

Density dependence in an experimental boreal forest understory community

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Abstract: Density-dependent regulation in plants may occur at the level of the entire community and may differ in magnitude and direction at different life history stages such as germination, survival and growth, and under different abiotic conditions. We constructed semi-natural communities of boreal forest understory species planting 10 of the most abundant species. The experimental communities were established from seed or from cuttings and grown in sandboxes at six densities that extended far above and below average natural field density, while maintaining constant relative species proportions (a community density series (CDS)). We used two watering and fertilization levels in a factorial design. At the community level, both emergence and final per-plant shoot mass were negatively density dependent, while survival to the end of the season was facilitative. The effect of water was positive at seed emergence, whereas fertilizer negatively affected survival. Species-specific responses were also dependent on life stage. We demonstrated that density dependence is important in structuring this unproductive boreal understory habitat. The CDS approach allows us to quantify the effects of plant competition at the community and species levels, and to determine whether the importance of these biotic interactions depend on abiotic factors.

Key words: boreal forest understory, competition, facilitation, fertilization, survival, watering.

Résumé : La régulation dépendant de la densité chez les plantes survient à l'échelle de la communauté entière et peut différer en importance et en direction selon les différents stades du cycle de vie comme la germination, la survie et la croissance, et selon diverses conditions abiotiques. Les auteurs ont construit des communautés semi-naturelles représentant les espèces du sous-étage de la forêt boréale, en plantant dix des espèces les plus abondantes. Ils ont établi les communautés expérimentales à partir de semences ou de boutures et les ont fait croître dans des boîtes de sable; six densités ont été utilisées allant de situations bien en-deçà et bien au-delà de la densité naturelle sur le terrain, tout en maintenant les proportions relatives entre les espèces [série de densité communautaire (CDS)]. Ils ont utilisé deux régimes de fertilisation et d'arrosage, selon un dispositif factoriel. À l'échelle de la communauté, la biomasse par tige à l'émergence aussi bien qu'à la fin s'est avérée négativement dépendante de la densité, alors que la survie jusqu'à la fin de la saison la facilite. L'effet de l'eau fut positif à l'émergence des plantules alors que la fertilisation a affecté négativement la survie. On observe que les réactions espèce-espèce dépendent également du stade du cycle de vie. Les auteurs démontrent que la dépendance sur la densité s'avère importante pour la structuration de cet habitat peu productif du sous-bois de la forêt boréale. L'approche CDS a permis aux auteurs de quantifier les effets de la compétition végétale à l'échelle de la communauté et des espèces, et de déterminer si l'importance de ces interactions biotiques dépend de facteurs abiotiques.

Mots-clés : sous-étage de la forêt boréale, compétition, facilitation, fertilisation, survie, irrigation.

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Introduction

There is abundant evidence showing that competition occurs within plant communities (Connell 1983; Schoener 1983; Goldberg and Barton 1992; Goldberg et al. 1999; Keddy 2001; Reynolds and Rajaniemi 2007), and there is a growing body of evidence documenting the prevalence of facilitation in plant communities (Callaway 1995; Bertness

1998; Brooker and Callaghan 1998; Brooker et al. 2008). Most of these studies only examine a small subset of species present in the community leaving the community-level consequences of biotic interactions unexplored and this is, at least in part, due to a lack of appropriate experimental methods (Goldberg et al. 1995). To evaluate the community consequences of biotic interactions, both the effects of competition and facilitation on the entire community, and not just a few select species, and their effects in varying abiotic conditions need to be quantified (Goldberg and Barton 1992; Goldberg and Scheiner 1993; Goldberg et al. 1995).

Here we use a community density series (CDS) to determine the role of biotic interactions and abiotic influences on an experimental community. The CDS uses the performance of the community at reduced densities to quantify the null community, the community without interactions, and to determine the effect of competition or facilitation at higher,

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natural, densities (Goldberg et al. 1995). This approach is a community-level modification of traditional density-yield experiments typically used for single species.

Goldberg et al. (2001) noted three key problems with approaches used to study density dependence. The first is that most studies that actually manipulate density, only focus on a single species. Yet, in nature, plants almost always live in mixtures. The second is that most studies are descriptive or mensurative rather than experimental. Obviously, natural gradients are useful for examining natural patterns; however, it is often difficult to untangle the effects due to density and those due to underlying environmental factors. Unfortunately, the experiments that have been done may not tell us much about the patterns of density dependence, since they are usually done to determine the effect of the presence of neighbours or focus on only one life history stage. The third problem is that most studies, even those that are experimental, only study one or a few species in the field, making it difficult to extrapolate to other plant species or to other environments. This does not mean that what happens to a single species is of no interest, for it maybe the most important issue in cases of conservation. However, it is unlikely that single-species responses are useful in predicting the community-level consequences of competition or facilitation.

Here we follow the terminology advocated by Crawley (1997), and used by others who have done community density experiments (Goldberg et al. 2001; Lortie and Turkington 2002; Shilo-Volin et al. 2005; Turkington et al. 2005; Rajaniemi et al. 2009). Negative density dependence, or competition, indicates the negative effects of increasing density, and positive density dependence, or facilitation, indicates positive effects of increasing density.

In this study, we recreated an understory plant community to investigate the role of density dependence at the community and species levels and to determine whether changing the productivity of the system alters these relationships. Specifically, we ask the following questions:

1. Do density dependent biotic interactions affect the species abundance and composition of this community?
2. Do these interactions affect emergence, survival, and growth differently?
3. Do these interactions affect the species in the community differently?
4. Does varying water and fertilizer modify productivity, and how does this affect species abundance and composition?

Materials and methods

Community description

We attempted to recreate the understory plant community of the boreal forest near Kluane Lake in southwestern Yukon. This ecosystem has been extensively studied for both its animal and plant components, and was used for the Kluane Boreal Ecosystem Project (Krebs et al. 2001). Previous research has shown that this ecosystem is nutrient limited (Turkington et al. 1998, 2002), may be water limited (Carrier and Krebs 2002), and that biotic interactions affect some plant species (Arii and Turkington 2002). The overstory is dominated by white spruce (*Picea glauca* (Moench)

Voss s.l.) with a shrub canopy of willows (predominantly *Salix glauca* L. s.l.) and some dwarf birch (*Betula glandulosa* Michx.). The 10 most common understory species were chosen as representative species for the community density series experiment. Eight of the species are herbaceous perennials: *Achillea millefolium* L. subsp. *borealis* (Bong.) Breitung (yarrow), *Anemone parviflora* Michx. (northern anemone), *Chamerion angustifolium* L. s.l. (fireweed), *Festuca altaica* Trin. (northern rough fescue), *Lupinus arcticus* Wats. (arctic lupine), *Mertensia paniculata* (Ait.) G. Don var. *paniculata* (bluebells), *Senecio lugens* Richardson (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. subsp. *americana* (twinline). All nomenclature follows Cody (2000). These 10 species account for 95% of the understory cover.

