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MALHAM TARN NATIONAL NATURE RESERVE: THE VEGETATION OF MALHAM TARN MOSS AND FENS

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ABSTRACT

This paper is a descriptive and interpretative account of the diverse and floristically-rich mire complex that occupies the western part of the basin of Malham Tarn, comprising the raised bog of the Tarn Moss and its associated calcareous fens. The course of development of the lake deposits, peats and vegetation during Post-glacial time is outlined, with a brief consideration of human impacts and the management history of the site. The present vegetation is described and mapped, and related to 'British National Vegetation Classification' types and to broad vegetation categories in general use in continental Europe. The major components are bog communities (largely dominated by *Eriophorum vaginatum* and *Calluna vulgaris*), *Molinia caerulea* vegetation and *Betula pubescens* woodland on the raised-bog peats, and small-sedge rich fens, fen meadow and fen carr (of *Salix phylicifolia*, *S. pentandra* and *S. cinerea*) on calcareous fen peats, with extensive *Filipendula ulmaria* stands on silted peats and adjacent mineral soil. There are smaller areas of *Carex rostrata* swamp, acid 'poor fen' and damp calcareous woodland. A general account is given of major environmental factors influencing bog and fen communities, including water and peat chemistry, limiting nutrients for plant growth, variation in water level and oxidation-reduction processes, and the influence of these factors on directions of variation and the pattern of distribution of the vegetation. The paper concludes with a discussion of successional processes, the scientific and educational value of the site, and conservation problems and objectives.

INTRODUCTION

Malham Tarn Moss and its associated fens together make up an outstandingly rich and interesting mire complex, occupying the western part of the basin of Malham Tarn, 20 km north-west of Skipton in the Yorkshire Pennines (Fig. 1). Sinker (1960) gave a good general account of the topography and character of the vegetation for the country immediately around the Tarn; a more detailed account of the vegetation of the Malham Tarn estate, and of the Tarn Moss and fens in particular, was given by Cooper (1993, 1994). There are

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papers on the vegetation of the North Fen by Proctor (1974) and by Adam, Birks, Huntley & Prentice (1975), and much useful information is summarised in the unpublished National Trust biological survey of the estate (Lister & Alexander, 1989). Malham Tarn itself is a shallow marl lake 62 ha in area, lying over an inlier of impermeable Silurian rocks (mostly covered by calcareous drift) and surrounded by Carboniferous Limestone, 375 m above sea level (Shaw 1982; Arthurton, Johnson & Mundy 1988). The Tarn Moss is a raised bog, covering about 40 ha, built up of acid *Sphagnum* and *Eriophorum vaginatum* peat overlying fen peats and lake sediments; its domed surface and water-table rise to some 5 m above the level of the adjacent calcareous drainage. It is an ombrogenous (or ombrotrophic) bog; that is, its water and solute supply is derived wholly from rain and other airborne sources. The surrounding calcareous fens – a broad belt of about 12 ha fringing the main inflow streams to the north, and a narrower 'lagg' to the south and west separating the bog from the neighbouring mineral ground – are fed by strongly calcareous water draining from the limestone and lime-rich drift. Except for parts of the south-west lagg, the fens lie within a narrow range of levels, not more than a few decimetres above the level of the water in the Tarn (Pigott & Pigott 1959, 1963; Proctor 1974).

HISTORICAL DEVELOPMENT

Post-Glacial history of the Malham Tarn basin and the Tarn Moss

A detailed account of the stratigraphy and vegetational history of the Tarn Moss is given by Pigott & Pigott (1959, 1963). In Late-Glacial times, open water extended over almost the whole area of the present tarn and the Tarn Moss and fens; there was a separate small area of open water at a slightly higher level in the area now occupied by Ha Mire east of the Tarn. The earliest deposit to be laid down was a silty clay with stone fragments but few organic remains, reflecting still-severe conditions in the earliest Late-Glacial (Fig. 2). With warming climate, this silty mineral material was followed by some 50 cm of a more compact bluish clay, richer in organic matter. This contains abundant pollen, indicating an open grass-dominated but species-rich vegetation, with patches of low scrub, whose closest modern counterparts would be found above the tree-line in the central European mountains. Above this, a layer of *ca* 20 cm of laminated silt and clay with occasional stones shows a setback to colder conditions for between 500 and 1,000 years. A return to a thin layer of blue-grey clay passing quickly into white calcareous marl then followed the rapid Post-Glacial rise to near-modern temperatures. The marl, consisting of precipitated calcium carbonate with 5-6% of silt and clay, contains abundant *Chara* oospores and shell fragments, and was evidently laid down in extensive *Chara* beds in clear, shallow open water, at a time when the pollen shows that the surrounding country was dominated by birch and pine, later with elm and the first traces of oak pollen. By 8,000-9,000 years ago, reedswamp had become established on the surface of the marl over much of the western part of the Tarn basin, building up a thin layer of peat full of grass and sedge remains set in a highly humified matrix with a substantial mineral content; as in many other lakes, almost no emergent vegetation established on the exposed shore of the east side of the Tarn. The reedswamp peat quickly gave way to fen and fen carr peats, humified and almost amorphous, often with wood fragments. These fen and brushwood peats locally continued to build up, sometimes to a depth a several metres, especially around the margins of the basin, and in parts of the fen reach to the present surface. In the more central parts of the basin, after a thin woody layer in the peat (mostly of birch), the frequency of *Sphagnum* increases until the disappearance of mineral material and an abrupt change to almost pure and less-humified *Sphagnum* peat marks the onset of ombrogenous bog growth. At Malham Tarn, as at many

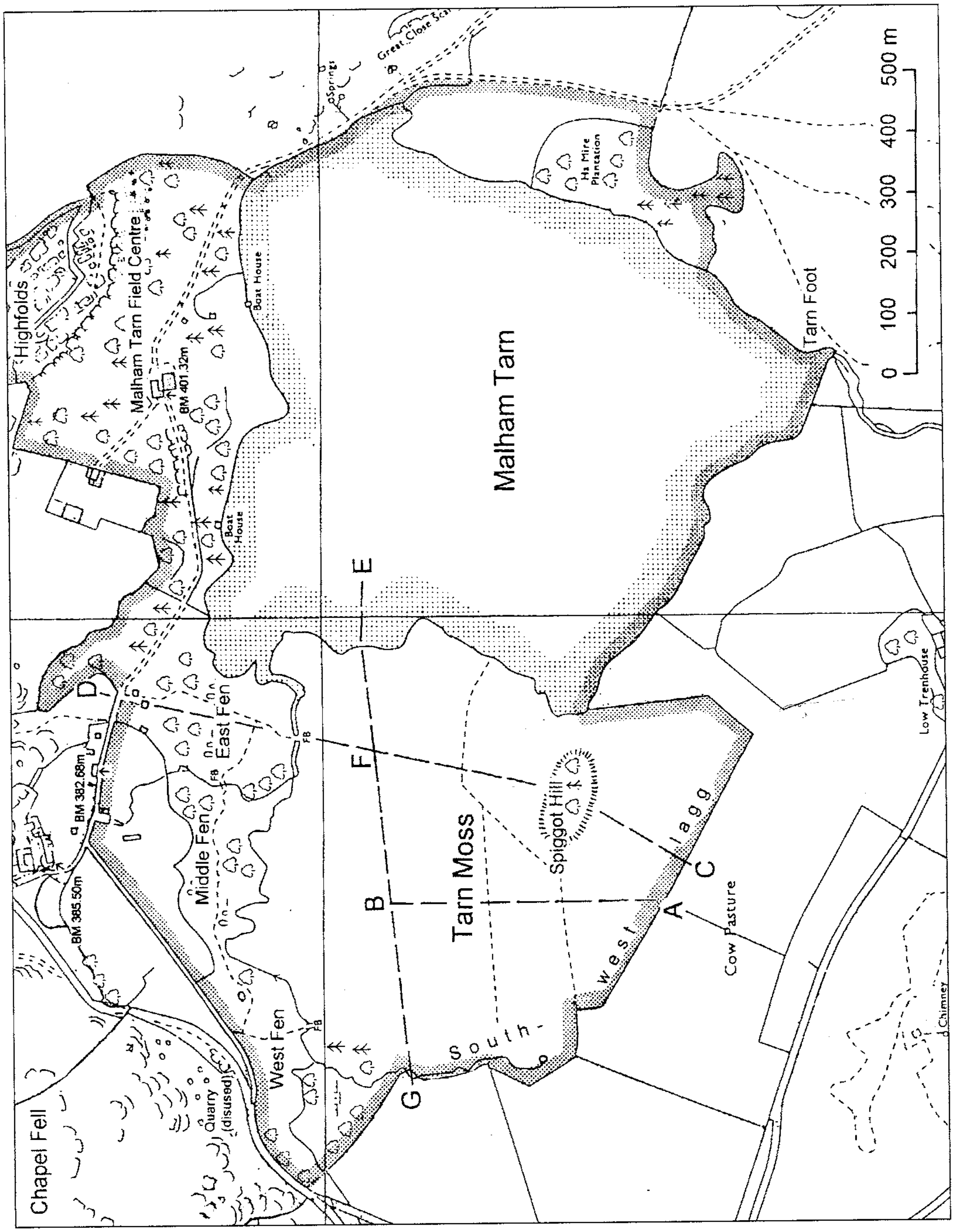

FIG. 1. Malham Tarn and its surroundings, showing the location of Tarn Moss and fens (with the sections shown in Fig. 2), and the boundary of the National Nature Reserve. Based on the Ordnance Survey 1:10,000 map, with permission.

other sites, this change roughly coincides with the appearance of abundant alder in the pollen record, and with the switch to a more oceanic climate that followed the filling of the North Sea basin around 7,000 years ago, so it may have been at least in part a consequence of changing climate. Ombrogenous peat has accumulated continuously since that time, attaining a depth of 5-6 m over much of the Tarn Moss. Through much of this depth the easily-recognised remains of *Sphagnum imbricatum* are prominent in the peat. This species was the dominant peat former across much of northwest Europe for much of the Post-Glacial, but has become a rare plant in Britain over the last few centuries and no longer grows on the Tarn Moss. Remains of the fibrous tussock bases of *Eriophorum vaginatum* with woody fragments of *Calluna vulgaris* root can be found through much of the ombrogenous peat, but become more numerous towards the surface, and form the bulk of the peat immediately beneath the present vegetation.

The sequence sketched in the last paragraph was not followed in detail everywhere. Large-scale successional development, especially the initiation of raised-bog growth, had impacts on other parts of the mire system, especially upstream and around the margins, as is clear from Fig. 2. Raised-bog development progressively constrained the calcareous drainage from the surrounding country into the present lagg and the broader belt of fen fringing the main inflow streams. As the surface of the raised bog rose, the belt of lagg fen around the morainic mound of Spiggot Hill and at the south edge of the Tarn Moss encroached progressively onto the mineral ground, the acid ombrogenous peat at the same time encroaching onto its inner margin. Although most of the fen was occupied by carr, the peat stratigraphy suggests that limited areas probably remained open throughout the Post Glacial.

As can be seen from the Ordnance Survey map, or from the high viewpoints of Chapel Fell or Highfolds, the main expanse of the Tarn Moss is the result of coalescence of three raised-bog domes – northeast, northwest and south of Spiggot Hill – each initiated on a different part of the undulating surface beneath the whole complex. The northeastern and northwestern domes are separated by a slight seepage, now marked by a partly clogged ditch, from the Spiggot Hill fen to the main inflow stream. There are several smaller areas of raised bog peat north of the main inflow stream.

The impact of Man: ownership and management history

Evidence from the pollen diagram points to at least local Neolithic and Bronze Age forest clearance in the limestone country surrounding the Tarn and, by the Medieval period, the landscape was probably little less open than now (cf. Fig. 1, p.279) Grazing by farm stock must have had some influence on the Tarn moss and fen since early times, tending to suppress the growth of trees and the fen-carr sallows, and to increase the area of open fen.

The plans in Thomas Lister's estate book from the 1780s (Anon, 1785-86; Fig. 3) show the North Fen divided into named compartments, and the area was evidently in active agricultural use. The present-day West Fen was divided into two compartments known as 'Moss Meadows'. The western third of Middle Fen was joined with Tarn Fen Meadow, making one large compartment called 'Long Meadow', and the remainder of Middle Fen was 'Kell Hill Meadow'. The present East Fen included the whole of 'Crooks', the bottom corner of 'Becks' (the field below Water Houses traversed by the North Inflow stream) and the southern edge of 'Tarn Close'. These field names suggest that at the time of the map the western parts of the fen were managed as meadow, mown either for hay or for litter. The symbols on the map suggest that all or most of East Fen was ombrogenous bog.

In 1791, the level of the Tarn was raised by about a metre by the construction of a weir and sluice in its southeast corner (Holmes, 1965). This extended the area of the Tarn slightly, inundating the lakeward edge of the Tarn Moss and probably about a hectare of fen around

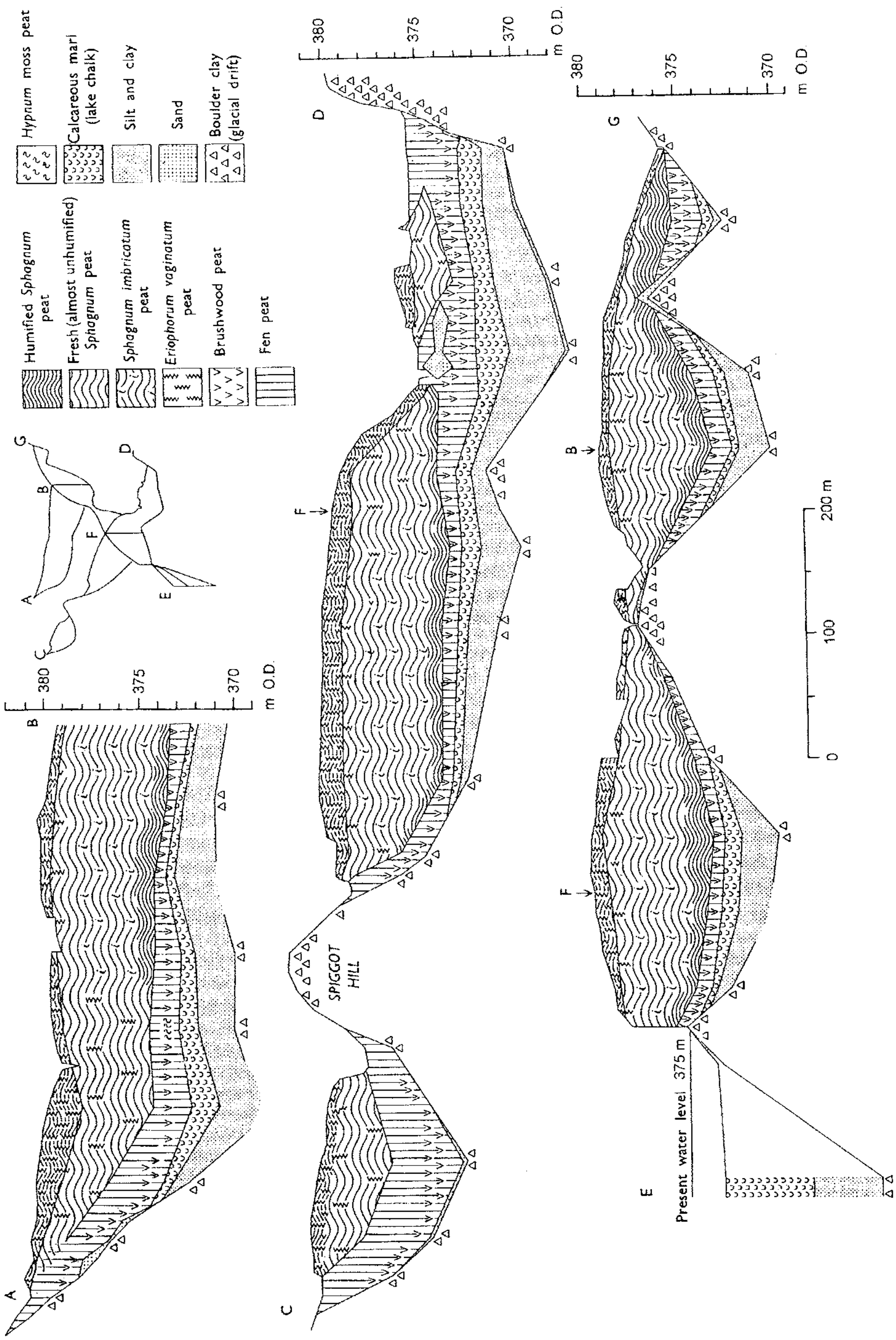

FIG. 2. Stratigraphy of Tarn Moss, Malham.
The relation of the three sections to each other is shown on the map (Fig. 1.) and illustrated in the sketch next to the key. The vertical scale is in metres above Ordnance Datum. Reproduced (with change to metric scale) from Pigott & Pigott (1959), with permission.

