

Facilitation in an unproductive boreal forest understorey community

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Abstract

Questions: We tested the hypothesis that if competition had a significant influence in structuring this boreal plant community, removal of neighbours, addition of fertilizer and addition of water would all benefit the transplanted seedlings. Alternatively, if facilitation had a greater influence, then removal of neighbours would be detrimental to the transplants but fertilization and watering would still be beneficial.

Location: Understorey of the boreal forest in southwestern Yukon Territory, Canada (138°22'W; 61°02'N).

Methods: Ten of the most common species were transplanted as seedlings into transects from which all neighbours had been removed, and also into transects with intact vegetation. We used a factorial design with two levels of watering and two levels of fertilization; this allowed us to test effects at both species and community level.

Results: The summed survival and total biomass of all transplants was significantly higher in the presence of neighbours than without neighbours, indicating a facilitative effect of neighbouring plants, but there were significant increases in only six of the ten species. The combined survival and biomass of all species increased with watering, survival decreased and biomass increased with fertilization, but only two species had significant responses to fertilization: *Anemone parviflora* decreased and *Mertensia paniculata* increased in biomass. Watering increased the biomass of *Achillea millefolium*, *Festuca altaica* and *Solidago multiradiata*; there were also some interaction effects.

Conclusions: (1) The presence of neighbours was generally facilitative. (2) Fertilization had negligible effects, and watering had minor beneficial effects. (3) This study demonstrates the importance of facilitation in structuring this boreal understorey community.

Keywords: Boreal forest understorey; Competition; Facilitation; Fertilization; Survival; Watering.

Nomenclature: Cody (2000).

Abbreviations: VWC, Volumetric water content; LAI, Leaf area index; PAR, Photosynthetically active radiation.

Introduction

Traditionally, studies on the factors structuring plant communities have focused on negative interactions such as competition (Connell 1983; Schoener 1983; Grace & Tilman 1990; Keddy 2001) and have tended to neglect positive interactions such as facilitation (Bertness & Callaway 1994; Callaway 1995). Only recently have researchers begun to thoroughly investigate the potential role of facilitation in community structure, especially in unproductive environments (Bertness 1998; Brooker & Callaghan 1998; Lortie & Turkington 2002; Brooker et al. 2008). In productive environments, plants may compete for resources because conditions are favourable, but if environmental conditions are harsh, the ability to capture resources may be restricted and any amelioration of these conditions by neighbouring plants may outweigh potential negative interactions (Brooker & Callaghan 1998). Others have argued that competition also occurs in unproductive environments (Goldberg et al. 1999, 2001; Shilo-Volin et al. 2005; Rajaniemi et al. 2009), although the particular plant strategies that would be optimal under those conditions are different from those in more productive environments (Newman 1973; Tilman 1988). More recently, Lamb & Cahill (2008) and Mitchell et al. (2009) have demonstrated, in rough fescue grassland and a subarctic-alpine community, respectively, that competition can be intense in unproductive communities without having a significant impact on community structure.

The boreal forest is generally considered to be limited by soil nutrients and can vary from extremely dry to extremely wet, and from cold and harsh to relatively temperate (Larsen 1980; Bonan & Shugart 1989). The boreal region of the southwestern Yukon, Canada, is dry, cool and nutrient-

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limited (Turkington et al. 1998, 2002); experimental studies by Carrier & Krebs (2002) showed that the understorey and shrub layers are not water-limited. Therefore, this region is an appropriate location to test the role of biotic interactions in low productivity habitats. Much of the knowledge on plant interactions in stressed, low productivity systems comes from arid ecosystems (Fowler 1986; Goldberg et al. 2001; Rajaniemi et al. 2009); however, for a review of studies focusing on biotic interactions in cold, harsh environments see Arie & Turkington (2002).

Specifically, we tested the hypothesis that if competition has an impact in structuring this boreal forest understorey community, removal of neighbours, addition of fertilizer and addition of water would all benefit the transplanted seedlings. Alternatively, if facilitation has a greater influence than competition, then removal of neighbours would be detrimental to the transplants, but fertilization and watering would still be beneficial.

Methods

Study site

The study site is located within the boreal forest, close to Kluane Lake, in the southwestern Yukon Territory (YT; 138°22'W; 61°02'N) at approximately 900-1000 m a.s.l. The closest climate station is Burwash Airport, YT, approximately 52 km to the north. At Burwash, the mean annual total precipitation is 279.7 mm (range 142-401 mm), of which 192.1 mm is rainfall (Whitfield et al. 2004; Environment Canada 1971-2000 Climate Normals); the 30-year normal precipitation (including some snow) for the months during which the study took place (June, July, August) is 158.2 mm. In 2001, the first year of the study, this value was 149.2 mm. In 2002, 104.2 mm of precipitation fell in July and August and no data are available for June. For these months, the 30-year normal daily average temperature was 11.1°C and the daily maximum and minimum were 18.0°C and 4.7°C, respectively.

