Distribution of biomass along hummock-hollow gradients: A comparison between a North American and a Scandinavian peat bog

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Abstract

This is an attempt to illustrate the universality of cause and effect of the plant interactions in hummock formation. Two bogs, both situated within boreonemoral zone, with comparable structure, but within completely different flora regions, were chosen to test whether the hummock-hollow structures on the surface were functionally comparable. In spite of different history of mires, it was obvious that the mire hummocks were clearly a product of the interactions between *Sphagnum* mosses and vertically growing dwarf shrubs. The height of the hummocks on the Meddybemps heath, was probably an effect of the comparatively high productivity of both mosses and dwarf shrubs resulting from nutrient enrichment by fire. The high hummocks were associated with a higher amount of biomass of vertically growing dwarf shrubs. Both sites on the Meddybemps heath had twice as much biomass as the Åkhult mire.

Key words: bogs, hummock formation, hummock-hollow structure, biomass

INTRODUCTION

The hummocks and the hollows on a bog surface form rather constant patterns in time, characterizing all ombrotrophic peat forming systems within the boreal and boreonemoral zone (Walker and Walker 1961, Barber 1981, Svensson 1988). This means that peat formation, measured as the volumetric growth rate, must take place at the same rate over most of the bog surface and be independent of the pattern of hummocks and hollows. Further, the rate of peat formation is much more depending on the decay of the peat litter and the consequent change in hydrodynamic properties of the peat, than of the productivity of the surface (Damman 1979, Clymo 1984).

As the plant litter forming the peat decomposes, it gradually loses its structure and the spaces between its plant remains become smaller (Johansson 1987). Consequently the capillary forces acting within the peat increase. A decrease in size of the spaces between the components of the peat, is related to an increase of the hydraulic conductance with approximately the fourth power. The runoff from this compacted peat is thus markedly hampered, and the water table tends to rise. Thus the degree of breakdown of the plant tissue is more or less directly responsible for regulating the ground water level of the bog, and consequently, the border between the upper, aerobic acrotelm and the lower, anaerobic catotelm (Ingram 1978). The position of this limit may affect the development of different ombrotrophic bog types. There is a clear change in height and shape of raised bogs, and a clear change in frequency, shape and size of hummocks and hummock strings, as well as hollows and hollow pools, from oceanic to more continental climatic conditions (Gränlund 1932, Euröla 1962, Dammann 1977, Sjörs 1983). There are, however features on peat bogs that appear to be primarily the result of interactions between plants growing on the surface, and only secondarily are dependent on hydrology. These are the hummocks and the hollows, when randomly distributed, star- or net like microtopographic structures, but not the hummock ridges perpendicular to the slope of the bog, or the pools and flarks which are supposed to be hydrologically conditioned.

Randomly distributed hummocks are the result of two main factors:

- 1) Different *Sphagnum* species decompose with different rates (Clymo 1965), probably mainly due to their varying content of phenolic compounds (Rudolph and Jöhnk 1982).

- 2) The quantitatively most important vascular plants are mainly concentrated to hummocks, as they cannot tolerate anaerobic rhizosphere-conditions. Beside that they double the production of biomass many times over (Wallén et al. 1988) (they contribute with approximately up to 90% of the total production on hummocks), they control the growth of the bottom layer species. They act as "scaffolds" to the growing *Sphagnum* individuals, which allows these to grow in loose cushions. Light can penetrate down to deeper layers and cause sections further down to assimilate, thus increasing the total productivity of the moss layer (Johansson and Linder 1980, Hayward and Clymo 1983). The vascular plants also reasonably create more favourable microclimatic conditions for the mosses, and probably also recirculate mineral nutrients to the moss surface (Malmer 1988). The most important plant group in this context are the ericaceous dwarf shrubs. Different species belonging to this group characterize the hummock vegetation on ombrotrophic peat bogs all over the world.

