Methods.

3.0 Introduction.

The reconstruction of mire development pathways, leading to the fen/bog transition, takes advantage of the unique ability of a wetland ecosystem to preserve a record of previous developmental stages (Barber 1994). A detailed examination of macrofossil remains preserved in stratified layers of peat can be used to estimate the composition and occurrence of past communities and to infer contemporary environmental conditions. The approach is based upon the principles of uniformitarianism, which assume that the biological, chemical and physical processes determining the present form of the natural world, have remained constant through time. Only the rate and intensity of their operation is variable (Gould 1965). The concept does not necessarily imply that modern plant communities can act as exact analogues for the fossil record. The further two equivalent ecosystems are removed from each other, in space or time, the greater are the differences between them. This is the principle of the 'Reddened Spectrum' (Williamson 1987). Analogy is, therefore, an important aspect of palaeoecology, because it provides an indication of the magnitude and rate of ecological change through time (Delcourt and Delcourt 1991).

The palaeoecologist's task is to extract the highest possible quality of data, from an often fragmentary record, thus providing a sound basis for inferring the processes that shaped the palaeoenvironment. Research directed at the reconstruction of past peat-forming communities must include the analysis of vegetative macrofossils. In autochthonous deposits (sediments forming *in situ*), such as raised peat, these plant remains provide unequivocal evidence for the existence of a taxon on or close to the sampling site (Grosse-Brauckmann 1986, Birks and Birks 1981) unlike pollen or seeds and fruits, which are subject to at least some degree of transport. (Tauber 1965, Wasylkowa 1979, Price and Moore 1984, Greatrex 1983 in Clarke 1988). Even in partially allochthonous (sediments composed of transported material) fen peats, the vast majority of the vegetative plant remains are deposited in the immediate vicinity of the parent vegetation, thus providing a record of local vegetation change.

However, the degree of preservation displayed by plant tissues differs widely between species (Coulson and Butterfield 1978, Birks and Birks 1981) and with variations in the sedimentary environment (Ohlson 1987). Consequently, some species may be under represented in the vegetative macrofossil archive, whilst others are absent. In addition certain plant remains are difficult to differentiate. Under these conditions the qualified use of other lines of evidence such as propagule macrofossil analysis, may substantially improve the breadth of the record enabling a more detailed reconstruction of the fen/bog transition. Therefore, all components of the macrofossil assemblage will be exploited in this project. Successful integration and accurate interpretation of the data provided by the different techniques requires a clear understanding of their respective strengths and limitations. These factors are discussed in Sections 3.4.1 to 3.4.2 and 3.5.1.

3.1 The rationale and design of the site distribution strategy.

In palaeoecology, as with other natural sciences, an understanding of the effect of differing spatial and temporal scales is required before attempting to infer the operation of processes from biostratigraphic data (Birks 1986 in Berglund). Within palynology, this principle is clearly illustrated by the work of Jacoson and Bradshaw (1981) on site size and pollen source area. The study of a small peat patch in a forest is useful for examining local vegetation processes and small scale human disturbances (Segerström 1991), whilst larger sites receive a greater proportion of far travelled pollen, enabling inferences to be drawn about regional vegetation change (eg. Dumayne 1992). Although macrofossil data are primarily derived from plants that grew within a few centimetres or metres of the sampling point, a consideration of scale is still required, particularly when attempting to evaluate the role of regionally acting environmental forces, such as climate change, on pathways of fen to bog development. Different explanations may be needed to account for small scale fluctuations in mire vegetation and stratigraphy than those required to explain changes to the entire peatland complex (Moore 1986 in Berglund). Aario (1932, in Birks and Birks 1981) recognized this distinction, using the terms 'Kleinform' and 'Grossform' respectively, to describe the two scales of variation. In the present project the equivalent terms large scale (or site scale) and small scale will be used. Within the mire system autogenic factors can mask evidence for the operation of large scale autogenic and allogenic processes, by causing localized fluctuations in macrofossil assemblages, ('Ecological noise', Stoneman 1993). Therefore successful differentiation of allogenic and autogenic processes affecting the fen / bog transition may require comparisons at the site scale and the inter-site scale. Whilst the identification of stratigraphic events that affect the whole mire simultaneously can provide clear evidence for allogenic forces such as climate change (Barber 1981, Barber *et al.* 1994a), the ability to demonstrate synchronous changes in the stratigraphy of hydrologically separate peatland systems would provide further strong evidence for controls on mire development.

Examination of the literature on peatland development (Chapter 2, see Section 2.3), indicates that climate change and, in coastal areas, sea level change, may be very significant allogenic forces affecting the switch from fens to bogs. Other allogenic factors such as human impact and river capture have also been identified as possible allogenic agents determining the course of the transition, therefore, the site distribution strategy has been designed to enable comparisons of the FBT at a range of scales.

Prior to undertaking the main analyses for this project one mire was selected to study the intra-site variability of the macrofossil record. Firstly, the study aims to examine the diversity of mire development pathways occurring in a single peatland, using a set of five macrofossil core sites and extensive field stratigraphy. Secondly, the multiple core analyses enable an assessment of the degree of 'ecological noise' in the data set. The findings from the intra-site analysis have been used to calculate the level of sampling required to identify the main mire wide stratigraphic changes from local phenomena. This information has been used to design the sampling strategy for analyses at the inter-site scale. The details of multiple core study are presented in Chapter 5.

The second part of this project, presented in Chapter 6, is an inter-site comparison of seven further mires. The study has been designed to examine the role of factors such as climate change, base level change, human impact and drainage basin change, on the character and timing of the FBT. To achieve this aim a set of paired sites was selected, running in a transect from Cumbria to Galway Bay, providing numerous possible comparisons. Whilst the specific details of the rationale for site distribution are dealt with in the introduction to Chapter 6, the general design of the strategy is outlined below:-

(1) Raised mires originating from small kettlehole lakes in northern England or Scotland, have been targetted to provide examples of early Holocene FBTs.

(2) Raised mires originating from larger wetland basins, with a longer reedswamp stage have been targetted as likely sources of mid-Holocene FBTs.

(3) **Pairing of two adjacent inland sites (separated by 1 - 5 km):** The selection of two adjacent but hydrologically separate mires enables a comparison of the FBT at sites, experiencing the same climatic conditions, and in glaciated areas, with a similar date for deglaciation. During the selection process sites with a similar basin size were sought for this comparison.

(4) **Inland and coastal paired sites:** Mires where the freshwater peat deposits are in close proximity to salt-marsh or estuarine clays, were sought for a comparison with sites hydrologically separated from the marine influence. The control sites could either be close to the coast but located on higher ground or the inland sites selected in step (2), above. Again mires with similar basin sizes were required for this comparison.

(5) **East-west comparison of sites:** Stratigraphies from sites in north-west England suggest that many peatlands developed into dry *Eriophorum vaginatum* / *Calluna vulgaris* dominated mire, immediately after the FBT. To further investigate that status of this relatively dry mire phase, a raised mire in the far west of Ireland was sought to compare and contrast the pathway of development in a mire from the most oceanic part of Britain. This aspect of the project is discussed further in Section 6.0.

(6) **Inland site in contact with a river system:** An inland raised bog site, in direct contact with a major river system, was sought to study the possible role of drainage basin change in determining the character of the FBT.

The final distribution of sites chosen for this project, after applying the selection criteria outlined in Section 3.2, are displayed on Figure 4.1 in Chapter 4.

3.2 Additional site selection criteria.

An examination of eight mires was considered to be manageable in the time available for the project. The selection of sites, within the framework summarized in table 3.1, is based on a literature survey of mires and field excursions. Selection criteria were established to build a short list of the most promising locations. Since the aim of the project is to target the transition between minerotrophic and ombrotrophic peat, which generally occurs near the base of mires, a wide range of sites was potentially useful because the present state of the mire surface is not important. The following criteria were, therefore applied to narrow down the choice:

(1) All sites have to contain at least one ombrotrophic phase over the majority of the site. Sites containing only minor acid patches were discounted. Blanket peats maintained by significant lateral flow were also rejected.

(2) All sites must contain at least a central focus of swamp or fen peat. Schwingmoor sites and mire that had developed solely from paludified ground were eliminated at this point.

Many suitable raised bogs remained at this stage of the selection process all of which could be readily investigated. The next stage of selection was based on the desired spatial distribution of sites. Northern Cumbria was selected as an ideal, initial testing ground for the project because of the concentration of well preserved deep peat deposits existing in relatively close proximity to each other.

(3) Further site selection was determined on the basis of the quantity and quality of existing data already available for a mire. In this respect consultation with the Wardens of English Nature and Countryside Council for Wales (C.C.W) reserves has proved to be valuable. The most desirable sites were considered to be those with an existing basic stratigraphy, pollen diagrams and radiocarbon dates. Some mires, particularly nature reserves and commercial peat workings have additional information, such as extensive peat depth maps, which provide valuable information for establishing the coring strategy. Table 3.2 illustrates the final selection process.

Table 3.1 Selection of study sites.

Nº	Site name	Comments.	Status
1	Abbeyknockmoy Bog	Macrofossil core on top 3 metres of peat accompanied by 10 radiocarbon dates. Oceanic location.	Selected
2	Bolton Fell Moss	Well documented surface cores and monoliths. Subject of detailed climatic reconstruction for the last 7000 years. Peat depth map and radiocarbon dates available.	Selected
3	Borth Bog	Pollen diagrams and long transect basic stratigraphy available.	Selected
4	Butterburn Flow	Little work available. Complex surface topography, with much of the site transitional or blanket mire.	Eliminated
5	Crymlyn Bog	Two pollen diagrams and macrofossil data available. But multiple coring showed complex history of local flooding events.	Eliminated
6	Felecia Moss	Levelling showed that the surface is not truly raised. Much of the bog is a transitional type close to blanket mire.	Eliminated
7	Glasson Moss	Extensive peat depth map available. Subject of a climate reconstruction on the surface peats.	Selected
8	Mongan Bog	Macrofossil diagram on the top 3 metres accompanied by 10 radiocarbon dates.	Selected
9	Raeburn Flow	Classic raised bog but no data available.	Eliminated
10	Scaleby Moss	Heavily cut bog, with basic stratigraphic data.	Eliminated
11	Solway Moss	Peat depth map and surface topography map available. Good quality marginal pollen and macrofossil diagrams with radiocarbon dates.	Selected
12	Thorntwaite Moss	Basic stratigraphy on one transect.	Eliminated
11	Tregaron North Bog	Classic raised bog, but no pollen, stratigraphy or radiocarbon determinations.	Eliminated
13	Tregaron West Bog	Less stratigraphy and pollen work than Tregaron South-East Bog, no radiocarbon dates.	Eliminated
14	Tregaron SE Bog	Stratigraphy and pollen diagram with 18 radiocarbon dates available. In direct contact with R. Teifi.	Selected
15	Walton Moss	Close proximity to Bolton Fell Moss. Subject of an English Nature sponsored coring programme involving radiocarbon dating	Selected
16	Wedholme Flow	Extensive mapping of the pre-Holocene surface and present surface. Only one coastal site required Glasson was chosen in preference because it is closer to the coast.	Eliminated

3.3 Core sampling.

3.3.1 Coring Strategy.

Choice of the location for the main Russian core on each mire was based on transects of field stratigraphy carried out prior to Russian sampling. Corers were located as near to the deepest point as possible. However, where the basal topography was very uneven, such as at Glasson moss, a core within 30 cm of the deepest existing record was accepted. To provide a context for the main, wide bore Russian cores, a stratigraphic survey of each site was completed, for sites where there was no pre-existing field stratigraphy (Bolton Fell Moss, Walton Moss, Glasson Moss, Mongan Bog and Abbeyknockmoy Bog). The survey consisted of two crossed transects at Walton Moss and single transects at the remaining four mires. The field stratigraphy for Solway Moss was kindly supplied by Dr C. Wells of the North-West Wetlands Survey. Stratigraphic transects produced by Godwin and Mitchell (1938) were used for the study of Tregaron South-East Bog. At Borth Bog, the stratigraphies completed by Moore (1963, in Slater 1972) and Williams Parry and Parker (1939, in Slater 1972) were used to locate the sample core.

Sample points for the survey were spaced at between 100 and 350m depending upon the size of the peatland. Samples for field stratigraphic analysis were collected using a narrow bore Russian corer. A selection of these have been retained for laboratory verification of peat types. This was considered to be necessary because of the difficulty of distinguishing between different peat types in the well humified basal sections of the mires.

3.3.2 Russian core recovery procedure.

Cores were extracted using two alternating bore holes, placed approximately 0.5m apart. Odd numbered cores were always extracted from the first borehole and even numbered cores from the second, using 5cm overlaps. Rods were pre-measured and marked with coloured electrical tape, bearing the depth and number of the core. Pegs were placed in the borehole not currently being sampled, to prevent loss of the hole.

Once samples reached the surface, the chamber was quickly laid horizontal and thoroughly cleaned prior to opening. Sediments were immediately described and photographed. Upon completion of field analyses, any obvious contamination was carefully removed from the fin plate and the surrounding metal work. Care was taken not to smear peat up and down the length of the fin plate. Cores were carefully turned out into either 30 or 50cm lengths of pre-labelled polythene drain pipe. This part of the procedure was always checked by both members of the coring team to ensure correct orientation of the tube labels. The labels themselves include a full site name, a three letter site code, the date, and the words 'top' and 'bottom', with the relevant depths, at each end of the tube.

Finally tubes were wrapped in airtight plastic bags, bound with electrical tape, labelled and packed horizontally in field bags, for transportation to the laboratory. Aluminium foil was not used for wrapping, since it can react with the peat.

3.3.3 Field Stratigraphy.

Field stratigraphy was noted on all major and minor cores using the Tröels-Smith (1955) convention. The order in which attributes were noted was standardized to avoid confusion and to increase efficiency. The colour and visible peat components were used as a guide for dividing up the descriptions. Colour was always noted as soon as the core chamber had been opened because oxidation and the consequent colour change is rapid on exposure to air. In addition the von Post (1924) 10 point scale for humification was also noted. This was used in preference to the five point Tröels-Smith scale.

3.4 Macrofossil analysis.

3.4.1 Interpretation of vegetative macrofossil data.

The degree to which the fossil assemblage reflects the composition of the original parent vegetation is affected by a whole range of processes, which must be taken into account when evaluating palaeoecological data. These processes may be broadly divided into factors controlled by species attributes and conditions of deposition.

Susceptibility to decomposition, and therefore the degree of preservation, varies between species. For example, within a hummock micro-habitat, stems of *S. fuscum* are more resistant to decay than those of *S. rubellum* (Johnson *et al.* 1990). Similarly species show differing degrees of resistance to the grazing of detritivores. *Calluna vulgaris* litter tends to be more heavily utilized than the remains of *Eriophorum vaginatum* (Coulson and Butterfield 1978).

Mire species exhibit a range of growth forms which affect the amount and type of material that a species contributes to the peat-forming system. *Sphagnum* grows continually from the tip. This results in burial of lower branches which die and become directly incorporated into the waterlogged peat substrate. Species such as *Trichophorum caepitosum* mimic this growth form, which favours the preservation of the whole plant (Malmer *et al.* 1994). In raised bogs, vascular plants, rooted in the anoxic catotelm, tend to contribute a greater proportion of root, rhizome and leaf base material to the peat because of the reduced decay potential in this zone. Aerial parts of these plants are only preserved when they fall by chance into an anaerobic part of the bog surface (Grosse-Brauckmann 1986).

Differences in decay rates have also been noted between micro-habitats. For example, Johnson and Damman (1993) demonstrated that species of *Sphagnum* inhabiting hummocks, decay more slowly than those living in hollows. *S. cuspidatum* loses mass at approximately twice the rate of the hummock species *S. rubellum*. This corroborates previous evidence (Johnson and Damman 1991, Rochefort *et al.* 1990, Johnson and Damman 1991). Hogg (1993) used the release of CO₂ from hummock and hollow *Sphagnum* peats to assess the long term rates of decay between the two environments. Conclusions from this monitoring programme agree with Johnson and Damman (1991) and Rochefort *et al.* (1990).

Depositional conditions have a large impact upon the degree of preservation of macrofossils. A single species may display a wide variation in the quality of sub-fossils preserved. Verhoeven and Arts (1992) show that fens are more favourable environments for the breakdown of cellulose than base-poor bogs. Within a fen environment a change in the nutrient status of the peat is important in determining the rate of decay. Ohlson (1987) has reported that significant variations in decomposition of a single *Carex* species may occur over distances as small as 30 metres, depending upon the local concentration of nitrogen (N) and potassium (K). Weight loss in the first twelve months of degeneration could range between 40% and 80% of the original mass.

In raised bogs the depth of the acrotelm controls the degradation of peat because it is in this zone that the majority of decay occurs (Clymo 1965). Under dry conditions the acrotelm is deeper, plant material therefore takes longer to pass through the oxic layer, providing a greater opportunity for microbially controlled humification (Aaby and Tauber 1975). Fluctuations in climatic conditions are, therefore, significant in controlling the quality of the ombrotrophic peat macrofossil record. In general the number of species that can be identified from any one peat type is inversely related to the degree of humification. Since decomposition tends to be greater in nutrient rich deposits. Fen peats, despite being formed by diverse communities may preserve no more species than fresh ombrogenous peats (Grosse-Brauckmann 1986).

Interpretation of the macrofossil record is further complicated by the fact that the roots and rhizomes of plants are generally younger than the peat matrix surrounding them. Sudden environmental change, inducing rapid replacement of the surface vegetation, may result in a layer of peat containing the sub-fossils of the younger community mixed with the remains of a substantially different older community. Weber (1930) called these mixed macrofossil assemblages displacement peats. However, such deposits are rare, being restricted to periods of very rapid species replacement. Generally peat-forming communities persist for many centuries, so that the majority of new material is deposited into a peat matrix of similar composition (Grosse-Brauckmann 1986).

3.4.2 Interpretation of the sub-fossil seed record.

Similar problems to those encountered in vegetative macrofossil analysis, must be addressed during the evaluation of a sub-fossil seed assemblage. To what extent do the seed macrofossil remains reflect the original composition of the vegetation? Seeds have the advantage of being more readily identified to species level, but interpretation of their presence is more problematic, due to the complex relationships between production, dispersal, and deposition. After inclusion in the peat body, seeds are subject to the same processes of differential decomposition between species that complicate vegetative macrofossil analyses (Wasylikowa 1986). Despite the traditional focus of macrofossil research on seeds and fruits, (Birks and Birks 1981), most of the work on preservation in peats has been directed at vegetative material. Therefore little is known about the variability of decay rates.

The taphonomy of propagules has been neglected in palaeoecology with the exception of a few studies such as Birks (1973). However, some information can be gained from ecological studies of seed bank dynamics, predation, production and dispersal.

Seed production varies widely between species (Grubb 1987) and within species, depending upon local conditions. Plants adopting a strategy of r- selection frequently produce large numbers of highly dispersible propagules, whereas K - strategists may display the opposite features. However, Grubb (1987) has noted that high values of r (the intrinsic rate of increase in a population.) may equally result from a moderate level of seed production coupled with low mortality rates. Year to year variability within one species may occur due to a whole spectrum of factors such as weather and soil conditions, and changes in inter and intra specific competition. Other responses reported in the literature include the finding that seed production in some species tends to decrease as a succession ages (Escarré and Thompson 1991) and that grazing may increase the reproductive effort of species such as *Molinia caerulea* (Clarke 1988).

Once propagules have been released into the environment, their method of transport will determine the radius of spread from the parent plant. *Betula* seeds are dispersed efficiently, because they are adapted for wind transport, whereas grass seed may be deposited no more than 6cm from the point of production, in an undisturbed community and up to 20cm away if the plants are subject to the passage of large animals. (Carey and Watkinson 1993). Even amongst propagules that are adapted for modes of dispersal other than wind transport, distributions around the parent plant may be slightly skewed away from the direction of the prevailing wind. Although much of the literature suggests dispersal is strictly limited in many species, some seeds are transported great distances in the gastric tracts of animals and birds. In the context of the wetland environment, waterfowl are particularly important in this respect.

Upon deposition, a number of processes affect the assemblage of propagules, such as concentration at the edges of lakes, re-deposition, and physical sorting in the surface layers of the soil, (Birks and Birks 1981, Wasylikowa 1986). Losses from the assemblage result particularly from predation by birds, rodents and soil fauna (Russi *et al.* 1992). Hulme (1994) has demonstrated that rodents have a strong tendency to exploit some species and ignore others and that large seeds are more likely to be selected when total seed numbers are low. Germination is a second significant source of loss from the initial propagule input. Rates of germination will depend upon the species (Carey and Watkinson 1993), the weather, competition (Wardle *et al.* 1995) and the availability of safe locations.

The seed bank which is left in the soil at any one time represents the sum total of all propagules reaching the surface, minus those lost through germination, predation and re-deposition. Few attempts have been made to study these assemblages with the aim of aiding the interpretation of macrofossil analysis. The work of Birks (1973) studying numbers of seeds in sediments in relation to the percentage of surrounding vegetation was carried out on a lake and therefore, it is not directly applicable to fen or bog environments. Seed bank studies conducted by Van der Valk and Verhoeven (1988) in fen carr woodland provide some

indication of the losses involved. Of the fifty nine species inhabiting the fen carr, thirty nine were also found in the seed bank. However, the macrofossil assemblage is one step further removed from the parent vegetation since it is subject to a period of losses due to decay.

Given the problems of interpreting seed macrofossil assemblages, the decision was taken to use this line of evidence mainly to corroborate the vegetative macrofossil record. For example, species level identifications of *Carex* seeds have been used to infer the identity of *Carex* leaves and roots when they occur side by side in the record. Single seeds have not generally been used to interpret the conditions of formation of an assemblage. In some instances the seeds of individual species occur in large numbers. In these circumstances a local origin is assumed, particularly if other remains are found and if the propagules are large. No attempt has been made to provide detailed quantification of seeds because the return, in terms of interpretative ability, was considered to be too low, when set against the time required. Instead seed data is presented on a 1 to 5 abundance scale.

3.4.3 Laboratory preparation and core sampling.

Cores were initially sampled at 16 cm intervals to provide skeleton diagrams broadly locating the stratigraphic changes of interest. Further samples were taken at 2 cm and 4 cm intervals to constrain the transitions more closely. Contiguous sampling for vegetative macrofossils has been avoided to reduce the risk of multiple sampling from the remains of an individual plant, (Berglund 1986). Each section of peat measuring 4cm³ was carefully removed from the centres of the cores, using individually cleaned scalpels and half centimetre spatulas. All roots and twigs were snipped through before sample removal.

Preparation of the peat for microscopy involved brisk sieving through a 125 µm mesh sieve, using cold tap water. The amount of water was standardized at 5 litres per sample to enable comparison of the quantity of unidentified organic matter (U.O.M.) remaining. The procedure enabled complete disaggregation of the peat remains without causing unacceptable damage. Consequently, there was no need to apply chemical treatments to the peat as suggested by Grosse-Brauckmann (1986). The washed residue, was briefly analysed, for the basic Tröels-Smith (1955) components using 10x magnification under a Nikon SMZ-10 binocular dissecting microscope. Results were noted in a laboratory notebook and used to update the sampling strategy. Preparations awaiting analysis were stored in screw capped sterilin tubes, containing a mixture of water and ethanol, (except samples for radiocarbon determinations).

3.4.4 Identification of fossil material.

3.4.4.1 The vegetative macrofossils of vascular plants.

The identification of vascular plants in peat is generally most reliable when a whole range of anatomical and macromorphological features can be distinguished. Equally, identification of different parts of a plant (e.g. seeds, leaves, rhizomes) increases the accuracy of the analysis (Grosse-Brauckmann 1986). Data collection for this project has therefore concentrated on recording all the surviving components of the original plants. These may include bud scales, rhizomes, leaves, leaf sheaths, stems, sclerenchyme

spindles, (e.g. of *Eriophorum vaginatum*) seed boxes and roots. Usually, the peat remains are individual organs or fragments of organs. Many of these may be very diagnostic of a species. For example the epidermal cells of *Phragmites*, *Molinia* and *Equisetum fluviatile* are most distinctive. Unfortunately, the epidermal cells of *Carex* species cannot usually be differentiated.

Macromorphology, the way in which several component organs fit together, may also be a significant aid to identification, as with the stem bases and basal leaves of *Trichophorum cespitosum* and the arrangement of leaves on stems of *Calluna vulgaris* and *Erica tetralix*.

Colour is not usually a good guide to identification, because the humic acids that are released during decomposition tend to stain most remains brown and the original pigments in plants usually degenerate. However, there are a few instances when colouration may be useful. For example, the rhizome material of *Eriophorum angustifolium* tends to be red/brown, whilst the roots of *Eriophorum vaginatum* are a very dark grey/brown. In reedswamp material, the epidermal and root material of *Equisetum fluviatile* can be readily distinguished because it is red/black, unlike any other common plant remains in peat. The wood of *Betula* and *Salix* may sometimes have a light pink tinge when the material is fresh. *Alnus* and *Pinus* are never pink (Grosse-Brauckmann 1986). This colouration disappears when the wood is brought into contact with air and is not always present.

Successful identification of vegetative macrofossils required the creation of a type material collection. Samples of common species were obtained directly, by the author, from the field. A number of sites were sampled from the New Forest. These include; the marshes, carr woodland and poor valley fen at Avon Water, the acid bog and flush areas of Cranesmoor, the valley bog at Churchmoor, an area of rich fen near Leap, and Hatchet's pond near Beaulieu. Other sites sampled for type material include, the mesotrophic fen at Crymlyn (South Wales), Brookland (Dungeness) and the six main coring sites. In addition to field collection, over 60 dried samples of less common wetland vascular plants, were obtained from the herbarium at the University of Reading.

The fresh and the dried plant material was 'artificially aged' by boiling in 5% KOH. This also served to rehydrate the dried specimens (Berghlund 1986). Type slides were made up from the prepared material by taking cell peels, using a sharp, clean surgical scalpel. The material was mounted in Aquamount fluid and the cover slips were completely sealed using clear cellulose varnish. Fresh material does not necessarily represent the morphology of the equivalent sub-fossil material, therefore, every effort has been made to use accurately identified fossil material where possible.

In addition to the type material, reference books were used, mainly to narrow down the choice of taxa, where identifications proved to be particularly problematic. Type material was always used to make the final identification. The literature on non-bryophyte, vegetative macrofossil identification is very sparse. The most useful texts have proved to be Grosse-Brauckmann (1964, 1972 and 1974, 1982), and Katz, Katz

and Skobeyeva (1977). The later publication is in Russian which causes problems when identifying different types of cell from a plant, however, the book has good line drawings, species coverage and full botanical names. The two principal difficulties that remain for the study of British vegetative macrofossils are the lack of English language literature and more seriously the lack of work on identification of fossil remains from British peatlands. Distinguishable remains of the species predominant in the fossil record from this study are described below.

Cyperaceae

All of the Cyperaceae have the characteristic rounded 'saw-tooth' edge to their epidermal cells. However, many genera, within the family, such as *Carex* cannot be satisfactorily separated on epidermal cell morphology alone. Those which can be identified from leaf fragments include the following:-

Eleocharis multicularis: This species has very long narrow epidermal cells with fine serrated edges. The ratio of the length to width of these cells is in the order of 12 : 1 to 15 : 1. Seeds may also be readily identified.

Rhynchospora alba: has a particularly distinctive cell pattern at the edges of leaves and particularly in leaf sheaths and leaf bases. At the edge the cells are twice as broad as they are long. In the centre of the leaves the opposite is the case. This species has distinctive seeds.

Eriophorum vaginatum: has very dark tough 'string-like' leaf veins that are very slow to decompose. Epidermal cells are often broken, with groups still clustered on part of the length of the vein. Cells typically have a length to breadth ratio of 8 : 1 or 9 : 1. The stem and rhizome material of *Eriophorum vaginatum* yields distinctive tapered spindles. These are characteristically striate. Roots are generally charcoal coloured and flattened.

Eriophorum angustifolium: This species may be distinguished by its much shorter squat epidermal cells, which do not completely join with neighbouring cells along their width. This gives each cell a characteristic wider section at the mid point of the long dimension. Rhizome material may be identified from the red/brown colour.

Trichophorum cespitosum: may be identified by the arrangement of short epidermal cells interspersed with chains of longer cells parallel to them. As noted above, the macromorphology of the leaf sheaths is also distinctive, however careful washing of the peat is required to maintain this feature.

Carex lepidocarpa: is one of the few *Carex* species that can be separated by the form of the epidermal cells. These cells tend not to be joined to neighbouring cells at the corners, creating small triangular voids. Care must be taken during identification since a similar morphology can arise from decay and dehydration of cells.

Roots: roots have been identified for a wide range of species by Katz *et al.* (1977). Discrimination depends on the arrangement of isolated incrassate cells on the fine rootlets. However, Grosse-Brauckmann (1982) has placed uncertainty on the usefulness of the technique. For the present project the incrassate cells have been used purely to isolate *Carex* spp. roots from *Phragmites australis* roots.

Scheuchzeria palustris: Rhizomes may be identified by smooth sided long cells with end walls that slant at a noticeable angle. These cells must be separated from *Menyanthes trifoliata*.

Menyanthes trifoliata:

Under x200 or x400 magnification the epidermal cells of *Menyanthes trifoliata* can be identified by the semi-rectangular smooth cells, one end of which usually slants or is rounded. The general cell pattern is also distinctly non-linear. At low magnification (x40 or less) fragments of *Menyanthes* can be easily separated because of the distinctive sheen that is preserved and the fact that large sheets of the cells tend to remain intact, even after vigorous sieving.

Poaceae.

The only members of the Poaceae that are readily identifiable in peat from their epidermal cells are *Phragmites australis* and *Molinia caerulea* (Grosse-Brauckmann 1982). Since the latter does not figure in the peats from any of the sites, only the former will be described.

Phragmites australis: This species is very distinct due to the occurrence of curved bean-shaped end cells, interspersed at intervals between the epidermal cells. Roots are separable in a mix of *Carex* spp. and *Phragmites* because they have no protruding cells.

Pteridophytes

Equisetum fluviatile: All parts of the *Equisetum* plant can be distinguished because they preserve a deep red/black colour after death, unlike any other wetland species. Epidermal cells are also distinctive, but examination under high power is rarely necessary.

Ericaceae.

Calluna vulgaris: The leaves, stems, seed boxes and seeds may all be easily identified. Leaves are small elliptic with overturned edges, with some fine hairs. Stems may be identified by the alternating pairs of petioles, whilst the bark has a texture distinctive to the Ericaceae. Any remnants of wood associated with the bark are likely to be white or grey/white. Seed boxes have a characteristic globe form.

Erica tetralix: Unlike *Calluna* leaves, those of *Erica tetralix* are rarely preserved in situ on stems. On the living plant, leaves are arranged in whorls of four around the stems forming a cross. This is preserved in the petioles on the stems. The leaves themselves are distinguished because they have coarser hairs. *E.*

tetralix is not to be confused with *Empetrum nigrum* which has more in-rolled leaf margins. These have the effect of producing an indented stripe down the under side of the leaf. In addition the species lacks the arrangement of four petioles.

Vaccinium oxycoccus: has heart shaped leaves that are larger than those of the above species. Stems are red, long and very straight. Sometimes red rootlets may still be attached.

Ericaceous rootlets: These rootlets may be the major component of the peat in some dry levels. It is difficult to assign a species identification to the rootlets alone. However a reasonable inference can be made from the associated Ericaceous leaves, seeds stems and seed boxes. Usually only one member of the Ericales dominates in any one level. The rootlets are very fine, red and have a visible cortex. Badly degraded rootlets may be represented as the cortex plus intermittent blocks of small red cells. Close inspection (x40) of each sample is required to separate rootlets from fine fungal hyphae. The hyphae are generally brown in colour with rather larger cells. However, both Ericaceous rootlets and hyphae look similar in gross morphology having small right angled branches.

Wood samples were identified using professionally prepared microtome sections of the common tree species. Additionally, Schweingruber (1978) was used to narrow down the choice of taxa.

For illustrations of the sub-fossil components described above refer to Grosse-Brauckmann (1963, 1964).

3.4.4.2 Bryophytes.

The main characteristics that enable the identification of fossil bryophytes are, leaf size and shape and cell structure. In non-*Sphagnum* mosses additional features may be important such as the presence or absence of a central vein, branching of the vein, leaf serrations or grading in the size of the cells between the base and tip of the leaf. Certain species are distinctive because they retain evidence of their former colouration, (e.g. *Polytrichum alpestre*). However, this feature cannot be regarded as diagnostic by itself. Most species do not retain any of their former colouration.

All identifications of bryophyte leaves were made using the Southampton Bryophyte type collection, in conjunction with Richards, Smith (1978) and Daniels and Eddy (1990). Where necessary the collection has been supplemented with material from the collection of Dr R.G. Scaife. A Nikon Optiphot light transmitting microscope was used to establish all identifications, using x100 and x400 magnifications and occasionally x60 to view larger leaves.

3.4.4.3 Fruits and seeds.

Seeds and bracts were identified using the type collections at Southampton University and Royal Holloway College, University of London. Additionally material has been examined from the collection of Dr Scaife. Literature used included general texts by Beijerinck (1947), Martin and Barkley (1961), Katz, Katz and

Kipiani (1965) and Berggren (1982). In addition Berggren (1969) and Korber-Grohne (1964) were used to aid the identification of seeds from the Cyperaceae family and the *Juncus* genus, respectively.

3.4.4.4. Faunal remains.

Faunal remains are relatively common in raised peats and may provide valuable ecological information. The most common sub-fossils found in this study were of Coleoptera and Acarid mites. Coleoptera analyses can yield high quality data for palaeotemperature reconstructions. The best data is gained from small basins that provide a high proportion of land dwelling species. Aquatic beetles are not so sensitive to climatic changes since the water body tends to dampen temperature oscillations. Since all of the basins chosen for the present study are relatively large inland and coastal sites, they are not ideally suited to Coleoptera based temperature reconstructions. Therefore, no attempt has been made to include them in the analysis.

Very little is known about the ecological preferences of the Acarid mites, therefore the decision was taken that the time and resources required for their analysis would not be worth the benefit of species identifications.

3.4.5 Quantification techniques in vegetative macrofossil analysis.

Traditionally bryophyte data have been expressed as presence or absence on diagrams (Janssens 1983). However, there is a considerable benefit to be gained from quantifying the relative proportions of bryophyte remains in peat.

The simplest level of quantification of the component parts of peat is to provide a subjective estimation of the proportions of each fraction. Hereafter this type of quantification will be referred to as Abundance Estimate Macrofossil Analysis or A.E.M.A). For example Moore (1977) and Tröels-Smith (1955) use three and four point systems respectively, whilst many other researchers employ a five point scale (Vasarie 1962, Haskins 1978, Barber 1981, Smith 1985, Wimble 1986, Wells 1991, 1992, 1993, 1994). The advantage of these methods is that they are very quick, enabling the analysis of many levels. However, lack of flexibility seriously hampers the ability to express differences in the abundance of components. This is particularly a problem when the manner in which co-dominant species vary is important to the palaeoenvironmental interpretation. Secondly results may vary between workers depending upon the individual's ability to judge proportions. Barber (1981) has been able to replicate results and trials for the present project have shown a very high degree of replication even when analyses were repeated several months after the first determinations were completed. The degree of variability in the data from one operator, can be reduced with practice.

In an attempt to provide a more rigorously quantified data set Clarke (1988) adopted a system of assessing percentage cover of macrofossils in a standard microscope view. To aid the estimation a grid graticule was used in the manner of an ecological quadrat. (This technique was also advocated by Grosse-Brauckmann

1986, although no details were provided). Clarke combined this technique with randomly sampled counts of *Sphagnum* leaves (after Barber 1981). Hereafter this form of quantification will be referred to as Quadrat and Leaf Count Macrofossil Analysis or QLCMA. These techniques substantially improve the accuracy of quantification. Both Haslam (1987) and Stoneman (1993) provide refinements to the method, to improve its application to climate change studies.

Other detailed methods for reconstruction of macrofossil assemblages are available. For example, Johnson, Damman and Malmer (1990) have described a procedure that treats intact *Sphagnum* plants differently to disarticulated plants:

(1) Intact plants are identified to species level (where possible). Subsequently the number of stems are counted and the cumulative length of the stems measured. Results are expressed as millimetres of stem per unit volume of peat sample.

(2) For disarticulated plants the cumulative stem length is measured and then the sample is dispersed in distilled water. A sub-sample is collected Using a 5mm glass tube and the sample, placed in a petri dish. After staining with methyl violet, between fifty and one hundred stem leaves are picked out mounted on a slide and identified.

Johnson *et al.* (1990) were able to directly use the number of stems per sample to indicate the proportion of each species because numbers of leaves per stem differed very little between species at their particular site. Janssens (1983) used a similar but more elaborate system of sampling involving the quantification of whole plants, branches stems and individual leaves. However, he found that the *Sphagnum* components of the bryophytes presented difficulties because they had a greater tendency to disarticulate. A total count of *Sphagnum* fragments, therefore, over estimated the original number of individuals. To overcome this problem he arbitrarily divided the number of branches counted by 10 and the number of leaves by 100. These results were then expressed as fragments of each bryophyte species per unit volume of peat.

These complicated and time consuming techniques are not necessary for the analysis of early Holocene peats because they rarely contain intact branches of bryophytes. Stems are also invariably degraded and sampling for leaves is hindered by the dominance of monocotyledon remains. Consequently, neither Janssen's nor Damman's analyses were employed. The techniques developed by Haslam (1987) and Clarke (1988), and refined by and Stoneman (1993), offer a much more promising basis for developing a methodology that can accommodate early Holocene peats. The principal benefit of the techniques are that they allow detailed quantification of monocotyledons and wood as well as bryophytes. However, the calculation of percentage cover of components does produce a major difficulty with the assessment of very small but often abundant sub-fossils.

3.4.6 The methodology for quantification of macrofossils.

The quantification of the macrofossil remains was organized into a standardized set of procedures which were carried out in the same order for each sample. The macrofossil remains stored in alcohol and water were placed in a large glass trough and spread out to achieve a monolayer of residue (Clarke 1988). Each sample was examined under x10 magnification, using the dissecting microscope, until all identifiable components had been located and recognized. Needle tweezers were used to tease apart any clumps that survived the sieving process and to look for smaller remains such as seeds and bud scales. Sub-samples of monocotyledon remains, wood, and leaves were extracted and mounted on slides to check identifications. Having become completely familiarized with all of the components present, the percentage cover of each main type was estimated. This was achieved with the aid of a 100 cell grid graticule, mounted in one eye piece of the microscope. Each sample of sieved residue was subjected to fifteen, randomly placed, replicate trough scans to give a reliable mean value for each component, with an acceptably small confidence limit. The required number of replicates was established by Clarke (1988) who developed a computer program to calculate the running standard error of the mean as the number of trough scans were increased.

Once the percentage cover of the main components had been established seeds were removed and their abundance expressed on a five point scale (rare, occasional, frequent, abundant very abundant) All other small macrofossils that constituted only a minor proportion of the total cover were quantified in a similar manner. These included Acrid mites, carbonized plant remains, carbon spheres, *Eriophorum* spindles, seed boxes, bud scales and fungal sclerotia. Seeds were treated in this manner rather than being expressed as concentrations because only small numbers were recovered from the Russian cores.

The proportions of *Sphagnum* and other bryophyte leaves were always determined last. This was necessary because they were often very scarce and removal prior to estimation of the main components would have significantly affected the data. Three techniques for bryophyte leaf quantification have been necessarily employed depending on the relative proportions of monocotyledons to bryophytes.

(1) Bryophyte leaves very scarce: In this situation the total presence of leaves has been extracted to gain a species list. Leaves were mounted on slides in Aquamount and identified at x100 and x400 magnification.

(2) Abundant bryophyte leaves mixed with abundant monocotyledon remains: In this case four randomly chosen grid squares were cleared of bryophyte remains until at least 100 leaves had been sub-sampled. Each grid square also came from a different randomly selected field of view. Clearance of grid squares prevented operator selection of better preserved or larger specimens. However, this technique is only completely valid if all the bryophyte leaves are disarticulated from their stems.

(3) Bryophytes dominant: In this case a sub-sample of the bryophytes could be drawn off and placed in a petri dish. Clearance of grid cells and identification could then proceed as described in part (2).

Where monocotyledons dominated the sample and were only distinguishable at high magnification a further stage was added to the analysis. Both epidermal cell fragments and root fragments were cleared from randomly chosen grid squares until fifty fragments had been sub-sampled. Roots were mounted on one slide. Epidermal cell fragments on a second slide. The fragments were identified under x100 and x400 magnification, where necessary, and the resulting proportions were used to divide the main percentage cover estimations. Using this technique much of the undifferentiated proportion of the main components has been accounted for.

3.4.7 Presentation of macrofossil data.

Macrofossil data are presented in two formats. Firstly, diagrams showing the percentage abundance or five point scale of abundance of each fossil type against depth have been produced for each of the study sites. These diagrams are organized so that fossils found in minerotrophic environments are to the left of the diagram, and those from oligotrophic sites to the right of the diagram. Species appearing in the middle of the diagram may either be present across the entire environmental gradient or they may represent transitional types. This standardized format has been selected to allow rapid and accurate comparison of sites and to provide a clear visual expression of the sequence of change.

3.5 Pollen analysis.

Pollen is produced by all flowering plants. Grains are usually resilient to microbial decay, produced in large numbers and are widely dispersed into the atmosphere. Any anaerobic sedimentary environment which continually accrues organic material may, therefore, entrain a temporal record of the pollen washed or deposited from the atmosphere. As with macrofossils the relationship between pollen percentages and the vegetation cover abundance is obscured by a range of biotic and abiotic processes (Moore *et al.* 1991). These problems are considered in the remaining sections of this chapter.

Pollen analysis has been employed in this project, primarily to correlate between the main macrofossil cores. Known regional pollen types, i.e. those originating from plants which do not grow in wetlands, can be used to identify distinct horizons within the pollen spectra at different core sites. This technique has been used to link radiocarbon dates from the main core at Solway Moss to the four multiple cores SOLA195, SOLA395, SOLA495 and SOLA595. Similarly the radiocarbon dates for Bolton Fell Moss have been transferred to Walton Moss, core WLM11, using pollen correlation.

Pollen can be used to provide an approximate chronology based on the abundance of non-mire tree pollen and selected herb types. The identification of regional pollen zones provides a cross check for the chronology constructed from radiocarbon determinations, although this kind of analysis requires careful consideration of the findings of Smith and Pilcher (1973). Smith and Pilcher's study has demonstrated that the empirical and rational limits of many tree species vary in radiocarbon age across the British Isles.

3.5.1 Pollen representation at a site.

The factors affecting pollen representation in a peat core are well documented. Therefore the following four sections will provide only a brief summary of the subject. The reader is referred to Birks and Birks (1981) and Moore *et al.* (1991) for more comprehensive syntheses.

3.5.1.1 Pollen production and liberation.

Flowering plants exhibit a large degree of variation in the quantity of pollen produced between species Birks and Birks (1981). Studies of selected European plants undertaken by Pohl (1937) recorded a range which varied from 72 pollen grains per flower for *Valisneria spiralis* to over 589,000 grains per flower for *Picea excelsa*. Differences in production of this magnitude clearly confound the relationship between the abundance of parent plants and their representation in the pollen rain. Wind pollinated species generally produce more pollen than insect pollinated plants. A second factor which significantly influences the composition of the pollen rain is the relative efficiency and timing of pollen liberation between species. Some plants, such as *Viola*, have flowers which do not open causing an extremely poor rate of liberation.

3.5.1.2 Pollen dispersal.

The majority of pollen grains are distributed throughout the environment via airborne dispersal, whilst a minority are conveyed due to the activities of insects and due to water transport through soligenous sediments and along water courses. Tauber (1965) proposed a model which describes the various mechanisms by which pollen can reach a site due to a variety of transport methods. The different components of the sub-fossil assemblage, for a site surrounded by woodland, can be classified as:

- (1) Trunk space component (Ct): Pollen from this source is mainly composed of pollen falling from the canopy mixed with pollen liberated from the woodland floor species.
- (2) Canopy component (Cc): The canopy component can be an important contributor to the regional pollen rain since air flowing across the top of the canopy can join with thermals to be transported to high altitudes, therefore settling out over greater distances.
- (3) Rain component (Cr): Pollen grains can act as nuclei for the formation of water droplets. Therefore pollen is efficiently removed from the atmosphere during rain storms, possibly accounting for the majority of pollen deposition. (Moore *et al.* 1991).
- (4) Local or gravity component (Cl): Plants growing locally on the wetland surface tend to contribute a large amount of pollen to their immediate surroundings. Most of this pollen arrives at the surface as dry deposition under the influence of gravity.
- (5) Inwash component (Cw): Pollen transported to a mire or lake by a water body may contain pollen deposited directly from the atmosphere or grains that have been reworked due to fluvial erosion. The latter

category of pollen grains may significantly predate the sub-fossils that are more directly incorporated into the sediment.

3.5.1.3 Pollen preservation and deterioration.

The relationship of the pollen producing plants to the recoverable sub-fossil assemblage is further complicated by differential preservation and destruction of pollen grains. The resilience of pollen is directly related to the quantity of sporopollenin contained in their cell walls. This may vary significantly between species. For example, *Populus* spp. (5.1% sporopollenin) is very susceptible to corrosion, whilst *Lycopodium clavatum* (23.4% sporopollenin) is very resistant. The quality of pollen preservation is also closely dependent upon the types of sediments that are sampled. Waterlogged organic samples are generally more favourable environments for preservation than drier, minerogenic sediments (Birks and Birks 1980).

3.5.1.4 The relationship of site size to pollen representation.

The size of a site has a significant affect upon the proportions of pollen reaching the sediment surface from local and regional sources (Jacobson and Bradshaw 1981). Small sites, of no more than 100 metres in diameter, tend to be dominated by 50 to 80% local pollen, whereas wetlands that are greater than 300 metres in diameter may contain over 70% regional pollen. The precise values and source areas will differ depending upon the direction of dominant air currents (Price and Moore 1984) and the structure of the mire vegetation.

3.5.2. Sampling for pollen analysis.

Samples of peat with a volume of 1 - 2cm.³ were extracted from a cleaned peat surface using fresh scalpels and spatulas. Between sampling, instruments were wiped and washed with distilled water. Initially the sampling interval was spaced at 16 cm throughout the core. Further sampling was located at significant changes in the stratigraphy, on the basis of the first batch of pollen counts and with reference to the macrofossil results.

3.5.3 Preparation for Pollen Analysis.

The preparation of pollen samples follows standard procedures described by Barber (1976) and Moore *et al.* (1991). All samples received at least one treatment of potassium hydroxide and three minutes of acetolysis. Where necessary dirty samples were subjected to a second treatment of potassium hydroxide and a treatment of hot hydrofluoric acid (HF). This was only required for basal peats which graded into the underlying clay. Pollen was recovered from the clay by sieving the preparations with a 10µm. mesh sieve followed by one treatment of hot hydrofluoric acid, boiled for 30 minutes and one of warm hydrochloric acid, simmered for 10 minutes. Preparations were stained with two drops of alcohol soluble 'Safranin' stain and mounted in silicone fluid. This mounting medium has the advantage of maintaining the integrity of the dimensions of the pollen grains (Praglowski 1970), unlike glycerine jelly which absorbs water from the

atmosphere causing pollen grains to swell (Faegri and Deuse 1960). The mobility of the silicone fluid also enables grains to be easily turned over.

The main disadvantage of using silicone oil is the difficulty of relocating problem grains. Mobility can be reduced somewhat by sealing the edges of the slides. In practice this proved sufficient to prevent most losses. In the light of this problem every effort was made to identify problem grains from the type material as they were encountered

3.5.4 Pollen Counting.

Pollen grains were routinely examined at x400 magnification using a Nikon Optiphot light transmitting microscope. Slides were counted in a systematic manner by taking traverses in the direction of the Y co-ordinate. At the end of a traverse the slide was moved three fields of view to the left along the X co-ordinates. This prevented the possibility of counting the same grains twice. The number and the direction of the traverses were noted down each time the slide was moved to enable breaks from counting to be taken, without losing the direction of movement across the slide. Most slides contained sufficient pollen to enable the pollen sum to be reached after no more than 6 to 8 traverses. Under these conditions, traverses were taken from the edge and the middle of at least two slides to reduce errors that result from sorting of pollen when the slide is made up.

3.5.5 Pollen Identification.

The identification of unknown pollen grains was undertaken using a x60 lens and a x100 lens (for use with immersion oil). These two lenses give magnifications of x600 and x1000 respectively when coupled with a pair of x10 binocular eye pieces. A ruler graticule with 100 divisions equal to 2.4µm each (at x400) was used to take measurements of grains. A first approximation of the identity of the grains was made with reference to Erdtman *et al.* (1961), Punt (1976), Moore and Webb (1978), Faegri *et al.* (1989), Punt and Clarke (1980, 1981, 1984) and Moore *et al.* (1991). The laboratory manuals were used to narrow down the choice of pollen types to be compared against the unidentified sub-fossil specimen. All identifications were finally made using the Southampton pollen reference collection and the private collection of Dr R.G. Scaife.

3.5.6 Presentation of Pollen Data.

The pollen diagrams have all been standardized to enable rapid comparison. Taxa are shown in the order; trees, shrubs, herbs, aquatics and spores. All taxa are shown as a percentage of tree pollen, unless specified otherwise. A pollen sum of at least 150 tree pollen has been adopted for all of the pollen correlation diagrams. Nomenclature follows Stace (1991).

Chapter 4

Sites investigated.

4.0 Introduction.

The rationale for selecting suitable sites for this project is presented in Chapter 3, (Section 3.1) The resulting distribution of mires, chosen for stratigraphic analyses, forms a transect of paired sites, ranging from Bolton Fell Moss and Walton Moss in northern Cumbria to Abbeyknockmoy Bog near Galway city in Western Ireland. (see Figure 4.1). The arrangement of sites allows comparisons on a variety of spatial scales and also between coastal and inland situations. This chapter provides an introduction to the geography of the study sites and a review of existing palaeoecological research relevant to them.

4.1 Cumbria.

The Cumbrian (Cumberland) lowland (Walker 1966) is blanketed in a deep layer of till belonging to the Bewcastle drift sequence and dating from the Devensian glacial period (Day 1970). On the coastal fringe the till is overlain by marine clay. Elsewhere, till alone separates the land surface from the underlying Permian and Triassic solid geology. Numerous sites suitable for peatland formation are provided within kettle hole depressions, formed by the melt-out of stagnant ice blocks and the grouping of drumlins. The oceanic climate has favoured raised mire development, with numerous examples, known locally as either 'Mosses' or 'Flows', spreading out onto the surrounding wooded landscape, beyond the confines of their originating hollows. Four of the mires selected in Chapter 3 are located in the Cumbrian lowlands, namely Glasson Moss, Solway Moss, Walton Moss and Bolton Fell Moss.

4.1.1 Bolton Fell Moss (NY490690).

Situated 12 Km. east of Carlisle, Bolton Fell Moss (Figure 4.1 and Figure 4.2) lies at an altitude of 110 metres O.D. The mire originally covered approximately 4 square kilometres prior to nineteenth century land reclamation and twentieth century peat extraction. Isopachyte maps, produced by the Boothby and Penicuik Peat Company, show a deep basin offset to the west of the mire centre, containing a maximum of 11 metres of peat. However, detailed stratigraphic survey work carried out for this project, has failed to find deposits any deeper than 10 metres. Presumably up to a metre of shrinkage has occurred since the large scale drainage of the ombrotrophic mire. This is also indicated by the significant altitude gain from the centre of the bog to the present western margin. Damage and compaction to the peat beds resulting from shrinkage should be restricted to deposits lying above the level of the deepest ditches (3.5 metres). To the north-east of the geographical centre of Bolton Fell Moss a mineral inlier rises to the surface of the peatland. This area is wooded with *Pinus sylvestris*, *Betula pendula* and *Quercus robur*. Fringing ditches reveal that the Bolton Fell Moss is underlain by a light brown sandy till thought to be of Devensian age (Day 1970). The contours of the isopachyte map suggest that a water course could have run from east to west through the peatland prior to blockage by thick peat deposits.

Bolton Fell Moss has been extensively exploited for peat. Since 1945 the majority of the surface vegetation has been removed to enable commercial peat milling and large drainage ditches have been constructed. A significant uncut area of bog remains as a nature reserve, incorporating the deepest part of the bog. One core (BFML) was extracted from the undisturbed area (see Figure 4.2 for location of core), for this project, in June 1993. Examinations of the surface vegetation by Ratcliffe (1957, unpublished, reported in Barber 1978), Barber (1978), Haslam (1987) and observations by the author in 1993 and 1994 indicate that the mire vegetation has changed considerably, towards a dry *Calluna vulgaris*, *Cladonia* sp. dominated community. *Pinus sylvestris* and *Betula pendula* invasion of the bog vegetation is widespread, whilst the population of *Sphagnum* species is much reduced, with the wettest communities existing on the uncut mire fringe near the western rand.

Palaeoecological studies at Bolton Fell Moss began with Barber's (1978, 1981) examination of the ombrotrophic peat stratigraphy. Detailed analysis of many peat sections in the hand cut ditches, coupled with analysis of surface monoliths enabled Barber (1978) to conclude that the mire had not developed via a succession of hummocks and hollows, as proposed by von Post and Sernander (1910) and popularized by Osvald (1923). Rather the stratigraphy indicates that surface wetness has changed over large areas of the mire at similar times. Subsequent studies by Haslam (1987), Stoneman (1993) and Barber *et al.* (1994a) have refined the reconstruction of bog surface wetness, proxy climate records. These studies used cores of up to 5 metres depth from three uncut areas of Bolton Fell Moss. Barber (1995, NCCE) has demonstrated replicability in the ombrotrophic macrofossil record, using a series of four short cores linked to core BFML by pollen correlation. Further pollen work by Dumayne (1992) has provided evidence for human impact in the area.

4.1.2 Walton Moss. (NY504667)

Walton Moss (Figure 4.2) is one of the last substantially intact raised mire systems in England, lying 2 Km. to the south-east of Bolton Fell Moss at an altitude of 93 to 103 metres O.D. (Figure 4.1). The two mosses lie on the same geology, separated by a small valley. The bog complex at Walton Moss consists of a deep basin to the north, with a maximum depth of 10 metres of peat (see Figure 6.2a). Borehole data suggests that the bog spread out to the south and south-east from this centre, paludifying *Betula* and *Corylus* woodland. Much of the mire to the south is between 5 and 6 metres deep, with all boreholes recording well preserved minerotrophic and ombrotrophic sediments. The greatest depth of fen peat coincides with the greatest total depth of peat in the northern basin.

Walton Moss is fringed by wet pasture, which has been maintained on thin peat deposits located beyond the margins of the rand. The Moss covers 283.9 ha. and is currently dominated by *Sphagnum magellanicum* and *S. cuspidatum*, with some parts of the surface supporting *Molinia caerulea*,

Eriophorum vaginatum and *Erica tetralix*. *Calluna vulgaris* is virtually absent due to grazing by sheep and deer. Fragmentary patches of birch scrub have colonized the marginal parts of the moss.

Small parts of the paludified area of Walton Moss have been drained in the past. These cuttings have completely refilled with *Sphagnum* and have not penetrated the basal peats. The edges of the mire have been slightly modified by traditional peat digging which continued until the 1930s, with minimal impact upon the drainage system. Some parts of the rand on the south side of the mire appear to be completely untouched, representing a rare feature in British raised bogs.

Three palaeoecological studies have been completed on the top 1.5 to 3.0 metres of Walton Moss. Dumayne (1992) has produced a detailed pollen diagram from the middle of the site with the aim of studying the impact of the Roman invasion, on the regional vegetation. Stoneman (1993) has undertaken a macrofossil reconstruction, also of the top three metres of peat from the middle of the mire. The macrofossil data have been used to provide mire surface wetness reconstructions, and proxy climatic records. This latter work has been extended by Barber (1996) in a NERC funded research project (GR9/01646), designed to test the replicability of the macrofossil record in ombrotrophic peat. Six, 50 cm deep monoliths, from sites spaced between 100 and 200 and 300 metres apart were analysed for macrofossils. All sites indicated a very good level of agreement with respect to the larger scale wet shifts and dry shifts in mire surface wetness. However, some local differences in macrofossil assemblages do occur between cores, as would be expected.

Two cores were recovered from Walton Moss for this project. A full archive core WLM11 was extracted from the deepest area of peat in the north basin (April 1995), in association with the NERC project and a shorter core (WLM 15) was sampled from the southern paludified area (October 1994). Two full stratigraphic transects of the moss were also completed as part of the same NERC project and provide the context for cores WLM 11 and WLM 15. There have been no previous detailed studies of the site stratigraphy below 3 metres depth. The locations of the two cores, sampled for macrofossils (WLM11 and WLM15) and the accompanying stratigraphic transects are given in Figure 4.2.

4.1.3 Glasson Moss. (NY238603).

West of Carlisle on the south side of the Solway firth, four ombrotrophic mosses dominate the landscape, namely, Bowness Common, Drumburgh Moss, Glasson Moss and Wedholme Flow, (Figure 4.3). All of the mires have been affected by peat extraction. However, drainage and cutting have only disrupted a limited area of basal peat at Glasson Moss (Walker 1966, Stratigraphic survey 1995: this project). The majority of the deepest peat deposits remain intact.

Glasson Moss is located 0.5 Km. from Glasson village (Figure 4.3). This lowland raised mire is 9.8 metres at the deepest point with a surface that lies at a mean altitude of 10 metres O. D. Certain areas of the basal

peats therefore lie up to 4 metres below the mean high water of the spring tide, whilst the northernmost edge of the reserve lies just 300 metres from the fringing salt-marshes of the Solway Firth. The deepest deposits under Glasson Moss are commonly composed of laminated sandy brown clays with some pebbles, (Walker 1966) which overlie till from the Bewcastle Drift series (Day 1970). A detailed map of peat depth based on a 10 metre grid (Mauby undated, English Nature unpublished) indicates an undulating basal topography consistent with the presence of small drumlins.

The Moss has a gentle cupola sloping most noticeably to the south, which is also the line of greatest water movement. The southern rim of the Moss is fringed by a *Phragmites* and *Carex* fen, which thrives on a mobile water supply derived from the moss. The capola's southerly slope has been increased by shrinkage resulting from commercial peat cutting between 1948 and 1951. The south part of the mire was drained by an intensive system of ditches, causing severe drying of the upper peats. (Lindsay 1977, N.C.C. unpublished). In addition four related fires between the years of 1956 and 1976 have compounded the serious damage and drying caused to the surface of the bog. The cut area of the mire was again burnt in 1995. Since the 1976 fire the surface vegetation has recovered remarkably well particularly in the uncut area. This has been facilitated by a scheme to block many of the larger drains. *Sphagnum cuspidatum*, *S. pulchrum* and *Rhynchospora alba* are now common in the wetter hollows. *Narthecium ossifragum*, *Erica tetralix*, *Andromeda polifolia* and *Drosera species* and *Eriophorum angustifolium* are also widespread in hollows.

Walker (1966) presents two stratigraphic cross sections of Glasson Moss (SW to NE and NW to SE) with maximum depths of 9 and 7.5 metres respectively. Much of the centre section of the largest transect remained unsampled. Peat classification was very broad describing the ombrotrophic peat as either *Sphagnum* peat with a Von Post and Sernander (1910) humification range H 1-4 or *Sphagnum* peat H 5-9. The stratigraphic survey undertaken for this thesis aimed to provide a more detailed classification of the peats in the deepest part of the basin. Four levels (from 705 cm to 735 cm) were sampled for pollen by Walker (1966) from a 2.4 metre core that reached a depth of 740 cm. The resulting pollen counts are tentatively assigned to zone VIIa (Godwin 1956) of the larger Bowness pollen diagram. Further palaeoecological work has been completed by Dumayne (1992) and Stoneman (1993) on human impact and climate change, respectively. Both of these studies used cores from the top 2.5 to 3.0 metres of peat. Therefore, the deeper peat deposits remain largely unstudied. Core GLM95 was sampled at a point 300 metres from the northern margin of the moss. The location of the core is shown in Figure 4.3.

