

PEAT¹

R.S. CLYMO

PEAT STRUCTURE

Peat is the accumulated remains of dead plants. There is no clear break in the continuum between a mineral soil with organic matter in it — as, for example, in the surface of a podzol — and an almost pure *Sphagnum* peat of which more than 99% is organic matter. Most peats contain less than 20% of unburnable inorganic matter, but some soil scientists allow up to 35%, and commercial standards may allow up to 55%. In Iceland, volcanic ash is widespread and peat commonly contains more than 20% ash (Bjarnason, 1968). The depth of peat deposits is similarly unbounded, though it is common to take an arbitrary minimum depth of about 30 cm. Few deposits in the Temperate and Boreal Zones exceed 15 m in depth². Peat accumulations in subtropical and tropical regions are mostly coastal or at high altitude, but may once have been more extensive than Temperate and Boreal Zone peats (Given and Dickinson, 1975). For example Anderson (1964) records 13 m depth of swamp forest peat accumulated during 4500 years on the coast of Sarawak, and Whitmore (1975), who summarized Anderson's work, noted that as much as 20 m of peat had been recorded. Tropical and subtropical peat may even now be more abundant than is commonly realised (Anderson, Part B, Ch. 6). For example, Coulter (1950, 1957) records about 800 000 ha of peatland in Malaya (about the same as the area in Scotland, where peat covers 10% of the land: Robertson, 1968), and Anderson calculates about 1.5×10^6 ha of peatland in Sarawak.

Peat is not a single homogeneous substance either in space or time. It starts as recently dead plant matter and begins a series of changes which are usually fast at first but slower later. Collectively

these changes are often called decay, decomposition, breakdown or humification. The meaning of these terms is rather vague, but the processes encompassed by them, with varying emphasis, are: (1) loss of organic matter, as gas or in solution, as a result of leaching and of attack by animals and micro-organisms; (2) loss of physical structure; and (3) change of chemical state — for example the production of new types of molecules by micro-organisms.

Peat is of interest to workers in many fields — agriculture, horticulture, chemistry, power generation, civil engineering, medicine and mining — as well as in ecology; so there is a great deal of published information about it. Much of this information may initially be of interest to workers in one particular field. For example, consolidation under load was of interest, originally, to engineers. More recently it has become of interest to ecologists too (Clymo, 1978; Hutchinson, 1980). These different interests are displayed in the four-yearly International Peat Congress. The Proceedings of these Congresses form a useful entrée to the literature, but are, with one exception, a bibliographer's nightmare, having neither editors nor publication date. They are quoted here with the year in which the Congress was held (see p. 224). A very useful account of those parts of peat science which have been of interest in Germany is that of Göttlich (1976).

Peat has numerous characters, most of which

¹Manuscript completed July, 1980.

²Florschütz et al. (1971) described a deposit near Padul, southern Spain, which had twelve alternating bands of peat and lake marl to a depth of 72 m. About half was peat, though of what botanical origin was not recorded. The peat at 10 m depth was about 4600 years old.

may be used in classification. Amongst the more generally important are:

1. Botanical composition
2. State of decomposition

Other characteristics which may be important for particular purposes are:

3. Concentration of inorganic matter (soluble and insoluble)
4. Concentration of inorganic solutes (especially calcium, potassium, ammonium and hydrogen ions, nitrate and phosphate)
5. Cation exchange capacity
6. Activity of micro-organisms
7. Bulk density (dry-matter mass per unit volume of peat)
8. Water content
9. Gas content
10. Drainage and water-retaining properties
11. Proportion of fibre (defined as a size class, and not fibre in the generally understood sense)
12. Structure (the arrangement of materials of different size class and type)
13. Heat of combustion
14. Colour
15. Age

Finally, there are three characters of the peat-forming system as a whole:

16. Topography and hydrology of the area which formed the peat
17. Morphology of the peat-forming system
18. History of the peat-forming system

These characteristics are independent in the sense that there is no compelling physical reason why most of them should not vary independently. In practice, however, there is high correlation between characteristics, so that knowledge of one or a few of them enables one to predict many others with considerable success. For example, the knowledge that a peat is composed mainly of undecomposed *Sphagnum* allows one to predict that it is probably light to medium brown, comes from raised bog (*Hochmoor*), has bulk density about 0.05 g cm^{-3} , holds (at field capacity) about fifteen times the dry mass of water and has about 50% gas space, has about 90% "fibre" (material retained by a 1.5-mm mesh sieve), a cation exchange capacity of about 1 mmol g^{-1} , a calorific content of about 17 to 20 kJ g^{-1} , an ash content of 1 to 2%, nitrogen concentration about 10 to 20 mg g^{-1} , phosphorus concentration about 1 mg g^{-1} , and so on.

For many practical purposes the chemical state and the origin of the peat can be predicted from botanical composition, and the physical properties from the state of decomposition. These two "key characters" may, to a considerable extent, be determined in the field. Colour often changes rapidly on exposure to air, probably as a result of oxidation, so it must be recorded in the field; delicate greens, blues, yellows, browns, oranges and reds visible in peat freshly exhumed from anaerobic conditions often change before one's eyes, and within an hour the peat is a uniform dark brown or black.

The other characteristics are normally measured in a laboratory, and more detailed determination of botanical composition and state of decomposition may need to be made there too. These characteristics are now considered in more detail.

Attributes of peat

Botanical composition

A broad distinction of three categories — **moss**, **herbaceous** (predominantly grasses and sedges) and **wood** — has been suggested (Kivinen, 1977).

There is a good case for subdividing the "moss" category into "*Sphagnum*" and "other" (mainly hypnoid) mosses, because hypnoid moss peat is commonly formed from plants supplied with water which has flowed through mineral soil, and frequently has a higher concentration of solutes than does *Sphagnum* moss peat, which commonly forms in ombrotrophic and oligotrophic conditions (see, for example, Mörnsjö, 1969). A few types of non-*Sphagnum* moss peat are oligotrophic (and mainly ombrotrophic). Examples are the subantarctic peats formed from the mosses *Chorisodontium aciphyllum* and *Polytrichum alpestre* (Collins, 1976; Fenton, 1978, 1980) and the *Racomitrium* peats of Andøya, northern Norway.

Identification of mosses to family or genus may be attempted in the field, but a microscope is usually necessary to confirm the identification and to extend it to lower levels. This may be of value. For example, the identification of *Sphagnum* to the level of Section *Acutifolia* (usually hummock species), *Sphagnum* (commonly lawn species) and *Cuspidata* (commonly pool species) made possible the reconstruction of the succession of communities on north temperate bogs, and gave rise to the constructively misleading hypothesis, commonly

attributed to Osvald (1923), about cyclic growth of hummocks and hollows (Tansley, 1939; Watt, 1947; Walker and Walker, 1961; Tallis, Chapter 9, this volume). Another example is the use of the distinctive comb-fibrils of *S. imbricatum* leaf cells to show that for nearly 7000 years this species dominated the peat in the bog at Malham Tarn, England (Pigott and Pigott, 1959), but that it rather suddenly vanished from the peat in recent times, and is now extremely rare in the surface vegetation of the whole region.

The "herbaceous" category of peat may usefully be divided too. In north temperate regions grasses and sedges predominate, and this type of peat (typically a product of Magnocaricion vegetation) has usually formed under the influence of mineral soil water. As Kulczyński (1949) pointed out the plants are rooted (unlike mosses) and the leaves fall onto the waterlogged peat surface. Such peats are usually denser than moss peats and have a higher concentration of ash and of inorganic solutes. The ecological conditions which give rise to *Phragmites* peat, *Carex* peat, and *Cladium* peat differ considerably, though from the gardener's point of view the differences may be unimportant. But the distinction between these and peat formed from the remains of *Eriophorum vaginatum* (cotton grass) is likely to be important to almost everyone using peat because *Eriophorum* grows, usually, in oligotrophic conditions.

In north temperate and arctic peat deposits, "wood" peat is usually found in one of three positions: at the base of a deposit, above a layer of herbaceous peat, or as a layer in moss peat. Wood peat at the base of a deposit is commonly of *Betula* or *Pinus*, the trees probably being the last generation rooted in mineral soil. Wood peat above herbaceous peat may be formed from fen carr, and commonly contains *Alnus*, *Betula* and some *Salix*. Wood layers in temperate moss peat often contain *Betula* or *Pinus* and formed at times when a bog surface dried temporarily. In the arctic, wood layers are commonly of birch — often *Betula michauxii*. In the tropics and subtropics complete deposits may be of wood peat — for example the coastal Sarawak peats (Anderson, 1964; and Part B, Ch. 6).

Many peats are an intimate mixture of moss, herbaceous and wood types. Yet others are so decomposed that their botanical composition is not, or not easily, identifiable.

State of decomposition

This character, usually called the state of humification, is partly assessed by the extent to which plant structure is visible, and partly by colour (though this may change rapidly). Field assessments are usually made using the H scale devised by Von Post and Granlund (1926). This is similar to the Beaufort scale of wind velocity in that it replaces an entirely subjective description by a numerical scale based on specific, more objective, criteria. These include the colour of the fluid expressed when peat is squeezed in the hand, and the proportion and character of the material which remains in the hand after squeezing the peat (Table 4.1).

Other methods of assessing the extent of humification rely on chemical extractants and measurement of the density of brown colour. One of the simplest is to shake equal volumes of peat and 5% w/v potassium hydroxide, or a saturated solution of sodium pyrophosphate, allow a few drops of the liquid to spread on a filter paper, and compare the colour with arbitrary standard colours, preferably Munsell chart colours.

More complex procedures are used too. For example, Bahnson (1968, translated in Aaby and Tauber, 1974), dries and grinds the samples, then boils 0.2 g with 100 ml 0.5% sodium hydroxide for 1 h, filters, and measures absorbance with a yellow filter (EEL 626). Other methods use neutral sodium pyrophosphate at room temperature for 24 h as extractant (Schnitzer and Kahn, 1972), or dissolve all but "humus" with acetyl bromide (Overbeck and Schneider, 1940). Von Naucke (1976) discussed these and other methods of assessing humification.

When comparisons of methods are made (for example, Aaby and Tauber, 1974) there is broad general agreement, though in detail the agreement is poor. Fig. 4.1 shows the correlation between the H scale and a colorimetric estimate. A more extensive series of 614 samples was found by Karesniemi (1972) to give an approximately linear relation between H and a (different) colorimetric estimate. The lack of detailed agreement is not surprising: peat is a mixture of still largely unknown chemical substances (Schnitzer and Kahn, 1972), and the techniques used for assessing humification (e.g. Schnitzer, 1973) are still comparatively crude. Nevertheless they can, used in a relative way, give useful insights into some of the processes of peat formation.

TABLE 4.1

Humification scale, translated and tabulated from Von Post and Granlund (1926, pp. 29-30)

Scale number	Description	Proportion of "dy"	Plant structure	Expressed fluid	Peat lost	Peat retained in the hand	
						consistency	colour
H1	completely unhumified	none		colourless, clear			
H2	virtually unhumified	none		yellow-brown, clear			
H3	little humified	small		noticeably turbid	none	not porridgey	
H4	poorly humified	modest		very turbid		somewhat porridgey	
H5	fairly humified, structure distinct	fair	plain, but somewhat obscured	strongly turbid	some	very porridgey	
H6	fairly humified, structure less distinct	fair	indistinct, but still clear		up to 1/3	very porridgey	
H7	quite well-humified	considerable	much still visible		about 1/2	gruel-like	very dark
H8	well-humified	large	vague		2/3	only fibrous matter and roots remain	
H9	almost completely humified	most	almost none visible		almost all	homogeneous	
H10	completely humified	all	none visible		all	porridge	

The often quoted Von Post (1924) reports the existence of this scale but gives no details. Peat is squeezed in the hand. The fluid which escapes is examined and so are the nature and amount of peat substance remaining in the hand.

The term "dy" introduced by Von Post has no direct equivalent in English. It is nowadays used for amorphous (colloidal) dark brown "humic" matter from which all trace of macroscopic plant-structure has disappeared.

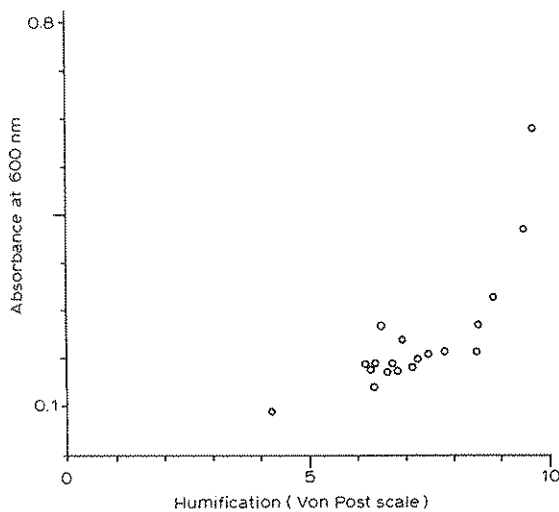


Fig. 4.1. Correlation of humification on the H scale with absorbance at 600 nm of an $\text{Na}_2\text{HPO}_4/\text{NaF}$ extract. Data of Mattson and Koutler-Andersson (1954).

In *Sphagnum* peats in Finland there is a positive and approximately linear regression between bulk density and the Von Post H scale value (summarized by Päivänen, 1969). The relationship is approximately:

$$\rho = 0.01 H + 0.04$$

where ρ = bulk density (g cm^{-3}); H = Von Post scale number (0-10). A remarkably similar relationship:

$$\rho = 0.01 H - 0.05$$

may be calculated from the results shown by Karesniemi (1972).

Humification may also be related to void proportion (see below).

Concentration of inorganic matter

This is easily measured after dry ashing (at 450-550°C) or after wet ashing with concentrated

strong acids, particularly nitric acid mixed with perchloric acid. Wet ashing is usually used only when chemical analyses are to be made, and the presence of perchloric acid is potentially dangerous. The mineralogy of the inorganic fraction may be a useful characteristic (Finney and Farnham, 1968), particularly the distinction between soil-derived quartz and plant-produced opaline silica (Chapman, 1964b).

Concentration of inorganic solutes

It is convenient to distinguish solutes in the water from those, probably nearly in equilibrium, in "exchangeable" forms. "Exchange" includes a variety of processes, including simple exchange, chelation and (for H^+) dissociation. Peat water may be expressed by pressure (Malmer, 1962b, p. 8), and "exchangeable" solutes extracted by 1M acetic acid, 1M ammonium acetate, or 0.5M barium acetate, at pH 7 (Puustjärvi, 1957) or by some other concentrated acid or salt. Different extractants give different results (Table 4.2A). Most of the H^+ , Na^+ , K^+ , Mg^{2+} and Ca^{2+} in ombrogenous peat is exchangeable (Gore and Allen, 1956; see also Table 4.2B).

The concentration (or, strictly, the activity) of H^+ in peat water is an especially important character. It is commonly reported as "pH", and is useful because, as Pearsall (1954) pointed out, it is often highly correlated with other characters. Taken together with the concentration of Ca^{2+} , or even with electrical conductivity (if the influence of coastal sea spray is not important), it can be used to assess the relative importance of rain water and mineral soil water.

Measurements of pH made by pressing a glass electrode into damp peat are usually lower than those of peat water, and are difficult to interpret. Measurements of pH in concentrated potassium chloride solution mixed with peat may be useful: essentially, the method measures total exchangeable H^+ , so the relative amounts of solution and dry peat mass should be recorded too (but rarely are).

Many chemical species change state as a result of the activities of micro-organisms or from purely chemical changes, especially between anaerobic and aerobic conditions. Examples are: Fe^{2+} and Fe^{3+} , Mn^+ and Mn^{2+} , S^{2-} and SO_4^{2-} . Investigation of these very important changes *in the field* has hardly begun.

TABLE 4.2

A. Concentration ($mmol\ dm^{-3}$) in peat from Åkhult mire, southern Sweden, of exchangeable cations extracted with 1M CH_3COONH_4 (Am) and corresponding value as % difference (D) extracted by 1M CH_3COOH . Selected from Malmer (1962a, pp. 304–307) (nd=not determined)

Am ($mmol\ dm^{-3}$)				D (%)			
Na ⁺	K ⁺	Mg ²⁺	Ca ²⁺	Na ⁺	K ⁺	Mg ²⁺	Ca ²⁺
Replicates from "mud-bottom", H3–H4							
0.57	0.22	3.1	4.2	–18	9	nd	–2
0.40	0.33	3.0	3.2	28	9	nd	16
0.40	0.11	2.7	3.7	–10	0	nd	–11
0.52	0.22	3.5	5.2	8	–14	nd	–4
0.50	0.16	3.2	4.5	48	131	nd	0
Wet area, <i>Eriophorum vaginatum</i> zone							
0.48	0.79	2.3	1.8	–2	–5	–22	–22
0.40	0.28	2.5	2.4	15	57	0	–37
0.32	0.17	1.9	1.9	–9	0	nd	–16
0.52	0.31	2.8	2.4	–17	16	4	–25
Wet area, <i>Menyanthes trifoliata</i> zone, H5–H6							
0.49	0.79	3.1	9.2	33	–10	nd	–4
0.59	0.64	2.5	12.7	–3	6	nd	2
0.82	nd	2.1	7.8	–2	nd	nd	–19
Wooded bog, H2							
0.83	0.88	2.4	2.3	–10	–41	17	0

B. Cation concentration in a *Sphagnum–Eriophorum* peat ($mmol\ dm^{-3}$) using four extractants, compared with total ($HClO_4–HNO_3$ wet ashing) (from Boatman and Roberts, 1963; bulk density assumed to be $0.1\ g\ cm^{-3}$)

	(Extract- ant pH)	Na ⁺	K ⁺	Mg ²⁺	Ca ²⁺
Wet ashed		1.2	0.7	3.1	3.1
Extracted with:					
HCl (50 $mmol\ dm^{-3}$)	c. 1.2	1.2	0.3	4.3	3.0
CH_3COOH (1 $mol\ dm^{-3}$)	c. 2.4	1.0	0.4	2.2	1.7
CH_3COOH (1 $mol\ dm^{-3}$, intermittent leaching)	c. 2.4	1.3	0.5	4.9	3.2
$BaCl_2$ (triethanolamine)	8.1	1.1	0.5	–	2.5

Cation exchange capacity

The term "cation exchange" is often used loosely, as it is here, as a description of experimental results. Besides cation exchange in the strict sense, there are other processes which can in general be described by equilibrium equations based on the law of mass

action and with a specific coefficient. Dissociation and chelation are such processes. One may set up mathematical models with sets of, say, three such equations for each cation, and use experimental results to get best estimates of the coefficients for each process. These are useful for predictive purposes (Clymo, 1967). Most workers assume, however, that they are dealing with a single process. If they work with Na^+ or K^+ they will probably call it "exchange", but if with Pb^{2+} they may prefer to speak of chelation. There is usually very little evidence adduced on which the distinction can be supported (but see Sikora and Keeney, Ch. 6), and indeed there may in reality be a mixture of processes, or ones of intermediate character. "Exchange" is used here in the broad sense.

Sphagnum has a relatively high cation exchange capacity (Skene, 1915) as a result of abundant long chain polymers of uronic acids (Theander, 1954), but *Eriophorum vaginatum*, for example, has an unusually low cation exchange capacity (Knight et al., 1961; Clymo, 1963). The cation exchange capacity of bog peats may vary noticeably, therefore, over quite short distances both horizontally and vertically (Fig. 4.2). The chemical potential of a cation is related to concentration (or, strictly, to

activity) in peat water, but the capacity of the peat to supply that ion is related to the cation exchange capacity (and to the concentration of solids such as calcium carbonate if present) and also to the concentration of other cations. Table 4.3 (from Malmer, 1962b) shows that, in accordance with expectation (Clymo, 1967), up to half the total (monovalent) Na^+ is in the peat water, but only 1 to 2% of the (divalent) Ca^{2+} .

Cation exchange capacity is commonly expressed per unit dry mass of peat, and measured by saturating the exchange sites with a polyvalent cation at a pH sufficiently high to ensure that the uronic acids are dissociated, followed by washing in distilled water to remove cations in solution, then displacing the saturating cation with strong acid or alkali and measuring the amount thus displaced. The washing step is unsatisfactory because some of the saturating cation comes out into the water as the system moves toward a new equilibrium. It is preferable therefore to use a different procedure. The peat is pressed as dry as possible, weighed and transferred to the extracting solution. From the pressed dry weight and the final dry weight the mass of solution transferred with the peat is calculated. The cation concentration in the saturating solution is measured, as well as in the extracting solution, and then the amount of cation transferred with the peat is subtracted. With well-pressed peat this correction is usually less than 10% of the total exchangeable cations.

TABLE 4.3

Proportions of peat cations (as % of total) in peat water in southern Swedish mires; the water was extracted with a pressure-plate apparatus at 14.5×10^5 Pa for 24 h (from Malmer, 1962a).

Site	Na^+	K^+	Mg^{2+}	Ca^{2+}
Mud bottom				
Bog, Åkhult	44	17.0	3.4	2.6
Poor fen, Åkhult	45	11.5	1.7	0.8
Rich fen, Nâthult	40	11.3	3.5	1.6
Hummock				
Bog, Åkhult	27	4.7	2.6	2.3
<i>Nartheceium ossifragum</i> community				
Åkhult	33	2.5	4.5	1.0
Kopporås	38	23.0	1.9	0.9
Tjörnarp	51	11.4	6.3	3.5

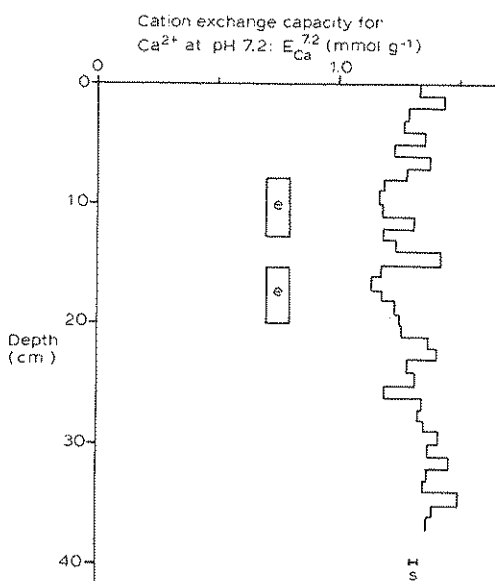


Fig. 4.2. Profile of cation exchange capacity of peat from Stordalen, Abisko, northern Sweden. Peat type *Sphagnum fuscum*, with some *Eriophorum* at points marked e. The standard deviation of the method is shown at s. (Clymo, unpubl.)

Because the COOH and OH groups dissociate as the pH is raised, the cation exchange capacity is very dependent on pH. Fig. 4.3 (redrawn from Belkevich and Chistova, 1968) illustrates this point. If E is the observed cation exchange capacity (mmol g^{-1}), and p is the pH, then: $E \approx 0.3(p - 3)$. For this reason it might be preferable to use cation exchange ability ($E_{\text{Ca}}^{7.2}$) to represent the measured capacity at a particular pH (7.2 in this example) and with a particular cation (calcium in this example), and to reserve the term "cation exchange capacity" for the maximum reached when all the exchange groups are ionized. The results depend on the concentration of the exchanger cation too (Clymo, 1963). Where detailed comparisons are to be made there is much to be said for allowing all samples, enclosed in individual net bags, to equilibrate together in the same bath of solution. The results in Fig. 4.2 were obtained in this way, and with the pressed-dry correction described above. The saturating solution was $\text{CaCl}_2 + \text{Ca(OH)}_2$ at pH 7.2, and the displacing solution was $0.1M \text{HNO}_3$. The cation Ba^{2+} has commonly been used, in spite of the chances of precipitation of barium carbonate or barium sulphate if the pH is not controlled. Puustjärvi (1956) used H^+ as saturating cation, and

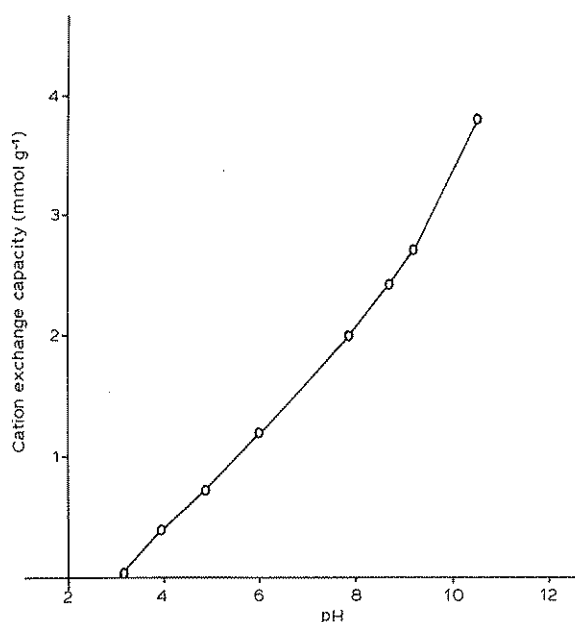


Fig. 4.3. Cation exchange capacity for Ba^{2+} of an *Eriophorum-Sphagnum* peat as a function of pH. Redrawn from Belkevich and Chistova (1968).

$0.25M$ barium acetate as displacer. He found values of $E_{\text{Ba}}^{6.5}$ from 0.07mmol g^{-1} in peat from a *rimpi fen* composed of *Carex* plus non-*Sphagnum* mosses up to 1.5 (or, in isolated cases, 1.7 and 1.9) mmol g^{-1} in *Sphagnum fuscum* peat.

Activity of micro-organisms

The nature and activities of micro-organisms (mainly fungi and bacteria) have been receiving much more attention since 1950, following a long period of neglect after the early work of Waksman and Tenney (1928) and Waksman and Stevens (1929c).

In blanket bog, Collins et al. (1978) found that estimates of biomass of bacteria by different methods differed by one to two orders of magnitude, and of fungi by about one order of magnitude. Within these broad limits there was no clear indication that either group was dominant. The abundance of both groups declined in the anaerobic zone, though this total masked conspicuously different behaviour by groups defined by physiological function. Even obligately anaerobic bacteria were less abundant in the anaerobic zone than they were in the surface layers, which contain a lot of water and must have a large total volume of microanaerobic sites scattered through the generally aerobic zone.

The biomass of bacteria and fungi is of course not a good indicator of their physiological activity. That such activities are localized can be suggested by enrichment cultures (Clymo, 1965) or, better, by direct measurement of the products of micro-organism activity, for example sulphide (Benda, 1957; Clymo, 1965; Urquhart and Gore, 1973), or carbon dioxide and methane (Clymo and Reddaway, 1971). In general, however, there is still relatively little known about the activities of micro-organisms and particularly about microbial interactions in peat. Reviews of the microbiology of peat have been made by Given and Dickinson (1975) and by Dickinson in this volume (Ch. 5). Here it is sufficient to point out that the activity (or inactivity) of micro-organisms is one of the main causes of the very existence of peat. At the other end of the scale, the excessive activity of micro-organisms perhaps especially of thermophilic fungi (see, for instance, Küster and Locci, 1964) can raise the temperature of milled peat to -70°C , at which point, if air is admitted, chemical reactions become

so fast that the peat burns spontaneously¹ (Strygin, 1968).

Bulk density, water content, gas content

There are many methods of making these measurements. Puustjärvi (1968, 1969) gives one example. In principle, four quantities must be known (Skaven-Haug, 1972).

A defined volume of peat is weighed. The peat is oven-dried and weighed again. A fourth quantity — the density of the peat dry matter — is needed. This may be determined by weighing the peat, suspended under water, after evacuation under water to remove gas (Clymo, 1970). Let:

V = volume of whole bulk of peat	V_d = volume of the dry peat substance
W_w = wet weight in air	M_w = wet mass in air
W_s = weight submerged in water	
W_d = dry weight in air	M_d = dry mass in air
ρ_w = density of water	

Then ρ_d , the density of peat dry matter, is given by:

$$\rho_d = \frac{M_d}{V_d} = \frac{\rho_w W_d}{(W_d - W_s)} \quad (1)$$

The dry matter density is defined in terms of *mass* per unit volume, but the simplest method for determining it depends on measuring the quotient of *weights*. The method should be accurate at any position on the earth's surface, but would be impossible if attempted in a condition of weightlessness. This is not likely to be a severe limitation in practice.

The *bulk* density, ρ , is given by:

$$\rho = M_d/V \quad (2)$$

The water content on a mass basis, ϕ_d , is given by:

$$\phi_d = \frac{(M_w - M_d)}{M_d} \quad (3)$$

¹Spontaneous combustion of peat should be distinguished from the phenomenon known as "will-o'-the-wisp" (= *ignis fatuus* = Jack-o'-lantern) which anecdotal accounts record from the surface of peat bogs. It is tempting to speculate that this may be bubbles of methane ignited by rapid oxidation of inorganic or organic sulphides.

and the water content on a volume basis, ϕ_v , by:

$$\phi_v = \frac{(M_w - M_d)}{\rho_w V} \quad (4)$$

The void proportion, E , is given by:

$$E = 1 - \frac{M_d}{V\rho_d} \quad (5)$$

Finally, the gas content per unit volume, G , is given by:

$$G = 1 - \phi_v - \frac{M_d}{V\rho_d} \quad (6)$$

If such measurements are made for ecological purposes, it may be important to avoid sample compaction. Hiller borer samples are virtually useless. Those collected with a "Russian pattern" borer (West, 1968), with which a half-cylinder of metal is rotated to trap the sample, gave results for bulk density which were consistently about 5% below those for samples taken by horizontal excavation of monoliths from a cut-back peat face (Clymo, unpubl.). The monolith samples were each about fifty times the volume of the "Russian pattern" samples.

For detailed investigations of the top 50 to 100 cm, then, a rectangular sampler (Fenton, 1978) may be useful. One side of the sampler runs in grooves and can be slid out lengthwise. The three-sided box, with a sharp-sloping end, is forced down into the peat, cutting down three sides but leaving the fourth attached. This attachment causes the whole block to resist compaction. The sharp-ended fourth side of the cutter is then thrust down, running in its grooves, to complete the vertical isolation of a peat block. The whole must then be excavated with a spade. Any movement of the surface can be seen, so faulty blocks may be rejected.

Other workers have used cylindrical samplers. One such (Clymo, unpubl.) allows one to draw a cutter plate across the sampler base, thus retaining the core in the tube while both are extracted. The natural profile of water and of gas space (Fig. 4.4) may be fairly easily and accurately captured in this way — something which is difficult to manage by

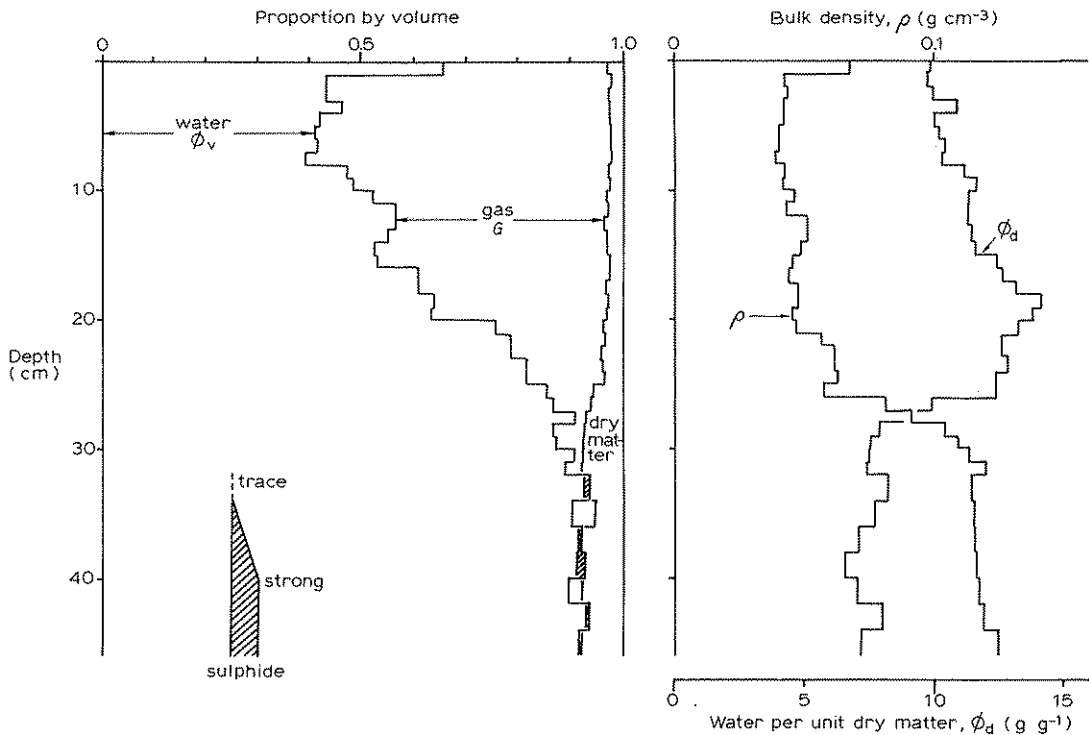


Fig. 4.4. Physical properties of a *Sphagnum fuscum* peat profile from Nordmjele, Andøya, northern Norway (Clymo, unpublished). The 20 cm diameter core was collected in a tube which was then sealed to prevent water loss. The core was later ejected, 1 cm at a time, and sliced with a sharp knife.

other methods. Again, faulty samples may easily be recognized and rejected.

Of the quantities defined above, bulk density and water content are determined routinely for commercial purposes (for example, Puustjärvi, 1968, 1969) but not as commonly as might be hoped for scientific purposes, and rather rarely on profiles (as opposed to isolated samples). An illustrative set of profiles is shown in Fig. 4.4. The void proportion (or quotient), E , is especially important in studies of the mechanical properties of peat (see, for example, Berry and Poskitt, 1972) and in studies of hydraulic conductance. The bulk density profile is important in studies of the rate of peat accumulation (Tallis and Switsur, 1973; Jones and Gore, 1978; Clymo, 1978) and ought to be measured whenever ^{14}C dates are determined.

The general features of *Sphagnum*-dominated profiles are that the bulk density in the top 1 cm is relatively high, but that immediately below the tightly packed capitula of the mosses it falls to about 0.02 g cm^{-3} (mosses of the Section

Sphagnum) or about 0.04 g cm^{-3} (Section *Acutifolia*). Below this ρ increases gradually, and then, at the point where the weakened moss can no longer support the load above (commonly 10–30 cm deep), ρ increases rapidly to about 0.1 g cm^{-3} . At greater depth there may be perhaps a 20% further increase (for example, see Jones and Gore, 1978). Highly humified peat (Päivänen, 1969; Tallis and Switsur, 1973) and *Eriophorum vaginatum* peat (Tallis and Switsur, 1973) have greater bulk density — about 0.12 to 0.15 g cm^{-3} . The values calculable from the data of Bellamy and Rieley (1967) — between 0.18 and 0.22 g cm^{-3} in *Sphagnum fuscum* peat — seem remarkably high for natural peat, though artificial means can raise ρ to 1.3 g cm^{-3} (Freistedt, 1968). The specific gravity of 0.2 to 0.8 reported by Mattson and Koutler-Andersson (1954), and density from 0.35 to 0.96 reported by Walsh and Barry (1958), probably refer to wet-mass. A similar pattern: $\rho = 0.15 \text{ g cm}^{-3}$ at the surface, declining to 0.09 g cm^{-3} at 15 cm depth, then increasing again deeper in the profile, is

reported by Fenton (1980) for Antarctic peats (though the explanation here is probably rather different — see p. 215). In all these peats the contribution of inorganic matter is negligible.

It is remarkable that in these peats no more than 3 to 10% by volume is organic matrix: the rest is water or gas. The proportions of water and gas are inversely related. The water-holding capacity of small peat samples which have been saturated and allowed to drain is closely related to bulk density (see, for example, Puustjärvi, 1968, 1972). In the field however the relationship is complicated by capillary phenomena. Apart from the top 1 cm, the surface peat contains 50% (*Acutifolia* peat) to 90% (*Sphagnum* peat) of gas, decreasing to zero at the water table. This has obvious consequences for the roots of vascular plants. The interrelationship of water-table, water-content profile, bulk density and decay is best discussed later.

For a wide range of commercial peats, Olsen (1968) has shown that humification H (on the Von Post scale) is related to ρ (g cm^{-3}) and E by:

$$H = (\rho - 0.023) / 0.015 \quad \left. \begin{array}{l} \text{(valid between } \rho = 0.03 \text{ and} \\ E = 1.01 - 0.67\rho \end{array} \right\} 0.20$$

Karesniemi (1972) and others report similar relationships.

The profile, *in situ*, of water content on a dry weight basis, ϕ_d , is affected by changes both in ϕ_v and in ρ , and quite complex shapes (for example, see Fig. 4.4) may result.

