Response surfaces of plant species along water-table depth and pH gradients in a poor mire on the southern Alps (Italy)

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Response surfaces along gradients of water-table depth and water pH were obtained for the commonest vascular and bryophyte species in a nutrient-poor mire on the southern Alps of Italy. Depth to the water table was the major factor, whereas the chemical gradient was of lower importance in structuring vegetation. The distributional pattern of vascular plants is considered to be determined by physiological tolerance along the gradient in depth to the water table. Hence, interspecific competition in the field layer is considered of minor importance, except for interactions between ericaceous shrubs. Bryophytes probably interact to a greater extent, especially in lawns and carpets. *Sphagnum* species appear to be better competitors, as they almost totally exclude other mosses from those habitats. Interactions between species mainly result in dominance patterns, rather than in a clear habitat partitioning along the water-table gradient. Strong dominance by single species rather than clear habitat partitioning along the water-table gradient is interpreted as a result of interactions between species. Species showing ruderal traits are more typical of wet habitats (carpets and hollows), where disturbance is likely to play a major role in structuring the vegetation in the bottom layer.

Key words: depth to the water table, environmental gradients, nutrient-poor mire, pH, response surfaces, southern Alps, species interactions

INTRODUCTION

Numerous studies of peatland vegetation indicate that water chemistry, depth to the water table and shade are the main factors controlling the local species distributions and the vegetation patterning (Sjörs 1948, 1950, Malmer 1962, Sonesson 1970a, Økland 1989a). Climate plays an important role at a regional scale in limiting the geographic distribution of species (Gignac & Vitt 1990, Glaser 1992) and the development and distribution of different mire complexes (Eurola 1962, Damman 1977).

The rank of single environmental gradients by importance to vegetation varies between areas and between studies, as determined by local conditions and the scale used for the study. Fine-scaled studies in ombrotrophic and weakly minerotrophic peatlands have emphasized gradients in depth to the water table and biotic interactions (Rydin 1986, Økland 1990a) while climatic gradients may be important on regional scales (Økland 1989b, Glaser 1992).

In general, depth to the water table and water pH are frequently used to describe the local distribution of peatland species, owing to the high proportion of variation in species abundance generally explained by these factors (Jeglum 1971, Vitt *et al*. 1975, Vitt & Slack 1975, Gerdol 1990, Vitt & Chee 1990).

The response curves for plant species have usually been drawn separately with respect to each gradient (Slack *et al*. 1980, Andrus *et al*. 1983, Vitt & Slack 1984, Økland 1986a, Gignac 1992, Gerdol & Bragazza 1994), although the relationships between coenoclines and the underlying ecological gradients have received much attention in recent works (Malmer 1986, Økland 1990a).

Nonetheless, a true multi-gradient approach has rarely been employed in peatland ecology. Recently, a multi-gradient analysis was addressed to draw response surfaces for mire bryophytes along climatic and ecological space at a regional scale, i.e. over broad areas (Gignac *et al*. 1991a, Gignac *et al*. 1991b).

In this study we aim at constructing species response curves along gradients in depth to the water table and water pH, using data on the distribution of plant species in a single mire. Our main objective was to determine the suitability of a multi-gradient approach for acquiring information about the local distribution and the niche relationships of plant species.

MATERIAL AND METHODS

Study area

The study site, Stallner Lacke or Stallner Loch, is located on the Sarntaler Alpen (Monti Sarentini), province of Bozen (Bolzano), northern Italy, at 1 720 m above sea level. The climate is temperate-continental with a mean annual temperature of 4.3˚C, a mean temperature of the coldest month (January) of – 3.2˚C, a mean temperature of the warmest month (July) of 14˚C and an average annual rainfall of 909 mm. Precipitation usually peaks in late spring–early summer.

Mire morphology and vegetation

The study site is a ca. 1.5 ha wide nutrient-poor mire, located on a saddle, showing a very gently sloping surface from the East to the West. The mire has an elliptic shape with the main axis ca. 200 m long and the longest secondary axis ca. 60 m wide (Fig. 1). Peat depth along the main axis varies from 0.5 m in drier parts up to 8 m in wetter parts.

