Patterns of species richness and vegetative performance in heath ecosystems at Þingvellir, Southwest Iceland

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SUMMARY

The *Racomitrium lanuginosum* (Hedw.) Brid. moss heath is a unique environment and is of great importance for co-occurring established vascular plants. A thick moss carpet can prevent or restrict the growth of vascular plants as they are exposed to more unfavourable growth conditions, but the effect on species richness and abundance is less known. To investigate the negative effects of a well-developed moss carpet on established vascular plants, patterns of species richness, shoot density, and number of leaves (*Carex bigelowii* Schwein. and *Thalictrum alpinum* L.) were studied in two different vegetation types, *Racomitrium lanuginosum* moss heath, and dwarf shrub heath in Þingvellir National Park, Southwest Iceland. Species richness was higher in dwarf shrub heath and increased proportionally with the size of the shrub patches. Total species richness and plant functional dominance did not differ between vegetation types. There were no differences found in shoot density, percentage of flowering and juveniles, number of leaves in *Carex bigelowii*, or shoot density, flowering percentage or number of leaves in *Thalictrum alpinum* between the vegetation types. However, leaf length of *Carex bigelowii* was higher in the dwarf shrubs heath, indicating more favourable growth conditions, shade or shelter effects. It is possible that translocation is taking place between the shoots of the clonal vascular plants in this study so that the plants themselves are counteracting unfavourable effects in the different vegetation types. The effect of global climatic change on moss heaths in Iceland is briefly discussed.

Key words: *Carex bigelowii*, *Racomitrium lanuginosum* moss heath, species richness, *Thalictrum alpinum*

YFIRLIT

Gamburmosaheiðin þar sem *Rachomitrium lanuginosum* (Hedw.) Brid. ræður ríkjum er sérstætt vistkerfi og er mikilvægt fyrir þær háplöntur sem í því vaxa. Þykkt mosalag getur hindrað eða dregið úr vexti háplantna vegna lakari vaxtarskilyrða, en áhrifin á tegundafjölbreytni eru minna þekkt. Til að rannsaka neikvæð áhrif vel þroskaðs mosalags á háplöntur voru dreifing í tegundafjölbreytni, sprotaþéttleiki og blaðafjöldi á stinnastör og brjóstagrasi rannsökuð í tveimur gróðursamfélögum, gamburmosaheiði og dvergrunnaheiði í Þjóðgarðinum á Þingvöllum. Tegundafjölbreytni var meiri í dvergrunnasamfélaginu og jókst hlutfallslega með stækkun runnasvæðanna, en heildar tegundafjölbreytni og virkar ríkjandi plöntur voru ekki marktækt mismundi á milli vistkerfa. Enginn munur mældist á milli vistkerfa í fjölda sprota, hlutfalli blóma og ungsprota og blaðafjölda hjá stinnastör né í þéttleika sprota, blómgunarhlutfalli og blaðafjölda hjá brjóstagrasi. Samt sem áður var blaðlengd stinnastarar meiri í dvergrunnasamfélaginu sem bendir til betri vaxtarkjara, skyggingar eða skjóláhrifa. Hugsanlega fer fram efnaflutningur á milli sprota hjá klónuðum háplöntum í þessari rannsókn, þannig að það vinni gegn óæskilegum umhverfisáhrifum í vistkerfunum tveimur. Áhrif væntanlegra loftslagsbreytinga eru rædd stuttlega.

INTRODUCTION

Bryophytes are important components in arctic and subarctic vegetation and they may develop extensive moss carpets that can dominate large areas (Longton 1982, 1984). Such well-developed moss carpets are not commonly found in terrestrial biomes, even though there is often a well-defined bryophyte layer in many vegetation types (Keizer *et al*. 1985). Extensive areas of moss heath vegetation dominated by *Racomitrium lanuginosum* (Hedw.) Brid. are common on islands with suitable soil conditions (e.g. porous volcanic soils) and an oceanic climate, although it is also a widespread vegetation type throughout the Arctic (Longton 1982). In Iceland, mosses are important in many natural ecosystems (Aradóttir *et al*. 2000) and *Racomitrium lanuginosum* in particular is common and dominant in many plant communities (Bjarnason 1991). The *Racomitrium* moss heath plays an important role in the primary succession of lava and other rock types (Bjarnason 1991, Thorsteinsson & Arnalds 1992) and in secondary succession of eroded land (Thorsteinsson & Arnalds 1992). Furthermore, the *Racomitrium* moss heath is also a prominent vegetation type at higher altitudes where growth conditions are too extreme for vascular plants (Thorsteinsson & Arnalds 1992).

