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METHODS FOR STUDYING BELOW-GROUND PRODUCTION IN MIRE ECOSYSTEMS

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Difficulties in separating fine roots from a purely organic matrix preclude the use of traditional root-harvesting techniques when studying the below-ground production of the field layer species in mires. Also methods based on different types of installations, such as ingrowth chambers or rhizotrons, cause a significant disturbance of the root environment. Indirect techniques using isotope-labelling avoid many of these problems and are the most suited for studying below-ground processes in peatlands. A technique based on translocation of ^{14}C to the peat through the fine roots is demonstrated to evaluate the vascular plant biomass distribution in hummocks of a subarctic and a boreonemoral peat bog respectively. The technique fails to distinguish between structural and labile carbon and overestimates therefore the fine root biomass, but is useful for comparative purposes. It is shown that different mire plants have species-specific below-ground distributions, and that a proportionately greater share of carbon is allocated to fine roots in subarctic conditions.

Keywords: *Andromeda*, *Calluna*, *Empetrum*, *Eriophorum*, ^{14}C, root biomass, *Rubus*, translocation

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INTRODUCTION

Peat accumulates because net production of plant mass exceeds the total loss through decay. Mires have been considered as systems where organic matter is added at the surface at a constant rate and steadily lost through decay below the surface, at a rate proportional to its remaining mass (Clymo 1978, 1987). A differential decay of the different plant litter fractions depletes the peat of the easily decomposable fractions during its passage through the acrotelm, and at the transition to the catotelm, the peat is quantitatively dominated by the most resistant fractions, the *Sphagnum* mosses (Clymo 1984).

The model described above assumes that the addition of biomass all takes place at the mire surface. It is thus appropriate, for example, for lawn and carpet sites on ombrotrophic bogs where most of the biomass consists of apically growing *Sphagnum* mosses. However, mires are — from a biomass and production point of view — generally dominated by vascular plants. Hummocks dominated by ericoid dwarf shrubs are characteristic features of all ombrotrophic bogs, and also occur in most of the fens, while the graminoid-dominated lawns and low hummocks characterize most of the fens (Sjörs 1948). Thus, there is a considerable continuous addition of biomass below the surface, even down into the catotelm, through the below-ground production of roots and rhizomes. Values for the share of total biomass formed below ground between 40% and 90% have been reported (Forrest 1971, Tyler et al. 1973, Wallén 1986, 1987). But few attempts have been made to determine the below-ground biomass and productivity of the vascular plants growing on mires (Vasander 1982, Backéus 1985). Undoubtedly, the main reason for this is the lack of a reliable method. The most important feature of mires which precludes the use of the most commonly used methods is the organic soil matrix.

On the other hand, the organic soil matrix facilitates the use of alternative techniques, e.g. radioisotope labelling.

In this paper I briefly review some methods for measuring the below-ground biomass and productivity of vascular plants. A comparative study of the vertical distribution of vascular plant biomass in subarctic and boreonemoral bog hummocks using a ^{14}C labelling technique is described in more detail. Hummocks are, from a peat accumulation point of view very important structures and can be considered as 'centra' for production of the mires. On hummocks, non-aquatic *Sphagna* and woody, ramifying vascular plants interact in 'putting up' the acrotelm, increasing the total living-space and the production potential (Barber 1981, Boatman 1983, Wallén 1983, 1987). Peat deposited under hummocks has a higher bulk density than peat deposited under lawns and hollows (Svensson 1988). Thus, the growth and expansion of hummocks is the main regulator of runoff and ground water levels (Streefkerk et al. 1989), and, consequently, of the growth of a mire as a whole.

GENERAL METHODS

There are four groups of methods for the studying of below-ground production: 1) Root standing crop estimates over various time spans using coring or profile wall techniques, 2) growth observation methods using rhizotrons , 3) root ingrowth methods, and 4) indirect methods using uptake of radioisotopes. Only some of these methods are possible in mire research.

Root sampling on mires means separating the below-ground vascular plant biomass from the organic peat matrix. As a considerable amount of fine roots tend to penetrate the cellular fractions of the soil matrix, all methods based on root extraction underestimate the biomass to a considerable extent (Reader 1978). Furthermore, as with above-ground harvesting techniques, root harvesting is based on the assumption that biomass increases can be calculated by subtracting the biomass at the start of a period from the biomass at the end of a period, an assumption that implies either a continuous growth during the time interval between the two samplings, or that the sampling occasions coincide with the root minimum and maximum respectively (Singh et al. 1984, Vogt et al. 1986, Kurz et al. 1987). However, below-ground mass is known not to grow synchronously with the above-ground biomass, neither during the life span of a plant nor during the growth season. Thus, root harvesting techniques are based on a set of assumptions that are difficult to quantify, particularly in peaty soils.