The mire can probably be typified as a very weakly minerotrophic fen. Five main vegetation types were recognised on this mire by Gerdol *et al*.(1994).

1) Marginal forest, partly covered by a tree layer of Norway spruce (*Picea abies*), developing over a shallow peat layer. Typical species are *Vaccinium myrtillus, V. uliginosum, V. vitis-idaea, Avenella flexuosa, Polytrichum commune, Dicranum scoparium* and *Sphagnum nemoreum*.

2) *Sphagnum nemoreum* high hummocks, restricted to the upslope dry part of the mire. Typical species are *Calluna vulgaris, Vaccinium vitis-idaea, V. uliginosum, Eriophorum vaginatum, Sphagnum nemoreum* and *Polytrichum strictum*.

3) *Sphagnum magellanicum* low hummocks covering large areas in the central part of mire. Typical species are *Carex pauciflora, Eriophorum vaginatum, Sphagnum magellanicum, S. fallax, S. russowii* and *Calliergon stramineum*.

4) *Sphagnum compactum* carpets occupying the central areas with shallow peat. Typical species are *Trichophorum caespitosum, Carex rostrata, Eriophorum vaginatum, Sphagnum compactum* and *Cladopodiella fluitans*.

5) Pools and hollows in the downslope wet part of the mire. Typical species are *Carex rostrata, C. limosa, Scheuchzeria palustris, Sphagnum subsecundum* and *Drepanocladus fluitans* (Fig. 1).

The climax vegetation of the surrounding area consists of Norway spruce forests.

Sampling design

At the beginning of the 1991 vegetative season, 170 sampling sites were established along one longitudinal transect, corresponding to the long axis of the mire, and fifteen transversal transects. The sampling plots were randomly placed along each transect. At each plot a perforated polyvinylchloride tube (inner diameter 14 mm, wall thickness 2 mm) was inserted into the peat. The apex of every tube was placed at the level of the mire surface. Eighty-one more sites were established in 1993. These were subjectively selected, after a preliminary survey of vegetation based on the 1991 data (see below), in order to provide even coverage of the whole range of variation in vegetation.

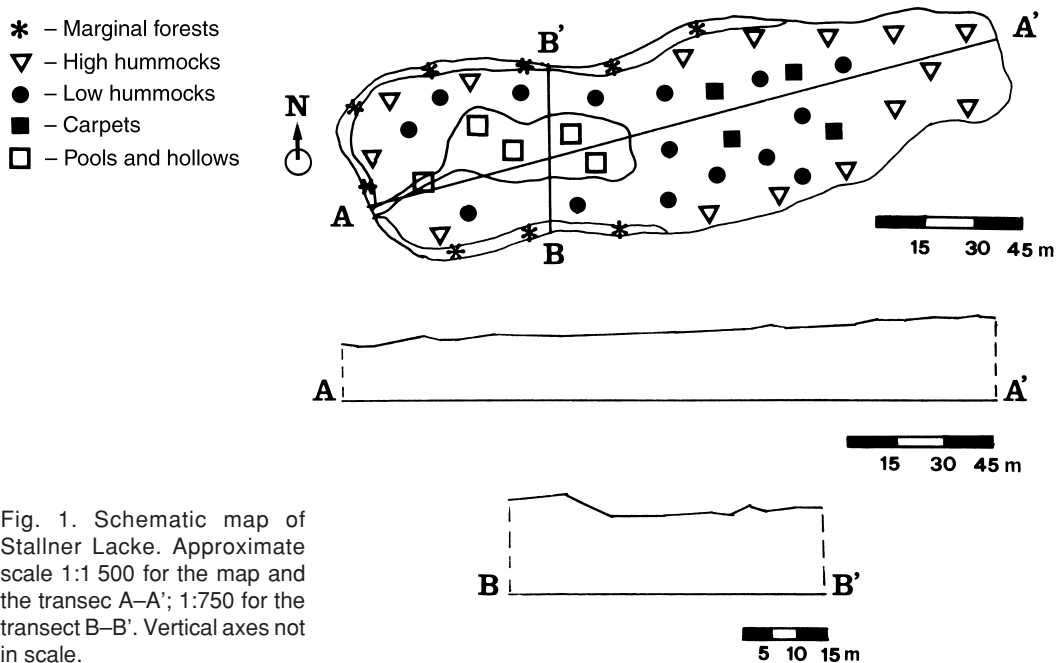The final sampling design thus included a total of 251 sites.