The moss heath is a unique ecosystem where the moss functions as the substrate for vascular plants (cf. peatlands, Malmer *et al.* 1994). The thick moss carpet may regulate a number of factors that are of great importance for the co-occurring vascular plants, e.g. temperature (Skre & Oechel 1979, van der Wal *et al*. 2001), thaw depth (Ng & Miller 1977, Miller *et al*. 1980, Tenhunen *et al*. 1992), decomposition rates (e.g. Russell 1990), and nutrient availability (e.g. Jónsdóttir *et al*. 1995). A dense moss layer may also restrict or prevent the growth of vascular plants as the plants are exposed to more unfavourable growth conditions (van der Wal *et al*. 2001). Less directly, the unfavourable growth conditions may also affect species richness and vegetative performance of vascular plants negatively. For example, in *Racomitrium* moss heath, it has been repeatedly noted that vascular plants are few and scattered (e.g. Tallis 1958, Thorsteinsson & Arnalds 1992).

Up to now the effects of a moss carpet on established vascular plants have received little attention (Herben & Wagnerová 2004), although two studies have been carried out. Van der Wal *et al*. (2001) showed that herbivores may influence the plant abundance by reducing the thickness of the moss layer, and Herben & Wagnerová (2004) showed that bryophyte removal in a grasslands positively affected graminoid species with a high ramet turnover. However, these studies have mainly focused on plant growth and rather small-scale spatial patterns (i.e. 1 m^2 and 50 x 50 cm plots, respectively). Knowledge of plant species richness and vegetative performance at larger scales are important in many respects, for example when translating ecological work from species to mesoscale or landscape levels, and may also be useful in the context of future environmental change. In the moss heath ecosystem it is not possible to experimentally remove the bryophyte layer in order to analyse neighbour interactions, as a removal would have detrimental effects on co-occurring vascular plants (these are often long-lived clonal plants). Instead, species richness and vegetative performance of the moss heath vegetation can be compared to other vegetation types. This descriptive study approach cannot separate causality relationships and is therefore scientifically rather limited. Nevertheless, irrespective of origin, significant differences may be informative and underpin the awareness of how established vascular plants are affected by a thick moss carpet, as well as increasing our ecological understanding of the function of moss dominated ecosystems.

The aims of this study were to:

Describe patterns of species richness in moss heath and dwarf shrub heath and to compare variation in shoot density and numbers of

Table 1. Species list, plant functional types and vegetation types, M=moss heath, S=dwarf shrub heath.

Species	**Plant functional type**	**Vegetation type**
Agrostis vinealis Schreb.	Graminoid	M, S
Bistorta vivipara (L.) S. Gray.	Forb	M, S
Carex bigelowii Schwein.	Graminoid	M, S
Cetraria islandica (L.) Ach.	Lichen	M
Deschampsia flexuosa (L.) Trin.	Graminoid	M, S
Empetrum nigrum L.	Evergreen shrub	M, S
Galium boreale L.	Forb	S
Galium normanii O. C. Dahl	Forb	S
Galium verum L.	Forb	S
Hylocomium splendens (Hedw.) Schimp.	Bryophyte	M, S
Juncus trifidus L.	Graminoid	M, S
Luzula multiflora (Retz.) Lej.	Graminoid	S
Pleurozium schreberi (Brid.) Mitt.	Bryophyte	S
Poa alpina L.	Graminoid	M, S
Poa glauca Vahl.	Graminoid	M, S
Racomitrium lanuginosum (Hedw.) Brid.	Bryophyte	M
Ranunculus acris L.	Forb	S
Salix herbacea L.	Deciduous shrub	S
Salix lanata L.	Deciduous shrub	S
Salix phylicifolia L.	Deciduous shrub	S
Thalictrum alpinum L.	Forb	M, S
Thymus praecox Opiz.	Forb	S

leaves between vegetation types in two clonal vascular plants.

