THE THERMAL REGIME OF HUMMOCK–HOLLOW COMPLEXES ON CLARA BOG, CO. OFFALY

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ABSTRACT

The thermal regime of the hummock–hollow complexes on Clara bog (Co. Offaly, Ireland) was studied during the summer of 1990 and the winter of 1991 and was found to be mainly dependent on the differences in physical properties of the peat and the interaction with vegetation structure. Differences in specific volumetric heat capacity and thermal conductivity between hummocks and hollows have implications for their thermal behaviour. Their varying thermal responses indicate that hummocks and hollows should be considered as interconnected but simultaneously independent systems. The lower water content of the hummock, resulting in a lower specific volumetric heat and thermal conductivity, means that its surface layers may not only heat up quickly but also act as an insulating blanket, protecting the deeper layers from cooling in the summer nights or heating up during the winter days. Larger diurnal amplitudes in temperature were found in the surface layer of the hollow compared with the slope and hummock. These result from higher maximum temperatures. Minimum temperatures in the hollow are higher than in the slope or hummock, since heat is supplied to the surface from the layers deeper down the profile, where it was stored during the day. Hummocks store little heat and temperatures therefore drop more during the night. Vertical variation in thermal regime, owing to delayed responses to warming or cooling of the surface, gives rise to horizontal thermal variation. The effect of this phenomenon on nutrient supply and water movement in the hummock–hollow complex is discussed.

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INTRODUCTION

A number of studies concerned with hummock–hollow complexes on Irish raised bogs have been carried out (e.g. Schouten 1981; 1984; 1990; van der Molen *et al.* 1992). The reason for studying hummock–hollow complexes is mainly because they incorporate the extremes of the bog surface on a small spatial scale. In these studies, emphasis was placed on the vegetation, hydrology and chemistry of the complex. Most ecological processes, however, are predominantly temperature-dependent (Baaijens 1982; Lewis Smith 1988; Rydin 1984). Temperatures are now easily recorded with comparatively low-cost equipment, but relatively few accounts of the thermal regime in raised bogs and temperature-related phenomena in mirelands exist (Clymo and Hayward 1982; Norgaard 1951; Rydin 1984; Schmeidl 1978; Takahashi *et al.* 1984; Williams 1968).

Temperatures within hummock–hollow complexes are dependent on the vegetation structure and the ensuing physical properties of the system. The bulk of the biomass in these systems is made up of *Sphagnum* species. These are ectohydric hygrophytic bryophytes, meaning they exchange water freely over their entire surface and do not possess well-developed conducting systems. They occur not more than a few decimetres above the water-table since the continuity of water movement via the pores depends on the presence of water in capillary spaces outside the hyaline cells. Evaporated water is replaced by a gradient in water potential, causing water movement from the level of the water-table to the capitula (Proctor 1979; 1982). Hummock–hollow complexes on Clara bog show a subdivision of the *Sphagnum* species into three groups: hummock species (*Sphagnum imbricatum* and *S. fuscum*), slope species (*S. capillifolium*, *S. magellanicum*, *Hypnum cupressiforme*, *S. tenellum* and *S. papillosum*) and the hollow species (*S. cuspidatum*). This division is less clearly reflected in the distribution of vascular plants: *Calluna vulgaris* and *Eriophorum vaginatum* are most abundant on the hummock, the slope is mainly dominated by *Erica tetralix*, *Andromeda polifolia* and *Narthecium ossifragum*, and the hollows contain *Eriophorum angustifolium* and *Rhynchospora alba*.

Fossil peat deposits provide records of past environmental conditions that result from the interplay of both local and regional factors. Only when the contributions of the local factors are known is it possible to assess the contributions of the regional factors. In order to obtain information on the local environmental factors, recent peat-forming vegetation types need to be studied. Since no living raised bogs exist in the Netherlands any more, peatlands in Ireland were chosen, which are considered to resemble the lost Dutch bogs closely.

Temperature not only influences obvious processes, such as production and decomposition, but may also govern factors such as nutrient distribution. This paper describes the thermal regime of hummock–hollow complexes on Clara bog. Observations were made in the two most important seasons—the summer and the winter—in an effort to examine the thermal extremes of the system.

SITE DESCRIPTION

Clara bog (665ha) is situated in a depression adjacent to a complex of esker ridges south of the town of Clara, Co. Offaly, Ireland (7°38′/53°19′) (Fig. 1). At present it is 4.24km long and 1.20km wide. The bog possesses so-called soak areas (small lakes, surrounded by minerotrophic vegetation) and well-developed microtopographical patterns.

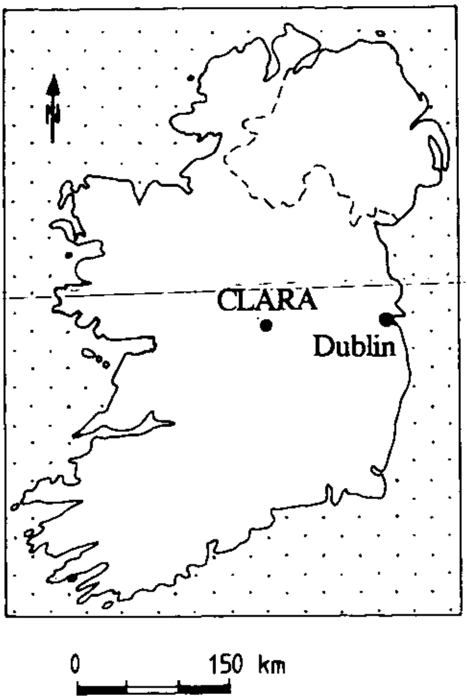

Fig. 1—Location of Clara bog.

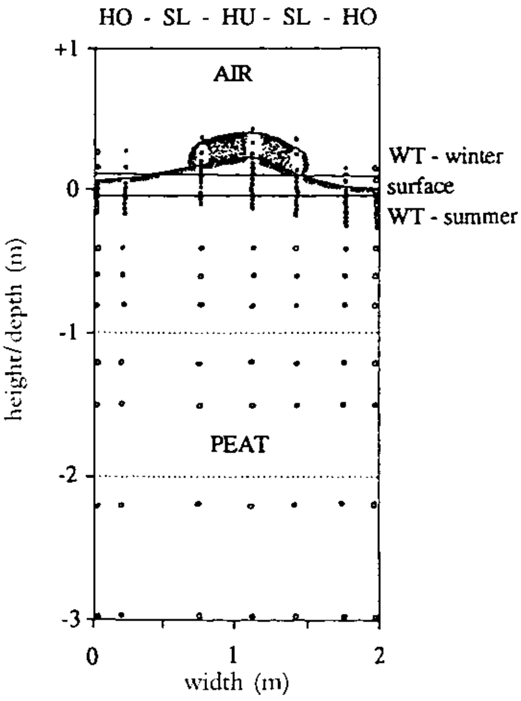

Fig. 2—Measuring points in the air and in peat of the hummock (HU), slope (SL) and hollow (HO). Water-tables are for summer 1990 and winter 1991. The closed circles are measured points. The open circles are points where measured data from comparable depths were used to complete the grid to facilitate calculations.