Fig. 1. Schematic map of Stallner Lacke. Approximate scale 1:1 500 for the map and the transec A–A'; 1:750 for the transect B–B'. Vertical axes not in scale.

Vegetation sampling

The vegetation of Stallner Lacke was preliminary surveyed during summer 1991. The cover of plant species (both bryophytes and vascular plants) was visually recorded in summer 1993 at each of the 251 sites using squares of 25×25 cm. The following scale, from 1 to 10, was adopted for estimating the cover degree of species: 1 = cover 1–10; 2 = cover 11–20%; 3 = cover 21–30%; 4 = cover 31–40%; 5 = cover 41–50%; 6 = cover 51–60%; 7 = cover 61–70%; 8 = cover 71–80%; 9 = cover 81–90%; 10 = cover 91–100%.

Nomenclature follows Pignatti (1982) for vascular plants and Frahm and Frey (1987) for bryophytes.

Hydrology and hydrochemistry

Depth to the water table in the 170 PVC tubes was measured at intervals of 10 ± 1 days from 21 May to 7 October 1991. The median value of depth to the water table was calculated for every site at the end of the 1991 vegetative season. Water-table depth was measured on a single day in July 1993, at all 251 sites. The 81 additional sites was assigned a median water-table depth equal to the mean of the medians of the tubes having the same water-table depth in July 1993. Indeed, Økland (1989a) showed that fractiles of the cumulative water-table curve can be confidently estimated from single measurements. The depth to the water table is always referred to the mire surface. Water pH was determined at all 251 sites immediately after measuring water-table depth, using a portable pH-meter.

Data processing

Only the species occurring in at least 10% of the sampling sites were included in the data analysis.

Three-dimensional response surfaces were generated along water pH and water-table depth gradients using a gridding process (Gignac *et al.* 1991b). Predicted values at each grid node were calculated as distance-weighted means of all observed values within a predetermined radius around each node, after removing outliers. The water-table depth axis was rescaled to 20 grid nodes and the pH axis to 10 grid nodes. For both gradients, a search radius of 2 was used to calculate distance-weighted averages at each grid node. A BASIC program was developed for the calculations.

RESULTS

Ecological space and interpretation of gradients

The ecological space represented in our study as a combination of median depth to the water table, rang-

ing from + 8 to – 72 cm, and water pH, ranging from 3.2 to 5.2 (Figs. 2–21), is representative of conditions normally found in nutrient-poor mires of the north-temperate and boreal regions (Jensen 1961, Malmer 1962, Sonesson 1970b, Damman & Dowhan 1981, Reinikainen *et al.* 1984, Galten 1987).

The water-table gradient can be interpreted as a complex-gradient (*sensu* Økland 1992), since water acts as a resource which can limit plant growth at the dry end of the gradient (Austin 1980) but, on the other hand, an excess of water may inhibit growth and increase plant mortality due to waterlogging (Backéus 1985).

The pH per se is unlikely to appreciably influence mire vegetation, at least within the range sampled in this study, but there is much evidence that nutrient availability usually increases with pH (Sjörs 1952, Daniels 1978, Glaser *et al.* 1981, Wells 1981). Therefore, we can reasonably interpret the gradient underlying the pH axis in terms of nutrient status.