Root observation methods have a long tradition within agriculture and horticulture with the root laboratories or the so-called rhizotrons that use flat-sided viewing panels for observing root growth *in situ*, or the mini-rhizotrons that use viewing tubes and fiber-optical registration instruments (Cheng & Coleman 1991). However, despite the recent improvements in minirhizotrone techniques with computerized analyses of miniature video images, the key problem still remains: how to transfer observations of rooting intensity (length of roots per unit window area) to rooting density (length of roots per unit volume) and biomass. In addition, the installation of the transparent observation tubes or chambers results in considerable disturbance of the below-ground environment. The extremely sensitive inter-individual capillary system is disturbed around the installations, especially on mires. Thus, this group of methods is of limited use in mire research.

Root ingrowth cores or mesh bag techniques have been used in mires for quantifying fine root production with some success (Backéus 1990). A given volume of peat is replaced by a root-free ingrowth medium, enclosed either in a plastic tube equipped with a set of open windows or a mesh bag (Persson 1979, Steen 1991). The ingrowth medium can be root-free peat, glass wool, filter wadding or some other material that physically resembles peat. An advantage with this method is that a comparatively large number of cores can be prepared and sampled. This allows repeated sampling for an analysis of the turnover of roots and makes a statistical analysis of the results possible. There are, however, serious objections. The cutting of the cores results in: 1) pruning of the roots at the beginning of the experiment and 2) drainage of the peat along the cores, and 3) differences in the physical properties between the ingrowth medium and the surrounding peat. The second objection can be minimized by a careful performance of the experiment, and the third objection by imitating the peat density in the original core. This is best done using root-free milled peat as ingrowth medium. However, using peat implies problems with the subsequent extraction of fine roots. Alternative, inert ingrowth materials, such as glass wool or filter wadding, should be tested, at least in comparative studies.

Indirect techniques using stable or radioisotopes, are the ones most suited for studying below-ground processes in mires. Generally, they do not involve any disturbance of the capillary system of the peat nor of the root growth itself during the experiments. As carbon is the principal constituent of organic matter, radioactive ^{14}C is the most commonly used tracer. However, ^{14}C-pulse labelling with a subsequent repeated sampling of below-ground biomass can not directly be used for determining root biomass turnover. A considerable, unknown amount of carbon, translocated below ground, is non-structural and labile (Newman 1985). Methods based on a decline in total ^{14}C after a pulse labelling do not distinguish between labile and structural carbon and therefore overestimate the below-ground biomass and its turnover. A restriction to analysing the dilution of ^{14}C incorporated in some well-defined structural component (e.g. cellulose or hemicellulose), eliminates the errors associated with translocation of labile carbon in and out of the roots (Caldwell et al. 1974, Milchunas et al. 1985, 1992). The ^{14}C dilution technique is based on a turnover coefficient for the structural carbon:

$$TC = (R_1C_1/R_2C_2) - 1$$

where R_1 and R_2 are relative ratios of ^{14}C and ^{12}C at two successive dates, and C_1 and C_2 denote the share of structural carbon component analysed of total tissue dry weight.

ESTIMATION OF BELOW-GROUND BIOMASS DISTRIBUTION IN BOG HUMMOCKS USING ^{14}C PULSE LABELLING

Background

In the following, an experiment in which ^{14}C is used to quantify the supply of organic matter to successive peat levels in bog hummocks is described in detail.

Extremely high root/shoot ratios have been reported from arctic and subarctic moor sites (Wielgolaski 1972). Below-ground/above-ground ratios have been reported to be 30 to 45 in graminoid species (mainly *Eriophorum* spp. and *Dupontia fisheri*) dominating wet tundra (Dennis & Johnson 1970), and 49 for *Andromeda polifolia* and *Rubus chamaemorus* and 9 for *Empetrum hermaphroditum* dominating subarctic ombrotrophic peat bog hummocks (Wallén 1986). Flower–Ellis (1980a, b) found that 91% and 97% of assimilated carbon was available for translocation to rhizomes and roots of *Andromeda* and *Rubus* respectively. On the same mire, manually extracted roots of *Andromeda* and *Empetrum* formed 24% and 17% of the total biomass respectively (Malmer, pers. comm.).

