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THE VEGETATION OF THE MALHAM TARN FENS

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The main features of the topography and vegetation of the fens at Malham Tarn are outlined. The principal plant communities are described, and their distribution is examined in relation to data on the height and variation of the water table, and chemical analyses of peats and plant material. It is concluded that the most important directions of variation are related to water level, to calcium concentration and pH (ombrogenous—soligenous) and to the availability of nutrients, including magnesium, potassium and phosphorus (oligotrophic—eutrophic). Successional relationships are briefly discussed.

CONTENTS

INTRODUCTION

THE word "fen" calls up a picture of the flat, willow-lined landscape of the Fens of East Anglia, and of the reeds, sedge, sallows and buckthorn of the few remaining fragments of undrained Fenland, but in fact smaller areas of fen—vegetation of wet, mineral-rich peat—occur very widely in the British Isles. The undrained remnants of the great Fenland owe their present condition to special and quite artificial circumstances. It is to the smaller, isolated fen areas that have escaped drainage that we must turn to see the most nearly natural fen vegetation at the present day, always remembering that any one of these small areas represents only a small fraction of the possible range of physical conditions and vegetation.

Fen is largely a lowland vegetation type in the British Isles, but not exclusively so. Small areas of mountain fen occur at altitudes up to 1,000 m. (3,000 ft.) or more in the Scottish Highlands (Ratcliffe, 1964*b*). Nevertheless, it is still true that, as Holdgate (1955*b*) pointed out, almost all published descriptions of fen vegetation in England relate to areas at modest altitudes. The Esthwaite fens described by Pearsall (1918, and in Tansley, 1939) are only some 65 m. (215 ft.) above sea level. The upland fens around Sunbiggin Tarn, Westmorland, described by Holdgate, lie at about 250 m. (825 ft.) and the area of fen at Semerwater (Ingram *et al.*, 1959), is at almost the same altitude. The Malham Tarn fens, at about 370 m. (1,230 ft.), are not only at a higher altitude but are considerably more extensive than either.

Malham Tarn lies on the drift-covered surface of impermeable Silurian rocks at the foot of an escarpment of Great Scar Limestone just north of the North Craven Fault. The mean annual rainfall is about 1,470 mm. (58 in.) (Manley, 1956). A good general account of the habitats and vegetation in the neighbourhood of the Tarn is given by Sinker (1960). Water flows into the Tarn basin principally from a group of strong springs near the base of the limestone to the north-west, which join to form the main inflow stream. There are other springs along the north shore of the Tarn, and a smaller stream enters the Tarn at its north-east corner from springs at the foot of Great Close Scar. The Tarn was once nearly double its present size. The western part of its basin is now occupied by the mire (or "wetland") complex that includes the Tarn Moss, and of which the fens form a part. Before we look at the fens in detail, we must look briefly at this mire complex as a whole.

The brow of the hill above High Stables affords an excellent view of the area. The dominant feature is the great raised bog of the Tarn Moss, a gently domed mass of acid peat, some 700–800 m. ($\frac{1}{2}$-mile) across and rising some 4–6 m. (15–20 ft.) above the level of the Tarn. In fact the Moss is made up of not one but of several more or less discrete domes, and there are some smaller isolated raised bog areas lying within the meanders and between the tributaries of the main inflow stream. These raised bog areas are dependent for their water supply entirely upon the rain falling on their surface. The mineral nutrient regime of the vegetation is determined by the balance between the rate at which material is brought in as blown dust or dissolved in rain-water or in other ways, and the rate at which it is lost in solution in the water draining out to the surroundings (Firbas, 1952). A mire of this kind is referred to as *ombrogenous* (Greek *ombros*, rain). Obviously, in such a situation, circulation of nutrients between the vegetation and the peat on which it is growing is likely to be of paramount importance.

Around the margins of the raised bog areas the peat comes under the influence of mineral-rich water draining from the surrounding country; the regime is *soligenous*. Where the sloping edge of the raised bog—the *rand*—abuts on mineral ground there is an intervening belt of fen—the *lagg*—sometimes very narrow, sometimes broader. Similarly, belts of fen vegetation mark the courses of the streams, and the seepages between the separate areas of raised bog. At Malham Tarn the most extensive fens are associated with the inflow streams entering the north-west of the Tarn Basin, forming a broad belt along the northern edge of the Tarn Moss. There are some smaller, but still interesting, areas of fen in the lagg on the south-west side of the Moss, and in the lagg around the moraine hillock of Spiggot Hill.

It is with the "North Fen"—the broad belt of fen fringing the main inflow streams —that this paper is chiefly concerned. I propose to consider the fens primarily in terms of the ecology of the present surface, but two points of history must be recorded at the outset. Firstly, it is obvious that a good deal of peat cutting has taken place in the past, and this has had a considerable influence on the diversity of habitat at the present day. Secondly, the level of the Tarn was raised by several feet in 1791, and probably altered again to some extent in about 1910. This initiated extensive secondary succession, whose results are often still clearly visible. The water level appears to have been raised slightly again (or returned to a former level) by repairs to the sluice at the Tarn Foot in September 1972.

Definitions and limits

The terms "bog" and "fen" have generally been used rather loosely in the British ecological literature, "bog" usually implying vegetation on acid peat, dominated mainly by bog-mosses (*Sphagnum* spp.), heather (*Calluna*), cotton-grass (*Eriophorum*), etc., and "fen" implying vegetation on circumneutral or alkaline peat, dominated principally by sedges (usually *Carex* spp.) and "brown mosses" (Hypnales, Bryales). These terms might be given more precision either by a more precise definition of the floristic differences that their common English usage reflects, or by defining them in terms of the distinction between ombrogenous and soligenous mires. There are arguments in favour of both courses. Duvigneaud (1949) considered at length the problem of the floristic subdivision of bog and fen vegetation, and concluded that no workable major boundaries can be drawn. Sjörs (1950) similarly concluded that the variation in Scandinavian fens is substantially continuous. A definition in terms of the ombrogenous/soligenous distinction is, of course, hydrological rather than botanical, and the boundary is reflected differently by the vegetation in different geographical areas. On the other hand, the ombrogenous/soligenous boundary (the "mineral soil water limit" of Du Rietz (1949); the boundary between hydrological systems I and II of Kulczynski is at least closely related to this) is clearly of high ecological significance, and within any particular area the major discontinuity in the vegetation is generally associated with it. This is certainly so at Malham, and for the purposes of this paper I shall follow Du Rietz and regard the mineral soil water limit as the boundary of the fen.

Topography and Vegetation

General Description

At first sight, the North Fen appears a forbiddingly complex and confusing area. However, as Fig. 1 shows, the distribution of the main vegetation types has a certain underlying simplicity and regularity. Within the fen there are six substantial areas of acid peat; the first and fourth of these (counting from east to west) have evidently been much cut, and are now reduced to mere remnants, though their influence is still obvious in the vegetation. In all of them the effect of mineral-rich ground water is apparent at least around the margins in acid fen communities ("poor fen" in Du Rietz's terminology) often rich in *Molinia* (purple moor grass). Extensive areas of fen wood or "carr" are particularly associated with the soligenous peat bordering the larger of these isolated patches of raised bog peat. *Carex* fens of various kinds occupy the broader spaces between them, and also many of the recolonized peat-cuttings; some of these are of considerable extent. The banks of the inflow streams,

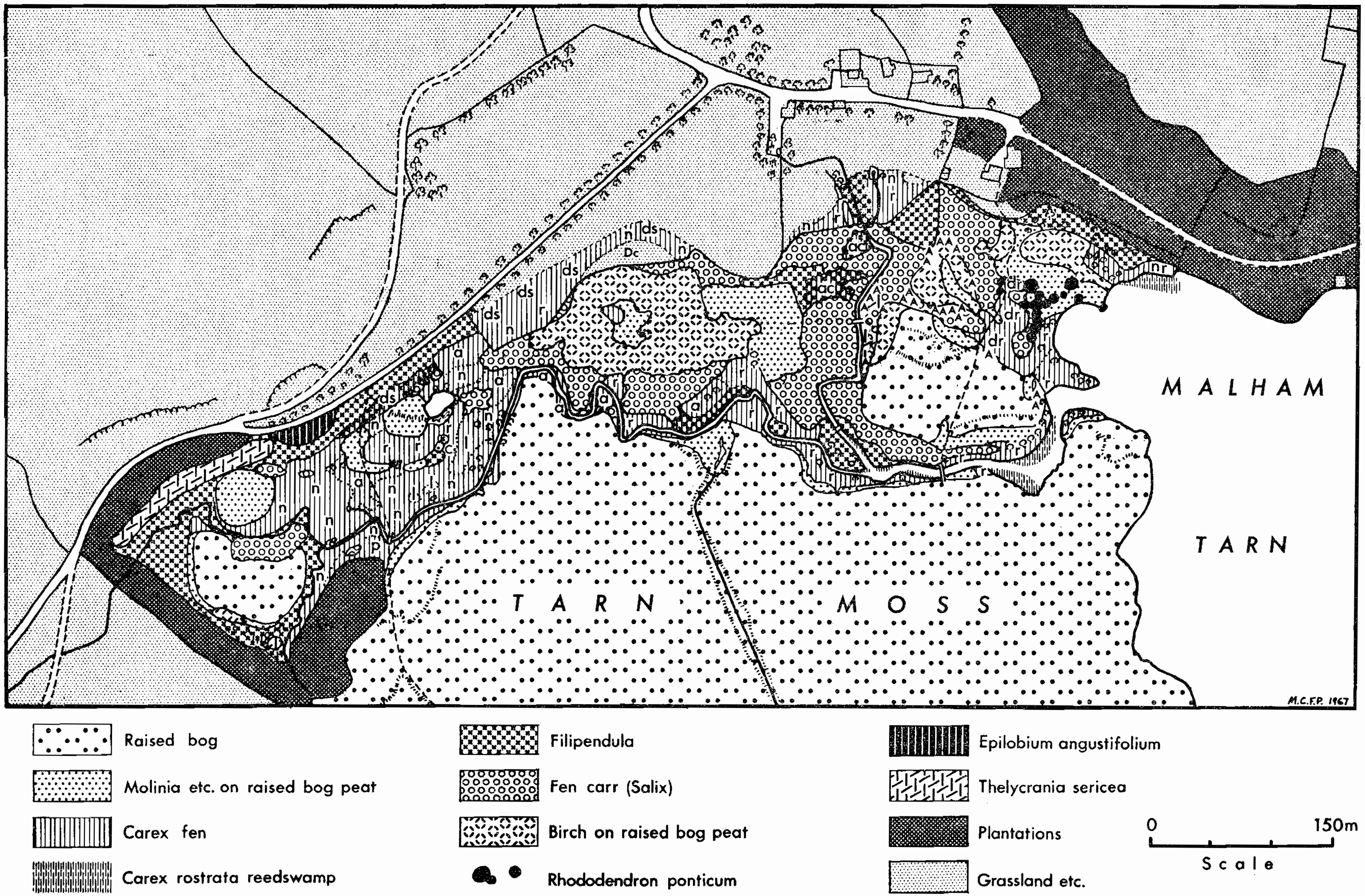

FIG. 1.

Sketch map showing approximate distribution of the main vegetation types within the "North Fen". For location and further topographical detail see Fig. 2. A = *Alnus glutinosa* (alder), a = *Carex appropinquata*, ac = *C. acutiformis*, Cs = *Calamagrostis stricta*, d = *Carex diandra*, Dc = *Deschampsia caespitosa*, ds = *Carex disticha*, l = *C. lasiocarpa*, n = *C. nigra*, p = *C. panicea*, r = *C. rostrata*.

and the contact between the fen and the surrounding mineral ground, are characteristically marked by a belt of vegetation dominated by *Filipendula ulmaria* (meadowsweet), while a low reedswamp of *Carex rostrata* (bottle sedge) fringes the broader and more sheltered parts of the inflow streams and the shore of the north-west corner of the Tarn.

For description it is convenient to divide the North Fen, as Sinker does, into a western, middle and eastern part. The "West Fen" between "Horseshoe Plantation" and the wall of the pasture some 300 m. south-west of Water Houses, probably includes the most natural areas, though there are still many signs of past disturbance. The main inflow stream enters the extreme western corner through a large and dense stand of *Filipendula*. After about 150 m. the stream is joined by a tributary from the lagg of the Tarn Moss. To the north of the main stream is a low area of acid peat dominated by *Molinia*; between the two streams is a better developed area of raised bog dominated by *Eriophorum vaginatum* (hare's-tail cotton-grass), and a good patch of fen carr. The remainder of the West Fen is occupied mainly by *Carex*-dominated communities, with a broad belt of *Filipendula* (and a patch of *Chamaenerion angustifolium* (rosebay willowherb) on formerly cultivated mineral soil) along the edge next to the road. A fairly uniform *Carex nigra* (common sedge) fen on rather firm peat, with scattered willows and a few small patches of carr, extends from the western end of this area along the north side of the stream; *Carex appropinquata* (fibrous tussock sedge) becomes dominant here and there, especially towards the eastern end. The central and northern part of the West Fen is more complex. There was evidently extensive acid peat here at one time, of which hummocks and banks and one larger patch remain, now covered with *Molinia*. A number of former pools have become almost entirely filled with spongy quaking mats of *Carex rostrata*, *Potentilla palustris* (marsh cinquefoil) and various bryophytes. One of these old pools was cleared in 1964 to recreate an area of open water. Nearer the inflow stream several patches of *Carex lasiocarpa* (slender sedge) may also occupy the sites of former pools. A small area on firmer peat is dominated by *Calamagrostis stricta* (narrow smallreed), which occurs also in some quantity in the Middle Fen. *Carex disticha* (brown sedge) is abundant in a narrow but regular zone at the lower edge of the marginal *Filipendula* belt, and continues in the corresponding position into the neighbouring pasture above the Middle Fen.

The "Middle Fen", which extends to the broad stream flowing due south to join the main inflow stream from springs near Waterhouses, is largely occupied by a large acid peat area. This is partly open and dominated by *Molinia* and *Deschampsia flexuosa* (wavy hair-grass) (the "Football Field", in which a number of new ponds were dug in 1971 and 1972) and partly overgrown with birch (*Betula pubescens*). It is surrounded by extensive areas of wet carr, especially on the sides next to the two streams. There are limited areas of *Carex appropinquata* and *C. rostrata* fen along the main inflow stream, the former on firm, the latter on softer peat probably representing fairly recent seral development. *Filipendula* is locally dominant along the stream and in the north-east corner of the area, where it is associated with two stands of *Carex acutiformis* (lesser pond-sedge) in gaps in the carr. Much of the birch wood is carpeted with *Sphagnum palustre*, *S. fimbriatum* and *Polytrichum commune*, with scattered plants of *Dryopteris dilatata* and *D. spinulosa* (broad and narrow buckler ferns). *Sphagnum squarrosum* is locally common, probably indicating more mineral-rich conditions, and in an open area near the middle of the wood there is a good deal of *S. teres*. At the northern edge of the same open patch an old pool has become recolonized by a floating mattress of *Phragmites* (common reed) and *Sphagnum*, though *Acrocladium stramineum* and other mosses in hollows among the *Sphagnum* indicate the mineral-rich character of the water close beneath the surface.