Experimental design

We tested for density dependence in an experimental community density series (CDS) of the most common understory plant species. The CDS is a multi-species refinement of the traditional single-species density-yield experiments (Harper 1977) and was first described by Goldberg et al. (1995). Traditionally, a single species is planted, or manipulated, such that density varies from very low to very high. Similarly, an entire community can be manipulated to densities above and below the “normal” or initial community density (ICD) while keeping the relative proportions of each species constant. It can be assumed that if we lower the density of the community such that the density precludes interactions, then we have characterized the null community (Zobel 1992; Goldberg et al. 1995). The CDS was successfully applied using plants from an annual community in the Negev desert (Goldberg et al. 2001; Lortie and Turkington 2002; Shilo-Volin et al. 2005; Turkington et al. 2005; Rajaniemi et al. 2009), and has been applied once in a perennial community (Rajaniemi and Goldberg 2000); however, the latter study only lasted one growing season and did not use densities greater than the natural plant density of the community.

This experiment was conducted during the summer of 2002 at the Arctic Institute of North America Kluane Lake Research Station (61°02'N, 138°25'W, altitude of 785 m a.s.l.). Six 120 cm wide × 240 cm long × 15 cm high boxes were built out of wood and each box was subdivided into 8 equal and smaller “plots” of approximately 60 cm × 60 cm with partitions of 2.5 cm thick wood. Some of the 60 cm × 60 cm plots were further subdivided into 30 cm × 30 cm plots using thin plywood partitions. The boxes were filled with beach sand, and the surface was sterilized with heat for 30 s using a propane torch. The sterilization was effective because no plant species growing on the beach germinated in the sandboxes during the experiment. Greenhouse frames were built and covered with a clear 6 mil (0.15 mm) plastic vapour barrier. This plastic transmitted 73% of the incoming photosynthetically active radiation to the sand surface (measured using a quantum sensor, Apogee Instruments Inc., Logan, Utah). The greenhouse cover allowed us to (i) vary the volume of water added to each plot individually, (ii) increase temperature and humidity to enhance germina-

tion and survival of seedlings, (iii) reduce damage from herbivores, and (iv) reduce the immigration of weed seeds into the plots. To ensure that the surface temperature of the plots did not increase to the point where it may injure seedlings, the greenhouse frames were propped open to allow air flow. On particularly hot days, the frames were removed. To reduce the impact of herbivores, especially granivorous mice and voles, snap-traps were set around the perimeter of the sandboxes.

The sandboxes were not treated as blocks. In an experiment conducted during the previous summer, the sandboxes were treated as blocks and there were no statistical differences between blocks for soil moisture, soil temperature, light at the soil surface, seedling emergence, seedling survival, or seedling growth. Therefore, this experiment is treated as a completely randomized design.

Treatments

A geometric series of six initial community densities (ICDs) was constructed: 1/8, 1/4, 1/2, 1, 2, and 4× the average natural field density. The ×1 density closely approximated the density of the vegetation estimated at a natural field site where another CDS experiment was established in 1999; this corresponded with a density of 132 plants·m⁻² (95% CI of 113 to 151 plants·m⁻²). The CDS was generated from mature seeds of the 10 most common plant species that were collected the previous summer and stored over winter. The average germination rate for each species was used to calculate how much seed was necessary to give the density of individuals desired to approximate the numbers observed in the field. Germination rates were estimated in the spring prior to this experiment using a standard method of Petri plates and moist sand (Baskin and Baskin 1998; Treberg and Turkington 2008).

For each plot, the exact numbers of seeds for each species were counted and all seeds were sown onto their respective plots and lightly raked into the surface of the sand. For example, for a plot with the treatment at the ×1 density, or average natural field density, we planted 1374 seeds·m⁻² for the expected 132 plants·m⁻². To conserve seeds, the highest density plots (×1, ×2, and ×4 densities) were sown in 30 cm × 30 cm plots rather than 60 cm × 60 cm plots used for the lower densities. In the previous experiment done in these sandboxes, no plot size effects were observed for seedling emergence, survival, or growth.

We were unable to germinate seeds of the two woody shrubs, *Arctostaphylos* and *Linnaea*. Instead we used cuttings of the appropriate numbers (in total, 252 of *Arctostaphylos* and 504 of *Linnaea*) to approximate the natural density. The stem cuttings were collected from close to the study area and were 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: Sure-Gro IP Inc., Brantford, Ontario) to promote root growth. *Anemone* seeds collected from the previous season exhibited particularly low germination rates. Therefore, we did not have sufficient seed numbers and did not include it in the CDS. All planting occurred on 13 June 2002. This coincided with the emergence of seedlings at the nearby field site.

There were two watering levels. Water was added as necessary to keep the low water level moist enough to prevent

obvious water stress and seedling death. The high water level was double the low water treatment and it was applied at the same time. Usually water was applied early morning, and again in the afternoon or evening if needed during hot or windy days. Water soluble fertilizer (Plant Prod[®] 20–20–20: Plant Products, Brampton, Ont.) was added as a solution every 2 weeks at the manufacturer's recommended rate; this was the low level treatment (4 mL fertilizer per 1 L H₂O). This amount was doubled for the high level treatment. Throughout the summer there were 5 fertilizer applications with a total addition of 11.4 g N·m⁻² and 22.8 g N·m⁻² added to the low and high treatment levels, respectively. This fertilizer had a manufacturer's 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. These values correspond to other fertilizer applications in this region that have produced significant plant responses (Turkington et al. 1998). There was no "control" treatment without fertilizer added because this experiment was done using sand, which is inherently nutrient poor and also has poor nutrient retention.

