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Improved water retention links high species richness with increased productivity in arctic tundra moss communities

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Abstract A positive relationship between plant species richness and ecosystem functioning has been found in a number of experimental studies. Positive species interactions at high species numbers have been suggested as a cause, but mechanisms driving positive interactions have not often been tested. In this experiment we asked three questions: (1) What is the relationship between species richness and productivity in experimentally constructed moss communities? (2) Is this relationship affected by plant density? and (3) Can changes in moisture absorption and retention explain observed relationships? To answer these questions we exposed arctic tundra moss communities of different species richness levels (1–11 species) and two different densities in the greenhouse to two levels of drought (short and long). Biomass (by the community and individual species), height and community moisture absorption and retention were measured as response variables. High species diversity increased productivity (more so in low-density plots than in high-density plots), but only when plots were watered regularly. Plot moisture retention was improved at high species richness as well, and plant height and variation in height was increased compared to plants in monoculture. Under high-density and short-drought conditions 10 out of 12 species grew better in mixture than in monoculture, but under the long drought treatment only six species did. A positive feedback loop between biomass and improved humidity under high diversity was supported by path analysis. We conclude that in this community the relationship between species richness and

productivity depends on moisture availability and density, with improved water absorption and retention likely to be the mechanism for increased plant growth when drought periods are short. Furthermore, since this is the opposite of what has been found for temperate moss communities, conclusions from one system cannot automatically be extrapolated to other systems.

Keywords Biodiversity · Bryophytes · Ecosystem functioning · Facilitation · Interior Alaska

Introduction

Over the past decade a large number of experimental studies (primarily using plants) have examined how species richness affects ecosystem functioning (for recent reviews, see Loreau et al. 2001; Kinzig 2002). For systems for which positive effects were found (e.g. Naeem et al. 1996; Tilman et al. 1996; Hector et al. 1999; Reich et al. 2001; Tilman et al. 2001), the extent to which this is due to sampling effects or species interactions has been extensively debated and statistically tested (e.g. Aarssen 1997; Huston 1997; Hector et al. 2000, 2002, Huston et al. 2000). In contrast, although potential positive interactions resulting from high species richness have been hypothesized for a number of systems (Cardinale et al. 2000; Loreau and Hector 2001; Mulder et al. 2001; Tilman et al. 2001), there have been few tests of mechanisms driving the positive interactions (but see Caldeira et al. 2001; Cardinale et al. 2002).

Positive interactions may be most important in stressful environmental conditions, where facilitator species can exhibit a positive effect on other species by ameliorating the harsh physical conditions (e.g. Bertness 1991; Bertness and Callaway 1994; Kitzberger et al. 2000; Tielborger and Kadmon 2000; Callaway et al. 2002). In experimental communities constructed using temperate bryophyte species (mosses and liverworts), Mulder et al. (2001) found a positive relationship be-

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tween species richness and biomass under drought stress, but not under control conditions. They hypothesized that the presence of multiple plant architectures resulted in increased humidity under drought conditions, but they did not test this hypothesis. Similarly, Pedersen et al. (2001) found positive density effects for boreal bryophytes and attributed this to improved moisture regime. In that study, increased density had a positive effect on some species by increasing water retention and a negative effect by increased competition for light. Thus, a close packing of shoots can improve humidity. In this study we examine the potential for increased moisture absorption and retention as the mechanism driving positive diversity–productivity relationships in a system likely to experience regular moisture extremes: arctic tundra moss communities. Several mechanisms may drive potential species richness effects on ecosystem functions in our experiment. First, the sampling effect, which describes a greater probability of including at least one species with a high water absorption capacity in high diversity plots, may enhance ecosystem function. Second, the inclusion of more species may result in a greater diversity of architecture, which in turn may reduce evaporation. For example, evaporation may be lower when taller species are included in the community. Third, increased species richness may increase complementarity, that is, intraspecific competition is greater than interspecific competition. This greenhouse experiment is a companion study to a field study, in which environmental conditions are realistic (C. Rixen and C. P. H. Mulder, unpublished data). Here, we test whether changes in moisture absorption and retention can explain productivity results, not whether they actually do so in nature.

Bryophytes represent major components and often dominate in arctic tundra and boreal forests, which cover 14% of the global land area (Beringer et al. 2001). For example, in five sites at Alaska's North Slope ranging from Arctic coast to the Brooks Range, the percent area covered by mosses and lichens comprised a mean of 25% (D.A. Walker personal communication). Unlike in temperate or tropical areas, where bryophytes are a prominent feature and where moisture tends to be high, variation in moisture availability to bryophytes in tundra of Interior Alaska can vary enormously in space and time. Much of Interior Alaska's tundra receives very little precipitation (e.g. annual precipitation at Eagle Summit, a tundra site close to where mosses were gathered for our experiment is 418 mm). Furthermore, high winds, long daylight hours during the growth season, and a lack of a high vascular plant canopy result in high evaporation rates (Bliss 1962). Most bryophyte species absorb water and nutrients over the whole surface of their shoots, but since they lack roots many bryophyte species have a very limited capacity to absorb moisture from the underlying substrate and depend on precipitation and runoff for their water (Longton 1988; Proctor 2000).

Bryophyte species of intermittently dry habitats tend to be ectohydric: water conduction occurs in an interconnecting network of capillary spaces on the outer surface (Longton 1988; Proctor 2000). For plants with large external storage of water there are only two conditions: plants are either at full turgor, or they are too dry to support active metabolism (Proctor 2000). Thus, an increase in the period during which they are at full turgor should increase productivity. However, some species (e.g. *Polytrichum* species) are endohydric and obtain more of their moisture from the substrate (Eckstein and Karlsson 1999; Proctor 2000).

Furthermore, most of the tundra is underlain by extensive permafrost (Ferrians 1998). In flat areas or hollows this results in very moist (often saturated) soil conditions, and species growing under these conditions (e.g. *Sphagnum* species) may have very little tolerance of desiccation.

Often, species with very different methods of obtaining water grow intermingled or at very short distances from each other, depending on local microtopography. For arctic tundra bryophyte communities we therefore expect that the ability of the community to absorb and retain moisture following a precipitation event will greatly affect productivity during the very short growth season, but the ability of individual species to tolerate drought is likely to differ greatly. Many of the species (e.g. *Pleurozium*, *Hylocomium* and *Sphagnum*) often grow in virtual monocultures (Longton 1988, and personal observation) but they can also occur in mixture (personal observation), thus making them particularly appropriate for this study.