The "East Fen" is largely taken up by two large areas of acid peat. Of these, the one nearer the inflow stream is substantially intact and retains its raised bog character. A series of irregular hollows along its northern edge contain areas of very wet *Sphagnum* carpet, mainly of *S. papillosum* and *S. cuspidatum* close to the main mass of peat, but with the beginning of poor fen conditions indicated by the appearance of *Drepanocladus fluitans* and *Sphagnum recurvum*. Especially at the eastern end, considerable areas of acid peat are influenced by base-rich water. Here, *Molinia*, *Deschampsia flexuosa*, *Potentilla erecta* (tormentil) and *Polytrichum commune* are abundant, and *Sphagnum fimbriatum*, *S. squarrosum* and *Carex curta* (white sedge) frequent and characteristic. The other area of acid peat, between Miss Hilary's Cottage and the shores of the Tarn, is fragmentary, much influenced by mineral-rich water, and overgrown by birch. *Rhododendron ponticum* grows on some of the remaining ridges and hummocks of acid peat. It is difficult to be sure now whether this was a coherent area of acid peat in the past, or whether it has always consisted of several small areas with mineral-rich seepages in between. As it stands now it is complex, and the pH at the surface varies widely within short distances; the higher parts are similar in character to the birch wood of the Middle Fen. Carr occupies much of the remainder of the East Fen, but there is a largish patch of very wet fen in the centre, dominated by *Carex rostrata* and *C. diandra* (lesser tussock sedge). In part this has developed in old peat cuttings, but in part it probably follows the line of natural seepages. Comparable wet fen along the inflow stream and on the north shore of the Tarn is evidently connected serally to the neighbouring *Carex rostrata* reedswamp. The patch of fen on the firm peat of the headland north of the mouth of the inflow stream is rich in species for its size, and looks as though it may be a relatively natural piece of open *Carex* fen of long standing.

The lagg of the Tarn Moss consists of an almost continuous, though sometimes narrow and fragmentary, belt of fen. There are some sizeable patches of calcareous fen in the lagg to the west and south-west of Spiggot Hill, and the lagg which surrounds Spiggot Hill itself broadens out on the north side into an interesting and species-rich patch of very wet fen, which includes *Carex lasiocarpa* and *Cinclidium stygium* amongst other things. The lagg is made conspicuous in late summer by the blue flowers of *Succisa pratensis* (devil's-bit scabious) and the light green leaves of *Molinia*. Where the ground is strongly calcareous the fen ranges from a wet community with *Carex rostrata* and *Potentilla palustris* and a carpet of sphagna and other bryophytes at one extreme, to drier areas with much *Carex panicea* (carnation sedge), *C. lepidocarpa* (long-stalked yellow-sedge) and *Parnassia palustris* (grass of Parnassus) at the other. Either may grade rapidly into the poor fen of the bog margin. This is especially so in the watershed areas of the lagg, where poor-fen and rich-fen species sometimes alternate in remarkably close proximity.

The Plant Communities

Reedswamps

Carex rostrata is the only reedswamp species of any consequence in the Tarn and its surroundings. Vigorous shoots colonize open water up to about 30 cm. depth,

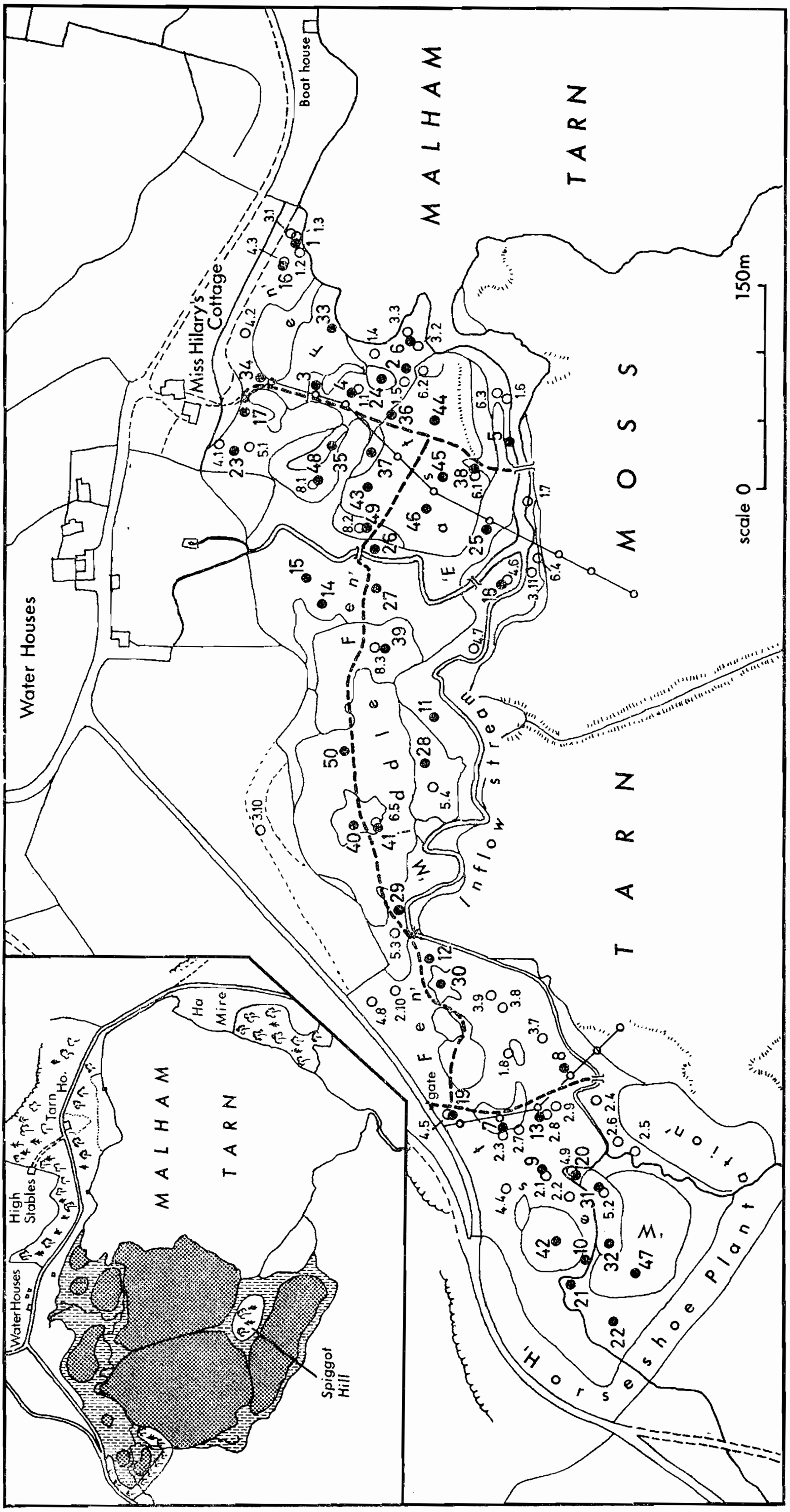

FIG. 2.

Location of the profiles shown in Figs. 3 and 4 (ruled lines; water-table sites shown as small circles), vegetation samples (open circles and small numerals: 5.2 is sample 2 in Table 5, etc.) and peat samples analysed in Table 10 (solid dots and large numerals). Inset: Tarn Moss and fens in relation to the Tarn and its surroundings.

forming a belt along the shore which may be several metres broad. Colonization by *Potentilla palustris* and bryophytes such as *Acrocladium giganteum* and *A. cordifolium* initiates the development to fen. *Carex rostrata* does not become established on exposed shores. Around the Tarn itself there is substantial growth only in the sheltered bays at the north-east and north-west corners. At the north-west corner of the Tarn and near the mouth of the main inflow stream there are areas of *C. rostrata* reedswamp which pass progressively into fen and are probably serally connected with it, but elsewhere there are patches which are probably static features and unlikely to develop further.

Equisetum fluviatile (water horsetail), *Sparganium erectum* (branched bur-reed), *Menyanthes trifoliata* (bogbean) and *Hippuris vulgaris* (mare's-tail) occur here and there as reedswamp plants. *Phragmites communis* is found in the North Fen, but sparingly, and mainly close to the inflow in the West Fen and in and around the large overgrown pools in the West Fen and Middle Fen. *Phalaris arundinacea* (reed canary-grass) is easily mistaken for *Phragmites* when it is not in flower, and is much commoner, but at Malham it is mainly a plant of stream banks and the shore of the Tarn, not reedswamp. *Typha latifolia* (bulrush) is limited to a single patch in the overgrown pool in the West Fen.

Carex rostrata communities occur widely in the British Isles, especially in oligotrophic areas of the north and west. The *Carex rostrata-Menyanthes* and *Carex rostrata-Acrocladium* sociations of Spence (1964) and some of the *Carex*-dominated communities at Semerwater (Ingram *et al.*, 1959) correspond in a general way to the *Carex rostrata* reedswamps and early transitional stages to fen at Malham (Table 1). *Carex rostrata* reedswamps are widespread also in the Lake District (Pearsall, 1918), Wales and Ireland (Braun-Blanquet and Tüxen, 1952, p. 267). These British *C. rostrata* communities correspond with the Continental Caricetum inflato-vesicariae (W. Koch, 1926), and fall within the alliance Magnocaricion (class Phragmitetea, order Magnocaricetalia) (see Shimwell, 1971).

Carex *fens*

(a) *Carex rostrata* reedswamps often grade into wet fen, dominated by *C. rostrata* or *C. diandra*, with a luxuriant understorey of large bryophytes including *Acrocladium cordifolium*, *A. giganteum*, *Drepanocladus revolvens*, *Marchantia polymorpha* and *Mnium pseudopunctatum*. Herbaceous associates are much more numerous and prominent than in the reedswamp. *Potentilla palustris* remains abundant and characteristic, alongside such species as *Caltha palustris* (marsh-marigold), *Carex nigra*, *Epilobium palustre* (marsh willow-herb), *Galium palustre* (marsh bedstraw), *Mentha aquatica* (water mint) and *Ranunculus flammula* (lesser spearwort). Along the inflow stream and at the north-west corner of the Tarn, fen of this kind forms a relatively narrow belt, but there are more extensive areas in recolonized peat cuttings and pools in the East and West Fen. For the purposes of the present paper we may call this community the *Potentilla palustris-Acrocladium* nodum (using *nodum* in Poore's sense as a general term for a plant community of unspecified rank). Although a fair number of species attain a high constancy in these fens, the floristic composition varies a good deal from place to place, probably reflecting partly the vagaries of dispersal and establishment in a developing situation, and partly the variation in physical factors of the habitat. For instance, in the strip along the inflow stream, *Acrocladium cordifolium* and

Table 1. Potentilla palustris-Acrocladium *nodum and related fens*

	1	2	3	4	5	6	7	8	9	10
Total field layer cover /10	7	6	7	10	10	9	6	8	10	9
Total moss cover /10	3	9	8	4	5	7	9	5	5	6
Area of sample (m^2)	100	4	4	4	4	4	4	4	4	4
Caltha palustris	4	3	1	3	3	4	4	–	3	2
Cardamine pratensis	1	2	1	1	2	2	1	–	–	–
Carex nigra	3	5	5	8	8	5	5	–	5	4
Carex rostrata	3	3	3	7	3	–	8	7	3	3
Epilobium palustre	3	3	3	2	3	2	2	–	–	–
Galium palustre	2	3	1	3	3	2	2	2	–	–
Menyanthes trifoliata	3	5	4	4	5	–	–	–	7	8
Potentilla palustris	5	5	7	4	4	6	2	7	4	2
Carex diandra	7	5	5	–	4	–	–	–	–	–
Filipendula ulmaria	1	1	2	–	1	2	–	–	–	–
Mentha aquatica	2	4	–	2	3	3	–	–	–	–
Ranunculus flammula	1	2	1	–	1	–	3	–	–	–
Agrostis stolonifera	–	2	2	1	–	2	4	–	3	–
Lychnis flos-cuculi	–	1	–	1	1	8	–	2	–	2
Myosotis palustris	1	–	–	2	2	–	3	–	–	–
Juncus articulatus	–	2	2	–	–	–	–	–	–	–
Succisa pratensis	1	–	–	–	1	–	–	1	4	–
Valeriana officinalis	1	–	–	1	–	3	–	–	–	–
Angelica sylvestris	1	–	–	–	–	1	–	–	–	–
Carex lepidocarpa	–	1	–	–	–	–	–	–	6	–
Eriophorum angustifolium	–	–	–	–	–	3	–	2	–	–
Equisetum fluviatile	–	3	–	–	–	–	–	–	4	2
Molinia caerulea	1	–	–	–	–	–	–	–	2	–
Parnassia palustris	1	–	–	–	–	2	–	–	–	–
Pedicularis palustris	–	2	–	–	–	1	–	–	–	–
Sparganium erectum	–	–	1	–	–	–	2	–	–	–
Veronica scutellata	–	–	–	–	–	1	3	–	–	–
Acrocladium giganteum	5	9	8	3	5	–	–	–	–	–
Marchantia polymorpha	1	4	3	5	6	6	–	4	–	–
Acrocladium cuspidatum	2	–	1	5	4	5	–	2	7	2
Bryum pseudotriquetrum	3	3	2	2	–	–	–	1	–	–
Cratoneuron filicinum	1	2	1	1	–	–	–	–	–	–
Mnium pseudopunctatum	5	2	–	1	4	4	–	4	–	–
Chiloscyphus pallescens	2	–	–	–	1	2	–	2	–	–
Mnium seligeri	1	–	5	–	–	–	–	–	–	–
Scorpidium scorpioides	1	–	4	–	–	–	–	–	–	–
Acrocladium stramineum	–	–	–	–	–	4	–	3	–	–
Aulacomnium palustre	–	–	–	–	–	1	–	5	–	–
Brachythecium rutabulum	–	–	–	–	–	3	–	–	–	2
Mnium rugicum	–	–	–	2	–	5	–	–	–	–
Lophocolea bidentata	–	–	–	–	–	–	–	2	–	3
Pellia endiviaefolia	1	–	–	–	–	–	–	2	–	–
Rhytidiadelphus squarrosus	–	–	–	–	–	4	–	–	–	3

Additional species: Acrocladium cordifolium 6, 2; Agrostis canina 6, 3; Calypogeia fissa 10, 2; Campylium stellatum 1, 4; Carex appropinquata 3, 1; C. disticha 6, 2; C. panicea 1, 3; Cirsium palustre 9, 1; 10, x; Dactylorhiza incarnata 10, 2; D. purpurella 9, x; Drepanocladus revolvens 1, 2; Equisetum palustre 10, 2; Fissidens adianthoides 1, 2; Fontinalis antipyretica 3, 1; Hippuris vulgaris 8, 2; Iris pseudacorus 2, 1; Festuca rubra 10, 3; Hookeria lucens 10, 3; Phragmites communis 8, 1; Potentilla erecta 10, 2; Riccardia pinguis 1, 1; Rumex acetosa 6, 1; Salix cinerea 1, 1; Sphagnum papillosum 10, 3; S. squarrosum 6, 2; Stellaria alsine 6, 1; Typha latifolia 8, 2; Utricularia neglecta 8, 4; Veronica beccabunga 7, 5; Viola palustris 10, x.