Drainage and water-retaining capacity

Relatively undecomposed peats have a high hydraulic conductance, and water flow through them follows Darcy's Law quite closely (Ingram et al., 1974; Rycroft et al., 1975a, b). The conductivity is about 10^{-1} to $10^{-3} \text{ cm s}^{-1}$. In decomposed peat the conductivity is much lower — perhaps $10^{-6} \text{ cm s}^{-1}$. Korpijaakko and Radforth (1972) reported an approximately linear relationship between conductivity, K_p (in cm min^{-1}) and the logarithm of humification on the Von Post scale:

$$K_p \approx -0.5 \log_{10} H + 0.6$$

Rycroft et al. (1975b) showed that flow in humified peat deviates from Darcy's Law, so it is not clear how far the results of Korpijaakko and Radforth

can be relied on. During periods of heavy precipitation (or snow melt) much of the water can flow vertically and then horizontally through layers of high conductance, but at other times, of low water table, movement may be very slow (e.g. Chapman, 1965).

The relationship of water content, ϕ_d , and equilibrium water potential, ψ , in peat is important, and depends primarily on the extent of humification and compaction. An example of the water potential capacity curve for a moderately humified peat is shown in Fig. 4.5 (capacity as ϕ_d rather than ϕ_v). Most of the water is removed between a potential corresponding to that in circular fully wettable water-filled pores between 1 and 20 μm diameter. This corresponds to the range of pore sizes commonly measured in peats, and one may conclude that most of the water in little-humified peat is held by capillary forces. "Wilting point" (at $-20 \times 10^5 \text{ Pa}$)¹ is well below this point (though the actual wilting point of most peat-inhabiting plants is not known), and is unlikely to be reached in natural conditions. Capillary forces in this range begin to overlap with other (stronger) chemical forces. In highly humified peats — H8 to H10 — the proportion of water with ψ below $-20 \times 10^5 \text{ Pa}$ is larger (Boelter, 1968). In less humified peat (Fig. 4.5) the whole curve is lower and extends to higher water

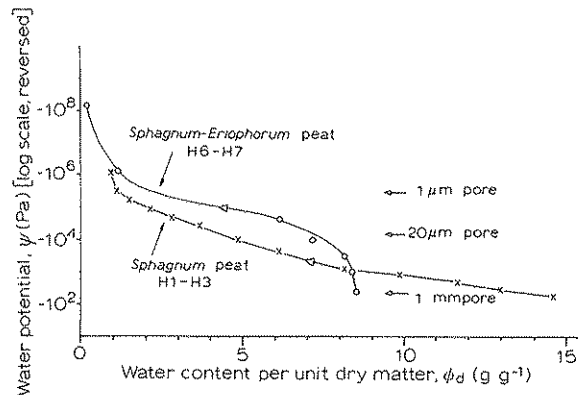


Fig. 4.5. Water potential/water content curves (drying, for *Sphagnum-Eriophorum* peat, H6-H7, and for *Sphagnum* peat, H1-H3). Redrawn from Van Dijk and Boekel (1968) and Puustjärvi (1968). The ψ value for cylindrical water-filled pores of 1 and 20 μm diameter is shown.

¹The SI unit of pressure, the Pascal, is related to the Newton and other units by: $10^5 \text{ Pa} = 10^5 \text{ N m}^{-2} \approx 1 \text{ bar} \approx 1 \text{ atm}$.

content because there are more and larger capillary spaces.

The exact shape of water potential/capacity curves varies with pretreatment. Changing the physical structure by freezing and thawing for example (Van Dijk and Boekel, 1968) has a marked effect, as does drying. If results are plotted on a volumetric basis the curves are similar, but shifted as a result of shrinkage on drying. In peats with some structure but low strength this shrinkage may be caused by the reduced hydrostatic pressure inside capillary films. The pressure is closely related to water potential in this case. This may account for the linear relationship between water loss and shrinkage (Irwin, 1968). In humified peats the process is more akin to the shrinking of a drying jelly. In unhumified peat in which the plant structures on the scale of 1 to 5 mm are preserved there is much less shrinkage on drying. Further information is given in Chapters 3 and 8.

Proportion of fibre

"Fibre" is the category of organic matter which fails to pass through a sieve of mesh size 1.5 mm. "Unrubbed" and "rubbed" fibre are distinguishable. Fragments of wood larger than 2 cm are excluded in this definition, but leaves are included (Day, 1968). The proportion of "fibre" must, ultimately, be measured, but with practice visual estimates on vertical (not horizontal) cleavage planes in the field may become accurate to within 10%. Technical details are given by Farnham (1968). In practice the bulk of material classified as "fibre" is not fibre in the sense of the botanical cell type, but consists of leaves and stems of *Sphagnum*, other bryophytes, segments of sedge leaves, fragments of wood from stems of dwarf shrubs, and so on. The main exception is undecomposed shoot bases of *Eriophorum* which contain a large proportion of fibres, and are fibrous in the technical and common senses of the word.

The proportion of fibre is usually closely linked with the extent of humification, and hence with the mechanical and hydraulic properties already discussed.

Structure

Structural features of primary importance are the size and distribution of pores, and the orientation of those components (if any) which have retained

structural integrity. These features have influence on the mechanical properties of peat (compressibility and creep behaviour) and on the hydraulic properties. MacFarlane and Radforth (1968) suggest from microscopic examination that the structure of moss peat may be approximated by a series of parallel cylinders, each with an incompressible core (the stem) surrounded by a compressible sheath (leaves). Ohira (1962) suggested a more abstract model of loosely packed spheres, with the space between them filled by smaller particles, gas and water. Some features of the pore size and pattern may also be deduced from the pattern of absorption and elution of non-adsorbed radioactive tracers (Volarovich and Churaev, 1968).

Heat of combustion

This character (also known as "calorific content" or "energy content") may be measured by the standard techniques of bomb calorimetry. Such measurements are made routinely for commercial purposes but are rarely published and are not usually related to the processes of peat genesis. The results in Fig. 4.6 show that in both profiles there is

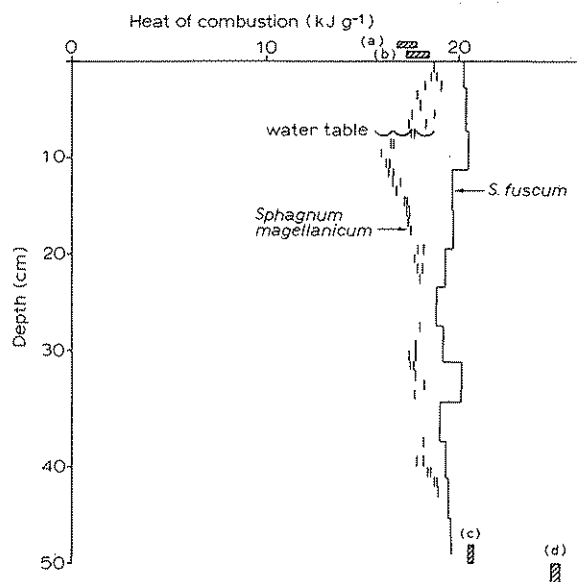


Fig. 4.6. Profiles of heat of combustion (= "energy content" = "calorific value"). *Sphagnum fuscum* profile (Bellamy and Rieley, 1967) from northern England. *S. magellanicum* profile (Clymo, unpublished) from Cranemoor, southern England. The four blocks are: (a) "*Sphagnum*" (Gorham and Sanger, 1967); (b) *S. capillifolium*, *S. papillosum*, *S. cuspidatum*, *S. recurvum* (E.D. Ford, quoted in Clymo, 1970); (c) "peat" (Duane et al., 1968; Kamula, 1968); (d) coal (average).

at first a decrease downwards in the heat of combustion, followed by an increase. This is clear in the *Sphagnum magellanicum* profile, where there are sufficient observations to make the trend plain. The *S. fuscum* profile shows the same trend (excepting the high value at 31 to 35 cm), though it is less well marked and the trough is at greater depth. The reversal may be connected with the change from aerobic to anaerobic conditions. The even higher values for commercial peat (used for fuel) and coal, and the results of Salmi (1954), suggest that the process continues.

Colour

Soil scientists have long recognised the need for objective descriptions of colour *in the field*, and commonly use standards such as Munsell charts. There are a surprising variety of delicate colours to be seen in freshly exposed peat, and these may be of ecological significance. For example, the distinction of upper "black-brown" peat above a layer described as "green" which in turn overlies "red-brown" peat has been associated with microbiological differences, which are, in turn, probably connected with the position and fluctuation of the water table (Collins et al., 1978). Reference to standard colours is rarely made however, probably because a complete set of such standards is expensive and only occasionally of use to ecologists.

Age

The age of peat is needed for the reconstruction of vegetation history and in studies of peat growth. For ages in the range from 200 to 20 000 yr the ^{14}C technique is satisfactory for ombrogenous peats unless there has been an abnormal amount of deep root growth, but may be less so for peat formed from plants growing with mineral soil water, particularly if this is highly calcareous. There is uncertainty about the calibration of ^{14}C ages (Pearson et al., 1977). There is probably little vertical movement of carbon-containing substances, though it may be that some substances present in small amounts, for example, amino acids (Swain et al., 1959) and pollen (Mackay, unpublished, 1976), are mobile in the top 20 cm of the peat.

Ages to 200 years cannot at present be measured accurately, though one particular event, the 1963 peak in ^{137}Cs produced by nuclear bomb tests, may be useful. Aaby et al. (1979) and Oldfield et al.

(1979) doubt this and prefer the amount of ^{210}Pb , believing that the mobility of lead is low (but see Figs. 4.17 and 4.18). Attempts have been made to use the cumulative total of magnesium or aluminium to provide a continuous scale (Clymo, 1978), but it is evident that many inorganic elements are surprisingly mobile in the surface layers of peat (Damman, 1978; Mackay, unpublished, 1976), so such methods are approximate at best.

The only other method in use at present is painstaking correlation of pollen abundance with historical records of tree planting, industrial activity (causing deposition of soot), changes in cereal abundance, and so on (Lee and Tallis, 1973; Livett et al., 1979).

Attributes of peat-forming systems

The three characters which follow differ from the earlier ones in being characters of the peat-forming system as a whole, rather than of the peat *substance*. The three characters are often closely interlinked.

Topography and hydrology of the area in which peat formed

Because of their dependence on water, peat-forming systems may be very sensitive to topography. In regions of continuous high humidity such as Ireland and Newfoundland, peat may form direct on slopes up to 20° or more, although such "blanket peats" on steep slopes are likely to "flow" or "burst". In drier climates, basins or valleys may be essential to give the necessary amplification or stabilization of the water supply. The peat itself affects the hydrology. These matters are considered in much detail elsewhere in this volume.

Morphology of the peat-forming system

Structures may be seen in peat-forming systems at all scales, but three scales are most conspicuous. First is the scale of the individual plant, centred on about 1 to 10 cm. Second is a scale of 1 to 20 m. This corresponds to pool and hummock topography. There is a great variety of structures from the extraordinary "strings" of the northern "string-bogs" which may be 2 m across, 1 m tall, and hundreds of metres long, to the approximately circular hummocks of more southerly bogs on the west coast of Europe. Finally, there is the large-scale structure of a whole peat-forming system, such as raised-bog, eccentric-domed bog, *Schwingmoor*,

etc. The scale here is hundreds or thousands of metres. Again, these structures are described in detail elsewhere in this volume.

History of the peat-forming system

The history of a peat-forming system is preserved, with distortion, in the peat substance. Except where cryoturbation has disturbed the sequence, the deepest peat is the oldest. Macrofossils — leaves, stems and roots — show what plants lived at that particular point. Microfossils — pollen, spores, etc. — may be local or regional. Different plants decay at different rates (see, for instance, Coulson and Butterfield, 1978; and Dickinson, Chapter 5, this volume) so it is not in general possible to reconstruct the vegetation history in detail, but major changes from, for example, *Phragmites* to *Sphagnum* (see, for instance, Chapman, 1964a) are of value as indicators of a change in the nature of the peat-forming vegetation. Sometimes the changes are surprising and would not have been expected from consideration of present topography and hydrology. For example, the sequence *Sphagnum* peat, *Cladium* peat, *Sphagnum* peat at Shapwick Heath, Somerset (Godwin, 1956, Fig. 14) probably resulted from flooding of a rainwater-dependent surface by calcareous mineral-soil water.

Classification of peat and peat-forming systems

There are a large number of classifications in use and disuse. A primary distinction is between classifications of peat *substance* and those of the peat-forming *system*. The general problems are well presented in the account of an International Peat Society Symposium (Kivinen et al., 1979).

Peat is of economic importance, so there are national commercial classifications of peat substance (summarized by Farnham, 1968) in, *inter alia*, the Soviet Union, Finland, Canada, the United States, Germany, Great Britain, Sweden, Poland, Norway and The Netherlands. [The order is that of the area, reported by Olenin (1968), of exploitable peat in each country.] Attempts are being made to produce an internationally agreed commercial classification (Kivinen, 1977) and this is shown in Appendix I.

Some classifications of peat-forming systems make use, in the main, of the peat substance charac-

ters and their vertical variation. An example of such a classification is that contained within the United States Department of Agriculture 7th Approximation soil classification. The relevant parts are shown in Appendix II. A similar classification is given by Farnham and Finney (1965), who give examples of other classifications too. These are "special classifications" in the same sense that a telephone directory is. They may be very good for one purpose, but useless for all others. The arbitrary definition of a "control section", 130 or 160 cm deep in the U.S.D.A. 7th Approximation, makes the classification of little value to those whose interest lies in the ecology or history of the peat-forming system, as Ingram (1978) points out.

Ecologists are likely to find the more "general" or so-called "natural" classifications of more use. There are very many of these, mostly making use of five main elements: topography and hydrology, present surface vegetation, morphology, water chemistry, and history. Amongst the earliest were those of Weber (1908) and Potonié (1908), and an influential later one is that of Sjörs (1948). An example of such a classification is shown in Appendix III, and others are given by Moore and Bellamy (1974) and elsewhere in this volume. Of particular interest are the classifications used in the Soviet Union, which contains perhaps 60% of the world's peat. Rather vague examples are given by Bradis and Andrienko (1972) and Elina (1972), and a more detailed description, but using Scandinavian and German terms, by Walter (1977); further discussion will be found in Chapter 4 of Part B.

Most of these schemes are intended for use within a limited geographic range: few of them would cope easily with the sub-Antarctic moss-peats (Fenton, 1978). Some interesting and very early "proto-classifications" are reviewed by Gorham (1953, 1957).

Most classifications recognize the fundamental importance of two factors: plant nutrition and source of water. The significance of these was first emphasized by Scandinavian ecologists, and is discussed elsewhere in this volume. Two extremes of each factor may be recognized. The water coming to the system may have a high concentration of plant "nutrients" (or a lower concentration but a constantly renewed supply, or both) in which case conditions may, inaccurately

but commonly, be called eutrophic. Water which has a low concentration of "nutrients" or which is not often renewed, causes oligotrophic conditions. The present surface vegetation may be entirely dependent on precipitation for its water supply ("ombrotrophic"), or most of its water may have flowed through rock or mineral soil or both ("minerotrophic"). The terms "bog" and "fen", with qualifiers, are freely used in classifications. Their relationship to nutrition and source of water is shown in Table 4.4.

Precipitation alone does not cause eutrophic conditions, and peat-forming systems which depend entirely on precipitation are almost universally recognized (nowadays) as "bog". The vegetation often contains much *Sphagnum*, which can make the water acid (Clymo, 1967), and a limited number of vascular plant species, particularly *Eriophorum* and dwarf shrubs, which can tolerate acid, oligotrophic, wet conditions. Water which has flowed through sedimentary rocks and acquired a high concentration of solutes usually gives conditions suited to a wider range of vascular plants, mostly of non-bog species, and is recognized as "fen". Classifications differ in their treatment of peat-forming systems which receive most of their water from weathering-resistant rock or mineral soil, and which are therefore oligotrophic and commonly have a vegetation similar to that of "bog". Sometimes the vegetation character is con-

sidered paramount, sometimes the origin of the water. On the whole such mires — a general term — have been called "bog" in Britain, but "fen" in Scandinavia where the "mineral soil water limit" is considered of great importance.

During its development a mire may have passed from fen to bog. Some classifications recognize this. Others ignore the history of the peat-forming system, but attach importance to morphology.

In general it is as well to remember that classifications are artificial, they are intended for *convenience*, and they should change to accommodate new knowledge. The quest for "the" classification of peat-forming systems has proved as difficult and as self-revealing (though not yet as deadly) as that for the Holy Grail, but there are now so many classifications in use (or disuse) that it should be possible to find one that is adequate for any specific limited purpose.

PEAT CHEMISTRY

Many factors affect the chemistry of peat. Amongst the most important are the nature of the original plant matter, the supply of inorganic solutes, the activities of plants and animals and of micro-organisms, environmental conditions (particularly temperature and the extent of waterlogging) and, finally, the age and history of the peat. These factors are not independent: the type and extent of microbiological activity depends on temperature and the extent of waterlogging; the nature of the original plants may change as eutrophic fen is succeeded by oligotrophic (ombrotrophic) bog, and so on.

There are marked vertical patterns in chemistry associated with gradients in these factors, and significant horizontal patterns within any one peat-forming community: one need only consider the "string bogs" of arctic regions (Ruuhijärvi, Part B, Ch. 2) to appreciate this.

It is convenient to consider the organic compounds in peat separately from the inorganic ones. Nitrogen and phosphorus do not fit easily into this scheme, and are considered at convenient points in both sections.

Organic constituents of peat

Peat begins to form when any one of a large number of plant species dies. At the outset therefore

TABLE 4.4

Broad outline of ecological classifications of northern peat-forming systems

Source of water	Nutrition	
	eutrophic	oligotrophic
Rock or soil	fen (a)	bog or fen (b)
Precipitation	—	bog (c)

Approximate equivalence of special terms:

Weber (1908)	Potonić (1908)	Sjörs (1948)	Tansley (1939)
(a) <i>Niedermoore</i>	<i>Flachmoore</i>	rich fen	fen
(b) <i>Übergangsmoore</i>	<i>Zwischenmoore</i>	poor fen	valley bog
(c) <i>Hochmoore</i>	<i>Hochmoore</i>	moss	raised bog; blanket bog

These terms are only approximately equivalent because different authors placed emphasis on different characters.

it contains the full range of chemical compounds found in the parent plants, dominated in quantity by the structural cell-wall carbohydrates. As the peat ages, its chemistry changes. Some substances are selectively removed. For example, plant pigments do not survive in acid peat, though they do in lake sediments (Gorham, 1961a). Other substances are formed *de novo*; the development of brown colour cannot be explained simply by removal of non-brown matter. Micro-organisms and, in the surface layers, small animals are known to be active (Coulson and Butterfield, 1978; see also Chapters 5, 10 and 11 of this volume), and it is tempting to suppose that these are the main agents of change. The extent to which slow chemical reactions, taking hundreds or thousands of years to become obvious, are involved is not known. Some animal activities are unexpected: the production of wax by the aphid *Colopha compressa* living on the roots of *Eriophorum* is an example (Wheatley et al., 1975). The wax is in interlinked fibres and contains paraffins, with some carbohydrate and secondary amides. It forms white aggregates up to 3 mm diameter which can be found to 6 m depth at least. Presumably the aggregates at lower depth are fossil. Those at 1 m depth show fewer fine fibres and less carbohydrate and amides. This example is sufficient to show that the chemistry of peat is likely to be very complex.

The usual approach to the organic chemistry of peat has been to extract the peat with a variety of solvents, and attack it with other chemicals to make it soluble, then to apply more precise methods to these fractions.

In general our knowledge of the organic composition of peat, and of the changes which occur, is fragmentary. Specialists have detected the presence, often in unmeasured concentration, of a wide range of organic substances. It is rarely possible to relate such studies to one another, however, because too little is recorded about the general properties, such as botanical composition, humification, depth or age of the sample. Notable exceptions are the works of Waksman and Stevens (1928a, b, 1929a, b, c), of Mattson and Koutler-Andersson (1954), and especially of Theander (1954): all fractionated peat from known positions in a profile. Some of their results are shown in Table 4.5 and Fig. 4.7.

The material soluble in non-polar solvents is often called peat "wax". The proportion of "wax"

increases with age and depth, or perhaps more specifically with humification, in the examples in both Table 4.5 and Fig. 4.7. This might be simply a result of selective survival; it does not seem to be associated with the presence of macroscopic remains of cuticularised plants, and there is no evidence for a concentration of aphid activity. The general problem illustrated here pervades the whole study of peat: to what extent is a difference observed now a record of historical differences in vegetation, and to what extent has it resulted from changes applied to the same material but over different time spans? Frenzel (Ch. 2) discusses this issue too.

The peat "wax" is a complex mixture of true waxes, "asphalt", and "resins" (Howard and Hamer, 1960) and includes at least some ligneous matter. It is also called "bitumen". Of these terms only wax (esters of fatty acids with alcohols other than glycerol; Fieser and Fieser, 1944) is at all clearly defined. For example, Gilliland and Howard (1968) made a further separation of peat "wax", using column chromatography. They recognised nine fractions, each of which was still a mixture, and identified, *inter alia*, alcohols with chain lengths of even numbers of carbon atoms from C₂₀ to C₃₀, and acids with chain lengths from C₁₇ to C₃₃ (with marked dominance of odd number lengths).

The compounds extracted from peat in polar solvents (Table 4.5: NH₃ or KOH and H₂O) were constant in proportion at different depths at about 14% of dry mass, although the proportion in *Sphagnum* (probably dead for a few years) was about 10%, of which at least 3% of the total dry mass was fructose, and a further 3% other sugars (galactose, glucose, mannose, arabinose, and xylose). In the lower peats about 1% was in these sugars, but no fructose was detectable. The concentration of free sugar is surprisingly high; media used for growing micro-organisms commonly contain 2 to 5% of sugars, and there is no shortage of active micro-organisms in the surface layers of peat, so it may be that these "solvents" attack the peat chemically too.

Further comparison of the fractions in Table 4.5 and Fig. 4.7 is far from easy. Waksman and Stevens (1928a, b, 1929a, b, c), and Mattson and Koutler-Andersson (1954) used two acid-hydrolysis stages. The first was mild, and may be assumed to have broken some polymeric carbohydrates into shorter sections. The second hydrolysis was more severe,

TABLE 4.5

Fractionation of organic compounds in surface *Sphagnum* and peat from southern Sweden (Theander, 1954)

Material	Depth (cm)	Age (yr)	Humification (Von Post scale)	Ash (%)	Successive extractions ¹ (%)						Residue	Lost ²	Last four columns = holocellulose
					C ₆ H ₆	CH ₃ OH	H ₂ O	bleach	NH ₃ then H ₂ O	KOH then H ₂ O			
<i>S. fuscum</i>	5	1-10	-	1.5	1.7	6.3	4.6	3.7	5.6	3.7	72.5	1.9	83.7
<i>S. imbricatum</i>	5	1-10	-	1.8	1.7	4.5	3.6	3.7	6.9	3.6	73.4	2.6	86.5
Peat A													
<i>S. imbricatum</i>	17	200-400	3	1.0	4.0	3.6	1.5	26.3	8.0	5.6	48.5	2.5	64.6
Peat B													
<i>S. tenellum</i> , <i>S. recurvum</i>	47	700-1000	4	1.1	3.1	4.5	2.0	24.7	8.5	5.5	47.8	3.9	65.7
Peat C													
<i>S. imbricatum</i>	57	900-1200	6	1.7	5.9	4.6	1.6	43.9	8.8	6.5	27.8	6.6	49.7
Peat D													
<i>S. imbricatum</i>	113	1900-2200	3	0.7	3.3	3.9	1.0	22.1	8.3	5.1	53.8	2.5	69.7
Peat E													
<i>Sphagnum</i> spp.	295	4300-4800	6-7	1.7	6.7	4.9	1.1	57.1	8.8	5.2	20.4	5.4	39.8

¹The fractionation procedure was: (1) C₆H₆ for two days; (2) CH₃OH five days; (3) dry and extract with H₂O 9 h; (4) Na hypochlorite + CH₃COOH at 60-65°C, 2-4 h; (5) swell in liquid ammonia, extract with H₂O; (6) 5% KOH under N₂, 8 h, extract with H₂O. Stages 1-3 are simple extractions causing little or no chemical modification. Stage 4 is a mild oxidation.

²Proportion lost from the holocellulose fraction during the preceding bleaching. This was estimated separately, and is excluded from the "bleach" fraction.

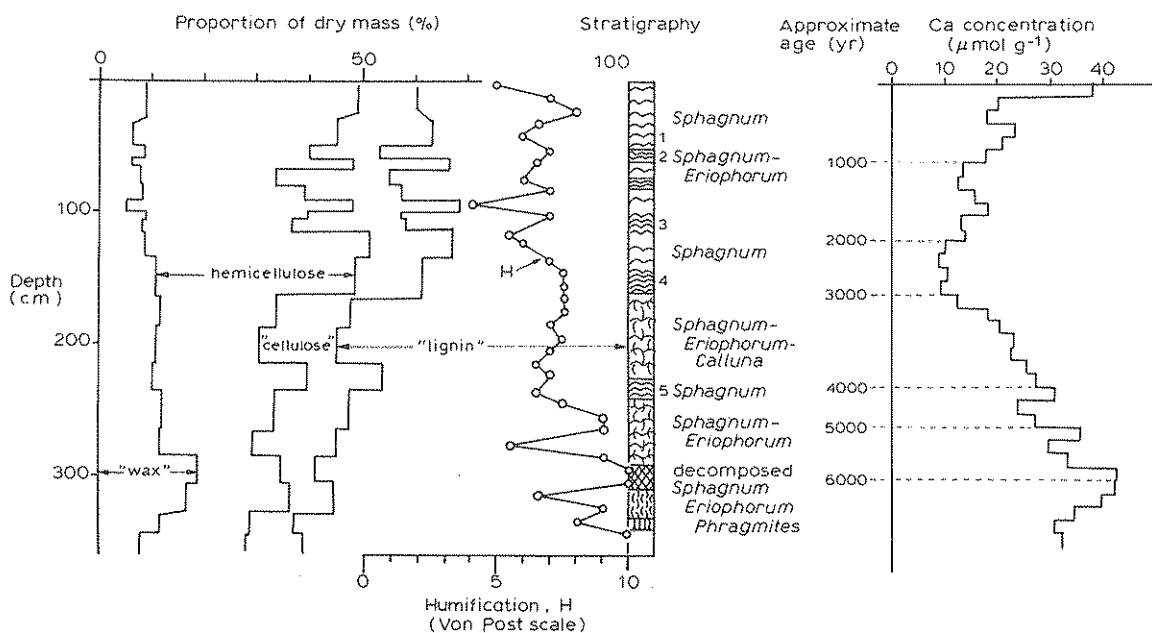


Fig. 4.7. Stratigraphy, botanical composition, humification (Von Post scale), age, exchangeable Ca concentration and organic fractions in Ramna bog, southern Sweden. The fractionation procedure was: (1) reflux in C₂H₅OH and C₆H₅ ("wax"); (2) 2% HCl, boil 1 h ("hemicellulose"); (3) 80% H₂SO₄ *in vacuo* 2½ h, dilute, boil 5 h ("cellulose"); (4) residue ("lignin"). Redrawn from Mattson and Koutler-Andersson (1954). The numbers 1-5 in the stratigraphy column are recurrence horizons.

but not exceptionally so. The fractions thus isolated they called "hemicellulose", "cellulose", and (the residue) "lignin". "Hemicellulose" is nowadays usually isolated by hydrolysis with alkali and after removal of lignins. The terms "cellulose" and "lignin" are valid only in the most general sense.

Theander (1954) used a mild hypochlorite oxidation to remove lignins before alkaline hydrolysis, which should then give some indication of hemicellulose proportions (Bonner, 1950).

If these equivalences are accepted, then the two sets of data do agree quite closely. Again it is the degree of humification which seems important; "lignin" forms about 30% of the total at H3, rising to 50 to 60% at H6-7. The amounts of "hemicellulose" (Fig. 4.7, Table 4.5) differ, but whether the difference lies in the peat or in the methods cannot be determined. The proportion of "hemicellulose" + "cellulose" (Fig. 4.7) and of KOH-solubilized + residue (Table 4.5) behave in much the same way, decreasing with humification from initial values of about 75% in newly dead *Sphagnum* to about 50% in the early stages of peat formation and later to about 25% in highly humified peat. Again it is impossible to assess the relative importance of historical difference and of development, but the drift of values over the middle section of Fig. 4.7, for the peat between 2000 and 4000 years old, which has little change in botanical composition, argues for continued slow changes.

The composition of the holocellulose (alkali-solubilized + residue) is shown in Table 4.6. In newly dead *Sphagnum* nearly 60% of the total mass

could be positively identified. Most of the sugars and uronic acids declined in the same way, but mannose increased for the first thousand years. The identity of about 20% of the total dry mass, all in the holocellulose fractions, remained unknown. This proportion did not appear to depend on humification or age. Theander (1954) suggested that it might be non-carbohydrate material, but the recorded amounts of uronic acids seem to be lower than those measured by other workers (Clymo, 1963; Spearing, 1972) and lower by 5 to 10%, on a dry-weight basis, than those necessary to account for the cation-exchange properties of *Sphagnum* (Clymo, 1963) and peat (Puustjärvi, 1956). These cation exchangers — polymers containing uronic acids — are of great importance in peat chemistry. They provide not only the possibility of a large reserve capacity for cations, but also reduce the capacity for anions because the concentration of anions in the charged phase is reduced (Donnan, 1911).

The standard procedure for further fractionating the fraction of soil organic matter soluble in alkali or neutral sodium pyrophosphate ("humic substances") is to add acid. The material which remains in solution is "fulvic acid". That which precipitates is treated with ethanol. Insoluble material is "humic acid", soluble is "hymatomelanolic acid". Schnitzer (1973) summarizes further procedures, and Schnitzer and Khan (1972) record hundreds of specific compounds isolated from soils by various procedures. These methods seem to have been applied to peat only infrequently. It is worth noting therefore (Table 4.6) that, in deeper and

TABLE 4.6

Sugars and uronic acids in acid hydrolysates of holocellulose fractions in Table 4.5; figures are proportion of total dry mass of peat (A = alkali-soluble (NH₃ and KOH solubilized); R = insoluble residue; + + = present but less than 2%; + = present but less than 0.5%)

Material	Humifi- cation	Uronic acids		Galac- tose		Glucose		Mannose		Arabi- nose		Xylose		Rham- nose		Peat proportion accounted for here	Holocellulose unaccounted for here
		A	R	A	R	A	R	A	R	A	R	A	R				
<i>S. fuscum</i>	1	3.3	15.6	+ 5.2		+ 26.8		+ + +		+ -		+ 3.9		+ +	58.2	23.6	
<i>S. imbricatum</i>	1	3.4	14.5	+ 5.3		+ 28.4		+ + +		+ -		+ 2.6		+ +	57.6	26.3	
Peat A	3	3.3	7.8	+ 2.6		+ + 21.8		+ 2.2		+ -		+ + 2.2		+ +	42.9	19.2	
Peat B	4	3.8	7.3	+ 3.0		+ + 18.9		+ 3.0		+ -		+ + 3.0		+ +	42.0	19.8	
Peat C	6	2.5	3.7	+ + +		+ + 13.6		+ + +		+ -		+ + + +		+ +	25.9	17.2	
Peat D	3	3.1	8.7	+ 3.4		+ + 22.3		+ 2.4		+ -		+ + 2.9		+ +	45.3	21.9	
Peat E	6-7	+ +	+ +	+ + +		+ + 11.4		+ + +		- -		+ +		+ +	18.1	16.3	

older horizons, 60% falling to 20% seems to consist of polymers of a few sugars — predominantly glucose — and uronic acids, and 5% rising to 15% of a variety of complex non-polar compounds ("wax"). Only 20%, and possibly less, falls in the class of "humic substances".

Peat also contains, or can be treated to yield, a great variety of phenolic compounds. Many of these may be extracted in the "lignin" fraction forming 4% rising to 60% of the total mass. *Sphagnum* itself contains unusual lignins (Bland et al., 1968), and so does peat (Morita, 1968). In hot-water extracts of *Sphagnum-Eriophorum* peat, Wildehain and Henske (1965) found vanillin; *p*-hydroxybenzaldehyde; 4-hydroxy-2-methoxyacetophenone; 2,4,6 trihydroxyacetophenone; 3,4 dihydroxypropio-phenone; glucoacetovanillone; *p*-hydroxybenzoic acid; vanillic acid; ferulic acid; protocatechuic acid; caffeic acid; *p*-hydroxyphenylpyruvic acid; 4-hydroxy-3-methoxyphenylpyruvic acid; and dehydrodivanillin. Such work is still at the stage of "finger printing" but eventually the amounts and origin of these substances must be known if the

crudely derived bulk chemical properties of peat "lignin" are to be explained.

There are many reports that peat and *Sphagnum* extracts affect the growth of bacteria, fungi, algae and vascular plants. Sometimes growth is increased; in other cases it is decreased (for examples see Květ, 1955; and Given and Dickinson, 1975). Very often there is an unsupported suspicion that phenolic compounds are having toxic effects. Control experiments with extracts of plants and humus from mineral soils, where decay is more complete, are the exception. It would be surprising if peat extracts did not have *some* effects. The important question is "How big are these effects in natural conditions?". It is difficult to answer this question.

The "lignin" fractions (insoluble in non-polar solvents, water, or sulphuric acid) as defined by Waksman and Stevens (1928a, b, 1929a, b, c) and by Mattson and Koutler-Andersson (1955) have some interesting gross chemical properties. For example, the proportion of lignin is closely correlated (Fig. 4.8) with the ability of the peat to

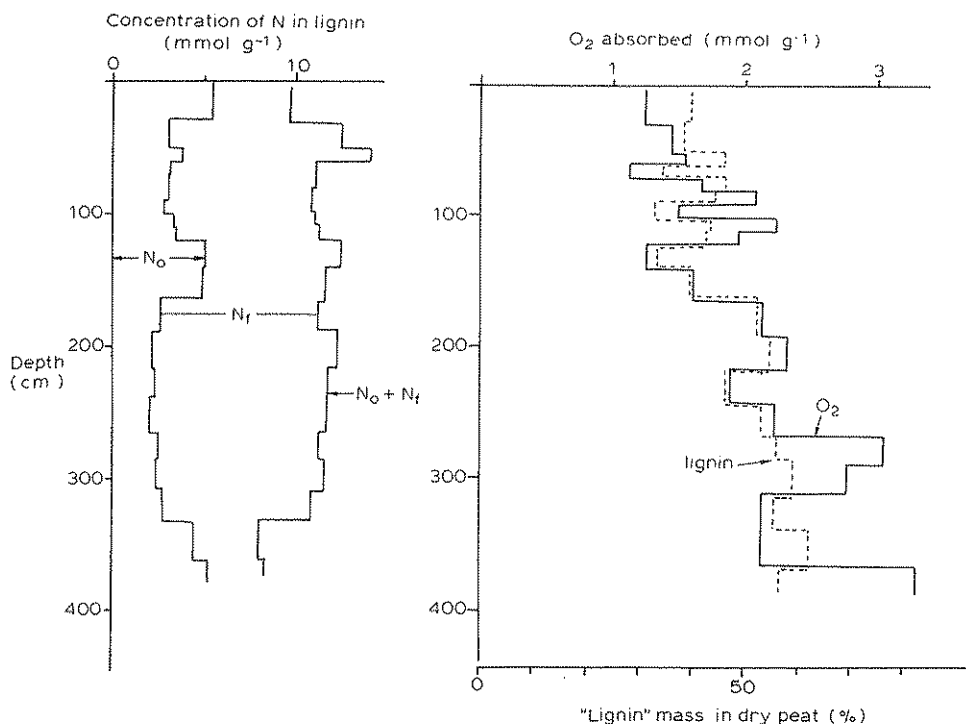


Fig. 4.8. Proportion of lignin, oxygen-absorbing capacity of peat, and properties of the "lignin" fraction of peat in Ramna bog, southern Sweden. N_o=nitrogen concentration in "lignin"; N_f=concentration of nitrogen absorbed into non-exchangeable form from dilute ammonia. Redrawn from Mattson and Koutler-Andersson (1955).