Species richness and dominance were compared between two vegetation types in Þingvellir National Park in Southwest Iceland, *Racomitrium* moss heath and dwarf shrub heath. Size of dwarf shrub patches was related to total species richness. Detailed studies were performed on two clonal vascular plants (*Carex bigelowii* Schwein. and *Thalictrum alpinum* L.) and compared between the two vegetation types. On *Carex bigelowii,* measurements were made on shoot density, percentage flowering and juveniles, number of leaves and leaf length. On *Thalictrum alpinum* shoot density, percentage flowering, and number of leaves were measured.

MATERIALS AND METHODS

Study site

The site is situated in Þingvellir National Park, Southwest Iceland (64°17'N, 21° 05'W, at 120 m.a.s.l.), in maritime subarctic climate. More specifically, the site is located north of Þingvallavatn on a more than 9,000 year old post-glacial Eldborgir lava field in the subsidence area between the fissures Almannagjá and Hrafnagjá that are parts of the axial rift zone in Southwest Iceland (Sæmundsson 1992). The study site was chosen as it is representative for *Racomitrium* moss heaths in Iceland and is dominated by a well-developed stand of the ecosystem. In the same area, dwarf shrub heath is common with *Salix* spp., grasses, and forbs (Thorsteinsson & Arnalds 1992). Dwarf shrubs occur as patches in the moss heath, which facilitates comparison. The study site is within the fenced and protected area of Þingvellir National Park. The soil is well drained on highly permeable bedrock (Thorsteinsson & Arnalds 1992). For June-August in 1996 and 1997 the mean temperature was 9.9°C, and 10.2°C, respectively (Stenström 1998). At Þingvellir the annual temperature is rather low, but the growth conditions are favourable for both plants and bryophytes as the summer temperatures are relatively high and the annual precipitation is 1300-1400 mm (Einarsson MÁ 1992, Thorsteinsson & Arnalds 1992). Snow cover rarely persists for more than a few weeks or a month (Einarsson MÁ 1992). Since the area was fenced from grazing in 1928, the vegetation has successively developed from small trees to the contemporary woodland, while outside the protected areas trees are absent (Thorsteinsson & Arnalds 1992). In the Thingvellir area moss heath is the most extensive plant community followed by dwarf shrub heath (Thorsteinsson & Arnalds 1992). The existence of the well-developed moss heath (sometimes 10-30 cm thick) is partly explained by the long-term absence of herbivores. The *Racomitrium* moss heath contained few vascular plants, while the patches of dwarf shrub heath (of *Salix* spp.) had a more species rich understorey vegetation of forbs and grasses (Table 1). *Carex bigelowii* and *Thalictrum alpinum* were chosen for a detailed study of vegetative performance as they were common at the site and are also frequently found in both moss heath and dwarf shrub vegetation.

Analyses

To investigate patterns of species richness, three analyses were performed: Firstly, (in June 1996), the total number of all plants, bryophytes, and lichen species were recorded along 1 m intervals in four 20 m long lines. The lines were placed at 10 m apart in a N-S direction. Secondly, to get a measurement of species composition and plant functional groups at smaller scale, species occurrence along 10 cm intervals in two 30 m lines was recorded in August 1997. Lines were placed on at least two rather large patches of dwarf shrubs ca. 20 m apart in a N-S direction, approximately 400 m south of the first analysis area. In both line analyses, classification of vegetation types was based on the occurrence of *Racomitrium lanuginosum*. When the moss occurred without dwarf shrubs it was classified as moss heath, while presence of both *Racomitrium lanuginosum* and dwarf shrubs was classified as ecotone. Presence of dwarf shrubs without *Racomitrium lanuginosum* was classified as dwarf shrub heath. Thirdly, 32 *Salix* spp. dwarf shrubs were analysed in June 1996 for total species number (i.e. vascular plants, bryophytes, and lichens) and area along two perpendicular lines on each shrub. The measurements were made over a rather extensive