1. *Carex diandra* fen by raised way south of Miss Hilary's Cottage.
2, 3. Landward side of *Carex rostrata* reedswamp at north-west corner of Tarn.
4. *Carex rostrata* fen, East Fen close to Tarn edge.
5. *Carex nigra-C. diandra* fen, south of carr between raised way and Tarn.
6. *Carex rostrata* fen on north bank of inflow stream, East Fen.
7. *Carex rostrata* fen at inner edge of reedswamp on south bank of inflow stream.
8. *Carex rostrata* fen, edge of large recolonized peat cutting, West Fen.
9, 10. Lagg of Tarn Moss, south-west of Spiggot Hill.

Cover-abundance values in this and succeeding tables on Domin's scale; "x" indicates nearby occurrence in same community but outside sample area.

Mnium rugicum largely replace *A. giganteum* and *M. pseudopunctatum* which are prominent in the nodum elsewhere in the Fen.

Fens of this general kind seem to be a widespread and characteristic type in the British Isles and on neighbouring parts of the Continent. For examples of comparable communities see Holdgate (1955*b*, p. 395), Ivimey-Cook and Proctor (1966, p. 258 and Table 31, *Carex nigra-Acrocladium giganteum* nodum), Spence (1964, p. 344 and Table 51, *Carex rostrata-Acrocladium* sociation, p. 350 and Table 52, *Carex nigra-Acrocladium* sociation, p. 352 and Table 53, *Potentilla palustris-Acrocladium* sociation), Ratcliffe (1964*a*, p. 438 and Table 56, *Carex rostrata*-brown moss mire), Segal (1966, p. 119, *Calliergon giganteum*, *Scorpidium* and *Pellia* phases, and p. 126, Table 1).

(b) The Middle and especially the West Fen include large areas of *Carex*-dominated vegetation on much firmer peat. This drier fen usually lacks *Potentilla palustris*, but *Angelica sylvestris* (wild angelica), *Carex panicea*, *Molinia caerulea*, *Sanguisorba officinalis* (great burnet), *Succisa pratensis* and *Valeriana dioica* (marsh valerian) occur with high constancy. The bryophyte layer is generally sparse, with *Acrocladium cuspidatum* the most constant species, and *Ctenidium molluscum*, *Campylium elodes*, *Lophocolea bidentata*, *Thuidium tamariscinum* and *Plagiochila asplenioides* frequent in small quantities. *Carex nigra* is the most widespread dominant, with the addition locally of *Carex appropinquata*. This somewhat variable but coherent range of fen communities may be grouped together as the *Carex nigra-Sanguisorba officinalis* nodum, with two facies dominated respectively by *Carex nigra* (Table 2, 1–6) and *C. appropinquata* (Table 2, 7–10). They give the appearance of being very much more stable and persistent than the fens of the last nodum, and are notably species-rich. Broadly comparable fen exists at Sunbiggin in Westmorland (Holdgate, 1955*b*, p. 396, "mixed fen"), and the Malham nodum is evidently related to a number of the types listed from Scotland by Spence (1964, Tables 51, 53).

(c) Sites on firm calcareous peat, especially around the fen margin, often carry fen vegetation in which *Carex panicea* and *C. lepidocarpa* are prominent in the field layer, with a bryophyte layer characteristically including *Drepanocladus revolvens*, *Riccardia pinguis* and *Acrocladium cuspidatum* (Table 3, 1–6). Each site is different from every other, so it would be premature to attempt to characterize a nodum from the rather fragmentary stands in and around the Fen, especially so without taking into account the extensive related communities of the calcareous mires east of the Tarn. Vascular plants often conspicuous in sites of this kind include *Parnassia palustris*, *Pedicularis palustris* (marsh lousewort), *Pinguicula vulgaris* (common butterwort), *Primula farinosa* (bird's-eye primrose) and *Selaginella selaginoides*.

These sites fall within the circle of affinity of a widespread complex of short, open calcareous marsh and fen communities; related communities are described from Westmorland (Holdgate, 1955*a*), Teesdale (Pigott, 1956, p. 555 ff., "Calcareous marshes"), Scotland (Ratcliffe, 1964*a*, p. 437 and Table 56, *Carex panicea-Campylium stellatum* mire; 1964*b*, p. 537 and Table 63, Alpine *Carex-Hypnum* mire; Spence, 1964, p. 350 and Table 52, *Carex nigra-C. panicea* sociation) and Ireland (Braun-Blanquet and Tüxen, 1952, pp. 312–316, *Schoenus nigricans-Cirsium dissectum* association and *Carex hostiana* Gesellschaft; Ivimey-Cook and Proctor, 1966, pp. 255–256 and Tables 31 and 32, *Schoenus nigricans-Cirsium dissectum* association and Burren *Carex demissa* nodum).

(d) *Carex lasiocarpa* is dominant locally in the West fen in several open areas south of the large infilled pool. Three species-lists from this area are given in Table 3, 7–9.

No doubt the sites were much wetter when they were first colonized by the sedge; at present their flora has much in common with that of the surrounding drier fen. In the fen north of Spiggot Hill *C. lasiocarpa* occurs in very much wetter conditions, and the general character of the vegetation is close to the *Potentilla palustris-Acrocladium* nodum; there is a strong tendency to surface acidification and vigorous growth of *Sphagnum*.

All of the fen communities considered above include a fair representation of species characteristic of the order Molinietalia of Continental authors, e.g. *Angelica sylvestris, Caltha palustris, Filipendula ulmaria* and *Lychnis flos-cuculi* (ragged robin). However, the total species-list leaves no doubt that they should be placed among the

Table 2. Carex nigra-Sanguisorba officinalis *nodum*

	1	2	3	4	5	6	7	8	9	10
Total field layer cover /10	8	8	9	10	10	9	9	10	10	10
Total moss cover /10	1	1	1	2	3	1	1	2	1	2
Angelica sylvestris	4	4	4	1	–	2	3	4	4	2
Carex nigra	8	8	6	7	2	5	5	5	5	2
Carex panicea	4	3	2	6	5	6	4	3	4	–
Crepis paludosa	3	3	1	2	2	2	3	3	3	1
Sanguisorba officinalis	3	4	6	3	4	4	2	3	3	–
Succisa pratensis	3	4	3	3	–	4	4	4	4	2
Valeriana dioica	5	3	3	2	2	3	3	3	3	3
Equisetum palustre	3	4	–	2	–	1	3	3	3	2
Filipendula ulmaria	2	4	2	–	–	2	5	–	4	5
Molinia caerulea	4	4	7	5	7	8	1	–	4	–
Potentilla erecta	2	–	–	2	3	2	4	1	1	–
Caltha palustris	1	2	–	–	–	1	–	1	1	2
Carex pulicaris	3	3	–	2	–	2	–	–	2	–
Cirsium palustre	1	–	1	–	1	1	–	–	–	2
Ranunculus acris	1	2	–	–	–	2	2	3	2	–
Anemone nemorosa	–	–	2	–	3	2	2	–	–	–
Anthoxanthum odoratum	–	2	–	–	–	–	2	2	–	–
Cardamine pratensis	–	2	–	–	–	–	1	2	–	1
Carex appropinquata	–	–	–	–	–	–	8	9	8	9
Carex disticha	–	1	1	–	–	–	3	–	–	–
Centaurea nigra	–	–	–	–	–	2	–	1	1	–
Festuca rubra	–	2	–	–	–	2	1	–	–	–
Galium palustre	1	2	–	–	–	–	–	–	–	3
G. uliginosum	–	2	–	–	–	–	–	3	2	2
Geum rivale	–	–	–	–	–	–	–	2	2	4
Juncus articulatus	–	–	–	1	1	2	–	–	–	–
Luzula multiflora	–	x	–	–	1	–	–	–	1	–
Mentha aquatica	–	2	–	–	–	–	–	2	1	–
Menyanthes trifoliata	–	–	2	4	–	–	5	4	–	–
Rumex acetosa	–	1	1	–	–	–	1	–	–	3
Serratula tinctoria	–	–	–	2	4	3	–	–	–	–
Trollius europaeus	2	–	–	–	3	2	–	2	–	–
Agrostis canina	–	–	–	–	1	–	–	–	–	1
Agrostis stolonifera	–	3	–	–	–	–	2	–	–	–
Arrhenatherum elatius	–	–	–	–	–	–	x	–	–	1
Carex flacca	–	–	–	–	2	1	–	–	–	–
Carex hostiana	–	–	–	–	5	–	–	2	–	–
Dactylorhiza purpurella	–	–	–	1	–	–	1	–	–	–
Equisetum fluviatile	–	1	–	–	2	–	–	–	–	–
Festuca ovina	–	–	–	–	1	–	–	–	1	–
Lathyrus pratensis	–	–	–	–	–	–	x	–	–	2
Lychnis flos-cuculi	–	–	–	–	–	–	–	1	–	2
Parnassia palustris	–	3	–	–	–	–	2	–	–	–
Phragmites communis	–	–	–	–	2	1	–	–	–	–
Potentilla palustris	1	–	–	–	–	–	–	–	–	1
Ranunculus auricomus	2	–	–	–	–	–	–	–	1	–

Table 2—*continued*

	1	2	3	4	5	6	7	8	9	10
Acrocladium cuspidatum	3	3	–	1	–	–	2	4	2	5
Aulacomnium palustre	1	2	3	–	–	–	2	–	–	2
Campylium elodes	3	2	–	–	–	–	1	3	1	–
Lophocolea bidentata	–	1	3	–	2	–	2	2	–	5
Plagiochila asplenioides	4	3	–	–	4	–	2	2	–	2
Campylium stellatum	–	–	–	5	–	–	–	4	4	–
Climacium dendroides	–	4	–	–	–	–	2	2	–	2
Ctenidium molluscum	2	–	–	–	1	–	4	1	–	–
Hylocomium splendens	1	–	–	3	–	–	1	–	–	–
Pseudoscleropodium purum	2	–	–	–	4	–	–	–	–	1
Rhytidiadelphus squarrosus	–	1	–	–	2	–	2	–	–	–
Thuidium tamariscinum	3	–	1	–	6	–	1	–	–	–
Dicranum bonjeanii	–	–	–	–	1	–	–	–	–	1
Eurhynchium praelongum	2	–	–	–	–	–	–	–	–	3
Fissidens adianthoides	–	–	–	–	–	–	–	3	1	–
Mnium pseudopunctatum	–	–	–	–	–	–	2	1	–	–
Mnium undulatum	–	–	–	–	–	–	2	–	–	4

Additional species: Ajuga reptans 7, 1; Deschampsia caespitosa 10, 2; D. flexuosa 3, 1; Epilobium palustre 5, 2; Eriophorum angustifolium 4, 1; E. vaginatum 3, 1; Holcus lanatus 10, 2; Juncus conglomeratus 6, 1; Primula farinosa 9, 1; Salix pentandra 8, 1; Acrocladium cordifolium 7, 1; Barbilophozia sp. 2, 1; Brachythecium rutabulum 3, 1; Bryum pseudotriquetrum 2, 1; Cratoneuron filicinum 8, 1; Drepanocladus uncinatus 9, 3; Hypnum cupressiforme 3, 4; Mnium hornum 7, 1; M. punctatum 10, 1; M. rugicum 4, 2.

1, 2. *Carex nigra*, middle of West Fen.
3. *Carex nigra*, West Fen, near water-table site 12.
4–6. *Carex nigra*, south edge of West Fen.
7–9. *Carex appropinquata*, West Fen, between water-table sites 12 and 14.
10. *Carex appropinquata*, near north-east corner of West Fen.

Table 3. *Miscellaneous* Carex *fens*

	1	2	3	4	5	6	7	8	9	10	11
Total field layer cover /10	10	8	9	9	9	9	10	10	8	9	9
Total moss cover /10	6	7	6	7	7	5	4	5	5	n.r.	5
Species differential for *Potentilla palustris-Acrocladium* nodum											
Cardamine pratensis	–	–	2	–	–	–	2	2	2	2	–
Carex rostrata	–	–	–	2	2	–	1	2	–	–	7
Epilobium palustre	–	–	–	–	–	–	1	2	–	1	2
Galium palustre	2	–	2	–	–	–	2	–	–	2	3
Menyanthes trifoliata	–	6	6	8	6	8	1	–	–	–	3
Potentilla palustris	–	1	2	–	–	–	2	5	6	4	5
Mentha aquatica	2	3	4	–	–	–	4	–	–	–	2
Ranunculus flammula	–	–	2	–	–	–	–	–	–	–	–
Acrocladium giganteum	–	4	4	–	–	–	–	–	–	–	–
Marchantia polymorpha	–	3	5	–	–	–	–	–	–	–	–
Bryum pseudotriquetrum	–	–	2	–	–	–	–	–	–	p	–
Cratoneuron filicinum	–	–	4	–	–	–	–	–	–	–	–
Mnium pseudopunctatum	–	8	5	7	4	4	–	–	1	p	5
Species differential for *Carex nigra-Sanguisorba officinalis* nodum											
Angelica sylvestris	2	2	2	–	–	–	–	4	2	2	1
Carex panicea	4	2	4	4	4	5	3	–	5	6	–
Crepis paludosa	–	–	–	–	–	–	2	1	1	–	–
Sanguisorba officinalis	1	–	–	–	–	–	3	2	1	–	–
Succisa pratensis	4	4	3	5	3	4	1	1	2	4	4
Valeriana dioica	5	6	3	–	–	–	4	3	4	3	–
Equisetum palustre	–	–	–	4	4	5	–	1	2	1	–
Molinia caerulea	–	4	4	1	8	6	3	–	–	4	–

