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Regeneration of bog liverworts

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SUMMARY

Leafy liverworts of many species regenerate in slabs cut at various depths from peat cores from two widely different sites. Two patterns are recognizable. Species such as *Calypogeia fissa* (L.) Raddi, *Lophocolea* spp., *Lophozia ventricosa* (Dicks.) Dum., *Barbilophozia floerkii* (Web. & Mohr) Loeske and *Riccardia latifrons* (Lindb.) Lindb., which lack underground axes, regenerate most abundantly at the surface but not below 9 cm depth. Other species such as *Kurzia pauciflora* (Dicks.) Grolle, *K. sylvatica* (Evans) Grolle, *Odontoschisma sphagni* (Dicks.) Dum., *O. denudatum* (Mart.) Dum., *Cladopodiella fluitans* (Nees) Buch, *Cephalozia bicuspidata* (L.) Dum. and *C. connivens* (Dicks.) Lindb. which have underground axes, may regenerate poorly at the surface, much better down to 12 cm or so, and are still found at 24–30 cm depth. These patterns were found in cores from a live *Sphagnum*-covered surface and from a much older cut peat surface recently recolonized by liverworts. These results suggest that regeneration is mainly from underground axes rather than from spores or gemmae. The biomass of the underground axes seems to be large. All the axes have fungal associates, and it possible that they are partially saprophytic or parasitic.

Key words: Hepatics, *Sphagnum*, peatland ecology, rhizoids, symbiotic fungi.

INTRODUCTION

A characteristic feature of many peat-bog communities is the presence of a wide variety of leafy liverworts. The most characteristic and widespread genera in Britain include *Lophozia*, *Barbilophozia*, *Mylia*, *Odontoschisma*, *Cephalozia*, *Cephaloziella*, *Kurzia*, *Calypogeia* and *Gymnocolea*. In habitats such as decaying hummocks and carpets of *Sphagnum*, in shallow pools, or under dense canopies of *Calluna vulgaris* (L.) Hull leafy liverworts are often the dominant bryophytes. Despite their importance in these communities little is known about the patterns of growth of these hepatics. Because sporophyte production is intermittent or rare it is generally assumed that the plants normally spread vegetatively either by lateral growth of surface stems or more widely by gemmae, though these are rare in some species, for example *Cephalozia macrostachya* Kaal., *Kurzia* spp. (Paton, 1986). In these habitats the leafy liverworts have 'underground' axes. The possibility that these axes are the main organs of perennation in some peat-bog hepatics has not been investigated.

Apart from the completely subterranean parasite

Cryptothallus mirabilis Malmb. (Pocock & Duckett, 1984), the calobryalian 'roots' in Calobryales (Grubb, 1970), and the virtually leafless subterranean axes in some antipodean genera in the Cephaloziineae and Lepidoziaceae (Schuster, 1963; 1966, p. 430; 1980) it seems to be generally believed that Northern Hemisphere hepatics have only rhizoids growing through the substratum. Although many taxa produce downwardly growing flagella the extent to which these extend into the substratum has not been explored in detail. However, a recent survey of rhizoids in British hepatics (Pocock & Duckett, 1985a) revealed that several genera, in particular *Kurzia*, *Lepidozia*, *Cladopodiella*, *Cephalozia* and *Odontoschisma*, possess systems of underground axes which appear to be as well developed and extensive as those in their Southern Hemisphere counterparts. These axes were traced to depths of 20 cm in peaty substrata and it was suggested that they might be important as organs which enable the plants to withstand drought and fire. The rapid recolonization of bare peat surfaces by such hepatics may be due to regeneration from their underground axes.

