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Growth of two peat-forming mosses in subarctic mires: species interactions and effects of simulated climate change

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In patches of co-occurring species in natural plant communities, there is a finely poised balance between species in the ways in which they respond to prevailing moisture and temperature regimes. However, environmental change scenarios, in which temperature, moisture and ultraviolet-B radiation are suggested to increase, may favour one of the species. The imbalance is likely to occur at the levels of interactions between patches of the different species and at the shoot level when neighbouring shoots belong to different species. We increased temperature and UV-B in a two-way factorial experiment and increased water supply independently in two subarctic mire communities dominated by the mosses *Sphagnum fuscum* and *Dicranum elongatum*. The effects of simulated increase in UV-B were studied using two separate radiation systems, i.e. a “square wave” system and a “modulated” system.

When precipitation was enhanced, both species showed an increase in growth but this was not sustained beyond 5 mm per day. *S. fuscum* showed a 50% greater response to enhanced precipitation than did *D. elongatum*, as would be expected from their habitat preferences. Under ambient temperature, *S. fuscum* grew 67% faster than *D. elongatum* and this relative difference in response was maintained after one year under a temperature enhancement. The response by species over the winter period was moderated by their neighbours. *S. fuscum* growth was enhanced when it grew next to *D. elongatum* whereas *D. elongatum* grew better with neighbours of its own species. Increased temperature and UV-B radiation did not affect the interaction between the species.

Although a balance was maintained between the two species over the short duration of the experiment, potential was shown for an imbalance to occur over longer periods and particularly if winter warming and precipitation are greater than those in summer.

During the peak growing season 20% increased UV-B over ambient had a negative effect on *S. fuscum* under increased temperature but there were no overall seasonal effects on either species, irrespective of method of UV supplementation.

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Approximately 3% of the Earth's land surface is covered with peat and about 75% of this is in boreal and arctic areas (Kivinen and Pakarinen 1980). Peatlands

sequester atmospheric carbon and store it in peat. They are estimated to contain 300 Gt carbon which is equivalent to about 40% of the carbon content of the atmo-

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sphere (Sjörs 1982). There is little doubt that both the formation and decomposition of peat and the factors controlling these processes are of great importance for the global atmospheric carbon balance, particularly if predicted climatic change occurs and peatlands shift from carbon sinks to source status (Billings et al. 1982, 1983, Oechel et al. 1993, 1995, IPCC 1996, Malmer and Wallén 1996).

Subarctic and arctic peatlands are on permafrost to a large extent (Kalela 1939, Kalliola 1939, Ruuhijärvi 1960, Sonesson 1970a, Botch and Masing 1983). This affects decomposition as well as the formation of plant biomass and hence peat. Where the permafrost surface is deep in the soil profile below a thick active layer, oxidising conditions exist and aerobic decomposition is rapid (Christensen et al. 2000). In contrast, a high permafrost table during the growing season leads in general to wet and anaerobic soil conditions in the unfrozen active layer which in turn prevents decomposition of surface peat. However, in a climate change scenario with an increase in temperature and precipitation (Maxwell 1992, Cattle and Crossley 1995), particularly in the northern areas which have already experienced warming of up to 1.5°C per decade (Chapman and Welsh quoted in Weller 2000), both decomposition and plant growth will be affected. However, plant growth and decomposition will probably not be affected to the same extent because temperature is likely to differ between aboveground plant organs and sub-surface peat.

An effect of increasing humidity may be increased thermal conductivity of the peat. This can then result in a lowering of the permafrost table and in combination with increased temperature enhance decomposition and flux of CO₂. However, if surface peat layers are oxidised, the remaining layers will be less labile and the decomposition of these is also less temperature sensitive (Christensen et al. 1999).

Increased precipitation and temperatures in combination will also improve plant growth which will counteract the effect of greater CO₂ emission from increased decomposition. Hence, to what extent the subarctic-arctic peatlands will be sources or sinks for carbon in the future may largely depend on the rate and magnitude of change in thermal conductivity of the peat and the rate and magnitude of biomass formation.

UV-B radiation associated with stratospheric ozone depletion may also have an effect on plant growth (Searles et al. 2001). However, studies on the effects on mosses are few and with conflicting results. Experimentally added UV-B has been found to either stimulate (Sonesson et al. 1996), depress (Gehrke et al. 1996, Gehrke 1998) or to have no effect (Björn et al. 1999, Gwynn-Jones et al. 1999, Searles et al. 1999) on the performance of bryophytes.

Two moss species are particularly important for ombrotrophic peat formation in subarctic (continental)

peatlands, viz. the hummock-forming *Sphagnum fuscum* Klinggr. and *Dicranum elongatum* Schleich. (Kalliola 1939, Ruuhijärvi 1960, Sonesson 1970a). They form structures that may often be large, elongated, surrounded by or adjacent to, wet depressions (Sonesson 1970a, 1980a). Normally *D. elongatum* and lichens are dominant on the summits and *S. fuscum* on the slopes. The plants rely nearly exclusively on water and nutrients from precipitation (Malmer and Nihlgård 1980). This makes them particularly strongly exposed to climatic impacts. Stratigraphic studies have shown that there is usually a progressive succession in these sites from moss communities of wet depressions to *S. fuscum*-dominated slopes to *D. elongatum*-dominated summit communities, i.e. there is a successive development towards drier stages (Sonesson 1970b). The opposite pattern has also been observed, however, when *S. fuscum* and even mosses of wet areas succeed *D. elongatum*. Regressive development may be brought about by changes in the hydrology of the ecosystem. How much of the change that is due to inherent properties of the ecosystem (e.g. species interactions) and how much is due to external environmental factors (such as weather) cannot usually be determined from stratigraphic studies only (Sonesson 1970b). However, by experimentally manipulating the live plant cover, information may be gathered about some of the major mechanisms involved.

This study has two main objectives. Firstly, we use environmental manipulation experiments to study the likely response of communities to increase in precipitation, temperature, and ultraviolet-B radiation. Secondly, we seek to understand how interaction between co-existing species may be affected by such climate change.