MATERIALS, METHODS AND DATA ANALYSIS

EQUIPMENT

For these studies a part of the permanent study site on Clara bog was chosen (van der Molen *et al.* 1992). At this site a representative hummock–hollow complex was chosen and data-logging equipment was installed, providing a flux of data automatically over longer time-spans, under any climatic conditions, with large numbers of probes, more or less simultaneously (compare Lewis Smith 1988). Across the microgradient at five locations, a series of copper-constantan thermocouples were inserted into the peat of the acrotelm (Ingram and Bragg 1984). A total of 64 thermocouples were used, spaced at 3cm intervals along five bamboo rods. The maximum depth was 0.40m below the lowest level, i.e. hollow surface. Thermocouples in small containers, covered with reflecting aluminium foil, were used to measure air temperatures above the surface. In addition to this, thermocouples were placed in one hollow location to a depth of 2.2m below the surface. The results of this deep probe were considered to be representative for the deeper layers underneath the entire complex. In this way a complete cross-section through a hummock–hollow complex to a depth of 2.2m could be reconstructed (Fig. 2). The thermocouples were connected to Campbell data-loggers. To one 21-OSX-O logger the 64 thermocouples for the profile were connected via two AM-32 multiplexers. Another 21-X logger was used for the other probes. The loggers sampled every ten minutes and stored the results in an intermediate memory. After 30 minutes the three readings were averaged and stored in a final memory. A Bondwell (BW-8-TH) laptop computer was used in the field to off-load the data from the logger onto floppy disk. Measurements were made in June 1989, December 1989, July 1990 and February 1991. The first two sets yielded some preliminary data that were used to obtain a first impression and to improve the techniques. The latter two sets are used in this paper because they are the largest in size and cover the most depths.

DATA ANALYSIS

The data were translated into EXCEL-files for the Apple Macintosh and OS-2 (IBM), where further treatment took place. The data were corrected for differences between the individual thermocouples. In order to accomplish this the difference from average was established for each thermocouple after calibration at 0 and 100 degrees Celsius. This corrected data set was used for all further calculations. The data spanned many days and were transformed into one average diurnal cycle (24 hours) for that period, eliminating incidental cloud cover. All times are in GMT wintertime.

Contour plots of the isotherms in cross-sections of the hummock–hollow complex were obtained by inserting the values for an average diurnal cycle into a coordinate system of all measuring points in the profile. Interpolation between the values at these coordinates was performed using distance-weighted least squaring with SYSTAT for the Apple Macintosh. This technique fits a surface through a set of points using least squares, while the contour line is allowed to flex locally, in order to fit the data. Extrapolations of temperatures to a depth of 3m were made. Separate profiles of air temperatures over the complex were obtained by extra- and interpolations using recorded temperatures at the *Sphagnum* surface, in the hummock Ericaceae canopy and above the vegetation of the hummock, slope and hollow.

The establishment of the average diurnal cycles of the two most extreme seasons enabled calculation of some physical characteristics of the peat along the microtransect for the summer and the winter period, using equations taken from Monteith and Unsworth 1990 and Barkman and Stoutjesdijk 1987 (Table 1).

The damping depth (D) was calculated after finding the depth at which the surface amplitude was reduced by a factor of 1/e or 0.37 (A_D). The surface values (A_s) used are those of the capitulum layer, in order to avoid problems with possible boundary layer conditions directly over the surface. It must be noted, however, that some damping might already have taken place in this capitulum layer.

From the damping depth a number of other variables were drawn. The water content (WC) (%), the specific volumetric heat ($p'c'$) (J m^{-3} K^{-1}) and the thermal conductivity (k') (J m^{-1} K^{-1} s^{-1}) were calculated using third-degree polynomial regression equations, which were derived from the peat data by Barkman and Stoutjesdijk (1987).

$$WC = -2631.1 + 1623.4\ D - 332.72\ D^2 + 22.903\ D^3 \qquad (1)$$

The maximum value for volumetric water content is 100%.

Table 1—Physical characteristics of the hummock, slope and hollow peat. A_s is the temperature amplitude in the surface layer of the capitula (°C); A_D is the inferred amplitude at damping depth (A_s * 0.37) (°C); D is the damping depth at which A_D is found (m rad^{-1}); WC is the water content (vol. %); $p'c'$ is the volumetric heat (J m^{-3} K^{-1}); k' is the thermal conductivity (J m^{-1} K^{-1} s^{-1}); w is the angular frequency of the oscillation (rad h^{-1}); πD is the depth at which the temperature wave is out of phase with the wave at the surface (m rad^{-1}); $\sqrt{2}D$ is the effective depth (m rad^{-1}) and wD is the rate of penetration of the temperature wave (m rad^{-1} h^{-1}).

Location	A_s	A_D	D	WC	$p'c'$	k'	w	πD	$\sqrt{2}D$	wD
SUMMER										
Hummock	13.49	4.99	0.060	75	3368992	0.44	0.26	0.187	0.084	0.016
Slope	13.47	4.98	0.061	87	3797447	0.51	0.26	0.191	0.086	0.016
Hollow	15.11	5.59	0.058	58	2736523	0.33	0.26	0.181	0.082	0.015
WINTER										
Hummock	3.91	1.45	0.198	>100	>4190000	>0.59	0.26	0.623	0.281	0.052
Slope	3.17	1.17	0.165	>100	>4190000	>0.59	0.26	0.519	0.234	0.043
Hollow	4.17	1.54	0.073	>100	>4190000	>0.59	0.26	0.228	0.103	0.019

