

Tundra in the Rain: Differential Vegetation Responses to Three Years of Experimentally Doubled Summer Precipitation in Siberian Shrub and Swedish Bog Tundra

Frida Keuper, Frans-Jan W. Parmentier, Daan Blok,
Peter M. van Bodegom, Ellen Dorrepaal, Jurgen R. van Hal,
Richard S. P. van Logtestijn, Rien Aerts

Abstract Precipitation amounts and patterns at high latitude sites have been predicted to change as a result of global climatic changes. We addressed vegetation responses to three years of experimentally increased summer precipitation in two previously unaddressed tundra types: *Betula nana*-dominated shrub tundra (northeast Siberia) and a dry *Sphagnum fuscum*-dominated bog (northern Sweden). Positive responses to approximately doubled ambient precipitation (an increase of 200 mm year⁻¹) were observed at the Siberian site, for *B. nana* (30 % larger length increments), *Salix pulchra* (leaf size and length increments) and *Arctagrostis latifolia* (leaf size and specific leaf area), but none were observed at the Swedish site. Total biomass production did not increase at either of the study sites. This study corroborates studies in other tundra vegetation types and shows that despite regional differences at the plant level, total tundra plant productivity is, at least at the short or medium term, largely unresponsive to experimentally increased summer precipitation.

Keywords Water addition · Plant traits · Irrigation · Primary production · Subarctic · High latitude

INTRODUCTION

Northern tundra ecosystems are important in the current context of a changing climate as they contain a large part of our global terrestrial soil carbon pool (Tarnocai et al. 2009). Despite their low primary productivity, tundra ecosystems act as a carbon sink due to their low decomposition rates. Climatic changes, which are currently increasing decomposition rates of old carbon, threaten to change the tundra from a carbon sink into a source (Dorrepaal et al. 2009). In contrast, enhanced vegetation

productivity in response to climatic changes may increase net storage of carbon in these systems in the near future (Qian et al. 2010). Hence, climatic changes alleviating growth-limiting factors of tundra vegetation have a potential to feed back to the global carbon cycle.

Plant productivity in northern tundra ecosystems is strongly constrained by the adverse physical environment. In addition to low temperature and low nutrient availability (Chapin et al. 1995; Shaver et al. 2001; Aerts et al. 2006; Elmendorf et al. 2012), water shortage is frequently listed as one of the growth-limiting factors for tundra vegetation (e.g. Bliss et al. 1994; Ostendorf and Reynolds 1998; Press et al. 1998a; Hodkinson et al. 1999; Kade et al. 2005; Qian et al. 2010). However, the notion that growth of tundra vegetation is water limited is largely based on observational evidence: the best-developed arctic plant communities are often found at sites where snowmelt water or seasonal streambeds keep the soil moist (Bliss et al. 1984, 1994; Kade et al. 2005). In addition, dendrochronological research suggests summer precipitation as one of the main climate drivers for shrub (*Betula nana*) growth in northeast-Siberian tundra (Blok et al. 2011). This is supported by modelling approaches, which reveal enhanced precipitation as the major driving factor for increasing growing season leaf area index trends in northeast-Siberian tundra as well as in northern Scandinavia from 1980 to 2000 (Piao et al. 2006).

In contrast with these correlative or modelling studies that postulate water as a limiting factor for arctic plant growth, direct measurements of plant water potential suggest that water is not a growth-limiting factor, at least for Alaskan arctic tundra vegetation (Oberbauer and Miller 1982). In addition, very few positive plant responses to experimentally increased summer precipitation in arctic ecosystems have been documented (for an overview of

performed experiments see Table 1). However, this experimental evidence is based on a limited number of experiments (seven) only, which were restricted to an even more limited number of geographic areas (Table 1). Moreover, only three of these increased summer precipitation experiments at higher latitudes were performed in tundra sites, as the other studies were executed in subarctic forest ecosystems (Table 1). As such, the tundra types covered in these three studies do not reflect the full diversity of tundra ecosystems (Walker et al. 2005).

Climate change predictions include increasing precipitation at high latitudes for the coming decades (IPCC 2007; Bengtsson et al. 2011), while long-term trends of both the increased precipitation amounts and the intensity have already been observed (IPCC 2007; Callaghan et al. 2010). If low water availability indeed poses a limitation to plant productivity, this may critically affect carbon uptake of northern ecosystems. Thus, there is clearly a need for additional studies on tundra plant water limitation in previously unaddressed tundra types in order to corroborate the conclusions of previous experiments (Table 1). Two tundra types, which have not been previously addressed, are northeast-Siberian shrub tundra ('dry heath', van Huissteden et al. 2005) and Swedish permafrost-underlain ombrotrophic bog tundra ('dry elevated palsa', Rydén 1976). Together, these dry tundra types represent a large part of the tundra biome (~30 %) (Gorham 1991; Walker et al. 2005). Moreover, both the shrub tundra and the bog tundra are important actors in the global carbon cycle: shrub tundra because of its long-term C-storage in woody biomass, and bog tundra because of their efficient C-storage capacity in slowly decomposing peat. Their responsiveness to increased moisture availability in a changing climate therefore needs to be known.