Materials and methods

Experimental sites and vegetation

Two mires on permafrost, situated ca 10 km apart, at Abisko (68°21'N; 18°49'E) and Stordalen (68°21'N; 19°04'E) were used for the field studies. The studies at the Stordalen site were completed in 1973, those at Abisko in 1997 and 1998. *S. fuscum* and *D. elongatum* are dominant mosses on the higher, ombrotrophic parts in both mires ("hummock sites", Sonesson 1970a). Plant communities in which these mosses are particularly prominent have been described by Sonesson (1970a, b, 1980a) as variants of an "*Empetrum hermaphroditum*–*Vaccinium microcarpum* association". Lichens dominate in variants of the driest habitats while moisture demanding mosses such as *Sphagnum balticum* (Sw.) Lange become prominent over the wettest habitats of the association. Extreme (dry or wet) habitats have been avoided in the present study. We

have concentrated on habitats in the moderately wet to moderately dry range. The seasonal median, total and interquartile range of water tables of the habitats in relation to the bryophyte surface are shown in Sonesson (1970b). For an extensive description of other aspects of these mires, i.e. their vegetation and general ecology, see also Sonesson (1970a, 1980a).

Data on temperature and precipitation during the study periods are shown in Table 1. The Stordalen site is located at the same altitude as the Abisko meteorological station, i.e. 390 m above sea level, and the mean temperatures are similar, whereas precipitation is on average about 6% higher at Stordalen (Rydén 1980).

Experimental design

Stordalen

Natural growth of the two species was measured in 16 plots (each approximately 10 × 10 cm) selected over a large sub-site (about 150 × 300 m) in each of three habitats for each species, viz. 2 (species) × 3 (habitats) × 16 (plots) = 96 plots in total (Sonesson and Johansson 1974). The statistical sampling design is described in Sonesson et al. (1980). The habitats were selected for being “moderately dry”, “intermediate”, and “moderately wet” according to community characteristics. The measurements were performed in 1973 between June 5 and September 15.

During part of the 1973 season the effect of increased precipitation on growth was simulated in an experiment on a neighbouring sub-site, using forty plots selected to represent moderately dry habitats of each species. The experiment started on July 1 and was finished on September 15. Distilled and deionized water was mist-sprayed onto plots twice a day on 20 rain-free days during the first four weeks after which no further

irrigation was carried out. The experimental design consisted of 2 species × 4 levels of daily water supply (control, 1, 5, 10 mm) × 5 replicate plots. Half of the daily water doses were applied in the mornings and half in the afternoons to minimize leaching effects. No irrigation was made during three rainy days during the first experimental period (July 1–15) and during five rainy days during the second period (July 16–27).

Abisko

Twenty-four years later, a two-way factorial experiment simulating increased temperature and ultraviolet-B radiation was established over a 30 × 75 m sub-site to study the effects on growth of the same two species.

Thirty plots were subjectively selected in moderately wet and intermediate habitats where *D. elongatum* and particularly *S. fuscum* were abundant. Each plot measured approximately 10 × 10 cm. The plots were distributed in a non-systematic way over the whole sub-site. Twenty plots were randomly selected for the experiment simulating future elevated UV-B levels using a modulated supplementation system (Bowles 1997, based on Caldwell et al. 1983) and ten plots were selected for a comparative experiment applying a “square wave technique” for UV-B supplementation (Johanson et al. 1995, Bertgren 1997, Gehrke 1998).

Temperature was increased by placing on the plots hexagonal open, UV-B-transparent plexiglas chambers of an ITEX-type (ITEX = International Tundra Experiment, Marion et al. 1997) that increase the average air temperature by about 2.0°C over ambient (Marion et al. 1997). The chambers were placed on small wooden blocks a few cm above the moss surface to improve ventilation (van Oijen et al. 1999) and to reduce possible effects of extreme warming events.

The UV dose was administered from small (15 cm) UV-B fluorescent tubes (Philips TL 12/4W) covered

Table 1. Monthly mean deviations (Δ) from the temperature and precipitation normals at Stordalen (Rydén 1980) and Abisko (30-year normals, 1961–1990, Andersson et al. 1996).

| | June | July | August | September |
|-------------------|------|------|--------|-----------|
| Stordalen | | | | |
| Temperature, °C | | | | |
| Normal | 8.4 | 11.0 | 9.7 | 5.2 |
| 1973 Δ | -0.7 | 0.3 | -3.3 | -3.2 |
| Precipitation, mm | | | | |
| Normal | 23 | 57 | 48 | 24 |
| 1973 Δ | -10 | -7 | 6 | 3 |
| Abisko | | | | |
| Temperature, °C | | | | |
| Normal | 8.4 | 11.0 | 9.7 | 5.2 |
| 1997 Δ | 1.2 | 2.2 | 1.8 | 2.0 |
| 1998 Δ | 0.1 | 1.9 | 0.2 | -0.2 |
| Precipitation, mm | | | | |
| Normal | 22 | 54 | 45 | 23 |
| 1997 Δ | -18 | -6 | -2 | -2 |
| 1998 Δ | 5 | 6 | 16 | 0 |

with 0.13 mm cellulose diacetate (Courtaulds, Derby, U.K.) to exclude UV-C radiation (Bertgren 1997). These were suspended under square frames on thin aluminium legs, 20 cm above the moss surface. The UV-B tubes were pre-burned for 48 h to get a stable output which was checked with a UV-B sensor. The UV-B dose over ambient corresponded to 20% ozone depletion under clear sky at this latitude. Control plots were equipped with UV-B frames under which 0.1 mm Mylar film/filters were placed to exclude all UV radiation below 318 nm. All filters were changed once a week to avoid the effects of ageing.

The modulated system measured ambient UV-B radiation continuously and added the difference between ambient radiation and that corresponding to a 20% ozone depletion level, taking seasonal ambient change into account (Björn and Murphy 1985). Five plots were equipped with similar frames and fluorescent tubes but with the total extra daily UV-B dose in a square wave centred on noon (Johanson et al. 1995, Bertgren 1997, Gehrke 1998). For the treatments and replicate numbers of the temperature and UV-B experiment, see Table 2.

All experiments were performed during two consecutive seasons. In 1997 work started on July 10 and was finished on September 5, in 1998 work started on June 12 and was finished on September 12. The equipment was removed during winter. The studies of the 1998 season comprised nearly a complete growing season in contrast to those of 1997. Thus we present results mainly from 1998.