Monitoring and harvesting

All newly germinated seedlings were counted on a weekly basis and identified to species. At the end of the season, on 29–31 August 2002, all individuals in the plots were identified to species and counted, and all aboveground biomass removed by clipping. The plant material was sorted to species and dried to prevent spoilage before being sent to the University of British Columbia, Vancouver, B.C., for final drying and weighing.

Analysis

The effects of density, water, and fertilizer on the experimental community were examined using analysis of covariance (ANCOVA) with density as the covariate, and water and fertilizer as categorical variables, each with 2 levels. All analyses were done using JMP 4 (SAS 1995).

The effect of density on the community was analyzed using an individual performance approach (Goldberg et al. 2001). In this method, the variable of interest is divided by the appropriate measure of density and the variable remains constant with density in the absence of interactions. An increase or decrease in the variable with increasing density would be indicative of facilitative or competitive interactions, respectively. To use ANCOVA, the density and response variables were transformed to best linearize the relationship. Four transformations were attempted: linear, power, semilog, and reciprocal. The best fitting model, with the highest *R*², is reported. These transformations also assisted in making the ANOVAs and ANCOVAs better meet statistical assumptions of normality and homogeneity of variances.

The effect of density was examined for three life-stages of the experimental community: emergence, survival, and final plant size. The appropriate covariate, or measure of density to use, varied in each of the analyses. For the emergence stage we used the initial planting density. We calculated an

Table 1. Regression coefficients for the community response variables and density relationships shown in Figs. 1, 2, and 3.

Variable	Model	df	Intercept	Slope	R^2	P
Emergence index	Semi-log	71	269.188	-37.046	0.097	0.008
Survival	Semi-log	71	0.177	0.083	0.252	<0.001
Shoot mass	Semi-log	71	0.779	-0.175	0.224	<0.001
Final plant density	Power	70	-2.276	1.045	0.805	<0.001
Total plant mass	Linear	70	9.749	0.094	0.556	<0.001
Species richness	Semi-log	70	1.882	0.738	0.401	<0.001
Evenness	Linear	70	0.343	-0.020	0.017	0.277

Note: The model type refers to the data transformation that best linearized the data. The degrees of freedom (df) are for the model and error combined. A negative slope indicates negative density dependence (or competition) and a positive slope indicates positive density dependence (or facilitation). Significant values ($P < 0.05$) are in bold.

index of emergence from the total number of seedlings emerged divided by the planting density. The measure of density used for the survival stage was the cumulative density of all emerged seedlings. Survival was the proportion of those seedlings that survived until the end of the season. For the final plant mass, the appropriate covariate was the final plant density. Plant mass was the total aboveground biomass of the plot divided by the final plant density. All of these analyses were also completed using the initial planting density as a covariate to determine if the choice of density measure affected the outcome of the statistical tests. There were no significant changes in test results.

The effect of density on species diversity in plots was also examined. For both species richness and evenness, the initial planting density was used as a covariate in the ANCOVA. The evenness index used was E_{var} (Smith and Wilson 1996). Because species richness is expected to increase with increased sampling, the expected species richness in the absence of interactions was also calculated from the null community following the procedure described by Goldberg and Estabrook (1998).

Species-specific effects of density were examined on the proportional survival and the final plant mass. Proportional survival was the final plant density divided by the total seed planting density. Because survival was a proportion and many numbers were close to, or at zero, all survival data were arcsine transformed such that $X' = \arcsine(p)^{1/2}$ (where X' = transformed value, and p = the proportion). Final plant mass was the mass of all individuals of that species in the plot, divided by the relative planting density. Those species with significant relationships were analyzed using ANCOVA with final plant density as the covariate and fertilizer and water treatments as categorical variables. If the species' survival or final plant mass demonstrated no relationship with density, an analysis of variance (ANOVA) of the water and fertilizer treatments was done.

Results

Density dependence of the community

Density dependence was evident at all three life stages (emergence, survival, and shoot mass) in the experimental communities, although it was not consistently competitive or facilitative (Tables 1 and 2; Fig. 1). Emergence was negatively related to planting density, with much higher germination in the lowest density plots and lower germination at

the highest density (Fig. 1a). Survival to the end of the season was positively associated with the cumulative density of emergents, indicating facilitative interactions at higher densities (Fig. 1b). The final stage, final per-plant shoot mass, was negatively related to final plant density, with extremely high shoot biomass only possible in the lowest density plots (Fig. 1c). The final density was strongly and positively related to the initial planting density, and the total plant mass in the plot was also positively related to the final plant density (Table 1; Fig. 2).

Species richness was also highly positively and linearly density dependent (Tables 1 and 2; Fig. 3). Because species richness increases as the number of individuals in a sample increases, we also calculated the expected species richness based on data from the null community. The expected species richness indicates how many species to expect due to the increased sampling. Generally, observed species richness is lower than the expected species richness (Fig. 3). There was no significant relationship between species evenness, E_{var} , and density (Table 1; Fig. 3).

Water and fertilizer effects on the community

The effects of water and fertilizer addition were not consistent among life stages. Watering significantly increased both the emergence of seedlings and the species richness (Table 2). The addition of fertilizer had the opposite effect, and reduced both seedling survival and the species richness (Table 2). Some interaction terms were significant. The density \times fertilizer interaction, and the water \times fertilizer interactions, were significant for the emergence index (Table 2). The low fertilizer treatment resulted in higher emergence at lower planting densities than the high fertilizer treatment. At high planting densities, there was no difference in emergence between the two fertilizer treatments. The low water and high fertilizer treatment resulted in significantly lower emergence than the low water and low fertilizer, high water and low fertilizer, or the high water and high fertilizer treatments. For the final shoot mass, the density \times water interaction was significant (Table 2), with the shoot mass in the low water treatment at low density being higher than that for the high water treatment. At high densities, there was no difference between the water treatments. For final plant density, the density and water interaction was also significant (Table 2) and exhibited the same pattern as for the emergence index, where only the low water and high fertilizer treatment was significantly lower than the other treatments,

and individually, water addition increased density while fertilizer addition decreased density. The total plant mass in the plot was not affected by water or fertilizer addition, although there was a significant third order interaction. Species richness increased with both density and water, and decreased with the addition of fertilizer.