Table 3—*continued*

	1	2	3	4	5	6	7	8	9	10	11
Other species											
Carex nigra	5	5	5	–	–	2	5	4	4	4	4
Eriophorum angustifolium	–	–	1	5	4	3	5	–	5	–	3
Pedicularis palustris	2	2	3	4	2	2	1	–	–	–	–
Caltha palustris	2	1	–	–	–	–	–	2	1	3	3
Equisetum fluviatile	–	1	1	7	–	5	1	–	1	–	–
Filipendula ulmaria	4	3	–	–	–	–	2	6	4	–	5
Parnassia palustris	2	2	2	–	–	–	–	1	1	2	–
Agrostis stolonifera	2	3	–	–	–	–	–	3	2	–	2
Carex lepidocarpa	–	3	3	8	3	6	–	–	–	–	–
Lychnis flos-cuculi	2	–	1	–	–	–	1	2	–	2	–
Triglochin palustris	–	–	2	–	2	5	–	–	1	–	–
Carex lasiocarpa	–	–	–	–	–	–	7	6	7	–	–
Dactylorhiza purpurella	1	–	1	x	–	–	–	–	–	–	–
Galium uliginosum	–	–	1	–	–	–	–	3	3	–	–
Salix repens	–	–	–	–	–	–	2	4	4	–	–
Salix seedlings excl. pentandra	1	2	1	–	–	–	–	–	–	–	–
Carex appropinquata	2	–	x	–	–	–	–	–	–	–	–
Carex dioica	–	–	–	1	–	5	–	–	–	–	–
Carex pulicaris	–	3	2	–	–	–	–	–	–	–	–
Festuca rubra	3	–	–	–	–	–	–	1	–	–	–
Geum rivale	–	–	–	–	–	–	–	1	1	–	–
Holcus lanatus	5	–	–	–	–	–	–	–	–	3	–
Phalaris arundinacea	–	–	–	–	–	–	–	–	–	1	4
Rumex acetosa	2	–	–	–	–	–	–	–	–	1	3
Salix pentandra (seedlings)	–	2	1	–	–	–	–	–	–	–	–
Vaccinium oxycoccos	–	–	–	–	–	–	2	–	1	–	–
Acrocladium cuspidatum	4	4	4	2	5	–	5	5	1	p	7
Campylium stellatum	–	–	–	2	–	1	4	–	–	–	–
Climacium dendroides	8	–	2	–	–	–	–	–	–	p	–
Drepanocladus revolvens	1	–	5	3	–	–	–	–	–	–	–
Fissidens adianthoides	–	–	4	–	–	x	1	–	–	–	–
Hylocomium splendens	–	–	–	–	–	2	–	2	4	–	–
Lophocolea bidentata	–	–	–	–	–	–	–	2	1	p	–
Rhytidiadelphus squarrosus	–	–	–	–	–	–	–	4	3	–	2
Riccardia pinguis	–	1	1	–	–	2	–	–	–	–	–
Aulacomnium palustre	–	–	–	–	–	–	–	4	5	–	–
Brachythecium rutabulum	–	–	–	–	–	–	–	4	–	p	–
Ctenidium molluscum	–	–	–	–	–	1	1	–	–	–	–
Mnium rugicum	–	–	–	–	–	–	–	2	–	–	1
Mnium seligeri	–	–	–	–	–	4	1	–	–	–	–
Pellia endiviaefolia	–	–	4	–	–	1	–	–	–	–	–
Plagiochila asplenioides	–	–	–	–	–	–	–	–	1	p	–
Pseudoscleropodium purum	–	–	–	–	–	–	–	1	1	–	–
Sphagnum plumulosum	–	–	–	–	–	3	–	4	–	–	–

Locations of samples (additional species in parentheses):

1. Margin of fen at north-west corner of Tarn (*Alchemilla glabra* 1, *Anthoxanthum odoratum* 1, *Festuca pratensis* 1, *Luzula multiflora* 1, *Prunella vulgaris* 1, *Ranunculus repens* 3, *Sagina nodosa* 1, *Mnium* sp. 1).

2, 3. Promontory north of mouth of inflow stream, East Fen (2: *Carex flacca* 1, *Scorpidium scorpioides* 1; 3: *Carex diandra* 1, *Equisetum variegatum* 1, *Juncus articulatus* 1, *Primula farinosa* 1, *Philonotis calcarea* 1).

4–6. Lagg of Tarn Moss south-east of Spiggot Hill (5: *Calluna vulgaris* 2, *Dactylorhiza incarnata* 2, *Pinguicula vulgaris* 1, *Lophocolea* sp. 4; 6: *Selaginella selaginoides* 1, *Calypogeia* sp. 1, *Mnium hornum* 2, *Riccardia multifida* 1, *Thuidium recognitum* 2).

7–9. Between inflow stream and large recolonized peat cutting in eastern part of West Fen (7: *Juncus acutiflorus* 2, *Sphagnum contortum* 6; 8: *Calamagrostis stricta* 6, *Eurhynchium praelongum* 4, *Mnium punctatum* 3; 9: *Barbilophozia* sp. 1, *Dicranum bonjeanii* 3, *Rhytidiadelphus triquetrus* 1, *Thuidium tamariscinum* 4, *Trichocolea tomentella* 5).

10. Lagg fen with *Carex disticha* in pasture north of Middle Fen; bryophyte cover values not recorded, p = present (*Agrostis canina* 2, *Carex disticha* 7, *Cerastium holosteoides* 1, *Ranunculus acris* 2).

11. Bank of main inflow stream near confluence (*Cochlearia officinalis* subsp. *alpina* 5, *Viola palustris* 1, *Acrocladium stramineum* 3).

fen communities of the class Caricetea nigrae. Most phytosociologists divide the communities of fens, as does Shimwell (1971), between the order Caricetalia nigrae of mineral-poor sites and the calcareous Tofieldietalia. At best, the floristic distinction is not sharp (see p. 3 and Duvigneaud, 1949). A number of species common in Caricetalia nigrae communities in Central Europe are mainly associated with highly calcareous sites in the British Isles, and there appears to be a shift in the expression of the significant rich-fen–poor-fen transition as one moves towards the western seaboard of Europe. There is much to be said for a radical reclassification of fen communities on the lines suggested by Segal (1966), taking much more account of the bryophytes, but it would be premature to attempt it here. The communities included under (c) above clearly belong in the Tofieldietalia of the traditional classifications, but no sharp boundary can be drawn between them and the remaining fens influenced by calcareous water. The *Carex acutiformis* stands referred to on p. 5 are species-poor, and their floristic relationships are with the surrounding *Filipendula* vegetation rather than with the other *Carex* fens.

Filipendula *communities*

Filipendula ulmaria is an uncompromising dominant in much of the *Filipendula*-rich vegetation that borders the inflow stream and the margins of the Fen. As the samples in Table 4 show, this vegetation is not particularly species-poor, but the associated species seldom make a large contribution to the vegetation, and few occur with high constancy. The most abundant are plants of wet eutrophic meadow (often occurring also in fen carr), such as *Angelica sylvestris*, *Geum rivale* (water avens), *Ranunculus repens* (creeping buttercup) and *Rumex acetosa* (common sorrel), and the bryophytes *Brachythecium rutabulum*, *Eurhynchium praelongum* and *Lophocolea bidentata*. Fen species are sporadic and poorly grown. There seems to be rather little difference between the marginal *Filipendula* stands and those along the stream, beyond a tendency for the former to be slightly richer in species.

Filipendula communities appear to have been little studied in the British Isles. Pearsall indicates the presence of a *Filipendula* society on the bank of the Black Beck in the Esthwaite fens (Tansley, 1939, pp. 641, 643) and a couple of examples from Semerwater are listed by Ingram *et al.*, (1959). Spence (1964) describes two *Filipendula*-rich sociations from the Scottish lochs. Both are evidently wetter than the bulk of the *Filipendula* vegetation at Malham and correspond most nearly to transitional stages between that and the *Potentilla palustris-Acrocladium* nodum. However, Spence's paper is concerned primarily with aquatic vegetation, and he comments that both of his sociations are "fen rather than swamp sociations but they are considered here because of their floristic and spatial connections with swamps". He indicates that his *Filipendula-Acrocladium* sociation occurs widely but sporadically on the shores of base-rich lochs; it is limited by the intolerance of *Filipendula* to grazing and burning.

Our *Filipendula* stands are certainly closely related floristically to the *Filipendula* communities which are widespread and well known on the Continent (order Molinietalia, alliance Filipendulion). Braun-Blanquet and Tüxen (1952) equated four *Filipendula*-rich stands from Ireland with the Filipenduleto-Geranietum palustris of W. Koch (1926) which they consider synonymous with the Valerianeto-Filipenduletum described by Sissingh (1946) from Holland and north-west Germany.

Table 4. Filipendula ulmaria *communities*

	1	2	3	4	5	6	7	8	9
Total field layer cover /10	10	10	9	10	10	9	9	9	10
Total moss cover /10	5	5	4	2	3	1	2	4	3
Filipendula ulmaria	8	9	8	10	9	8	9	9	8
Rumex acetosa	3	1	2	1	1	2	2	–	–
Angelica sylvestris	2	1	x	–	–	4	1	–	1
Galium palustre	–	3	2	–	–	1	1	–	x
Geum rivale	5	–	–	4	6	–	–	5	7
Juncus effusus	2	3	3	x	–	–	1	–	–
Ranunculus repens	–	2	–	–	5	6	7	–	6
Cardamine flexuosa	2	2	3	1	–	–	–	–	–
Carex rostrata	–	–	3	–	–	5	2	–	x
Valeriana officinalis	3	4	2	–	–	–	4	–	–
Equisetum arvense	5	3	2	–	–	–	–	–	–
Caltha palustris	–	1	2	–	–	–	2	–	–
Cardamine pratensis	–	–	–	–	–	2	2	–	3
Carex disticha	–	–	–	2	3	–	–	1	–
Carex nigra	–	2	4	1	–	–	–	–	–
Cirsium palustre	2	3	–	–	–	–	–	1	–
Deschampsia caespitosa	1	–	–	1	–	–	–	–	x
Lychnis flos-cuculi	–	1	2	–	–	–	–	–	1
Poa trivialis	–	3	–	–	–	1	2	–	–
Equisetum palustre	–	1	–	–	–	–	–	2	2
Alchemilla glabra	5	–	–	–	2	–	–	–	–
Chrysosplenium oppositifolium	–	–	–	–	–	2	2	–	–
Crepis paludosa	–	–	1	1	–	–	–	–	–
Myosotis palustris	–	–	–	–	–	2	1	–	–
Sanguisorba officinalis	–	–	–	2	2	–	–	–	–
Mentha aquatica	–	–	–	–	–	–	3	–	2
Equisetum fluviatile	–	–	1	–	–	–	–	–	1
Brachythecium rutabulum	6	–	6	4	5	4	4	4	4
Eurhynchium praelongum	5	6	2	–	4	–	4	5	5
Lophocolea bidentata	4	5	4	5	2	–	–	3	–
Acrocladium cuspidatum	–	4	4	–	–	3	–	–	4
Mnium undulatum	3	4	–	3	–	–	–	–	–
Thuidium tamariscinum	–	–	5	–	1	–	–	5	–
Eurhynchium swartzii	4	–	–	–	2	–	–	–	–
Plagiochila asplenioides	1	–	–	–	–	–	–	4	–

Additional species: Acrocladium cordifolium 6, 1; Arrhenatherum elatius 1, 4; Cirriphyllum piliferum 5, 1; Cirsium heterophyllum 4, 4; Climacium dendroides 6, 1; Cochlearia officinalis 6, 1; Dactylis glomerata 1, 1; Epilobium palustre 1, 1; Festuca rubra 4, 2; Holcus lanatus 2, 1; Iris pseudacorus 3, x; Lathyrus pratensis 6, 3; Menyanthes trifoliata 2, 2; Mnium punctatum 2, 2; M. rugicum 7, 2; M. seligeri 9, 1; Pellia endiviaefolia 2, 1; Phalaris arundinacea 6, 4; Phragmites communis 9, x; Potentilla palustris, 2, 1; Primula vulgaris 1, 1; Rumex obtusifolius 1, 1; Rhytidiadelphus squarrosus 4, 4; Succisa pratensis 2, 1; Urtica dioica 2, 1; Valeriana dioica 3, 3; Veronica chamaedrys 1, 2; Stellaria alsine 7, 4; S. media 6, 3.

1. Margin of East Fen south-west of Miss Hilary's Cottage.
2. Margin of East Fen south-east of Miss Hilary's Cottage.
3. Margin of East Fen near north-west corner of Tarn.
4. Margin of West Fen near west end of *Chamaenerion angustifolium* area.
5. Margin of West Fen near West Drive gate.
6. By inflow stream close to confluence at east end of Middle Fen.
7. By inflow stream *c.* 100 m. upstream from last.
8. Near fen margin at north-east corner of West Fen.
9. By inflow stream, inside meander at east end of large carr on West Fen.

All samples 4 m^2.

Similar communities are described by Duvigneaud (1958) from Belgium and Géhu (1961) from northern France.

Fen carr

The fen at Malham is rich in species of *Salix* (willows and sallows), and these are by far the most important woody species in the fen carr. There are scattered alders (*Alnus glutinosa*) along the north branch of the inflow, and bordering seepages across the East Fen. There are a number of dense but circumscribed thickets of the introduced North American dogwood *Thelycrania sericea* in the carr in various parts of the fen. Birch (*Betula pubescens*) dominates areas of acid peat, but encroaches little into calcareous fen or carr. Other woody species, such as the guelder rose (*Viburnum opulus*) and the buckthorns (*Rhamnus catharticus* and *Frangula alnus*) which are abundant in many fen carrs in East Anglia and elsewhere, are notably absent at Malham. Much of the carr is dominated either by *Salix pentandra* (bay willow), or by *S. phylicifolia* (tea-leaved willow) and a hybrid swarm between that species and *S. nigricans* (dark-leaved willow). *S. cinerea* (grey willow) is less abundant, but still widespread and locally dominant; *S. purpurea* (purple willow) is much more localized, but dominates a small area of carr south of Water Houses.

The field layer of the carr has many species in common with the *Filipendula* vegetation that commonly adjoins it. *Filipendula ulmaria* itself is an abundant and regular constituent; *Angelica sylvestris*, *Cardamine pratensis* (cuckoo-flower), *Crepis paludosa* (marsh hawksbeard), *Geum rivale*, *Poa trivialis* (rough meadow-grass) and *Ranunculus repens* occur with moderate to high constancy. A few fen species remain common (e.g. *Mentha aquatica*) and others are locally conspicuous, probably as relics of pre-existing fen (e.g. *Carex appropinquata*). The most characteristic bryophytes of the ground layer in the carr are *Mnium rugicum* and *Climacium dendroides*. Both occur elsewhere in the fen, but it is in the carr that they grow best and most abundantly. Apart from these, most of the bryophytes are common species of wet woodland. The more notable include *Drepanocladus uncinatus*, frequent on the bases of the shrubs, *Ptilidium pulcherrimum*, widely scattered through the carr on sloping surfaces of trunks and the lower branches, and *Nowellia curvifolia*, which has been found very locally on decaying branches.

The fen carr at Malham has many species in common with alder and sallow carrs in East Anglia and the south of England (Tansley, 1939; Rose, 1950; Lambert, 1951) and its ecological relationship with them is clear. However, many species common and characteristic in carr in lowland England, e.g. *Solanum dulcamara* (bitter-sweet), *Thelypteris palustris* (marsh fern), *Eupatorium cannabinum* (hemp-agrimony) and *Lythrum salicaria* (purple loosestrife), in addition to the woody species mentioned above, are rare or absent at Malham, while, for instance, *Salix pentandra*, *S. phylicifolia*, *S. nigricans* and *Crepis paludosa* do not occur in the lowland carrs. The "closed carr" at Esthwaite described by Pearsall (see Tansley, 1939) and the *Salix* carr at Semerwater in Wensleydale (Ingram *et al.*, 1959) are both broadly comparable with parts of the Malham carr. So, too, are the *Salix cinerea* communities described from Ireland by Braun-Blanquet and Tüxen (1952), though these apparently contain rather little *Filipendula*. The carr at Malham evidently belongs floristically to the class Alnetea glutinosae (see Lohmeyer *et al.*, 1962) to which Braun-Blanquet and Tüxen refer their Irish communities, and of which a range of north German examples are set out by Passarge (1961); in Shimwell's scheme they fall in the Salicetea cinereae.