White spruce (*Picea glauca* (Moench) Voss s.l.) is the dominant tree species, with a density of 583 stems ha⁻¹ (95% CI of 486-697 ha⁻¹). Many willows (predominantly *Salix glauca* L. s.l.) and some dwarf birch (*Betula glandulosa* Michx.) make up the shrub understorey. The ground layer or understorey species had a mean biomass of 367 g m⁻² (n = nine 1-m² quadrats, 95% CI of 186-548 g m⁻²) in 1999. The cover of moss and lichens is <5%. Although

there are herbivores such as snowshoe hares, red squirrels and microtine rodents at this site, the abundance of the ground layer is more affected by the limited soil nutrients than by herbivores (John & Turkington 1995; Turkington et al. 2002).

Study species

Ten of the most common understorey species were chosen as representative of the community. Eight of the species are herbaceous perennials: *Achillea millefolium* L. ssp. *borealis* (Bong.) Breitung (yarrow), *Anemone parviflora* Michx. (northern anemone), *Epilobium angustifolium* L. s.l. (fireweed), *Festuca altaica* Trin. (northern rough fescue), *Lupinus arcticus* Wats. (arctic lupine), *Mertensia paniculata* (Ait.) G. Don var. *paniculata* (bluebell), *Senecio lugens* Richards. (black-tipped groundsel), *Solidago multiradiata* Ait. (goldenrod). The remaining two species are woody perennials: *Arctostaphylos uva-ursi* (L.) Spreng. s.l. (bearberry) and *Linnaea borealis* L. ssp. *americana* (twinflower). Hereafter we will refer to species using their generic name. These ten species have the highest density of the plants found in the understorey and account for approximately 95% of its aboveground biomass.

Experimental design

The role of biotic interactions in structuring the boreal forest understorey was tested using a 2×2×2 fully factorial design using two levels of each treatment (neighbour removal, fertilization and watering), ten understorey species and three replicates per treatment. In mid-June 2001, immediately after snowmelt, we laid out 24 transects, each 3.3-m long and 0.3-m wide, with at least 1 m separating each transect. Half of the transects were randomly assigned to the neighbour removal treatment and were sprayed with a non-selective systemic herbicide (RoundUp™, active ingredient glyphosate; Monsanto, Winnipeg, MB, CA), which is known to quickly break down in the soil. At weekly intervals, a 1:20 ratio of glyphosate to water was sprayed on the neighbour removal transects until vegetation was completely covered with solution. This was repeated until all plants within the 3.3 m×0.3 m area were dead. Some species were resistant to glyphosate and complete death did not occur until mid-July; litter was not removed. Throughout the remainder of the study to August 2002, no regrowth occurred in the sprayed areas and all natural seedling recruits were removed manually.

Transplants were prepared in late May or early June using seed collected the previous year. Seeds of all species except *Arctostaphylos* and *Linnaea* were germinated in peat plugs that were 2.5-cm wide by 5-cm deep following the protocol of Treberg & Turkington (2008). For *Arctostaphylos* and *Linnaea*, we used cuttings grown in peat plugs to make the transplants. The cuttings were taken from healthy plants growing close to the study site. Each was 5-cm long with half of the length left as leaves and half stripped of leaves and treated with a growth hormone (Wilson Roots[®] Liquid Root Stimulator; Brantford, ON, CA) to promote root growth. An individual transplant of each of the ten study species was planted in the peat plug in which it had originally germinated into each transect in mid-July 2001, about 3-4 weeks before the end of the growing season, after all plants in the removal transects had died. The transplants were planted down the centre line of the 3.3-m transect, approximately 0.3-m apart. Transplants that died within the first 10 days were replaced. At the beginning of the 2002 season (early-mid June), all transplants that had died during the previous season or during winter were replaced with seedlings germinated in May 2002, or in the case of *Arctostaphylos* and *Linnaea*, with fresh cuttings.