the mouth of the main inflow stream. It also flooded old peat cuttings, and brought some low areas of ombrogenous peat within the influence of calcareous water. In the fen, this initiated a good deal of local secondary succession. Flooding of the edge of the raised bog by calcareous water led to the erosion of a peat cliff, now a couple of metres high. There must have been some flooding of the fen bordering the inflow streams (of which the present stands of *Carex appropinquata* in the Middle and West Fen may be a legacy), but this cannot have been very extensive because, except near the mouth where the maps and the stratigraphy both suggest some lateral shift, the course of the streams marked on the 1785-6 map matches the modern 1:10,000 map with remarkable fidelity. Around 1820 two large ponds were excavated in the West Fen, and used to hold young trout (Woof & Jackson, 1988). They were abandoned around 1880, and by the 1940s had become largely infilled with *Carex rostrata* and a patchy quaking mat of *Sphagnum* spp., with some *Phragmites australis* and a little *Typha latifolia*.

Tarn Moss itself has probably long been used for rough grazing, and was no doubt at least sporadically burnt, but the 1785-6 map shows the Moss divided into three compartments, and these may have rather different management histories. From the latter part of the 19th Century onwards, grip drains were put in radially across the main raised bog. In the late 1940s the vegetation was dominated by *Eriophorum vaginatum* with abundant *Deschampsia flexuosa*, with little heather, very little *Sphagnum* except in flooded peat pits, and profuse growth of the mosses *Pohlia nutans* and *Tetraphis pellucida* reflecting recent severe burning.

The Malham Tarn estate was donated to the National Trust (NT) in 1947. From then until 1986 the reserve was managed by the Field Studies Council (FSC). Since then, it has been managed jointly by the NT (responsible for physical management) and the FSC (responsible for education and research). The first management plan for the site was written in 1975 by Dr R. H. L. Disney, then warden of the Field Centre (Disney, 1975a); the current management plan was written by the NT head warden and naturalist at Malham, A. J. Clunas (Clunas, 1992). In 1992 Malham Tarn was designated a National Nature Reserve (NNR) and, since then, English Nature have provided advice and help to the joint management committee. Blocking of grip drains on the main bog, begun experimentally around 1970 (Prof. C. D. Pigott, *in litt.*) and pursued systematically since 1987, has significantly raised the water table. This, together with the exclusion of grazing and burning, has led to slow progressive (but still incomplete) recovery of the raised bog vegetation. On parts of East Fen and on the Tarn Moss there has been an ongoing commitment to removal of willow and birch and, throughout the reserve, to the eradication of the aggressive exotics *Rhododendron ponticum* and *Thelycrania sericea*.

Malham Tarn NNR is located within the Yorkshire Dales National Park, forms part of the 5,000 ha Malham-Arncliffe SSSI, is a Ramsar site, and falls within the Pennine Dales Environmentally Sensitive Area (ESA).

THE VEGETATION OF THE TARN MOSS AND FENS

The description of the vegetation which follows is based on a National Vegetation Classification (NVC) survey of the Malham Tarn NNR (Cooper, 1993), and a more detailed survey of the North Fen (Cooper, 1994), and builds on the earlier vegetation survey of Proctor (1974). The NVC surveys mapped the boundaries between vegetation types on a scale of 1:2500. Representative homogeneous areas of each vegetation type were selected for sampling. Either 2 x 2 or 4 x 4 m quadrats were used to sample herbaceous vegetation, depending on scale, and usually 10 x10 m or equivalent in area for the woodland, since stands were often small in extent. The data were analysed and handled

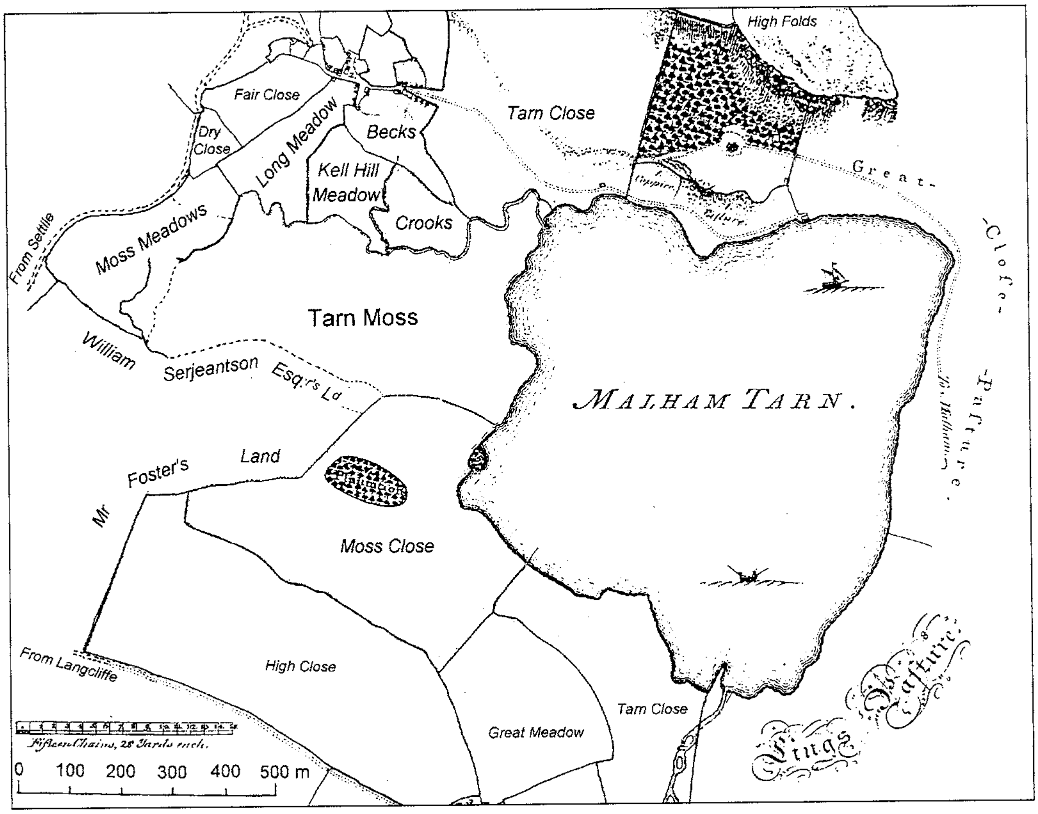

FIG. 3. Malham Tarn and its surroundings in the 1780s, compiled and in part redrawn from the plans in Thomas Lister's estate book (Anon, 1785-86). Compartments including parts of the Tarn Moss and fen are lettered in larger type. Spiggot Hill was marked as 'Plantation'; the two small compartments bordering the Tarn below Tarn House were marked as 'Coppice' and 'Pasture' respectively. The estate and its boundaries were surveyed very accurately and, with appropriate adjustment of scale and orientation, can be superimposed on the modern Ordnance Survey 1:10,000 map with remarkable precision, apart from the east shore of the Tarn which appears to have been sketched-in only roughly. Notice the greater area of fen that existed before the Tarn water level was raised in 1791; inundation appears to have cut back the edge of the raised bog by some 10-20 m from its 18th Century position, and flooded a belt of fen 30-40 m wide east of Spiggot Hill and about a hectare of fen around the mouth of the main inflow stream. Changes to the steep north shore were relatively slight, but substantial areas were inundated on the gently shelving southern shore.

using VESPAN II (Malloch, 1995), which incorporates TWINSPAN (Hill, 1979). Endgroups were compared with and described and named in terms of *British Plant Communities* (Rodwell, 1991a, b, 1992, 1995).

For simplicity, the account is arranged under the broad ecological headings of bog vegetation, 'poor fen', 'rich fen' (both *sensu* Du Rietz, 1949), and carr and woodland as outlined on p.284. The distribution of the vegetation types is mapped in Figs 4 and 5; a summary of the species composition of the main communities is given in Table 1.

Bog vegetation (Erico-Sphagnion, Junco-Molinion)

M2 *Sphagnum cuspidatum/recurvum* bog pool community

M18 *Erica tetralix-Sphagnum papillosum* raised and blanket mire community ('Raised bog vegetation', *p.p.*, Proctor, 1974).

M19 *Calluna vulgaris-Eriophorum vaginatum* mire ('Raised bog vegetation', p.p., Proctor, 1974).

M25 *Molinia caerulea-Potentilla erecta* mire ('Marginal raised bog communities', Proctor, 1974).

Poor fens (Caricion curto-nigrae)

M5 *Carex rostrata-Sphagnum squarrosum* mire ('Poor fen vegetation', *p.p.*, Proctor, 1974).

M6 *Carex echinata-Sphagnum recurvum/auriculatum* mire ('Poor fen vegetation', *p.p.*, Proctor, 1974).

Rich fens and associated swamps and tall-herb vegetation (Magnocaricion, Caricion davallianae, Filipendulion).

S27 *Carex rostrata-Potentilla palustris* swamp ('*Carex* fen, *Potentilla palustris-Acrocladium nodum*', *p.p.*, Proctor, 1974).

M9 *Carex rostrata-Calliergon cuspidatum/giganteum* mire ('*Carex* fen, *Potentilla palustris-Acrocladium nodum*', *p.p.*, Proctor, 1974).

M26 *Molinia caerulea-Crepis paludosa* mire ('*Carex* fen, *Carex nigra-Sanguisorba officinalis* nodum', Proctor, 1974).

Carr and woodland (Salicion cinereae, Betulion pubescentis)

W3 Salix pentandra-*Carex rostrata* woodland ('Fen carr', Proctor, 1974)

W4 *Betula pubescens-Molinia caerulea* woodland ('Birch woods on raised bog peats', Proctor, 1974).

W6 *Alnus glutinosa-Urtica dioica* woodland

Terminology

The ecological terminology relating to fens and bogs is often used inconsistently and can be confusing; we use the terms in the following ways. *Mire* is an umbrella term for any peat-forming vegetation, bog or fen, and its peat substrate (it is convenient to stretch this definition slightly to include some closely related communities which may not actually be forming peat). *Peatland* includes bogs and fens, and also drained and cultivated peat areas. Both fens and bogs are generally permanently waterlogged, with the water table close to the surface at least for much of the year. *Fens* receive water and nutrients from mineral soil or the underlying rock and are described as *minerotrophic*. They may occur in basins or valley bottoms (topogenous) or be fed by water issuing on slopes (soligenous). They contrast with *bogs* which are *ombrogenous* (or *ombrotrophic*), receiving their water and nutrients from the atmosphere – either in rain, or by dry deposition of gases and wind-borne dust – and are generally nutrient-poor and acid, with a pH of 3.5-4.5. The Swedish ecologist Du Rietz (1949) divided fens into *poor fens*, fed by non-calcareous waters, with pH typically between 4.5 and 6.0 and usually dominated by base-tolerant *Sphagnum* species, and calcareous *rich fens*, with abundant 'brown mosses' such as *Campylium stellatum* and *Scorpidium scorpioides* with pH generally around 6.5-7.5.

TABLE 1. *Floristic table illustrating the transition at Malham Tarn Fen from swamp colonising open water, through tall-herb fen, base-rich small-sedge mire and wet woodland (with the corresponding fen-meadow community) to acid small-sedge mire and raised bog vegetation.*

The Roman numerals indicate species frequency in classes 81-100% (V), 61-80% (IV), 41-60% (III) and 21-40% (II). The lowest frequency class has been omitted from the table, unless the species are of especial ecological significance. The frequencies are derived from survey data and do not necessarily relate to those in the published tables of *British Plant Communities.* The species listed represent only those present within the samples taken and the list is therefore not comprehensive for the whole site. Canopy species in the fen carr are indicated by (c).