4.1.4 Solway Moss. (NY345688)

Solway Moss (Figure 4.4) is located 2 Km. from the north coast of the Solway Firth and 1.5 Km. from Gretna Green, on an interfluvium between the Esk and Sark rivers. The site is approximately 1.5 Km. square and the present uncut surface lies 21 metres above sea level. The mire is underlain by pale green and red sandy till. Much of the moss has been extensively milled for commercial peat extraction, removing the top

4 metres of peat. The milling process has accelerated the rate of peat removal to the extent that large areas of ombrotrophic peat have been cut down almost to the fen peat level, thus ruining much of the basal sequence. The small fragment of the original surface remaining has been severely affected by drainage. However the deepest peat beds which lie near the geographical centre of the mire have remained intact. Sufficient fen and ombrogenous peat remains for the site to be useful to this project. In addition Wells (1994 North West Wetlands Survey N.W.W.S. unpublished) undertook an extensive stratigraphic survey of the Moss using five radial transects based on the centre post erected by the Richardson Peat Company. This data has been kindly made available for the present project, providing an extensive context for more detailed stratigraphic analyses of the fen bog transition. One main core (SOLA295) and four subsidiary cores (SOLA195, SOLA395, SOLA495 and SOLA595) were recovered for this project after careful examination of the data provided by N.W.W.S.. The locations of these cores are detailed in Figures 4.4 and 5.1.

An account dating from 1771 by Gilpin, (quoted in Turner and Scaife 1995) indicates that a major bog burst occurred on Solway Moss, which enveloped 200 hectares of the surrounding farmland. The area affected by the mire collapse is on the northern fringe of the Moss some 600 metres distant from the core locations. In addition, the core samples should be protected from stratigraphic disturbance resulting from the bog burst, due to their location in a deeper basin. A preliminary study of the macrofossil assemblages from SOLA295 using 1 - 5 abundance estimates, indicated that the stratigraphy was intact.

Following the discovery of a buried sheep on Solway Moss excavations and accompanying palaeoecological investigations were carried out in 1991 and 1992 (Wells 1992). A number of radiocarbon age determinations were conducted on the sheep remains giving a mid-point for the combined dates of 1660 (Wells 1993). Wells (1993) and Huckerby (1993) have produced macrofossil and pollen studies, respectively, from a core located next to the sheep find. The present depth of peat in this area is just 175 cm. Six radiocarbon dates are available for the two diagrams. The basal peat assemblage indicates a paludification sequence from *Betula* woodland and dates to 7940 years cal. B.P. This diagram provides a good opportunity to compare the centrally located core (SOLA295) with the marginal core next to the sheep. Cores SOLA195, SOLA395, SOLA495 and SOLA595 are positioned between SOLA295 and the sheep find (Figure 5.1) providing a transect of five cores.

4.2 Wales.

4.2.1 Tregaron Bog. (SN685622).

At Tregaron village, 15 Km south-east of Aberystwyth, the glaciated valley of the River Teifi is traversed by a moraine ridge which caused damming of the river waters and the formation of a large lake of Devensian age. The Tregaron peatland complex, which originally consisted of five distinct mires, developed within the waterlogged basin, with the River Teifi forming a channel through the centre. Three

bogs have survived to the present date, the north-east bog, the west bog and the south-east bog. The present study is concerned with the south-east bog which is bounded by the Teifi to the west and north-west, by sharply rising ground to the east and by farmland or woodland to the south and north-east. The mire is approximately 1200 metres in length, 800 metres wide and lies at an altitude of 165 metres O.D. Whilst large parts of the mire have been cut (marked on maps published by Godwin and Mitchell 1938) there are significant areas that remain untouched and none of the deeper peats have been disturbed.

The coring site for TSE94 was located in the approximate centre of the mire on undisturbed peat. The vegetation of the site was predominantly *S. magellanicum*, *S. papillosum* and *Rhynchospora alba*, with some *Eriophorum vaginatum* and *Erica tetralix*. The field stratigraphy published by Godwin and Mitchell (1938) was used to locate the position of the main sample core and to provide all the field stratigraphic information for the site. No further field description of the sediments was undertaken.

The Tregaron mire complex has been the focus of a range of palaeoecological studies. Erdtman (1928) carried out preliminary investigations in the peatlands and published a single stratigraphic profile from one of the eastern mires. Pollen samples were taken, although a full diagram was never published. Two stratigraphic transects traversing the south-east and west bogs were completed by Godwin and Mitchell (1938). Four pollen diagrams presenting tree species alone were also published to accompany the stratigraphies. Subsequently, Turner (1964 and 1965) has undertaken more detailed pollen work on the upper *Sphagnum* peats to examine the record of forest clearance. A full Holocene pollen sequence has been published by Hibbert and Switsur (1976) for the south-east bog. The diagram was produced as part of the project to radiocarbon date Flandrian pollen zones in Wales and Northern England. Therefore, the pollen record is accompanied by 18 radiocarbon dates some of which have been used to compare the synchronicity of changes in the stratigraphy at the margin of the mire with changes recognized from the centrally located core TSE94 (this project). Further radiocarbon dates for Tregaron Bog have been reported by Godwin (1960) and Godwin and Willis (1969).

In 1936 and 1937 the west bog was extensively surveyed to study the modern ecology of raised mire vegetation. The spatial distributions of mire species were mapped from numerous quadrats and a classification of community types was produced (Godwin and Conway 1939).

4.2.2 Borth Bog. (SN625915)

At the mouth of the Dovey estuary the great expanse of Borth Bog is located behind the shingle barrier of Borth beach. To the south and east, the mire is fringed by steeply rising hills, which are drained by the rivers Clettwr and Leri. These two rivers pass east and west of the mire centre, draining to the north through salt-marshes into the Dovey estuary. The River Leri dissects the peat beds (Figure 4.6) flowing parallel to the line of the shingle beach. The northern margin of the mire runs into the salt-marshes that fringe the southern shore of the estuary. The entire wetland complex rests on a virtually flat bed of blue

salt-marsh clay at an altitude of approximately 0.6 metres O.D. Analyses of the Foraminifera within the clay, completed by Macfadyen for Godwin (1943), indicated brackish water conditions near the upper contact, suggesting a gradual removal of the salt-marsh conditions. Two, radiocarbon assays taken just above the gradational contact of the clay with reedswamp peat (Godwin and Willis 1969 and this project) both give dates of c. 7000 cal B.P. for the conversion to freshwater conditions.

Stratigraphies from Borth Bog have been produced by Moore (1963, published in Slater 1972) and Williams-Parry and Parker (1939, published in Slater 1972). Moore's profiles traverse the mire from NE to SW and from NW to SE. The transects reveal basal *Phragmites* and brushwood peats overlain by humified and then less humified raised bog peats. Accompanying diagrams demonstrate the existence of a liquid core in the peat deposits, which formed as a secondary feature after the development of the mire. The transects of Williams-Parry and Parker (1939) are less detailed. However, the north-south orientation of the main profile depicts the tongue of salt-marsh clay which overlies the highly humified raised mire peat, and was first described by Godwin (1943).

At Ynyslas, beds of submerged peat containing many tree stumps outcrop on the beach at low tide. These have been examined by the late Mrs Campbell James (Godwin and Newton 1938) who considered that the peats were contiguous with the deposits of Borth Bog. Subsequent stratigraphic analyses reported by Godwin (1943) support the interpretation that the beds represent the eroded base of the bog, exposed by the landward movement of the shingle beach over the mire.

Pollen diagrams of tree and shrub taxa have been published by Godwin (1943) and Godwin and Newton (1938) for the main mire and the submerged peat, respectively. A full diagram was prepared by Moore (1968) to study the impact of humans upon the surrounding vegetation. The results of the latter study suggest that Neolithic people were the first colonizers of the area and that this population was probably very small.

Shi and Lamb (1991) provide a detailed examination of the evolution of the Dovey estuary and the formation of the salt-marshes. They suggested that the estuary has passed through four distinct phases including; (1) shallow water, high energy, fluvially dominated phase; (2) deep water, low energy estuarine phase; (3) shallow water, tidally dominated phase representing a quiet water estuary, and (4) infilling of the estuary and the approach of equilibrium with sea level rise. Borth Bog began to form, at the boundary between stages 2 and 3, with the change to a quieter regime in the estuary. The sample core BTH94 was located 1 km east of the River Leri, in the approximate centre of the mire. The location of the core is shown in Figure 4.6.

4.3 Eire.

4.3.1 Mongan Bog, Co. Offaly. (N004302)

The grey limestone of the Clonmacnoise area of Eire is covered by limestone rich Devensian till and crossed by numerous fluvioglacial features such as eskers. The waterlogging that created the 3 km long Devensian lake at Mongan was caused by the confinement of drainage between two approximately parallel eskers that eventually converge near the east bank of the River Shannon, 8 km from the village of Shannon bridge (Figures 4.1 and 4.7). The peatland that subsequently developed over the lake now covers the entire basin, measuring 4 km by 1.5 km at the widest point. To the north and south, Mongan bog is surrounded by the vast peatlands of Blackwater Bog and Bloomhill Bog. These mires have been extensively mined for peat and have little or no undisturbed stratigraphy. By contrast, much of Mongan Bog is substantially intact. Only the easternmost lobe of the site has been exploited.

Mongan Bogs is one of the very few almost undisturbed sites left in Eire, consequently it has been the focus of a range of palaeoecological and ecological studies. Pollen analyses have been completed to study the forest history and human impact of the area. For an overview see Bradshaw (1987, in Turbidity ed.). Pollen frequencies indicate that the first major anthropogenic impacts in the mire's pollen catchment date to the Neolithic period. No disturbance has been detected from earlier periods although hunters and gatherers probably occupied the region in small numbers during the Mesolithic.

Kneale (1987) used Mongan Bog to provide field data during the testing of the sensitivity of the groundwater mound model for predicting mire topography. Barber *et al.* (1994b) have also taken advantage of the undisturbed upper stratigraphy to reconstruct the record of mire surface wetness, as part of the Palaeoclimate Special Topic grant (ref, GST/02/539). Aspects of the modern ecology of the mire complex have been studied by a number of researchers. For example, Doyle and Dowding (1990) have examined the decomposition and various aspects of the physical environment in experimental plots at Mongan bog, whilst Madden and Doyle (1990) have studied the primary production of the mire.

During the field visit to Mongan Bog in September 1995 an east-west transect of field stratigraphy was completed across the long axis of the mire (Figure 6.6). Core MOG95 was located at the deepest point of the transect which is close to the centre of the site (see Figure 4.7).

4.3.2 Abbeyknockmoy Bog, Co. Galway. (M409492)

Abbeyknockmoy bog lies 25 km north-east of Galway city in Co. Galway, Ireland, at 30 metres above sea level (Figure 4.1 and 4.8). The site is 4.5 metres deep and approximately circular, with a diameter of 2.5 Km. It is the most westerly of the sites. The geology of the area is composed of carboniferous limestone overlain by glacial deposits. The mire occupies the site of a former calcareous lake. Thick marl deposits were encountered during coring for the description of field stratigraphy. These proved to be too stiff to

core through into the underlying parent material. Much of the eastern side of the mire has been cut down to the level of the fen peat leaving a 2 km long peat 'cliff' which reveals a remarkable layered stratigraphy within the raised mire deposits. Pool layers may be traced laterally for 20 to 30 metres at numerous locations. The three metre high 'cliff' was exploited during the climate study carried out as part of the Palaeoclimate Special Topic Grant (GST/02/539, Barber *et al.* 1994b). 10 radiocarbon dates were sampled from the upper *Sphagnum* peat to establish a chronology for the climate reconstructions.

The work carried out for the Palaeoclimate Special Topic is believed to be the first palaeoecological investigation at Abbeyknockmoy Bog. Core locations for the climate project were readily located in lawn environments by examining the extensive sections. However, the sections do not penetrate to the FBT. Therefore in the absence of published stratigraphies, a transect of borings was completed as part of the present project, from the north-east to the south-west side of the mire, prior to locating the main sample core. The radiocarbon dates from Barber *et al.* (1994b) were used to provide an approximate estimate of the age of the lower raised mire peats for the purpose of submitting the radiocarbon application.

The vegetation of the cut area nearest the peat face, is very degraded and mainly composed of *Calluna vulgaris* and *Eriophorum vaginatum* with very few bryophytes and no *Sphagna*. In some areas large tussocks of *E. vaginatum* are growing on an otherwise bare peat surface. Much of the driest part of the mire is fissured and some blocks have begun to slump. Despite this, some areas within a few metres of the peat 'cliff' retain pools on the elevated surface for several days after rain. The uncut area furthest from the most disturbed parts of the mire support thick carpets of *S. magellanicum* and *S. papillosum* amongst other *Sphagna*, brown moss carpets and a full range of raised mire vascular plants. Core AKM95 was located 150 metres from the deep cuttings (Figures 4.8 and 6.7) well within the *Sphagnum* lawns.

Chapter 5:

Reconstructing the fen/bog transition at the intra-site scale: Solway Moss.

5.0 Introduction.

The approach to palaeoecological reconstruction of the FBT may be considered to be a process composed of five basic stages. These include, (1) definition of the problem under examination, (2) design of a sampling strategy, appropriate to the project aims, (3) analysis of biostratigraphy to provide a record of macrofossil and pollen assemblage changes at a coring site, (4) the use of fossil assemblage data to infer mire surface conditions and (5) the use of biostratigraphic data from one or a number of cores and sites to assess the influence of allogenic processes on mire development, at the inter-site scale.

The ability to undertake analyses at stage five requires careful design and implementation of the preceding four stages. Having considered the background to the research aims in Chapters 1 and 2 and the design of the sampling procedure in Chapter 3, the next stage in the process is to assess the variability of the FBT in one mire system, before moving on to draw comparisons between widely separated palaeoecological records. An important issue that requires consideration, in this context, is the degree to which one sample core represents a record of environmental change at the wider scale. If one core is not representative, what is the minimum amount of data required to identify the main large scale (mire scale) stratigraphic changes surrounding the transition to raised mire? A multiple coring strategy was adopted to examine the intra-site variability of pathways culminating in the FBT (Section 5.2). The resulting data will be used to address the following objectives.

5.1 Objectives of the chapter.

- To characterize the pathways leading to the FBT at multiple core sites arranged along a transect, using reconstructions of vegetative and propagule macrofossil assemblages.
- To assess the spatial extent of fossil mire communities using data from the multiple coring programme and comprehensive field stratigraphy.
- To study the variability of mire development pathways.
- To assess the degree of 'ecological noise' in the macrofossil core assemblages, and to distinguish between large scale and small scale changes in the biostratigraphy.

- To gauge the degree to which a single macrofossil core can represent the main large scale changes in the mire system.
- To examine the timing of the fen/bog transition across one site and the rate of mire community change through time and to assess the evidence for allogenic and autogenic controls on mire stratigraphy.

Conclusions drawn from this chapter will be used to design and implement the research questions relevant to stage five of the analysis of the FBT, presented in Chapter 6.

5.2 The approach to reconstructing the fen/bog transition at the intra-site scale.

The assessment of local mire changes requires a large volume of field data. Therefore, sites have been selected wherever possible to take advantage of pre-existing stratigraphic information (Chapter 3). The discovery of two prehistoric cow heads in a pool peat at Solway Moss and the remains of a sheep on the same mire (Wells 1992, 1993) stimulated several palaeoecological investigations, designed to provide an understanding of the context of the finds. These studies, outlined in section 4.1.4 include one pollen diagram and one macrofossil diagram from a core adjacent to the sheep find, with five accompanying radiocarbon age determinations. Subsequently, the North West Wetlands Survey (NWWS) completed a detailed survey of field stratigraphy at Solway Moss, using crossed transects (Figure 5.1). Spot check samples have been analysed in the laboratory from each of the boreholes by Dr C Wells. At the time of undertaking field work for this project (April 1994) these studies represented one of the best concentrations of stratigraphic data available, at a single site, for the peat levels relevant to this project.¹ Therefore, Solway Moss was selected for the intra-site scale study of the FBT.

The field stratigraphy data supplied by the NWWS provides a basis for work on the FBT (Figures 5.2a, 5.2b and 5.3). Analysis of the spatial distribution of fossil plant communities in the basal peats was used to locate the transect for the multiple coring programme (selection criteria are discussed in section 5.3). Five cores, SOLA195 to SOLA595 were recovered at 150 metre intervals, using a 4 cm wide, Russian pattern corer (Figure 5.1). The sampling locations were levelled with a Geodimeter, to a permanent bench mark post, which penetrates through the full sequence of peat, into the underlying silts and clays.

Cores were analysed for macrofossils at 16 cm intervals, using the 5 point scale of abundance method of quantification (Abundance Estimates Macrofossil Analysis, A.E.M.A. Section 3.3.5). The resulting skeleton diagrams provided the necessary information to target more detailed analyses. Skeleton pollen diagrams or spot check pollen samples were also completed to estimate the time span covered by the cores.

¹ Subsequently, the N.W.W.S. has published detailed field stratigraphies for sites in Lancashire and Manchester (Middleton 1995 and 1996) which could prove to be valuable locations for future mire development studies.

SOLA295 proved to contain the most complete sequence of mire development, therefore, this core location was chosen for detailed analysis of the FBT using both macrofossils and pollen.

SOLA295 was recovered using a 9 cm diameter Russian pattern corer (Barber 1984) to provide sufficient material for more detailed vegetative and propagule macrofossil analyses, pollen analysis and bulk radiocarbon age determinations. A master macrofossil diagram was produced, using Quadrat and Leaf Count Macrofossil Analysis (Q.L.C.M.A. for a description of the methods see section 3.3.5), targetted on the period of the transition to ombrotrophic peat and the transition to *Sphagnum imbricatum* domination. An interval of 4 cm was used near the main transitions with intervals of 8 and 16 cm used elsewhere (Figure 5.4). The four remaining skeleton macrofossil cores were completed using an 8 cm sampling interval and the A.E.M.A. five point scale of abundance (Figures 5.5, 5.6, 5.7 and 5.8).

The chronology established for SOLA295, using four radiocarbon age determinations, has been used to provide age estimates for stratigraphic changes in the other four cores, using pollen correlation between the main pollen diagram (Figure 5.9) and the skeleton pollen diagrams (Figures 5.10, 5.11, 5.12 and 5.13). The consistency of the radiocarbon age estimates undertaken on SOLA295 for this project has been cross-checked against the ages for the Solway Sheep site using the same method.

5.3 Gross stratigraphy of Solway Moss.

Examination of the gross stratigraphy at Solway Moss (Figure 5.2a, 5.2b and 5.3) shows that the mire developed on an undulating surface that dips gently (approx. 1 : 150) to the south. The majority of the peatland expanse is underlain by pre-Holocene silts and clays containing a significant coarse sand fraction and occasional stones, which may represent floodplain sedimentation from the adjacent River Sark. At the margins of the moss to the north (core S14, see Figure 5.1) and to the south (site of the Solway Sheep find, core S1) the peat is underlain by sand. Core 14 is close to the banks of the Sark and may have developed over a former channel. In the south part of the mire, a transect of ten cores, sampled at close intervals across the find area of the sheep (Wells 1993, Figure 5.1), reveals more steeply sloping underlying geology, possibly accounting for the coarser inorganic sediments in this area. Additional augering at points A to E (Figure 5.1), using a 2 cm diameter Dutch gouge, penetrated the silts (up to 20cm depth) revealing a pinky grey clay. Walker (1966) describes similar deposits from the Solway plain which are assigned to the Bewcastle drift series, (section 4.1.4) and considered to be of Devensian age by Day (1970).

At four sites, S6, S7, S8 and S11, which coincide with depressions in the underlying geology (Figures 5.2a, 5.2b and 5.3), the basal inorganic sediments are composed of finer materials than those found in surrounding areas. The sequences contain either silts, clayey silts or clays, often with a significant organic content. In addition several of the cores record a fining upwards sequence, suggesting the existence of closed water bodies. Two borehole logs in the deepest areas of the mire centre, S11 and core SOLA295

(Figure 5.4) reveal a stratigraphy commencing with silts and clays which grade into amorphous peat. These deposits are subsequently overlain by sandy silt containing some organic material and then the main peat body. This stratigraphy implies a period of catchment erosion possibly caused by reduced vegetation cover and a deteriorating climate.

Both the borehole data and an examination of the main drainage ditches dug by the Richardson Peat Co. at Solway Moss reveal that *Betula pendula* woodland was widespread across the Sark floodplain at the onset of peat accumulation. The stratigraphy described by Wells (1993) for the Solway Sheep site (S1) is typical of mire development from the widespread wood peats. At core S1 wood peat began to accumulate after c. 6000-6500 BC (7950-8450 cal. BP). This mire phase was regularly punctuated by fires which Wells (1993) tentatively attributes to Mesolithic human disturbance. Analysis of the borehole data across the whole mire demonstrates evidence for widespread charcoal layers in the basal peat, across the southern and eastern sectors of the mire (e.g. cores S2, S3, S4, S5, S7, S9, S10, S12, S20, S21, S22, Wells unpublished data). Peat inception in the larger depressions was largely free of charcoal as may be expected in these wetter areas. In addition, if the burning phases were anthropogenic, the deepest peats in the basins may be sufficiently old to predate the occurrence of human induced fires.

A *Polytrichum* spp. and *Sphagnum* sect. *Acutifolia* association, possibly representing damp 'heath-like' vegetation, rapidly displaced the woodland communities, dominating large areas of the moss (see borehole logs appendix 1) prior to the appearance of *Eriophorum vaginatum* and shortly afterwards *Calluna vulgaris*. At core S1, Wells (1993) dates the appearance of *Eriophorum vaginatum* to c. 5000 cal BC. With the exception of a brief wet phase dated to 3360-2890 Cal BC (5310-4840 cal. BP) (Wells 1993) this community persisted until the rise to dominance of *Sphagnum imbricatum*.

The borehole logs identify at least three main shallow depressions underlying Solway Moss (or one sinuous basin), centred on cores S7, S11 and S20, (Figures 5.2a 5.2b and 5.3) in which fen peats have accumulated. Remains of *Phragmites australis* and *Equisetum* spp. could be discerned in the field with the aid of a hand lens or field microscope. Field stratigraphy indicates that these fen deposits were either short lived or accumulated very slowly, laying down only a few decimetres of peat. In common with surrounding areas, the fen peat is superseded by acid communities reminiscent of damp heath, containing an abundance of *Polytrichum* spp. Again, *Eriophorum vaginatum* and *Calluna vulgaris* displace this community in some but not all cores. Further evidence for a wet phase prior to the rise of *Sphagnum imbricatum* can be discerned in the *Eriophorum* peat lying above the fen depressions. In virtually all cores the *Polytrichum* spp. and *Eriophorum vaginatum*/*Calluna vulgaris* dominated peats are highly humified varying from H7 to H9 on the von Post scale (von Post 1924). The resulting band of dark comminuted peats may be easily separated by visual examination in the field from the overlying lighter peats which coincide with the spread of *Rhynchospora alba*, pool species such as *Sphagnum cuspidatum*, and with the increase in *Sphagnum imbricatum*.

5.4 The selection of the multiple core sites.

All three of the basins containing fen peats were considered for a more detailed study of the FBT. The basin centred on cores S9 to S11 was selected after further preliminary coring, designed to establish the extent of the fen peats, for two reasons. Firstly, this basin appeared to offer the largest single area of fen deposits, ideal for testing ideas concerning the lateral extent of stratigraphic changes and, secondly, the occurrence of a basal mineral inwash layer suggested that the area may contain peats dating from the beginning of the Holocene. Identification of a full sequence of sedimentation at the site was considered to be desirable so that the first record of mire acidification could be examined. The five replicate Russian sample cores SOLA195 through to SOLA595 were laid out to cover a complete cross section of the chosen basin, between boreholes S6 to S10. (Figure 5.1).

5.5 Components of the macrofossil diagrams.

5.5.1 Depth.

The depth scale represents the centimetre depth from the present cut or uncut mire surface. Core sections have been analysed from the contact with underlying inorganic strata to the level at which the main raised bog forming mosses (principally *Sphagnum imbricatum* and *Sphagnum cuspidatum*) become dominant for the first time. Radiocarbon dates presented in section 5.10.2 have been used to convert the depth scale into an estimated age scale using linear extrapolation between dates.

5.5.2 Aggregate macrofossil curves.

Aggregate macrofossil curves have been included as solid black histograms on the right hand side of the percentage diagrams to provide a summary of the main peat components. These types include the sum of all monocotyledon remains, total identified *Sphagnum* and unidentifiable organic matter (U.O.M.). The summary curves represent percentage cover of the microscope graticule (Section 3.5). The category of U.O.M. is applied to organic material that is humified to the extent that all structure is lost.

5.5.3 Macrofossil components.

Each main macrofossil diagram contains data quantified in three ways. Components, such as monocotyledon and *Ericaceae* remains that form a large part of the peat matrix have been assessed as percentage cover of the microscope graticule. The frequencies for each taxon are displayed in the diagrams as joined histograms with depth bars centred on the sampling point. The proportions of individual bryophyte species have been quantified using the Q.L.C.M.A. system outlined in Chapter 3. The leaf counts have been used to divide up the total percentage cover of bryophytes between the various taxa present. Therefore, individual moss species are also represented by joined histograms.

Small macrofossils such as fruits, seeds, bud scales, spindles and fungal sclerotia (and charcoal) are frequently numerous, yet cover only a very minor percentage of the microscope graticule. Therefore, these

components were quantified using the five point scale of abundance (Section 3.5). Taxa assessed using this system have been represented by unlinked histograms in the macrofossil diagrams. The thickness of an individual bar is equivalent to the sample thickness on the diagram's depth scale.

The multiple macrofossil cores from Solway Moss differ from the main diagram (SOLA295) in that all of the taxa have been quantified using the five point scale, to make the volume of analyses manageable in the time available. In this case all of the components are represented by unlinked histograms.

The overall organization of the diagrams is designed to aid comparisons between cores and sites. Taxa have been placed in approximate order of their first major appearance in the record. Therefore, fen species usually occur on the left hand side of diagrams and acid mire species on the right. Components such as undifferentiated monocotyledon remains have been plotted in the middle. The placement of species is not in strict order since they have also been grouped, wherever possible, into phanerogams, shrub species, bryophytes etc.

5.6 Zonation of the macrofossil and pollen diagrams.

Horizontal zonation lines are commonly used in pollen diagrams to aid the interpretation of complex biostratigraphy consisting of many levels and species (Birks and Birks (1980). The technique has also been applied to macrofossil diagrams (e.g. Barber 1981, 1994, Stoneman 1993, Almquist-Jacobsen and Foster 1995). The most widely used subdivision in Quaternary palaeoecology is the assemblage zone defined by Hedberg (1972) as:

'a body of strata whose contents of fossils, or of fossils of a certain kind, taken in its entirety, constitutes a natural assemblage or association which distinguishes it in biostratigraphic character from adjacent strata.' (p223)

In this study macrofossil diagrams are divided into local macrofossil assemblage zones (LMZ) These are quoted with the core code followed by the letter label for the zone (e.g. LMZ-SOLA2-C). For pollen diagrams a similar system is used with the prefix LPZ standing for local pollen assemblage zone and numbers replace letters for the zone labels (e.g. LPZ-SOLA2-3). To aid pollen correlation between multiple pollen cores at Solway Moss and Walton Moss, mire pollen zones have been recognized and labelled with the prefix MPZ followed by the site code and a zone number (e.g. MPZ-SOL-1).

Birks and Birks (1981) state that pollen diagrams should be zoned only on the basis of the observed pollen stratigraphy. Numerical methods such as cluster analyses may provide an objective method of performing this task, eliminating human bias. However, these techniques have problems of their own. For example, cluster analysis frequently fails to pick out the *Ulmus* decline as a significant stratigraphic change in pollen diagrams because the total change in the pollen spectra may be small. The same may be true in the

macrofossil diagrams from this study where the appearance or disappearance of indicator species from assemblages dominated by one species such as *Phragmites australis*, may be significant. Similarly cluster analysis may pick out large changes in the macrofossil assemblages such as the frequent fluctuations between *Sphagnum* sect. *Acutifolia* and *Eriophorum* which do not represent a significant change in the water or nutrient levels of the mire. Therefore, macrofossil diagrams were zoned by eye but with the aid of the groupings produced by detrended correspondence analysis (DCA). Once the zonations were complete they were compared against the CONISS cluster analysis option in the TILIA plotting programme. The resulting dendrograms usually confirmed the original zonation, however they are not included on the diagrams due to lack of room.

The macrofossil diagrams are presented in Figures 5.4 to 5.8

5.7 The ecology of species identified in the macrofossil assemblages.

The following sections provide an introduction to the ecology of the taxa identified in the macrofossil record, at Solway Moss. The species or genera are grouped into the major sub-fossil assemblages recorded from cores SOLA1 to SOLA5. Within each assemblage the species are generally treated individually and a short summary of the inferred conditions for peat formation is provided at the end of each section. Taxa occurring throughout the record are introduced in the assemblage where they make their first major appearance.

In most circumstances a uniformitarian approach may be adopted to draw inferences about the nature of a palaeoenvironment, based on the modern ecology of the constituent taxa. However, caution is required when undertaking this kind of analysis. Species do not always maintain their full niche within a community, over millennial time-scales. For example *Sphagnum imbricatum* once dominated most raised mires in the British Isles and western Europe (Green 1968). Several phases of extinction over the last 700 years have greatly reduced the species' distribution to the extent that it is now rare in Britain (Stoneman *et al.* 1993).

A second source of error in examining fossil assemblages relates to the geographic shift in the ecology of some species. For example *Sphagnum magellanicum* has a narrower niche with respect to pH and depth to the water-table in continental Canadian mires, when compared with oceanic sites (Slack 1990). Barkman (1992) found similar variations in *S. magellanicum* in Europe. *Sphagnum subnitens* ranges between oligotrophic and mesotrophic habitats depending upon the degree of oceanicity (Daniels and Eddy 1990), whilst *Sphagnum imbricatum* sub-species *austinii* becomes more minerotrophic at the limits of its distribution (Flatberg 1986). Clearly, fluctuations in macroclimate over the duration of the Holocene, may have significant implications for the interpretation of some species. However, the process of extracting ecological information from fossil assemblages, where the ecology of one or more of the main species has altered over time, may be aided by examining the widest possible range of accompanying taxa.

The macrofossil assemblages described in the following sections have been recognized from the zonation of the main macrofossil diagrams (Figures 5.4-5.8 and 6.8-6.15). Zonations were initially delimited by eye and subsequently checked using both the CONISS cluster analysis option of the TILIA plotting programme and the Detrended Correspondence Analysis option (DCA) of the CANOCO environmental gradient analysis package. DCA proved to be particularly useful for objectively identifying the FBT in the macrofossil data. (Figures 5.15-5.33 and 6.25-6.55).

Macrofossil assemblages described in this project are not directly comparable to modern phytosociological assemblages. The species represented in the sub-fossil record may not accurately reflect the original composition of the peat-forming vegetation due to processes such as transport, differential decomposition and the penetration of roots and rhizomes into older peats. These factors are discussed further in Section 3.3.1.

5.7.1 *Phragmites australis* / *Carex* spp. / *Salix* spp. assemblage.

The *Phragmites* / *Carex* spp. / *Salix* spp assemblage is relatively species rich. Therefore, the following examination of the modern ecology of its constituent plants will focus on the main indicator species. Other species will be examined in the discussion where relevant.

***Phragmites australis*.**

The latitudinal distribution of *Phragmites australis* is wide, ranging from the tropics up to 70°N. In the northern part of its range the species is sterile, reproducing vegetatively and forming large clonal stands in favourable conditions. In Britain most apices are sterile and sexual reproduction is rare (Haslam 1972).

Phragmites is capable of tolerating a large water-table range in conditions of high nutrient availability, relatively high pH and warm temperatures, although sudden changes may be deleterious (Haslam 1970, Hellings and Gallagher 1992). In Britain, water-table changes may be limiting above and below 1 metre from the substrate surface. Within this range the only significant affect of vertical water-table movement is through the potential impact upon *P. australis*' competitors (Haslam 1972).

Haslam (1970) has found that nutrient status is more significant than water supply as a limiting factor on the performance of *P. australis* in northern Britain. However, in the south interspecific competition becomes more significant where site conditions are drier. In undisturbed stands in the middle of its range, the performance of *P. australis* may be predicted successfully from the factors of soil, water and light regimes. (Haslam 1971). *P. australis* is intolerant of much water movement, occurring in stagnant water habitats where flow is subdued. Under conditions of moderate to severe scour the species is absent.

pH values vary considerably from 3.6 to 8.6 for substrata supporting *P. australis* communities. However, the optimum range for growth may be nearer to pH 5.5 to 7.5 (Spence 1964). In oligotrophic habitats where competition is low the species may be able to persist as a relic of a previous community in areas that are no longer suitable for colonization. (Chapman 1964, Haslam 1972, Barber 1981, p49). Where this occurs the reed may be able to grow in relatively dry surface peat due to its great rooting depth and the low level of competition.

Burning, particularly in spring and Autumn, stimulates the production of above ground biomass in *P. australis* (Thompson and Shay 1985). However, shoots are damaged by severe frost and growth ceases between September and April in Britain (Haslam 1972).

Carex spp.

Carex rostrata inhabits peatlands and lake margins with a constantly high water-table, where the pH lies between 4.5 and 6.5 units (Jermy *et al.* 1982). The sedge is also found in flushes receiving water with a low base saturation and in quaking mat vegetation (Catling 1996). On raised bogs *C. rostrata* is commonly associated with *Sphagnum* carpets in the low lawn part of the hummock/hollow gradient.

C. vesicaria is a plant of wet peatlands with a slightly more mesotrophic character than *C. rostrata* (Jermy *et al.* 1982). In the southern part of its distribution, turnover of above ground biomass may be continuous, with up to seven distinct cohorts per year. The species can take advantage of the annual die back in a reedswamp community by producing a cohort in the winter when above ground biomass of competitors is negligible (Danaï 1986).

Both *C. vesicaria* and *C. rostrata* will hybridize with *C. riparia*. The latter species also inhabits areas with a high water-table, frequently around the edges of ditches, ponds, beside slow flowing rivers and in fens. At present *C. riparia* is commonly associated with *C. acuta* and *C. acutiformis*, forming large colonies where water stands for long periods throughout the spring (Jermy *et al.* 1982). Significantly, the modern distributions of these latter three species has a southern bias, becoming rare or absent north of the Scottish lowlands.

C. nigra type: Achenes of this type proved to be difficult to separate in the fossil state, particularly when the utricle was absent. The group contains seven species of which *C. aquatilis*, *C. elata* and *C. nigra* are most frequently associated with the other *Carex* species identified in this assemblage. Table 5.1 summarizes the ecology of the group.

Table 5.1 Summary of the ecology of the *Carex nigra* group.

Species.	Ecology.
<i>Carex recta</i>	V. local, in estuaries and lower riverine habitats on stiff peaty alluvium or sand.
<i>Carex aquatilis</i>	A swamp species accompanied by <i>C. rostrata</i> & <i>C. vesicaria</i> , but alone in rivers.
<i>Carex acuta</i>	In marshes, freshwater margins and other wet places.
<i>Carex nigra</i>	Wide habitat tolerance, usually found in peatlands with some mineral water input. Found in upland flushes, lowland fen, dune slacks and stream sides.
<i>Carex elata</i>	In eutrophic mires with some seasonal flooding. Common by fen ditches/lakes.
<i>Carex bigelowii</i>	Mountain plant occurring above 600m in <i>Rhacomitrium/Vaccinium</i> /lichen heath.
<i>Carex trinervis</i>	A dune slack species.

Source: Jermy *et al.* (1982).

***Salix* / *Populus* type.**

The *Salix* genus is relatively large including tree, shrub and dwarf shrub species. The main macrofossil remains of this genus are wood fragments, although highly degraded fragments of bud scales and the remains of dicotyledon leaves are found in the wood peat. It is not possible to differentiate between species of *Salix* or *Populus* on the basis of wood anatomy alone. Many native species of *Salix* live in damp to wet environments either beside or in streams, in fens, marshes and carr woodlands (Meikle 1984). However, the macrofossil remains could represent the presence of *Salix herbacea* which is a plant of high altitudes at present, becoming rare below 600 metres. This dwarf *Salix* species usually grows on moist, exposed rock ledges, on rocky summits and in Alpine damp turf with *Carex* spp. and a range of *Poaceae* species (Meikle 1984).

5.7.2 *Phragmites australis* / *Equisetum* spp. assemblage.

Equisetum fluviatile* / *E. palustre

The optimum conditions for *Equisetum fluviatile* are found in shallow water (typically up to 65cm depth¹) at the edges of lakes ponds or ditches. Frequently, the species extends from the margins of a mire into open water (Grime *et al.* 1988). *E. fluviatile* occurs in substrates with a pH range between 4.0 and 7.5 although it is mainly found growing at pH 6.0 to 7.0. The diversity of associated species is usually low, however the plant may be present in species rich soligenous mires (Grime *et al.* 1988). *E. palustre* is frequent in soligenous mires, often marginal to open water and temporarily flooded situations, however,

¹ Spence (1964) has recorded some individuals of *Equisetum fluviatile* growing at depths up to 1.5 metres in Scottish Lochs.

the species is absent from submerged sites. *E. palustre* occurs on soils with a pH greater than 5.0 up to pH 8.0.

In this assemblage *Equisetum* spp. is accompanied solely by an abundance of *Phragmites australis* remains suggesting that it is *E. fluviatile* that is present, indicating swamp conditions and shallow standing water.

5.7.3 *Phragmites australis/Equisetum/Sphagnum recurvum/Menyanthes trifoliata/Scheuchzeria palustris* assemblage.

Sphagnum recurvum.

Sphagnum recurvum exhibits a shift in ecology depending upon geography. In Sweden and Finland the species occupies mesotrophic habitats, whereas in Germany it is more strictly a species of ombrotrophic *Sphagnum* bogs, occupying an intermediate position on the hummock/hollow gradient. In the British Isles it is weakly minerotrophic growing on the fringes of carr woodland, in the lags surrounding raised mires (Daniels and Eddy 1990), in poor fens and oligotrophic valley mires (personal observations). Occurrence of the species is indicative of a degree of water movement through the mire substrate or across the mire surface.

Menyanthes trifoliata.

The water-level in a community containing *Menyanthes trifoliata* is usually at or above the substratum level. Under drought conditions individuals may tolerate exposure of the substratum so long as it remains moist. The species usually occurs on gleys or peats with an organic content of 13 to 92 percent and a pH in the range 4.5 to 7.1 units. The communities in which *M. trifoliata* appears may be broadly classified into:

- (1) Habitats flushed by groundwater. These may be upland or lowland sites each with characteristic associations of phanerogams and aquatic species. In these habitats *M. trifoliata* occupies the wetter areas where groundwater flow is most marked.
- (2) Communities marginal to lakes or ponds, partially or completely filled by peat. These communities have many similarities to flushes. In the lakeside habitat *M. trifoliata* is commonly associated with *Phragmites* and *Cladium mariscus*. A whole range of aquatic and fen herbs may also be associated, depending upon the particular site conditions. *M. trifoliata* grows best in marginal situations because it is excluded by heavy shade and intense competition for nutrients from species such as *Phragmites australis*. However, *M. trifoliata* can withstand a degree of competition for light, by making phenotypic adjustments, including increased leaf blade area and earlier expansion of leaves in the growing season (Haraguchi 1993).

(3) Occasionally *M. trifoliata* may be found in drainage channels formed between the roots of trees in carr woodland. In these circumstances it is only found beneath a break in the canopy.

Scheuchzeria palustris.

Throughout its range *Scheuchzeria palustris* is confined to oligotrophic mires with a permanently high water-table (Tallis and Birks 1965). The species is usually associated with *Sphagnum* in mud-bottom communities and flarks on raised bogs, in floating raft vegetation and in poor fens (Tallis and Birks 1965).

The present distribution of *S. palustris* covers much of central and eastern Europe from northern Scandinavia to the Massif Centrale. In Britain the rush is confined to just one site on Rannoch Moor, although macrofossil evidence proves that it was once much more common (see for example, Moore 1955 in Ireland and Sledge 1949 in Scotland). The more constant modern associates of *Scheuchzeria palustris* include *Equisetum fluviatile*, *Menyanthes trifoliata*, *Eriophorum* spp., a range of *Sphagna* and *Carex* spp. All of these species and others have been found with *Scheuchzeria palustris* in peats from across Britain and Europe. Therefore, Tallis and Birks (1965) have concluded that 'in the past *Scheuchzeria* probably flourished in similar situations to those in which it occurs at the present day.' (p288). However, the appearance of distinctive bands of peat rich in the remains of *Scheuchzeria palustris* have been used to infer flooding of raised bogs or poor fens by base-poor waters, particularly where the remains overlie fossil assemblages indicative of dry mire conditions (Tallis and Birks 1965).

The modern ecology of the four main species in this assemblage suggests that the peat formed in conditions of moderate surface flow or flushing within the peat. The water passing through the system would have been moderately acidic with a low base saturation and the water-table was probably continually at or above the surface of the peat, throughout the year.

5.7.4 *Eriophorum vaginatum* / *Calluna vulgaris* / *Cenococcum grandiforme* assemblage (often with charcoal).

Eriophorum vaginatum.

Eriophorum vaginatum has the ability to grow in a wide range of moisture conditions (Wein 1973). Hammond *et al.* (1990) quote a range of 0-28 cm depth to water-table (Table 5.3). The species dominates modern communities that have annually fluctuating water-levels. These may be high enough to flood tussock bases in the spring, falling considerably in late summer (Tansley 1939, Gimingham 1964). In the British Isles the greatest concentration of *E. vaginatum* is found in areas of blanket peat receiving over 1500 mm of annual precipitation (Perring and Walters 1962). However, in Arctic tundra it may grow where annual precipitation is just 250 mm (Wein 1973).

E. vaginatum occurs in strongly oligotrophic areas containing stagnant water (Gore and Urquhart 1966). pH values for deep peat communities may be as low as 2.98 units (Ratcliffe 1959). Gimingham (1964) recorded values between pH 3.6 and 3.8, with a base saturation of 30%, in *E. vaginatum* wet heath vegetation in Scotland. In common with many species of strongly oligotrophic habitats, including the *Sphagna* and *Rhynchospora alba*, *E. vaginatum* has a high cation exchange capacity particularly for phosphorous (P) (Chapin and Tyron (1982). Exchange of nutrients appears to be possible even in completely anaerobic conditions which would preclude *Sphagna* (Boggie *et al.* 1958). However, *E. vaginatum* also adopts a strategy of annual nutrient translocation between rhizomes and above ground biomass (Jonasson and Chapin 1991).

Drought is not a serious problem for *E. vaginatum* because it produces annual roots that grow vertically down into the peat (Kummerow *et al.* 1988), to a depth of 60 cm (Wein 1973). This enables the sedge to persist for long periods after former bog communities have been drained. Often *E. vaginatum* becomes more luxuriant and tussocky as the bog dries out (Wein 1973) because it can exploit the release of nutrients caused by the accompanying higher rate of mineralization (Malmer *et al.* 1994). Shaver *et al.* (1986) have demonstrated significant increases in growth rate after applications of P, potassium (K) and to a lesser extent, Nitrogen (N). By contrast, Gebauer *et al.* (1995) found that *E. vaginatum* growth rates could increase with a change to wetter soil conditions. However, this was only recorded if N availability was very high. Under low N conditions (as found in raised mires) growth in flooded soils was significantly reduced compared to more aerated substrates.

In many disturbed and undisturbed raised mire communities *E. vaginatum* may form the dominant species on hummocks. In the Silver Flowe, Boatman (1983) observed that *E. vaginatum* favoured drier parts of the mire in conjunction with *E. tetralix* and *S. capillifolium*. Barber (1978) reported similar findings from Bolton Fell Moss which also agree with Katz (1926 in Barber 1978). Detailed analysis of the hummock/hollow complex at Clara Bog, Co. Ofaly, recorded the greatest percentage cover for *E. vaginatum* on high hummocks although the species was present in all height classes (Van der Molen *et al.* 1994). Osvald (1923), Wein (1973), Barber (1978) and (pers. obs.) have all noted that *E. vaginatum* may invade pools although these are often shallow and ephemeral.

Calluna vulgaris.

Calluna vulgaris is indicative of dry mire conditions (Tansley 1939). The roots of *C. vulgaris* are fairly shallow, reaching 15 cm depth and cannot tolerate waterlogged conditions (Rutter 1955, Malmer 1962) due to the lack of aerenchyma cells. During dry phases *C. vulgaris* is a very successful species on raised mires. Penetration of its roots into underlying peat may result in significant secondary decomposition (Middeldorp 1986) caused by increased aeration (Casparie 1993). *C. vulgaris* is closely associated with mycorrhiza (*Pezizella ericae*) which may stimulate the production of adventitious roots important for

regeneration by layering (Scandrett and Gimingham 1989). This fungal activity is also limited by anaerobic conditions resulting from waterlogging.

The maximum above ground biomass production by *C. vulgaris* is achieved on hummock tops, it then decreases steadily down the hummock/hollow gradient (Wallen 1987) to a limit 10 cm above the water-table (Hammond *et al.* 1990). Van der Molen *et al.* (1994) registered a similar pattern for the percentage cover of *Calluna* along the same gradient.

A decumbent sometimes trailing growth habit allows *C. vulgaris* to survive in a continuously growing *Sphagnum* mat. The ability to rejuvenate below ground biomass by forming adventitious roots on buried segments of stem, termed layering (Macdonald *et al.* (1995) , makes *C. vulgaris* virtually immortal in that environment. There is some evidence to suggest that the presence of *Sphagnum* and the *Pleurocarpus* mosses (except *Hypnum* spp.) actually stimulate the layering process (Macdonald *et al.* (1995). Layering is also linked to the nature of the substrate, being common on partially anoxic wet heath soils and bog peats but absent from dry heath soils (Forrest 1971, Rawes and Hobbs 1979, Hobbs 1984).

Cenococcum grandiforme

This species of fungus is typical of mor and peat soils. It is found growing under a wide diversity of moisture conditions and vegetation types, including *Betula* spp. woods growing on peat, *Calluna* moorland, wet *Sphagnum* carpets and grassland. The distinctive black spherical sclerotia of *Cenococcum grandiforme* usually occur just below the soil surface; however they have also been observed amongst surface vegetation, on bare soil and on sandy substrates (Ferdinandsen and Winge 1925). The species appears to be particularly abundant under *Calluna* and *Betula* spp. cover. The geographical range of the fungus appears to be mainly limited to Europe with no known recordings from either alpine regions or the Arctic (Ferdinandsen and Winge 1925).

The *Eriophorum vaginatum* / *Calluna vulgaris* / *Cenococcum grandiforme* assemblage may be interpreted as a dry oligotrophic or ombrotrophic bog community. Whilst *C. grandiforme* and *E. vaginatum* can tolerate widely varying water-levels, the presence of significant quantities of *C. vulgaris* remains and the virtual absence of *Sphagna* and brown mosses suggests the existence of a mire community similar to dry heath vegetation with a relatively low water-table in the range of 10 to 60 cm below the growing surface. Blanket mire vegetation may also be dominated by a *Calluna* / *Eriophorum vaginatum* association but, the surface layers remain sufficiently aerated for *Calluna vulgaris* growth due to the significant slope angle of these mires.

The occurrence of charcoal bands associated with this assemblage indicates frequent burning.

Eriophorum vaginatum has a well protected leaf apex providing a high level of resistance to burning (Philips 1954). However, woody heath and bog species, such as *Calluna vulgaris*, are less resistant to fire

(Ratcliffe 1959). *Eriophorum vaginatum* benefits from the nutrients released after burning, spreading to produce a fire climax (Wein 1973). In *Calluna vulgaris* / *Eriophorum vaginatum* communities, Gore and Ohlson (1967) found that a species composition resembling the pre-fire state took twenty years to redevelop, therefore, mires dominated by *Eriophorum vaginatum* with little *Calluna vulgaris* may be maintained over protracted periods of time if the burning cycle is short (Hobbs 1984).

5.7.5 *Eriophorum vaginatum* / *Sphagnum* sect. *Acutifolia* / *Calluna vulgaris* / Brown mosses assemblage.

This assemblage is distinguished from the preceding one by the presence of *Sphagnum* and brown mosses. *Sphagnum* sect. *Acutifolia*, *Polytrichum* spp. and *Aulacomnium palustre* are the most common species. *Dicranum scoparium* and *Pohlia nutans* are also represented.

***Sphagnum* sect. *Acutifolia*.**

The family *Sphagnaceae* was divided into groups of similar species called sections by Isovilta (1966). Section *Acutifolia* contains 11 species all of which are medium sized, with small lanceolate or ovate-lanceolate branch leaves (Daniels and Eddy 1990). In the sub-fossil form most species are difficult to separate using branch leaf morphology alone, however *Sphagnum molle* is an exception. In the present project the frequently high degree of decomposition of peats containing *S.s. Acutifolia* remains precluded any attempts to break the section down further. This presents a problem for the interpretation of assemblages where *S.s. Acutifolia* appears with few associates.

The section may be divided into two main groups on the basis of nutrient status:

(1) Eutrophic to mesotrophic species requiring varying degrees of mineral water input and water movement. This group includes *S. warnstorffii*, *S. russowii*, *S. fimbriatum*, *S. girgensohnii*, *S. subfulvum*¹ and *S. angermanicum*².

(2) Oligotrophic or ombrotrophic species. This group may be split further into three groups³ on the basis of their position on the hummock/hollow gradient (Table 5.2).

¹ and ² These species are not recorded in Britain at present (Daniels and Eddy 1990). They are also absent from Dickson's (1973) records for the Pleistocene, therefore, they may never have been native to the British Isles.

³ *Sphagnum quinquefarium* is excluded from the classification because it is not usually a mire species. (Smith 1978, Daniels and Eddy 1990).

Table 5.2 The division of oligotrophic members of *Sphagnum* sect. *Acutifolia*.

Environment	Species
2a High hummock	<i>Sphagnum capillifolium</i> var. <i>rubellum</i> and <i>Sphagnum fuscum</i>
2b Low hummock	<i>Sphagnum capillifolium</i> var. <i>capillifolium</i>
2c Lawn	<i>Sphagnum subnitens</i> and <i>Sphagnum molle</i>

Source: Daniels and Eddy (1990).

The common occurrence of *Eriophorum vaginatum*, *Calluna vulgaris* and *Polytrichum alpestre* type with *S.s. Acutifolia* suggests that much of the assemblage contains one or more of the oligotrophic hummock species *S. fuscum*, *S. capillifolium* var. *rubellum* or *S. capillifolium* var. *capillifolium*. However, this kind of interpretation requires some caution. The ombrotrophic hollow environment is within the fundamental niche of many lawn and hummock species which may only occupy these niches due to biotic factors (Slack 1990). Therefore, some species may vary in their position on the hummock/hollow gradient depending upon which other species are present. Rydin (1985a) found that *S. fuscum* occupied higher hummock locations in the presence of *S. capillifolium* var. *rubellum* although the former species can grow in wetter parts of the gradient (Cronberg 1989).

***Aulacomnium palustre*.**

Aulacomnium palustre has a wide pH tolerance appearing in ombrotrophic bogs, poor fens and moderately rich fens, that range from pH 3.5 to 7.7. Consequently the species is widely distributed occurring at all sites investigated by Janssens (1992) in the Minnesota peatlands. The presence of *A. palustre* in a mire community is usually interpreted as representing a degree of nutrient enrichment, for example Nicholson and Gignac (1995) registered the greatest abundance of the species at pH 6, with a water-table depth of 10 cm, in Canadian peatlands. However, Li and Vitt (1994) found that the occurrence of *A. palustre* bore little relationship to nutrient availability but rather to its ability to regenerate quickly in disturbed micro-habitats. The species is able to utilize resources efficiently during establishment allowing rapid colonization, but individuals have poor survival rates, thus hampering competitive ability. Therefore, *A. palustre* is excluded from mature *Sphagnum* and *Eriophorum vaginatum* communities by competition (Li and Vitt 1994) despite having a high cation exchange capacity approaching that of *Sphagnum* (Proctor 1982a).

***Polytrichum* spp.**

The *Polytrichaceae* are well known species of acid soils (Proctor 1982b). pH values for the mean abundance of *P. commune* and *P. alpestre* (*P. strictum*) were recorded as 4.1 and 4.2 respectively by Anderson *et al.* (1995). Nicholson and Gignac (1995) found that *P. alpestre* was most abundant at pH values < 5.5 although the species was found in mires ranging from pH 3.5 to 7.5. *P. alpestre* is abundant in intermediate moist habitats in the range of 15 to 17 cm depth to the water-table. However, *P. alpestre*

and *P. commune* are well adapted to withstand long periods of desiccation; for example, Bayfield (1973) noted that *P. commune* was able to reduce water loss using a series of complex adjustments in leaf orientation. *Polytrichum* spp. also translocate water efficiently through the central strand of the leaves and in the stem cortex, under high evaporative flux and externally under moderate flux (Bayfield 1973). The leaves themselves have a well developed cuticle, further cutting water loss (Proctor 1982b), consequently, *Polytrichum alpestre* is frequently associated with *Sphagnum* hummocks. Gignac *et al.* (1991) consider the species to be an indicator of dry oligotrophic bogs and poor fens.

Dicranum scoparium* and *Pohlia nutans

Dicranum scoparium may be found growing on rocks, walls, trees and logs as well as on acidic peat soils (Smith 1978) at an average pH of 5.0. The species is tolerant of considerable desiccation and extreme temperatures in the desiccated state (Proctor 1982b). An ability to live well above the water-table is facilitated by external structures which allow rapid translocation of water (Bowen 1931). *Pohlia nutans* is also a species capable of living on rock, decaying bark and peat (Smith 1978), preferring strongly acidic conditions (pH 4.0, Anderson *et al.* 1995) and either wet or dry habitats.

The *Eriophorum/Calluna/Sphagnum* sect. *Acutifolia*/Brown moss fossil assemblage is reminiscent of hummock communities on ombrotrophic *Sphagnum* bogs. This assemblage represents a relatively dry bog but probably less so than the *Eriophorum/Calluna* assemblage described in section 5.7.4.

5.7.6 *Rhynchospora alba*/Eriophorum vaginatum.

Rhynchospora alba.

Rhynchospora alba is the dominant component of this fossil assemblage. The species is typical of wet mud bottom areas in strongly oligotrophic mires where vegetation cover and competition are limited (Ohlson and Malmer 1990). Godwin and Conway (1939), working at Tregaron Bog, recorded *R. alba* growing on low lawns surrounding pools and in the shallower parts of the pools themselves. However, the species was rarely observed in deeper water, suggesting a lack of tolerance to perennial inundation. A detailed study of mire species distributions and water-table depth measurements, at Lodge Bog Co. Kildare, indicates that *Rhynchospora alba* can tolerate a water-table depth range of 0 to 10 cm (Hammond *et al.* 1990, see also Table 5.3). Similar studies at Kisselbergmosen in Norway (Økland 1990) give a median depth to the water-table of 5 to 7 cm for the species. A shallow rooting system prevents the species from occupying higher levels on the mire (Ohlson and Malmer 1990).

The replacement of *Eriophorum vaginatum* / *Calluna ulgaris* mire by *Rhynchospora alba* may represent a significant increase in the mire water-table. Whilst *Eriophorum vaginatum* can invade pools (Barber 1981) it grows less vigorously under conditions of prolonged waterlogging (Wein 1973). *Rhynchospora alba* may be able to rapidly invade the mire surface, if bare areas of peat are exposed, due to death amongst the

dominant mire species. Similarly, *R. alba* is often one of the first species to appear on bare peat after severe trampling or deep burning of the mire vegetation. However, the regrowth of species after a fire may be expected to displace *R. alba*, since it prefers areas with low competition.

5.7.7 *Sphagnum imbricatum* / *Rhynchospora alba* assemblage.

Sphagnum imbricatum.

Three sub-species of *Sphagnum imbricatum* are recognised by Flatberg (1984). Of these two are found in Europe. Subspecies *affine* is minerotrophic and distinguished by sparse comb lamellae located in the basal areas of the branch leaves. By contrast sub-species *austinii* occupies ombrotrophic habitats with a pH range of 4.5 to 6.5 (Andrus 1986) and has densely packed comb lamellae throughout the length of the branch leaves (Flatberg 1986).

The arrangement of lamellae in the fossil material from the *Sphagnum imbricatum*/*Rhynchospora alba* assemblage at Solway Moss, indicates the presence of sub-species *austinii*. Flatberg (1986) notes that the subspecies '*prefers a relatively high level position on hummocks (although) the cushions only rarely arch over the summits*'. p69. The tightly packed cushions usually occur well above the groundwater-table and the lower limit for *Calluna* growth (Section 5.7.4). *Sphagnum fuscum* is the only other member of the European Sphagna to assume such a high niche, displacing sub-species *austinii* in sub-alpine (above 300 m a.s.l., Flatberg 1986), continental and sub-arctic mires, in Norway. Usually very few *Sphagnum* species intermingle with sub-species *austinii*. *Sphagnum capillifolium* var *rubellum* is the most common exception.

Occasionally, sub-species *austinii* is found growing on low hummocks and lawns in association with *Sphagnum papillosum*. However, competition with other Sphagna usually limits its growth at lower levels (Flatberg 1986). Stoneman *et al.* (1993) points out that modern growth rates for *Sphagnum imbricatum* are slow in comparison to other Sphagna (Green 1968). However, laboratory measurements conducted by Green (1968) demonstrated that samples of *Sphagnum imbricatum* from ombrotrophic hummocks (therefore almost certainly sub-species *austinii*) '*showed the most rapid shoot elongation under conditions of highest water-level.*' (pg 50). Tallis (1962) carried out similar experiments, concluding that observed differences in habitat, colour and growth form could be accounted for by phenotypic variation within one species. This conclusion is difficult to reconcile with the findings of Flatberg (1986). A re-examination of Tallis's material by Hill (1988) revealed that all specimens used in the transplant experiments belong to Flatberg's sub-species *austinii*. Therefore, the results of Tallis (1962) demonstrate that '*sub-species austinii can produce lax greenish forms in certain very wet conditions*' (Hill 1988 p109).

Overbeck (1975), Barber (1981) and Stoneman (1993) conclude that the modern distribution of sub-species *austinii* on ombrotrophic hummock tops, represents the only niche where the subspecies can still

out compete other *Sphagna*, despite growth conditions being suboptimal. Whilst *Sphagnum imbricatum* has the best desiccation tolerance of eight species tested by Green (1968), the ability of mosses to withstand dry phases is severely limited if the wetting and drying cycles are frequent (Proctor 1982b). Therefore, sub-species *austinii* is restricted to oceanic climates where desiccation is intermittent.

Associated species.

Common associates of *Rhynchospora alba* in modern raised bogs include species indicative of very wet mires such as *Sphagnum auriculatum* [M1], *Sphagnum cuspidatum*/*Sphagnum recurvum* [M2] and *Erica tetralix*/*Sphagnum papillosum* [M18] (Rodwell 1991). The species also occurs in wet heath communities [M16], blanket mires [M17, M18] and oligotrophic valley mires [M21]. In the fossil assemblage *Rhynchospora alba* and *Sphagnum imbricatum* are accompanied by *Vaccinium oxycoccos*, *Erica tetralix* and a trace of *Sphagnum cuspidatum*.

Erica tetralix.

Erica tetralix can tolerate a relatively wide range of soil moisture conditions, growing to within 5cm of the water-table (Hammond *et al.* 1990, table 5.3). The species is commonly associated with *Calluna vulgaris* (Bannister 1964). However, since *Erica tetralix* is more tolerant of water logging it finds its greatest expression in wet oligotrophic mires (Bannister 1964, Davis 1984). In particular, Rutter (1955) has shown that a change from a fluctuating water-table to a constantly high water-table is correlated with a decrease in the importance of *Calluna vulgaris* and an increase in *Erica tetralix*.

In raised bogs and oligotrophic flushes *Erica tetralix* is found in pH conditions that range from 4.0 to 5.0 with a base saturation of 21 - 44%. Whilst the species is usually found on oligotrophic peat soils, it can tolerate pH values as high as 6.1 and base saturation levels of 78%, in mesotrophic to eutrophic mires. In these conditions the species only forms a subordinate component of the communities.

Sphagnum cuspidatum.

Sphagnum cuspidatum is a common species of wet oligotrophic sites where it is often found growing submerged in pools or on pool margins (Daniels and Eddy 1990). Økland (1990) has recorded the species growing at an average pH of 4.5 at Kisselbergmosen where it dominated low-lying carpets. *Sphagnum cuspidatum* is common or dominant between pH 3.5 and 5.5. However, it may be found in small quantities up to pH 6.0 (Andrus 1986). Very small traces of *Sphagnum cuspidatum* in the fossil assemblage do not necessarily indicate a high water-table because a few individuals may be supported in hummock communities lying well above the natural water-level for the species, by the superior water conducting properties of hummock mosses (Proctor 1982b).

The presence of species indicative of high water-tables and oligotrophic conditions occurring with *Sphagnum imbricatum* in the fossil assemblage is interesting because it suggests that sub-species *austinii*

was once able to occupy a broader niche, growing as the lax form identified by Hill (1988) as well as on hummock tops. This finding is in agreement with Stoneman (1993).

Table 5.3 The relationship between water-table depth and the occurrence of selected raised mire species at Lodge Bog, Co. Kildare Ireland. (The last column indicates the depth to water-table above which 90% of occurrences for a species were recorded).

