Boreal conifer seedling responses to experimental competition removal during summer drought

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Abstract. The southern range limit of white spruce (Picea glauca) in western Canada is believed to arise from effects of moisture limitation on seedling recruitment. Within stands near white spruce's range limit, the adverse effects of water limitation on seedling growth and survival may be compounded by competition from neighboring understory plants and trees. To test this hypothesis, we conducted a competition removal experiment on white spruce seedlings in the Cypress Hills, an isolated forest landscape within the Canadian Prairies. We measured the height and diameter at root collar of 371 natural seedlings, and then we manually cleared all vegetation within a 75-cm radius of 83 seedlings to remove local competition from neighboring plants. In addition to removal of neighboring plants, we excavated a 75-cm radius trench around another 46 of these seedlings to remove competition for belowground resources. We took hemispherical photographs above each seedling to calculate canopy openness (a proxy for light availability) and re-measured height and diameter over two years to calculate pre- and post-treatment growth. There was a pronounced difference in precipitation between the two years of our experiment, with spring–summer precipitation 58% higher than average in the pre-treatment year and 62% lower than average in the post-treatment year. The diameter growth and survival of seedlings growing without competition showed smaller decreases in the dry post-treatment year than control seedlings. Removing competition by trenching increased the height growth of seedlings located under an open canopy, but not of those growing under heavy shade. These interactions suggest that white spruce regeneration in water-limited areas is sensitive to both light availability and local competition. Competition exacerbated drought effects on seedlings, which suggests that frequent droughts could have greater negative impacts on boreal tree seedlings that are growing under a closed canopy.

Key words: below-ground competition; drought; height growth; light; nitrogen; radial growth; soil moisture.

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INTRODUCTION

Precipitation is becoming more irregular and unpredictable because of climate change (Dai 2012, Pfahl et al. 2017). Such changes can alter the geographic distribution of northern tree species through their effects on growth, recruitment, and mortality rates (Silva et al. 2012, Vanderwel et al. 2013). Seedlings tolerate a narrower range of environmental conditions than later life-history stages (Purdy et al. 2002), which implies that a tree species’ ability to persist in changing environments may often be determined by its regeneration success. Although the regeneration of some northern conifers has been related to climate (Hogg 1994, Hogg and Schwarz 1997),
studies to date have not often considered how climate change may affect inter-specific competition through changes in resource availability (Adler et al. 2009, Lu et al. 2019). Changes in the strength of competition across resource gradients may have comparable impacts to direct climate effects on species performance (Grant et al. 2014). To better understand how the distribution of northern tree species may shift under climate change, it is thus important to consider how seedling performance responds to environment-related changes in competition for resources.

Tree seedlings’ susceptibility to competition from their neighbors varies with resource availability. For both shade-tolerant and shade-intolerant species, competition for light is most pronounced in locations with greater levels of water and/or nutrients (DeMalach et al. 2017). In such locations, fast growth enabled by ample below-ground resources creates asymmetrical competition between taller individuals that cast shade, and shorter ones that must grow under it. Competition for below-ground resources is not as size asymmetric (Casper and Jackson 1997), but can vary with both light and moisture. Under shade, seedlings are typically limited by low light conditions, and therefore, competition for water or nutrients is not necessarily apparent (Barbier et al. 2008). Conversely, trenching experiments have shown that seedling growth is often sensitive to competition for below-ground resources under an open canopy (Coomes and Grubb 2000). While both water and nutrients can potentially affect competition for light, competition may not change along light gradients in areas where soil moisture is not limiting (Ricard et al. 2003).

There are different views on how and why competition intensity changes with below-ground resource availability. Esch et al. (2018) found that below-ground competition for soil moisture was more intense when moisture was abundant. This finding is supported by isotopic studies showing that various growth forms take up water from shallow soil layers when soil moisture is abundant, and take up water from different depths during the late growing season when soil moisture is scarce (Nippert and Knapp 2007, Kulmatiski and Beard 2013, Guo et al. 2018). As a result, niche overlap is greatest when soil moisture is abundant, and niche segregation is greatest when soil moisture is low. High competition intensity in areas with abundant moisture can thus reduce seedling performance and even reverse the effects of high resource availability (Esch et al. 2018). Similar findings have been reported for soil nutrients, with higher nutrient concentrations leading to stronger competition and reduced seedling performance (Ceulemans et al. 2017).

Alternatively, competition for water may be stronger in areas where soil moisture and nutrient availability are low (Casper and Jackson 1997, Fotelli et al. 2001). Niche overlap between competing individuals can increase during drought as species adopt similar strategies for water uptake (Matias et al. 2018). For example, Nilsson and Orlander (1999) showed that grasses and Norway spruce seedlings (Picea abies) both took water from the upper soil surface in drought years. As seedlings depend on summer rainfall from the upper soil (Cavender-Bares and Bazzaz 2000), this leads them to compete more strongly with grasses, herbs, and other small plants (Prechsl et al. 2015), and less strongly with trees that take up water from deeper sources in dry years (Phillips and Ehleringer 1995). Niche overlap can likewise increase in nitrogen-poor soils, producing stronger competition for available nutrients (Wilson and Tilman 1993).