Growth measurements

Straight stainless wires (\varnothing 0.6 mm) were inserted into the bryophyte carpet (extending from ca 10 cm underneath to 3 cm above the bryophyte surface) to serve as reference points for growth increment measurement (Sonesson and Johansson 1974, Sonesson 1980b). Points shaded by vascular plants were avoided. Leaves of *Rubus chamaemorus* L. in particular, expanding over the points were cut and removed. Every wire was marked with paint in a way that it could be individually recognized. Readings of the length increments were made using a thin (2 mm) glass tube (0.23 g) with a

Table 2. Treatments and replicate numbers of the temperature and UV-B supplementation experiment.

| Modulated system | Number of plots |
|--------------------|-----------------|
| UV-B | 5 |
| UV-B+temperature | 5 |
| Temperature | 5 |
| Control | 5 |
| Square wave system | |
| UV-B | 5 |
| Control | 5 |

fused millimetre scale and equipped with a narrow flat collar at the lower end (Sonesson and Johansson 1974, Sonesson 1980b). The maximum error in reading was estimated to be ± 0.2 mm (Sonesson and Johansson 1974). All measurements were made by the same person. The wire method was a variant of a method proposed and pioneered by Clymo (1970). Ten wires were inserted in each plot at Stordalen. The mean value of the ten readings was the replicate value of the plot.

Growth interactions between *D. elongatum* and *S. fuscum* and the effects of increased UV-B and temperature were studied at Abisko in each plot by inserting wires so that they touched individuals of the same species or adjacent individuals of both species. In this way growth of individuals surrounded by individuals of the same species was measured, i.e. *S. fuscum* in *S. fuscum* (S/S) and *D. elongatum* in *D. elongatum* (D/D), and of individuals immediately adjacent to/surrounded by the other species, i.e. *S. fuscum* at/in *D. elongatum* (S/D) and *D. elongatum* at/in *S. fuscum* (D/S). Four points for each combination of individuals in each plot were equipped with wires, i.e. 4×4 wires per plot. For the evaluation of interactions, mean values of each set of four wires were the replicate values of each plot. For the evaluation of the effects of temperature and UV-B, mean values of the eight wire measurements of each species (S/S + S/D and D/D + D/S, respectively) were the replicate values of each plot.

Growth of the same individual *S. fuscum* capitula was easy to follow throughout the seasons while the glass tube usually hit more than one apex of the tiny *D. elongatum* individuals. This was probably the reason why bending of the *D. elongatum* apices caused by the weight of the tube was only rarely observed.

Possible movements of the wires due to thawing and freezing during early winter and early spring were controlled using three sets of ten wires which were inserted in three different parts of the Abisko site. They were inserted in moss carpets dominated by either of the two mosses studied or by a combination of both. The distance between these wires was approximately 10 cm. The experiment was established on September 9, 1997 when the levels of the wire tops were carefully determined using a precision levelling instrument. This procedure was repeated on June 9, 1998 (after thaw). There was nothing in the measurements that could be explained by instabilities of the reference wires due to frost heaving. The variance ratios (Zar 1984) between the autumn and spring readings were for Set 1 = 1.93, $P > 0.20$; Set 2 = 1.25, $P > 0.20$; Set 3 = 1.23, $P > 0.20$.

Data analysis

Natural growth and the precipitation experiments were analysed using three-way ANOVAs with Species, Habitat/Irrigation level and Time of season as independent

factors. For the two-way factorial experiment at Abisko, means of length increments over the summer season were analysed with a repeated-measures ANOVA with Time of season as a within-subject factor and Species, Neighbour identity, Temperature, and UV-B flux as between-subject factors. A separate two-way ANOVA with Species and Neighbour identity as factors was run for the winter season. All analyses were carried out using SPSS for Windows 10.0 (SPSS Inc., Chicago, IL).

Results

Natural growth

Growth was clearly related to type of habitat for both species ($P < 0.001$, Fig. 1, Table 3). The lowest increment was measured for dry habitats and the highest for wet habitats. This was particularly evident during the early and peak summer periods (Habitat \times Time of season interaction, $P < 0.001$, Table 3). The increment of *D. elongatum* in wet habitats was much higher than

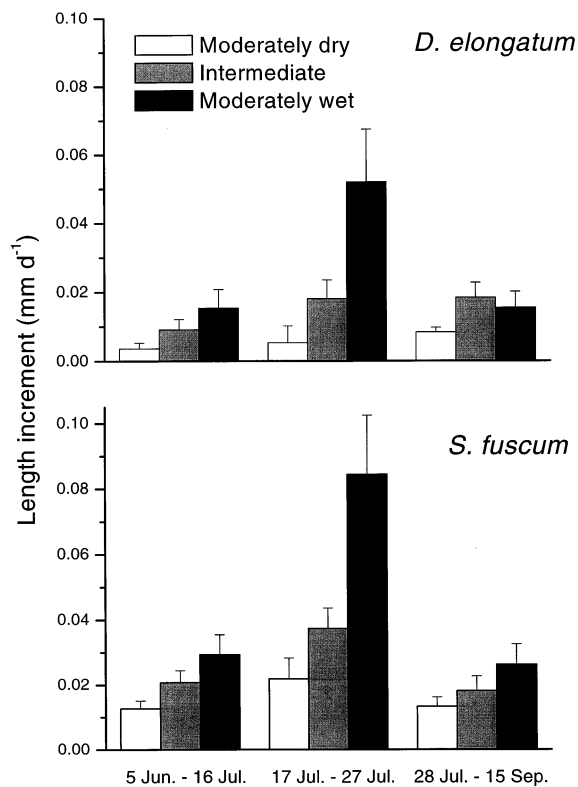


Fig. 1. Mean daily length increment ($\text{mm} \pm 1 \text{ SE}$) of *Dicranum elongatum* and *Sphagnum fuscum* under natural conditions in three habitats at Stordalen during three periods of the summer 1973. $N = 16$. The relation between growth and habitats was significant at $P < 0.001$ (Table 3).