Water-soluble fertilizer (Plant Prod[®] 20-20-20; Brampton, ON, CA) was applied as a solution every 2 weeks at 4-ml fertilizer per 11 H₂O for the high fertilization treatment. This fertilizer has a manufacturer guaranteed analysis of 20% nitrogen (3.85% ammonium nitrogen, 5.9% nitrate nitrogen, 10.25% urea nitrogen), 20% available phosphate, 20% soluble potash, 0.02% boron, 0.05% chelated copper, 0.10% chelated iron, 0.05% chelated manganese, 0.0005% molybdenum and 0.05% chelated zinc. The total application of nitrogen, phosphorus and potassium was 12 g m⁻² each for the 2002 season. In 2001, approximately half of this amount was added. This fertilizer addition rate corresponds with other experiments conducted in this system that demonstrated significant vegetation responses to nutrient addition (Turkington et al. 1998, 2002; Dlott & Turkington 2000; Arii & Turkington 2002). The low nutrient treatment had no fertilizer added, to serve as a control.

For the watering treatments, water was added at a rate of 31 m⁻² (which corresponds to a rainfall of 3 mm) for the low level and 61 m⁻² (6 mm of rain) for the high level. Water was added every other day throughout the season, and total application was approximately 120 mm and 240 mm for the low and high treatments respectively for 2002. The previous

season was shorter due to site preparation and, as a result, only about half of this total amount was added.

Environmental variables were measured three times during both growing seasons. Volumetric water content (VWC) was measured using a CS620 HydroSense[®] Water Content sensor (Campbell Scientific Inc., Logan, UT, US). Soil temperature at 5 cm was measured using a digital thermometer (Model TPD 32, Omega, Laval, QC, CA). Two measures of the abundance of neighbouring plants along the transects were estimated. The leaf area index (LAI) was calculated by lowering a pin through the vegetation every 10 cm along the 3.3-m long transect and recording the number of times the pin intercepted leaves. We also estimated the percentage of light transmitted through the vegetation by measuring incoming photosynthetically active radiation (PAR) above the vegetation and at the soil surface at three points along the transects. PAR was measured using a line quantum sensor (Apogee Instruments Inc., Logan, UT, US). The three sets of measurements for each environmental variable were averaged for analysis.

Statistical analysis

The effects of neighbours, fertilization and watering were analysed for survival and total biomass of all species in each transect combined using the standard 2×2×2 fully factorial design ANOVA with SYSTAT (SYSTAT Software Inc., 2002; Version 10, Richmond, CA, US). ANOVAs were also carried out to analyse the biomass of the ten species individually. During preliminary data analysis, the planting date of each transplant was included as a covariate to remove size effects due to differences in age. But, for none of the species was planting date a statistically significant covariate (data not shown). For each ANOVA, the usual assumptions of independence, homogeneity of variance and normality were checked. All data conformed to the assumption of independence. Survival data were not transformed prior to ANOVA because assumptions about variance and normality were met (Zar 1984). Most species lost some individuals in some of the transects. If an individual died before the end of the experiment, its final biomass was not recorded. This led to zero values and skewed distributions when the treatment effects on the biomass of the individuals of each species were individually tested in ANOVA. To remove some of the skewness and to meet the assumption of homogeneity of variance, all of the biomass data for each individual species were

square-root transformed with $X' = (X)1/2 + (X+1)1/2$. This transformation is useful when data values are small ($X \leq 2$) and contain some zero values (Zar 1984). Although the data had variances that were similar, the normality assumption was not met for any of the ten study species. However, ANOVA is robust to violation of the normality assumption, especially when the experiment is large (having either many samples or many treatments) and the samples are balanced, such as in this experiment (Zar 1984; Underwood 1997). Differences between treatment means, or multiple comparisons, were tested using Tukey's HSD (honestly significant difference) test (Zar 1984).

Results

The summed survival of all transplants (Table 1a, Fig. 1) and their total biomass (Table 1b, Fig. 2) were both significantly higher in the presence of neighbours ($P < 0.05$). The combined biomass of all species showed an increase with fertilization ($P = 0.056$), while the combined survival decreased with fertilization ($P = 0.058$) and increased with watering ($P = 0.096$, Table 1).

Transplants of six of the ten species had significantly higher biomass with neighbours than without (Table 2, Fig. 3). However, only two species had significant responses to fertilization, with *Anemone* decreasing and *Mertensia* increasing in biomass (Table 2, Fig. 3). Watering increased the

Table 1. Summary of ANOVA for (a) the summed percentage survival of all transplants along a transect and (b) the summed biomass of all transplants along a transect. Main effects are Neighbours (N), Fertilization (F) and Watering (W). Values in bold are significant at $P < 0.05$, and those in *italics* are significant at $P < 0.10$.