In this article we record the regenerative behaviour

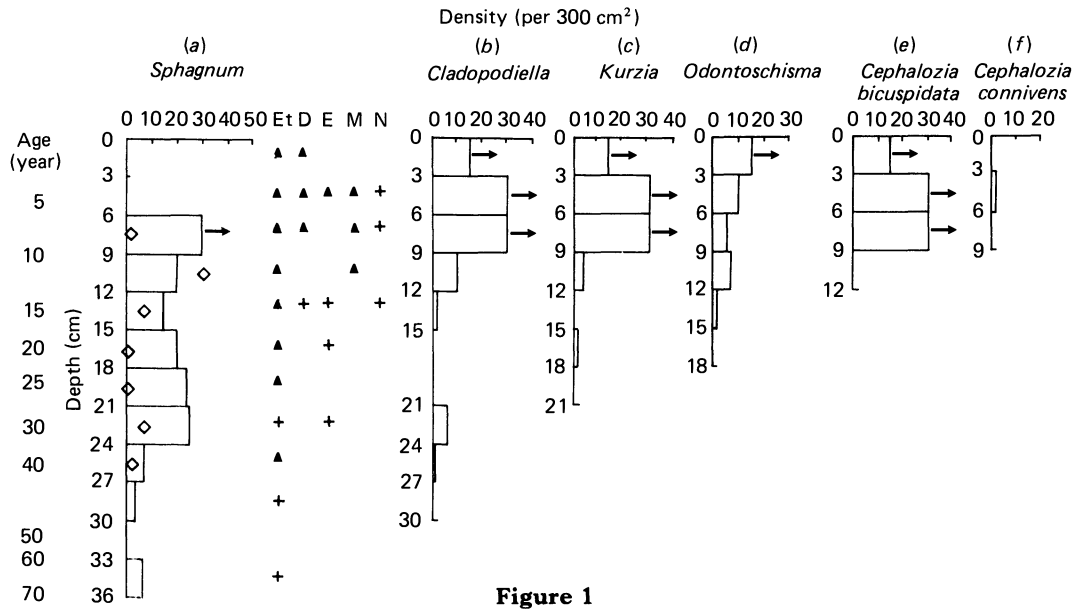


Figure 1

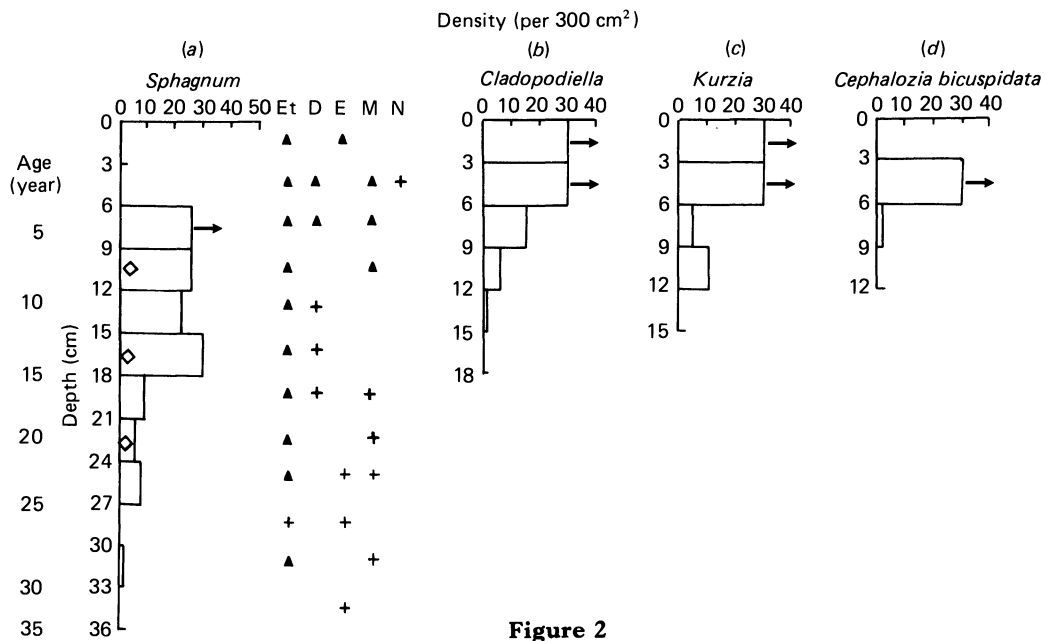


Figure 2

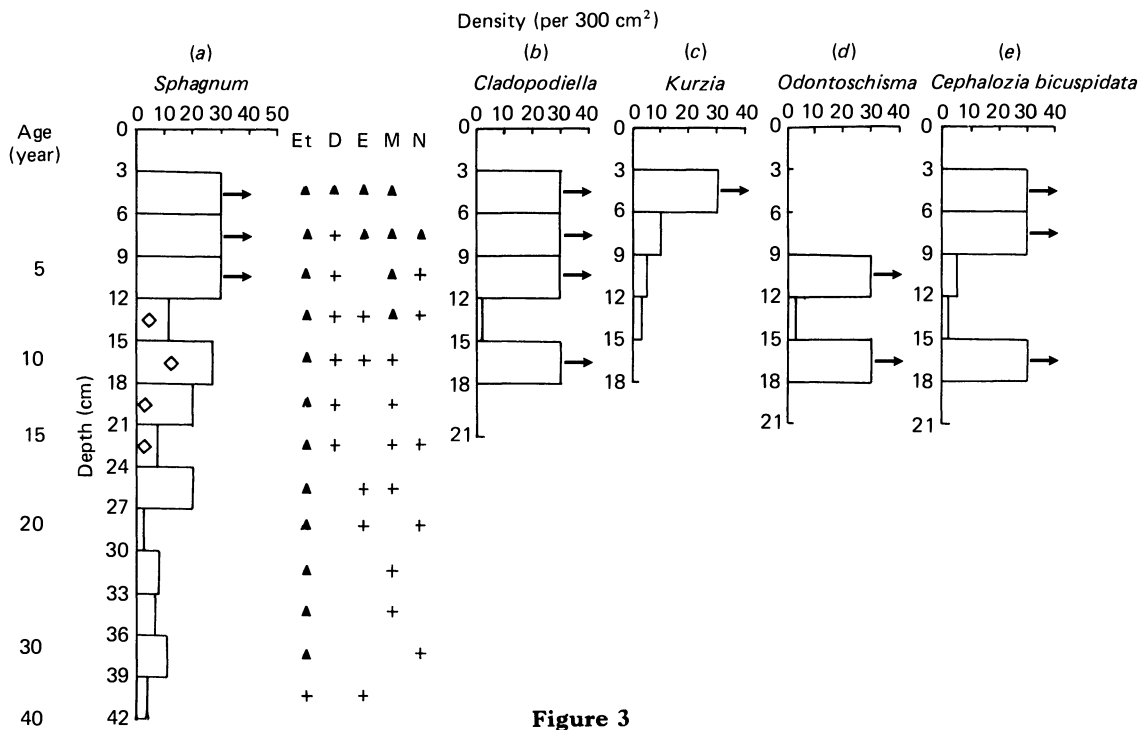


Figure 3

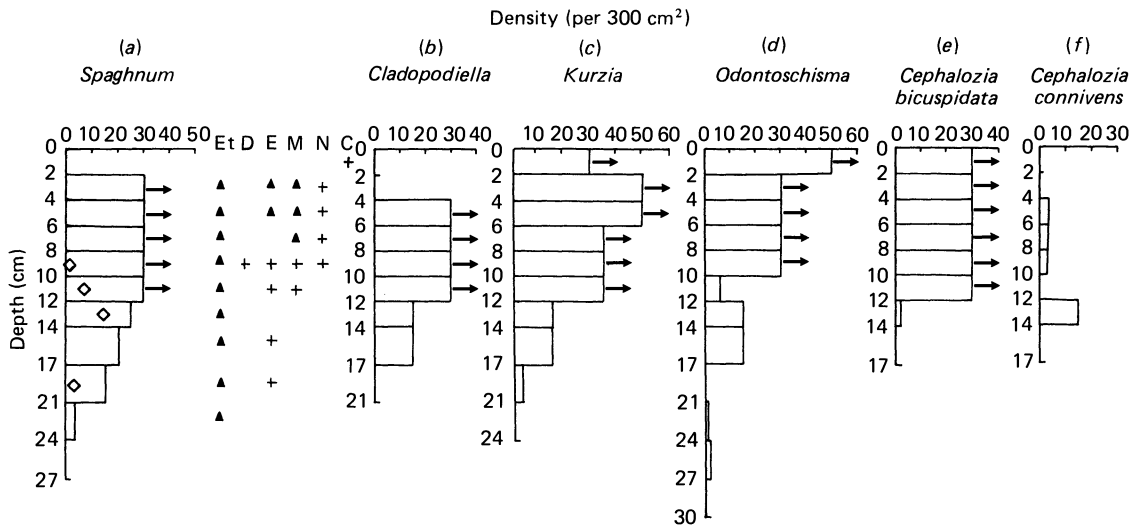


Figure 4

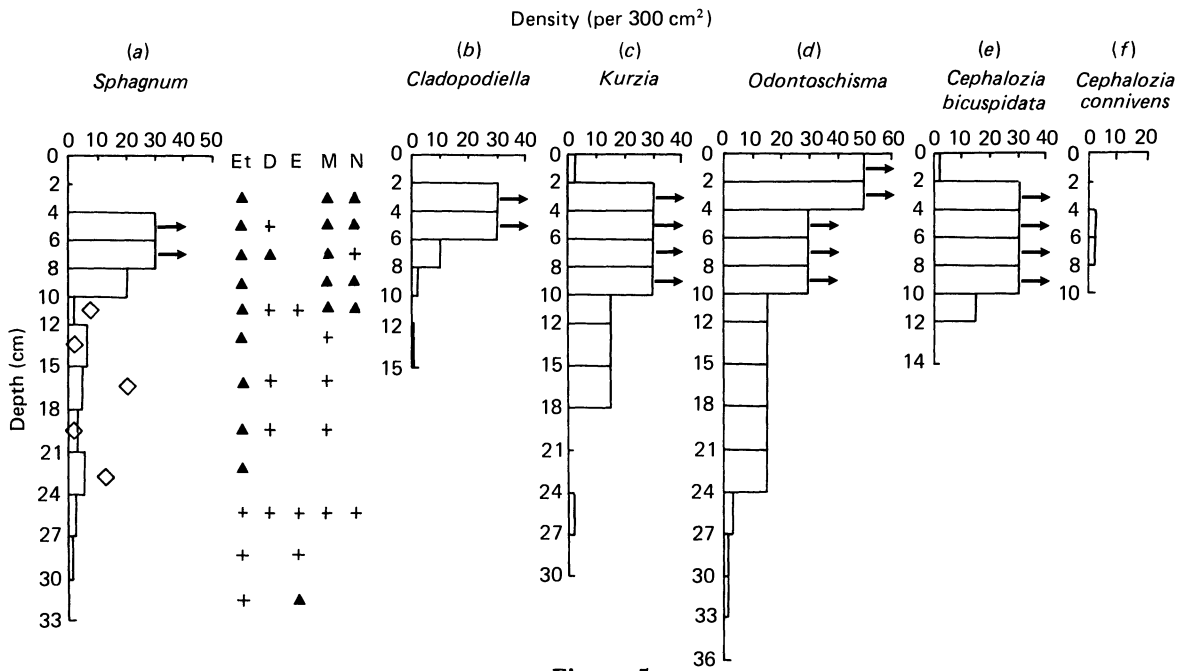


Figure 5

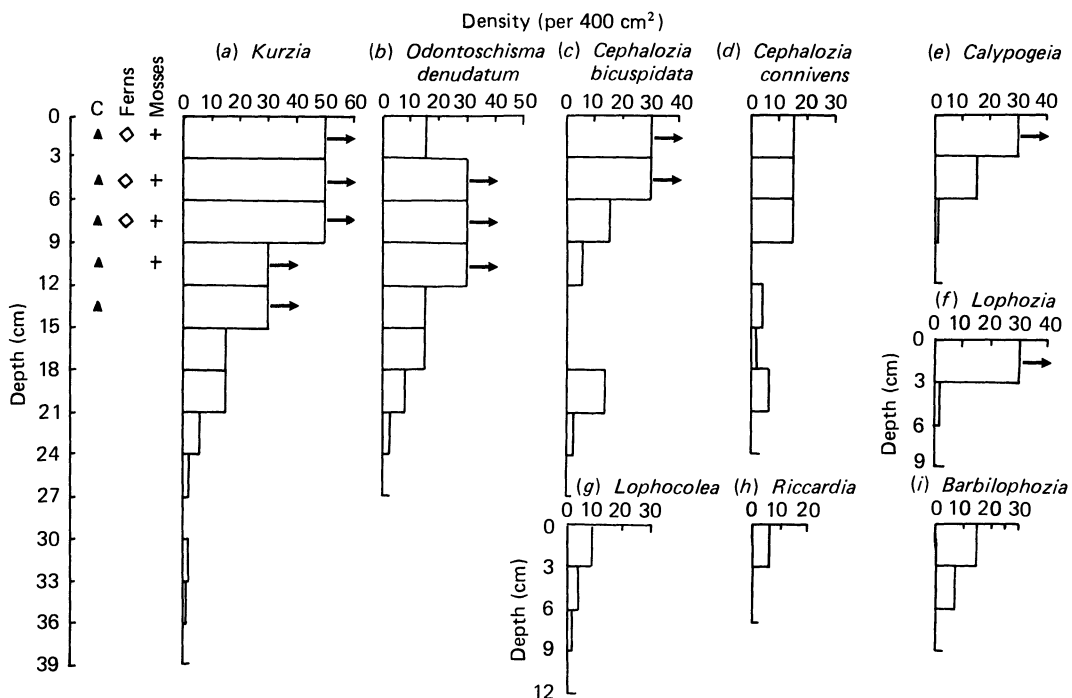


Figure 6

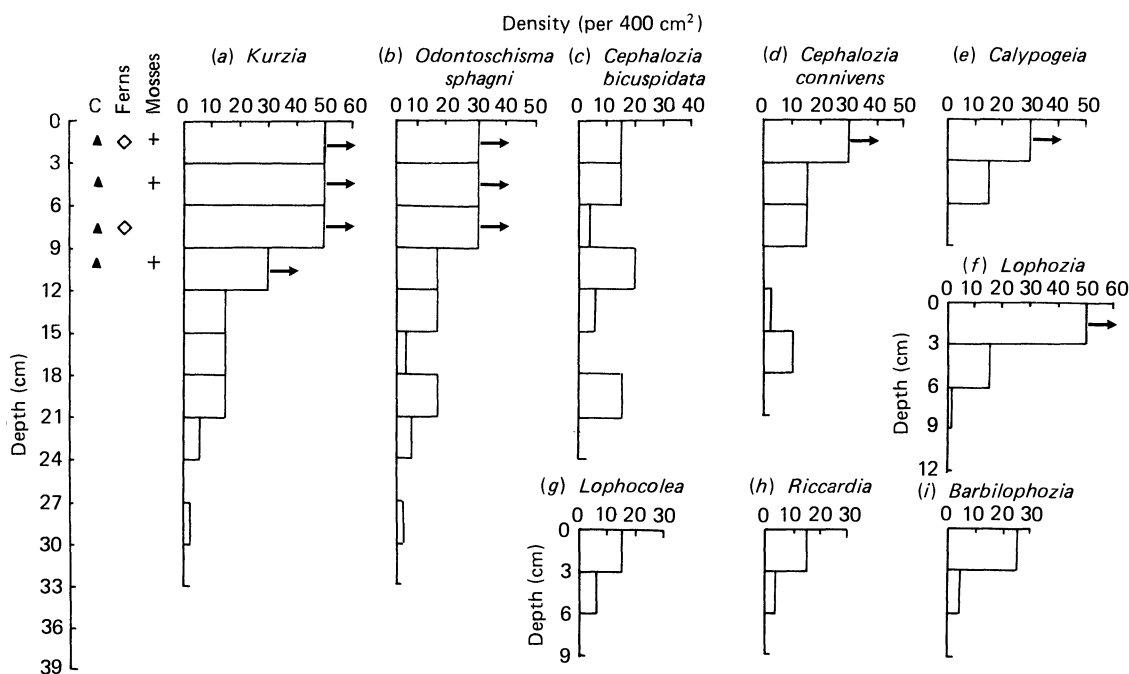


Figure 7

Figures 1–7. Regeneration from peat cores. Figures 1–5: cores from Cranesmoor (CM1, 4, 6, 2 and 7 respectively). Figures 6, 7: cores from Woodfield (WF1, WF2). (a) profile of density of new shoots of *Sphagnum* from both protonema and innovations (modified from Clymo & Duckett, 1986). \diamond , fern gametophytes and vascular plants shown by + (0–9 plants) or \blacktriangle (10 or more). Those found were: Et, *Erica tetralix*; D, *Drosera rotundifolia*; E, *Eriophorum angustifolium*; M, *Molinia caerulea*; N, *Narthecium ossifragum* and C, *Calluna vulgaris*. At left in Figures 1–3 are tentative probable minimum ages inferred from ^{137}Cs and bulk density measurements (Clymo & Duckett, 1986). (b–i) Profiles of density of new shoots of hepatics as named. Where the densities were high exact counts were not made: arrows indicates ‘more than’.