When analysing data on species composition by multivariate techiniques, depth to the water table appeared as the main factor influencing the vegetation of poor mires (Singsaas 1989, Økland 1990a). The poor-rich gradient plays a much greater role when the analysis is extended to moderate and rich fens (Edlinger & Hegger 1984, Vitt & Chee 1990, Gerdol 1995).

Shape of response curves

Vascular plants

Most vascular species exhibit more or less sharply truncated surfaces along the water-table axis, whereas almost all surfaces span the entire range of pH (Figs. 2–12).

Vascular plants are separated into two main groups as regards their response pattern along the water-table gradient. The first group mainly consists of graminoids. *Carex rostrata* (Fig. 2), *C. limosa* (Fig. 3) and *Scheuchzeria palustris* (Fig. 4) are clearly concentrated in the wettest part of the water-table gradient. The response patterns of all three species along the pH gradient are similar to each other, albeit *S. palustris* prefers more acidic habitats than *Carex rostrata* and *C. limosa*. All three species possess root aerenchyma, a common adaptation to fre-

quent waterlogging (Metsävainio 1931). The response surface of *C. rostrata* extends somewhat more towards intermediate depths to the water-table, as a probable consequence of its greater rooting depth.

The fourth graminoid in this group is *Trichophorum caespitosum* (Fig. 5). It also prefers wet habitats but avoids the wettest end of the gradient. *Trichophorum caespitosum* can be found at drier sites, as it has a higher tolerance against desiccation (Persson 1962). In spite of a considerable niche overlap along both gradients, *T. caespitosum* segregates from most graminoids along a third gradient, viz. that associated with peat-producing ability. Indeed, *T. caespitosum* is often well represented at sites with a low rate of peat accretion especially in high-altitude peatlands of central Europe (Gams 1958).

The first group further includes *Drosera rotundifolia* (Fig. 6). It exhibits a general hydrophytic morphology (Firbas 1931), but differs from all of the other vascular species by its insectivorous habit (Stewart & Nilsen 1992).