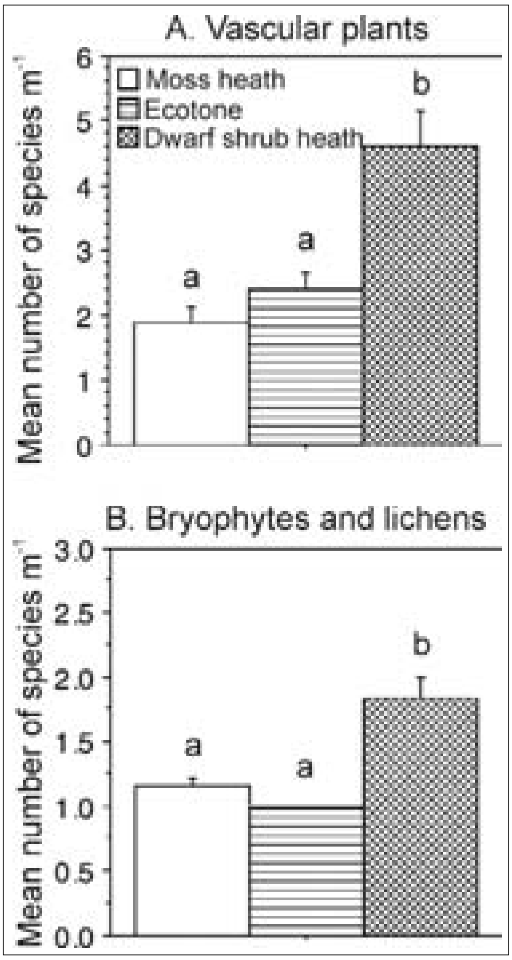


Figure 1. Relative species richness in the different vegetation types at Þingvellir per unit length (1 m). A: Vascular plant species. B: Bryophytes and lichens. Mean number ± 1 S.E. Bars with different letters were significantly different at P<0.05. n=numbers of 1 m intervals along four 20 m long lines. n=57 moss heath, n=5 ecotone, n=18 dwarf shrub heath.

area situated approximately 500 m north of the first analysis area.

To analyse vegetative performance in *Carex bigelowii* and *Thalictrum alpinum* in moss heath and dwarf shrub heath, an area ca 100 m west of the second analysis area was chosen in July 1997. In a 30 x 30 m plot, the size of 20 *Salix* spp. shrubs was measured. In the moss heath just beside (1-3 m) a plot of the same size as the *Salix* spp. shrub was established. *Carex bigelowii* and *Thalictrum alpinum* were only found beneath 16 of these shrubs. The number of individuals (i.e. tillers), flowering percentage, and the number of leaves of *Carex bigelowii* and *Thalictrum alpinum* in each patch of dwarf shrubs and the corresponding moss heath plot were counted. For *Carex bigelowii,* leaf length and juvenile percentage were also measured. Leaf length was measured once, as green leaves on vegetative tillers. The relative age of leaves was determined, as the new leaves develop from the main stem and are produced in chronological order. Old leaves may overwinter and continue to grow from intercalary meristems (Carlsson & Callaghan 1990). Plant species, plant functional groups, and the vegetation type for species occurrences are listed in Table 1. Nomenclature follows Einarsson E (1992) for vascular plants in the Þingvellir area, Thorsteinsson & Arnalds (1992) for vegetation type classification, Söderström & Hedenäs (1998) for bryophytes and Moberg & Holmåsen (1982) for lichens. Plant functional groups follow Chapin *et al*. (1996).

Statistical analyses

Data from the line analyses did not meet the assumptions of normality, hence, when testing for differences between number of species among moss heath, dwarf shrub heath, and the ecotone, the nonparametric Kruskal-Wallis test was employed. If significant differences were detected, a subsequent Mann-Whitney U-test was used (Sokal & Rohlf 1995). Relative species richness was calculated by dividing the total number of species with the total line length for each vegetation type or ecotone. Dominance was calculated by dividing the occurrence of plant functional groups with the total number of intervals for that vegetation type or ecotone (e.g. *Racomitrium lanuginosum* plant dominance in the moss heath was 1). Wilcoxon's signed rank test (Sokal & Rohlf 1995) was used to analyse for significant differences in plant functional group composition between vegetation types. Relationship between size of dwarf shrubs and species richness was analysed using correlation analysis. For all measurements in *Carex bigelowii* and *Thalictrum alpinum*, data that did not meet assumptions of normality were logarithmic transformed. A paired t-test was used to analyse for differences between the patches of

Table 2. Mean ± 1 S.E. for plant variables measured in *Carex bigelowii* and *Thalictrum alpinum* in the two different vegetation types at Þingvellir. All cases were non-significant ($P > 0.05$). n=16.