In this study we used a greenhouse experiment to address three questions: (1) What is the relationship between species richness and productivity in arctic tundra moss communities? (2) Is this relationship affected by plant density? and (3) How does species richness affect moisture absorption and retention, and can this mechanism explain relationships between species richness and productivity? We predict that increased species richness will improve moisture retention and thereby increase moss productivity; an increase in species richness should therefore have a greater positive effect (either absolutely or proportionally) under long-drought than under short-drought conditions. Low-density communities will have a lower total biomass and consequently a lower ability to retain moisture; we predict that an increase in species richness will have a greater impact (either absolutely or proportionally) on these more drought-sensitive communities than on high-density ones. Based on information about water dependency of the studied mosses (Vitt et al. 1988), we expect those species that are neither complete drought specialists nor highly dependent on high moisture to respond the most to a moderate improvement in moisture conditions. Responses of individual species to being grown in polyculture will be greater at high density than at low density.

Materials and methods

Design and treatments

We conducted a greenhouse experiment in which species richness, moisture regime, and plant density were manipulated. The experimental design was fully factorial with five levels of species richness crossed with two moisture regimes (short-drought and long drought) and two density levels (high and low). Moss communities were constructed with 1, 2, 4, or 8 moss species randomly selected from a larger pool of 12 species (Table 1). These species represented the most common moss species found in the dwarf-shrub heath tundra of the hills in Interior Alaska (C. Rixen, personal observation). The levels of species richness are representative of natural tundra communities that we observed at the locations where the mosses were collected (C. Rixen, personal observation). All species in this experiment were grown in monocultures with four replicates, one for each of the four treatments. The 2-, 4-, and 8-species levels were represented by 8, 6, and 5 different mixtures, respectively, representing true replication of the species richness treatment. Four replicates of each unique mixture were grown, one for each combination of density and moisture regime. The total number of plots was 124 (31 mixtures \times 4 treatments).

Plants were grown in the greenhouse using seeding of moss fragments. Mosses were collected from Murphy Dome (64°57' N, 148°21' W) and Twelvemile Summit (65° 23' N, 145° 58' W), two tundra locations near Fairbanks, Alaska. Moss communities were planted on 1 September 2002 by spreading moss fragments. We created "stock solutions" (suspensions of approximately 2-mm moss fragments in water) of each moss species by blending 10 g of fresh moss of each species (30 g of *Sphagnum girgensohnii* due to the extraordinary water content potential of up to 20 times the dry weight; Clymo and Hayward 1982) in 500 ml of water in a kitchen blender for approximately 10 s. Species mixtures were produced by mixing equal quantities of stock solution of each component species; pilot experiments had established that all of these species were capable of regeneration using this method. The moss-water mix was spread on trays (size: 40 \times 40 cm) filled with fine unsterilized peat (Sunshine Canadian Peat Moss) to a depth of 4 cm, and divided into four smaller areas (19 \times 19 cm) with wooden dividers to the bottom of the tray. Each of these smaller plots was planted with a different mixture and treated as an independent replicate. Plots were planted at two densities: 80 ml per plot for high density (equivalent to 44 g m⁻² of fresh moss and 133 g m⁻² of *Sphagnum*, respectively) and 10 ml per plot for low density (equivalent to 5.5 g m⁻² of fresh moss and 16.6 g m⁻² of *Sphagnum*, respectively).

Table 1 Species composition of the bryophyte assemblages. Nomenclature follows Anderson et al. (1990) and, Vitt et al. (1988) for the mosses and Vitt et al. (1988) for *Marchantia polymorpha* (a liverwort). Non-assemblage mosses ("weeds") were *Aulacomnium palustre* (Hedw.) Schwaegr., *Brachythecium* sp., *M. polymorpha* L. and *Pohlia* sp

1 species	2 species	4 species	8 species	
1a	2a	4a	8a	8d
<i>Aulacomnium turgidum</i> (Wahlenb.) Schwaegr.	<i>Pleurozium sch.</i>	<i>Polytrichum co.</i>	<i>Dicranum sc.</i>	<i>Dicranum sp.</i>
1b	<i>Dicranum sp.</i>	<i>Pertilium cr.</i>	<i>Pleurozium sch.</i>	<i>Hylocomium sp.</i>
<i>Dicranum scoparium</i> Hedw.	2b	<i>Rhytidium ru.</i>	<i>Polytrichum co.</i>	<i>Hypnum cu.</i>
1c	<i>Sgiphagnum gi.</i>	<i>Sphagnum gi.</i>	<i>Ptilium cr.</i>	<i>Pleurozium sch.</i>
<i>Dicranum sp.</i>	<i>Hypnum cu.</i>	4b	<i>Racomitrium ca.</i>	<i>Polytrichumco.</i>
1d	2c	<i>Dicranum sp.</i>	<i>Rhytidium ru.</i>	<i>Ptilium cr.</i>
<i>Hylocomium splendens</i> (Hedw.) B.S.G.	<i>Dicranum sc.</i>	<i>Ptilium cr.</i>	<i>Sanionia un.</i>	<i>Racomitrium ca.</i>
1e	<i>Pleurozium sch.</i>	<i>Rhytidium ru.</i>	<i>Sphagnum gi.</i>	<i>Sphagnum gi.</i>
<i>Hypnum cupressiforme</i> Hedw.	2d	<i>Sphagnum gi.</i>	8b	8e
1f	<i>Hypnum cu.</i>	4c	<i>Dicranum sp.</i>	<i>Aulacomnium tu.</i>
<i>Pleurozium schreberi</i> (Brid.) Mitt.	<i>Hylocomium sp.</i>	<i>Dicranum sc.</i>	<i>Dicranum sc.</i>	<i>Dicranum sp.</i>
1g	2e	<i>Hylocomium sp.</i>	<i>Hypnum cu.</i>	<i>Dicranum sc.</i>
<i>Polytrichum commune</i> Hedw.	<i>Sphagnum gi.</i>	<i>Hypnum cu.</i>	<i>Pleurozium sch.</i>	<i>Pleurozium sch.</i>
1h	<i>Ptilium cr.</i>	<i>Racomitrium ca.</i>	<i>Polytrichum co.</i>	<i>Ptilium cr.</i>
<i>Ptilium crista-castrensis</i> (Hedw.) De Not.	2f	4d	<i>Ptilium cr.</i>	<i>Racomitrium ca.</i>
1i	<i>Racomitrium ca.</i>	<i>Aulacomnium tu.</i>	<i>Rhytidium ru.</i>	<i>Rhytidium ru.</i>
<i>Racomitrium canescens</i> (Hedw.) Brid.	<i>Dicranum sc.</i>	<i>Racomitrium ca.</i>	<i>Sanionia un.</i>	<i>Sanionia un.</i>
1j	2g	<i>Dicranum sc.</i>	8c	
<i>Rhytidium rugosum</i> (Hedw.) Kindb.	<i>Hylocomium sp.</i>	<i>Sanionia un.</i>	<i>Dicranum sp.</i>	
1k	<i>Dicranum sc.</i>	4e	<i>Dicranum sc.</i>	
<i>Sanionia uncinata</i> (Hedw.) Loeske	2h	<i>Aulacomnium tu.</i>	<i>Pleurozium sch.</i>	
1l	<i>Sanionia un.</i>	<i>Dicranum sc.</i>	<i>Ptilium cr.</i>	
<i>Sphagnum girgensohnii</i> Russ.	<i>Pleurozium sch.</i>	<i>Hylocomium sp.</i>	<i>Racomitrium ca.</i>	
		<i>Rhytidium ru.</i>	<i>Rhytidium ru.</i>	
		4f	<i>Sanionia un.</i>	
		<i>Aulacomnium tu.</i>	<i>Sphagnum gi.</i>	
		<i>Hypnum cu.</i>		
		<i>Polytrichum co.</i>		
		<i>Sanionia un.</i>		