Table 3. ANOVA results for the natural growth investigation at Stordalen 1973.

| Source | Df | MS | F | P |
|----------------------------------------|-----|--------|------|-----------|
| Species | 1 | 0.0116 | 16.4 | <0.001*** |
| Habitat | 2 | 0.0157 | 22.3 | <0.001*** |
| Time | 2 | 0.0130 | 18.5 | <0.001*** |
| Species \times Habitat | 2 | 0.0005 | 0.78 | 0.46 |
| Species \times Time | 2 | 0.0018 | 2.51 | 0.084 |
| Habitat \times Time | 4 | 0.0051 | 7.23 | <0.001*** |
| Species \times Habitat \times Time | 4 | 0.0001 | 0.16 | 0.96 |
| Error | 255 | 0.0007 | | |

*** $P < 0.001$.

that in dry habitats, fivefold during the early period, tenfold during the peak season. Overall, *S. fuscum* had a 67% larger increase in length than *D. elongatum* ($P < 0.001$) although the relative differences between the habitats were smaller in comparison with those of *D. elongatum*. The highest increments were measured during the peak season when growth in the wet habitats was ten times higher and nearly four times higher than in the dry habitats for *D. elongatum* and *S. fuscum*, respectively.

Simulated climate change

Increased precipitation had a significant effect on growth which generally increased ($P < 0.01$, Fig. 2, Table 4). This was particularly evident for plots irrigated at 1 mm per day, whereas the higher amounts resulted in no enhanced growth in comparison with the control ($P > 0.05$). During the early season, a 1 mm increase in precipitation nearly trebled the growth of *D. elongatum*. During the late season when irrigation had ceased, mean length increase was still about two thirds greater than that of the controls. Overall *S. fuscum* showed a 50% larger response than *D. elongatum* to enhanced precipitation ($P < 0.001$). An increase in precipitation by 1 mm (during the first two periods) tended to increase growth of *S. fuscum* by half over the controls during the early season and by approximately one third during the peak and late season. The insignificant effects of precipitation at a rate higher than 1 mm per day were similar to those for *D. elongatum*.

Increased temperature had a strong positive effect on the growth of both mosses ($P < 0.001$, Fig. 3, Table 5). Over the whole summer season of 1998 (June 12–September 12), *S. fuscum* increased 23% more than *D. elongatum* ($P = 0.064$, Fig. 3, Table 5). Significant interactions involving “Time of season”, “Species”, and “Temperature” indicated, however, that as the season progressed, the difference in growth between the two species increased, especially in plots with increased temperature (Fig. 4).

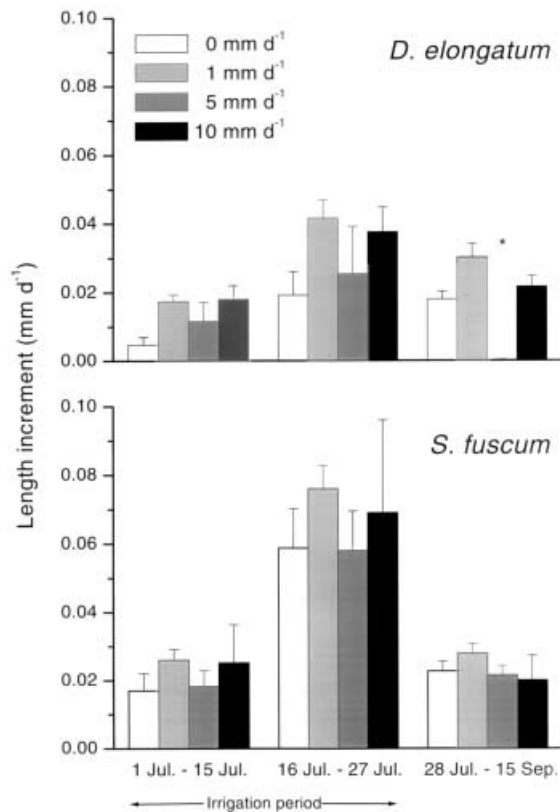


Fig. 2. Mean daily length increment ($\text{mm} \pm 1 \text{ SE}$) of *Dicranum elongatum* and *Sphagnum fuscum* in moderately dry habitats at Stordalen during three summer periods (1973). Three intensities of increased precipitation over ambient were simulated. Irrigation was made during the first two periods only. (*Note that the mean figure and SE for the third period at 5 mm for *D. elongatum* were negligible, 0.0002 and ± 0.0001 , respectively). $N = 5$. Increased precipitation had a significant effect on growth for both species ($P < 0.001$). *S. fuscum* had an overall 50% larger response than *D. elongatum* ($P < 0.001$, Table 4).

Increased UV-B had no statistically significant overall effect regardless of experimental system. However, there was a significant Time \times UV-B interaction ($P = 0.03$, Table 5), which was mainly caused by *S. fuscum* responding negatively to increased UV-B under increased temperature at the peak of the growing season (Fig. 4, Table 5).

Table 4. ANOVA results for the irrigation experiment at Stordalen 1973.

| Source | Df | MS | F | P |
|-------------------------------------------|----|--------|------|-----------|
| Species | 1 | 0.0072 | 22.9 | <0.001*** |
| Irrigation | 3 | 0.0013 | 4.14 | 0.008** |
| Time | 2 | 0.0106 | 33.7 | <0.001*** |
| Species \times Irrigation | 3 | 0.0001 | 0.39 | 0.76 |
| Species \times Time | 2 | 0.0022 | 7.08 | 0.001** |
| Irrigation \times Time | 6 | 0.0002 | 0.49 | 0.81 |
| Species \times Irrigation \times Time | 6 | 0.0001 | 0.36 | 0.90 |
| Error | 96 | 0.0003 | | |

** $P < 0.01$, *** $P < 0.001$.

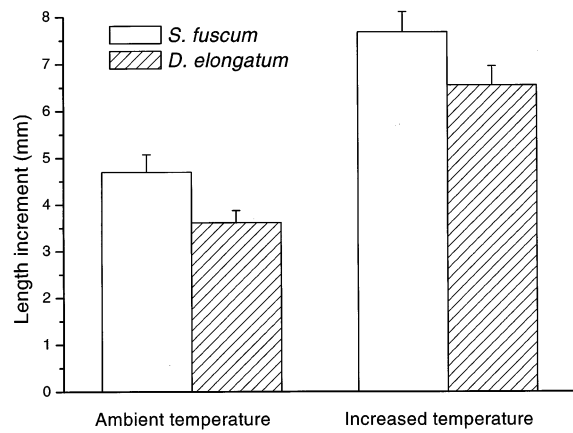


Fig. 3. Effect of increased temperature on growth at Abisko during the summer season 1998 (June 12–September 12) for *Dicranum elongatum* and *Sphagnum fuscum* in. Error bars are 1 SE. $N = 10$. The overall temperature effect for both species was significant at $P < 0.001$. *S. fuscum* increased 23% more than *D. elongatum* ($P = 0.064$, Table 5).