TABLE 4.7

Fractionation of minerotrophic and ombrotrophic peat, and of newly dead plants (values are % of dry mass)

Depth (cm)	Peat type	Fraction ¹							Lost
		1 "wax"	2 or 3	4 "hemi- cellulose"	5 "cellulose"	6 "lignin"	7 "protein"	8 "ash"	
<i>A. Raised bog, Cherryfield, Me (U.S.A.)²</i>									
1-8	<i>Sphagnum</i>	2.4	1.5	26.5	16.9	27.2	4.1	2.0	19.4
8-20	<i>Sphagnum</i>	2.6	1.9	25.2	14.7	29.2	4.3	1.1	21.0
20-30	<i>Sphagnum</i>	2.8	1.8	24.6	16.0	28.9	5.1	1.0	19.8
30-46	<i>Sphagnum</i>	2.6	2.1	22.3	13.7	32.2	5.2	0.9	21.0
46-61	<i>Sphagnum</i>	3.0	3.2	18.5	14.7	33.2	4.8	1.1	21.5
183-214	<i>Sphagnum</i>	4.0	3.2	15.9	15.6	37.4	4.4	1.0	18.5
460-480	<i>Sphagnum</i>	4.9	4.3	12.7	11.9	44.8	4.7	1.1	15.6
550-580	sedge	6.0	5.1	6.0	5.1	54.1	11.5	2.8	9.4
<i>B. Ramna bog, southern Sweden³</i>									
60-65	<i>Sphagnum</i>	6.0		42.1	18.0	38.4	6.4 ⁴	0.8 ⁴	
67-79	<i>Sphagnum</i>	7.7		25.5	21.2	36.6			
190-216	<i>Sphagnum</i>	10.3		19.8	15.1	48.4	5.0	1.5 ⁴	
217-238	<i>Sphagnum</i>	10.0		29.6	14.0	39.9			
<i>C. Lowmoor, Newton, N.J. (U.S.A.)²</i>									
12	?	0.7		10.3	0	38.4	22.5	13.2	
18	?	1.1		9.0	0	50.3	18.7	10.1	
160-180	?	0.5		7.0	0	57.8	14.8	10.2	
<i>D. Everglades, Cladium peat²</i>									
0-65	surface	4.3	1.2	6.9	0.3	43.7	22.8	12.1	8.8
65-26	upper fibrous	4.7	1.1	6.4	0.3	46.1	23.1	10.0	8.4
26-40	pure <i>Cladium</i>	4.8	1.3	8.0	0.4	44.9	22.3	6.9	11.4
40-50	lower fibrous	4.7	1.4	7.6	0.4	47.6	21.3	8.1	9.0
50-62	upper colloidal	4.1	0.5	2.2	0	19.3	9.0	59.6	5.4
62-70	lower colloidal	2.3	0.7	2.6	0	28.5	13.0	42.3	10.6
110-120	lower fibrous	2.4	1.2	4.3	0	48.4	20.4	15.1	8.1
<i>E. Newly dead plant material</i>									
	<i>Carex</i> leaves	2.5	12.6	18.4	28.2	21.1	7.1	3.3	6.9
	<i>Carex</i> rhizomes	1.7	3.2	20.9	11.8	41.7	14.6	4.6	1.6
	<i>Cladium</i> leaves	1.1	6.9	21.5	28.3	29.1	7.2	3.9	2.1
	<i>Cladium</i> rhizomes	0.9	5.2	20.8	30.7	30.9	3.8	3.6	4.1
	<i>Hypnum</i> (moss)	4.6	8.4	18.9	24.8	21.1	4.2	4.3	13.7
	<i>Sphagnum</i>	1.6	1.6	24.5	15.9	19.2	1.9	19.9	13.5
	<i>Pinus strobus</i> leaves	11.4	7.3	19.0	16.4	22.7	2.2	2.5	6.0
	Oak leaves	4.0	15.3	15.6	17.2	29.7	3.5	4.7	10.1

¹Extractants and fractions: (1) ether; (2) cold and hot water; (3) C₂H₅OH (boiling 95%), 1-2 h; (4) 2% HCl, boil, 5 h = "hemicellulose"; (5) 80% H₂SO₄ cold, 2 h then dilute and reflux, 5 h = "cellulose"; (6) residue, excluding (7) and (8) = "lignin"; (7) Kjeldahl N × 6.25 = "protein"; (8) inorganic ash.

²From Waksman and Stevens (1928a, b, 1929a, b, c).

³From Mattson and Koutler-Andersson, (1954).

⁴Approximate mean for the range.

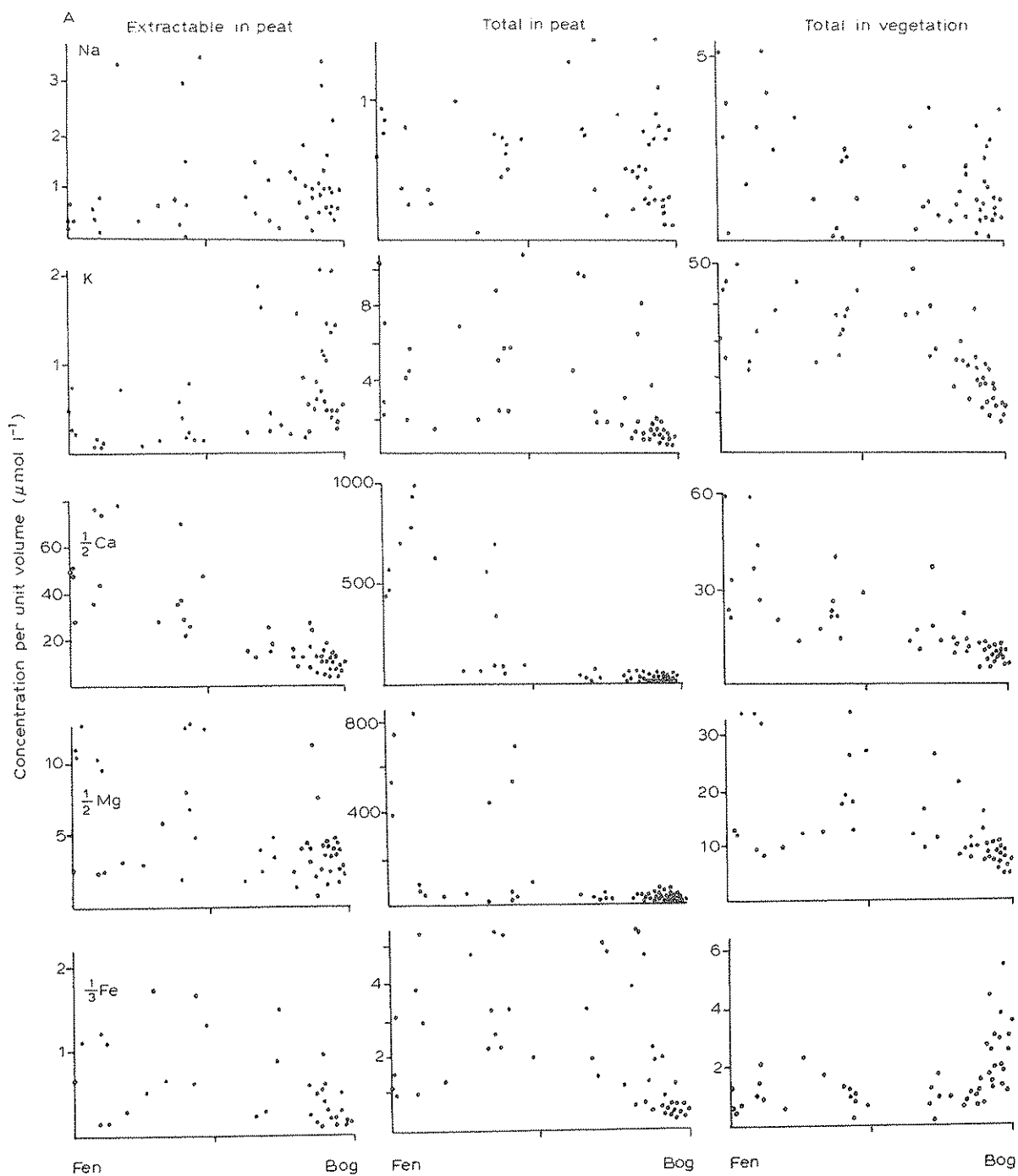


Fig. 4.9A.

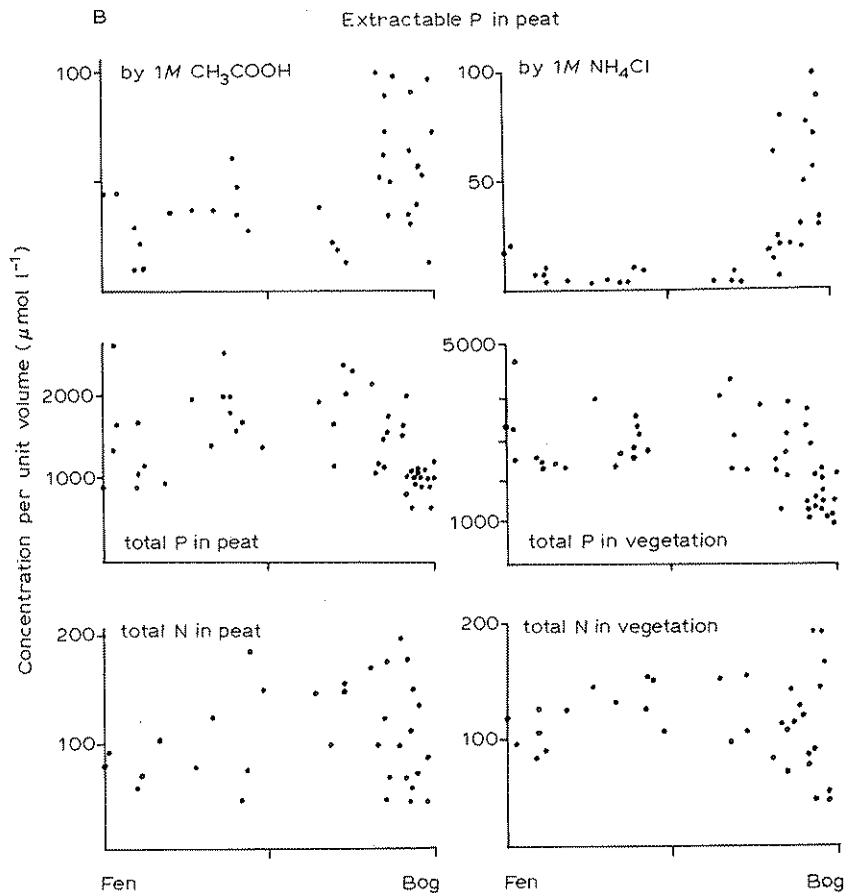


Fig. 4.9. Exchangeable and total concentration of elements in peat, and total in vegetation, in mires in southern Germany. The sites for samples were arranged using reciprocal averaging (Hill, 1973) of the vegetation. Fen is to the left, bog to the right. Na, K, Ca, Mg, Fe in Fig. A; N and P in Fig. B. Redrawn from Waughman (1980) assuming that peat and plants have bulk density of 0.1 g cm^{-3} .

combine chemically with O_2 . The total Kjeldahl-nitrogen content of the "lignin", N_0 , varies by a factor of three, but the Kjeldahl-nitrogen, after shaking with 12% ammonia solution in an atmosphere of oxygen, then washing with 0.1M HCl and with water (i.e. the non-exchangeable N) is remarkably constant except for the top 50 cm and the base. It seems as if the "lignin" has a nearly constant "nitrogen capacity" which is filled to a greater or lesser extent at different depths. The combination of ammonia with the peat is accompanied by an oxidation. Mattson and Koutler-Andersson (1955) also found N_0 to be correlated with the pH of electro-dialyzed peat, and inversely with "excess base", but the correlation with the

proportion of "lignin" in the peat is almost as high.

Much of this account has been concerned with *Sphagnum*-dominated peat. It is of interest to compare these peats with other types. Table 4.7 shows some of the results obtained by Waksman and Stevens (1928a, b, 1929a, b, c) and Mattson and Koutler-Andersson (1954). The freshly dead plant materials differ in composition, but far less than the minerogenic and ombrogenic peats. In particular the minerogenic peats contain smaller proportions of "hemicellulose" and "cellulose", even after a relatively short time. On the other hand they have more "lignin" and "protein" (and ash). Again, it is impossible to separate the effects of original composition from those of development,

but it seems clear that the changes during decay are at a different rate, or perhaps even of a different kind, in microgenetic peat and ombrogenous peat (see Sikora and Keeney, Ch. 6). The fractionation procedures are unable to distinguish readily metabolizable from resistant chemicals in the different fractions.

Inorganic constituents of peat

Some idea of the range of concentration of elements in peat can be obtained from Fig. 4.9, assembled from Waughman (1980). The peat samples on which these analyses were made came from the top 20 cm of sites in mires in southern Germany. The sites were ordinated by reciprocal averaging using vegetation composition, and are arranged from fen at the left to bog at the right. The vegetation ordination provides a quasi-objective means of positioning the sites on the fen–bog axis. The interrelation of vegetation and mire chemistry is thereby revealed. At the bog end occur species such as *Sphagnum* spp. and *Eriophorum vaginatum*; in the centre are *Menyanthes trifoliata*, *Carex rostrata* and *Equisetum fluviatile*; and at the fen end *Schoenus ferrugineus*, *Juncus subnodulosus*, and *Scorpidium scorpioides*. In fens, with pH about 7.5, the dominant cations in peat are Ca^{2+} ($\text{Ca}^{2+} \approx 500 \mu\text{mol l}^{-1}$, of which about 1/20 is easily extractable) and Mg^{2+} ($\text{Mg}^{2+} \approx 300 \mu\text{mol l}^{-1}$, of which about 1/50 is easily extractable). In bogs, with pH about 4.0, the total concentration is only one-tenth that in fens, or less, though the concentration of extractable Ca^{2+} and Mg^{2+} is not reduced by quite so much. The concentration of iron and phosphorus is also low in bogs, and higher towards the fen end of the continuum, but with some indications of lower concentrations again in rich fens. Sodium and nitrogen show no clear pattern, but total potassium shows a pattern similar to that of iron, though extractable potassium and phosphorus are present in smaller concentration in fens than in bogs. [The concentration of extractable phosphorus depends considerably on the extractant (Fig. 4.9B), and the concentration of phosphorus in peat water is much lower than either “extractable” or total phosphorus — see p. 187 below.] On the whole the concentration in the vegetation reflects the total concentration in peat, with the exception of iron which is more concentrated in bog vegetation than it is in bog peat, and less in fen vegetation than in fen peat.

The majority of analyses of inorganic constituents of peat have been made on north-temperate and boreal peatlands (but see Anderson, Vol. B, Ch. 6). Any account of the inorganic chemistry of peat must therefore be biased. It is convenient to consider first the processes affecting the profile of concentration of inorganic constituents, next examples of the vertical distribution in deep profiles and the pattern of horizontal variation, and thirdly the details in the top 50 cm — the so-called “active layer” (Romanov, 1968).

Processes affecting the inorganic constitution of peat

There are several processes which may combine to determine the concentration of an inorganic substance in peat.

Initial concentration in the plant or in the water in the peat. The biggest difference is between plants growing under the influence of mineral soil water, which usually has a relatively high concentration of, *inter alia*, calcium, iron, aluminium and manganese, and plants dependent on precipitation and dry deposition. The concentration in precipitation of elements such as sodium, magnesium and chlorine, which originate principally in sea spray, increases markedly towards coasts (for examples see Gorham, 1958; Boatman, 1961; and Sonesson, 1970). Other elements in precipitation and dry deposition, such as aluminium, manganese and iron, probably derive from soil dust (Peirson et al., 1973). Other distinguishable sources are industrial and domestic gases (sulphur dioxide, ammonia), smoke, industrial dusts, road dust (Tamm and Troedsson, 1955), volcanic ash, and extra-terrestrial particles (meteorites). Volcanic ash is of local importance, in Iceland for example. Meteorites are generally of negligible importance, though locally they can be catastrophic.

The supply of industrial and domestic gases, particles and solutes has undoubtedly increased and the increases, in a general way, are abundantly documented. Attempts to demonstrate increases in, for example, lead in Arctic and Antarctic snow and ice have posed extremely difficult analytical problems because of the low concentration (Murozumi et al., 1969), but the “concentration” of such elements by mosses including *Sphagnum* has made such work much simpler with bryophytes (Rühling

and Tyler, 1971, 1973). The recent increase in acidity of precipitation (attributable to oxidation of sulphur dioxide) in Scandinavia has been documented (Granat, 1972; Brackke, 1976), and may have had some marked effects on fish populations. Earlier increases are suspected but are less well established. For example, Conway (1949) noted that a change of peat type at Ringinglow in the Pennines preceded the appearance of layers of soot, and drew attention to the high concentration of sulphur dioxide in the air and the low pH (about 3.1) of the present bog surface.

The concentration of inorganic constituents in dry deposition and in precipitation varies with place and fluctuates with season (Cawse, 1974) and, for example, with agricultural practice (Boatman et al., 1975). Long-term changes are superimposed on these fluctuations. Generalization is therefore difficult. There are numerous measurements of the concentration of solutes in precipitation, notably those in the network of stations (principally Scandinavian) described by Eriksson (1955) and in subsequent quarterly reports in *Tellus*. There are considerable technical difficulties in making such measurements (Paterson and Scorer, 1973) and in interpolating between stations (Granat, 1975), so there are few cases where precipitation chemistry can be compared directly with peat chemistry. One example, from the Pennine hills of England, is shown in Table 4.8. The peat came from the top 10 cm (A.J.P. Gore, pers. comm., 1979). The last line shows that the apparent effectiveness of trapping is $N > P > Ca \approx Mg > K \gg Na$. The order for the last four is approximately that to be expected if these elements are trapped on cation exchange sites, and indeed, for these four elements, most is exchangeable (Gore and Allen, 1956; Smith, undated; Sonesson, 1970). Very little of the nitrogen and phosphorus is exchangeable, consistent with their presence in organic combination.

Nitrogen may be supplied in significant amounts as ammonia gas, which may be absorbed directly by acid peat (Ingham, 1950), or in special cases by "fixation" of atmospheric nitrogen (assessed by acetylene reduction) by root nodules of *Myrica gale* (Sprent et al., 1978) or — at a rate independent of pH between 4.5 and 7.5 — by blue-green algae associated with *Sphagnum* or other semi-aquatic bryophytes (Basilier, 1973; Basilier et al., 1978; Dickinson, Ch. 5).

Decay and loss as gas of peat organic matter. This would cause a non-selective increase in concentration of all inorganic solutes.

Relocation of inorganic constituents by physico-chemical processes. The hydraulic conductivity of humified peat is low (Rycroft et al., 1975b) and in permanently waterlogged peat of this kind the mass movement of water is very slow (Knight et al., 1972), so there is probably little mass redistribution of inorganic solutes below the surface 50 cm of peat. Diffusion may occur. There are few measurements of the diffusion rate of solutes in saturated peat. Giles (1977) found the diffusion coefficient of labelled (^{32}P) phosphate in saturated peat was about $10^{-6} \text{ cm}^2 \text{ s}^{-1}$, compared with about $10^{-5} \text{ cm}^2 \text{ s}^{-1}$ in water and much lower values — around 10^{-8} to $10^{-10} \text{ cm}^2 \text{ s}^{-1}$ — in unsaturated soils (Nye and Tinker, 1977). There seem to be no records of diffusion coefficients of cations in saturated peat, but one might expect the value to be lower than for phosphate because the high cation exchange capacity effectively enlarges the volume of the peat.

Given the diffusion coefficient and concentration gradient, then Fick's Law may be used to calculate the amount of solute moved. For example, if the diffusion coefficient were $10^{-6} \text{ cm}^2 \text{ s}^{-1}$ and the concentration gradient that of calcium in Fig. 4.12 below (assuming bulk density of 0.1 g cm^{-3} gives a gradient of about $0.3 \mu\text{mol cm}^{-1}$ in the region just above the *Carex*-moss peat), then the flux would be about $10 \mu\text{mol cm}^{-2} \text{ yr}^{-1}$. The total calcium in the 250 cm above the *Carex*-moss peat is about $400 \mu\text{mol cm}^{-2}$, representing about forty years of diffusion at this rate. The real elapsed time since the *Carex*-moss boundary is probably nearer to 4000 years, suggesting that, if diffusion is indeed the main process affecting the calcium profile in these conditions, then the diffusion coefficient must be about $10^{-8} \text{ cm}^2 \text{ s}^{-1}$ — only about one hundredth that of phosphate. This would be consistent with experimental measurements on cation exchange resins (Helfferich, 1962). If diffusion were the principal controlling factor one would also expect that the profile would be a hollow curve (which it is) and that trivalent cations would have even lower diffusion coefficients. The behaviour of iron in Fig. 4.12 is consistent with this. One would also expect there to be little change in concentration associated with changes in humification. This too

TABLE 4.8

Influx of solutes and particles (wet and dry deposition) on blanket bog at Moor House, England, and concentration of the corresponding elements in the top 10 cm of peat: the peat contains *Sphagnum*, *Calluna*, and *Eriophorum*

A. Influx in precipitation

Year	Precipitation (mm)	Influx ^b ($\mu\text{mol cm}^{-2} \text{ yr}^{-1}$)					
		NH ₄ + NO ₃	PO ₄	Na	K	Mg	Ca
1959-60	1790	—	0.11	14.8	1.4	1.0	2.6
1960-61	1910	—	0.30	12.2	1.2	—	3.3
1961-62	2060	7.6	0.09	12.9	0.9	—	3.1
1962-63	1870	8.9	0.60	24.1	1.5	—	5.7
1963-64	1800	10.3	0.19	10.2	0.8	—	2.2
1964-65	1770	13.3	0.35	17.2	1.6	1.6	2.8
Mean		10.0	0.27	15.2	1.2	1.3	3.3

B. Concentration in peat

		Concentration ($\mu\text{mol cm}^{-3}$)					
		total N	total P	Na	K	Mg	Ca
Site 2 ^a				1.0	1.3	2.6	3.0
Site 3 ^a				0.7	1.0	3.2	3.0
Ten sites ^c	lowest	58	0.9	0.3	0.2	0.7	2.4
	highest	136	1.7	0.8	0.7	5.2	10.5

C. Approximate proportion of annual influx in 1 cm³ of peat (median for top 10 cm)

	N	P	Na	K	Mg	Ca
	10	5	0.05	0.7	4.0	4.0

^aFrom Gore and Allen (1956). ^bFrom Gore (1968), assuming peat bulk density is 0.1 g cm⁻³. ^cFrom Smith (undated).

seems to be generally true (for example calcium in Fig. 4.7). But there is a wide gap between the conclusion that diffusion *could* account for part of the profile, and the conclusion that it *does*. Some elements in Fig. 4.12 — sodium, potassium, magnesium and aluminium — do not fit this hypothesis at all. If diffusion is important in these cases it must be superimposed on other processes.

The rate of relocation may be much influenced by changes of chemical state. Phosphate may be released into solution if peat is frozen then thawed (Sæbø, 1969); iron and manganese change valence

between oxidized and reduced forms (aerobic and anaerobic peat); some elements (for example iron, manganese, lead and copper) can form relatively insoluble sulphides, and probably become less mobile in consequence when they pass into the anaerobic zone where sulphide is produced. They may also form relatively stable complexes with organic constituents in the peat (Sikora and Keeney, Ch. 6). The elements nitrogen and phosphorus are present in relatively low concentration but in a wide range of compounds which may be actively metabolized; the rate of "mineralization" of nitrogen is an im-

portant character if peat is used commercially as a plant substrate, and is related to the level of the water table (probably through the aerobic/anaerobic transition and microbial activity) in a complex way (Williams, 1974).

Relocation by washing through the surface layers is considered later.

Relocation of inorganic constituents by biological processes. The main processes are absorption of solutes by plant roots, then movement up into the rhizomes and leaves, and downward movement when roots grow down into the peat. Bog species differ in the vertical distribution of their roots, and more particularly in the profile of radioactive solute uptake (Boggie et al., 1958; Giles, 1977). Most species cycle solutes through the top 20 cm of peat, but the bog species *Eriophorum* may be effective to a depth of 60 cm or more. The roots of the fen plant *Cladium mariscus* extend to this depth (Conway, 1937), as probably do some roots of *Calamagrostis* spp. (Luck, 1964) and of the larger species of *Carex*. In *Sphagnum fuscum*-dominated bogs in the Abisko area of northern Sweden, *Rubus chamaemorus* is common. The rhizomes produce two types of roots: fine, surface-ramifying ones, and large (1–2 mm diameter) vertical roots at a density of about one per centimetre of rhizome. These vertical roots drill straight down to near the water table — perhaps from 10 to 60 cm down — with few or no laterals, then explode in a dense network of very fine branches. Stavset (1973) reports *R. chamaemorus* roots down to 180 cm in peat on Andøy in northern Norway.

The quantitative importance of roots of various bog plants in relocating phosphate has been examined by Giles (1977). Phosphate was used as a convenient tracer — ^{32}P has a half-life of about ten days and produces moderately energetic β radiation — but the concentration of soluble phosphorus in peat is but a tiny fraction of the total (see later). The exploitation of peat by a plant root is probably diffusion-limited, because the deep roots (at least) of bog plants appear to lack the mycorrhizal associations (Dickinson, Ch. 5) which might effectively extend out from the roots the zone from which rapid transport is possible (Sparling and Tinker, 1978a, b, c). It is, therefore, the length of root produced which is the most important measure of exploitation potential. Giles, taking into account

the length of life and period of activity of roots, calculated an effective depletion cylinder of about 4 mm for most species. Table 4.9 shows the present proportions of species on a site in a valley bog in southern England, and the time needed for 95% of the peat volume at various depths to have been within the exploitation range of a root. Peak above-ground biomass is a fair estimator of productivity in this community, and is about the same as litter fall. Above-ground production is about six times the production of roots, and *Eriophorum* has a greater proportion of its roots at greater depths than other species. It is the main contributor in this community to relocation of phosphate from greater depths, as shown by the time for $P=0.95$ depletion. Given the usual rate of peat "growth" of about 1 cm yr^{-1} at the surface decreasing to about 1 mm yr^{-1} at 50 cm depth, it is apparent that there is a high probability that soluble phosphate will be kept in circulation at the surface. For cations, with smaller diffusion coefficients, exploitation even as close as 10 cm to the surface is probably much lower. The last line of Table 4.9, corresponding to a depletion cylinder of negligible thickness, gives some indication of the chance of exploitation of a totally immobile substance.

In general, one might expect there to be significant biological relocation of anions to a depth of 50 cm, but to a much smaller depth for cations. There is a great deal of internal cycling between root, rhizome and shoot — in some bog species at least (Sæbø, 1968, 1970, 1973, 1977; Chapin et al., 1975, 1978, 1979; Shaver et al., 1979). This internal cycling is considered in detail elsewhere in this volume.

The relocation of inorganic solutes by vascular plants is not surprising, but relocation in the surface layers by bryophytes is more so. *Sphagnum papillosum* plants supplied with $\text{H}^{14}\text{CO}_3^-$ incorporate ^{14}C , about 80% of which is in the alcohol-insoluble fraction after 24 h (Clymo, 1965); yet three months later, after the plants had grown on average 3.2 cm, as much as 35% of the ^{14}C in the plants after 24 h was found in the capitulum formed since the original treatment, and only 5% at and below the original treatment level. (Of the rest, 25% was in stem and branches which were probably part of the capitulum at the time of treatment.) This movement may have been partly outside the plant (as carbon dioxide respired and then reabsorbed),

TABLE 4.9

Shoot and root productivity, and the calculated time for 95% of peat to be exploited by plant roots, at a site in the valley bog at Cranemoor, southern England

	<i>Eriophorum angustifolium</i>	<i>Molinia caerulea</i>	<i>Narthecium ossifragum</i>	<i>Rhynchospora alba</i>	Ericaceae	All five taxa
<i>Biomass and dry mass productivity</i>						
Maximum above-surface live biomass ¹ (g m ⁻²)	7	12	16	19	8	61
Root productivity (mg dm ⁻³ yr ⁻¹)						
At depth 10 cm	3.6	14.2	18.4	8.9	1.6	47
20 cm	4.2	3.3	6.9	1.3	0.1	16
35 cm	0.5	0.5	0.02	<0.1	<0.1	1.2
Root productivity summed to 60 cm depth (g m ⁻² yr ⁻¹)	0.9	2.6	3.7	1.5	0.3	9.0
<i>Root growth in length</i>						
Rate of root growth (m dm ⁻³ yr ⁻¹)						
At depth 10 cm	0.29	1.18	1.58	0.55	0.35	3.9
20 cm	0.47	0.15	0.42	0.15	0.01	1.2
35 cm	0.04	0.02	0.01	<0.01	<0.01	0.1
Rate of root growth summed to 60 cm depth (m dm ⁻³ yr ⁻¹)	110	200	290	100	54	750
<i>Time (yr) for the depletion zone of roots to sum to 95% of the peat volume</i>						
At depth 10 cm	180	50	30	100	210	13
20 cm	110	360	130	370	7500	44
35 cm	1250	2700	5500	>8000	>8000	750

The five taxa shown grow intermixed and account for about 98% of the biomass of rooted plants. *Sphagnum* is the other major component of the vegetation. Biomass and productivity of rhizomes are not included. Data of Giles (1977).

¹ Minimum was near zero, so these values approximate productivity. Litter-fall was 56 g m⁻² (cf. 61 g m⁻² maximum live biomass).

but it seems probable that most was within the moss.

The relocation of ¹³⁷Cs is another example. The radioactive ¹³⁷Cs produced during nuclear bomb tests reached a sharp peak in concentration in deposition in 1963. This is a useful date marker now well established in use on lake sediments (Ravera and Premazzi, 1972; Pennington et al., 1973, 1976). It has been used on peat profiles too (Clymo, 1978, and unpublished). Examples are shown in Figs. 4.10 and 4.18 below. The most notable feature is that most of the ¹³⁷Cs which has fallen is retained in the top 1 or 2 cm of live surface moss. In these cases vascular plants are hardly involved because the samples were from a nearly pure *Sphagnum* lawn.

In almost all cores there is a lower peak at a depth consistent with it having been laid down in 1963 and subsequently moved down and become spread over a greater depth. This lower peak in con-

centration of soluble ¹³⁷Cs may be not at all conspicuous in a single profile, as Fig. 4.10 shows, but it appears consistently. The concentration of insoluble ¹³⁷Cs, perhaps in glassy particles, is usually more conspicuous and rather higher up, perhaps because the peak has moved less.

These relocation processes are summarized in Fig. 4.11.

Deep peat-profiles

As an example, Fig. 4.12 (from data of Mörnsjö, 1968) shows the variation of concentration in a variety of substances at Fjällmossen, southern Sweden, in a concentrically domed peat bog with *Sphagnum* peat overlying *Carex*-moss peat over *Alnus* wood peat. There are several other profiles of the concentration of several elements on samples taken at intervals of from 10 to 5 cm to a depth of more than 2 m, *inter alia*, those of Sillanpää

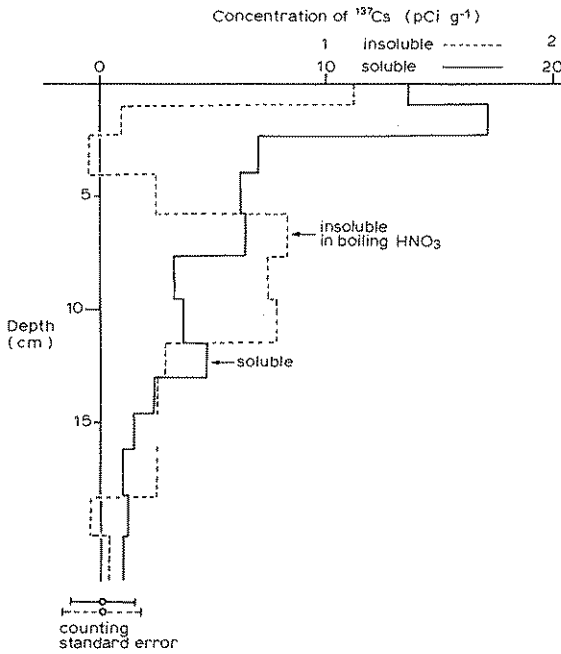


Fig. 4.10. Concentration of ^{137}Cs in HNO_3 -soluble and insoluble fractions of peat collected in 1973 from Bohult mire, southern Sweden. Note the ten-fold difference in scale. Both fractions have a surface peak and a smaller peak further down which may be connected with the 1963 peak in ^{137}Cs produced by nuclear bomb tests. Results of Clymo (unpublished).

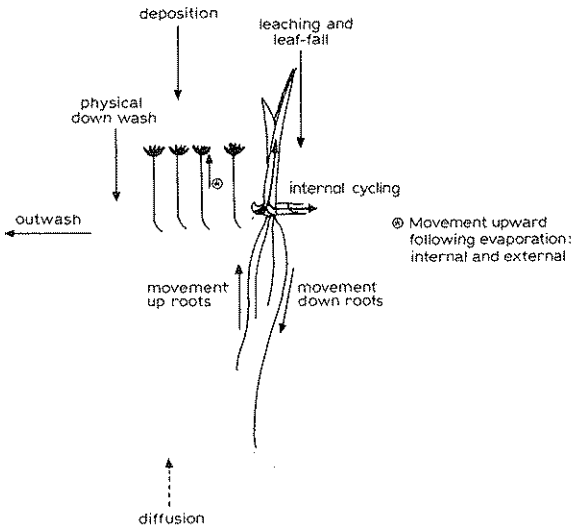


Fig. 4.11. Summary of processes causing movement of inorganic solutes (and particles) in peat. The surface contains stylized *Sphagnum* and a vascular plant.

(1972) from Finland; Mattson and Koutler-Andersson (1955), Sonesson (1970) and Damman (1978) from Sweden; Schneider (1968) from Germany; Chapman (1964b) and Green and Pearson (1977) from England; and Walsh and Barry (1958) from Ireland. Excluding the *Schwingmoor* and blanket bog the profiles all have features in common. Their stratigraphy shows a transition from fen communities (with or without trees) to bog. The basal and surface peats have high concentrations of silica (" SiO_2 ", or "insoluble ash"), calcium and iron, but the middle peat has lower concentrations. The same pattern, though less conspicuous, is shown by aluminium and manganese, while potassium has a particularly pronounced surface peak. Other elements such as magnesium are more variable, but sodium and hydrogen ions tend to increase in concentration from the bottom to the top of the profile. Nitrogen and phosphorus have been more rarely measured. They have high concentrations at the surface, but remain fairly constant below that (Mattson and Koutler-Andersson, 1955; Damman, 1978).

The high concentration in the top 30 to 50 cm may reasonably be connected with the relocating activities of live plants and animals, and with the change from aerobic to anaerobic conditions. The details of the processes operating in this horizon are considered later. The transition from high concentrations at the base to lower ones in the mid-section is commonly associated with the change from a eutrophic, mineral-soil-water-dependent, fen peat to an oligotrophic, precipitation-dependent, bog peat. For some substances the decline in concentration is abrupt: iron, aluminium and " SiO_2 " are examples. For calcium, however, the decline is more gradual and occupies a metre or more. The possible role of diffusion in creating this shape has already been mentioned. In course of time either diffusion or biological relocation would smear an initially sharp transition. Mattson et al. (1944) drew attention to the usefulness of the Ca:Mg ratio as an indicator of the limit of influence of mineral soil water. In atomic units, the concentration of calcium in soil water usually exceeds that of magnesium, but in precipitation the sea-derived magnesium exceeds calcium in concentration, though the ratio depends on dust supply and on distance from the sea (for example, see Sonesson, 1970). Mattson and Koutler-Andersson

(1954) adopted the ratio of 1:1, though it is evident from their figure 7 that the erratic behaviour of the magnesium profile makes this nothing more than a rule of thumb. Chapman (1964b) used the same ratio, though perhaps with mass instead of atomic units of concentration, and found it a very good guide. The same atomic ratio is reached in Mörnsjö's Fjällmossen profile (Fig. 4.12) about 100 cm above the minerotrophic *Carex*-moss peat limit. It is exactly on the wood peat limit in Walsh and Barry's (1958) Clonreen profile, but is 200 cm above the fen carr peat in their west coast raised bog at Kilmacshane. At Vassijaure (Sonesson, 1970) the ratio is more than 1:1 at all depths. It seems clear that no universal rule exists, and in view of the different sources of these two elements one would not expect one.