Variables	Vegetation type	
	Moss heath	Dwarf shrub heath
Carex bigelowii		
Shoots m^{-2}	10.45 ± 1.69	10.78 ± 2.36
Percentage juvenile shoots	15.29 ± 2.60	20.63 ± 4.03
Percentage flowering shoots	2.35 ± 1.83	4.38 ± 1.57
Number of leaves	4.62 ± 0.15	4.92 ± 0.15
Thalictrum alpinum		
Shoots m^{-2}	13.36 ± 3.40	17.46 ± 3.86
Percentage flowering shoots	4.21 ± 1.92	2.18 ± 0.94
Number of leaves	2.08 ± 0.13	1.99 ± 0.12

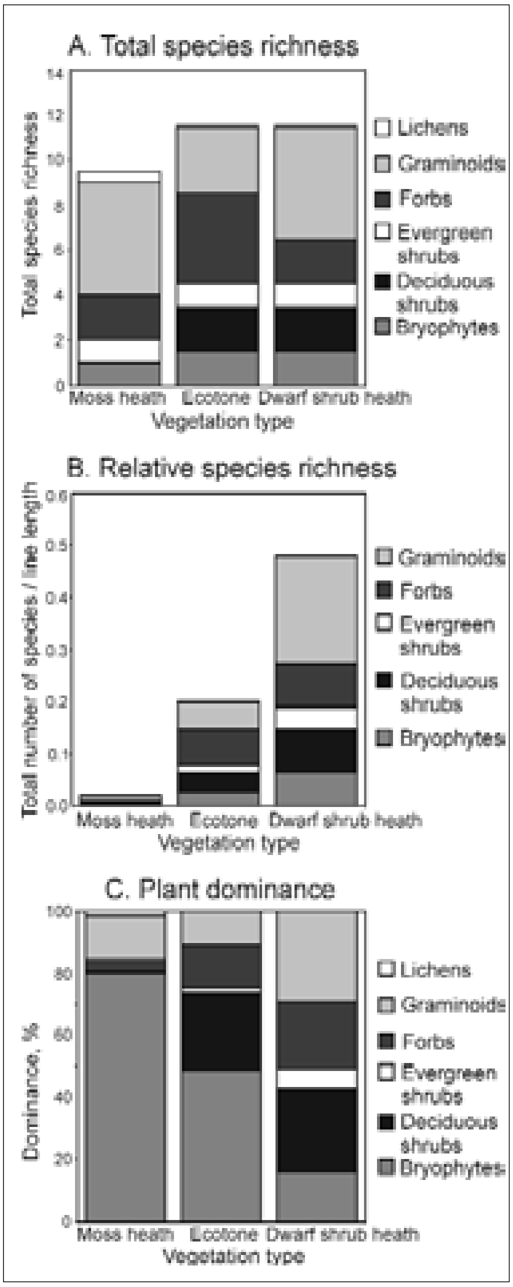


Figure 2. A: Total species richness at Thingvellir. B: Relative species richness (number of species per unit length, 10 cm). C: Plant dominance. n= numbers of 10 cm intervals along two 30 m long lines. n= 511 moss heath, n= 58 ecotone, n= 24 dwarf shrub heath. For species list and plant functional groups see Table 1.

dwarf shrubs and the corresponding moss heath plot.