Species interactions

Neighbour identity had no effect on the length increment of either species during the summer season, neither in itself nor in interactions involving temperature or UV-B (Table 5). During the “winter period”, however, *S. fuscum* performed much better when growing with *D. elongatum* as a neighbour than in monoculture (Fig. 5). This was manifest as a significant Species \times Neighbour interaction ($P = 0.01$; Table 6).

Discussion

Humidity and temperature effects

As humidity and temperature increased so did moss growth both in the specific habitats where the species grow and in the experimental manipulations. Overall there was 50% larger growth in *S. fuscum* than in *D. elongatum* due to enhanced precipitation. The experiment indicated that ambient precipitation is sub-optimal for growth of both species. The optimum value is unknown but seems to be closer to an extra 1 mm per

day than to higher quantities. Some of the insignificant or negative effects of the higher precipitation may be an artefact of the method of application. Leaching of nutrients from the plants and ensuing reduced growth is difficult to avoid using distilled water even when precautions are taken to minimize such effects. Natural precipitation water contains nutrients of importance for growth, particularly in ombrotrophic sites (Malmer and Nihlgård 1980). Hence an increase of natural precipitation exceeding 1 mm per day together with its content of nutrients may enhance growth in contrast to what was indicated by the experiment. Our simulated 1 mm daily addition, however, corresponded to 55%–135% increase over the present normal summer values, which was much more than the predicted annual 20–25% increase for the middle of this century, particularly during winter (Maxwell 1992).

Increased temperature too has a large effect on growth even when increases are only approximately 2°C over ambient, corresponding to the lower range of predicted values for the middle of the 21st century (Maxwell 1992). As length and biomass are positively correlated (Sonesson and Johansson 1974), a combination of enhanced temperature by 2°C and precipitation by 20–25% may substantially increase the sequestering of carbon in habitats typical of the species. The superior growth of *S. fuscum* should result in a dominance over *D. elongatum* in moderately wet to moderately dry habitats. Also the natural growth today under ambient conditions indicates superior growth of *S. fuscum*.

Mosses are strongly dependent on environmental conditions due to their poikilohydric nature (Sveinbjörnsson and Oechel 1992, Tenhunen et al. 1992, Green and Lange 1994). Hydration has a direct effect on performance and temperature has an indirect effect through its control of hydration. Thus, the interaction

between hydration and temperature may be particularly important for moss performance. Growth in *Hylocomium splendens* was found to be highest in humid and mild temperature sites (Callaghan et al. 1997) and there was an increase in biomass and rates of ramification during years with wetter climate than normal (Økland 1997). Increased hydration and temperature together resulted in increased length in *Polytrichum commune* (Potter et al. 1995), whereas irrigation alone stimulated length growth of *Dicranum majus* (Hanslin et al. 2001).

During winter (i.e. late autumn-spring), *S. fuscum* grew better with *D. elongatum* as neighbour than in monoculture, whereas the opposite was true for *D. elongatum* itself (Fig. 5). An explanation for the negative length values could be a dehydration of peat during winter and differences in mechanical strength between the two species. The strength of *S. fuscum* shoots appears to be much lower than that of *D. elongatum* and dehydration might cause the shoots to collapse. Differences in mechanical strength of the stems of *Hylocomium splendens* have been shown to be related to erect and prostrate growth forms (Ross et al. 1998). The decrease may also be an effect of surface tension due to a lowering water level of the peat (Clymo, pers. comm.). During winter, *S. fuscum* individuals growing adjacent to *D. elongatum* will get support resulting in improved growth. After the thaw of seasonal frost above the permafrost table, hydration of the *S. fuscum* mats will be restored and the shoots will return to their former shape.

UV effects

The negative UV-B effect on *S. fuscum* during the peak season might have been an interaction with a drought

Table 5. ANOVA results for the experimental summer period at Abisko 1998 (June 12–September 12).

| Source | df | MS | F | P |
|------------------------|--------|------|------|-----------|
| Time of season | 2, 208 | 10.8 | 23.7 | <0.001*** |
| Species | 1, 104 | 8.39 | 3.49 | 0.064+ |
| Neighbour identity | 1, 104 | 0.17 | 0.07 | 0.79 |
| Temperature | 1, 104 | 70.5 | 29.3 | <0.001*** |
| UV-B | 1, 104 | 0.12 | 0.05 | 0.82 |
| Time × Species | 2, 208 | 2.37 | 5.20 | 0.006** |
| Time × Neighbour | 2, 208 | 0.99 | 2.18 | 0.12 |
| Time × Temp. | 2, 208 | 2.85 | 6.24 | 0.002** |
| Time × UV-B | 2, 208 | 1.62 | 3.55 | 0.030* |
| Species × Neighbour | 1, 104 | 0.08 | 0.03 | 0.86 |
| Species × Temp. | 1, 104 | 0.18 | 0.08 | 0.78 |
| Species × UV-B | 1, 104 | 2.62 | 1.09 | 0.30 |
| Neighbour × Temp. | 1, 104 | 1.22 | 0.51 | 0.48 |
| Neighbour × UV-B | 1, 104 | 2.75 | 1.15 | 0.29 |
| Temp. × UV-B | 1, 104 | 1.24 | 0.52 | 0.47 |
| Time × Species × Temp. | 2, 208 | 1.82 | 3.99 | 0.020* |
| Time × Species × UV-B | 2, 208 | 1.06 | 2.31 | 0.10+ |
| Time × Temp. × UV-B | 2, 208 | 1.36 | 2.99 | 0.053+ |