Where aluminium and iron have both been measured (Mattson and Koutler-Andersson, 1955;

Chapman, 1964b; Mörnsjö, 1968; Sonesson, 1970; Damman, 1978; Clymo, unpublished) they usually show the pattern of Fig. 4.12. At the base, the atomic concentration of iron exceeds that of aluminium, and both are high. In the bulk of the ombrotrophic peat the concentration is low and both elements have about the same concentration. In the surface layers aluminium exceeds iron. As will be shown later, the thick 10 or 20 cm slices average out a much greater range of concentration in thin layers near the surface. The concentration of iron at the base of a peat deposit may be so high that iron-containing minerals such as siderite and vivianite (Casparie, 1972) are formed, as well as more amorphous deposits of "bog iron" (Newbould, 1960). The basal iron and aluminium are probably derived from the mineral soil water. In ombrotrophic conditions the iron and aluminium are probably derived from soil dust (Peirson et al.,

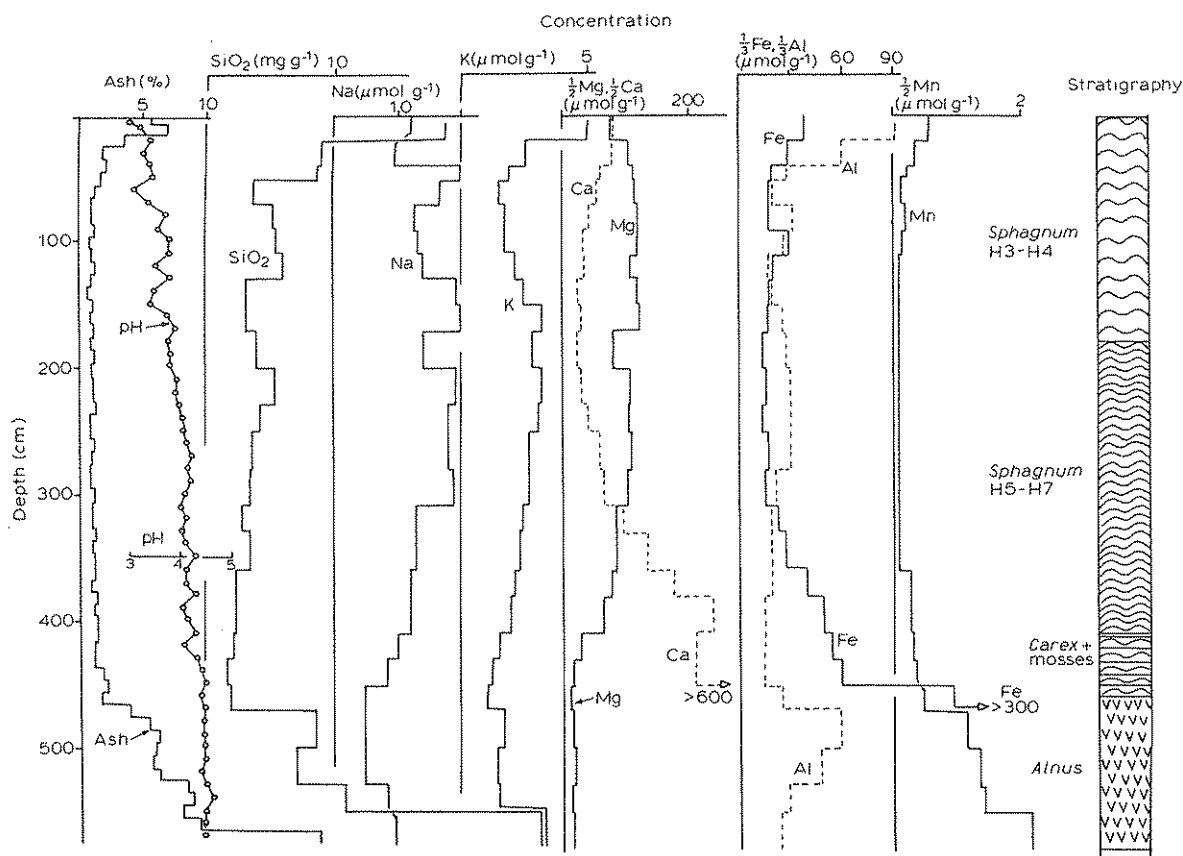


Fig. 4.12. Concentration of inorganic constituents in a peat profile from Fjällmossen, southern Sweden. The bog is (today) concentrically domed. Redrawn from Mörnsjö (1968).

TABLE 4.10

Concentration (per unit dry mass) of inorganic constituents in the mid-section of deep profiles (the sites are in north-south order; values are reliable only within a factor of 2)

Site	Concentration ($\mu\text{mol g}^{-1}$)									Source
	Na	K	Mg	Ca	Mn	Fe	Al	"SiO ₂ "	pH	
Vassijaure (arctic Sweden)	4	1	30	50	0.1	20	30	0.2	4.0	Sonesson (1970)
Ramna ¹ (central Sweden)	—	—	60 ²	20 ²	0.2	2	15	0.05	—	Mattson and Koutler-Andersson (1954)
Fjällmossen (southern Sweden)	20	3	40	20	0.05	5	10	0.01	4.0	Mörnsjö (1968)
Traneröds Mosse (southern Sweden)	15	2	40	25	0.2	4	10	0.3	—	Damman (1978)
Cruden Moss (northeastern Scotland)	50 ³	2	80	20	—	20	—	0.2	—	Stewart and Robertson (1968)
Coom Rigg Moss (northern England)	20	5	—	40	—	2	20	0.2	4.2	Chapman (1964b)
Cloncreen (Ireland)	20	4	60	30	—	4	—	0.1	4.7	Walsh and Barry (1958)

¹Original data on air-dry mass. Assumed oven-dry mass is 80% of air-dry mass. ²Exchangeable. ³The Na profile is inverted, with the highest concentration in the mid-section.

1973). If this is so, then some of the differences in their profiles probably result from differences in the amount of relocation. The concentration of most of these elements in the central "fossil ombrotrophic" section of many profiles is surprisingly similar. Some results are collected in Table 4.10. The most variable of the elements commonly measured is iron, with a range from about 2 to 20 $\mu\text{mol g}^{-1}$. Total cation concentration is about 100 to 150 $\mu\text{mol g}^{-1}$. It is possible that this seeming uniformity is imposed by the cation exchange properties of the peat.

Isolated measurements of total nitrogen and phosphorus in peat have been frequently reported, but *profiles* have been less commonly measured. The relative expense of the methods rather than the importance of the subject must account for this. The chemical state of nitrogen and phosphorus is even more vaguely known than is that of the metals. Thus, it is possible to measure "total nitrogen" and "total phosphorus" or the exact species NH_4^+ , NO_3^- , NO_2^- and the various forms of orthophosphate. The complex (probably organic) forms predominate. The range of concentration of inorganic phosphate in suction water from peat from the Åkhult mire (Malmer and Sjörs, 1955; Malmer,

1962b) was from 0.003 to 0.035 mmol l^{-1} . Sæbø (1968) recorded similar values. The concentration of extractable phosphate depends on the extractant. Malmer and Sjörs (1955) and Malmer (1962b) recorded, per unit volume of wet peat, from 0.03 to 0.37 mmol dm^{-3} extractable by 1M acetic acid, and Waughman (1980; see Fig. 4.9) recorded a range from 0.01 to 0.1 mmol dm^{-3} , the lower values being in fen peats. Waughman also showed that 1M ammonium chloride extracted less than acetic acid from fen peat, but about the same from bog peats. The total concentration of phosphorus in peat is much greater; Malmer and Sjörs (1955) and Malmer (1962b) found 0.8 to 3.2 mmol dm^{-3} , Smith (undated) recorded 2 to 5 mmol dm^{-3} in Pennine blanket peat, Bellamy and Rieley (1967) found 1 mmol dm^{-3} in *Sphagnum fuscum* peat, and Waughman (Fig. 4.9) recorded about 2 mmol dm^{-3} in fen and bog peats. In round figures the ratio of water-soluble:extractable:total is about 1:10:100. In the Alaskan tundra, however, the "reserve" in exchangeable form seems to be much greater (Chapin et al., 1978) although the concentration of soluble inorganic phosphate is about the same. Similar differences exist for nitrogen. Sæbø (1970) recorded 0.1 to 0.3 $\mu\text{mol dm}^{-3}$ NH_4 in

suction water, but total nitrogen has been commonly recorded in the range 30 to 200 mmol dm^{-3} in peats from a wide range of temperate, boreal and arctic sites (for examples see Waksman and Stevens, 1929a, b; Malmer and Sjörs, 1955; Walsh and Barry, 1958; Gorham, 1961b; Malmer, 1962b; Stewart and Robertson, 1968; and Smith, undated) and from other regions, such as the Antarctic (Allen et al., 1967) and Borneo (Richards, 1963). Between 0.5 and 3% by weight seems to be the usual range. This is less than is found in most live plants, but not notably less than in *Sphagnum* (for example, see Malmer and Sjörs, 1955; and Malmer, 1962b). Much of the nitrogen seems to be associated with the "lignin" fraction (Fig. 4.8) and the relative constancy of binding capacity for non-exchangeable nitrogen in the "lignin" has already been mentioned. Mattson and Koutler-Andersson (1955) drew attention to the fact that the "lignin" in the top 50 cm is nearer to saturation than that in the rest of the profile (except the base, which might be expected to show minerogenic influences). They suggested that the surface anomaly is a result of direct absorption of ammonia from the air — ammonia produced in increasing amounts as a result of industrialization. The amounts they found correspond to about $11.6 \text{ kg ha}^{-1} \text{ yr}^{-1}$ since 1000 A.D., compared to precipitation measurements of about $3.5 \text{ kg ha}^{-1} \text{ yr}^{-1}$. But there is good reason to suppose that the biological and physico-chemical processes in the top 50 cm of peat are markedly different from those lower down, and valid measurements of ammonia in precipitation are notoriously difficult to make. The surface anomaly *may* be a result of industrial activity, but it may be a normal feature of the surface.

Much the same can be said of the profiles of total phosphorus (Fig. 4.13), though the basal high values seem to be missing.

One factor which is always difficult to assess is the extent to which a particular vertical profile reflects very local changes — for example the difference between hummock and hollow. In some cases it can be demonstrated that what would appear in a single core of a few centimetres diameter as a "recurrence surface" (see Tallis, Ch. 9) extends at most a few metres (Walker and Walker, 1961; Casparie, 1972). The position is not clarified by the general lack of any reference to replication of analyses, let alone of samples, so that the precision

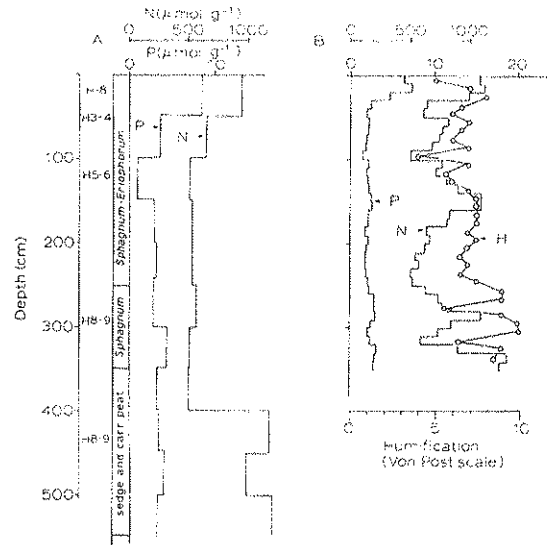


Fig. 4.13. Humufication (Von Post scale) and concentration of N and P in two bog profiles. A. Raised bog at Cloncreen, Ireland. (B) Raised bog at Ramna, southern Sweden. Redrawn from Walsh and Barry (1958) and Mattson and Koutler-Andersson (1954).

and accuracy of published values can only be guessed. It is most unlikely that they justify the three or even four significant digits commonly reported. One exception to the lack of replication is the work of Stewart and Robertson (1968). They collected 110 samples from eighteen levels in a blanket peat site to a depth of just over 100 cm, spread over a lateral distance of about 410 cm. One vertical series of eighteen samples formed a profile, the other samples were taken at random. The peat in the top 40 cm was of a series of interdigitating patches of *Calluna*, *Sphagnum*, and *Eriophorum* in varying proportions. Below this the botanical composition was unclear but the peat was "fibrous" to a depth of about 90 cm, where it became "amorphous". Most of the measured substances showed the smallest range of concentration in the mid-depth zone between 40 and 80 cm deep. As a proportion of the whole range, the range in this zone was about 0.3 for nitrogen, 0.3 for phosphorus, 0.3 for sodium, 0.8 for potassium, 0.7 for calcium, 0.3 for magnesium and 0.3 for sulphur. For all but sulphur the range was proportionately greater in the "mixed" peat layers: about 0.4 for nitrogen, 0.5 for phosphorus, 1.0 for calcium, and so on. Only for sulphur, and perhaps magnesium,

was the range about the same at all depths. The chosen profile also showed marked patterns in relation to the range of two elements: sodium was consistently high in the mid-layers, but low in the bottom layer; potassium was low in all but the bottom layers. The other elements showed no consistent pattern. Even in this work, however, it is not possible to separate sampling and analytical errors.

One may perhaps conclude that, in the absence of botanical information, erratic individual differences in concentration in adjacent samples by a factor of less than two may be uninterpretable, though a change of the same magnitude occurring gradually but steadily over several samples may be more meaningful.

Profiles of the surface layers

The surface layers (the top 50 cm or so) of a peat-forming community are specially important because within them rapid changes are in progress and much relocation of inorganic substances may occur. This upper layer has sometimes been called the "active" layer, overlying the "inert" layer. This is an unhappy choice of words, prejudicing consideration of what changes are going on in the lower layer. There is much to recommend the suggestion of Ingram (1978; see also Ch. 3) that the layers be called the acrotelm and catotelm, respectively.

Small differences in rate in the acrotelm may have a disproportionate effect on peat accumulation (Clymo, 1978; Jones and Gore, 1978). Perhaps the most useful indicator in this zone is the "redox potential". In practice this is measured as the electrical potential between a platinum probe and a calomel (or similar) reference junction. A KCl salt bridge, usually saturated, is used to connect the calomel to the peat (for the same reason that it is used in pH measurements) and its exact position is usually unimportant — anywhere within 1 to 100 cm will usually leave the potential unchanged. The potential may be changed however by the pretreatment of the platinum. Some workers (Urquhart and Gore, 1973) boil the platinum in concentrated oxidizing acids, and use one electrode for only one or at most a few measurements. Results which are *reproducible* may be had with no preparation of the platinum apart from a few immersions to 10 cm or so in the peat. This process seems to prepare the surface in some undefined

way, so that on subsequent removal to sites of different redox potential the reading stabilizes within a few seconds. With platinum prepared by the long process, the reading usually drifts, and some arbitrary time must be chosen for the measurement. The less carefully prepared platinum may drift in oxidizing conditions, but very little in reducing conditions.

"Redox potential" is also affected by pH, and it is usual to apply a "correction" of about 58 mV per pH unit to an arbitrary standard, often to pH5 (E_5). Temperature affects the readings too, reducing the potential as temperature rises by about 0.8 mV per °C, and a correction to a standard temperature is usually made.

Potentials are usually reported relative to the calomel half cell. They may be changed to the standard hydrogen cell by adding about 242 mV. If the KCl bridge is not saturated, the shift is different (Conway, 1952).

It will be obvious that "redox potential", as measured in the field or on fresh peat newly returned to the laboratory, may be usefully compared within any one set of measurements but should not be compared too closely between sets, particularly if different methods have been used.

Three other features are commonly correlated with "redox potential" profiles: the position of the water table, the presence of sulphides, and the oxygen concentration. In acid peat and even in alkaline peat a sulphidic smell, usually attributed on no other evidence to hydrogen sulphide, is often conspicuous. The blackening of a freshly cleaned silver or copper wire or plate (Burgeff, 1961; Clymo, 1965; Urquhart, 1966) may be used in a semi-quantitative way. At low temperature particularly (as shown for example in Fig. 4.8) the sulphidic smell may be quite strong and yet there may be no detectable blackening of silver within an hour. The kinetics of blackening have not been investigated, but are obviously complex. Many profiles similar to that of Fig. 4.14 have been reported (for example, by Mörnsjö, 1969; and Urquhart and Gore, 1973). Most of these agree in showing the upper limit of S^{2-} to correspond to " E_5 " about +200 mV. This is a figure similar to that found for the transition from SO_4^{2-} to S^{2-} in lake muds by Mortimer (1942). Urquhart and Gore (1973) reported that " E_4 " showed a minimum at 12

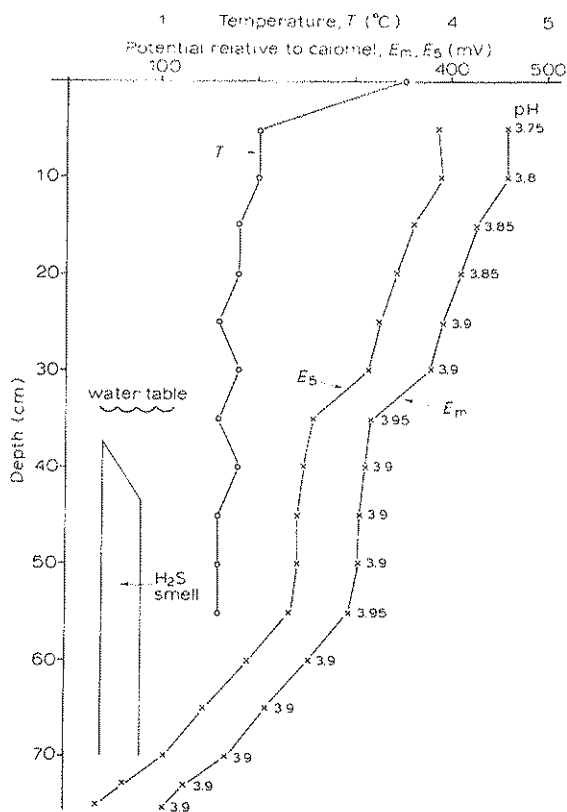


Fig. 4.14. "Redox potential" profile on September 17 in *Sphagnum fuscum* peat near Abisko, northern Sweden. E_m = as measured; E_s = calculated at pH 5 using the temperature profile and pH value by each point. A platinum-tipped probe was used with a calomel reference junction. Results of Clymo (unpublished).

to 20 cm deep, but the evidence for this is much less strong than that for a large surface drop. Nevertheless, the profiles they reported are remarkably similar to those found in lakes in winter (Mortimer, 1942), and the parallel between mire surfaces and lake muds might be illuminating.

The sulphide zone seems to be of limited thickness (Mörnsjö, 1968; Urquhart and Gore, 1973). What happens to S^{2-} at the lower limit has not been investigated, but the seasonal variation in concentration of sulphide — lower in winter — perhaps indicates that sulphide is normally removed by chemical conversion to other forms, and that which is observed has been recently produced by microbiological means. The finding by Gorham (1956) of increased concentration of SO_4^{2-} in pools during dry weather in mid-May is consistent with this hypothesis.

If waterlogged peat is drained the oxidation of large amounts of sulphide may produce so much sulphate (as H_2SO_4) that the peat becomes extremely acid. Hart (1962) recorded that the pH of a drained mangrove swamp fell during six months from 6.2 to 3.8, and even greater acidity has been recorded in these circumstances. The seasonal variation of "redox potential" and the extent of blackening on a silver plate has been most thoroughly investigated by Urquhart and Gore (1973). They found that in wet sites (lowland, and 560 m altitude) E_4 fell, as temperature increased, by about 5 mV per °C between 12 and 20 cm depth, and by about 8 mV per °C between 22 and 30 cm depth. In drier sites the effects were erratic, and mostly of lower statistical significance. Blackening of a silver plate was clearly correlated with "wetness" — it was most intense (after 1 hr) in the wet sites, and in one case where the plate crossed the boundary between hummock and hollow the top of blackening was within 2 cm of the hollow surface, but 15 cm below the hummock surface and was actually lower (in altitude) below the hummock than below the hollow. Unfortunately the wet sites were examined in May and June and the dry sites in August, and common experience is that sulphidic smells on bogs are generally most noticeable in early summer, so this difference between sites may have been a result of measuring at different seasons of the year.

The interrelations of "redox potential" and sulphide content with water table in peat are obvious in general, but unclear in detail. One may deduce that during the measurements of Urquhart and Gore (1973) the top of the sulphide zone was usually just below the water table, and the data reported by Clymo (1965), Smith (undated) and those in Fig. 4.14 here show this too. On the other hand, Boggie (1972) found the mean water table was about 4 cm below the mean upper limit of blackening on silver-plated copper. His silvered plates were left in the peat for about a month however, compared to the period of one hour or so used by other workers, and it is to be expected that traces of sulphide not detectable in one hour would be conspicuous after 600 h. The problem is further complicated by the fact that the water table can, when near the surface, fluctuate by 5 to 10 cm over one to two days (Chapman, 1965); and the very idea of a water table (as such) in humified peat is as dubious as the existence of a water table in a

domestic jelly, though there may be a clear and rapidly changing water table in a well in that jelly. Sulphide production is likely to be related to wetness of the peat and not, in general, to a free water table in an inspection pit, unless the hydraulic conductivity at the level is high. The following hypothesis seems to be consistent with most of the known facts. During winter the water level rises and covers some newly dead plant matter containing readily decomposable compounds, but temperature is low, so microbiological activity is low too. In late spring the temperature increases, and with it microbiological activity. The rate of oxygen diffusion (about 10^{-4} of the rate in air) is insufficient to support this activity, so the peat a few centimetres below the water table becomes anaerobic, as shown by a fall of "redox potential" by an average of about 150 mV (Urquhart and Gore, 1973). A different set of microbiological processes is then favoured, resulting in the relatively rapid production of sulphide. Later in the summer, as the water table falls and the readily metabolized material is exhausted, the rate of sulphide production declines, and more of the existing sulphide is reconverted to sulphate either chemically or by micro-organisms. It may be that production of methane is partly linked to this pattern.

There is a need for concerted studies of chemistry (both organic and inorganic) and of microbiology *in the field* at the same site. Tentative steps in this direction were taken during the International Biological Programme (for example, see the various accounts in Sonesson, 1973; Flower-Ellis, 1974; and Heal and Perkins, 1978), but far more needs to be done. The interrelations of "redox potential", sulphide concentration, and the concentration and movement of inorganic substances is equally unclear. The correlation between a particular chemi-

cal transition and redox potential is probably mediated by microbial activities. Table 4.11 gives four of the important transitions recorded in lake muds by Mortimer (1941, 1942). These are not the potentials for the chemical reactions, but the potentials which happen to be correlated with them. To what extent the bacteria cause the potentials or are favoured by them is obscure.

There seem to be no published measurements of valence states and few of sulphide or oxygen concentration in peat. Webster (1962) made measurements in ground water of a wet-heath community, but this ground water was probably moving through, and perhaps in, a mineral soil. That the concentration of oxygen and sulphide could be important is suggested by Fig. 4.15, which shows the maximum concentration of metals which may, in theory, remain in solution at various concentrations of sulphide and other anions. Ponnamperna (1972) considered these and other equilibria. The order of precipitation from equimolar ionic solutions is: Ag^+ first, then Cu^+ (if it

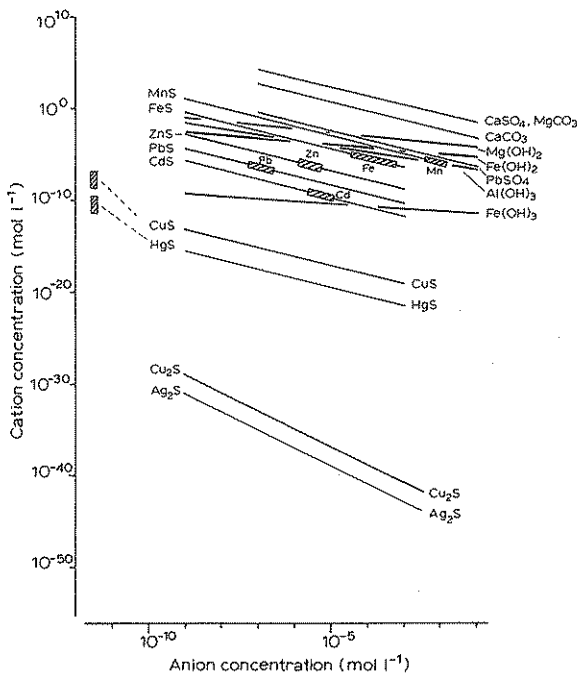


Fig. 4.15. Calculated relationship of cation and anion concentration for some sparingly soluble salts. Above the line the solution would be supersaturated. Hatched bars show the approximate peak volumetric concentration of the cation in bog peat. Calculated from solubility products in Weast (1965).

TABLE 4.11

Correlation of chemical transition with "redox potential" in mud from Lake Windermere [data from Mortimer (1942), adjusted to E_5 from E_7 ; relative to calomel]

Transition	"Redox potential", E_5 (mV)
$\text{NO}_3^- \rightarrow \text{NO}_2^-$	570–520
$\text{NO}_2^- \rightarrow \text{NH}_3$	520–470
$\text{Fe}^{3+} \rightarrow \text{Fe}^{2+}$	420–320
$\text{SO}_4^{2-} \rightarrow \text{S}^{2-}$	220–180

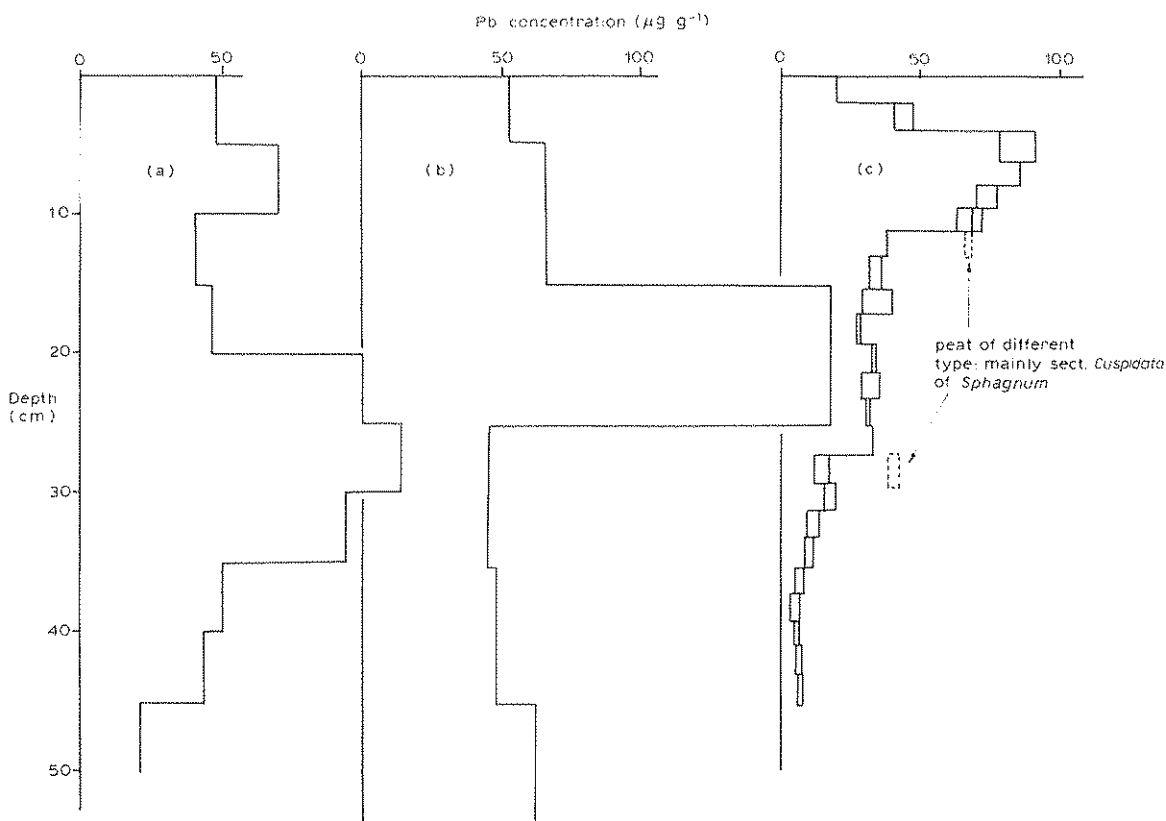


Fig. 4.16. Concentration of lead in three ombrotrophic peats from 60° N latitude: (a) Fjällmossen, southern Sweden; (b) Myras, southern Finland, *Sphagnum fuscum* peat; (c) Os, southern Sweden, *S. magellanicum* peat. Redrawn from Tyler (1972), Pakarinen and Tolonen (1977), and results of Clymo (unpublished).

forms), followed by Hg^{2+} and Cu^{2+} , then after a gap Cd^{2+} , Pb^{2+} , Zn^{2+} , Fe^{2+} and Mn^{2+} in that order. The actual formation of metal sulphides should be influenced by the solution concentration — strictly, activity — of the metals. As a first approximation the volumetric concentration in peat (Clymo, 1978, unpubl.; Damman, 1978) is shown, though this is probably higher than the solution concentration by a factor of perhaps 1000. All the sulphides shown are with divalent metals, so the slopes in Fig. 4.15 are all -1 , and if the concentration of the metal is reduced by a factor $1/v$ then that of sulphide must be increased by a factor v . If the metal concentration in the peat water is a thousand-fold less, then the sulphide concentration must be a thousand-fold more. Applying this to Fig. 4.15, with a sulphide concentration of 1 mmol l^{-1} one would expect no MnS , but possibly some FeS , CdS and ZnS . The compounds PbS and,

especially, CuS and HgS seem to have a high probability of forming. The blackening of silver and copper is some support for this prediction, but there are no reliable direct measurements of S^{2-} activity in peat, and H_2S is such a weak acid that one would expect only low S^{2-} concentration in acid conditions.

Detailed profiles of metal concentration in the top 20 to 50 cm are beginning to be available (largely as a result of the development of atomic absorption flame spectrophotometry). The resolution of such profiles has usually been 5 to 10 cm (Bellamy and Rieley, 1967; Sonesson, 1970; Sillanpää, 1972; Tyler, 1972; Pakarinen and Tolonen, 1977; Damman, 1978). It seems to be a common feature of such profiles that they show sporadic peaks — single samples with unusually high or low values; but there is almost never any replication of samples, so it is difficult to decide

how to regard such one-sample peaks or troughs. Profiles sampled at 1-cm intervals (Clymo, 1978, unpublished; Aaby and Jacobsen, 1979; Aaby et al., 1979; see Figs. 4.16, 4.18) reduce these problems because the trends are usually clearly distinguishable against the sampling and analytical "noise". In the one published instance of replicate cores, sampled a year apart in time and analyzed by different workers with different equipment (Clymo, 1978), the mean difference in concentration of lead in 36 pairs of samples, each pair from the same depth down the profile, was 70 ppm, but the general trend was from a concentration of about 200 ppm in the top 19 cm, rising to 600 ppm at 29 cm, then falling to 80 ppm at 36 cm. This general point is illustrated in Fig. 4.16, which shows three lead profiles from peats at about the same latitude.

Even with these reservations it is possible to make some generalizations. The most interesting work of Damman (1978) reproduced in Fig. 4.17 may be used together with Fig. 4.18 to illustrate features which are found repeatedly in ombrotrophic mires. The element potassium has very high concentration in the top 1 to 2 cm of live *Sphagnum*, falling from 3500 ppm (0.1 mmol g^{-1}) to 150 to 200 ppm at 10 cm depth and to 25 ppm at 40 cm depth. The very high surface values are associated with the live moss; in dead patches the values are about 50 ppm (Clymo, unpublished). The element sodium, also monovalent, shows similar behaviour, though less extreme, with surface values of 400 ppm falling to 150 ppm at 20 cm depth. Granat (1975) reports the ratio of Na:K in precipitation about 100 km inland from the west coast of Sweden, and 200 km to the north of these peat sites, as about 1:1 (mass basis). The 6:1 ratio in peat at 40 cm is therefore rather surprising unless there has been selective loss of potassium by leaching.

The element manganese shows a characteristic pattern of very high surface concentration — 200 to 300 ppm — in the surface of hummocks, falling sharply from the surface to 5 to 10 cm above the water table. In peat formed by *Sphagnum magellanicum* growing in a "lawn" just above the water table, the surface concentration is about 50 ppm, and falls very steadily to about 1 to 2 ppm at 40 cm depth.

Other elements increase in concentration with depth and reach a peak at about the mean water table. In the case of iron and lead the peak is very marked. For zinc it may be less so, when the

discrimination is fine. For yet other elements (aluminium, magnesium, calcium, phosphorus and nitrogen) the peak is even more obscure. For copper and cadmium there is no obvious pattern, though for copper (at least) replicates agree closely, so the small drifts in concentration may be of significance.

There are marked differences too in the prominence of peaks compared to the concentration at 40 cm depth. The peak is prominent for potassium, manganese, lead and zinc, but less so for sodium, and inconspicuous for aluminium, iron, magnesium and calcium.

The elements also differ in concentration in different peat types (Fig. 4.18). Conspicuously higher in concentration in *Eriophorum* peat than in *Sphagnum cuspidatum* peat are potassium, aluminium and insoluble ash. Slightly higher are lead, copper, cadmium, sodium, iron and calcium, but slightly lower are manganese, zinc and magnesium.

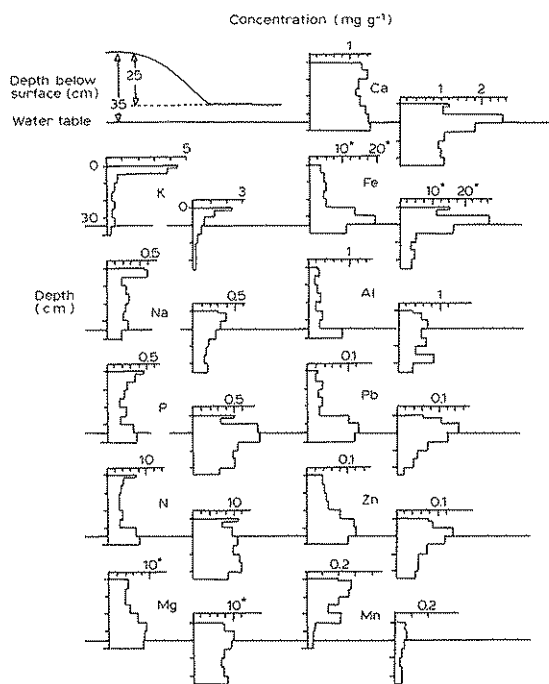


Fig. 4.17. Concentration, per unit dry mass of peat, of eleven elements in surface profiles of ombrotrophic peat from Storemosse, southern Sweden. Left columns: *Sphagnum fuscum*. Right columns: *S. magellanicum*. Roots of vascular plants were removed before analysis. Redrawn from Damman (1978). (It seems likely, from other results in Damman's paper, that the Mg peak should be about 1 mg g^{-1} , not 10, and the Fe peak about 2 mg g^{-1} , not 20. If this is true, the scales should be reduced by a factor of ten.)

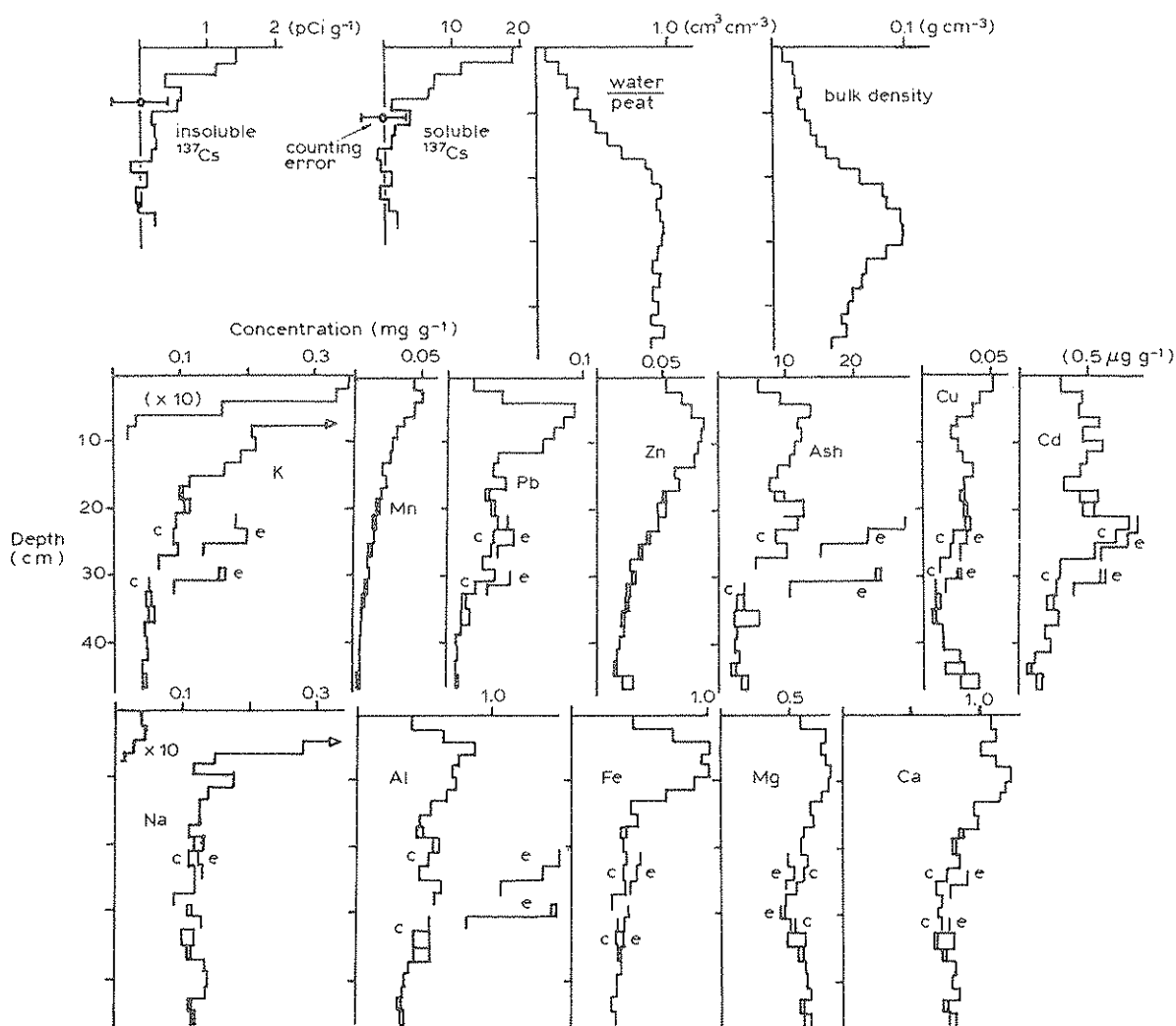


Fig. 4.18. Physical variables and concentration, per unit dry mass of peat, of twelve elements and of ash (%), in a surface profile of ombrotrophic peat from Os, Southern Sweden. Chemical units are mg g^{-1} except Cd and ^{137}Cs . The peat was predominantly *Sphagnum magellanicum* in the top 20 cm, but below that the proportion of *Eriophorum vaginatum* (e) and of the *Cuspidata* section of *Sphagnum* (c) increased and was analyzed separately. Roots were removed before analysis. Results of Clymo (unpublished).