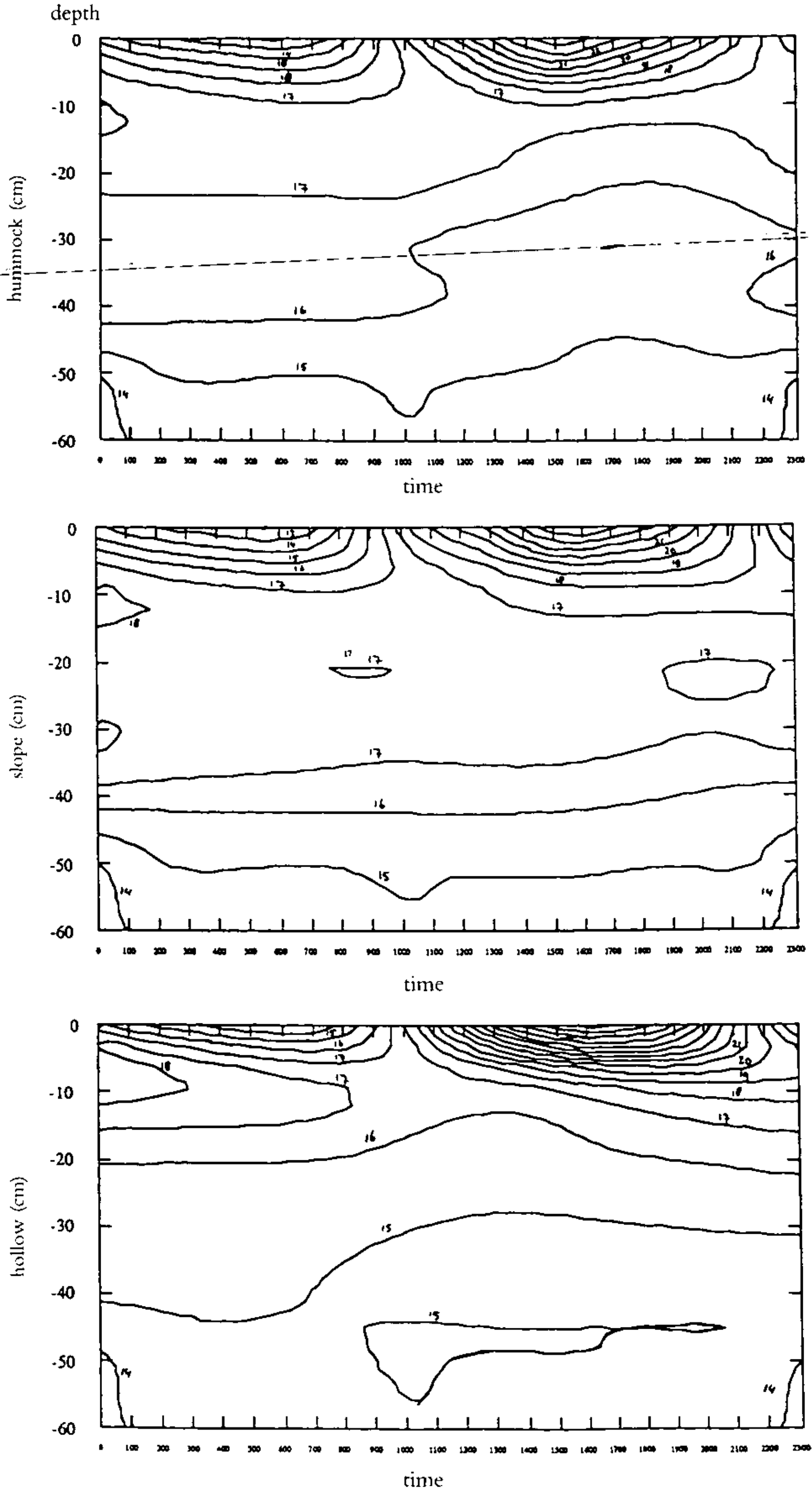

Fig. 3—Isotherm profiles during an average day (24 hours) from the surface to a depth of 60cm. (A) Summer 1990: hummock, slope and hollow. (B) Winter 1991: hummock, slope and hollow.