In this study, we assessed how increased summer precipitation, through modulating water availability, will affect vegetation productivity and species-specific growth responses in dry heath and dry elevated palsa types. Hence, we performed increased summer precipitation experiments in both the habitats for three consecutive growing seasons and approximately doubled the ambient summer precipitation. If water indeed inhibits growth of tundra vegetation, we hypothesize vegetation productivity to increase in response to additional summer precipitation. Given the high spatial heterogeneity that is commonly observed in biomass sampling studies (Whittaker and Marks 1975) (and accordingly low statistical power), total annual vascular production might not represent the most sensitive vegetation variable. We therefore also determined more sensitive species-specific stem growth responses of dominant species. Traits allow sensitive detection of vegetation responses to environmental drivers (e.g. Wright et al. 2005;

Ordóñez et al. 2009). Commonly measured traits that are known to be particularly sensitive to drought stress include leaf size and specific leaf area (SLA) of dominant individual species (Cornwell and Ackerly 2009). Therefore, we hypothesized that leaf size would increase and SLA would decrease if moisture is indeed inhibiting growth in dry elevated palsa and dry heath. In addition, because stem growth of subarctic shrub species has been shown to respond strongly to a release of inhibiting factors (Bret-Harte et al. 2001), we additionally determined more sensitive species-specific stem growth responses of dominant species.

MATERIAL AND METHODS

Study Sites

Siberia

The first site (Fig. 1a) is a low-Arctic tundra site within the Kytalyk nature reserve in NE-Siberia, Russia (70°49'N, 147°28'E, elevation 48 m.a.s.l.), previously described by Van Huissteden et al. (2005). Mean annual precipitation is 205 mm, most of which falls during the summer months. July is the wettest month with an average precipitation of 32 mm (Tank et al. 2002). Regional climate data [Chokurdakh weather station (WMO station 21946), <http://climexp.knmi.nl/>, 1948–2006] show mean annual air temperatures of –13.9 °C and average July temperatures of 10.5 °C. In 2007, the growing season was longer than usual, with snowmelt occurring 3 weeks earlier than the other measured years and average temperatures were higher than normal. The following years were more typical for this region, with 2009 being the coldest of the studied 3-year period (Parmentier et al. 2012). The same holds true for wetness, where 2007 was the wettest, 2008 in between and 2009 the driest (Parmentier, pers. obs.). The experiment was set up on an elevated dry palsa, with a maximum active layer thickness of around 25 cm (measured at the end of the growing season, in each plot at three replicate points, by probing a 0.5-cm diameter graduated stainless steel rod into the soil to refusal). The subsoil is silt clay overlain by 10–15 cm of highly organic soil, carpeted with an ~4- to 5-cm thick moss layer [consisting of 35–45 % *Aulacomnium turgidum* (Wahlenb.) Schwägr.]. The vascular plant community consists of the deciduous shrubs *B. nana* subsp. *exilis* (93 % of total aboveground biomass) and *Salix pulchra* (4 %), the graminoid *Arctagrostis latifolia* (2 %), and the forbs *Saxifraga* spp. (<1 %) and *Pyrola rotundifolia* (<1 %) and has been classified as dry heath (van Huissteden et al. 2005).

Table 1 Summary of the results of summer water addition experiments on vascular arctic tundra vegetation, arranged by geographical region and vegetation type

	Geographical region	Vegetation type	Treatment	Effect	Studies
1.	Swedish Lapland (subarctic)	Birch forest, <i>V. vitis-idaea</i>	4.5 mm each fortnight (≈ 18 mm season ⁻¹); NP = 120 mm	'0' (<i>V. uliginosum</i>); '+ ' (<i>V. vitis-idaea</i> leaf-weight/shoot-weight; number of leaves per shoot)	1
2.	Swedish Lapland (subarctic)	Dwarf shrub heath, open birch forest	4.5 mm week ⁻¹ (≈ 60 mm season ⁻¹); NP = 120 mm	'0' (overall mean biomass; flowering frequency; shoot production)	2–6
3.	Swedish Lapland (subarctic)	Dwarf shrub heath, open birch forest	9 mm week ⁻¹ (≈ 100 mm season ⁻¹); NP = 120 mm	'0' (overall stem growth and branching; cover percentage; leaf thickness <i>V. myrtillus</i> and <i>V. vitis-idaea</i>) '+' (flowering and berry production <i>V. myrtillus</i> ; stem growth <i>E. hermaphroditum</i> in one out of four measured years)	7
4.	Finnish Lapland (subarctic)	Birch forest, dwarf shrub heath, <i>V. vitis-idaea</i> , <i>E. nigrum</i>	Weekly watering (≈ 130 mm season ⁻¹); NP = 240 mm	'+' (shoot production <i>V. vitis-idaea</i>); '-' (shoot production <i>E. nigrum</i>)	8
5.	Svalbard (high Arctic)	Polar <i>Dryas octopetala</i> semi desert community	45 mm season ⁻¹ , divided over 6 times, 60 % increase compared to NP	'0' (cover; green biomass; all photosynthetic parameters; all reproductive parameters; seedling establishment); '+' (SLA <i>Dryas octopetala</i>)	9–12
6.	Canadian Arctic (high arctic)	1. Wet sedge meadow; 2. mesic <i>Cassiope</i> heath; 3. dry-mesic <i>Dryas</i> heath	33 mm each 10 days (≈ 100 mm season ⁻¹); NP ≈ 10 mm	'0' (green and total standing crop of any species, on all sites)	13
7.	Alaska (high arctic)	Montane <i>Dryas octopetala</i> tundra, fellfield	5 mm 1–2 \times week ⁻¹ (≈ 30 –50 mm season ⁻¹); NP = NA	'0' (mean leaf number per shoot; shoot growth rates; aboveground production)	14

Background shading colour indicates similarity between geographical regions. Natural summer precipitation (NP) values are given under 'treatment', unless unavailable (NA), while no data were available for influx from glaciers or thawing permafrost. Effect is indicated as positive (+), negative (–) or no effect (0), with the measured variable between parentheses. To the best of our knowledge, this list of experiments is complete. All studies listed have been reviewed previously by Dormann and Woodin (2002)