Source	<i>df</i>	MS	<i>F</i> -ratio	<i>P</i>
<i>(a) Survival</i>				
N	1	70.042	31.130	<.001
F	1	9.375	4.167	<i>0.058</i>
W	1	7.042	3.130	<i>0.096</i>
N×F	1	0.042	0.019	0.894
N×W	1	0.375	0.167	0.689
F×W	1	1.042	0.463	0.506
N×F×W	1	1.042	0.463	0.506
Error	16	2.250		
<i>(b) Biomass</i>				
N	1	0.407	20.364	<.001
F	1	0.085	4.240	<i>0.056</i>
W	1	0.014	0.716	0.410
N×F	1	0.022	1.093	0.311
N×W	1	0.000	0.001	0.973
F×W	1	0.005	0.230	0.638
N×F×W	1	0.008	0.393	0.540
Error	16	0.020		

biomass of three species, *Achillea*, *Festuca* and *Solidago* (Table 2, Fig. 3). *Arctostaphylos*, *Festuca* and *Solidago* had interaction effects so some caution is required in interpretation (Table 2). For example, for *Festuca* all first-order interactions were significant and both neighbours and watering were significant (Table 2). The interactions of neighbours and fertilization, and of neighbours and watering, both showed higher biomass in the higher fertilization or watering treatments but only with neighbours present (Fig. 3). The interaction between water and nutrients indicates higher biomass for *Festuca* but only when nutrients and water are high (Fig. 3). Therefore, the main treatment effects that were significant, neighbours and watering, were due largely to the interaction effects. A second-order

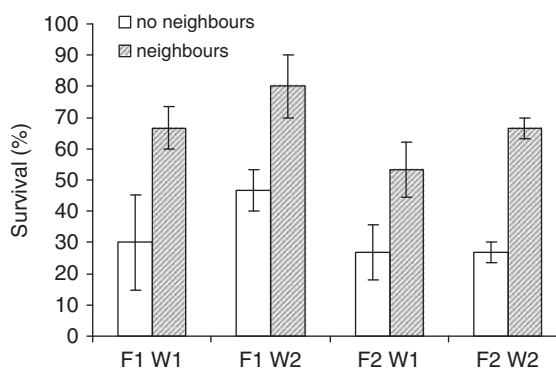


Fig. 1. The percentage survival (± 1 SE) of all transplants summed per transect with or without neighbours at low (F1) and high (F2) fertilizer addition and at low (W1) and high (W2) watering. The effect of neighbours was statistically significant at $\alpha = 0.05$ and the effect of fertilizer and watering was significant at $\alpha = 0.10$.

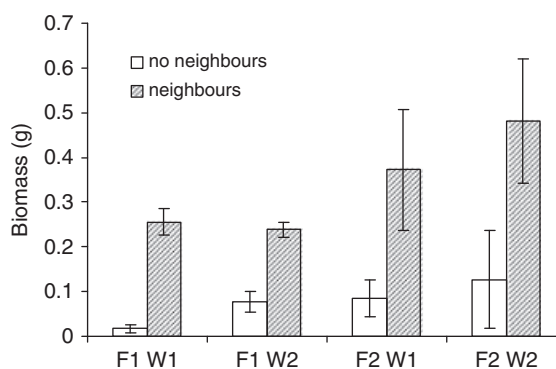


Fig. 2. Total aboveground biomass ($g \pm 1$ SE) of all transplants summed per transect with or without neighbours at low (F1) and high (F2) fertilizer addition and at low (W1) and high (W2) watering. The effect of neighbours was statistically significant at $\alpha = 0.05$ and the effect of fertilizer was significant at $\alpha = 0.10$.

Table 2. Probabilities derived from ANOVAs for the biomass of each of the ten species. Values in bold are significant ($P < 0.05$).

Species	N	F	W	N×F	N×W	F×W	N×F×W
<i>Achillea millefolium</i>	0.010	0.251	0.024	0.801	0.388	0.088	0.594
<i>Anemone parviflora</i>	0.904	0.008	0.337	0.117	0.208	0.593	0.829
<i>Arctostaphylos uva-ursi</i>	<.001	0.827	0.892	0.562	0.618	0.453	0.020
<i>Epilobium angustifolium</i>	0.712	0.309	0.890	0.520	0.393	0.591	0.217
<i>Festuca altaica</i>	0.002	0.110	0.012	0.011	0.003	0.048	0.277
<i>Linnaea borealis</i>	0.012	0.803	0.430	0.696	0.163	0.163	0.430
<i>Lupinus arcticus</i>	0.023	0.823	0.462	0.823	0.462	0.064	0.064
<i>Mertensia paniculata</i>	0.172	0.037	0.427	0.105	0.278	0.806	0.414
<i>Senecio lugens</i>	0.580	0.505	0.457	0.948	0.752	0.908	0.616
<i>Solidago canadensis</i>	<.001	0.833	0.023	0.118	0.098	0.033	0.007

interaction (F×W) was significant for *Solidago* (Table 2). The high fertilizer and high water with neighbours treatment had significantly higher biomass for *Solidago* than for all other treatments, with the exception of the low fertilizer and low water with neighbours treatment, which was the same as all others (Fig. 3). The high and low water treatments were different within the high fertilizer effect, but there was no difference between any of the other nutrient and water treatments (Fig. 3). As for *Festuca*, the significant effects of the neighbour and water treatments for *Solidago* were due to the significant interaction terms.