of hepatics in peat cores taken from two widely separate and ecologically distinct sites, one in southern England the other in central Ireland. The results show that underground axes are indeed important sources of regeneration of hepatics particularly on damaged peat surfaces and areas of decaying *Sphagnum*.

MATERIALS AND METHODS

Sites and sampling procedures

Peat cores were collected from two sites: Cranesmoor a valley bog in the New Forest (National Grid reference SU 185029) on 2 February 1985, and Woodfield Bog, a raised bog complex in County Offaly, Eire on 17 June 1987. Details of the sites and their climate are given in Clymo & Duckett (1986) and Doyle & Duckett (1985). Five cylindrical cores, 20 cm diameter and 50–60 cm deep, were collected in PVC tubes from Cranesmoor. Two square cores, 20 cm side and 40 cm deep, were cut from Woodfield Bog with a spade and placed in sealed polythene bags.

Treatment of the cylindrical (Cranesmoor) cores is described in detail by Clymo & Duckett (1986). The square (Woodfield) cores were treated similarly. Both were cut transversely into 2–3 cm slabs. Each slab was placed separately in a polythene bag with

the open end of the bag folded under to limit evaporation. The bags were not hermetically sealed and gases could enter or leave through small gaps and by diffusion through the polythene. Water which drained at first from the wetter slabs was removed. The top two or three slabs showed signs of drying out and were given distilled water as necessary. After 20 weeks (from 5 February to 5 July 1985) for the Cranesmoor cores and 25 weeks (from 18 August 1987 to 6 January 1988) for the Woodfield ones the plants growing on the slabs were identified and counted under a dissecting microscope and when necessary photographed with a Leitz Dialux microscope.

Sample age

The age of slabs in some cores was estimated conservatively by the accumulation of dry mass, calibrated by the 1963 peak in concentration of ^{137}Cs . This method ignores decay of organic matter and downward leaching of ^{137}Cs , and thus underestimates the true age. Details are given in Clymo & Duckett (1986).