	Species	Minimum depth (cm)	Maximum depth (cm)	90% of occurrences (cm)
Surface water-table	<i>Sphagnum cuspidatum</i>	0	8	5
	<i>Rhynchospora alba</i>	0	10	8
	<i>Drosera anglica</i>	0	25	20
	<i>Sphagnum papillosum</i>	5	28	23
	<i>Eriophorum angustifolium</i>	0	28	24
	<i>Eriophorum vaginatum</i>	0	28	24
	<i>Sphagnum magellanicum</i>	12	28	24
	<i>Trichophorum cespitosum</i>	5	33	25
	<i>Narthecium ossifragum</i>	5	52	30
	<i>Erica tetralix</i>	5	52	35
	<i>Cladonia implexa</i>	10	52	35
	<i>Calluna vulgaris</i>	10	52	30
Deep water-table	<i>Drosera rotundifolia</i>	12	52	45

(After Hammond *et al.* in Doyle (ed.) 1990).

5.8 Summaries of the macrofossil stratigraphies

5.8.1 Summary of the macrofossil stratigraphy of core SOLA195.

(Figure 5.5)

Peat accumulation began on a substrate of sandy silt with the development of a *Carex* spp. dominated fen (LMZ-SOLA1-A). In the basal sample at 315 cm the frequent occurrence of macroscopic charcoal fragments (typically 0.5 to 2.5 mm) indicates local burning either prior to peat initiation or very soon afterwards. *Phragmites australis* was present in the pioneer community although not abundant. Wood fragments occurring in the lowermost peat were too degraded to allow further analysis, however, examination of the equivalent level in the pollen diagram prepared for core SOLA195 (Figure 5.10, LPZ-

SOLA1-1) indicates high levels of *Salix* spp. pollen, which is usually under represented in pollen assemblages, due to low production and poor dispersal. Therefore, the presence of *Salix* spp. pollen may be interpreted as evidence for the genus being present at or very near to the sample site. In the middle of LMZ-SOLA1-A *Calliergon stramineum* dominates the macrofossil assemblage indicating wet mesotrophic fen conditions (Smith 1978). Towards the top of the zone woody roots accompanied by the propagules of *Betula* spp. suggest slightly drier conditions and the appearance of *Sphagnum* sect. *Acutifolia* signals the onset of mire acidification.

A range of oligotrophic mire species, including *Sphagnum* sect. *Acutifolia*, *Eriophorum vaginatum*, *Aulacomnium palustre* and *Polytrichum* spp. displace the fen community in LMZ-SOLA1-B. Most of the species present are indicative of hummock communities on raised bogs. However, the presence of *Aulacomnium palustre* may be a response to very slight base enrichment, either caused by occasional groundwater supply or the release of breakdown products in an environment favouring peat humification. *Polytrichum* spp. is abundant at the top of LMZ-SOLA1-B prior to the establishment of a stable *Eriophorum vaginatum* / *Calluna vulgaris* bog in LMZ-SOLA1-C. The *Eriophorum vaginatum* / *Calluna vulgaris* association, represents dry 'heath-like' bog conditions also indicated by the presence of the sclerotia of *Cenococcum* spp., *Empetrum nigrum*, frequent burning events and high levels of U.O.M.

A wetter phase of mire development defined by a peak in *Rhynchospora alba* at 156 cm (LMZ-SOLA1-D) ends the domination of *Eriophorum vaginatum*. Finally, in LMZ-SOLA1-E both *Sphagnum* sect. *Acutifolia* and *Eriophorum vaginatum* return and are initially co-dominant. A lack of *Cenococcum* spp. and the presence of *Vaccinium oxycoccos* tends to suggest a significantly higher water-table than that of LMZ-SOLA1-C.

5.8.2 Summary of the macrofossil stratigraphy of core SOLA295.

(Figure 5.4)

The onset of organic sedimentation is characterized by a highly humified (H8) gyttja containing a species poor *Phragmites australis*, *Equisetum* spp. assemblage. *Salix* spp. / *Populus* type wood is also present in small amounts in zone LMZ-SOLA2-A. Again the pollen assemblage for the zone registers a high frequency for *Salix* spp. indicating that it is this genus rather than *Populus* that is represented at the site. LMZ-SOLA2-B is differentiated by a large decrease in the proportion of *Phragmites australis*, the lack of *Salix* spp. wood, an increase in the abundance of *Equisetum* spp. and a marked decrease in the proportion of U.O.M. In addition a significant quantity of inorganic inwash, composed of clays, silts, medium calibre quartz and silica sand, of up to 500µm, is registered between 360 and 365 cm.

At the opening of LMZ-SOLA2-C the proportion of *Salix* spp. wood and U.O.M. increases significantly and carices such as *C. rostrata*, *C. acuta*, *C. pseudocyperus*, *C. vesicaria* and *C. aquatilis* enter the assemblage, represented by undifferentiated vegetative remains and propagules. A marked increase in herb types such as *Potentilla paustris*, *Galium palustre* and *Valeriana diocia* and *Ranunculus Batrachium*-type completes the picture of a relatively species rich fen. *Phragmites australis* returns as a co-dominant. This increased species diversity ends abruptly at the zone boundary between LMZ-SOLA2-C and D, accompanied by sharp declines in both *Phragmites australis* and *Carex* spp.

The superseding oligotrophic mire assemblage that appears in the lower part of LMZ-SOLA2-D is completely dominated by *Sphagnum* sect. *Acutifolia*. The only other components identified in this highly humified (H7 to H9) brown/black peat are a trace of *Betula pendula* wood, charcoal and *Cenococcum* spp. By the middle of the zone the *Sphagnum* component is joined by both *Eriophorum vaginatum* and *Eriophorum angustifolium*, brown mosses such as *Pohlia nutans* and *Aulacomnium palustre* and *Ericaceae* rootlets, although *Sphagnum* remains dominant.

The early part of LMZ-SOLA2-Ea is marked by rapid changes in the macrofossil composition, with *Eriophorum vaginatum* and *Sphagnum* sect. *Acutifolia* alternately comprising the majority of the hummock assemblage. Above 320cm *Eriophorum vaginatum* is accompanied by *Calluna vulgaris* to form a very stable association, with *S.s. Acutifolia* peaks becoming more widely spaced. Other components appearing in this zone include *Cenococcum* spp., *Aulacomnium palustre*, *Polytrichum* spp. and *Polytrichum alpestre/ juniperinum* type and frequent occurrences of charcoal.

The virtual disappearance of *Sphagnum* from the record, a lack of brown mosses and a significant rise in the quantity of U.O.M differentiates zone LMZ-SOLA2-Eb from zone -Ea. Peat humification remains very high varying between H7 and H9.

A marked change in peat humification to H5/H6 heralds the end of the *Eriophorum vaginatum/Calluna vulgaris* bog. The lighter peat contains *Rhynchospora alba* and both *Sphagnum* sect. *Acutifolia* and *S. imbricatum* (LMZ-SOLA2-F). LMZ-SOLA2-G marks the initiation of *Sphagnum imbricatum* domination on the raised mire, beginning at 185 cm.

5.8.3 Summary of the macrofossil stratigraphy of core SOLA395.

(Figure 5.6)

Both *Carex* spp. and undifferentiated wood fragments form significant components in a highly humified (H8) basal *Phragmites australis* fen peat (LMZ-SOLA3-A) which also contains the propagules of *Lycopus europaeus*, *Cirsium dissectum* and *Juncus* spp. Occasional poorly preserved branch leaves of *Sphagnum*

sect. *Acutifolia* may also be distinguished. The occurrence of 18% *Salix* spp. pollen in the basal sample of core SOLA395 suggests that this genus is represented by the undifferentiated wood fragments in common with several other multiple cores. *Phragmites australis* continues to form a major part of the assemblage in LMZ-SOLA3-B whilst the proportion of *Sphagnum* sect. *Acutifolia*, in this well humified H7/H8 peat, increases to abundance level 5 and undifferentiated wood fragments are replaced by both the wood and bud scales of *Betula* spp., These two changes suggest a significant increase in acidity in a fen carr environment. *Polytrichum alpestre*/ type and *Sphagnum* sect. *Acutifolia* are co-dominant throughout zone LMZ-SOLA3-C, whilst *Eriophorum vaginatum* is found continuously at low levels.

Zone LMZ-SOLA3-D marks a rise in *Eriophorum vaginatum*, however, this stratigraphic change is coincident with a reappearance of *Phragmites australis* epidermis fragments in the assemblage, accompanied by both *Erica tetralix*, *Sphagnum cuspidatum* and a lower degree of humification (H6). The Root material from *P. australis* penetrates through the peat column occurring in the preceding zone (LMZ-SOLA3-C). A stable *Eriophorum vaginatum*/*Calluna vulgaris* association is established in LMZ-SOLA3-E, accompanied by an unbroken record of charcoal fragments and a return to very dark brown/black H7 to H9 peat. *Sphagnum* sect. *Acutifolia* also occurs throughout, registering characteristic intermittent peaks. *Polytrichum alpestre* appears in the lower half of the unit to be replaced by a continuous low-level occurrence of *Sphagnum imbricatum* from 230cm. A second reappearance of *Phragmites australis* epidermal fragments occurs early in LMZ-SOLA3-E, however unlike LMZ-SOLA3-D, there are no other coincident wet indicating mire species. *Rhynchospora alba* and *Sphagnum cuspidatum* join the *Eriophorum vaginatum*/*Calluna vulgaris* association in zone LMZ-SOLA3-F, before a return to an assemblage reminiscent of the preceding unit in LMZ-SOLA3-G. At the top of the diagram (LMZ-SOLA3-H) *Sphagnum cuspidatum* dominates accompanied by *Rhynchospora alba*.

5.8.4 Summary of the macrofossil stratigraphy of core SOLA495.

(Figure 5.7)

Just 8 cm of *Phragmites australis*/ *Carex* spp./*Equisetum* spp. fen peat is recorded (LMZ-SOLA4-A) prior to the rapid increase in undifferentiated wood fragments and *Sphagnum palustre* (LMZ-SOLA4- B). *Carex* spp. persists throughout the wood horizon into LMZ-SOLA4- C. The base of this latter zone marks the arrival of oligotrophic taxa such as *Eriophorum vaginatum*, *Empetrum nigrum*, *Sphagnum* sect. *Acutifolia* and *Polytrichum alpestre* type. By comparison with the other replicate cores an unusual stratigraphic change occurs in LMZ-SOLA4- D which registers the return of *Phragmites australis* and *Equisetum*, accompanied by *Sphagnum recurvum*, *Menyanthes trifoliata* and *Scheuchzeria palustris*, indicating the presence of surface flooding. The zone also records a significant decrease in peat humification from H7/H8 in the previous three zones to H6 and a drop in the proportion of U.O.M.

The familiar *Eriophorum vaginatum*/*Calluna vulgaris* association replaces the *Sphagnum recurvum* dominated peat of LMZ-SOLA4- E. Initially the assemblage includes *Polytrichum* spp. and abundant *Cenococcum* spp., however these taxa disappear after 215 cm and 175 cm respectively, whilst traces of *Sphagnum imbricatum* become more frequent towards the top of the zone. LMZ-SOLA4- F is characterized by the dominance of *Sphagnum imbricatum* heralding higher mire water-levels.

5.8.5 Summary of the macrofossil stratigraphy of core SOLA595.

(Figure 5.8)

In common with all but one (SOLA195) of the multiple macrofossil cores, *Phragmites australis* and *Equisetum* spp. are the main components of the well humified (H7/H8) basal fen peat unit. However, wood fragments are more abundant than in previous cores. These proved to be too degraded to allow further identification, but pollen data from the same zone suggests the presence of *Betula* spp. rather than *Salix* spp. (Figure 5.13, LPZ-SOLA5-1). In sub-zone LMZ-SOLA5-Ba, undifferentiated *Carex* spp. assumes co-dominance with *Phragmites australis* whilst the proportion of wood fragments declines and *Sphagnum palustre* becomes more frequent. The appearance of *Sphagnum imbricatum* at trace levels in this unit is assumed to represent *S. imbricatum* var. *affine*, although attempts at identifications proved to be difficult due to poor preservation. Sub-zone LMZ-SOLA5-Bb differs from the preceding zone only in the proportion of wood fragments which increase again and in the disappearance of *Sphagnum palustre*.

The coarse 8 cm sampling interval resulted in a failure to identify transitional samples between sub-zone LMZ-SOLA5-Bb and LMZ-SOLA5-C. This latter zone indicates an abrupt change to oligotrophic mire, including species such as *Eriophorum vaginatum* and *Calluna vulgaris*. Significantly, and in contrast to the other multiple cores this association is accompanied by *Rhynchospora alba* and *Sphagnum imbricatum*, although these two species are sub-dominant initially. Finally, *Sphagnum imbricatum* displaces the dominance of *Eriophorum vaginatum* in zone LMZ-SOLA5-D, however, *Calluna vulgaris*, and *Cenococcum* spp. persist at similar abundances to those found in the previous zone.

5.9 Summary of pollen stratigraphy from core SOLA295.

(Figure 5.9a, 5.9b)

5.9.1 LPZ-SOLA2-1 (370-364 cm Cyperaceae/Poaceae/*Betula*/*Pinus*/*Salix*/*Juniperus*)

Godwin Zone II.

The arboreal pollen component of the basal zone, which represents just 6% of the total pollen sum, is mainly composed of *Betula* with *Pinus sylvestris* occurring at very low levels. Both *Salix* and *Juniperus*

are present in the assemblage, also at low frequencies, suggesting that the pollen source for these taxa was at some distance from the sampling site. By contrast Cyperaceae dominates accompanied by over 25% Poaceae, although both taxa decline towards the top of the zone. A range of herb types such as *Thalictrum*, *Potentilla*, *Filipendula*, Ranunculaceae and *Equisetum* are coincident with the high incidence of Cyperaceae and Poaceae indicating local fen or swamp conditions.

The presence of a number of taxa such as *Artemisia*-type, *Botrychium*, *Locopodium annotinum*, *Selaginella selaginoides* and *Juniperus* suggests that the peat bed, represented by LPZ-SOLA2-1, which was discovered overlain by a mineral inwash layer, may date from the Allerød period.

5.9.2 LPZ-SOLA2-2 (364-361 cm Poaceae/Cyperaceae/*Artemisia*-type/ Monolete spores)

Godwin Zone III.

Preparation of the 4cm thick sandy silt inwash layer revealed a limited pollen assemblage characterized by an abundance of Poaceae, Cyperaceae and monolete spores. Just five arboreal pollen grains (Three *Betula* and two *Pinus*) were encountered from a count of 350 total pollen grains minus spores. Figure 5.9a over represents the proportion of arboreal pollen in the zone because the locally abundant taxa, Poaceae and Cyperaceae have been removed from the sum to enable examination of the herb component. Figure 5.9b which is based on a total pollen sum excluding only spores, demonstrates that arboreal pollen forms a relatively small percentage of the total pollen spectra. The abundance of Poaceae and Cyperaceae pollen in the sandy silt layer suggests that fen or swamp conditions persisted through at least part of zone III, despite increased erosion and deposition from surrounding slopes. However, species diversity was considerably reduced. Herb taxa appearing in the zone include *Artemisia*-type, *Thalictrum*, *Empetrum*, Caryophyllaceae and *Rumex*. Most other types including *Salix* are poorly represented or absent.

5.9.3 LPZ-SOLA2-3 (362-347 cm *Salix*/*Betula*/*Pinus*/Poaceae/Cyperaceae/*Juniperus*)

Godwin Zone IV, Local Cumbrian Zone C9 (Walker 1966).

The base of LPZ3 marks the re-establishment of peat-forming conditions. The zone is characterised by very high counts of *Salix* pollen indicating the presence of either *Salix herbacea* scrub or tree *Salix* on the sampling site. Unfortunately, the macrofossil components were too humified to distinguish *Salix herbacea* since, only small fragments of veins survived from the leaf litter and the genus cannot be separated on the basis of wood anatomy. *Betula* and *Pinus* together register values below 15% of the total pollen assemblage (Figure 5.9b). However, the diversity of herb taxa increases considerably compared to the preceding units. *Caltha*, *Epilobium*, Rosaceae, *Urtica* and Apiaceae type 2 all join a fen or swamp community similar to that described in zone LPZ-SOLA2-1. A large increase in *Galium* to 10% of total pollen at the base of the zone may be due to the underlying mineral inwash layer. The presence of a

greater diversity of aquatic elements in the pollen spectra such as *Myriophyllum spicatum*, *Nymphaea alba* and *Typha latifolia* indicates the existence of local open water bodies. These may have existed in previous zones, inhabited by submerged macrophytes such as *Equisetum fluviatile*. The change to a more diverse aquatic pollen assemblage may represent the development of hydrosere succession and the establishment of floating leaved and emergent species.

5.9.4 LPZ-SOLA2-4 (347-305 cm *Betula*/*Pinus*/*Corylus*/*Salix*)

Godwin Zone V, Local Cumbrian Zone C9.

The opening of the zone marks a significant change across most taxa in the pollen assemblage, both local and regional. Cyperaceae and Poaceae decline to a quarter of their former abundance, *Salix* having registered a similar decline at the top of zone LPZ-SOLA2-3. Most of the herb types accompanying the fen community also disappear, whilst taxa indicating acidic conditions, such as *Sphagnum* and *Calluna vulgaris*, appear for the first time or become more abundant (e.g. *Empetrum nigrum*). The frequency of *Sphagnum* spores in particular demonstrates a very rapid increase across the boundary with the preceding zone. Some herb types such as monolet spores, *Filipendula*, *Rumex acetosa*, and Apiaceae type 2 persist throughout the zone possibly representing longer distance transport or the continued existence of fen in another part of the basin. The lower boundary of the zone also marks the empirical limit of *Corylus* and the rational limit of *Betula*.

5.9.5 LPZ-SOLA2-5 (307-263 cm *Betula*/*Pinus*/*Corylus*/*Ulmus*)

Godwin Zone VI, Local Cumbrian Zone C10.

Acid mire taxa continue to dominate the local pollen spectra throughout the unit. At 295 cm the occurrence of both *Salix* and *Filipendula* becomes discontinuous. Coincidentally, *Rumex acetosa* disappears from the record and the proportion of monolet spores dwindles from nearly 10% of total pollen minus exclusions, to less than 1%, indicating a further reduction in the extent of fen and carr communities resident in the sampled basin or in adjacent ones.

The base of the zone is defined by the rational limit of *Corylus* with the empirical limit of *Ulmus* occurring just inside the zone boundary. LPZ-SOLA2-5, therefore, correlates with the opening of zone VI in the Standard British Zonation scheme.

5.9.6 LPZ-SOLA2-6 (263-195 cm *Betula*/*Pinus*/*Ulmus*/*Quercus*/*Corylus*)

Godwin Zone VI, Local Cumbrian Zone C11.

Calluna vulgaris dominates the mire pollen assemblage maintaining constant frequencies throughout the zone. By contrast, *Sphagnum* spores, having declined to less than 10% of the pollen sum (TP-exclusions)

near the top of the preceding zone, remain subdued. Between 235 cm and 215 cm the genus declines further to trace levels. This suggests the development of a heath-like mire community. Towards the upper boundary with zone LPZ-SOLA2-7 *Sphagnum* in particular returns to values greater than 10% of the pollen sum.

Changes in the non-mire taxa are comparatively small, with *Betula*, *Pinus*, *Ulmus* and *Corylus* maintaining virtually constant proportions within the unit. However, the base of the zone is characterized by the rational limit of *Ulmus* and the empirical limit of *Quercus*.

5.9.7 LPZ-SOLA2-7 (195-185 cm *Corylus/Alnus/Betula/Pinus/Ulmus/Quercus*)

Godwin Zone VIIa, Local Cumbrian Zone C12.

The representation of both *Sphagnum* and Cyperaceae increases significantly in the uppermost unit of SOLA2, whilst drier bog species such as *Empetrum nigrum* decline to trace levels. The change in the mire taxa is coincident with the rational limit of *Alnus*, which marks the zone VIc to VIIa boundary in the Godwin Zonation scheme. The first traces of *Tilia* accompany the rise in *Alnus*, however, some taxa such as *Ulmus* record lower frequencies probably due to the interdependency of the percentage based curves.

5.10 Chronology.

The ability to construct a sound chronology for recorded events is vital, for a project concerned with the synchronicity of stratigraphic changes within and between mires and with rates of mire community development. There are a number of techniques available for estimating the age of peat. The analysis of spheroidal carbonaceous particle (SCP) concentrations and ^{210}Pb activity allow age estimations to be produced for lake and peat sediments that have accumulated since the industrial revolution. Both radiometric and accelerator mass spectrometry (AMS) radiocarbon dating are widely used, for older peat samples up to 50000 years (Pilcher 1991). More recently a system of stratigraphic marker horizons has been established using tephra shards from volcanic ash fall out. These horizons are securely dated using a combination of dendrochronology and multiple high precision radiocarbon dating (Pilcher and Hall 1992, Pilcher *et al.* 1995).

The chronology for this project is based upon conventional radiocarbon age estimates. The National Environmental Research Council (NERC) supported, in full, an application for 26 assays from seven mires, for this study. Analysis was carried out at the NERC high precision radiocarbon laboratory at East Kilbride. Eight radiocarbon dates, which were awarded for core BFML as part of the Palaeoclimate Special Topic Grant (code GST/02/539), also relate directly to macrofossil samples analysed as part of this project (Chapter 6). A further five radiocarbon dates from Solway Moss, requested by the North West Wetlands Survey (NWS) have also been exploited using pollen correlation. Time and cost restraints

have precluded the use of tephrochronology, however, this technique should be seriously considered for future research into the FBT.

5.10.1 Radiocarbon dating.

5.10.1.1 Background to the technique.

Cosmic rays interacting with the upper atmosphere produce a continuous supply of the radioactive carbon 14 isotope (^{14}C , radiocarbon), which reacts with oxygen to produce $^{14}\text{CO}_2$. This provides the basis for radiocarbon dating. In common with all radioactive material ^{14}C is subject to continual decay at a constant rate [this rate is defined by the half life, set at 5570 ± 30 years for the purposes of radiocarbon date calculation, by the Fifth Radiocarbon Dating Conference in 1962 (Godwin 1962)], therefore, the concentration of the isotope in the atmosphere is a function of the balance between production and decay. So long as this process is maintained in dynamic equilibrium the concentration of ^{14}C in the atmosphere will be constant. As a consequence of the continual exchange of CO_2 between the atmosphere and the biosphere, living organisms absorb ^{14}C . Assuming equal and efficient rates of gaseous exchange, all organisms will be in equilibrium with the atmospheric level of radiocarbon. This equilibrium is lost upon death since gaseous exchange ceases, whilst radioactive decay continues. If the decay rate of ^{14}C is known and its atmospheric concentration has remained constant, the time since the death of an organism can be calculated by undertaking a radiocarbon assay (Pilcher 1991).

5.10.1.2 Problems associated with radiocarbon dating.

The assumption that the specific activity of radiocarbon in the atmosphere has remained constant is not valid (Stuiver and Reimer 1993b). The level of ^{14}C has fluctuated over time (Stuiver and Braziunas 1993) due to variations in the intensity of cosmic rays (Suess 1965). Consequently, the initial ^{14}C activity of sample material, which provides the baseline for calculating radiocarbon age estimates, has also varied depending upon the time of death of constituent organisms.

Radiocarbon age estimates may be corrected to account for fluctuations in ^{14}C production using empirical calibration curves. These are calculated by performing high precision radiocarbon age estimations on tree rings of known age. Dendrochronological records constructed by Linick *et al.* (1986), Pearson *et al.* (1993), Pearson and Stuiver (1993), Stuiver and Becker (1993) and Stuiver and Pearson (1993) form the basis of the computer programme Calib V 3.0. which was used to perform the calibrations for this project. A bi-decadal data set covers the last 9840 cal yr. This has been extended to 11,390 cal yr using a more tentative floating tree ring record compiled by Kromer and Becker (1993) and Becker *et al.* (1991), quoted in Stuiver and Reimer (1993b). The calibration relationship is not uniform. As a result a single radiocarbon age may intersect the calibration curve at a number of points representing several true ages or an age range. This problem may be addressed by calculating probabilities for the calibrated mid-point of

each intersection, using Calib V 3.0. The calibrated age estimates quoted in the text represent the mid-point of the full range of intersects with the calibration curve for the 2σ confidence interval.

A second set of problems relate to the assumption that organisms are in equilibrium with atmospheric CO_2 . There are several reasons why this may not be true:

- (1) Plants exhibit fractionation of carbon isotopes. Different taxa absorb carbon isotopes in slightly different ratios from the atmosphere (Plicher 1991). Any selective absorption also affects the proportion of the more abundant ^{13}C isotope. Therefore, laboratories routinely measure the $^{12}\text{C}/^{13}\text{C}$ ratio in samples to provide a correction factor. This process is aided in peats if the constituent parts of the sample have been identified because typical fractionation ratios are known for different plant types (Pilcher 1991).
- (2) Some plants assimilate CO_2 from carbonate rich water derived from the underlying geology. This source of carbon is low in ^{14}C , resulting in an overestimation of the age of radiocarbon samples, termed the 'hard-water effect' (Pilcher 1991).
- (3) Many plants also derive a significant proportion of CO_2 from sediment. This can produce a range of apparent reservoir ages (Olsson 1986), since the CO_2 content of organic material is then dependent upon the composition and accumulation rate of the sediment. Olsson (1986) has identified this affect in lake, fen and even raised bog samples, although the latter environment showed only very slight discrepancies compared to atmospheric ^{14}C activity.
- (4) Ocean surface waters are continually mixed with deeper water with a low ^{14}C activity. Consequently, organic samples derived from a marine source have apparent ages approximately 400 years older than their true age (Pilcher 1991). In brackish conditions this reservoir effect is less predictable.
- (5) The fact that different fractions of peat from the same level may yield different age estimates gives an indication of the scale of the problem. Olsson (1986) recommends using only identifiable peat components for dating.

The subject matter of this project requires the examination of peats formed under the influence of groundwater supply by species possessing large root systems. AMS dating of bracts and seeds preserved in the fen peat represents the best solution for overcoming the problems outlined above. However, access to AMS facilities was not available since it is limited to projects funded by NERC. Therefore, the following steps were taken to minimize errors in conventional bulk radiocarbon age estimates.

(1) Samples derived from poor fen environments were targetted on bryophyte-rich layers, usually composed of *Sphagnum palustre* or *Sphagnum recurvum*; rootlets were extracted and discarded if possible, using clean stainless steel instruments.

(2) Wherever possible samples from swamp and fen peats were located in wood-rich layers.

(3) Where sufficient wood fragments were present all the matrix and other peat remains were removed and discarded.

(4) Obvious remains of *Cladium mariscus* were removed from the peat (Olsson 1986). This only applied to one sample from Mongan Bog.

Raised bog peats are usually considered to provide relatively reliable radiocarbon age estimates subject to the normal calibration process (Olsson 1986). However, Kilian *et al.* (1995) have uncovered a possible reservoir affect relating to the mass of very fine Ericaceae rootlets that commonly occur in peat. AMS dating of 99-100% pure *Sphagnum* yielded results comparable to the high precision dates of the calibration curve. However, similar samples containing Ericaceae rootlets produced apparent ages that were 100 - 150 years too old. Normally rootlet penetration would be expected to cause a younger apparent age. Kilian *et al.* (1995) have tentatively suggested that this reservoir affect is caused by the production of CH₄ in the catotelm which is oxidized by methane consuming bacteria once it reaches the rooting zone, providing a source of 'old' CO₂. The 'old' carbon could enter rootlets after death due to fungal activity.

A number of other problems may affect radiocarbon age determinations:

(1) Significant systematic errors have been identified in international comparison exercises between radiocarbon laboratories (Scott *et al.* 1990). As a result (Scott *et al.* 1991) published proposals for rigorous quality controls in ¹⁴C dating. The NERC radiocarbon Laboratory at East Kilbride has been at the forefront of devising and implementing these measures.

(2) Contamination of samples with modern or recent carbon during laboratory preparation is possible due to careless handling, incorrect storage, and the use of carbon based tools and packaging materials. All samples for this project were stored in refrigerators at 4°C to prevent fungal growth. Sampling was conducted wearing protective clothing and gloves, using stainless steel tools, cleaned in distilled water. The outer few millimetres of each sample were skimmed off and discarded prior to packaging in clean aluminium foil.

(3) Radioactive tracer experiments involving ^{14}C are frequently used in biology departments. Sampling for radiocarbon dating within the same building is a potential source of contamination (Pilcher 1991). However, tracer experiments have never been conducted in the building that houses the Southampton Palaeoecology Laboratory.

5.10.2 The radiocarbon chronology at Solway Moss.

The requirement to date seven mires (see Chapter 6) and the high cost of radiocarbon assays (c.£350) strictly limits the number of dates available per site. Therefore, the chronology for the multiple core project at Solway Moss has been constructed using a combination of ^{14}C dating and pollen correlation. Four radiocarbon assays were undertaken on core SOLA295 for which detailed macrofossil and pollen analyses have been completed. Cores SOLA195, SOLA395, SOLA495 and SOLA595 have been linked to the main core using skeletal pollen diagrams (Section 5.10.4).

The radiocarbon dating strategy for core SOLA295 and the cores studied in Chapter 6 was designed with the following aims in mind:

- To study the difference in accumulation rates between the fen and bog peats.
- To calculate the approximate lifespan of mire stages either side of the fen/bog transition.
- To look for a possible hiatus in peat growth between the end of the fen phase and the beginning of raised mire development.
- To date comparable points in the mire sequence at each site, to allow inter-site comparisons.

Therefore, samples from SOLA295 were located in (1) basal wood peat, (2 and 3) either side of the FBT and (4) at the first major occurrence of *Sphagnum imbricatum*.

Age depth curves (Figure 5.14) have been constructed assuming constant peat accumulation between radiocarbon dated samples. This is only a sound assumption within a specific peat type, such as ombrotrophic *Sphagnum*-rich peat. Closely dated full mire sequences reveal significant changes in peat growth rates between some fen and raised mire deposits (see for example, BFML accumulation curve, Figure 6.16). Therefore, where sufficient radiocarbon dates and suitable material were available, two or more assays were sampled from the fen and the raised bog peats with two dates straddling the FBT. Calibrated dates are quoted as cal. BP (calibrated Before Present). These dates represent the mid-point of the 2σ range for the full age probability distribution, derived from the calibration curve (see Dumayne *et al.* 1995).

Table 5.4 Radiocarbon dates from SOLA295 and the Solway Sheep find site.

Sample No.	Core site	Depth (cm)	Date \pm error (BP)	Cal. mid point of date (BP)	2 σ confidence limit (BP)
SSR-5645	SOLA295	186-194	7020 \pm 45	7850	7950-7750
SSR-5646	SOLA295	334-342	7985 \pm 45	8840	9030-8655
SSR-5647	SOLA295	346-354	9370 \pm 45	10430	10570-10290
SSR-5648	SOLA295	362-370	11610 \pm 50	13630	13835-13425
GU-5313	SOL sheep	20-25	4400 \pm 80	5070	5300-4840
GU-5275	SOL sheep	45-50	5110 \pm 60	5860	5985-5730
GU-5276	SOL sheep	87-94	5470 \pm 60	6265	6410-6115
GU-5315	SOL sheep	142-150	6180 \pm 60	7040	7190-6890
GU-5277	SOL sheep	160-170	7080 \pm 50	7885	8030-7740

Source of dates: SOLA295 = this project, SOL Sheep = NWWS 1993.

5.10.3 Pollen correlation.

The four skeletal pollen diagrams of between 4 and 8 samples each have been assigned local pollen assemblage zones (LPZ) on the basis of changes in selected taxa including the main tree species and some of the dominant mire types. The diagrams presented in figures 5.10 to 5.13 are based on a sum of 100 arboreal pollen grains. They have been correlated with the main pollen diagram (Figure 5.4) which is also based on an arboreal pollen sum, to give the mire assemblage zones (MPZ). The results of the pollen correlation exercise are presented in tables 5.5 to 5.8.

Table 5.5 SOLA195 pollen correlation table.

Local pollen zone	Depth (cm)	Main species	Mire zone
LPZ-SOLA1-4	120-182	<i>Corylus/Alnus/ Quercus/Ulmus</i>	MPZ-SOL-7
LPZ-SOLA1-3	182-220	<i>Corylus/Quercus/ Ulmus/Betula</i>	MPZ-SOL-6
LPZ-SOLA1-1	220-260	<i>Corylus/Ulmus/ Betula</i>	MPZ-SOL-6
LPZ-SOLA1-1	260-310	<i>Betula/Poaceae/ Cyperaceae/Salix</i>	MPZ-SOL-4/5

Table 5.6 SOLA395 pollen correlation table.

Local pollen zone	Depth (cm)	Main species	Mire zone
LPZ-SOLA3-6	150-163	<i>Corylus/Alnus/ Quercus/Ulmus</i>	MPZ-SOL-7
LPZ-SOLA3-5	163-212	<i>Corylus/Quercus/ Ulmus/Betula</i>	MPZ-SOL-6
LPZ-SOLA3-4	212-237	<i>Corylus/Ulmus/ Betula</i>	MPZ-SOL-6
LPZ-SOLA3-3	237-262	<i>Corylus/Betula</i>	MPZ-SOL-5
LPZ-SOLA3-2	262-317	<i>Betula</i>	MPZ-SOL-4
LPZ-SOLA3-1	317-335	<i>Betula/Poaceae/ Cyperaceae/Salix</i>	MPZ-SOL-4

Table 5.7 SOLA495 pollen correlation table.

Local pollen zone	Depth (cm)	Main species	Mire zone
LPZ-SOLA4-6	150-167	<i>Corylus/Alnus/ Quercus/Ulmus</i>	MPZ-SOL-7
LPZ-SOLA4-5	167-213	<i>Corylus/Quercus/ Ulmus/Betula</i>	MPZ-SOL-6
LPZ-SOLA4-4	213-237	<i>Corylus/Ulmus Betula</i>	MPZ-SOL-6
LPZ-SOLA4-3	237-263	<i>Corylus/Betula</i>	MPZ-SOL-5
LPZ-SOLA4-2	263-287	<i>Betula/Corylus</i>	MPZ-SOL-4/5
LPZ-SOLA4-1	287-300	<i>Betula/Poaceae Cyperaceae/Salix</i>	MPZ-SOL-4

Table 5.8 SOLA595 pollen correlation table.

Local pollen zone	Depth (cm)	Main species	Mire zone
LPZ-SOLA5-3	60-85	<i>Corylus/Alnus/ Quercus/Ulmus/ Betula</i>	MPZ-SOL-7
LPZ-SOLA5-2	85-102	<i>Corylus/Quercus/ Ulmus/Betula</i>	MPZ-SOL-6
LPZ-SOLA5-1	102-110	<i>Corylus/Betula/ Pinus</i>	MPZ-SOL-5

5.11 Characterizing environmental gradients within the macrofossil data.

5.11.1 Introduction.

Ordering of the macrofossil diagrams to display fen species on the left and acid mire species on the right reveals an obvious diagonal structure to most of the data sets. It is reasonable to assume that the observed species turnover constituting the FBT is an expression of one or a number of unidentified (or latent) controlling ecological factors. These determinants may be difficult to interpret accurately from raw macrofossil counts alone, due to the multidimensional character of species data (ter Braak 1987a). Ordination techniques have been specifically developed to facilitate such analyses.

Ecologists commonly use Principal Components Analysis (PCA), Correspondence Analysis (CA) and derivatives of CA such as Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) to perform ordinations with the choice of technique determined by the composition of the data set and the aim of the analysis.

PCA identifies uncorrelated axes, representing groupings of the original data, which may be treated as new aggregate variables (Kovach 1995). The reduced number of dimensions enables easy graphical representation of results, facilitating interpretation. Whilst this technique may give meaningful results using count and presence / absence data, it was specifically designed to detect latent structures in continuous measurement data assuming a linear response model (ter Braak 1987a, Kovach 1995).

Most species display non-linear responses to a particular environmental gradient, occurring in abundance at optima and becoming rare or absent at high and low values of the explanatory variable (ter Braak 1987b in Maddy and Brew 1995). Therefore, the Gaussian curve (bell shaped) was proposed as a simple approximation of this unimodal ecological response (Gauch and Whittaker (1972) for use in statistical

modelling.¹ Indirect ordination techniques such as CA, DCA and CCA were specifically developed to handle species abundance data containing many zero values and assuming the non-linear response of species to environmental variables.

It is essential to investigate whether a linear or unimodal response model is most appropriate for a particular ecological data set. The choice is dependant upon the length of the environmental gradient sampled. A short gradient approximates to a linear relationship (ter Braak 1987a), therefore, techniques such as PCA may be used. For data sets describing long gradients in which species turnover is high and samples from either end of the axis have widely differing taxonomic compositions, a Gaussian response model is more appropriate (Birks 1995).

A simple method for investigating the length of a gradient (measured in standard deviation units, SD), involves the use of DCA with detrending by segments (Section 5.11.2). The tolerance of a species response curve along a scaled DCA axis is assumed to be close to 1 SD (Birks 1995). As a result a species appears, rises to its greatest abundance and disappears over approximately 4 SD. Therefore, DCA samples separated by a distance of > 4 SD along an axis probably have no taxa in common and a long section of the gradient is present in the data set. Unimodal techniques are considered to be appropriate for gradients longer than 2 SD, which will contain the optima of several species (Birks 1995). Application of DCA to the FBT data demonstrated that all of the sites had gradients longer than 2 SD for both axis 1 and axis 2, therefore unimodal techniques were selected for further analysis.

Since the aim of applying ordination techniques to the macrofossil data is to interpret the unknown or latent gradients in the data set, indirect ordination routines such as, CA and DCA were considered. By contrast direct ordination (e.g. CCA) requires the input of field measurements for explanatory variables (Kovach 1995), such as pH or water-level, which are unavailable for the plant macrofossil records.

5.11.2 Detrended correspondence analysis.

Ordination may be defined as a system of assigning suitably selected weights to a multi-species community (or assemblage) to give a score for each sample unit (depth level) reflecting the aggregate species response to an environmental variable (Pielou 1984). The scores for the sample units may be ordered along an axis to visualize an environmental gradient. This process is a one dimensional ordination. Different weighting systems may be applied to give a set of one dimensional ordinations representing different environmental gradients.

Correspondence analysis and its derivative DCA differ from other ordinations techniques in the methods employed to assign weights to species. These indirect methods are extensions of weighted averaging (for a

¹ Species responses are commonly more complex than the relationship described by the Gaussian response curve, however, the model is useful as a robust approximation (Maddy and Brew 1995).

good explanation of the background to this technique see ter Braak 1987a in Jongman *et al.*). In simple weighted averaging, if the indicator value of a species is known (equivalent to the species score in CA) the value of the relevant environmental variable at a site can be calculated directly using the abundance of each species present. The resulting weighted average (sample score) may be ranked to show the response of species to the identified variable. Clearly, this method requires prior knowledge of the variable affecting the species. If this is unknown CA can construct species and sample scores for a theoretical variable by applying the weighted averaging process to both species and samples in an iterative routine (ter Braak 1987a).

The computer programme 'CANOCO' was used to carry out this reciprocal averaging process (ter Braak 1987b) which is composed of the following steps:

(1) To provide a starting point for the ordination arbitrary trial values are selected for either sample or species scores. In the accompanying example (Table 5.9 a) the numbers 1 -10 are used as the first sample scores.

(2) The first trial species scores are derived by calculating the weighted average of the initial sample scores using equation 5.1 where the abundance of species k at site i is represented by y_{ki} , the score of species k by u_k and the score of sample i by x_i .

$$u_k = \frac{\sum_{i=1}^n y_{ki} x_i}{\sum_{i=1}^n y_{ki}} \quad \text{Equation 5.1}$$

source: ter Braak 1987a, in Jongman *et al.*

(3) Next the species scores are recalculated by taking the weighted average of the sample scores from step 2, using equation 5.2.

$$x_i = \frac{\sum_{k=1}^m y_{ki} u_k}{\sum_{k=1}^m y_{ki}} \quad \text{Equation 5.2}$$

source: ter Braak 1987a, in Jongman *et al.*

(4) Then new sample scores are recalculated by finding the weighted average of the new species scores from step 3. The iteration process described above, continues until the values for the species scores and sample scores stabilize. Hill (1973) demonstrated that the initial arbitrary values have no effect on the final result. However, one consequence of the averaging process is that the resulting numerical range of the scores reduces. Therefore, after the first iteration, a standardization procedure is applied to rescale the scores. This procedure maintains the relative distance between the scores and is purely a practical method to prevent them from becoming indistinguishable after further iterations. The details of the method are described fully by ter Braak 1987, in Jongman *et al.*

Table 5.9a, b and c illustrate the ordination process, using a test data set of 7 *Sphagnum* species sampled from 10 plots along a transect.

Table 5.9a The raw data set with arbitrary values for sample scores (x_i) set at 1-10.

<i>Sphagnum</i> species (k)	Sites (i)										Species score u_k
	0	0	0	0	0	0	0	0	0	1	
	1	2	3	4	5	6	7	8	9	0	
<i>S. magellanicum</i>	5	1	3		1		1	2	3		
<i>S. papillosum</i>		2		3	3			3	2	3	
<i>S. subsecundum</i>		1				5				3	
<i>S. imbricatum</i>	4	1	2	2	4			3	4		
<i>S. acutifolia</i>	4		5				3	2	3		
<i>S. fuscum</i>	3		3				6		2		
<i>S. cuspidatum</i>		1		2	1	2				4	
	x_i	0	0	0	0	0	0	0	0	1	
		1	2	3	4	5	6	7	8	9	0

The raw data set has no apparent diagonal structure that would suggest unimodal species response to an environmental gradient. However, examination of the data matrix after the first CA iteration indicates the emergence of some apparent structure, table 5.9b.

Table 5.9b The *Sphagnum* test data after the first CA iteration.

<i>Sphagnum</i> species (k)	Sites (x_i)										Species score u_k
	0	0	0	0	0	0	0	0	0	1	
	1	3	9	8	7	5	4	2	6	0	
<i>S. imbricatum</i>	4	2	4	3		4	2	1			4.00
<i>S. magellanicum</i>	5	3	3	2	1	1		1			4.44
<i>S. acutifolia</i>	4	5	3	2	3						4.88
<i>S. fuscum</i>	3	3	2		6						5.14
<i>S. papillosum</i>			2	3		3	3	2		3	6.44
<i>S. cuspidatum</i>						1	2	1	2	4	6.80
<i>S. subsecundum</i>								1	5	3	7.75
	x_i	4	4	4	4	4	5	5	5	6	6
		5	7	7	9	9	2	8	9	5	9
		7	0	9	0	9	0	5	8	1	8

Further iterations gradually improve the dispersal of the data points. In the *Sphagnum* species example, the species and sample score derived from this simple data set stabilize after 3 iterations, marking the end point of the routine. Ordering of the samples and species according to these scores reveals a strong diagonal structure representing an ordination of the first CA axis. The axis is interpreted by considering the position of species along the gradient in the light of their ecology. The example gradient reflects mire water-levels.

Table 5.9c: The completed CA ordination of the *Sphagnum* species data for axis one.

<i>Sphagnum</i> species (k)	Sites (x_i)										Species score u_k
	0	0	0	0	0	0	0	0	1	0	
	7	3	1	9	8	5	4	2	0	6	
<i>S. fuscum</i>	6	3	3	2							-50
<i>S. acutifolia</i>	3	5	4	3	2						54
<i>S. magellanicum</i>	1	3	5	3	2	1		1			138
<i>S. imbricatum</i>		2	4	4	3	4	2	1			199
<i>S. papillosum</i>				2	3	3	3	2	3		285
<i>S. cuspidatum</i>						1	2	1	4	2	362
<i>S. subsecundum</i>								1	3	5	493
	0	0	0	1	1	2	2	2	3	4	Eigen value for axis 1 = 0.76 (equals the degree of dispersion of species scores on axis 1)
x_i	0	7	9	3	8	3	8	9	7	5	
	0	2	7	1	3	9	2	4	8	6	

Ordination scores for subsequent axes may be obtained using a similar iteration routine with an added stage, designed to ensure that the scores for axis two are uncorrelated with axis one. For each iteration the scores for axis two are plotted against those for axis one and a linear regression line is fitted. The residuals from this regression form the new scores for the next weighted averaging cycle. A process called orthogonalization provides a short cut, performing the same function. This technique and the whole subject of CA and DCA ordination are described fully in ter Braak (1987a)

DCA is a modification of CA designed to correct two faults which arise as artefacts of the computation process (Hill and Gauch 1980). The first of these is the arch effect so called because the ordination scores describe an arch along the first two axes of the CA rather than the expected linear relationship. Each axis is supposed to be uncorrelated and independent of the first. However CA is not constrained to provide the latter condition (Hill and Gauch 1980). The arch effect arises when a long environmental gradient has been sampled, (ter Braak 1987a). If most of the variation in the species data is accounted for by the first

axis, the CA computation may extract a second axis by folding the first midway along its length (Peeting *et al.* 1988). Although spurious, the resulting axis has no linear correlation with axis one thus fulfilling the rules for its calculation. The arch effect can occur when there is a real second gradient within the data, provided the dispersion of ordination points along this gradient is less than that provided by the folded axis (ter Braak 1987a).

The detrending process in DCA corrects the arch effect by dividing the first two axes, derived from the reciprocal averaging routine, into segments of equal length. The scores for the ordination points lying on the second axis are then altered so that the mean value of each segment equals that of other segments. Kovach (1995) has described the process as being analogous to cutting a scatterplot into vertical strips and moving each one until the arch in the scatter has been corrected to a straight line.

The second fault arising in CA produces distortion of axes particularly near their outer limits where compression may be severe. The distortion occurs because estimates of niche breadth and within-sample variance (of species scores) are smaller near the ends of the axes. This is a consequence of the partial sampling of species response curves where the optima of some species lie outside the recorded section of the gradient (Peeting *et al.* 1988).

Hill and Gauch (1980) corrected this error by undertaking non-linear rescaling of the first DCA axis so that the Gaussian species response curve widths for all species were approximately equal. To recap, the unimodal model for species response assumes a tolerance (standard deviation) of 1 with the whole curve arising, peaking and falling over 4 standard deviations. Hill and Gauch (1980) found that the variance in the optima of species occurring within a sample unit (level) provided an estimate of the actual average squared standard deviation of the species. Therefore, the width of response curves (measured in standard deviation units, SD) may be standardized in the following way. First the axis is divided up into segments. Then the species ordination is expanded for segments containing samples with low within-sample variance (for species scores) and contracted for segments with a high variance. Once the species ordination has been corrected in this way the final site scores are calculated using the normal weighted averages routine (ter Braak 1987).

The benefit of re-scaling is that distance along the axis now relates directly to species turnover (Peeting *et al.* 1988). The gradient length may be defined by the amount of species turnover, with length expressed as standard deviation units (SD). This facilitates comparisons between ordinations from different macrofossil records.

5.11.3 Problems with DCA.

Whilst DCA provides a significantly improved ordination (Hill and Gauch 1980), it has drawbacks of its own. Some of the problems identified by Hill and Gauch (1980) during the development phase of DCA include the following:

- (1) Outliers: Species placed at the far edges of the axes are often rare. They may have their optima in extreme environmental conditions or their infrequent distribution may reflect a chance occurrence at a marginal site. If the outlier is widely separated from other species it may dominate the first axis although it is only a small part of the data. Without further information it is impossible to decide between these two options. The only way to deal with extreme outliers is to remove them from the ordination.
- (2) Species at the centre of an ordination diagram may be placed in this location either because their optima lie there or because their response curve is bi-modal. Examination of the ordination points in a matrix such as 5.9c will address this problem.
- (3) Where large discontinuities exist in the response of species along a gradient, the size of gaps may be poorly estimated. This is unlikely to be a problem in the FBT data.
- (4) Interpretation of an axis extracted by the ordination can be difficult, particularly if it represents a compound environmental gradient. There may be no way to clarify such a gradient.
- (5) Species ordinations may be unreliable when there is a strong second gradient at one end of the axis and not the other. This needs to be examined in the context of the FBT data.

5.11.4 DCA of the main macrofossil core, SOLA295.

Canoco offers several different methods for detrending. Initial investigations of the SOLA295 data set showed that the best separation of species along the ordination axes was achieved using detrending by segments, rather than by first, second or third order polynomials. To enable direct comparisons between different ordinations the number of segments used in the detrending process was held constant at 26. The rescaling option was applied to all ordinations using default settings.

A trial detrended correspondence analysis was applied to the complete data set, treating all species and samples equally. Examination of the species scores revealed that some rare taxa were located on the extreme ends of the axes, thus compressing the distribution of the remaining ordination points. Rare species may genuinely occupy extreme parts of the gradient or they may be placed there erroneously by the ordination because only a very small portion of their distribution is present in the data set. To address this problem rare species were down weighted.

DCA axis one for the whole data set accounts for 86% of the dispersion in the ordination points. Analysis of the biplot of axis one versus axis two scores reveals a relatively long gradient (approx. 4 SD) from fen and swamp communities through carr woodland to acid raised bog species (Figure 5.15). Very few samples locate in the centre of the axis whilst the fen and oligotrophic mire communities are widely separated. This suggests a very rapid transition between the mire types, with few overlapping species. A plot of axis one sample scores against depth clearly illustrates the rapidity of the change which is also evident in the macrofossil diagram (Figure 5.16). The fact that one sample (at 344 cm) lies exactly half way between the fen and the bog sections of the gradient suggests that the acid mire developed from the fen community rather than pioneering on a bare peat surface after a major hiatus. Alternatively, samples occupying a halfway position on the gradient could represent displacement peats (Section 3.3.1). However, the macrofossil diagram (Figure 5.4) shows that the sample at 344cm is composed of a mixture of *Phragmites* and *Sphagnum* sect. *Acutifolia*. Since this level is the last one to register any *Phragmites*, contamination by rootlet penetration from above may be ruled out. However, the exact status of this community is difficult to interpret because *Phragmites* can persist in a depauperate state in ombrotrophic conditions, whilst *S.s. Acutifolia* contains species of both oligotrophic and more minerotrophic habitats. One clue is provided in the biplot of the ordination scores which places *S.s. Acutifolia* firmly amongst the oligotrophic species. If a more minerotrophic species had been present in the transition community, the group as a whole may be expected to have a bimodal response curve. Such a taxon would be difficult to relate to the unimodal response model and would register as being unrelated to the gradient, thus appearing in the centre of the scatter plot. Therefore, the sample may represent a very brief phase in which poor fen conditions prevailed on the mire surface.

The second DCA axis explains 42% of the remaining variation, placing *Polytrichum alpestre* type, *Dicranum scoparium* and *Eriophorum vaginatum* at one end of the axis and *Sphagnum papillosum*, *Vaccinium oxycoccos*, *S. cuspidatum* and *S. imbricatum* at the other end (Figure 5.15). This grouping resembles a hummock/hollow gradient in the raised mire samples. However, DCA provides a poor representation of a crossed gradient, which occurs in just one half of the primary axis (Hill and Gauch 1980). Therefore, the plot of axis two scores against depth (Figure 5.17) is likely to be an unreliable estimate of the change in the hummock/hollow gradient through the core.

A second DCA was undertaken to investigate the structure of the raised mire samples alone. The resulting biplot (Figure 5.18, again of axis one vs. axis two scores) describes a primary gradient accounting for 49.2% of the variation, in which *Eriophorum vaginatum* and *Sphagnum* sect. *Acutifolia* occupy opposite extremes. Most of the wetter acid mire species such as *Rhynchospora alba*, *Sphagnum cuspidatum*, *S. imbricatum*, *Vaccinium oxycoccos* and *Erica tetralix* are grouped in the centre of the axis suggesting that they are unrelated to it. The axis appears to represent the fluctuation between *Sphagnum* sect. *Acutifolia* and *Eriophorum vaginatum* dominated hummock environments. The plot of axis one scores against depth (Figure 5.19) shows the frequent interactions between the two species, which may represent a response to

burning of the mire surface. The macrofossil diagram records many charcoal layers associated with the hummock communities. Dominance by *Eriophorum vaginatum* could reflect a reduced return period for burning events, since it is considerably more resistant to fire than *Sphagnum* sect. *Acutifolia*.

The second DCA axis extracted from the acid mire samples indicates a clear hummock, hollow gradient reflecting change in mire surface wetness (Figure 5.18). *Sphagnum papillosum*, *Rhynchospora alba* and *S. cuspidatum* cluster at one end of the axis with *Polytrichum* sp. *Eriophorum vaginatum* and *Sphagnum* sect. *Acutifolia* at the other. The short length of this gradient (1.6 SD) suggests that changes in mire water-tables were of relatively low amplitude. A plot of axis two score against depth illustrates these changes (Figure 5.20).

To test the hypothesis that DCA axis 2, from the ombrotrophic samples, is a reliable estimation of mire surface wetness a modified Dupont Moisture Index was calculated for the relevant levels. This computation is a one-way weighted average ordination based upon equation 5.1 (Section 5.11.2). The weighting factors applied to the species in this direct ordination are shown in Table 5.10. The Table 5.10 also gives the weights employed by Dupont (1986), Haslam (1987) and Stoneman (1993). Most of the weights used in the present project follow Stoneman (1993), to avoid artificial gaps in the index. Dupont (1986) did not assign species to weighting factors '4' or '7'. The weight of '4' used for *S. imbricatum*, by Stoneman (1993) is preferred to that used by Dupont (1986) and Haslam (1987) because the macrofossil assemblages suggest that it is the wet, lax form of sub-species *austinii*, that is represented in the stratigraphy.



Table 5.10 Comparison of the weighting factors used in the modified Dupont Moisture Index for this project, with those of Stoneman (1993) and Dupont (1986).

Macrofossil element	Present project	Stoneman (1993)	Haslam (1987)	Dupont (1986)
Unidentified organic matter	7	7	8	8
<i>Ericaceae</i> rootlets	7	7	8	8
Monocots undiff.	--	6	--	--
<i>Eriophorum vaginatum</i>	6	--	--	--
<i>Eriophorum angustifolium</i>	3	--	--	--
<i>Rhynchospora alba</i>	3	--	--	--
<i>Sphagnum palustre</i>	4	--	--	--
<i>Sphagnum</i> sect. <i>Acutifolia</i>	5	5	6	6
<i>Sphagnum imbricatum</i>	4	4	5	5
<i>Sphagnum magellanicum</i>	--	4	3	3
<i>Sphagnum papillosum</i>	2	4	2	2
<i>Sphagnum cuspidatum</i>	1	2	1	1
<i>Polytrichum alpestre</i> type	5	--	--	--
<i>Empetrum nigrum</i>	6	--	--	--
<i>Calluna vulgaris</i> wood	7	--	--	--
<i>Erica tetralix</i> wood	4	--		--

The modified Dupont Moisture Index (Figure 5.21) plotted against depth indicates close agreement with the equivalent plot for axis two scores from the DCA of the ombrotrophic samples. The moisture index and the DCA scores both show that low water-tables dominated the raised bog environment from the time of the FBT at c. 10000 cal. BP for 2000 years until 7850 cal. BP, with only minor fluctuations in the intervening centuries. It is interesting to note that the modified Dupont Index appears to register more small scale changes in surface wetness. Hill and Gauch (1980) have noted that DCA may result in the loss of some finer data structures.

5.11.5 DCA of core SOLA195 macrofossil data.

Cores SOLA195, SOLA395, SOLA495 and SOLA595 were analysed using the 5 point scale of abundance. Categorical data is unsuitable for DCA therefore each of these data sets has been converted to presence / absence format to facilitate computation.

The biplot of axis one versus axis two scores for an ordination of the complete macrofossil data set (Figure 5.22) uncovers a long fen to ombrotrophic bog gradient (6 SD) on the first axis, accounting for 66.4% of the dispersion in the ordination points. *Sphagnum* sect. *Acutifolia* is placed in the centre of this gradient because it possesses a bimodal distribution appearing at the FBT and again towards the top of the macrofossil diagram. Domination of the mire surface by *Eriophorum vaginatum* in zone C may account for this distribution. Figure 5.23 displays the depth profile for axis one scores, revealing a relatively rapid fen/bog transition which occurred over approximately 15cm depth. The second DCA axis, which explains just 6.6% of the total variation, is difficult to interpret. Most of the main raised mire species are separated by less than 1 SD. along the axis. This suggests that the raised bog samples represent a relatively stable community. Removal of fen species resulted in very little change in the ordination.

5.11.6 DCA of core SOLA395 macrofossil data.

DCA axis one extracted from the whole macrofossil record describes a paludification gradient, representing 39.3% of the variation (Figure 5.24). Woody roots, *Betula* spp. wood and Dicotyledon wood cluster within one SD. of taxa such as *Phragmites australis*, *Equisetum* spp. and *Carex* spp. The ombrotrophic mire community is placed at the other extreme of this long gradient (5.7 SD). In common with SOLA195, *Sphagnum* sect. *Acutifolia* occurs in the centre of the axis due to its bimodal distribution. This *Sphagnum* section occurs in the early paludification assemblage in association with *Polytrichum alpestre* type and *Betula* spp. wood. It also accompanies the *Eriophorum vaginatum* dominated raised mire components, suggesting that in both cases *Sphagnum* sect. *Acutifolia* is represented by oligotrophic species. The plot of axis one scores against depth (Figure 5.25) reveals an attenuated transition between the paludification community and the raised mire. This may be accounted for by the presence of *Polytrichum alpestre* type and *Sphagnum* sect. *Acutifolia* in both communities.

All of the oligotrophic species cluster tightly in the centre of the second DCA axis suggesting that they are unrelated to it. *Betula* spp. wood fragments and Dicotyledon leaves are placed at opposing extremes of the gradient, however, both of these macrofossil elements are rare and should be discounted from the interpretation. The DCA was calculated using down weighting for rare species therefore, the remaining plots are not significantly affected by these two anomalous points. Axis two (6.8% of overall variation) appears to describe a weak nutrient depletion or combined nutrient water-level gradient within the paludification assemblage.

5.11.7 DCA of core SOLA495 macrofossil data.

In common with the preceding sites the ordination of the macrofossil data from SOLA495, extracts the fen/bog gradient on axis one, accounting for 54.3% of the variation (Figure 5.26). However, both *Eriophorum vaginatum* and *Polytrichum alpestre* type occupy unusual positions in the middle of the axis. Examination of the macrofossil diagram shows that these two species have bimodal distributions because they are briefly displaced by *Sphagnum recurvum*, *Menyanthes trifoliata* and *Scheuchzeria palustris* in

zone D. The plot of axis one scores through the depth profile (Figure 5.27) shows the false start to the FBT at 286 cm and the final more rapid transition to ombrotrophic conditions at 230 cm.

DCA axis two clearly represent the species response to flooding and the consequent water movement on the mire surface. *Scheuchzeria palustris*, *Sphagnum recurvum* and *Menyanthes trifoliata* all occupy the extreme negative part of the axis representing the flooded conditions with most other species arranged in the stagnant water section of the gradient. Both *Phragmites australis* and *Equisetum* sp. occupy central positions due to their bimodal distributions. Axis two scores plotted against depth (Figure 5.28) illustrate the flooding phase between 262 and 230 cm depth.

5.11.8 DCA of core SOLA595 macrofossil data.

SOLA5 is a small record of 14 levels analysed at 8 cm intervals. The coarse sampling strategy may be responsible for the wide gap in the gradient represented on axis one of the DCA (Figure 5.29). Fen species and Woody roots and wood fragments again figure prominently at one end of the axis. Raised mire species are located at the other extreme indicating the familiar gradient from fen carr to raised bog (representing 74.3% of the dispersion in the data). Figure 5.30 of axis one scores against depth illustrates the rapidity of the transition to ombrotrophic bog conditions.

Axis two appears to represent a water-level gradient in the acid mire assemblage, however, much of the dispersion of the ordination points is accounted for by the anomalous position of rare species such as *Erica tetralix*. Removal of the fen taxa and down weighting of rare species demonstrate that this gradient is not significant, with most species plotting near its centre.

5.12 Interpretation.

The fen deposits at Solway Moss form a thin mantle 15 - 60 cm deep over the gently sloping central basin. Careful levelling using a Geodimeter mounted on railway sleepers revealed an average gradient of just 1 in 200 for the contact between peat and the underlying inorganic sediments (Figure 5.31). Core SOLA295 which was sampled at the deepest point of the depression, contains the only record of a 7cm thick band of detritus mud and peat, that accumulated in a reedswamp environment, dominated by *Phragmites australis* (Figure 5.4). The contemporary pollen record from SOLA295 (Figure 5.9a and b) contains taxa such *Artemisia*-type, *Brassicaceae*, *Botrychium*, *Lycopodium annotinum*, *Empetrum nigrum* and *Selaginella selaginoides*, which point to a Devensian Late-glacial date for the deposit. A basal peat sample centred on 366 cm in zone LMZ-SOLA2-A was submitted for radiocarbon assay, yielding a result of 13630 cal BP. This indicates that the first peat accumulation occurred just after the end of the Oldest Dryas (Birks and Birks 1981). If the radiocarbon assay is a true reflection of the sample's age it suggests that the narrow basal reedswamp deposit has been eroded. The abrupt contact of the unit with a 5cm thick layer of minerogenic inwash (zone SOLA2AB), composed of clays, silts and sand sized quartz grains, supports this interpretation.