There are as yet too few reports to be sure which of these patterns are common and which are particular to one or a few sites, but it does seem clear that there is a variety of patterns, and that some of these are correlated with the type of peat and with the oxidation-reduction state of the peat. The order of depth of the peaks of manganese, iron, zinc and copper is the reverse order to that of their sulphide solubility.

In several cases it has been assumed that bryophytes (Rühling and Tyler, 1971; Pakarinen and Tolonen, 1977) or peat profiles (Lee and Tallis,

1973; Livett et al., 1979) or both may record the history of deposition in the same way that ice accumulations do, but without the technical difficulties of that case (Murozumi et al., 1969) and with fewer geographic constraints. In one instance (Clymo, 1978, using information available in 1972) the cumulative amounts of magnesium, aluminium and titanium were used as indicators of age in the surface layers. It is important therefore to consider the extent and mechanism of movements of solutes in the surface layers, to a depth of perhaps 10 cm below the mean water table.

In a few cases it is possible to make crude estimates of the proportion of deposited matter which is retained. For a *Sphagnum magellanicum* profile in the Pennines (England) about 30 to 40% of magnesium and about 50% of caesium (^{137}Cs) were retained (Clymo, 1978). The calculations were possible because the profile for magnesium was relatively free of peaks, and most of the ^{137}Cs input is recent and fairly accurately known. For most other elements however the peaks imply relocation, so the best that can be done is to use the mean concentration in the lower "central" anaerobic section (Table 4.10) on the assumption that these approach "steady state" values and that in this section there is little relocation. These very crude calculations (Table 4.12) suggest that retention may be related to valence, ranging from values of 1 to 3% for sodium and potassium to 40% for aluminium. The valence state of manganese and iron is uncertain, but one might expect them to be in the reduced form.

The retention values in Table 4.12 are about 0.1 to 0.2 of those in Table 4.8. The calculations used in Table 4.8 were for the top 10 cm, and assumed about 1 cm of vertical growth per year, whilst those for Table 4.12 assumed that at greater depth only 1 mm of that is left.

The incomplete retention and the variety of profiles indicate that at least some elements are relocated. Equally clearly the processes of re-

location differ in importance. In ombrotrophic peat-forming systems the following may be considered:

(1) Biological cycling of various kinds, particularly the movement from roots to shoots, and return either internally to rhizomes in winter, or externally by leaching and leaf-fall. These processes are considered in detail by Dickinson (Ch. 5), and are of obvious importance for elements such as potassium and caesium.

(2) Diffusion, which is probably of less importance because the available time is relatively short (perhaps 10 to 50 years) and the pathway is dissected and tortuous.

(3) Movement by mass flow, similar to the elution of a column of exchange resin or microporous gel. That such elution (or leaching) does occur seems nearly certain, and the relation of retention to valence is consistent with elution of cations from an exchange phase. If the surface layers have high hydraulic conductivity, as is often the case, then water probably flows down to the water table rapidly, and then laterally. The details are obviously complex; the profiles of Fig. 4.18 are not simply explicable by this mechanism, but have biological cycling and probably valence change as well as recent changes in deposition rate (of lead, for example) superimposed. One might expect Cs^+ to behave in a manner similar to K^+ , and the pattern for ^{137}Cs (Figs. 4.10, 4.18), most of which

TABLE 4.12

Retention of deposited substances by the central section of peat deposits

	Na	K	Mg	Ca	Mn	Fe	Al	Precipitation (mm)
Concentration range in peat (Table 4.13) ($\mu\text{mol g}^{-1}$)	4 50	1 5	30 80	20 50	0.05 0.2	2 20	10 30	
Deposition flux ($\mu\text{mol cm}^{-2} \text{yr}^{-1}$)								
Chilton, 1973	5.2	0.8	0.9	1.9	0.02	0.48	1.2	574
Wraymires, 1973	18.3	0.9	2.3	1.4	0.01	0.23	0.6	1482
Approximate ¹ retention (%)	1	3	30	20	10	30	40	

The peat concentrations are taken from Table 4.10. The deposition rates, selected from Cawse (1974), are from Chilton (central southern England, low precipitation, 90 km from sea, rural, predominantly arable) and Wraymires (English Lake District, high precipitation, 25 km from sea, rural, little arable, some industrial influence).

¹Assuming peat growth of 1 mm yr^{-1} , density 0.1 g cm^{-3} .

fell in precipitation during 1963, does perhaps support this view. Much of the acid-soluble ^{137}Cs is still "suspended" biologically at the surface, with a small peak, probably representing the 1963 input, at about 10 cm in this profile. The acid-insoluble ^{137}Cs , perhaps glassy particles, peaks at about 8 cm depth, with a larger surface peak. The difference of 2 cm may represent elution of the soluble fraction in the ten years since it was deposited. The process cannot be as simple as this, however: Clymo (1978) reported that about 50% of the deposited ^{137}Cs was not recovered from peat profiles, and elution experiments in the field and laboratory (Mackay, unpublished, 1976) indicated that a substantial part of caesium and other cations added to *Sphagnum* is eluted. The same experiments indicate however that a fraction remains where it was applied. There may be one fraction which can be readily eluted and another which moves much more slowly.

The surface peak of acid-insoluble ^{137}Cs is rather surprising, but Mackay (unpublished, 1976) has shown that upward movement of particles and solutes occurs around *Sphagnum* during dry conditions. The top of the plants is the limit to movement in that direction, so particles may accumulate there. In the downward direction there is no limit, so particles moving in that direction may be dispersed and, eventually, lost laterally.

One may conclude that there is still much to be learned about the chemistry of peat.

ACCUMULATION OF PEAT

Peat accumulation results when the rate of addition of dry matter exceeds the rate of decay.

Matter is added mostly at the surface, and may be measured as productivity. For mosses — mainly *Sphagnum* in bogs or hypnoid mosses in fens — all the new matter is added at the surface, but vascular plants produce rhizomes and roots, and these add matter perhaps as much as 2 m below the surface in exceptional cases (Stavset, 1973). Most of the matter is added in the top 10 cm, however.

Decay on the other hand may occur not only at the surface but through the whole peat depth. The rate of decay seems to be highest in the surface layers, and to be much lower in waterlogged peat. In addition, some species — particularly some species of *Sphagnum* — seem to decay at a lower

rate than others. These differences have several consequences: the depth of the water table is very important; a very low decay rate operating over 5 m of peat may be as important as a hundred-fold greater rate restricted to a 5 cm layer; selective decay of species may result in a peat dominated by one or a few only of the species which grew on the surface which formed it.

It is convenient to consider productivity first, then decay, and lastly models of the peat accumulation process.

Productivity

The productivity of vascular plants in peat-forming systems is reviewed by Bradbury and Grace (Ch. 8). Particularly valuable accounts of primary productivity of blanket-bog are given by Smith and Forrest (1978) and by Grace and Marks (1978), so only the contribution of bryophytes is considered here. In these acid habitats vascular plant productivity ranges from about 100 to about $800 \text{ g m}^{-2} \text{ yr}^{-1}$. In fens, the contribution from non-vascular green plants — mostly hypnoid mosses — is probably small compared to that from vascular plants. In bogs, the contribution from non-vascular plants may be important and is usually dominated by *Sphagnum*. Exceptions include, for example, *Polytrichum commune* on the edge of some valley bogs in southern England. Individual plants up to 150 cm long may be recovered with annual increment of 12 cm and productivity up to $1400 \text{ g m}^{-2} \text{ yr}^{-1}$. This productivity was maintained for a few years only during a transient rise in the water table, and over an area of about 1 ha only. Other cases where mosses are important are the "moss-banks" of the maritime Antarctic. On Signy Island, Baker (1972) estimated the net productivity of the moss *Chorisodontium aciphyllum* at $440 \text{ g m}^{-2} \text{ yr}^{-1}$, and Fenton (1980) estimated the net productivity of *C. aciphyllum* and *Polytrichum alpestre* to be from 160 to $350 \text{ g m}^{-2} \text{ yr}^{-1}$. For systems with pH 4, a growing season of about five months, and a mean maximum temperature of 0°C , these seem at first to be surprisingly high values. They are probably explicable by adaptation to low temperature, but it may be that the mean monthly temperature of 0°C obscures the fact that the temperature is above 0°C for most of the growing season. If the mosses are able to respond to change in light-flux or in

temperature as rapidly as aquatic subantarctic mosses can (Priddle, 1980a, b), then the productivity is less surprising.

These cases of relatively high productivity are all exceptional, and of interest only in pointing to what may be possible. On a world scale they are trivial; the only bryophytes whose production is important on this scale are a few species of *Sphagnum*. On blanket-bog in Britain their productivity in pure stands ranges from about $150 \text{ g m}^{-2} \text{ yr}^{-1}$ on hummocks to about $500 \text{ g m}^{-2} \text{ yr}^{-1}$ in lawns, but up to $800 \text{ g m}^{-2} \text{ yr}^{-1}$ in pools (Clymo, 1970). The methods of measurement have rather large inherent inaccuracy — perhaps $\pm 50\%$. As a component of shrub-dominated blanket bog *Sphagnum* contributes about 100 to $300 \text{ g m}^{-2} \text{ yr}^{-1}$ (summary in Smith and Forrest, 1978). The species of *Sphagnum* commonly grow in different micro-habitats, particularly in relation to the water table. Thus *S. capillifolium* (*S. rubellum*, *S. acutifolium*) commonly grows some way above the water table, *S. papillosum* and *S. magellanicum* grow just above the water table, and species of the section *Cuspidata* usually grow in the water or close to it. It is of some interest that species seem to grow in that habitat in which their productivity is greater than that of competing species of *Sphagnum* rather than that in which they grow best. For example, *S. capillifolium* grew best in pools, but better than other species tested on hummocks (Clymo and Reddaway, 1971; see also Fig. 4.19). Similar productivity — 100 to $600 \text{ g m}^{-2} \text{ yr}^{-1}$ — was reported by Sonesson (1973), who also found a similar difference between the drier hummocks and wetter depressions near Abisko in Arctic Sweden. Greater productivity by *Sphagnum* may occur in special habitats such as slow-flowing streams draining peatlands (where *S. subsecundum* shoots may grow more than 120 cm in a season) or, transiently, in the furrows made when preparing the ground for afforestation. Up to $1500 \text{ g m}^{-2} \text{ yr}^{-1}$ may be produced. Excepting these special cases, it is of interest to find the same range of values appearing for such diverse climates. If the value of $200 \text{ g m}^{-2} \text{ yr}^{-1}$ applied to all acid peatlands — say two-thirds of the $150 \times 10^6 \text{ ha}$ reported by Tibbetts (1968) — then the world annual production by *Sphagnum* would be about $200 \times 10^6 \text{ t}$. Woodwell et al. (1978) estimated total productivity on the continents — that is, excluding that in seas and oceans — to be about $72 \times 10^9 \text{ t yr}^{-1}$. *Sphag-*

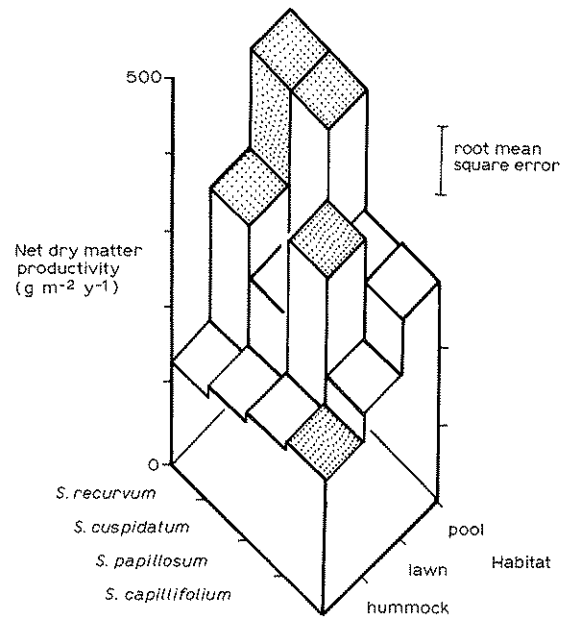


Fig. 4.19. Net productivity of four species of *Sphagnum* in three habitats on blanket bog at Moor House (England). The plants were put experimentally in all three habitats. Dotted area shows the usual natural habitat for each species. Redrawn from Clymo and Reddaway (1971).

num may thus contribute about 0.3% of the total. It would be interesting to know how many other families contribute as much (though the family is a rather arbitrary division: the Sphagnales are a clearly isolated group). If the efficiency is calculated per unit of nitrogen or phosphorus employed, rather than per unit area, the importance of *Sphagnum* is even greater (Clymo, 1970).

Plant productivity, by vascular plants and bryophytes, in fens and bogs is clearly not exceptional for temperate regions. Yet peat accumulates, so the rate of decay must be exceptionally low. To this I now turn.

Decay rate

Some indication of the overall decay rate may be had by calculating how much of what was produced has remained as peat. Assuming productivity of $300 \text{ g m}^{-2} \text{ yr}^{-1}$, no decay, and peat bulk density of 0.1 g cm^{-3} , then after 5000 years there would be 15 m depth of peat. Such a depth is uncommon — 2 to 5 m is perhaps more usual — so one may expect

to find that half or more of the plant material decays. But it seems likely that there may be a rather delicate relationship between production and decay, so that a small change in either may have a big effect on how much remains in peat. The rate of decay is usually measured by one or more of five methods: by direct measurement of mass loss; by direct measurement of gas evolution; by indirect estimate from change in properties of a standard substance; by indirect estimate as a parameter of a model; or by indirect estimate as the result of simulation. These methods are considered in turn.

Direct measurement of mass loss

The commonest method is the "litter bag". The mesh size may be large (c. 1 cm), allowing animals ready access; medium (commonly c. 1 mm), restricting access by large soil animals and preventing the removal of whole chunks; or very small (c. 20 μm), preventing access by all but the smallest animals such as nematodes and protozoa. The nature of pretreatment of the plant material may have an important effect on results. In particular there may be quite a large fraction of the original plant mass which can be removed by simple leaching. For example, Coulson and Butterfield (1978) found that, if freshly gathered leaves were dried in vacuum at 50°C and put into water for seven days, then the loss in mass was 25% from *Rubus chamaemorus*, 14% from *Calluna vulgaris*, 5% from *Eriophorum vaginatum*, and 0% from *Sphagnum recurvum* (see Fig. 4.23). Another important technical point is the method of drying. *Sphagnum papillosum* dried at 105°C decayed less than half as fast as air-dried material (Clymo, 1965). Even air-drying may change the ease with which the plant is attacked.

A major problem with large-mesh litter bags is the possibility of loss of large fragments of litter. This danger becomes greater as time passes and plant structure breaks down. The amount remaining may therefore become increasingly biased on the low side. This effect is likely to be extreme in cases where individual leaves are tethered by a thread but not enclosed. Frankland (1966) used this technique with *Pteridium aquilinum* petioles on peat and found the rate of loss appeared to increase between the fourth and seventh years. The opposite effect — gain from material moving in — is occasionally found (e.g. Clymo, 1965).

A particularly elegant method can be applied in the special case of Antarctic moss peats (Baker, 1972; Fenton, 1978, 1980) in which the annual growth pattern of the moss is preserved for 200 years or more. Assuming that there has been no change in the average mass of a newly produced segment it is possible to calculate the loss after a known time. The plant material has been completely undisturbed. Fenton (1980) gives decay rate for ages as great as 170 years, whereas the best litter bag results (for example, Heal et al., 1978) rarely extend to more than five years. In all cases, however, difficulties develop by the time that less than 20% of the original mass remains.

Direct measurement of gas evolution

In this method it is the gaseous products of decay which are measured. There are many reports of the rate of evolution of carbon dioxide from mineral soils, forest litter, and so on, but few of the flux of carbon dioxide from peat. There are even fewer measurements of the flux of other carbon-containing gases such as methane. The fact that decaying organic matter may evolve methane has been known for 180 years (Dalton, 1802), and with the advent of gas chromatography it has become possible to show that small amounts of other paraffins (ethane, propane) may be evolved as well. Bog peat evolves easily measurable amounts of carbon dioxide and methane (Clymo and Reddaway, 1971; Svensson, 1974). The three main problems with this method are that enclosures used to collect the gas change the conditions (particularly temperature), the flux of gas varies during the day-night cycle, and the flux (especially of methane) is subject to erratic surges, probably associated with the escape of bubbles.

Indirect estimates on standard materials

The best-known method depends on the reduction in tensile strength of unbleached calico strips (Heal et al., 1974). The method can be calibrated, though not very precisely, against other measures of decay. It allows comparisons between sites to be made easily, but the almost pure cellulose is a "foreign" substrate and the results cannot be generalized.

Loss in mass from sheets of standard cellulose has been used in the same way (Rosswall, 1974).

Indirect estimates from models of peat growth

Suppose that the rate of addition of dry matter, p , is constant and that the rate of loss is a constant proportion, α , of the accumulated mass of peat, x . Then:

$$\frac{dx}{dt} = p - \alpha x \quad (7)$$

Here it is assumed that the time scale for the annual march of p and α is so short, compared to the time of interest, that the annual fluctuations can be treated as high-frequency components which have negligible effect on the low frequency trends, and p and α can be assumed constant. The solution to eq. 7 has been known since Newton's day and is:

$$x = \frac{p}{\alpha} (1 - e^{-\alpha t}) \quad (8)$$

This equation, illustrated in Fig. 4.26, has important consequences which are considered later. It can be shown (Clymo, *in lit.*) that where V is the peat mass measured from the surface downwards (i.e. backwards in time) and T is the age of the peat at a given depth, relative to that at the surface, then:

$$V = \frac{p}{\alpha} (1 - e^{-\alpha T}) \quad (9)$$

The variable V , the peat mass to a given depth below the surface, may be called the "depth in mass units". If the bulk density of dry peat were the same at all depths then V would be directly proportional to linear depth. In fact, of course, it rarely is so. Where mass of peat accumulated is being considered then V is a more useful variable than the linear depth.

The relationship (eq. 9) is formally the same as the relationship between the mass of peat accumulated and time elapsed (eq. 8). In effect one redefines zero time anywhere one wishes and looks backward. Given three depths (in mass units) and the corresponding ages, then the decay rate, α , is defined by:

$$\frac{V_2 - V_1}{V_3 - V_2} = \frac{1 - e^{-\alpha(T_2 - T_1)}}{1 - e^{-\alpha(T_3 - T_2)}} \quad (10)$$

This can be solved (by iteration) and, as a bonus, p may be obtained from eq. 9.

Published examples of dated profiles almost all relate to linear depth (measured in units of length) rather than depth in mass units. In such cases the calculation can be made for length in place of mass, but only if the bulk density profile is assumed constant — that is, there has been no consolidation. Jones and Gore (1978) and Clymo (1978) have given several profiles of bulk density, from which it is clear that there are variations within a profile and between profiles, so that the assumption of a uniform value could lead to non-trivial errors. To illustrate the principle of the method a very detailed profile from Draved Mose, Denmark (Aaby and Tauber, 1974) is shown in Fig. 4.20. Here eq. 9 has been fitted, by minimization of weighted squares of deviations, to all the points (not just to three) assuming no consolidation. The simple model gives a surprisingly complete description, with the decay parameter α estimated as $2 \times 10^{-4} \text{ yr}^{-1}$.

A more complex model, including consolidation effects (Clymo, 1978), when applied to blanket-bog peat at Moor House gave most estimates between 10^{-3} and 10^{-5} yr^{-1} .

Indirect estimates from simulations

Simulations may be used to calculate the overall rate of decay from a knowledge of the rate and functional relationships of component processes. For example, Bunnell and Tait (1974) and Flanagan and Bunnell (1976) included the effects of temperature, moisture content and nature of plant substrate on microbial respiration rate. Given the march of temperature and moisture content, the model gives decay. Simulations of this kind have been used for litter of *Carex aquatilis* and *Eriophorum angustifolium*, but not for older peat.

Factors affecting the rate of decay

The rate of decay of plant material in peat-accumulating systems is affected, *inter alia*, by temperature, water supply, oxygen supply, nature of the plant material, and nature of the micro-organisms and invertebrates in the peat. These factors are not always independent, and all may be correlated with depth in the peat and with age. Their effects may interact, too. The rate of oxygen consumption by litter of *Eriophorum angustifolium*

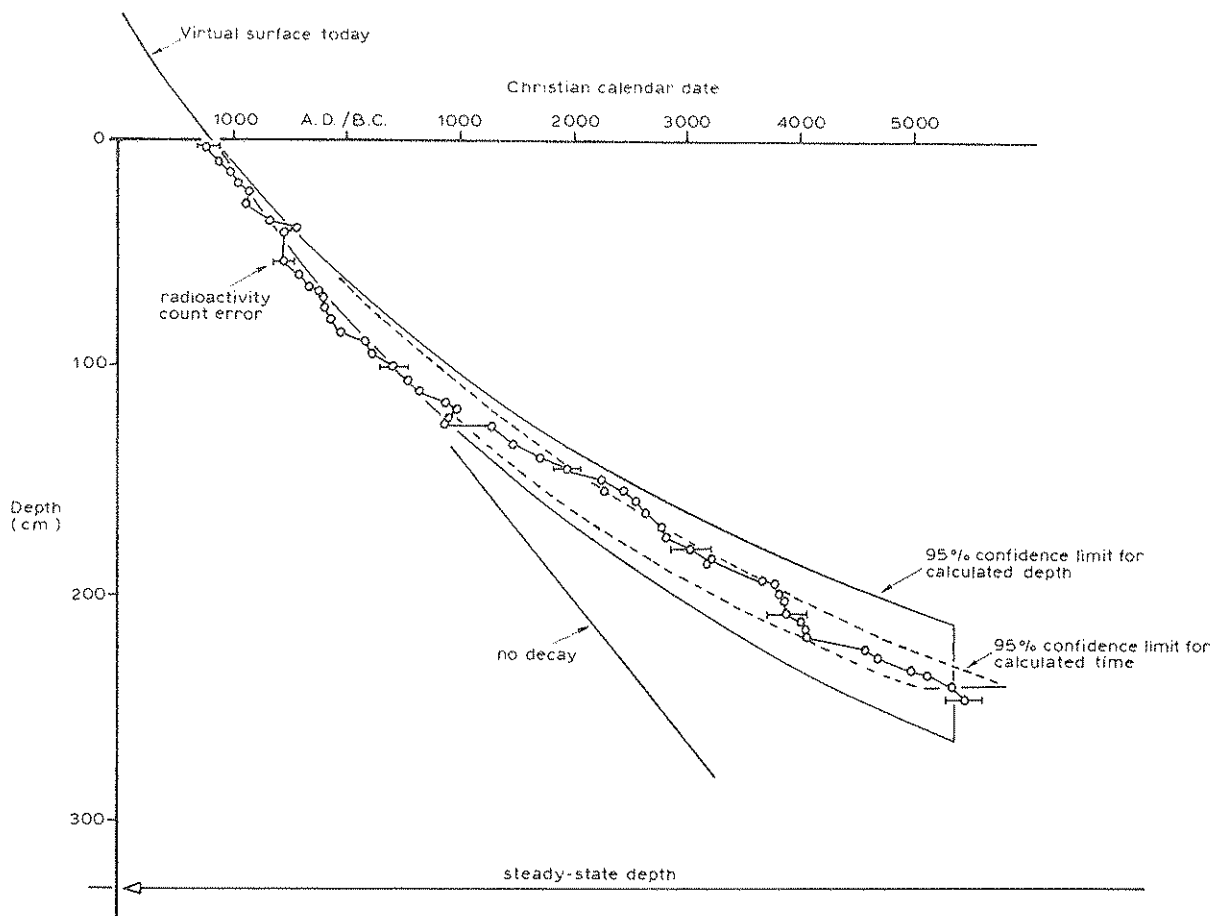


Fig. 4.20. Age (by ^{14}C counting) against depth curve for Draved Mose (Denmark). Results of Aaby and Tauber (1974). The 55 dated depths are shown by circles, seven of which have, for illustration, a horizontal bar giving the 95% confidence interval. Eq. 9 was fitted to these points (see text), assuming a uniform bulk density of 0.1 g cm^{-3} . The parameter estimates, \pm standard error, are: productivity (p) = $6.4 \times 10^{-3} \pm 2.8 \times 10^{-4} \text{ g cm}^{-2} \text{ yr}^{-1}$; decay rate (α) = $1.9 \times 10^{-4} \pm 1.9 \times 10^{-5} \text{ yr}^{-1}$. The 95% confidence bands are shown assuming that error is all in the depth or all in the age. The diagonal straight line shows what would be expected for the same productivity, but no decay. The lower horizontal line at 330 cm is the steady-state depth (see text). The surface of this bog has been cut for fuel, so the whole bog may be considered haplotelmic (only the catotelm remaining; Ingram, 1978). The fitted line is extrapolated up to today, giving a "virtual surface" at about 55 cm above the actual surface. From Clymo (*in lit*).

at 20% water content is about $130 \mu\text{l g}^{-1} \text{ h}^{-1}$ over the temperature range -4°C to 8°C (Flanagan and Bunnell, 1976; see also Fig. 4.21). At -4°C the rate is little changed over a range of "water" content from 20% to 320% at least. At a temperature above -2°C however, water content has a considerable effect. At 8°C and 320% water content the rate of oxygen consumption is double that at 20% water content. More usually, the relation between rate of oxygen consumption and temperature is a hollow curve. At 10% water content *Rubus chamaemorus* litter consumed oxygen at 5 to $8 \mu\text{l g}^{-1} \text{ h}^{-1}$ at -5°C , increasing to 30 to $50 \mu\text{l g}^{-1} \text{ h}^{-1}$ at 10°C and 240 to

$360 \mu\text{l g}^{-1} \text{ h}^{-1}$ at 30°C (Rosswall, 1974). *Carex aquatilis* litter gives similar results (Flanagan and Veum, 1974). These results show — not surprisingly — that temperature has an effect on the rate of oxygen consumption, and hence of decay rate, of litter. They also show that the process is significant at surprisingly low temperatures. Micro-organisms adapted to the general thermal environment seem to be the rule, so that the mean temperature is of less consequence than might be supposed. That psychrophilic micro-organisms occur in peat is known (see, for instance, Janota-Bassalik, 1963). What is not known is how fast the micro-organisms

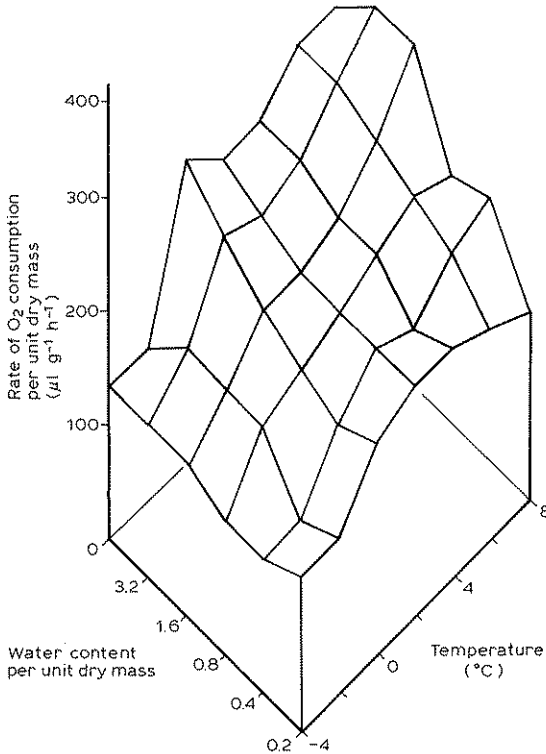


Fig. 4.21. "Respiration rate", measured in a respirometer, of dead leaves of *Eriophorum angustifolium* gathered at Barrow (Alaska, U.S.A.) in relation to water content and temperature. Redrawn from Flanagan and Bunnell (1976).

can adapt to temperature change. This may be important because peat, even water-saturated peat, is a fairly effective thermal insulator. The amplitude of temperature fluctuations is rapidly damped. The damping depth — that depth at which the amplitude of a sinusoidal oscillation has been reduced to $1/e=0.37$ of that at the surface — is about 5 cm for the daily cycle and $5 \times \sqrt{365}$ cm (≈ 1 m) for the annual cycle in peat (Monteith, 1973). At a depth three times the damping depth the amplitude is $e^{-3}=0.05$ of that at the surface. At 15 cm depth, therefore, daily fluctuations in temperature are small, but at the surface they are twenty times larger, and the total amount of decay may be critically dependent on the speed with which decay organisms respond to change. This is particularly so if the relation between temperature and oxygen consumption rate is non-linear. It can be shown (Clymo, *in lit.*) that rapid response to a non-linear relation coupled with a smaller-amplitude thermal regime (though at the same mean temperature)

should reduce the overall decay rate of *Rubus chamaemorus* at mean temperature 0°C from 0.35 yr^{-1} at the surface to 0.14 yr^{-1} at 100 cm depth, and at mean temperature 5°C from 0.62 yr^{-1} to 0.42 yr^{-1} . Of course *Rubus* litter is unlikely to survive in identifiable form to such a depth, but the same sort of effect should hold for material which does. It is this effect which makes the use of day-degree sums dubious.

Measurements of oxygen consumption by litter are necessarily made in artificial conditions; respirometers with shaken flasks are usual. The same material is often taken through a series of increases in temperature with no check of the extent of adaptation or damage. It is therefore of interest to find that measurements of decay of *Rubus chamaemorus* litter (in bags) in the field range from about 0.2 yr^{-1} (Rosswall, 1974) through 0.4 yr^{-1} (Heal et al., 1978) to 0.7 yr^{-1} (Coulson and Butterfield, 1978). These rates agree fairly well with those calculated from the respirometer measurements. Direct comparisons in the field at sites with different mean temperature have been made for standard cellulose material (Rosswall, 1974) and for uniform *Sphagnum* material of several species (Clymo, 1965). There are several reports of the rate of decay of plants of the same species, for example *Eriophorum vaginatum*, but these are not easy to compare because the plants were in all cases local to the site at which the measurements were made. In general the rate of decay of cellulose increases with temperature, or with time at a given temperature, and the decay of *Sphagnum* was about 0.05 yr^{-1} faster at a site with mean temperature about 4°C higher, but with the same amplitude.

The effects of oxygen supply on rate of decay have rarely been measured directly, but are deduced from the change in decay rate with depth. Waterlogged peat rapidly becomes deoxygenated because the rate of diffusion of oxygen in water is too slow (about 0.0001 of that in air) to replace that used in aerobic metabolism of micro-organisms. There are micro-anoxic patches in unwaterlogged peat too. The consequent change in the activities of micro-organisms is considered elsewhere in this volume. Here only the measured effects on decay are considered.

That decay rates can be low may be deduced in general from the fact that macroscopic and microscopic plant structures (not only pollen) are still

identifiable after several thousand years as peat. This argues for a decay rate of less than 0.0001 yr^{-1} . In exceptional cases it may be even less. For example, between 2400 and 2600 years ago at Tregaron Bog (Wales) *Sphagnum magellanicum* was abundant (Turner, 1964). Even today there remains the equivalent of a productivity during that time of $3 \text{ t ha}^{-1} \text{ yr}^{-1}$. This would be a respectable rate before decay had begun. Other instances are known too. There are records of about 700 discoveries of human bodies buried in peat (Dieck, quoted by Glob, 1969). In many cases the body was buried and fixed down in an old peat cutting. Usually the skin is well-preserved, and bones and other tissues may be too. Clearly, the processes of decay have been slower than in the aerobic conditions of the more conventional places for burial.

Direct measurements of plant loss by litter bag techniques have given results which differ in detail but show that there is a general reduction in decay rate of material in waterlogged peat when compared with the same material placed above the water table. *Sphagnum papillosum* decay rate fell

abruptly from about 0.12 yr^{-1} at the surface of Thursley Bog to 0.07 yr^{-1} between 5 and 18 cm depth, and to 0.01 to 0.02 yr^{-1} below 18 cm depth — the mean depth of the water table (Clymo, 1965; see also Fig. 4.22). A similar surface decline and then abrupt drop of decay rate of *Calluna* stems at 18 cm depth in Moor House (England) blanket peat was found by Heal et al. (1978), and losses in tensile strength of cellulose strips at nine sites at Moor House, and in a wet site at Abisko (northern Sweden) all show the same abrupt drop (Heal et al., 1974), as do strips in an Antarctic *Rostkovia magellanica* peat bog (Anonymous, 1978). The only conspicuous exception is the decay of roots of *Eriophorum vaginatum*, which increases steadily from about 0.07 yr^{-1} at the surface of blanket bog at Moor House to about 0.19 yr^{-1} at 25 cm deep (Heal et al., 1978). The decay rate below the water table appears in most cases to be only 0.01 to 0.04 yr^{-1} . This is close to, or beyond, the accuracy of the litter bag techniques. An alternative is to measure the evolution of methane. At Moor House, on a wet blanket bog 3 m deep, the rate of evolution

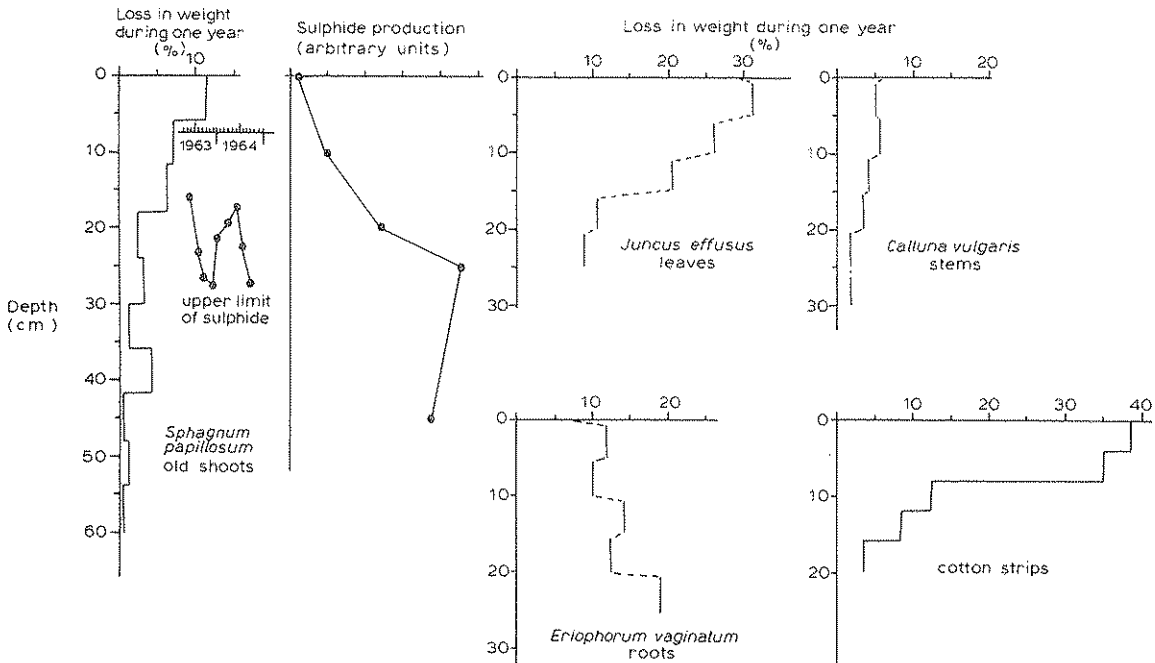


Fig. 4.22. Decay during the first year after death of a variety of materials at various depths in peat. For *Sphagnum papillosum* at Thursley, southern England, the annual cycle in the upper level of sulphide (detected by blackening of a silver wire) is shown, and the sulphide production, on a single occasion, of water samples added to an enrichment culture. The other four materials were measured at Moor House, northern England. Redrawn from Clymo (1965) and Heal et al. (1978).

of methane gas, calculated as carbon, was 1 to $7 \text{ g m}^{-2} \text{ yr}^{-1}$, with least from hummocks and most from pools (Clymo and Reddaway, 1971). At Abisko, Svensson (1974) found similar rates of methane evolution. At Moor House the efflux of carbon dioxide, calculated as carbon, was 31 to $54 \text{ g m}^{-2} \text{ yr}^{-1}$. If the methane is being produced at all depths, is the only product of decay, and reaches the surface by diffusion, then the decay rate is about 10^{-5} yr^{-1} (Clymo, 1978). This is certainly too simple a view: the erratic appearance of high methane concentration in traps suggests the evolution of gas bubbles; some of the methane may be oxidized and appear as carbon dioxide (Svensson, 1974); and there is no direct evidence that methane production is not localized near the current water table, with "fossil" methane in solution or even as trapped bubbles lower down. Svensson (1974) showed that a lot of methane is present in peat at a depth of 50 cm, but it is not clear how much of this is "fossil". There is much scope for experiment.