The second main group of vascular plants includes the ericaceous shrubs, whose response surfaces are clearly centred in the dry part of the water-table gradient. Again, the lower limit of these species along the water-table gradient is related to a well-known set of morpho-physiological adaptations since the associated mycorrhizal fungi do not endure waterlogging (Miller 1982, Lindholm & Markkula 1984, Wallén 1987). The evergreen species *Calluna vulgaris* (Fig. 9) and *Vaccinium vitis-idaea* (Fig. 10) show a unimodal response to pH, with a peak in the central part of the gradient, while the deciduous species *V. myrtillus* (Fig. 11) and *V. uliginosum* (Fig. 12) have a bimodal pattern peaking at the two extremes. This probably is associated with variation along a mire margin–mire expanse gradient. The vegetational variation along this gradient has usually been disregarded in mires of central Europe, mainly because well-preserved mire margins are almost absent in this region (Dierßen & Dierßen 1984, Grünig *et al.* 1986, Steiner 1992). There are, however, some indications that both *V. myrtillus* and *V. uliginosum* are much commoner in shaded sites in the marginal strip, while *V. vitis-idaea* and *Calluna vulgaris* extend deeply into the central open area, as is usually the case in Fennoscandian mires (Malmer 1962, Økland 1989a). The bimodal responses of *V. myrtillus* and *V. uliginosum* along the pH axis can
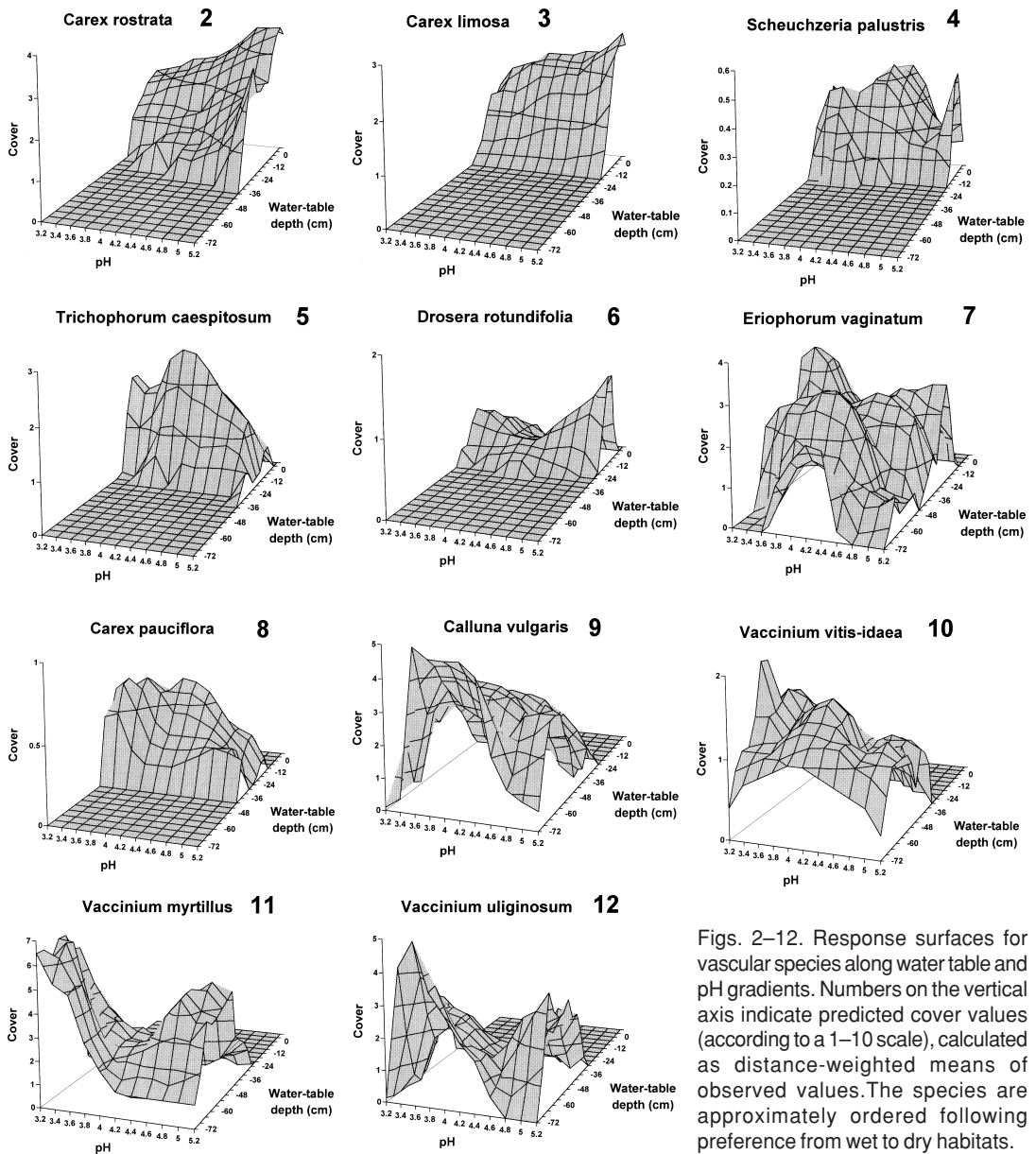
Figs. 2–12. Response surfaces for vascular species along water table and pH gradients. Numbers on the vertical axis indicate predicted cover values (according to a 1–10 scale), calculated as distance-weighted means of observed values. The species are approximately ordered following preference from wet to dry habitats.

be easily explained considering that the combination of intermediate pH and mire margin was not represented among the samples.

Eriophorum vaginatum (Fig. 7) and *Carex pauciflora* (Fig. 8) exhibit symmetric response surfaces compared to all species in the above two groups. Both surfaces span the entire pH range but with a slight peak towards the acid end of the axis. *Eriophorum vaginatum* has the widest surface among all of the vascular plants analysed in our study. This species tolerates both desiccation and waterlogging and possesses a series of physiological adaptations to nutrient deficiency, such as efficient uptake of nutrients under anaerobic conditions (Gore & Urquhart 1966) and a great ability to retain nutrients in storage organs and to allocate them to the growing tillers (Chapin *et al.* 1979, Jonasson & Chapin 1991, Francez 1995). This is likely to be why

E. vaginatum is evenly distributed in nutrient-poor mires, where it covers a wide range of habitats as far as depth to the water table is concerned (Malmer 1962, Økland 1986a).