The present study is an attempt to illustrate the universality of the cause and effect of the plant interactions in hummock formation by examining the vertical distribution of vascular plants along hummock-hollow gradients on ombrotro-

phic bogs. Two bogs, both situated within the boreonemoral zone (Sjörs 1963), with comparable main structure, but within completely different flora regions, were chosen to test whether the hummock-hollow structures on the surface were functionally comparable.

METHODS

STUDY SITE

The Meddybemps heath (45°2'N, 67°23'W) in Maine, USA, is representative of the convex, raised inland bogs of the coastal area along the Bay of Fundy (Dammann 1977). The climate within the area is characterized of an average temperature of the warmest month (July) of 18°C, and of the coldest month (January) of -7°C. The annual precipitation is 1100 mm, and the mean monthly precipitation is more than 60 mm in all months. The mean annual potential evapotranspiration is about 50% of precipitation.

The bog is characterized of several raised areas separated by drainage channels. The bog centre is mainly characterized of *Gaylussacia* — heath, with *Sphagnum fuscum* (Schimp.) Klinggr. dominating the bottom layer and *Gaylussacia baccata* (Wang.) K. Koch and *G. dumosa* (Andr.) T. & G. the field layer. Sparse scrubby individuals of *Picea mariana* (Miller) BSP. and *Pinus strobus* L. occur, often associated with bog pools. The gentle slope (about 1:100) is characterized by a *Kalmia*-heath with *Kalmia angustifolia* L. dominating the field layer and *Sphagnum fuscum* dominating the bottom layer.

The dwarf shrubs of both the *Gaylussacia*- and the *Kalmia*-heaths are concentrated on hummocks, mainly dominated by *Sphagnum fuscum* and *S. rubellum* Wils. in the bottom layer. The depressions in between are characterized by lichens, mainly *Cladonia* species. Accidental fires from the surrounding blueberry barrens are known to occur on the bog, which might be the reason for the relative richness in lichens (Dammann 1977).

The Åkhult-mire is situated within the boreonemoral region, in Götaland, southern Sweden (14°30'E, 57°5'N). The average temperature of the warmest month (July) is 15°C, and of the coldest (February) -3°C. The annual precipitation is 730 mm, with 40–50 mm month⁻¹ during February to May, and more than 60 mm month⁻¹ during rest of the year. The mean annual potential evapotranspiration is roughly 55% of precipitation.

The vegetation of the mire has been monographed by Malmér (1962). It is an eccentrically dome-shaped bog, extending over 0.7 km². The surface of the bog centre and the slopes are characterized by a pattern of randomly dispersed hummocks and hollows. The vegetation can be classified into hummock, lawn, carpet- and mudbottom communities according to Sjörs (1950). The hummocks are dominated by ericaceous scrubs (above all of *Calluna vulgaris* (L.) Hull), *Eriophorum vaginatum* L., *Sphagnum rubellum*, and *Sphagnum fuscum*; the

lawns by *Eriophorum vaginatum* and *Sphagnum magellanicum* Brid.; the carpets and mud bottoms by *Rhynchospora alba* (L.) Vahl. and *Sphagnum cuspidatum* Hoffm.

FIELD METHODS

The field sampling was carried out in September 1983 on the Åkhult mire, and in August 1984 on the Meddybemps heath. On the Åkhult mire seven 2 m long transects, extending from a hummock top to a nearby hollow, were laid out on the bog plain. At 20 cm intervals along the transects the height of the moss surface, and the depth to the water level below was measured in 12 mm diameter pipes. The sampling for the vascular plant above-ground biomass was made within contiguous 20 cm x 20 cm quadrats. The plants were clipped at the moss surface. The moss biomass and the below-ground biomass was sampled with a 10 cm diameter (surface area 0.785 dm²) corer in the middle of each quadrat. The cores were cut into 5-cm thick slices in field.