KEY:
S9 *Carex rostrata* swamp
S27a *Carex rostrata-Potentilla palustris* swamp, *Carex-Equisetum* sub-community
M27a *Filipendula ulmaria-Angelica sylvestris* tall-herb community, *Valeriana-Rumex* sub-community
M9b *Carex rostrata-Calliergon cuspidatum/giganteum* mire, *Carex-Calliergon* sub-community
W3 *Salix pentandra-Carex rostrata* woodland
M26a *Molinia caerulea-Crepis paludosa* mire, *Sanguisorba* sub-community
M6b *Carex echinata-Sphagnum recurvum/auriculatum* mire, *Carex-Nardus* sub-community
M25a *Molinia caerulea-Potentilla erecta* mire, *Erica cinerea* sub-community
M19a *Calluna vulgaris-Eriophorum vaginatum* mire, *Erica tetralix* sub-community

	S9	S27a	M27a	M9b	W3	M26a	M6b	M25a	M19a
Carex rostrata	**V**	**V**	II	**V**	III	•	I		
Equisetum fluviatile	III	II		II	II	II			
Calliergon cuspidatum	•	**IV**	II	**V**	**IV**	**IV**			
Galium palustre	I	**V**	III	**V**	**V**	III			
Caltha palustris	I	**IV**	II	**V**	III	III			
Filipendula ulmaria	•	**V**	**V**	**V**	**V**	**IV**			
Angelica sylvestris	•	**V**	III	III	III	**V**			
Potentilla palustris	II	**V**		**V**	II	I			
Menyanthes trifoliata	II	**IV**		**V**	II	II			
Epilobium palustre	I	**V**		**V**	I	•			
Calliergon giganteum	I	**IV**		**V**	I	•			
Agrostis stolonifera	I	**V**		III		II			
Valeriana officinalis	•	**IV**	II		**IV**	•			
Succisa pratensis	•	**IV**		III	I	**V**	I		
Lychnis flos-cuculi	•	**IV**		III	II	•			
Rumex acetosa	•	**IV**		•	•	II			
Cochlearia officinalis		**IV**							
Phalaris arundinacea		III							
Viola palustris		III							
Galium uliginosum	•	III				II			
Juncus acutiflorus	I	II		II	II	•			
Plagiomnium elatum		II		II					
Mentha aquatica	I	II			I	•			
Brachythecium rutabulum	•	I	**V**			•			

	S9	S27a	M27a	M9b	W3	M26a	M6b	M25a	M19a
Poa trivialis	•	I	III			•			
Eurhynchium praelongum	•	•	III		II	•			
Ranunculus repens	•	II	III		III	•			
Chrysosplenium oppositifolium		II	III						
Geum rivale	•	•	III		I	I			
Cirsium helenioides			II						
Geranium sylvaticum			II						
Myosotis scorpioides			II		II				
Calliergon cordifolium	•		I		I	•			
Carex nigra	I	I		**V**	I	**V**	**V**		
Cardamine pratensis	I	III	III	**V**	II	•			
Rhizomnium pseudopunctatum		III		**V**	III	•			
Ranunculus flammula	I	II		**V**	I	•			
Carex diandra	•	I		**V**	•	•			
Bryum pseudotriquetrum	•	I		**V**	•	•			
Marchantia polymorpha				**V**					
Cratoneuron filicinum				**IV**					
Cirsium palustre	•	I		III	I	III			
Myosotis scorpioides		II		III					
Phragmites australis	•	I		II	I	II			
Holcus lanatus	•	I		II	II	•			
Parnassia palustris				II					
Scorpidium scorpioides				II					
Aneura pinguis				II					
Carex lepidocarpa				II					
Carex panicea		I		II					
Salix pentandra (c)	•	•			**V**	•			
Ajuga reptans	•	•		•	**IV**	•			
Mnium hornum	•	•			III	•			
Plagiomnium affine	•	•			II	•			
Salix phylicifolia (c)					II				
Salix cinerea (c)	•	I			II	•			
Salix nigricans (c)					II				
Molinia caerulea	•			II	II	**V**	I	**V**	II
Crepis paludosa	•	•		I	III	**V**			
Carex panicea	•	•		III	•	**V**			
Valeriana dioica	•	•			I	**V**			
Equisetum palustre	•	I		III	III	**V**			
Potentilla erecta	•	•		I	•	**IV**	**IV**	III	I
Sanguisorba officinalis	•	•		•	•	**V**			
Ranunculus acris	•	•		II	II	III			
Juncus articulatus	I	I		II	•	III			
Lophocolea bidentata	•	I		•	I	III			

	S9	S27a	M27a	M9b	W3	M26a	M6b	M25a	M19a
Trollius europaeus	•	•		•	I	III			
Carex pulicaris	•	•		•	•	III			
Anemone nemorosa	•	•		•	•	III			
Campylium stellatum	•	I		I	•	III			
Thuidium tamariscinum	•	•		•	•	III			
Ctenidium molluscum	•	•		I	•	III			
Serratula tinctoria	•	•		•	•	III			
Campylium elodes	•	•		•	•	III			
Plagiochila asplenoides	•	•		•	•	III			
Rhytidiadelphus squarrosus	•	I		•	•	II			
Carex disticha	•	•		•	•	II			
Carex flacca	•	•		I	•	II			
Pseudoscleropodium purum	•	•		•	•	II			
Centaurea nigra	•	•		•	•	II			
Ranunculus auricomus	•	•		•	•	II			
Deschampsia flexuosa							**V**	**V**	**V**
Sphagnum recurvum							**V**	**V**	II
Aulacomnium palustre	•	•		I	•	III	**V**	I	II
Polytrichum commune							**V**	II	II
Carex curta							II		
Eriophorum vaginatum							I	**V**	**V**
Sphagnum palustre							III	**V**	**IV**
Sphagnum papillosum								II	II
Sphagnum cuspidatum								II	II
Galium saxatile							I	II	I
Calluna vulgaris								III	**V**
Erica tetralix								II	**V**
Sphagnum capillifolium								II	**V**
Cephalozia bicuspidata								I	**IV**
Eriophorum angustifolium								II	**IV**
Hypnum jutlandicum									**IV**
Calypogeia muelleriana									**IV**
Sphagnum fimbriatum							II	II	III
Scirpus cespitosus								I	III
Campylopus paradoxus								I	III
Lophozia ventricosa								I	III
Mylia taylori									III
Pleurozium schreberi							I	I	II
Hypnum cupressiforme							I	I	II
Narthecium ossifragum								I	II
Polytrichum alpestre								I	II
Vaccinium myrtillus								I	II
Vaccinium oxycoccos								I	II
Dicranum scoparium									II
Cladonia pyxidata									II
Sphagnum magellanicum								I	I
Empetrum nigrum ssp. nigrum								I	I

Vegetation in which the water level is above the surface of the peat for much or most of the year is referred to as *swamp* (or '*reedswamp*'). Wet sites rich in the growth-limiting nutrients N, P and K are often dominated by luxuriant tall herb vegetation, in which the vigorous persistent dominants often make any clear distinction between 'swamp' and 'fen' difficult or impossible. Vegetation of this kind is conveniently called '*tall herb fen*'.

Bog vegetation

The raised acid peat at Malham supports predominantly Erico-Sphagnion mire of the *Erica tetralix* sub-community of the *Calluna vulgaris-Eriophorum vaginatum* mire (M19a). It is found across the three domes of the main Tarn Moss raised bog and also on the isolated lenses of peat that occur within the North Fen. *Calluna-Eriophorum* mire is the typical blanket-bog vegetation of high-altitude ombrogenous peats that have accumulated in the wet cool climate of the uplands of northern Britain (Rodwell, 1991b). It can also be derived from repeated burning and grazing of *Erica tetralix-Sphagnum papillosum* mire (M18) and this is its likely origin at Malham.

This vegetation at Malham is characteristically dominated by an uneven tussocky growth of *Eriophorum vaginatum*, with *Deschampsia flexuosa*, ericoid sub-shrubs and patches of sphagna and hypnoid mosses. Of the ericoids, *Calluna vulgaris* is the commonest and most conspicuous, but varies locally in abundance, probably because of differences in burning history, heather-beetle damage and water level. *Erica tetralix* is frequent and locally abundant; *Empetrum nigrum* is widely but more thinly scattered. Other frequent associates, often locally abundant, include *Scirpus cespitosus*, *Narthecium ossifragum*, *Eriophorum angustifolium* and *Vaccinium oxycoccos*. *S. cespitosus* has spread particularly where trampling has compacted the peat along pathways, as on the beaten track from East Fen bridge to Spiggot Hill. Bryophytes are dominated by local patches of *Sphagnum capillifolium*[1] with frequent *S. papillosum* and occasional *S. fimbriatum* and *S. recurvum*. Of the hypnoid mosses, *Hypnum jutlandicum* is the commonest and tends to be associated with *Calluna*. There is frequently some *Pleurozium schreberi* too, and a range of leafy hepatics including *Cephalozia bicuspidata*, *Calypogeia muelleriana*, *Lophozia ventricosa*, *Mylia taylori*, *Odontoschisma sphagni*, *Mylia anomala*, *Ptilidium ciliare* and *Barbilophozia floerkei*.

The *Vaccinium-Hylocomium* sub-community of the *Calluna-Eriophorum* mire (M19b) occurs fragmentarily along the steep margin (Rand) of the Tarn Moss at its northern and eastern edge. Here the vegetation is dominated by *Calluna vulgaris* and *Vaccinium myrtillus*, with locally frequent *Vaccinium vitis-idaea* and *Rubus chamaemorus* (confined to the northern edge). *Sphagnum capillifolium* remains frequent, along with frequent *Hypnum jutlandicum* and *Pleurozium schreberi*, but *Hylocomium splendens*, *Cladonia arbuscula* and *C. uncialis*, common associates of this community elsewhere, are rare or absent on the Tarn Moss.

Bog pools are poorly developed at Malham. Where they do occur, e.g. in old peat cuttings just north of Spiggot Hill and on the bog area in East Fen, or as small natural pools (mainly in the raised bog south of Spiggot Hill), they are of *the Sphagnum cuspidatum/recurvum* type (M2). Around the margins of these pools, sphagna such as *S. papillosum* and *S. capillifolium* become more abundant; *S. magellanicum* appears in this situation near the Spiggot Hill peat pools. Here too, *Vaccinium oxycoccos* and *Drosera rotundifolia* increase in frequency, all combining to shift the composition of the vegetation closer to the *Sphagnum magellanicum-Andromeda polifolia* sub-community of the *Erica tetralix-Sphagnum papillosum* raised and blanket mire community (M18a), which is well developed on the lowland raised bogs of the south side of the Solway. Of other species

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[1] Most or all of the '*Sphagnum capillifolium*' in the NNR is subsp. *rubellum*, which some experts once again regard as a distinct species.

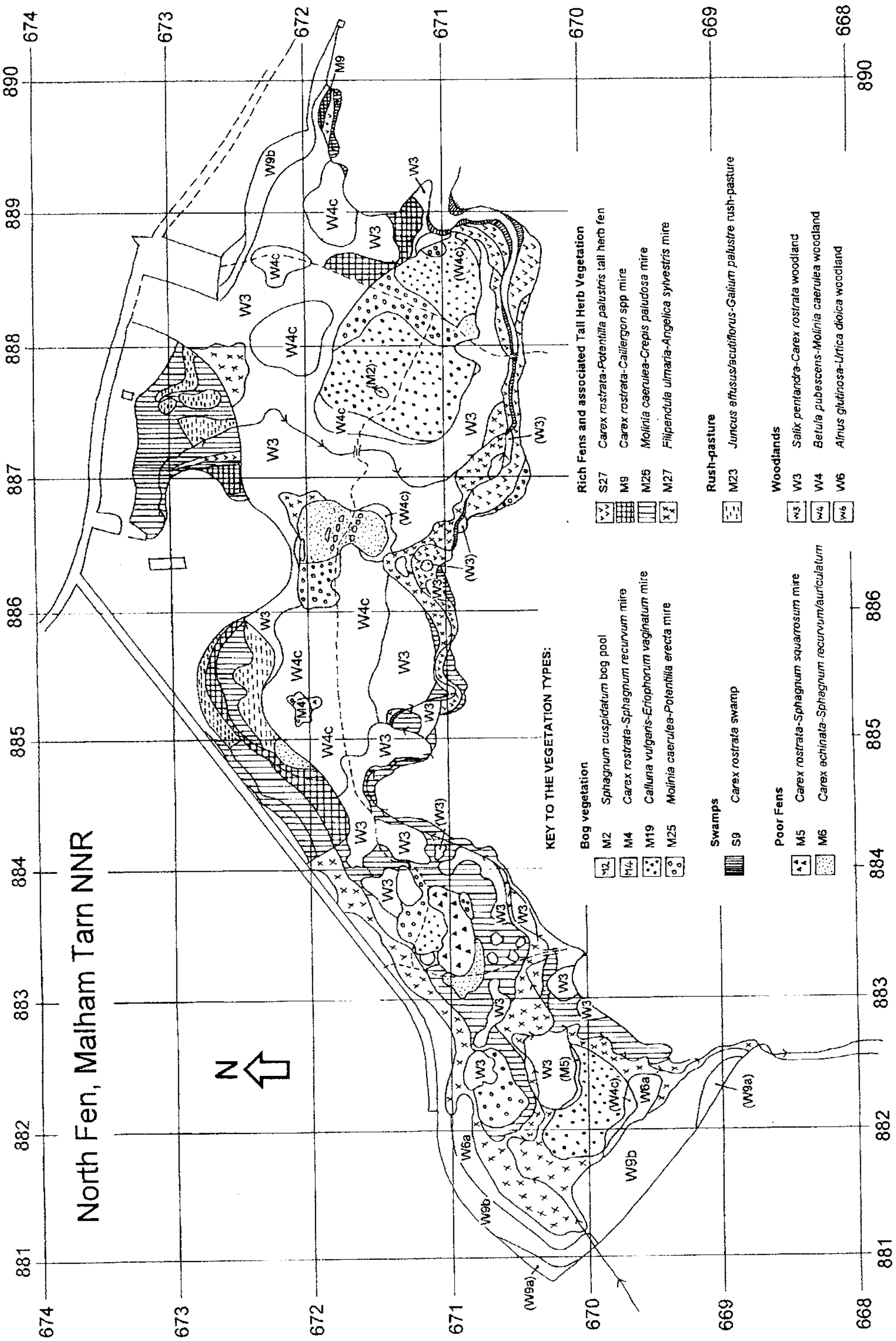

FIG. 4. Map of vegetation types on Malham Tarn North Fen, with 100 m squares of the National Grid. Surveyed by E. A. Cooper, August 1994.

characteristic of this community, *Andromeda polifolia* and *Sphagnum tenellum* are uncommon and thinly scattered on Tarn Moss (though *A. polifolia* grows in abundance only a few km away on Helwith Moss in Ribblesdale); *Rhynchospora alba* is absent from Malham but still occurred on Helwith Moss 40 years ago.

Around the rand of the bog, and where the surface of the peat has been disturbed by peat digging, *M. caerulea* often becomes prominent, forming the *Erica tetralix* sub-community of the *Molinia caerulea-Potentilla erecta* mire. Good examples can be seen on the north edge of Tarn Moss above the inflow stream, on the acid peat area of East Fen, and associated with the various pools and old peat diggings in the Middle and West Fen.

Poor Fens

Some areas of wet acidic peat close to the influence of mildly base-rich water (and often sites of past disturbance) are occupied by a rather particular form of the *Carex echinata* sub-community of the *Carex echinata-Sphagnum recurvum* mire (M6a), rich in *Carex curta*. The pH of these areas is little higher than in the raised-bog communities, but cation content is slightly greater and mineralisation of nutrients, especially N and P, is probably more rapid. The most frequent sedges are usually *Carex echinata*, *C. nigra* and *C. curta*. Of the sphagna, *S. recurvum* is usually dominant, but *S. palustre* and (more locally) *S. fimbriatum* are also frequent. Also distinctive is the local abundance of *Polytrichum commune*. The *Carex nigra-Nardus stricta* sub-community (M6b) is developed locally around the south-western lagg of Tarn Moss, and very locally the *Juncus effusus* (M6c) and *J. acutiflorus* (M6d) sub-communities occur in old grip drains and more recent experimental peat diggings on the west side of Tarn Moss. The dicotyledonous associates are few in this kind of poor-fen vegetation at Malham, and are generally restricted to *Potentilla erecta* and occasional *Rumex acetosa*, *Succisa pratensis*, *Viola palustris* and *Galium saxatile*. *M. caerulea* is often common, and this vegetation intergrades with M26a.