No three- or higher-order interactions other than those reported significant at or below $P=0.10$, + $P<0.10$, * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

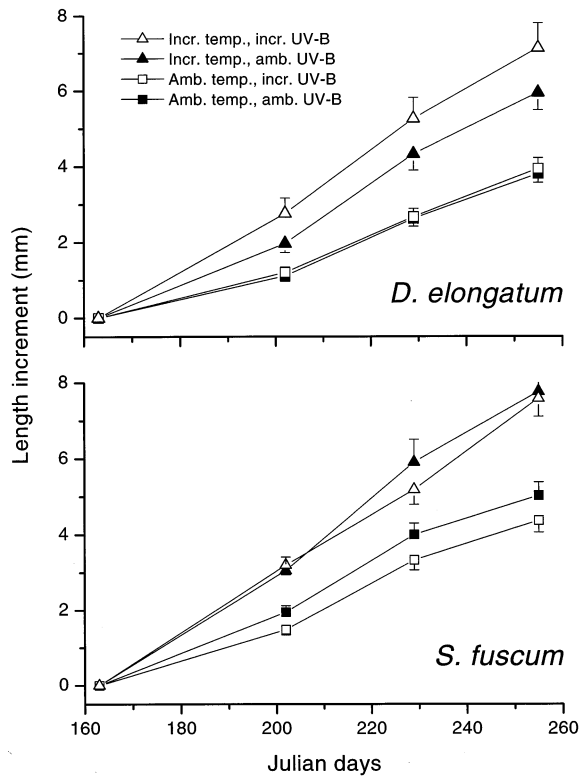


Fig. 4. Length increments for three periods at Abisko during the summer season 1998 (June 12–September 12) for *Sphagnum fuscum* and *Dicranum elongatum* growing under different levels of temperature and UV-B. Error bars are 1 SE. $N = 5-10$. During the peak season increased UV-B had a negative effect on *S. fuscum* under increased temperature ($P = 0.03$). There were no overall seasonal UV effects on either species (Table 5).

effect due to the occurrence of temperatures higher than at the beginning and end of the experimental period. Although the overall seasonal temperature effect on growth was positive, which suggests adequate (although not necessarily optimal) hydration, high temperatures during the peak season might have resulted in some water limitation (Fig. 1).

The result of the enhanced UV-B-radiation experiment was in contrast to our expectations from previous experiments on *S. fuscum* in the area. Apart from the significantly negative effect during the peak season, which could be due to an interaction with drought, there was no overall seasonal UV-B effect. Nor were there any significant effects on biomasses or the chlorophyll and flavonoid contents in either moss species (data not shown). In a similar experiment on a similar mire site (500 m distant from ours), for which the square-wave technique alone was applied, Gehrke (1998) found significantly negative UV-B effects on *S. fuscum* which were more or less consistent throughout the 1994 and 1995 seasons. The coefficient of variation of our length measurements was 64% and that of

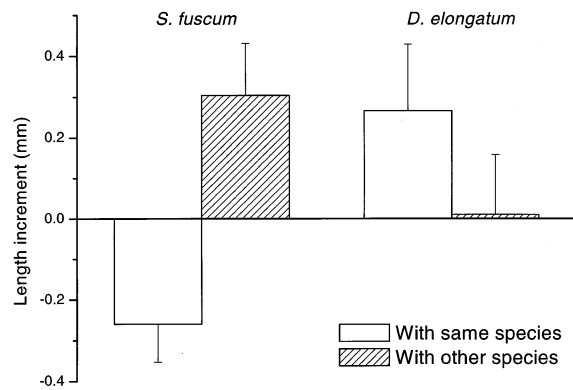


Fig. 5. Length increments at Abisko during the “winter period”, i.e. September 5, 1997–June 12, 1998, for *Sphagnum fuscum* and *Dicranum elongatum* growing with the same or with the other species as neighbour. Error bars are 1 SE. $N = 10$. The neighbour effect was significant at $P = 0.01$ (Table 6).

Gehrke’s was about 55%, however (estimated from the figures in Gehrke 1998). This slight (possible) difference in variability cannot explain the disagreeing results. Different weather conditions during the experimental periods might have been a cause. The precipitation figures were approximately similar, but the mean air temperatures were $0.1^{\circ}\text{C}-2^{\circ}\text{C}$ lower than normal in 1994 and in 1995 but $1^{\circ}\text{C}-2^{\circ}\text{C}$ warmer in 1998. It is known that the enzyme system for DNA repair works better at higher temperatures (Takeuchi et al. 1996, Pakker et al. 2000, Paulsson and Björn 2001). The higher temperatures in 1998 might have reduced the sensitivity of the mosses to UV-B in contrast to the effects in 1994–95.

The insignificant or lack of effect of enhanced UV-B in our experiment is similar to what was reported for other mosses in the Arctic (Björn et al. 1999, Gwynn-Jones et al. 1999) and for the Antarctic population of *Sphagnum magellanicum* (Searles et al. 1999).

Long-term effects

If temperatures and precipitation increase, *D. elongatum* is likely to be hampered by shading from the overtopping *S. fuscum* and may eventually become extinct in wet to moderately dry habitats. However, this

Table 6. ANOVA results for the “winter period” at Abisko, i.e. September 5, 1997–June 12, 1998.

| Source | df | MS | F | P |
|----------------------------|----|------|------|---------|
| Species | 1 | 0.27 | 0.54 | 0.46 |
| Neighbour identity | 1 | 0.47 | 0.94 | 0.33 |
| Species \times Neighbour | 1 | 3.36 | 6.72 | 0.010** |
| Error | 76 | 0.50 | | |

** $P < 0.01$.

may not apply to the “extreme dry habitats”, i.e. on the summits of the hummocks, where *S. fuscum* does not grow. The only competitors to *D. elongatum* on these tops seem to be lichens. *D. elongatum* might survive in these habitats even in the next 50–100 year climate scenario (Maxwell 1992, Cattle and Crossley 1995). However, temperature and climate are changing concurrently with other environmental factors such as nitrogen deposition. Over the last 20 years, many of the ombrotrophic parts of the Stordalen mire have become more eutrophic and formerly abundant *S. fuscum* has become very restricted in abundance (Svensson et al. 1999). Although this study has identified the relative importance of three environmental change factors for two moss species, responses to other factors in combination need to be studied before implications for bog growth and atmospheric carbon sequestration can be made.