Table 5. *Fen carr*

	1	2	3	4
Total shrub cover /10	8	9	9	8
Total herb cover /10	8	6	6	8
Total moss cover /10	9	7	8	5
Salix pentandra	9	4	10	8
Salix nigricans } S. phylicifolia }	4	9	–	–
Salix cinerea	–	–	–	7
Cardamine pratensis	2	3	3	2
Filipendula ulmaria	6	5	5	5
Galium palustre	3	2	1	3
Ajuga reptans	–	1	3	4
Geum rivale	–	5	5	6
Mentha aquatica	5	2	3	–
Poa trivialis	–	1	1	2
Valeriana dioica	4	1	5	–
Valeriana officinalis	5	–	1	3
Equisetum palustre	3	1	1	–
Angelica sylvestris	2	–	–	2
Caltha palustris	2	2	–	–
Carex rostrata	–	1	4	–
Crepis paludosa	3	–	1	–
Myosotis palustris	–	2	–	2
Ranunculus repens	–	3	–	7
Urtica dioica	–	4	–	5
Equisetum fluviatile	3	–	2	–
Carex appropinquata	–	–	4	–
Chrysosplenium oppositifolium	–	–	–	8
Menyanthes trifoliata	5	–	–	–
Acrocladium cuspidatum	–	5	4	3
Drepanocladus uncinatus	–	3	2	3
Eurhynchium praelongum	–	3	2	3
Mnium hornum	2	2	3	–
Mnium punctatum	7	4	7	–
Mnium rugicum	8	–	2	7
Brachythecium rutabulum	–	3	–	4
Climacium dendroides	2	–	5	–
Aulacomnium androgynum	–	2	–	–
Conocephalum conicum	–	–	–	2
Lophocolea cuspidata	–	3	–	–
Lophocolea heterophylla	–	–	3	–
Mnium seligeri	–	8	–	–
Mnium undulatum	–	–	5	–

Additional species: Chiloscyphus pallescens 2, 1; Dicranoweisia cirrata 4, 1; Epilobium palustre 4, 1; Fissidens adianthoides 2, 1; Galium aparine 2, 1; Hypnum cupressiforme 2, 1; Lychnis flos-cuculi; Parnassia palustris 3, 1; Pellia endiviaefolia 1, 1; Phalaris arundinacea 3, 1; Plagiochila asplenioides 1, 1; Succisa pratensis 1, 1; Trollius europaeus 3, 1.

1. Carr south-west of Miss Hilary's Cottage.
2. Large carr by inflow stream in West Fen.
3. *Salix pentandra* carr at west end of Middle Fen.
4. Carr south of main birch area, Middle Fen.

All samples 25 m^2.

Communities of acid peat

(a) *Poor fen communities.* The two extremes of edaphic variation in the Tarn Moss and fen are relatively stable and are represented by extensive and well-characterized noda. Vegetation transitional between ombrogenous bog and rich fen is diverse, fragmented and often varies greatly from place to place even within small areas. There is a strong tendency for the vascular plants and the bryophytes to behave as independent synusiae. Consequently it is difficult to systematize the vegetation of poor fen sites at Malham in a wholly satisfactory way.

A general trend can be recognized leading from the *Potentilla palustris-Acrocladium* nodum to communities with progressively more *Sphagnum* in the ground layer. The most base-tolerant of the sphagna, *S. contortum*, is typically associated with "brown mosses" rather than other sphagna. *S. squarrosum* forms extensive carpets which often dominate the ground layer, but always in fairly close proximity to calcareous water, as for instance in a belt along the south side of the main inflow stream, and around the margins of the acid peat areas of the East and Middle Fen. *S. teres* occupies a similar but more restricted ecological niche. *S. squarrosum* and *S. teres* are often

Table 6. *Poor-fen vegetation*

	1	2	3	4	5
Total field layer cover	8	6	6	8	4
Total moss cover	6	8	7	8	10
Agrostis canina	2	1	3	–	2
Carex nigra	5	–	5	–	3
C. rostrata	–	6	–	8	6
Deschampsia flexuosa	6	4	4	1	–
Eriophorum angustifolium	–	4	3	–	4
Juncus effusus	–	–	–	1	1
Molinia caerulea	–	4	–	–	–
Caltha palustris	–	–	–	3	–
Luzula multiflora	–	–	3	–	–
Menyanthes trifoliata	–	–	3	–	–
Potentilla erecta	7	2	–	–	–
P. palustris	–	–	5	9	4
Rumex acetosa	–	–	3	3	–
Succisa pratensis	–	–	4	2	4
Acrocladium stramineum	–	–	3	3	2
Aulacomnium palustre	3	5	4	–	2
Polytrichum commune	5	–	–	–	4
Sphagnum fimbriatum	7	–	4	x	–
S. palustre	2	–	1	–	4
S. plumulosum	–	–	4	–	–
S. recurvum	7	7	2	–	–
S. squarrosum	–	6	6	9	4
S. teres	–	–	–	–	9

Locations of samples (additional species in parentheses):

1. South edge of East Fen raised bog (*Carex curta* 1, *Eriophorum vaginatum* 2, *Hypnum cupressiforme* var. *ericetorum* 2, *Pleurozium schreberi* 1, *Polytrichum alpestre* 1).
2. Near east edge of East Fen raised bog.
3. South edge of East Fen raised bog, above *Carex rostrata* reedswamp and rich fen (*Salix* cf. *nigricans* seedling).
4. North edge of Tarn Moss, near confluence of inflow streams (*Phragmites communis* 2, *Epilobivm palustre* 2, *Filipendula ulmaria* 2, *Galium palustre* 2, *Viola palustris* 2).
5. Open area in birch wood, Middle Fen (*Calluna vulgaris* 2).

All samples 4 m^2.

accompanied by *S. fimbriatum*, *S. palustre* and *S. recurvum*, which extend into less calcareous sites and give way in their turn to *S. papillosum* and the other raised bog species. *S. palustre*, *S. fimbriatum*, *S. recurvum* and *S. squarrosum*, together with *Polytrichum commune*, *Molinia* and *Carex nigra*, form an understorey to wet birchwood in the East and Middle Fen. A few species are particularly characteristic of poor fens within our area, notably *Acrocladium stramineum*, *Aulacomnium palustre*, *Carex curta* and *C. echinata* (star sedge). The poor fens fall into the alliance Caricion curto-nigrae of the order Caricetalia nigrae (Shimwell, 1971).

(b) *Marginal raised bog communities.* The rand of the Tarn Moss along the south bank of the main inflow stream carries a dense cover of *Molinia*. This is a species-poor community; the main associates are common calcifuge bryophytes including *Dicranum scoparium*, *Campylopus flexuosus*, *Barbilophozia floerkei*, *Calypogeia* spp., *Lepidozia reptans*, *Lophozia ventricosa* and sphagna including *S. fimbriatum*, *S. plumulosum* and *S. recurvum*. A similar assemblage of species reappears on the marginal or lower-lying parts of the isolated areas of raised bog peat north of the inflow stream. These *Molinia* communities have been included with the poor fens in a single broad category in Fig. 1.

(c) *Raised bog.* The usual dominant of the raised bog surface at Malham is *Eriophorum vaginatum*, associated with abundant *Deschampsia flexuosa* and variable amounts of *Calluna vulgaris*, *Vaccinium myrtillus* (bilberry), *V. oxycoccos* (common cranberry) and *V. vitis-idaea* (cowberry). Sphagna are locally abundant, but over much of the area a large part of the ground layer is made up of other bryophytes, e.g. *Campylopus flexuosus*, *Hypnum cupressiforme* var. *ericetorum*, *Lophozia ventricosa*, *Calypogeia* spp. and *Odontoschisma sphagni*. A few examples from the Tarn Moss near Spiggot Hill are listed in Table 7.

Table 7. *Vegetation samples from Tarn Moss, near Spiggot Hill*

	1	2	3	4	5	6
Total field layer cover	8	9	9	9	8	8
Total moss cover	6	5	6	2	4	4
Calluna vulgaris	7	6	7	5	6	8
Eriophorum vaginatum	4	5	6	6	5	7
Deschampsia flexuosa	8	8	4	4	8	–
Erica tetralix	4	4	–	–	2	2
Empetrum nigrum	–	–	–	–	2	–
Eriophorum angustifolium	–	–	–	–	–	6
Vaccinium myrtillus	–	–	–	–	–	1
Cladonia spp.	1	x	2	–	2	2
Campylopus flexuosus	4	1	3	–	–	2
Calypogeia fissa	–	–	2	–	2	5
Dicranum scoparium	4	4	–	–	–	3
Lophozia ventricosa	2	–	3	–	4	–
Barbilophozia floerkei	x	–	1	–	–	–
Odontoschisma sphagni	x	–	–	–	3	–
Sphagnum papillosum	3	–	–	3	–	–
Sphagnum rubellum	–	4	–	5	–	–
Hypogymnia physodes	–	–	–	–	–	2
Mylia anomala	–	–	–	–	2	–
Pohlia nutans	1	–	–	–	–	–
Polytrichum formosum	–	4	–	–	–	–

All samples 4 m^2.

The more *Sphagnum*-rich parts of the raised bog surface fall clearly within the class Oxycocco-Sphagnetea, order Sphagnetalia magellanici (Moore, 1968), and can reasonably be regarded as an impoverished version of his Erico-Sphagnetum magellanici. The more drastically altered parts of the raised bog surface and the marginal *Molinia* community are more difficult to place, but perhaps find their nearest affinities in the Nardetalia (class Calluno-Ulicetea).

(d) *Birch woods on raised bog peat.* Birchwood occupies a substantial part of the remaining areas of raised bog peat north of the main inflow stream. *Betula pubescens* is the dominant and practically the only woody species. In wetter areas the floor of the wood is occupied by *Sphagnum-Molinia* communities of the kind indicated on p. 19, with much *Eriophorum vaginatum* and *Deschampsia flexuosa* where there is slightly better drainage. In the higher and drier areas *Deschampsia flexuosa* is dominant in the field layer, often with abundant *Dryopteris dilatata* and *D. carthusiana* (*D. spinulosa*), and calcifuge pleurocarpous mosses such as *Pleurozium schreberi* assume dominance in the ground layer. Two samples from birch wood on well-drained peat are listed in Table 8. Although very species-poor these birch woods have a good deal in common, both floristically and ecologically, with the Continental Betuletum pubescentis (order Vaccinio-Piceetalia; see Ellenberg, 1963, p. 376), and fall readily into place as an oceanic end-point to the series of woodland types on peat summarized by Matuszkiewicz (1963, p. 153).

The Vegetation in Relation to Environmental Factors

The Water Table

It is obvious on the ground, and borne out by the sections illustrated in Figs. 3 and 4, that there is variation in the height of the water table on different parts of the fen, and that this is at least to some extent related to variation in the vegetation. Thus the fens of the *Potentilla palustris-Acrocladium* nodum are clearly wetter than those of the *Carex nigra-Sanguisorba officinalis* nodum. The fen carr is probably on average slightly drier than the open fen within any particular part of the area, but the difference is not great, and to establish it conclusively would require more observations than are set out in Table 9. Some of the fen carr is certainly very wet, with water at or above the surface of the peat when the general water level of the fen is high after a spell of wet weather. The relation of *Filipendula* to the water table is, on the face of it, puzzling. At first sight it appears from Fig. 4 to be associated with a belt of relatively low water level along the edge of the fen and the well-drained bank of the stream. However, its habitats are not always as dry as they were when the profile was surveyed for Fig. 4, and inspection of a larger sample of its habitats makes a simple relation with water level seem unlikely to be the main explanation of its distribution. *Carex* fens of various kinds are found in some equally dry habitats, and *Filipendula* is dominant in some very wet ones. In general, within the obvious sequence open water-fen-dry land, the picture over the fen as a whole is of a wide range of vegetation types occurring with remarkably little variation in the height of the water table relative to the peat surface. The domed profile of the water table leading to the establishment of ombrogenous conditions is very clearly shown in Fig. 3. However, the fen itself is very nearly flat, and there is normally no more than 15 or 20 cm. difference between the level of the inflow stream in the West Fen and the level of the Tarn.

Table 8. *Birch woods, etc., on raised bog peat*

	1	2	3
Total tree cover /10	6	7	–
Total field layer cover /10	9	9	8
Total moss cover /10	4	5	6
Area of sample (m^2)	100	100	4
Betula pubescens	7	8	–
Alnus glutinosa	4	–	–
Agrostis canina	–	–	2
Carex nigra	4	–	2
Deschampsia flexuosa	9	8	8
Eriophorum vaginatum	1	5	–
Molinia caerulea	1	1	4
Calluna vulgaris	–	1	–
Dryopteris carthusiana	3	–	–
D. dilatata	7	6	–
Galium saxatile	3	1	–
Potentilla erecta	–	–	5
Vaccinium myrtillus	–	2	–
Dicranum scoparium	(e)	2	6
Eurhynchium praelongum	1	–	–
Hypnum cupressiforme var. ericetorum	4	2	2
Orthodontium lineare	(e)	(e)	–
Plagiothecium undulatum	5	2	–
Pleurozium schreberi	1	4	7
Pohlia nutans	–	–	1
Polytrichum commune	2	3	3
Rhytidiadelphus squarrosus	1	–	–
Tetraphis pellucida	(e)	–	–
Sphagnum capillaceum	–	5	–
S. fimbriatum	–	3	2
S. palustre	5	5	–
Calypogeia fissa	–	–	1
C. muellerana	–	2	–
Cephalozia bicuspidata	–	–	1
Cephaloziella sp.	–	–	1
Lepidozia reptans	(e)	–	1
Lophocolea bidentata	2	2	–
Lophozia ventricosa	–	(e)	–
Ptilidium ciliare	–	1	–

1. Birch wood on isolated acid peat area south-south-west of Miss Hilary's Cottage.
2. Birch wood at western edge of main raised bog area on East Fen.
3. *Deschampsia flexuosa* grassland east of Middle Fen birch wood.

(e) = epiphytic.