Trays were randomized and placed in a greenhouse (temperature 23°C, photoperiod = 24 h), where they were maintained for 6 months. Trays were misted until saturated daily. This resulted in daily wet–dry cycles (mean soil moisture shortly after watering was 63% and 24 h after watering 43%; see also Results for considerable water absorption under short-drought treatment, fig 3). This type of daily cycle was similar to what plants might experience in the field during a relatively wet part of the summer (personal observation). Trays were fertilized with a commercial liquid fertilizer every 2 weeks (Champion 17-17-17, that is, 5.5 mg of each N, P₂O₅, and K₂O per plot). All plots were weeded during the first two weeks of February by manually removing all species not planted; pilot experiments had demonstrated that in the absence of such weeding in the surface area early in the experiment would quickly be dominated by *Marchantia polymorpha*. Due to this early intervention, only approximately 3 g of *M. polymorpha* was removed on all plots combined. Other weed species re-grew effectively during the course of the experiment due to which they were included in the analyses (see Statistical analyses).

Drought treatments were conducted during the seventh month, between 12 March and 9 April 2003. At that time the mosses had re-grown from the fragments and in most cases formed a closed canopy in the high-density plots (98 ± 7% mean cover) and an open canopy in the low-density plots (75 ± 21% mean cover). Trays receiving the long-drought treatment were watered every third day for the first two weeks, and every fifth day for the next two weeks. Short-drought plots continued to receive once-daily mistings. After the drought treatments the frequency of watering was increased to twice-daily for all trays during a 4-week recovery period, after which the experiment was terminated. After the four week recovery period, the plants had recovered from obvious short-term drought stress, but we still expected to observe longer-term impacts, e.g. through changes in species composition.

Measurements

Plant performance

Vegetation height was measured before the drought period (10 measurements per plot). The above-ground biomass of all plots was harvested at the end of the experiment and dry weight (following 48 h in a 55°C drying oven) was obtained. A random sub-sample (10%) taken from different parts of the plot of the total biomass per plot was sorted into the individual species including weeds (species not planted).

Water absorption and retention measurements

During the drought period, three different measurements of community moisture retention were taken in all plots. These allow us to distinguish between effects driven by

changes in total plant biomass, effects resulting from differences in the water-holding capacity of individual species, and those resulting from differences in evaporation rates (a combination of the other two factors plus any interactions between them).

Water absorption capacity

The *water absorption capacity* is a measure of the total amount of water that can be absorbed by the community, and is affected by both the moss biomass and by the water-holding capacity of the particular species planted in the plot. Water absorption capacity of all plots (long- and short-drought) was measured at the end of a 5-day drought period towards the end of the drought treatment by spraying 300 ml of water on each plot, collecting the amount of water that percolated through the moss cover and peat soil, and subtracting the amount of water recovered from that added.

Water retention capacity

The *water retention capacity* of the community is affected by both water absorption and subsequent evaporation. Two measures reflect whole-community water retention capacity. Soil moisture of the plots was measured four times using a Delta-T HH2 and ML2 sensor (Delta-T Devices Ltd, Cambridge, UK): two times before the drought treatment, immediately, and 24 h after watering, respectively; then following a 5-day drought towards the end of the entire drought period, and again after rewetting at the end of the experiment. The mean value of four measurements per plot and time was used.

Maximum whole-plot water retention was measured at the beginning (amount of water retained by the entirely water-saturated peat in ml per m²) and at the end of the experiment (sum of soil moisture before rewetting, water content in the moss biomass before rewetting, and water absorption at final rewetting in ml per m²). Minimum whole-plot water retention was calculated as the sum of soil moisture and water content in the moss biomass before rewetting in ml per m².

Water retention per gram dry weight of moss

Water retention per g dry weight of moss was measured on the last day of the drought treatment period just before watering of all plots. Thus, the long-drought plots had not received water for 5 days and the short-drought plots for 1 day. Three randomly-selected small sub-samples (approximately 0.04 g) were clipped from each plot, weighed immediately, and after drying at 55°C for 48 h, the water content was calculated. Since this measure is independent of biomass it allows us to distinguish between community level effects due to changes in total biomass and changes in ability of plants to absorb and retain moisture.

Statistical analyses

We can distinguish interactions between species from effects due to the particular species composition by comparing the performance of each polyculture with that expected if all species in the mixture performed as in monoculture. Expected biomass for each plot was calculated by averaging, for all species planted in the mix, the biomass in monoculture under the appropriate condition (i.e., short-drought, low-density conditions for short-drought, low-density plots, long drought, low-density conditions for long drought, low-density plots, etc.). The difference between the observed and expected values (DIFF) indicated whether each community had a greater (DIFF > 0) or lesser (DIFF < 0) biomass than predicted by the performance of the member species when grown in monoculture. The same calculations were also made for height and absorption variables. To examine the performance of individual species in response to growth in mixtures, biomass per individual planted in monoculture at the given treatment was subtracted from mean biomass per individual planted in mixtures (corrected for initial seeding) for each species. The difference between those two values was termed "SDIFF".

Data were analyzed in SPSS 10.0.5 (SPSS 1999). Means are given as mean \pm SEM unless indicated otherwise. Where differences are reported, statistical significance was assessed at $\alpha=0.05$. Explanatory variables in the ANOVA included density (high versus low), drought treatment, species richness (number of species in the plot as a linear variable), and all two- and three-way interactions. To test whether plots within a tray were independent, we tested for a tray effect after including density in the model. As the factor tray did not significantly change the results of the analysis, including it in the model would preclude examining interactions between density and species richness, and hence we left it out of the full model.

Actual and planted species numbers were highly correlated ($r^2 = 0.80$, $P < 0.0001$), but not identical. This difference was due to additional species not planted in that plot but present in the design, plus four additional invading species (Table 1). Weeds contributed significantly to the mean species richness of the plots: they represented a mean of 2.6 species. All weeds comprised a mean of 3.4% of the total plot biomass (half of which is species in the species pool but not planted in the plot, and half is the other species). Given the difference in contribution of weeds to species richness (large) and biomass (minor), we analyzed the data in two ways: (1) using total species richness (including weeds) and their biomass (actual species number); and (2) excluding weed biomass and weed contribution to species richness (planted species richness). For the analyses of all other variables and the differences between the observed and expected values (DIFF), the influence of weeds had to be neglected because it could not be separated from the influence of the planted species. The difference between

actual and expected biomass for each individual species (SDIFF) was calculated excluding weeds and weed biomass. However, analyses of actual and planted species number are presented for all variables.