In contrast, *Carex pauciflora* has a narrower range along the water-table gradient. This is presumably due to interactions with other gradients rather than by physiological limitations related to water balance. *Carex pauciflora* is almost completely excluded from the dry areas of the mire margin (Økland 1989a), presumably owing to low shade tolerance.

Bryophytes

A distinct species group with response surfaces peaking close to the wet end of the water-table gradient can also be recognised among bryophytes. This group includes two species of *Sphagnum*, viz. *S. subsecundum* (Fig. 13) and *S. compactum* (Fig. 14), one moss species (*Drepanocladus fluitans*; Fig. 15) and *Cladopodiella fluitans* (Fig. 16), the only common hepatic in the mire investigated.

The responses of these four species to pH differ rather strongly. *Sphagnum subsecundum*, *Drepanocladus fluitans* and *Cladopodiella fluitans* show unimodal responses, peaking at higher, intermediate and lower pH, respectively. In contrast, *Sphagnum compactum* exhibits a bimodal response pattern along the pH gradient with two distinct peaks at the opposite extremes. *Sphagnum subsecundum* is known to prefer fairly rich sites with relatively high pH and electrolyte concentrations (Andrus 1986). Its lower limit along the pH gradient is unlikely to be set by physiological intolerance against acidity, since this species was found to grow well at low pH in pure culture (Clymo 1973). Interactions with the peat-productivity gradient may determine the sharp contrast between the response of *S. compactum*, on one side, and those of *Drepanocladus fluitans* and *Cladopodiella fluitans* on the other side. *Cladopodiella fluitans* usually reaches highest abundancce in carpets and hollows where disturbance may produce open space sufficiently often to avoid competitive exclusion by more productive species. Such habitats appear also suitable for the moss *Drepanocladus fluitans*, which rarely threatens to bury the hepatic shoots owing to the looseness of its mats. In

contrast, *Sphagnum compactum* generally acts as a colonizer (Økland 1990b). This species often expands, in spite of its low growth rates (Clymo 1973), forming too dense a carpet and thus lowering the vitality of *Cladopodiella fluitans*.

The response surfaces of other *Sphagnum* species are more or less clearly separated from each other along the water-table gradient. All of them cover the whole pH range, although with a peak close to the acid end.

Sphagnum fallax (Fig. 17) and *S. magellanicum* (Fig. 18) are most frequent at relatively low depths to the water table. However, the response surface of *S. magellanicum* declines more gradually towards the dry end of the gradient, whereas *S. fallax* disappears as soon as the median depth to the water table exceeds – 50 cm. By contrast, the surface of *Sphagnum russowii* (Fig. 19) peaks at moderately dry, and that of *S. capillifolium* (Fig. 20) at even drier sites.

A common feature of the response surfaces of all four *Sphagnum* species is their abrupt decline towards the wet end of the gradient. This lower limit is certainly not set by physiological intolerance against flooding since all species exhibit an active growth at higher water levels provided other conditions are optimal (Clymo & Hayward 1982, Rydin & McDonald 1985). Nor is this likely to derive from negative interactions with more productive inhabitants of carpets and hollows, such as *S. cuspidatum* and *S. majus*, since these species do not occur in the mire investigated. A possible explanation for the lack of highly productive *Sphagna* at high water levels resides in the increasing incidence of disturbance from dry to wet habitats, as will be further discussed below.

Polytrichum strictum is most abundant on hummocks but is fairly common also in wetter areas (Fig. 21).