The variation in water level at 21 recording sites, between August 1965 and February 1967, is shown in Figs. 5 and 6. The first important feature to note is that the fluctuations in water level observed over this period are quite small, and with a few exceptions do not vary greatly from place to place. The fluctuations are somewhat greater in the West Fen than in the East Fen, but for most sites the total annual fluctuation does not exceed 20 cm. This is comparable with the annual fluctuation recorded by Godwin (1931) and Godwin and Bharucha (1932) from Wicken Fen, Cambs., and is very much less than that found by Poore (1956) at Woodwalton Fen, Hunts. (*c.* 50–90 cm.) or by Small (1931) and White (1932) in the fens around Lough Neagh in Northern Ireland (normal range *c.* 120 cm.). One consequence of this small annual fluctuation is that there is only a small range of

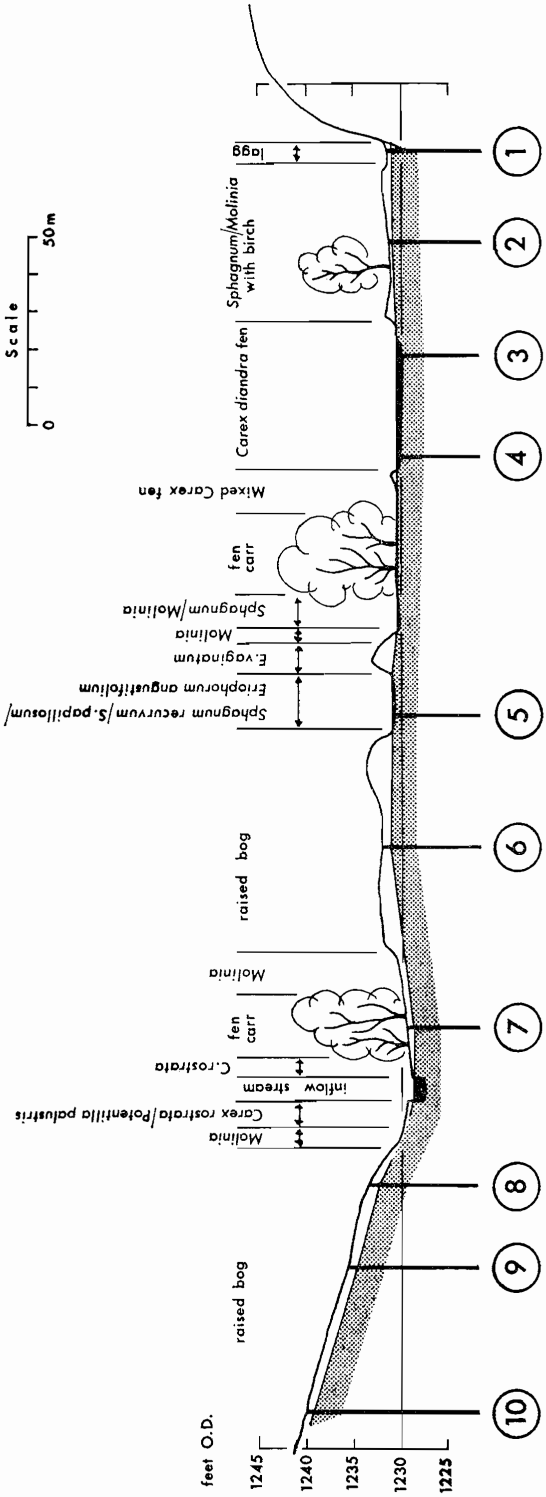

FIG. 3.

Levelled profile across the East Fen from near Miss Hilary's Cottage to the Tarn Moss. Fen carr shrubs not to scale. Large numerals show the position of the water-table sites of Fig. 5.

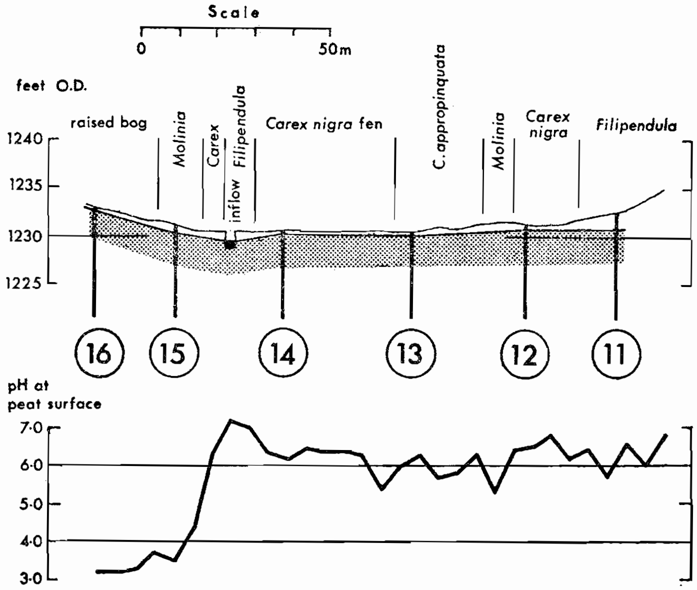

FIG. 4.

Levelled profile across the West Fen from near the gate in the West Drive to the Tarn Moss; (bottom) pH of peat surface measured at 5 m. intervals. Large numerals show the position of the water-table sites of Fig. 6.

Table 9. *Depth of water table below surface, 27 September 1972. For locations see corresponding water table and peat sampling sites in Fig. 2*

Site	Depth (cm.)
East Fen:	
Carex diandra fen (water-table site 4)	9
Salix pentandra carr near last (peat sample 24)	10
Carex diandra fen (water-table site 3)	11
Carex rostrata fen by main inflow below bridge (cf. Table 1, 6)	12
Fen north of mouth of inflow stream (peat sample 6)	19*
Carr near confluence of inflow streams (*S. cinerea*, *S. pentandra*, *S. phylicifolia*; water-table site 7)	28
Carr below Miss Hilary's Cottage (peat sample 23 and cf. Table 5, 1)	39
Carr by north inflow (*S. cinerea*; peat sample 26)	47
Middle Fen:	
Carr near south edge of birch wood (*Salix pentandra*, *S. phylicifolia*; peat sample 28)	19
Carex appropinquata fen (tussocks to *c.* 25 cm. above surface; peat sample 11)	20
Carr at east end of Middle Fen (*Salix cinerea*, *S. pentandra*, *S. phylicifolia*; peat sample 27)	26
Carr at west end of Middle Fen (*S. pentandra*, *S. phylicifolia*; peat sample 29)	26
Carex acutiformis (peat sample 14)	>30
West Fen:	
Isolated patch of carr at east end of West Fen (*S. phylicifolia*; peat sample 30)	20
Carex appropinquata fen (tussocks to *c.* 20 cm. above surface; peat sample 12)	21
West end of large carr (*Salix pentandra*, *S. cinerea*, *S. phylicifolia*; peat sample 32)	26
Carex nigra fen (tussocks to *c.* 15 cm. above surface; water-table site 14)	27
Carr north of open water pool (*Salix phylicifolia*)	27
Carex nigra fen (water-table site 12)	28
Carex appropinquata fen (tussocks to *c.* 25 cm. above surface; water-table site 13)	28
East end of large carr (peat sample 31)	30
Carex nigra fen (peat sample 9)	31
Small patch of carr near last (*Salix phylicifolia*)	34
Carex nigra fen (peat sample 10)	35

* Site possibly affected by lowering of Tarn level for repairs to sluice.

level within which the fen is not liable to colonization by fen carr. As Figs. 5 and 6 show, both short-and long-term fluctuations in water level are greatest at the margin of the fen and next to the inflow stream (cf. Godwin and Bharucha, 1932, pp. 162–163). This suggests at least the possibility that *Filipendula* sites are characterized by relatively large fluctuations in water level. Dierschke (1969) and others have demonstrated similar contrasts between the pattern of variation of water level in different vegetation types on the Continent. In the present instance there can be little doubt that a relationship exists, but it is probably not clear cut. General observation suggests that a good deal of the fen carr, occupying similar streamside sites to the *Filipendula*, also experiences relatively large fluctuations of water level. Ingram (1967) discusses the possibility that water movement by itself may determine the occurrence of vegetation normally associated with more eutrophic conditions. In the present case, data considered below allow a more direct explanation of the

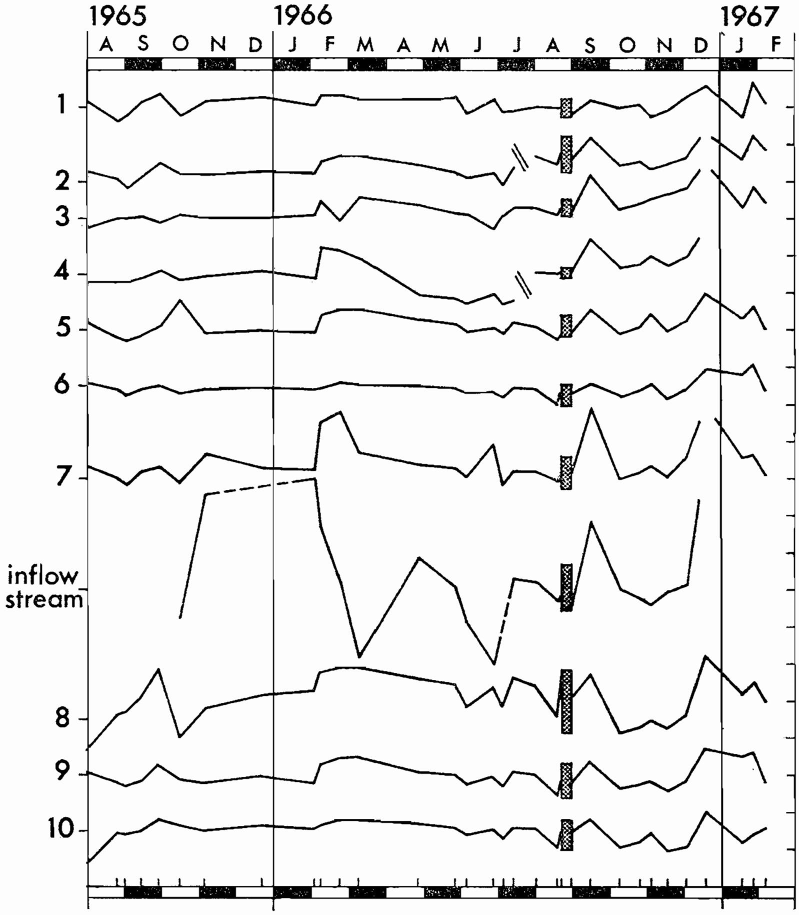

FIG. 5.

Recorded levels of the water table at the sites shown in Fig. 3, from August 1965 to February 1967. Levels were recorded in relation to a separate arbitrary datum for each site. The reference stakes at sites 2 and 4 were disturbed during July 1966; in each case the two parts of the record refer to different datum levels. The shaded blocks show the range of levels recorded between 21 August and 1 September 1966. The right-hand margin is scaled in 10 cm. intervals. Sampling dates are indicated in the bottom margin.

distribution of the vegetation. However, there is evidence that variations in soil aeration associated with water movement may have important effects on the uptake of phosphorus and other nutrients (Armstrong and Boatman, 1967); some of the mechanisms envisaged by Ingram may well have played a part in establishing the situation that now exists at Malham.

Chemical Characteristics of the Peat

Ash content

The ash content of 50 samples of surface peat from various vegetation types is given in Table 10. Although there is a good deal of variation within each vegetation type, a very clear general correlation exists. The lowest values, ranging up to about 5 per cent, are found among the raised bog samples. Samples from poor fen and marginal raised bog sites have a somewhat higher ash content, usually between about 4 and 10 per cent. The peats underlying *Carex* fens are much more variable, with ash contents from around 10 per cent to 50 per cent or more. In general, the

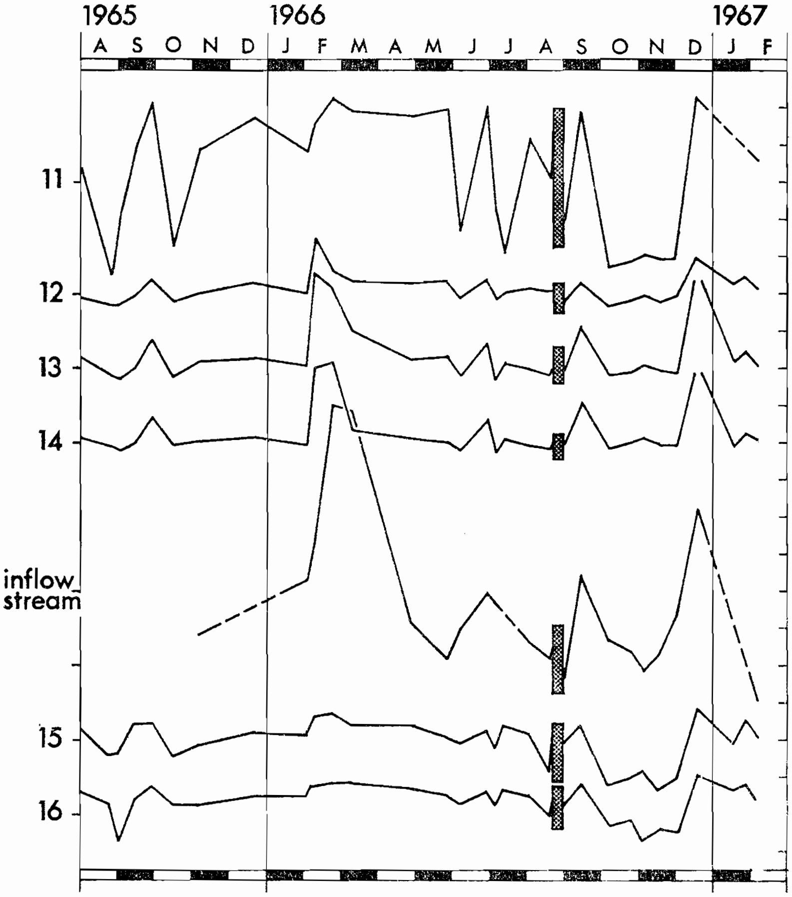

Fig. 6.

Recorded levels of the water table at the sites shown in Fig. 4, from August 1965 to February 1967. Conventions and sampling dates as for Fig. 5.