Marking the junction between the raised-bog acidic peats and the calcareous fens is the *Carex rostrata-Sphagnum squarrosum* mire (M5). This poor-fen community typically forms a narrow zone between the *Molinia-Potentilla* mire (M25) on the sloping edge of the acid peat (or the *Calluna-Eriophorum* mire, M19, where the junction is more abrupt) and the lower-lying *Carex rostrata-Calliergon* mire (M9) or, along the course of the inflow stream, the *Carex rostrata-Potentilla palustris* swamp (S27). The same zonation is visible in the wet woods; wherever the acid *Betula-Molinia* woodland (W4) abuts onto the *Salix cinerea* carr (W3), there is a band with *Sphagnum squarrosum*, *S. palustre* and *S. fimbriatum* dominant in the ground layer, reflecting its derivation from *Carex rostrata-Sphagnum squarrosum* mire. The community is also extensively developed in the Middle Fen, where it occupies almost the whole of a former pool, dug in the 19th Century as a holding pond for fish, but now filled with a quaking mat of *Sphagnum* much invaded by *Phragmites*.

The *Carex rostrata-Sphagnum squarrosum* mire (M5) is a rather heterogeneous vegetation characterised overall by the dominance of *Carex rostrata* and other sedges with some of the less exacting fen herbs over a carpet of base-tolerant sphagna. The vascular plants vary in their prominence at Malham. *Potentilla palustris* is the most consistent associate, with more locally frequent *Succisa pratensis*, *Eriophorum angustifolium*, *Viola palustris*, *Epilobium palustre*, *Agrostis canina* and *Lychnis flos-cuculi*. The bryophyte carpet is distinctive. The sphagna, dominated by the mildly base-tolerant *S. squarrosum*, *S. palustre*, *S. fimbriatum*, *S. angustifolium* and, very locally at Malham, *S. teres*, tend to form discontinuous hummocks, often with a ramifying network of pools in between that support *Calliergon stramineum* and, where the water is deeper, *Utricularia neglecta*. *Aulacomnium palustre* is often conspicuous on the tops of the *Sphagnum* hummocks. The community is a good illustration of the 'synusia' concept (Barkman, 1978), in that the vascular

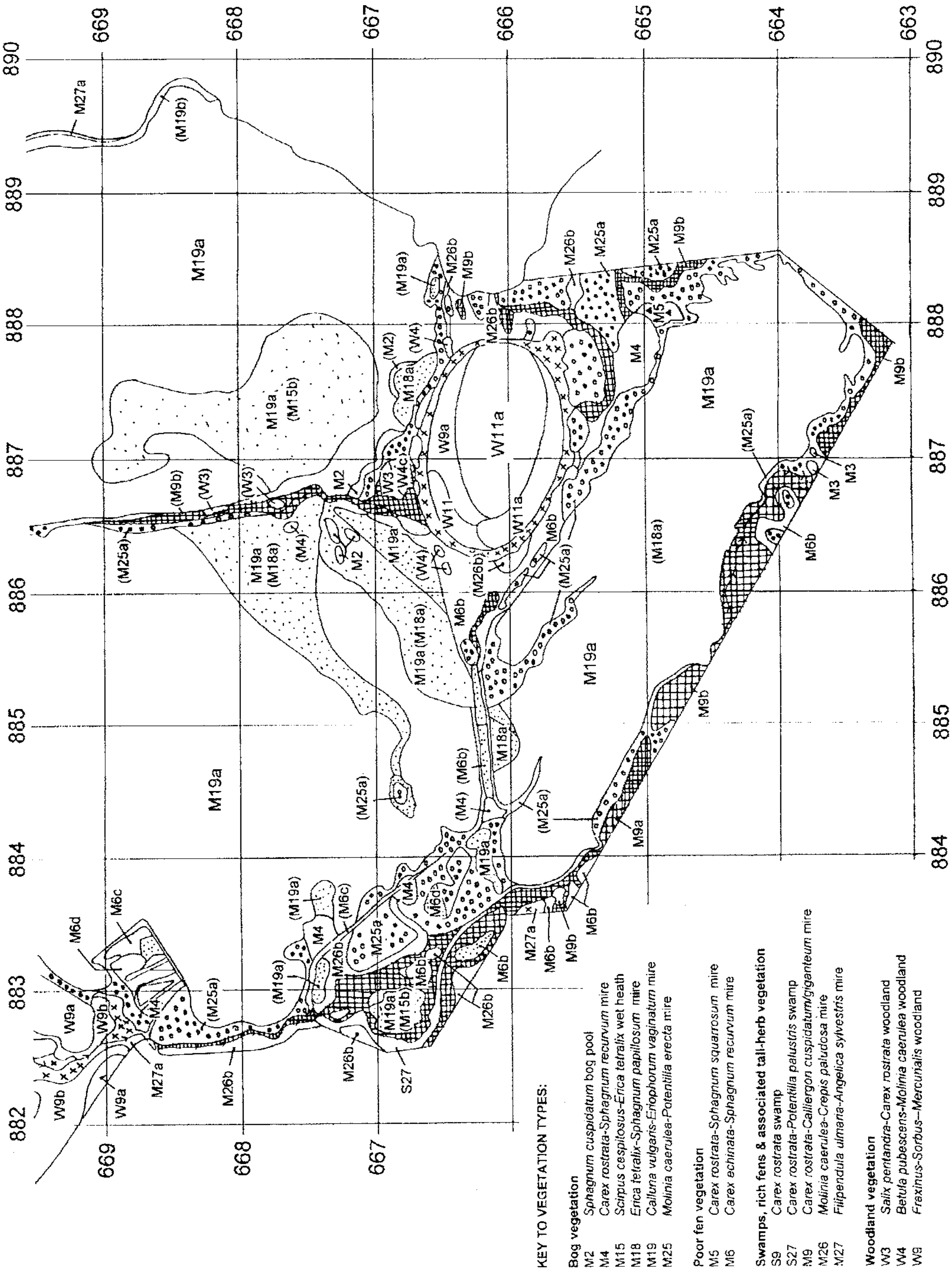

FIG. 5. Map of the vegetation of Spiggot Hill, the southern part of the Tarn Moss, and the south-west lagg, with 100 m squares of the National Grid. Surveyed by E. A. Cooper, 1993.

plants and the moss layer vary to a large extent independently. A very similar suite of vascular plants is found in the *Carex rostrata-Potentilla palustris* swamp (S27), and as in that community the list of vascular plants depends very much on how calcareous the groundwater is. If this is very calcareous, the *Sphagnum* cover becomes more discontinuous and the present community intergrades into the rich-fen communities described below; an instance is seen at the western edge of the filled-in pool in West Fen, where cushions of *Sphagnum teres*, *S. palustre*, *S. subnitens* and *S. warnstorfii* stand above water with a pH between 6 and 7 (Fig. 9, Table 3).

Rich Fens and associated swamp and tall-herb vegetation

In the Middle Fen, and more extensively in the East Fen, where the channel broadens and the flow slackens, *Carex rostrata* has been able to colonise the margins of the inflow stream. In such situations, a narrow zone of *Carex rostrata* swamp (S9) in open water fronts a broader floating raft of *Carex rostrata-Potentilla palustris* swamp (S27). Similar fringing vegetation occurs in the sheltered bays at the northeast and northwest corners of the Tarn.

At Malham, the *Carex rostrata-Potentilla palustris* swamp is exclusively formed by the more species-poor and open vegetation of the *Carex-Equisetum* sub-community (S27a). *Carex rostrata*, the most consistently frequent member of this community, dominates over a floating raft of the rhizomatous *Potentilla palustris* and *Menyanthes trifoliata*. Characteristic and frequent associates are *Equisetum fluviatile*, *Ranunculus flammula*, *Myosotis scorpioides*, *Caltha palustris*, and trailing shoots of *Agrostis stolonifera* and *Galium palustre*. The abundance of large mosses – *Calliergon* species, *Rhizomnium pseudopunctatum* and *Plagiomnium elatum* – in the ground layer reflects the intergradation of this community with the *Carex rostrata-Calliergon* mire (M9), and the frequency of *Filipendula ulmaria*, *Valeriana officinalis*, *Cochlearia pyrenaica*, *Rumex acetosa*, *Galium uliginosum* and *Phalaris arundinacea* is indicative of the silted conditions associated in higher and drier situations with the *Filipendula-Angelica* mire (M27).

It is only in East Fen and around the south-western lagg that peats kept permanently moist with calcareous groundwater have remained poor enough in growth-limiting nutrients for the development of *Carex rostrata-Calliergon* mire (M9), a very characteristic rich-fen type. This community varies in composition, even within individual stands, but it is generally characterised by a rich assemblage of vascular plants amongst which sedges (*Carex rostrata* and various others) are dominant over a luxuriant carpet of bulky 'brown mosses', typically including such calcicolous fen species as *Campylium stellatum*, *Drepanocladus revolvens* ssp. *intermedius*, *Calliergon giganteum*, and *Scorpidium scorpioides*. Frequent associates include *Carex lepidocarpa*, *C. panicea*, *Menyanthes trifoliata*, *Galium palustre*, *Potentilla palustris*, *Equisetum fluviatile*, *Epilobium palustre*, *Ranunculus flammula*, *Succisa pratensis*, *Pedicularis palustris*, *Valeriana dioica*, *Molinia caerulea* and *Rhizomnium pseudopunctatum*, sometimes with the very base-tolerant *Sphagnum contortum* forming low patches just above the level of the calcareous groundwater.

On the North Fen remaining stands of this vegetation are almost exclusively of the *Carex diandra-Calliergon giganteum* sub-community (M9b), east of the boardwalk below Sandhill (Miss Hilary's) Cottage. This sub-community also occurs locally in the central wettest zone of the Spiggot Hill lagg. The stand in East Fen was much more extensive in the past but, perhaps because of the abundant seed from the vigorous neighbouring carr and the influx of nutrients from winter floodwater, it has been especially prone to invasion by *Salix* species. In this sub-community, *Carex rostrata* is still usually present, but it may be exceeded or replaced altogether by *C. diandra*. Taller dicotyledons are numerous and can constitute a lush and quite species-rich cover, frequently including *Angelica sylvestris*, *Lychnis flos-cuculi*, *Caltha palustris* and *Cirsium palustre*. It is in this sub-community that *Calliergon giganteum* typically grows best, along with *Calliergonella cuspidata*, *Rhizomnium pseudopunctatum*, *Plagiomnium elatum*, *Campylium stellatum* and *Drepanocladus revolvens* ssp. *intermedius*. All of these mosses vary in prominence and relative abundance from season to season. The small area of wet fen beside Spiggot Hill has some notable species including *Carex lasiocarpa*, *C. limosa* at its only Malham site, and the moss *Cinclidium stygium* which has not been seen on North Fen for several decades.

The limited extent of this community on the North Fen and at Spiggot Hill underlines the importance of the belt of open rich-fen vegetation along the south-western lagg of Tarn Moss. This is very varied, but much of it is best placed in the *Campylium-Scorpidium* sub-community of the *Carex rostrata-Calliergon* mire (M9a). A variety of sedges occur, frequently including *Carex panicea*, *C. lepidocarpa*, *C. nigra* and *C. echinata*. Herbaceous associates tend to be rather sparse, giving the vegetation a rather open look. *Menyanthes trifoliata* and *Potentilla palustris* are patchily abundant, but for the most part the community is made up of scattered individuals of such species as *Succisa pratensis*, *Equisetum fluviatile*, *Epilobium palustre*, *Ranunculus flammula* and *Pedicularis palustris*. Mosses are often prominent, forming an extensive patchwork round the bases of the vascular plants, with 'brown mosses' including *Campylium stellatum*, *Scorpidium scorpioides*, *Drepanocladus revolvens* ssp. *intermedius*, *Calliergon* spp. and Mniaceae frequent throughout the ground layer. Wet spots support aquatic plants such as *Potamogeton polygonifolius*, *Juncus bulbosus* and *Utricularia neglecta*. Where the lagg fen abuts the neighbouring pasture on limestone drift, the occurrence of *Primula farinosa*, *Parnassia palustris*, *Pinguicula vulgaris Carex dioica* and *Eleocharis quinqueflora* marks the transition to the *Pinguicula vulgaris-Carex dioica* mire (M10), which occurs much more extensively on limestone and calcareous drift east of the Tarn, as on Ha Mire, Great Close Mire and near Mastiles Bridge. Several of these species recur, along with patches of the moss *Philonotis calcarea*, in an interesting area close to the Tarn edge in East Fen, possibly indicating an upwelling of calcareous groundwater.

In West Fen, the regular deposition of nutrient-rich silt along the banks of the stream and the inwashing of silt around the fen margins has favoured the growth of the *Filipendula ulmaria-Angelica sylvestris* mire (M27). The dense waist-high stands (which die down to the ground in winter) are overwhelmingly dominated by *Filipendula ulmaria*, with a suite of other tall herbs which are able to grow up through the canopy, and are a particularly prominent feature of the *Valeriana officinalis-Rumex acetosa* sub-community (M27a). The commonest species of this group on the Fen are *Angelica sylvestris*, *Rumex acetosa*, *Lathyrus pratensis*, *Valeriana officinalis* and, strikingly around the margins of West Fen, *Cirsium helenioides*. Although not typical for the community nationally, at Malham there is often a lower-growing herb layer with occasional *Geum rivale*, *Ranunculus repens*, *Cardamine pratensis*, *Chrysosplenium oppositifolium*, *Mentha aquatica*, *Myosotis scorpioides*, and more towards the woodland margin *Alchemilla glabra* and *Geranium sylvaticum*. Within individual stands on North Fen, *Carex acutiformis*, *Phalaris arundinacea* or *Phragmites australis* may appear as conspicuous components of the vegetation, but the essential composition of the community is otherwise little changed. Downstream from West Fen bridge, the *Filipendula ulmaria* fringe along the stream thins out, and in Middle and East Fen it becomes sparse and fragmentary.

The most extensively-developed kind of rich-fen vegetation on the North Fen is the *Sanguisorba officinalis* sub-community of the *Molinia caerulea-Crepis paludosa* mire (M26a). This kind of vegetation is intermediate between the swamps and mires on the one hand, and damp mesotrophic grasslands on the other. Traditionally it would have been managed as fen meadow, and it may owe much of its present character to that. Much the most extensive stands are on West Fen, where the *Molinia-Crepis* mire covers the broad zone between the swamp and tall-herb communities fringing the stream and fen margin, and the relic areas of acid peat.