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References

- Andersson, N. Å., Callaghan, T. V. and Karlsson, P. S. 1996. The Abisko Scientific Research Station. – *Ecol. Bull.* 45: 11–14.
- Bertgren, M. 1997. Effects of increased UV-B radiation on mosses in a subarctic climate with a square-wave and a modulated irradiation system. – Degree project in Plant Physiology at Dept. Plant Physiology, Univ. of Lund, Sweden and Dept. of Applied Science Mid Sweden Univ., Härnösand, Sweden.
- Billings, W. D., Luken, J. O., Mortensen, D. A. and Peterson, K. M. 1982. Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment. – *Oecologia* 53: 7–11.
- Billings, W. D., Luken, J. O., Mortensen, D. A. and Peterson, K. M. 1983. Increasing atmospheric carbon dioxide: possible effects on arctic tundra. – *Oecologia* 58: 286–289.
- Björn, L. O. and Murphy, T. M. 1985. Computer calculations of solar ultraviolet radiation at ground level. – *Physiol. Vég.* 23: 555–561.
- Björn, L. O., Callaghan, T. V., Gehrke, C. et al. 1999. Ozone depletion ultraviolet radiation and plant life. – *Chemosphere: Global Change Sci.* 1: 449–454.
- Botch, M. S. and Masing, V. V. 1983. Mire ecosystems in the U.S.S.R. – In: Gore, A. J. P. (ed.), *Mires: swamp, bog, fen and moor. Regional studies. Ecosystems of the World 4B*. Elsevier, pp. 187–223.
- Bowles, F. P. 1997. The description of the Abisko UV-B modulator. – Technical Paper, Research Designs, Woods Hole MA 02543, USA.
- Caldwell, M. M., Gold, W. G., Harris, G. and Ashurst, C. W. 1983. A modulated lamp system for solar UV-B (280–320 nm) supplementation studies in the field. – *Photochem. Photobiol.* 37: 479–485.
- Callaghan, T. V., Carlsson, B. Å., Sonesson, M. and Temesváry, A. 1997. Between-year variation in climate-related growth of circumpolar populations of the moss *Hylocomium splendens*. – *Funct. Ecol.* 11: 157–165.
- Cattle, H. and Crossley, J. 1995. Modelling Arctic climate change. – *Philos. Trans. R. Soc. Lond. A* 352: 201–213.
- Chapman and Welsh (unpublished) cited in Weller, G. 2000. The weather and climate of the Arctic. – In: Nutall, M. and Callaghan, T. V. (eds), *The Arctic: environment, people, policy*. Harwood Academic publishers, pp. 143–160.
- Christensen, T. R., Jonasson, S., Callaghan, T. V. and Havström, M. 1999. On the potential CO₂ release from tundra soils in a changing climate. – *Appl. Soil Ecol.* 11: 127–134.
- Christensen, T. R., Friborg, T., Sommerkorn, M. et al. 2000. Trace gas exchange in a high arctic valley 1: Variations in CO₂ and CH₄ flux between tundra vegetation types. – *Global Biogeochem. Cycles* 14: 701–714.
- Clymo, R. S. 1970. The growth of *Sphagnum*: methods of measurements. – *J. Ecol.* 58: 13–49.
- Gehrke, C. 1998. Effects of enhanced UV-B radiation on production-related properties of a *Sphagnum fuscum* dominated subarctic bog. – *Funct. Ecol.* 12: 940–947.
- Gehrke, C., Johanson, U., Gwynn-Jones, D. et al. 1996. Effects of enhanced ultraviolet-B radiation on terrestrial subarctic ecosystems and implications for interactions with increased atmospheric CO₂. – In: Karlsson, P. S. and Callaghan, T. V. (eds), *Plant ecology in the subarctic Swedish Lapland*. *Ecol. Bull.* 45: 192–203.
- Green, T. G. A. and Lange, O. L. 1994. Photosynthesis in poikilohydric plants: a comparison of lichens and bryophytes. – In: Schulze, E. D. and Caldwell, M. M. (eds), *Ecophysiology of photosynthesis*. Springer-Verlag, pp. 319–344.
- Gwynn-Jones, D., Johanson, U., Phoenix, G. K. et al. 1999. UV-B impacts and interactions with other co-occurring variables of environmental change: an arctic perspective. – In: Rozema, J. (ed.), *Stratospheric ozone depletion: the effects of enhanced UV-B radiation*. Backhuys Publisher, pp. 187–201.
- Hanslin, H. M., Bakken, S. and Pedersen, B. 2001. The impact of watering regime and ambient relative humidity on the effect of density on growth in two boreal forest mosses, *Dicranum majus* and *Rhytidiadelphus loreus*. – *J. Bryol.* 23: 43–54.
- IPCC 1996. *Climate Change 1995. Impacts, adaptations and mitigation of climate change: scientific–technical analyses*. Cambridge Univ. Press.
- Johanson, U., Gehrke, C., Björn, L. O. et al. 1995. The effects of enhanced UV-B radiation on a subarctic heath ecosystem. – *Ambio* 24: 106–111.
- Kalela, A. 1939. Über Wiesen und wiesenartige Pflanzengesellschaften auf der Fischerhalbinsel in Petsamo Lappland. – *Acta Forest. Fenn.* 48: 1–523.
- Kalliola, R. 1939. Pflanzensociologische Untersuchungen in der alpinen Stufe Finnisch-Lapplands. – *Ann. Bot. Soc. Zool. Bot. Fenn. 'Vanamo'* 13: 1–321.
- Kivinen, E. and Pakarinen, P. 1980. Peatland areas and the proportion of virgin peatlands in different countries. – *Proc. 6th Int. Peat Congr., Duluth*, pp. 52–54.
- Malmer, N. and Nihlgård, B. 1980. Supply and transport of mineral nutrients in a subarctic mire. – *Ecol. Bull.* 30: 63–95.
- Malmer, N. and Wallén, B. 1996. Peat formation and mass balance in subarctic ombrotrophic peatlands around Abisko, northern Scandinavia. – In: Karlsson, P. S. and Callaghan, T. V. (eds), *Plant ecology in the subarctic Swedish Lapland*. *Ecol. Bull.* 45: 79–92.
- Marion, G. M., Henry, G. H. R., Freckman, D. W. et al. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. – *Global Change Biol.* 3 (suppl.): 20–32.
- Maxwell, B. 1992. Arctic climate: potential for change under global warming. – In: Chapin III, F. S., Jeffries, R. L., Reynolds, J. F. et al. (eds), *Arctic ecosystems in a changing*