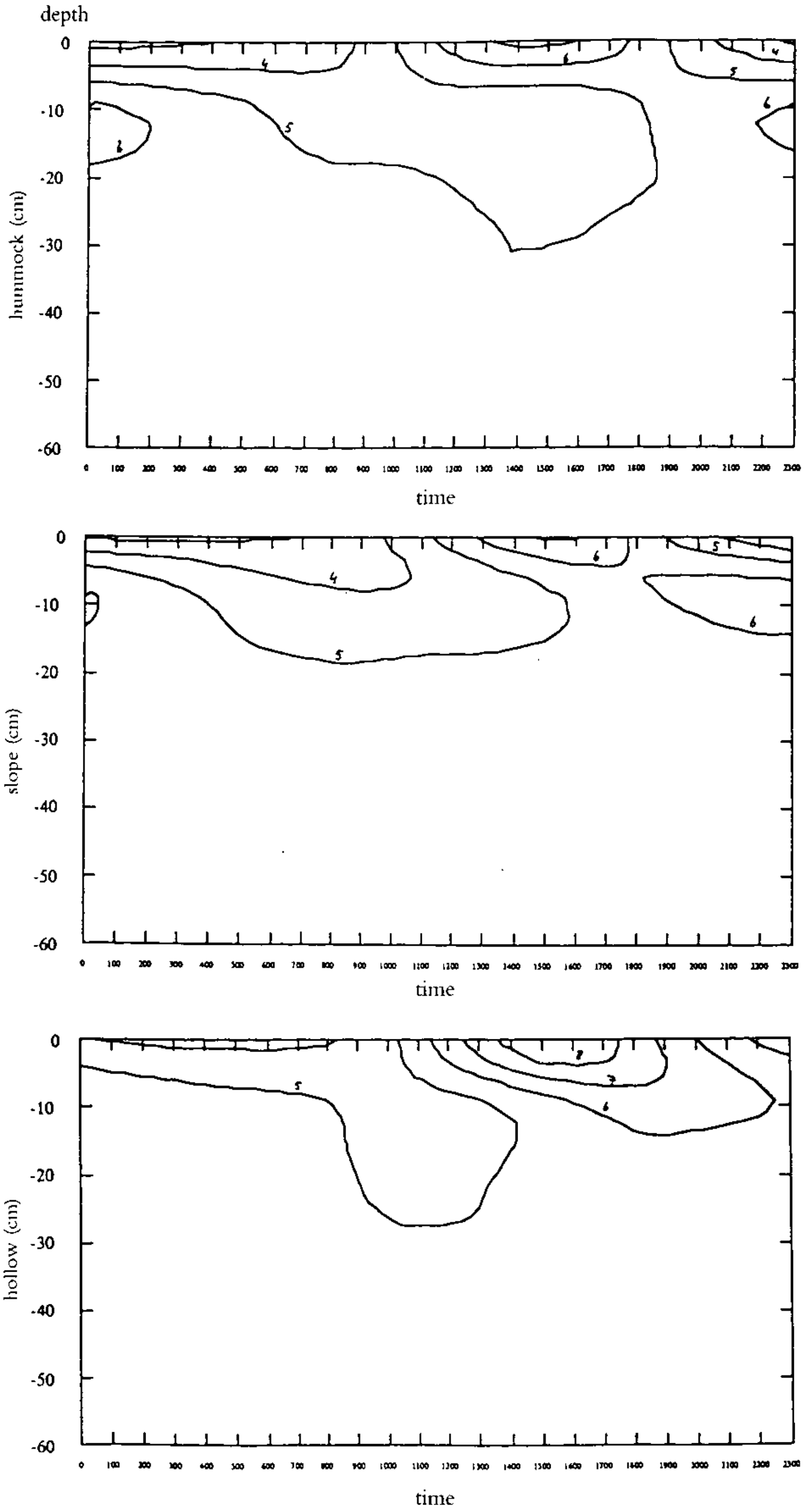

Fig. 3—Continued

S

$$p'c' = -74.694 + 46.366\ D - 9.5638\ D^2 + 0.6680\ D^3 \qquad (2)$$

The maximum value for the volumetric heat is 4,190,000J $m^{-3}\ K^{-1}$.

$$k' = -104.39 + 66.498\ D - 14.145\ D^2 + 1.0149\ D^3 \qquad (3)$$

The maximum value for the thermal conductivity is 0.59J $m^{-1}\ K^{-1}\ s^{-1}$.

This method had to be followed since no *in situ* water content of the peat could be established without damaging the structure of the studied hummock–hollow complex. The results are therefore estimations and the equations can only be used to the maximum damping depth for 100% water (0.062m).

The w is the angular frequency of the oscillation (rad h^{-1}) and was calculated following

$$w = 2\pi / P, \qquad (4)$$

which means that for daily cycles $w = (2\pi/24)\ h^{-1}$ The πD is the depth at which the temperature wave is exactly out of phase with the wave at the surface (m rad^{-1}). When the surface temperature reaches a maximum, the temperature at πD reaches a minimum and vice versa. The maximum heat flow is the flow of heat that would be maintained through a soil layer with the thickness $\sqrt{2}D$, provided that one side of the layer would be kept at the maximum and the other at the minimum temperature of the surface. The thickness $\sqrt{2}D$ (m rad^{-1}) is therefore also called the effective depth for heat flow. The wD is the rate of penetration of the temperature wave (m $rad^{-1}\ h^{-1}$).

RESULTS

PHYSICAL THERMAL PROPERTIES OF THE PEAT

Calculations show that damping depths (D), where the amplitude of the temperature wave is $1/e$ or 0.37 times the amplitude at the surface, are much deeper in the winter than in the summer. The average damping depth for the hummock–hollow complex is 0.145m below the surface in winter and 0.059m in summer, a difference of a factor of *c.* 2.5. The cause of this dissimilarity lies in the difference in water content of the peat in the winter and the summer. The water-table is generally high during the winter period and hollows become completely filled. The water-table in hummocks is at the same level as in the hollows, but capillary rise of the water causes an increase in the water content of the top layers as well (van der Molen *et al.* 1992). Therefore, since the peat contains more water in the winter and because water possesses a higher thermal conductivity (k'), the damping depth (D), the out of phase depth (πD), the effective depth ($\sqrt{2}D$) and the rate of penetration of the temperature wave (wD) will therefore be higher as well. The average out of phase depth, at which the temperature wave is exactly out of phase with the wave at the surface, is 0.186m in the summer and 0.456m in the winter. The average effective depth is 0.084m in the winter and 0.206m in the summer. The rate of penetration of the temperature wave is also more than twice as high in the winter (0.038m h^{-1}) as in the summer (0.016m h^{-1}).

TEMPERATURE PROFILES OF AN AVERAGE DAY FOR SUMMER AND WINTER

Isotherms were calculated for a full average diurnal cycle (24 hours, summer and winter) for the hummock, slope and hollow for the first 0.6m (Fig. 3). The profiles in Fig. 3 show a clear reduction of the thermal dynamics below a depth of *c.* 0.2m at all three locations. The temperature profiles can be separated into two groups for the summer as well as for the winter period, depending on the way a separation develops between a regularly stratified temperature profile or one with anomalies in the form of warmer or colder pockets.

During the summer days heat is stored in the surface layers to a depth of *c.* 0.20m. At night only the top 0.05–0.10m cool down. Below this level higher temperatures remain present for another 0.10–0.3m. Underneath this warmer region temperatures drop again. In this way an unstable temperature profile develops, with a narrow band of higher temperatures maintained throughout the night between the surface and the deeper peat layers. This temperature inversion ends around 09.00h in the morning. A regularly stratified profile is observed during the day from 09.00h on until 23.00h in the evening, when the inversion sets in again.

In the winter period a similar temperature inversion develops during the day. During the night the surface layers cool. When they are heated in the morning a cold tongue becomes trapped in the peat. As a result, an unstable temperature profile develops, with a narrow band of lower temperatures existing between the surface and the deeper peat layers. This inversion sets in around 09.30h in the morning and lasts to about 18.30h in the evening, especially in the hummock. During the night the profile is stable and stratified. Below a depth of *c.* 30cm the summer profile is always regularly stratified, although during winter the distances between the temperature intervals are much larger, sometimes beyond the scale of the diagram.