Description of the cores

Nomenclature in this article follows that of Clapham,

Tutin & Warburg (1981) for vascular plants and Corley & Hill (1981) for bryophytes.

Three of the Cranesmoor cores were also used to study regeneration of *Sphagnum*: descriptions are given in Clymo & Duckett (1986). Cores CM1 and CM4 came from extensive carpets of *Sphagnum papillosum* Lindb. Careful examination revealed scattered stems of *Cladopodiella fluitans* (Nees) Buch, *Cephalozia bicuspidata* (L.) Dum., *Kurzia pauciflora* (Dicks.) Grolle. and *Odontoschisma sphagni* (Dicks.) Dum. growing between the *Sphagnum capitula*. Core CM6 contained the same hepatics, but in much smaller amounts amid the dominating *S. magellanicum* Brid.

Cores CM2 and CM7, not reported in Clymo & Duckett (1986), were specifically selected to include an abundance of hepatics (the same species as in the previous cores) on the surface. In both cores approximately 20% of the surface was covered with *Odontoschisma sphagni*. Core CM2 was dominated by *Sphagnum capillifolium* (Ehrh.) Hedw. with a few stems of *S. papillosum* plus scattered plants of *Calluna vulgaris*, *Eriophorum angustifolium* Honck., *Erica tetralix* L., *Molinia caerulea* (L.) Moench. and *Rhynchospora alba* (L.) Vahl. Cores CM6 and CM7 were only 20 cm apart. Both had dominant *S. magellanicum* and the same vascular plants, with the addition in CM7 of *Juncus acutiflorus* Hoffm. and *Drosera rotundifolia* L. In CM7 leafy liverworts were conspicuous and abundant on the surface; in CM6 they were inconspicuous. The water table was at 3 cm (CM1, CM4), 5 cm (CM2) and 6 cm (CM6, CM7) below the surface.

The Woodfield cores (WF1, WF2) were cut from beneath a stand of mature *Calluna vulgaris* 30–40 cm tall and with approx. 60–80% cover. It is important to note that the area had been cut for peat over 20 years previously. The exposed *Sphagnum* peat had recolonized but there is no live *Sphagnum* today. Beneath the *Calluna* canopy was a continuous bryophyte carpet dominated by *Kurzia pauciflora* and *K. sylvatica* with small quantities of other hepatics (approximately 15% cover) and the mosses *Dicranella heteromalla* (Hedw.) Schimp., *Campylopus paradoxus* Wils., *C. introflexus* (Hedw.) Brid., *Pohlia nutans* (Hedw.) Lindb. and *Hypnum jutlandicum* Holmen & Warncke (approximately 20% cover). The water table was deeper than 40 cm below the surface. There was standing water in an old peat cutting approximately 1.5 m below and 10 m from the core sites.

RESULTS

The results of these experiments cannot easily be analysed by the usual statistical procedures because the differences between cores are often qualitative. But repeating patterns of behaviour do reveal themselves in Figures 1–7. All five Cranesmoor cores

(Figs 1–5) produced extensive regeneration of *Sphagnum*. The patterns of *Sphagnum* regeneration were much the same in CM2 and CM7 as in those previously reported (Clymo & Duckett, 1986). In each case several vascular plants appeared together with fern gametophytes.

The patterns of hepatic regeneration were broadly similar for all five cores, even those where hepatics were scarce on the surface (Figs 1–3). In many cases there were fewer hepatic shoots in the top slab of those cores which contained actively growing *Sphagnum capitula*, than in those immediately below. This was especially striking where the hepatics in question were not recorded at the surface. For example *Cephalozia connivens* (Dicks.) Lindb. in Figures 1, 4 and 5; *C. bicuspidata* in Figures 2 and 3, *Cladopodiella fluitans* in Figures 3–5, and both *Kurzia pauciflora* and *Odontoschisma sphagni* in Figure 3. In some cores over 50 separate shoot systems of each species were picked off the peat slabs from the upper 10–12 cm. On slabs below this level the number of shoots declined. The maximum depths from which each species regenerated ranged from 10–24 cm for *Cladopodiella fluitans*, 9–24 cm for *Kurzia pauciflora*, 12–23 cm for *Odontoschisma sphagni*, 6–15 cm for *Cephalozia bicuspidata* and 3–12 cm for *C. connivens*.

The cores from Woodfield Bog (Figs 6, 7) produced the same general patterns of regeneration for *Cephalozia bicuspidata*, *C. connivens*, *Kurzia pauciflora* (and presumably *K. sylvatica* (Evans) Grolle: both species were identified from perianths in the surface layers of both the Woodfield cores but no attempt was made to identify the regenerating shoots to the species level). Two species of *Odontoschisma* were found: *O. sphagni* in WF1 and *O. denudatum* (Mart.) Dum. in WF2. Their behaviour was similar. From both cores the top 12–15 cm produced an abundance of new shoots of all these species. Shoot abundance declined below this depth with the last records at 33 cm for *Kurzia* spp., 21 cm for *Cephalozia bicuspidata*, 18 cm for *C. connivens*, 21 cm for *Odontoschisma denudatum* and 27 cm for *O. sphagni*.

The behaviour of the other five hepatics *Lophozia ventricosa* (Dicks.) Dum., *Barbilophozia floerkii* (Web. & Mohr) Loeske, *Calypogeia fissa* (L.) Raddi, *Lophocolea* sp. and *Riccardia latifrons* (Lindb.) Lindb. was very different. The number of stems which regenerated was greatest in the surface slab and declined rapidly with depth, disappearing below 9 cm.

In contrast to Cranesmoor no *Sphagnum* plants appeared on the core slabs (made up mainly of *Sphagnum imbricatum* Hornsch. ex Russ. peat) but fern gametophytes and mosses were noted in the top 6 cm and shoots of *Calluna* down to 15 cm. We do not know whether *Calluna* originated from shoots or from seeds.