RESULTS

The mean number of species of vascular plants, bryophytes, and lichens on 1 m was significantly higher in the dwarf shrub heath (Figure 1 A, B). Total species richness (Figure 2 A) was not significantly different between the vegetation types or the ecotone (significance levels not shown). Relative species richness (total number of species on line length; Figure 2 B) was significantly higher in both dwarf shrub heath ($P = 0.0109$) and ecotone ($P = 0.0109$) compared with moss heath. Plant dominance (Figure 2 C) was not significantly different between the vegetation types or ecotone. The correlation in dwarf shrub size and the number of species was significant ($r = 0.85$, $P < 0.001$; Figure 3).

In *Carex bigelowii*, no significant differences between vegetation types were found in the number of shoots m^{-2}, the percent of juvenile shoots, or number of leaves (Table 2, significance levels not shown). The percentage of flowering individuals was higher in dwarf shrub heath vegetation compared with moss heath, although not significant ($P=0.055$, Table 2). *Carex bigelowii* had longer leaves when growing in dwarf shrub heath vegetation as there were significant differences for leaf length from the youngest leaf up to leaf 6 (Figure 4). In *Thalictrum alpinum,* no significant differences were found in the number of shoots m^{-2}, number of leaves, or percentage of flowering between plants in moss heath or dwarf shrub heath vegetation (Table 2).

DISCUSSION

The relative species richness of vascular plants, bryophytes, and lichens was higher in the dwarf shrub heath. This indicates that the dwarf shrub heath vegetation type is generally a more favourable habitat for vascular plants (see also Thorsteinsson & Arnalds 1992) than the moss heath, perhaps because of better soil nutrient conditions. However, the total plant species richness did not differ between the vegetation types, i.e. over the examined area the different vegetation types and the ecotone contained similar numbers of species. As the line length for moss heath vegetation (n=511) was much larger than for the ecotone (n=58) and dwarf shrub heath (n=24), the total species richness should have been higher. The lack of relationship between species richness and area in the moss heath might have been a consequence of the extremely low relative species richness. Dwarf shrub patches examined for species richness in relation to size showed a normal relationship between area and species number. It seems as if the larger shrubs act as species hotspots, probably providing a more beneficial environment for vascular plants (i.e. "facilitation"; Callaway 1998). They are therefore important components in maintaining species richness in the area.

Plant dominance was not different between the vegetation types or the ecotone, although the trend is an increase of deciduous shrubs, forbs, and graminoids in the dwarf shrub heath and ecotone compared to moss heath. It is also possible that the statistical testing with only two replicates (the two line analyses) was unreliable as variation was high. Bryophytes were dominant and frequently found in all the vegetation types and the ecotone. For example, *Hylocomium splendens* (Hedw.) Schimp. was occasionally very abundant in the dwarf shrub heath.

Contrary to earlier indications of the negative effects of a thick moss carpet (van der Wal *et al*. 2001), there were no differences found in shoot density, percentage of flowering and juveniles, number of leaves in *Carex bigelowii*, or shoot density, flowering percentage or number of leaves in *Thalictrum alpinum* between the vegetation types. It therefore seems that in these variables, the two vascular plants studied here do not experience the very thick *Racomitrium* moss carpet as an unfavourable environment, or at least not more unfavourable than growing in the dwarf shrub heath. However, leaf length of *Carex bigelowii* was

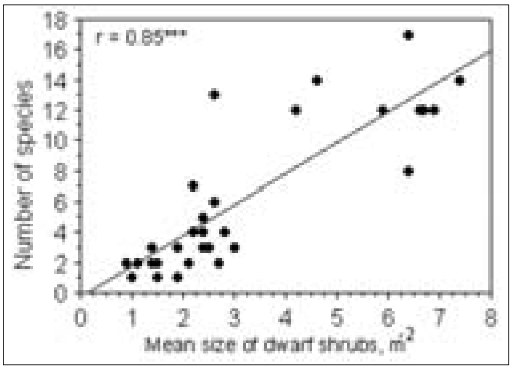
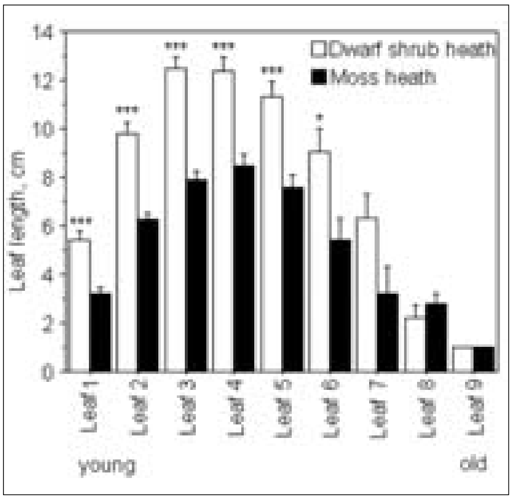