The other method of estimating decay at depth is from ^{14}C dates and a model of the peat accumulation process. The results from Draved Mose (Denmark) already quoted give a decay rate of about $2 \times 10^{-4} \text{ yr}^{-1}$, which is (considering the inaccuracy of all existing methods) not inconsistent with 10^{-5} yr^{-1} from methane evolution at a different site.

These rates of decay in the anaerobic zone seem low, but they are not negligible, because they apply over perhaps 20 to 50 times the depth and 40 to 100 times the mass that the aerobic rates do, and they apply for a very long time. Just how important such rates are is shown later.

The effects of nutrition and of the spectrum of micro-organisms and invertebrates are closely connected with the nature, history and location in the peat of the plant material. The organic material itself is the main "nutrient" for the organisms of decay. They attack the different chemical constituents selectively, and may themselves produce new organic substances. Molecules which were attackable by aerobic organisms may be unavailable to anaerobic ones, and *vice versa*.

It has already been shown that the decay rate is lower in waterlogged peat whatever the plant material. In the surface layers, however, the rates of decay of different species and parts of species differ widely. One of the earliest demonstrations

of this was made by Waksman and Tenney (1928). They measured carbon dioxide efflux at 26°C from air-dried and ground plant materials mixed with two or five times their own weight of water and inoculated with a "suspension of a good field soil". The rate of flux of carbon dioxide from maize stalks was about three times that from rye straw, pine needles, or *Sphagnum*. When small amounts of ammonium salts and phosphates were added, the efflux of carbon dioxide from all the materials except *Sphagnum* increased two- to five-fold, but the efflux from *Sphagnum* was unchanged unless the *Sphagnum* had been treated with acid, causing partial hydrolysis. These experiments were, of course, in very unnatural conditions and excluded the natural fauna, but they did show that "ordinary" soil micro-organisms could attack *Sphagnum* at much the same rate as they do several other plant materials, and that, uniquely among the materials tested, the rate of attack on *Sphagnum* could not be increased by adding inorganic nutrients alone. The rate of attack in this case seemed to be limited by organic nutrients alone. This may explain the observation (Strygin, 1968) that the rate of heating in piles of milled peat can be increased by the addition of hay or straw as sources of easily attacked organic nutrients, and that *Sphagnum papillosum* capitula, which presumably contain a relatively high concentration of easily attacked organic compounds as well as higher concentrations of nitrogen and phosphorus, decay about three times as rapidly as do newly dead stems and branches, whilst the addition of inorganic nitrogen and phosphorus has no significant effect on decay rate (Clymo, 1965). In a particularly elegant way, Coulson and Butterfield (1978) have confirmed these findings and have shown the importance of invertebrate grazers in decay in the aerobic zone. This is of particular interest because, whereas about 60% of the plant material on mineral soils adjacent to blanket bog at Moor House is assimilated, so that it is animal faeces which are the main food for the rest of the decomposers, only 5% of plant production on blanket bog is assimilated (Coulson and Whittaker, 1978). In particular, *Sphagnum* is scarcely ingested at all, except perhaps accidentally. Three species (the craneflies *Tipula subnodicornis* and *Molophilus ater*, and the enchytraeid worm *Cognettia sphagnetorum*) form about three-quarters of the biomass and account for about three-

quarters of the assimilated plants. Coulson and Butterfield used litter bags and made four comparisons: of large-mesh (*c.* 1 mm) with fine-mesh (*c.* 20 μ m) litter bags, thus allowing or preventing access by most of the soil fauna; of decay on mineral soil with that on peat; of a variety of species naturally occurring on the mineral soil or on the bog; and of plant material as it occurred naturally with that grown on plots fertilized with either nitrogen or phosphorus, and thus having larger concentrations of these elements. The first three of these comparisons are shown in Fig. 4.23. The species are arranged in rank of nitrogen con-

centration in the material used. Animals accounted for an important proportion of the weight loss of *Phleum pratense* on mineral soil. *Rubus chamaemorus* on mineral soil and on peat, *Calluna vulgaris* on both soils, *Festuca ovina* on peat, and *Sphagnum recurvum* on mineral soil. Animals had no effect on weight loss of *Eriophorum vaginatum* on either soil, or of *Sphagnum recurvum* on peat. Comparing soil types (with free access by animals) *Phleum* lost notably more weight on the mineral soil than on peat, whilst *Rubus* and to some extent *Calluna* showed a reverse effect. *Rubus* leaves recovered from peat after three months contained more en-

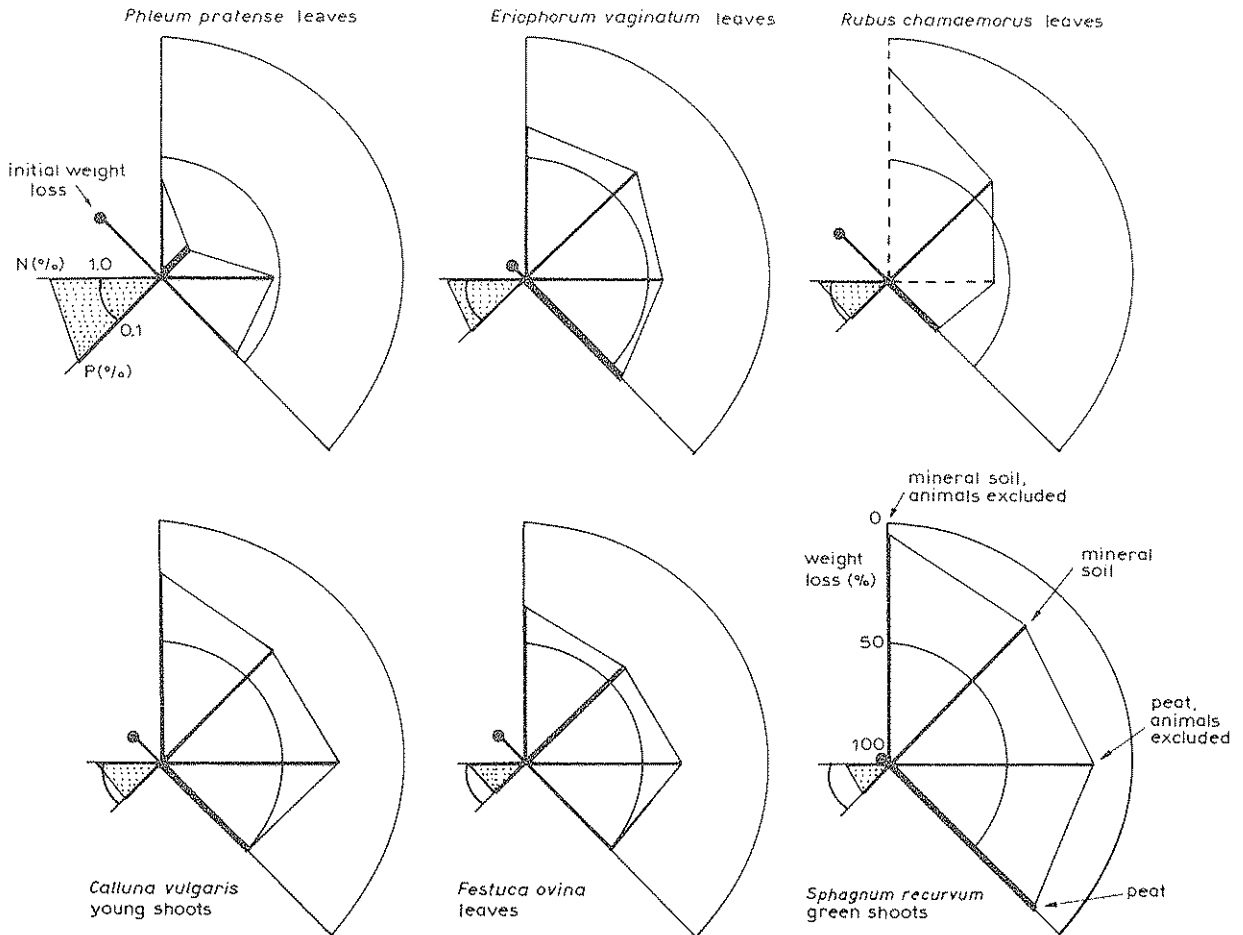


Fig. 4.23. Weight loss during one year from litter bags filled with plant material of one of six species. The bag mesh size was 20 μ m (excludes most animals) or 0.8 mm, and bags were buried in mineral soil adjacent to blanket bog at Moor House (England) or in peat there. Arcs define 0% and 50% loss. The results for the four treatments are joined by straight lines, forming a polygon. *Rubus chamaemorus* in small-mesh bags was measured for 3 months only. The results have been calculated in the same proportion as that found for 3-month and 12-month measurements on large-mesh bags. The northwesterly "stick-and-knob" shows the leaching loss during the first seven days. All material was leached before the experiment began. To west and southwest are the initial concentrations of nitrogen and phosphorus. Thick bars show the natural habitat. Drawn from results of Coulson and Butterfield (1978).

chytraeids, dipteran larvae, mites and Collembola (by a factor of from 2 to 5) than did similar leaves on mineral soil.

Taken together, those results show a surprising range of rather specific effects. Invertebrates on peat are clearly important agents in the decay of *Rubus chamaemorus* leaves, but of little importance in the decay of *Eriophorum* leaves or *Sphagnum* shoots.

There are potentially important differences between species in the absolute rate of decay, measured over the first year, too (Table 4.13). The rank order of decay rate is much the same where it has been measured more than once, but the absolute values differ. There are uncontrolled differences between different sets of measurements, even for the same experimenters (e.g. Fig. 4.24). Water content can have a big effect. For example, Heal et al. (1978) showed that the relationship between loss in weight of *Rubus chamaemorus* leaves and water content is approximately hyperbolic with half-maximum rate (0.3 yr^{-1}) at about 200% water content. In very wet conditions the rate was 0.6 yr^{-1} . Overall, however, it is clear that some parts of the species, such as leaves of *Rubus chamaemorus*, *Narthecium ossifragum* and *Calluna vulgaris*, decay rather rapidly, whilst stems and roots of *Calluna* and *Eriophorum*, and *Sphagnum*,

decay more slowly. There is a tendency for materials with relatively high nitrogen and phosphorus concentration to lose weight more rapidly, whether they are available to animals or not (Figs. 4.23, 4.24). Coulson and Butterfield experimented with blanket bog which had been fertilized with ammonium nitrate or superphosphate (a mixture of calcium sulphate and calcium phosphate). The concentration of nitrogen and phosphorus in plants growing on these plots increased (by from 10 to 30%), and so did the abundance of many of the invertebrates. The decay rate of plants grown on unfertilized bog, but transferred to fertilized bog, was no different from similar material on fertilized bog, but plants grown on nitrogen-fertilized bog, and having a higher concentration of nitrogen, decayed more rapidly than did normal plants when put on unfertilized bog (Fig. 4.24). The decay rate of plants on phosphorus-fertilized bog was not more rapid, however. Indeed the loss of *S. recurvum* was only 10%, compared to 18% for unenriched plants.

The differences in the nitrogen experiment were rather small, but because the experiment was large and carefully designed the differences were significant at the 1 in 20 level. Earlier reports that nutrition was without effect probably mean that those experiments were not sufficiently sensitive to

TABLE 4.13

Rate of weight loss (yr^{-1}) from dead plants in large-mesh bags during one year on blanket bog at Moor House, England.

	Source		
	Heal et al. (1978)	Coulson and Butterfield (1978)	Clymo (1965)
<i>Narthecium ossifragum</i> leaves	0.45		
<i>Rubus chamaemorus</i> leaves	0.36	0.78 ²	
<i>Eriophorum angustifolium</i> leaves	0.24		
<i>Eriophorum vaginatum</i> leaves	0.22	0.46 ²	
<i>Calluna vulgaris</i> shoots	0.20	0.55 ²	
<i>Sphagnum capillifolium</i> shoots ¹			0.16
<i>S. recurvum</i> shoots		0.14 ²	
<i>S. cuspidatum</i> shoots ¹			0.15
<i>S. papillosum</i> shoots ¹			0.08
<i>C. vulgaris</i> above-ground stems	0.08		
<i>C. vulgaris</i> roots	0.05		
<i>E. vaginatum</i> roots	0.01		

¹ Excludes capitulum. ² Pre-leached to remove readily soluble materials. Values recalculated to include these lost materials, to allow comparison with the first column.

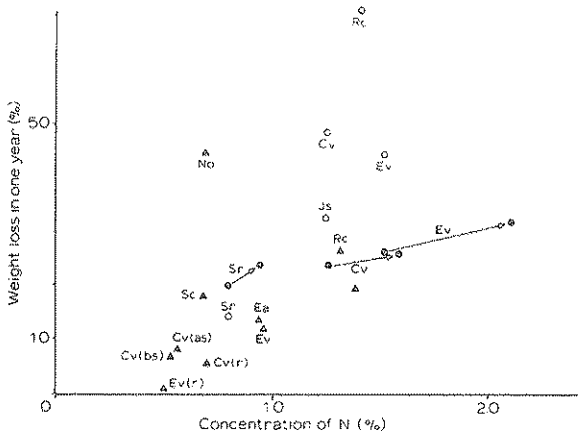


Fig. 4.24. Decay rate in relation to initial concentration of nitrogen in plant material in litter bags at Moor House (England):

- Cv* = *Calluna vulgaris* shoots
Cv(as) = *C. vulgaris* above-ground stems
Cv(bs) = *C. vulgaris* below-ground stems
Cv(r) = *C. vulgaris* roots
Ea = *Eriophorum angustifolium* leaves
Ev = *E. vaginatum* leaves
Ev(r) = *E. vaginatum* roots
Js = *Juncus squarrosus* leaves
No = *Narthecium ossifragum* leaves
Rc = *Rubus chamaemorus* leaves
Sc = *Scirpus cespitosus* shoots
Sr = *Sphagnum recurvum* shoots

Results from: ▲, Heal et al. (1978); ○, Coulson and Butterfield (1978), first experiment; ●, Coulson and Butterfield (1978), nutrition experiment. Arrow-heads point to the experimentally nitrogen-enriched material

detect the differences. The change in nitrogen concentration on fertilized bog was not large either, when considered as a proportion of the range shown in Fig. 4.24. Nevertheless, the results are important because there is high intercorrelation between the concentration of different elements in plants. Complex descriptive equations, such as that used by Heal et al. (1978) using (P+Ca) and (lignin × tannin) give no insight into mechanisms. Only by *experiment* is it possible to isolate the differences and to discover causal links.

Not only do different species and macroscopic parts of species disappear at different rates (Fig. 4.23), but so do different parts of cells. For example, the abaxial and adaxial surface of the cells in leaves of *Sphagnum* break down more rapidly than do the thickening bands and the enclosed cells

(Dickinson and Maggs, 1974), and the attack is sporadic: some leaves are extensively damaged whilst others close by are virtually undamaged.

The time course of decay is difficult to measure and difficult to interpret. Broken litter may be lost from litter bags. The bags themselves become covered, and thus move to a different environment. Different chemical fractions decay at different rates. Equations for the time course of decay can therefore be nothing more than descriptions, but are essential if models of the peat accumulation process are to be made.

Two assumptions have commonly been made. The first (e.g. Baker, 1972) is that the rate of decay is constant, so that a constant proportion of the *original* mass disappears during each time interval. Thus, if the decay rate is 0.2 of the original mass per year, then the material will have disappeared in five years. A much commoner assumption, inspired by the observation that some peat is thousands of years old, and ignoring the fact that such peat if put in aerobic conditions will decay quite rapidly, is that the rate of decay is a constant proportion of what is left. Jenny et al. (1949) used this assumption, and have generally been followed, though with little or no evidence in support. The two assumptions may be expressed:

$$\frac{dm}{dt} = -\beta m \quad (11)$$

$$\frac{dm}{dt} = -\alpha m \quad (12)$$

where m is the mass of peat, t is time, β a decay parameter (dimensions $M T^{-1}$) and α a decay parameter (dimension T^{-1}). These equations, when solved for m , give:

$$m_t = m_0 - \beta t \quad (13)$$

$$m_t = m_0 e^{-\alpha t} \quad (14)$$

Eq. 14 can be put in linear form as:

$$\ln(m_t/m_0) = -\alpha t \quad (15)$$

The same results, plotted according to eqs. 13 and 15, are shown in Fig 4.25. There is little reason to claim that one set is closer to a straight line than the

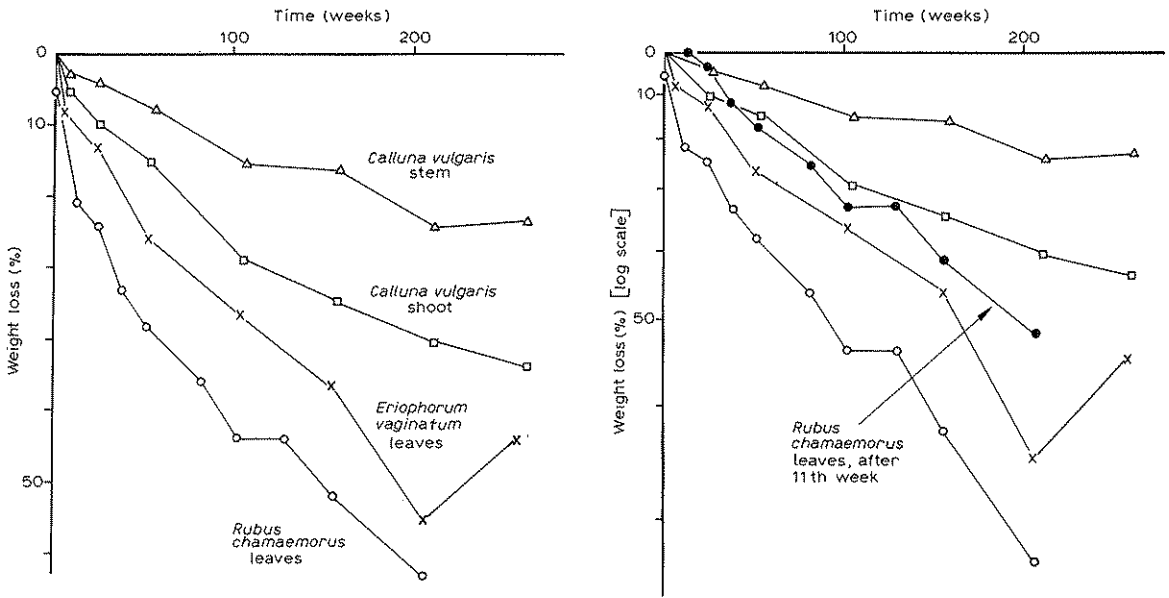


Fig. 4.25. Weight loss of various plant materials in litter bags during five years in peat at Moor House (England). On the left graph, a straight line would indicate that a constant proportion of the original weight was lost per unit time. On the right graph a straight line would indicate that the rate of loss is a constant proportion of the amount left at any time. *Rubus chamaemorus* is plotted again (filled circles) restarting at eleven weeks after the initial rapid loss in weight. Results of Heal et al. (1978), redrawn from Clymo (1978).

other, though there is some indication that there is a fraction — up to about 20% in *Rubus chamaemorus* — which decays within ten weeks. For the next 250 weeks, either assumption seems to fit equally well. Given a coefficient of variation of about 10 to 20%, which it is very difficult to reduce in experiments of this kind, it is unlikely that the evidence from litter bags will favour one assumption rather than the other until about 80% of the original mass has been lost. By that stage of course most of the structure has gone too, and litter bags become increasingly inaccurate. This is true also of Baker's (1972) method of measuring the loss from Antarctic *Chorisodontium aciphyllum* which had never been disturbed: the measurements fit either assumption fairly well, and become inaccurate beyond about 60% loss (Clymo, 1978, figure 1). Finally, one may perhaps have doubts about cases such as the last two points for *Eriophorum vaginatum* leaves in Fig. 4.25 where the precision is high but the accuracy is obviously much lower; errors of accuracy in long-term measurements are commonly unknown but are quite possibly much larger than errors in precision.

This uncertainty about which assumption is correct may appear to be unimportant, as it seems

to matter only when the mass left is less than 30% of the original mass. That this is not true, and that the exact form of the decay curve is of vital importance, is best revealed by calculations on models, extended over hundreds or thousands of years. The existing evidence about decay is in some respects unsatisfactory and will probably have to remain so. The biggest single gap is the lack of reliable estimates of the actual rate of decay deep in the peat.

Before turning to models of peat accumulation it is worth summarizing the factors which are known to be important determinants of decay: (1) temperature; (2) water supply (at the surface of the peat-forming system); (3) oxygen concentration; (4) nature of the plant material; and (5) nature and activity of soil animals and micro-organisms. These interact with each other and with position in the profile, and they change with time.

Models of peat accumulation

The chief purposes of models of peat accumulation are: to test our understanding of the accumulation process; to reveal the consequences of assumed processes; and to estimate parameters, such as the rate of anaerobic decay over hundreds

of years, which cannot be measured directly. There is much confusion about the reliability and value of model results. The apparent precision of symbols and numbers is often belied by grotesquely unlikely predictions. Some explanation is therefore necessary.

Models can be expressed in one or more (simultaneous) equations of the general form:

$$R_c = f(V_e, V_i, P) \quad (16)$$

where R_c is the calculated result; V_e are external (driving) variables, such as temperature; V_i are internal (state) variables, such as the mass of some component; and P are parameters. These equations embody the assumptions about the *processes* and their interactions, if any. If there is evidence that a particular relationship does actually exist, and its functional form is known, then the ultimate test of understanding is likely to be more stringent because fewer arbitrary assumptions need be made; but lack of evidence has rarely inhibited the making of more or less credible assumptions. This stage of model making may start from assumptions about a process — for example, that decay rate is proportional to the amount of material — and derive equations algebraically. Alternatively it may be simply an *ad hoc* description, in symbols, of an observed geometric relationship (typically a graph) but enshrining no understanding of why the shape is as it is. Even in such cases there is room for choice: a hyperbola can be understood as some sort of saturating process, and is generally therefore a more illuminating assumption than a quadratic (or higher-degree polynomial) description which gives an equally good 'fit' to the observations. In choosing descriptions it is important to remember that in reality there are physical boundaries to the validity of any description; mass cannot be negative, rate cannot increase exponentially without limit. If these features are not included the model will, sooner or later, become unrealistic.

The fundamental strength of a model may, therefore, be tested by asking questions such as: Is there evidence that the processes occur over the range of variables to be used? Has the possibility of interaction between processes been considered? Do the descriptions arise from clear postulates, or are they *ad hoc*? Do the descriptions allow for discontinuity or non-linearity or both? When tested in this

way, most of the models of peat accumulation are rather weak.

Models have been used in many ways. The simplest is to supply values for all the variables (V_e , V_i) and parameters (P) and to calculate the results R_c . This is a direct simulation. The results may be compared with measured values R_m . Such comparison may be of a crude "by eye" type, or may involve some numerical measure of badness of fit. There are difficult problems of weighting — the model may be a good fit in some places and bad in others, and this may or may not be expected. Essentially this is a direct test of the model. If agreement between R_c and R_m is poor then it may be that the *processes* are inaccurately described (the wrong shapes on graphs) or incompletely described, or it may be that the variable or parameter *values* are inaccurate (or both). The sensitivity of the model to errors in the values supplied may be examined analytically or by numerical trial. If agreement between R_c and R_m is close, then the model may be accepted as a useful working description, and as *confirmatory* evidence that the processes and values used are fairly accurate. The more complex the pattern of R_c , the greater the confirmatory value.

A more complex, indirect, way of using a model is to omit some or all the parameter values (P). Trial values are assumed and R_c calculated. Using known values of R_m , a measure of badness of fit is calculated. The values of P are then changed to arrive at a least bad fit between R_c and R_m . An example is the use already mentioned as a means for estimating the decay in anaerobic conditions over 5000 years at Draved Mose. This sort of use does test the description of processes to some extent; it might prove impossible to get an acceptable fit over the whole time span by any combination of p and α . But on the whole the test is not very strong. An equally close fit could be got by using an arbitrary quadratic (which has three parameters). This does not mean the model is "wrong" — only that the accuracy of the processes included in it cannot be well confirmed by this test.

The adjustment of parameter values is best done systematically. There are many ways of doing this, and choice of which is best is a matter for specialists. In general, there is no method of guaranteeing that *the* best combination of parameters has been found, but in practice it usually happens that

much the same set of values is reached from different starting points, and this is taken to show that something near the best has been reached. Sometimes this minimization is done "by hand". A trial is made, then a new parameter value guessed and another trial made, and so on. This was the method used by Jones and Gore (1978) in estimating the decay rate that best fitted their model of the blanket bog at Moor House, England. They combined this approach with changes in the assumptions about processes too. It will be obvious that such "fitting" methods are likely to be inefficient. The parameters are usually estimated with different precision, and the estimates may be weakly or strongly correlated.

The earliest explicit model of organic matter accumulation was that of Jenny et al. (1949). They postulated an annual instantaneous injection of organic matter as litter fall from deciduous plants, and decay of a constant proportion of the accumulated organic matter during each year. This is mathematically awkward, so they assumed that both litter fall and decay were continuous, and arrived at the equivalent of eq. 8 on page 199:

$$x = \frac{p}{\alpha} (1 - e^{-\alpha t})$$

where p is net productivity ($M L^{-2} T^{-1}$) and x the mass accumulated at time t . This is shown in Fig. 4.26. If one assumes that litter addition is instantaneous but decay is continuous then one gets a graph similar to those in Fig. 4.26 but with annual negative exponential "teeth" superimposed.

Eq. 8 has interesting implications. One is that after a long time the whole system tends, asymptotically, towards a steady-state mass. More precisely, as $t \rightarrow \infty$, $x \rightarrow p/\alpha$. Suppose, for illustration, that present-day peat-forming systems are in a steady state. Forrest (1971) believed this to be true of the Moor House blanket bog, and one may deduce from curves relating peat depth to precipitation and bog diameter (Granlund, 1932; Wickman, 1951) that some Scandinavian peat-forming systems are approaching, or in, this state. If the peat is 5 m deep with bulk density 0.1 g cm^{-3} and if surface productivity is $200 \text{ g m}^{-2} \text{ yr}^{-1}$, then α is $0.4 \times 10^{-3} \text{ yr}^{-1}$. The model of eq. 8 makes no allowance for differences in rate of decay of different species or parts of species, or for position in

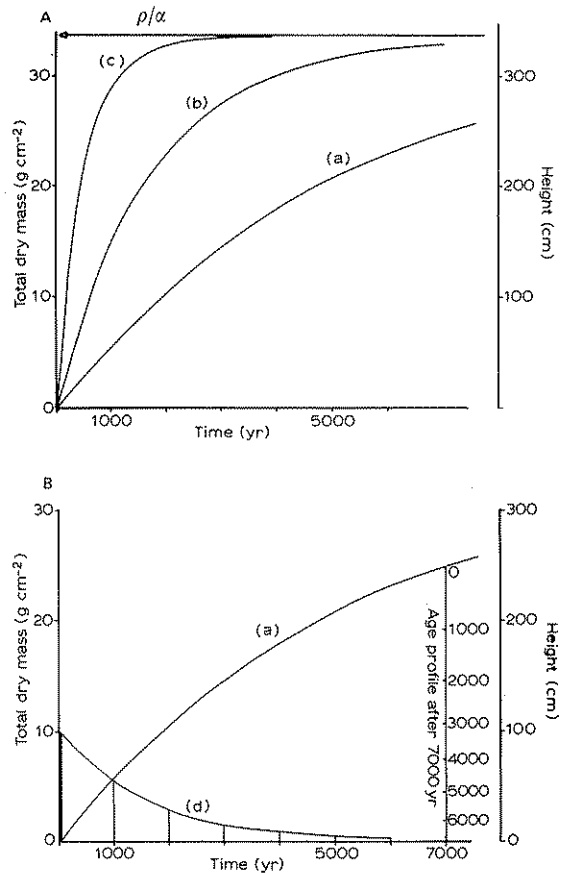


Fig. 4.26. A. Accumulation of a single-component peat according to eq. 8. The left axis shows mass, the right axis shows height assuming bulk density (ρ) to be 0.1 g cm^{-3} . The three curves (a), (b) and (c) have the same ratio of productivity (p , $\text{g cm}^{-2} \text{ yr}^{-1}$) to decay rate (α , yr^{-1}). The steady state approached by all three is shown at p/α . The parameter values are:

	(a)	(b)	(c)
$p(\text{g cm}^{-2} \text{ yr}^{-1})$	6.4×10^{-3}	1.9×10^{-2}	6.4×10^{-2}
$\alpha(\text{yr}^{-1})$	1.9×10^{-4}	0.57×10^{-3}	1.9×10^{-3}

The values for (a) are those which best fit the Draved Mose data (Fig. 4.20).

B. Accumulation of a single-component peat [curve (a) repeated from Fig. 4.26A] and course of decay (d) of an initial mass of peat of 10 g cm^{-2} with the same decay rate as that of curve (a). The age profile of curve (a) at the arbitrary time of 7000 yr is shown.

relation to the water table, but a second implication is that a very low decay rate — 0.04% — is sufficient to change the accumulation curve from an indefinitely accumulating peat mass to one which has reached a steady state at a relatively modest depth of 5 m. A decay rate of 0.04% is very difficult to measure in the field. Litter bags are much too

imprecise and inaccurate. Gas evolution rates are better, but it is not easy to determine where the gas comes from. Indirect estimates, from models, may be sensitive enough but suffer from inaccuracy in their assumptions.

A third implication is now obvious: surface productivity, p , may be finite and perhaps large *and yet the rate of peat accumulation may be very small or zero*. It may even be negative, with a net loss of carbon to the atmosphere, if the rate of decay at depth has increased — perhaps because of an increase in temperature, or as a result of draining (e.g. Hutchinson, 1980) during the last century or two. The possible consequences of this were considered by Woodwell et al. (1978). The stable state may be seen formally in eq. 7 where, if $p = \alpha x$, then $dx/dt = 0$, the rate of production, which is limited to the surface, is balanced by the rate of loss *summed over the whole depth* of peat.

The assumption that the peat-forming system has reached a steady state may be unimportant. It is easy to show that if Q is the proportion of the final asymptotic steady-state mass, x_x , which has been reached by t_Q then:

$$t_Q = -\frac{\ln(1-Q)}{\alpha} \quad (17)$$

For the example already used, the peat will have reached 90% ($Q = 0.9$) of the steady state after about 5800 years. It is interesting to note that the time needed depends on the decay rate but not on the productivity.

The independence of rate of peat accumulation, dx/dt , and productivity, p , appears in another important context. It has become increasingly common to see layers of peat dated by ^{14}C age or by cross-reference of pollen zones to other ^{14}C -dated profiles. The distance between two such layers may be divided by the difference in dates, and a "peat accumulation rate" reported. There are two objections to this practice (apart from possible errors in the dating technique). First, the peat may have consolidated — a general term for elastic and plastic reduction in depth. That such consolidation may occur has been shown in experiments by, *inter alia*, Berry and Poskitt (1972) and Clymo (1978), and on a large scale in the English fens (partly as a result of drainage) by Hutchinson (1980). This problem could be avoided if peat accumulation

rates were expressed on a mass basis rather than as depth. If this is to be done then a bulk density profile is needed, but those who take samples for ^{14}C measurements rarely measure bulk density too.

The second objection to such estimates of "peat accumulation rate" is that the calculation is valid only if the decay rate is zero. Suppose, for example, that ^{14}C dating establishes that a peat sample is 1000 years old, and another from 100 cm deeper is 2000 years old. Assume further that there is no consolidation. If there is no decay at all, then in another 5000 years this layer of peat will still be 100 cm thick. If the decay rate is as little as 0.04% per year, however, the peat layer will be only 13.5 cm thick (the general shape of the decay curve is shown in Fig. 4.26) and the peat accumulation rate would, wrongly, be reported as $13.5/5000 = 0.03 \text{ mm yr}^{-1}$. Nor is the accumulation rate really $100/5000 = 0.2 \text{ mm yr}^{-1}$ because the youngest part of the layer is 1000 years old but the oldest is 2000 years old.

The solution to this problem is to use a minimum of three dated levels and apply eq. 10 and then eq. 9 to get first α and then p . More useful is to use the minimization technique already described to estimate p and α , as shown in Fig. 4.20. The values thus obtained ($p = 64 \text{ g m}^{-2} \text{ yr}^{-1}$, $\alpha = 2.8 \times 10^{-4} \text{ yr}^{-1}$) are small and refer to the zone of low decay — the anaerobic zone, or catotelm of Ingram (1978). In particular, p is the rate at which matter is added to the *anaerobic* zone — the material which has run the gauntlet of the aerobic acrotelm and reached the comparative safety of the anaerobic catotelm. Of course the material itself has not necessarily moved in space, but new plant production above it has gradually buried the original material, and the water table usually keeps at an approximately constant mean depth below the surface, so, as the water table rises, the material moves down *relative to the water table*. The rate at which material passes into the anaerobic catotelm is of much greater importance in determining the amount of peat accumulated than is the net primary productivity at the surface. For Draved Mose the rate of entry to the anaerobic zone is perhaps one-fifth to one-tenth of the net primary productivity. The value of $64 \text{ g m}^{-2} \text{ yr}^{-1}$ may be compared with $32 \text{ g m}^{-2} \text{ yr}^{-1}$ estimated by a different method for blanket bog in Ireland (Moore, 1972).

Differences in decay rate lead to changes in the

representation of different components too (components here mean chemical substances, tissues or whole plant parts). There is some experimental evidence for this in pine-needle litter (Minderman, 1968). It appears as a bend or as two lines joined by a curve on graphs similar to Fig. 4.25B. *Rubus chamaemorus* is a good example. The sort of effects to be expected are shown in Fig. 4.27. For two components with decay rates of 0.5 and 0.1 yr⁻¹ and initially in equal proportions, then after ten years the proportions will be 0.2 and 0.8, and will change very little thereafter. If the decay rates are, say, ten times smaller, then it takes ten times as long to reach the same proportion. It seems that decay rate actually drops by a factor of about 100 when the catotelm is reached, so most of the selection probably happens in the first few years after death.

It is helpful, for illustration, to consider the results of a model which combines two layers and two components, giving four independent components of the mass variable m , and two independent decay parameters (α_a) in the aerobic acrotelm and two (α_c) in the anaerobic catotelm. There are two independent net primary productivity parameters, p_a and a fixed depth (in mass terms) for the acrotelm, giving seven parameters in all (Table 4.14). The output rate from the acrotelm is then the input p_c to the catotelm and is determined by the other p , α , and depth parameters. It is this p_c which can be estimated from the Draved Mose results. Starting from nothing, the acrotelm accumulates to the fixed depth, taking a characteristic time, t , determined by the p_a and α_a parameters,

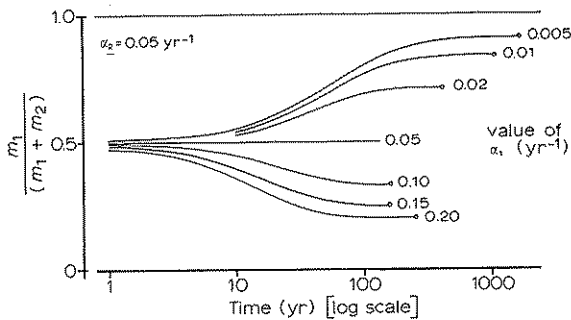


Fig. 4.27. Proportion that component 1 (mass = m_1) forms of the total mass ($m_1 + m_2$) in a two-component mixture in relation to time and decay rate (α). If both decay rates are multiplied by a factor, then the same graphs may be used, but with the time axis divided by the same factor. For example, if decay rates are multiplied by 10 then the time axis values must be divided by 10.

to do so. Thereafter the acrotelm is in a steady state and feeds matter at a constant rate to the catotelm. For matter added at the surface it takes the characteristic time for the catotelm to grow up and claim it, and at the end of that time whatever survives is in the catotelm. Some exploratory results of this model are shown in Table 4.14. The first case, which acts as a reference for all the others, gives the components equal productivity, but there is a four-fold difference in decay rates and a fifty-fold difference in decay rate between acrotelm and catotelm. The net productivity (1000 g m⁻²) is between likely values for bog and fen. The acrotelm depth, assuming the approximately linear trend in bulk density from 0.01 g cm⁻³ at the surface to 0.1 g cm⁻³ lower down, corresponds to a depth of about 16 cm. It takes about sixteen years before the catotelm can claim newly produced organic matter. Only 24% survives so long, and of *this* only about 8% is of the faster decaying component 1, which originally formed 50% of the total. The final steady state corresponds to about 220 cm depth of peat; component 1 forms only 2% of all this, and much less than 1% in the lowest layers.