The treatments had few statistically significant effects on the environmental variables measured along the transects (Table 3, Fig. 4). The volumetric water capacity was significantly higher in the high water treatment (mean = 16.4%, 95% CI 14.4–18.4%) than the low water treatment (mean = 12.6%, 95% CI 11.0–14.2%). There was significantly more light transmitted to the surface in the neighbour removal transects, although this is not surprising given that there was no live vegetation. The fertilization and watering had no effect on either the percentage transmittance or LAI.

Discussion

The importance of neighbours

The presence of neighbours did not show a suppressing or competitive effect on the survival or growth of transplants. Rather, their presence significantly increased the survival and the biomass of most of the transplants, while fertilization and watering slightly increased the survival and biomass. Given the results reported from previous research conducted near this site, we would not have predicted the importance of neighbours for the success

of seedling establishment and growth. All of these study species have been included in previous experiments examining the role of nutrient availability and herbivory (John & Turkington 1995; Turkington et al. 1998, 2002; Dlott & Turkington 2000), and four of the species were included in a study specifically examining the role of competition (Arii & Turkington 2002). Here, we assumed that if we expanded the number of species to include more than the four species examined in Arii & Turkington (2002), we would detect additional evidence of suppression by neighbours. Surprisingly, we found that both survival and biomass of most of the transplanted species were higher when neighbours were present, indicating a positive interaction rather than a competitive one. The use of seedlings in this study, compared to adults in these previous studies, likely accounts for some of the observed differences in results, a topic we discuss later. The positive effect of neighbours has been previously reported from an experiment conducted in alpine tundra < 10 km from our study site (Callaway et al. 2002). Callaway et al. (2002) used elevation as a stress gradient and hypothesized that with increasing elevation, the importance of facilitation would also increase. They reported that the target species at both low and high elevation had a significantly positive neighbour effect, and that both elevations were highly stressed (Callaway et al. 2002). The idea that positive interactions become more important as stress increases is not new (Bertness & Callaway 1994; Callaway 1995, 1997; Brooker & Callaghan 1998). The positive effect of neighbours has been observed at many other low productivity, high-stress sites in subarctic forests (e.g. Shevtsova et al. 1995, 1997) in alpine tundra (Carlsson & Callaghan 1991; Aksenova et al. 1998; Gerdol et al. 2000) and in arctic tundra (Jonasson 1992). Mitchell et al. (2009) completed a study about 20-km north of our sites but at higher elevation in a subarctic-alpine site. They also