Species-specific responses

Four species' survival was significantly related to increased density, with two (*Achillea* and *Arctostaphylos*) responding negatively, and two (*Festuca* and *Solidago*) responding positively (Table 3; Fig. 4). Only *Festuca* demonstrated a significant, positive, density dependent relationship, between initial planting density and final plant biomass (Table 3; Fig. 5). *Mertensia* was the only species to show any positive response (increased survival) to fertilizer addition (Table 4). All others, except *Lupinus* and *Solidago*, showed significant decreases in survival with increased fertilizer (Table 4). Three species, *Arctostaphylos*, *Linnaea*, and *Senecio*, responded negatively to increased fertilizer (decreased biomass) (Table 4). No species responded with increased growth to fertilizer addition. Increased water aided survival for *Festuca*, *Linnaea*, *Lupinus*, and *Mertensia*, while *Lupinus* and *Mertensia* all increased in mass (Table 4). No species responded negatively to increased water. No interaction terms in the ANOVAs or ANCOVAs were significant. *Chamerion* seeds did germinate in the sandbox plots; however, no seedlings survived to the end of the season.

Discussion

It is often assumed that in northern environments, abiotic factors are the predominant factors that structure plant communities. While the importance of abiotic stress in tundra, arid, and semi-arid environments is unquestionable, biotic interactions such as competition also play a role in structuring such plant communities (Goldberg et al. 2001). There are also many examples of facilitation in arid environments (Callaway 1995; Callaway and Walker 1997) leading some to suggest that facilitation may be more common in severely stressed communities (Brooker et al. 2008). There are many examples of both competition (Arii and Turkington 2002) and facilitation (Callaway et al. 2002) in northern stressed environments such as arctic or alpine tundra. Here we show that density-dependent process also play a major role in structuring these boreal forest understory plant communities. However, Goldberg et al. (2001) identified many problems with our past and current methods of investigating density dependence, the principal one being the investigation of only a single or few species while apparently ignoring the possibility that regulation may occur at the community level. This traditional approach tells us little about how the focal species interacts with other species and what the overall consequences of community density are for either the population of the species studied or the community as a whole. The experimental approach utilized in the CDS avoids this problem by manipulating the density of the entire community and examining the relationship of density with individual species and the community (Goldberg et al. 1995, 2001).

In this study, all of the life history stages examined demonstrated density dependence at the community level; how-

ever, whether the density dependence was positive or negative depended on the life history stage examined. While seed germination and the final mean plant mass were negatively related to density, indicating competitive interactions, survival was positively related, indicating facilitative interactions. These patterns of density dependence parallel those of Goldberg et al. (2001) and are similar to those of Lortie and Turkington (2002), although Lortie and Turkington (2002) did not demonstrate density dependence for survival. The major distinction between these studies is that Goldberg et al. (2001) and Lortie and Turkington (2002) used desert *annual* plant communities, whereas we have applied the CDS to boreal understory *perennial* species grown from seed over one growing season. Only one other study (Rajaniemi and Goldberg 2000) has used perennial species, with old field species grown from seed at natural densities and in thinned plots (approximately 1/20 the natural density). All of these studies, regardless of habitat or community studied, demonstrate that lower than naturally occurring densities of plants have higher mean mass than the normal ($\times 1$) density. It is surprising that such similar patterns of density dependence occur in such distinctly different systems.

In this study, germination rate was significantly reduced at the higher planting densities, indicating negative density dependent emergence. This means that seeds in high density plots were somehow "sensing" their high density. Other studies have also observed negative density dependent germination (McMurray et al. 1997; Murray 1998; Goldberg et al. 2001; Lortie and Turkington 2002), while others have observed that increased seed density can be facilitative (McMurray et al. 1997; Dyer et al. 2000). Although Murray (1998) reported that 4 species out of 12 demonstrated negative density dependence, he detected no relationship between density and germination for any of the other species in his study. A possible mechanism for the negative density dependent response could be the release of leachates from the seed coat that directly inhibits germination (Murray 1998). This may lead to earlier germination and emergence, (Dyer et al. 2000), which may be an adaptive response to get a head start in competitive environments, or to decreased germination (Murray 1998; Goldberg et al. 2001; Lortie and Turkington 2002) or delayed germination (Turkington et al. 2005). Any of these responses may have subsequent effects on later life history stages such as survival and growth. Turkington et al. (2005) observed that delayed germination did not significantly effect survival, although seedlings that germinated earlier, tended to be larger at the end of the growing season. In this study there was no relationship between number of seeds emerging and date (data not shown) suggesting that there was no change in the timing of emergence.

Adding water significantly increased emergence independently of density; however, there was also a significant interaction of fertilizer and water. The low water treatment coupled with high fertilizer had significantly lower emergence than any other combination with water. Although it has been demonstrated that fertilizer addition can reduce survival of one species common to this system, *Anemone* (Arii and Turkington 2002), there is no other evidence to suggest that increased fertilization reduces germination. The overall effect of water is to increase germination rates and

Table 2. Summary of ANCOVAs and ANOVA for the response variables to density manipulations in the experimental communities.