The *Sanguisorba officinalis* sub-community is structurally dominated by the major graminoid species within the stand, usually *M. caerulea*, although at Malham this can be wholly or partly replaced by *Carex nigra* (in an unusual tussocky form, var. *subcaespitosa*), or in particular situations by other species. The strongly tussocky sedge *Carex appropinquata* is dominant locally close to the inflow stream; there are also several patches of *Carex lasiocarpa*, probably marking the position of former pools. Herbs capable of moderate to tall growth among the tussocky dominants are an important component of the vegetation. Most frequent on the North Fen are *Succisa pratensis*, *Angelica sylvestris*, *Valeriana dioica*, *Filipendula ulmaria*, *Sanguisorba officinalis*, the continental northern *Crepis paludosa* and the northern montane *Trollius europaeus* – these last two adding a distinctive regional look to the vegetation. Less frequent associates include *Equisetum palustre*, *Parnassia palustris*, *Serratula tinctoria*, *Anemone nemorosa*, *Ranunculus auricomus*, *Dactylorhiza purpurella* and *Cirsium palustre*. Bryophytes are much less prominent than in the *Carex rostrata-Calliergon* mire (M9), and the common rich-fen 'brown mosses' are sparse or absent. The commonest species are the ubiquitous and shade-tolerant *Calliergonella cuspidata*, *Rhytidiadelphus squarrosus*, *Eurhynchium praelongum* and *Lophocolea bidentata*, all common grassland plants. These are occasionally joined by *Plagiochila asplenioides*, *Campylium stellatum*, *Ctenidium molluscum*, *Rhizomnium pseudopunctatum*, *Aulacomnium palustre*, and in the more swampy areas *Campylium elodes*; a wide diversity of species occur in smaller quantities. There is a suite of herbs specifically associated with the more swampy areas where the big *Carex* species replace *Molinia caerulea*; the most frequent are *Lychnis flos-cuculi*, *Galium uliginosum*, *G. palustre*, *Potentilla palustris*, *Mentha aquatica* and *Equisetum fluviatile*.

Vegetation that clearly belongs to the *Molinia caerulea-Crepis paludosa* mire in its overall species composition can look very different in different situations or under different regimes of management. In the more eutrophic, cattle-grazed and slightly drier situation of Tarn Fen Meadow, the *Festuca rubra* sub-community (M26b) is rank and grassy and lacks *M. caerulea* altogether. At the other extreme, in the permanently wet, nutrient poor and undisturbed conditions along the north side of the main inflow stream in West and Middle Fen, stands which resemble swamp with large dominant tussocks of *Carex appropinquata* or *Carex nigra* also lack *M. caerulea*. Throughout, however, there is a solid block of frequent associates in common with the more typical forms of the two sub-communities. Part of the difficulty in deciding at what scale to define and describe the variation within the *Molinia-Crepis* mire arises because so few stands of this kind of vegetation remain in Britain with which to compare the floristics of the assemblages occurring at Malham.

Carr and woodland

Shrub and tree-dominated communities on the Tarn Moss and fen are of two main types. The fen carr mostly corresponds to *Salix pentandra-Carex rostrata* woodland (W3). Several of the low-lying areas of ombrogenous peat in the North Fen have become colonised by birch, forming locally extensive stands of *Betula pubescens-Molinia caerulea* woodland (W4). A narrow zone of woody vegetation round the margin of the West Fen (and fragments elsewhere) can be seen as a discontinuous fringe of *Alnus glutinosa-Urtica dioica* woodland (W6). Of the remaining wooded areas, Spiggot Hill appears as a plantation on the 1785-86 map; 'Horseshoe Plantation', round the end of West Fen, was planted in the 19th Century. The field layer of both approximates to that of the local (usually ash-dominated) *Fraxinus-Sorbus-Mercurialis* woodland (W9).

The *Salix-Carex* carr (W3) is extensively developed across the low-lying parts of the North Fen irrigated by calcareous water, and fragmentarily on Spiggot Hill fen. It has evidently originated by shrub invasion of various fen communities, including *Carex-Calliergon* mire (M9), *Molinia-Crepis* mire (M26) and *Filipendula-Angelica* mire (M27), as well as swamp communities dominated by *Carex appropinquata* that are no longer present in unwooded form on the fen. From photographic evidence and observation over the years (Ball, 1994), the carr is known to be expanding its area on the fen, but at different rates in different places. Some selective removal of developing carr is essential to maintain the more-open mire communities.

The *Salix pentandra-Carex rostrata* carr (W3) is a very distinctive woodland type with clear northern European affinities in its flora. The canopy is dominated by a low (3-6 m), often uneven-topped cover of bushy willows, here mainly *Salix pentandra* and S. *phylicifolia*, with some *S. cinerea* and a little *S. nigricans*; the last three species hybridise freely, so the exact identification of individual bushes can sometimes be difficult. The canopy tends to open up with age, the low spreading branches of *S. pentandra* often reaching down to the ground and re-rooting; older areas of carr are often a near-impenetrable tangle.

The composition of the field layer is closely related to that of the preceding fen vegetation. Indeed, there is little that is uniquely distinctive about the herbaceous element of the understorey, many of the fen species being somewhat shade-tolerant so that they continue to survive under the relatively open canopy. The taller broad-leaved herbs are generally the most prominent component of the field layer. The commoner species include *Filipendula ulmaria*, *Angelica sylvestris*, *Valeriana officinalis*, *Geum rivale*, *Cirsium palustre*, and *Succisa pratensis*. Of more distinctively northern species, *Crepis paludosa* is frequent, and *Trollius europaeus* is locally conspicuous when it flowers in early summer. Shorter herbs, including *Caltha palustris*, *Lychnis flos-cuculi*, *Ranunculus repens*, *Mentha aquatica* and *Potentilla palustris* form a patchy lower tier to the vegetation. Although various grasses and a range of *Carex* species can be found within this community, in the stands sampled *C. rostrata* and *C. appropinquata* are the only frequent monocotyledonous associates, and are locally abundant. The remaining striking feature of the community is the abundance of large bryophytes which in some stands form a virtually continuous carpet over the ground. The most conspicuous and abundant species include *Calliergonella cuspidata*, *Calliergon cordifolium*, *Climacium dendroides* and various large Mniaceae, especially *Plagiomnium ovatum* and *Rhizomnium punctatum*.

The *Sphagnum* sub-community of the *Betula pubescens-Molinia caerulea* woodland (W4c) is most extensive on the islands of acid peat across the North Fen, but also occurs locally along the northern side of the Spiggot Hill lagg and at the northeastern tip of Tarn Moss by the main outflow. Without continual removal of young birches on the open area of *Calluna-Eriophorum* mire (M19a) in East Fen, the extent of this woodland would undoubtedly increase rapidly. The canopy is dominated by *Betula pubescens*, with a little *Salix cinerea* in the shrub layer. The field layer is typically species poor, with *Molinia caerulea* and variable amounts of *Eriophorum vaginatum* amongst a prominent carpet of sphagna. The most conspicuous associated vascular plants are the ferns *Dryopteris dilatata* and *D. carthusiana*, thinly scattered through the field layer, especially around the drier tree bases. The commonest sphagna are three rather base-tolerant species, *Sphagnum palustre*, *S. recurvum* and *S. fimbriatum* (which fruits freely in summer), often accompanied by tall patches of *Polytrichum commune*; *Sphagnum russowii* is frequent locally. Around the margins of the acid peat areas, where the irrigating waters become more base rich, *Sphagnum squarrosum* often becomes dominant in the ground layer, and is highly diagnostic of this transition zone, where the surface pH is around 5.8.

Alnus glutinosa-Urtica dioica woodland (W6) is restricted to the northern margins of West and Middle Fen, where it forms a narrow zone on silty soil between the *Filipendula-Angelica* mire (M27) and the perimeter woodland formed by the *Crepis paludosa* sub-community of the *Fraxinus-Sorbus-Mercurialis* woodland (W9b). Here it has a canopy of *Alnus glutinosa* or *Salix* spp. over a species-poor field layer overwhelmingly dominated by *Urtica dioica*. The most frequent associates are *Poa trivialis*, *Galium aparine*, *Filipendula ulmaria* and *Silene dioica*, with

TABLE 2. *The composition of some natural waters in the Malham Tarn National Nature Reserve expressed in micro equivalents per litre (meq.l⁻¹).*

	pH	Ca^{2+}	Mg^{2+}	K^+	Na^+	Cl^-	SO_4^{2-}	NO_3^-	NH_4^+	HCO_3^-
Rainwater (1986-1988)	**4.51**[1]	**27**[2] **[13.5]**	**24**	**[7.1**[3]**]**	**98**	**124**	**60**	**22**	**28**	**0**
[relative to Cl^-]	-	.218[3] [.109]	.194	[.057]	.790	1.000	.484	.177	.226	.000
Tarn Moss (1992-1995)	**3.94**	**32**	**48**	**9.8**	**167**	**179**	**123**	**2**	**[3.8**[4]**]**	**0**
[relative to Cl^-]	-	.179	.268	.055	.933	1.000	.687	.011	.021	.000
North inflow (1992)	**7.51**	**2920**	**57**	**10.3**	**196**	**218**	**139**	**64**	**-**	**2790**
[relative to Cl^-]		13.4	.261	.047	.899	1.000	.638			

1 from mean H^+ concentration of rainwater.
2 includes a very high and probably atypical value from 1986; the bracketed figure is the mean for 1987-88.
3 mean from 7 sites in northern England; for authors see Proctor (1992).
4 mean Dec. 1993-Nov. 1994.
- indicates not determined or not applicable

an underlayer of *Ranunculus repens*. The abundance of *F. ulmaria* is unusual for this community, but is simply a reflection of the close proximity of the *Filipendula-Angelica* mire. Locally, usually by fallen trunks, there may be bare areas of mud with occasional *Caltha palustris* and *Ranunculus repens* dominating the field layer. Some stands, with low-growing herbs such as *Geum rivale* and *Mercurialis perennis* frequent in the field layer are transitional to the adjacent *Fraxinus-Acer-Mercurialis* woodland (W9b). Bryophytes are limited to straggly mats of *Calliergonella cuspidata*, *Brachythecium rutabulum* and *Eurhynchium praelongum*.

ENVIRONMENTAL FACTORS, PLANT GROWTH, AND VEGETATION

Cation concentrations and pH

The most striking contrast within the vegetation is that between the acid raised-bog areas and the calcareous fens that surround them. This reflects the very great contrast in the character of their water and solute inputs (Fig. 6; Table 2) (Proctor, 1995b). The ombrotrophic bog areas are fed directly by rainwater, with some additional contribution of solutes from dry deposition of gases and dust from the atmosphere, and some input of material by the movements of animals (Proctor, 1992, 1994, 1995a). The fen areas are fed by water issuing from springs at the base of the limestone to the north, or draining from the calcareous drift to the south; most of the solutes in this water come from the rocks and mineral soils though which it has flowed. Table 3 summarises chemical analyses of surface water samples from a number of different communities in 1992.

The mean total ionic concentration of rainwater at Malham Tarn is about 400 µeq.l⁻¹ (UKRGAR, 1990)[2], and the mean total ionic concentration of surface water on the raised bog

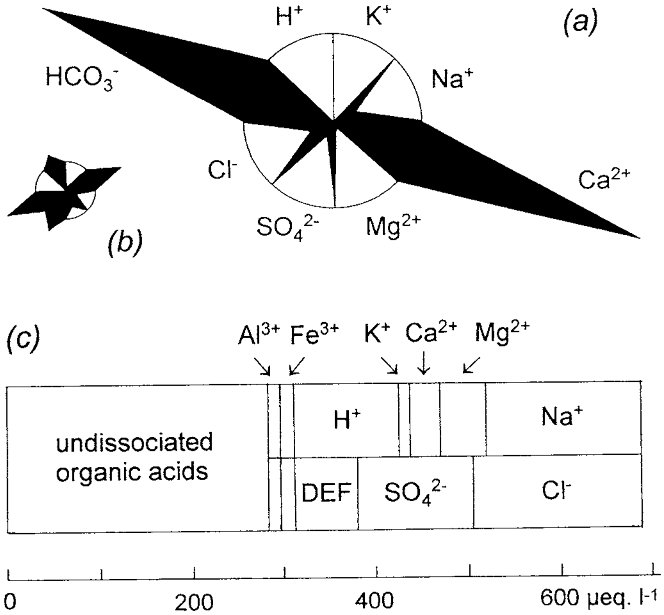

FIG. 6. *(a, b)* Maucha diagrams of two contrasted natural waters at Malham Tarn. *(a)* Mean composition of water in the North Inflow stream, Mar.-Dec. 1992. *(b)* Mean composition of water samples from Malham Tarn Moss, Mar.-Dec. 1992. *(c)* Block diagram illustrating the solute composition and ionic balance in water on Malham Tarn Moss. The major inorganic ions are from the same data as (b); aluminium (measured in Nov. 1992 samples) and iron are mainly complexed with dissolved organic matter. The undissociated organic acids were estimated by titration, on samples collected in Aug. 1996.

from March 1992 to December 1995 was about 550 $\mu eq.l^{-1}$. The average concentration of calcium in raised-bog water over this period was about 27 $\mu eq.l^{-1}$ (0.54 mg l^{-1}) but, as Fig. 7 shows, the concentration varied substantially with varying rainwater composition and changing balance of precipitation and evaporation. Magnesium exceeded calcium when calculated on a molar or equivalent basis, with a mean concentration of 39 $\mu eq.l^{-1}$ (0.47 mg l^{-1}). Potassium was generally found at lower concentrations than either of these elements, averaging 8.8 $\mu eq.l^{-1}$ (0.34 mg l^{-1}), but was very variable, reflecting its major role as an essential element for both plants and animals and its rapid biological turnover. Sodium, by contrast, is the dominant metallic cation, and was the least variable (mean 143 $\mu eq.l^{-1}$; 3.29 mg l^{-1}). The average pH of rain at Malham Tarn from 1986-88 was about 4.5; the 1992-95 average pH of surface water on the Tarn Moss was about 4.0 ([H^+] *ca* 100 $\mu eq.l^{-1}$). The acidity of raised bogs arises mainly from the organic acids produced by the plants, especially the polyuronic acids of the cell wall materials of *Sphagnum* and other plants; the organic acid groups of the peat give it a high buffering capacity.

Water in the springs and streams entering the Tarn basin is close to saturation with calcium bicarbonate, or more strictly, the calcium concentration determined by the carbonate/bicarbonate equilibrium and the solubility product of calcite (Stumm & Morgan, 1981; Pentecost 1981, 1992). It has a total ion content of 6,000-10,000 $\mu eq.l^{-1}$, and an average calcium concentration of *ca* 3,000 $\mu eq.l^{-1}$ (60 $mg.l^{-1}$). The Carboniferous limestone north of the Tarn is remarkably pure calcium carbonate, and over half of the magnesium in

[2] For convenience of reference, we have retained the old term 'equivalent', still widely used in environmental chemistry, in this context corresponding to (and numerically identical with) the mole of ionic charge.