We did also run the analyses using \log_2 of the species richness, but as this did not change the results significantly we do not report them here. Response variables included mean plant height, standard deviation in plant height, biomass, water absorption, water retention, moss water content, and height-DIFF, biomass-DIFF, absorption-DIFF, and moss water content-DIFF (the differences between observed and expected based on monoculture data). ANOVAs for species richness effects on biomass test for differences in slope, that is, differences in change in biomass per species added to the mix. However, if mean biomass for density or diversity treatments is significantly different, then a similar effect of species richness on absolute biomass will represent a change in proportional biomass (and vice versa). Therefore, where there were significant differences in mean biomass between density or drought treatments, we repeated the biomass analyses using standardized biomass values (dividing by mean). Transformations to meet the assumptions of parametric statistical analysis were not necessary. Running second-order regressions instead did not improve the fit of the model so we report first-order regression results only.

We expected many of the variables measured to be correlated with each other. To get a clearer picture of the likely causal relationships between species richness, water variables, and biomass, we constructed path diagrams for each of the four treatment groups. Path analysis (Wright 1934) allows one to test models of causal relationships among several independent and dependent variables from the correlations, which exist between variables (Schemske and Horvitz 1988). The magnitude of the path coefficient (standardized regression coefficient) indicates the strength of the direct effect of an independent variable on a dependent variable. Causality is assumed rather than demonstrated, since additional unmeasured variables may be the true cause of correlations. In our case, we could examine the extent to which species richness, community water absorption, and community water retention could explain community biomass directly and indirectly, but we could not distinguish between direct effects of water retention and absorption on biomass and feedback from biomass to these variables.

Results

Overall effects of the drought treatments

The long-drought treatment had a large effect on the water content of the mosses (results for statistical tests for this and the following three sections are given in Table 2 if not indicated otherwise): water constituted 72% of the biomass of mosses after 1 day of drought

Table 2 ANOVA-tables with results: biomass, height, soil moisture (after drought treatment), water absorption, and moss water content during drought. Significance levels are indicated as follows: ⁺ $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Source	df	<i>F</i> height	<i>F</i> biomass	<i>F</i> soil moisture	<i>F</i> water absorption	<i>F</i> moss water cont. during drought
Model R^2 values		0.622	0.548	0.114	0.392	0.707
Density	1	167.012***	126.836***	2.880 ⁺	45.060***	5.108*
Drought	1	0.030	0.773	4.292*	12.236***	266.785***
Actual species number	1	19.795***	7.734**	3.314 ⁺	9.347**	3.349 ⁺
Drought * Density	1	0.142	0.466	0.574	4.399*	0.058
Drought * Species number	1	3.235 ⁺	2.078	1.482	2.726 ⁺	0.111
Density * Species number	1	0.424	2.594	2.333	0.001	1.711
Drought * Density * Species number	1	0.470	0.075	0.000	1.103	2.598
Error	116					
Total	123					

(short-drought plots), but only 24% water after 5 days of drought. This was reflected in the higher water absorption capacity in the long-drought plots (3.50 l m⁻² in long versus 3.24 l m⁻² in short-drought), lower soil moisture (12% in the long-drought plots, compared with 44% in the short-drought plots), and lower minimum whole-community water retention (10.6 l m⁻² (36%) in long-drought versus 19.9 l m⁻² (64%) in short plots). However, the long-drought period did not significantly lower moss biomass in either density, although direction of the results was as expected (short-drought mean 206 g m⁻², long-drought mean 193 g m⁻²). We observed that overall plants under the long-drought treatment turned slightly brown, which reversed slowly during the recovery period.

Overall effects of planting density

Higher planting density resulted in higher biomass at the end of the experiment (mean \pm sd: 283 \pm 87 g m⁻² at high density and 117 \pm 82 g m⁻² at low density; Table 2) and a greater mean plant height (17 \pm 4 mm at high density versus 9 \pm 3 mm at low density). Mosses in the high density treatment retained more water (52 \pm 29% at high density versus 45 \pm 26% at low density). This was reflected in higher whole-plot water absorption capacity (3.62 \pm 0.41 l m⁻² at high density versus 3.12 \pm 0.49 l m⁻² at low density), higher soil moisture (69 \pm 10% at high density versus 56 \pm 9% at low density; before the drought treatment), greater minimum whole-plot water retention (9.30 \pm 5.67 l m⁻² at high density versus 7.56 \pm 6.27 l m⁻² at low density) and a higher water content of mosses during long-drought periods (52 \pm 29% at high density versus 45 \pm 30% at low density). In all treatments, species in mixtures were distributed across the plot and not aggregated in monospecific patches.

Plant responses to diversity manipulations

For the whole dataset, biomass increased with actual species richness by approximately 30% from 150 g m⁻²

at the one-species level to 200 g m⁻² at the 11-species level (Fig. 1, Table 2). The diversity effect was not significantly different between the drought treatments (species richness by drought interaction: $F_{(1,116)} = 2.08$, $P = 0.15$). All treatments except the dense long-drought plots showed a positive relationship between species number and biomass production. The steepest slope was found for the low-density, short-drought treatment with an increase from 40 g m⁻² at 1-species level to 200 g m⁻² at the 11-species level. Biomass-DIFF (the difference between actual and expected biomass) also showed an increase of 35 g m⁻² from the 1- to the 11-species mixtures ($F_{(1,116)} = 14.117$, $P < 0.001$). Biomass was not significantly increased by planted species richness ($F_{(1,116)} = 1.43$, $P = 0.23$), however, biomass-DIFF was increased ($F_{(1,116)} = 4.18$, $P < 0.05$).

Biomass increased similarly with actual species richness in high- and low-density plots (there was no species richness by density interaction; Table 2). However, since high-density plots had a much greater mean biomass, we ran analyses using standardized biomass (divided by mean for each density treatment to test for proportional changes. Proportional changes were higher at low-density plots (Interaction density \times actual species number: $F_{(1,116)} = 7.476$, $P < 0.01$).

Greater actual species richness resulted in a significant increase in plant height (Table 2): in the most diverse mixtures plant height was almost 50% greater than in monocultures (mean \pm sd: 17 \pm 4 versus 10 \pm 6 mm; Fig. 1a). However, there was no interaction between drought duration and density (Fig 1a): plant height increased similarly in both treatments. The difference between the observed and expected height values (height-DIFF) indicated that increase in plant height with species richness (4.5 mm from monocultures to 11 species) was greater than would have been expected from the values of the monocultures ($F_{(1,116)} = 24.082$, $P < 0.001$). Height variability (the standard deviation of plant height) also increased with increasing species numbers ($F_{(1,116)} = 4.527$, $P < 0.05$), from 2 mm at the one-species level to 3 mm at the 11-species level. Planted species richness increased plant height marginally significantly ($F_{(1,116)} = 3.52$, $P = 0.063$) and height-DIFF highly significantly ($F_{(1,116)} = 9.46$, $P = 0.003$).