Table 10. *Chemical analyses of peat samples. For locations, see Fig. 2*

Site no.	Notes	Ash (per cent)	Dry wt. (g./litre)	Exchangeable cations in NH_4NO_3 extract (mM/litre wet peat)				Cations in water extract (mg./litre of extract)		Total P (mg./litre of peat)
				Ca	Mg	K	Na	Fe	Mn	
Potentilla palustris-Acrocladium nodum										
1	*Carex diandra, C. rostrata*	26	123	52	·57	·55	4·3	—	1·0	3·7
2	*C. diandra, C. rostrata*	12	69	20	·37	1·8	2·6	—	—	3·5
3	*Carex diandra*	42	136	14	·29	·65	2·2	—	—	11
4	*Carex diandra*	8·4	84	17	·24	·67	2·5	—	—	24
5	*C. rostrata* by inflow stream	59	179	24	·24	·81	2·9	0·1	—	27
6	*Carex lepidocarpa*, etc. (cf. Table 3, 2 and 3)	11	73	30	·33	·67	3·1	—	—	5·1
Carex nigra-Sanguisorba officinalis nodum (*C. nigra* variant)										
7		34	169	40	·43	·65	1·4	—	—	39
8		21	128	33	·20	·67	2·6	0·1	—	138
9		34	136	22	·16	1·0	2·0	0·4	—	60
10		30	169	27	·13	·74	1·5	—	—	63
Carex nigra-Sanguisorba officinalis nodum (*C. appropinquata* variant)										
11	Middle Fen	8·3	107	23	·33	·87	2·5	—	1·3	123
12	East end of West Fen	9·4	109	21	·40	·83	2·1	—	—	21
13	West Fen	12	129	32	·27	·95	2·3	—	—	129
Carex acutiformis stands										
14		66	374	46	·19	·78	4·3	0·2	—	82
15		34	132	38	·27	·53	3·2	0·3	—	22
Filipendula communities										
16	North-east corner of East Fen	17	121	47	·49	1·5	4·8	0·4	—	18
17	Lagg below Miss Hilary's	29	130	34	·43	1·7	4·3	0·2	—	38
18	By inflow near confluence	16	117	29	·22	·99	2·9	0·1	—	31
19	Margin of West Fen	65	253	43	·30	·90	2·2	0·3	—	165
20	Bank of inflow, West Fen	51	226	53	·13	1·4	2·4	0·4	—	90
21	By inflow stream, West Fen	49	202	56	·29	1·1	2·0	0·1	—	51
22	Margin, west end of West Fen	72	324	36	·96	1·2	2·4	0·4	—	32
Fen carr										
23	Cf. Table 5, 1	66	296	35	·60	1·2	3·6	0·1	—	18
24	*S. pentandra*, by *Carex diandra* fen	8·9	84	27	·37	·58	2·8	—	—	71
25	By inflow stream, East Fen	47	155	41	·66	1·3	3·8	4·5	—	141
26	By north inflow, East Fen	70	299	49	·52	1·1	4·5	1·8	—	36
27	Near north inflow, Middle Fen	68	207	40	·33	·65	3·8	0·1	—	33
28	South of birch area, Middle Fen	9·5	100	19	·91	1·1	2·5	—	—	126
29	*S. pentandra*, Middle Fen	14	101	35	·53	·64	3·0	—	—	53
30	Isolated patch in West Fen	8·7	101	33	·57	1·0	2·6	—	—	17
31	Large carr in West Fen	34	162	47	·20	·80	2·8	—	—	49
32	Large carr in West Fen	12	132	28	·52	1·1	1·7	—	—	20
Poor fen and *Molinia* sites										
33	*Molinia/Sphagnum* by Tarn	4·9	98	8·3	1·0	·99	2·6	—	—	13
34	*Molinia/Sphagnum*	4·5	75	5·1	·73	·46	1·5	—	—	22
35	*Sphagnum/Potentilla palustris/Molinia*, etc.	4·5	62	6·4	·92	·65	1·7	—	—	50
36	*Sphagnum squarrosum*	2·7	50	2·4	·79	·87	1·5	—	—	32
37	Bog margin, *S. fimbriatum*	6·5	73	8·3	·76	1·2	2·1	—	—	8·3
38	*Carex curta/Sphagnum*	5·6	98	3·5	·47	·28	1·6	—	0·2	33
39	*Deschampsia flexuosa*, etc.	25	116	3·5	·14	·28	3·6	—	—	36
40	*Sphagnum/Phragmites* mat	7·3	56	8·6	·34	·27	1·4	—	—	5·6
41	*Sphagnum teres*, etc.	4·2	65	9·5	·95	·97	1·5	—	0·8	5·2
42	*Molinia* on raised bog peat	17	121	4·3	·40	·71	1·6	—	—	125

Table 10—*continued*

Site no.	Notes	Ash (per cent)	Dry wt. (g./litre)	Exchangeable cations in NH_4NO_3 extract (mE/litre wet peat)				Cations in water extract (mg./litre of extract)		Total P (mg./litre of peat)
				Ca	Mg	K	Na	Fe	Mn	
Raised bog										
43	Pool with *Drepanocladus fluitans*, *Sphagnum cuspidatum*, etc.	2·0	68	1·6	·95	·32	1·5	—	—	21
44	East Fen	4·5	107	2·7	1·0	·67	1·3	—	—	22
45	East fen	3·8	107	8·6	·86	·48	2·5	--	—	63
46	East fen	·74	92	3·0	1·6	·37	2·0	—	—	17
47	West Fen	3·5	98	6·0	1·2	·74	·92	—	—	13
Birch wood on raised bog peat										
48	East Fen	3·9	103	4·3	1·4	·57	1·6	—	—	65
49	East Fen	1·8	116	4·7	1·6	·48	2·3	—	—	7·0
50	West Fen	6·0	113	2·9	·65	·35	1·5	—	—	16

lower values come from sites well away from the inflow streams or the fen margin. The peats are variable in both the *Potentilla palustris-Acrocladium* and the *Carex nigra-Sanguisorba officinalis* noda, and there is not enough evidence to establish any consistent difference between them. The fen carr samples are again variable, spanning virtually the entire range of the fens, and extending on to silt-rich peats with an ash content up to about 70 per cent. The *Filipendula* sites occupy the higher end of this range; the lowest value recorded is 15·7 per cent and the highest is 71·8 per cent.

Exchangeable cations

In columns 3–6 of Table 10 the quantities of the principal cations extracted by M/2 ammonium nitrate solution are expressed in terms of unit volume of wet peat. A rough conversion to a dry weight basis can be made using the dry weights in column 2. If the sites are grouped according to the noda and other vegetation types they represent, a number of broad conclusions emerge. Calcium increases progressively in the order: raised bog (and birch wood), *Molinia* and poor fen, rich fen, fen carr, *Filipendula*. Magnesium shows a largely opposite trend, highest in the raised bog peats. High magnesium levels are a well-known characteristic of ombrogenous peats, but in none of the present samples does magnesium exceed calcium—a suggested criterion for distinguishing ombrogenous from soligenous peats (see Chapman, 1964). The lowest magnesium values are found in the three groups of rich fen sites, not in the carr and *Filipendula* which show the highest calcium values. The distribution of potassium follows that of calcium, but its variation is much less. The ratio of the highest and lowest means for the groups is only about 2·7, compared with 10·7 for calcium. Sodium shows a similar distribution, but with less variation again. However, there is a major contrast in the calcium figures between the ombrogenous and transitional groups, with less than 10 mM/litre, and the remaining groups which all average more than 25 mM/litre. This is not reflected in the distribution of the other cations.

There is a good deal of detailed variation between the figures for individual sites; in particular the *Molinia* and poor fen group are obviously very heterogeneous.

However, the major features of the data may be interpreted in terms of two broad trends. One, reflected most simply by calcium, is the direction of variation from ombrogenous to soligenous conditions. Superimposed on this is a second trend reflected in part by the distribution of magnesium within the more calcareous sites, and in part by the distribution of potassium, representing an oligotrophic-eutrophic direction of variation (cf. Ellenberg, 1963, p. 414). A comparable contrast between unsilted "headwater fens" and silted and eutrophic "valley fens" in the Breckland of East Anglia is discussed by Haslam (1965).

Other cations may be important in particular instances. All the peats from *Filipendula* sites, several of the carr sites and a few others released measurable quantities of iron (approximately 0·1 mg./litre or more) into water extracts. Manganese appeared in comparable amounts in only a few sporadic instances, and is probably not generally important in shaping plant distribution within the area, either through deficiency or excess.

Cations in surface waters

Measurements of cation concentrations in surface water are less useful than measurements on peat samples for elucidating the detailed relation between vegetation and cation availability, if only because possible sampling sites are limited in number. However, such measurements are easily made and have been widely used, so they provide a useful basis for comparison between different areas.

Some data from the Malham Tarn fens are set out in Table 11; analyses of the water of the Tarn and the main inflow are given by Lund (1961). In general, the results from Malham fall within the range that would be expected from comparable sites elsewhere (see, e.g. Gorham and Pearsall, 1956; Gorham, 1956; Bellamy and Bellamy, 1967). Sodium concentrations are, predictably, somewhat lower than those recorded from the Lake District and Ireland, while calcium figures from pools on ombrogenous peat at Malham are somewhat higher than those obtained from Irish ombrogenous bogs by the Bellamys or myself (unpublished), or by Chapman (1965) from Northumberland.

pH

The pH value is closely correlated with base-saturation and therefore, since calcium is the most abundant metallic cation within the area, it is closely related to calcium concentration. The pH of bulk samples of peat or of surface water samples (Fig. 7) shows much the same relation to vegetation as exchangeable calcium in peat or the calcium concentration in open water. The pH values from open water in different vegetation types correspond well with Sjörs's results from northern Sweden (Sjörs, 1950) and with the data of Gorham and Pearsall and Bellamy and Bellamy from the British Isles.

The pH of the peat surface, and even more so of the bryophytes growing upon it, varies much more intricately from place to place. Differences of 2 pH units or more within a decimetre are common. The role of *Sphagnum* in bringing about surface acidification is well known (see Clymo, 1963). Other mosses, too, can produce large pH gradients, e.g. *Mnium pseudopunctatum*, and the phenomenon is quite general. Some good examples from Marcham Bog near Oxford are quoted by Clapham (1940).

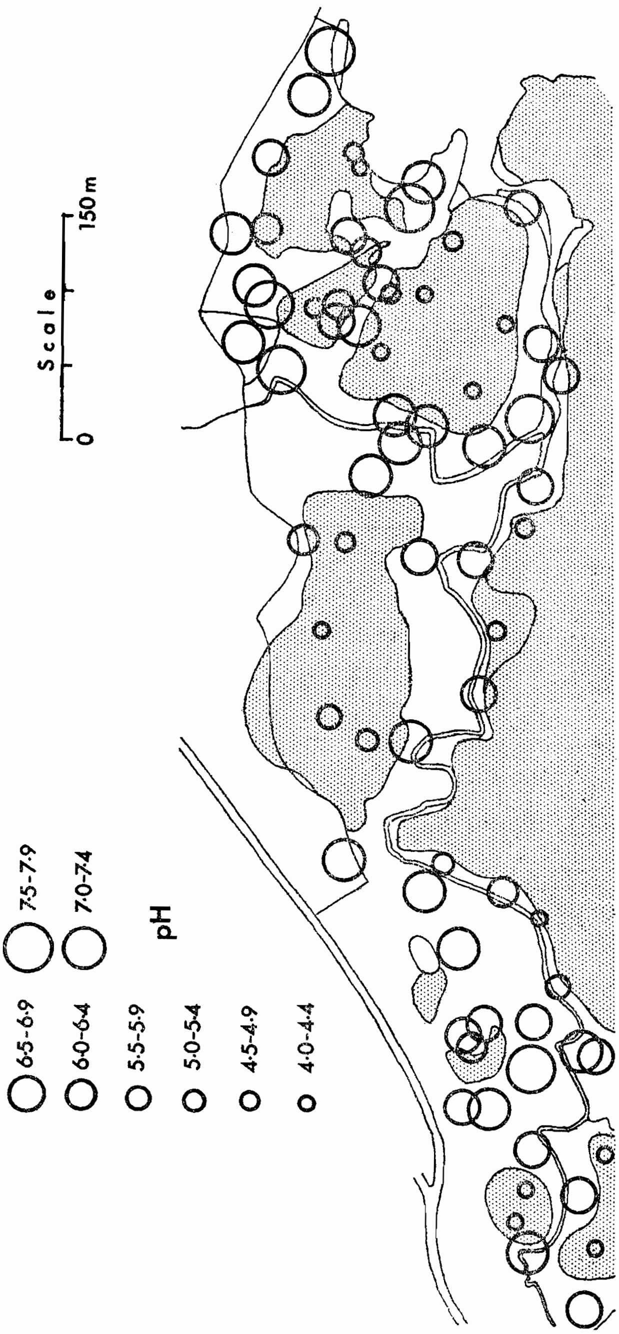

FIG. 7.
pH values in surface water on the "North Fen", September 1962.

Table 11. *Ionic concentrations in surface water, 18 July 1973. Except for samples marked thus *, the sites are close to (but in most cases not identical with) those indicated on the maps in Proctor (1960, p. 75). The pH values were determined electrometrically in the field. Calcium and magnesium were estimated by atomic absorption, and potassium and sodium by flame emission, on a Unicam SP-90. Bicarbonate was estimated by titration to pH 4·5. Concentrations are expressed in mE (mg. ions × valency)/litre.*

	pH	Ca^{++}	Mg^{++}	K^{+}	Na^{+}	HCO_3^{-}
Rich fen sites						
1. *Carex diandra* fen (cf. Table 1.1)	7·2	2·7	·054	·010	·27	2·30
*2. *Carex diandra* fen (cf. Table 1.5)	6·8	1·8	·043	·008	·24	1·46
3. Fen near Tarn edge (cf. Table 3.2–3)	7·3	2·4	·055	·009	·26	1·80
4. *Carex rostrata-C. diandra* fen at north-west corner of Tarn (cf. Table 1.2–3)	7·0	2·4	·050	·015	·24	1·94
5. Recolonized peat cutting in West Fen with *Carex rostrata* (north-east of site of Table 1.8)	5·6	1·6	·045	·009	·37	1·20
*6. *Carex appropinquata*, West Fen (cf. Table 2.8–9)	6·9	3·3	·059	·015	·84	2·51
*7. *Carex nigra*, West Fen (cf. peat-sample site 8)	6·6	1·8	·038	·010	·35	1·23
8. Spiggot Hill fen; *Carex nigra, C. lasiocarpa, Menyanthes trifoliata, Potentilla palustris, Drepanocladus revolvens*, etc.	7·5	2·4	·089	·008	·37	1·82
9. Lagg of Tarn Moss south of Spiggot Hill; *Carex rostrata, C. lepidocarpa, Menyanthes trifoliata, Campylium stellatum*, etc.	7·6	3·0	·174	·010	·15	2·71
10. Lagg of Tarn Moss near source of south-west inflow stream; *Carex rostrata, C. nigra, C. panicea, Eriophorum angustifolium, Caltha palustris, Potentilla palustris*, etc.	7·5	2·8	·153	·008	·16	2·49
11. Fen carr, eastern end of Middle Fen (cf. peat-sample site 15)	6·9	3·5	·066	·022	·25	3·11
Poor fen and transitional sites						
12. Recolonized peat cutting, Middle Fen; *Phragmites communis, Sphagnum* spp., *Acrocladium stramineum*, etc. (cf. post-sample site 40)	5·6	·55	·031	·013	·15	·26
13. *Sphagnum teres-S. squarrosum* carpet, with *Menyanthes trifoliata, Carex curta*, etc. (cf. Table 6.5)	3·9	·20	·046	·006	·22	0·0
14. Southern edge of acid peat area, Middle Fen; *Carex appropinquata, Mnium pseudopunctatum, Menyanthes trifoliata, Potentilla palustris, Sphagnum plumulosum, Mnium hornum*	5·4	·80	·055	·014	·21	·27
15. West side of Spiggot Hill lagg; *Molinia, Narthecium, Menyanthes*, etc.	6·7	1·2	·082	·010	·18	·85
16. Lagg of Tarn Moss near "Horseshoe Plantation"; *Carex rostrata, C. curta, Sphagnum fimbriatum, S. recurvum, Polytrichum commune*, etc.	4·8	1·2	·036	·009	·15	·16