The macrofossil diagram for SOLA295 registers the continued presence of *Phragmites australis* and *Equisetum* spp. through the inwash horizon (LMZ-SOLA2-B), however, these species are entirely represented by root fragments. Examination of the silts and clays, using a hand lens prior to sieving, showed that the sparse roots were aligned vertically in the deposits rather than occurring as detritus in bedding planes, therefore, they probably penetrated into the unit from above.¹ In contrast to sedimentary silts and clays from other sites such as Tregaron Bog (Section 6.3.5) the horizon contained no trace of fruits and seeds or fragments of aerial plant structures. This suggests that very few if any macrofossils were contemporary with the inwash phase. *Phragmites* can thrive in conditions of high inorganic sedimentation, but, the northern distribution of the species is limited by low temperatures (Haslam 1970a). *Phragmites australis* is also sensitive to rapid water movement and erosion (Haslam 1970b). All three of these factors may have contributed to the apparent demise of the species.

Pollen spectra sampled from LPZ-SOLA2-2 (equivalent to LMZ-SOLA2-B) indicate an increase in disturbed and open ground indicators such as *Artemisia*-type and *Rumex acetosa*, and the disappearance of many fen herb types. The assemblage is also characterized by a large peak in monolete spores, *Poaceae* and *Cyperaceae* and a decline in *Salix*. These changes support the interpretation that the silts and clays of zone LMZ-SOLA2-B date from a stadial period. A sample of fen carr peat immediately overlying LMZ-SOLA2-B dates to 10430 cal. BP (10290-10570, SRR5647) suggesting that the former unit represents the Younger Dryas. Pollen assemblages from Younger Dryas deposits at Blelham Bog have a comparable composition (Pennington 1970). Both *Betula* and *Pinus* pollen continue to be recorded in LMZ-SOLA2-B, however many of the grains identified were badly broken and corroded, indicating that they may have been reworked and transported to the site. Alternatively, the poor pollen preservation of these species may be a result of post depositional abrasion with angular silt and sand grains. However, other taxa including many monolete spores present in the same level are preserved in good condition.

A comparative study of the five pollen diagrams from the multiple cores (Figures 5.9 to 5.13) shows that the first continuous peat accumulation began during the Preboreal period (Zone IV), under a species rich *Salix* fen carr at SOLA295 (represented by LMZ-SOLA2-C). The pollen assemblage for this zone pre-dates the empirical limit of *Corylus* at Solway Moss, containing an abundance of *Salix* pollen and between 5 and 10% *Juniperus* pollen (MPZ-SOL-3). The radiocarbon date of 10430 cal. BP (10290-10570, SRR5647) for peat sampled from 346 to 354 cm in core SOLA295 supports the age interpretation derived from the pollen evidence and correlates closely with basal radiocarbon and pollen samples from Scaleby Moss (Walker 1966) and Bolton Fell Moss (Chapter 6).

¹ In the macrofossil diagrams roots have not been separated from stem and leaf fragments due to the difficulty of estimating the relative proportions of each element in the highly humified basal peats.

The rapid establishment of *Sphagnum* sect. *Acutifolia* dominated mire at the main core site (zone LMZ-SOLA2-D) is clearly illustrated in the DCA axis 1 sample scores and the SOLA295 macrofossil diagram (Figures 5.16 and 5.4 respectively) and occurs at the beginning of the Boreal period, coinciding with the zone IV/V boundary in the pollen record. A DCA biplot for the complete data set from SOLA295 demonstrates that *Sphagnum* sect. *Acutifolia* has a unimodal response to the fen/bog gradient. This suggests that the section is represented by one species or several species with similar tolerances to the environmental gradient. In the mid to upper half of the macrofossil zone, *Eriophorum vaginatum* and *Polytrichum alpestre* type appear in the assemblage indicating that the *S.s. Acutifolia* peat represents the establishment of strongly oligotrophic conditions. The pollen spectra in LMZ-SOLA2-D register the acidification with a sharp increase in *Sphagnum* spores, the first appearance of *Calluna vulgaris* pollen and a rapid decline in *Poaceae*, *Cyperaceae* together with virtually all of the fen herb types.

Regional pollen types are particularly distinctive at the level of the FBT in SOLA295. *Corylus* appears for the first time at 5 - 12 % of arboreal pollen (Figure 5.9b), whilst *Juniperus* occurs at 5 - 8 % of AP until a level 8 cm above the transition at which point it declines to trace levels. These changes define the Preboreal/Boreal boundary. The pollen diagrams for SOLA195, SOLA395 and SOLA495 indicate that peat inception took place at all three of these sites in early MPZ-SOL-4 correlating with the *Juniperus/Corylus* <12% phase. Therefore, the peat formation began at these locations during or very soon after the FBT in SOLA295.

Both *Polytrichum alpestre* type and *Sphagnum* sect. *Acutifolia* are well represented from the base of core SOLA395, occurring in a 15 cm deep *Betula* carr peat. The early presence of oligotrophic taxa in the carr suggests that the onset of acidification at cores SOLA295 and SOLA395 was approximately synchronous. The two cores are both located on the floor of the basin, separated by 150 metres. Cores SOLA195 and SOLA495 occupy slightly higher positions on the sides of the depression. At these two sites 5 to 15 cm of poor fen peat, characterized by *Phragmites australis*, *Carex* spp., *Calliergon stramineum* and *Sphagnum palustre* accumulated prior to the rapid displacement of these communities by *Sphagnum* sect. *Acutifolia* and *Polytrichum alpestre* type. This suggests a brief lag in the establishment of strongly oligotrophic species between the floor and the shallow slopes of the basin. However, the presence of *Sphagnum palustre* and *Calliergon stramineum* in the basal peat of SOLA195 and SOLA495 (LMZ-SOLA1-A and LMZ-SOLA4-A respectively) shows that these deposits were formed under poor fen communities (Figures 5.5 - 5.7). Therefore, the whole basin shows evidence for acidification at the time of the Preboreal/Boreal transition, with the strength of the process dependent upon the location within the basin.

The composition of the first oligotrophic (or possibly ombrotrophic) community to inhabit the old fen surface represents the widespread formation of 'hummock type' vegetation, indicative of a low mire water-table. *Polytrichum alpestre*, which is the most likely representative of *P. alpestre* type on deep peat, grows at a mean height of 15 to 17 cm above the water-table and commonly occurs in the tops of dry hummocks

on ombrotrophic bogs (Gignac *et al.* 1991). *P. juniperinum*, the other member of this type grows on free draining acidic heath soils and rocks (Smith 1978). The association of *S.s. Acutifolia* with *Polytrichum alpestre* type and *Eriophorum vaginatum* suggests that the section is represented by one or more of the hummock species *S. fuscum*, *S. capillifolium* var. *rubellum* or *S. capillifolium* var. *capillifolium*. This inference is supported by routine analyses of *S.s. Acutifolia* leaves conducted during the quantification procedure. Two *S.s. Acutifolia* species, *S. molle* and *S. subnitens* that grow on raised bogs in lawn communities may be separated from the rest of the section using branch leaf morphology. None of the observed leaves displayed the resorption furrow present in *S. molle* or the larger leaf size of *S. subnitens*. A significant proportion of the branch leaves were too degraded for detailed examination of their margins, but this shortcoming was compensated for by examining at least 100 leaves per level. The difficulty of separating the remaining *S.s. Acutifolia* species prevents any further interpretation of the height of the hummock communities.

Figure 5.14 shows the age depth curve for the main core site SOLA295. Two radiocarbon dates straddling the FBT (SRR5646 and SRR5647) are separated by 1500 years and just 12cm in depth, giving a peat accumulation rate of 134 years per centimetre. A typical accumulation rate for a raised bog is closer to 10 - 15 yr cm⁻¹ (e.g. Bolton Fell Moss, average accumulation 12.4 yr cm⁻¹, Barber 1994). Therefore, peat growth may have halted on one or a number of occasions during the time in which the hummock vegetation developed on Solway Moss. This would explain the poor state of macrofossil preservation and the high degree of humification (H7/8) of the *S.s. acutifolia* peats. It is also possible that erosion of the peat surface occurred during this period. The DCA plots for the complete data set of core SOLA295 support this interpretation. The plot of axis 1 scores versus depth (Figure 5.16) clearly shows a wide separation between the fen and the bog samples of up to 3 S.D, indicating that the two communities have few species in common. Furthermore, the transition between fen and bog samples is very sharp with just one level registering an intermediate sample score. This sample could represent a displacement peat rather than a transitional mire community.

As a consequence of the very slow accumulation rate, the 8 cm interval in core SOLA295, characterized by low *Corylus* and 5-8% *Juniperus* pollen, which correlates with the FBT in SOLA195, SOLA395 and SOLA495, accounts for 1070 years of peat formation.

Eriophorum vaginatum and *Calluna vulgaris* mire supersedes the pioneer oligotrophic community in the central part of the basin, at core sites SOLA195, SOLA295 and SOLA395. The switch to sedge dominated hummock communities may represent a response to more frequent burning events since the assemblage is accompanied by numerous bands of charcoal. *Eriophorum vaginatum* is highly fire resistant in contrast to *Sphagnum* and benefits from the resulting supply of phosphorous. A marked increase in the abundance of *Cenococcum* spp. sclerotia also implies that the peat surface was aerated. During LMZ-SOLA2-Ea the macrofossil assemblages contains brief peaks of *S.s. Acutifolia* which correlate with levels containing less

charcoal. However, throughout zone LMZ-SOLA2-Eb bryophytes are virtually absent (with the exception of one level). This may represent more complete suppression of the moss flora by fire, with charcoal occurring in greater quantities in every level throughout the zone.

Regular burning and the success of *Eriophorum vaginatum* may provide evidence to support the traditional idea of a protracted phase of dry, more continental climatic conditions in the Boreal. Height above the summer water-table is an important determinant of species distributions in the hummock / hollow complex (Van der Molen *et al.* 1994). Even without the benefits of burning, an increase in depth to the water-table during the summer would favour *Eriophorum vaginatum*. The species is particularly successful under conditions of annually fluctuating water-table depths, with relatively high levels in spring dropping deep below the peat surface by the late summer. Continental climatic conditions in the Boreal could have provided melt waters from snow cover in spring and tinder dry summers creating these ideal conditions.

The radiocarbon date (SRR5646) placed just above the boundary between *Eriophorum vaginatum* peat and *Rhynchospora alba*/*Sphagnum imbricatum* peat, at 185-193 cm, yields an age estimate of 7850 cal. BP (7950-7750). Therefore the replacement of *Eriophorum* bog by *Sphagnum imbricatum* correlates to the beginning of the Atlantic period. Figure 5.14 shows that the resulting peat accumulation rate for the *Eriophorum*/*Calluna* assemblage is 6.7 yr cm^{-1} representing a dramatic increase compared to the preceding *S.s. Acutifolia* peat.

The decomposition rate of peat in hummocks is slower compared to hollows (Rochefort *et al.* 1990). Furthermore the rapid build up in hummock peat may be facilitated by support from vascular plants (Boatman and Armstrong 1968, Barber 1981 p203, Økland 1990) such as *Calluna vulgaris*, which regenerate vigorously by layering when buried under litter. Rhizomes of *E. vaginatum* are also very resistant to decay, with fibres surviving in highly humified peat. However, the exceptionally high rate of accumulation (Figure 5.14) recorded in LMZ-SOLA2-E, from a peat containing *Cenococcum* spp., indicative of good aeration, strongly suggests that there is a problem with the radiocarbon time-scale. In addition, five radiocarbon dates from a very similar *Eriophorum*/*Calluna* assemblage containing *Cenococcum* spp. and charcoal, occurring just above the FBT at Bolton Fell Moss, demonstrate an even rate of accumulation of 13.4 yr cm^{-1} (refer to Figure 6.16)

The limited number of radiocarbon dates available per site presents a difficulty for constructing a reliable age/depth curve. A single outlier may have a large influence upon the estimated accumulation rate. The radiocarbon date placed immediately above the FBT in SOLA295 (SRR5646) is the most prone to contamination by younger root material penetrating from above because the *Sphagnum* layers from which it is derived are overlain by *Eriophorum* peat. SRR5647 from the *Salix* spp. fen carr and SRR5645 from the *Sphagnum imbricatum* peat are less likely to be affected because they are directly overlain by *Sphagnum* peat. Furthermore a radiocarbon date (7885 cal. BP, 8030-7740, GU-5277) taken from the first

major increase in *Alnus* in the pollen record from the Solway Sheep site (Huckerby 1993, Figure 5.34) compares directly with the uppermost date from the *Alnus* / *S. imbricatum* rise in core SOLA295.

The age of the *S.s. Acutifolia* peat dated by SRR5647 was re-estimated by performing a linear extrapolation back from the level of the *Alnus/Sphagnum imbricatum* rise, using the average accumulation for *Eriophorum/Calluna* peat at Bolton Fell Moss. The calculation gives an age of 9850 cal BP for the establishment of the pioneer oligotrophic community and the empirical limit of *Corylus* pollen at Solway Moss. The recalculated estimate ties in more closely with radiocarbon dates from nearby Scaleby Moss for the Preboreal/Boreal boundary defined by the rise in *Corylus* and decline of *Juniperus* (9560-9740 cal. BP, Walker 1966).

If the re-estimated age is assumed to be accurate, the peat accumulation rate over the transition is still very slow at 50.8 yr cm^{-1} suggesting that peat growth did indeed halt for a period during the acidification of the mire. The FBTs in the four deepest multiple cores now correlate to a pollen phase lasting 400 years, giving the maximum time span in which acidification of the 0.5 km wide central basin took place.

The establishment of a *Sphagnum imbricatum/Rhynchospora alba* community in LMZ-SOLA2-F and -G, at the beginning of the Atlantic period marks a significant increase in mire water-levels. The increased surface moisture is expressed in all of the multiple cores at the time of the *Alnus* rise. In SOLA195 *Rhynchospora alba* colonized the mire followed by *Sphagnum* sect. *Acutifolia*. Leaf measurement suggest that the section is represented by the lawn species *Sphagnum subnitens*. In SOLA395 *Rhynchospora alba* is joined by *Sphagnum cuspidatum*, whilst in SOLA495 and SOLA595 the switch is to *S. imbricatum*. Therefore, the mire displays a consistent response over a distance of half a kilometre, with the altitude of the wet shift in the four deep cores varying by just 40 cm in 0.5 km. The wet shift can be traced further across Solway Moss using the field stratigraphy. Figure 5.33 shows the altitudes for the empirical and rational limits of *Sphagnum imbricatum* for an east-west transect across Solway Moss. Stratigraphy cores S9, S12 and S13 are located on higher ground (Figure 5.2b). However, all the remaining cores are positioned in the two main basins. Here the rational limit of *Sphagnum imbricatum* occurs at virtually the same altitude across one kilometre. On an isolated inland ombrotrophic mire such a widespread increase in the height of the water-table almost certainly reflects a significant increase in effective precipitation (Barber 1981, 1994, Smith 1985 Wimble 1986, Stoneman 1993).

SOLA595 is marginal to the main basin, located on higher ground. Here 60 cm of *Phragmites australis* and *Carex* spp. peats have accumulated in a fringing fen environment prior to a late FBT which occurred just before the *Alnus* rise. The actual transitional assemblage is dominated by *Eriophorum vaginatum* with some *Sphagnum imbricatum*, in zone LMZ-SOLA5-C, however this community was quickly displaced at the beginning of the Atlantic period by a mire dominated by *Sphagnum imbricatum* containing

Rhynchospora alba and *S. cuspidatum*. Therefore, this late transition has rather a different character which may reflect the ameliorating climate.

Finally, SOLA495 records a brief flooding episode in zone LMZ-SOLA495-C shortly after the transition to a dry bog containing abundant *Polytrichum alpestre*-type, *E. vaginatum* and *Empetrum nigrum*. The flooding is characterized by recolonization of *Phragmites australis*, the appearance of *S. recurvum* and *Scheuchzeria palustris*. This phase is recorded very briefly in just one other core SOLA395 (zone LMZ-SOLA3-D) suggesting that the phenomenon was local in extent. The flooding by acidic waters probably reflects the formation of a low point on the raised mire caused by peat accumulation in the centre of the basin.

5.13 Summary and concluding remarks.

To conclude, the multiple macrofossil records from Solway Moss reveal striking similarities in the pathways of mire development over large expanses of the moss (Figure 5.32). In the shallow central basin where Holocene peat accumulation began at approximately 10400 cal. B.P. in a fen environment, a maximum of just 15 cm of peat formed before acidic hummock communities displaced the pioneer vegetation. Similar hummock environments developed throughout the low lying basins, depositing a highly humified oligotrophic peat. A combination of radiocarbon dates and pollen evidence suggests that the first establishment of acid mire occurred at c. 9900 cal. B.P. and that the community had completely occupied the 0.5 km depression within four hundred years. The FBT may have been even more rapid than this across the old fen surface. However, the very slow accumulation rate and the limitations of radiocarbon dating prevent a more accurate estimation of the timing of the event. Certainly, the switch to oligotrophic species is very sudden in the main macrofossil diagram with few levels containing species tolerant of intermediate conditions. This is clearly illustrated by the DCA plots of axis 1 scores versus depth for the complete data set from core SOLA295 (Figure 5.16).

Analysis of the field stratigraphy demonstrates that *Sphagnum* sect. *Acutifolia* peat displaced *Betula* woodland over the majority of the plains lying beyond the basins. (Radiocarbon dates sampled at the Solway Sheep site (Figure 5.34, Huckerby 1993), located on the southern margin of the mire suggest that much of the area presently occupied by Solway Moss was paludified by 7800 cal. B.P.). A period of 2500 years of *Eriophorum vaginatum* / *Calluna vulgaris* dominated peat accumulation followed the FBT, punctuated by frequent burning events. The peat produced by this community is reminiscent of that accumulated by freely draining blanket bog systems which are wet in the winter but may dry out considerably in the summer. Yet this mire community occurred on a level plain, possibly indicating a protracted period of severe summer dryness. All of the data produced for Solway Moss points to a significant increase in mire water-levels right across the central plain of the moss at 7800 cal. B.P. This strongly suggests an increase in the level of effective annual precipitation at this time. Within the earlier *Eriophorum* / *Calluna* mire phase, significant localized flooding events were recorded in two of the

multiple cores, relating to differential peat accumulation . The identification of such features highlights the problem of relying on just one core to undertake palaeoenvironmental reconstructions, particularly in groundwater dominated peatlands. However, careful examination of detailed field stratigraphy prior to sampling enabled the successful location of the main core in an unaffected area. The resulting macrofossil record from SOLA295 provides a good representation of the main mire-wide stratigraphic changes in the central mire basin.

Experience of the basal peats at Solway Moss suggests that a simple broad classification of fen peat, black highly humified *Sphagnum* peat, highly humified *Eriophorum/Calluna* peat and fresher *Sphagnum* / *Rhynchospora* peat is clearly distinguishable in coherent layers from a combination of field observations and laboratory checks. The literature suggests that this zonation is very widespread (Section 2.4), although many humified *Eriophorum* peats may have been misclassified as *Sphagnum* peat in the past. As the humification of monocotyledon peat increases, the physical characteristics change from a fibrous structure to a crumb structure (Okruszko 1993). This can be very difficult to distinguish from humified *Sphagnum* peat in the field. Detailed laboratory work, for the present project and for NERC grant GR9/01646 (Barber 1996), focussed on Walton Moss, has demonstrated the value of undertaking regular checks on field stratigraphy descriptions.

The analyses undertaken in this chapter indicate that, it should be possible, using detailed field stratigraphy, backed up by spot check levels for humified *Sphagnum*, to locate one main sample core to give a representative record of the earliest phase of mire acidification and the basin wide stratigraphic changes in the ombrotrophic peat thereafter.

Chapter 6

Allogenic or autogenic mire development?: The fen/bog transition at the inter-site scale.

6.0 Introduction.

The central debate to emerge from the literature review presented in Chapter 2, concerns the relative importance of allogenic and autogenic processes in driving the transition from fen to raised mire. The traditional model of raised mire formation assumes that decoupling from the groundwater is a result of continuous autogenic peat accumulation, to a level above the regional water-table. A major assumption underlying this model is that boundary conditions have remained constant. In his study of hydroseres, Walker (1970) stated that the analysis included only those sites free from allogenic disturbance. However, advances in palaeoecology over the last century have clearly demonstrated that climate and sea level have been anything but stable over the duration of the Holocene. Change in these systems may be expected to have a profound influence upon all aspects of wetland development. This view is accepted in many accounts of raised mire development. For example, the formation of raised mires is frequently attributed to increased effective precipitation (eg. Weber 1908, Granlund 1932, Godwin 1946, Conway 1948, 1954, Walker and Walker 1961, Berglund *et al.* 1983). Whilst regeneration and accelerated growth in ombrotrophic systems may clearly correlate to this factor, several recent studies based on stratigraphic analyses suggest that the transitions, in some Scandinavian mires, coincide with periods of drier climate and low lake levels (Svensson 1988a, Almquist-Jacobson and Foster 1995). The detailed macrofossil analyses from Solway Moss seem to support this latter view, since relatively dry 'heath-like' oligotrophic mire replaces the fen or carr stage in all of the multiple cores.

This chapter aims to further investigate the controlling factors affecting the FBT, by comparing the character and timing of the event at Solway Moss with a further three sites originating from similar, small kettlehole lakes, in the Cumbrian lowlands. The following specific research questions will be addressed:

- (1) Have the four former kettlehole lakes developed along comparable pathways in their minerotrophic phases?
- (2) Is the transition to dry ombrotrophic mire, recorded at Solway Moss, commonplace?
- (3) Do FBTs of a similar type occur at similar rates, with constituent stages possessing comparable lifespans?

(4) Is *Sphagnum* always a dominant part of the flora in transitional stages? Is there any evidence for other species performing the ecosystem engineering role usually attributed to *Sphagnum*?

(5) Do FBTs display evidence for climatic forcing on a regional scale? (e.g. accelerated succession, reversed succession, or synchronous change between mires, not accounted for by similarities in the pathways of development)

(6) In the case of the coastal mire, Glasson Moss; do flooding events correlate with positive sea level tendencies and retardation phases with negative tendencies? Do any of these events coincide with the FBT?

In larger basins the greater depth of water dictates a relatively long period of infilling dominated by reedswamp, fen and carr communities, before conditions become suitable for raised mire formation. Therefore, it is reasonable to anticipate that peatlands developing from large glacial lakes will possess younger transitions than those forming in shallow kettleholes. This aspect of peatland development will be exploited in the next section of the chapter, in order to compare the character of the FBTs recorded in the Cumbrian mires with those of different time periods and different climatic or hydrological conditions. Sites located in the far west of the British Isles will also be used to study the character of the FBT in an oceanic climate, with the aim of comparing the resulting mire development records with those of the Cumbrian mires.

The concentric raised bog located on the south-east side of the Tregaron mire complex provides an ideal opportunity to study a younger FBT than those examined in Cumbria. Well preserved ombrotrophic peat is underlain by more than three metres of *Phragmites australis*/*Cladium mariscus* peat deposits. Furthermore, the site is already well studied possessing a full stratigraphy, compiled by Godwin and Mitchell (1938), and a detailed pollen diagram accompanied by 18 radiocarbon age estimates (Hibbert and Switsur 1976). Examination of the basic field stratigraphy and the pollen diagram suggests that ombrotrophic conditions established over much of the mire at c. 7300 cal. B.P. This correlates with the early part of the *Sphagnum imbricatum*/*Rhynchospora alba* phase identified right across Solway Moss (commencing 7800 cal. B.P., see Chapter 5). If the extensive synchronous wet phase at Solway Moss can be regarded as evidence for increased effective precipitation at the opening of the Atlantic, then the FBT data gathered at Tregaron South-East Bog should provide insight into raised bog formation during a humid climatic phase. However, the Tregaron peatland complex is also dissected by the River Teifi, which forms the western boundary to the south-east bog. Therefore, the aim of the study at Tregaron will be to examine the character of the transition to raised mire conditions during a wet climatic phase, in a peatland dominated by a major river system. What impact does the proximity of the river have on the peatland complex and the FBT in particular?

Borth Bog provides a second chance to study a relatively young transition (mid-Holocene), since the mire originates from a Boreal salt-marsh. The coastal site was chosen for study to undertake a paired site comparison with Tregaron South-East Bog and to investigate any possible impacts of base level change on the FBT.

Abbeyknockmoy Bog, originating from a large Devensian lake, was chosen to provide a representative site for analyses of the FBT in an oceanic part of the British Isles. Modern weather statistics for the meteorological recording station in Galway Bay, which lies *c.* 25 km from Abbeyknockmoy Bog, register an average annual precipitation level of 1800 mm yr.⁻¹, with maxima and minima of 2050 and 1630 mm respectively for the period from 1963 to 1983 (The Meteorological Office of Eire). Prior to sampling for radiocarbon assays, estimates of the age of the FBT at Abbeyknockmoy Bog were calculated by extrapolating back from radiocarbon dates, sampled on the upper 3 metres of peat from the mire, as part of the Palaeoclimate Special Topic (GST/02/539, Barber *et al.* 1994). The results of the extrapolation exercise suggest that the FBT occurred at 7000 to 8000 cal. B.P. Preliminary examinations of the lake status records for Eire (Yu and Harrison 1995, Guiot *et al.* 1993) indicate that the east-west climate gradient across Eire may have been more pronounced in the past, particularly during the early Holocene, with westerly mires such as Abbeyknockmoy Bog experiencing an even wetter climatic regime than at present. In addition, the estimated time interval for the FBT at Abbeyknockmoy Bog coincides with an inferred period of generally wetter climatic conditions in Northern Europe (Digerfeldt 1988, Figure 7.6). Therefore, Abbeyknockmoy Bog should provide interesting information concerning the character of mire development, at the FBT, in a mire unaffected by a major river system but experiencing a very wet climatic regime.

Mongan Bog, located on the edge of the River Shannon, in the centre of Eire, represents an interesting contrast to the conditions in Galway Bay. Meteorological statistics from Blackwater Bog, situated *c.* 1 km from Mongan Bog, record an average of 820 mm of precipitation per water year, for the period from 1963 to 1983, with a maximum value of 1086 mm yr.⁻¹ and a minimum of 608 mm yr.⁻¹. The precipitation values indicate a significant modern rainfall gradient between the two Irish sites. As mentioned above this gradient may have been stronger in the early Holocene. Mongan Bog receives almost exactly the same level of precipitation (average annual precipitation of 825 mm at Carlisle) as the four Cumbrian Mosses, which are the most easterly sites in the transect studied for the present project.

An estimate of the age of the FBT at Mongan Bog of 5000 to 6000 cal. B.P. was calculated in a similar manner to that of Abbeyknockmoy Bog, also using radiocarbon dates from the Palaeoclimate Special Topic (GST/02/539, Barber *et al.* 1994). Climate records (Dubois and Ferguson 1985, Digerfeldt 1988, Barber *et al.* 1994) indicate lower levels of effective precipitation at this time. Therefore, Mongan Bog was selected, not only as a paired site for Abbeyknockmoy Bog, but also to compare the pathway of development with those of the Cumbrian mires and Solway Moss in particular, which appears to have developed initially into

a relatively dry ombrotrophic mire possibly reflecting a climate that was not sufficiently humid to support wet raised mires. Does Mongan Bog develop along a parallel successional pathway to Solway Moss?

Specific research questions relating to the FBT in large wetland basins include the following:

- (1) Do the successional pathways differ between mires originating in large and small basins?
- (2) Does dry 'hummock-level' raised mire, such as that recorded at Solway Moss (Chapter 5) ever form the pioneer ombrotrophic community in large basin mires that develop into raised mires during humid climatic phases?
- (3) Are FBTs in very wet climates more gradual?
- (4) Are *Sphagnum* spp. more important in FBTs occurring in very wet conditions?
- (5) Is drainage basin change an important factor in triggering the FBT at Tregaron South-East Bog? Does the presence of the river system at Tregaron South-East Bog result in a different type of FBT when compared to sites that are not connected to a major river system, which experienced a similar climatic regime at the FBT?
- (6) Does base level change affect the character of the FBT at coastal sites such as Borth Bog?
- (7) Does the character of the FBT at the oceanic site, Abbeyknockmoy Bog, differ significantly from sites located in drier parts of the east-west gradient and in drier time periods?

The examination of multiple cores from one site, presented in Chapter 5, demonstrated a considerable degree of coherence in the five macrofossil diagrams and the field stratigraphies. Large scale stratigraphic changes could be traced over extensive areas of the central mire basins and events in the ombrotrophic peat in particular appeared to be broadly synchronous. The use of field stratigraphy proved to be particularly valuable for selecting a main sample core with the minimum of local scale disturbances. In this chapter a transect of field stratigraphy from each wetland is used to locate one main sample core, designed to represent the large scale stratigraphic changes of the whole mire.

Although the FBT at Solway Moss correlates with a relatively narrow time and depth interval over the majority of the central basin, this cannot be assumed to be the case at all sites because minerotrophic wetlands may be subjected to the vagaries of many more local factors than their ombrotrophic counterparts. However, it is important to compare like with like, when attempting to correlate events from

different mire systems. Therefore, macrofossil cores were selected with the aim of comparing the first point at which ombrotrophic mire established on each mire.

6.1 Objectives of the chapter.

- To characterize the pathways of mire development at seven sites ranging from Cumbria to Galway, using vegetative macrofossils, fruits and seeds.
- To study the timing of the FBT and other major stratigraphic changes using radiocarbon dating and pollen correlation.
- To examine the evidence for allogenic controls (e.g. climate change and sea level change) on mire stratigraphy and the FBT in particular, using inter-site correlation.

6.2 Gross stratigraphies of the study mires.

The gross stratigraphies for each of the seven mires introduced in this chapter are presented in Figures 6.1 to 6.7. In each case the mire displays a very familiar stratigraphy that may be divided into a simplified classification containing three basic peat types:

(1) Reedswamp and fen peat dominated by *Phragmites australis* remains, usually with a brushwood component that increases towards the upper boundary.

(2) Highly humified (H6 - H9) raised mire peat: a dark brown to black peat containing the remains of *Eriophorum vaginatum*, *Calluna vulgaris* and variable amounts of *S.s. Acutifolia*, often dominated by very fine, orange Ericaceae rootlets and containing numerous bands of charcoal.

(3) Fresh Sphagnum peat (H2 - H5): A well preserved peat containing abundant remains of *Sphagnum* which often form over 90% of the peat matrix.

Comparisons of Figures 6.1 to 6.7 show that all of the mires follow the basic three-part division described above. The stratigraphies usually become more complicated towards the edges of the mire where the effects of runoff from the surrounding land and disturbance are greatest. The main function of each of the stratigraphies is to provide a context for locating a Russian sample core. Therefore the individual stratigraphies are not discussed in detail. However, the rationale for positioning the sample cores along each transect is presented in Section 6.2.1

6.2.1 The rationale for core site selection.

Bolton Fell Moss (core BFML):

Fig 6.1 shows that the deepest part of the basin is described by three stratigraphy cores (2, 3 and 4). Although core 2 records the deepest FBT, the site is located close to the junction of two main drainage ditches. The peat in the sample area appeared to be disturbed and had experienced shrinkage due to de-watering. Therefore, core BFML was sited four hundred metres away from the main drain within the area of the deep basin still covered by an uncut peat surface. Figure 1 shows that cores 3 and 4, (both within this area) have level fen/bog contacts, probably representing the true level of the former fen surface, across the whole mire basin.

Glasson Moss (GLM95), Walton Moss (centre core, WLM11) , Tregaron Bog (TSE94), Borth Bog (BTH94) and Mongan Bog (MOG95):

All of the core sites in these mires are located a long way from any large scale disturbances, therefore there were few constraints upon core location. In each case the sample core has been recovered from the field stratigraphy borehole that recorded the deepest FBT. This should provide a record of the earliest date for raised mire inception.

Abbeyknockmoy Bog:

The sample core from this mire is located in the deepest part of the pre-Holocene lake basin (core 5) which coincides with the deepest point at which oligotrophic peats are found. The core site was at least 150 metres from the main peat cutting face, which has caused drying and local slumping of the bog surface.

Walton Moss (marginal core WLM15):

Core WLM15 was located on a steeply sloping section of the paludified fringing peatland surrounding the central basin at Walton Moss.

6.3 Summary of the macrofossil stratigraphies.

6.3.1 Summary of the macrofossil stratigraphy of Bolton Fell Moss (BFML).

Figure 6.8 (The location of core BFML is given in Figure 4.2).

The Holocene peat beds at Bolton Fell Moss overlies silty clays which contain some sand. In common with Solway Moss these inorganic sediments are typical of a low energy water body. The marked lack of organic material in the clays suggests that the unit was deposited in an unproductive environment such as a kettlehole lake. An intercalated 5 cm band of peat lying at a depth of 1006 to 1011 cm closely resembles

the sequence from Solway Moss and Blelham Tarn, and probably represents the Windermere interstadial period.

The lowermost macrofossil assemblage from the continuous peat sequence (LMZ-BFML-A) is composed of over 60% U.O.M and originates from a highly humified (H8/9) wood peat containing numerous fragments of *Phragmites australis*. Larger twigs were sectioned and tentatively identified as *Salix/Populus* type. High *Salix* pollen frequencies in LPZ-BFML-1 suggest that the wood is from the *Salix* genus, however, further identification was not attempted since the accompanying leaf remains were too small. The orange/black roots of *Equisetum* spp. are the only other macrofossils to survive in this zone. *Phragmites australis/Betula* spp. wet fen carr peat (or possibly swamp carr) replaces the *Salix* assemblage in LMZ-BFML-B. *Carex paniculata* achenes occur in small numbers throughout the zone, accompanied by a trace of vegetative *Carex* spp. remains and *Menyanthes trifoliata*. A tussock fen surface may have begun to develop with *Betula* spp. growing on the drier tussock tops, and *Menyanthes trifoliata* colonizing the intervening depressions. Towards the upper boundary of LMZ-BFML-B *P. australis* begins to be displaced by *Carex* spp. A coincident increase in the abundance of *C. paniculata* achenes and *Menyanthes trifoliata* point to further development of a tussocky reedswamp community. Towards the upper boundary of LMZ-BFML-C *Carex* spp. completely dominates the macrofossil assemblage. A poor fen community (LMZ-BFML-D) composed of *Calliargon stramineum* and *Drepanocladus fluitans* marks an abrupt change in the macrofossil record. Whilst *Menyanthes trifoliata* remains in the assemblage most other fen species disappear and *Eriophorum vaginatum* is recorded for the first time. This implies a significant increase in the acidity of the mire. In LMZ-BFML-E *Sphagnum palustre* replaces the brown mosses and *Eriophorum vaginatum* increases to 40% of the assemblage. The transition to ombrotrophic mire is finally recorded at the lower boundary of LMZ-BFML-F, marked by the disappearance of *S. palustre*, the more complete dominance of *Eriophorum vaginatum* and the first continuous record of *Calluna vulgaris* and *Sphagnum* sect. *Acutifolia*. This mire community lasted for approximately 2100 years from 9605 to 7510 cal. B.P. and remained remarkably stable in composition. The establishment of the *Eriophorum vaginatum* bog is coincident with the beginning of the charcoal record. Regular burning events and the species composition suggest a long period of low mire water-table conditions similar to those at Solway Moss. Again, the frequent occurrence of *Cenococcum* spp. supports this interpretation. *Sphagnum* sect. *Acutifolia* occurs as small isolated peaks correlating with horizons containing little or no charcoal. This supports the findings from Solway Moss which suggest that the interaction of *Eriophorum vaginatum* and *S.s. Acutifolia* is a result of the degree of burning. In zone LMZ-BFML-G *Sphagnum* sect. *Acutifolia* becomes a more prominent part of the assemblage. This change precedes the establishment of *Rhynchospora alba* which is continuously recorded from 575 cm depth (6700 cal. B.P.). The upper two zones LMZ-BFML-H and I are characterized by greater than 40% *Rhynchospora alba* and 5% *Sphagnum cuspidatum*, indicating significantly wetter mire surface conditions similar to those succeeding the *Eriophorum vaginatum/Calluna vulgaris* mire at Solway Moss. In LMZ-BFML-I *Sphagnum imbricatum* becomes co-dominant with *Rhynchospora alba*. Table 6.1 summarizes the stratigraphy of core BFML.

Table 6.1 Summary of the stratigraphy of core BFML

Bolton Fell Moss (BFML)				
Wetland type	Depth (cm)	Zone LMZ-BFML	Date range (cal. BP)	Lifespan (years)
<i>Sphagnum imbricatum</i> bog	500-504	I	5250-	N/A
<i>Rhynchospora</i> bog	504-540	H	5250-6220	970
<i>Calluna</i> / <i>S.s. Acutifolia</i> bog	540-650	G	6220-7510	1290
<i>Eriophorum</i> / <i>Calluna</i> bog	650-826	F	7510-9640	2130
<i>S. palustre</i> poor fen	826-846	E	9640-9760	120
<i>D. fluitans</i> Poor fen	846-854	D	9760-9810	50
<i>Carex</i> fen	854-885	C	9810-9930	120
<i>Betula</i> swamp carr	885-960	B	9930-10215	290
<i>Salix</i> carr	960-984	A	10215-10250	35
Total				5005

6.3.2 Summary of the macrofossil stratigraphy of Walton Moss (WLM11).

Refer to Figure 6.9 (The location of core WLM11 is given in Figure 4.2).

Peat accumulation commenced in a fen environment containing *Phragmites australis*, *Carex vesicaria* and *Potentilla palustris* (LMZ-WLM11-A). This community developed into a tussocky *Betula* spp. fen or swamp carr in zone LMZ-WLM11-B similar to that at Bolton Fell Moss. *Sphagnum* sect. *Acutifolia* is recorded at a number of levels in the carr phase possibly indicating the presence of some of the more minerotrophic members of the section. Thereafter, the mire development pathway is close to that found at Bolton Fell Moss. In zone LMZ-WLM11-C *Sphagnum palustre* rises to dominance and the first traces of acid species such as *Eriophorum vaginatum* and *Calluna vulgaris* are registered whilst fen species such as *Phragmites australis* and *Menyanthes trifoliata* disappear. At the upper boundary of LMZ-WLM11-C the swamp carr assemblage composed of *Carex paniculata* and *Betula* spp. is finally replaced by *Sphagnum palustre* and *Eriophorum vaginatum* (LMZ-WLM11-D). The first ombrotrophic bog peat is dominated by *Eriophorum vaginatum* and *Calluna vulgaris* macrofossils with frequent occurrences of *Cenococcum* spp. and charcoal. The U.O.M content also remains high throughout zones LMZ-WLM11-Ea and Eb implying that mire surface water-levels were low, for at least part of the year. The latter of the these two zones is differentiated by a shift towards the dominance of *Calluna vulgaris*, possibly representing further drying out of the bog surface. However, this trend is reversed in LMZ-WLM11-F with the formation of a *Sphagnum* sect. *Acutifolia*/*Eriophorum vaginatum* association. The associated decline in U.O.M and

Cenococcum spp. suggests a shift towards higher mire water-tables. Measurements taken on the leaf size of the *S.s. Acutifolia* also reveal a slightly larger than average size distribution indicating the presence of the lawn species *Sphagnum subnitens*. At 630 cm depth the pool species *Sphagnum cuspidatum* colonizes the mire, indicating a major rise in mire surface wetness. This change is associated with the appearance of *Eriophorum angustifolium*, large numbers of Acrid mites and a significant decline in *Calluna vulgaris* (LMZ-WLM11-G). A brief summary of the stratigraphy is presented in table 6.2.

Table 6.2 Summary of the stratigraphy of core WLM11.

Walton Moss (centre) (WLM11)				
Wetland type	Depth (cm)	Zone LMZ-WLM11	Date range (cal. BP)	Lifespan (years)
<i>S. cuspidatum</i> bog	-635	G	-7380	N/A
<i>S.s. Acutifolia</i> bog	635-664	F	7380-7635	255
<i>Eriophorum/Calluna</i> bog	664-869	E	7635-9840	2205
<i>S. palustre</i> poor fen	869-885	D	9840-9950	110
<i>Betula</i> swamp carr	885-975	B&C	9950-10200	250
<i>Phragmites</i> fen	975-1000	A	10200-10265	65
Total				2890

6.3.3 Summary of the macrofossil stratigraphy of Walton Moss (WLM15).

Refer to Figure 6.10 (location of WLM11 is given in Figure 4.2)

A wet *Alnus* carr containing *Phragmites australis* and *Juncus* provides the starting point for the paludification sequence, from the margin of Walton Moss (LMZ-WLM15-A). Signs of acidification are encountered after just 30 cm of peat accumulation with the arrival of *Sphagnum palustre* and a change in composition of the carr to *Betula* (LMZ-WLM15-B). The following zone, characterized by a brief dominance by *S. recurvum* (LMZ-WLM15-C), immediately precedes the transition to oligotrophic mire vegetation in zone LMZ-WLM15-D. The macrofossils preserved from the first oligotrophic mire community are almost entirely composed of two familiar species, *Eriophorum vaginatum* and *Calluna vulgaris*, representing dry surface mire conditions. Minor isolated occurrences of *Polytrichum alpestre*-type and *Aulacomnium palustre* are also recorded in this zone. LMZ-WLM15-Ea is defined by a large increase in the rootlets of *Calluna vulgaris* and a corresponding drop in *Eriophorum vaginatum*. The assemblage is also accompanied by a greater frequency of *Aulacomnium* and *Cenococcum* spp. suggesting further drying out of the mire surface and a slight increase in nutrient availability from decomposition. The beginning of LMZ-WLM15-Eb is marked by a brief wet pulse in which *Rhynchospora* enters the

record for just one level. Above the *Rhynchospora* level *S.s. Acutifolia* registers a response, indicating the gradual return to low and then higher hummock level communities as the water-table sinks to its former level. Zone LMZ-WLM15-Fa marks the irregular increase of *S. imbricatum* on the mire prior to the major rise in the species at the beginning of zone LMZ-WLM15-Fb. Species such as *Vaccinium*, *Erica tetralix* and *Eriophorum angustifolium* increase with *S. imbricatum* confirming the presence of the lax form of the *Sphagnum* species, indicative of wet lawn conditions. Table 6.3 provides a brief summary of the stratigraphy.

Table 6.3 Summary of the stratigraphy of core WLM15.

Walton Moss (margin) (WLM15)				
Wetland type	Depth (cm)	Zone LMZ-WLM15	Date range (cal. BP)	Lifespan (years)
<i>S. imbricatum</i> bog	214-244	Fb	-2350	N/A
<i>Eriophorum</i> / <i>S. imbricatum</i> bog	244-290	Fa	2350-2975	625
<i>Calluna</i> / <i>Eriophorum</i> bog / <i>R. alba</i>	290-350	Eb	2975-3795	820
<i>Calluna</i> / <i>Eriophorum</i>	350-396	Ea	3795-4420	625
<i>Eriophorum</i> / <i>Calluna</i> bog	396-470	D	4420-5460	1040
<i>S. palustre</i> / <i>S. recurvum</i> poor fen	470-475	C	5460-5555	95
<i>Betula</i> carr	475-514	B	5555-7180	1625
<i>Alnus</i> carr	514-550	A	7180-	N/A

6.3.4 Summary of the macrofossil stratigraphy of Glasson Moss (GLM95).

Refer to Figure 6.11 (The location of core GLM95 is given in Figure 4.3).

The clays underlying Glasson Moss are similar in character to those at the preceding sites. Macrofossils of *Scirpus lacustris* and *Daphnia* spp. demonstrate that the unit was deposited in a shallow water body (LMZ-GLM95-A). The first peat deposit is highly humified and virtually amorphous, containing over 80% U.O.M with traces of *Equisetum* spp. and *Phragmites australis* rootlets, *Ranunculus flammula* and *Salix* spp. leaves (LMZ-GLM95-B). In zone MZ-GLM95-Ca a wet fen developed, principally composed of *Phragmites australis* and *Carex vesicaria*, with *Carex rostrata* and a range of fen herbs, including *Potentilla palustris*, *R. flammula* and *R. batrichium*-type. The upper part of the zone (LMZ-GLM95-Cb) is characterized by a shift towards *Carex* spp. domination, accompanied by *Menyanthes trifoliata*. Towards the upper part of LMZ-GLM95-Cb and in LMZ-GLM95-D acidification of the mire is signalled by the

appearance of species such as *Scheuchzeria palustris*, *Sphagnum palustre* and *S.s. Acutifolia*, which indicate the development of a wet poor fen. Other indicators of acidification coincident with these levels include the propagules of *Eriophorum angustifolium* and *Rhynchospora alba*. The poor fen phase is rapidly displaced by drier ombrotrophic bog peat at 895 cm, represented by *Eriophorum vaginatum*, *Empetrum nigrum* and relatively high percentages of U.O.M. (LMZ-GLM95-E). In zone LMZ-GLM95-F a *Sphagnum palustre* dominated assemblage returns indicating a reverse succession towards a more minerotrophic community. This is superseded by a second dry bog phase in zone LMZ-GLM95-G, characterized by the usual *Eriophorum vaginatum*/*Calluna vulgaris* association, with larger charcoal peaks and a more frequent record of *Cenococcum* spp. *Sphagnum* sect. *Acutifolia* again correlates with levels containing little or no charcoal. Zone LMZ-GLM95-H records the rise of *Rhynchospora alba* at 750 cm depth. This is followed by a brief dry shift in LMZ-GLM95-I prior to the rapid displacement of hummock and lawn environments by a pool peat at 670 cm, indicated by the arrival of *Sphagnum cuspidatum* (LMZ-GLM95-J). Table 6.4 gives a summary of the stratigraphy.

Table 6.4 Summary of the stratigraphy of core GLM95.

Glasson Moss (GLM95)				
Wetland type	Depth (cm)	Zone LMZ-GLM95	Date range (cal. BP)	Lifespan (years)
<i>S. cuspidatum</i> bog	-672	J	-7695	N/A
<i>Eriophorum</i> / <i>Calluna</i> bog	672-695	I	7695-7975	280
<i>Eriophorum</i> / <i>Rhynchospora</i> bog	695-750	H	7975-8650	675
<i>Eriophorum</i> / <i>Calluna</i> bog	750-800	G	8650-9265	615
<i>S. palustre</i> poor fen	800-838	F	9265-9720	455
<i>Eriophorum</i> bog	838-885	E	9720-9975	255
<i>Scheuchzeria</i> / <i>S. palustre</i> bog	885-895	D	9975-10400	425
<i>Phragmites</i> / <i>Carex</i> / <i>Menyanthes</i>	895-914	Cb	10400-10770*	370
<i>Phragmites</i> / <i>Carex</i> fen	914-938	Ca	10770-10950*	180
<i>Equisetum</i> / <i>Phragmites</i> swamp	938-948	B	10950-11000*	50
Unproductive water	948-	A	11000*-	N/A
Total				3305

* Estimated from pollen data.

6.3.5. Summary of the macrofossil stratigraphy of Tregaron Bog (TSE94).

Refer to Figure 6.12 (The location of core TSE94 is given in Figure 4.5).

The peat beds of Tregaron South-East bog overlies finely laminated lake clays containing the macrofossils of *Myriophyllum spicatum* and *Chara* oospores, which indicate that the waters were calcareous. Reedswamp development is recorded in LMZ-TSE94-B with rootlets from the main species, *Typha latifolia* and *Phragmites australis* penetrating into the preceding amorphous peat unit. The presence of *Potamogeton natans* propagules and the remains of leaves from the same genus suggest that water depths were no greater than one metre in this zone. The character of the reedswamp assemblage changes in LMZ-TSE94-C with the displacement of *Typha latifolia* by *Cladium mariscus*. This is followed by the beginning of fen carr development in zone LMZ-TSE94-Da which is indicated by the decline of *Cladium mariscus* and the appearance of many wood fragments in the *Phragmites australis* peat. Initially the wood remains were too small and degraded to allow satisfactory sectioning. Accompanying leaf fragments were also highly humified preventing further examination. However, above 640 cm depth (zone LMZ-TSE94-Db) the macrofossils of *Alnus glutinosa* are recorded in the form of wood and propagules. Figure 6.12 also registers the rational limit of *Alnus* pollen at this level. In the upper part of LMZ-TSE94-Db *Carex paniculata* propagules become a prominent part of the fen carr assemblage pointing to the development of a tussocky mire surface. Carr conditions continue into zone LMZ-TSE94-E, where *Betula* spp. replaces *Alnus glutinosa*, possibly due to base depletion on the tussock tops. The transition to a poor fen occurs over a depth of 4 cm at the boundary with LMZ-TSE94-F. The principal species in this phase are *Sphagnum palustre*, *Aulacomnium palustre* and *Eriophorum vaginatum*. In the following zone a familiar *E. vaginatum*/*Calluna vulgaris* association forms the first ombrotrophic community. Again, this assemblage is accompanied by high numbers of *Cenococcum* spp. Sub-zone LMZ-TSE94-Gb is differentiated by the disappearance of *Cenococcum* spp. and the arrival of *Rhynchospora alba* suggesting increasing anaerobiosis. In zone LMZ-TSE94-H the lawn and pool edge species *Rhynchospora alba* dominates the mire prior to the sudden increase to complete dominance of *Sphagnum imbricatum* in LMZ-TSE94-I. Table 6.5 gives a brief summary of the stratigraphy.

Table 6.5 Summary of the stratigraphy of core TSE94.

Tregaron Bog (TSE94 Core)				
Wetland type	Depth (cm)	Zone LMZ-TSE94	Date range (cal. BP)	Lifespan (years)
<i>S. imbricatum</i> bog	363-	I	4850	N/A
<i>Rhynchospora</i> bog	363-440	H	4850-5950	1100
<i>Eriophorum</i> <i>Calluna/R. alba</i> Bog	440-482	Gb	5950-6525	575
<i>Eriophorum</i> <i>/ Calluna/ Cenococcum</i>	482-545	Ga	6525-7360	835
<i>S. palustre</i> poor fen	545-555	F	7360-7460	100
<i>Phragmites/Carex/Betula</i> swamp carr	555-572	E	7460-7640	180
<i>Phragmites/Carex/Alnus</i> swamp carr	572-635	Db	7640-8410	770
<i>Phragmites/ Carex</i>	635-700	Da	8410-9200	790
<i>Phragmites/Cladium</i> swamp	700-810	C	9200-10540	1340
<i>Phragmites/Typha</i> reedswamp	810-840	B	10540-10910	370
Productive open water	840-855	A	10910-11100	190
Total				6250

6.3.6. Summary of the macrofossil stratigraphy of Borth Bog (BTH94).

Refer to Figure 6.13 (The location of core BTH94 is given in Figure 4.6).

Peat accumulation began at Borth Bog in a salt-marsh environment. The basal zone LMZ-BTH94-A is a mixture of fine marine clay containing numerous Foraminifera and *Phragmites australis* rootlets. In the superseding zone (LMZ-BTH94-B) Foraminifera disappear suggesting the development of freshwater conditions. *Phragmites australis* dominates the zone accompanied by the macrofossils of tree roots that penetrated down into the unit from higher levels. Towards the top of LMZ-BTH94-B the vegetative remains of *Carex* spp. are recorded, accompanied by large numbers of *Carex paniculata* propagules. This heralds the replacement of the reedswamp with an *Alnus glutinosa*/*Carex paniculata* dominated swamp carr in LMZ-BTH94-C although *Phragmites australis* persists at 10 to 20% of the assemblage, presumably surviving in the wetter hollows between the *Carex paniculata* tussocks. *Betula* spp. replaces *Alnus glutinosa* in the swamp carr in zone LMZ-BTH94-Da, signalling the onset of acidification on the

hummock tops. Above 620 cm depth *Betula* spp. completely replaces *C. paniculata* to form a fen carr with *Phragmites australis* and *Hydrocotyle vulgaris* (LMZ-BTH94-Db). The major switch to oligotrophic conditions is registered in zone LMZ-BTH94-E with the replacement of the carr community by an *Eriophorum vaginatum*/*Pinus sylvestris* bog. Brown mosses such as *Pleurozium schreberei*, *Pseudoscleropodium purum* and *Aulacomnium palustre* accompany the acidic dry bog community. It is interesting to note that the macrofossils of *Phragmites australis* continue to occur at 2 - 5% of the assemblage right into the *Pinus sylvestris* bog phase. This possibly indicates the persistence of a tussocky mire surface. In the top four mire zones Borth Bog follows a typical sequence of raised bog development. LMZ-BTH94-F is characterized by the appearance of *Sphagnum* sect. *Acutifolia*, *Calluna vulgaris*, *Erica tetralix* and *Polytrichum alpestre*-type, and the virtual absence of *Eriophorum*. This 'hummock type' vegetation is replaced by a dry *Eriophorum vaginatum*/*Calluna vulgaris* bog in zone LMZ-BTH94-G prior to a dramatic increase in mire surface wetness and the formation of *Rhynchospora alba* lawn in LMZ-BTH94-H. As with many of the other sites examined in this project, the *Rhynchospora alba* phase is closely followed by the rapid rise to dominance of *Sphagnum imbricatum* in zone LMZ-BTH94-I. A resume of the stratigraphy is presented in table 6.6.

Table 6.6 Summary of the stratigraphy of core BTH94.

Borth Bog (Core BTH94)				
Wetland type	Depth (cm)	Zone LMZ-BTH94	Date range (cal. BP)	Lifespan (years)
<i>S. imbricatum</i>	284	I	3270	N/A
<i>Rhynchospora alba</i>	284-392	H	3270-4425	1155
<i>Eriophorum/Calluna</i>	392-490	G	4425-5475	1050
<i>S.s. Acutifolia</i>	490-558	F	5475-6135	660
<i>Pinus/Eriophorum</i>	558-590	E	6135-6225	90
<i>Betula</i> carr	590-635	D	6255-6380	125
<i>Alnus</i> carr	635-660	C	6380-6430	50
<i>Phragmites</i> swamp	660-700	B	6430-7035	605
	700-	A	7035-	N/A
Total				3765

6.3.7 Summary of the macrofossil stratigraphy of Mongan Bog (MOG95).

Refer to Figure 6.14 (The location of core MOG95 is given in Figure 4.7).

The mire complex at Mongan developed from a calcareous lake similar to that found at Tregaron. Fine silty lake clays, containing a range of mollusc species and *Chara* oospores, grade into an organic detritus mud composed of *Scirpus lacustris* macrofossils (LMZ-MOG95-A). This assemblage is quickly replaced by reedswamp peat, principally composed of *Phragmites australis* and *Cladium mariscus* in zone LMZ-MOG95-Ba. The point at which reedswamp developed into fen is hard to gauge. However at least until 675 cm standing water existed at the core site. This is demonstrated by the presence of the propagules of *Nymphaea alba* and *Mentha aquatica* and the spikelets of *Myriophyllum* spp. and *Ranunculus flammula*. In LMZ-MOG95-Bb, *Phragmites australis* becomes subdominant to *Cladium mariscus* for the first time. The presence of *Eupatorium cannabinum* and larger numbers of *Carex* spp. propagules may indicate the development of fen. *Drepanocladus fluitans* is also recorded in the assemblage, suggesting wet relatively acidic conditions. The record of *Polytrichum alpestre* type towards the top of the sub-zone also points to increasing acidification. *Cladium mariscus* is usually found on neutral or alkaline soils. However, it may be able to persist in poor fen due to its deep rooting system. Again the transition to fully oligotrophic peat is relatively sharp, occurring over 4 to 8 cm depth between 504 and 496 cm. In common with all the preceding sites the first oligotrophic community (LMZ-MOG95-C) is indicative of dry bogs and contains *Eriophorum vaginatum*, *Calluna vulgaris*, *Pinus sylvestris* and *Pleurozium schreberei*. An abundance of *Cenococcum* spp. also indicates an aerated mire surface. LMZ-MOG95-D is defined by the disappearance of the *Pinus sylvestris* assemblage but dry mire conditions persist until the beginning of LMZ-MOG95-E. In this zone lawn species including *Rhynchospora alba* and *Erica tetralix* become much more frequent, indicating an increase in surface wetness. It is also noticeable that *Cenococcum* spp. declines at this point. Again the *Rhynchospora alba* phase is closely followed by the arrival of *Sphagnum imbricatum* at 300 cm depth. (LMZ-MOG95-F). Table 6.7 gives a brief resume of the stratigraphy of core MOG95.

Table 6.7 Summary of the stratigraphy of core MOG95.

Mongan Bog (MOG95)				
Wetland type	Depth (cm)	Zone LMZ-MOG95	Date range (cal. BP)	Lifespan (years)
<i>S. imbricatum</i> bog	-304	F	-2630	N/A
<i>Rhynchospora/Eriophorum</i> bog	304-400	E	2630-3855	1225
<i>Eriophorum</i> bog	400-462	D	3855-4625	770
<i>Pinus/Eriophorum</i> bog	462-506	C	4625-5445	820
<i>Cladium/Phragmites</i> fen	506-550	Bb	5445-	N/A
<i>Phragmites/Cladium</i> reedswamp	550-782	Ba	No data	N/A
<i>Myriophyllum/Chara</i> calcareous lake	782-805	A	No data	N/A

6.3.8 Summary of the macrofossil stratigraphy of Abbeyknockmoy Bog (AKM95).

Refer to Figure 6.15 (The location of core AKM95 is given in Figure 4.8).

The basal macrofossil assemblage at Abbeyknockmoy Bog is derived from a lake marl and includes a range of mollusc species and the rootlets of *Cladium mariscus* and *Phragmites australis*. A reedswamp community typical of high calcium concentrations is recorded from zone LMZ-AKM95-B. The dominant species is *Cladium mariscus*. Other taxa present include *Chara* oospores, *Phragmites australis*, *Mentha aquatica* and *Menyanthes trifoliata*. Zone LMZ-AKM95-C represents a fen phase in which *Carex* spp. is the most abundant macrofossil component having displaced *Cladium mariscus*. Analysis of the *Carex* achenes present suggests that the main species was *Carex lepidocarpa* which occurs predominantly in peaty habitats where the concentration of calcium is greater than 20 ppm and the pH is 5 - 7.5 (Jermy *et al.* 1982). Again it may be possible for the species to persist even when surface conditions have changed beyond these limits because roots can draw Calcium from deeper levels. However, in zone LMZ-AKM95-D, *C. lepidocarpa* is replaced by other undifferentiated *Carex* species, and *Phragmites australis* registers a rise to dominance. The macrofossils of *Potentilla erecta*, *Rhynchospora alba* and *Sphagnum* sect. *Acutifolia* are also registered for the first time, indicating acidification of the fen. In contrast to all of the other developmental pathways studied in this project the first oligotrophic community is dominated by wet mire species including *Rhynchospora alba* and *Eriophorum angustifolium* (LMZ-AKM95-E). The transition is also notable for the absence of *Cenococcum* spp. and *Calluna vulgaris*. The latter species only appears in the assemblage towards the top of LMZ-AKM95-E. Zone LMZ-AKM95-F is characterized by

an abundance of *Eriophorum vaginatum* and *Calluna vulgaris*, however, the macrofossils of wetter lawn species continue to be recorded throughout the zone. Sub-zone Fb is differentiated by the appearance of the leaf epidermal remains of *Phragmites australis*, possibly indicating a flooding episode. The roots of *P. australis* are visible penetrating into LMZ-AKM95-Fa. The response of *Sphagnum* is lagged, occurring in zone LMZ-AKM95-G when *S. cuspidatum* and *S. subnitens* briefly colonize the area. The flooding levels also mark the first continuous presence of *Rhynchospora*. In zone LMZ-AKM95-I *Sphagnum imbricatum* again replaces the *Rhynchospora alba*/*Erica tetralix* lawn community, rising to complete dominance. Table 6.8 gives a brief summary of the stratigraphy.

Table 6.8 Summary of the stratigraphy of core AKM95.