Individual species responses

Most species grew better in mixture than in monoculture (positive SDIFF, the per-gram-planted differences between growth in monoculture and growth in mixture; $F_{(1,116)}=14.117$, $P<0.001$; Fig. 2). Consistent with our predictions, responses of individual species to being grown in polyculture (whether positive or negative) were much greater at high density than at low density (Fig. 2). However, whereas 10 out of 12 species showed strong positive responses to polyculture in the high-density short-drought plots, only half of the species exhibited positive responses in the other three treatments, suggesting that for those treatments the higher mean biomass at higher species richness was due to positive effects on a few species. The species that were most positively affected by growing in mixture were several feather

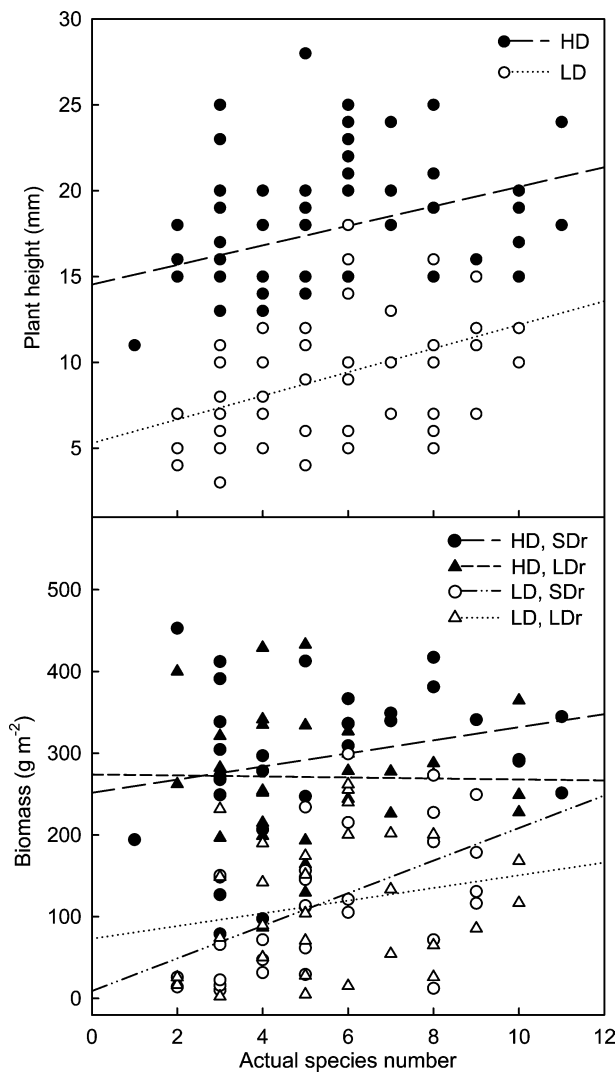


Fig. 1 Relationship between plant variables and species richness (actual number of species in the plots, including weeds) by treatment. **a** plant height by drought treatment. **b** biomass by drought and density treatments. Treatments: *HD* high density, *LD* Low density, *SDr* short-drought, *LDr* long drought

mosses (*Hypnum cupressiforme*, *Ptilium crista-castrensis*, *Sanionia uncinata*). Peat moss (*S. girgensohnii*) was the most negatively affected by growing in mixture. The drought-adapted *Racomitrium canescens* was affected only a little by growing in mixture.

Water absorption and retention

Whole-tray water absorption was increased at higher actual species numbers (Table 2, Fig. 3). The species richness effect was marginally stronger in short-drought plots than in long-drought plots at both densities (interaction species richness×drought: $F_{(1,116)}=2.726$, $P=0.1$). However, all treatments except the low-density long-drought plots showed a positive relationship between species number and water absorption, with the strongest effect for the low-density short-drought plots. Similarly, absorption-DIFF (the difference between observed and expected absorption based on species composition) showed an increase of approximately 300 ml m⁻² from the 1- to the 11-species mixtures

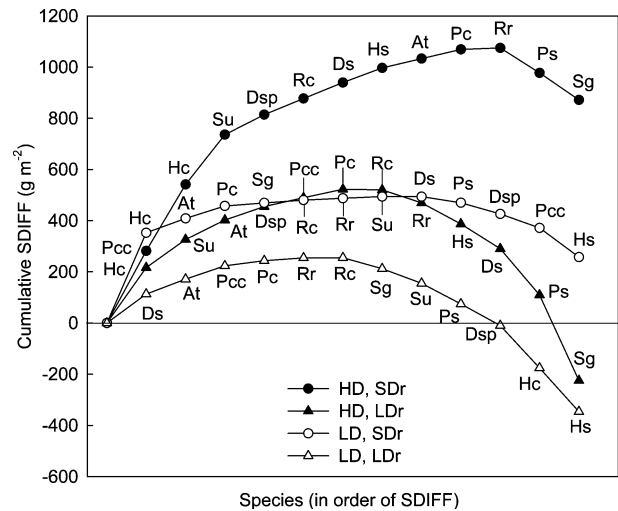


Fig. 2 Differences in final biomass ("SDIFF" values) per gram planted between plants in monoculture and in mixture for individual species. For each species, biomass per individual planted in monoculture at the given treatment was subtracted from mean biomass per individual planted in mixtures (corrected for initial seeding). These differences were ranked from high to low and presented cumulatively. The highest point on each curve is the switch from species that have positive to those that have negative contributions to DIFF. The sums of these DIFFs (the last point of each line) correspond to the mean DIFF across all plots at that treatment. Species identities: At = *Aulacomnium turgidum*, Ds = *Dicranum scoparium*, Dsp = *Dicranum spec.*, Hc = *Hypnum cupressiforme*, Hs = *Hylocomium splendens*, Pc = *Polytrichum commune*, Pcc = *Ptilium crista-castrensis*, Ps = *Pleurozium schreberi*, Rc = *Racomitrium canescens*, Rr = *Rhytidium rugosum*, Sg = *Sphagnum girgensohnii*, Su = *Sanionia uncinata*. Treatments: *HD* high density, *LD* low density, *SDr* short-drought, *LDr* long drought. Overall positive effect of species number on SDIFF ($F_{(1,116)}=14.117$, $P<0.001$). *HD, SDr*: ($F_{(1,29)}=9.960$, $P<0.01$). *HD, LDr*: ($F_{(1,29)}=0.660$, $P>0.05$). *LD, SDr*: ($F_{(1,29)}=8.542$, $P<0.01$). *LD, LDr*: ($F_{(1,29)}=0.439$, $P>0.05$)

($F_{(1,116)} = 10.203$, $P = 0.002$). In contrast, water retention in the soil did not change significantly with actual species richness for any treatment (although there was a marginally positive relationship for the low-density short-drought treatment: $F_{(1,29)} = 3.654$, $P = 0.066$). Community water loss over time (difference between maximum water retention at the beginning and maximum water retention at the end of the experiment in 1 m^{-2}) was marginally lower at higher actual species numbers (14 l m^{-2} in monoculture versus 9 l m^{-2} in 11-species mixtures; $F_{(1,116)} = 3.323$, $P = 0.071$). Thus, the diverse communities that absorbed more water may have retained this water longer during the drought period than the less diverse communities.