Studies: 1, Karlsson (1985); 2–3, Parsons et al. (1994, 1995); 4, Potter et al. (1995); 5, 6, Press et al. (1998a, b); 7, Phoenix et al. (2001); 8, Shevtsova et al. (1997); 9, Welker et al. (1993); 10, 11, Wookey et al. (1993, 1995); 12, Robinson et al. (1998); 13, Henry et al. (1986); 14, McGraw (1985)

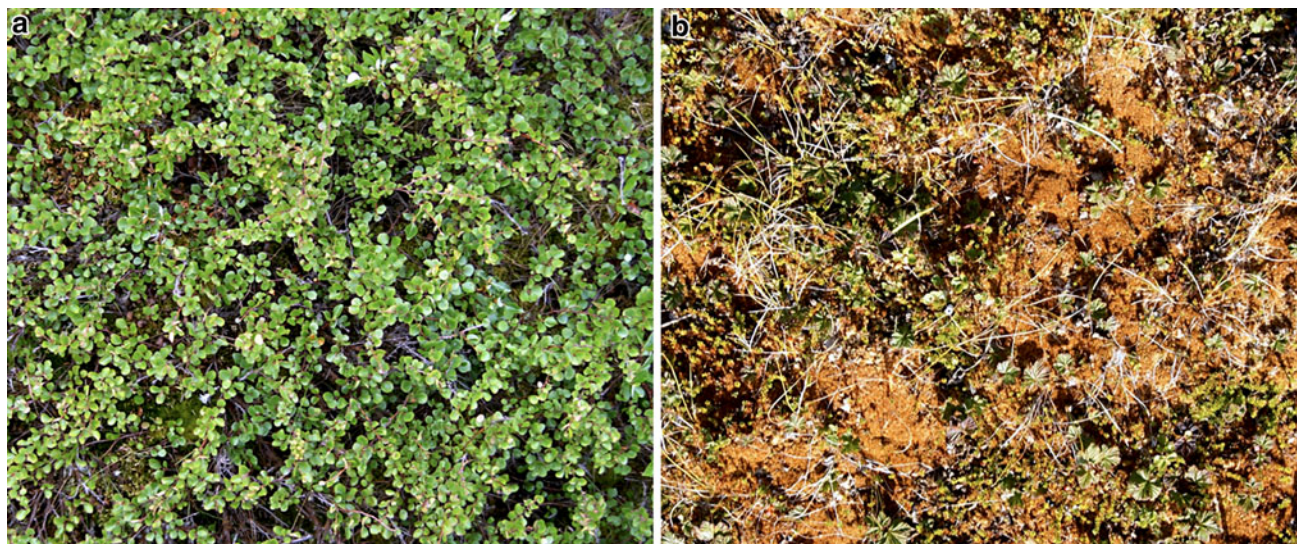


Fig. 1 Tundra types addressed in this study, showing dense cover at the *Betula nana*-dominated heath (northeast Siberia) site (a); and a low and open but *S. fuscum*-dominated vegetation at the ombrotrophic palsa site (northern Sweden) (b). (Photos by F. Keuper and J.L. Ramsay)

Sweden

The second study site (Fig. 1b) is at the Stordalen nature reserve in northern Sweden (68°21'N, 19°03'E, 351 m.a.s.l.) which has been described in full detail by Sonesson (1980). Annual precipitation in the area is around 300 mm year⁻¹ (1913–2006; Johansson et al. 2009). Summer precipitation at the site in the years of the experiment equalled 287 mm in 2007, 228 mm in 2008 and 190 mm in 2009; with a mean of 235 mm ± 49 SD (Olefeldt and Roulet 2012). The mean summer temperature at the site is 7 °C, the mean winter temperature is -6 °C. The experiment was set up on an elevated, dry (Rydén 1976; Sonesson 1980), ombrotrophic *Sphagnum fuscum* (Schimp.)-dominated palsa, with an active layer thickness of around 50 cm. The vascular plant community consists of the evergreen dwarf shrubs *Empetrum hermaphroditum* L. (56 % of total aboveground biomass) and *Andromeda polifolia* L. (9 %), the deciduous dwarf shrubs *B. nana* L. subsp. *nana* (6 %) and *Vaccinium uliginosum* (7 %), the forb *Rubus chamaemorus* L. (15 %), and the graminoid *Eriophorum vaginatum* L. (8 %) and has been classified as dry-growing elevated palsa vegetation by Madsen and Widell (1974).

Treatment and Experimental Design

At both sites, 16 visually similar plots of 1 m² were laid out at the beginning of the growing season in 2007. Following a completely randomized design, the plots were assigned to one of the precipitation treatments (ambient or increased

precipitation, $n = 8$). The plots with increased precipitation were evenly watered 16 times during each growing season with 12.5 l of water per plot per time. This resulted in a total of 200 mm extra precipitation per growing season, i.e. an approximate doubling of the ambient summer precipitation. Both the experiments lasted three growing seasons.

At the Siberian site, water for additional precipitation was taken from nearby clear-water pools and the Berelekh (Yelon) River, a tributary of the Indigirka River. Total inorganic nitrogen was 0.4 ± 0.2 mg l⁻¹ (data based on water samples used for the treatment, taken in 2007 and analysed using a SA-40 auto-analyser, Skalar, Breda, The Netherlands).

At the Swedish site, water for additional precipitation was taken from the stream adjacent to the experimental site and had a conductivity of 50.0 ± 11.5 μS cm⁻¹, pH 6.7 ± 0.2, dissolved organic carbon content of (DOC) 10.6 ± 2.6 mg l⁻¹, and total nitrogen of (TN) 0.3 ± 0.2 mg l⁻¹ (data based on measurements from two separate spots in the stream from the end of April until the end of September 2008) (Olefeldt and Roulet 2012). Given these low nutrient concentrations in neither site, nutrient addition does not seem to have been a confounding factor in our set-up.