Figures 8 and 9 illustrate the morphology of the

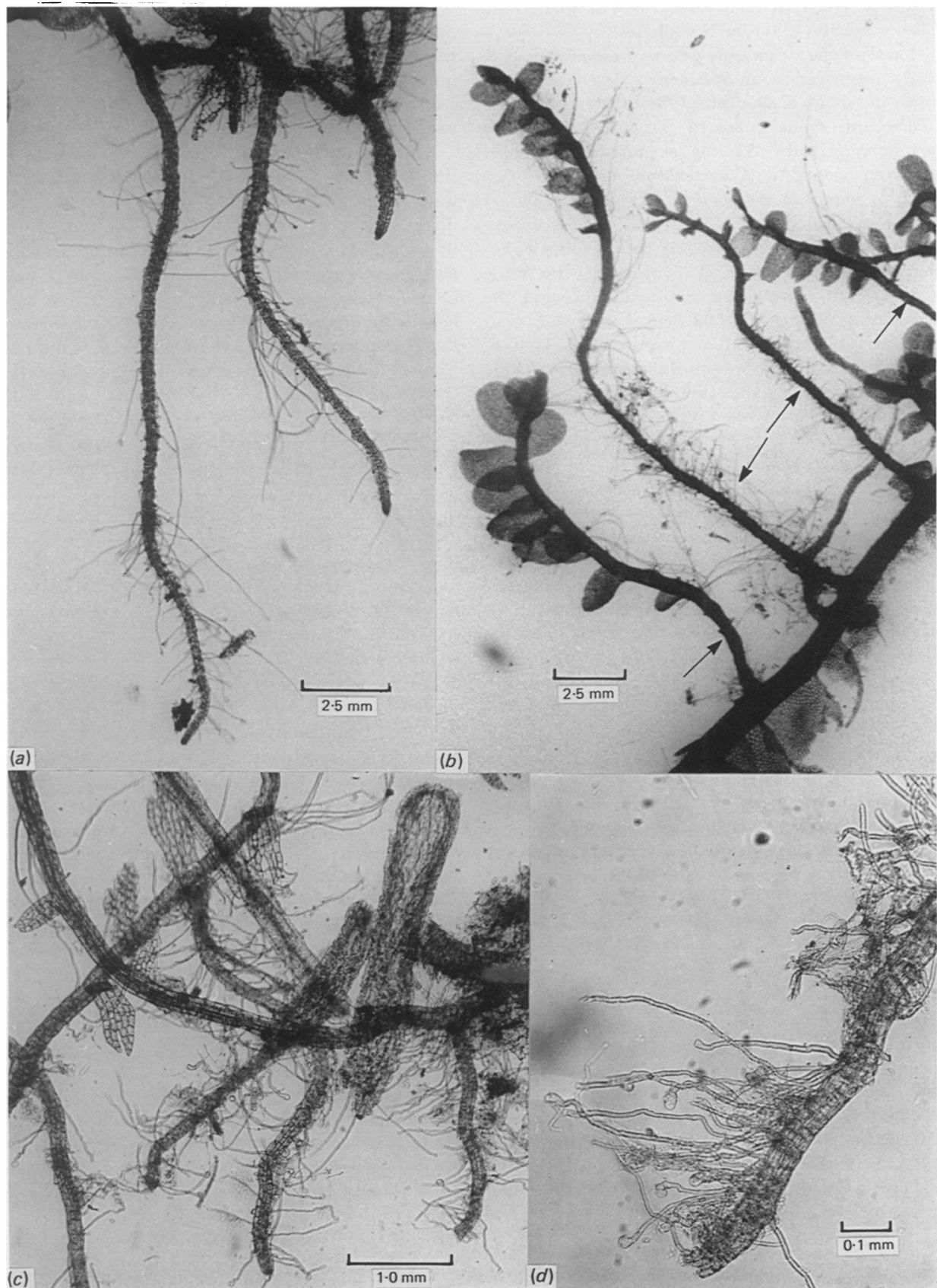


Figure 8. Photomicrographs of regenerating bog hepatics. (a, b) *Odontoschisma sphagni*. (a) Radially symmetrical flagellar branches bearing numerous rhizoids; from 18 cm below the Woodfield Bog surface, $\times 6$. (b) Leafy shoots regenerating from flagellar branches; (arrowed); from 3 cm below the Cranesmoor Bog surface, $\times 5.5$. (c-d) *Cladopodiella fluitans*. (c) Leafless shoots with numerous rhizoids; from 9 cm below the Cranesmoor Bog surface, $\times 18$. (d) The tip of a leafless shoot bearing numerous rhizoids with swollen tips, $\times 85$.