Corresponding data from sites in temperate and subtemperate regions are lacking. Only some data based on manual root extractions are available. Forrest (1971) estimated the below-ground/above-ground ratio to be ca. 1 for *Calluna vulgaris* in a blanket bog in northern England. Tyler et al. (1973) estimated the ratio to be ca. 1.5 for a *Calluna vulgaris–Erica tetralix*-dominated coastal wet heath in South Sweden, while Wallén (1987) estimated the ratio to be 0.55–1 for *Calluna* on an ombrotrophic peat bog in South Sweden.

In the following, the biomass distribution of the dominant vascular plant species growing on hummocks on an ombrotrophic peat bog in south Sweden is compared with the biomass distribution of the dominant species at a comparable site on a subarctic mire (Wallén 1986). An indirect method based on ^{14}C translocation, is used for estimating the fine root biomass. The method has been previously described by Wallén (1986).

The sites

Two ombrotrophic mires, one at Stordalen, Abisko in northern Sweden (68°22′N, 19°03′E) and the other at Åkhult in southern Sweden (57°06′N, 14°33′E), were investigated.

The Stordalen mire is situated within the subarctic region, approximately 200 km north of the Arctic Circle, and is characterized by permafrost conditions. The sampling for the present study was made within an ombrotrophic, elevated hummock area with *Sphagnum fuscum* (Schimp.) Klinggr. in the bottom layer and evenly distributed *Empetrum hermaphroditum* Hagerup, *Andromeda polifolia* L. and *Rubus chamaemorus* L. dominating the field layer. The sampling was carried out in 1985 and the results have been described by Wallén (1986).

The Åkhult mire, ca. 30 km NW of the city of Växjö, is a boreonemoral mire with a large ombrotrophic bog. It has been described by Malmer (1962). The surface of the mire is characterized by randomly distributed, irregularly shaped small hummocks dominated by *Sphagnum rubellum* Wils. and *Sphagnum fuscum* in the bottom layer, and *Calluna vulgaris* (L.) Hull and *Eriophorum vaginatum* L. in the field layer. *Empetrum nigrum* L. occurs on high, secondary hummocks (Du Rietz 1949) only.

The methods

The study concentrated on the vertical distribution of vascular plant biomass. The above-ground fractions were determined by clipping at the top of the moss surface within 20 x 20 cm squares, replicated 30 times on the Stordalen mire and 10 times on the Åkhult mire. The below-ground coarse fractions were extracted and partitioned into species from 2.5-cm thick slices of 10-cm diameter cores taken in the centre of each square. All coarse fractions (diameter >0.5 mm) were dried at 85°C and weighed. The fine root biomass, in this context the thin, wiry fine roots with a diameter <1 mm, was determined indirectly using a ^{14}C labelling technique: Each of the 20 x 20 cm plots were clipped so that all shoots of the vascular plants but one species, were clipped at the moss surface. Thus, plots containing either *Andromeda, Empetrum* or *Rubus* on Stordalen mire, and either *Calluna* or *Eriophorum* on Åkhult mire, were prepared. Each plot was covered with a transparent perspex chamber, 20 x 20 x 40 cm, pushed down ca. 5 cm into the peat. The effective volume of the chamber was ca. 12 dm^3. Each chamber was supplied with 100 µCi ^{14}C by acidification of sodium ^{14}C-bicarbonate inside the chamber. The treatment lasted for three hours. Three days after the initial labelling, cylindrical cores, 10 cm in diameter, were cut out in the centre of each plot. The cores were transferred into PVC tubes and deep frozen within 3 hours. The deep frozen cores could then be cut up into 2.5 cm slices very exactly with an ordinary band saw. Each cut took ca. 1 mm. After all coarse fractions had been extracted by hand, together with all fine roots attached to rhizomes or below-ground stems belonging to the species left above-ground, the peat was thoroughly homogenized in a food blender. All fractions were dried at 85°C and weighed.