Vegetation Measurements

Total Annual Productivity

We chose to present annual vascular production instead of total aboveground biomass, as the latter is bound to be

largely unresponsive to perturbations due to dilution of the current season's growth by material produced in previous years (cf. Parsons et al. 1994). After three growing seasons, all aboveground biomass, defined as all plant material emerging above the moss layer, was harvested. The total annual vascular production was subsequently calculated as the sum of: (1) the aboveground green biomass of all graminoids and forbs (*A. latifolia*, *Saxifraga* spp., *P. rotundifolia* for the Siberian site and *E. vaginatum* and *R. chamaemorus* for the Swedish site), (2) the leaf biomass and length increment biomass of all deciduous shrubs (*B. nana* subsp. *exilis* and *S. pulchra* for the Siberian site and *B. nana* subsp. *nana* and *V. uliginosum* for the Swedish site) and (3) all new growth of the evergreen species, which were only present at the Swedish site. Total biomass of the evergreen's new growth was calculated by multiplying the total aboveground biomass with the ratio of current-year's growth biomass to total shoot biomass. This ratio was determined on samples of 20 randomly picked shoots for *E. hermaphroditum*, whereas the ratio for *A. polifolia* was estimated to be 1:3 (Aerts, pers. comm., data from a site 200 m from the present study site).

Because the most productive species at the Swedish site is the peat moss *S. fuscum*, productivity of this bryophyte was measured separately. The length growth of *S. fuscum* was measured in all plots, using a modification (Dorrepal et al. 2004) of the cranked wire technique (Clymo 1970), with four wires per plot. Although length growth was measured in last 2 years of the experiments, bulk density of the moss was determined (destructively, on the top 1 cm of the moss carpet), in the last year of the experiment (on two samples per plot, dry weight per volume). Therefore, annual production was calculated only for the last year of the experiment (by multiplying bulk density with length growth). However, to check for temporal consistency, length growth was analysed with repeated measures (RM)-ANOVA (within-subject factor year and between-subject factor treatment) for the last 2 years of the experiment.

Species-Specific Growth Responses

In addition to the integrative measure of total annual production, several more sensitive key variables of species-specific plant performance were measured (leaf size, SLA, length increments and biomass per length increment).

Two traits known to be particularly responsive to drought, leaf size and SLA, were measured in the last year of the experiment on randomly picked leaves (number of leaves per plot) of the most abundant broad-leaved species [*B. nana* subsp. *exilis* (twenty), *S. pulchra* (five) and *A. latifolia* (five) at the Siberian site, and *B. nana* subsp. *nana* (ten), *V. uliginosum* (ten) and *A. polifolia* (ten) at the Swedish site]. Leaf size and SLA were measured and

calculated according to the standard protocol described in Cornelissen et al. (2003).

Current-year apical stem length increments of the dominant shrub species were determined as measures of growth responses. At the Siberian site, all stem length increments of five randomly selected individual shrubs of *B. nana* subsp. *exilis* per plot were measured of the last two years' growth. The length of all shoots (both the short and the long shoots) of these individuals was determined in order to obtain a reliable measurement. Apical stem length increments of all *S. pulchra* plants per plot (min. three, max. nine) were measured during the last year of the experiment. Current-year length increments were identified using colour differences of the stem and scars of the terminal bud. At the Swedish site, length increments of ten randomly selected *E. hermaphroditum* shoots per plot were measured during the last 2 years of the experiment. Current-year growth was identified using colour differences of the stem, bud scars and changes in leaf length between the growth segments of the different years (Keuper et al. 2011). *B. nana* subsp. *nana* length increments at the Swedish site were measured as the distance from a marked point on the stem until the tip of the shoot, both at the beginning (early June) and at the end (early September) of the growing season. Only the first 2 years were measured because the destructive end harvest in the last year of the experiment interfered with these measurements.

Statistics

All data were tested for normality and homogeneity of residual variances by visual inspection of residual and probability plots. Log transformation improved the homogeneity of residual variances for the total vascular production data and for the *B. nana* subsp. *nana* length increment data. For all other variables residual variance was approximately normal and homogeneous.

Total vascular production in the last year of the experiment at both the sites was analysed simultaneously with a two-factor ANOVA (with treatment and site as independent factors) in order to reduce the chance of Type I error.

Leaf size and SLA were analysed with separate MANOVAs for the two sites, with treatment as independent factor and the leaf traits (leaf size and SLA) as dependent variables with the species identities acting as multivariates.

Differences in length increments and biomass per new stem length of the dominant shrubs were analysed using separate RM-ANOVAs for species and site when data for 2 years were available (*B. nana*, *E. hermaphroditum*), with year as a within-subject factor and treatment as a between-subject factor. A one-way ANOVA was used when only 1 year of measurements was available (stem length

increments of *S. pulchra*, number of *B. nana* leaves on the new stem, weight per unit new stem length, and production of the dominant peat moss *S. fuscum* for the Swedish site).

Before statistical analysis, values for each variable were averaged per plot, and all analyses were performed with SPSS 15.0 for Windows. Given the high intrinsic variability of many of the vegetation response measures, the statistical power is generally low and therefore we also discuss results with $P < 0.1$.

RESULTS

Total Aboveground Biomass Production

Total annual aboveground biomass production of the vascular plant communities at the Siberian and the Swedish site was not affected by precipitation addition ($F = 2.0$; $p > 0.1$). Although vascular production was higher at the Siberian site (Fig. 2; $F = 85.7$; $p < 0.001$), there was no interaction ($F = 0.35$; $p > 0.1$) between site and treatment (Fig. 2).