Effect	df	SS	F ratio	P
Emergence index				
Initial planting density	1	138471	11.300	0.001
Water	1	333268	27.196	<0.001
Fertilizer	1	26565	2.168	0.146
Density×Water	1	2738	0.223	0.638
Density×Fertilizer	1	64733	5.282	0.025
Water×Fertilizer	1	81574	6.657	0.012
Density×Water×Fertilizer	1	623	0.051	0.822
Error	64	784284		
Survival				
Cumulative density	1	0.451	17.032	<0.001
Water	1	0.066	2.492	0.119
Fertilizer	1	0.276	10.437	0.002
Density×Water	1	0.032	1.226	0.272
Density×Fertilizer	1	0.000	0.013	0.909
Water×Fertilizer	1	0.008	0.320	0.574
Density×Water×Fertilizer	1	0.010	0.391	0.534
Error	64	1.695		
Shoot mass				
Final plant density	1	0.956	13.276	<0.001
Water	1	0.234	3.249	0.076
Fertilizer	1	0.005	0.067	0.796
Density×Water	1	0.362	5.032	0.028
Density×Fertilizer	1	0.176	2.450	0.123
Water×Fertilizer	1	0.041	0.564	0.455
Density×Water×Fertilizer	1	0.089	1.232	0.271
Error	64	4.537		
Final plant density				
Initial planting density	1	96.499	190.127	<0.001
Water	1	11.576	22.914	<0.001
Fertilizer	1	5.235	10.362	0.002
Density×Water	1	0.004	0.007	0.935
Density×Fertilizer	1	0.256	0.508	0.479
Water×Fertilizer	1	2.206	4.367	0.041
Density×Water×Fertilizer	1	0.185	0.367	0.547
Error	64			
Total plant mass				
Final plant density	1	46033	76.062	<0.001
Water	1	935.64	1.546	0.218
Fertilizer	1	751.32	1.241	0.269
Density×Water	1	617.57	1.020	0.316
Density×Fertilizer	1	896.25	1.481	0.228
Water×Fertilizer	1	2064.1	3.411	0.070
Density×Water×Fertilizer	1	2943.5	4.864	0.031
Error	63	38128		
Species richness				
Final plant density	1	37.181	27.214	<0.001
Water	1	16.701	12.224	<0.001
Fertilizer	1	8.795	6.438	0.014
Density×Water	1	0.829	0.607	0.439
Density×Fertilizer	1	0.003	0.002	0.965
Water×Fertilizer	1	2.525	1.848	0.179
Density×Water×Fertilizer	1	0.042	0.031	0.861
Error	63	86.073		

Table 2 (concluded).

Effect	df	SS	F ratio	P
Evenness (E_{var})				
Water	1	0.000	0.001	0.975
Fertilizer	1	0.065	1.479	0.228
Water×Fertilizer	1	0.031	0.709	0.403
Error	67	2.938		

Note: Significant values ($P < 0.05$) are in bold.

Fig. 1. The effect of density on the performance of seedlings in the experimental communities. In (a) emergence is negatively related to density, with the highest germination in the lowest density plots; (b) survival to the end of the season is positively associated with density, indicating facilitative interactions at higher densities; and (c) final per-plant shoot mass is negatively related to density, with extremely high shoot biomass only possible in the lowest density plots. The coefficients for the best fit curve for each graph are given in Table 1.

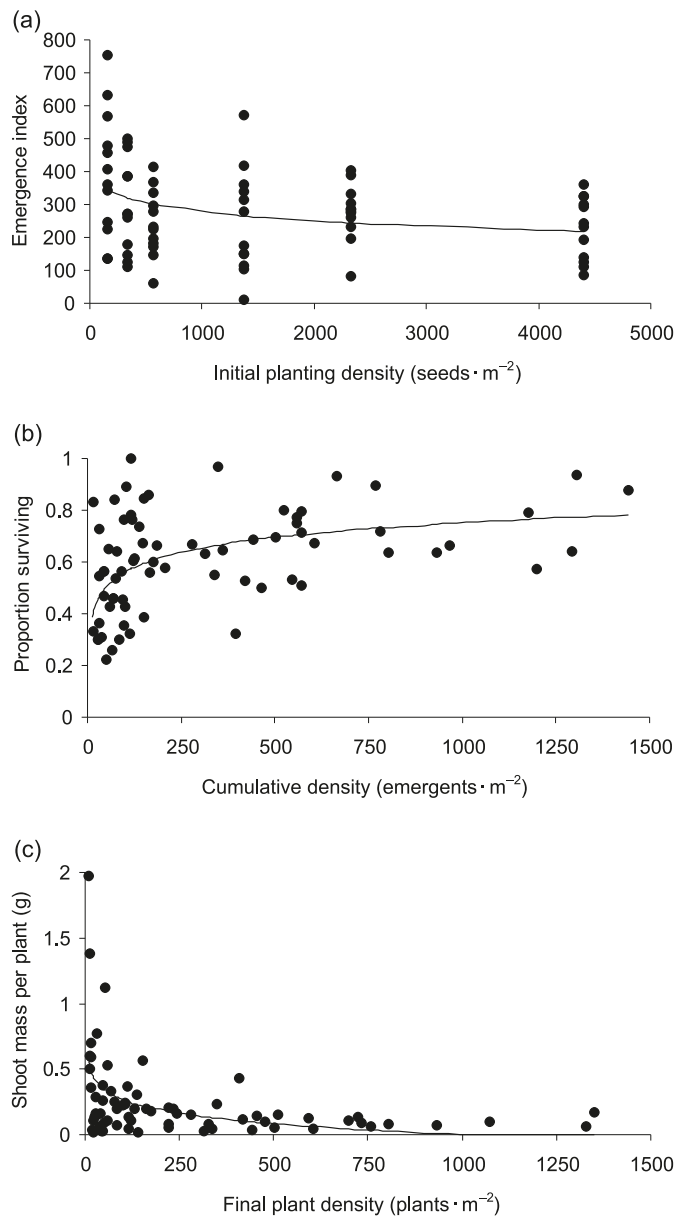
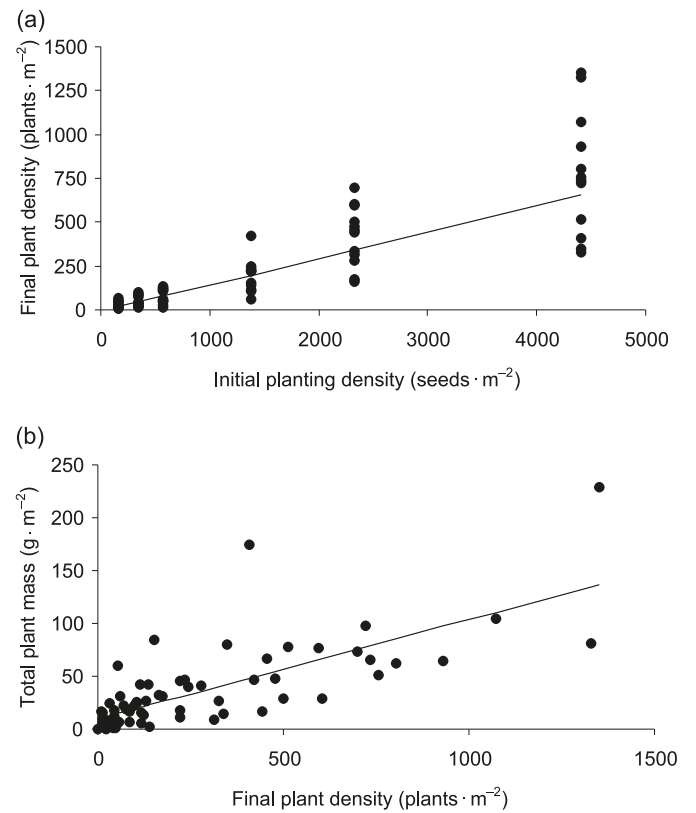