On the Meddybemps heath two transects from hummock to hollow were laid out, one in the *Kalmia* heath vegetation on the gentle slope of the bog (2.5 m long) and one in the *Gaylussacia* heath vegetation on the central plain area of the bog (2 m long). Both transects were levelled at 25 cm intervals. The above-ground biomass was clipped at the moss surface within contiguous 25 cm x 25 cm quadrats. The below-ground vascular plant biomass and the bottom layer biomass was sampled using a 11.3 cm diameter corer (1 dm² surface area). The cores were cut into 5 cm slices in field.

The living biomass of the bottom layer species was removed from the uppermost sections of the cores. This included the green or reddish upper section of the mosses. The number of individuals of each *Sphagnum* species was counted. From the rest of the sample, as well as from all subsequent lower slices of the cores, all living vascular plant parts were extracted. In the cores from the Åkhult mire these vascular plant below-ground fractions could be divided into species. This was not possible in the cores from Meddybemps heath due to the much greater number of dwarf shrub species there. All fractions, both above-ground and below-ground, were dried at 85°C and weighed.

RESULTS

DISTRIBUTION OF ABOVE-GROUND PLANT BIOMASS

Although similarly distributed on the surface, the hummocks on the Meddybemps heath were distinctly higher than on the Åkhult mire (Fig. 1). The height above the bottom of the hollow varied around 30 cm, while on the Åkhult mire around 20 cm. The horizontal distance from hummock top to hollow was in

both cases about 2 m. Other differences visible in the field were that the depressions on the Meddybemps heath were drier compared to the Åkhult mire. They were mostly dominated by lichens which indicated that the ground-water level was rarely reaching the surface level of the hollows. On the Åkhult mire the mean water table was at level of the surface of the hollow.

Fig. 1. Surface topography within the *Kalmia*-zone on the Meddybemps heath and on the Åkhult mire respectively

The Meddybemps heath was characterized by the dominance of several dwarf shrub species over the entire surface. Only the proportions of the species varied from the hummock tops to the bottom of the depressions. Within the *Gaylussacia*-zone, the hummock tops were dominated by *Gaylussacia baccata* (about 250 g m^{-2}), while *Kalmia angustifolia* and *K. polifolia* Wang., and *Chamaedaphne calyculata* (L.) Moench were rather evenly distributed with c 50 g m^{-2} (Fig. 2). Within the *Kalmia* zone, the two *Kalmia* species were dominating with $100\text{--}200 \text{ g m}^{-2}$ except in the hollows where *Chamaedaphne* was more prominent. *Gaylussacia* was within this zone concentrated in small amounts to the hummock tops.

On the Åkhult mire *Calluna vulgaris* was the only dwarf shrub dominating on the hummocks (Fig. 3). *Andromeda polifolia* L. and *Vaccinium oxycoccus* L. were found over the whole transect, but never in structurally dominating amounts. *Eriophorum vaginatum*, occurred with ca 50 g m^{-2} over most of the bog surface, from the hummock top down to the lawn level. The hollows were mainly free from vascular plants.

Fig. 2. Distribution of above-ground biomass (g m^{-2}) along hummock-hollow transects A — within the *Gaylussacia*-zone, and B — within the *Kalmia*-zone on the Meddybemps heath

Fig. 3. Distribution of above-ground biomass (g m^{-2}) along a hummock-hollow gradient on the Åkhult mire. Mean of transects from seven hummock-hollow gradients

On both of the Meddybemps-sites, *Sphagnum fuscum* dominated the hummock tops, *S. rubellum* the slopes, and in most of the hollows *Cladonia arbuscula* was predominant (Fig. 4). The total assimilating moss biomass on the Meddybemps-site varied between 200 and 300 g m^{-2} (In figure 4, the biomass of lichens is based on the whole lichen mat. This mass is probably not really comparable with the moss biomass.).

Fig. 4. Distribution of bottom layer biomass (g m^{-2}) along hummock-hollow transects within A — the *Gaylussacia*-zone, B — the *Kalmia*-zone on the Meddybemps heath, and C — on the Åkhult mire

On the Åkhult mire there was a shift from *S. rubellum* dominating the hummock tops to *S. magellanicum* dominating the slopes, to *S. cuspidatum* dominating the hollows. The peak assimilating moss biomass, c 100 g m^{-2} was found in the lawn vegetation, while on the hummock top and in the hollow the bottom layer contained about 50 g m^{-2} assimilating moss biomass.