TABLE 3. *Median concentrations of ions (μeq.l⁻¹) in surface waters associated with different plant communities at Malham Tarn NNR, from six sampling occasions, 28th March, 26th May, 24th July, 4th September, 16th November and 18th December 1992.*

Community and site	pH	Ca^{2+}	Mg^{2+}	K^+	Na^+	Cl^-	SO_4^{2-}	NO_3^-	HCO_3^-
Raised bog, (M18/19): Tarn Moss NE	4.08	19	28	8.1	140	155	46	0.0	0
Raised bog, (M18/19): Tarn Moss S	3.96	21	33	6.2	137	152	69	0.6	0
Peat pit in poor fen (M6) with *Carex curta* and *C. nigra*, Middle Fen	4.68	86	26	1.3	119	138	28	0.1	0
Birch-Molinia wood (W4) on acid peat, with *Sphagnum fimbriatum* etc., Middle Fen	4.00	141	44	8.9	185	222	69	0.0	0
Carex diandra–brown-moss fen (M9), East Fen	6.90	2122	48	20.9	208	234	96	0.6	1886
Carex diandra–brown-moss fen (S27/M9), Spiggot Hill fen	6.79	2153	110	9.4	521	580	228	23.1	1960
Wet calcareous fen in old peat pit (nr M9), with *Sphagnum teres*, *S. warnstorfii* etc., West Fen	6.66	1275	37	4.7	399	438	113	0.1	1045
Molinia-Crepis paludosa fen meadow (M26), West Fen	6.67	2267	56	3.3	585	536	241	1.75	2200
Salix pentandra-S. phylicifolia fen carr (W3), East Fen	6.89	2362	50	21.0	214	226	89	1.1	2049

these calcareous waters is of marine origin, brought in (with the sodium) by rain. The dominant anion is bicarbonate, and the pH of the water is determined by the carbon dioxide-bicarbonate equilibrium (Golterman, Clymo & Ohnstad, 1978; Stumm & Morgan, 1981). In well-aerated springs, pH is between 7 and 8, but the pH of water amongst the fen plants is often below 7 because of the high concentration of carbon dioxide from respiration. The bicarbonate acts as a buffer, tending to maintain a near-neutral pH; its effectiveness is greatly increased if solid calcite is also present.

The anions

The positively-charged cations are balanced by negatively-charged anions. In ombrotrophic-bog waters the predominant inorganic anions are generally chloride and sulphate. The chloride is of marine origin. Some sulphate also comes from seawater, the remainder from sulphur dioxide emissions from the burning of fossil fuels. At Malham, this 'non-marine sulphate' accounts for about 85% of the total. Sulphur is an essential element

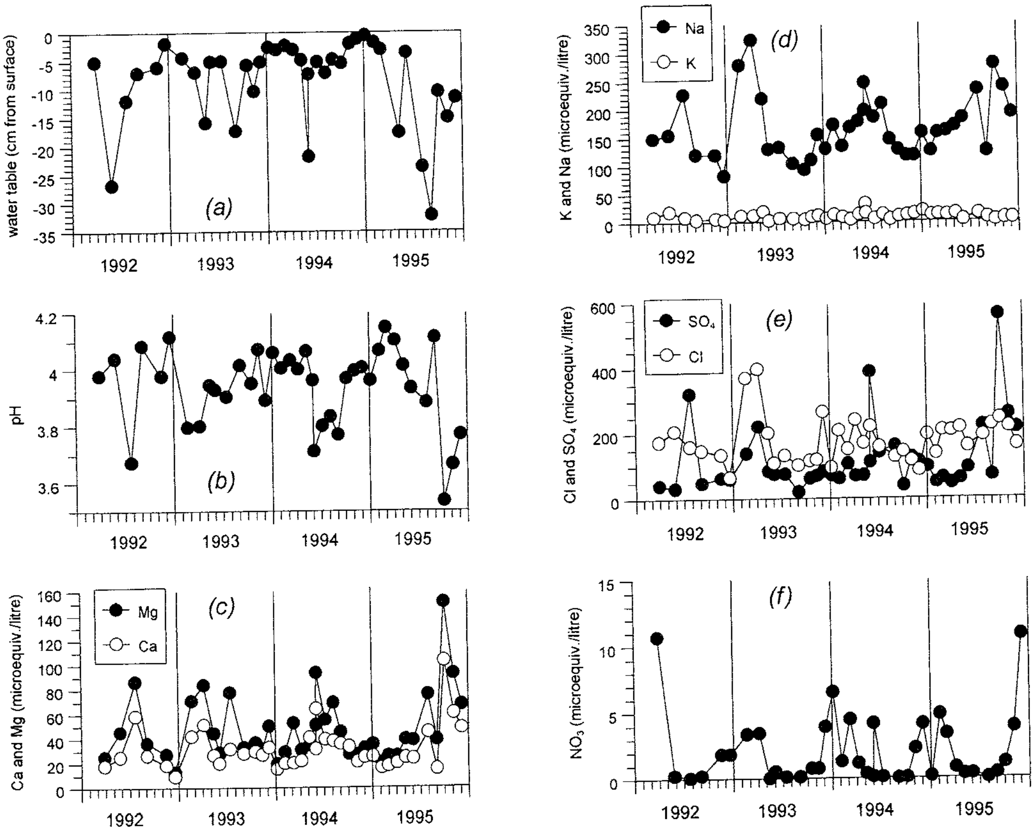

FIG. 7. Water levels and concentrations of major ions in surface-water samples from Tarn Moss, 1992-1995. (a) Water level; (b) pH; (c) calcium and magnesium; (d) sodium and potassium; (e) chloride and sulphate; (f) nitrate. All the cations tend to show higher concentrations during dry periods and in summer; note the peak in sodium, chloride and other ions following high input in rain during a stormy period in February and March 1993. Sulphate shows high peaks coinciding with sharp falls in pH after periods of low water level as in June 1992, July 1994 and October 1995. Nitrate appears in significant amounts only during cold periods in winter or immediately after rain.

for plant growth but in Britain is rarely limiting. It is important ecologically for the oxidation-reduction transformations that sulphate and sulphide undergo. A substantial part of the sulphate deposited on an ombrogenous bog is reduced to sulphide in the waterlogged peat (Gorham, Eisenreich, Ford & Santelmann, 1985), where it may accumulate in the organic matter or as insoluble iron sulphides (Brown, 1985, 1986; Brown & Macqueen, 1986). If the water level falls during a dry summer, sulphide can be oxidised back to sulphate, resulting in a flush of sulphuric acid in the drainage water following subsequent rain. This was well shown on the Tarn Moss by the peak in sulphate and the sharp fall in pH that followed the dry summer of 1992, and even more strongly after the prolonged drought of 1995 (Fig. 7).

Rainwater at Malham Tarn contains on average about 22 μeq.l^{-1} of nitrate (UKRGAR, 1990), but this ion is rapidly taken up by organisms and it is unusual for more than trace amounts to appear in surface water on the Tarn Moss except during cold periods in winter. The fate and transformations of nitrogen are discussed further below.

On ombrotrophic bogs, the sum of the negative charges of the inorganic anions is generally substantially less than the sum of the positive charges of the cations. The difference, the 'anion deficit', is made up by the negative charges carried by the ionised acidic groups of the dissolved organic matter, which may amount to 20% or more of the total anionic charge (Urban, Bayley & Eisenreich, 1989; Proctor 1995a).

In the calcareous waters, the dominant anion is bicarbonate, which roughly balances calcium. Chloride and sulphate are also present, in rather higher concentrations than on the Tarn Moss, but making up only a modest proportion of the whole. They are generally in roughly the same proportions as in rainwater, and roughly balance the cations from the same source. As in bogs, sulphate may be reduced to sulphide under waterlogged conditions, and sulphide oxidised back again to sulphate when the water level falls. Usually the high concentration of bicarbonate will prevent violent changes in pH, but the sulphate produced in the dry summer of 1992 was sufficient to replace most of the bicarbonate in some sites on the fen (Proctor, 1995b).

Water and peat chemistry and plant nutrition

Among the major ions just considered, Ca^{2+}, Mg^{2+}, K^+, SO_4^{2-} and NO_3^- (or NH_4^+) are essential for plant growth. Because such striking vegetational differences are associated with the contrast between acid, base-poor soils and bog peats on the one hand and near-neutral calcareous soils and fen peats on the other, it is often assumed that calcicole species have a high nutritional requirement for calcium. To some extent this is undoubtedly true, but its nutrient role is easily overemphasised. As the dominant metallic cation in limestone and other basic rocks, calcium also has an important role in determining the cation:anion balance and hence the pH of soils and peats, and through this the form and availability for plant uptake of many other ions. The part it plays in calcicole-calcifuge relationships may, therefore, often be secondary. Magnesium is probably here always present in ample quantity. Potassium is required in large amounts by plants; calculations suggests that uptake during the growing season might substantially deplete the surface layers of the peat, and there is some indication from water analyses that this may sometimes happen. But potassium is a very mobile element, and it seems seldom to be limiting under the conditions on the Tarn Moss and fen.

Two elements certainly important in limiting growth are nitrogen and phosphorus. Aerts, Wallén & Malmer (1992) showed that *Sphagnum* growth in a bog in Swedish Lapland, with a rainwater nitrogen input of only 0.06-0.20 g N m^{-2}y^{-1}, was limited by nitrogen availability, whereas in a raised bog in south Sweden, with a corresponding annual nitrogen input of 0.7-0.9 g N m^{-2}y^{-1}, growth was limited by phosphorus. At Malham Tarn, the total wet deposition of nitrate + ammonium nitrogen is *ca* 0.9 g m^{-2}y^{-1}, suggesting that here too we should expect phosphorus to be limiting; nutrient-addition experiments with a range of species on Malham Tarn peats bear this out (MCFP, unpublished). In particular, phosphorus availability is a critical factor determining the luxuriant growth of *Filipendula ulmaria* and *Geum rivale* around the margins of the fen and along the silted banks of the inflow streams. Nitrate and ammonium deposited from the atmosphere or released by mineralisation are rapidly taken up by plants or microorganisms, so concentrations in surface water are usually very low (but highest in winter). Phosphate is also generally taken up as soon as it is mineralised, so it is rare for the concentration in surface-water samples to exceed 1 μeq.l^{-1}, and it is often undetectable.

Measurements in 1992 showed nitrate constantly present at concentrations between 38 and 130 µeq.l^{-1} in the two main inflow streams (which are inflows *to* the Tarn but drain *from* the bog and fen as well as from the surroundings). The calcareous peats (and the surrounding grasslands) would be expected to be nitrifying, at least in their aerated upper layers; the acid peats would not (Lee & Stewart, 1987; Dickinson, 1983), and in general this is so. An indication of the rate at which nitrate is being utilised is given by the activity in the plant of the enzyme nitrate reductase (Stewart, 1993). Leaves of plants on the fen generally show substantial activity (median 0.62 nkat g[FW]$^{-1}$), whereas plants on the raised bog show generally show little or none (median 0.03 nkat g[FW]$^{-1}$). The highest activities on raised-bog peat were shown by *Molinia caerulea* on the rand at the north edge of Tarn Moss (0.11 nkat g[FW]$^{-1}$), and birch around the peat ponds on the Middle Fen (0.40 nkat g[FW]$^{-1}$. The usual assumption is that most plants on acid peats take up their nitrogen as ammonium ions, but mycorrhizal species such as *Calluna vulgaris* acquire organic nitrogen through their fungal symbionts (Read, 1991), and Chapin, Moilanen & Kielland (1988) have shown that the non-mycorrhizal *Eriophorum vaginatum* may take up nitrogen largely in the form of free amino acids. *Sphagnum* species show substantial nitrate reductase activity, and apparently obtain nitrogen largely from rainwater nitrate (Press & Lee, 1982; Woodin, Press & Lee, 1985; Press, Woodin & Lee, 1986; Rudolph & Voigt, 1986).

Ombrotrophic peats typically have low bulk densities, in the region of 0.05- 0.10 (Table 4), and a very low ash content (Proctor, 1974). Bulk densities and ash contents of fen peats are typically higher, but over much the Malham fen this difference is not great. This is probably partly because the many of the fen peats have grown quickly since the Tarn water level was raised in 1791, and partly because there has been little silt input over much of the site. The C/N and C/P quotients of the peats give some measure of the long-term availability of N and P in the communities growing on them.

Water levels, seasonal changes and oxidation-reduction processes

It is characteristic of bogs and fens that the water table is high, and the peat waterlogged, for much or most of the year. Some differences in the vegetation of the Tarn Moss and fens reflect differences in water level, but much of the variation in vegetation is accompanied by little difference in water levels. Except for dry periods in summer, the Tarn Moss and fens are wet enough to call for gumboots almost everywhere, but only some of the peat pits and fringing *Carex* swamps would need waders. Almost the whole of the area shows substantial variations in water level with the seasons and with changing weather. These variations are least close to the Tarn, and greatest in the immediate vicinity of the main inflow streams, and around the margins of the fen. The changing balance of precipitation and evaporation with the seasons is one of the factors influencing the concentrations of solutes in mire waters, and there is some tendency for all to be higher in summer than in winter. Other factors are important too, including varying solute concentrations in rainwater, and non-seasonal variations in weather. Because peat acts as a cation-exchange medium, and the quantities of cations held on the exchange sites are generally much greater than those in the water, changes in the different cations are closely linked. Thus a large input of, e.g., sodium in rain will result in peaks in surface-water concentrations of other cations (including H^+) as well.

Waterlogging results in depletion of oxygen, so that conditions become anaerobic and reducing. As water level falls, the surface layers of the peat become aerated, and oxidising conditions return. A number of important chemical processes in soils and peats are sensitive to 'redox' changes of this kind. Even mildly reducing conditions suffice to reduce nitrate to ammonium, and to bring manganese into solution as Mn^{2+}. More strongly reducing conditions are needed to reduce ferric to ferrous iron, and stronger again for the reduction

TABLE 4. *Bulk density, total carbon content, C:N and C:P quotients of peats at Malham Tarn NNR.*

Site	bulk density kg dm^{-3}	total C %DM	C:N quotient	C:P quotient
South raised bog (i) (M18/19)	0.106	46.4	32.4	1034
South raised bog (ii) (M18/19)	0.077	43.1	30.6	678
Northeast raised bog (M18/M19)	0.150	44.4	31.7	2041
	0.077	45.8	43.9	1188
Raised bog N of main inflow (M18/M19)	0.104	45.6	27.9	991
	0.106	47.5	33.2	963
M6 with *Carex curta*, East Fen	0.082	41.8	28.0	525
	0.106	45.6	25.9	684
	0.068	44.4	25.4	453
M6 with *Carex curta*, Middle Fen	0.191	26.0	14.7	143
	0.212	35.3	15.7	275
	0.121	46.1	20.1	368
M9, East Fen	0.064	40.7	17.6	324
	0.062	40.3	22.3	421
M9/M10, East Fen	0.071	43.7	19.4	480
M10, South Lagg	0.110	37.4	17.3	305
M26 *Molinia caerulea-Crepis paludosa* mire,	0.147	34.2	15.0	329
West Fen	0.120	46.1	17.4	360
	0.167	34.5	14.5	288
M27 *Filipendula ulmaria*, Spiggot Hill lagg	0.473	14.8	12.9	185
M27 *Filipendula ulmaria*, West Fen gate	0.319	16.4	13.5	107
	0.672	8.4	10.7	65
M27 *Filipendula ulmaria*, West Fen bridge	0.262	23.1	14.0	167
	0.287	22.7	13.1	171
W3 *Salix pentandra-Carex rostrata* carr	0.103	52.9	23.8	437
	0.233	22.2	13.2	125
	0.150	38.1	16.3	271
W4 *Betula pubescens-Molinia caerulea*	0.084	47.1	25.2	525
woodland	0.117	46.8	21.1	602

of sulphate to sulphide or the production of methane from organic matter. Many of these transformations are mediated by peat microorganisms.