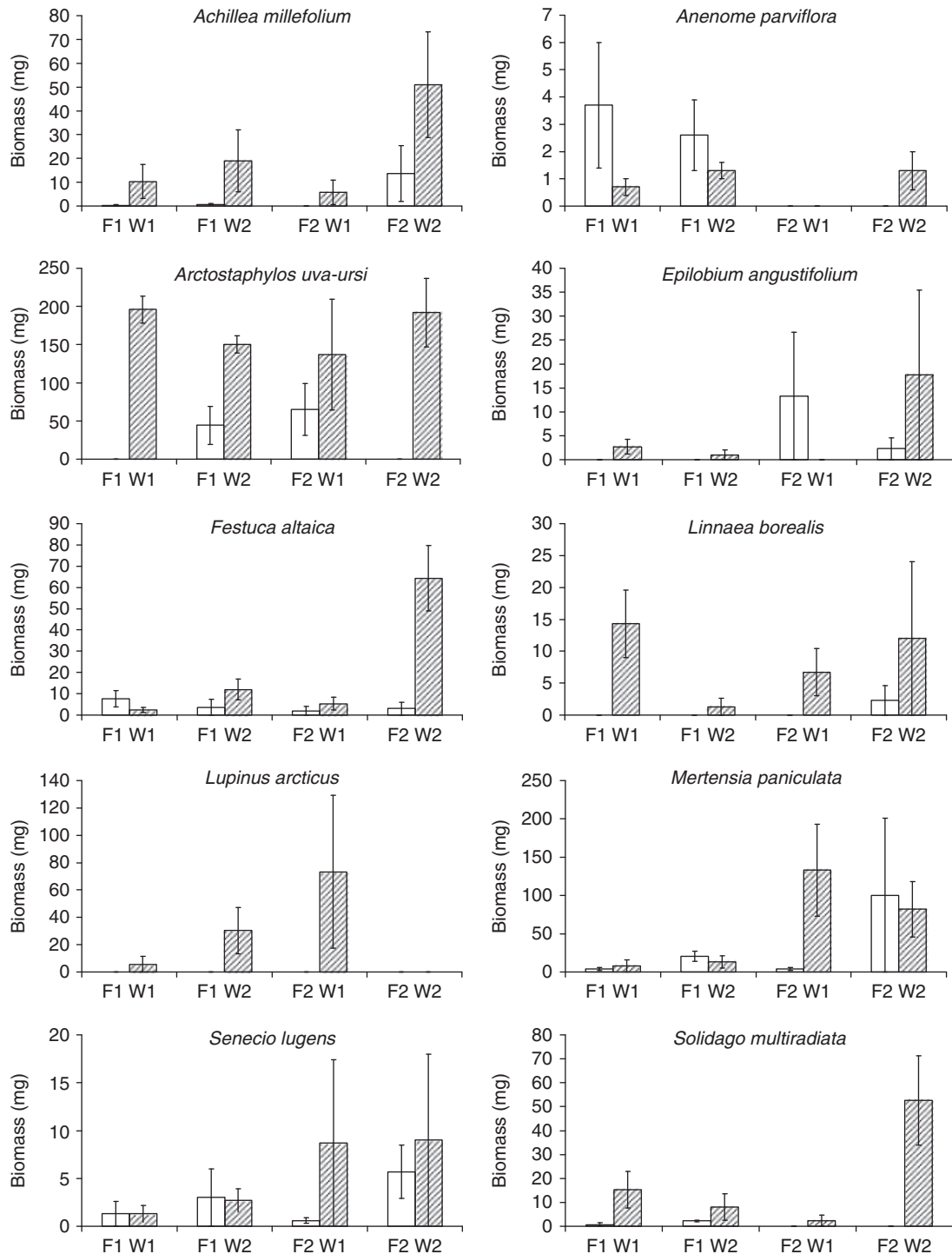


Fig. 3. Total aboveground biomass ($g \pm 1$ SE) of all species with (shaded bars) or without (open bars) neighbours at low (F1) and high (F2) fertilizer addition and at low (W1) and high (W2) watering. A summary of the ANOVA for each species is presented in Table 2.

showed that plant interactions were not important to community structure, even though in many cases the interactions were intense. In their study, plant interactions may reduce individual growth but this

was not important in structuring the community. It has been argued that the relative importance of facilitation should increase with increasing environmental stress (Bertness & Callaway 1994; Callaway

Table 3. Probabilities derived from ANOVAs for the environmental variables monitored in the transect. Neighbours are not included in the ANOVA for LAI because there were no live plants in plots with the neighbours removed. Values in bold are significant ($P < 0.05$).

Variable	N	F	W	N×F	N×W	F×W	N×F×W
Soil temperature	0.746	0.888	0.556	1.000	0.388	0.231	0.352
Volumetric water content	0.815	0.397	0.008	0.519	0.605	0.795	0.471
Percentage light transmittance	<0.001	0.622	0.637	0.523	0.697	0.764	0.917
Leaf area index		0.800	0.723		0.983		