The concentration of ^{14}C was measured both in the attached fine roots (C_{ro}) and in the homogenized peat (C_{Pr}) fractions. The ^{14}C analyses were made by combustion of dried and weighed samples in a Packard-Tri-Carb sample oxidizer, trapping the $^{14}CO_2$ in a carbosorb-solution with scintillation fluid added, and counting the disintegrations of ^{14}C in a Packard-Tri-Carb scintillation counter. The mass of fine roots (including non-structural carbon) in the homogenized peat (W_{ro}) was then determined as:

$$(1) \qquad W_{ro} = W_{Pr} \frac{C_{Pr}}{C_{ro}}$$

where W_{Pr} is the total dry weight of peat. This method of determining fine roots is based on the assumption that the only way for ^{14}C to reach a certain depth in the peat is through the rooting system of the species left to assimilate in the chamber. This condition was probably not fulfilled in the uppermost layer, as an unknown amount of ^{14}C had probably been supplied to the peat through the living *Sphagna* (Rydin & Clymo 1989). For these samples, a correction for the content of ^{14}C in root-free moss litter (C_P) therefore had to be made:

$$(2) \qquad W_{ro} = W_{Pr} \frac{C_{Pr} - C_P}{C_{ro} - C_P}$$

Results

The ^{14}C in fine roots, and in peat decreased according to a negative exponential with depth both on Stordalen and on Åkhult (Fig. 1). At both sites, the non-dwarf shrubs, *Eriophorum* on Åkhult and *Rubus* on Stordalen, translocated ^{14}C comparatively deeper than the dwarf shrubs. The main differences between the sites were in the degree of translocation to the deep peat levels. The distribution of ^{14}C within the dwarf shrub fine root fractions reveals a quite different picture. The ^{14}C within *Andromeda* and *Empetrum* at Stordalen decreased according to a negative exponential to 1.1% and 1.4% of the top layer respectively at 10 cm depth, while *Calluna* at Åkhult had an activity of about 9% of that in the top layer at the corresponding level (corresponding values for *Eriophorum* and *Rubus* were 16% and 41% respectively).

The total fine root mass down to 25 cm, according to equations (1) and (2), did not differ significantly between the two mires (Fig. 2). On Stordalen there was a total vascular plant fine root mass down to a 25-cm depth of ca. 2 kg m^{-2}, of which roughly 50% was *Andromeda*, 30% *Empetrum* and 20% *Rubus*. The corresponding value for Åkhult was 1.8 kg m^{-2} of which 30% was *Calluna* and 70% *Eriophorum*. Neither *Vaccinium oxycoccus* fine roots nor fine roots below a 25-cm depth are included in these values. However, despite the similar total amounts of fine roots, the vertical distribution differs greatly between Stordalen and Åkhult.

On Åkhult the total fine root mass was evenly distributed throughout the profile, with between 150 g m^{-2} and 250 g m^{-2} at each 2.5 cm level and with *Calluna* dominating above 10 cm and