A measure of the level of oxidising or reducing conditions is provided by the *redox potential* measured between a standard electrode and a platinum electrode (Pearsall, 1938; Armstrong, 1982; Stumm & Morgan, 1981), which reflects the state of chemical equilibrium between oxidants and reductants in the water or peat. Redox potentials are expressed in millivolts relative to the standard hydrogen electrode (or as pe values, analogous to pH, obtained by dividing this potential by 54-58 mV, depending on temperature). Practical measurements are usually made with a saturated calomel reference electrode, which has a potential of about +250 mV relative to the hydrogen electrode. A fully aerated soil or water usually gives a potential of about +500 mV; a near-zero or negative value implies strongly reducing conditions. Redox changes are not abrupt; chemical equilibria shift progressively over a range of redox potential. Redox processes involving exchanges of hydrogen ions as well as electron transfer are sensitive to pH; equilibrium moves in favour of many common

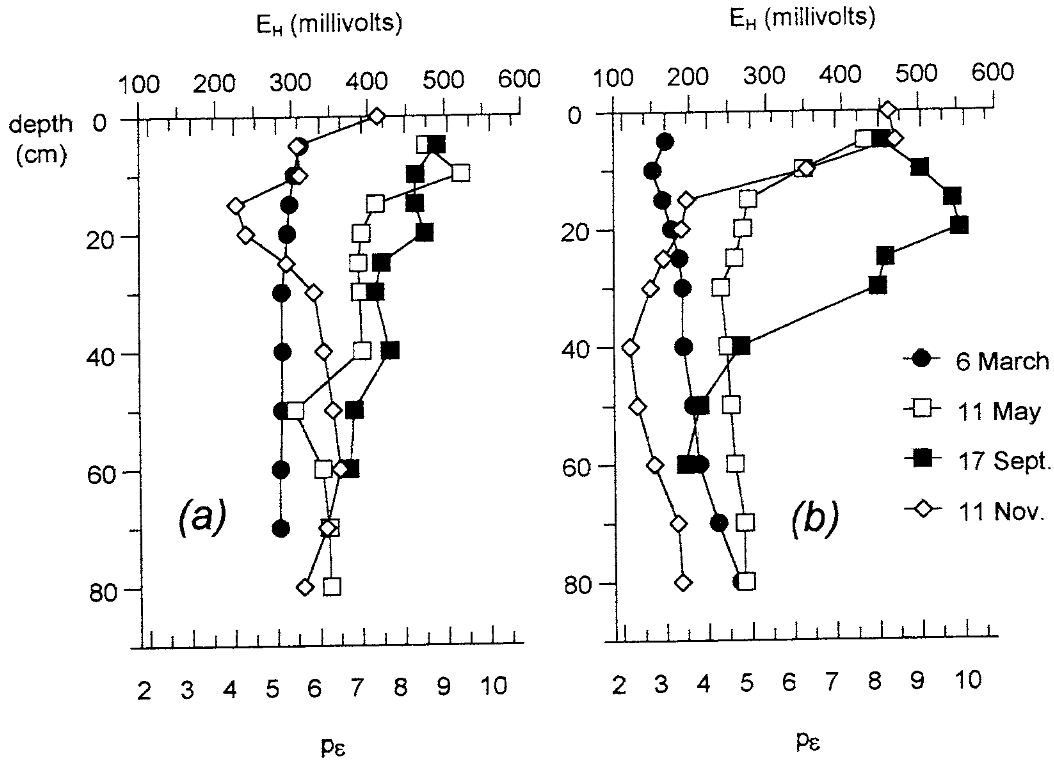

FIG. 8. Profiles of redox potential, (a) in Tarn Moss, north of Spiggot Hill (pH approx. 4.0); (b) in wet fen (M9) by boardwalk below Sandhill (Miss Hilary's) Cottage (pH approx. 6.5). The measurements on 6 March 1995 came at the end of an exceptionally wet winter, and both profiles are reducing throughout; somewhat higher E_H at the base of the fen profile is perhaps due to seepage of water from the substrate. By 11 May there had been several weeks of dry weather, water levels had dropped, and the surface layers had become oxidising. The summer was dry, and by 17 September oxidising conditions extended down to 30-40 cm. By 11 November, following a moderate amount of rain, both profiles were returning towards normal winter conditions. E_H in the Tarn Moss profile was generally higher than in the fen profile; as expected from the difference in pH between the sites.

reduction processes with falling pH. Thus a given redox potential implies generally more strongly reducing conditions in a bog at pH 4 than in a fen at pH 6.5. Some examples of redox profiles on the Tarn Moss and fens are given in Fig. 8.

Directions of variation, and vegetation patterns

Many of the chemical and physical factors of the bog and fen environment can be thought of in terms of three major directions of variation: (1) the height of the peat surface in relation to water level, (2) variation in cations (especially Ca^{2+}) and pH, and (3) the availability of the potentially limiting plant nutrients N and P. Of these, the first two have long been widely recognised in studies of mire vegetation (Sjörs, 1948, 1950; Malmer, 1986). The third has become widely recognised only in recent decades (Haslam, 1965; Wheeler, 1980a-c; 1983; Wheeler & Giller, 1982; Wheeler & Shaw, 1995).

The interplay of ombrogenous-bog surface water (or rainwater falling directly on the vegetation), and the groundwater of the surrounding limestone country, underlies much of the pattern of vegetation in the Malham Tarn fens. Calcareous groundwater emerges in a line of springs and seepages along the foot of the limestone escarpment north of the Tarn. Springs emerge below water level along the north shore of the Tarn, and, farther east, below Great Close Scar, feeding a small stream running into the northeast corner of the Tarn and the upper parts of Ha Mire and Great Close Mire. The lower-lying parts of the Malham Tarn fens are flooded when the inflow streams are in spate, but never deeply; water can be ankle deep over the boardwalk near the West Fen bridge, and can sweep through the fen carr and wet fen below Sandhill Cottage. Much of the fen is above flood level, and water-chemistry suggests that parts at least of the northern edge may be fed largely by diffuse seepage from the limestone (Proctor 1995b).

The calcareous water becomes progressively diluted by rain falling directly on the surface of the fen, and there is mixing where calcareous water meets water draining from ombrogenous peat. But in the absence of processes promoting active mixing, these different water sources tend strongly to preserve their identity, and gradients between them are often steep. There is indeed a zone of mixing around the ombrogenous peat areas, often marked by base-tolerant sphagna such as *Sphagnum palustre*, *S. squarrosum* and *S. recurvum*. However, this is usually narrow, and it is often noticeably impermanent in position and extent over the years. Rain-fed carpets of *Sphagnum* often extend over calcareous groundwater in this zone of transition. The tendency for *Sphagnum* to establish above the level of calcareous groundwater is widely evident even in extensive areas of calcareous fen. The most tolerant species of *Sphagnum* to calcareous water is *S. contortum*, but others commonly occurring in this situation are *S. palustre*, *S. subnitens*, *S. fimbriatum*, *S. squarrosum* and, more locally, *S. teres* and *S. warnstorfii*. During the growing season differences of several pH units can build up over a distance of only a decimetre or so between the surface of *Sphagnum* cushions and the surrounding calcareous water and peat (Fig. 9). This property is not unique to *Sphagnum*; similar pH contrasts can be found in patches of other bryophytes, such as *Rhizomnium pseudopunctatum*. The pH tends to rise again at least round the edges of the moss cushions during winter and early spring, but the process is one which may lead over a period of time to the replacement of calcareous fen by acid *Sphagnum* bog.

These spatial relationships, together with the chemistry of the buffering systems considered in Section 4.1, lead to a strong bimodality in water pH on the Tarn Moss and fens. There are large areas of bog with pH below 4.5, and of fen with pH above 6, but little in between (Fig. 10). The nutrient (N, P)-rich–nutrient-poor direction of variation is well displayed in the Malham Tarn fens, most strikingly in the belt of *Filipendula ulmaria*-dominated herb-rich vegetation fringing the inflow streams and northern edge of the fen. Growth experiments with *F. ulmaria* and *Geum rivale* on West-Fen peats suggest that this is determined primarily by availability of phosphorus.

This may be brought into the fen as stream-borne silt, as inwashed mineral material, or as leaf-fall from trees around the margins. If there is no substantial drain of nutrients by cropping of hay or grazing livestock, P will tend gradually to accumulate, and this must clearly have taken place in the development of the fen carr. A more subtle nutrient-related contrast is seen between the ombrogenous bog areas (M18/19) and the acid poor-fen areas (M6) on marginal or disturbed ombrogenous peat. In pot experiments, *Holcus lanatus* grows much better on peats under M6 than from those of the extensive raised-bog communities, although there is little or no difference in pH. The contrast is probably related to more rapid mineralisation of N in the M6 sites.

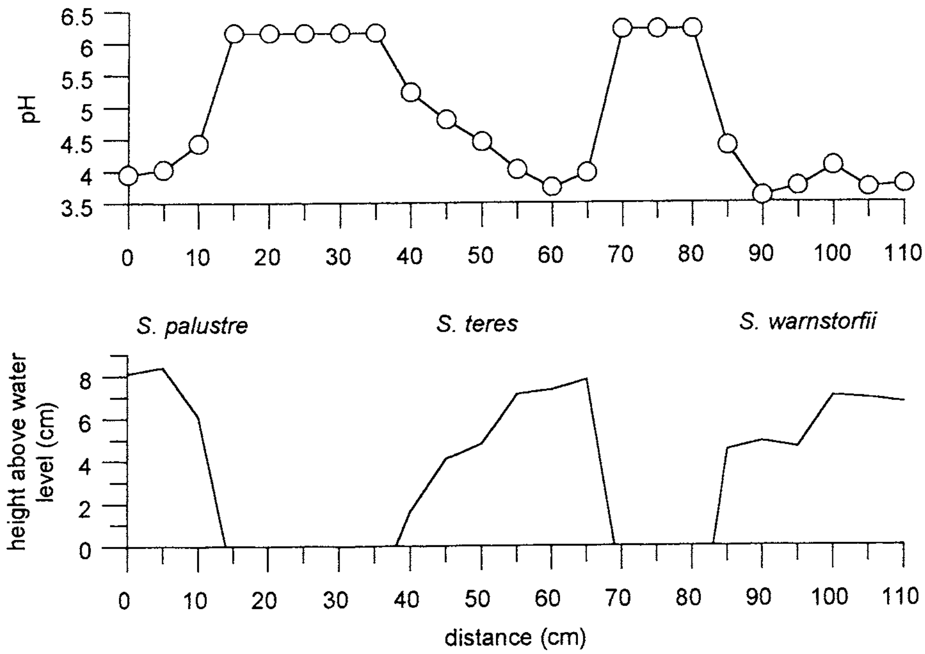

FIG. 9. Levelled profile across three *Sphagnum* hummocks in a wet calcareous area of the West Fen. The measurements were made at the end of the season in November 1995, following a dry summer.

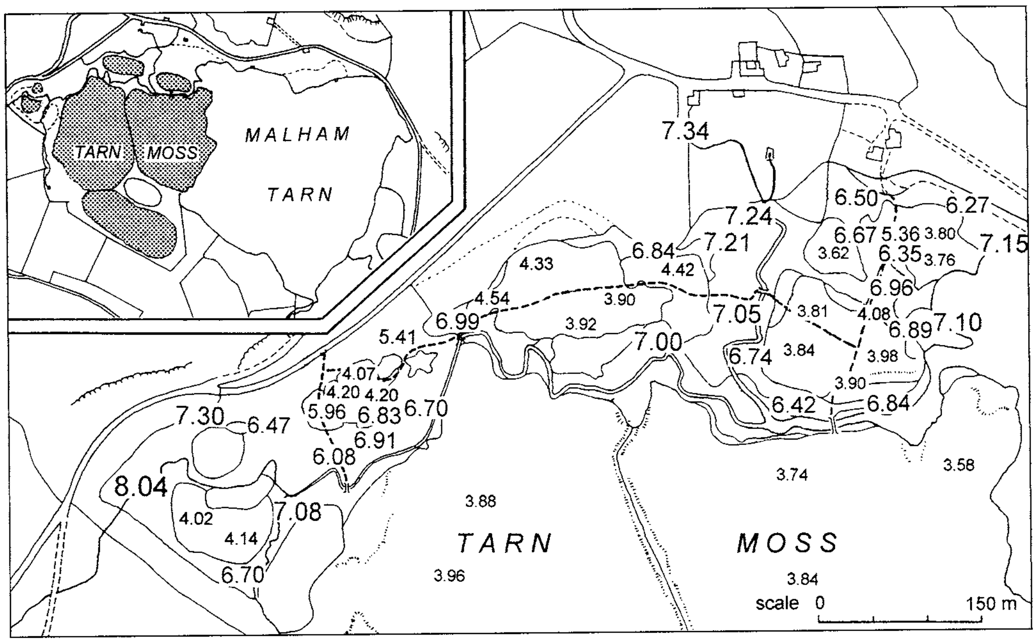

FIG. 10. Measurements of pH in surface water on the North Fen and northern part of Tarn Moss, 26-28 August 1994. The inset shows the approximate location of the larger areas of ombrogenous peat (shaded); there are more fragmentary areas of ombrogenous acid peat in the northern parts of East Fen and in West Fen.