Figure 3. Correlation between size of the dwarf shrub patches of *Salix* spp. and the number of plant species at Þingvellir. n=32.

greater when plants grew in the dwarf shrub heath. This may indicate more favourable growth conditions, but may also indicate increased shade or shelter effects (e.g. Carlsson & Callaghan 1991). Nutrients are assumed to be more available in the dwarf shrub heath (with *Hylocomium splendens*) than in the *Racomitrium* moss heath. *Racomitrium lanuginosum* and *Hylocomium splendens* are very different in nutrient terms as nitrogen concentration in *Racomitrium lanuginosum* is



Figur 4. Leaf length of *Carex bigelowii* in moss heath and in dwarf shrub vegetation at Thingvellir. *** $P < 0.001$, * $P < 0.05$. Leaf number 1 youngest, leaf number 9 oldest. Mean values ± 1 S.E. n=16.

extremely low (e.g. Vitt & Pakarinen 1977), whereas nitrogen productivity of *Hylocomium splendens* is comparable with woody evergreen vascular plants (Eckstein 2000). Nitrogen content in *Racomitrium lanuginosum* was lower than in *Hylocomium splendens* at Þingvellir (Jägerbrand, unpublished). Litter with lower nitrogen content will decompose more slowly so that the nitrogen content of the moss will affect the nutrients available for all plants. Additionally, the shrubs may trap drifting snow in winter thereby decreasing temperature variation (e.g. Carlsson & Callaghan 1991).

It is difficult to analyse the effect of a thick moss carpet on the vascular plants without knowing the exact effect or how it affects plant expressions. Future studies in this area should therefore involve more exact measurements of the moss carpet (e.g. thermal properties, water-retention capacities and nutrient status, see van der Wal *et al.* 2001) concurrently with studies of how these factors may influence vascular plants.

There are competitive as well as beneficial effects of a thick moss carpet that may influence vascular plants. Some of the competitive effects are related to space, nutrients, light, and temperature. The moss carpet is continuously growing upwards and thereby putting vascular plants at the risk of being over-grown (Malmer *et al*. 1994, Svensson 1995). However, clonal vascular plants may escape competition from the moss carpet by producing new tillers. *Carex bigelowii* has been shown to have physiological integration of interconnected tillers and that translocation may take place from one or two year old tillers into nine to eleven year old tillers (Jónsdóttir & Callaghan 1988). Consequently, it is possible that translocation is taking place between shoots in the two different vegetation types so that the plants themselves are counteracting or buffering unfavourable effects in the environment. It is not known what influence the ability of translocation between tillers has had on this investigation.

The moss heath plays a significant role as a part of the ecosystems in terms of e.g. primary production, carbon, and nutrient cycling. The moss *Racomitrium lanuginosum* is one of the most common mosses found in Iceland, often covering vast unproductive areas and protecting against erosion. A potential threat against the moss heath vegetation is the global climate change. The anticipated global warming will probably cause changes in the moss heath ecosystems as *Racomitrium lanuginosum* has been shown to operate with 5°C as its optimum temperature for net photosynthesis (Kallio & Heinonen 1973). Therefore, it is likely that an elevated temperature will cause a decreased growth of the moss. However, Jónsdóttir *et al*. (submitted) showed that there were no effects of an experimentally increased temperature on the plant community in a *Racomitrium* moss heath in Iceland, whereas in a dwarf shrub heath, the deciduous and evergreen shrubs increased and bryophytes decreased. Increased shrub abundance and dominance (mainly by *Betula nana* L.) have also been shown in Alaska under conditions of both experimental and observed warming (Chapin *et al*. 1995, Sturm *et al*. 2001). The possible shrub increase will probably cause decreases in the moss heath ecosystems with unknown secondary consequences.

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