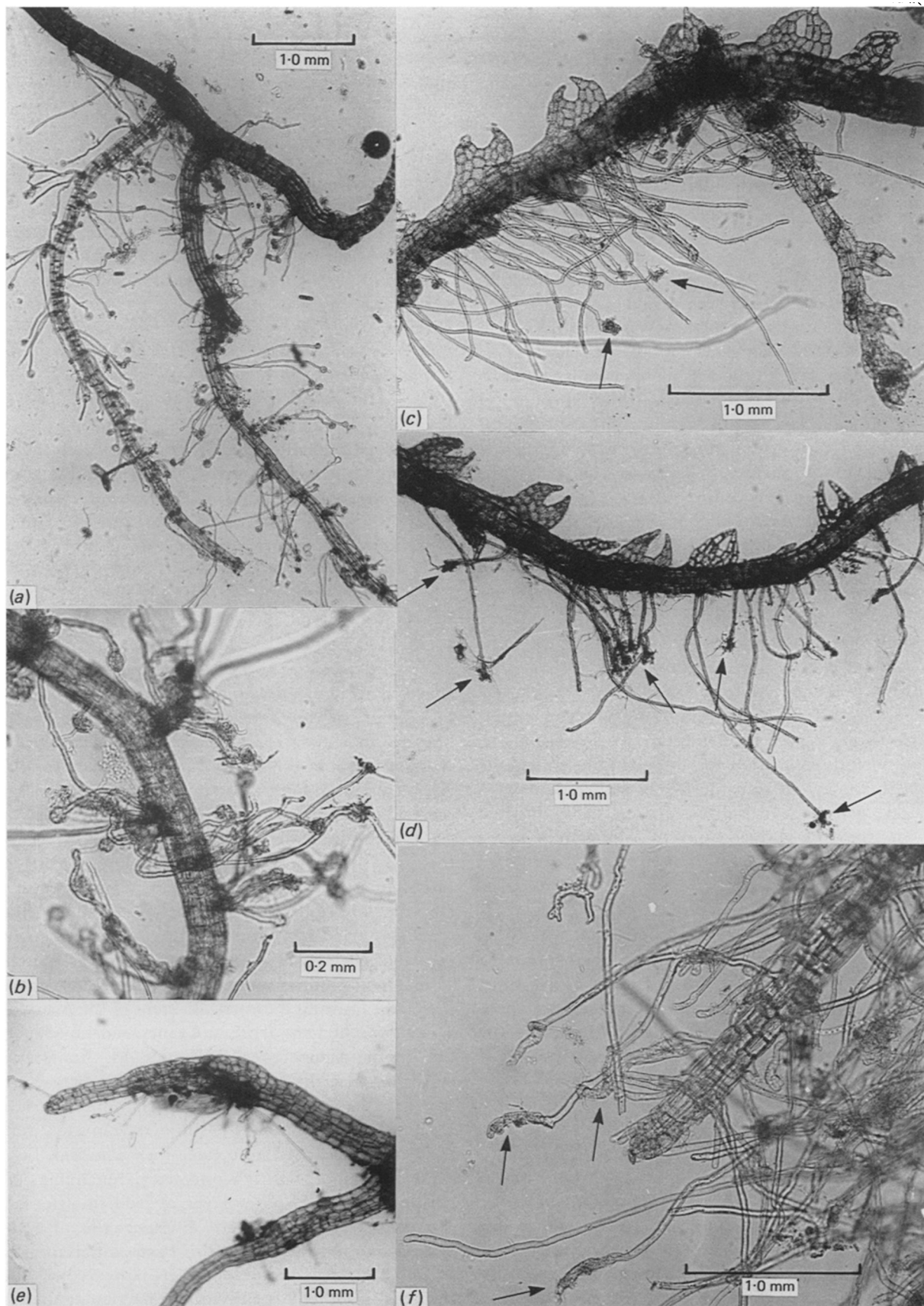


Figure 9. Photomicrographs of regenerating bog hepatics. (a, b) *Kurzia pauciflora*. (a) Axes with widely spaced rudimentary leaves bearing fascicles of swollen-tipped rhizoids; from 18 cm below the Cranesmoor bog surface, $\times 18$. (b) Swollen-tipped rhizoids packed with fungal hyphae, $\times 65$. (c) *Cephalozia connivens*, shoots regenerating from 12 cm below the Cranesmoor bog surface. Some of the rhizoids have swollen, fungus-filled tips (arrowed), $\times 28$. (d-f) *Cephalozia bicuspidata*. (d) Shoot regenerating from 15 cm below the Woodfield Bog surface bearing normal leaves and rhizoids with swollen fungus-filled tips (arrowed), $\times 21$. (e) Leafless axes from 18 cm below the Woodfield Bog surface, $\times 16$. (f) Tip of an axis from 15 cm below the Cranesmoor bog surface bearing numerous rhizoids, some with fungus-filled tips (arrowed), $\times 32$.

subterranean axes and regenerants of *Odontoschisma*, *Cladopodiella*, *Kurzia* and *Cephalozia*. In *Odontoschisma* (Fig. 8a, b) *Cladopodiella* (Fig. 8c, d) and *Cephalozia* (Fig. 9e, f) the subterranean axes are leafless and radially symmetrical but in *Kurzia* (Fig. 9a, b) they bear widely spaced rudimentary leaves. All the axes produce numerous rhizoids many of which have swollen, fungus-containing tips.

DISCUSSION

These results show that several peat bog hepatics possess remarkable powers of regeneration; from two highly contrasting sites new shoots were produced from peat from depths down to 30 cm. We will consider in turn the various questions raised by these results. What is the origin of the regenerants? Why do some species regenerate from depths of as much as 30 cm while others are limited to slabs much nearer the surface. What factors determine the lower limits of regeneration? What are the ecological implications of our findings?

Of the species which appeared on slabs from depths of 20–30 cm *Kurzia pauciflora*, *K. sylvatica*, *Odontoschisma sphagni* and *Cephalozia connivens* are known to possess an extensive system of underground axes (Pocock & Duckett, 1985a). The Woodfield peat surface, exposed as a result of peat cutting, was much more ancient than the native bog surface from Cranesmoor yet both produced similar patterns of hepatic regeneration. We infer that the most likely explanation for these results is that the new shoots came from these axes rather than from spores, gemmae or bulbils (Paton, 1986) washed down from the surface or from a long-lived spore bank (see discussion in Clymo & Duckett, 1986).

The much more restricted regeneration of vascular plants and fern gametophytes at Woodfield is consistent with this argument as plants of these groups probably regenerate mainly from seeds or spores, and these seem unlikely to be washed down below 6–9 cm. The absence of *Sphagnum* protonemata on any of the Woodfield slabs and the absence of other moss protonemata below 6 cm is further circumstantial evidence against washdown. Several species of *Sphagnum* were producing abundant capsules in the immediate vicinity of the Woodfield cores, as were *Camylopus introflexus* and *Pohlia nutans*. The depth of rhizoid penetration probably limited the mosses from Woodfield to the upper peat slabs. The possibility that a high water table is important in maintaining the viability of *Sphagnum* spores still requires investigation.