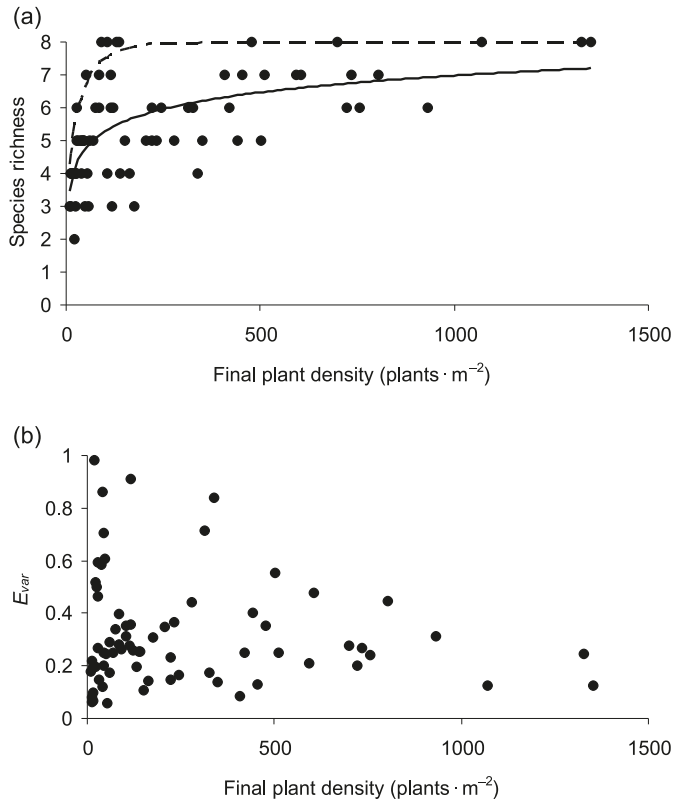
Fig. 2. Final density is strongly and positively related to the initial planting density, and the total plant mass in the plot is positively related to the final plant density. The coefficients for the best fit line are given in Table 1.



counter any negative effect of fertilizer addition. Given that the water and density interaction term is not significant, it is not likely that exploitive competition for water was important at least at the emergence stage. It is possible that allelochemicals or leachates would be washed away in the high water treatment; however, there was still a significant relationship between density and emergence and this was not related to water (i.e., the interaction term was not significant). Seeds are somehow inhibited from germinating because of their high density, and increased water may simply increase germination rates, as has been demonstrated for some arctic species (Oberbauer and Miller 1982). Although it seems unlikely that exploitive competition occurs at the emergence stage, we can only speculate that direct interference competition is important.

Survival at the community level (i.e., counting all seedlings regardless of species identity) was positively related to density indicating a facilitative relationship. The only plots

Fig. 3. Species richness is positively and linearly density dependent (a), and there is no significant relationship between species evenness, E_{var} , and density (b). The best fit curve for species richness is shown as a solid line and the coefficients are given in Table 1. The broken line is the expected value of the species richness as calculated from the null community.



that had low survival were the lowest density plots where the potential for interactions between plants are presumed to be the lowest. Although there is a well established negative relationship between density and fitness, there has not been a general realization that increased population density can also increase survival (Bruno et al. 2003). Positive interactions between plants has only recently become a common research topic (Callaway 1995; Brooker and Callaghan 1998; Brooker et al. 2008).

The specific mechanism for the increased survival detected in high density plots is not clear. Often seedlings benefit by having adult neighbours, or in studies with traditional nurse plant effects where the larger adult plant shelters the smaller plants, thereby reducing evapotranspiration losses and moderating temperature extremes (Callaway 1995; Holmgren et al. 1997). In this study we did not have the usual disparity between the sizes of neighbours. If low water was important, we would expect that the addition of water would alleviate some of this effect. Although water did not have a significant effect on seedling survival at the community level, when examined at the species level, half of the plant species demonstrated a positive response to watering with no species showing a negative reaction. Surprisingly, of the four species that demonstrated a significant relationship with density, half of those responded positively and half negatively to increased density. So although the community as a whole benefited from increasing density,

not all species did. Fertilizer was more consistent in its effect by reducing survival at the community level and for five out of the eight species that survived to the end of the study. Only one species, *Mertensia*, had increased survival with fertilization. As already mentioned, in some previous studies *Anemone* responded negatively to fertilization showing both decreased survival and growth; (Arii and Turkington (2002) speculated that this may be a toxic reaction to the fertilizer. Overall, it is possible that close proximity to neighbours reduces the surface temperature of both the soil surface and the leaf surface to reduce evaporation and transpiration as in the nurse plant effect.

Commonly, increased densities of neighbours leads to decreased growth (Goldberg et al. 1999, 2001). The final mean plant mass at the community-level was negatively related to density; however, at the species-level only one species was positively related to density. The species-specific observations are a very poor predictor of community-level patterns. Also, fertilizing decreased the mass of three species and watering increased the mass of two species. Neither fertilizer nor water alone had a significant effect on the community-level mean plant biomass. Water and density interacted such that the highest plot biomass was achieved in plots with the lowest planting density with the low water treatment. If exploitive interspecific competition is occurring, we would expect the observed decrease in growth with an increase in density; however, it is not clear what specifically the plants are competing for.

Our results are parallel to Goldberg et al. (2001) who demonstrated a switch in biotic interactions from competitive to facilitative and back to competitive as life history stages progressed. In general, studies that have measured the effect of competition through different life history stages tend to show that neighbours are less likely to negatively affect survival even though they may have severe negative effects on subsequent growth (Goldberg et al. 1999; Howard and Goldberg 2001). On the whole, the effect of neighbours on developing seedlings may be neutral if competitive interactions and facilitative interactions are occurring simultaneously (Callaway and Walker 1997; Holmgren et al. 1997; Brooker and Callaghan 1998; Howard and Goldberg 2001). The positive influence of neighbours early in the development of seedlings, especially during emergence and early survival, is usually associated with the beneficial shading of larger neighbours that reduce temperature and moisture extremes (Callaway 1995; Callaway and Walker 1997). There are also other examples showing a switch from facilitation being important early in a seedling's life because of the neighbours sheltering them from predators, followed by a switch to neighbours competing with them as growing plants (Zanini et al. 2006).