Table 11—*continued*

	pH	Ca++	Mg++	K+	Na+	HCO3–
17. Tarn Moss, central soak; *Molinia, Succisa pratensis, Potentilla palustris, Sphagnum fimbriatum, Mnium pseudo-punctatum*, etc.	6·2	·70	·048	·004	·16	·42
Raised bog sites						
18. *Sphagnum cuspidatum* pool, East Fen	3·6	·10	·039	·008	·18	0·0
19. *Sphagnum cuspidatum* pool, East Fen	4·0	·09	·038	·008	·16	0·0
20. Birch wood on peat, Middle Fen	3·8	·17	·084	·013	·32	0·0
21. Crown of east dome of Tarn Moss; *Eriophorum vaginatum, Deschampsia flexuosa, Mylia taylori*	4·0	·09	·040	·004	·16	0·0
22. Crown of west dome of Tarn Moss; *Eriophorum vaginatum, Deschampsia flexuosa, Erica tetralix*	3·9	·11	·048	·005	·18	0·0
23. East dome of Tarn Moss near Spiggot Hill; *Eriophorum vaginatum, Deschampsia flexuosa, Narthecium ossifragum, Erica tetralix, Sphagnum papillosum, S. rubellum, Polytrichum alpestre*, etc.	4·0	·09	·039	·005	·15	0·0
24. South dome of Tarn Moss; *Eriophorum vaginatum, Erica tetralix, Deschampsia flexuosa, Calluna vulgaris, Narthecium ossifragum, Sphagnum papillosum, Mylia taylori*, etc.	4·4	·09	·044	·005	·16	0·0
Tarn inflow stream						
25. Main inflow at bridge	7·2	4·3	·095	·019	·34	3·75

Phosphorus

Estimates of total phosphorus in the peat samples are given in the last column of Table 10. Such estimates must always be approached with the reservation that some proportion of the phosphorus is likely to be unavailable. The results for all the groups of sites are very variable, but there is a fairly clear division between the raised bog peats, the poor fens and the *Potentilla palustris-Acrocladium* nodum on the one hand, almost always with less than 35 mg./litre, and the remaining groups on the other. These, although with some low values, all average more than 50 mg./litre. Pigott and Taylor (1964) found comparable quantities of *available* phosphorus in soils under vigorous stands of *Urtica dioica*, and that such concentrations supplied as soluble inorganic phosphate to phosphorus-deficient woodland soils allowed good growth of this phosphorus-demanding species. However, they also found that proto-rendzina and mull soils under *Mercurialis*, deficient in available phosphate, generally had a total phosphorus content of 30–80 mg./100 g. dry soil—on a dry weight basis very similar to our peats.

Chemical Analysis of Plant Material

Analyses of material harvested from 0·25 m.² plots at six sites are set out in Table 12. The sites fall into three groups. A and B, from raised bog peats, are low

Table 12. *Chemical analyses of plant material*

(a) Quantities of elements expressed as percentage of dry weight of plant material.

	Ca	Mg	K	P	Fe	Mn
A Raised bog, East Fen						
1. Field layer (mainly *Eriophorum vaginatum*)	·04	·04	·27	·025	·030	·007
2. Moss layer (*Sphagnum rubellum*)	·06	·05	·31	·009	·028	·006
B *Molinia*, margin of Tarn Moss	·04	·07	·51	·047	·020	·011
C *Carex diandra* fen (*Potentilla palustris-Acrocladium* nodum), East Fen						
1. *Carex*	·33	·07	·50	·028	·020	·019
2. Dicotyledons (mainly *Potentilla palustris*)	·68	·17	1·11	·056	·037	·027
3. *Acrocladium giganteum*	·75	·07	·75	·046	·113	·070
D *Carex nigra* fen (*Carex nigra-Sanguisorba officinalis* nodum), West Fen						
1. *Carex*	·35	·07	·98	·036	·018	·013
2. Dicotyledons	·87	·33	1·44	·052	·010	·008
3. Moss layer (mainly *Ctenidium molluscum*)	·56	·06	·37	·040	·078	·022
E *Filipendula*, East fen near confluence of inflow streams						
1. Field layer	·61	·28	1·39	·091	·046	·016
2. Moss layer (mainly *Brachythecium rutabulum*)	·18	·23	·63	·093	·173	·041
F *Filipendula/Geum rivale*, West Fen near gate to West Drive	·78	·53	1·34	·106	·010	·007

(b) Quantities of elements expressed in g/m² of vegetation.

		Dry weight	Ca	Mg	K	P	Fe	Mn
A	1.	1120	·45	·45	3·02	·28	·34	·08
	2.	197	·12	·10	·61	·02	·06	·01
	Total	1217	·57	·55	3·63	·30	·39	·09
B		958	·38	·67	4·88	·45	·19	·11
C	1.	406	1·34	·28	2·03	·11	·08	·08
	2.	186	1·27	·32	2·07	·10	·07	·05
	3.	264	1·98	·19	1·98	·12	·30	·19
	Total	856	4·59	·79	6·08	·34	·45	·31
D	1.	752	2·63	·46	7·37	·27	·14	·10
	2.	37	·32	·12	·53	·02	·004	·003
	3.	58	·33	·04	·22	·02	·05	·01
	Total	837	3·28	·61	8·12	·31	·19	·11
E	1.	596	3·64	1·67	8·28	·54	·27	·10
	2.	32	·06	·07	·20	·03	·06	·01
	Total	628	3·69	1·74	8·48	·57	·33	·11
F		552	4·31	2·93	7·40	·59	·06	·04

in calcium and oligotrophic; C and D are calcareous fens, oligotrophic but rich in calcium; E and F are eutrophic *Filipendula* stands. If only the dominant vascular plants are considered, the potassium content is seen to increase progressively from the raised bog to the *Filipendula* sites. Magnesium and phosphorus occur in similar concentrations in the raised bog and fen dominants, but phosphorus increases by a factor of 2 or 3, and magnesium by a factor of 4 or more in the *Filipendula* sites. Calcium behaves predictably, with very much lower values in the raised bog sites than in any of the others. It is noteworthy that *Molinia* is nearly twice as rich in magnesium and phosphorus as the dominant *Eriophorum vaginatum* of the raised bog, and that the dicotyledonous herbs in the fen samples are as rich in potassium and calcium and almost as rich in magnesium as dominant *Filipendula*; their phosphorus content is also roughly double that of the dominant *Carex* in each case. The distributions of iron and manganese are apparently capricious—iron is unusually high in one of the *Filipendula* samples, unusually low in the other. The high percentages of both elements recorded for the moss layer in samples C, D and E may be partly due to extraneous material, which was difficult to remove completely from the plants.

Fig. 8 shows the results of analyses of samples of *Filipendula* at 2·5 m. intervals along a transect through the marginal *Filipendula* belt into *Carex nigra* fen on the line of the section in Fig. 4. Although the differences shown are hardly spectacular, the general trend to more eutrophic conditions at the margin of the fen emerges clearly

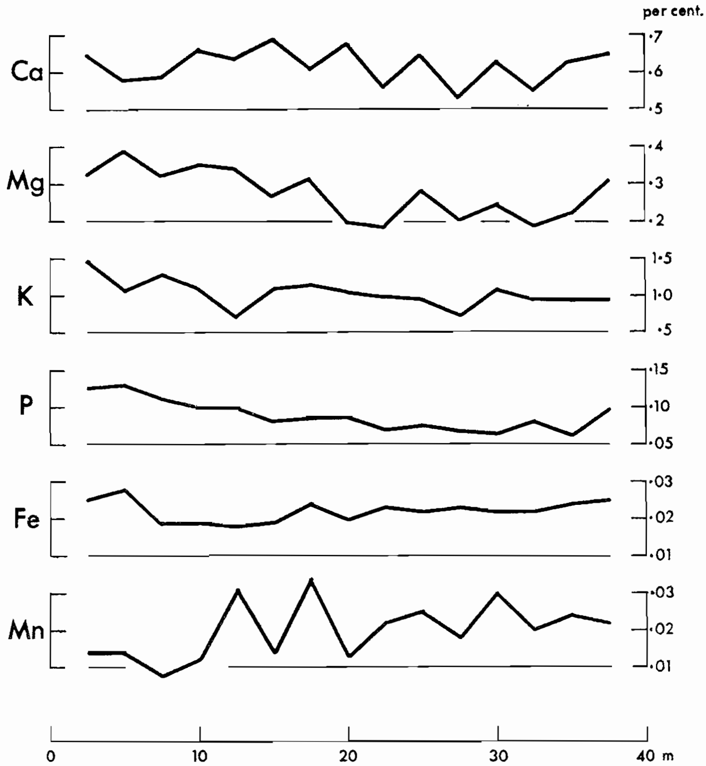

FIG. 8.

Chemical analyses of samples of *Filipendula ulmaria* collected at 2·5 m. intervals along a transect from the north edge of the West Fen on the line of the profile in Fig. 4.

enough in the distributions of magnesium, potassium and phosphorus; manganese shows some tendency to a reverse distribution. It must be remembered that these curves show changes in nutrient content of (and presumably reflect changes of nutrient availability to) a single species, which is varying in vigour and density along the transect. The data of Table 12 suggest that there would be very much larger differences in the total nutrient content of the vegetation.

DISCUSSION: SPATIAL AND SUCCESSIONAL RELATIONSHIPS

Much of the variation in the present vegetation of the Malham fens can thus be accounted for in terms of variation in the level of the water table and in the quantities of a number of the common mineral nutrients. Naturally, the correspondence is not perfect. One is not dealing with a simple system of cause and effect, but with a dynamic system of interacting parts. Any one part is a portion of the environment of the remainder. In any particular spot, various features of the immediate physical environment, including the level and form of the water table, the chemical composition of the ground water, and the microclimate are influenced by the growth and behaviour of other parts of the mire complex. The oligotrophic-eutrophic direction of variation in particular needs to be understood in terms of processes taking place within the ecosystem. Some of the "oligotrophic" fens at Malham possess considerable total amounts of phosphorus in the peat, but much of this is probably unavailable and thus effectively outside the ecosystem. In some places the occurrences of particular species (e.g. *Carex lasiocarpa* in the West Fen, or fen species in *Sphagnum* carpets) appear as instances of "biological inertia" (Gorham, 1957, p. 149). Again, the composition of the vegetation at a particular point reflects the reproductive potential of the species available from its not necessarily identical surroundings, with effects which are indicated (in a different context) by MacArthur and Wilson (1967, p. 16). Individuals of all species have limited life-spans (Tamm, 1948, 1956), and a further random element of variation is added by the hazards of dispersal and establishment.

The mire complex is, of course, the product of successional change. Its history, at least in broad terms, can be reconstructed from the stratigraphical data of Pigott and Pigott (1959, 1963). The greater part of the area (apart from the margins and a number of islands of glacial drift) is underlain by grey silt and clay, laid down in biologically unproductive water in an open late-glacial landscape. This is followed by calcareous marl, which in turn is followed by fen peat. In the central parts of the Tarn Moss the fen (and brushwood) peat is often less than a metre thick; after an irregular layer of birch fragments it rapidly gives place to raised bog peat. The sequence open water—reedswamp—fen—fen carr—bog was found by Walker (1970) to be one of the commonest in the "large inland basins" among which he included Malham Tarn, although here the reedswamp stage was evidently very brief. Around the periphery of the basin, fen peat is more persistent. As the level of the raised bog surface rose, the fen peat spread out over the neighbouring boulder clay without an intervening layer of aquatic deposits. Open fen sometimes replaced pre-existing carr, and in turn gave way to bog. Malham Tarn clearly offers no exception to Walker's general picture of long persistent open water and bog, linked by a short reedswamp stage and considerably longer-lived fen and fen carr stages. However, succession in much of the basin does seem to have been rather rapid. The Pigott's pollen diagram suggests a transition from open water to bog completed in about 1,500 years. This is about half the modal time suggested by Walker, but is by no means exceptionally short. At Malham one can readily endorse Walker's suggestion that "all the indications are that *Sphagnum*, once established, expands very rapidly indeed and quickly imposes its dominating influence on any further development".

Examples of all the main transitions indicated above can be found in the fens at the present day, but sometimes one must look for them in what are obviously secondary successions. The correspondence between succession and zonation is often pointed out, but it will be clear from what has been said about the variation in the vegetation that the correspondence cannot be more than partial. Some interesting illustrative zonations can be seen on the north bank of the inflow stream east of the main bridge, but these give only a meagre picture of the succession that was taking place over a large part of the Tarn basin eight thousand years ago. A relevant account of the early stages in acidification of the surface peat and the establishment of *Sphagnum* under fen carr in the Norfolk Broads is given by Godwin and Turner (1933).

It may be asked what further changes are to be expected in the vegetation of the Malham Tarn fens as they now stand. In some places it is quite clear that rapid change is taking place. Some of the fens in recolonized peat-cuttings would soon progress to fen carr if left undisturbed. In other parts of the fen it is hard to say whether the fen carr shrubs are tending to increase or decrease. Evidence can be found both of colonization, and of death of established shrubs, and systematic observation and recording over long periods is needed to find out what real changes are taking place in different parts of the fen. Probably, quite extensive colonization by birch could take place on the Tarn Moss; if it occurred, this might be an interesting addition to the diversity of the area. Some areas of rich fen with substantial amounts of *Sphagnum* seem destined to change to poor fen and perhaps ultimately to bog. However, these are merely minor and marginal changes, and the broad pattern of the Tarn Moss and fens seems likely to change very little. The succession that led to the development of the Tarn Moss cannot go to completion over the whole of a drainage basin. The more closely the mineral-rich drainage water is confined by the development of raised bogs, the more unsuitable conditions become for further succession in the remaining fen. The result is that the whole complex tends to reach a steady-state pattern of ombrogenous bog and lagg fen. The Pigotts's sections suggest that the Tarn Moss had indeed approached a steady state of this kind. It is noteworthy that Kulczynski (1949), writing of a very large series of mire complexes, saw succession at the present day largely as a matter of readjustment of the vegetation to natural or artificial disturbance of the habitat. The massive succession during the past 10,000 years of which our peat deposits record the evidence followed the massive topographic and climatic upheavals of the last glaciation. Succession is a matter of balance between species and between processes, within a broad framework of externally imposed major habitat factors; it is a gross oversimplification to see every wet peat site in terms of an inexorable succession to "climatic climax" forest or ombrogenous bog. Rates of peat accumulation can vary very greatly, but an average for a wide range of post-glacial deposits is about 5 cm. per century (Walker, 1970). This is equivalent to less than 5 per cent of the net annual production, so fairly small changes in the factors affecting the breakdown of organic matter (see Clymo, 1965) can have a disproportionately large effect on the rate of accumulation. Even if peat does accumulate, this may not raise the level of the surface relative to the water table or cause any substantial change in the character or pattern of distribution of the vegetation; that will depend on what is happening elsewhere in the mire complex. Hydrosere succession has undoubtedly taken place on a massive scale in the past, and is clearly taking place locally on a limited scale now. However, its general occurrence should not be taken as an axiom to be assumed, but as a hypothesis to be tested.

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