PEAT STRUCTURE

In all peat cores from the Meddybemps heath, except in those from the hummock tops, the bulk density increased downwards, from about 20 g dm^{-3} in the surface peat, to $60\text{--}100 \text{ g dm}^{-3}$. On the hummock tops no marked increase in bulk density down the cores was noted. Below the lichen-covered surface the lowest bulk densities in the surface was about 40 g dm^{-3} . In the *Gaylussacia*-zone there was an almost level horizon with relatively highly-humified peat ($60\text{--}70 \text{ g dm}^{-3}$) (Fig. 5) at a depth of c 10 cm below the level of the hollow. This layer changed abruptly to low-humified peat above which was intermingled with mainly vertically oriented rhizomes and roots. In this highly-humified border zone (marked with arrows in Figs. 5 and 6), the dwarf shrub rhizomes were more or less horizontally oriented, and the peat between the rhizomes was highly-humified and amorphous.

Fig. 6. Vertical distribution of vascular plant biomass (g m^{-2} within 5 cm thick peat layers), and bulk density (g dm^{-3}), at 25 cm intervals along a hummock-hollow gradient within the *Kalmia* zone on the Meddybemps heath

The vascular plants appeared to be rooted at this level and from there extend upwards through the moss litter and living moss surface above. This highly-humified layer seemed to extend to the bottom of most of the cores. In the *Kalmia*-zone a corresponding highly-humified layer with bulk densities exceeding 100 g dm^{-3} occurred below the surface, however it was not level but roughly followed the undulating surface pattern (Fig. 6). In both of the transects from the Meddybemps heath, the peat above the high-humified layer consisted of litter of the *Sphagnum* species dominating the surface vegetation.

Fig. 7. Vertical distribution of vascular plant biomass (g m^{-2} within 5 cm thick peat layers), and bulk density (g dm^{-3}), at 20 cm intervals along a hummock-hollow gradient on the Åkhult mire. Mean of seven transects

On the Åkhult mire, there was also a clear boundary between the rather loose, low-humified peat litter overlaying an amorphous, dense, peat (Fig. 7). However, this layer was not as well-defined as on the Meddybemps heath, especially not with respect to the orientation and structure of the vascular plant rhizomes and roots. Nor did it show any traces of charcoal.

DISTRIBUTION OF THE BELOW-GROUND BIOMASS

The vertical distribution of the below-ground biomass in the two transects on the Meddybemps heath mirrored mainly the main structure of the peat, and not so much the above-ground biomass. Above the dense peat layer, each 5 cm peat layer contained roughly between 200 and 300 g m⁻² rhizome and root mass, most of it living (Figs. 5 and 6). In the highly-humified layer, the rhizome and root mass increased markedly to c 400 to 700 g m⁻². Below the dense zone the vascular plant mass seemed to decrease again. The share of dead rhizome increased markedly at and below the dense zone.

On the Åkhult mire, in contrast to the Meddybemps heath, the quantity of the below-ground biomass decreased clearly along the transect from hummock top to hollow (Fig. 7). The total below-ground biomass measured within 30 cm depth decreased almost linearly, from c 600 g m⁻² on hummock top to c 30 g m⁻² in hollow. In all cores along the transect, the dwarf-shrubs were quantitatively dominating, especially *Calluna* rhizomes. *Eriophorum* rhizome and root occurred mainly in the cores between 60 and 120 cm from hummock top (roughly 5-10 cm above hollow). In contrast to the Meddybemps-profiles, the living dwarf-shrub rooting systems were concentrated mainly to the uppermost 10 cm of peat. On the hummock top, dead dwarf-shrub rhizome dominated below c 10 cm. Further down along the transect, *Eriophorum* rhizome was more prominent, and in the hollow *Vaccinium oxycoccus* in the surface layers constituted the only vascular plant fraction.