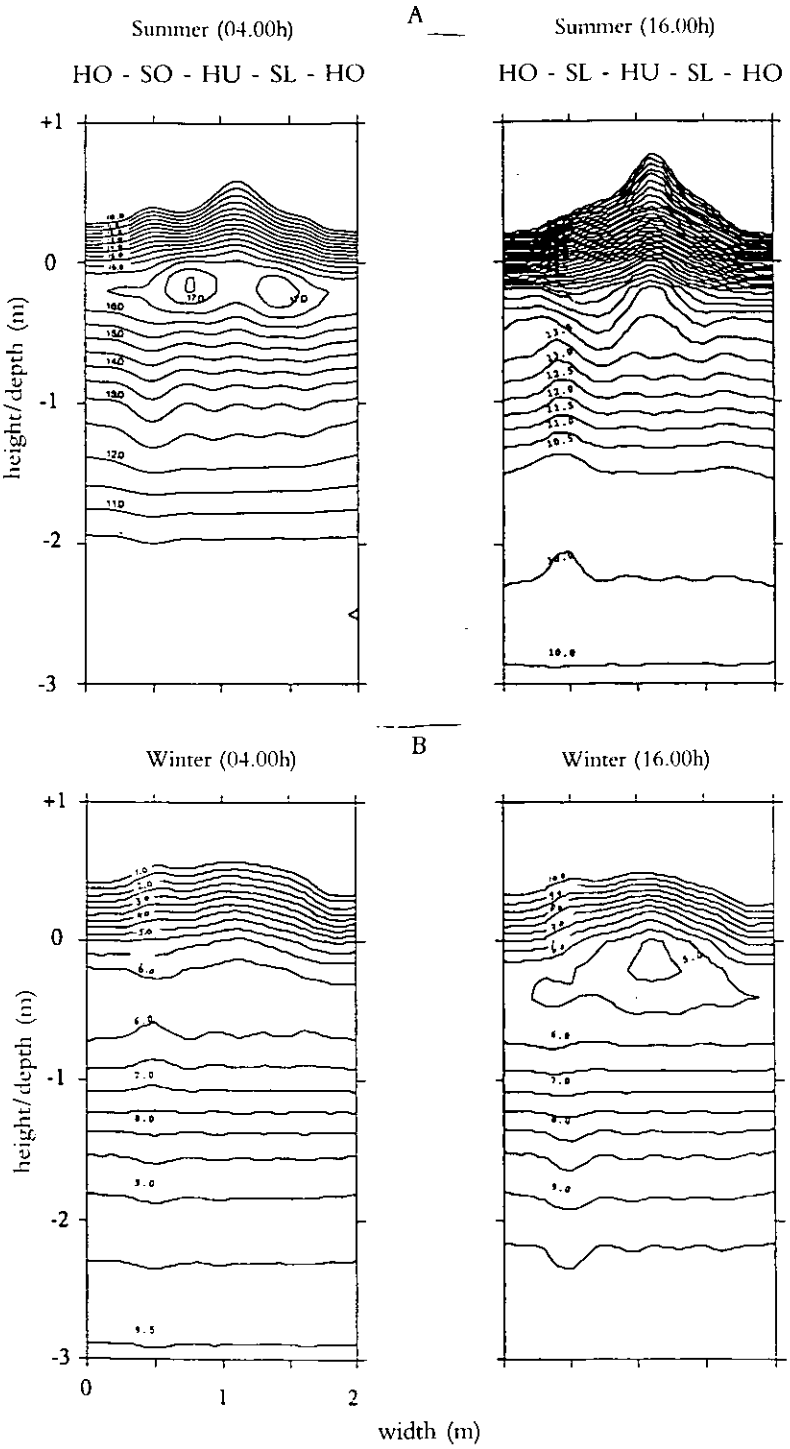

Fig. 4—Temperature profiles of the hummock, slope and hollow from 1m above to 3m below the surface. (A) Summer 1990, with profile at 04.00h and 16.00h. (B) Winter 1991, with profile at 04.00h and 16.00h. HO = hollow, SL = slope and HU = hummock.

The inferred differences in specific volumetric heat capacity and thermal conductivity between hummocks and hollows have large implications for their thermal behaviour. A drier vegetation will have a lower specific volumetric heat capacity and thermal conductivity. Initially, with increasing water content, the specific volumetric heat capacity increases faster than the thermal conductivity, which results in a higher thermal diffusivity. At some stage, however, the thermal conductivity will

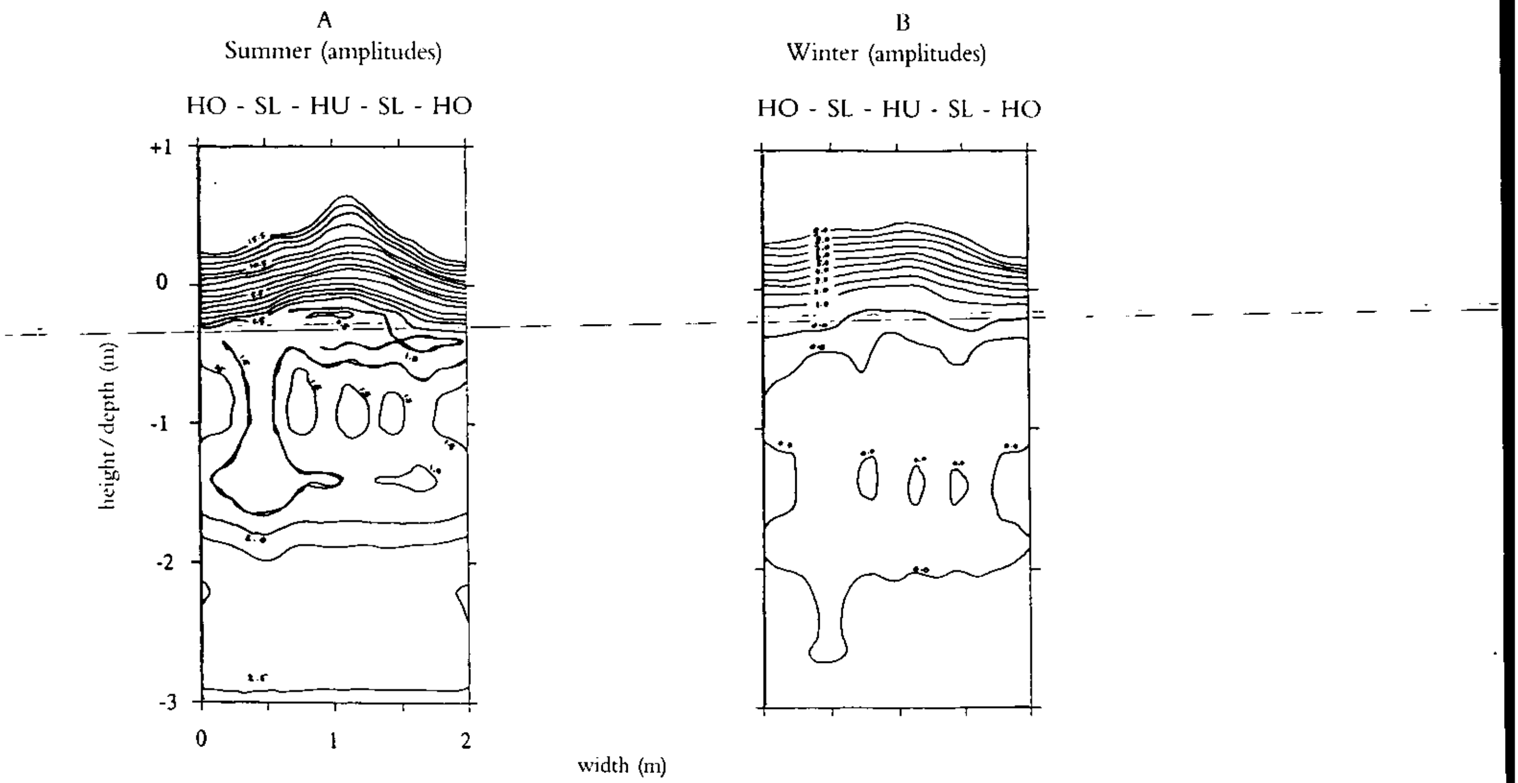

Fig. 5—Profiles of the diurnal temperature amplitudes of the hummock, slope and hollow from 1m above to 3m below the surface. (A) Summer 1990. (B) Winter 1991. HO = hollow, SL = slope and HU = hummock.

rise more quickly than the specific volumetric heat capacity, leading to a decrease of thermal diffusivity with water content (Monteith and Unsworth 1990). In practical terms, this means that the surface layers of the hummocks will warm faster, through a higher thermal diffusivity, than the waterlogged hollows, but cannot store the same amount of heat (Schmeidl 1978). This response difference is visible especially in the summer (Fig. 3A), but the advantage is short-lived.