Abbeyknockmoy Bog (AKM95)				
Wetland type	Depth (cm)	Zone LMZ-AKM95	Date range (cal. BP)	Lifespan (years)
<i>S. imbricatum</i> bog	-260	I	-4760	N/A
<i>Rhynchospora</i> / <i>Eriophorum</i> bog	260-350	H	4760-6555	1795
<i>Eriophorum</i> / <i>R. alba</i> / <i>S. cuspidatum</i> bog	350-375	G	6555-6770	215
<i>Phragmites</i> / <i>Eriophorum</i> bog	375-388	Fb	6770-6940	170
<i>Eriophorum</i> / <i>Erica tetralix</i> / <i>Calluna</i> bog	388-465	Fa	6940-7920	980
<i>Rhynchospora</i> / <i>Phragmites</i> bog	465-480	E	7920-8170	250
<i>Phragmites</i> / <i>Rhynchospora</i> bog	480-492	D	8170-	N/A
<i>Carex</i> / <i>Phragmites</i> fen	492-530	C	No data	N/A
<i>Cladium</i> / <i>Phragmites</i> reedswamp	530-592	B	No data	N/A
Calcareous lake	592-	A	No data	N/A

6.4 Chronology.

6.4.1 Radiocarbon dates.

The sampling strategy for radiocarbon dating the FBT generally follows the format used for Solway Moss (Section 5.10.2) with one sample placed either side of the transition and one at the main switch from sedge mire to *Sphagnum* mire. Sufficient dates were obtained for further levels to be dated at some sites. For example, at Bolton Fell Moss the project was able to take advantage of 9 dates sampled from BFML for another research project (Barber unpublished results). The resulting chronology has also been transferred to Walton Moss core WLM11 using pollen correlation (see Section 6.4.2) This has enabled the dates

allocated for Walton Moss to be placed in a marginal core, to draw comparisons between the mire pathway at a paludified site, situated on sloping ground and the dry *Eriophorum vaginatum*-dominated mire overlying the FBT. (This aspect of the study will be discussed in Section 6.7. At Borth two extra dates were placed in the fen peats to study the rate of accumulation between the carr woodland and the transition to *Pinus sylvestris* bog. The age/ depth curves for each site are presented in Figures 6.16 to 6.22.

Calibrated radiocarbon dates have been calculated in the manner described in Chapter 5 (Section 5.10.2). The calibrated dates quoted in the text, figures and tables represent the mid-point of the 2σ range for the full age probability distribution derived from the calibration curve (see Dumayne *et al.* 1995). All radiocarbon dates are presented as 'cal. BP' (calibrated Before Present).

Table 6.9 Radiocarbon dates awarded for the FBT project.

Sample No.	Core site	Depth (cm)	Date \pm error (BP)	Cal. mid-point of date (BP)	2σ confidence limit (BP)
SRR-4937	BFML	500-508	4575 \pm 45	5250	5445-5053
SRR-4938	BFML	560-568	5860 \pm 45	6705	6845-6562
SRR-4939	BFML	620-628	6335 \pm 50	7285	7402-7169
SRR-4940	BFML	680-688	7005 \pm 50	7810	7639-7679
SRR-4941	BFML	740-748	7660 \pm 45	8460	8549-8369
SRR-4942	BFML	800-808	8470 \pm 50	9445	9510-9376
SRR-4943	BFML	860-868	8840 \pm 45	9810	9966-9653
SRR-4944	BFML	920-928	9165 \pm 50	10145	10289-9998
SRR-4945	BFML	970-978	9305 \pm 45	10215	10380-10048
SRR-5638	WLM15	236-244	2235 \pm 45	2240	2340-2140
SRR-5639	WLM15	452-460	4555 \pm 45	5185	5320-5045
SRR-5640	WLM15	476-484	4910 \pm 45	5650	5730-5585
SRR-5641	WLM15	516-524	6645 \pm 45	7465	7540-7400
SRR-5725	GLM95	660-668	6790 \pm 45	7595	7655-7530
SRR-5726	GLM95	832-840	8740 \pm 45	9705	9865-9540
SRR-5727	GLM95	876-884	9010 \pm 45	9975	10040-9910
SRR-5728	GLM95	896-904	9535 \pm 45	10655	10895-10410
SRR-5642	TSE94	338-346	4035 \pm 45	4605	4805-4410
SRR-5643	TSE94	536-544	6480 \pm 45	7320	7400-7240
SRR-5644	TSE94	562-570	6775 \pm 50	7565	7650-7480
SRR-5633	BTH94	280-288	3080 \pm 45	3270	3380-3155
SRR-5634	BTH94	548-556	5355 \pm 50	6135	6280-5990
SRR-5635	BTH94	592-600	5460 \pm 45	6255	6395-6110
SRR-5636	BTH94	652-660	5660 \pm 45	6430	6550-6315
SRR-5637	BTH94	690-698	6155 \pm 45	7035	7165-6900
SRR-5732	AKM95	247-252	4010 \pm 45	4575	4795-4350
SRR-5733	AKM95	354-362	5750 \pm 40	6555	6665-6445
SRR-5734	AKM95	481-489	7420 \pm 45	8170	8320-8020
SRR-5729	MOG95	300-308	2630 \pm 45	2700	2850-2545
SRR-5730	MOG95	460-468	4085 \pm 45	4625	4815-4430
SRR-5731	MOG95	508-516	4705 \pm 45	5445	5575-5315

6.4.2 Pollen correlation.

At Walton Moss radiocarbon dates have been targeted on the diagram prepared from the blanket type peat occurring on the south side of the moss, (see Section 6.7). Therefore, the main macrofossil diagram taken from the deepest part of the basin (WLM11) has been dated using pollen correlation to transfer radiocarbon dates from core BFML at Bolton Fell Moss. The two pollen diagrams prepared for pollen correlation are based on sums of 150 arboreal pollen grains. The diagrams appear in Figures 6.23 and 6.24. Tables 6.10 and 6.11 show the pollen zonation and the interpolated dates for the upper boundary of each zone.

Table 6.10 Pollen correlation table for Bolton Fell Moss core BFML.

Local pollen zone	Depth (cm)	Main species	Godwin zone	Interpolated date, upper boundary
LPZ-BFML-E	800-820	<i>Betula / Ulmus / Quercus / Corylus</i>	Zone VI	----
LPZ-BFML-D	820-882	<i>Betula / Ulmus / Pinus / Corylus</i>	Zone VI	9545 cal. BP
LPZ-BFML-C	882-907	<i>Betula / Pinus / Corylus</i>	zone V	9915 cal. BP
LPZ-BFML-B	907-972	<i>Betula / Pinus / Salix</i>	Zone IV	10060 cal. BP
LPZ-BFML-A	972-980	<i>Betula / Pinus / Salix</i>	Zone IV	10215 cal. BP*

Table 6.11 Pollen correlation table for Walton Moss core WLM11.

Local pollen zone	Depth (cm)	Main species	Godwin zone	Interpolated date, upper boundary
LPZ-WLM11-E	800-832	<i>Betula / Ulmus / Quercus / Corylus</i>	Zone VI	- - ----
LPZ-WLM11-D	832-885	<i>Betula / Ulmus / Pinus / Corylus</i>	Zone VI	9545 cal. BP
LPZ-WLM11-C	885-910	<i>Betula / Pinus / Corylus / Salix</i>	Zone V	9915 cal. BP
LPZ-WLM11-B	910-962	<i>Betula / Pinus / Salix</i>	Zone IV	10060 cal. BP
LPZ-WLM11-A	962-985	<i>Betula / Pinus / Salix</i>	Zone IV	10215 cal. BP*

* actual radiocarbon date.

6.5 Detrended correspondence analysis.

6.5.1 DCA of core BFML from Bolton Fell Moss.

DCA of the whole data set from Bolton Fell Moss reveals a sharp division between fen and bog samples accounting for 93% of the variation along axis one (Figures 6.25 and 6.26). However, the biplot of axis 1 vs axis 2 scores (Figure 6.25) also shows the grouping of acid mire sample and species scores in the middle of axis 2, whilst the fen equivalents are widely dispersed. This indicates that axis 2 represents a gradient restricted to minerotrophic levels. The fen gradient is clearly indicated in the plot of axis 2 sample scores vs depth, for the whole data set (Figure 6.27).

A second DCA was performed to investigate the structure of the fen data without the influence of the ombrotrophic bog samples. Figure 6.28 shows the biplot of axis 1 vs axis 2 scores for the fen levels. The first axis accounts for 66% of the variation and clearly describes a gradient from reedswamp and fen carr species such as *Phragmites australis* and *Equisetum* spp., through swamp carr to poor fen and raised bog taxa, such as *Drepanocladus* and *Eriophorum vaginatum*, respectively. The lower sections of the gradient relate to the replacement of *Phragmites australis* by *Carex paniculata*. Both species thrive in base-rich conditions, and high water-levels. However, *Carex paniculata* may become more competitive under conditions of annually fluctuating water-levels. The second part of the gradient clearly records the acidification of the mire. In contrast to the equivalent DCA plots for mires such as Solway Moss and Glasson Moss (Figures 5.15, 5.16 and 6.35, 6.36) the axis 1 scores for the fen samples show that the development of the site towards poor fen was gradual at first, with sample scores declining from 3 to 1.7 S.D. over a depth of 40 cm. The final switch to oligotrophic conditions at 856 cm depth appears to be rather less abrupt than is suggested by Figure 6.26 (axis 1 scores for the whole data set), once the influence of the oligotrophic mire samples has been removed from the DCA calculation. Nevertheless, the samples straddling the switch from poor fen to bog (848-856 cm) are separated by almost 2 S.D. and only 8 cm of peat accumulation, suggesting that the final species turnover that created the *Eriophorum vaginatum*/*calluna vulgaris*-dominated mire was significantly more rapid than the preceding species replacements occurring in the fen and poor fen stages.

Examination of the raised bog species alone, reveals further gradients. A biplot of axis 1 vs axis 2 scores for the upper 54 samples suggest a water-level gradient on the first axis representing 53% of the variation (6.30). A plot of axis 1 score vs depth (Figure 6.31) shows the apparent changes in raised bog surface wetness as reconstructed by the DCA routine. From 820 to 668. cm depth the trace is continually at the drier end of the gradient with regular relatively minor fluctuations of less than one S.D. Up to 540 cm the scores continue to plot at the dry end of the gradient although the magnitude of short-lived fluctuations increases. Finally at 540 cm the plot records a major wet shift.

To check the validity of the surface wetness curve as depicted by DCA, a weighted average ordination (WAO) was calculated for the ombrotrophic samples using the weights specified in Table 5.10. Figure 6.32 shows that the WAO for Bolton Fell Moss broadly agrees with the DCA reconstruction. Dry conditions are recorded between 820 and 548 cm with minor fluctuations which increase in amplitude above 668 cm depth. The major wet shift at 540 cm is also in agreement with the two reconstructions. However, it is interesting to note that not all of the peaks and troughs match in the dry hummock-like bog phase. The DCA reconstruction appears to record some fluctuations ignored by WAO. A possible explanation for this may be that the DCA has included a lesser gradient with the dominant water-level one. Examination of the biplot of axis 1 and 2 scores (Figure 6.30) shows that the hummock taxa *Sphagnum* sect., *Acutifolia* and *Calluna vulgaris* are widely separated from *Eriophorum vaginatum* along the gradient. Therefore, some of the fluctuations in the dry phase may relate to interactions in the hummock communities. The DCA fails to detach the hummock level fluctuations from the main water-level gradient because both *Calluna vulgaris* and *Sphagnum* sect. *Acutifolia* appear in all the macrofossil assemblages. This illustrates that care must be exercised when inferring surface wetness changes from DCA plots.

6.5.2 DCA of core WLM11 from Walton Moss.

Macrofossils from WLM11 were quantified using the five point scale of abundance. This type of categorical data is not suitable for DCA manipulation. Therefore the data set was converted into presence/absence format for statistical analysis. The biplot of axis 1 and 2 scores for whole data set (Figure 6.33) shows the clear fen/oligotrophic bog gradient on axis 1 accounting for 37% of the variation. *Sphagnum palustre* and wood fragments occupy the middle part of the axis, which depicts the development of an intermediate *Betula* carr phase. The plot of axis 1 scores versus depth (Figure 6.34) shows a relatively gradual FBT occurring over c. 30 cm depth (10 sample levels). Although both the fen and the bog levels appear to contain slight trends, separate analyses of these levels failed to recover meaningful gradients.

6.5.3 DCA of core GLM95 from Glasson Moss.

DCA of the whole data set from core GLM95 recovers a strong gradient on axis 1 accounting for 88% of the variation. Analysis of the biplot of axis 1 versus axis 2 scores (Figure 6.35) shows that taxa align along the axis in the order, fen, fen carr, dry acid mire and finally wet acid mire. Therefore, the gradient may be considered to be a composite including the FBT and the hummock/hollow gradient of the raised mire stage. The plot of axis 1 scores versus depth (Figure 6.36) clearly shows a sharp fen/bog transition on the right hand side of the diagram, at 890 cm depth, with just one truly intermediate level. This sample might represent a displacement peat, in which the macrofossil remains from two distinct communities may be mixed at the boundary, due to the penetration of rootlets from above or due to the mixing of litter from two assemblages under conditions of rapid ecological change (Grosse-Brauckmann 1986 and Section 3.3.1) In contrast to previous analyses the axis shows significant structure within the acid mire samples which may

be interpreted as representing mire surface wetness. Figure 6.35 also describes a strong gradient on axis 2 (Eigen value 0.44) which is restricted entirely to the ombrotrophic samples. To further investigate these acid mire gradients, the DCA was recalculated without the fen samples. The results are shown in Figures 6.37 and 6.38. The classic hummock/hollow gradient is again located on axis 1 (Eigen value 0.78). However, without the fen levels the amplitude of fluctuations is described more accurately. Figure 6.38 shows two wet shifts at 750 and 700 cm depth prior to the main wet shift at 670 to 650 cm. Axis 2 records the displacement of *E. vaginatum* by *Sphagnum palustre*. This clearly represents a phase of higher water-tables and slight eutrophication, possibly caused by flowing surface water or reconnection to the groundwater supply. Figure 6.39 and the macrofossil diagram Figure 6.11 show that this gradient refers to two phases of *Sphagnum palustre* invasion of the *Eriophorum* mire between 800 and 850 cm depth. Taken together, axis 1 and 2 from the ombrotrophic levels may represent the full record of raised mire surface wetness. A weighted averages ordination was calculated to check the accuracy of the DCA. Figure 6.40 indicates that there is close agreement between the two types of reconstruction.

6.5.4 DCA of core TSE94 from Tregaron Bog.

The DCA gradient represented by axis 1, for core TSE94, shows a composite gradient containing the FTB and changes in the acid mire community. Figure 6.41 registers a 2.5 SD separation between the main grouping of fen species on the right hand side of the biplot and the acid species on the left, indicating that there is little overlap between the two communities. *Sphagnum palustre* is the only species to occur in an intermediate position bridging the transition. The plot of axis 1 scores versus depth (Figure 6.42) again shows a sharp transition at 560 cm depth. The changes identified in the acid mire samples by the DCA relate to the replacement of sedge dominated mire by *Sphagnum imbricatum*. As a result of the total dominance of *Sphagnum imbricatum* the analysis does not identify the normal hummock/hollow gradient. Therefore, species such as *Rhynchospora alba*, indicative of lawn habitats, are grouped close to hummock species such as *Eriophorum vaginatum* and *Calluna vulgaris* with respect to axis 1 (Figure 6.43 and 6.44). Recalculation of the DCA without the fen levels has little effect upon the results for the acid mire stage. However, the second axis clearly represents the change from dry *Eriophorum vaginatum* bog to wetter *Rhynchospora* bog (Figure 6.43). The WAO for the ombrotrophic data set demonstrates that the hummock/hollow gradient is not perfectly described by the DCA due to the failure of the technique to separate *Rhynchospora* from *Eriophorum vaginatum*. Figure 6.44b shows that the mire surface wetness increased significantly prior to the arrival of *S. imbricatum*, contrary to the interpretation resulting from the DCA routine.

6.5.5 DCA of core BTH94 from Borth Bog.

Over 90% (eigen value 0.93) of the variation in the total data set is extracted as a single gradient on axis 1 of the DCA (complete data set, Figure 6.45). Fen car elements cluster at the far right hand side of the diagram. The carr woodland community is replaced by acid *Pinus sylvestris* bog in the middle of the axis, followed by dry open raised bog and finally wet raised bog. This zonation is also clear in the macrofossil

diagram. Curiously the initial step in the succession, namely from *Phragmites australis* reedswamp to fen carr, has been separated by the DCA and occurs on axis two. This occurs because there is little overlap in the species of these adjacent stages, whereas there is a higher degree of species overlap between most subsequent mire stages. For example *Phragmites australis* persists from the *Betula* spp. fen carr into the *Pinus sylvestris* bog stage, whilst *Eriophorum vaginatum* first colonizes late in the *Betula* spp. carr and rises to dominance in the *P. sylvestris* bog. The plot of axis 1 scores versus depth (Figure 6.46) reveals a more gradual, stepped transition than recorded at previous sites, occurring over a depth of approximately 50 to 60 cm. However, the change from reedswamp to carr appears to have been sharper. Similarly, the final switch to ombrotrophic mire at 590 cm is relatively abrupt. Separate DCA calculations performed on the ombrotrophic samples show little deviation from the original analysis. The gradient in the ombrotrophic mire may also be considered to be composite. The levels from 590 to 395 cm represent the change from treed dry bog to open dry *E. vaginatum* / *S.s. Acutifolia* mire. Above 395 cm depth the gradient records the increase in mire surface wetness and the colonization of lawn species including *Rhynchospora alba* and the lax form of *Sphagnum imbricatum*. Figure 6.47, the plot of axis 1 scores for the ombrotrophic samples versus depth, describes these changes.

6.5.6 DCA of core MOG95 from Mongan Bog.

Prior to statistical analysis, the 5 point scale of abundance data from Mongan and Abbeyknockmoy Bogs were converted into presence/absence format.

In core MOG95 the first axis of variation (eigen value 0.58) illustrates a clear fen/bog gradient (Figure 6.48). The plot of axis 1 scores versus depth (Figure 6.49) reveals a very sharp transition at 510 cm depth after a long reedswamp phase. The acid samples display little variation with respect to axis 1, varying by no more than 0.5 SD. However, analysis of the DCA biplot for the whole data set (Figure 6.48), suggests that raised mire species align along a water-level gradient on the second axis. After removing the fen species the DCA calculation shows a clear wet bog / dry bog gradient on axis 1 (Figure 6.50) with *P. sylvestris* and *Pleurozium schreberei* at one end of the gradient and *Rhynchospora alba* and *Erica tetralix* at the other end. Without the ability to take account of the abundance of taxa the DCA places species that occur throughout the core, such as *Eriophorum vaginatum* and *S. imbricatum*, in the centre of the biplot. Figure 6.51 shows the tentative reconstruction of mire surface wetness based on DCA axis 1 for the ombrotrophic samples. This record was not checked against the WAO technique because the latter is not compatible with presence/absence data. Two main wet shifts are apparent, centred on 400 and 320 cm depth. The upper of these two represents the dominance of *Rhynchospora alba* and *Sphagnum imbricatum*.

6.5.7 DCA of core AKM95 from Abbeyknockmoy Bog.

The DCA (complete data set) for the most oceanic mire in the study group, depicts a much more gradual transition from poor fen to wet raised bog. At least ten intermediate sample levels, spanning a depth of 44 cm, straddle the switch to ombrotrophic conditions (Figure 6.52). The biplot of axis 1 versus axis 2 scores

for the complete data set, shows the clear fen/bog gradient (Figure 6.53, eigen value 0.49). However, in sharp contrast to many of the sites examined, the first ombrotrophic community is composed of species indicative of wetter acid mires such as *Rhynchospora alba*, *Eriophorum angustifolium* and *Sphagnum tenellum*. These species plot in the middle of the axis separating the fen stage from species, such as *Eriophorum vaginatum* and *Calluna vulgaris*, which are usually amongst the first colonists of the ombrotrophic habitat. *Sphagnum* sect. *Acutifolia* also occupies the central part of the gradient in common with many other sites, possibly because it is found throughout the macrofossil record. DCA axis 2 from the full data set displays only a weak gradient which is difficult to interpret. However, when the ombrotrophic samples are analysed in isolation the latent structure is easier to interpret. Figure 6.54, the biplot of axis 1 versus axis 2 scores for the ombrotrophic samples, depicts a relatively long composite gradient. The right hand side of the diagram represents a lawn to low hummock gradient, whilst the left hand part of the biplot shows the gradient from Ericaceae and sedge dominated communities to *Sphagnum imbricatum* domination. The plot of axis 1 versus depth for the ombrotrophic samples clearly shows the wet mire conditions at the time of the FBT (468 cm depth) and a major wet shift at 380 to 350 cm depth (Figure 6.55).

6.6. Inter-site comparisons.

6.6.1 The Cumbrian Mosses.

The four Cumbrian mosses studied for this project have very similar physical settings. Each one is located in a former kettlehole or similar depression in the Bewcastle drift that drapes the landscape of the Cumbrian lowlands. The greatest separation of the four sites is no more than 24 km. Consequently, regional climatic indicators such as effective precipitation, the number of rain days and the date of ice retreat from the area will have differed little between the mosses. The altitudinal range of the group is also no more than one hundred metres.

Despite having similar physical circumstances, the macrofossil records for each site (Figures 5.4, 6.8, 6.9 and 6.11) show that the mires have followed varied pathways during their minerotrophic phases of development. At Bolton Fell Moss peat accumulation commenced under a *Salix* spp./*Phragmites australis* community which subsequently developed into a *Betula* spp. swamp carr, whilst at Walton Moss, *Phragmites australis*/*Equisetum* reedswamp and *Carex vesicaria* fen preceded a *Betula pendula* swamp carr. The pioneer peat forming community at Glasson Moss was dominated by *Equisetum fluviatile*. This was superseded by a *Phragmites australis*/*Carex* fen, a *Carex*/*Menyanthes* fen and finally a *Menyanthes*/*Scheuchzeria* poor fen, prior to ombrotrophic mire formation. At Solway Moss pre-Holocene reedswamp and open water wetland phases were followed by just one Preboreal *Phragmites australis*/*Carex*/*Salix* community before the FBT.

Tables 6.12 and 6.13 provide a comparison of the lifespans of fen stages at Bolton Fell Moss and Walton Moss. Although the pathways of development have differed between the two sites, comparable communities do appear to have similar lifespans as suggested by Walker (1970). For example *Betula* spp. swamp carr thrived for approximately 300 years at both sites whilst open *Sphagnum palustre* poor fen existed for 120 years at Bolton Fell Moss and for 110 years at Walton Moss. A similar community was recorded at Tregaron Bog with a comparable lifespan of 100 years.

Table 6.12 The lifespan of minerotrophic wetland stages at Bolton Fell Moss.

Bolton Fell Moss				
Wetland type	Depth (cm)	Unit thickness (cm)	Date range (cal. BP)	Lifespan (years)
<i>S. palustre</i> poor fen	826-846	20	9640-9760	120
<i>D. fluitans</i> Poor fen	846-854	8	9760-9810	50
<i>Carex</i> fen	854-885	31	9810-9930	120
<i>Betula</i> swamp carr	885-960	75	9930-10215	290
<i>Salix</i> carr	960-984	24	10215-10250	35
Total				615

All interpolated dates are rounded to the nearest 5 years.

Table 6.13 The lifespan of minerotrophic wetland stages at Walton Moss.

Walton Moss (Core WLM11)				
Wetland type	Depth (cm)	Unit thickness (cm)	Date range (cal. BP)	Lifespan (years)
<i>S. palustre</i> poor fen	869-885	16	9840-9950	110
<i>Betula</i> swamp carr	885-975	90	9950-10200	250
<i>Phragmites</i> fen	975-1000	25	10200-10265	65
Total				425

At Solway Moss and Glasson Moss the only levels in the fen peat to have been dated are the upper contacts with the overlying ombrotrophic peats. In the case of Solway Moss, the fen deposit was too thin to allow two bulk peat samples to be extracted from the 10 cm diameter Russian core. At Glasson Moss radiocarbon dating priority was given to a flooding level appearing just after the FBT. To provide an estimate of the age of the basal peat and to allow an approximate chronology for the fen communities to be constructed, pollen samples were examined from the basal peat beds at the two sites (see Figure 5.9 and Table 6.14).

In Chapter 5 the mineral inwash layer at Solway Moss was interpreted as belonging to the Loch Lomond Stadial. The upper contact of the inorganic unit with the Holocene peat is gradational suggesting

continuity of sedimentation. The pollen spectra also register a 30 cm thick basal zone (LPZ-SOLA295-1) containing an abundance of *Salix* and *Juniperus* grains. Given that the top of this zone is radiocarbon dated to 10430 cal. B.P. (SRR-5647) it is reasonable to assume that Godwin zone IV is preserved in its entirety and that the base of the zone dates to approximately 11000 cal. B.P.

At Glasson Moss the upper surface of the fen peat (at 900 cm) is radiocarbon dated to 10655 cal. B.P. (SRR 5728). Forty five centimetres of *Phragmites/Carex* peat underlie this level. Check pollen analyses, presented in Table 6.14, demonstrate that the *Phragmites* reedswamp (LMZ-GLM95-B, -Ca and -Cb) again correlates to Godwin zone IV. In parallel with Solway Moss, the lower contact of the peat with the underlying laminated pre-Holocene lake clays, is gradational. Therefore, a basal date of c. 11000 cal. B.P. is also suggested for Glasson Moss.

Table 6.14: Pollen spectra from Godwin Zone IV at Glasson Moss (900-946 cm) represented as a percentage of arboreal pollen

Glasson	Depth (cms)						
Species	900	908	916	924	932	940	945
<i>Betula</i>	96	97.2	98.9	88.8	92.3	86	88
<i>Pinus</i>	4	1.4	1.1	5.5	7.8	13.6	12
<i>Corylus</i>	11.7	14.4	3.3	4	—	—	—
<i>Salix</i>	11.2	8.4	13.3	27.8	38.5	209	223
<i>Juniperus</i>	—	1	4	38.9	40	54	36

Pollen sum: 150 arboreal pollen grains

The total lifespans of the fully minerotrophic wetland stages at Solway Moss and Glasson Moss are 570 and 600 years respectively, assuming that the inferred date for peat inception at each site is accurate. The comparable figure for Bolton Fell Moss is 615 years and for Walton Moss, 430 years. Therefore, the reedswamp and fen phases at all four mosses were short-lived, accounting for between 3 and 6 % of the total duration of Holocene peat accumulation.

A comparison of the transitional communities immediately preceding the FBT (Table 6.15) shows that they also have brief lifespans ranging between 90 and 175 years. This demonstrates that the final stage of acidification was relatively rapid in the kettlehole basins. However, Solway Moss and Glasson Moss appear to have developed along distinctly different pathways immediately prior to raised mire formation, compared to Bolton Fell Moss and Walton Moss. At the former two sites, the radiocarbon dates indicate that there was an hiatus in peat formation during or just before the FBT on both mosses (see Figures 5.14 and 6.18). This interpretation is supported by the DCA plots for the two sites (Figures 5.16 and 6.36). Axis 1 scores versus depth, for the complete data sets show that fen samples are abruptly separated from raised

bog samples by up to 3 S.D. units. In both cases just one or two sample scores lie in intermediate positions between the fen and raised bog levels, possibly representing displacement peats. Analysis of fen samples alone, for Solway Moss and Glasson Moss, failed to recover significant gradients in the minerotrophic peat leading up to the transitions.

By contrast the FBTs at Bolton Fell Moss and Walton Moss show no evidence for coincident breaks in peat accumulation. Both sites pass through several transitional poor fen types before developing into raised mires. (Figures 6.8, 6.9 and 6.16). The DCA plots for Bolton Fell Moss and Walton Moss both indicate that significant gradients exist in the fen and poor fen samples leading upto the FBT (Figures 6.27, 6.29 and 6.34).

Table 6.15 Comparison of the transitional communities immediately preceding raised bog formation in the Cumbrian mosses.

Cumbria				
Mire	Wetland type	Depth (cm)	Date range (cal. BP)	Lifespan (years)
Bolton Fell Moss	<i>S. palustre</i> poor fen	830-846	9605-9750	145
Walton Moss	<i>S. palustre</i> poor fen	869-885	9840-9930	90
Solway Moss	No poor fen phase	-----	-----	-----
Glasson Moss	<i>Scheuchzeria</i> poor fen	891-895	9975-10150	175

Although the four Cumbrian mosses have followed individual pathways of development, composed of differing numbers of wetland stages, the dates for raised mire inception at each site fall into a relatively narrow time interval of 370 years (Table 6.16). The earliest FBT is recorded at Glasson Moss, dating to 9975 cal. B.P. (SRR-5727), with the youngest at Bolton Fell Moss occurring at 9605 cal. B.P. (Interpolation from SRR-4942 and SRR-4943, Table 6.9). Analysis of the 2σ confidence intervals accompanying each of the calibrated radiocarbon age estimates, shows that adjacent dates are not significantly different from each other, whilst the minimum significant age separation between Bolton Fell Moss and Glasson Moss is reduced to just 240 years. In the context of Holocene peatland development the four raised mire inception dates may be regarded as virtually synchronous.

Table 6.16 Comparison of the wetland communities at the time of raised mire inception in the Cumbrian mosses.

Cumbria.				
Mire	Main species of the first ombrotrophic mire	Depth (cm)	Raised mire inception (cal. BP)	2 σ confidence interval
Bolton Fell Moss	<i>Eriophorum</i> / <i>Calluna</i>	830	9605	9535-9670
Solway Moss	<i>Sphagnum</i> sect. <i>Acutifolia</i>	342*	9850	-----
Walton Moss	<i>Eriophorum</i> / <i>Calluna</i>	870	9845	9685-10000
Glasson Moss	<i>Eriophorum</i> / <i>Empetrum nigrum</i>	887	9975	9910-10040

(* Depth from cut peat surface).

In common with Solway Moss, the oligotrophic mire vegetation that first colonized Bolton Fell Moss, Walton Moss and Glasson Moss, is indicative of low water-tables and relatively dry surface conditions. At Bolton Fell Moss the pioneer community (LMZ-BFML-F) is dominated by *Eriophorum vaginatum* and *Calluna vulgaris*. Very few *Sphagnum* mosses are recorded and wet mire species are completely absent. The fungal sclerotia of *Cenococcum* spp. are also numerous in the zone, indicating the existence of well aerated surface peats. The situation at Walton Moss is virtually identical although the hummock taxon *Polytrichum alpestre*-type is better represented (zone LMZ-WLM11-E). At Glasson Moss the main Ericaceae species accompanying *Eriophorum vaginatum* in the equivalent zone, is *Empetrum nigrum*. This species is also indicative of relatively dry mire.

If the four fledging oligotrophic mires were truly ombrotrophic and recording a proxy climatic signal of effective precipitation in a similar manner to modern, undisturbed raised mires, then the evidence presented above suggests that the Cumbrian FBTs occurred during a period of reduced effective precipitation. Each site displays a record of rapid decoupling from the groundwater-table. Poor fen communities last for no more than 90-120 years, whilst the form of the transitions appears to be abrupt in two cases (Solway Moss and Glasson Moss). Furthermore the inception of the dry 'heath-like' mires is broadly contemporaneous despite the fact that the underlying fen deposits accumulated at different rates (Figure 6.16 to 6.18) and through site specific pathways.

To further examine the status of the dry pioneer oligotrophic mires, the main macrofossil diagrams (Figures 5.4, 6.8, 6.9 and 6.11) were extended to cover the complete lifespan of these wetland phases and their transitions with superceding mire types. A comparison of these analyses is provided in Table 6.17.

Figure 6.17 Comparison of the oligotrophic mire stratigraphy in the Cumbrian mires.

Transect of sites			
Mire	Lifespan of dry mire (years)	Arrival of first lawn or pool community (Years cal. BP)	Rise to dominance of lawn and pool <i>Sphagnum</i> species (Years cal. BP)
Bolton Fell Moss	2100	7510 (<i>S. subnitens</i>)	7510 (<i>S. subnitens</i>)
Walton Moss	2415	7430 (<i>S. cuspidatum</i>)	7430 (<i>S. cuspidatum</i>)
Solway Moss	2000	7880 (<i>Rhynchospora alba</i>)	7850 (<i>S. imbricatum</i>)
Glasson Moss	270	9705 (<i>S. palustre</i>) 8700 (<i>Rhynchospora alba</i>)	7595 (<i>S. cuspidatum</i>)

With the exception of Glasson Moss, dry sedge mire thrived on the Cumbrian mosses for over two millennia resulting in the accumulation of between 1.50 and 2.40 metres of highly humified hummock peat. At Glasson Moss the oligotrophic pathway of development was interrupted between 800 and 845 cm depth (zone LMZ-GLM95-F, 9705-9265 cal. B.P.) when *Sphagnum palustre* re-invaded the moss, indicating a significant reversal in the mire succession. The brief dominance of *S. palustre* may be a response to rising groundwater-levels caused by rapid early Holocene sea level rise. This aspect of the mire stratigraphy will be discussed further in Chapter 7. However, it is interesting to note that the second transition to oligotrophic conditions at Glasson Moss, dating to 9265 cal. B.P. (LMZ-GLM95-G) also results in the formation of a dry *Eriophorum vaginatum*/*Calluna vulgaris* dominated mire. Glasson Moss displays another difference in its pathway of development compared to the other three mosses. Between 750 and 695 cm depth (LMZ-GLM95-H) *Rhynchospora alba* colonizes the mire surface indicating an increase in surface wetness lasting from 8700 B.P. to 7980 cal B.P. At this time the other three Cumbrian mires register consistently dry conditions. Again this wet phase may be a function of base level change or local mire conditions.

The termination of the sedge mire phase is very distinctive in all four mosses, since it is marked by a dramatic increase in lawn and pool *Sphagnum* mosses. At Bolton Fell Moss the lawn species *Sphagnum subnitens* displaces *Eriophorum vaginatum* at 7510 cal. B.P., prior to the first appearance of *Sphagnum imbricatum* at 5250 cal. B.P. (SRR-4937). Pool peats composed of *Sphagnum cuspidatum* replace the *Eriophorum vaginatum*/*Calluna vulgaris* mire on Walton Moss at 7430 cal. B.P. (The date for this change was established by means of pollen correlation of the *Alnus* rise, with the radiocarbon dated core from Bolton Fell Moss.). A directly comparable stratigraphic change is recorded at Glasson Moss dating to 7595 cal. B.P. (SRR-5725), whilst at Solway Moss *Sphagnum imbricatum* rises to dominance at 7850 cal. B.P. (SRR-5645), accompanied by *Rhynchospora alba* also indicating the emplacement of lawn conditions.

The hummock/hollow gradient resulting from the replacement of *Eriophorum vaginatum*/*Calluna vulgaris* mire by low lawn and pool *Sphagnum* species, is represented in the biplots of axis 1 scores versus axis 2 scores, for the acid mire samples, from each site. (Figures 6.23, 30 to 6.37). At Bolton Fell moss, Solway Moss and Glasson Moss the hummock/hollow variation is selected by the DCA, to form the primary gradient, in the ombrotrophic samples, accounting for 50 to 78% of the total variation in the data sets. The plots of axis 1 scores against depth demonstrate that this variation is almost entirely accounted for by the arrival of the main ombrotrophic *Sphagnum* species. The DCA routine fails to recover the hummock/hollow gradient at Walton Moss due to the presence/absence data format and the fact that many of the *Sphagnum* species occur at trace levels throughout the dry bog phase.

The data presented in Chapter 5 for Solway Moss, show that the onset of *Sphagnum* domination on the mire is synchronous over a kilometre wide area of the central dome, providing strong evidence for an increase in effective precipitation dated to 7850 cal. B.P. (SRR-5645). The fact that the rise to dominance of wet, ombrotrophic *Sphagnum* species correlates to within 430 years of this date at a further three sites, provides significant support for a change towards a wetter climate at the beginning of the Atlantic period.

If the replacement of *Eriophorum vaginatum*/*Calluna vulgaris* mire by wet *Sphagnum* bog can be related to increased effective precipitation, it follows that the dry conditions prevailing on the Cumbrian mosses immediately before the wet shift were a result of lower effective precipitation. With the exception of Glasson Moss the *Eriophorum vaginatum*/*Calluna vulgaris*/*S.s. Acutifolia* mire appears to have changed very little in the preceding 1900-2400 year period since the FBT at each site. Therefore, it is possible that the dry mire conditions reflect a protracted period of low effective precipitation, beginning prior to 9975 cal. B.P. and lasting until approximately 7800 cal B.P. This is illustrated by the DCA plots for the ombrotrophic samples and the WAO reconstructions of mire surface wetness (Figure 6.39 and 6.40, respectively). Similar water-level gradients have been reconstructed at Solway Moss (Figures 5.20 and 5.21) and Bolton Fell Moss (Figures 6.31 and 6.32).

The evidence presented so far, from the oligotrophic mire stratigraphy, tends to support the interpretation that the Cumbrian FBTs occurred during a period of reduced effective precipitation. However, is it safe to assume that a newly formed oligotrophic mire of 20 to 50 cm thickness, accurately records a proxy record of effective precipitation, in the same manner as a mire that has accumulated over 2 metres of well humified acid peat? Without a well developed catotelm, a new raised mire may pass through a phase when it remains at least partially aerated under conditions of relatively high effective precipitation, due to a high rate of seepage. The validity of this argument may be tested by examining the character of the FBT in a mire that became ombrotrophic during a period of increased effective precipitation. This is explored further in Chapter 7 (Section 7.3).

6.6.2 The Irish mires.

6.6.2.1 Abbeyknockmoy Bog.

Having recovered evidence for dry FBTs at all four of the mires studied in Cumbria, Abbeyknockmoy Bog was investigated to see if wet lawn mire communities were involved in the FBT at a site located in the wettest parts of the British Isles.

Conditions at the time of the FBT (8170 cal. B.P., SRR-5734) on Abbeyknockmoy Bog differed substantially from the Cumbrian Mosses. The DCA plot of axis 1 scores (fen/bog gradient) against depth, for the whole data set from AKM95, records a much more progressive change from fen to bog. The onset of the transition occurs at 496 cm depth (LMZ-AKM95-D) and spans *c.* 40 cm, equivalent to 250 years of peat accumulation. The DCA plot of axis 1 sample scores versus depth, for the complete data set at Abbeyknockmoy Bog (Figure 6.52), clearly shows that 8 samples occur in an intermediate position between the fen and the bog levels. The form of the DCA plot contrasts sharply with the 'cliff-like' shape of the equivalent diagrams for Solway Moss core SOLA295 and Glasson Moss. (refer to Figures 5.16 and 6.36 respectively).

The contrast between the character of the FBTs at Bolton Fell Moss/Walton Moss and Abbeyknockmoy Bog is less dramatic. (see Figures 6.27 and 6.34 respectively). Nevertheless, the final switches to *Eriophorum vaginatum* / *Calluna vulgaris* dominated mire in both Bolton Fell Moss and Walton Moss are relatively abrupt, indicating the rapid displacement of poor fen species, rather than the process of gradual species replacement, inferred for Abbeyknockmoy Bog.

In marked contrast to all of the sites studied so far, the first raised mire assemblage at Abbeyknockmoy contains a number of lawn species including *Rhynchospora alba*, *Eriophorum angustifolium*, *Erica tetralix* and *Sphagnum tenellum*. This assemblage suggests that mire water-tables remained close to the growing surface throughout the acidification process. Judging from the selection of mires sampled for the present project, this appears to be a relatively rare situation at the point of the FBT.

Although the macrofossil diagram for Abbeyknockmoy registers distinctly wetter mire communities throughout the ombrotrophic phase of development, *Sphagnum* is a surprisingly small component of the assemblages, both at the FBT and in zones LMZ-AKM95-Fa, -Fb and -H. The *Rhynchospora*/*E. angustifolium*/*Phragmites australis* community presented at the transition (LMZ-AKM95-E) initially contains only a few leaves of *S.s. Acutifolia* and *S. imbricatum* in contrast to the drier Cumbrian mires where a short-lived abundance of *Sphagnum palustre* or *Sphagnum* sect. *Acutifolia* is usually recorded. At Abbeyknockmoy, *Rhynchospora alba*, in particular, appears to occupy the position of *S. palustre*, possibly performing a similar role in the acidification process. Further research would be required to establish whether the *Rhynchospora alba*, phase is widespread across the mire.

After the flooding phase (LMZ-AKM95-Fb and -G) at Abbeyknockmoy (6555 - 7000 cal. B.P.) the ombrotrophic mire development takes a course that is very similar to Mongan Bog, Solway Moss and the two Welsh mires. A long phase of *Rhynchospora alba* domination is brought to a close by the first major rise in *S. imbricatum*. A comparison of the timing of the *S. imbricatum* rise, across the large wetland basins, shows that the event is only synchronous at two sites, Abbeyknockmoy Bog and Tregaron Bog (Table 6.18). Analysis of independent proxy climate records for the Holocene, may aid the interpretation of the observed stratigraphic changes. This is undertaken in Chapter 7.

Figure 6.18 Comparison of the raised bog stratigraphy across the east/west transect.

Transect of site.		
Mire	Arrival of first lawn or pool community (Years cal. BP)	Rise to dominance of lawn and pool <i>Sphagnum</i> species (Years cal. BP)
Tregaron Bog	6495 (<i>Rhynchospora alba</i>)	4605 (<i>S. imbricatum</i>)
Borth Bog	4425 (<i>Rhynchospora alba</i>)	3270 (<i>S. imbricatum</i>)
Mongan Bog	3770 (<i>Rhynchospora alba</i>)	2630 (<i>S. imbricatum</i>)
Abbeyknockmoy Bog	8170 (<i>Rhynchospora alba</i>)	4575 (<i>S. imbricatum</i>)

6.6.2.2 Mongan Bog.

The macrofossil diagram for Mongan Bog registers the FBT at five metres depth, with a date of 5445 cal. B.P. (SRR-5729). The form of the transition is very abrupt. A fen community, composed principally of *Phragmites australis* and *Cladium mariscus*, is replaced within four centimetres of peat accumulation by a completely different community containing *Polytrichum alpestre*-type, *Pleurozium schreberei*, *Pinus sylvestris* and *Eriophorum vaginatum*. *Sphagnum palustre* is present at the FBT although it only appears in one level directly on the transition. The abrupt nature of the transition is very clearly depicted in the DCA plots for Mongan Bog (Figures 6.48 and 6.49). Figure 6.49, the plot of axis 1 scores versus depth for the whole data set, registers a drop of 2.7 S.D. over just four samples (equivalent to a depth of 12 cm). Examination of the stratigraphy diagram for Mongan Bog (Figure 6.6) shows that the divide between fen peat and humified *Eriophorum vaginatum*-dominated peat may be traced across the majority of the bog at an altitude of 56.5 to 57 metres O.D. This strongly suggests that the fen was replaced by oligotrophic communities, at much the same time, over a wide area of the basin. In this respect, the analyses from Mongan Bog demonstrate a dramatic difference in the character of the FBTs between the two Irish sites. Table 6.19 gives a comparison of the first raised mire communities at Mongan Bog and Abbeyknockmoy Bog.

Table 6.19 Comparison of the wetland communities at the time of raised mire inception in the Irish bogs.

Transect of sites				
Mire	Main species of the first ombrotrophic mire	Depth (cm)	Raised mire inception (cal. BP)	Lifespan of 'dry' mire (years)
Abbeyknockmoy	<i>Eriophorum</i> / <i>E. tetralix</i> / <i>Calluna</i> / <i>Rhynchospora</i> bog	440*	8170	-----
Mongan Bog	<i>Pinus</i> / <i>Eriophorum</i> / <i>Calluna</i>	504	5240	1675

[* From cut peat surface.]

The course of the FBT at Mongan Bog is remarkably similar to that recorded for Borth Bog. It is also much closer in character to the relatively dry transitions recorded in the Cumbrian mires, than to the FBT found at Abbeyknockmoy Bog. The comparison between Mongan Bog and the Cumbrian mires is investigated further in Chapter 7.

6.6.3 The Welsh Mires.

6.6.3.1 Tregaron Bog.

At Tregaron South-East Bog, situated on the east bank of the River Teifi, the FBT occurs at 7320 cal. B.P. (SRR-5643) in the early part of the Atlantic period. All the relevant evidence from Cumbria points to a major climatic shift towards wet conditions beginning up to 530 years prior to this date. Further evidence from Abbeyknockmoy Bog in western Ireland and a second core at Walton Moss also indicates an increase in effective precipitation dating to the early Atlantic. At Walton Moss basal peat on the paludified slopes surrounding the main mire basin has an age of 7465 cal. BP (SRR-5641). Whilst at Abbeyknockmoy Bog (Figure 6.15) a flooding phase is recorded in the ombrotrophic peat (zone LMZ-AKM95-Fb and -G) from c.7000 to 6555 cal BP (lower date, interpolation from Figure 6.22, upper date SRR-5733). Therefore, Tregaron South-East Bog was selected for study to provide an example of a mire, that became raised during an inferred period of wetter climate, and developed in close contact with a major river system.

The macrofossil diagram for Tregaron Bog (Figure 6.12) reveals a long reedswamp and swamp carr phase that resulted in the accumulation of three metres of minerotrophic peat (zones LMZ-TSE94-B, -C -D and -E). Radiocarbon dates transferred from Hibbert and Switsur (1976) by means of pollen correlation, show that infilling of the preceding glacial lake began at 11100 cal. BP with the formation of a nekron mud in open water. The subsequent reedswamp phases, dominated by *Phragmites australis*, lasted for 3500 years

(Table 6.5) ending with the invasion of *Sphagnum palustre* at 7520 cal. B.P. (Interpolation from the age depth curve for TSE94, Figure 6.19). The switch to *S. palustre* bog is rather sudden with little overlap between succeeding species. This is neatly reflected in the DCA diagrams for Tregaron Bog. The plot of axis 1 scores against depth (Figure 6.42) shows a 'cliff-like' drop in the sample scores occurring across just three samples at the point of the FBT (8 cm depth). Similarly the biplot of axis 1 against axis 2 scores for the whole data set (Figure 6.41) shows that the minerotrophic and oligotrophic species are widely separated by at least 3.25 standard deviation units.

Table 6.5 shows that the lifespan of the transitional *S. palustre* poor fen is just one hundred years. This figure compares very closely with the lifespans recorded for open *S. palustre* mire at Bolton Fell Moss and Walton Moss. The poor fen community is replaced as rapidly as it colonized, by a community principally composed of *Eriophorum vaginatum*, *Calluna vulgaris* and *Aulacomnium palustre* (LMZ-TSE94-Ga). This pioneer raised mire vegetation also contains an abundance of *Cenococcum* spp. confirming the presence of well aerated mire surface conditions. Therefore, the FBT at Tregaron Bog is remarkably similar in character to equivalent transitions at Bolton Fell Moss and Walton Moss in particular, and differs significantly from the character of the FBT recorded in the most oceanic mire of the study group, at Abbeyknockmoy.

The existence of a 'hummock-type' community immediately after the FBT at Tregaron demonstrates that the newly formed raised mire did not maintain a permanently high water-table, even in a period of increased effective precipitation. However, the major difference in the ombrotrophic pathways from Tregaron and the Cumbria Mosses lies in the lifespan of the dry *Eriophorum vaginatum* mire. At Tregaron *Cenococcum* spp. disappears from the macrofossil record in zone LMZ-TSE94-Gb, to be replaced by the first discontinuous record of *Rhynchospora alba*. This stratigraphic change registers the end of aerated surface conditions, prior to the major increase in *R. alba* at the beginning of LMZ-TSE94-H. The lifespan of the dry hummock community is, therefore, just c. 830 years (Table 6.5) compared to an average of 2100 years for the equivalent mire phases in Cumbria. The point at which *Eriophorum vaginatum* / *Calluna vulgaris* vegetation is replaced by a low lawn environment, may represent the first time that the raised mire accurately reflects the prevailing climatic conditions.

Change in the drainage characteristics of the of River Teifi may account for the significant differences in the FBT at Tregaron South-East Bog, when compared to the pathway of development recorded at Abbeyknockmoy in Galway Bay. The possible role of drainage basin change in altering the course of mire development at Tregaron South-East Bog, is discussed further in Chapter 7 (Section 7.4), in the light of previous studies, conducted on the stratigraphy of the Tregaron Mire complex.

6.6.3.2 Borth Bog.

Borth Bog, having developed from a salt-marsh deposited in the Boreal period, offers the chance to study a second relatively young FBT (6255 cal. B.P., SRR-5635) at a site with very different origins from the mires studied so far. The proximity to Tregaron Bog also provides an interesting opportunity to draw comparisons between the coastal and inland peatland systems in mid-Wales. In the light of the findings from Section 6.6.2.1, it will be interesting to investigate whether Borth Bog passed through a dry *Eriophorum vaginatum*/*Calluna vulgaris* mire phase after the FBT, with a lifespan comparable to the communities recorded at Tregaron Bog.

The radiocarbon date of 7035 cal. B.P. (SRR-5637) for basal peat from core BTH94 compares closely with a date of 6910 cal. B.P. (uncal. 6026 ± 110 B.P.) recorded by Godwin and Willis (1969) on *Phragmites australis* peat immediately overlying the salt-marsh clays. Thus freshwater or brackish reedswamp development probably began over a large area of the estuarine embayment at much the same time. Table 6.6 records the lifespans of the various wetland stages leading to ombrotrophic bog initiation. The carr phases in particular, are short-lived, lasting 50 and 120 years respectively. However, the macrofossil diagram (Figure 6.13) shows that over 75 cm of peat accumulated in this time. The rapid accumulation rate is clearly visible in the age depth curve, presented in Figure 6.20.

The rapidity of peat growth (producing a coarse open structure) in zones LMZ-BTH94-C and -D possibly accounts for the character of the first ombrotrophic community, which differs in species composition from that found at the equivalent stages in Tregaron Bog and in the Cumbria Mosses. The macrofossil diagram for Borth Bog shows that *Pinus sylvestris*, *Eriophorum vaginatum* and *Pleurozium schreberei* are the first occupants of the raised mire, indicating high hummock conditions. The FBT is also notable for the lack of *Sphagnum*, in contrast to many of the mires studied so far. Figure 6.20 reveals that peat growth in the *Pinus sylvestris* mire community equalled that of the preceding carr phases at 2.6 years per centimetre.

The succeeding low hummock raised mire phases composed of *Sphagnum* sect. *Acutifolia* (LMZ-BTH94-F) and *Eriophorum vaginatum*/*Calluna vulgaris* (LMZ-BTH94-G) have a considerably longer combined lifespan than the *Eriophorum* phase at Tregaron (1710 years at Borth [zones F and G] compared to 835 years at Tregaron, Table 6.5 and 6.6). This suggests that Borth Bog took longer to develop a stable high, water-table, again possibly due to the rapid peat accumulation of previous mire stages. However, this interpretation needs to be verified by analysing the evidence for the prevailing climatic and sea level conditions of the time. This comparison is undertaken in the discussion chapter. (Chapter 7).

Despite the proximity of Borth Bog to the Dovey estuary the general format of the ombrotrophic pathway appears to be no different from inland mires such as Tregaron Bog. A phase of dry mire is superseded by *Rhynchospora alba* lawn and finally *Sphagnum* bog dominated by *S. imbricatum* (Figure 6.13). However, base level change and climate change might produce similar species responses, once the growing surface

of the mire is insulated from the general groundwater-level by several metres of oligotrophic peat. The status of the change to the *Rhynchospora* and *S. imbricatum* mire phases will be investigated further in the discussion chapter by means of comparisons with independent climatic proxy records and the Holocene sea level record for Cardigan Bay.

6.7 Paludification at Walton Moss.

Having studied eight lowland mires, seven of which developed into dry *Eriophorum vaginatum* / *Calluna vulgaris* bogs, the final part of this chapter examines the FBT at a site located on sloping ground, where relatively free drainage may be expected to have dominated the mire development pathway. The resulting macrofossil records should provide an interesting comparison with the dry 'hummock-like' communities that developed on the level fen surfaces. In the light of the previous results, one aspect of this comparison is of particular interest, namely the species response to conditions of high effective precipitation and relatively free drainage, in a lowland mire.

Walton Moss was selected for this study because it possesses a wide fringe of transitional mire on the slopes surrounding the deep northern basin. The peat is remarkably undisturbed over much of the paludified slopes. Examination of aerial photographs shows that only the thinnest fringe of peat has been cut in the past.

Peat accumulation began shortly before 7465 cal. B.P. (SRR-5641) under wet *Alnus* woodland sustained by slope runoff. Analyses from Bolton Fell Moss, Walton Moss, Glasson Moss and Solway Moss confirm that the *Alnus* phase (LMZ-WLM15-B, Figure 6.10) correlates with a major increase in mire surface wetness right across the Cumbrian lowlands. The transition to oligotrophic mire finally occurs at 5650 cal. B.P. Figure 6.10 shows that the acid phase in the sloping, transitional peatland very closely resembles the *Eriophorum vaginatum*/*Calluna vulgaris* mires at many of the other sites. *Cenococcum* spp. again forms a major part of the assemblage. That the community developing on a sloping peatland dominated by water-table fluctuation should so closely resemble the pioneer raised bogs developing from level fen, gives a strong indication of the degree of water-table fluctuation that may take place prior to the development of a significant catotelm in a lowland raised bog.

The development pathway in the upper zones of WLM15 (LMZ-WLM15-Fa and Fb) differs from that of the mire centre. The pioneer species *Rhynchospora alba* is absent from the first lawn community. *S. imbricatum* is the first species to respond to a sustained high water-table, directly displacing *Eriophorum vaginatum*. This probably represents the expansion of moss cushions from foci elsewhere on the mire. *Sphagnum imbricatum* is recorded at 5 metres depth from WLM11, equivalent to a date of approximately 5000 cal. B.P.

6.8 Summary.

- The four kettlehole mires (Cumbrian sites) follow diverse pathways in the reedswamp and fen phases. Development after the FBT, is strikingly similar at each site, with the exception of Glasson Moss.
- The transitional communities involved in the FBT are usually short-lived, having lifespans of 90 to 150 years. *Sphagnum palustre* is a frequent component of these mires, appearing at Bolton Fell Moss, Walton Moss and Tregaron Bog. In all of these mires the lifespan of the *S. palustre* phase is comparable, lasting c. 100 years
- Dry hummock-like raised mire replaces fen and fen carr in seven out of eight of the FBTs studied.
- The hiatus in peat accumulation at Solway Moss and Glasson Moss, coupled with evidence for very abrupt transitions at these two sites and the broadly synchronous timing of the transitions across all four Cumbrian Mosses, suggest that a regional controlling factor, such as climate change, may be significant in determining the character and timing of these FBTs.
- Dry *Eriophorum vaginatum* mire dominates the Cumbrian mosses for a duration of approximately 2000 years (with the exception of Glasson Moss) prior to the increase in the main wet ombrotrophic bog mosses. DCA analyses of the ombrotrophic samples indicate the presence of hummock/hollow-level moisture gradients in the raised mire stratigraphies. The DCA plots compare favourably with similar reconstructions, using WAO. The broadly synchronous end to the sedge mire phase strongly suggests a major increase in effective precipitation at the beginning of the Atlantic period (7800 cal. B.P.). This also suggests that the previous *Eriophorum* phase was, at least in part, maintained due to lower effective precipitation.
- The pathway of mire development at Glasson Moss differs from the other Cumbrian mires studied. At one point the succession is reversed. The proximity of the mire to the coast and the fact that basal layers lie below the present mean high-water mark, suggest that some of the differences may be related to sea level change (see Chapter 7).
- Abbeyknockmoy Bog, situated in western Ireland, is the only site that records a FBT developing into a wet raised mire. Even so *Sphagnum* forms a relatively minor component of the actual transition. Although the assemblage immediately overlying the FBT is wetter in character than the other seven, studied in this project, it is drier than might be expected from the strongly oceanic location of the mire. The FBT at Abbeyknockmoy Bog is more gradual than most of the equivalent stages from other mires. Interestingly, *Rhynchospora alba* dominates the FBT, rather than *Sphagnum*.

- In addition to Abbeyknockmoy Bog, the transitions at Mongan Bog, Borth Bog and Glasson Moss have very little or no *Sphagnum*.
- The FBT at Mongan Bog is very abrupt and develops into a dry *Eriophorum/Pinus* mire immediately after the FBT. In these respects, the mire development pathway at Mongan has more similarities with the Cumbrian mires and Borth Bog, than with the most oceanic site in the study, namely Abbeyknockmoy Bog.
- At Tregaron South-East Bog the FBT occurs in a wet climatic phase. However, the transition is abrupt and leads to the development of a dry mire. This suggests the operation of an allogenic factor, other than climate change, such as drainage basin change. The analyses at Tregaron Bog indicate that there may be a lag period after the FBT during which time the raised mire water-table is insensitive to the prevailing climate.
- The FBT at Borth Bog shows no evidence for disturbance caused by changes in base level.
- At most of the sites studied *Rhynchospora alba* plays a major pioneering role in responding to increased raised mire surface wetness. The species usually precedes the arrival of a variety of oligotrophic *Sphagnum* species.
- *Sphagnum imbricatum* supersedes *Rhynchospora alba* in six of the eight mires. At the remaining two sites the equivalent species is *Sphagnum cuspidatum*. The rise of *S. imbricatum* is synchronous in two of the three mires originating from large basins. Mongan Bog is the exception. Here the pathway of development may have been significantly affected by local factors, such as change in the course of the Shannon river.
- Similar successional pathways have been recorded in both the kettlehole and larger basins, just before and after the FBT. Pathways differ more in the reedswamp and fen phases, as may be expected.

Chapter 7

Discussion.

7.0 Introduction.

Examination of the detailed macrofossil records for the eight mires, presented in Chapters 5 and 6, strongly suggests that a number of the development pathways have deviated from the route predicted by traditional models of autogenic raised mire formation (Weber 1908, Walker 1970, Bellamy 1972). The emphasis of the autogenic models is upon gradual development and species turnover. The mechanisms of raised mire formation on reedswamp, fen or fen carr described by Walker (1970) and Bellamy (1972) suggest that ombrotrophic foci should occur in one or a number of favoured locations and then spread progressively across the mire surface. Some autogenic mechanisms that involve simultaneous colonization by *Sphagnum* to produce ombrotrophic mire conditions have been identified. However, these do not involve a reedswamp fen or carr stage (e.g. Ingram 1967, colonization of bare ground, and Walker 1970, formation of schwingmoor). *Sphagnum* in particular has been identified as a very important factor in the autogenic development of raised mires (Walker 1970). The species plays an ecosystem engineering role, progressively modifying the mire surface environment to create strongly oligotrophic conditions (Clymo 1983, van Breeman 1995).

The results from the present project demonstrate that the FBT can be very rapid, with some transitional communities lasting for no more than 90 to 120 years at sites such as Tregaron Bog, whilst in other mires, including Mongan Bog and Solway Moss, transitional mesotrophic communities appear to be missing. In some cases the radiocarbon dates for transitions that proceed straight from reedswamp or fen to fully oligotrophic conditions indicate that a break in peat accumulation occurred prior to the FBT. Further evidence for allogenic forcing of the transitions may be seen in the field stratigraphies for certain sites. Tregaron Bog is a good example (Figure 6.4). Here the stratigraphic change from reedswamp peat to humified acid peat is sharp and occurs at virtually the same altitude across the whole of the south-east bog. A comparison of radiocarbon dates from Hibbert and Switsur (1976) and from this project supports the interpretation that the FBT at Tregaron was synchronous across the entire mire.

The temporal grouping of all four FBTs within the Cumbrian mires in the latter half of the tenth millennium B.P. is also suggestive of a regional controlling factor operating upon the mire systems at the time of raised peat formation. In Chapter 6, climate change was suggested as the most likely cause for the observed pattern between the four paired sites.

Similarly, the lack of *Sphagnum* or the low level of occurrence of the genus, at sites such as Glasson Moss, Borth Bog, and Mongan Bog at the time of the FBT, represents a major departure from the suggested (e.g. Walker 1970) autogenic routes of raised mire formation. The continued lack of *Sphagnum* in the pioneer

oligotrophic communities of many of the study mires is also notable. Species such as *Eriophorum vaginatum*, *Calluna vulgaris* and *Pinus sylvestris* indicative of much drier bogs are widely recorded. Only *Sphagnum sect. Acutifolia* occurs in any significant quantity in the early raised mire assemblages and even this section appears sporadically. Analyses of spore frequencies indicate that the low occurrence of *Sphagnum* in the highly humified basal peats is not simply a consequence of differential preservation.

To gain a greater understanding of the causes of the stratigraphic features noted above, Sections 7.2 to 7.6 aim to compare the macrofossil records, field stratigraphies and pollen diagrams presented in the previous two chapters with the records for allogenic events such as climate change, sea level change, river channel change and human impact. An overview of early to mid-Holocene climate change is presented in Section 7.1 prior to the discussion of the implications of the climate record for interpreting stratigraphic changes associated with the FBT. The records for other allogenic factors are introduced where relevant, within the subsequent discussion Sections.

7.1 Overview of climate change in the early to mid-Holocene.

During the last two decades major advances have been made in a number of approaches concerning the recovery of climatic signals from palaeoecological data. Barber (1978) demonstrated that oceanic lowland raised mires could be sensitive to changes in the effective precipitation balance. This work has been refined in subsequent years by Haslam (1987), Stoneman (1993), Barber *et al.* (1994a) and most recently by Mauquoy (forthcoming).