SECCESSIONAL CHANGE, CONSERVATION AND MANAGEMENT

Vegetation succession on the Tarn Moss and fens

An extensive, diverse mire complex including a lake arouses expectations of zonations reflecting hydrosere succession. It is clear from the record in the peat that dramatic successional changes took place at Malham Tarn in the interval between the Late-Glacial period and the beginning of growth of the raised bog some seven thousand years ago, but by the time Neolithic and Bronze Age man had begun to clear the forest the Tarn Moss and its surroundings had settled to a pattern not greatly different from what we see now (Fig. 11). Vegetation succession can be seen as a process of ecosystem readjustment to changed conditions, leading towards a new position of stability. In those terms the large-scale succession in the Tarn basin was a response to the climatic and topographical upheaval of the last glaciation, and we are six or eight thousand years too late to see really spectacular hydrosere development and the zonations that went with it. The raising of the Tarn water level in 1791 set in train its own readjustments and initiated a good deal of small-scale succession along the inflow streams and in old peat diggings; in the Tarn itself it had the obvious (and intended) effect of putting back succession towards open water. There are indeed zonations around the mouth of the main inflow stream and elsewhere which are nicely illustrate the succession from open water to raised bog - in terms of NVC vegetation types, S9 S27 [M9] W3 W4 or M6[M25] M19 (see Table 1) - but these are now mostly short and steep and must be relatively stable.

Peat growth reflects the balance between production and breakdown of plant organic matter; in an actively growing bog or fen the rate of accumulation is commonly around 0.5-1 mm a year, representing some 10-20% of net primary production, but it requires only a relatively modest increase in the rate of breakdown for net peat growth to be zero.

The obvious successional change that *is* taking place rapidly at the present day is expansion of carr and birch wood over open fen and raised-bog peat. This is largely due to the relaxation of traditional farming practices. It is clear from the peat record that much of

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FIG. 11. Schematic diagrams of the zonation of vegetation types, (a) from open water to raised bog over a terrestrialised fen basin, and (b) from the open water on the shore of a lake to the uplands on the Carboniferous rocks of the country around Malham Tarn. Both diagrams show a sequence of tree-covered and a sequence of open communities. In general, under natural conditions the landscape would have been forested except for the swamps bordering the lake, limited areas of nutrient-poor fen, and the wet ombrogenous-bog vegetation of the raised bog and the blanket peats of the plateau. With the all-pervasive grazing of a pastoral hill-farming economy most of the forest is replaced by grasslands of various kinds; peat-cutting and surface drainage allow birch to become established on ombrogenous peats which under natural conditions would be largely treeless.

KEY TO VEGETATION TYPES.

Bog vegetation: M2, *Sphagnum cuspidatum* bog pool; M16, *Erica tetralix-Sphagnum compactum* wet heath; M18, *Erica tetralix-Sphagnum papillosum* mire; M19, *Calluna vulgaris-Eriophorum vaginatum* mire; M25, *Molinia caerulea-Potentilla erecta* mire.

Swamps, rich fens, and associated tall-herb vegetation: S9, *Carex rostrata* swamp; S27, *Carex rostrata-Potentilla palustris* swamp; M9, *Carex rostrata-Calliergon cuspidatum/giganteum* mire; M26, *Molinia caerulea-Crepis paludosa* mire; M27, *Filipendula ulmaria-Angelica sylvestris* mire.

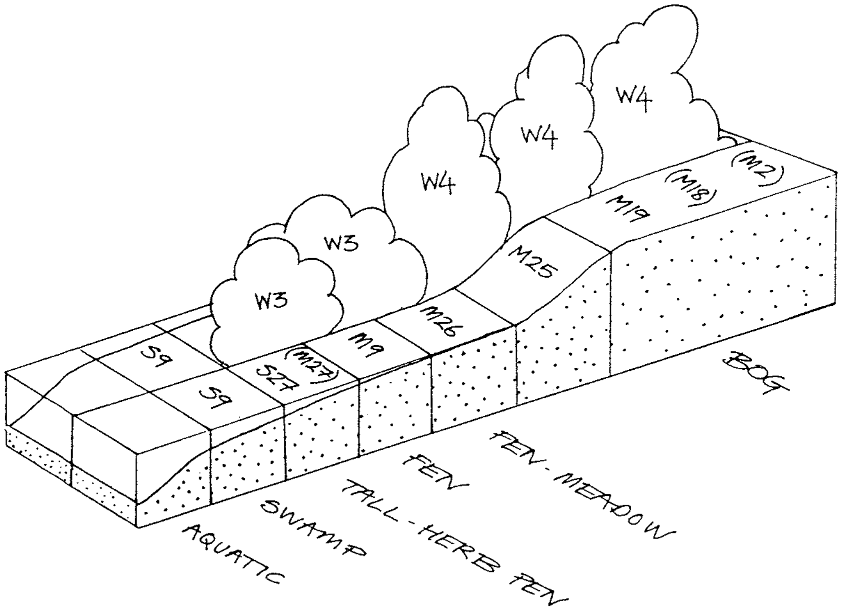
Grassland vegetation: CG9, *Sesleria albicans-Galium sterneri* grassland; CG10, *Festuca ovina-Agrostis capillaris-Thymus praecox* grassland; U4, *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland; U5, *Nardus stricta-Galium saxatile* grassland.

Fern-crevice vegetation: U22, *Asplenium trichomanes-A. ruta-muraria* community; U23, *Asplenium viride-Cystopteris fragilis* community.

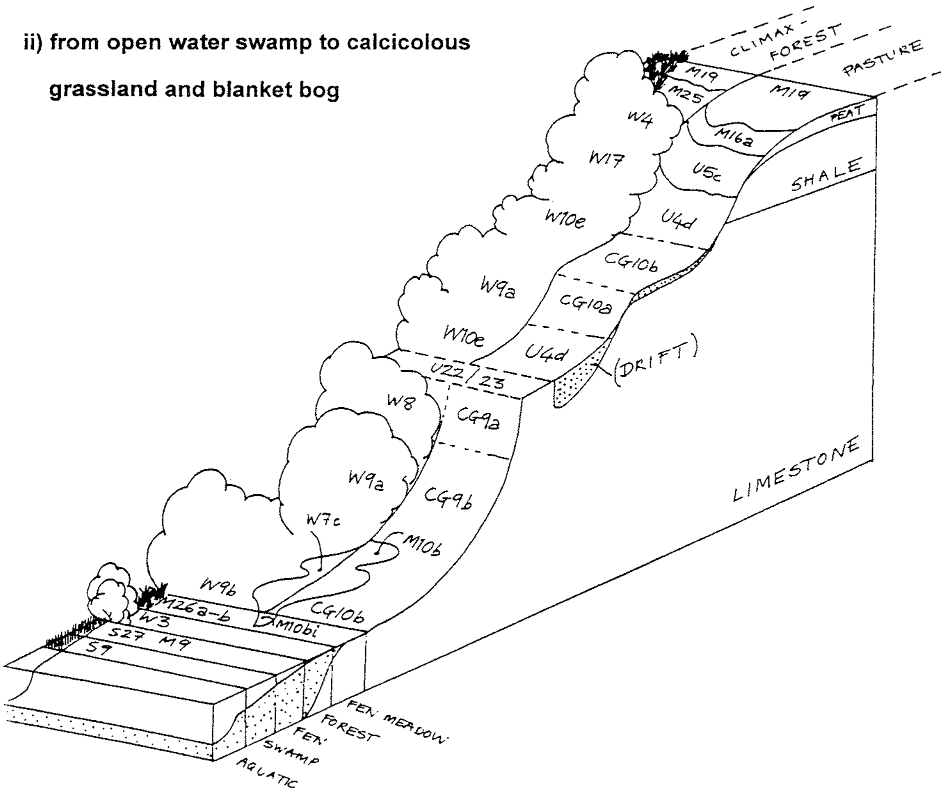
Woodland vegetation: W3, *Salix pentandra-Carex rostrata* woodland; W4, *Betula pubescens-Molinia caerulea* woodland; W7, *Alnus-Fraxinus-Lysimachia* woodland; W9, *Fraxinus-Sorbus-Mercurialis* woodland; W10, *Quercus-Pteridium-Rubus* woodland.

Schematic diagram of zonation of vegetation types:

i) from open water swamp to raised bog developed over fen basin



ii) from open water swamp to calcicolous grassland and blanket bog



the fen would naturally have been occupied by carr, yet in the late 1940s carr was limited to compact and evidently long-established areas beside the inflow stream in West Fen and close to the North inflow stream on the boundary of Middle and East Fen, fringes around the then much more patchy areas of birchwood on acid peat in Middle and East Fen, and scattered willow bushes elsewhere. Over the last 50 years carr has expanded almost everywhere, but at very different rates in different places (Ball, 1994). Carr colonisation has been rapid and very vigorous in East Fen, especially east of the boardwalk, where the area of open fen is now much less than in 1949, and most of what now remains depends on continual removal of colonising willow bushes. The growth and spread of carr has been slower in much of the Middle and (especially) West Fen, and in a small area of East Fen, perhaps spring fed, close to the Tarn edge. Here the willows are often small leaved, stunted and have grown only slowly. Why this is so is not entirely clear, but it probably reflects nutrient (especially phosphate) limitation and the time needed to accumulate the necessary nutrient capital for the bulky carr bushes. Very locally, examples can be seen of carr die-back, as at the eastern corner of the main acid peat area on East Fen, where a former patch of carr has succumbed to waterlogging and expanding growth of *Sphagnum*, a nicely illustrative picture of a process that took place widely when the *Sphagnum* peat of the Tarn Moss began to grow six or seven thousand years ago.

Some thoughts on the scientific and educational value of the Malham Tarn NNR

What do we value about the Malham Tarn reserve, and why? The most immediately obvious answer is that the reserve encompasses within a small area an extraordinarily wide diversity of species and habitats, many of them rare in the country as a whole. A small patch of sedge once thought to be *Carex flava* (known elsewhere in Britain only from Roudsea Wood in Cumbria) is now considered to be the hybrid *C. flava* x *lepidocarpa*, but remains interesting. There are many species at Malham Tarn which are rare in Britain as a whole, or which here are at or near the southern limit of their English range, such as *Crepis paludosa*, *Trollius europaeus*, the sedge *Carex appropinquata*, the grass *Calamagrostis stricta*, mosses including *Tomenthypnum nitens* and *Cinclidium stygium*, and the liverwort *Barbilophozia kunzeana*. There have been losses, and also new discoveries. The beautiful fen moss *Helodium blandowii* which once occurred at Malham Tarn in the highest of its few British localities has not been seen here (or anywhere else in Britain) for many years, and *T. nitens* and *C. stygium* are much less plentiful at Malham than they were half a century ago. On the other hand, the bog-mosses *Sphagnum riparium* and *S. warnstorfii*, both notable occurrences at Malham, have been found only within the last couple of decades. Some particular fen and bog habitats are equalled or bettered elsewhere, but probably nowhere can such a range, and so many of their characteristic species, be seen within so short a distance. The Malham Tarn NNR is a remarkable microcosm of the mire habitats and species of upland Britain. The interest of the present-day vegetation and flora is enhanced by the historical record in the peat – the record of past vegetation inherent in the character of the peats themselves, as well as the regional record from the surrounding country provided by pollen, and the detailed local evidence of species at the site itself from seeds and other macrofossils.

All of these things make the reserve a rich educational resource, whether it is seen as a geographical entity, as a living demonstration of historical and ecological process, as a series of contrasted functioning ecosystems, or as habitat for individual species. The greatest problem is to balance the use of the reserve with the restraints needed to ensure its continued richness and value. It has so much to offer as an education experience that it would be as wrong not to use it at all for teaching, as it would be to over-use fragile parts of the site and spoil them for the future. 'Scientific interest' is perhaps indefinable; 'science' has more to do with an attitude of mind, an approach to understanding the world, than with subject matter.

Nevertheless, Malham Tarn NNR poses many scientific questions, often of significance far beyond the reserve, and provides an ideal working site for their study and solution. This is reflected in the range of papers on the reserve that have been published over the years, on subjects as diverse as palaeoecology (Pigott & Pigott, 1959, 1963), hydrochemistry (Woof & Jackson, 1988; Pentecost, 1992; Proctor, 1995), vegetation ecology Proctor, 1974; Adam *et al.*, 1975), entomology (Flint, 1963; Disney, 1975b, 1976a, b, 1984, 1986), euglenoid algae (Pentecost, 1982) and testate amoebae (Corbet, 1973); these are surely only a beginning.

Conservation and management

The reserve as we know it is not static; it is the product of a long historical process of change, which still continues. Probably all perceptive visitors would agree that to maintain its diversity and interest, active management is necessary. The problem is to decide first, what the aims of this management should be, and second, how these can be achieved. The first question is not an easy one, but is fundamental. Regarding the reserve simply in terms of biodiversity, it would have been nice to preserve it exactly as it was in 1950 (or some other arbitrary date). But we value a fen and bog site like this also as a demonstration of processes of vegetation change which, allowed to go to completion, would see most or all of the fen covered with dense fen carr. Some of the individual communities we want to preserve are inherently seral – stages in the process of succession – and we cannot preserve them unchanged indefinitely. We may need to recreate their starting points.

Any plan of management for a site as diverse as the Malham Tarn NNR has to avoid too-facile or simplistic assumptions. The history of the site can provide clues to appropriate management. The evidence from the 1785-86 estate book suggest that the Middle and West fen were probably formerly managed as [mowing] meadow. This could justify a regime of periodic cutting, perhaps intermittent late-season grazing, and removal of established willow bushes from substantial parts of this area, because the situation we value is a product of past farming practice, and not in any strict sense 'natural'. In East Fen the problems are different. Again, the situation is artificial in that at least some of the diversity has arisen from the flooding of old peat cuttings when the level of the Tarn was raised two centuries ago. Carr growth (presumably formerly limited by grazing) has been vigorous and has greatly reduced the area of open fen, so maintenance of fen here is dependent on clearance of willow, and a case could be made for reinstating former open fen by clearing some areas of established carr. But carr removal should not go too far. Carr has an interest and value of its own, and there is considerable ecological interest in the establishment and growth, fast or slow, of the willows.

The control of willow colonisation is an immediate and practical problem of management. A more subtle but pervasive problem is the gradual build-up of nutrients with time in the course of succession. This problem is much more intractable in the fertile agricultural landscape of lowland Britain, but the Malham NNR does not escape it completely. Raised bog is an inherently nutrient-poor ecosystem; small-sedge fens of the sort seen in East Fen and the south lagg of Tarn Moss characteristically grow in situations rich in calcium, but relatively poor in N and P. Over much of present-day Britain there is a substantial pollutant input of N in rain, and these communities are generally P-limited. Traditional farming practices – mowing and grazing – probably led to a gradual net drain of P from the fen, whereas the trend now is probably a slow net accumulation which, too, needs to be taken account of in management.

The intention of these last paragraphs is not to provide a prescription, but to indicate something of the complex and dynamic nature, and the problems of maintaining, this extraordinarily fascinating and beautiful area.

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Note added in proof

Since the preparation of the vegetation maps (Figs. 4 and 5) and the submission of this paper for publication, extensive clearance of *Salix* carr has taken place in the fen north of the main inflow stream. The West Fen was cleared in the winter of 1996-97, and the East Fen in the winter of 1997-98. The cut material was removed from the site. The distribution of carr in both these areas now approximates to the situation in 1950. It will be particularly interesting to observe the redevelopment of vegetation in the areas cleared of carr colonisation in the East Fen that were open fen at that time.