A better view of the implications of these temperature inversions can be obtained by studying cross-sections of the hummock–hollow complex. Two moments in time were chosen, representing the extremes of the thermal dynamics as observed above: 04.00h and 16.00h. In Fig. 4 a series of temperature profiles through the hummock–hollow complex are presented from 1m above the surface of the hollow to 3m below it. In the summer period (Fig. 4A) a stable, stratified temperature profile exists during the day. At night, however, the centre of the hummock is warmer than its surroundings. In the winter period (Fig. 4B) the situation is reversed. During the day the centre of the hummock is colder than its surroundings, while the night profile is regularly stratified. This is consistent with the field observations that on mornings after severe night frost the hummocks were found to be frozen solid, while the water in the hollows was either open or covered with a thin layer of ice.

DIURNAL AMPLITUDE AND TEMPERATURE RANGES

Temperature amplitudes are an important measure of the thermal dynamics of a particular location (Fig. 5). However, not only the magnitude of the amplitudes but also the absolute temperature ranges are of great importance, and are shown in Fig. 6 and Table 2. It must be remembered, however, that the observed thermal regime not only influences the ecology of the species involved but is also a result of the microtopography formed by the same species, creating a feedback.

The graphs of the diurnal amplitude of the summer and winter periods in Fig. 5 show a division of the profiles into an upper and a lower part. In the upper parts of the profiles the amplitudes increase towards the surface. Table 2 shows that during the summer period the amplitudes can reach values of about 16.4–18.5°C in the air above the vegetation and directly above the capitula. During the winter period air temperatures reach amplitudes of between 7.7°C and 8.2°C above the vegetation, while directly above the *Sphagnum* capitula these amplitudes are reduced to between 7.0°C and 8.0°C.

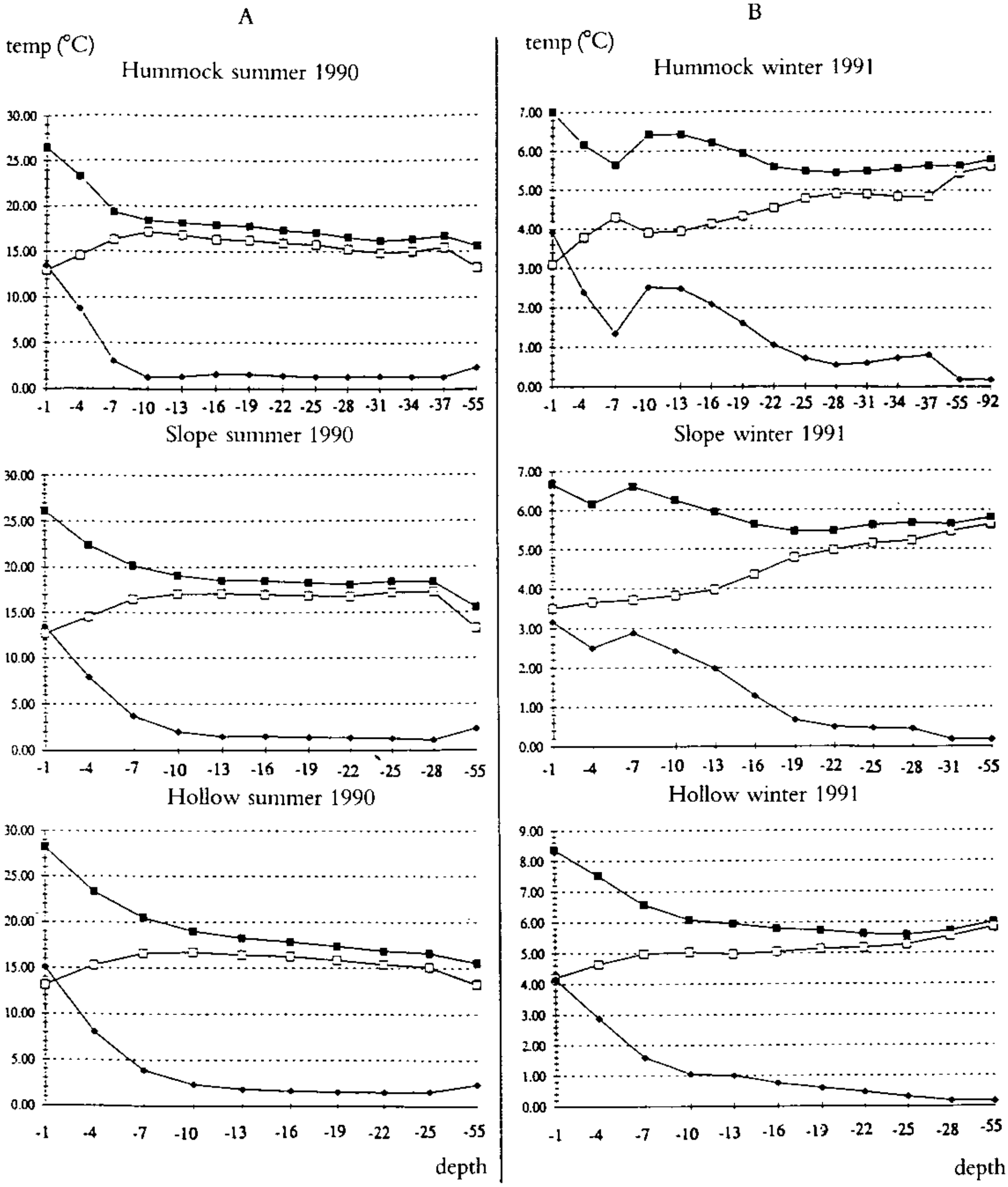

Fig. 6—Minimum and maximum temperatures and amplitudes. (A) Summer 1990 and (B) winter 1991: hummocks, slopes and hollows (■ maximum; □ minimum; ♦ amplitude).