Colorimetric determination of the degree of peat humification has also proved to be a useful climatic indicator both in raised bogs (Aaby and Tauber 1975, Mauquoy (forthcoming) and in blanket peat (Blackford 1990). Further techniques aimed at extracting climatic signals from peat include the use of isotope geochemistry (Dupont 1986), non pollen microfossils (van Geel 1978b, Blackford 1990) and the study of pollen spectra (e.g. Huntley and Prentice 1988).

The coverage of Holocene climatic change by peat based signals is necessarily constrained by the availability of suitable deposits. Very few lowland mires in Britain contain ombrotrophic *Sphagnum* rich peats older than 6000 years. Bolton Fell Moss yields one of the longest surface wetness curves extending back to 6500 cal. B.P. The record of climate change from blanket peats is similarly limited in time. Pollen evidence suggests that early human disturbance was instrumental in causing blanket peat formation at many sites (e.g. Chapman 1964, Moore 1973 and 1975) with dates for inception ranging from the Mesolithic to the Iron Age period (Moore 1993). The temporal limitations of the peat based proxy climate records limit their usefulness to studies of the younger mire sequences at Tregaron, Borth and Mongan Bogs.

Interest in the dramatic environmental changes of the last glacial/interglacial transition has resulted in a second concentration of palaeoclimatic records derived from sources such as Coleoptera analysis, for the period from 15000 - 10000 cal. B.P. However, these studies rarely extend further into the early Holocene. Consequently, there are significantly fewer sources to draw upon for the period from c. 10000 to 6500 cal. B.P. The overview of early to mid-Holocene climatic change, presented in Section 7.1.2, necessarily draws upon a wide range of often fragmentary proxy indicators.

7.1.1 Orbital variations.

Predictions of past climatic parameters have been calculated by Berger (1978) using numerical models based on Milankovitch cycles and astronomically controlled variations in the amount of radiation received by the Earth. At 10000 cal. B.P. perihelion was in the northern hemisphere summer, rather than in the winter, as it is today. In addition, the tilt of the Earth was at its greatest declination. As a result of these orbital changes, the Earth received up to 8% more solar radiation in the Northern Hemisphere summer than at present and correspondingly less in the winter months (COHMAP members 1988). Whilst reduced winter insolation has a significant impact on the mid latitudes, there is little effect in the high latitudes due to continual darkness. Combined with the greater exposed land area surrounding the British Isles during the early Holocene, the differences in insolation may be expected to favour relatively warm summers and cold winters.

7.1.2 Proxy indicators of palaeotemperature.

The analysis of fossil Coleoptera provides one of the best methods of recovering an actual proxy indicator of past temperature changes. Atkinson *et al.* (1987) have presented a detailed temperature curve for a number of time intervals covering the last 22000 years, reconstructed using the Mutual Climatic Range (MCR) technique (Figure 7.1, Average temperature of the coldest and warmest month). This approach assumes that if the present climatic tolerance of a beetle species is known then the occurrence of that species within the record implies a palaeoclimate within the same tolerance range. Generally the palaeotemperature is more tightly defined when a large number of species are represented. Figure 7.1 shows that average temperatures for the coldest month of the year rose sharply between c11200 and 11000 cal. B.P. (10200 - 10000 radiocarbon years B.P.) marking the transition from the Loch Lomond Stadial to the Holocene. The pattern of change was similar for the temperature of the warmest month although the magnitude was less. After the first major warming, there is evidence for a significant reversal between 10500 and 10000 cal. B.P. that affected both winter and summer averages. A second rise in summer and winter values occurred in the following 500 years from 10000 to 9500 cal. B.P. This change brought the average temperature for the warmest month to within 0.5 °C of present values. By contrast the coldest month of the year was up to 3 °C colder than present. The period from 9000 to 6000 cal. B.P. is not

represented in the Coleoptera record presented by Atkinson *et al.* (1987), therefore other lines of evidence are required to investigate early and mid-Holocene temperature change.

Data from the Greenland ice cores have the advantage of full Holocene coverage. O'Brien *et al.* (1995) conducted ion chromatography on 5114 Holocene samples from the Summit ice core (GISP 2) to determine the relative abundance of salts derived from marine and terrestrial sources. Changes in the chemical flux values from each source are believed to represent changes in the composition of the atmosphere and temperatures in particular. Brian *et al.* (1995) used a statistical function to combine the records of each chemical species through the ice core to provide a palaeotemperature signal for the entire Holocene (Figure 7.2). Five specific cold events have been identified, beginning with the Loch Lomond Stadial, which ended at 11200 cal. B.P. according to the GISP2 record. Other apparent cold events occur at 8300, 6000 - 5000, 2900 cal. B.P. and during the Little Ice Age (*c.* 1420 to 1850 A.D., Lamb 1977). It is interesting to note that a long relatively warm period is inferred for 11200 to 8300 cal. B.P.

The Intergovernmental Panel on Climate Change (IPCC 1990) has used a suite of palaeoclimatic indicators to construct a generalized curve for the inferred change in average Northern Hemisphere temperatures over the last 11000 years. The curve is presented in Figure 7.3.

7.1.3 Proxy indicators of past precipitation levels.

Measurements taken on the level of deuterium (δD) in precipitation have shown that values vary according to the intensity of the rainfall. (Dansgaard 1964, in Dubois and Ferguson 1985). Trees record, at least in part the deuterium/hydrogen (D/H) ratio of precipitation water absorbed through their root systems because the water is used to manufacture cellulose. Dubois and Ferguson (1985) have analysed the δD content of cellulose from a large number of radiocarbon dated pine macrofossils, from the Cairngorm Mountains, in order to reconstruct a record of past changes in precipitation. Excessively low δD values are considered to be indicative of very heavy rainfall, termed 'pluvial phases'. Four distinct rainy phases have been identified during the Holocene (Figure 7.4), the oldest of which has a minimum date of *c.* 8100 cal. B.P. (7300 B.P. uncal.). The second pluvial phase occurs from *c.* 7100 cal. B.P. to *c.* 6700 cal. B.P. with the remaining two at *c.* 4500 cal B.P. and 3500 cal. B.P. Again this record is fragmentary with no data available for the early Holocene. D/H analysis is also a relatively insensitive technique that can only distinguish the phases of heaviest rainfall.

Guiot *et al.* (1993) have attempted to reconstruct precipitation patterns for the whole of Europe for 10000, 7000 and 3000 cal. B.P. Estimates of effective precipitation have been inferred from pollen data. These were subsequently compared with the status of neighbouring lakes. Any anomalies were rejected from the data set and precipitation levels were then estimated by correcting for variations in evaporation caused by change in palaeotemperatures. Figure 7.5 shows the results of the analysis for the British isles at *c.* 10000 and *c.* 7000 cal. B.P. At the former date, Scotland, the Cumbrian lowlands and the Isle of Man were

apparently drier than the present, with conditions similar to the present recorded for much of England and Ireland. By 7000 cal. B.P. the reconstruction suggests that northern England had become wetter, with a shift to drier conditions in southern England.

7.1.4 Proxy indicators of past effective precipitation.

In the absence of ombrogenous mire surface wetness records for the early Holocene, lake level reconstructions provide another possible source of data for gauging the level of past effective precipitation, since humidity is one of the primary controls determining lake levels. Digerfeldt (1988) has identified a range of broadly synchronous lake status changes from nine sites in Scandinavia. These provide the basis for the curve presented in Figure 7.6. The lake level fluctuations suggest a phase of decreasing effective precipitation from 11000 cal. B.P. to 10200 cal. B.P. (10000 - 9200 B.P. uncal.). Thereafter the trend is reversed with the highest lake levels recorded at c. 7800 cal. B.P. (7000 B.P. uncal.). A second dry phase is inferred for the period between 7600 and 2700 cal. B.P. (6600 - 2700 B.P. uncal.). However, this second phase was not uniformly dry. Digerfeldt notes that the lake status record bears some similarities to the postulated course of Holocene climate change described by Sernander and Lundquist (in Digerfeldt 1988). The early Holocene low lake levels correspond to the 'Boreal dry period'. A similar set of lake status changes has been reported from the Jura mountains of France, where low levels have been inferred between 10000 cal. B.P. and 9800 cal. B.P., with higher levels from 9800 to 9000 cal. B.P. Thereafter, a long dry phase is recorded, ending at 8000 cal. B.P. (Magny 1992). Results reported by Hobby (1990) also support this scheme of lake status changes.

Yu and Harrison (1995) have collated biological evidence for lake level change from 87 sites in northern Europe, spanning the duration of the Holocene. Although the lake status records are continuous, comparisons with modern lake levels have been made at c. 1000 year intervals for the last 11000 years. Figure 7.7 presents the water-level anomaly maps for 11000 to 7800 years cal. B.P (10000 - 7000 uncal.). The results for the British Isles are rather sparse and not entirely harmonious. However, the map for 11000 years B.P. shows that all of the sites in England registered conditions that were drier or much drier than present. The only wetter sites are found in the extreme west of Ireland, on the north side of Galway Bay, and in the far north of Scotland. At 10000 B.P. most of the British lakes register levels similar to present, with the exception of the site in Galway and one in Snowdonia which indicate wetter conditions. The Welsh lake sites record drier conditions at 9000 B.P, with sites in East Anglia, Ireland and Scotland all wetter than present. Finally, at 7800 cal. B.P (7000 uncal. B.P.) drier conditions than present are inferred for East Anglia, South Wales and the East Coast of Scotland. Most other areas are similar to present with the exception of one wet site near Glasgow.

Oceanic ombrotrophic mires are mantled by a micro-topography of hummocks, lawns and hollows. Each level has a characteristic flora of *Sphagna*, and vascular plants, sensitive to changes in the water-table. During wet phases pools expand over neighbouring lawns and low hummocks. The resulting stratigraphic

changes depicted in the turnover of species may be recognized as a wet shift. Conversely, hummocks expand during dry phases, covering lawn areas, whilst pools contract. Therefore, a core located in a lawn microtope provides a particularly sensitive record of past mire surface wetness changes. This in turn provides a record of change in past effective precipitation because the domed water-table of a raised mire only receives water from precipitation (Barber 1978). Water losses occur due to a low, relatively constant level of lateral seepage and due to evaporation (Ingram 1982). Barber (1978) demonstrated that wet shifts in mire surface stratigraphy could be traced laterally over considerable distances, suggesting that one core could be representative of the changes in the general ombrotrophic peat stratigraphy of the whole mire. Analyses undertaken on multiple cores from Bolton Fell Moss and Walton Moss clearly demonstrate the replicability of the macrofossil climate reconstruction techniques based on core sampling (Barber 1995 and 1996).

Colorimetric determination of the degree of peat decomposition closely supports the inferred surface wetness reconstructed from macrofossils (Mauquoy forthcoming), therefore, macrofossil data alone will be used to represent the record of past effective precipitation from ombrotrophic bogs. Figure 7.8 shows the mire surface wetness curve for Bolton Fell Moss, covering the period from 1000 to 6500 cal. B.P. The curve registers a set of eight major wet shifts. Those relevant to the mid-Holocene include one centred on 6200 cal. B.P, with others at 5800, 5200, and 4440 cal. B.P. The macrofossil based reconstruction of effective precipitation identifies a greater number of changes in humidity than the lake status record covering the same time period. This probably represents a greater degree of sensitivity to climate change within the peatland system. Dupont (1986) has undertaken similar macrofossil reconstruction of mire surface wetness for a site located in the north east of the Netherlands. Results are broadly comparable to those from Bolton Fell Moss (Figure 7.8).

7.1.5 Other pollen and macrofossil evidence for early Holocene climate change.

A large number of pollen studies provide evidence for climate change during the Holocene. Dutch researchers in particular have combined detailed pollen work with the analysis of macrofossils and non-pollen microfossils to provide highly detailed palaeoecological accounts of mire development and climate change. The large volume of material precludes a detailed review; therefore, only a selection of works that add to the picture of climate change, already established in the previous sections, will be discussed.

Analysis of pollen diagrams from Europe suggest that the Preboreal period may be divided into three distinct climatic phases, which Behre (1978) called the Friesland (IVa), the Youngest Dryas (IVb) and the Late Preboreal. The Friesland period was characterized by rising mean summer temperatures. The Youngest Dryas (termed the 'Rammeltebeek phase' by Van Geel *et al.* 1980/81) had a more continental climate with warmer summer temperatures, increasingly cold winters and significantly reduced precipitation. This phase lasted from approximately 10900 to 10700 cal B.P. (9000 - 9700 B.P. uncal., van Geel *et al.* 1980/81). The late Preboreal marked a return to more humid conditions in Europe, with

summers that were sufficiently humid for the domination of *Sphagnum* on mires in the north-east Netherlands (Van Geel *et al.* 1980/81). Records in support of a climatic deterioration in the mid-Preboreal (equivalent to the Youngest Dryas) have been reported from elsewhere in northern Europe, including the Isle of Skye (Benn *et al.* 1992), the eastern Highlands of Scotland (Huntley 1994) and Fife (Whittington *et al.* 1996). However, most proxy records agree that the later part of the Preboreal and the beginning of the Boreal represented a time of low humidity. (Digerfeldt 1988, Starkel 1991, Harrison *et al.* 1993, Walker *et al.* 1993).

7.2 The implications of the climate record for the FBTs in Cumbrian mosses.

7.2.1 Glasson Moss and Solway Moss.

Radiocarbon chronologies for Glasson Moss and Solway Moss suggest that peat growth halted prior to the establishment of the first oligotrophic 'hummock-type' vegetation on the mires. The end of fen peat formation at Glasson Moss is radiocarbon dated to 10655 cal. B.P. (SRR-5728). Just one transitional poor fen level is recorded in the macrofossil record before the complete replacement of the assemblage by *Eriophorum vaginatum* peat at 9975 cal. B.P. The two radiocarbon samples straddling the FBT are separated by a depth of 16 cm (as measured from their respective mid-points) giving a peat accumulation rate of more than 42 yr. cm⁻¹ for the transitional levels. This compares to an average peat growth rate of 11 yr cm⁻¹ in the overlying *Eriophorum vaginatum* mire phases (LMZ-GLM95-E to -I). It is unlikely that peat accumulation in the transitional *Scheuchzeria palustris*/*Menyanthes trifoliata*/*S. palustre* mire would have been substantially slower than in the superseding *Eriophorum vaginatum* mire, therefore an hiatus in peat formation may be inferred between zones LMZ-GLM95-D and -E. This interpretation is supported by the sudden switch to *Eriophorum vaginatum* peat. A significant increase in the unidentifiable organic matter (U.O.M.) content of the upper fen and poor fen peat is also registered in the macrofossil diagram (Figure 6.11) indicating that these levels became aerated (zone LMZ-GLM95-Cb and -D). The presence of species indicative of relatively high water-levels in the more humified fen and poor fen peat, suggests that decomposition was secondary and that it occurred due to falling groundwater-levels.

A similar situation is recorded at Solway Moss where the sudden end of fen peat formation is dated to 10430 cal. B.P. Oligotrophic mire peat dominated by *Sphagnum sect. Acutifolia* lies directly over the fen peat. A radiocarbon assay sampled from the lowermost levels of the *S.s. Acutifolia* assemblage registers an age estimate of 8840 cal. B.P. (SRR-5646). However, this date is almost certainly 'too young' due to contamination from rootlets penetrating down from overlying levels. In Section 5.12 a revised estimate for the age of SRR-5646 of c. 9850 cal. B.P. was suggested from pollen correlation between Bolton Fell Moss and Solway Moss (refer to Figures 5.9 and 6.23). If the amended date is accepted, the rate of peat accumulation at the time of the FBT was c. 35 yr cm⁻¹, which is more than twice the average for ombrotrophic peat. This suggests that conditions were unsuitable for significant peat growth immediately before the FBT. However, in common with Glasson Moss, species indicative of very wet fen carr are found

in the minerotrophic peat. The high percentage of accompanying U.O.M. may indicate secondary decomposition and lowering of the water-table, although at least part of this feature of the stratigraphy may be due to the primary breakdown of litter from the *Salix spp* carr.

The DCA results for both Glasson Moss and Solway Moss support the interpretation that peat growth halted for a period during the two FBTs. Figures 5.16 and 6.36 show that just one sample level bridges the gap between fen and ombrotrophic mire assemblages at each site. The fen and raised mire sample scores are widely separated and display no evidence for gradual development from one state to the other. The isolated transitional sample scores may be accounted for by the presence of displacement peats, in which mixed assemblages are recorded because species replacement was rapid. The one centimetre macrofossil samples may either have bridged the boundary between two distinct peat types or roots from the succeeding vegetation may have penetrated into the underlying peat.

Proxy palaeoclimatic indicators such as lake status change (Digerfeldt 1988, Figure 7.6, Walker 1993), dendrochronology (Becker and Kromer 1993) and fluvial records (Starkel 1991) provide evidence for reduced levels of effective precipitation across Europe during the period of minerotrophic mire development at Solway Moss and Glasson Moss, from 11000 to 10400 cal. B.P. For example, Walker *et al.* (1993) have reported a period of water-level reduction at Llangorse lake which lasted well into the early Holocene. The contemporary pollen zones show that *Artemisia*-type was well represented in the catchment until at least 10,400 cal. B.P. This pollen type is frequently used to infer the presence of dry conditions. Similarly, the integrated pollen and lake level study by Guiot *et al.* (1993) indicates dry conditions for northern Britain at 10000 cal B.P.

The period of Preboreal and early Boreal dryness would account for falling water-levels in the kettlehole basins at Glasson Moss and Solway Moss. Climatically induced removal of the groundwater effect from the growing surface of the mires, effectively represents an acceleration of the autogenic process of gradual isolation from minerogenic water, due to the build up of peat above the level of the water-table. In a dry climate this would leave a layer of 'perched' fen peat lacking a sufficient water supply to maintain peat growth. Due to the possibility of surface peat erosion and wastage, the radiocarbon dates for the upper contacts of the fen peat represent the maximum age at which accumulation stopped.

A number of studies of the effects of drying out in fen peats have shown that a suite of physical and chemical changes take place when the groundwater-level drops. In addition to loss of mass and buoyancy, de-watering causes shrinkage and subsidence as a consequence of changes in the physical structure of the peat. (Koerselman and Verhoeven 1992). If subsidence of the peat surface due to this process is insufficient to bring it back into contact with the groundwater, longer term processes of peat humification become significant. Petersen and Breuning-Madsen (1978) found that nitrogen (N) mobilization, as nitrate, was significant when fen peats dried out. Other plant nutrients were also liberated. The release of

nutrients due to humification may be expected to cause eutrophication and reversed succession. This effect is certainly recorded in some mires when de-watering is severe, as would be the case when a peat surface is artificially drained. For example, Harding (1993) recorded significant increases in soil fertility at Redgrave and Lopham fens, East Anglia, as a result of large falls in the water-table, caused by the abstraction of groundwater from the underlying chalk aquifer.

However, at Glasson Moss and Solway Moss the macrofossil evidence suggests that oligotrophic vegetation colonized the mires after the dry phase, marked by the hiatus in peat accumulation. Further studies into the reaction of modern fen peats to surface drying may provide at least part of the answer to the problem identified above. For example, research into the cycling of nitrogen compounds in wetlands has shown that the mineralization of organically bound nitrogen to nitrate, as a consequence of peat aeration, produces a significant proton load. Kazda (1995) found that desiccation of the top 10 cm of fen peat in an *Alnus spp.* carr resulted in the production of 140 - 280 K mol H⁺ ha.⁻¹ and the depletion of organic N compounds, during the study period. This process occurs to a lesser extent, in undisturbed habitats, wherever aeration of N rich soil occurs. Miegroef and Cole (1985) have measured a yearly H⁺ production of 4.5 Kmol ha⁻¹ in an undisturbed *Alnus rubra* woodland growing on mineral soil.

Oxidation of compounds such as sulphides may also produce significant amounts of H⁺ ions in desiccated peat. Gosling and Baker (1980) have recorded large scale increases in acidity at Calthorpe Broad, Norfolk, resulting from the aeration of sulphide rich surface peat. Improved drainage in surrounding farmland left the water-table in the Calthorpe Broad peatland perched above the general groundwater-level. Until 1969 the water-table in the fen was controlled by damming. Damage to the main dam resulted in a seasonally fluctuating water-table. Gosling and Baker (1980) found that significant quantities of sulphuric acid were liberated into the mire waters once rewetting of oxidized levels occurred during the winter months. Proctor (1994) has also noted large annual fluctuations in the pH of peatlands associated with the oxidation of sulphides in the peat when water-tables are at their lowest in late summer. Even in the calcareous valley-head fens studied by Harding (1993) marginal areas with peat rich in sulphide became strongly oligotrophic when the permanent fall in the water-table exposed the peat surface to the atmosphere. Harding recorded pH values as low as 2.3 in the worst affected areas.

Drained or dried out fen peat soils switch from a groundwater to a rainwater dominated hydrology, (Kulczynski 1949, Casparie 1972, 1992, Grootjans *et al.* 1988, Harding 1993). In drained areas Grootjans *et al.* (1988) found that precipitation water could replace groundwater to a considerable depth (1 - 1.5 m). Although the switch to an ombrotrophic hydrology is likely to be less dramatic on a fen surface that has dried out naturally, the leaching of bases from surface peats is likely to be significant in both cases (Gosling and Baker 1980, Grootjans *et al.* 1988, Wiegers 1990). This would tend to cause a reduction in the ability of the peatland waters to buffer pH changes, resulting in more rapid acidification of the peat after dry spells (Gosling and Baker 1980).

Okruszek (1993, 1995) has also carried out detailed studies of the effect of drainage on fen peats. One consequence of peat humification noted was that the absorptive ability of the peats increased, bringing about a reduction in the availability of some cations, such as calcium (Ca) and iron (Fe), for use by plants. In addition Okruszek (1993) found a simultaneous increase in the level of humic acids and phosphorous (P).

The studies outlined above suggest that the chemical composition of the fen peat prior to aeration is one of the most important factors determining the changes that take place during oxidation. Other researchers have reached similar conclusions (e.g. Petersen and Breuning-Madsen 1978, Koerselman *et al.* 1993). However, the degree of de-watering is also likely to be important. Anthropogenic drainage is usually far more severe than the drying out caused by natural processes. Severe de-watering may be expected to result in much more complete breakdown of the peat and the liberation of significantly higher concentrations of plant nutrients. The transformation of the peat to a crumb structure also makes it more vulnerable to over drying (Okruszek 1995). The resulting changes in the floristic composition of artificially drained fens may be considerable. For example, data presented by Fojt and Harding (1995) from three Suffolk fens showed that all fen associates and bryophytes were lost from drained areas during the thirty year study period. The species replacing the fen communities were principally tall ruderal herbs and shrubs, indicative of dry scrub habitats.

The less severe de-watering experienced by naturally dried out peats may provide a more suitable template for the colonization of oligotrophic mire species, such as *E. vaginatum*, which can thrive in dried out peat so long as the water-table remains above a depth of 60 cm from the surface. If oxidation causes a decrease in pH and an increase in the availability of P, *E. vaginatum* could grow particularly vigorously (Wein 1973).

The development of oligotrophic peats, dominated by *Eriophorum vaginatum* and *S.s. Acutifolia* at the end of the retardation phases at Solway Moss and Glasson Moss strongly suggests that the liberation of H⁺ ions, as a by-product of humification, was significant at both sites.

Renewed peat accumulation after 10000 cal. B. P. in the two Solway lowland mosses probably reflects an increase in regional humidity, bringing the mires back into a climatic regime suitable for peat growth. Digerfeldt (1988) has suggested that effective precipitation increased in northern Europe after 10200 cal. B.P. (9200 uncal. B.P.) as shown by progressively rising lake levels from this date until c. 7800 cal. B.P. (7000 uncal. B.P., Figure 7.6). However, Harrison and Digerfeldt (1993) have argued that the observed changes in the status of Boreal lakes need not reflect significantly increased precipitation. Insolation changes could account for at least part of the long term gradual rise in water-levels as perihelion started to shift from the northern summer towards autumn and winter (COHMAP members 1988).

Certainly the 'hummock-type' oligotrophic communities that first colonized Solway Moss and Glasson Moss do not reflect a large shift towards a wetter climate. Rybníček and Rybníková (1968) have described a very similar oligotrophic peat type found in south-eastern Czechoslovakia. In common with Solway Moss and Glasson Moss the main constituents of the peat were found to be *Eriophorum vaginatum*, *Calluna vulgaris* and various *Sphagnum* species indicative of hummock tops. Rybníček and Rybníková (1968) compared these macrofossil assemblages with the distribution of comparable modern communities. They concluded that the past and present communities were significantly different compared to true raised bogs, and frequently showed signs of greater nutrient enrichment. Therefore, they coined the term 'pseudohochmoor' ('pseudo-raised bog') to describe the *Eriophorum vaginatum*-dominated mire. Rybníček and Rybníková (1968) also found that this mire type was common in regions where precipitation levels were too low to allow the development of true ombrotrophic, *Sphagnum* dominated, raised bogs.

The macrofossil assemblages from the two Solway lowland mosses display many of the characteristics described by Rybníček and Rybníková (1968). For example, the peat components in zones LMZ-SOLA2-D and -Ea (Figure 5.4) from Solway Moss and zone LMZ-GLM95-E (Figure 6.11) from Glasson Moss register some signs of continued nutrient enrichment, indicated by the presence of moss species such as *Aulacomnium palustre*, in the *Eriophorum vaginatum* peat. This probably reflects the release of breakdown products in the highly humified peat.

However, it is also possible that the dry surface conditions in the newly formed pseudo-raised mires are partly a result of a lack of sufficient catotelmic peat to maintain a permanently high water-table, thus creating a lag phase, during which time mire surface wetness might not provide an accurate reflection of the prevailing climatic conditions. This aspect of the mire stratigraphy is discussed further in Section 7.2.5 and 7.3.

7.2.2 Bolton Fell Moss and Walton Moss.

Although the *Eriophorum vaginatum*/*Calluna vulgaris* macrofossil assemblages recorded at Bolton Fell Moss and Walton Moss, after the FBT, are very similar to those found in the two Solway lowland mosses, the course of development in the fen and poor fen communities differs significantly between the two sets of paired sites. At Bolton Fell Moss and Walton Moss there is no evidence for a marked break in peat development prior to the FBT. At both sites bryophyte assemblages span the switch from *Carex spp.* fen and *Betula spp.* carr to *Eriophorum vaginatum*/*Calluna vulgaris* mire. In addition, the radiocarbon chronology for Bolton Fell Moss and pollen correlation with Walton Moss show that the fen peat at the two sites accumulated rapidly after inception at c. 10300 cal. B.P.

The size and water depth in the originating lake basins could be one of the most important factors contributing to the observed differences in the mire development pathways between the Solway lowland

and inland sites. At Bolton Fell Moss the interpolated date for the change from lake clay sedimentation to peat accumulation suggests that open water existed at the site for up to 700 years after peat growth began at Solway Moss and Glasson Moss. The absence of a significant *Juniperus/Salix spp.* zone in the pollen diagrams for both Bolton Fell Moss and Walton Moss (Figures 6.23 and 6.24) also indicates that the Preboreal and early Boreal periods are missing from the peat record at these two sites.

The change from open water to *Salix spp.* carr registered in Bolton Fell Moss (LMZ-BFML-Aa to -Ab, Figure 6.8) at or just before 10300 cal. B.P. represents a significant lowering of the water-level in the enclosed lake basin and coincides with the latter part of the inferred period of Boreal dryness (Digerfeldt 1988). Relatively rapid fen peat formation is recorded for the period after 10215 cal. B.P. until the FBT, suggesting that water supply was not a limiting factor in the *Betula spp.* carrs and *Carex paniculata* tussock fen. Again this phase of mire development coincides with the inferred increase in humidity after 10200 cal B.P. (Digerfeldt 1988). However, these correlations must be treated with some caution because of the uncertainties involved in radiocarbon dating and in lake level reconstructions.

The FBTs at Bolton Fell Moss and Walton Moss probably represent relatively undisturbed successions to 'pseudo-raised bog' dominated by *Eriophorum vaginatum*, again under a climatic regime with insufficient effective precipitation to allow classical ombrotrophic mire formation. Contemporary lake status records indicate very low lake levels although they had begun to rise by the time of the two FBTs (Digerfeldt 1988, Figure 7. 5). The short lifespans of 90 - 120 years for the poor fens bridging the fen and *Eriophorum vaginatum* communities are a distinctive feature of the two transitions. Comparable communities in a very wet mire such, as Abbeyknockmoy Bog in the far west of Ireland, last for more than 250 years. The transitions in a relatively dry climate may be accelerated due to frequent drying out, which would increase the rate of oxidation and acidification.

Both *Carex paniculata* and carr woodland species such as *Salix spp.* and *Betula spp.* may have an important part to play in the acidification process, by providing locally isolated tussock tops (Walker 1970) and raised peat around root boles. Wiegiers (1986, 1990) has observed that rainwater tends to pond up in the locally raised areas of peat on the floor of fen carr woodland. A similar process may occur in *Carex paniculata* tussocks. With the conversion to a predominantly ombrotrophic hydrology, the surface areas of peat would be affected by leaching of bases. However, decoupling from the groundwater would be intermittent for a while until peat accumulated above the level of the highest inundation events. Seasonal drying of the peat surface may release H^+ ions due to the oxidation organic N compounds and sulphides (Section 7.2.1). These conditions favour the growth of *Sphagnum palustre* and other poor fen mosses such as *Calliergon stramineum*. The arrival of *Sphagnum* in a peatland systems marks a turning point in the mire's development (Walker 1970) since the species has a high cation exchange capacity with which to acidify the environment (Clymo 1964, Gagnon and Glimé 1992, Van Breeman 1995).

However, it is interesting to note that once the influence of minerogenic water had been removed from both Bolton Fell Moss and Walton Moss, as indicated by the demise of *Sphagnum palustre*, it was again dry mire species such as *E. vaginatum* and *Calluna vulgaris* that replaced the poor fen. The *Eriophorum vaginatum* dominated communities at Bolton Fell Moss, Walton Moss and Solway Moss had lifespans of approximately 2000 years. This is significantly longer than the dry *Eriophorum vaginatum* dominated lag phases recorded in two sites (Abbeyknockmoy Bog and Tregaron Bog) that became ombrotrophic during humid climatic phases (refer to Sections 7.2.3, 7.2.5 and 7.3). Therefore, the long pseudo-raised mire stages registered in the Cumbrian sites probably reflect a 2000 year period in which climatic conditions were too marginal for the development of true raised bogs. Until 10000 cal. B.P. the early Boreal climate was probably too dry to allow any form of raised oligotrophic peat formation, as indicated by the macrofossil evidence for breaks in peat formation, from Glasson Moss and Solway Moss. The lake level record (Digerfeldt 1988, Figure 7.6) indicates that effective precipitation levels rose only gradually from 10000 cal. B.P. enabling the onset of humified *Eriophorum vaginatum* peat accumulation. The relatively slow rate of climatic change might account for the persistence of *E. vaginatum* on the Cumbrian mires for over 2000 years, since a wet shift of considerable magnitude would have been required, to transform the dry early Boreal mires into oceanic *Sphagnum*-dominated raised bogs.

Several factors may enable the accumulation of *Eriophorum vaginatum* peats in conditions that are marginal for classical raised peat growth. The first is that *E. vaginatum* has very tough rhizomes and leaf vein fibres that are not readily broken down by micro-organisms. These elements are often the last remaining macrofossils in highly degraded peats (pers. obs.). Secondly, fibrous peats retain interstitial water better than a soil with a crumb structure (Okruszko 1993). Therefore, even when the water-table has dropped to a low level during a continental summer, *Eriophorum vaginatum* peat is likely to be able to retain interstitial water longer than many other peat types. This effect may be sufficient to prevent severe wastage or erosion during short dry spells. Thirdly, winter freezing of peat in a continental climate would prevent decomposition for a considerable period of the year. This would have the effect of significantly reducing the average annual rate of decomposition in the peatland, offsetting relatively high summer decomposition rates.

Eriophorum vaginatum is well adapted to cope with long periods of winter freezing since it is a common species of tundra vegetation (Wein 1973). The sedge is also relatively drought tolerant because its roots penetrate vertically down into the peat mass for depths up to 60 cm (Kummerow *et al.* 1988). *E. vaginatum* may even benefit from drying out of the surface peat in the late summer when it can take advantage of nutrients released by peat humification (Malmer 1993). It is particularly responsive to the release of P (Shaver *et al.* 1986), during peat humification. As the pH of the peat is reduced P increases in solubility, further increasing its availability for plant nutrition (Okruszko 1993).

The clustering of the four Cumbrian transitions in the latter half of the tenth millennium cal. B.P. is partly due to the fact that raised peat growth at Solway Moss and Glasson Moss was not possible during the time that their basal fens first developed above the water-table. These sites were probably prevented from developing any further until an amelioration in the climatic conditions occurred. This allowed sufficient time for Bolton Fell Moss and Walton Moss to develop up to the level of the general groundwater-table. These latter sites must have arrived at the point of accumulating above the water-table just after conditions became sufficiently humid for this to occur. The pollen diagrams for Bolton Fell Moss and Walton Moss (Figures 6.23 and 6.24) demonstrate that the date of peat initiation and accumulation rates at the two sites have been very similar, therefore it is not surprising that these two sites arrived at the FBT within a 380 years of each other. The similar physical settings of these two mires could be responsible for the apparent synchronicity of the basal stratigraphy.

7.2.3 Tregaron Bog.

Independent climate evidence suggests that the FBT at Tregaron, (7300 cal. B.P.) did indeed occur during a phase of significantly higher effective precipitation. The lake status record shows that water-levels were at their highest in the Scandinavian lakes at c. 7500 cal. B.P. (Digerfeldt 1988, Figure 7.6). Deuterium levels in the Scots pine record from the Cairngorms also indicate the presence of a marked pluvial phase at 7300 cal. B.P. (Dubois and Ferguson 1985, Figure 7.4). As noted in Section 6.6.2.1, the character of the transition at Tregaron differs little from the four Cumbrian sites where the existence of a relatively dry climate has been suggested as the cause of pseudo-raised mire development. The only difference in the development pathway at Tregaron is the much shorter lifespan of the *Eriophorum vaginatum* / *Calluna vulgaris* mire, before the emplacement of lawn conditions. However, the peatland complex at Tregaron differs significantly from the enclosed basins of the Cumbrian mires since it is dominated by the presence of the River Teifi. The role of change in the fluvial system and its impact on the surrounding peatlands is discussed in Section 7.4 in the light of the mismatch between peat stratigraphy and independent palaeoclimatic records.

7.2.4 Borth Bog and Mongan Bog.

The displacement of *Alnus glutinosa* by *Betula spp.* in the tussock tops of the swamp carr at Borth Bog (LMZ-BTH95-C and D) represents the first signs of base depletion at the site. However, it is noticeable that this change is not accompanied by a significant increase in the representation of *Sphagnum* macrofossils. Pollen samples taken from the carr levels also indicate low levels of *Sphagnum* spores at less than 1% of the pollen sum. The two records may indicate that surface conditions in the *Betula spp.* carr were too dry to allow significant *Sphagnum* growth. Walker (1970) suggests that under these circumstances further development of the mire sequence may be prohibited. However, in this case, the *Betula spp.* community lasted just 90 years before it was replaced by the pioneer oligotrophic mire, principally composed of *Pinus sylvestris*, *Eriophorum vaginatum* and *Pleurozium schreberei* at 6255 cal. B.P. (SRR- 5635). This assemblage (LMZ-BTH94-E) is indicative of a deep mire water-table.

At the time of the FBT in Borth Bog the surface wetness curve for Bolton Fell Moss registers dry conditions (Figure 7.8), in accordance with the lake level record from Scandinavia which reaches a low point at c. 6200 cal. B.P. (5500 uncal. B.P., Figure 7.6, Digerfeldt 1988). The deuterium record from the Cairngorms also registers weakly negative values from this time indicating the existence of a relatively less rainy period in Scotland (Figure 7.4). This suggests that the deep mire water-table was the result of a change to relatively drier climatic conditions, although rapid peat accumulation in the *Betula spp.* carr phase (see Figure 6.20) may also have contributed to the relatively dry mire surface.

Acidification in core BTH94 appears to have occurred without the intervention of *Sphagnum*. The production of H^+ ions as a by-product of nitrogen mineralization in the aerobic layers of the carr peat, may have been sufficient to create conditions suitable for the establishment of *Eriophorum vaginatum* and *Pinus sylvestris*. Once *P. sylvestris* has colonized a mire its presence contributes to further acidification. *Pinus* needles are rich in resin acids which produce a highly acidic peat upon decomposition (Buratti *et al.* 1990). In addition extracts from *Pinus* sapwood efficiently inhibit microbial decay (Bruce and Munro 1995). These two factors may account for the relatively rapid rate of oligotrophic peat formation in a period of inferred low effective precipitation. The end of the *Pinus* phase at Borth Bog is marked by a large increase in *Sphagnum sect. Acutifolia*. This may reflect a shift from a high hummock environment to low hummock conditions, reflecting a slight rise in the water-table sufficient to cause increased waterlogging in the rooting zone of the *Pinus* trees.

At Mongan Bog the macrofossil record of mire development strongly suggests a drop in mire water-levels at the time of the FBT. The *Phragmites* / *Cladium* fen of zone LMZ-MOG95-Bb ends abruptly at 5445 cal. B.P. (SRR-5731) to be replaced by dry *Pinus* / *Eriophorum vaginatum* / *Pleurozium schreberei* bog. Additionally, the field stratigraphy (Figure 6.6) shows that the FBT may be traced across more than 600 metres of the central part of the wetland basin, at the same altitude. This suggests that the transition was broadly synchronous across the middle of the mire and that the FBT registered in core MOG95 is representative of the main development pathway.

At the time of the FBT, just after 5445 cal. B.P. (SRR-5731), the mire surface wetness (Bolton Fell Moss), lake level and deuterium records all indicate an episode of drier climatic conditions, (see Figure 7.8, 7.6 and 7.4, respectively) suggesting that a reduction in effective precipitation was responsible for the fall in mire water-levels. In common with Borth Bog, the *Sphagnum* genus is poorly represented at the transition again indicating that acidification was primarily the result of peat humification and colonization by *Pinus sylvestris*.

However, the period of lower effective precipitation is unlikely to have been as severe as that experienced in the early Boreal period when Glasson Moss and Solway Moss were becoming ombrotrophic because

there is no evidence for a break in peat accumulation associated with the FBT at Mongan Bog. The accumulation rate calculated from the two dates straddling the FBT is virtually the same as that calculated from the two dates in the ombrotrophic peat (Figure 6.21).

To summarize, the evidence for Mongan Bog suggests that falling water-levels in the mire, which correlate to a period of reduced effective precipitation, enabled the surface layers to become more aerated and humified, causing acidification and the colonization of *Pinus sylvestris* and *Eriophorum vaginatum*. A similar process probably occurred at Borth Bog although the rapid accumulation of *Betula spp.* peat may have been partly responsible for the dry mire surface. It is interesting to note the distinct similarities between the pathways of development at Mongan Bog, Borth Bog and the Cumbrian mires, given that lake status records (Digerfeldt 1988) indicate that the FBTs at these sites occurred at times when water-levels were low, indicating periods of reduced effective precipitation.

7.2.5 Abbeyknockmoy Bog.

The pattern of lake status changes reported for northern Europe (Yu and Harrison 1995) indicate that western coasts were wetter than present at 11200 cal. B.P. (10000 uncal.). Changes in lake levels suggest that westerly winds became stronger by c. 10000 cal. B.P. although they probably followed a more northerly direction than present, skirting up the west coast of Ireland. Figure 7.7 shows that the lake site from Galway Bay, studied by Yu and Harrison (1995) registered consistently wetter conditions than present from 11200 (10000 uncal.) through to 9000 cal B.P. (8000 uncal.) with levels similar to the present day prevailing by 7800 cal B.P. (7000 uncal.).

Therefore, the FBT at Abbeyknockmoy Bog, dated to 8170 cal B.P. (SRR-5734), occurred at a time when precipitation levels were probably a little higher than or similar to the modern levels of 2000 mm yr⁻¹ for Galway Bay (Wallen 1970). The strongly oceanic climate is evident in the character of the transition to raised mire. Abbeyknockmoy Bog is the only site out of the eight studied for this project in which oligotrophic lawn species such as *Rhynchospora alba*, *Eriophorum angustifolium* and *Sphagnum tenellum* occur in the pioneer raised mire community. The FBT is also more gradual than most of the others studied for this project, taking twice as long as the FBT at Tregaron, for example.

Although the newly raised mire is distinctly wetter than similar communities identified from all the other sites there is a remarkable under representation of *Sphagnum*, considering the oceanic location of the site. *Rhynchospora alba* appears to take the place of the *Sphagnum* genus in the transitional communities. *Sphagnum tenellum* only appears in the record towards the top of LMZ-AKM95-E once *Rhynchospora alba* is well established. Whilst other *Sphagna* such as *S.s. Acutifolia* and *S. imbricatum*, are present in zone LMZ-AKM95-E and Fa they are rare. Additional short cores similar to those sampled at Solway

Moss would be required to establish whether this phenomenon was local or more widespread across the mire.

The lack of *Sphagna* and the strong presence of *Calluna vulgaris* in LMZ-AKM95-Fa (Figure 6.15) may indicate that the newly formed raised mire did not maintain a permanently high water-table throughout the year. *Eriophorum vaginatum* (Wein 1973) and other sedge species were able to grow vigorously under a regime of fluctuating water-table levels, possibly to the extent that *Sphagna* were excluded due to competition. One possible reason for an unstable water-table may be the lack of highly impermeable catotelmic peat just after the transition. The role of the peat structure in the course of the FBT is discussed in Section 7.3.

7.3 Edaphic factors influencing the character of the FBT.

Ingram (1982) proposed that the formation of a domed groundwater-table depended upon the presence of a layer of humified catotelmic peat possessing a low hydraulic conductivity. Thus the raised water-table would be maintained in dynamic equilibrium with the atmosphere due to impeded lateral water flow. Clearly, until sufficient humified catotelmic peat is present in a raised peatland system, high water-levels would tend to subside after rainstorms preventing the development of mire communities, indicative of low lawns and pools, even in a relatively wet climate. Capillary forces may contribute to raising the water-table in the first 50 cm of ombrotrophic peat accumulation (Granlund 1932). However, this height is likely to be less in peat dominated by *Eriophorum vaginatum* and *Calluna vulgaris* than in *Sphagnum* peat, due to the larger pore spaces created by supportive branches, twigs and rhizomes.

The production of a well aerated peat, either by drainage, uplifting by tree roots or by accumulation above the groundwater-table, would promote the formation of well humified peat through increased microbial activity. The rate of decay in the acrotelm is three orders of magnitude higher than in the catotelm (Clymo 1984b). Therefore, a phase of increased surface aeration, producing humified peat, may aid the formation of a domed water-table.

If the presence of occluded methane in the raised peat is important or even essential for the formation of a domed water-table, as suggested by Brown *et al.* (1989), a similar lag time, may be expected before the newly raised bog could maintain a permanently high water-table in response to high effective precipitation. The trapping of methane produced by the decomposition of peat depends upon the development of a sufficiently thick overburden. At present the shallowest depth at which occluded methane has been measured is 45 cm, in *Sphagnum* peat (Mathur *et al.* (1991). But this depth may vary according to the constituents of the peat and the peat structure. Although, the highest rates of methane production have been recorded from the acrotelm, most of this gas is released straight to the atmosphere.

The end of *Eriophorum vaginatum* / *Calluna vulgaris* domination at Abbeyknockmoy Bog, and Tregaron Bog, (both of which became ombrotrophic in periods of inferred higher effective precipitation) may represent the point at which the mire water-tables stabilized due to the accumulation of sufficient catotelmic peat to maintain a permanently wet mire surface throughout the year. Therefore, the rise to dominance of *Rhynchospora alba* probably represents the first time that the two mires closely reflect the prevailing climatic conditions. Similar autogenically controlled lags are probably present in the other six mires studied. However, in the Cumbrian mires in particular, the phase of dry raised peat formation continued much longer than the observed lag time at Tregaron Bog and Abbeyknockmoy Bog. The average lifespan for the dry raised mire communities in Cumbria is 2100 years compared to 1350 and 1270 years for Tregaron and Abbeyknockmoy Bog respectively. This suggests that the Cumbrian mires recorded a long phase of relatively dry climatic conditions after an initial lag period in which they may not have retained a reliable archive of the prevailing climate. However, as noted in Section 7.1, the lake level record and a number of other proxy records of climate change indicate that periods of relatively low effective precipitation occurred just before, or at, the time of the FBTs in the Cumbrian mosses, Borth Bog and Mongan Bog. The record of climate change contained within the raised peat is discussed further in Section 7.8.

Rhynchospora alba appears to be an important pioneer species in the newly formed lawn communities that follow the *Eriophorum vaginatum* / *Calluna vulgaris* phase. *R. alba* normally grows in mud bottom sites or in sparsely vegetated areas where competition is relatively low (Ohlson and Malmer 1990). Therefore, the species may be able to take advantage of the reduced vigour of competitors such as *Eriophorum vaginatum* under conditions of more continuous waterlogging.

7.4 Drainage basin change and the FBT at Tregaron Bog.

The circumstances surrounding the FBT at Tregaron South-East Bog are complicated by the presence of a major river system running through the middle of the peatland complex. Godwin and Mitchell (1938) have presented a wealth of interesting field stratigraphy and pollen data for the west bog, the south-east bog and the contact of the wetlands with the channel of the River Teifi. Several important points emerge from their study. The first is that the *Phragmites* beds of the south-east bog have extended up the valley sides and then retreated back again on a number of occasions, as revealed by the intercalation of *Phragmites* and brush wood peats (Figure 7.9). This indicates that the water-levels in the lake and reedswamp environments must have fluctuated on a number of occasions. Godwin and Mitchell (1938) have suggested that the reasons for these hydrological changes are linked to the accumulation of peat in the basin and changes in the fluvial system. On at least one occasion the competence of the Teifi increased sufficiently to enable the river to incise a channel through the *Phragmites* peat into the underlying silts and clays, prior to renewed ponding and the resumption of sedimentation in a low energy environment.

Secondly, Godwin and Mitchell (1938) have noted that the transition to raised mire, on the south-east bog, occurred immediately after a phase when open water was being rapidly overgrown by renewed *Phragmites* growth at the edge of the river channel whilst, at the margins of the mire, brushwood peat was recorded as extending out over the *Phragmites* beds. These stratigraphic changes are consistent with a significant fall in the general water-level of the wetland basin (Figure 7.9) at the time of the transition to raised bog. Furthermore, Figure 6.4 shows that the FBT is recorded at virtually the same altitude along a transect from the railway line to the channel of the Teifi, indicating that acidification occurred across the mire at much the same time. This interpretation is supported by radiocarbon dates sampled from the FBT by Hibbert and Switsur (1976) and also for the present project. Hibbert and Switsur (1976) examined a core approximately 100 metres from the eastern margin of the south-east bog, reporting a date of 7380 cal. B.P. (6530±110, Q939) for the upper contact of the *Phragmites* peat with the overlying raised mire peat. The equivalent date from core TSE94, sampled from the centre of the same mire, is 7320 cal. B.P. (SRR-5643).

The synchronicity of the transition across the mire supports the view that acidification resulted from a single trigger that affected the whole basin. Autogenic growth of oligotrophic peat above the level of the groundwater-table may be expected to start at one or a number of foci where the growing surface is sufficiently protected from inundation by mineral rich groundwater (Giller and Wheeler 1988), and then progressively spreads out over the surrounding fen once the surface has been raised by further peat accumulation. A comparison of pollen evidence and field stratigraphy / macrofossil records from the same core may be used to check whether there is a lag time between the increase in acid species in the pollen spectra and the arrival of those species at the core site. The pollen diagram from Hibbert and Switsur (1976) clearly shows that Ericaceae pollen rises at the FBT and not before. Similarly *Sphagnum* spores record a dramatic increase at the transition, from levels of less than 5% throughout much of the fen phase. Isolated peaks in the fen peat may have originated from minerotrophic *Sphagna*. Pollen levels were also completed from core TSE94 for the purpose of estimating the age of radiocarbon samples. Again pollen types from oligotrophic habitats are only registered within the raised mire peat, indicating that little or no oligotrophic mire vegetation existed in the basin until the simultaneous increase in these taxa at both the marginal and the central core sites. However, the pollen core sampled from the centre of the mire (TSE94) differs significantly from the margin in that it registers a lower frequency of *Sphagnum* spores.

To summarize, the evidence from Tregaron South-East Bog suggests that improved drainage in the wider Tregaron peatland basin caused the water-level of the mire to fall, thus decoupling the growing surface from the effects of mineral rich groundwater. This event occurred at a time when proxy climate indicators register a period of increased effective precipitation. The combination of falling groundwater-levels, leaving a perched fen peat layer, and relatively high levels of effective precipitation appear to have strongly favoured the rapid establishment of ombrotrophic mire.

Similar circumstances have been suggested for the formation of raised mire on part of the Emmen Bog complex in the Netherlands. Casparie (1972) found that humified ombrotrophic peat overlay an old fen surface which showed evidence for rapid drainage. An archaeological style excavation of the upper fen peat contact revealed numerous large desiccation cracks running across the surface. Casparie (1972, 1992/93) correlated the drainage event with a phase of hydrological change in the drainage network of the wider basin. Kulczynski (1949) inferred a similar set of processes for raised mire formation on fen peat in the Pripet Marshes driven by an autogenic mechanism. The locality studied by Kulczynski has a very subdued relief with permeable base-poor geology. Under these conditions most ombrotrophic mires were found to have formed without basal fens, on water partings where water flow was minimal. Fens were found to be located in the intervening valleys where water flow was greater. In the rare cases where fen preceded ombrotrophic mire Kulczynski proposed that fen peat accumulation would continue until it overtopped the sides of the shallow valleys. Once this had occurred the water could drain over the water parting in a new direction, reducing the input of minerotrophic waters to the surface fen peat. Raised mire would then form as a result of the switch to a predominantly ombrotrophic hydrology at the growing surface.

7.5 The impact of sea level change at Glasson Moss and Borth Bog.

The boundary of Glasson Moss lies within 500 metres of the south shore of the Solway Firth, with the uncut peat surfaces rising to between 10 to 15 metres above O.D. Core GLM95 is located 450 metres into the mire from the northern margin at an altitude of 11.8 metres O.D. The base of the 9.5 metre core lies at 2.3 metres O.D, which is approximately 1.7 metres below the present mean high-water mark of spring tides.

Figure 7.10, (Sea level curve for the eastern Solway Firth, after Haggart 1989) shows that the FBT at Glasson Moss (dated to 10655 - 9975 cal. B.P., 9935±45 - 9010±45 uncal. B.P.), occurred at a time when mean sea level in the eastern Solway Firth was rising rapidly. However, the apparent hiatus in peat growth at the FBT (Section 7.2.1) suggests that the mire system had not been affected by the rising base level at that time or that other factors such as climate change had more than compensated for the impact of sea level rise.

In zone LMZ-GLM95-F, *Sphagnum palustre* recolonized the mire indicating a re-coupling of the groundwater supply to the growing surface. Glasson Moss is the only one of the four Cumbrian mires studied to display this stratigraphic feature. The retrogressive succession may be a consequence of the rapidly rising sea level at 9705 cal. B.P. (8740±45 uncal. B.P., SRR-5726) causing backing up of the fresh groundwater supply. The macrofossil assemblages in LMZ-GLM95-F display two distinct fluctuations between domination by *S. palustre* and domination by *E. vaginatum*. These changes may reflect differences in the rates of water-level rise and peat accumulation, with *Eriophorum vaginatum* displacing

S. palustre, either when the rate of water-level rise was not so rapid or when the rate of peat accumulation accelerated.

The macrofossil diagram for Glasson Moss indicates a second phase of higher mire water-levels in LMZ-GLM95-H, as shown by the appearance of *Rhynchospora alba*. Again there are no comparable wet phases at the inland sites suggesting that the high water-levels are either a consequence of the continued rise in sea level or a result of the development of sufficient peat to maintain a relatively high mire water-table. There is insufficient data to distinguish between these two alternatives. Further radiocarbon dating and bulk density measurements might demonstrate whether peat accumulation slowed down prior to the wet phase enabling the rise in base level to outpace the rise in the growing surface of the mire.

The *Sphagnum cuspidatum* pool phase registered in LMZ-GLM95-J occurred at a time (7595 cal. B.P., 6790±45 uncal. B.P., SRR- 5725) when the rise of sea level had slackened to less than a quarter of the early Holocene rate (Figure 7.10). Therefore, it would seem unlikely that base level change was the trigger for the pool phase thus strengthening the argument, presented in Section 7.2.1, that an increase in effective precipitation was responsible for the wet shift.

At Borth Bog there appears to be little or no evidence to suggest that base level change affected the character of the succession to raised bog. Indeed the macrofossil record of the newly formed raised mire community is remarkably similar to the equivalent ombrotrophic vegetation at Mongan Bog, in the centre of Ireland. The base of the sequence at Borth indicates a removal of the marine influence from the core site shortly before 7035 cal. B.P. (6155±45 uncal. B.P., SRR-5637). This is illustrated in the macrofossil diagram (Figure 6.13) by the gradational contact between the underlying clay, containing brackish water foraminifera (analysed by Macfadyen for Godwin 1943) and freshwater *Phragmites* reedswamp peat (zones LMZ-BTH94-A to B). The generalized sea level curve for Cardigan bay at this time, shows that base level was rising, although at a considerably slower rate than that recorded for the earlier part of the Holocene. However, Wilks (1979) has proposed that a barrier began to form across the estuary mouth prior to c. 6400 cal. B.P. (5500 uncal. B.P.). This would have had the effect of reducing the tidal scour and increasing sedimentation rates in the estuary. Thus the onset of freshwater peat formation could have resulted directly from the protection afforded by the presence of the barrier.

After freshwater peat inception, accumulation rates in the reedswamp and carr phases were rapid, raising the mire surface at an average rate of 1 cm in 8.2 years, up to the time of the FBT. This magnitude of peat accumulation probably increased the altitudinal difference between mean sea level and the mire's growing surface, ensuring that the growing surface was protected from the much reduced rate of sea level rise (Figure 7.11) inferred for the phase of raised mire inception (at 6255 cal. B.P., 5460±45 uncal. B.P.).

The stratigraphy for Borth Bog, produced by William's, Parry and Parker (in Slater 1972), shows that a wedge of salt-marsh clay overlies raised bog peat at the mire's northern boundary with the Dovey estuary, indicating a renewed marine transgression. The clay bed occurs at the contact of the *Rhynchospora alba* / *E. vaginatum* peat, with fresh *S. imbricatum* peat. Godwin and Willis (1969) have radiocarbon dated the lower contact of the salt-marsh clay to c. 3000 cal. B.P (2900±110 B.P. uncal.).

Shi and Lamb (1991) have proposed that there were several minor oscillations in sea level registered in the sediments at the mouth of the Dovey estuary during the mid-Holocene. At the same level as the intercalated salt-marsh clay, a band of *Molinia caerulea* rich peat stretches across the bog almost to the centre. This is not recorded in core BTH95, however after the *Molinia* phase *S. imbricatum* mire developed at 3270 cal B.P. (3080±45 uncal. B.P., SRR-5633). It is possible that this change represents the backing up of acid mire waters as a consequence of salt-marsh clay deposition in the rand area, which would have the effect of creating an impermeable seal around a significant percentage of the mire's unconstrained boundary. More research using multiple macrofossil cores might help to shed light on this aspect of the mires development.

7.6 Human impact and the FBT.

Human activities such as burning, catchment deforestation, mire drainage, peat cutting, mowing and the grazing of livestock, have caused a variety of changes in wetland systems. Perhaps the most relevant of these anthropogenic impacts in the prehistoric context are catchment deforestation and burning.

The felling of trees in a catchment would result in increased runoff and leaching of soils. The effect may be similar to that of increased rainfall causing base depletion in soils (Frenzel 1983). Tallis (1973) has noted that woodland clearance could have been one of the factors driving base depletion in the Cheshire meres, where *Sphagnum* dominated schwingmoor developed directly over the open water. Pennington *et al.* (1972) have also considered the effect of deforestation in lake catchments concluding that large scale clearance produces similar changes in lake sediments to natural soil maturation.

Tipping (1995b) has proposed that prehistoric clearance may have been responsible for the transition to raised bog at a site in eastern Dumfriesshire. At Burnfoothill Moss the FBT is radiocarbon dated to 7700 cal. B.P. At this time the pollen spectra indicate evidence for 'anthropogenic interference' in the surrounding dry woodland with accompanying increases in the frequency of charcoal records in the mire. Tipping (1995b) has therefore suggested that increased runoff generated by deforestation, caused waterlogging of the fen surface, resulting in the establishment of ombrogenous plant communities. The field stratigraphy presented for Burnfoothill moss suggests that *Sphagnum*-rich peat immediately overlies the fen levels. However, the individual species have not been identified.

Only four of the mires studied for the present project have transitions that are young enough to have been potentially affected by a significant level of forest clearance, namely Borth, Tregaron, Mongan and Abbeyknockmoy Bogs. At Tregaron Bog the pollen diagram produced by Hibbert and Switsur (1976) shows no evidence of disturbance in the dry woodland immediately before or at the time of the FBT. The first increase in the main ruderal pollen types also postdates the transition. Pollen levels prepared for estimating the age of the peat prior to radiocarbon dating were checked for microscopic charcoal, with only very few fragments being recorded.

At Borth Bog pollen work completed by Moore (1968) suggests that the first anthropogenic impacts on the surrounding vegetation were only slight. The main clearance phases occur well after the FBT, with no apparent evidence for deforestation at the time of raised peat inception. Analysis of pollen slides prepared for the present project, for the depths covering the transition, revealed almost no microscopic charcoal. Similarly the record of macroscopic charcoal presented in the macrofossil diagram (Figure 613) shows that no records occur before the raised mire peat developed.

Pollen results for Mongan Bog (Bradshaw 1987) indicate that the first forest clearance phases occurred during the Neolithic period, with the main phases of clearance postdating the *Ulmus* decline and the FBT. Again analyses of microscopic and macroscopic charcoal provide no evidence for increased burning just prior to the inception of raised peat.

There are no comprehensive pollen records for Abbeyknockmoy Bog, however, pollen slides prepared for estimating the age of radiocarbon samples show similar results to the other three sites. Pollen frequencies indicate full forest cover at the time of the transition, with few traces of Poaceae pollen or microscopic charcoal. Therefore, the evidence from all four sites suggests that the surrounding catchments were largely undisturbed at the time of the FBTs. If there was human activity in the catchments, it was too small or localized to be recorded in the pollen and charcoal records and probably not of a sufficient magnitude to affect mire hydrology.

7.7 Models of raised mire inception.

Four basic models of ombrotrophic mire development may be recognized from the development pathways contained within the eight study mires. The first is the autogenic model, driven primarily by peat accumulation, in which other factors such as climate change are subordinate. The second and third models are closely related. Both propose that fluctuations in the level of effective precipitation provide the trigger for raised peat inception. The fourth model proposes drainage basin change as a trigger for raised mire inception. The four models are elaborated in the following sections.

7.7.1 Model 1 Autogenic raised mire inception.

In the autogenic model, peat accumulates up to the level of the water-table in a stable climate or at least during a period when changes in climate are too small to alter appreciably, the natural direction and rate of change. Further deposition of litter raises the peat surface above the level of permanent inundation. Two communities strongly favour the accumulation of peat well above the level of the water-table in the minerotrophic peatlands sampled for the present study. The first community is a *Carex paniculata* dominated tussocky swamp. *Carex paniculata* forms high tussocks that produce large quantities of litter, providing areas where the mire surface is locally isolated from the groundwater supply. Carr species, such as *Betula spp.* and *Alnus glutinosa* also produces large volumes of annual litter resulting in rapid peat accumulation (eg. Borth Bog, Figure 6.20). The growth of tree roots near the surface of the peat and the development of root boles also provides locally raised areas of peat.

The tussock tops and higher areas of the carr woodland floor become predominantly irrigated by rainwater, resulting in the leaching of bases. The surface layers of the peat also become aerated, particularly during the summer months, resulting in increased decomposition and acidification as the result of the mineralization of nitrogen compounds and the release of humic acids. These conditions enable mesotrophic Sphagna such as *S. palustre* to dominate, resulting in further acidification.

Continued accumulation above the level of the water-table favours the establishment of oligotrophic 'hummock-level' taxa such as *Eriophorum vaginatum*, *Calluna vulgaris* and *S.s. Acutifolia*, rather than aquatic or lawn species (except in the very wettest climates of the west of Ireland). These communities persist on the mire until sufficient catotelmic peat has developed to inhibit lateral drainage. The presence of humified catotelmic peat ensures that the water-table remains high throughout the summer months. Once this situation is achieved lawn communities frequently, dominated by *Rhynchospora alba*, establish on the mire.