Species-Specific Responses to the Precipitation Treatment

Leaf Traits

At the Siberian study site, leaf size of *B. nana* subsp. *exilis* was not affected by the treatment ($F = 0.068$; $p > 0.1$), but leaf size of both *S. pulchra* ($F = 5.4$; $p < 0.05$) and *A. latifolia* ($F = 11.1$; $p < 0.01$) were 25 and 113 % larger in the plots with additional precipitation, respectively (Fig. 3a; Table 2). In contrast to leaf size, SLA ($\text{cm}^2 \text{g}^{-1}$) of *B. nana* subsp. *exilis* was only slightly larger in the irrigated plots ($F = 3.75$; $p < 0.1$). SLA of *A. latifolia* was even ~25 % larger in the irrigated plots ($F = 12.9$; $p < 0.001$). In contrast, SLA of *S. pulchra* was not affected by treatment ($F = 3.04$; $p > 0.1$) (Fig. 3c). At the Swedish site, neither leaf size nor SLA of any of the examined species (*B. nana* subsp. *nana*, *V. uliginosum*, *A. polifolia*) were affected by treatment ($p > 0.05$ for all species) (Fig. 3b, d).

Stem Traits

At the Siberian study site, length increments of the dominant shrub *B. nana* subsp. *exilis* were about 30 % larger in the irrigated plots both in the penultimate and in the last year of the experiment ($F = 17.1$; $p < 0.01$). There was a marginally significant difference in growth among the years ($F = 3.6$; $p < 0.1$), while there was no interaction between treatment and year ($p > 0.1$) (Fig. 4a). These

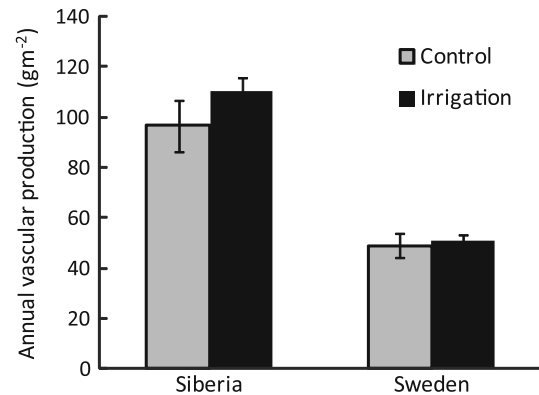


Fig. 2 Mean (± 1 SE) annual vascular production after three years of water addition compared to control plots ($n = 8$). There were no significant effects of the treatment (two-way ANOVA with independent factors site and treatment ($p > 0.1$))

elongated *B. nana* subsp. *exilis* stems produced about one leaf per cm stem length less (–25 %, last experimental year data only) ($F = 13.7$; $p < 0.01$). The treatment did not affect biomass per unit length of the new stem growth ($F = 2.4$; $p > 0.1$). Length increment of the subdominant shrub *S. pulchra* at the Siberian site was also 32 % larger in the last year of the experiment ($18.1 \text{ cm} \pm 3.9 \text{ SD}$ for the irrigated plots vs. $13.7 \text{ cm} \pm 3.4 \text{ SD}$ for the control plots, $F = 4.8$; $p < 0.05$), but the number of leaves per new stem length remained unchanged (3 per cm stem, $F = 2.4$; $p > 0.1$) and biomass of the new stem growth was not affected either ($F = 0.73$; $p > 0.1$).

At the Swedish study site, the length increments of the dominant shrub *E. hermaphroditum* were not affected by additional precipitation ($F = 0.059$; $p > 0.1$) and there was no effect of year, nor an interaction between year and treatment ($p > 0.1$) (Fig. 4b). Biomass per unit length of the new growth was neither affected by treatment ($1.49 \pm 0.24 \text{ SD mg mm}^{-1} \text{ year}^{-1}$ for control and $1.36 \pm 0.26 \text{ SD mg mm}^{-1} \text{ year}^{-1}$ for plots with additional precipitation; $F = 0.89$; $p > 0.1$) and no effect of year nor an interaction between year and treatment was observed ($p > 0.1$). Similarly with the other Swedish results but in contrast to the Siberian results for this species, *B. nana* subsp. *nana* length increments were not affected by additional precipitation at the Swedish site ($5.9 \pm 5.1 \text{ SD mm}^{-1} \text{ year}^{-1}$ for control and $3.6 \pm 2.7 \text{ SD mm}^{-1} \text{ year}^{-1}$ for plots with additional precipitation; $F = 0.93$; $p > 0.1$), nor was there an effect of year ($F = 0.66$; $p > 0.1$) or an interaction between year and treatment ($F = 0.77$; $p > 0.1$). Length growth of the dominant bryophyte *S. fuscum* was not different from the control in the plots with additional precipitation during the last 2 years of the experiment ($4.10 \pm 2.2 \text{ SD mm year}^{-1}$ in the control plots and $4.73 \pm 1.9 \text{ SD mm year}^{-1}$ in the treatment plots:

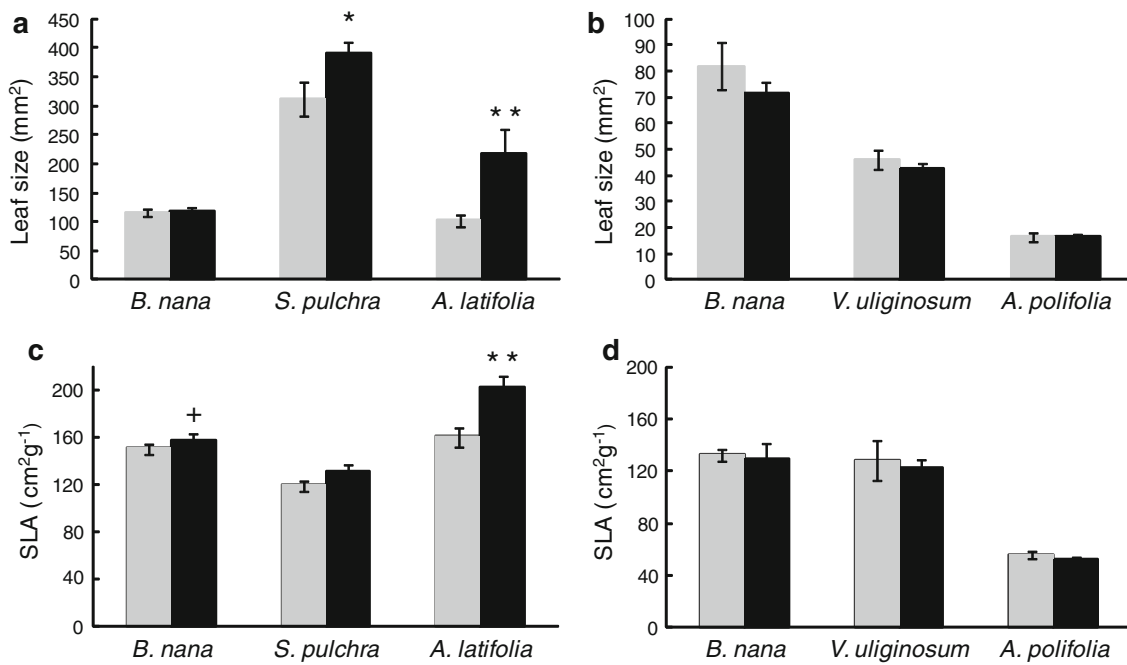


Fig. 3 Mean (± 1 SE) leaf size and SLA at the Siberian (a, c) and the Swedish (b, d) study site in the third year of the experiment in water addition (black bars) compared to control (grey bars) plots ($n = 8$).

Significant differences between water addition and controls per species are indicated with ⁺ $P < 0.1$, * $p < 0.05$ and ** $p < 0.01$ (see main text for details on statistical analysis)

Table 2 Summary of species-specific responses to summer water addition in the two sites addressed in this study (see main text for details)

Geographical region	Vegetation type	Species-specific responses
Northeast Siberia (arctic)	<i>B. nana</i> -dominated dwarf shrub heath	“+” (<i>B. nana</i> SLA and length increments; <i>S. pulchra</i> leaf size and length increment; <i>A. latifolia</i> leaf size and SLA); “0” (<i>B. nana</i> leaf size and biomass per length growth; <i>S. pulchra</i> SLA and number of leaves per cm stem; biomass per length growth); “-” (number of <i>B. nana</i> leaves per stem)
Swedish Lapland (subarctic)	<i>S. fuscum</i> -dominated ombrotrophic peatland	“0” (<i>B. nana</i> , <i>V. uliginosum</i> , <i>A. polifolia</i> leaf size and SLA; <i>E. hermaphroditum</i> , <i>B. nana</i> , <i>S. fuscum</i> length increments; <i>E. hermaphroditum</i> , <i>S. fuscum</i> biomass per length growth)

Background shading colour indicates similarity between geographical regions including those presented in Table 1. Response is indicated as positive (+), negative (-) or no effect (0), with the species and measured variable between parentheses. See main text for effect sizes and F values

$F = 0.57$; $p > 0.1$). *Sphagnum* length growth was significantly different in the two measured years ($F = 20.8$; $p = 0.00$), but there was no significant interaction between treatment and year ($F = 0.11$; $p > 0.1$). Biomass

production of the peat moss was not affected by the precipitation treatment (288 ± 170 SD g m⁻² in the control plots and 313 ± 141 SD g m⁻² in the plots with additional precipitation: $F = 0.10$; $p > 0.1$).

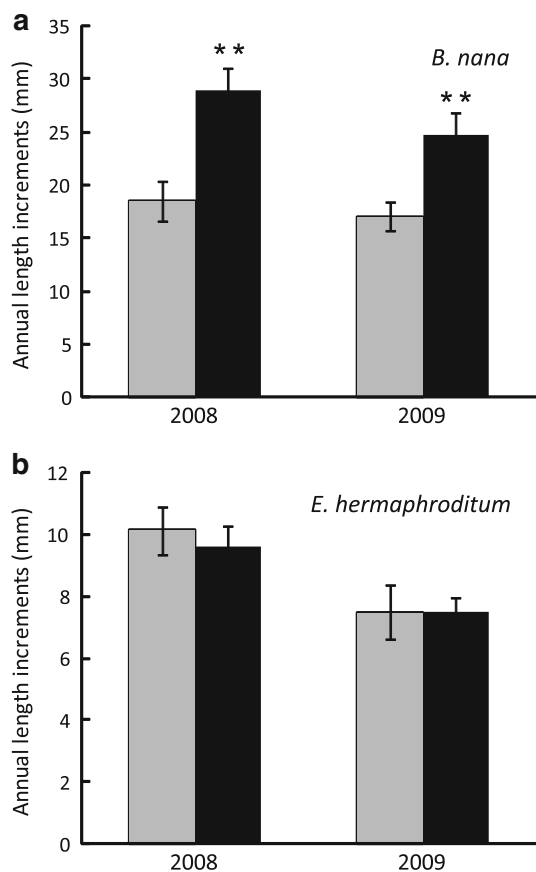


Fig. 4 Mean (± 1 SE) apical annual growth of the dominant dwarf shrubs in both the study sites in response to summer water addition (black bars) or control treatment (grey bars) in the last 2 years of the experiment: **a** *Betula nana* subsp. *exilis* at the Siberian site and **b** *Empetrum hermaphroditum* at the Swedish site ($n = 8$). Significant differences between water addition and controls per species are indicated with $^+P < 0.1$, $*P < 0.05$ and $***P < 0.01$ (see main text for details on statistical analysis)