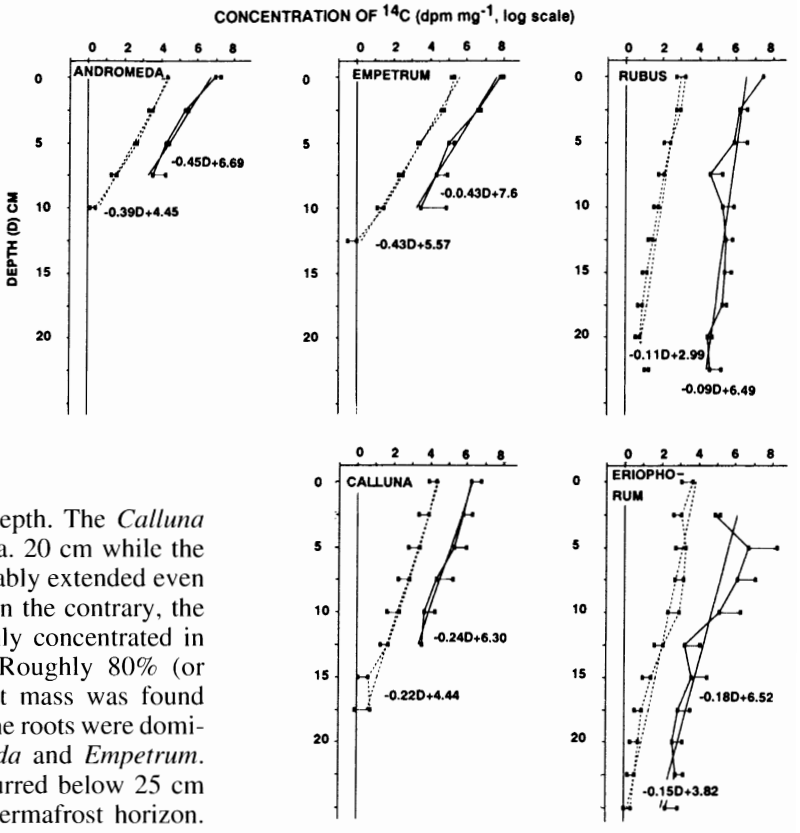

Fig. 1. Average concentrations of ^{14}C (log scale) with + 1 SE and linear regressions against peat depth (dotted lines) and in fine roots (solid lines) of the dominating vascular plants of bog hummocks on the Stordalen mire (*Andromeda, Empetrum* and *Rubus*), and on the Åkhult mire (*Calluna* and *Eriophorum*).

Eriophorum below a 10 cm depth. The *Calluna* fine roots extended down to ca. 20 cm while the fine roots of *Eriophorum* probably extended even below 25 cm. On Stordalen, on the contrary, the total fine root mass was mainly concentrated in the uppermost 10 cm peat. Roughly 80% (or 1.6 kg m^{-2}) of total fine root mass was found between 0 and 10 cm. These fine roots were dominated (ca. 85%) by *Andromeda* and *Empetrum*. Probably no root activity occurred below 25 cm due to the proximity of the permafrost horizon.

The total biomass above the moss surface was about 1.5 times higher on the Åkhult mire than on the Stordalen mire (Fig. 3). If the uppermost 2.5-cm moss layer is included in the comparison (which is quite reasonable because this layer contains overgrown basal stem parts) the difference between Åkhult and Stordalen becomes much

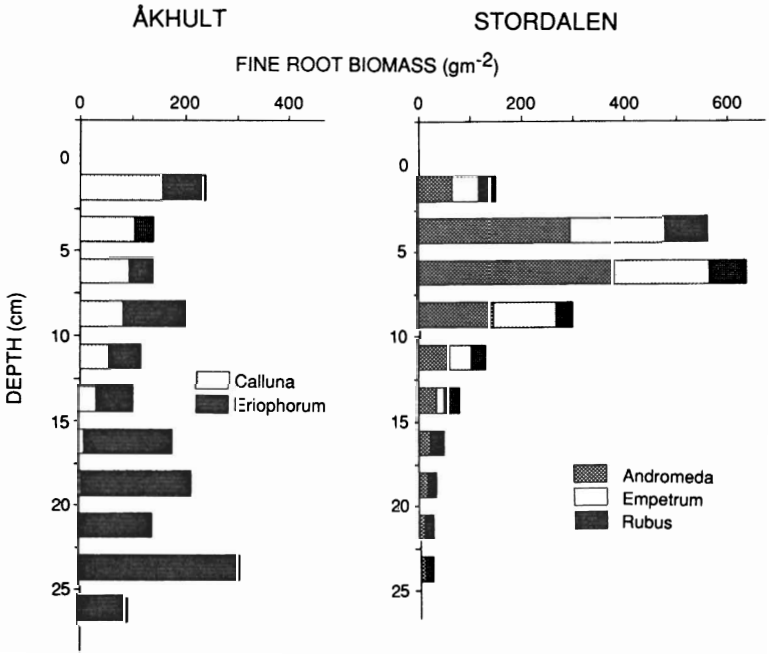

Fig. 2. Vertical distribution of fine root mass (g m^{-2} in successive 2.5-cm sections) of the dominating vascular plants on the mires at Åkhult and Stordalen.

greater. In spite of the difference in biomass above ground, the total biomass below moss surface (0–25 cm depth) is similar — ca. 2.8 kg m^{-2} on Åkhult and 2.7 kg m^{-2} on Stordalen. Thus, the ratios between the biomass below and above the moss surface on Stordalen is 19 and on Åkhult 13, but decreases to 6 and 2, respectively, if the biomass within the uppermost 2.5 cm of peat is counted as above ground.

Both the vertical distribution and the proportion of fine roots in the below-ground biomass differs between the two sites. On the Stordalen mire, the bulk of the below-ground biomass (roughly 70%) is concentrated to the 2.5–10-cm level. Below the 15-cm level comparatively little biomass is found. In contrast, on the Åkhult mire, there is a rather even distribution of biomass below the 5 cm depth to the bottom of the cores, with ca. 200 g m^{-2} at each 2.5 cm level. However, above 5 cm there is a marked concentration of biomass, especially of *Calluna* woody parts. On Stordalen, 80% of the below-ground biomass was composed of fine roots, mainly in the 2.5 and 10-cm layer. In contrast, on Åkhult, the fine root fraction constituted ca. 65% of total below-ground biomass and was more or less evenly distributed throughout the peat, with *Calluna* fine roots dominating the upper layers and *Eriophorum* fine roots the deeper layers.