If climatic conditions are too dry to enable the development of true raised mire, supporting carpets of lawn and pool Sphagna, the *E. vaginatum* / *Calluna vulgaris* phase may persist until the climate becomes sufficiently humid. The resulting oligotrophic mire is similar in character to present day vegetation described from central Europe and has been termed 'pseudohochmoor' (pseudo-raised bog).

The model presented above is similar to that described by Walker (1970).

7.7.2 Model 2 Dry shift climate change model.

In model 2 the trigger for acidification is a decline in the level of effective precipitation. This causes the mire water-table to fall, leaving a layer of poor fen peat perched above the water-table (Figure 7.12). This peat is leached by rainfall and will begin to humify in the aerobic conditions, causing acidification and the release of a range of plant nutrients (The precise response of peat to de-watering depends upon the peat

type). *Eriophorum vaginatum* is able to cope with these conditions because it has a deep rooting system. Additionally, phosphorous (P) becomes more widely available partly due to release upon decomposition and partly because it becomes more soluble at lower pH values. *Eriophorum vaginatum* responds particularly vigorously to a high availability of P in oligotrophic habitats. Consequently, *Eriophorum vaginatum* frequently dominates the pioneer oligotrophic community.

Several processes may favour the accumulation of *E. vaginatum* peat above the water-table in a climate that is marginal or too dry for other types of peat formation. These include annual freezing of the peatland which prevents the rapid breakdown of the previous summer's litter layer. Secondly, *Eriophorum vaginatum* has very tough leaves and rhizomes that are not readily broken down by microbial activity.

The resulting pseudohochmoor may persist for several millennia until an increase in effective precipitation enables lawn conditions to establish on the highly humified and undoubtedly very impermeable *E. vaginatum* peat.

7.7.3 Model 3 Dry -wet climate oscillation model.

Model 3 proposes that a change towards very dry conditions causes the end of peat accumulation in the fen and the production of a retardation layer. Some erosion may be associated with this event. The resulting aeration causes humification and acidification of the surface peat, in a similar manner to that suggested for both models 1 and 2. However, the change to a drier climate produces conditions that are unsuitable even for *Eriophorum vaginatum* peat formation. A subsequent increase in effective precipitation brings the peatland back into a climatic regime favourable for peat accumulation. *Eriophorum vaginatum* is again one of the main mire species in conjunction with other hummock-level species such as *Calluna vulgaris* and certain members of *S.s. Acutifolia*, such as *S. capillifolium* var. *rubellum* and *S. fuscum*. The mire development pathway proceeds in a similar way to model 2 from this point.

7.7.4 Model 4 Drainage basin change model.

In model 4 the trigger for acidification is increased drainage in the wider peatland complex. Improved drainage may be a result of river incision into a peat, alluvium or clay bed, as a result of increased competence. The release of a blockage or the cutting of a wide meander may have a similar affect. The groundwater-level in the peatland may fall sharply leaving a perched fen peat bed. If this occurs under a climatic regime of high effective precipitation, the establishment of oligotrophic mire conditions may be very rapid. The perched fen peat will undergo leaching by rainwater and acidification as a result of increased humification in aerobic conditions. Again *E. vaginatum* / *Calluna vulgaris* dominated mire is favoured, until the establishment of a sufficiently thick catotelmic peat layer results in stabilization of the raised mire water-table at a permanently high position.

7.8 The record of climate change within the ombrotrophic peat.

7.8.1 The Cumbrian mosses (Kettlehole mires).

All four Cumbrian mosses register major wet shifts in a relatively narrow temporal range from 7850 - 7430 cal. B.P. In chapter six these stratigraphic features were interpreted as representing a major increase in effective precipitation. The multiple coring work from Solway Moss, demonstrates very clearly, the synchronicity of the change over a very wide area of the peatland complex.

The lake status records from Scandinavia (Digerfeldt 1988) show that water-levels were at their highest between 8000 - 7500 cal B.P. (7300- 6700 uncal. B.P.). Similarly, the deuterium analyses from the Cairngorms register the presence of a significant pluvial phase at 7400 cal B.P (Figure 7.4) which possibly began earlier, although this is not known since 7400 cal. B.P. marks the beginning of the record. Therefore, the peat stratigraphy noted from Cumbria broadly agrees with other proxy records of effective precipitation.

The four hundred year spread in the dates for the wet shift in the four mosses may be partly a consequence of errors involved in radiocarbon dating and pollen correlation. The radiocarbon laboratory errors alone, could account for 90 years of the age range. Further errors are involved in the calibration process. When the 2σ confidence limits are taken into considered for the group of four dates the minimum age separation is just 210 years between the oldest and youngest assays. Equally the age range may relate to real lags in the response of individual mires to the increase in effective precipitation. The sensitivity of the mire would tend to depend upon the precise level of the mire water-table below the mire surface prior to the wet shift.

The detailed multiple coring work from Solway Moss (Chapter 5) showed that the mire response to a single wet shift varied locally. At some places lawn communities replaced hummock type vegetation, whilst in other places pools developed. The variety of lawn and pool species registered between the four Cumbrian mosses probably reflects a similar internal variability within each mire, controlled by site specific processes.

7.8.2 The large basin and floodplain mires.

Only two of the four bogs in the large basin and floodplain mire category demonstrate synchronous changes with respect to the first major colonization of lawn or pool *Sphagna*. Tregaron bog became an *S. imbricatum* mire at 4605 cal. B.P. whilst Abbeyknockmoy Bog developed into a similar mire at 4575 cal. B.P. The rise in *S. imbricatum* may reflect increased oceanic conditions. The stratigraphic changes certainly coincide with a marked decrease in the frequency of charcoal in the macrofossil assemblages of both sites. They also date to within 300 years of the major wet-shift registered at Bolton Fell Moss and in the deuterium record from the Cairngorms, dated to 4300 cal. B.P.

The mire sequences at Borth and Mongan Bogs are the youngest of the group, therefore their development pathways were less advanced at the time of the inferred wet shift. However, the first appearance of lawn species at Borth is recorded at 4425 cal. B.P. The records from Bolton Fell Moss and the Cairngorms suggest that the wet shift centred on 4300 cal B.P. was an event of considerable magnitude, therefore even the relatively insensitive fledgling raised mire may be expected to register some changes in vegetation composition. The FBT at Mongan Bog is the youngest of all, dated to 5445 cal. B.P. (SRR-5731). Consequently, this mire may be expected to be the least responsive to a mid-Holocene increase in effective precipitation. Examination of the relevant macrofossil diagram (Figure 6.14) suggests that this is indeed the case. However, Mongan Bog does register a significant stratigraphic change at 4625 cal B.P. (SRR-5730), marked by the sudden disappearance of *Pinus sylvestris* from the macrofossil record (zone LMZ-MOG95-C/D boundary). The replacement of *P. sylvestris* by *E. vaginatum* / *Calluna vulgaris* mire may represent a change from a high hummock to a low hummock environment, with the death of *P. sylvestris* triggered by flooding of the deeper rooting zone.

As discussed in Section 7.5 the rise of *S. imbricatum* at Borth Bog appears to be related to base level change and not climate. At Mongan Bog the first rise in *Sphagnum imbricatum* occurs at 2700 cal. B.P. (SRR-5729). This does correlate with a distinct wet shift at Bolton Fell Moss (Figure 7.8). Whilst there is insufficient data in the deuterium record to back up the correlation (Figure 7.4), the Scandinavian lake status record indicates that water-levels were rising rapidly through the relevant time period (Figure 7.6).

7.9 Summary of mire development pathways.

Walker (1970) classified the sequences of wetland development in his study of the rate and direction of change in British hydroseres, into 12 simplified types to enable comparative analysis of mire pathways (see Section 2.3.2.1). A similar approach has been adopted to provide a summary of mire development for the mires examined in the present study. Walker's original classification has been modified and extended to differentiate between wet and dry raised mire types. The generalized vegetation types are presented in table 7.1, which acts as the key to the transition matrices appearing in Figures 7.13a, 7.13b and 7.14 and to Tables 7.2 to 7.4.

Table 7.1 Classification of wetland types, modified from Walker (1970).

No.	Wetland type.
1	Salt-marsh
2	Unproductive water
3	Micro-organisms in open water and molluscs in open water.
4	Totally submerged macrophytes (or flowers only emerged)
5	Floating -leaved macrophytes, usually with some intervening open water
6	Reedswamp, rooted in the substratum and standing in more or less perennial water
7	Sedge tussock swamp, rooted in the substratum and standing in more or less perennial water
8	Fen, rooted in minerotrophic peat and waterlogged for much of the year.
9	Swamp carr, formed by trees growing on unstable sedge tussocks, with intervening pools
10	Fen carr, dominated by trees, with a ground layer of grasses and fen herbs all rooted in a physically stable peat mass.
11	Poor fen containing grasses sedges and a range of mesotrophic bryophytes
12	<i>Rhynchospora alba</i> , <i>Sphagnum tenellum</i> , <i>E. tetralix</i> ombrotrophic mire
13	<i>Eriophorum vaginatum</i> , <i>Calluna vulgaris</i> , <i>S.s. Acutifolia</i> , <i>Pinus sylvestris</i> ombrotrophic mire
14	<i>Rhynchospora alba</i> , <i>Eriophorum vaginatum</i> ombrotrophic mire
15	Lawn and pool <i>Sphagnum</i> dominated ombrotrophic mire.

Tables 7.2 and 7.3 provide a summary of the pathways of development for the 4 Cumbrian mosses and the large basin and floodplain mires respectively. The information contained within these 2 tables has been used to create the transition matrices appearing in Figures 7.13a and b and 7.14.

The transition matrix for the four Cumbrian mires (Figure 7.13a) shows that two of the four mires developed via a reedswamp phase whilst the remaining two mires passed directly from open water to swamp carr and fen carr. By contrast the matrix for the large basin mires (Figure 7.13b) shows that all sites contained reedswamp. This probably reflects the greater initial depth of water in the preceding lakes.

After the reedswamp phase the pathways of development become more varied with the transitions to oligotrophic mire communities immediately preceded by wetland stages 8 or 10 or 11, in the large and small basins. With the exception of one mire (Abbeyknockmoy Bog) all of the FBTs pass directly to stage 13 (*Eriophorum vaginatum* / *Calluna vulgaris* / *Pinus sylvestris* / *S.s. Acutifolia*) which represents a mire with a deep water-table. At Abbeyknockmoy Bog stage 12 (*Rhynchospora alba*, *S. tenellum*) precedes stage 13, probably reflecting the oceanic location of the mire.

Both the small basin and large basin mire transition matrices (Figures 7.13a and 7.13b) indicate that the ombrotrophic mire could either pass directly from 13 to 15 (*Eriophorum vaginatum* and associates to lawn

and pool *Sphagnum*) or passes through an intermediate phase, stage 14 (*R. alba*, *R. alba*/*E. vaginatum*). However, table 7.4 shows that the latter pathway is much more common. *Rhynchospora alba* clearly forms an important component of the development of the ombrotrophic mires. The species appears to be able to displace the *Eriophorum vaginatum* dominated communities that existed on many of the mires for between 1200 and 2100 years. Since *R. alba* is an annual species of wet mud bottom sites where competition is relatively low, the change to stage 15 may represent a reaction to die back in the *Eriophorum vaginatum* communities as a response to a rising water-table. *R. alba* is able to colonize disturbed or bare peat very quickly, creating a relatively continuous ground cover. This was observed at three of the vegetated core sites which were revisited 12 months after sampling with a Russian corer. In each case both trampled *Eriophorum vaginatum* tussocks and *Sphagnum* carpets lying close to the water-table had been superseded by a cover of *Rhynchospora alba*. The rapid colonization of *R. alba* may initially reduce the ability of *Sphagnum* species to react to the higher water-levels. Godwin and Conway (1939) found similar mud bottom *Rhynchospora alba* communities at Tregaron Bog that were very poor in *Sphagna*.

The stabilization of a previously fluctuating water-table, sea level rise or climate change may have caused the end of the *Eriophorum vaginatum* dominated stages noted in the macrofossil record. Although *E. vaginatum* may be found growing in shallow pools these are often ephemeral. The species grows vigorously when mire water-levels are high in the early spring and drop significantly by the end of the summer. Permanent waterlogging reduces the vigour of the species (Wein 1973).

The final stages of all of the sequences are *Sphagnum* lawns or pools. This simply reflects the cut off point used for examining the FBT macrofossil sequences.

Figure 7.14 represents a combination of the transition matrices for the small and large basins and therefore it is a concise summary of the entire data set examined for this project. Bold arrows indicate the dominant pathways of mire development. Although all of the mires followed different pathways, two dominant routes can be recognized leading up to the reedswamp stage, 2 - 3 - 6 and 2 - 4 - 6. Similarly there are two main pathways after the reedswamp stage 6 - 8 - 13 - 14 - 15 and 6 - 9 - 11 - 13 - 14 - 15. Figures 13a and 13b demonstrate that both of the principal pathways of mire development from *Phragmites australis* fen or reedswamp to raised bog occur in the large and the small basin mires.

The summary outlined above supports the findings of Walker (1970) which stressed that successions could be varied and reversible although a limited number of dominant mire development pathways could be discerned. Walker also highlighted the role of key communities such as *Phragmites australis*-dominated reedswamp which appear in most successions. Dry *Eriophorum vaginatum* / *Calluna vulgaris* raised mire and possibly wet *Rhynchospora alba* mire may be added to the list of key successional stages.

Table 7.2 Summary of mire development pathways in the Cumbrian mosses.

Cumbrian mosses	Summary of the mire development pathway.
Bolton Fell Moss	2 - 9 - 11 - 13 - 15 - 14 - 15
Walton Moss	2 - 6 - 9 - 11 - 13 - 15
Solway Moss	2 - 10 - 13 - 14 - 15
Glasson Moss	2 - 3 - 6 - 8 - 13 - 11 - 13 - 14 - 15

Table 7.3 Summary of the mire development pathways of the large basin and floodplain peatlands.

Large basin & floodplain mires	Summary of the mire development pathway.
Tregaron Bog	2 - 4 - 6 - 9 - 11 - 13 - 14 - 15
Borth Bog	1 - 6 - 10 - 13 - 14 - 15
Mongan Bog	2 - 4 - 6 - 8 - 13 - 14 - 15
Bog	2 - 3 - 6 - 8 - 12 - 13 - 15 - 14 - 15

Table 7.4 shows the frequencies of transitions between the separate wetland stages. The x-axis of the matrix represents the superseding vegetation stages, whilst the y-axis represents the antecedent wetland stages.

Table 7.4 Frequencies of transitions between vegetation stages for all eight mires.

		S	U	C	C	E	E	D	I	N	G	V	E	G	.		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	T
A	1						1										1
N	2			2	2		1			1	1						7
T	3						2										2
E	4						2										2
C	5																0
E	6								3	2	1						6
D	7																0
E	8												1	2			3
N	9											3					3
T	10													2			2
	11													4			4
V	12													1			1
E	13											1			5	3	9
G	14															7	7
.	15														2		2
	T	0	0	2	2	0	6	0	3	3	2	4	1	9	7	10	49

Chapter 8

Conclusions and Future Research.

8.1 Conclusions.

Detailed examinations of macrofossil records, field stratigraphies and independent proxy records of environmental change, indicate that allogenic processes may be identified as triggers for the fen/bog transition (FBT) in some mires. The operation of allogenic processes at the time of raised mire inception may be inferred from features such as retardation layers and breaks in peat accumulation immediately prior to the appearance of raised mire species. In addition some transitions display remarkable synchronicity across the entire mire expanse with rapid switches between reedswamp or fen communities and dry pseudo-raised mire. Radiocarbon dating clearly demonstrates the rapidity with which many of the transitions occurred. The cliff-like appearance of the DCA axis 1 scores at the transitions of Tregaron bog, Solway Moss, Glasson Moss and Mongan Bog clearly depict the rapid species replacements.

Four basic models of raised peat inception may be recognized from the group of eight mires studied for this project. The first is the autogenic model of peat accumulation, which is broadly parallel to that described by Walker (1970). The second model proposes that removal of the groundwater effect due to a dry shift in effective precipitation may cause the inception of pseudo-raised bog. The third model is similar and suggests that a climatic oscillation, of dry followed by relatively wetter conditions, may trigger raised peat growth. The fourth model suggests that a drainage basin change, which causes the water-table to fall in a groundwater-fed peatland, will facilitate the development of oligotrophic mire communities. Mire drainage due to change in the wider drainage basin seems to cause very rapid acidification, particularly if the trigger occurs during a humid climatic phase.

The general conclusion arising from the four models of mire development is that acidification is favoured when the growing surface of the mire becomes decoupled from the mineral rich groundwater supply, whether this is caused by a rising peat surface, as a consequence of peat accumulation and bioturbation, or by a falling water-table (or both).

The review of the literature suggests that other mechanisms of raised mire formation may be possible. Deforestation, leaching and the flooding of a fen surface with base-poor surface runoff may provide a very different route to ombrotrophic mire formation in which aquatic and lawn *Sphagna* play a dominant role at the transition.

Sphagnum is an important component of the mire community in four of the eight FBTs studied. *S. palustre* is the most common mesotrophic representative of the genus. However, the absence or very low occurrence

of *Sphagnum* in the other four transitions suggests that acidification of the peat to fully oligotrophic conditions is possible without the presence of *Sphagnum*. Transitional assemblages registering little or no *Sphagnum* have been found at Borth Bog, Mongan Bog, Abbeyknockmoy Bog and Glasson Moss.

Studies reviewed from the literature suggest that oxidation of previously anaerobic fen peats can lead to the liberation of a significant proton load. Peats rich in organically bound nitrogen compounds and Sulphides are particularly prone to acidification upon desiccation. These processes may account for the onset of acidification in the sites that experienced significant drying of the fen peat surface, due to accumulation above the water-table, reduced effective precipitation or change in the drainage basin network. However, the precise changes in the chemical composition of the peat after aeration are strongly dependent upon the original quality of the fen peat.

Artificial drainage must be distinguished from natural drying out of the fen surface. Artificial drainage is likely to enable much more complete humification of the peat liberating far greater concentrations of plant nutrients and is more likely to cause eutrophication of the peat. Severe drainage also results in the transformation of the peat from a fibrous to a crumb structure, making the rooting medium more prone to overdrying. All of these factors plus the very deep water-table tend to favour the development of poor heath or scrub, rather than mire vegetation.

Aerated conditions in the surface fen peat favour the establishment of *Eriophorum vaginatum* / *Calluna vulgaris* or *E. vaginatum* / *Pinus sylvestris* mire. This type of mire forms an important intermediate phase, in all of the peatlands studied, before the formation of true lowland ombrotrophic bogs dominated by lawn and pool *Sphagna*. The character of the *Eriophorum vaginatum*-dominated phase in Abbeyknockmoy Bog is rather wetter than that found at other sites and this is probably a reflection of the strongly oceanic conditions.

The initial dry surface (pseudo-raised bog) conditions in the four Cumbrian Mosses, Borth Bog and Mongan Bog may be the consequence of effective precipitation levels that were too marginal for the development of true *Sphagnum* dominated raised mires. This interpretation is supported by independent proxy climatic records (lake status changes), which register low water-levels at the time of the FBT, in Mongan Bog, Borth Bog and the Cumbrian Mosses.

However, the initial pseudo-raised bog phases may also form as the result of insufficient catotelmic peat to maintain a stable permanently high water-table. If this process was significant, the raised mire stratigraphy would register a lag period, immediately after the FBT, in which the mire communities are not necessarily a reliable indicator of the prevailing level of effective precipitation.

Abbeyknockmoy Bog and Tregaron Bog, both became ombrotrophic in conditions of inferred high effective precipitation. Both mires record *Eriophorum vaginatum* / *Calluna vulgaris* dominated phases just after the FBT. These communities would tend to confirm the existence of a lag phase. However, at Tregaron Bog the lag may be a result of continued decreases in the general peatland groundwater-level, caused by improved fluvial drainage. Abbeyknockmoy Bog is drier than may be expected from its oceanic position in the far west of Ireland. Contemporary lake level data indicates that effective precipitation values for Galway Bay were probably similar to present at the time of the FBT.

The pollen and macrofossil records from all eight mires suggest that any anthropogenic activity in the surrounding catchments was too limited to affect the hydrological regime of the mires during the periods when raised mire formation took place. None of the pollen records examined show any evidence for significant opening up of the forest canopy at the time of the transitions. Similarly, the records of macro and microscopic charcoal show that burning was relatively infrequent or absent from the surrounding areas immediately before and during the FBTs.

Neither Glasson Moss nor Borth Bog appear to have been affected by the rising sea levels in these two areas at the time of the FBT. Both sites developed dry *Eriophorum vaginatum* dominated mire vegetation, similar to that found in most of the other mires, at the equivalent stage in the development pathway. Comparisons of the macrofossil sequence from Glasson Moss with the other three Cumbrian mires suggest that the effects of base level rise and ponding of fresh groundwater were registered in Glasson Moss during two separate phases. In the first phase the oligotrophic peat was only a thin layer when ponding occurred, resulting in re-coupling of the mire to the groundwater system. In the second phase the oligotrophic peat was significantly thicker, therefore the rising water-table resulted in the establishment of oligotrophic lawn species, notably dominated by *Rhynchospora alba*. A similar stratigraphy has been found at Borth Bog where the displacement of *Eriophorum vaginatum* by *Rhynchospora alba* coincided with the extension of salt-marsh communities onto the northern margin of the raised mire.

Rhynchospora alba plays an important role in the development pathways of nearly all the mires studied. The species is often the first indicator of lawn conditions on the mires at the end of the *Eriophorum vaginatum* mire phases, whether the wet surface conditions are the result of autogenic soil development, climate change or base level rise. *Rhynchospora alba* may be taking advantage of the reduced vigour of *Eriophorum vaginatum* in permanently wet conditions. Whilst *Eriophorum vaginatum* may grow in wet habitats and has been recorded growing on pool margins, the species prefers a fluctuating water-table. *Rhynchospora alba* is a species of mud bottom sites where competition is low. Therefore, the appearance of *R. alba* may indicate die back in the *Eriophorum vaginatum* stands leaving exposed mud areas.

The raised mire peat stratigraphy records two main phases of lawn and pool *Sphagnum* establishment at c 7800 and c.4600 B.P. These phases appear to coincide with periods of high effective precipitation which

have been inferred from independent proxy records of effective precipitation. The wet shifts may have provided the trigger for the displacement of *Rhynchospora alba* and other sedge species by *Sphagna*.

8.2 Future research.

8.2.1 Chronology.

The use of conventional radiocarbon dating in the present study has placed constraints upon the conclusions that may be drawn. Dating errors arise from a number of the steps in the processing of a radiocarbon assay, as described in Section 5.10.1.2. Imprecision is introduced immediately into the dating process by the use of an 8 cm slice of peat from the Russian peat sampler. Subsequently, laboratory preparation and processing errors result in a degree of inaccuracy in the order of 80 to 100 years (for the samples presented in this project), for the final uncalibrated date. Calibration introduces further uncertainties into the age estimate. The concentration of radiocarbon in the atmosphere has not changed in a linear fashion over time, consequently a single age estimate may intersect the calibration curve at more than one place, giving several possible calibrated dates for the original assay. Once these factors have been considered, it must be remembered that the activity of the peat sample, as it is extracted from the ground may not be a true reflection of the sample's age due to a number of sources of natural contamination, such as rootlet penetration and the hard water effect (see Section 5.10.1.2.)

As far as possible steps were taken to minimize errors. For example obvious root material was extracted from the peat matrix, using clean stainless steel tweezers, prior to dating. In most cases radiocarbon samples were placed to take advantage of wood layers in the fen peat so that the dating of *Phragmites* remains could be avoided. *Phragmites* has very deep rooting systems which could introduce considerable error. *Phragmites* was dated when it was immediately overlain by acid peat because it was easy to distinguish any stray roots from species such as *Eriophorum vaginatum*. In the oligotrophic peat, *Sphagnum* levels were targeted for dating so that root material could be more readily avoided.

The results of the radiocarbon dating programme show that none of the dates are inverted with respect to their depths even though many of the assays are closely spaced. Skeleton pollen diagrams, prepared to check for problems in the radiocarbon dates, indicate that only SRR-5646 is obviously inaccurate. This date is placed just above the FBT at Solway Moss and appears to have been contaminated by younger carbon from penetrating rootlets. Other dates may suffer from the same problem; however any inaccuracies are not of sufficient magnitude to be obvious.

Further research into rates of change in peatlands and the synchronicity of stratigraphic events would benefit greatly from the use of additional dating techniques such as tephrochronology and accelerator mass spectrometry (AMS) radiocarbon dating. A number of distinct tephra layers have been identified in Ireland (Pilcher and Hall 1992), Scotland (Dugmore *et al.* 1995) and Northern England (Mauquoy forthcoming)

that provide accurately dated isochrones. Further investigations at sites as far south as Church Moor in the New Forest and the Somerset levels, may significantly extend the coverage of the tephrochronology in the near future (pers. comm. Dr Hall and Prof. Pilcher). The increased precision offered by the use of tephra dating would enable the degree of synchronicity to be more closely assessed. It would offer the ability to distinguish lags between events from dating error and provide the precision required to undertake more detailed studies of rates of change in wetland systems.

Tephrochronology has the disadvantage that dated levels cannot be placed at interesting points in the stratigraphy. Where this kind of dating is required, AMS samples may offer a significant advantage over bulk assays particularly in fen and oligotrophic sedge dominated peats. The very small sample size required, enables individual seeds or leaves to be dated. This would allow dates to be positioned closer together if necessary. Two dates could be placed in a very thin fen deposit where the depth would normally allow only one bulk date. Fewer compromises would have to be made in the positioning of sample levels, as there would be no need to restrict sampling to specific peat types. AMS dates also overcome the problem of having to use an 8 cm slice of peat.

8.2.2 Integrating the peatland record with changes in early Holocene climate.

One of the main difficulties encountered during the study of the various peatland development pathways is the relative lack of independent local climate records covering the early to mid-Holocene. The period from 10000 cal. B.P. to approximately 6500 cal. B.P. appears to be particularly under represented in the U.K., since it postdates the time interval covered by most researchers interested in the Late-glacial period and pre-dates the start of most peat based proxy records.

The ability to integrate a local proxy record of change in effective precipitation with changes in fen and raised bog stratigraphy could significantly improve the understanding of mire development processes. One possible way of achieving this aim would be to conduct a paired site analysis of a neighbouring lake and raised bog. An examination of the change in lake status could be used to provide the necessary proxy record of change in effective precipitation in the locality of the raised bog. The Cheshire meres may provide an opportunity to undertake this kind of research.

8.2.3 More precise indicators of mire water-levels.

Both testate amoebae and non-pollen microfossil analyses offer further opportunities to study changes in mire water-levels at the time of the FBT. Woodland (1996) has established the ecology of the main oligotrophic testate amoebae species. These animals are sensitive to changes in water-levels and may be used to distinguish between wetter and drier phases within the tolerance of vegetative communities. The rapid life cycle of testate amoebae (six to seven generations per year) means that it may be possible to distinguish phases of fluctuating water-tables as shown by mixed assemblages of wet and dry species. *Sphagnum* forms the main habitat for the amoebae, therefore *Sphagnum*-poor *Eriophorum*

vaginatum/*Calluna vulgaris* peat may provide a rather poor fauna. In addition, little is known yet of the ecology of the fen species. Therefore, further research would be required to examine the ecology of fen types if these species are to be used as indicators of water-levels. Since pH is also thought to be a significant determinant in the distribution of testate amoebae it may be possible to use reconstructed faunas to infer changes in palaeo-pH level within peat.

Testate amoebae are generally less robust than pollen grains, although some species do survive pollen preparations. Therefore the degree of differential preservation in different kinds of fen and carr environments may require examination.

Some of the non-pollen microfossil types identified by Van Geel (1978) indicate wet or dry mire conditions, offering another method of improving the detail of water-level reconstructions. Blackford (1990) has used a selection of indicator types for studying climate change in blanket peats. Similar analyses could be extended to the study of the FBT levels, using pollen slides that have already been prepared for pollen correlation.

8.2.4 Multiple macrofossil analyses from a single mire.

The multiple coring programme undertaken at Solway Moss, significantly increased the understanding of the way in which the mire developed. Further research into the FBT may benefit from similar analyses at further sites. Abbeyknockmoy Bog would provide an interesting candidate for this kind of study since it would reveal how widespread the *Rhynchospira alba* community is at the transition. It would also show whether or not *Sphagnum* was a significant part of the FBT at this most westerly site.

8.2.5 The Tregaron mire complex.

Skeletal pollen analyses from the west mire in the Tregaron peatland complex (Godwin and Mitchell (1938) suggest that the FBT differed in character from the south-east bog studied as part of the present project. In the west bog the pollen of oligotrophic taxa such as *Calluna vulgaris* rises well before the field stratigraphy registers the presence of macrofossils of the same species in at the sample site. The field stratigraphy also suggests that the contact between fen and raised mire peat is more gradational. A second macrofossil diagram from the west bog may provide an insight into how the east bog might have developed under conditions of stable or rising groundwater, providing an interesting comparison of the effects of differing hydrological regimes.

8.3 A final remark.

The detailed investigation of early to mid-Holocene peat deposits, using evidence from the full macrofossil record, pollen analysis and radiocarbon dating, has provided a fresh perspective on one of the most fascinating landscape changes of the last 11,000 years, namely the transition from diverse minerotrophic peatlands to lowland raised mires. This thesis stresses the importance of both allogenic and autogenic

factors in determining the course of the FBT and the diversity of parallel mechanisms involved in the process. Further research, including the application of tephrochronology to the study of the FBT and the integration of mire development reconstructions with independent climate reconstructions, will undoubtedly advance the understanding of this important subject area. An appreciation of the ways in which lowland ombrotrophic mires developed in the past may prove to be particularly valuable for peat-based climate change research and for present and future rehabilitation programmes, at sites damaged by peat extraction.

References.

- Aaby B. 1976 Cyclic climatic variations in climate over the past 5,500 yr reflected in raised bogs. *Nature* **263**, 281-284.
- Aaby B. and Tauber H. 1975 Rates of peat formation in relation to degree of humification and local environment, as shown by studies of raised bog in Denmark. *Boreas* **4**, 1-17.
- Aerts R. , Wallén B. and Malmer N. 1992 Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. *J.Ecol.* **80**, 131-140.
- Allemeersch L. 1991 Peat in the Belgian eastern coastal plain. In Gullentops F. ed., *Wetlands in Flanders. Contributions to palaeohydrology of the temperate zone in the last 15000 years.* pp 1-53. Aardkundige Mededelingen **6**, Leuven University Press.
- Almendinger J.C., Almendinger J.E. and Glaser P.H. 1986 Topographic fluctuations across a spring fen and raised bog in the lost river peatland, northern Minnesota. *J. Ecol.* **74**, 393-401.
- Almquist-Jacobson H. and Foster D.R. 1995 Towards an integrated model for raised-bog development: theory and field evidence. *Ecology* **76**(8), 2503-2516.
- Anderson D.S., Davis R.B. and Janssens J.A. 1995 Relationships of bryophytes and lichens to environmental gradients in Maine peatlands. *Vegetatio* **120**, 147-159.
- Andrus R.E. 1986 Some aspects of the *Sphagnum* ecology. *Can. J. Bot.* **64**, 416-426.
- Armesto J.J. and Pickett S.T.A. 1986 Removal experiments to test mechanisms of plant succession in oldfields. *Vegetatio*. **66**, 85-93.
- Arnold G. 1992 Soil acidification as caused by the nitrogen uptake pattern of Scots pine (*pinus sylvestris*). *Plant and Soil*. **142**(1), 41-51.
- Atkinson M. D. 1992 *Betula pendula* Roth *B. verrucosa* Ehrh. and *B. pubescens* Ehrh. *J. Ecol.* **80**, 837-870.
- Atkinson T.C., Briffa K.R. and Coope G.R. 1987 Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature* **325**, 587-592.
- Backéus I. 1972 Bog vegetation re-mapped after sixty years - a review. *Oikos*. **23**, 384-393.
- Backéus I. 1990 The cyclic regeneration on bogs - an hypothesis that became an established truth. *Striae* **31**, 33-35.
- Bannister P. 1964 The water relations of certain heath plants with reference to their ecological amplitude. III Experimental studies: general conclusions. *J. Ecol.* **53**, 500-509.
- Barber K.E. 1976 History of vegetation. In Chapman S.B. ed., *Methods in plant ecology.* pp 5-83. Blackwell, Oxford.
- Barber K.E. 1978 *A palaeoecological test of the theory of cyclic peat bog regeneration.* Unpublished Ph.D. thesis, University of Southampton.
- Barber K.E. 1981 *Peat stratigraphy and climate change. A palaeoecological test of the theory of cyclic peat bog regeneration.* A A Balkema Press, Rotterdam.

- Barber K.E. 1984 A large-capacity Russian-pattern sediment sampler. *Quaternary Newsletter*, 28-31.
- Barber K.E. 1987 *Wessex and Isle of Wight field guide*. p33-44. Quaternary Research Association, Cambridge.
- Barber K.E. 1993 Peatlands as scientific archives of past biodiversity. *Biodiversity and Conservation* 2, 474-489.
- Barber K.E. 1994 Deriving Holocene palaeoclimates from peat stratigraphy: some misconceptions regarding the sensitivity and continuity of the record. *Quaternary Newsletter* 72, 1-9.
- Barber K.E. 1995 *Palaeoecological research on Bolton Fell Moss: recent changes in the macrofossil stratigraphy of Bolton Fell Moss, Cumbria, and the prediction of bog response to higher water tables*. Final report to the Nature Conservancy Council of England, Contract No: F14/01/440. Department of Geography, Southampton University.
- Barber K.E. 1996 *Assessing the variability of the palaeoecological and palaeoclimatic record of Walton Moss and Bolton Fell Moss, Cumbria*. Final report to NERC on research grant GR9/01646. Department of Geography, Southampton University.
- Barber K.E. and Clarke. M.J. 1987 Cranes Moor, New Forest: palynology and macrofossil stratigraphy. In Barber K.E. ed., *Wessex and Isle of Wight field guide*. p33-44. Quaternary Research Association, Cambridge.
- Barber K.E., Chambers F.M. and Maddy D. 1994 (b) *Spatial and temporal variability of Late Holocene palaeoclimates derived from peat stratigraphy*. Final report to NERC on Palaeoclimate Special Topic Grant GST/02/539, 1-22.
- Barber K.E., Chambers F.M., Maddy D. and Stoneman R. 1994 (a) A sensitive high-resolution record of late Holocene climatic change from a raised bog in Northern England. *The Holocene* 4(2), 198-205.
- Barkman J.J. 1992 Plant communities and synecology of bogs and heath pools in the Netherlands. In Verhoeven J.T.A. ed., *Fens and bogs in the Netherlands: vegetation history, nutrient dynamics and conservation*. Geobotany 18. Kluwer Academic Publishers.
- Barkman J.J. and Sykora K. V. 1988 *Dependent plant communities*. SPB Academic Publishing, The Hague.
- Bartley D.D. 1960 Rosgoch Common, Radnorshire: stratigraphy and pollen analysis. *New Phytol.* 59, 238.
- Bartley D.D. 1966 Pollen analysis of some lake deposits near Bamburgh in Northumberland. *New Phytol.* 65, 141.
- Bayfield N.G. 1973 Notes on water relations of *Polytrichum commune* Hedw. *J. Bryol.* 7, 607-617.
- Becker B. and Kromer B. 1993 The continental tree-ring record - absolute chronology, ^{14}C calibration and climatic change at 11 ka. *Palaeogeography, Palaeoclimatology, Palaeoecology* 103, 67-71.
- Beckett S.C. and Hibbert F.A. 1979 Vegetational change and the influence of prehistoric man in the Somerset Levels. *New Phytol.* 83, 577-600.
- Behre K.E. 1978 Die Klimaschwankungen im europäischen Præboreal. *Petermanns Geographische Mitteilungen* 2, 97-102.
- Beijerinck W. 1947 *Zadenatlas der Nederlandsche flora*. Veenman, Wageningen.

- Bellamy D. 1968 An ecological approach to the classification of European mires. *Proc. 3rd Int. Peat Congr.* 74-79, International Peat Society, Quebec.
- Bellamy D. 1972 Templates of peat formation. *Proc. 4th Int. Peat Congress.* Helsinki. Vol. 1, 7-17.
- Bellamy D.J. and Rieley J. 1967 Some ecological statistics of a "miniature bog". *Oikos* 18, 33-40.
- Benn D.I., Lowe J.J and Walker M.J.C. 1992 Glacier response to climatic change during the Loch Lomond Stadial and early Flandrian: geomorphological and palynological evidence from the Isle of Skye, Scotland. *J. Quat. Sci.* 7(2), 125-144.
- Bennett K.D. 1983 Postglacial population expansion of forest trees in Norfolk, U.K. *Nature*. 303, 161-167.
- Berger A.L 1978 Long-term variations of daily insolation and Quaternary climatic changes. *J. Atmos. Sci.* 35, 2362-2367.
- Berggren G. 1969 *Atlas of seeds and small fruits of northwest European plant species, with morphological descriptions. Part 2. Cyperaceae.* SNSRC, Stockholm.
- Berggren G. 1982 *Atlas of seeds and small fruits of northwest European plant species, with morphological descriptions. Part 3.* SNSRC, Stockholm.
- Berglund B.E. 1986 *Handbook of Holocene palaeoecology and palaeohydrology.* Wiley, Chichester.
- Berglund B.E. 1979 *Palaeohydrological changes in the temperate zone in the last 15,000 years, subproject B. lake and mire environments.* Vol 3, pp340, International Geological Correlation Programme, Project 158, Lund.
- Berglund B.E. 1986 *Handbook of Holocene palaeoecology and palaeohydrology.* John Wiley and Sons, Chichester.
- Berglund B.E., Aaby B., Digerfeldt G., Fredskild B., Huttenen P., Hyvarinen H., Kaland P.E., Mue D. and Vascari Y. 1983 Palaeoclimatic changes in Scandinavia and on Greenland - a tentative correlation based on lake and stratigraphical studies. *Quaternary Studies in Poland* 4, 27-44.
- Birks H.H. 1973 Modern macrofossil assemblages in lake sediments in Minnesota. In Birks H.J.B. and West R. G. eds. *Quaternary Plant Ecology.* pp 173-189. Blackwell, Oxford.
- Birks H.J.B. 1965 Late-glacial deposits at Bagmere, Cheshire and Chat Moss, Lancashire. *New Phytol.* 64, 270.
- Birks H.J.B. 1989 Holocene isochrone maps and patterns of tree-spreading in the British Isles. *J. Biogeog.* 16, 503-540.
- Birks H.J.B. 1995 Statistical modelling of Quaternary science data. In Maddy D. and Brew J.S. eds. *Statistical modelling of Quaternary science data.* Technical Guide No.5, Quaternary Research Association. Cambridge.
- Birks H.J.B. and Birks H.H. 1981 *Quaternary paleoecology.* Arnold, London.
- Birks H.J.B. and West R.G. 1973 *Quaternary plant ecology.* 173-189. Blackwell, Oxford.
- Birse E.L. 1980 *Plant communities of Scotland: A preliminary phytocoenonia.* Macaulay Institute for Soil Research, Aberdeen.

- Birse E.L. 1984 *The phytocoenonia of Scotland: additions and revisions*. Macaulay Institute for Soil Research, Aberdeen.
- Blackford J.J. 1990 *Blanket mires and climatic change: a palaeoecological study based on peat humification and macrofossil analyses*. Unpublished Ph.D. thesis, Keele University.
- Boatman D.J. 1983 The Silver Flowe nature reserve, Galloway, Scotland. *J. Biogeog.* **10**, 163-274.
- Boatman D.J. and Armstrong W. 1968 A bog type in north-west Sutherland. *J.Ecol.* **56**, 129-141.
- Boggie R., Hunter R.F. and Knight A.H. 1958 Studies of the root development of plants in the field using radioactive tracers. *J. Ecol.* **46**, 621-639.
- Bowen E.J. 1931 Water conduction in *Polytrichum commune*. *Ann. Bot.* **45**, 175-200.
- Bradshaw R 1987 The early impact of man. In Tubridy M ed., *The heritage of Clonmacnoise*. Environmental Sciences Unit, Trinity College, Co. Offaly.
- Braun E.L. 1950 *Deciduous forests of eastern North America*. Blakiston, Philadelphia.
- Braun-Blanquet J. 1928 *Pflanzensoziologie. Grundzuge der vegetationskunde*. Springer, Berlin.
- Brown A., Mathur S.P. and Kushner D.J. 1989 An ombrotrophic bog as a methane reservoir. *Global Biogeochem. Cycles* **3**, 205-213.
- Brown A.D. and Overend R.P. 1993 Methane metabolism in raised bogs of northern wetlands. *Geomicrobiol. J.* **11**, 35-48.
- Bruce P.R.W and Munro A.G. 1995 The effect of water soluble Scots pine (PS) and sitka spruce [*Picea sitchensis* (BONG) carr] heartwood and sapwood extracts on the growth of selected *Trichoderma* species. *International Biodeterioration and Biodegradation.* **35(4)**, 355-367.
- Burratti L., Allais J.P. and Barbier M. 1990 A resin acid from *Pinus sylvestris* needles. *Phytochemistry* **29(8)**, 2708-2709.
- Carey P.D. and Watkinson A.R. 1993 The dispersal and fates of seeds of the winter annual grass *Vulpia ciliata*. *J. Ecol.* **81**, 759-767.
- Casparie W.A. 1972 Bog development in south-eastern Drenthe. *Vegetatio.* **25**, 1-271.
- Casparie W.A. 1993 The Bourtanger Moor: endurance and vulnerability of a raised bog system. *Hydrobiologia* **265**, 203-215.
- Casparie W.A. and Streefker K. 1992 Climatological stratigraphic and paleo-ecological aspects of mire development. In Verhoeven J.T.A. ed., *Fens and bogs in the Netherlands: Vegetation history, nutrient dynamics and conservation*, 85-133. Geobotany 18. Kluwer Academic Publishers
- Catling P.M. 1996 *Carex oligosperma* x *Carex rostrata*, a new natural hybrid in section visicariae from northern Ontario. *Can. J. Bot.* **74(1)**, 91-97.
- Chambers F.M. ed. 1993 *Climate change and human impact on the landscape*. Chapman and Hall, London.
- Chambers F.M. and Price S.M. 1985 Palaeoecology of *Alnus* (alder): early post glacial rise in a valley mire in northwest Wales. *New Phytol.* **101**, 333-344.

- Chapman S.B. 1964 The ecology of Coom Rigg Moss, Northumberland. I Stratigraphy and present vegetation. *J. Ecol.* **52**, 299-313.
- Chapman S.B. 1965 The ecology of Coom Rigg Moss, Northumberland. III. Some water relations of the bog system. *J. Ecol.* **53**, 371-384.
- Chapin F.S. III and Tyron P.R. 1982 Phosphate absorption and root respiration of different plant growth forms from northern Alaska. *Holarctic Ecology* **5**, 164-171.
- Clarke M.J. 1988 *Past and present mire communities of the New Forest and their conservation*. Unpublished Ph.D thesis, University of Southampton.
- Clements F.E. 1916 Plant succession: an analysis of the development of vegetation. *Carnegie Institute of Washington Publication*. **242**, 1-512.
- Clymo R.S. 1963 Ion exchange in *Sphagnum* and its relation to bog ecology. *Ann. Bot. N.S.* **27**, 310-324.
- Clymo R.S. 1964 The origin of acidity in *Sphagnum* bogs. *Bryologist*. **67**, 427-431.
- Clymo R.S. 1965 Experiments on breakdown of *Sphagnum* in two bogs. *J. Ecol.* **53**, 747-757.
- Clymo R.S. 1978 A model of peat bog growth. In Heal O.W. and Perkins D.F. eds. *Ecological studies 27: Production ecology of British moors and montane grasslands*. Springer-Verlag, Berlin.
- Clymo R.S. 1981 Peat growth. In Simmons I.G. and Tooley M. eds. *The environment in British prehistory*, Gerald Duckworth and Co., London.
- Clymo R.S. 1983 Peat. In Gore A.J.P. ed., *Ecosystems of the world 4A. mires: swamp, bog, fen and moor. General studies*. 159-224. Elsevier Science, Amsterdam.
- Clymo R.S. 1984a *Sphagnum*-dominated peat bog: a naturally acid system. *Phil. Trans. Roy. Soc. Lond.* **B 305**, 487-499.
- Clymo R.S. 1984b The limits to peat bog growth. *Phil. Trans. Roy Soc. Lond.* **B 303**, 605-654.
- Clymo R.S. 1992 Productivity and decomposition of peatland ecosystems. In Bragg O.M., Hulme P.D., Ingram H.A.P. and Robertson, *Peatland ecosystems and man; an impact assessment*. University of Dundee, Dundee.
- Clymo R.S. 1992 /1993 Models of peat growth. *Suo* **43(4-5)**, 127-136.
- COHMAP Members 1988 Climatic changes in the last 18,000 years: observations and model simulations. *Science* **241**, 544-547.
- Colinvaux P. 1986 *Ecology 2*. John Wiley and Sons, New York.
- Connel J.H. and Slatyer R.O. 1977 Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* **111**, 1119-1144.
- Connel J.H., Noble I.R. and Slatyer R.O. 1987 On the mechanisms producing successional change. *Oikos*. **50**, 136-137.
- Conway V.M. 1948 von Posts's work on climatic rhythms. *New Phytol.* **47**, 220-237.
- Conway V.M. 1954 Stratigraphy and pollen analysis of southern Pennine blanket peats. *J. Ecol.* **42**, 117-147.

- Constantz J.W.N., Herkelrath and Murphy F. 1988 Air encapsulation during infiltration. *Soil Sci. Soc. Am. J.* **52** 10-16.
- Cooper W.S. 1926 The fundamentals of vegetation change. *Ecology* **7**, 391-413.
- Coulson J.C. and Butterfield J. 1978 An Investigation of the biotic factors determining the rates of plant decomposition on blanket bog. *J. Ecol.* **66**, 631-650.
- Cowles H.C. 1899 The ecological relations of the vegetation on the sand dunes of Lake Michigan I. Geographical relations of the sand dune flora. *Bot. Gaz.* **27**, 95-117, 167-202, 281-308, 361-391.
- Cowles H.C. 1901 The physiographic ecology of Chicago and vicinity: a study of the origin, development and classification of communities. *Bot. Gaz.* **31**, 73-108, 145-182.
- Cowles H.C. 1911 The causes of vegetative cycles: Contributions from the Hull Botanical Laboratory, 143. *Bot. Gaz.* **51**, 161-183.
- Cronberg N. 1989 Patterns of variation in morphological characters and isoenzymes in populations of *Sphagnum capillifolium* (Ehrh.) Hedw. and *S. rubellum* Wils. from two bogs in southern Sweden. *J. Bryol.* **15**, 683-696.
- Damman A.W.H. 1979 Geographic patterns in peatland development in eastern North America. *Proc. Int. Symp. on Classification of Peat and Peatlands, Hyytala, Finland*. International Peat Society.
- Damman A.W.H. 1986 Hydrology, development and biogeochemistry of ombrogenous peat bogs with special reference to nutrient relocation in a western Newfoundland bog. *Can. J. Bot.* **64**, 384-394.
- Danaï M. 1986 The influence of some environmental factors on the production of *Carex vesicaria* and *Phalaris arundinacea*. *Vegetatio* **67(1)**, 45-46.
- Daniels R.E. and Eddy A. 1990 *A handbook of European Sphagna*. Natural Environmental Research Council, Swindon.
- Davis A.M. 1984 Ombrotrophic peatlands in Newfoundland, Canada: their origins, development and trans-Atlantic affinities. *Chemical Geology*. **44**, 287-309.
- Davies G. and Turner J. 1979 Pollen diagrams for Northumberland. *New Phytol.* **82**, 783-804.
- Davies M.S. 1984 The response of contrasting populations of *Erica cineraria* and *E. tetralix* to soil type and waterlogging. *J. Ecol.* **72**, 197-208.
- Davis W.M. 1909 *Geographical essays*. Ginn, Boston.
- Day J.B.W. 1970 *Geology of the country around Bewcastle*. NERC IGS. HMSO. pp 357.
- Delcourt H.R. and Delcourt P.A. 1991 *Quaternary ecology: a palaeoecological perspective*. Chapman and Hall, London.
- Den Held A.J., Schmitz M. and Van Wirdum G. 1992 Types of terrestrializing fen vegetation in the Netherlands. In Verhoeven J.T.A. ed., *Fens and bogs in the Netherlands: Vegetation history, nutrient dynamics and conservation*, 237-321. Geobotany 18. Kluwer Academic Publishers.
- Denys L. and Verbruggen C. 1989 A case of drowning - the end of subatlantic peat growth and related palaeoenvironmental changes in the lower Scheldt basin Belgium based on diatom and pollen analysis. *Rev. Palaeobot. Palynol.* **59**, 7-36.

- Dickson J.H. 1973 *Bryophytes of the Pleistocene*. Cambridge University Press, Cambridge.
- Digerfeldt G. 1988 Reconstruction and regional correlation of Holocene lake-level fluctuations in Lake Bysjön, South Sweden. *Boreas* 17, 165-182.
- Dilks T.J.K. and Procter M.C.F. 1974 The pattern of recovery of bryophytes after desiccation. *J. Bryol.* 8, 97-115.
- Dinel H., Mathur S.P., Brown A. and Levesque M. 1988 A field study of the effect of depth on methane production in peatland waters: equipment and preliminary results. *J. Ecol.* 76, 1083-1091.
- Doyle G.J. ed. 1990 *Ecology and conservation of Irish peatlands*. Royal Irish Academy, Dublin.
- Doyle T. and Dowding P. 1990 Decomposition and aspects of the physical environment in the surface layers of Mongan Bog. In Doyle G.J. ed., *Ecology and conservation of Irish peatlands*. Royal Irish Academy, Dublin.
- Drury W.H. and Nisbet I.C.T. 1973 Succession. *Arnold Arbor. J.* 54, 331-368.
- Dubois A.D. and Ferguson D.K. 1985 The climatic history of pine in the Cairngorms based on radiocarbon dates and stable isotope analysis, with an account of the events leading up to its colonization. *Rev. Palaeobot. Palynol.* 46, 55-80.
- Dumayne L. 1992 *Late Holocene palaeoecology and human impact on the environment of northern Britain*. Unpublished Ph.D. thesis, University of Southampton.
- Dumayne L., Stoneman R.E., Barber K.E. and Harkness D.D. 1995 Problems associated with correlating calibrated radiocarbon-dated pollen diagrams with historical events. *The Holocene* 5, 118-123.
- Dupont L.M. 1986 Temperature and rainfall variation in the Holocene based on comparative palaeoecology and isotope geology of a hummock and a hollow (Bourtangerveen, The Netherlands). *Rev. Palaeobot. Palynol.* 48, 71-159.
- Dupont L.M. 1987 Paleoeological reconstruction of the successive stands of vegetation leading to a raised bog in the Meerstalblok area (The Netherlands). *Rev. Palaeobot. Palynol.* 51, 271-287.
- Dureau de la Malle A.J.C.A. 1825 Memoire sur l'alternance ou sur ce probleme: la succession alternative dans la reproduction des especes vegetales vivant en societe, est elle une loi generale de la nature? *Annales des Science Naturelles*. 5, 353-381.
- Du Rietz G.E. 1924 Studien über die vegetation der alpen, mit derjenigen Skandinaviens verglichen. *Veroff. Geobot. Inst. Rubel, Zurich*. 1, 31-138.
- Du Rietz G.E. 1930 *Vegetationsforschung auf soziationsanalytischer grundlage*. Abderbalden E. ed., Handb. Biol. Arbeitsmeth. E. XI. 5, 293-480.
- Du Rietz G.E. 1949 Huvudenhetrr pch huvudgranser i Svensk myrvegetation. *Svensk Bot. Tidskr.* 43, 274-309.
- Egler F.E. 1954 Vegetation science concepts. I. Initial floristic composition: a factor in old-field vegetation development. *Vegetatio*. 4, 412-417.
- Erdtman G. 1928 Studies in the post-Artic history of the forests of northwestern Europe. I. Investigations in the British Isles. *Geol. Foren Stock. Forh.* 50.

- Erdtman G., Berglund B. and Praglowski J. 1961 *An introduction to the Scandinavian pollen flora. Grana Palynologica*. 2, No 3. Almqvist and Wiskell, Stockholm.
- Escarré J. and Thompson J.D. 1991 The effects of successional habitat variation and time of flowering on seed production in *Rumex acetosella*. *J. Ecol.* 79, 1099-1112.
- Faegri K. 1937 Some recent publications on phytogeography in Scandinavia. *Bot. Rev.* 3, 425-456.
- Faegri K. and Deuse P. 1960 Size variations in pollen grains with different treatments. *Pollen et spores*. 2, 293-298.
- Faegri K., Kaland P.E. and Krzywinski K. 1989 *Textbook of pollen analysis*. Fourth Edition, John Wiley and Sons, Chichester.
- Fanta F. ed. 1986 *Forest dynamics research in western and central Europe*. pp 135-144. PUDCC. Wageningen.
- Fenton J.H.C. 1980 The rate of peat accumulation in Antarctic moss banks. *J. Ecol.* 68, 211-228.
- Ferdinandsen C. and Winge O. 1925 *Cenococcum* FR. pp 332-382. Kongelige Veterinær - OG Landbohøjskoles Aasskrift.
- Finegan B. 1984 Forest succession. *Nature*. 311, 109-114.
- Flatberg K.I. 1984 A taxonomic revision of the *Sphagnum imbricatum* complex K. *Norske Vidensk* 3, 1-80.
- Flatburg K.I. 1986 Taxonomy morphovariation, distribution and ecology of the *Sphagnum imbricatum* complex with reference to Norway. *Gunneria* 54, 1-118.
- Fojt W. and Harding M. 1995 Thirty years of change in the vegetation communities of three valley mires in Suffolk, England. *J. App. Ecol.* 32, 561-577.
- Forrest G.I. 1971 Structure and production of north Pennine blanket bog vegetation. *J. Ecol.* 59, 453-479.
- Foster D.R. and Fritz S.C. 1987 Mire development, pool formation and landscape processes on patterned fens in Dalarna, central Sweden. *J.Ecol.* 75, 409-437.
- Foster D.R. and Wright H.E. Jr. 1990. Role of ecosystem development and climate change in bog formation in central Sweden. *Ecology* 71(2), 450-463.
- Foster D.E., Wright H.E. Jr., Thelaus M. and King G.A. 1988 Bog development and landform dynamics in central Sweden and south-eastern Labrador, Canada. *J. Ecol.* 76, 1164-1185.
- Fossit J.A. 1996 Late Quaternary vegetation history of the Western Isles of Scotland. *New Phytol.* 132, 171-196.
- Frenzel B. 1983 In Gore A.J.P. ed., *Ecosystems of the world 4A. mires: swamp, bog, fen and moor. General studies*. Elsevier Science, Amsterdam
- Gagnon Z.E. and Glime J.M. 1992 The pH-Lowering ability of *Sphagnum magellanicum* Brid. *J. Bryol.* 17, 47-57.
- Gardiner A.S. 1968 *The reputation of birch for soil improvement: a literature review*. Forestry Commission Research and Development Paper 67. H.M.S.O., London.

- Gauch H.G. and Whittaker R.H. 1972 Coenocline simulation. *Ecology* **53**, 446-451.
- Gebauer R.L.E., Reynolds J.F. and Tenhunen J.D. 1995 Growth and allocation of the arctic sedges *Eriophorum angustifolium* and *E. vaginatum*: effects of variable soil and nutrient availability. *Oecologia* **104**, 330-349.
- Gignac L.D., Vitt D.H. and Bayley S.E. 1991 Bryophyte response surfaces along ecological and climatic gradients. *Vegetatio* **93**, 29-45.
- Giller K.E. 1982 *Aspects of the plant ecology of a flood-plain mire in Broadland, Norfolk*. Unpublished Ph.D. thesis, University of Sheffield.
- Giller K.E. and Wheeler B.D. 1988 Acidification and succession in a flood-plain mire in the Norfolk Broadland, U.K. *J.Ecol.* **76**, 849-866.
- Gimingham C.H. 1964 Dwarf shrub heaths. In Burnett J.H. ed., *The vegetation of Scotland*. pp 232-287. Oliver and Boyd, Edinburgh.
- Glaser P.H. 1992 Raised bogs in eastern North America - regional controls for species richness and floristic assemblages. *J. Ecol.* **80**, 535-554.
- Glaser P.H. and Janssens J.A. 1986 Raised bogs in eastern North America: transitions in landforms and gross stratigraphy. *Can. J. Bot.* **64**, 395-415.
- Glaser P.H., Wheeler G.A., Gorham E. and Wright H.E. Jnr. 1981 The patterned mires of the Red Lake peatland, northern Minnesota: vegetation, water chemistry and landforms. *J. Ecol.* **69**, 575-599.
- Gleason H.A. 1917 The structure and development of the plant association. *Memoirs. Torrey Bot. Club.* **53**, 7-26.
- Gleason H.A. 1926 The individualistic concept of the plant association. *Am. Mid. Nat.* **21**, 92-110.
- Gleason H.A. 1927 Further views on the succession concept. *Ecology* **8**, 299-326.
- Gleason H.A. 1975 Delving into the history of American ecology. *Bull. Ecol. Soc. Am.* **56** 4, 7-10
- Glime Y., LI J.M. and Liao C. 1992 Responses of two interacting *Sphagnum* species to water level. *J. Bryol.* **17**, 59-70.
- Godwin H. 1936 Studies in the ecology of Wicken Fen. III The establishment of fen carr (scrub). *J. Ecol.* **24**, 82-116.
- Godwin H. 1941 The factors which differentiate marsh fen, bog and heath. *Chronica Bot.* **6**. 11.
- Godwin H. 1943 Coastal peat beds of the British Isles and North Sea. *J. Ecol.* **31**(2), 199-247.
- Godwin H. 1946 The relationship of bog stratigraphy to climate-change and archaeology. *Proc. Prehist. Soc.* **12**, pl.
- Godwin H. 1954 Recurrence - surfaces. *Dansk. Geol. Unders.* II Nr **80**, 22-30.
- Godwin H. 1956 *The history of the British flora: a factual basis for phytogeography*. Cambridge Univeristy Press, Cambridge.
- Godwin H. 1960 Radiocarbon dating and Quaternary history in Britain. *Proc. Roy. Soc. [B]* **153**, 287-320.

- Godwin H. 1962 The half-life of radiocarbon. *Nature* **195**, 984.
- Godwin H. 1975 *History of the British flora: a factual basis for phytogeography*. Second edition. Cambridge University Press, Cambridge.
- Godwin H. and Clifford M.H. 1938 Studies of the post-glacial history of British vegetation. I. Origin and stratigraphy of fenland deposits near Woodwalton, Hunts. II Origin and stratigraphy of deposits in southern fenland. *Phil. Trans. Roy. Soc. Lond.* **B 229**, 323.
- Godwin H and Conway V.M. 1939 The ecology of a raised bog near Tregaron, Cardiganshire. *J. Ecol.* **27**(2), 313-363.
- Godwin H. and Mitchell G.F. 1938 Stratigraphy and development of two raised bogs near Tregaron, Cardiganshire. *New Phytol.* **37**, 425-450.
- Godwin H. and Newton L. 1938 The submerged forest at Borth and Ynyslas, Cardiganshire. *New Phytol.* **37**, 333-345.
- Godwin H. and Turner J.S. 1933 Soil acidity in relation to vegetational succession in Calthorpe Broad, Norfolk. *J. Ecol.* **21**, 235-262.
- Godwin H. and Willis E.H. 1969 Borth Bog, Cardiganshire. *Radiocarbon* **6**, 128.
- Godwin L.M., Cowles D.R. and Huntley B. 1974 Studies in the ecology of Wicken Fen and the development of fen carr. *J. Ecol.* **62**, 197-214.
- Golley F.B. 1977 *Ecological succession: benchmark papers in ecology, vol. 5*. Dowden, Hutchinson and Ross Inc., Stroudsburg.
- Gore A.J.P. ed. 1983 *Ecosystems of the world 4A. mires: swamp, bog, fen and moor. General studies*. Elsevier Science, Amsterdam
- Gore A.J.P. and Urquhart C. 1966 The effects of waterlogging on the growth of *Molinia caerulea* and *Eriophorum vaginatum*. *J. Ecol.* **54**, 617-633.
- Gore A.J.P. and Olson J.S. 1967 Preliminary models for accumulation of organic matter in an *Eriophorum/Calluna* ecosystem. *Aquilo, Ser. Botanica.* **6**, 297-313.
- Gorham E. 1950 Variation in some chemical features along the borders of a *Canex lasiocarpa* fen community. *Oikos* **2**, 217-240.
- Gorham E. 1953 Some early ideas concerning the nature, origin and development of peatlands. *J. Ecol.* **41**, 257-274.
- Gosling L.M. and Baker S.J. 1980 Acidity fluctuations at a broadlands site in Norfolk. *J. App Ecol.* **17**, 479-490.
- Gould S. J. 1965 Is uniformitarianism necessary? *Am. J. Sci.* **5**, 223-228.
- Granlund E. 1932 De svenska hogmossarnas geologi. Sverig. *Geol. Undersokn. Ser. C. No. 373*. Stockholm.
- Gray A.J., Crawley M. J., and Edwards P.J. 1987 *Colonization, Succession and Stability*. The 26th Symposium of the British Ecological Society, held jointly with the Linnean Society of London. Blackwell Scientific Publications, Oxford..