DISCUSSION

Ecological studies dealing with species performance along environmental gradients, as well as with niche dimension and niche overlap, have often led to inferences about interspecific relationships such as habitat partitioning and competition. Species interactions in peat-forming systems have usually been analysed taking into sepa-
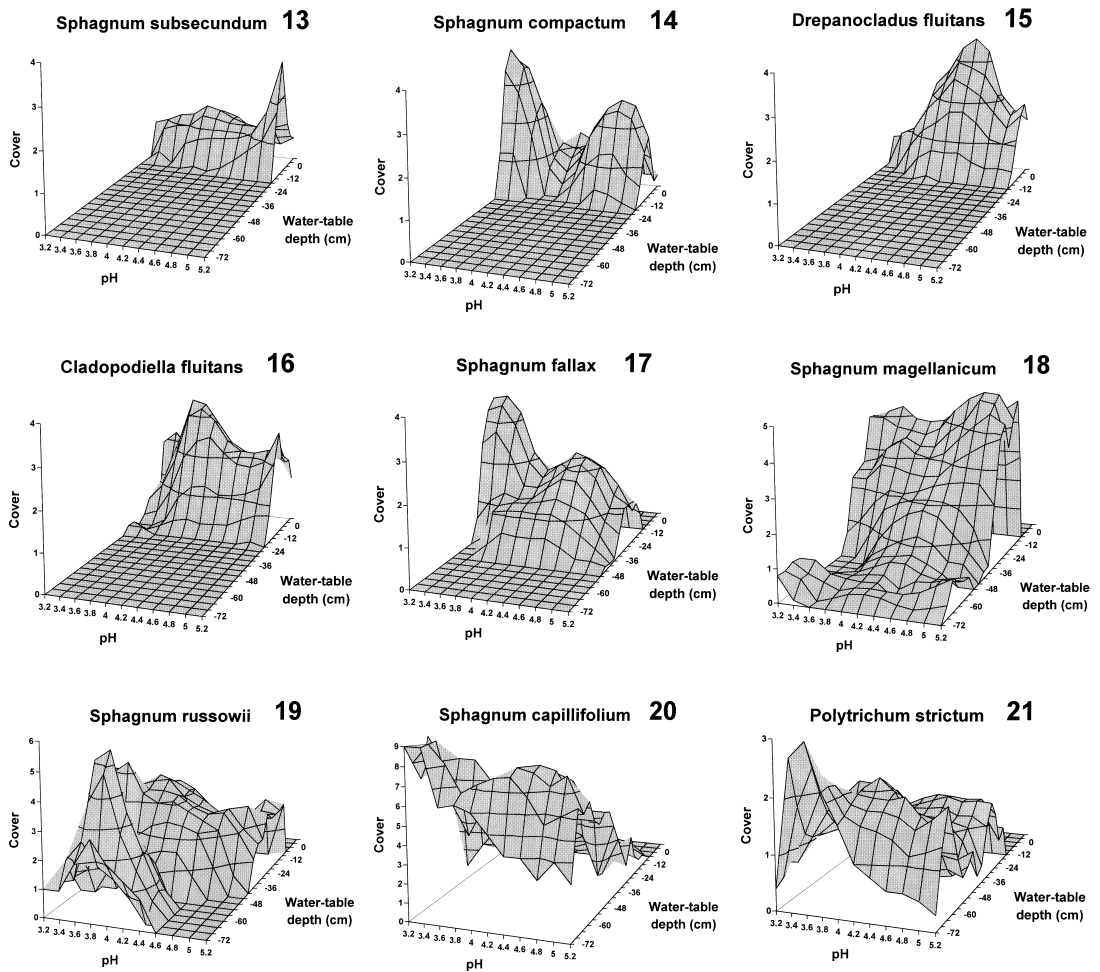
Figs. 13–21. Response surfaces for bryophyte species along water table and pH gradients. Numbers on the vertical axis indicate predicted cover values (according to a 1–10 scale), calculated as distance-weighted means of observed values. The species are approximately ordered following preference from wet to dry habitats.

rate accounts the vascular species in the field layer and the bryophyte species in the bottom layer since interactions between species in different strata are considered unimportant (Økland 1990b). A similar approach was adopted in this paper, although some of our results suggest that significant interactions may occur in some cases between mosses and vascular plants.