DISCUSSION

The most conspicuous difference in the composition of vegetation between the two bogs in the present study, was the comparative importance of *S. fuscum* on the hummocks and the lack of hollows with lawn and soft-carpet vegetation on the Meddybemps-heath. The bottom-layer was characterized of lichens dominating the depressions, *Sphagnum rubellum* dominating the intermediate zones, and *S. fuscum* dominating the hummock tops. The corresponding zonation on the Åkhult-mire was *Sphagnum cuspidatum*, *S. magellanicum* and *S. rubellum*. The overall reason to these differences can be ascribed the climatic differences between eastern N. Amerika compared to southern Scandinavia (Dammann 1979). However, also differences in recent history of the mires might explain the differences in vegetation-structure.

When planning the field work for this study, no information about the history of the Meddybemps-heath was available. The Meddybemps-heath was thought to be a representative of a more or less virgin inland mire. However, during the analysis of the peat cores it became obvious that the mire surface had been seriously burned not very long ago. The vegetation on the mire surface thus represented a post-fire successional stage. The mire is surrounded by blueberry-barrens, which are burned regularly to increase the blueberry production.

Obviously fire from these burnings spreads accidentally on to the mire. This is probably a regularly recurring even in this type of mires (D a m m a n 1977). The post-fire succession leads to the development of a surface structure of ever increasing sensitivity to fires: towards an accumulation of inflammable dwarf shrub and peat litter material. Mires with similar history and vegetation dynamics are found above all in Scotland, adjacent to areas which are managed by burning.

Both of the mires in the present study revealed similarities in their peat structure: on both mires there was a comparatively high-humified, dense peat layer on about a level with the bottom of the hollows. Although similar in structure, the origin of this layer was quite different. On the Meddybemps-heath this layer indicated a fire-surface, while on the Åkhult-mire it was a result of the breakdown of the peat due to decomposition, and thus constituted the approximate limit between acrotelm and catotelm (C l y m o 1984, M a l m e r and H o l m 1984).

The total number of vascular plant species did differ markedly between the Meddybemps-sites and the Åkhult mire. In spite of that, the total above-ground plant biomass did not differ to any greater extent between the sites. In all transects this biomass decreased from 300–400 g m² on the hummock tops to no above-ground vascular plant biomass in the hollows. The living moss biomass differed however considerably between the three sites, both quantitatively and qualitatively, and there seems to be a strong interaction between the dwarf shrubs and the mosses. In spite of different history of the mires, it was obvious that the mire hummocks were clearly a product of the interaction between the *Sphagnum* mosses (*S. fuscum* and *S. rubellum*) and vertically growing dwarf shrubs. The hummocks were thus reinforced by a perennial, woody framework of roots and rhizomes, which prevented them from settling. Dwarf shrubs with a trailing growth pattern and grasses, do not seem to support the hummocks to the same extent. The height of the hummocks on the Meddybemps heath, was probably an effect of the comparatively high productivity of both mosses and dwarf shrubs resulting from nutrient enrichment by fire. The high hummocks were associated with a higher amount of biomass of vertically growing dwarf shrubs. Both sites on the Meddybemps-heath had roughly twice as much biomass as the Åkhult mire.

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Zróźnicowanie biomasy w gradiencie kępowo-dolinkowym: porównanie torfowisk z Północnej Ameryki i Skandynawii

Streszczenie

Porównano dwa torfowiska leżące w strefie boreonemoralnej, posiadające analogiczną strukturę florystyczną lecz znajdujące się w kompletnie odmiennych regionach florystycznych. Pomimo różnej historii torfowisk okazało się, że ich układ kęp i dolinek jest wynikiem interakcji we wzroście torfowców (zwłaszcza *Sphagnum fuscum* i *Sph. rubellum*) oraz wykazujących pionowy wzrost licznych krzewinek.