- climate. An ecophysiological perspective. Academic Press, pp. 11–34.
- Oechel, W. C., Hastings, S. T., Vourlitis, G. et al. 1993. Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. – *Nature* 361: 520–523.
- Oechel, W. C., Vourlitis, G. L., Hastings, S. J. and Bochkarev, S. A. 1995. Change in arctic CO₂ flux over two decades: effects of climate change at Barrow, Alaska. – *Ecol. Appl.* 5: 846–855.
- Økland, R. H. 1997. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. III. Six-year demographic variation in two areas. – *Lindbergia* 22: 49–68.
- Pakker, H., Martins, R., Boelen, P. et al. 2000. Effects of temperature on the photoreactivation of ultraviolet-B-induced DNA damage in *Palmaria palmata* (Rhodophyta). – *J. Phycol.* 36: 334–341.
- Paulsson, L. M. and Björn, L. O. 2001. Temperature-dependent formation and photorepair of DNA damage induced by UV-B radiation in suspension-cultured tobacco cells. – *J. Photochem., Photobiol. B: Biol.* (in press).
- Potter, J. A., Press, M. C., Callaghan, T. V. and Lee, J. A. 1995. Growth responses of *Polytrichum commune* and *Hylocomium splendens* to simulated environmental change in the subarctic. – *New Phytol.* 131: 533–541.
- Ross, S. E., Callaghan, T. V., Ennos, A. R. and Sheffield, E. 1998. Biomechanics and growth form of the moss *Hylocomium splendens*. – *Ann. Bot.* 82: 787–793.
- Ruuhijärvi, R. 1960. Über die regionale Einteilung der nordfinnischen Moore. – *Ann. Bot. Soc. Zool. Bot. Fenn. 'Vanamo'* 31: 1–360.
- Rydén, B. E. 1980. Climatic representativeness of a project period – epilogue of a tundra study. – *Ecol. Bull.* 30: 55–62.
- Searles, P. S., Flint, S. D., Dias, S. B. et al. 1999. Solar ultraviolet-B radiation influence on *Sphagnum* bog and *Carex* fen ecosystems: first field season findings in Tierra del Fuego, Argentina. – *Global Change Biol.* 5: 225–234.
- Searles, P. S., Flint, S. D. and Caldwell, M. M. 2001. A meta analysis of plant field studies simulating stratospheric ozone depletion. – *Oecologia* 127: 1–10.
- Sjörs, H. 1982. The zonation of northern peatlands and their importance for the carbon balance of the atmosphere. – In: Gobal, R., Turner, R. E., Wetzal, R. G. and Whigham, D. F. (eds), *Wetlands: ecology and management*. National Inst. Ecol., Jaipur, pp. 11–13.
- Sonesson, M. 1970a. Studies on mire vegetation in the Torne-träsk area. Northern Sweden. III. Communities of the poor mires. – *Opera Bot.* 26: 1–122.
- Sonesson, M. 1970b. Studies on mire vegetation in the Torne-träsk area. Northern Sweden. IV. Some habitat conditions of their poor mires. – *Botaniska Notiser* 123: 7–25.
- Sonesson, M. (ed.) 1980a. Ecology of a subarctic mire. – *Ecol. Bull.* 30: 1–313.
- Sonesson, M. 1980b. Growth of *Sphagnum riparium* Ångstr. in relation to some environmental factors in the Stordalen mire. – *Ecol. Bull.* 30: 191–207.
- Sonesson, M. and Johansson (now Halling), S. 1974. Bryophyte growth, Stordalen 1973. – In: Flower-Ellis, J. G. K. (ed.), *Progress report 1973*. Technical Report No. 16 of the Swedish IBP Tundra Biome Project. Swedish Natural Science Research Council. Stockholm, pp. 17–27.
- Sonesson, M., Jonsson, S., Rosswall, T. and Rydén, B. E. 1980. The Swedish IBP/Tundra Biome Project. Objective-Planning-Site. – *Ecol. Bull.* 30: 7–25.
- Sonesson, M., Callaghan, T. V. and Carlsson, B. Å. 1996. Effects of enhanced ultraviolet radiation and carbon dioxide concentration on the moss *Hylocomium splendens*. – *Global Change Biol.* 2: 67–73.
- Sveinbjörnsson, B. and Oechel, W. C. 1992. Controls on growth and productivity of bryophytes: environmental limitations under current and anticipated conditions. – In: Bates, J. W. and Farmer, A. M. (eds), *Bryophytes and lichens in a changing environment*. Oxford Scientific Publications, pp. 77–102.
- Svensson, B. H., Christensen, T. R., Johansson, E. and Öquist, M. 1999. Interdecadal changes in CO₂ and CH₄ fluxes of a subarctic mire: Stordalen revisited after 20 years. – *Oikos* 85: 22–30.
- Takeuchi, Y., Murakami, M., Nakajima, N. et al. 1996. Induction and repair of damage to DNA in cucumber cotyledons irradiated with UV-B. – *Plant Cell Physiol.* 37: 181–187.
- Tenhunen, J. D., Lange, O. L., Hahn, S. et al. 1992. The ecosystem role of poikilohydric tundra plants. – In: Chapin III, F. S., Jefferies, R. L., Reynolds, J. F. et al. (eds), *Arctic ecosystems in a changing climate*. Academic Press, pp. 213–237.
- van Oijen, M., Schapendonk, H. C. M., Jansen, M. J. H. et al. 1999. Do open-top chambers overestimate the effects of rising CO₂ on plants? An analysis using spring wheat. – *Global Change Biol.* 5: 411–421.
- Zar, J. H. 1984. *Biostatistical analysis*. – Prentice-Hall.