The similar regeneration patterns of the hepatics which frequently produce spores (*Cephalozia bicuspidata*) and of those whose spore production is infrequent (*Kurzia* spp.) or very rare (*Odontoschisma* spp.) is yet further support for the notion that the new shoots of these species do not derive from spores either preserved in the peat or washed down from

above. Similarly the fact that *Odontoschisma sphagni*, which lacks gemmae, produced the same pattern as the highly gemmiferous *O. denudatum* indicates that the regenerants did not derive from gemmae. *Calypogeia*, *Lophozia* and *Barbilophozia* all produce abundant gemmae but not subterranean axes and their survival was restricted to the surface or immediately subsurface slabs.

To test further the hypothesis that the liverworts regenerated from subterranean axes, peat samples adjacent to the cores were thoroughly soaked out in water and liverwort axes dissected out. Extensive networks were revealed of non-green stems not only of *Kurzia* spp. *Odontoschisma sphagni* and *Cephalozia connivens* but also of *C. bicuspidata*, *Odontoschisma denudatum* and *Cladopodiella fluitans*. Their presence in the last three species was overlooked by Pocock & Duckett (1985a), probably because these axes are extremely fragile and break off at the junction with the leafy stem. They tend to be left *in situ* by normal collecting methods where adherent substratum is kept to a minimum and are thus poorly represented in herbarium specimens, all the more so since these axes do not feature in identification. In water cultures fragments of the subterranean axes rapidly turn green and readily regenerate into leafy shoots (Duckett & Renzaglia, 1988a). The responses of both surface and subterranean axes in relation to gravity and light are being investigated.

A feature of the Cranesmoor cores was the smaller number of shoots of some species of liverwort in slabs containing actively growing *Sphagnum* capitula when compared with those immediately below. The most likely explanation for these results is that the capitula produce allelopathic chemicals which inhibit the growth of other plants including *Sphagnum* protonemata (Clymo & Duckett, 1986). With a labyrinth of axes already present beneath the surface it is easy to visualize in this context why decaying or damaged *Sphagnum* is rapidly overrun by hepatics.

The height of the water table can be eliminated as the factor limiting the vertical extent of the liverwort axes: it was at 5 cm depth at Cranesmoor, but below the depth of the cores at Woodfield. Anatomical constraints on the translocation of assimilates from the surface would appear to be much more critical. It is quite remarkable that the subterranean axes attain the lengths recorded here since they comprise but a central group of slightly elongated parenchyma cells surrounded by an outer layer of isodiametric cells (Schuster, 1966; Duckett & Renzaglia, 1988b). There is no indication that this tissue differentiation in relation to conduction even approaches that recorded in other bryophytes. In particular there is nothing resembling the central strand of highly elongated cells in the underground organs of Calobryales (Grubb, 1970; Héban, 1977, 1979; Schofield & Héban, 1984). Labelling experiments on assimilate movement through these apparently unspecialized parenchyma cells would be of interest.

Such investigations must however take account of the fact that all the bog species with subterranean axes belong to the small group of hepatics in which swollen-tipped rhizoids are most highly developed, namely Lepidozioideae, Cephalozioideae and Odonotoschismatoideae (rhizoids are absent from calobryalean roots).

Associated with these rhizoids are ascomycetous fungi (Duckett & Renzaglia, 1988*a*) whereas the mycobionts in other Jungermanniales (including *Lophozia* & *Barbilophozia*) are basidiomycetes (Pocock & Duckett, 1985*b*). The cytology of the fungus–rhizoid associations is reported elsewhere (Duckett & Renzaglia, 1988*a*) but it should be noted that they have several similarities with ericoid mycorrhiza. The notion that the hepatics may be acting as alternative host to ericaceous shrubs for the mycorrhizal fungi – with attendant possibilities for lateral movement of assimilates – may explain the remarkable penetration of axes lacking well developed conducting elements. The bulk of the biomass of these liverworts appears to be in underground axes and this adds credence to the suggestion that they may be receiving organic assimilates from their associated fungi (Pocock *et al.* 1984) – either indirectly from ericaceous vascular plants or directly from the breakdown of organic matter in the substratum. This possibility of partial parasitism on ascomycetous fungi by bog hepatics invites further investigation. It is interesting that Wallén (1986) has shown that in a subarctic peat bog as much as 95% of new biomass of the vascular plants *Andromeda polifolia* L., *Empetrum hermaphroditum* Hagerup and *Rubus chamaemorus* L. appears below-ground, though there is no suggestion that this is not-all produced by the above-ground leaves of these species.

We do not know the extent to which the underground axes have grown downward, like roots. If they are simply old axes left *in situ*, as the source of many of the *Sphagnum* regenerates seems to be (Clymo & Duckett, 1986), then some of the older ones at Cranesmoor seem to be at least 10–40 years old. This is a rather astonishing age for such a fragile tissue. The Woodfield cores were from a cut peat surface however, and in this case the liverworts' axes must have grown down from above.

We suggest that other species with swollen rhizoids and subterranean axes such as *Cephalozia leucantha* Spruce, *C. loitlesbergeri* Schiffn., *C. macrostachya* Kaal. *Kurzia trichoclados* (K. Muell.) Grolle and *Cladopodiella francisci* (Hook.) Buch ex Jørg. – a species whose creeping and leafless axes are specifically noted by MacVicar (1926) – will have similar regenerative capabilities to those recorded here. In montane rain forest in the tropics, where the hepatic carpet often exceeds 1 m in depth (Duckett, unpublished observations), species with swollen rhizoids on largely leafless achlorophyllous axes are

particularly numerous (Pocock *et al.*, 1984). It may be that in such habitats subterranean axes develop to a much greater extent than they do in acidic bogs at higher latitudes.

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