DISCUSSION

Water Limited Plant Growth in Tundra? No Response in Total Annual Productivity

Three years of experimentally increased summer precipitation did not affect total aboveground vascular biomass production at either of the studied tundra sites. Total annual production is the integrative measure of all species-specific growth responses. Hence, this finding shows that overall, primary production of Siberian *B. nana* heath and Swedish ombrotrophic bog tundra vegetation is at the short to medium term not limited by water availability, even though some specific-species growth responses to the treatment were observed. Our results extend the established pattern of negligible tundra plant productivity responses to experimentally increased summer precipitation (reviewed by Dormann and Woodin 2002) with two previously unaddressed tundra types.

Although the investigated systems generally receive little natural precipitation (between 150 and 300 mm on average, Remer 2009), there are several potential explanations for their resistance in plant productivity to changes in summer precipitation. First, plant productivity may be more limited by other factors such as nutrient availability and/or temperature to such extent that positive responses to alleviation of water limitation are hampered or masked. This explanation is supported by the study of Parsons et al. (1995) (Table 1), who only found a significant effect of watering on graminoid biomass if watering was applied in combinations with either increased temperature or fertilizer. Second, although summer precipitation in tundra may be low, total evapotranspiration is also low, ensuring that in general tundra soils remain relatively wet throughout the summer (polar deserts excluded). Moreover, soils are driest in late summer (Rydén 1976), while most growth takes place in early summer (Sonesson 1980; Karlsson and Callaghan 1996). At the beginning of the growing season, moisture may still be available from snowmelt, while drainage is limited due to the shallowness of the active layer (McGraw 1985). Finally, total productivity responses to water addition might be hard to detect due to spatial heterogeneity in initial biomass and a relatively short duration of the experiment (three years).

Species-Specific Responses: Signs of Drought Stress-Release and Growth Responses

While the overall productivity was unaffected, species-specific growth responses to increased summer precipitation differed remarkably between species and sites (Table 2). The increased leaf size in response to irrigation observed for the deciduous shrub *S. pulchra* and the grass *A. latifolia* at the Siberian study site suggests that growth of these species is water limited, in line with our hypotheses. SLA of *S. pulchra* remained constant, but for *A. latifolia* the increased leaf size co-occurred with thinner leaves, again in line with our hypotheses. Leaves of the dominant shrub *B. nana* subsp. *exilis* (93 % of aboveground biomass) also became slightly thinner ($p < 0.1$) (Fig. 3b) while its leaf size remained unchanged in response to irrigation (Fig. 3a). While nutrient deficiency and drought stress are known to have very similar effects on vegetative plant characteristics (Small 1973), the very low nutrient concentrations in our irrigation water decrease possible interferences by increased nutrient availability as confounding factor. Together, the species-specific vegetation responses to the water addition suggest that growth of the vegetation is water limited at the Siberian dry heath. Alleviation of this water limitation allowed length increments of *B. nana* subsp. *exilis* to increase with around 30 %, while length increments of *S. pulchra* increased as well (Fig. 4a). The

fact that these growth responses were not sufficient to increase the overall productivity at the Siberian site might be explained by the relatively small contribution of *B. nana* subsp. *exilis* length increments (4 %) to total annual productivity, compared to the contribution of total *B. nana* subsp. *exilis* leaf biomass (84 %, results not shown), which did not differ among treatments (results not shown). However, note should be taken that we did not take growth (thickening of the stems) into account. Such secondary growth can amount up to an annual production of ~15 % of total standing biomass (Bret-Harte et al. 2002) and has previously been reported responsive to natural summer precipitation patterns (Blok et al. 2011). Given the relatively large contribution of the ‘old’ woody biomass to the total standing biomass at the Siberian site (84 %, results not shown) secondary growth might have contributed considerably to annual total productivity in the plots with additional precipitation.

In contrast, at the Swedish site, the absence of any responses in leaf size and SLA and the absence of increased length increments of all measured species, including *S. fuscum*, suggests that in this habitat, drought stress was not a condition that limited the plants during the period of leaf and stem development (Figs. 3b, d, 4b). *Empetrum* (56 % of aboveground biomass at the Swedish site) is assumed to be tolerant to variations in soil water content (Bell and Tallis 1973) and has previously been found unresponsive to experimentally increased summer precipitation (Shevtsova et al. 1997) (Table 1). Although *S. fuscum* is sensitive to water availability and has previously been shown to respond to small increases in summer precipitation (up to 20 mm year⁻¹) (Sonesson et al. 2002), larger increases, such as provided in this study, may also negatively affect productivity through increased leaching of nutrients (Sonesson et al. 2002). This would explain the absence of net effects of increased summer precipitation.