The second case gives both components the same decay rate in anaerobic conditions. This has little effect on the final steady-state depth (and the proportion of component 2 does not change in the catotelm).

In the third case, increasing the anaerobic decay rate of both components five-fold reduces the catotelm steady state in proportion to give a total depth of about 50 cm. It is very clear that the difference between a decay rate of 0.4% and 2% in the catotelm has a marked effect on the steady-state depth. It is the *proportional* change, not the absolute change, which matters.

The fourth case shows the effect of a four-fold decrease in the aerobic decay rate for the faster component. This results in a shorter time (ten years) for *both* components in the dangerous acrotelm. The steady-state depth approaches 4 m.

The same sort of effect is seen in the fifth case, in which the productivity of component 2 is doubled. The acrotelm is traversed in only seven years, so the input to the catotelm is great and the steady-state depth is over 7 m.

In the sixth case, the acrotelm has been deepened from about 16 cm to about 20 cm. This small difference results in a marked increase (from 16 to

CORE VOL 15

TABLE 4.14

Parameter values and calculated results for a two-layer, two-component peat accumulating system (~ indicates the same value as in Case 1; an asterisk shows that the value is that of a parameter which is specified; other values are calculated results; bold type indicates the parameter value(s) in which each other case differs from Case 1)

Case	Component	Aerobic zone (acrotelm)					Anaerobic zone (catotelm)			Total	
		P_a ($\text{g cm}^{-2} \text{ yr}^{-1}$)	α_a (yr^{-1})	$m_a(t_c)$ (g cm^{-2})	$m_a(\infty)$ (g cm^{-2})†	t_c (yr)	p_c ($\text{g cm}^{-2} \text{ yr}^{-1}$)	α_c (yr^{-1})	$m_c(\infty)$ (g cm^{-2})†	Q_{2500} (%)	$m_a(t_c) + m_c(\infty)$ (g cm^{-2})†
1	1	*0.05	*0.20	0.24	0.25		0.002	*0.004	0.47		0.71
	2	*0.05	*0.05	0.56	1.00		0.022	*0.001	22.0		22.6
	Total	0.10		*0.80	1.25	16.4	0.024		22.5	92	23.3
2	1	*~	*~	~	~	~		*0.001	1.88		2.12
	2	*~	*~	~	~	~		*~	22.0		22.6
	Total	~	~	*~	~	~	~		23.9	92	24.7
3	1	*~	*~	~	~	~		*0.020	0.09		0.33
	2	*~	*~	~	~	~		*0.005	4.41		4.97
	Total	~	~	*~	~	~	~		4.5	100	5.3
4	1	*~	*0.05	0.40	1.00		0.030	*~	7.50		7.90
	2	*~	*~	0.40	~		0.030	*~	30.0		30.0
	Total	~	~	*~	2.00	10.2	0.060		37.5	84	37.9
5	1	*~	*~	0.19	~		0.012	*~	2.93		3.12
	2	*0.10	*~	0.61	2.00		0.070	*~	69.6		70.2
	Total	0.15	~	*~	2.25	7.3	0.082		72.5	92	73.3
6	1	*~	*~	0.25	~		<0.001	*~	0.05		0.30
	2	*~	*~	0.75	~		0.012	*~	12.5		13.2
	Total	~	~	*1.00	~	27.8	0.012		12.5	92	13.5

¹Symbols: p_a =net productivity (must be specified); α_a =aerobic decay rate (must be specified); $m_a(t_c)$ =depth of aerobic zone in mass units (total must be specified); t_c =characteristic time that matter stays in the aerobic zone before being claimed by the rising anaerobic zone; $m_a(\infty)$ =steady-state mass which would have been reached by the aerobic zone alone; p_c =rate at which matter passes from the aerobic to the anaerobic zone; α_c =anaerobic decay rate (must be specified); $m_c(\infty)$ =steady-state mass in the anaerobic zone; Q_{2500} =proportion (as %) of the final steady state reached after 2500 years.

†An approximate value for depth (cm) may be obtained by multiplying the value for mass in g cm^{-2} by 10. This assumes that the bulk density is 0.1 g cm^{-3} . For the aerobic layer a factor of 20 would be more accurate because bulk density increases from 0.01 to about 0.10 g cm^{-3} .

28 years) in the time needed to traverse the acrotelm. In consequence, nearly all component 1 disappears. The steady-state depth is about 140 cm, but component 1 forms less than 0.4% of the whole mass. A 4 cm change in acrotelm depth has had a remarkable effect on the relative survival of the two components.

These few examples are sufficient to show that simple assumptions about the growth and decay

processes can produce a great variety of effects.

Various modifications and extensions of this simple model have been used. The first (Gore and Olsen, 1967) was to increase the number of compartments (equivalent to zones) to include transfers of "net primary production" to "live plant" and thence to "dead plant" and "peat", with provision for transfer from live plant direct to peat (presumably as root and rhizome). The model was

programmed for an analogue computer — at that time this was a sensible choice — but it is unclear from Gore and Olsen's account precisely what processes were supposed to be operating or where. The parameters of the model were adjusted by trial and error to fit the time course of matter in the different categories to that measured on a blanket bog recovering from cutting.

Subsequently, Jones and Gore (1978) devised another model which allowed several components to be put in at the surface at constant rate, but in which the rate of decay was a linear function of depth, decay decreasing at greater depth. This implies, of course, a potentially negative decay rate, and it is not clear what Jones and Gore did to prevent this happening. They showed that, if less dense leaves decay more slowly than denser wood does, then peat bulk density might increase for this reason alone. This effect has not been considered by other workers, and might be of some importance if the peat contained much wood. The simulated age–depth profiles did not agree closely with the observed ones down to 150 cm and 2500 years, and were particularly sensitive to changes in the depth–decay regression slope. Jones and Gore then tried *ad hoc* adjustment of parameters and of assumptions about the way in which decay rate changed with depth, but without much improvement in fit to the field results.

A different elaboration is to try to account for the effects of consolidation. At least two different effects must be considered. First is an “elastic” compression: a load, rapidly applied to and removed from peat which still retains macroscopic structure, produces elastic deformation. Over small ranges the stress–strain relation is linear (Hooke's Law) but over the range of interest, with compression over 20% or more, a negative exponential is a better description. The force involved is produced by the weight of the accumulated peat and of water above the water table. More important is long-term creep or plastic flow. Hanrahan (1954), Berry and Poskitt (1972) and Clymo (1978) have all shown experimentally that the amount of consolidation from this cause is proportional to the logarithm of time. These two processes can be combined with a two-zone (aerobic and anaerobic) single component model (Clymo, 1978). This model, which has seven parameters (p , α_a , α_c , rate of growth in length of plants, compression parameter, creep

parameter, and depth of the acrotelm, which is equivalent to the transition from aerobic to anaerobic conditions) produces calculated profiles of bulk density and age. Initial tests of this model using measured parameter values were much less ambitious than those tried by Jones and Gore, and showed agreement within the 95% confidence bands for age and bulk density for about half the top 30 cm, corresponding to fifty years. It was obvious, however, that agreement varied systematically (Fig. 4.28). The model was particularly sensitive to the depth of the acrotelm, just as the one illustrated in Table 4.16 was, and just as Jones and Gore's model was to change in the regression slope. All these effects come from the same cause: the length of time spent in the zone of high decay rate is crucial to survival into the comparative safety of the anaerobic peat.

The consolidation model was also used to estimate the parameters for a fixed aerobic/anaerobic transition depth. The remaining six parameters were chosen at random on a logarithmic scale extending from 10^{-6} to 10^6 times the measured value, and then adjusted to minimize a weighted sum of squares of deviations of observed bulk density and age from calculated bulk density and age. This process was repeated 28 times using different randomly chosen sets of parameter values to start the minimization. The frequency distribution of parameter values obtained after minimization is shown in Fig. 4.29. (The frequency distribution of *starting* values was, of course, much broader, even for anaerobic decay which is shown on a logarithmic scale.) In general the estimated biological parameters (except for anaerobic decay, which was ill-determined) agreed fairly well with the measured values, but the two physical ones did not agree.

Part of the explanation of this lack of agreement may be that the model takes no account of a process which certainly happens — the catastrophic collapse of mosses, with attendant increase in bulk density, when structure has been so weakened that it can no longer support the overlying weight of shoots and capillary water. Fenton (1978, 1980) worked with the very interesting and particularly favourable Antarctic “moss-banks”. These contain no vascular plants and a negligible number of invertebrate grazers; they can be monospecific; the mosses retain their structure at all depths; and one species shows annual growth increments. Below 20

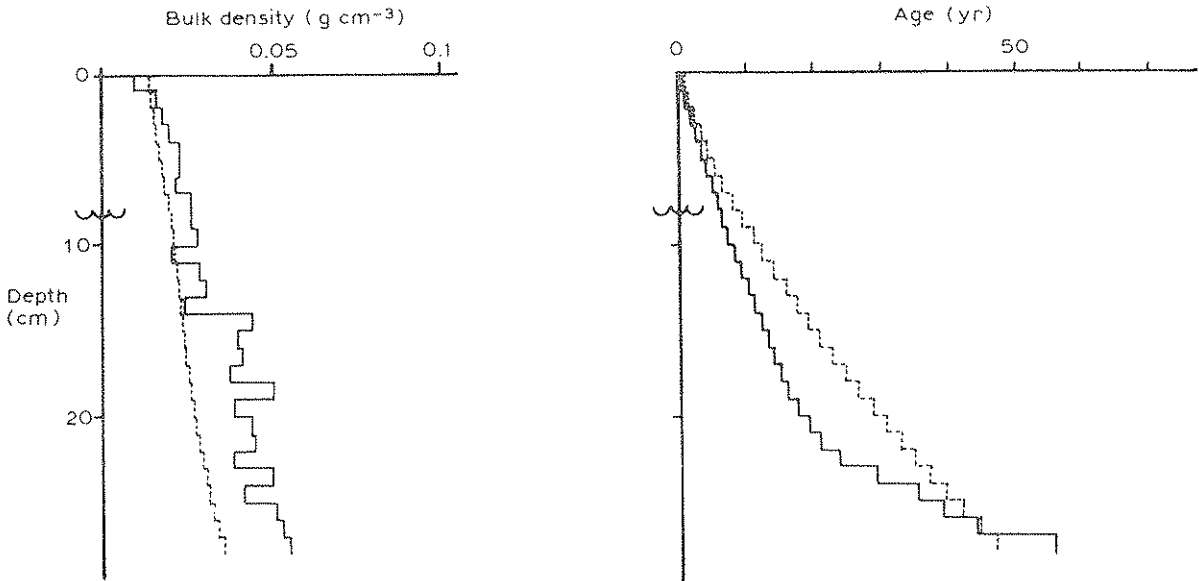


Fig. 4.28. Measured (full line) and calculated (dashed line) profiles of bulk density and age of the surface layer of peat at Moor House (England). The model included compression and creep. The transition from aerobic to anaerobic decay rate was at the water table at 8 cm depth. Measured values of the seven model parameters were used in the calculation. Redrawn from Clymo (1978).

to 30 cm the peat is permanently frozen, and, uniquely, the peat is nowhere anaerobic. Fenton assumed that the decay rate in the permafrost zone was zero and this zone might therefore be considered as the catotelm. The permafrost is at a depth below the surface which is approximately constant. It rises as the surface does, just as the anaerobic zone does in temperate peats. The special feature of the model which Fenton devised is that it allows for the observed fact that the shoots of mosses are parallel and upright at first, but at about 10 cm below the surface the combined effects of loss of strength and increasing weight of material above cause the shoots to bend. The bending may start as a catastrophic event, perhaps during the early autumn when there is a surface load of snow and ice, but during which the peat between the surface and the permafrost has not yet frozen.

The importance of this effect on bulk density can be quantified (Fig. 4.30). If the original depth of a layer is h_0 , the depth after collapse is h , the shoot angle after collapse is θ , and the mean distance between shoots, normal to the shoot direction, is u_0 originally and u after collapse, then:

$$c = \frac{h}{h_0} = \frac{u}{u_0} = \sin \theta \quad (18)$$

where c is the reciprocal of consolidation. Because the growth increments were preserved, all three measurements (thickness, intershoot distance, and angle) could be made. In other places it is unlikely that all three would be measurable, but in *Sphagnum fuscum* peat at Abisko (northern Sweden) h and h_0 were measurable (Clymo, unpublished). If this consolidation were all that were happening one would expect bulk density to be constant until collapse, and then to increase in proportion to consolidation. In fact it does not do this (Fig. 4.31) but decreases down to 10 cm depth and then increases. Fenton attributed the difference to decay, and pointed out that growth, collapse and decay might be combined in a model the parameters of which may be measured and the results checked. The measurements available are profiles of collapse, decay (assuming constant productivity), bulk density and age, and the annual growth in length of plants. Which is considered dependent is a matter of choice. The agreement between calculated and observed bulk density, for example, is quite close. Peat is reaching the permafrost zone (catotelm) at a rate of 90 to 160 $\text{g m}^{-2} \text{yr}^{-1}$ — a rate similar to that at which it reaches the anaerobic zone in temperate bogs: 64 $\text{g m}^{-2} \text{yr}^{-1}$ at Draved Mose, 32 at Glenamoy, Ireland (Moore, 1972), and 48 to 180 at

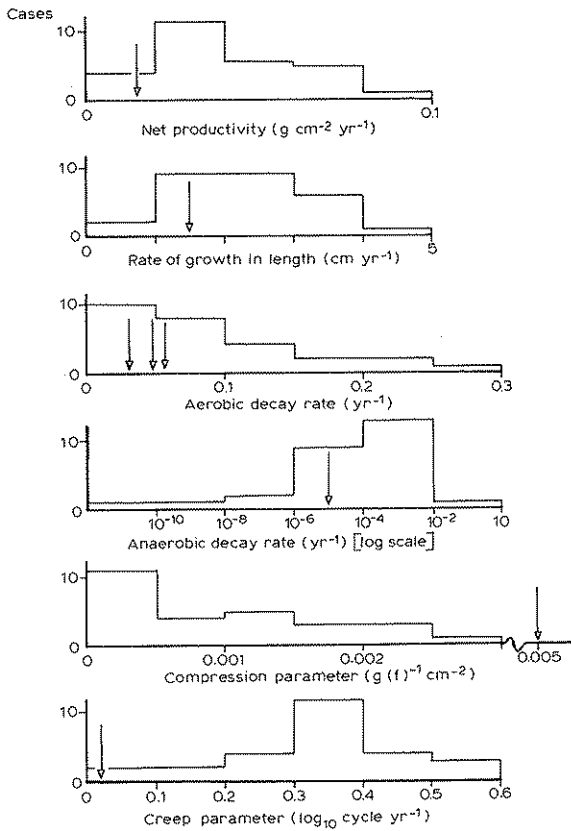


Fig. 4.29. Distribution of six parameter estimates minimizing a function of observed and calculated profiles of bulk density and of time in Fig. 4.28. The seventh parameter, water-table depth, was fixed at the measured depth of 8 cm. The distribution results from starting the minimization at different trial values. Vertical arrows show the measured values. None of the parameters is tightly constrained. The distribution of estimates of the top four (biological) parameters does not centre at or near the measured value. For the bottom two (physical) parameters agreement is very poor. Redrawn from Clymo (1978).

Moor House (Clymo, 1978).

A major problem with models of complex systems — and models of peat growth are no exception — is that of how to assess the accuracy and reliable range of the model. In the simplest case considered here — that of a single component decay fitted to the Draved Mose age–depth profile — the estimated values of rate of transfer to the anaerobic zone and of decay rate are not incredible, and the general shape of the curve fits that postulated. But these tests are not stringent; the profile could be explained in part or whole by a steady increase of bulk density with depth (so that the value at 250 cm depth was about double that at the present-day

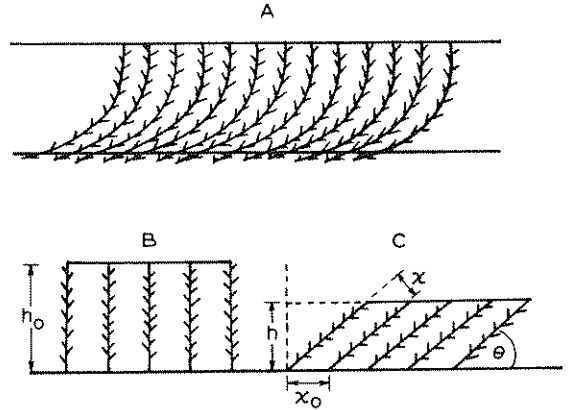


Fig. 4.30. A. Bending of moss shoots, with consequent increase in bulk density. B. Original upright shoots. C. After bending. See text for explanation and use of symbols. Redrawn from Fenton (1980).

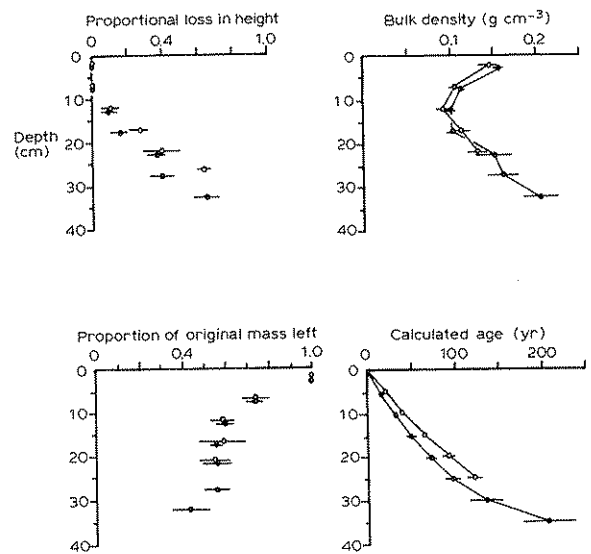


Fig. 4.31. Measured compression, bulk density and decay, and calculated age of *Polytrichum alpestre* moss-peat at two sites in the maritime Antarctic. Redrawn from Fenton (1980).

surface) and no decay at all. The addition of two zones and of consolidation (Clymo, 1978) or of several components and linear decrease of decay rate (Jones and Gore, 1978) allows tests of the profile of two variables (age and bulk density). But again, the expected shapes are simple curves, which could be explained by many different simple hypotheses. The way forward seems to be to include more variables, and to reach a point where much more complex curves are expected and may be

measured. Forrester (1961) considered that the *pattern* of behaviour was all that was worth examining in complex models of industrial systems. These contained interlocking and nested feedback loops, however, whereas the existing models of peat forming systems have nothing more than simple feedback loops. Bunnell and Scoullar (1975) described a model of carbon flow in tundra which has 96 parameters. "Soil organic matter" and "soil humus" are only two of fourteen variables, however, and their account gives no results for these two variables. An ambitious attempt to make a complex model of a peat-forming system is that made by Wildi (1978). His model includes five variables (amount of peat, amount of water, amount of "nutrients", biomass of bog plants and biomass of fen plants) and twenty parameters. The variables are specified for each element of the model, and adjacent elements can be put at different height, so there is flow of water and "nutrients" between elements.

The complete model is so large that it is impracticable to use it for parameter minimization, but parameter values for a part, for example those controlling water-flow, were optimized. The whole model is able to simulate peat growth in relation to topography, and in a crude way to simulate succession of bog and fen plants (Fig. 4.32). There are clearly a large number of testable results. Unfortunately the tests which have actually been made are few and qualitative: "peat thickness ... comes very close to what can be observed in the field"; "the minimum water table is in the center of the bog"; "the high nutrient concentration at the upper limit on the slope which is occupied by a definite fen vegetation". Many of Wildi's assumptions about processes are necessarily simplistic, as he realized. The flow of water through peat, for example, does not always follow Darcy's Law (Rycroft et al., 1975b), the assumption that "the concentration of Ca^{++} may be the limiting factor in peat bogs" is less than certain, and the equation of "cations" with

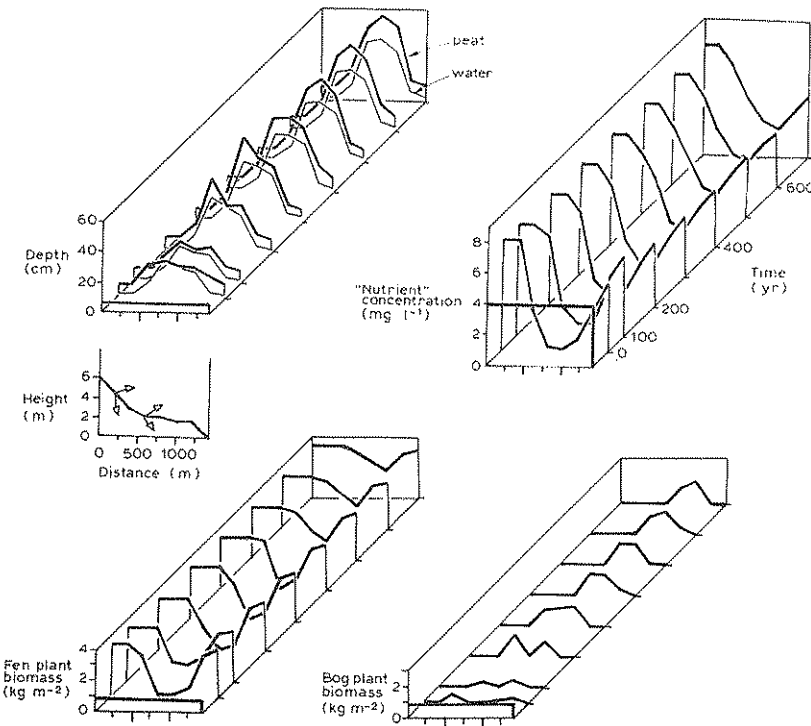


Fig. 4.32. Change in five variables during simulation of peat-bog growth on a sloping surface. The mineral soil surface level is shown at the centre left. Arrows indicate that at two places the water is allowed to flow laterally (or percolate into the ground). On all graphs, downhill is to the right. The peat and water are given as depth *above* the mineral soil surface defined in the small graph. Redrawn from Wildi (1978).

“nutrients” is even less so. Nevertheless such complex models have great promise because they give a large number of testable results, and, perhaps most important of all, they focus attention on those areas where ignorance is not bliss but a bane. The movement of water and “nutrients”, and their effects on the growth and decay of bog and fen plants, are such areas.

ACKNOWLEDGMENTS

I thank Mrs. P. Ratnesar and T. Clymo for technical help, Professors Nils Malmer and Mats Sonesson for making possible the unpublished work reported here, and Professor D.W. Goodall for numerous helpful suggestions.

APPENDIX I: OUTLINE OF A COMMERCIAL CLASSIFICATION OF PEATS (Kivinen, 1977)

Three characters are used

1. Botanical composition
 - (a) moss peat: >75% moss, <10% wood
 - (b) herbaceous peat: >75% herbaceous plants, <10% wood
 - (c) wood peat: >35% wood
 - (d) mixed peat: any other type
2. Decomposition
 - (a) little decomposed
 - (b) medium
 - (c) highly decomposed
3. Nutritional state
 - (a) oligotrophic
 - (b) mesotrophic
 - (c) eutrophic

This scheme is the basis for the proposed International Classification.

APPENDIX II: TREATMENT OF ORGANIC SOILS IN THE U.S.D.A. 7th APPROXIMATION SOIL CLASSIFICATION (after Ragg and Clayden, 1973; Buol et al., 1973)

The ten orders of soils are:

- (1) Entisols — recent soils
- (2) Vertisols — clay soils with marked shrinking and swelling
- (3) Inceptisols — embryonic soils
- (4) Aridisols — arid region soils
- (5) Mollisols — soils of steppe and prairie grassland
- (6) Spodosols — soils with subsoil accumulations of iron and aluminium oxides and humus
- (7) Alfisols — forest soils of high-base status
- (8) Ulfisols — forest soils of low-base status
- (9) Oxisols — highly weathered, sesquioxide-rich tropical soils
- (10) Histosols — organic soils

During development a soil may pass from one order to another. The Histosols, in which peats fall, are perhaps the most outlying order, and have, on the whole, been neglected by soil surveyors. Histosols are defined as follows:

Soils with organic soil matter containing:

- (1) no mineral layer 40 cm or more thick with upper boundary at or within 40 cm of the surface;
 - (2) less than 40 cm cumulative mineral layers in the top 80 cm.
- The depth of organic matter must be one of:
- (1) 60 cm or more if three-quarters or more (by volume) is fibric moss, or the bulk density is less than 0.1 g cm^{-3} ;
 - (2) 40 cm or more if: (a) the material is water-saturated for more than six months or is artificially drained; and (b) the organic material consists of sapric (H9–10) or hemic (H6–8) materials, or fibric (H1–5) materials if less than three-quarters by volume of fibric moss, and with a bulk density 0.1 g cm^{-3} or more;
 - (3) a layer more than twice the thickness of a mineral layer above and within 10 cm of the junction;
 - (4) any depth if the organic matter rests on fragmented mineral material with interstices partially or wholly filled by organic matter.

Sub-orders of Histosols

A depth of up to 130 cm (or 160 cm if the top 60 cm has three-quarters or more of fibric moss) is arbitrarily used for description (“control section”). Three layers (“tiers”) are arbitrarily defined: upper 30 cm (or 60 cm if more than three-quarters of fibric moss), subsurface 60 cm, bottom 40 cm.

After separating Folist (see below), the main divisions are based on the state of decomposition. Within the suborders the main divisive criterion is the mean annual temperature, T_a .

- (1) Folist — not water-saturated for more than a few days per year; less than three-quarters fibric *Sphagnum* and lithic material within 100 cm of surface
- (2) Fibrists — humification about H1 to H5
 - Cryofibrists — frozen in some part two months after summer solstice
 - Sphagnofibrists — at least three-quarters fibric *Sphagnum* in top 90 cm.
 - Borofibrists — T_a less than 8°C
 - Tropofibrists — mean summer and mean winter temperatures differ by less than 5°C
 - Medifibrists — other fibrists with less than 2 cm humiluvic matter
 - Luvifibrists — others
- (3) Hemists — humification about H6 to H8

<ol style="list-style-type: none"> Cryochemists Borochemists Tropochemists Medichemists 	}	as for corresponding Fibrists
<ol style="list-style-type: none"> Sulfhemists — sulphidic within 100 cm of surface Sulfohemists — sulphidic within 50 cm of surface Luvihemists — as for corresponding Fibrist 		

(4) Sapristis - humification about H9 to H10

Cryosapristis	} as for corresponding Fibrists
Borosapristis	
Troposapristis	
Medisapristis	
Luvisapristis	

APPENDIX III: OUTLINE OF A GEOLOGICAL/ECOLOGICAL CLASSIFICATION OF BIOGENIC SEDIMENTS (after West, 1968)

The classification is based on peat origin; symbols for use in stratigraphic diagrams are suggested by Troels-Smith (1955)

There are three main groups, of which only the second and third contain peats.

1. Sedimentary (allochthonous) deposits laid down in lakes, most with a large proportion of inorganic matter
2. Sedentary (autochthonous) deposits
 - (i) Limnic peats, formed by plants growing in water, for example:
 - (a) *Phragmites*
 - (b) lake *Scirpus*
 - (c) *Typha*
 - (ii) Telmatic peats, formed by plants growing between low and high water

Eutrophic types — examples:

 - (a) *Cladium* peat
 - (b) *Magnocaricetum* peat (formed from tall sedges)
 - (c) fen moss peat (hypnoid mosses)

Oligotrophic types — examples:

 - (d) *Sphagnum cuspidatum* peat
 - (e) *Eriophorum vaginatum* peat
3. Terrestrial peats, formed at or above high water mark

Eutrophic types — examples:

 - (a) *Parvocaricetum* peat (formed from small sedges)
 - (b) fen wood peat (especially birch and alder)

Oligotrophic types — examples:

 - (a) *Sphagnum* peat formed by hummock species
 - (b) *Sphagnum* + *Calluna* peat
 - (c) bog shrub peat (*Myrica*, ericaceous shrubs other than *Calluna*)
 - (d) bog wood peat (mainly *Betula*, but sometimes *Pinus*)
 - (e) *Eriophorum vaginatum* peat [indistinguishable from 2(ii)(e)]
 - (f) *Scirpus cespitosus* peat

REFERENCES

Aaby, B. and Jacobsen, J., 1979. Changes in biotic conditions and metal deposition in the last millennium as reflected in ombrotrophic peat in Draved Mose, Denmark. *Dan. Geol. Unders., Arb.*, 1978; 5-43.

Aaby, B., Jacobsen, J. and Jacobsen, O.S., 1979. Pb-210 dating and lead deposition in the ombrotrophic peat bog, Draved Mose, Denmark. *Dan. Geol. Unders., Arb.*, 1978; 45-68.

Aaby, B. and Tauber, H., 1974. Rates of peat formation in relation to degree of humification and local environment, as shown by studies of a raised bog in Denmark. *Boreas*, 4: 1-17.

Allen, S.E., Grimshaw, H.M. and Holdgate, M.W., 1967. Factors affecting the availability of plant nutrients on an Antarctic island. *J. Ecol.*, 55: 381-396.

Anderson, J.A.R., 1964. The structure and development of the peat swamps of Sarawak and Brunei. *J. Trop. Geogr.*, 18: 7-16.

Anonymous, 1978. *British Antarctic Survey, Annual Report 1977-78*, p. 78.

Bahnsen, H., 1968. Kolorimetrisk bestemmelse af humificeringstal i højmostorv fra Fuglso mose på Djursland. *Medd. Dan. Geol. Foren.*, 18: 55-63.

Baker, J.H., 1972. The rate of production and decomposition of *Chorisodontium aciphyllum* (Hook. f. and Wils.) Broth. *Bull. Br. Antarct. Surv.*, 27: 123-129.

Basilier, K., 1973. Investigations on nitrogen fixation in moss communities. In: J.G.K. Flower-Ellis (Editor). *International Biological Programme, Swedish Tundra Biome Project. Tech. Rep.*, 16: 83-95.

Basilier, K., Granhall, V. and Stenström, T.-A., 1978. Nitrogen fixation in wet microtrophic moss communities of a subarctic mire. *Oikos*, 31: 236-246.

Belkevich, P.I. and Chistova, L.R., 1968. Exchange capacity of peat with respect to alkali and alkaline-earth metals. In: R.A. Robertson (Editor). *Proc. 2nd Int. Peat Congress, Leningrad, 1963*, pp. 909-918.

Bellamy, D.J. and Ricley, J., 1967. Some ecological statistics of a "miniature bog". *Oikos*, 18: 33-40.

Benda, I., 1957. Mikrobiologische Untersuchungen über das Auftreten von Schwefelwasserstoff in den anaeroben Zonen des Hochmoores. *Arch. Mikrobiol.*, 27: 337-374.

Berry, P.L. and Poskitt, T.J., 1972. The consolidation of peat. *Géotechnique*, 22: 27-52.

Bjarnason, O.B., 1968. Chemical investigation of Icelandic peat. In: R.A. Robertson (Editor). *Proc. 2nd Int. Peat Congress, Leningrad, 1963*, pp. 69-73.

Bland, D.E., Logan, A., Menshun, M. and Sternhell, S., 1968. The lignin of *Sphagnum*. *Phytochemistry*, 7: 1373-1377.

Boatman, D.J., 1961. Vegetation and peat characteristics of blanket bogs in County Kerry. *J. Ecol.*, 49: 507-517.

Boatman, D.J. and Roberts, J., 1963. The amounts of certain nutrients leached from peat by various extractants. *J. Ecol.*, 51: 187-189.

Boatman, D.J., Hulme, P.D. and Tomlinson, R.W., 1975. Monthly determinations of the concentrations of sodium, potassium, magnesium and calcium in the rain and in pools on the Silver Flowe National Nature Reserve. *J. Ecol.*, 63: 903-912.

Boelter, D.H., 1968. Important physical properties of peat materials. In: C. Lafleur and J. Butler (Editors). *Proc. 3rd Int. Peat Congress, Quebec, 1968*, pp. 150-154.

Boggie, R., 1972. Effect of water-table height on root development of *Pinus contorta* on deep peat in Scotland. *Oikos*, 23: 304-312.

- Boggie, R., Hunter, R.F. and Knight, A.H., 1958. Studies of the root development of plants in the field using radioactive tracers. *J. Ecol.*, 46: 621-639.
- Bonner, J., 1950. *Plant Biochemistry*. Academic Press, New York, N.Y., 537 pp.
- Brackke, F.H. (Editor), 1976. *Impact of Acid Precipitation on Forests and Freshwater Ecosystems in Norway*. SNSF report 6, Oslo-Ås, 111 pp.
- Bradis, E.M. and Andrienko, T.L., 1972. Bogs of the Ukrainian SSR. In: *Proc. 4th Int. Peat Congress, Otaniemi, 1972*, pp. 41-48.
- Bunnell, F.L. and Scoullar, K.A., 1975. Abisko II. A computer simulation model of carbon flux in tundra ecosystems. In: T. Rosswall and O.W. Heal (Editors), *Structure and Function of Tundra Ecosystems*. *Ecol. Bull.*, No. 20. Swedish Natural Science Research Council, Stockholm, pp. 425-448.
- Bunnell, F.L. and Tait, D.E.N., 1974. Mathematical simulation models of decomposition processes. In: A.J. Holding, O.W. Heal, S.F. Maclean Jr. and P.W. Flanagan (Editors), *Soil Organisms and Decomposition in Tundra*. Tundra Biome Steering Committee, Stockholm, pp. 207-225.
- Buol, S.W., Hole, F.D. and McCrackern, R.J., 1973. *Soil Genesis and Classification*. Iowa State University Press, Ames, Iowa.
- Burgeff, H., 1961. *Mikrobiologie des Hochmoores*. Fischer, Stuttgart.
- Casparie, W.A., 1972. Bog development in south eastern Drenthe (The Netherlands). *Vegetatio*, 25: 1-271.
- Cawse, P.A., 1974. *A Survey of Atmospheric Trace Elements in the U.K. (1972-73)*. A.E.R.E.-R 7669. H.M.S.O., London.
- Chapin, F.S. III, Van Cleve, K. and Tieszen, L.L., 1975. Seasonal nutrient dynamics of tundra vegetation at Barrow, Alaska. *Arct. Alp. Res.*, 7: 209-226.
- Chapin, F.S. III, Barsdate, R.J. and Barèl, D., 1978. Phosphorus cycling in Alaskan coastal tundra: a hypothesis for the regulation of nutrient cycling. *Oikos*, 31: 189-199.
- Chapin, F.S. III, Van Cleve, K. and Chapin, M.C., 1979. Soil temperature and nutrient cycling in the tussock growth form of *Eriophorum vaginatum*. *J. Ecol.*, 67: 169-189.
- Chapman, S.B., 1964a. The ecology of Coom Rigg Moss, Northumberland. I. Stratigraphy and present vegetation. *J. Ecol.*, 52: 299-313.
- Chapman, S.B., 1964b. The ecology of Coom Rigg Moss, Northumberland. II. The chemistry of peat profiles and the development of the bog system. *J. Ecol.*, 52: 315-321.
- Chapman, S.B., 1965. The ecology of Coom Rigg Moss, Northumberland. III. Some water relations of the bog system. *J. Ecol.*, 53: 371-384.
- Clymo, R.S., 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. *Ann. Bot. (Lond.) N.S.*, 27: 309-324.
- Clymo, R.S., 1965. Experiments on breakdown of *Sphagnum* in two bogs. *J. Ecol.*, 53: 747-758.
- Clymo, R.S., 1967. Control of cation concentrations, and in particular of pH, in *Sphagnum* dominated communities. In: H.L. Golterman and R.S. Clymo (Editors), *Chemical Environment in the Aquatic Habitat*. North-Holland, Amsterdam, pp. 273-284.
- Clymo, R.S., 1970. The growth of *Sphagnum*: methods of measurement. *J. Ecol.*, 58: 13-49.
- Clymo, R.S., 1978. A model of peat bog growth. In: O.W. Heal and D.F. Perkins, with W.M. Brown (Editors), *Production Ecology of British Moors and Montane Grasslands*. Springer-Verlag, Berlin, pp. 187-223.
- Clymo, R.S. and Reddaway, E.J.F., 1971. Productivity of *Sphagnum* (bog-moss) and peat accumulation. *Hidrobiologia*, 12: 181-192. [A shorter version, without arbitrary cuts, appears as: A tentative dry matter balance sheet for the wet blanket bog on Burnt Hill, Moor House NNR. *Moor House Occas. Pap.*, No. 3 (1972): 15 pp.]
- Collins, N.J., 1976. The development of moss-peat banks in relation to changing climate and ice cover on Signy Island in the maritime Antarctic. *Br. Antarct. Surv. Bull.*, 43: 85-102.
- Collins, V.G., D'Sylva, B.T. and Latter, P.M., 1978. Microbial populations in peat. In: O.W. Heal and D.F. Perkins, with W.M. Brown (Editors), *Production Ecology of British Moors and Montane Grasslands*. Springer-Verlag, Berlin, pp. 94-112.
- Conway, B.E., 1952. *Electrochemical Data*. Elsevier, Amsterdam, 374 pp.
- Conway, V.M., 1937. Studies in the autecology of *Cladium mariscus* R. Br. III. The aeration of the subterranean parts of the plant. *New Phytol.*, 36: 64-96.
- Conway, V.M., 1949. Ringinglow Bog near Sheffield. Part II. The present surface. *J. Ecol.*, 37: 148-170.
- Coulson, J.C. and Butterfield, J.E., 1978. An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. *J. Ecol.*, 66: 631-650.
- Coulson, J.C. and Whittaker, J.B., 1978. Ecology of moorland animals. In: O.W. Heal and D.F. Perkins, with W.M. Brown (Editors), *Production Ecology of British Moors and Montane Grasslands*. Springer-Verlag, Berlin, pp. 52-93.
- Coulter, J.K., 1950. Peat formations in Malaya. *Malay. Agric. J.*, 33: 63-81.
- Coulter, J.K., 1957. Development of the peat soils of Malaya. *Malay. Agric. J.*, 40: 188-199.
- Dalton, J., 1802. *Experimental Enquiry Into the Proportion of the Several Gases or Elastic Fluids Constituting the Atmosphere*. Manchester Philosophical Society.
- Damman, A.W.H., 1978. Distribution and movement of elements in ombrotrophic peat bogs. *Oikos*, 30: 480-495.
- Day, J.H., 1968. The classification of organic soils in Canada. In: C. Lafleur and J. Butler (Editors), *Proc. 3rd Int. Peat Congress, Quebec, 1968*, pp. 80-84.
- Dickinson, C.H. and Maggs, G.H., 1974. Aspects of the decomposition of *Sphagnum* leaves in an ombrophilous mire. *New Phytol.*, 73: 1249-1257.
- Donnan, F.G., 1911. Theorie der Membrangleichgewichte und Membranpotentiale bei Vorhandensein von nicht dialysierenden Elektrolyten. *Z. Elektrochem.*, 17: 572-581.
- Duane, J., O'Brien, J.C. and Treacy, K., 1968. Recent work on milled peat in Ireland. In: C. Lafleur and J. Butler (Editors), *Proc. 3rd Int. Peat Congress, Quebec, 1968*, pp. 300-306.
- Elna, G.A., 1972. Types of swamps in Northern Karelia of the USSR. In: *Proc. 4th Int. Peat Congress, Otaniemi, 1972*, pp. 59-74.
- Eriksson, E., 1955. Current data on the chemical composition of air and precipitation. *Tellus*, 1: 134-139 [and in subsequent volumes].