Temperature amplitudes in the capitulum layer (1cm below the upper parts of the capitula) are between 13.5°C and 15.1°C in the summer and between 3.2°C and 4.2°C in the winter period. The amplitudes in the capitulum layer are higher in the hollows (15.1°C in the summer and 4.2°C in the winter) than in the hummocks (summer: 13.5°C; winter: 3.9°C) and slopes (summer: 13.5°C; winter: 3.2°C).

A reduction of amplitudes can be observed downwards in the profile. At 4cm below the capitulum layer, summer amplitudes are between 7.9°C and 8.8°C and between 2.4°C and 2.9°C in winter. This is a reduction in amplitudes of *c.* 10°C and 5°C for the summer and the winter periods respectively when compared with the amplitudes at the surface. The amplitudes in the lower parts of the profiles are much reduced and fluctuate between 0°C and 2.5°C both in the summer and winter periods. The stratification of the amplitudes in the upper parts of the profiles in both seasons is laminar and does not contain pockets as were found in the individual profiles for the summer nights and the winter days.

The absolute temperature ranges indicated in Fig. 6 and Table 1 show that in the summer period maximum temperature values of 26.3–28.2°C are reached in the air above the vegetation and 26.4–28.6°C directly above the capitula. During the winter period the maximum air temperatures above the vegetation range from 9.1°C to 9.4°C, while directly above the *Sphagnum* capitula these maxima are reduced to 8.6–9.2°C. The maximum summer temperatures in the capitulum layer (−1cm) are about the same as in the air above—25.5–28.2°C—while in the winter period they are reduced by 1–2.5° to 6.7–8.4°C. Below the capitulum layer (−4cm) maximum temperatures are reduced by 3–4° to 22.5–23.4°C in the summer and to 6.2–7.5°C in the winter.

The minimum air temperatures above the vegetation vary from 9.7°C to 9.9°C in the summer and from 1.2°C to 1.4°C in the winter. Directly above the surface they are slightly higher, and become 9.8–10.2°C in the summer and 1.2–1.6°C in the winter. The differences between the maximum temperatures above and in the surface was not very large and amounted to a reduction of 1–2.5°C, as we have seen above. The difference between the minimum temperatures above and in the surface, however, is nearly twice as large, and amounts to a temperature increase of 2.5–3°C. The summer minima, therefore, in the surface are 12.7–13.1°C, while the winter minima are 3.1–4.2°C. Below the capitulum layer the minimum temperatures increase further by 0.5–2°C, and become 14.5–15.3°C in the summer and 3.7–4.6°C in the winter.

The data in Table 1 show that there is no clear gradient in the thermal regime along the transect from the hummock, via the slope to hollow, but that individual elements of the microtopography may react more or less in their own specific way. This is in line with the conclusions drawn by van der Molen *et al.* (1992) about the subdivisions of the hummock–hollow complex.

THE TEMPERATURES OF DRY AND WET *SPHAGNUM CUSPIDATUM* CARPETS

The water-table in the hummock–hollow complex on Clara bog behaves as a plane. This is due to the high hydraulic conductivity of the acrotelm peat, allowing rapid lateral water movement. As a consequence, high soil water tensions exist in the hummock capitulum layer, even though water in the hummock is raised above the hollow level by capillary forces.

A number of studies have shown that moss species on the hummock–hollow microgradient have an upper rather than a lower limit (e.g. Bragg 1982; Clymo and Hayward 1982). The upper limit of the species is set by the capacity to transport water to the photosynthetically active parts. As can be deduced from the situation outlined above, the work involved differs for the hummock and the hollow. Hummock species can still remain moist, although their evapotranspiration rate is high and their desiccation tolerance is low. In the hollow environment species have an unfavourable water balance; however, they are adapted to major water deficits since they possess a high desiccation tolerance (Titus and Wagner 1984; Wagner and Titus 1984).

One way in which *Sphagnum* species can reduce their evapotranspiration rate is by increasing their albedo. Water loss from the hyaline cells leads to air entry, and the green chlorophyll-containing cells no longer shine through the water of their

Table 2—Temperatures of the air, the surface, and in and below the capitulum layer (−1cm and −4cm respectively) of hummocks, slopes and hollows in summer and winter (all values are mean °C per microtopographical element of an average diurnal cycle for each season).

Location	*Air*		*Surface*		*In capitula (−1cm)*		*Below capitula (−4cm)*	
	Max	*Min*	*Max*	*Min*	*Max*	*Min*	*Max*	*Min*
SUMMER (mean of 7 days)								
Hummock	26.32	9.92	26.44	10.09	26.45	12.96	23.28	14.52
Slope	27.20	9.72	28.56	10.15	26.17	12.71	22.45	14.53
Hollow	28.20	9.73	28.35	9.79	28.23	13.13	23.36	15.30
WINTER (mean of 11 days)								
Hummock	9.07	1.41	9.04	1.45	7.00	3.09	6.16	3.78
Slope	9.27	1.27	8.60	1.63	6.67	3.50	6.16	3.66
Hollow	9.37	1.16	9.16	1.16	8.37	4.20	7.52	4.64

neighbouring cells, which results in a white-coloured plant. Since white surfaces reflect more light than green ones, this reduces the temperature of the plant (Clymo and Hayward 1982). No data were available, however, to corroborate this hypothesis. Therefore, in a short experiment temperatures were recorded below the capitula of green and white (collapsed) carpets of *S. cuspidatum* on two occasions (in May 1989 and in July 1990). The results presented in Table 3 and Fig. 7 indicate that temperatures below the surface of the white *S. cuspidatum* carpets can be substantially lower than below the green carpets. Average differences over the day amount to 0.8°C, with maxima on the hottest part of the day of 1.4–3.2°C. Figure 7 also shows that white *S. cuspidatum* plants are consistently cooler throughout the measured period.

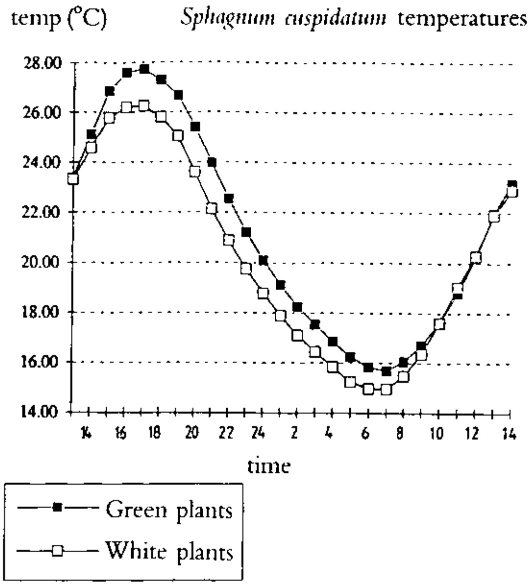

Fig. 7—Temperature fluctuation below green and white patches of *Sphagnum cuspidatum* (22–23 July 1990).