The difference in *B. nana* responsiveness among the sites may be due to the occurrence of different ‘ecotypes’ of *B. nana* at the two sites: different responses to experimental manipulation in different geographical areas (Alaska, Northern Sweden) have previously been observed for this species (Van Wijk et al. 2004). Previous observations of plant responses to water drainage patterns in Alaskan tundra (Matthes-Sears et al. 1988) showed that both *B. nana* as well as *S. pulchra* had higher aboveground biomass in water tracks. Growth of *B. nana* at the Siberian site might also have been more drought stressed ambiently, and might have contributed to drying of the soil because it comprised 93 % of the total biomass and thus had a relatively large transpiring leaf area. Finally, at the Siberian site, *B. nana* subsp. *exilis* supposedly had superficial roots only due to the shallow active layer thickness (max. 25 cm

compared to 50 cm at the Swedish site) and could thus only exploit a much smaller reservoir of soil water.

Long-Term Implications for Species Composition

Despite species-specific responses to the treatment at the Siberian study site, no changes in species composition indices were found on either site (results not shown). Hence, this study shows that even doubling of yearly summer precipitation does not induce a shift in species composition during the first three years. For the Swedish site, impacts on vegetation composition through species interactions are not expected due to the low total species cover in the plots and the complete absence of responses. However, at the Siberian site, the increased leaf size of *S. pulchra* and *A. latifolia* suggests that these species are drought stressed and may, if the tundra gets wetter, on the long-term benefit from wetter conditions. Enhanced responses in tundra ecosystems in terms of species composition and total productivity to additional precipitation seem even more likely in a future climate when changes in temperature and nutrient availability are predicted to co-occur with increased summer precipitation (Parsons et al. 1994) and when permafrost degradation drastically affects local hydrology, the first signs of which are already apparent (Molau 2010).

CONCLUSIONS

The plant level responses for the Swedish site indicate that increased summer precipitation alone will not have major effects on ombrotrophic peatland vegetation productivity. For the Siberian *B. nana* dominated dry heath site on the other hand, the fact that several individual plant measurements show a positive response to the precipitation treatment, suggests that in the long-term biomass production may increase in response to increased summer precipitation. However, over the course of this three-year experiment, primary production did not increase in response to the treatment at either of the study sites. Hence, despite regional differences at the plant level, our study shows that total tundra plant productivity shows at the short term no response to experimentally increased summer precipitation, corroborating previous studies on tundra plant productivity responses to summer precipitation. This contrasts with the results of nutrient addition experiments and suggests that water in most tundra ecosystems not be the primary growth-limiting factor but a co-limiting growth factor. This study extends the available knowledge with two previously unaddressed tundra types.

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AUTHOR BIOGRAPHIES

Frida Keuper (✉) is a PhD student at the department of Ecological Science at the VU University Amsterdam. Her research interests include the effects of climate change on vegetation, with special emphasis on plant–soil interactions in response to permafrost thawing. *Address:* Systems Ecology, Department of Ecological Science, Faculty of Earth and Life Sciences, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands. *Address:* Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, 981 07 Abisko, Sweden. e-mail: fridakeuper@gmail.com

Frans-Jan W. Parmentier is a postdoctoral researcher at the Department of Physical Geography and Ecosystem Science of Lund University, Sweden. His research interest involves the greenhouse gas balance of the Arctic, and ranges from the exchange of CO₂ and methane from tundra on the local scale to large scale teleconnections across the Arctic. *Address:* Lund University, Sölvegatan 12, 22362 Lund, Sweden. e-mail: frans-jan.parmentier@nateko.lu.se

Daan Blok is a postdoc at the Centre for Permafrost Dynamics in Greenland (CENPERM), University of Copenhagen. His research interests include the feedbacks between climate, vegetation and permafrost dynamics in Arctic tundra ecosystems. *Address:* University of Copenhagen, Øster Voldgade 10, 1350 Copenhagen K, Denmark. e-mail: daanblok@gmail.com

Peter M. van Bodegom is an associate professor at the VU University Amsterdam, working at the interface between community ecology, macroecology and earth system modelling. With his group, he aims at quantifying globally applicable functional relationships between vegetation, soil micro-organisms and their environment by targeted experiments, meta-analyses and process-based modelling. He applies the ecological relations thus derived to climate-proof modelling of soil-vegetation dynamics in collaboration with earth system modellers. *Address:* Systems Ecology, Department of Ecological Science, Faculty of Earth and Life Sciences, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands. e-mail: peter.van.bodegom@falw.vu.nl

Ellen Dorrepaal is an assistant professor in terrestrial ecology at the Climate Impacts Research Centre in Abisko, Umeå University. Her research focuses on how plant–soil interactions drive the feedbacks of arctic and boreal ecosystems to climate change. *Address:* Systems Ecology, Department of Ecological Science, Faculty of Earth and Life Sciences, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands. *Address:* Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, 981 07 Abisko, Sweden. e-mail: ellen.dorrepaal@emg.umu.se

Jurgen R. van Hal is a research technician at the VU University Amsterdam. His research interests include plant- and animal-ecology. *Address:* Systems Ecology, Department of Ecological Science, Faculty of Earth and Life Sciences, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands. e-mail: j.r.van.hal@vu.nl

Richard S. P. van Logtestijn is a research technician at Systems Ecology, VU University Amsterdam. He specialises in global change ecology of northern ecosystems and carbon and nutrient cycling processes. He frequently applies stable isotope techniques to track carbon and nitrogen through ecosystems and organisms at different trophic levels. *Address:* Systems Ecology, Department of Ecological Science, Faculty of Earth and Life Sciences, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands. e-mail: richard.van.logtestijn@vu.nl

Rien Aerts is a professor in Systems Ecology at the department of Ecological Science at the VU University Amsterdam in the Netherlands. His research interests include the effects of climate change on the interactions between vegetation, soil and hydrosphere, with special emphasis on cool and cold biomes. *Address:* Systems Ecology, Department of Ecological Science, Faculty of Earth and Life Sciences, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands. e-mail: rien.aerts@falw.vu.nl