Planted species richness had no significant effect on whole-tray water absorption ($F_{(1,116)} = 1.73$, $P = 0.19$), water retention ($F_{(1,116)} = 0.94$, $P = 0.33$), and community water loss over time ($F_{(1,116)} = 0.03$, $P = 0.87$) but significantly increased absorption-DIFF ($F_{(1,116)} = 4.69$, $P = 0.032$).

Moss water content

Actual species richness had a positive effect on water content of the mosses during the drought period (Table 2, Fig. 3). Surprisingly, this effect was strongest for the low-density long-drought plots, although the overall relationship between species richness and water content was positive for all treatments (all $P < 0.059$) except the high-density long-drought treatment, which showed a slightly negative relationship. The moss water content-DIFF showed an increase of 10% from the 1- to the 11-species mixtures ($F_{(1,116)} = 8.093$, $P = 0.005$). As the water content of the mosses was independent of the total biomass, these results show that the improved community-level water balance was not only the result of increased biomass but also of increased water retention by individual plants. Planted species richness had no effect on moss water content ($F_{(1,116)} = 1.3$, $P = 0.26$) but increased moss water content-DIFF marginally significantly ($F_{(1,116)} = 2.83$, $P < 0.1$).

The water content of the individual species in monocultures (Table 3) shows the different strategies regarding water retention. The species from the wettest habitats, *S. girgensohnii*, had the highest water content under short-drought conditions but a very low water content under long-drought and low-density. Some of the feather mosses that profited most from growing in mixtures with other species (*H. cupressiforme*, *S. uncinata*) were at intermediate to high levels. The drought-adapted species *R. canescens* had a low water content in all of the treatments.

Path analyses

The path diagrams constructed for each of the four treatments clarify some of the direct and indirect relationships found (Fig. 4). Only in the short-drought plots (Fig. 4a, c) did actual species richness affect biomass, and in both high and low density this was an indirect effect mediated through increased water absorption following drought. In long-drought plots, species richness had no direct or indirect effect on biomass (Fig. 4b, d), although water absorption and biomass were strongly correlated. Although water retention also explained variation in biomass in all treatments except low

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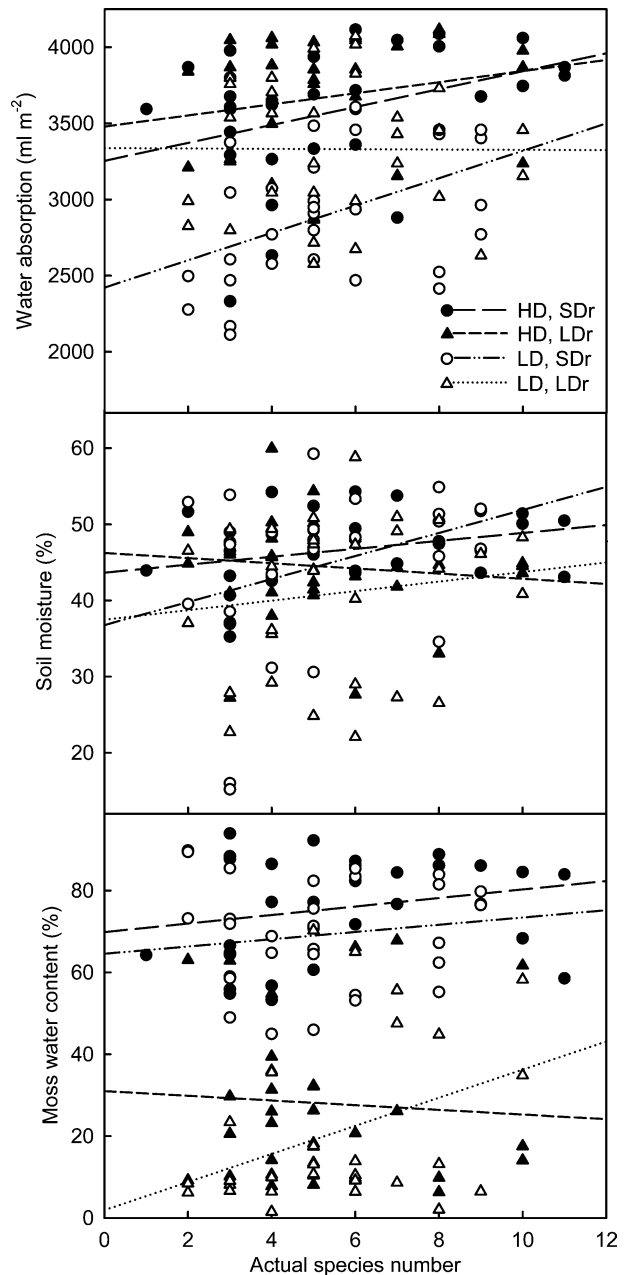


Fig. 3 Effects of density, species richness, and drought treatments on water absorption and retention. **a** results for whole-tray water absorption. **b** results for soil water retention measured as soil moisture (after drought treatment). **c** results for water content of moss during the drought treatment. Treatments: *HD* high density, *LD* low density, *SDr* short-drought, *LDr* long drought

Table 3 Effects of density and drought treatments on moss water content of individual species in monocultures during drought (all values in percent)

	High density		Low density		Mean \pm standard deviation	High density; percent drop from short to long drought	Low density; percent drop from short to long drought
	short-drought	Long drought	short-drought	Long drought			
<i>Aulacomnium turgidum</i>	55	30	64	10	40 \pm 25	45	84
<i>Dicranum scoparium</i>	77	63	71	11	56 \pm 30	18	85
<i>Dicranum</i> sp.	64	63	72	7	52 \pm 30	2	90
<i>Hylocomium splendens</i>	82	23	76	11	48 \pm 36	72	86
<i>Hypnum cupressiforme</i>	90	9	73	23	49 \pm 39	90	68
<i>Pleurozium schreberi</i>	87	14	45	36	46 \pm 31	84	20
<i>Polytrichum commune</i>	59	36	59	6	40 \pm 25	39	90
<i>Ptilium crista-castrensis</i>	56	21	86	8	43 \pm 35	63	91
<i>Racomitrium canescens</i>	57	8	49	8	31 \pm 26	86	84
<i>Rhytidium rugosum</i>	61	39	59	13	43 \pm 22	36	78
<i>Sanionia uncinata</i>	67	10	82	9	42 \pm 38	85	89
<i>Sphagnum girgensohnii</i>	94	55	89	9	62 \pm 39	41	90

density short drought in no case did species richness affect the variable, short drought. Finally, for low-density treatments the model explained variation in biomass very well ($>73\%$), but explanatory power was a bit weaker for high-density short-drought plots (62%) and weakest for the high-density long-drought plots (30%).