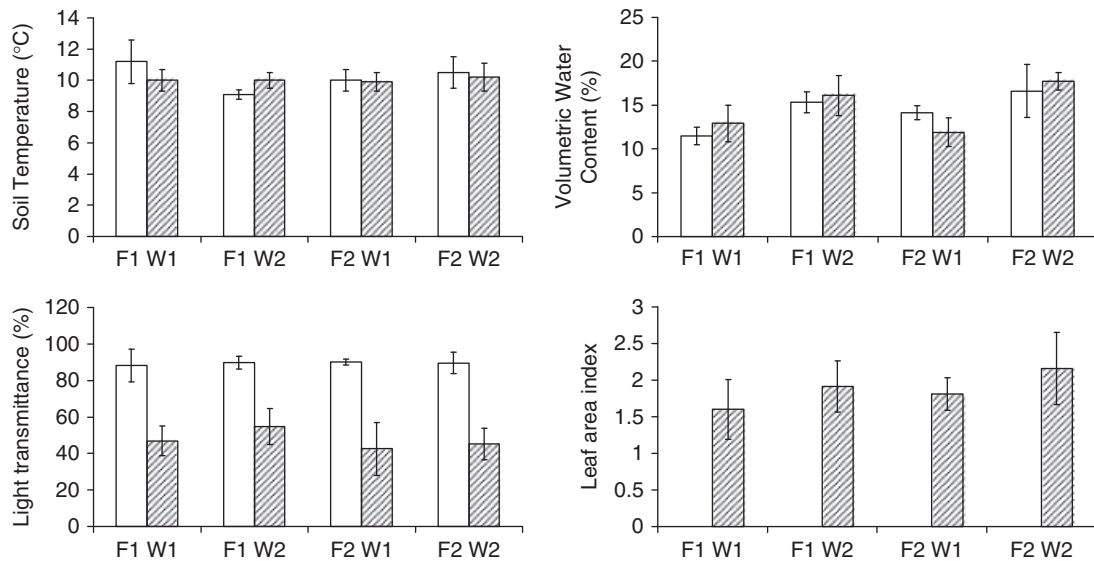


Fig. 4. Measures of three environmental variables, and LAI (± 1 SE) in transects with (shaded bars) or without (open bars) neighbours at low (F1) and high (F2) fertilizer addition and at low (W1) and high (W2) watering. A summary of the ANOVA for each variable is presented in Table 3.

& Walker 1997; Brooker & Callaghan 1998). However, Maestre et al. (2005) recently criticized this as not being consistent with field results from arid and semi-arid systems, and that both facilitation and competition occur in stressful environments. A re-examination of these results using meta-analysis suggests that there is insufficient evidence to reject the stress gradient hypothesis (Lortie & Callaway 2006). A meta-analysis examining the role of positive and negative interactions along productivity gradients (Goldberg et al. 1999) reported that facilitative interactions were common at low standing crop when biomass and growth rates were examined. Given the abundance of literature that demonstrates the role of positive interactions in highly stressed systems (Bertness & Callaway 1994; Callaway 1995; Callaway & Walker 1997; Brooker & Callaghan 1998; Brooker et al. 2008), it is clear that facilitation is a significant process, and our results add to the growing list of studies that support this conclusion.

There have been a number of proposals to explain the positive effects of neighbours on survival

and biomass. These include moderation of temperature and water extremes by providing shade (Callaway 1995; Holmgren et al. 1997), although we did not detect any significant differences between neighbour or no neighbour transects in either the 5-cm soil temperature or soil VWC (Table 3). Unfortunately, we did not determine the soil or plant surface temperature, measurements that would be more important to the individual transplants. The cover provided by even a very low canopy of herbaceous vegetation and low shrubs would absorb and reflect much of the incoming solar radiation and would highly modify the surface microclimate. For example, in a clearcut in a British Columbia Southern Interior forest, soil surface temperatures were significantly higher during the daytime when neighbours were removed using glyphosate compared to untreated areas with intact vegetation; this was due to interception of incoming solar radiation by the grass canopy (Fleming et al. 1998). It would not be unreasonable to assume that surface temperatures of our transplants were also much higher in the

absence of a protective canopy of neighbours. The benefits of the presence of neighbours do not negate the probability that negative interactions also occur between the transplants and canopy plants (Holmgren et al. 1997). In this particular case it is clear that the net outcome for transplants is positive simply because of the increased chance of survival.

Previous demonstrations of competitive interactions in this study location were with existing individuals (Graham & Turkington 2000; Arie & Turkington 2002) rather than with transplanted seedlings and cuttings. The use of seedlings versus adults likely accounts for some of the observed differences in results. Seedlings may only be able to survive if there is a facilitative neighbour present, with the interaction between species becoming negative once the seedling develops into adulthood (Callaway & Walker 1997). Relatively few studies have explicitly attempted to examine changes in biotic interactions as a function of life-history stages, and most of those studies focus on changes in competition intensity or ability (Howard & Goldberg 2001; Lamb & Cahill 2006). Goldberg et al. (2001) observed changes in the importance of facilitation and competition among life stages in desert annual plant species. They observed strong interference competition at the emergence stage, followed by neutral or mildly facilitative interactions at the survival stage, and the growth stage was dominated by exploitation competition. Our study does not include the emergence stage. However, the survival and growth of seedlings was increased in the presence of neighbours, indicating a primarily facilitative role. It would have been interesting to extend this experiment to determine whether the role of neighbours switched from facilitative to more competitive as seedlings became larger.