DISCUSSION

The thermal regime in the hummock–hollow complex is mainly dependent on the differences in physical properties of the peat and the interaction with vegetation structure. The surface of the vegetation obviously bears the brunt of the temperature fluctuations. Maximum temperature values range from 26°C to 28.5°C and are in line with values found in cushion plants in the Scandinavian tundra (Fischer and Kuhn 1984). They are, however, substantially lower than some values presented by Rydin (1984) and Schmeidl (1978), which range between *c.* 42°C and 62°C. This discrepancy can partly be attributed to variation in continentality or regional climate, but also to microtopographical variation such as inclination.

The inferred physical characteristics show that the relatively wet hollows have a higher specific volumetric heat ($p'c'$) and a higher thermal conductivity (k') than the relatively drier hummocks. Because of this, hollows can store heat while hummocks cannot. However, when looking at Table 1, these conditions are not immediately evident.

During the summer, the water-table is lowered in the bog. This means that the *Sphagnum cuspidatum* plants, which normally float in the water, collapse on the bottom of the hollow after the water-table has fallen to a level below that. This results in a skin of white-coloured *Sphagnum* plants that possess a greater albedo. As we have seen, turning white seems to be a reasonably effective mechanism to reduce temperatures during drought periods. This skin also effectively seals the hollow bottom from exchange with the air above it. Since the physical properties of the hollow are altered, the summer hollow values deviate from any expected trend from hummock to hollow.

When studying half of the transect, from hummock to slope, it is clear that the specific volumetric heat and the thermal conductivity increase with increasing water content. The hollow values deviate from this trend because of the above-mentioned mechanism. The winter hollow values are also obscured since the established damping depths result in estimates for the water content, specific volumetric heat and thermal conductivity

Table 3—Temperatures (°C) below carpets of *Sphagnum cuspidatum* on Clara bog.

S. cuspidatum	*Mean*	*S.D.*	*Maximum*	*Minimum*	*Amplitude*
31 (12.05h–13.35h)/05/1989					
Green	18.01	1.08	19.77	16.62	3.15
White	15.51	0.59	16.57	14.76	1.82
Difference	**2.51**		**3.20**	**1.87**	**1.33**
22 (12.25h)–23 (14.00h)/07/1990					
Green	21.32	3.94	27.72	15.68	12.04
White	20.52	3.79	26.28	14.88	11.40
Difference	**0.80**		**1.44**	**0.80**	**0.64**

above the maximum possible values, owing to the calculation method. This could only have been avoided if techniques had been available to assess the water content directly.

As a result of all this, surface layers of hummocks can warm up more quickly, but their advantage is soon overtaken by the hollows, which are also able to store more heat. In contrast to the results of Clymo and Hayward (1982) and Björkbäck (in Rydin 1984), larger diurnal amplitudes were found in the surface layer of the hollow than in the slope and hummock. Minimum temperatures in the hollow are higher than in the slope or hummock since heat is supplied to the surface from the layers deeper down the profile, where it was stored during the day. Hummocks do not store so much heat and temperatures will therefore drop more during the night. Since minimum temperatures are lower for the hummock than for the hollow, larger amplitudes in the hollow stem from higher maximum temperatures.

The phenomenon of the summer and winter temperature inversions can be explained by the above-mentioned physical properties of the peat layers of the hummocks and hollows. The lower water content of the hummock (Lindholm and Markkula 1984) results in a lower specific volumetric heat and thermal conductivity. This means that the surface layers of the hummock act as an insulating blanket, protecting the deeper layers from cooling in the summer nights or heating up during the winter days.

Therefore, in the summer period the deeper peat layers lose their heat only slowly during the night. Later in the morning the cooling of these layers matches the warming up of the outer layers and the profile becomes stable and stratified again.

In the winter, the outer insulating moss layer acts in the reverse manner: it delays the warming up of the deeper layers during the day. Only in the early evening, when the cooling of the outer layers matches the temperature of the deeper layers, do the profiles become stable and stratified again. The profiles also show a volume of peat with relatively constant temperatures in the deeper layers. At a depth of *c.* 3m the temperature is about 10°C throughout the year. This implies that in the summer the deeper peat layers will act as a heat sink but that in the winter period they will act as a source of heat for the surface layers.

Differences in specific volumetric heat capacity and thermal conductivity between hummocks and hollows and the implications for their thermal behaviour again indicate that hummocks and hollows should be considered as interconnected but simultaneously independent systems. Rydin (1984) points out that the response to environmental conditions of a species is of great importance when it occurs with others in the same habitat. Vegetation changes (and consequential stratigraphical changes) could result from different responses of the metabolically active parts of the plants to low water content in combination with higher temperatures. This is especially important in a raised bog vegetation, where small differences in ecophysiology and ecomorphology of the *Sphagnum* species give rise to a comparatively strong habitat segregation. Extrapolation of results obtained by using species stemming from different habitats is sometimes done for want of better data, but is dangerous and often irrelevant. Therefore the need exists for accurate information on a number of physiological characteristics of *Sphagnum* species, such as the location of metabolically active parts of a plant, the temperature and dessication tolerance, and the photosynthetic capacity at differing moisture contents.

Variation in the thermal behaviour of the various parts of the hummock–hollow complex has consequences for the invertebrate fauna as well. Some evidence for this is provided by Norgaard (1951: spiders) and Schmeidl (1978: ants), and indicates that insects look for well-defined habitats with specific temperature and moisture conditions. It is not inconceivable that they will migrate, according to the time of year, up, down or around the microtopography, looking for the best suitable conditions according to the season. These dynamics are not yet incorporated in macrofossil analysis and will doubtless be of importance with the increasing interest in invertebrate remains.

Deeper strata, especially below the hummocks, are insulated by the upper peat layers, giving rise to delayed responses to warming or cooling of the surface, a fact also observed in cushion plants (Fischer and Kuhn 1984). Vertical variation in thermal regime will thus give rise to horizontal thermal variation. This phenomenon has an important bearing on nutrient supply and water movement in the hummock–hollow complex. Below the water-table differences in temperature lead to density differences, which will give rise to movement of water (Schwoerbel 1971). The formation of horizontal and vertical circulation cells is well known from oceanic systems (Krantz *et al.* 1988; Whitehead 1989) and its importance for *Sphagnum* vegetation types has been speculated on (Baaijens 1982), but no evidence has been produced yet.

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13