Discussion

Effects of species richness on biomass in the four treatments

Overall, increased actual moss species richness had a positive effect on biomass and plant height, whether measured in absolute terms or as the difference between observed and expected responses based on monoculture. This is consistent with other studies on biodiversity and ecosystem functioning (e.g. Naeem et al. 1996, 2001; Tilman et al. 1996; Hector et al. 1999; Reich et al. 2001). The findings are also consistent with the findings of a companion field study in Arctic tundra, where a reduction in species richness by species removal decreased the performance of remaining vascular plant species (C. Rixen and C. P. H. Mulder, unpublished data). As expected, communities planted at low density had a lower biomass and plant height than plants at high density. We had predicted a stronger relationship between species richness and biomass in low-density than in high-density communities, because we expected the low biomass of low-density plots to make them particularly vulnerable to drought effects, thereby increasing the potential benefits of multiple species. There was no significant interaction between species richness and density in effects on biomass: in absolute terms, changes were identical. However, an equivalent increase in biomass represented a significantly greater proportional increase for the low-density communities (approximately 150% versus 15% in high-density communities). Thus, the proportional increase in biomass was much greater in

low-density communities, supporting our hypothesis. This is also supported by the much higher biomass R^2 values in the path analyses for the low-density plots.

We predicted that the positive effects of multiple species would be more apparent under long-drought conditions than under short-drought conditions. Our results showed the opposite: only the short-drought plots (those watered once a day during the treatment period) showed a significant positive response to species richness. This is confirmed by analyses of responses of individual species: in short-drought plots most species (ten in high density, 9 in low density) had better growth in mixture than in monoculture. In contrast, overall long-drought plots (those exposed to 3–5 day drought periods) showed no significant relationship, and only six species grew better in mixture than in monoculture. Responses of individual species to being grown in polyculture were greater at high than at low density, as we predicted.

The analysis of the actual species richness including weed species was the more appropriate one than analysis of planted species because weeds were, in some cases, as prevalent or more prevalent than planted species and therefore likely to have played an important role. Therefore, the actual species richness was a better descriptor of the diversity gradient in the experiment than the planted species richness. However, overall analyses pointed in the same direction of positive species richness effects.

Comparisons with other studies

This study found the opposite of what Mulder et al. (2001) found for temperate bryophytes: in their study, positive effects of high species richness exhibited themselves only under drought conditions. There were several differences between the two studies that may account for these conflicting results. First, light levels in this study were considerably higher (>20000 lumen m^{-2} versus $<$

300 lumen m⁻²), resulting in more rapid drying. Control plots in Mulder et al.'s study were covered in plastic and therefore remained very moist (90+ % humidity), while control (short-drought) plots in this study went through a considerably daily drying cycle (see Methods section). Second, the moisture regimes, which the two groups of species experience in nature differ. The bryophytes in Mulder et al.'s study were located under a dense canopy of evergreen tree species and seldom exposed to dry conditions (C. Mulder, personal observation); thus they are unlikely to have evolved adaptations to repeated wetting and drying cycles. In contrast, tundra communities are frequently exposed to long periods with little precipitation, high wind and high light conditions, and are likely to be adapted to repeated wetting and drying cycles. Tundra species may respond to a reduction in moisture by drying out rapidly and becoming metabolically inactive; in that case there would be little advantage to the small increase in moisture provided by a community with higher species richness.

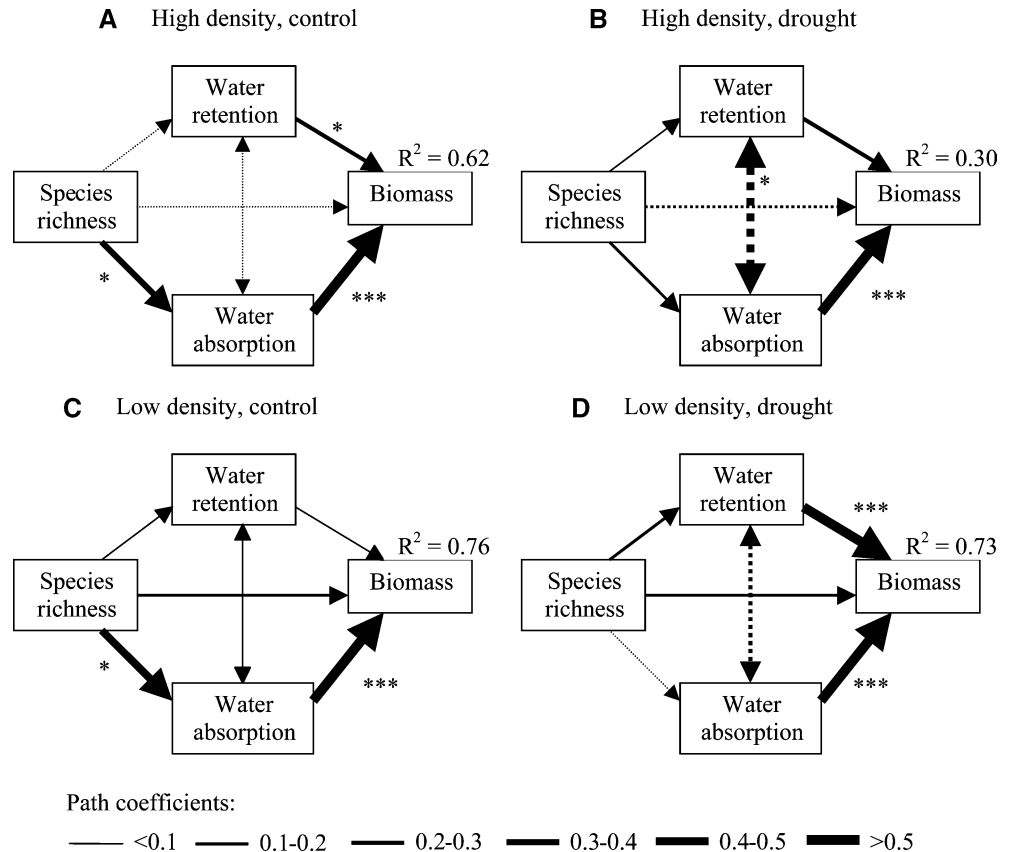
Pedersen et al. (2001) suggested that for their moss species, the advantages of greater moisture retention at high densities outweighed the negative effects of greater competition for light (up to a certain density). Our results are consistent with this: even at high density most species (including the weeds) showed increased growth compared with monocultures when watered regularly. This indicates that complementarity or facilitation due to increased water retention exceeded competition due to lower light availability in our study. However, our

results do not allow us to predict what will happen at other points on the density and moisture spectrum, as we only included two density and two moisture levels in the experiment. The complexity of the system created may be not sufficiently addressed by our experimental protocol. Thus, the results only point out that environmental conditions affect the relationship of species richness and ecosystem functions and that moisture absorption can help explain this.