The addition of fertilizer had a significant negative effect on plant survival at the community- and species-level in this study, and this resulted in reduced final plant density and reduced species richness. Normally, increased fertilizer increases community biomass and decreases diversity (DiTommaso and Aarssen 1989; Gough et al. 2000; Rajaniemi 2003). While the specific shape of the relationship between productivity and diversity is often debated and may be either linear, curvilinear, or unimodal, nevertheless, it is generally agreed that competition plays an important part in

Table 3. Regression coefficients for the relationship between each species' survival or mean plant mass biomass and density in the experimental communities.

Species	Model	Intercept	Slope	R^2	P
Survival					
<i>Achillea</i>	Linear	0.984	-7.6×10^{-5}	0.061	0.037
<i>Arctostaphylos</i>	Semilog	1.887	-0.110	0.063	0.033
<i>Festuca</i>	Semilog	0.218	0.054	0.064	0.033
<i>Linnaea</i>	Linear	0.064	5.4×10^{-6}	0.009	0.437
<i>Lupinus</i>	Semilog	0.625	-0.048	0.024	0.197
<i>Mertensia</i>	Semilog	-0.014	0.018	0.027	0.166
<i>Senecio</i>	Semilog	0.153	0.016	0.002	0.693
<i>Solidago</i>	Semilog	-0.172	0.106	0.086	0.013
Mean plant mass					
<i>Achillea</i>	Semilog	2.366	-0.194	0.030	0.147
<i>Arctostaphylos</i>	Semilog	0.074	-6.1×10^{-3}	0.048	0.067
<i>Festuca</i>	Linear	0.011	1.3×10^{-5}	0.203	<0.001
<i>Linnaea</i>	Semilog	0.001	-2.8×10^{-3}	0.045	0.075
<i>Lupinus</i>	Linear	0.054	-2.7×10^{-5}	0.001	0.922
<i>Mertensia</i>	Semilog	0.003	0.013	0.027	0.172
<i>Senecio</i>	Semilog	-0.010	-8.0×10^{-3}	0.028	0.163
<i>Solidago</i>	Semilog	0.004	0.016	0.037	0.109

Note: The proportional survival is the number of individuals of that species per plot, divided by the initial planting density; mean plant mass is the mass of that species per plot, divided by the relative initial density. The model type refers to the transformation required to best linearize the data. The degrees of freedom = 71 in all cases, and are for the model and error combined. Significant values ($P < 0.05$) are in bold.

Fig. 4. The survival of four species is significantly related to increased planting density, with two of them (*Achillea* and *Arctostaphylos*) responding negatively, and two (*Festuca* and *Solidago*) responding positively. The best fitting curves are described in Table 3. Species whose survival was not significantly related to initial planting density are not shown.

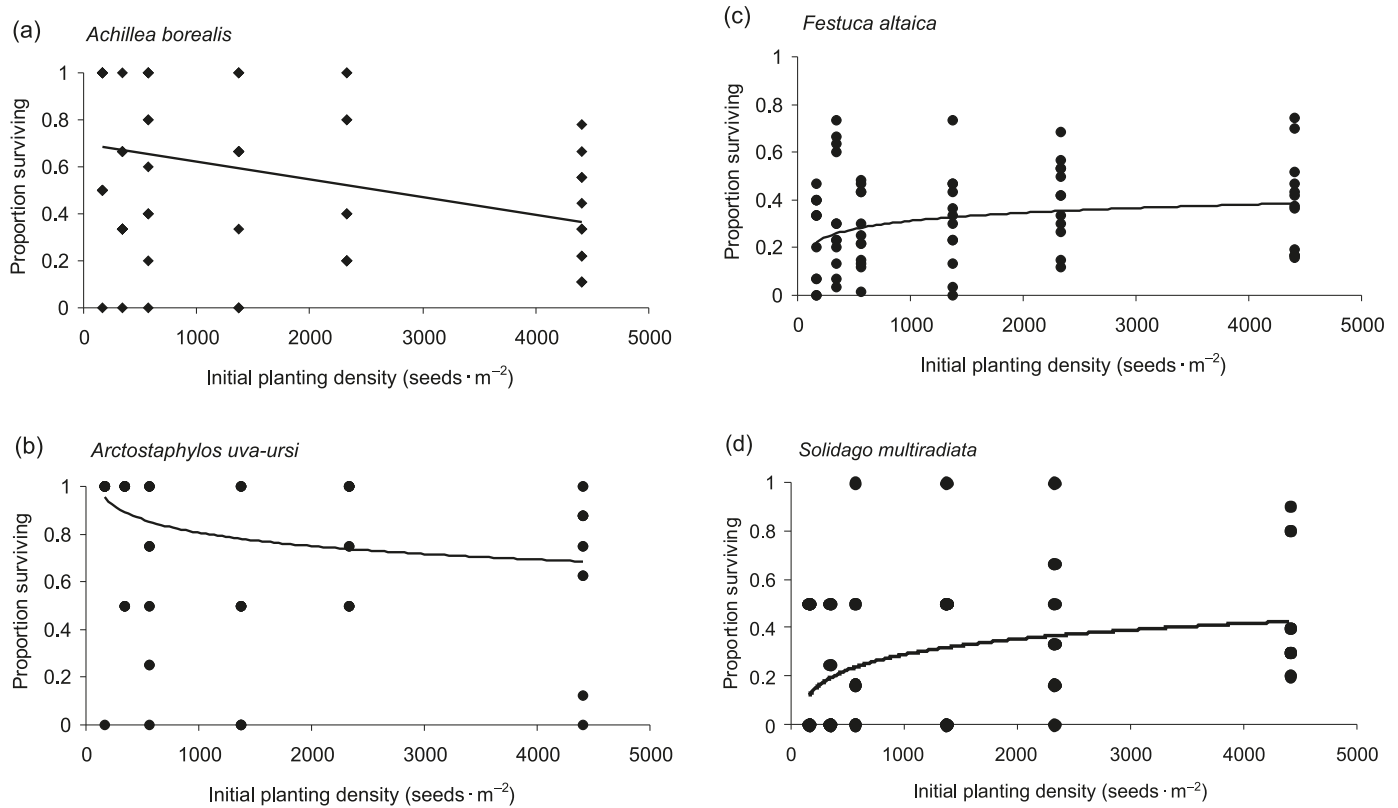


Table 4. *P* values from ANOVAs and ANCOVAs for each species using the proportional survival or the total biomass of each species per plot divided by the density.