- Greatrex P.A. 1983 Interpretation of macrofossil assemblages from surface sampling of macroscopic remains in mire communities. *J. Ecol* **71**, 47-58.
- Green B.H. 1968 Factors influencing the spatial and temporal distribution of *Sphagnum imbricatum* Hornsch. Ex Russ. in the British Isles. *J. Ecol.* **56**, 245-267.
- Green Winkler M. 1988 Effect of climate on development of two *Sphagnum* bogs in South-central Wisconsin. *Ecology* **69**(4), 1032-1043.
- Griffin K.O. 1977 Paleoecological aspects of the Red Lake Peatland, northern Minnesota. *Can. J. Bot.* **55**, 172-192.
- Grime J.P., Hodgson J.G. and Hunt R. 1988 *Comparative plant ecology*. Unwin Hyman, London.
- Grootjans A.P., van Diggelen R., Wassen M.J. and Wiersinga W.A. 1988 The effects of drainage on groundwater quality and plant species distribution in stream valley meadows. *Vegetatio* **75**, 47-48.
- Grosse-Brauckmann G. 1963 Über die Artenzusammensetzung von Torfen aus dem Nordwestdeutschen Marshen-Randgebiet. *Vegetatio* **11**, 325-41.
- Grosse-Brauckmann G. 1964 Zur Artenzusammensetzung von Torfen. Einige Befund und Überlegungen zur Frage der Zersetzlichkeit und Erhaltungsfähigkeit von Pflanzenresten. *Ber. Dtsch. Botan. Ges.* **26**, 22-37.
- Grosse-Brauckmann G. 1968 Einige Ergebnisse einer Vegetationskundlichen Auswertung Botanischer Torfuntersuchungen besonders im Hinblick auf Sukzessionsfragen. *Acta Bot. Neerl.* **17**, 59-69.
- Grosse-Brauckmann G. 1972 Über Pflanzliche Makrofossilien Mittel-Europäischer Torfe. I. Geweagereste Krautiger Pflanzen und ihre Merkmale. *Telma* **2**, 19-55.
- Grosse-Brauckmann G. 1976 Zum Verlauf der Verlandung bei einem eutrophen Flässe (nach quartarbotanischen Untersuchungen am Steinhuder Meer). II Die Sukzessionen, ihr Ablauf und ihre Bedingungen *Flora* **165**, 415-455.
- Grosse-Brauckmann G 1982 Vegetative plant macrofossils. In Berglund B.E. ed., *Palaeohydrological changes in the temperate zone in the last 15,000 years, subproject B. Lake and mire environments*. Vol. **3**, pp 111-130. International Geological Correlation Programme, Project 158, Lund.
- Grosse-Brauckmann G. 1986 Analysis of vegetative plant macrofossils. In Berglund B.E. ed., *Handbook of Holocene palaeoecology and palaeohydrology*. pp 591-618. John Wiley and Sons, Chichester.
- Grubb P.J. 1987 Some generalizing ideas about colonization and succession in green plants and fungi. In Gray A.J., Crawley M. J., and Edwards P.J. eds. *Colonization, succession and stability*. The 26th Symposium of the British Ecological Society, held jointly with the Linnean Society of London. Blackwell Scientific Publications, Oxford.
- Guiot J., Harrison S.P. and Prentice I.C. 1993 Reconstruction of Holocene Precipitation Patterns in Europe using pollen and lake-level data. *Quaternary Research*. **40**, 139-149.
- Gullentops F. 1995 (ed.), *Wetlands in Flanders. Contributions to palaeohydrology of the temperate zone in the last 15000 years*. Aardkundige Mededelingen **6**, Leuven University Press.

- Haggart A.B. 1989 Variations in the pattern and rate of isostatic uplift indicated by a comparison of Holocene sea-level curves from Scotland. *J. Quat. Sci.* **4**(1), 67-76.
- Hall D., Wells C.E. and Huckerby E. 1995 *The wetlands of Greater Manchester*. pp 1-167. North West Wetlands Survey 2.
- Hammond R.F., Van der Krogt G. and Osinga T. 1990 Vegetation and water tables on two raised bog remnants in County Kildare. In Doyle G.J. ed., *Ecology and conservation of Irish peatlands*. pp 121-134. Royal Irish Academy, Dublin.
- Haraguchi A. 1993 Phenotypic and phenological plasticity of an aquatic macrophyte *Menyanthes trifoliata* L. *J of Plant Research* **106** (no 1081), 31-35.
- Harding M. 1993 Redgrave and Lopham fens, East Anglia, England: a case study of change in flora and fauna due to groundwater abstraction. *Biol. Conserv.* **66**, 35-45.
- Harrison S.P. and Digerfeldt G. 1993 European lakes as palaeohydrological and palaeoclimatic indicators. *Quat. Sci. Rev.* **12**, 233-248.
- Harrison S.P., Prentice I.C. and Guiot J. 1993 Climatic controls on Holocene lake-level changes in Europe. *Climate Dynamics* **8**, 189-200.
- Haskins L.E. 1978 *The vegetation history of south-east Dorset*. Unpublished Ph.D. thesis, University of Southampton.
- Haslam C. 1987 *Late Holocene peat stratigraphy and climate change - a macrofossil investigation from the mires of north-western Europe*. Unpublished Ph.D. thesis, University of Southampton.
- Haslam S.M. 1969 *Phragmites communis* Trin. *Biol. Flora Br. Is. J. Ecol.* 585-610
- Haslam S.M. 1970 The performance of *Phragmites communis* Trin. in relation to water-supply. *Ann. Bot.* **34**, 867-877.
- Haslam S.M. 1971 Community regulation in *Phragmites communis* Trin. II Mixed stands. *J. Ecol.* **59**, 75-88.
- Haslam S.M. 1972 Biological flora of the British Isles, No 128, *Phragmites communis* Trin. *J. Ecol.* **60**, 585-610.
- Heinselman M.L. 1970 Landscape evolution, peatland types and the environment in the lake Agassiz Peatlands Natural Area, Minnesota. *Ecol. Mono.* **40**, 235-260.
- Hellings S.E. and Gallagher J.L. 1992 The effects of salinity and flooding on *Phragmites australis*. *J. App. Ecol.* **29**, 41-49.
- Hester A.J., Miles J.G and Gimingham C.H.. 1991a Succession from heather moorland to birch woodland. I. Experimental conditions in the field. *J. Ecol.* **79**, 303-315.
- Hester A.J., Miles J.G. and Gimingham C.H.. 1991b Succession from heather moorland to birch woodland. II. Growth and competition between *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Agrostis capillaris*. *J. Ecol.* **79**, 317-328.
- Hibbert F.A. and Switsur V.R. 1976 Radiocarbon dating Flandrian pollen zones in Wales and northern England. *New Phytol.* **77**, 793-807.
- Hill M.O. 1973 Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* **61**, 237-249.

- Hill M.O. 1988 *Sphagnum imbricatum* spp. *austinii* Sull. Flatberg and ssp. *affine* Ren. & Card. Flatberg in Britain and Ireland. *J. Bryol.* **15**, 109-115.
- Hill M.O. and Gauch H.G. Jr. 1980 Detrend correspondence analysis: an improved ordination technique. *Vegetatio* **42**, 47-58.
- Hobbs R.J. 1984 Length of burning rotation and community composition in high-level *Calluna-Eriophorum* bog in north England. *Vegetatio* **57**, 126-136.
- Hobby R. 1990 *The palaeoenvironmental significance of Holocene lake level fluctuations in Shropshire*. Unpublished Ph. D. Thesis, University of Southampton.
- Hogg E.H. 1993 Decay potential of hummock and hollow sphagnum peats at different depths in a Swedish raised bog. *Oikos* **66**, 269-278.
- Hogg P., Squires P., and Fitter A.H. 1995 Acidification, nitrogen deposition and rapid vegetational change in a small valley mire in Yorkshire. *Biological Conservation* **71**, 143-153.
- Hogg E.H. and Wein R.W. 1988 The contribution of *Typha* components to floating mat buoyancy. *Ecology*. **69**, 1025-1031.
- Houghton J.T., Jenkins G.J. and Ephraums J.J. eds. 1990 *Climate Change. The IPCC scientific assessment*. Cambridge Press, Cambridge.
- Hu F.S. and Davis R.B. 1994 Postglacial development of a Maine bog and paleoenvironmental implications. *Can. J. Bot.* **72**, 638-649.
- Huckerby E. 1993 In Middleton R. ed., *Recent work at Solway Moss, Cumbria*. North West Wetlands Survey, Annual Report.
- Hughes P.D.M. 1993 *Human impact and vegetation history in Swansea Bay as recorded in Crymlyn Bog*. Unpublished BSc thesis, Southampton University.
- Hulme P.E. 1994 Post-dispersal seed predation in grassland: Its magnitude and sources of variation. *J. Ecol.* **82**, 645-652.
- Huntley B. 1994 Late Devensian and Holocene palaeoecology and palaeoenvironments of the Morrone Birkwoods, Aberdeenshire, Scotland. *J. Quat. Sci.* **9**, 311-336.
- Huntley B. and Birks H.J.B. 1983 *An atlas of past and present pollen maps for Europe: 0 - 13000 years ago*. Cambridge University Press, Cambridge.
- Huntley B. and Prentice I.C. 1988 July temperatures in Europe from pollen data 6000 years before present. *Science*. **241**, 687-690.
- Ingram H.A.P. 1967 Problems of hydrology and plant distribution in mires. *J. Ecol.* **55**, 711-724.
- Ingram H.A.P. 1978 Soil layers in mires: function and terminology. *J. Soil Sci.* **29**, 224-227.
- Ingram H.A.P. 1982 Size and shape in raised mire ecosystems: a geophysical model. *Nature* **297**, 300-303.
- Ingram H.A.P. 1983 Hydrology. In Gore A.J.P. ed., *Ecosystems of the world 4A. mires: swamp, bog, fen and moor. General studies*. pp 67-158. Elsevier Science, Amsterdam.

- Isovilta P. 1966 Studies on *Sphagnum* L. I Nomenclatural revision of the European taxa. *Ann. Bot. Fenn.* **3**, 199-264.
- Ivanov K.E. 1981 *Water movement in mirelands.* (Vodoobmen v bolotnykh landshaftakh). Translated from Russian by Thompson A. and Ingram H.A.P., Academic Press.
- Iversen J. 1964 Retrogressive vegetational succession in the Post-glacial. In Macfadyen A. and Newbold P.J. eds. *Jubilee Symposium Supplement to the Journal of Ecology, Vol 52, and the Journal of Animal Ecology, Vol 33.* Blackwell Scientific Publishers, Oxford.
- Jacobson G.L. and Bradshaw R.W.H. 1981 The selection of sites for palaeoecological studies. *Quaternary Research*. **16**, 80-96.
- Jansen C.R. 1975 Ecologic and paleoecologic studies in the Fiegné d'Artimont (Vosges, France). *Vegetatio* **30**, 165-178.
- Janssens J.A. 1983 A quantitative method for stratigraphic analysis of bryophytes in Holocene peat. *J. Ecol* **71**, 189-196.
- Janssens J.A. 1992 Development of a raised bog complex. In Wright H.E., Coffin B.A. and Aaseng N.E. eds. *Patterned peatlands of Minnesota.* University of Minnesota Press, Minneapolis.
- Jermyn A.C., Chater A.O. and David R.W. 1982 *Sedges of the British Isles*, 2nd edition. Botanical Society of the British Isles, London.
- Johnson L. C. and Damman A.W.H. 1991 Species-controlled *Sphagnum* decay on a south Swedish raised bog. *Oikos* **61**, 234-242.
- Johnson L.C. and Damman A.W.H. 1993 Decay and its regulation in *Sphagnum* peatlands. *Adv. Bryol.* **5**, 249-296.
- Johnson L.C, Damman A.W.H and Malmer N. 1990 *Sphagnum* macrostructure as an indicator of decay and compaction in peat cores from an ombrotrophic south Swedish peat-bog. *J. Ecol* **78**, 633-647.
- Jonasson S. and Chapin F. III 1991 Seasonal uptake and allocation of phosphorus in *Eriophorum vaginatum* L. measured by labelling with ³²P. *New Phytol.* **118**, 349-357.
- Jongman R.H.G., ter Braak C.J.F. and van Tongeren O.F.R. 1987 *Data analysis in community and landscape ecology.* Pudoc, Wageningen.
- Katz N.J., Katz S.V. and Kipiani M.G. 1965 *Atlas and keys of fruits and seeds occurring in the quaternary deposits of the USSR.* Nauka, Moscow.
- Katz N.J., Katz S.V. and Skobeyeva E.I. 1977 *Atlas of plant remains in peats.* Nedra, Moscow.
- Kazda M. 1995 Changes in alder fens following a decrease in the ground water table: results of a geographical information system application. *J. App. Ecol.* **32**, 100-110.
- Kidson C. and Heyworth A. 1973 The Flandrian sea-level rise in the Bristol Channel. *Proc. Ussher Soc.* **2**, 565-584.
- Kilian M.R., Van der Plicht, J. and Van Geel B. 1995 Dating raised bogs: new aspects of AMS ¹⁴C wiggle matching, a reservoir effect and climatic change. *Quaternary Science Reviews* **14**, 959-966.
- Kivinen E. 1935 Über Elektrolytgehalt und Reaktion der Moorsasser - Muatalouskoclaitoksen muatulkimusosasto Agrogeol. Julkaisuja 38 Helsingfors.

- Klinger L.F. 1990 Global patterns in community succession. 1. Bryophytes and forest decline. *Memoirs of the Torrey Botanical Club*. **24**, 1-50.
- Klinger L.F. 1991 Peatland formation and ice ages: A possible Gaian mechanism related to community succession. In Schneider S.H. and Boston P.J. eds. *Scientists on Gaia*. pp 247-255. MIT Press. Cambridge, Mass.
- Klinger L.F. 1996 The myth of the classic hydrosere model of bog succession. *Arctic and Alpine Research* **28**, 1-9.
- Klinger L.F., Elias S.A., Behan-Pelletier V.M. and Williams N.E. 1990 The bog climax hypothesis: fossil arthropod and stratigraphic evidence in peat sections from south-east Alaska, USA. *Holarctic Ecol.* **13**, 72-80.
- Klinger L.F., Zimmerman P.R., Greenberg J.P., Heidt L.E. and Guenther A.B. 1994 Carbon trace gas fluxes along a successional gradient in the Hudson Bay lowland. *J. Geophys. Res.* **99**, 1469-1494.
- Kneale P.E. 1987 Sensitivity of the groundwater mound model for predicting mire topography. *Nordic Hydrology* **18**, 193-202.
- Koerselman W., Van Kerkhoven M.B. and Verhoeven J.T.A. 1993 Release of inorganic N, P and K in peat soils: effect of temperature, water chemistry and water level. *Biogeochemistry*. **20**, 63-81.
- Koerselman W. and Verhoeven J.T.A. 1992 Nutrient dynamics in mires of various trophic states: nutrient inputs and outputs and the internal cycle. In Verhoeven J.T.A. ed., *Fens and bogs in the Netherlands: vegetation history nutrient dynamics and conservation*. pp 397-432. *Goebotany* **18**, Kluwer Academic Publishers, Netherlands.
- Korber-Grohne U. 1964 Bestimmungsschlüssel für Subfossile Juncus Samen und Gramineen Früchte. *Probleme der Küstenforschung in Südlichen Nordseegebiet*. **7**, 33-47.
- Korhola A. 1990 Palaeolimnology and hydroseral development of the Kotasio bog, southern Finland, with special reference to Cladocera Annales. *Annales Academiae Scientiarum Fennicae AIII*. **155**, pp40.
- Korhola A. 1992 The Early Holocene hydrosere in a small acid hill-top basin studied using crustacean sedimentary remains. *J. Paleolim.* **7**, 1-22.
- Korhola A.A. 1994 Radiocarbon evidence for rates of lateral expansion in raised mires in southernland Finland. *Quaternary Research*. **42**, 299-307.
- Korhola A.A. 1995 Holocene climatic variations in southern Finland reconstructed from peat-initiation data. *Holocene* **5**, 43-58.
- Kovach W.L. 1995 Multivariate data analysis. In Maddy D. and Brew J.S. eds. *Statistical modelling of Quaternary science data: a practical manual*. Quaternary Research Association, Cambridge.
- Kratz K. and DeWitt C.B. 1986 Internal factors controlling peatland-lake ecosystems development. *Ecology* **67**(1), 100-107.
- Kromer B. and Becker B. 1993 German oak and pine 14C calibration, 7,200 BC - 9,400 BC. *Radiocarbon* **35**, 125-135.
- Kubiw H., Hickman M. and Vitt D.H. 1989 The development history of peatlands at Musiki and Marguerite lakes, Alberta. *Can. J. Bot.* **67**, 3534-3544.

- Kuhry P. 1985 Transgression of a raised bog across a coversand ridge originally covered with an oak - lime forest. *Rev. Palaeobot. Palynol.* **44**, 303-353.
- Kuhry P. 1994 The role of fire in the development of sphagnum dominated peatlands in western boreal Canada. *J. Ecol.* **82**, 899-910.
- Kuhry P., Hasley, L.A., Bayley S.E. and Vitt D.H. 1992 Peatland development in relation to Holocene climatic change in Manitoba and Saskatchewan (Canada). *Can. J. Earth Sci.* **29**, 1070-1090.
- Kulczynski S. 1949 Peat bogs of Polesie. *Mem. de l'Acad. Polon. des Sciences et des Lettres. Serie B*: 1-356.
- Kummerow J., Mills J.M., Ellis B.A. and Kummerow A. 1988 Growth dynamics of cotton grass (*Eriophorum vaginatum*). *Can. J. Bot.* **66**, 253-256.
- Kutzbatch J.E. and Guetter P.J. 1986 The influence of changing orbital parameters and surface boundary conditions on climate simulations for the past 18,000 years. *J. Atmos Sci.* **43**(16), 1276-1759.
- Lamb H.H. 1977 The Late Quaternary history of the climate of the British Isles. In Shotton F.W. ed., *British Quaternary Studies - recent advances*. pp 283-298. Oxford University Press, Oxford.
- Lambert J.M. 1951 Alluvial stratigraphy and vegetational succession in the region of the Bure Valley Broad. II Detailed vegetational stratigraphical relationships. *J.Ecol.* **39**, 120-148.
- Lawton J.H. 1987 Are there assembly rules for successional communities? In Gray A.J., Crawley M. J., and Edwards P.J. eds. *Colonization, Succession and Stability: The 26th Symposium of the British Ecological Society, held jointly with the Linnean Society of London*. Blackwell Scientific Publications, Oxford..
- Li V. and Vitt D.H. 1994 The dynamics of cross-establishment: temporal responses to nutrient gradients. *The Bryologist* **97**, 357-364.
- Lindsay R.A. 1977 *Glasson Moss NWR and the 1976 fire*. CST Report No 137. Nature Conservancy Council, London..
- Linick T.W., Long A., Damon P.E. and Ferguson C.W. 1986 High-precision radiocarbon dating of Bristlecone Pine from 6,554 to 5,350 BC. *Radiocarbon* **28**, 943-953.
- Luken J. O., Billings W. D. and Peterson K. M. 1985 Succession and biomass as controlled by *Sphagnum* in an Alaskan peatland. *Can. J. Bot.* **63**, 1500-1507.
- MacArthur R.H. and Connell J.H. 1966 *The biology of populations*. John Wiley and Sons, New York.
- Macdonald A.J., Kirkpatrick A.H., Hester A.J. and Sydes C. 1995 Regeneration by natural layering of heather *Calluna Vulgaris*: frequency and characteristics in upland Britain. *J. App.Ecol.* **32**, 85-99.
- Mackay A.W. and Tallis J.H. 1996 Summit-type blanket mire erosion in the Forest of Bowland, Lancashire, UK: predisposing factors and implications for conservation. *Biological Conservation* **76**, 31-44.
- Madden B. and Doyle G.J. 1990 Primary production on Mongan Bog. In Doyle G.J. ed., *Ecology and conservation of Irish peatlands*. pp147-161. Royal Irish Academy, Dublin.
- Maddy D. and Brew J.S. eds. 1995 *Statistical Modelling of Quaternary Science Data. Technical Guide No 5*, Quaternary Research Association, Cambridge.

- Magny M. 1992 Holocene lake-level fluctuations in Jura and the northern subalpine ranges, France: regional pattern and climatic implications. *Boreas* **21**, 319-334.
- Malmer N. 1962 Studies on mire vegetation in the archean area of south-western Gotaland, (south Sweden). II. Vegetation and habitat conditions on the Khult Mire. *Opera Bot.* **7** 1-322.
- Malmer N. 1986 Vegetational gradients in relation to environmental conditions in northwestern European mires. *Can. J. Bot.* **64**, 375-383.
- Malmer N. 1988 Patterns in the growth and accumulation of inorganic constituents in the *Sphagnum* cover on ombrotrophic bogs in Scandinavia. *Oikos*. **53**, 105-120.
- Malmer N. 1993 Mineral nutrients in vegetation and surface layers of *Sphagnum*-dominated peat-forming systems. *Adv. Bryol.* **5**, 223-248.
- Malmer N., Horton D.G. and Vitt D.H. 1992 Element concentrations in mosses and surface waters of western Canadian mires relative to precipitation chemistry and hydrology. *Ecography* **15**, 114-128.
- Malmer N., Svensson B. M. and Wallén B. 1994 Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. *Folia. Geobot. Phytotax. Praha.* **29**, 483-496.
- Martin A.C. and Barkley W. D. 1961 *Seed Identification manual*. University of California Press.
- Mathews E. and Fung I. 1987 Methane emission from natural wetlands: global distribution, area and environmental characteristics of sources. *Global Biogeochemical Cycles* **1**, 61-86.
- Mathur S.P., Brown A., Dinel H., Butler A. and Levesque M. 1991 The role of methane gas in peat hydrology: a new concept. In Jeglum J.K. and Overand R.P. eds. *Proceedings of the symposium on peat and peatlands diversification and innovation. Vol 1 Peatland forestry*. The Canadian Society for Peat and Peatlands.
- Mathur S.P. and Levesque M. 1985 Negative effect of depth on saturated hydraulic conductivity of histosols. *Soil Science* **140**, 462-466.
- Mauquoy D. (Forthcoming) *Testing the sensitivity of the palaeoclimatic signal from raised peat stratigraphy*. Unpublished Ph.D. thesis, University of Southampton.
- McCormick J. 1968 *Succession VIA*. Student Publication, p22-35, Graduate School of Fine Arts, Univ. Pennsylvania.
- McVean D.N. 1956a Ecology of *Alnus glutinosa* L. Gaertn.: III Seedling establishment. *J. Ecol.* **44**, 195-218.
- McVean D.N. 1956b Ecology of *Alnus glutinosa* L. Gaertn.: IV Root system. *J. Ecol.* **44**, 219-225.
- Meikle R.D. 1984 *Willows and poplars of Great Britain and Ireland*. BSBI Handbook No. 4, Bot. Soc. British Isles, London.
- Middeldorp A.A. 1986 Functional palaeoecology of the Hahnenmoor raised bog ecosystem - a study of vegetation history, production and decomposition by means of pollen density dating. *Rev. Palaeobot. Palynol.* **49**, 1-73.
- Middleton R., Wells C.E. and Huckerby E. 1995 *The wetlands of Lancashire. 7, The detailed palaeoecological studies*. pp 141-189. North West Wetlands Survey 3.

- Miles J. 1979 *Vegetation dynamics*. Chapman and Hall, London.
- Miles J. 1987 I. Vegetation succession: past and present perceptions. In Gray A.J., Crawley M. J., and Edwards P.J. eds. *Colonization, Succession and Stability: The 26th Symposium of the British Ecological Society*, held jointly with the Linnean Society of London. Blackwell Scientific Publications, Oxford.
- Mitsch W.J. 1994 *Global Wetlands: Old World and New*. Elsevier Science, Amsterdam.
- Moore J.J. 1955 The distribution and ecology of *Scheuchzeria palustris* L on reused bog in Offaly. *Ir. Nat. J.* **11**, 1-8.
- Moore P.D. 1963 *An investigation of the stratigraphy and water content of Borth Bog, Cardiganshire*. Unpublished BSc Thesis, University of Wales. In Slater F.M. 1972 *Contributions to the ecology of Borth Bog, Wales. I. General considerations. Proc. 4th Int. Peat Cong I-IV, Helsinki.* 277-288.
- Moore P.D. 1968 Human influence upon vegetational history in north Cardiganshire. *Nature* **217**, 1006-1009.
- Moore P.D. 1973 The influence of prehistoric cultures upon the initiation and spread of blanket bog in upland Wales. *Nature*. **241**, 350-353.
- Moore P.D. 1975 Origin of blanket mires. *Nature*. **256**, 267-269.
- Moore P.D. 1977 Stratigraphy and pollen analysis of Claissh Moss, North West Scotland: significance for the origin of surface pools and forest history. *J. Ecol.* **65**, 375-397.
- Moore P.D. 1984 *European mires*. Academic Press, London.
- Moore P.D. 1986 Hydrological changes in mires. In Berglund B.E. ed., *Handbook of Holocene palaeoecology and palaeohydrology*. John Wiley and Sons, Chichester.
- Moore P.D. 1993 The origin of blanket mires revisited. In Chambers F.M. ed. *Climate change and human impact on the landscape*. Chapman and Hall, London.
- Moore P.D. and Bellamy D.J. 1973 *Peatlands*. 18. Elek, London.
- Moore P.D., Merryfield D.L. and Price. 1984 The vegetation and development of blanket mires. In Moore P.D. ed., *European mires*. pp 203-236. Academic Press, London.
- Moore P.D. and Webb J.A. 1978 *An illustrated guide to pollen analysis*. Hodder and Stoughton, London.
- Moore P.D., Webb J.A. and Collinson M.E. 1991 *Pollen Analysis*. Blackwell Scientific Publications, Oxford.
- Mortimer A.M. 1987 Contributions of plant population dynamics to understanding early succession. In Gray A.J., Crawley M. J., and Edwards P.J. 1987 *Colonization, Succession and Stability: The 26th Symposium of the British Ecological Society*, held jointly with the Linnean Society of London. Blackwell Scientific Publications, Oxford.
- Nicholson B.J. and Gignac L.D. 1995 Ecotope dimensions of peatland Bryophyte indicator species along gradients in the Mackenzie river basin, Canada. *The Bryologist*. **98**(4), 437-451.
- Nilsson M. and Bohlin E. 1993 Methane and carbon dioxide concentrations in bogs and fens - with special reference to the effects of the botanical composition of the peat. *J. Ecol.* **81**, 615-625.

- Noble M.G., Lawrence D.B. and Streveler G.P. 1984 Sphagnum invasion beneath an evergreen forest canopy in southeastern Alaska. *Bryologist* **87**, 119-127.
- O'Brien S.R., Mayewski P.A., Meeker L.D., Meese D.A. M.S. and Whitlow S.I. 1995 Complexity of Holocene climate as reconstructed from a Greenland ice core. *Science* **270**, 1962-1964.
- Odum E.P. 1969 The strategy of ecosystem development. *Science* **164**, 262-270.
- Ohlson I.V. 1986 A study of errors in 164 dates of peat and sediment. *Radiocarbon* **28(2a)**, 429-435.
- Ohlson M. 1987 Spatial variation in decomposition rate of *Carex Rostrata* leaves on a Swedish mire. *J. Ecol* **75**, 1191-1197.
- Ohlson M. and Malmer N. 1990 Total nutrient accumulation and seasonal variation in resource allocation in the bog plant *Rhynchospora alba*. *Oikos* **58**, 100-108.
- Ohlson M. and Zackrisson O. 1992 Tree establishment and microhabitat relationships in north Swedish peatlands. *Can. J. For Res.* **22**, 1869-1877.
- Okland R.H. 1986 Rescaling of ecological gradients. III. The effect of scale and niche breadth measurements. *Nord. J. Bot.* **65**, 671-677.
- Okland R.H. 1990 A phytoecological study of the mire Northern Kisselbergmossen, south-east Norway. III Diveristy and habitat niche relationships. *Nord. J. Bot.* **10**, 191-220.
- Okruszko H. 1993 Transformation of fen-peat soils under the impact of draining. *Zeszyty Problemowe Postepow Nauk Polniczych* **406**, 4-73.
- Okruszko H. 1995 In Wheeler B.D., Shaw S.C., Fojt W.J. and Robertson R.A. eds, *Restoration of temperate wetlands*. John Wiley and Sons, New York.
- Oosting H.J. 1948 *The study of plant communities: an introduction to plant ecology*. Freeman, San Francisco.
- Osvald H. 1923 Die vegetation des hochmoores Komosse. *Svensk. Vaxtsoc. Sallsk. Handl.* **1**.
- Ovenden L. 1990 Peat accumulation in northern wetlands. *Quat. Res.* **33**, 377-386.
- Overbeck F. 1975 *Botanisch - geologische Moorkunde*. Karl Wacholtz Verlag, Neuminster.
- Pearce F. 1994 Forests destined to end in the mire. *New Scientist*, May 7th, p16.
- Pearsall W.H. 1918 The aquatic and marsh vegetation of Estwaite Water. *J. Ecol.* **6**, 53-74
- Pearson G.W., Becker B. and Qua F. 1993 High precision 14C measurement of German and Irish oaks to show the natural 14C variations from 7,890 to 5,000 BC. *Radiocarbon* **35**, 93-104.
- Pearson G.W. and Stuiver M. 1993 High precision bidecadal calibration of the radiocarbon time scale 500-2,500 BC. *Radiocarbon* **35**, 25-33.
- Pearson M.C. 1960 Muckle Moss, Northumberland. *J. Ecol.* **48**, 647.
- Peeting R.K., Knox R.G., Ceise J.S. and Allen R.B. 1988 Putting things in order: the advantages of detrended correspondence analysis. *American Naturalist* **131**, 924-934.

- Pennington W. 1970 Vegetation history in the north-west of England: a regional synthesis. In Walker D. and West R.G. eds. pp 41-79 *Studies in the vegetation history of the British Isles*. Cambridge University Press, Cambridge.
- Pennington W. 1986 Lags in adjustment of vegetation to climate caused by the pace of soil development: evidence from Britain. *Vegetatio* **67**, 105-118.
- Perring F.H. and Walters S.M. 1962 *Atlas of the British Flora*. Nelson, Edinburgh.
- Petersen L. and Breuning-Madsen H. 1978 Possible effects of ground water lowering on some peat soils in Sjælland. *Geografisk Tidsskrift* **77**, 25-35.
- Phillips M.E. 1954 Studies in the quantitative morphology and ecology of the *Eriophorum angustifolium* Roth III. The leafy shoot. *New Phytol.* **53**, 312-343.
- Pielou E.C. 1984 *The interpretation of ecological data*. John Wiley and Sons, Chichester.
- Pigott M.E and Pigott C.D. 1959 Stratigraphy and pollen analysis of Malham Tarn and Tarn Moss. *Field Studies* **1**(1), 1.
- Pigott C.D. and Wilson J.F. 1978 The vegetation of North Fen at Esthwaite in 1967-69. *Proc. Roy. Soc. Lond. B.* **200**, 331-351.
- Pilcher J.R. 1991 Radiocarbon dating. In Smart P.L. and Francis P.D. eds, *Quaternary dating methods - a users' guide. Technical Guide 4*. Quaternary Research Association, Cambridge.
- Pilcher J.R. and Hall V.A. 1992 Towards a tephrochronology for the Holocene of the north of Ireland. *The Holocene* **2**, 255-259.
- Pilcher J.R., Hall V.A. and Macormac F.G. 1995 Dates of Holocene Icelandic volcanic eruptions from tephra layers in Irish peats. *The Holocene* **5**, 103-110.
- Pohl F. 1937 Die Pollenzeugung der Windbluter. *Botanisch Centralblatt* **56A**, 365-470.
- Pons L.J. 1992 Holocene peat formation in the lower parts of the Netherlands. In Verhoeven J.T.A. ed., *Fens and bogs in the Netherlands: Vegetation history, nutrient dynamics and conservation*. Geobotany 18. Kluwer Academic Publishers.
- Poore M.E.D. and Walker D. 1958-59 Wybunbury Moss, Cheshire. *Mem. Manchr. Lit. Soc.* **101**, 1-24.
- Praglowksi J. 1970 The effects of pre-treatment and the embedding media on the shape of pollen grains. *Rev. Palaeobot. Palynol* **10**, 203-208.
- Price M.D.R. and Moore P.D. 1984 Pollen dispersion in the hills of Wales: a pollen shed hypothesis. *Pollen et Spores* **26**, 127-136.
- Proctor M.C.F. 1982a Physiological ecology of Bryophytes. *Physiological Ecology* **1**, 80-131.
- Proctor M.C.F. 1982b Physiological ecology : water relations, light and temperature responses, carbon balance. In Smith A.J.E ed., *Bryophyte ecology*. pp 333-381. Chapman and Hall, London.
- Proctor M.C.F. 1992 Regional and local variation in the chemical composition of ombrogenous mire waters in Britain and Ireland. *J.Ecol.* **80**, 719-736.
- Proctor M.C.F. 1994 Seasonal and shorter-term changes in surface-water chemistry on four English ombrogenous bogs. *J. Ecol.* **82**, 597-610.

- Punt W. ed. 1976 *The north-west European pollen flora 1* Elsevier Scientific Publishing Company, Amsterdam.
- Punt W. and Clarke C.G.S. eds. 1980 *The north-west European pollen flora 2* Elsevier Scientific Publishing Company, Amsterdam
- Punt W. and Clarke C.G.S. eds. 1981 *The north-west European pollen flora 3* Elsevier Scientific Publishing Company, Amsterdam
- Punt W. and Clarke C.G.S. eds. 1984 *The north-west European pollen flora 4* Elsevier Scientific Publishing Company, Amsterdam
- Ratcliffe D.A. 1959 The vegetation of the Carneddau, North Wales. I Grasslands, heaths and bogs. *J. Ecol.* **47**, 371-413.
- Ratcliffe D.A. and Walker D. 1958 The Silver Flowe, Galloway, Scotland. *J. Ecol.* **40**, 407-445.
- Rawes M. and Hobbs R. 1979 Management of semi-natural blanket bog in the northern Pennines. *J. Ecol.* **67**, 789-807.
- Rocheft L., Vitt D. H. and Bayley S.E. 1990 Growth and decomposition dynamics of *Sphagnum* under natural conditions and experimentally acidified conditions. *Ecology* **71**(5), 1986-2000.
- Rodwell J.S. 1991 *British plant communities Volume 2: mires and heaths*. Cambridge University Press, Cambridge.
- Rowell T.A. and Harvey H.J. 1988 The recent history of Wicken Fen, Cambridgeshire, England. A guide to ecological development. *J. Ecol.* **76**, 73-90.
- Rowell T.K. and Turner J. 1985 Litho-, humic- and pollen stratigraphy at Quick Moss, Northumberland. *J. Ecol.* **73**, 11-25.
- Russi L., Cocks P.S. and Roberts E. H. 1992 Seed bank dynamics in a Mediterranean grassland. *J. Appl. Ecol.* **29**, 763-771.
- Rutter A.J. 1955 The comparison of wet-heath vegetation in relation to the water-table. *J. Ecol.* **43**, 507-543.
- Rybníček K. 1973 A comparison of the present and past mire communities of central Europe. In Birks H.J.B. and West R.G. eds, *Quaternary Plant Ecology*. Blackwell, Oxford.
- Rybníček K. and Rybníčková E. 1968 The history of flora and vegetation on the Blato mire in southeastern Bohemia, Czechoslovakia. *Folia Geobot. Phytotax.* **3**, 117-142.
- Rycroft T.A., Williams D.J.A. and Ingram H.A.P. 1975 The transmission of water through peat. *J. Ecol.* **63**, 535-568.
- Rydin H. 1985a Competition and niche separation in *Sphagnum*. *Can. J. Bot.* **64**, 1817-1824.
- Rydin H. 1985b Effect of water level on desiccation of *Sphagnum* in relation to surrounding *Sphagna*. *Oikos* **45**, 374-379.
- Rydin H. 1985c Tolerance of *Sphagnum* to water level. *J. Bryol.* **13**, 571-578.

- Rydin H. 1993a Mechanisms of interactions among *Sphagnum* species along water-level gradients. *Advances in Bryology* **5**, 153-185.
- Rydin H. 1993b Interspecific competition between *Sphagnum* mosses on a raised bog. *Oikos*. **66**, 413-423.
- Scandrett E. and Gimingham C.H. 1989 Vegetative regeneration by layering in *Calluna vulgaris* (L.) Hull. *Trans. Bot. Soc. Edinburgh* **45**, 323-333.
- Schmidt W. 1988 An experimental study of old-field succession in relation to different environmental factors. *Vegetatio*. **77**, 103-114.
- Schweingruber F.H. 1978 *Microscope Wood Anatomy*. Swiss Federal Institute of Forestry Research, Zurcher.
- Scott E.M., Harkness D.D., Cook G.T., Aitchison T.C. and Baxter M.S. 1991 Future quality assurance in ¹⁴C dating. Special Proceedings, Volume 1. Quaternary Research Association.
- Scott E.M., Long A. and Kra R. eds. 1990 Proceedings of the international workshop on intercomparison of radiocarbon laboratories. *Radiocarbon* **32**, 253-397.
- Sernander R. 1910 Ausstellung zur belichtung der entwicklung - geschichte der schwedischen torfmoore. *Compt. Rend. XI Cong. Geol. Internat.* 203.
- Sergerström U. 1991 Soil pollen analysis - an application for tracing ancient arable patches. *J. Archaeological Sci.* **18**, 165-175.
- Shaver G.R., Chapin F.III, Gartner L. 1986 Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. *J. Ecol.* **74**, 257-278
- Shennan I. 1989 Holocene crustal movements and sea-level changes in Great Britain. *J. Quat. Sci.* **4**, 77-89.
- Shennan I. 1994a Late Devensian and Holocene relative sea-level changes at Locch nan Eala, near Aisaig, northwest Scotland, *J. Quat. Sci.* **9**, 261-283.
- Shennan I. 1994b Depositional environments. In Waller M. ed., *The Fenland project No.9: Flandrian environmental change in Fenland*. East Anglian Archaeology, Cambridgeshire County Council.
- Shi Z. and Lamb H.F. 1991 Post-glacial sedimentary evolution of a microtidal estuary, Dyfi Estuary, west Wales, U.K. *Sedimentary Geology* **73**, 227-246.
- Siegel D.I. 1983 Ground water and the evolution of patterned mires, glacial Lake Agassiz peatlands, northern Minnesota. *J.Ecol.* **71**, 913-921.
- Siegel D.I. 1992 Groundwater hydrology. In Wright H.E., Coffin B.A. and Aaseng N.E. *The patterned peatlands of Minnesota*. Minnesota University Press, Minnesota.
- Siegel D.I. and Glaser P.H. 1987 Groundwater flow in a bog-fen complex, Lost River Peatland, northern Minnesota. *J. Ecol.* **75**, 743-754.
- Silvola J. and Hanski I. 1979 Carbon accumulation in a raised bog. *Oecologica (Berl)* **37**, 285-295.
- Simmons I.G. and Tooley M. 1981 *The environment in British prehistory*, Gerald Duckworth and Co., London.

- Sjörs H. 1950 On the relationship between vegetation and electrolytes in North Swedish mire waters. *Oikos* **2:2**, 247-257.
- Sjörs H. 1980 An arrangement of changes along gradients, with examples from succession in boreal peatland. *Vegetatio* **43**, 1-4.
- Sjörs H. 1990 Divergent successions in mires, a comparative study. *Aquilo Ser. Bot.* **28**, 67-77.
- Slack N.G. 1990 Bryophytes and ecological niche theory. *Bot J. Linnean Soc.* **104**, 187-213.
- Slater F.M. 1972 Contributions to the ecology of Borth Bog, Wales. I. General considerations. *Proc. 4th Int. Peat Cong I-IV, Helsinki.* 277-288.
- Sledge W.A. 1949 The distribution and ecology of *Scheuchzeria palustris* L. *Watsonia* **1**, 24-35.
- Smart P.J. 1982 Stratigraphy of a site in the Munsary Dubh Lochs, Caithness, Northern Scotland: development of the present pattern. *J. Ecol.* **70**, 549-558.
- Smith A.G. 1959 The mires of south-western Westmorland: stratigraphy and pollen analysis. *New Phytol.* **58**, 105.
- Smith A.G. and Goddard I.C. 1991 A 12,500 year record of vegetational history at Sluggan bog, Co. Antrim, N. Ireland (incorporating a pollen zone scheme for the non-specialist). *New Phytol.* **118**, 167-187.
- Smith A.G. and Morgan L.A. 1989 A succession to ombrotrophic bog in the Gwent Levels, and its demise: a Welsh parallel to the peats of the Somerset Levels. *New Phytol.* **107**, 145-167.
- Smith A.G. and Pilcher J. R. 1973 Radiocarbon dates and vegetation history of the British Isles. *New Phytol.* **72**, 903-14.
- Smith A.J.E. 1978 *The Moss Flora of Britain and Ireland*. Cambridge University Press, Cambridge.
- Smith B.M. 1985 *A Palaeoecological Study of Raised Mires in the Humberhead Levels*. Unpublished Ph.D. thesis, University of Wales, Cardiff.
- Spence D.H.N. 1964 The macrophytic vegetation of freshwater lochs, swamps and associated fens. In Burnett J.H. ed., *The vegetation of Scotland*. pp 306-425. Oliver and Boyd, Edinburgh.
- Stace J. 1991 *New flora of the British Isles*. Cambridge University Press, Cambridge.
- Starkel L. 1991 Environmental changes at the Younger Dryas-Preboreal transition and during the early Holocene: some distinctive aspects in central Europe. *The Holocene* **1(3)**, 234-242.
- Stoneman R. 1993 *Holocene palaeoclimates from stratigraphy: extending and refining the model*. Unpublished Ph.D. thesis, University of Southampton.
- Stoneman R., Barber K. and Maddy D. 1993 Present and past ecology of *Sphagnum imbricatum* and its significance in raised peat - climate modelling. *Quaternary Newsletter* **70**, 14-22.
- Strefkerk J.G. and Casparie W.A. 1987 *De hydrologie van hoogveen systemen*. Staatsbosbeheer, Utrecht.
- Stuiver M. and Becker B. 1993 High-precision calibration of the radiocarbon time scale AD 1,950 - 6,000 BC. *Radiocarbon* **35**, 35-65.
- Stuiver M. and Braziunas T.F. 1993 Modelling atmospheric ^{14}C influences and ^{14}C ages of marine samples back to 10,000 BC. *Radiocarbon* **35**, 137-189.

- Stuiver M., Braziunas T.F., Becker B. and Kromer B. 1991 Climatic solar oceanic and geomagnetic influences of Late-glacial and Holocene atmospheric $^{14}\text{C}/^{12}\text{C}$ change. *Quaternary Research* **35**, 1-14.
- Stuiver M. and Pearson G.W. 1993 High-precision bidecadal calibration of the radiocarbon time scales, AD 1,950 - 500 BC and 2,500 - 6,000 BC. *Radiocarbon* **35**, 1-23.
- Stuiver M. and Reimer P.J. 1993a Extended ^{14}C database and revised CALIB radiocarbon calibration program. *Radiocarbon* **35**, 215-230.
- Stuiver M. and Reimer P.J. 1993b *CALIB users guide, rev 3.0*. Quaternary Research Center AK-60, University of Washington, Seattle.
- Suess H.E. 1965 Secular variations in the cosmic-ray produced carbon-14 in the atmosphere and their interpretations. *J. Geophys. Res.* **70**, 5937-5950.
- Sundstrom E. 1995 The impact of climate, drainage and fertilization on the survival and growth of *Pinus sylvestris* in afforestation of open low production peatlands. *Scandinavian J. of Forest Research* **10**, 190-203.
- Svensson B.H. and Rosswall T. 1984 In situ methane production from acid peat in plant communities with different moisture regimes in a subarctic mire. *Oikos* **43**, 341-350.
- Svensson G. 1988a Bog development and environmental conditions as shown by the stratigraphy of Store Mosse mire in southern Sweden. *Boreas* **17**, 89-111.
- Svensson G. 1988b Fossil plant communities and regeneration patterns on a raised bog in south Sweden. *J. Ecol.* **76**, 41-59.
- Swarzenski C.M., Swenson E.M., Sasser C.E. and Gosselink J.G. 1991 Marsh mat flotation in the Louisiana delta plain. *J.Ecol.* **79**, 999-1011.
- Tallis J.H. 1962 Some observations on *Sphagnum imbricatum*. *Trans. Br. Bryol. Soc.* **4**, 384-385.
- Tallis J.H. 1973 The terrestrialization of lake basins in north Cheshire, with special reference to the development of a 'schwingmoor' structure. *J.Ecol.* **61**, 537-567.
- Tallis J.H. 1983 Changes in wetland communities. In Gore A.J.P. ed., *Ecosystems of the world 4A: mires: swamp, bog, fen and moor. General studies*. Elsevier Science, Amsterdam
- Tallis J.H. and Birks H.J.B. 1965 The past and present distribution of *Scheuchzeria Palustris* L. in Europe. *J. Ecol.* **53**, 287-298.
- Tallis J.H. and Livett E.A. 1994 Pool-and -hummock patterning in a southern Pennine blanket mire. I. Stratigraphic profiles for the last 2800 years. *J. Ecol.* **82**, 775-788.
- Tansley A.G. 1911 *Types of British vegetation*. Cambridge University Press, Cambridge.
- Tansley A.G. 1939 *The British Islands and their vegetation*. Cambridge University Press, Cambridge.
- Tauber H. 1965 Differential pollen dispersal, and the interpretation of pollen diagrams. *Danm. Geol. Unders.* **11R 89**, 1-69.
- Taylor J.A. and Smith R.T. 1972 Climatic peat - a misnomer? *Proc. 4th Int. Peat Cong. Helsinki*. 471-484.

- Taylor J.A. and Smith R.T. 1980 The role of pedogenic factors in the initiation of peat formation and in the classification of mires. *Proc. 6th Int. Peat Cong. Duluth*. 109-118.
- ter Braak C.J.F. 1987a The analysis of vegetation - environment relationships by canonical correspondence analysis. *Vegetatio* **64**, 69-77.
- ter Braak C.J.F. 1987b Ordination. In Jongman R.H.G., ter Braak C.J.F. and van Tongeren O.F.R eds. *Data analysis in community and landscape ecology*. pp 91-173. Pudoc, Wageningen.
- ter Braak C.J.F. 1987c CANOCO - a Fortran program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1). T.W.O. Institute of Applied Computer Science, Wageningen.
- Thomas K.W. 1965 The stratigraphy and pollen analysis of a raised peat bog at Llanllwch, near Carmarthen. *New Phytol.* **64**, 101-116.
- Thompson D. J. and Shay J.M. 1985 The effects of fire on *Phragmites australis* in the Delta Marsh, Manitoba. *Can. J. Bot.* **63**, 1864-1869.
- Tipping R. 1995a Holocene evolution of a lowland Scottish landscape. Part 1, peat- and pollen-stratigraphic evidence for raised moss development and climatic change. *The Holocene* **5**, 69-81.
- Tipping R. 1995b Holocene landscape change at Carn Dubh, near Pitlochry, Perthshire, Scotland. *J. Quat. Sci.* **10**, 59-75.
- Tolonen K., Huttunen P. and Jungner H. 1985 Regeneration of two coastal raised bogs in eastern North America. *Annales Academiae Scientiarum Fennicae, Series A.* **13(d)**, 1-15.
- Tröels-Smith J. 1955 Characterisation of unconsolidated sediments. *Danm. Geol. Unders.* **4. R. 3**, No10.
- Tubridy M. ed. 1987 *The heritage of Clonmacnoise*. Environmental Sciences Unit, Trinity College, Co. Offaly.
- Turner J. 1964 The anthropogenic factor in vegetational history I: Tregaron and Whixal Mosses. *New phytol.* **63**, 73-89.
- Turner J. 1965 A contribution to the history of forest clearance. *Proc. Roy. Soc.* **161**, 343-355.
- Turner R.C. and Scaife R.G. eds. 1995 *Bog bodies: new discoveries and new perspectives*. British Museum Press, London.
- Tuxen R. 1937 Die pflanzengesellschaften Nordwestdeutschlands. *Mitteilungen der Floristsoziologischen Arbeitsgemeinschaft*. **3**, 1-170.
- Van Breeman N. 1995 How *Sphagnum* bogs down other plants. *Tree* **10 (7)**, 270-275.
- Van der Molen P.C. and Hoekstra S.P. 1988 A palaeoecological study of a hummock-hollow complex from Engbertsdijksveen, in the Netherlands. *Rev. Palaeobot. Palynol.* **56**, 213-274.
- Van der Molen P.C., Schalkoort M. and Smit R. 1994 Vegetation and ecology of hummock-hollow complexes on an Irish raised bog. *Proc. Royal Irish Academy* **94B(2)**, 145-175.

- Van der Putten W. H. 1993 Assessing ecological change in European Wetlands: How to know what parameters should be monitored to evaluate the die-back of common reed *Phragmites australis*? In Aubrecht G. and Crawford-Prentice G. D. 1993 Monitoring of ecological change in wetlands of middle Europe: *Proceedings of an International workshop in Linz, Austria, October 1993*, Stapfia 1WRB Publication No 30. (1994).
- Van der Valk A.G. 1981 Succession in wetlands: A Gleasonian approach. *Ecology* **62**, 688-696.
- Van der Valk A.G. and Verhoeven J.T.A. 1988 Potential role of seed banks and understorey species in restoring quaking fens from floating forests. *Vegetatio*. **76**, 3-13.
- Van Geel B. 1978a A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands. *Rev. Palaeobot. Palynol.* **25**, 1-20.
- Van Geel B. 1978b Tentative explanation of the late-glacial and early Holocene climatic changes in north-western Europe. *Geologie en Mijnbouw* **57**, 87-89.
- Van Geel B., Bohncke S.J.P. and Dee H. 1980/81 A palaeoecological study of an upper late glacial and Holocene sequence from "De Borchert", the Netherlands. *Rev. Palaeobot. Palynol.* **31**, 367-448.
- Van Geel B. and Middelorp A.A. 1988 Vegetational history of Carbury Bog (Co. Kildane, Ireland) during the last 850 years and a test of the temperature indicator value of the 2H/'H measurements of peat samples in relation to the historical sources and meteorological data. *New Phytol.* **109**, 377-392.
- van Miegroet H. and Cole D.W. 1985 Acidification sources in red alder and Douglas fir soils: importance of nitrification. *Soil Science Society of America Journal*. **49**, 1274-1279.
- Vasari Y. 1962 A study of the vegetational history of the Kuusamo District, North East Finland during the late-Quaternary period. *Annales Botanici. Fennici.* **33**, 1-140.
- Verhoeven J.T.A. 1986 Nutrient dynamics in mesotrophic peat mires. *Aquat. Bot.* **25**, 117-138.
- Verhoeven J.T.A. ed. 1992 *Fens and bogs in the Netherlands: Vegetation history, nutrient dynamics and conservation*. Geobotany **18**. Kluwer Academic Publishers.
- Verhoeven J.T.A., and Arts H.H.M. 1992 *Carex* litter decomposition and nutrient release in mires with different water chemistry. *Aquatic Botony* **43**, 365-377.
- von Marilaun A.K. 1863 *Das pflanzenleben des donaulander*. Translated by H.S. Conard in *The background to plant ecology*. Iowa State College Press. Ames
- von Post L. 1924 *Da genetische system der organogeneu Bildugen Schwedens*. *Comite International de Pedologie IV Commission No 22*.
- von Post L. and Sernander R. 1910 *Pflanzen - physiognomische studien auf Torfmooren in Narke*. Livretguide des excursion en Suede du 11eme Congress Geologie Internationale. **14**, 1-48.
- Walker D. 1966 The quaternary history of the Cumberland lowland. *Phil. Trans. Roy. Soc. Lond.* **B 251**, 1-120.
- Walker D. 1970 Direction and rate of change in some British postglacial hydroses. In Walker D. and West R.G. eds. *Studies in the vegetation history of the British Isles*. pp 117-139. Cambridge Univ. Press, Cambridge.

- Walker D. and Walker P.M. 1961 Stratigraphic evidence of regeneration in some Irish bogs. *J. Ecol.* **49**, 169-185.
- Walker D. and West R.G. eds. 1970 *Studies in the vegetation history of the British Isles*. pp 117-139. Cambridge University Press, Cambridge.
- Walker L.R. and Chapin F.S. 1987 Interactions among processes controlling successional change. *Oikos*. **50**, 131-135.
- Walker M.J.C., Griffiths H.I., Ringwood V. and Evans J.G. 1993 An early-Holocene pollen, mollusc and ostracod sequence from lake marl at Langorse Lake, South Wales, UK. *The Holocene* **3**(2), 138-149.
- Wallen B. 1987 Growth pattern and distribution of biomass in *Calluna vulgaris* on an ombrotrophic peat bog. *Holarctic Ecol.* **10**, 73-79.
- Wallen B. 1992 Methods for studying below ground production in mire ecosystems. *Suo.* **43**, 155-162.
- Wallen C.C. 1970 Introduction. In Wallen C.C. ed., *Climates of northern and western Europe*. pp 1-22. Elsevier, Amsterdam.
- Waller M. 1994 *The Fenland project No.9: Flandrian environmental change in Fenland*. East Anglian Archaeology., Cambridgeshire County Council.
- Wardle D.A., Nicholson K.S., Ahmed M. and Rahman A.R. 1995 Influence of pasture forage species on seedling emergence, growth and development of *Carduus nutans*. *J. Appl. Ecol.* **32**, 225-233.
- Warming E. 1895 *Plantensamfund. Grundtrak auf den ekologiska plantedeografi*. German edition published 1896 by Borntrager, Berlin.
- Warner B.G., Clymo R.S. and Tolnen K. 1993 Implications of peat accumulation at Point Escuminac, New Brunswick. *Quaternary Research* **39**, 245-248.
- Wasylikowa K. 1979 Plant macrofossil analysis. In Berglund B.E. ed., *Palaeohydrological changes in the temperate zone in the last 15,000 years, subproject B. lake and mire environments*. Vol. **3**, pp 291-313. International Geological Correlation Programme, Project 158, Lund.
- Wasylikowa K. 1986 Analysis of fossil fruits and seeds. In Berglund B. E., ed., *Handbook of Holocene palaeoecology and palaeohydrology*. John Wiley and Sons, Chichester.
- Watson E.V. 1968 *British mosses and liverworts*. Cambridge University Press, Cambridge.
- Waughman G.J. 1980 Chemical aspects of the ecology of some south German peatlands. *J. Ecol.* **68**, 1025-1046.
- Weber C.A. 1908 Aufbau und vegetation der moore Norddeutschlands. *Englers Bot. Jahrb. Beibl.* **90**. Leipzig.
- Weber C.A. 1930 Grenzhorizont und alterer *Sphagnum* torf. *Abhandl. Naturwiss. Verein. Bremen*, **28**, 57-65.
- Wein R.W. 1973 Biological flora of the British Isles: *Eriophorum vaginatum*. *J. Ecol.* **61**, 601-615.
- Wells C. 1991 In Middleton R. ed., *North West Wetlands Survey, Annual Report*, 1991.
- Wells C. 1992 In Middleton R. ed., *North West Wetlands survey, Annual Report*, 1992.

- Wells C. 1993 In Middleton R. ed., *North West Wetlands Survey, Annual Report*, 1993.
- Wells C. 1994 In Middleton R. ed., *North West Wetlands Survey, Annual Report*, 1994.
- Wheeler A.J. 1992 Vegetational succession, acidification and allogenic events as recorded in Flandrian peat deposits from an isolated Fenland embayment. *New Phytol.* **122**, 745-756.
- Wheeler B.D. 1980a Plant communities of rich-fen systems in England and Wales. I. Introduction. tall sedges and reed communities. *J. Ecol.* **68**, 365-395.
- Wheeler B. D. 1980b Plant communities of rich-fen systems in England and Wales. II. Communities of calcareous mires. *J. Ecol.* **68**, 405-420.
- Wheeler B.D. 1980c Plant communities of rich-fen systems in England and Wales. III. Fen meadows, fen grassland and fen woodland communities, and contact communities. *J. Ecol.* **68**, 761-788.
- Wheeler B.D. 1984 British fens: a review. In Moore P.D. ed., *European mires*. pp 337-282. Academic Press, London.
- Wheeler B.D. and Giller K.E. 1982 Species richness of herbaceous fen vegetation in Broadland, Norfolk, in relation to the quantity of above-ground plant material. *J. Ecol.* **70**, 179-200.
- Whittaker R.H. 1953 A consideration of climax theory: the climax as population and pattern. *Ecol. Monogr.* **23**, 41-78.
- Whittington G., Fallick A.E. and Edwards K.J. 1996 Stable oxygen isotope and pollen records from eastern Scotland and a consideration of Late-glacial and early Holocene climate change for Europe. *J. Quat. Sci.* **11**(4), 327-340.
- Wickman F.E. 1951 The maximum height of raised bogs and a note on the motion of water in soligenous mires. *Geol. Fören Förhandl.* **73**, 413-422.
- Wiegiers J. 1986 Succession in fen-woodlands in the Dutch Haf district. In Fanta F. ed., *Forest dynamics research in western and central Europe*, pp 135-144. PUDCC, Wageningen.
- Wiegiers J. 1988 Some bryophyte communities in a wetland forest: Their species composition, spatial relations and groundwater characteristics. In Barkman J.J. and Sykora K. V. eds. *Dependent plant communities*. SPB Academic Publishing, The Hague.
- Wiegiers J. 1990 Kragge-woodland in the Netherlands as a new community-type within the Alnion glutinosae. *Vegetatio*. **89**, 79-85.
- Wiegiers J. 1992 Carr vegetation: plant communities and succession of the dominant tree species. In Verhoeven J.T.A. ed., *Fens and bogs of the Netherlands: Vegetation history, nutrient dynamics and conservation*. pp 361-395. Kluwer Academic Publishers.
- Wildi O. 1978 Simulating the development of peat bogs. *Vegetatio* **37**(1), 1-17.
- Wilks P.J. 1979 Mid-Holocene sea-level and sedimentation interactions in the Dovey estuary area, Wales. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **26**, 17-36.
- Williamson M. 1987 Are communities ever stable? In Gray A.J., Crawley M.J., and Edwards P.J. eds, *Colonization, Succession and Stability: The 26th Symposium of the British Ecological Society, held jointly with the Linnean Society of London*. Blackwell Scientific Publications, Oxford.

Williams Parry M. and Parker L.A. 1939 *A general investigation of Cors Fochno*. Unpublished B.Sc. thesis, University of Wales. In Slater F.M. 1972 Contributions to the ecology of Borth Bog, Wales. I. General considerations. *Proc. 4th Int. Peat Cong I-IV, Helsinki*. 277-288.

Wimble G. A. 1986 The palaeoecology of the lowland coastal raised mires of south Cumbria. Unpublished Ph.D. thesis, University of Wales, Cardiff.

Winston R.B. 1994 Models of the geomorphology, hydrology and development of domed peat bodies. *Geol. Soc. America Bull.* **106**, 1594-1604.

Woodland W. 1996 Unpublished Ph.D. thesis. University of Plymouth.

Yu G. and Harrison S.P. 1995 Holocene changes in atmospheric circulation patterns as shown by lake status changes in northern Europe. *Boreas* **24**, 260-268.

Zielinski G.A., Mayewski P.A., Meeker L.D., Whitlow S., Twickler M.S., Morrison M., Meese D.A., Gow A.J. and Alley R.B. 1994 Record of volcanism since 7,000 B.C. from the GISP2 Greenland ice core and implications for the volcano-climate system. *Science* **264**, 948-951.

Zobel M. 1988 Autogenic succession in boreal mires - a review. *Folia Geobot. Phytotax.* **23**, 417-445.