- Farnham, R.S., 1968. Classification of peat in the U.S.A. In: R.A. Robertson (Editor), *Proc. 2nd Int. Peat Congress, Leningrad, 1963*, pp. 115-132.
- Farnham, R.S. and Finney, H.R., 1965. Classification and properties of organic soils. *Adv. Agron.*, 17: 115-162.
- Fenton, J.H.C., 1978. *The Growth of Antarctic Moss Peat Banks*. Thesis, University of London, London, 162 pp.
- Fenton, J.H.C., 1980. The rate of peat accumulation in antarctic moss banks. *J. Ecol.*, 68: 211-228.
- Fieser, L.F. and Fieser, M., 1944. *Organic Chemistry*. Heath, Boston, Mass., 1091 pp.
- Finney, H.R. and Farnham, R.S., 1968. Mineralogy of the inorganic fraction of peat from two raised bogs in Northern Minnesota. In: C. Laffeur and J. Butler (Editors), *Proc. 3rd Int. Peat Congress, Quebec, 1968*, pp. 102-108.
- Flanagan, P.W. and Bunnell, F.L., 1976. Decomposition models based on climatic variables, microbial respiration and production. In: J.M. Anderson and A. Macfadyan (Editors), *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*. Blackwell, Oxford, pp. 437-457.
- Flanagan, P.W. and Veum, A.K., 1974. Relationships between respiration, weight loss, temperature and moisture in organic residues in tundra. In: A.J. Holding, O.W. Heal, S.F. Maclean, Jr. and P.W. Flanagan (Editors), *Soil Organisms and Decomposition in Tundra*. Tundra Biome Steering Committee, Stockholm, pp. 249-277.
- Florschütz, F., Menéndez Amor, J. and Wijmstra, T.A., 1971. Palynology of a thick Quaternary succession in Southern Spain. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 10: 233-264.
- Flower-Ellis, J.G.K., 1974. Progress Report 1973. *International Biological Programme, Swedish Tundra Biome Project, Tech. Rep.*, 16: 212 pp.
- Forrest, I., 1971. Structure and production of North Pennine blanket bog vegetation. *J. Ecol.*, 59: 453-479.
- Forrester, J.W., 1961. *Industrial Dynamics*. M.I.T. Press, Cambridge, Mass., 464 pp.
- Frankland, J.C., 1966. Succession of fungi on decaying petioles of *Pteridium aquilinum*. *J. Ecol.*, 54: 41-63.
- Freistedt, E., 1968. Experiences in the design and construction of equipment for complete peat briquetting factories. In: C. Laffeur and J. Butler (Editors), *Proc. 3rd Int. Peat Congress, Quebec, 1968*, pp. 296-299.
- Giles, B.R., 1977. *Root Function in Eriophorum angustifolium*. Thesis, University of London, London, 182 pp.
- Gilliland, M.R. and Howard, A.J., 1968. Some constituents of peat wax separated by column chromatography. In: R.A. Robertson (Editor), *Proc. 2nd Int. Peat Congress, Leningrad, 1963*, pp. 877-886.
- Given, P.H. and Dickinson, C.H., 1975. Biochemistry and microbiology of peats. In: E.A. Paul and D. Maclaren (Editors), *Soil Biochemistry*, 3, pp. 123-212.
- Glob, P.V., 1969. *Mosefolket: Jernalderens mennesker bevaret i 2000 Ar*. Gyldendal, Copenhagen.
- Godwin, H., 1956. *The History of the British Flora*. University Press, Cambridge, 384 pp.
- Gore, A.J.P., 1968. The supply of six elements by rain to an upland peat area. *J. Ecol.*, 56: 483-495.
- Gore, A.J.P. and Allen, S.E., 1956. Measurement of exchangeable and total cation content for H⁺, Na⁺, Mg⁺⁺, Ca⁺⁺ and iron, in high level blanket peat. *Oikos*, 7: 48-55.
- Gore, A.J.P. and Olsen, J.S., 1967. Preliminary models for accumulation of organic matter in an *Eriophorum, Calluna* ecosystem. *Aquilo, Ser. Bot.*, 6: 297-313.
- Gorham, E., 1953. Some early ideas concerning the nature, origin and development of peat lands. *J. Ecol.*, 41: 257-274.
- Gorham, E., 1956. On the chemical composition of some waters from the Moor House nature reserve. *J. Ecol.*, 44: 375-382.
- Gorham, E., 1957. The development of peatlands. *Q. Rev. Biol.*, 32: 145-166.
- Gorham, E., 1958. The influence and importance of daily weather conditions in the supply of chloride, sulphate and other ions to fresh waters from atmospheric precipitation. *Philos. Trans. R. Soc. Lond.*, B241: 147-178.
- Gorham, E., 1961a. Chlorophyll derivatives, sulphur, and carbon in sediment cores from two English lakes. *Can. J. Bot.*, 39: 333-338.
- Gorham, E., 1961b. Water, ash, nitrogen and acidity of some bog peats and other organic soils. *J. Ecol.*, 49: 103-106.
- Gorham, E. and Sanger, J., 1967. Caloric values of organic matter in woodland, swamp, and lake soils. *Ecology*, 48: 492-493.
- Göttlich, K.-H. (Editor), 1976. *Moore- und Torfkunde*. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 269 pp.
- Grace, J. and Marks, T.C., 1978. Physiological aspects of bog production at Moor House. In: O.W. Heal and D.F. Perkins, with W.M. Brown (Editors), *Production Ecology of British Moors and Montane Grasslands*. Springer-Verlag, Berlin, pp. 38-51.
- Granat, L., 1972. *Deposition of Sulphate and Acid with Precipitation over Northern Europe*. Institute of Meteorology, University of Stockholm, Stockholm, Report AC-20, 30+19 pp.
- Granat, L., 1975. *On the Variability of Rainwater Composition and Errors in Estimates of Areal Wet Deposition*. Department of Meteorology, University of Stockholm, Stockholm, Report AC-30, 34 pp.
- Granlund, E., 1932. De svenska hogmossarnas geologi. *Sver. Geol. Unders. Aft.*, 26: 1-193.
- Green, B.H. and Pearson, M.C., 1977. The ecology of Wybunbury Moss, Cheshire. II. Post-glacial history and the formation of the Cheshire Mere and Mire landscape. *J. Ecol.*, 65: 793-814.
- Hanrahan, E.T., 1954. Factors affecting strength and deformation of peat. In: *Proc. 1st Int. Peat Congress, Dublin, 1954, Section b-3.2*.
- Hart, M.G.R., 1962. Observations on the source of acid in empoldered mangrove soils. I. Formation of elemental sulphur. *Plant Soil*, 17: 87-98.
- Heal, O.W. and Perkins, D.F., with Brown, W.M. (Editors), 1978. *Production Ecology of British Moors and Montane Grasslands*. Springer-Verlag, Berlin, 426 pp.
- Heal, O.W., Howson, G., French, D.D. and Jeffers, J.N.R., 1974. Decomposition of cotton strips in tundra. In: A.J. Holding, O.W. Heal, S.F. Maclean Jr. and P.W. Flanagan (Editors), *Soil Organisms and Decomposition in Tundra*. Tundra Biome Steering Committee, Stockholm, pp. 341-362.
- Heal, O.W., Latter, P.M. and Howson, G., 1978. A study of the

- rates of decomposition of organic matter. In: O.W. Heal and D.F. Perkins, with W.M. Brown, (Editors), *Production Ecology of British Moors and Montane Grasslands*. Springer-Verlag, Berlin, pp. 136–159.
- Helfferich, F., 1962. *Ion Exchange*. McGraw-Hill, New York, N.Y., 472 pp.
- Hill, M.O., 1973. Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.*, 61: 237–249.
- Howard, A.J. and Hamer, D., 1960. The extraction and constitution of peat wax: a review of peat wax chemistry. *J. Am. Oil Chem. Soc.*, 37: 478–481.
- Hutchinson, J.N., 1980. The record of peat wastage in the East Anglian fenlands at Holme Post, 1848–1978 A.D. *J. Ecol.*, 68: 229–249.
- Ingham, G., 1950. The mineral content of air and rain and its importance to agriculture. *J. Agric. Sci.*, 40: 55–61.
- Ingram, H.A.P., 1978. Soil layers in mires: function and terminology. *J. Soil Sci.*, 29: 224–227.
- Ingram, H.A.P., Rycroft, D.W. and Williams, D.J.A., 1974. Anomalous transmission of water through certain peats. *J. Hydrol.*, 22: 213–218.
- Irwin, R.W., 1968. Soil water characteristics of some Ontario peats. In: C. Lafleur and J. Butler, (Editors), *Proc. 3rd Int. Peat Congress, Quebec, 1968*, pp. 219–223.
- Janota-Bassalik, L., 1963. Psychrophiles in low-moor peat. *Acta Microbiol. Pol.*, 12: 25–40.
- Jenny, H., Gessel, S.P. and Bingham, F.T., 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. *Soil Sci.*, 68: 419–432.
- Jones, H.E. and Gore, A.J.P., 1978. A simulation of production and decay in blanket bog. In: O.W. Heal and D.F. Perkins, with W.M. Brown (Editors), *Production Ecology of British Moors and Montane Grasslands*. Springer-Verlag, Berlin, pp. 160–186.
- Kamula, A., 1968. Some observations on the autothermal gasification of peat dust on an industrial scale. In: R.A. Robertson (Editor), *Proc. 2nd Int. Peat Congr., Leningrad, 1963*, pp. 941–944.
- Karesniemi, K., 1972. Dependence of humification degree on certain properties of peat. In: *Proc. 4th Int. Peat Congr., Otaniemi, 1972*, 2: 273–282.
- Kivinen, E., 1977. Survey, classification, ecology and conservation of peatlands. *Bull. Int. Peat Soc.*, 8: 24–25.
- Kivinen, E., Heikurainen, L. and Pakarinen, P., 1979. *Classification of Peat and Peatlands*. International Peat Society, V.V.T. Fuel Research Lab., Espo, 367 pp.
- Knight, A.H., Croke, W.M. and Inkson, R.H.E., 1961. Cation exchange capacities of tissues of higher and lower plants and their related uronic acid contents. *Nature (Lond.)*, 192: 142–143.
- Knight, A.H., Boggie, R. and Shepherd, H., 1972. The effect of ground water level on water movement in peat: a study using tritiated water. *J. Appl. Ecol.*, 9: 633–642.
- Korpijaakko, M. and Radforth, N.W., 1972. Studies of the hydraulic conductivity of peat. In: *Proc. 4th Int. Peat Congress, Otaniemi, 1972*, 3: 323–334.
- Kulczyński, S., 1949. Peat bogs of Polesie. *Mem. Acad. Sci. Cracovie B*, 336 pp.
- Küster, E. and Locci, R., 1964. Studies on peat and peat microorganisms. II. Occurrence of thermophilic fungi in peat. *Arch. Mikrobiol.*, 48: 319–324.
- Květ, J., 1955. *Biologické Působiání Ráseliny a Ráseliniku*. Biologika Fakulta, University Karlovy, Prague, 105 pp.
- Lee, J.A. and Tallis, J.H., 1973. Regional and historical aspects of lead pollution. *Nature (Lond.)*, 245: 216–218.
- Livett, E.A., Lee, J.A. and Tallis, J.H., 1979. Lead, zinc and copper analyses of British blanket peats. *J. Ecol.*, 67: 865–891.
- Luck, K.E., 1964. *Studies in the Autecology of Calamagrostis epigeios (L.) Roth and C. canescens (Weber) Roth*. Thesis, University of Cambridge, Cambridge, 165 pp.
- MacFarlane, I.C. and Radforth, N.W., 1968. Structure as a base of peat classification. In: C. Lafleur and J. Butler (Editors), *Proc. 3rd Int. Peat Congress, Quebec, 1968*, pp. 91–97.
- Malmer, N., 1962a. Studies on mire vegetation in the Archaean area of south western Götaland (south Sweden). I. Vegetation and habitat conditions on the Åkhult mire. *Opera Bot.*, 7(1): 1–322.
- Malmer, N., 1962b. Studies on mire vegetation in the Archaean area of south western Götaland (south Sweden). II. Distribution and seasonal variation in elementary constituents on some mire sites. *Opera Bot.*, 7(2): 1–67.
- Malmer, N. and Sjörs, H., 1955. Some determinations of elementary constituents in mire plants and peat. *Bot. Not.*, 108: 46–80.
- Mattson, S. and Koutler-Andersson, E., 1954. Geochemistry of a raised bog. *K. Lantbrukshögsk. Ann.*, 21: 321–366.
- Mattson, S. and Koutler-Andersson, E., 1955. Geochemistry of a raised bog. II. Some nitrogen relationships. *K. Lantbrukshögsk. Ann.*, 22: 219–224.
- Mattson, S., Sandberg, G. and Terning, R.E., 1944. Electrochemistry of soil formation VI. Atmospheric salts in relation to soil and peat formation and plant composition. *K. Lantbrukshögsk. Ann.*, 12: 101–118.
- Minderman, G., 1968. Addition, decomposition and accumulation of organic matter in forests. *J. Ecol.*, 56: 355–362.
- Monteith, J.L., 1973. *Principles of Environmental Physics*. Arnold, London, 241 pp.
- Moore, J.J., 1972. Report of the Glenamoy (Ireland) ecosystem study for 1971. In: F.E. Wielgolaski and T. Rosswall (Editors), *Proceedings IV. International Meeting on the Biological Productivity of Tundra*. Tundra Biome Steering Committee, Stockholm, pp. 281–282.
- Moore, P.D. and Bellamy, D.J., 1974. *Peatlands*. Elek Science, London, 221 pp.
- Morita, H., 1968. Polyphenols in the extractives of an organic soil. In: C. Lafleur and J. Butler (Editors), *Proc. 3rd Int. Peat Congress, Quebec, 1968*, pp. 28–31.
- Mörnsjö, T., 1968. Stratigraphical and chemical studies on two peatlands in Scania, South Sweden. *Bot. Not.*, 121: 343–360.
- Mörnsjö, T., 1969. Studies on vegetation and development of a peatland in Scania, South Sweden. *Opera Bot.*, 24: 1–187.
- Mortimer, C.H., 1941. The exchange of dissolved substances between mud and water in lakes. I–II. *J. Ecol.*, 29: 280–329.
- Mortimer, C.H., 1942. The exchange of dissolved substances between mud and water in lakes. III–IV. *J. Ecol.*, 30: 147–201.
- Murozumi, M., Chow, T.J. and Patterson, C., 1969. Chemical concentrations of pollutant lead aerosols, terrestrial dusts

- and sea-salts in Greenland and Antarctic snow-strata. *Geochim. Cosmochim. Acta*, 33: 1247-1294.
- Newbould, P.J., 1960. The ecology of Cranesmoor, a New Forest valley bog. *J. Ecol.*, 48: 361-383.
- Nye, P.H. and Tinker, P.B., 1977. *Solute Movement in the Soil-Root System*. Blackwell, Oxford, 342 pp.
- Ohira, Y., 1962. Some engineering researches on the experiments of the physical properties of the peat and on the sounding explorations of the peaty area in Hokkaido, Japan. *Mem. Defence Acad.* 11(2): 253-282.
- Oldfield, F., Appleby, P.G., Cambray, R.S., Eakins, J.D., Barber, K.E., Battarbee, R.W., Pearson, G.R. and Williams, T.M., 1979. ^{210}Pb , ^{137}Cs and ^{239}Pu profile in ombrotrophic peat. *Oikos*, 33: 40-45.
- Olenin, A.S., 1968. Peat resources of the USSR. In: R.A. Robertson (Editor). *Proc. 2nd Int. Peat Congress, Leningrad, 1963*, pp. 1-14.
- Olsen, O.B., 1968. Peat and other substances. In: C. Lalleur and J. Butler (Editors), *Proc. 3rd Int. Peat Congress, Quebec, 1968*, pp. 264-267.
- Osvald, H., 1923. Die Vegetation des Hochmoores Komosse. *Sven. Växtsociol. Sällsk. Handl.*, 1: 1-434.
- Overbeck, F. and Schneider, S., 1940. Torfsetzung und Grenzhorizont, ein Beitrag zur Frage der Hochmoorentwicklung in Niedersachsen. *Angew. Bot.*, 22: 321-379.
- Päivänen, J., 1969. The bulk density of peat and its determination. *Silva Fenn.*, 3: 11-12.
- Pakarinen, P. and Tolonen, S., 1977. Distribution of lead in *Sphagnum fuscum* profiles in Finland. *Oikos*, 28: 69-73.
- Paterson, M.P. and Scorer, R.S., 1973. Data quality and the European air chemistry network. *Atmos. Environ.*, 7: 1162-1171.
- Pearsall, W.H., 1954. The pH of natural soils and its ecological significance. *J. Soil Sci.*, 3: 41-51.
- Pearson, G.W., Pilcher, J.R., Baillie, M.G.L. and Hillam, J., 1977. Absolute radiocarbon dating using a low altitude European tree-ring calibration. *Nature (Lond.)*, 270: 25-28.
- Pearson, D.H., Cawse, P.A., Salmon, L. and Cambray, R.S., 1973. Trace elements in the atmospheric environment. *Nature (Lond.)*, 241: 252-256.
- Pennington, W., Cambray, R.S. and Fisher, E.M., 1973. Observations on lake sediments using ^{137}Cs as a tracer. *Nature (Lond.)*, 242: 324-326.
- Pennington, W., Cambray, R.S., Eakins, J.D. and Harkness, D.D., 1976. Radionuclide dating of the recent sediments of Blenheim Tarn. *Freshwater Biol.*, 6: 317-331.
- Pigott, M.E. and Pigott, C.D., 1959. Stratigraphy and pollen analysis of Malham Tarn and Tarn Moss. *Field Stud.*, 1: 1-18.
- Ponnamperuma, F.N., 1972. The chemistry of submerged soils. *Adv. Agron.*, 24: 29-96.
- Potonié, R., 1908. Aufbau und Vegetation der Moore Norddeutschlands. *Englers Bot. Jahrb.*, 90.
- Priddle, J., 1980a. The production ecology of benthic plants in some antarctic lakes. I. *In situ* production studies. *J. Ecol.*, 68: 141-153.
- Priddle, J., 1980b. The production ecology of benthic plants in some antarctic lakes. II. Laboratory physiology studies. *J. Ecol.*, 68: 155-166.
- Puustjärvi, V., 1956. On the cation exchange capacity of peats. *Acta Agric. Scand.*, 6: 410-449.
- Puustjärvi, V., 1968. Standards for peat used in peat culture. *Peat Plant News*, 1: 19-26.
- Puustjärvi, V., 1969. Fixing peat standards. *Peat Plant News*, 2: 3-8.
- Puustjärvi, V., 1972. Standardization of peat products. In: *Proc. 4th Int. Peat Congress, Otaniemi, 1972*, 1: 415-420.
- Ragg, J.M. and Clayden, B., 1973. The classification of some British soils according to the comprehensive system of the United States. *Soil Surv. Tech. Monogr.*, 3.
- Ravera, O. and Premazzi, G., 1972. A method to study the history of any persistent pollution in a lake by the concentration of Cs-137 from fall-out in sediments. *Proc. Int. Symp. Radioecology Applied to the Protection of Man and his Environment*, 1: 703-722.
- Richards, P.W., 1963. Soil conditions in some Bornean lowland plant communities. In: *Symposium on Ecological Research in Humid Tropics Vegetation*. Kuching, Sarawak, pp. 198-204.
- Robertson, R.A., 1968. Scottish peat resources. In: R.A. Robertson (Editor). *Proc. 2nd Int. Peat Congress, Leningrad, 1963*, pp. 29-35.
- Romanov, V.V., 1968. *Hydro-physics of Bogs*. Israel Programme for Scientific Translations, Jerusalem.
- Rosswall, T., 1974. Cellulose decomposition studies on the Tundra. In: A.J. Holding, O.W. Heal, S.F. Maclean, Jr. and P. Flanagan (Editors). *Soil Organisms and Decomposition in Tundra*. Tundra Biome Steering Committee, Stockholm, pp. 325-340.
- Rühling, Å. and Tyler, G., 1971. Regional differences in the deposition of heavy metals over Scandinavia. *J. Appl. Ecol.*, 8: 497-507.
- Rühling, Å. and Tyler, G., 1973. Heavy metal deposition in Scandinavia. *Water, Air Soil Pollut.*, 2: 445-455.
- Rycroft, D.W., Williams, D.J.A. and Ingram, H.A.P., 1975a. The transmission of water through peat. I. Review. *J. Ecol.*, 63: 535-556.
- Rycroft, D.W., Williams, D.J.A. and Ingram, H.A.P., 1975b. The transmission of water through peat. II. Field experiments. *J. Ecol.*, 63: 557-568.
- Sæbø, S., 1968. The autecology of *Rubus chamaemorus* L. I. Phosphorus economy of *Rubus chamaemorus* in an ombrotrophic mire. *Meld. Nor. Landbrukshogsk.*, 47(1): 1-67.
- Sæbø, S., 1969. On the mechanism behind the effect of freezing and thawing on dissolved phosphorus in *Sphagnum fuscum* peat. *Meld. Nor. Landbrukshogsk.*, 48(14): 1-10.
- Sæbø, S., 1970. The autecology of *Rubus chamaemorus* L. II. Nitrogen economy of *Rubus chamaemorus* in an ombrotrophic mire. *Meld. Nor. Landbrukshogsk.*, 49(9): 1-37.
- Sæbø, S., 1973. The autecology of *Rubus chamaemorus* L. III. Some aspects of calcium and magnesium nutrition of *Rubus chamaemorus* in an ombrotrophic mire. *Meld. Nor. Landbrukshogsk.*, 52(5): 1-29.
- Sæbø, S., 1977. The autecology of *Rubus chamaemorus* L. IV. Potassium relations of *Rubus chamaemorus* in an ombrotrophic mire. *Meld. Nor. Landbrukshogsk.*, 56(26): 1-20.
- Salmi, M., 1954. Investigation of the calorific values of peats in Finland. In: *Proc. 1st Int. Peat Congress, Dublin, 1954*, B3: 1-9.

- Schneider, S., 1968. Chemical and stratigraphical investigations of high-moor profiles in north-west Germany. In: R.A. Robertson (Editor), *Proc. 2nd Int. Peat Congress, Leningrad, 1963*, 1: 75-90.
- Schnitzer, M., 1973. Chemical, spectroscopic, and thermal methods for the classification and characterization of humic substances. In: D. Povoledo and H.L. Golterman (Editors), *Humic Substances. Their Structure and Function in the Biosphere*. Centre for Agricultural Publishing and Documentation, Wageningen, pp. 293-310.
- Schnitzer, M. and Kahn, S.U., 1972. *Humic Substances in the Environment*. Marcel Dekker, New York, N.Y.
- Shaver, G.R., Chapin, F.S. III, and Billings, W.D., 1979. Ecotypic differentiation in *Carex aquatilis* on ice-wedge polygons in the Alaskan coastal tundra. *J. Ecol.*, 67: 1025-1046.
- Sillanpää, M., 1972. Distribution of trace elements in peat profiles. In: *Proc. 4th Int. Peat Congress, Otaniemi, 1972*, 5: 185-191.
- Sjörs, H., 1948. Myrvegetation i bergslagen. *Acta Phytogeog. Suec.*, 21: 1-299.
- Skaven-Haug, S., 1972. Volumetric relations in soil materials. In: *Proc. 4th Int. Peat Congress, Otaniemi, 1972*, 2: 222-228.
- Skene, M., 1915. The acidity of *Sphagnum* and its relation to chalk and mineral salts. *Ann. Bot. (Lond.)*, 29: 65-87.
- Smith, R.A.H., undated. The environmental parameters of IBP experimental sites at Moor House. Aspects of the Ecology of the Northern Pennines *Moor House Occas. Pap.*, No. 4.
- Smith, R.A.H. and Forrest, I., 1978. Field estimates of primary production. In: O.W. Heal and D.F. Perkins, with W.M. Brown (Editors), *Production Ecology of British Moors and Montane Grasslands*. Springer-Verlag, Berlin, pp. 17-37.
- Sonesson, M., 1970. Studies on mire vegetation in the Torneträsk area, Northern Sweden. IV. Some habitat conditions of the poor mires. *Bot. Not.*, 123: 67-111.
- Sonesson, M. (Editor), 1973. Progress Report 1972. *International Biological Programme, Swedish Tundra Biome Project, Tech. Rep.*, 14: 194.
- Sparling, G.P. and Tinker, P.B., 1978a. Mycorrhizal infection in Pennine grassland. I. Levels of infection in the field. *J. Appl. Ecol.*, 15: 943-950.
- Sparling, G.P. and Tinker, P.B., 1978b. Mycorrhizal infection in Pennine grassland. II. Effects of mycorrhizal infection on the growth of some upland grasses on γ -irradiated soils. *J. Appl. Ecol.*, 15: 951-958.
- Sparling, G.P. and Tinker, P.B., 1978c. Mycorrhizal infection in Pennine grassland. III. Effects of mycorrhizal infection on the growth of white clover. *J. Appl. Ecol.*, 15: 959-964.
- Spearing, A.M., 1972. Cation-exchange capacity and galacturonic acid content of several species of *Sphagnum* in Sandy Ridge Bog, Central New York State. *Bryologist*, 75: 154-158.
- Sprent, J.I., Scott, R. and Perry, K.M., 1978. The nitrogen economy of *Myrica gale* in the field. *J. Ecol.*, 66: 657-668.
- Stavset, K., 1973. Registering om molte i Andøy 1970-1972. *Medd. Nor. Myrselsk.*, 4: 153-156.
- Stewart, J.M. and Robertson, R.A., 1968. The chemical status of an exposed peat face. In: C. Lafleur and J. Butler (Editors), *Proc. 3rd Int. Peat Congress, Quebec, 1968*, pp. 190-194.
- Strygin, N.N., 1968. Research on spontaneous combustion processes in peat and their prevention. In: R.A. Robertson (Editor), *Proc. 2nd Int. Peat Congress, Leningrad, 1963*, pp. 509-513.
- Svensson, B.H., 1974. Production of methane and carbon dioxide from a subarctic mire. In: J.G.K. Flower-Ellis (Editor), *International Biological Programme, Swedish Tundra Biome Project. Progress Report 1973*, pp. 123-143.
- Swain, F.M., Blumentals, A. and Millers, R., 1959. Stratigraphic distribution of amino acids in peats from Cedar Creek Bog, Minnesota, and Dismal Swamp, Virginia. *Limnol. Oceanogr.*, 4: 119-127.
- Tallis, J.H. and Switsur, V.R., 1973. Studies on Southern Pennine Peats. VI. A radiocarbon-dated pollen diagram from Featherbed Moss, Derbyshire. *J. Ecol.*, 61: 743-751.
- Tamm, C.O. and Troedsson, T., 1955. An example of the amount of plant nutrients supplied to the ground in road dust. *Oikos*, 6: 61-70.
- Tansley, A.G., 1939. *The British Islands and their Vegetation*. Cambridge University Press, London, 930 pp.
- Theander, O., 1954. Studies on *Sphagnum* peat. III. A quantitative study on the carbohydrate constituents of *Sphagnum* mosses and *Sphagnum* peat. *Acta Chem. Scand.*, 8: 989-1000.
- Tibbetts, T.E., 1968. Peat resources of the World — a review. In: C. Lafleur and J. Butler (Editors), *Proc. 3rd Int. Peat Congress, Quebec, 1968*, pp. 8-22.
- Troels-Smith, J., 1955. Characterization of unconsolidated sediments. *Dan. Geol. Unders.*, IV Raekke, 3 (10).
- Turner, J., 1964. The anthropogenic factor in vegetational history. I. Tregaron and Whixall Mosses. *New Phytol.*, 63: 73-90.
- Tyler, G., 1972. Heavy metals pollute Nature, may reduce productivity. *Ambio*, 1: 52-59.
- Urquhart, C., 1966. An improved method for demonstrating the distribution of sulphide in peat soils. *Nature (Lond.)*, 211: 550.
- Urquhart, C. and Gore, A.J.P., 1973. The redox characteristics of four peat profiles. *Soil Biol. Biochem.*, 5: 659-672.
- Van Dijk, H. and Boekel, P., 1968. Effect of drying and freezing on certain physical properties of peat. In: R.A. Robertson (Editor), *Proc. 2nd Int. Peat Congress, Leningrad, 1963*, pp. 1051-1062.
- Volarovich, M.P. and Churaev, N.V., 1968. Application of the methods of physics and physical chemistry to the study of peat. In: R.A. Robertson (Editor), *Proc. 2nd Int. Peat Congress, Leningrad, 1963*, pp. 819-831.
- Von Naucke, W., 1976. Chemie von Moor und Torf. In: K.-H. Göttlich (Editor), *Moore- und Torfkunde*. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 134-148.
- Von Post, L., 1924. The genetic system of the organogen formations of Sweden. *Actes IVième Conf. Int. Pedologie*, p. 496.
- Von Post, L. and Granlund, E., 1926. Södra Sveriges torvtillgångar I. *Sven. Geol. Unders.*, C: 335.
- Waksman, S.A. and Stevens, K.R., 1928a. Contribution to the chemical composition of peat: I. Chemical nature of organic complexes in peat and methods of analysis. *Soil Sci.*, 26: 113-137.

- Waksman, S.A. and Stevens, K.R., 1928b. Contribution to the chemical composition of peat: II. Chemical composition of various peat profiles. *Soil Sci.*, 26: 239-251.
- Waksman, S.A. and Stevens, K.R., 1929a. Contribution to the chemical composition of peat: III. Chemical studies of two Florida peat profiles. *Soil Sci.*, 27: 271-281.
- Waksman, S.A. and Stevens, K.R., 1929b. Contribution to the chemical composition of peat: IV. Chemical studies of highmoor peat profiles from Maine. *Soil Sci.*, 27: 389-398.
- Waksman, S.A. and Stevens, K.R., 1929c. Contribution to the chemical composition of peat: V. The role of microorganisms in peat formation and decomposition. *Soil Sci.*, 28: 315-340.
- Waksman, S.A. and Tenney, F.G., 1928. Composition of natural organic materials and their decomposition in the soil: III. The influence of nature of plant upon the rapidity of its decomposition. *Soil Sci.*, 26: 155-171.
- Walker, D. and Walker, P.M., 1961. Stratigraphic evidence of regeneration in some Irish bogs. *J. Ecol.*, 49: 169-185.
- Walsh, T. and Barry, T.A., 1958. The chemical composition of some Irish peats. *Proc. R. Ir. Acad.*, 59B: 305-328.
- Walter, H., 1977. The oligotrophic peatlands of Western Siberia — the largest peino-helobiome in the world. *Vegetatio*, 34: 167-178.
- Watt, A.S., 1947. Pattern and process in the plant community. *J. Ecol.*, 35: 1-22.
- Waghman, G.J., 1980. Chemical aspects of the ecology of some South German peatlands. *J. Ecol.*, 68: 1025-1046.
- Weast, R.C. (Editor), 1965. *Handbook of Chemistry and Physics*. Chemical Rubber Co., Cleveland, Ohio, 46th ed.
- Weber, C.A., 1908. Aufbau und Vegetation der Moore Norddeutschlands. *Englers Bot. Jahrb.*, p. 90.
- Webster, J.R., 1962. The composition of wet-heath vegetation in relation to aeration of the ground-water and soil. I. Field studies of ground-water and soil aeration in several communities. *J. Ecol.*, 50: 619-637.
- West, R.G., 1968. *Pleistocene Geology and Biology*. Longmans, London, 377 pp.
- Wheatley, R.E., Greaves, M.P. and Russell, J.D., 1975. The occurrence of aphid wax in peat. *Soil Biol. Biochem.*, 7: 35-38.
- Whitmore, T.C., 1975. *Tropical Rain Forests of the Far East*. Clarendon Press, Oxford, 282 pp.
- Wickman, F.E., 1951. The maximum height of raised bogs. *Geol. för. Stockh. Förh.*, 73: 413-422.
- Wildehain, W. and Henske, G., 1965. Organische Verbindungen aus Hochmoortorfextrakten. *Z. Chem.*, 5: 457-458.

- Wildt, O., 1978. Simulating the development of peat bogs. *Vegetatio*, 37: 1-17.
- Williams, B.L., 1974. Effect of water-table level on nitrogen mineralization in peat. *Forestry*, 47: 195-202.
- Woodwell, G.M., Whittaker, R.H., Reiners, W.A., Likens, G.E., Delwiche, C.C. and Botkin, D.B., 1978. The biota and the world carbon budget. *Science*, 199: 141-146.

INTERNATIONAL PEAT CONGRESSES

The Proceedings of these Congresses are frequently referred to in these pages, and are an important source of information for the subject. They are bibliographically diverse, and not always easy of access, so it may be useful to give full details here:

- Proceedings 1st International Peat Congress, Dublin, 1954. No Editor. No publication date.
- Proceedings 2nd International Peat Congress, Leningrad, 1963. Edited by R.A. Robertson. H.M.S.O., London. Published 1968. 2 vols., 1090 pp.
- Proceedings 3rd International Peat Congress, Quebec, 1968. Edited by C. Lafleur and J. Butler. No Publisher, but "Sponsored by Department of Energy, Mines and Resources, Ottawa, Canada and National Research Council of Canada". No publication date. 405 pp.
- Proceedings 4th International Peat Congress, Otaniemi, Finland, 1972. No editor. No publisher. No publication date. 5 vols.: 484, 353, 569, 303, 284 pp.
- Proceedings 5th International Peat Congress, Poznań, Poland, 1976. No editor. Wydawnictwa Czasopism Technicznych Not, Warszawa. No publication date. 4 vols.: 482, 336, 335, 396 pp.
- Proceeding 6th International Peat Congress, Duluth, Minn., 1980. No Editor. No Publisher. No publication date, 735 pp.

0487-8 105

NOTE ADDED IN PROOF

A recent book summarizes a great deal of information about the organic chemistry and industrial uses of peat. It is:

- Fuchsman, C.H., 1980. *Peat: Industrial Chemistry and Technology*. Academic Press, New York, N.Y., 279 pp.