Species	Fertilizer	Water	Density	Fertilizer × Water	Fertilizer × Density	Water × Density	Fertilizer × Water × Density
Survival							
<i>Achillea</i>	0.009	0.561	0.031	0.316	0.141	0.567	0.798
<i>Arctostaphylos</i>	0.008	0.159	0.027	0.865	0.475	0.510	0.236
<i>Festuca</i>	<0.001	<0.001	0.003	0.114	0.134	0.464	0.317
<i>Linnaea</i>	0.007	0.010	—	0.332	—	—	—
<i>Lupinus</i>	0.603	<0.001	—	0.478	—	—	—
<i>Mertensia</i>	<0.001	0.021	—	0.317	—	—	—
<i>Senecio</i>	0.002	0.164	—	0.844	—	—	—
<i>Solidago</i>	0.195	0.812	0.014	0.209	0.445	0.817	0.821
Mean plant mass							
<i>Achillea</i>	0.617	0.232	—	0.625	—	—	—
<i>Arctostaphylos</i>	0.044	0.986	—	0.673	—	—	—
<i>Festuca</i>	0.125	0.986	<.001	0.054	0.253	0.694	0.778
<i>Linnaea</i>	0.034	0.162	—	0.212	—	—	—
<i>Lupinus</i>	0.180	0.072	—	0.908	—	—	—
<i>Mertensia</i>	0.195	0.003	—	0.690	—	—	—
<i>Senecio</i>	0.005	0.803	—	0.946	—	—	—
<i>Solidago</i>	0.181	0.557	—	0.412	—	—	—

Note: Significant values ($P < 0.05$) are in bold.

the reduction of diversity (Grime 1973; Huston 1979; Tilman 1982; DiTommaso and Aarssen 1989; Gough et al. 2000; Rajaniemi 2003). Recently, Storm and Suss (2008) demonstrated increased productivity in response to fertilizing a low-productivity sand system, but without an effect on diversity. In our study, although species richness declined with fertilization, there was no increase in final biomass and the largest effect of fertilizer was to increase the mortality rate at the survival stage. Both adding water and increasing density increased survival at the species- and community-levels, resulting in an increase in species richness. Overall, watering consistently increased survival at the community level and increased emergence, survival, and shoot mass for some of the species. These opposing effects of fertilizer and water have recently been reported by Stevens et al. (2006). Our results differ in that we did not observe any increase in community-wide mean plant biomass with fertilizing or watering, although two individual species did increase in mean mass with watering. The increase in species richness was predominately due to increased emergence and survival, which increased the chance of at least one individual from each species surviving until the end of the season. Although species richness is expected to increase with density simply because more individuals are sampled (Goldberg and Estabrook 1998), we observed lower species richness than would be predicted from the null community. Results similar to these have been purported to show that competition, specifically competitive exclusion, leads to reduced species richness (Goldberg and Estabrook 1998). In our study, species richness may be lower than expected owing to a number of factors, such as reduced germination with increased density or negative fertilizer effects acting on either germination or survival. These factors have been shown to affect species differently and may be the cause for lower than expected species richness.

These species-specific responses highlight a problem with traditional approaches to density dependence and to competition studies in general. Here, species within a community mixture responded very differently to the treatments. Little could be said about general trends if only one or two species were chosen in a study unless all species performed similarly. If species are affected differently by competition, there will be the potential for changes in diversity (Rajaniemi and Goldberg 2000). In a similar study in an old field community, Rajaniemi and Goldberg (2000) reported that species' individual growth responded to increased competition, yet there was no corresponding change in diversity. Both that study and this demonstrate that individual-level patterns are not necessarily useful for predicting community-level changes, the level where most theory on competition focuses. It is also important to measure the species' and community's responses over more than one life stage since one stage may not respond the same as another, even within the same species (Goldberg et al. 2001; Lortie and Turkington 2002).

The CDS technique offers a novel approach to investigate questions about how both regulation and limitation at the species- and community-level affect community structure. Other approaches have been used to generate a null community, which is one without interactions, such as the combined monocultures (CM) approach (Campbell and Grime 1992; Goldberg 1994). The CM compares the performance of a species in monocultures to standardize the performance of a species in mixtures. It has been shown that the CDS gives more consistent results which are less likely to depend on abundance than the CM approach (Zamfir and Goldberg 2000). The amount of variation explained in the relationships between community-level responses and density ranged from 10%–80% and only some species-level responses were significant with R^2 ranging between 6%–9%

for four species' survival, and only one species had a significant relationship between mean plant mass and density with an R^2 of 20%. Density is clearly not the only factor responsible for structuring this artificial community, and although the observations here fit a generally emerging pattern regarding the role of density dependence on community structure, more work is necessary to determine whether similar patterns occur in the boreal understory forest and similar communities.

A potentially interesting question arising from these results is the role that community density has in recruitment of new seedlings. Given that higher densities facilitate the survival of seedlings and the presence of neighbours increases survival and biomass of transplants, we might predict that a moderate to high density community would be the ideal place for new seeds to germinate and grow in this community. Similarly, areas with lower density might have lower seedling survival. This may make areas of low vegetation cover especially slow to colonize.

Studies conducted under artificial conditions are always subject to the scrutiny of how well the results can be transferred to the real world. The experiment described here was conducted under extremely artificial conditions and the plants were not grown in a boreal forest understory environment, did not have normal soil mineralogy or horizons, were well-watered in a greenhouse frame, and did not have the normal complement of associated symbionts. To extrapolate from these conditions to the real world is large leap. Nevertheless, this study demonstrated what was possible using different these plant species under different watering and fertilizing regimes and prompted us to conduct a much larger experiment under real boreal forest understory conditions.

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