Individual species responses

The species that profited most from the improved moisture regime at high species numbers were feather mosses (*H. cupressiforme*, *P. crista-castrensis*, *S. uncinata*). These species are moderately drought tolerant (Vitt et al. 1988) and, therefore, had the greatest capacity to benefit from a moderate improvement in moisture conditions. In contrast, the peat moss (*S. girgensohnii*), which generally grows under more or less constantly wet conditions (Smith 1978), was the most negatively affected by an increase in species richness. This species has a higher water retention capacity than other moss species; the substitution in mixture of other species for peat moss would therefore have reduced the overall water holding capacity of the community, with negative consequences for the highly moisture-dependent peat species. The drought-tolerant species *R. canescens* (Vitt et al. 1988), on the other hand, was

Fig. 4 Results of path analyses for the different densities and drought treatments. Water related variables are whole-plot water absorption and minimum whole-plot water retention. *Solid lines* indicate positive relationships, *dashed lines* indicate negative relationships. Relationships are significant at $P < 0.05$ (*), $P < 0.01$ (**), or $P < 0.001$ (***). Values are path coefficients. Model R^2 values are indicated for biomass. Additional unknown sources of variation are not shown



only moderately affected by the improved moisture regime or the long-drought treatment. This species probably does not show high growth rates at favorable conditions but tolerates drought without harm. Also the other species used in this experiment (mostly not feather mosses) reacted only moderately to the changed moisture regime. In general, the effects of our diversity treatments on individual species correspond well to the frequency with which species are found in monoculture in the field: species usually found in monoculture (e.g. *Sphagnum*, *Pleurozium*, *Hylocomium*) were either negatively affected or only very slightly positively affected by being planted in polyculture.

Moisture absorption and retention as mechanisms driving biomass differences

As expected, higher planting density resulted in increased water absorption, soil moisture, and whole-community water retention. There was also a difference in moisture content between high-density and low-density plants following long droughts, suggesting that the increased moisture content of the community was not simply a result of more biomass but of improved moisture conditions overall. Changes in morphology (as reflected in the greater plant height) may be in part responsible for the increased per-gram water retention, although we did not test this directly.

Our results are consistent with the hypothesis that the mechanism by which higher species richness results in biomass is through increased moisture availability (absorption and/or retention): most moisture variables (water absorption, soil moisture, and per gram moisture content, but not whole-community water retention) increased with species richness in the short-drought conditions. Our path analyses suggest that the positive effect of species richness in the short-drought plots was primarily an indirect effect: species richness increased community water absorption, which in turn increased biomass. In contrast, there is little evidence for a direct effect of species richness on moisture retention. Since increased biomass likely increases water absorption capacity (as suggested by the low versus high density comparison), which in turn feeds back to biomass in a positive feedback loop, we cannot rule out the possibility that higher species richness resulted in increased biomass for a different reason, which set this feedback loop in motion. However, the lack of any direct positive effect of species richness on biomass in the path diagram suggests that the primary effect of species richness is mediated through moisture absorption.

This increase in water absorption with greater species richness may be explained by two different mechanisms. First, it may be a sampling effect: a greater probability of including at least one species with a very high absorption capacity in high diversity plots. The individual species responses do not support this hypothesis: the species with the highest moisture absorption (*S.gir-*

gensohnii) was the most negatively affected by being planted in polyculture, resulting in a decline in its biomass over time (and a loss of the benefits of its inclusion). However, there may be other characteristics of species that we did not measure (e.g. ability to grow under very low moisture conditions) that do support this hypothesis, so we cannot reject it completely. The second explanation (and the one put forth by Mulder et al. 2001) is that the inclusion of more species results in a greater diversity of architectures. The inclusion of taller species may result in lower evaporation, while mat species that are in contact with the soil may release more moisture from the soil into the subcanopy space. In our communities greater species richness resulted in both increased mean plant height and increased variation in plant height. However, the positive effects were greater for moisture absorption than for moisture retention. Possibly the more complex architecture of the high-diversity plots slows down the rate at which water hitting the top of the canopy reaches the soil and increases the amount absorbed.

An alternative explanation for increased biomass under increased species richness is complementarity: intraspecific competition is greater than interspecific competition, and as species richness increases so do the proportion of interactions between different species. We did not test for this directly and cannot exclude such an effect; the two mechanisms (facilitation and complementarity) are not mutually exclusive. However, there is little indication of this: our path analyses show no unexplained (direct) effects of species richness beyond those through water absorption.

Regardless of the mechanism by which biomass is initially increased in high-diversity communities, our data suggest that multiple feedback loops reinforce the positive relationship: greater moisture retention leads to less drying out of the soil, which in turn results in a greater capacity to reabsorb moisture (because very dry peat does not absorb moisture easily; Heathwaite 1993), and allows mosses to remain active for longer, which in turn results in greater productivity and greater moisture retention.

Although greenhouse conditions in this experiment are not identical to field conditions, and regeneration from fragments may not lead to plants with the exact same morphology as in the field, our aim in this experiment was to test whether observed relationships between species richness and productivity could be altered by moisture regime and density (and if so, whether moisture absorption and retention changes could account for this). Field experiments designed to test for actual effects of removal of individual species will be reported in other manuscripts.

Conclusions

In this experiment we asked three questions: (1) What is the relationship between species richness and produc-

tivity in arctic tundra moss communities? (2) Is this relationship affected by plant density? and (3) Can changes in moisture absorption and retention explain observed relationships?

We conclude that in this community the relationship between species richness and productivity depends on density and moisture availability with improved water absorption and retention likely to be the mechanism for increased plant growth when drought periods are short. Furthermore, since this is the opposite of what has been found for temperate moss communities, conclusions from one system cannot simply be extrapolated to other systems.

This study suggests that increased moss species richness can result in greater biomass production. Likely mechanisms are an improved community humidity that are expressed by higher water absorption, water retention, and soil moisture. Our analyses indicate a positive feedback loop between humidity and biomass with higher species diversity improving plot moisture, thus prolonging the time during which mosses remain metabolically active before they dry out and, consequently, increasing biomass production. Increased biomass in turn increase community humidity leading to a self-enhancing effect. Therefore, our results suggest improved water absorption (and possibly retention) as a cause for facilitation among species. This is further supported by the positive effects of high plant density on community moisture and productivity of mosses.

However, positive effects of high species richness occurred only when drought periods were short, which is the opposite of what has been found for temperate moss communities (Mulder et al. 2001). Therefore, conclusions from one system cannot simply be extrapolated to another. Differing from species in temperate forests, many tundra moss species are often exposed to long drought periods during which they stay metabolically inactive without harm. Thus, experimental drought may not have the negative effects on tundra mosses that it would have on less drought-adapted species. Therefore, facilitative effects among tundra moss species may only occur under moderate drought.

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