The lack of importance of fertilization

In general, transplants tended to have lower survival and higher biomass when fertilized, yet only two species had a significant response. The overall lack of species-specific responses to fertilization is surprising given the previous positive responses to nutrient addition both in other low-nutrient systems (Storm & Suss 2008) and in this system (Turkington et al. 1998, 2002). Furthermore, the soil is known to be low in nutrients, particularly nitrogen, which was previously measured as $0.005 \text{ g total N kg}^{-1}$ of soil (Arie & Turkington 2002). Also, the LAI of the fertilized vegetation did not increase in transects in which neighbours were not removed, a response normally expected in a nutrient-limited system. The

only transplanted species that responded positively, *Mertensia*, has been shown to respond favourably to the addition of fertilizer in other studies (John & Turkington 1995; Arie & Turkington 2002; Turkington et al. 2002). We could speculate that the lack of response to fertilization was influenced by water addition to the experiment, which may have increased the rate of nitrogen cycling in all plots, and thus reduced or eliminated any potential fertilization effect. If this were the only study done in this region, this explanation would probably have carried some weight. However, at least three other studies listed above have been conducted within 400 m of these plots, and these studies showed significant responses by most species to fertilization, even when the fertilizer was added as a water-soluble solution. A more plausible explanation is that the seedlings and transplants were too small to adequately capture the additional resources added to the system or, in the case where neighbours were present, were “out-competed” for them.

It has been speculated that plants in this community have such slow growth that they are unable to adequately capture short-term increases in nutrients (Graham & Turkington 2000). This idea is consistent with Grime's (1977) strategy of stress tolerators, where it is assumed that species evolved to persist in harsh ecosystems with low productivity also have slow potential growth rates.

The negative response of *Anemone* to fertilization has been observed in this system previously (John & Turkington 1997; Turkington et al. 1998; Arie & Turkington 2002). This is probably a direct toxic reaction to the fertilizer, given the rapid response observed in this experiment and in Arie & Turkington (2002). In other experiments, the decline in *Anemone* took a few years, and it was thought that the reduction might be due to increased competition imposed by other species using the added fertilizer (John & Turkington 1997).

Most of the previous studies exhibiting significant responses to fertilization in this region have used naturally growing individuals of unknown age. These divergent results demonstrate the importance of investigating different life-history stages because, in experiments using seedlings, the responses to fertilization are quite different from the generally positive response observed when using already established plants.

How important is water?

Water limitation has not been studied to the same degree as nutrient limitation for the boreal

ecosystem. With one exception (Carrier & Krebs 2002), we know of no other experiments that have attempted to manipulate the water availability to boreal forest understorey plants. In our study, three out of ten species showed a significant increase in biomass due to watering and, in general, overall survival and biomass increased. In the low water treatment we supplied approximately 75% more precipitation than the 30-yr annual average in an attempt to prevent death of our seedlings. Initially, we intended that the low watering treatment would only be slightly more than the normal precipitation. However, it quickly became apparent that we would have had considerable death of transplanted seedlings. By increasing the amount of water applied we weakened our test because we reduced the ability to detect whether the system is water-limited. It is possible that the low watering treatment provided sufficient water such that the seedlings were no longer water-limited, even though the naturally occurring vegetation would normally be water-limited. Therefore, there may not be a biologically significant difference between the low and high watering even though there was a statistical difference. Nevertheless, the biomass increased for three of the transplanted species with increased watering and the overall survival increased and was weakly significant ($P = 0.096$), indicating some water limitation. Although we have not observed direct evidence for competition, given that three species at the seedling stage responded positively to increased water, it seems likely that competition for water may be of some importance in shaping the structure of this community. It is important to note that, although we may have observed water limitations, it does not necessarily mean that there will also be competition for water (Casper & Jackson 1997). Many of the examples of competition for water come from arid systems (Fowler 1986; Goldberg et al. 2001), although there are examples from other stressed ecosystems such as alpine meadows (Theodose & Bowman 1997) and oldfields (Stevens et al. 2006). It would be interesting to conduct a more detailed experiment examining the negative and positive interactions of plant communities in this dry boreal ecosystem along a water gradient.

Conclusions

Previous research on the factors structuring this boreal forest understorey community focused on the role of nutrient limitation and competitive interactions, with little emphasis on the role of water

limitation and facilitative interactions. However, in this study, the presence of neighbours resulted in increased biomass and survival of seedlings, additional water had minor beneficial effects and nutrient addition had negligible effects. We can tentatively tie these results together by noting that naturally occurring seedlings are observed in the field in years of higher than average rainfall, such as in 2000 when rainfall was 54% above average. Most of the species are almost entirely clonal, and it is plausible that establishment from seeds and seedlings occurs only in higher rainfall years, but successful seedling survival will be enhanced in the presence of neighbouring vegetation. This study highlights the important role that facilitation may have in structuring this boreal understorey community. The occurrence of these positive interactions may in part be due to the life-history stage examined. These results provide further evidence that facilitative interactions are important in structuring plant communities in stressed environments.

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