Discussion

In this three-day experiment, deposition of non-structural root material may have been a quite significant sink for ^{14}C. The ^{14}C recovered from the different peat levels had been deposited as soluble exudates (sugars, amino acids and organic acids), carbon dioxide, mycorrhiza, mucigel, sloughed root tissue or as tissue of roots themselves (Newman 1985). The ^{14}C pulse labelling technique fails to distinguish between these different fractions and, therefore, overestimates the fine root biomass to an unknown degree. Available evidence suggests that the deposition of non-structural material (soluble and insoluble) can be of about 10–500 mg g^{-1} root (Newman 1985). The method is, however, useful for estimating the total carbon allocation below ground for comparative purposes provided that the specific activity of ^{14}C is the same in the roots and their products, and that the ratio of C:dry weight is comparable.

The study indicates two things: 1) the proportionately greater share of carbon allocated to fine roots in the subarctic bog hummock, especially when considering comparable dwarf shrubs, suggests that plants growing in subarctic conditions have to spend comparatively more of their energy on mineral nutrient uptake than those growing in similar warmer sites, and 2) in both studied mires, the dwarf shrub below-ground biomass is concentrated in the uppermost fifteen centimetres of the peat, or above the level of the maximum water table.

The different mire plants thus have species-specific below-ground distributions, varying from a concentration to the uppermost few centimetres of the acrotelm to down into the catotelm. In mire sites with vascular plants, there is therefore a continuous input of organic matter, mainly as rhizomes, roots, and root exudates, to the successive peat layers down the acrotelm. This might

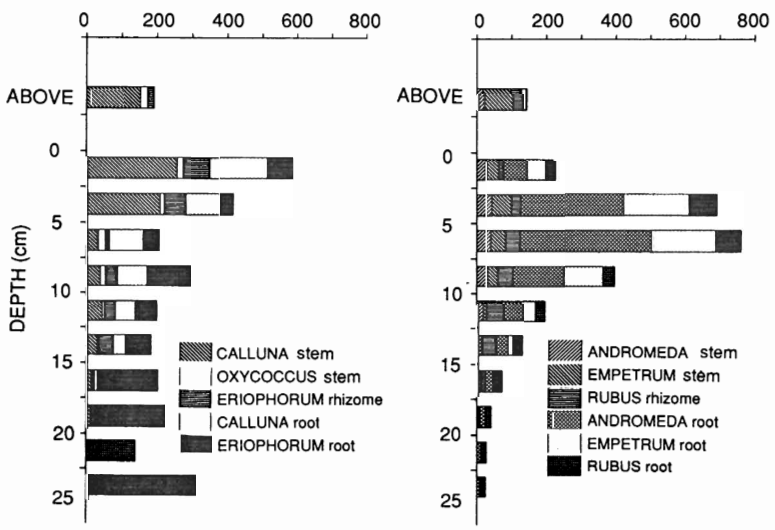

Fig. 3. Vertical distribution of total biomass (g m^{-2} above the moss surface, and in successive 2.5-cm sections) of the dominating vascular plants on the Åkhult (left) and Stordalen (right) mires.