The majority of vascular plants and bryophytes exhibited narrower response curves along the gradient in depth to the water table than along the pH gradient. At first sight, this would seem to support the idea that chemical gradients are of relatively scarce importance in nutrient-poor mires

(Karlin & Bliss 1984). However, as niche breadth is conditioned by the scaling of axes (Økland 1986b) there is no way of comparing in terms of compositional turnover the water-table and the pH axes when these are scaled in units of physical and chemical variables.

The sharp limits of the response curves of vascular plants towards the central part of the water-table gradient, as well as the grouping of these species into two main functional groups (xerophytes vs. hygrophytes) indicate that their distribution is mainly set by physiological tolerance, favoured by morpho-physiological adaptations either to drought stress or to waterlogging. The broad niche overlap

among hygrophytes indicates a low degree of mutual interactions (Lindholm 1980, Økland 1990b). *Drosera rotundifolia* avoids competition by exploiting a resource not available to the other vascular species. The response surface of *D. rotundifolia* largely coincides with those of peat mosses rather than with those of other mosses over its whole range of depth to the water table. This probably reflects some positive interactions between plants in different strata, since *D. rotundifolia* may benefit from the water-conducting capacity of *Sphagnum* mosses for its water supply (Malmer *et al.* 1994).

The niche segregation of ericaceous shrubs along the pH gradient is at least partly determined by variation along correlated gradients, as discussed in detail above. However, experimental evidence obtained by neighbour removal experiments, showed that growth of evergreen species, such as *Vaccinium vitis-idaea*, may be limited by competition with more productive deciduous species, such as *V. uliginosum* and *V. myrtillus* (Shevtsova *et al.* 1995).

The overlap of bryophyte response surfaces is much greater at the wet extreme of the gradient in depth to the water table than in the remaining sector of the gradient. This may be due to some ruderal and/or opportunistic traits of the species involved, as already hypothesized by Økland (1990b) at least for *Sphagnum compactum* and *Cladopodiella fluitans*. Such species would benefit from an increasing probability of disturbance in the bottom layer from hummocks to hollows (Økland 1989b). In contrast, the higher parts of the water-table gradient are mainly characterized by *Sphagnum* species. Their optimal responses along the water-table gradient are more or less clearly segregated but most of them have rather broad response surfaces, with a considerable degree of mutual overlap. This need not contrast with previous findings, considering at least lawn *Sphagna* as efficient competitors as indicated by their narrow niches along environmental gradients, with a low degree of mutual overlap (Gignac 1992). Indeed, lawn species showed a poor overlap when habitat niche breadth was recorded in units of compositional turnover, the latter being much stronger at the wet end than at the dry end of the water-table gradient (Økland 1986b, 1990b, 1992).

The extent to which competition is effectively involved in determining the distribution of bryophytes cannot be exactly evaluated on the basis of this study. It seems, however, that at least competition for space does play an important role since bryophytes often achieve 100% cover in the bottom layer (Rydin 1993). Competition may result in dominance patterns along the water-table gradient, more productive peat-moss species in the sections *Sphagnum* and *Cuspidata* being enhanced at habitats not subject to prolonged desiccation. Indeed, up to six species were found within one plot. This may even reflect a protocooperation (Li *et al.* 1992), such as in the case of isolated individuals of *Sphagnum fallax* and *S. magellanicum* growing within a matrix of *S. capillifolium* on hummocks (Lange 1969, Rydin 1985), where they benefit from the superior capillary conduction and reduced evaporation loss of the latter species (Titus & Wagner 1984).

True mosses seem to be outcompeted by the more productive peat mosses along the largest part of the water-table gradient, viz. from lawns to hummocks. *Polytrichum strictum* is the only moss species frequently growing intermingled with *Sphagna* owing to its ability to keep pace with the upward growth of peat mosses.

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