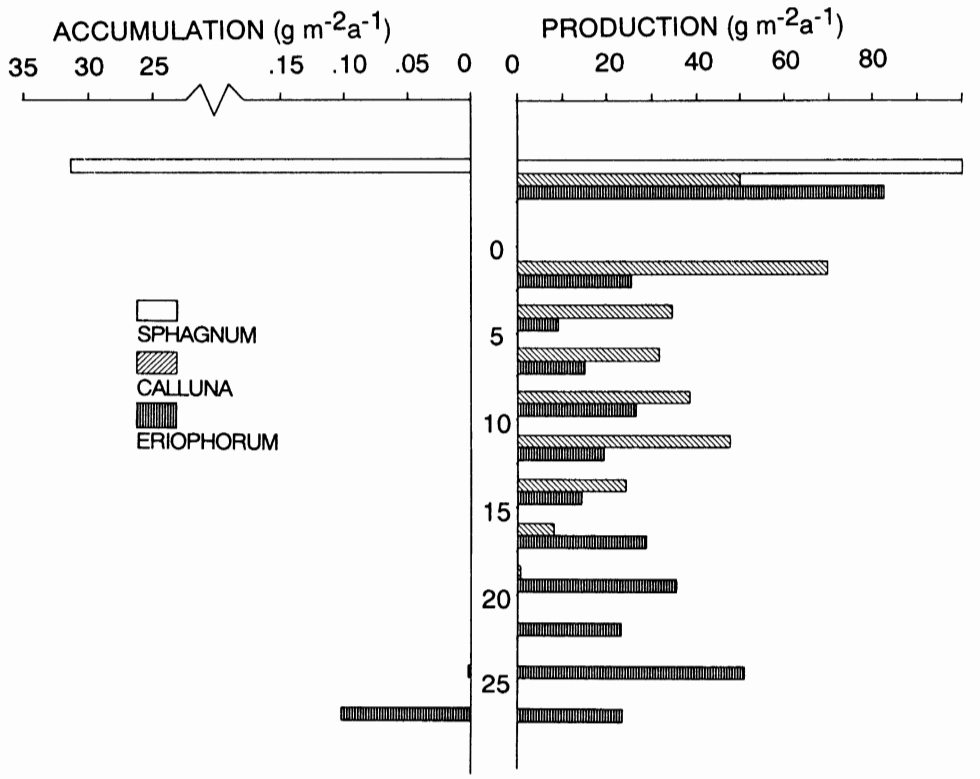

Fig. 4. Mass remaining at the transition from acrotelm to catotelm (left), of total biomass production (right) in successive 2.5-cm peat sections. The diagram is based on the production estimations derived from the biomass relations in Fig. 3. A turnover rate of 1 for *Eriophorum* above-ground biomass, 0.2 for the rest of the coarse fractions and 0.5 for the fine root fractions are assumed. The diagram on the left shows the biomass remaining after a proportional decay for each 2.5-cm layer. The rate for the passage of mass through the acrotelm is calculated from accumulation of nitrogen in hummocks at Åkhultmyren: age = exp {2.089 + 0.079 * depth}. The age of the peat at a 25-cm depth is hereby 60 yrs. The decay parameters used for the *Calluna* and *Eriophorum* coarse fractions are 0.27 and 0.34 respectively, and for *Sphagnum fuscum* 0.016 (determined experimentally as rate of CO_2-released at 5.7°C, which is the annual mean temperature at a 10-cm depth). Decay parameters for the fine root fractions were approximated to be 0.27 and 0.34 for *Calluna* and *Eriophorum* respectively.

have two main consequences: 1) a continuous filling up of vascular plant mass in the successive layers throughout the acrotelm, continuously changing the potential proportions between the different peat fractions, and 2) a continuous addition of a comparatively easily available carbon source to the rhizosphere, increasing the decay potential (Bottner et al. 1991).

The present study indicates that the below-ground production constitutes the major source of organic matter input to peat bog hummocks. The remaining mass of the total produced at successive 2.5-cm peat layers at the transition from acrotelm to catotelm is shown in Fig. 4. The figure is based on the biomass estimates at the Åkhult mire and relies on the assumption that there is a steady state with respect to the supply rate of biomass. Over longer periods of time this is certainly true, but in a short perspective of time, there is a stochastic variation in the environmental parameters, which cause unpredictable fluctuations in the growth of the plants. Although based on very rough approximations of the below-ground biomass turnover and of the time-course for the passage of the mass through the acrotelm, the figure shows that the most important components in modelling peat accumulation are the decay parameters for the component fractions and not the production parameters. In spite of a much higher production of mass (in this model about ten times the *Sphagnum* production), and most (80%) of it below ground, the peat is totally domi-

nated by *Sphagnum* remnants at the transition to catotelm. Of the ca. 30 g m^{-2} transferred annually into catotelm from the total production of ca. 800 g m^{-2}, 99.5% was *Sphagnum* peat. The remaining 0.5% mass mainly originated from root litter produced by the deepest rooted vascular plants, close to the transition to the catotelm.

However, the continuous addition of comparatively fast decomposable vascular plant litter to the different peat levels has a very important influence on the physical properties of the peat. It results in an increase in the share of amorphous, non-structural organic matter contributing to the impedance of water seeping through the peat.

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