White spruce (Picea glauca) is considered a moderately shade-tolerant tree species (Lieffers and Stadt 1994), but variation in its susceptibility to competition along above- and below-ground resource gradients is not well understood. In the present study, we conducted a field experiment to evaluate how resource availability and competition from neighboring understory plants and trees each influence the growth and survival of white spruce seedlings. We selected natural seedlings growing under different levels of soil moisture, nitrogen, and light, and applied competition removal treatments to assess how this species responds to competition from neighbors. Our study area experienced a summer drought in the post-treatment year of our experiment, which allowed us to test for effects of competition under unusually dry conditions. We hypothesized that (1) seedling growth and survival are limited by competition for resources during summer drought; (2) competition for resources is stronger in open canopy areas; and
(3) competition for resources is stronger in areas with low soil moisture and nitrogen. Accordingly, we expected that the removal of competition would alleviate decreases in seedling growth and survival experienced during a summer drought and that improvements in growth and survival would be greatest in areas with an open canopy, and in those with dry or nitrogen-poor soils.

**Methods**

**Study area**

This study was conducted within Cypress Hills Interprovincial Park, which is located on the southern Alberta–Saskatchewan border in western Canada (49°40'N, 110°15'W). Mean annual and growing season temperatures are 4° and 13°C, respectively. The area receives mean annual precipitation of 556 mm, of which 312 mm falls during the growing season (Environment and Natural Resources 2019). The Cypress Hills landscape comprises a mix of fescue prairie and forests dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), and occasionally balsam poplar (*Populus balsamifera*). The most common forest understory plants include *Poa pratensis*, *Symphoricarpos albus*, *Rosa acicularis*, and *Viola rugulosa* (Shovon et al. 2020). The distribution of vegetation communities in the Cypress Hills is closely related to topography and soil moisture (Newsome and Dix 1968). Most of the present forest originated between 1880 and 1890 following large fires (Strauss 2001). In the absence of fire, the major disturbances to understory plant communities and seedlings include occasional grazing by cattle and wild ungulates (Hegel et al. 2009).

The two growth years of our study (2016 and 2017) experienced contrasting summer precipitation: Summer precipitation in 2016 was 57% higher than average, while in 2017, it was 62% below average. These were among the most extreme precipitation levels recorded over the 24-yr period for which data are available from the nearest weather station (Fig. 1).

**Study design**

In the summer of 2016, we tagged and measured 454 white spruce seedlings of natural origin across 26 forest stands. Among these stands, nine were dominated by white spruce, seven were dominated by trembling aspen, and 10 were dominated by lodgepole pine. In each stand, we located and selected 18 seedlings within an approximately 1-ha area. Half of the seedlings were under a relatively closed canopy, and the other half were chosen to be in or near canopy gaps. All seedlings appeared healthy and were between 30 and 100 cm in height, under 30 mm in diameter, at least 2 m apart from one another, at least 1 m away from a large tree, and not growing on a rotted log. We measured and...
re-measured both the height and the diameter at root collar of the seedlings over three years (2016–2018). Eighty-three seedlings that had a tree fall on them or were otherwise broken, bent, or trampled during this period were excluded from the experiment, leaving 371 seedlings.

Between June and August 2017, following the second set of measurements on each seedling, we randomly assigned 46 of the final seedlings (~2 per stand) to a trenching treatment and 83 of the seedlings (~4 per stand) to a clipping treatment. The remaining 240 seedlings that were not subjected to these treatments served as controls. For each seedling receiving the trenching treatment, we excavated a 20–30 cm deep trench around the circumference of a 75-cm radius circle centered on the seedling, then backfilled it with soil and rocks for hydrological continuity. We also manually cleared all vascular plants (many of which were taller than the seedlings) between the seedling and the circular trench. Major lateral roots and fine roots (80–90% of all roots) of northern forests and temperate grasslands are generally concentrated in the top 30 cm of soil (Jackson et al. 1996). In severing these roots within the trench, we aimed to remove most of the competition for below-ground resources that these seedlings experienced from neighboring plants. In the clipping treatment, we manually removed all vascular plants within a 75-cm radius of the seedlings but did not dig trenches around them.

While both treatments temporarily removed competitors within 75 cm of the seedlings, the trenching treatment further removed competition for water and nutrients from more distant neighbors (larger shrubs and trees). Trenches were cut, and understory vegetation was removed only once during the experiment. All the seedlings were included in an analysis of survival, but only the 348 that survived to 2018 (44 with trenching, 81 with clipping, 223 control) were included in our growth analysis.

**Seedling growth measurement**

Seedling growth was calculated as the difference in either height or diameter at root collar between successive years. As seedlings were measured on different dates from June to August in each year, we applied a correction factor to scale the observed growth to an annual rate. To do this, we multiplied observed growth by GDDA/GDDM, where GDDA represents the summed growing degree-days from 1 May of one year to 30 April of the next, and GDDM represents the summed growing degree-days from the initial measurement date to the subsequent measurement date. For example, the correction factor for a seedling that was measured on 8 August 2016 and again on 27 July 2017 would have GDDM = 1477.5 and GDDA = 1524.65, for a correction factor of 1.03. In this case, the measured growth increment would be corrected upwards because there was less opportunity for growth between the measurement dates than over a standard 12-month period. Growing degree-day values were calculated from daily temperature data for the Cypress Hills (Environment Canada 2019).

**Environmental variables**

Within each stand, we established two soil sampling locations 30–50 m apart from one another. At each sampling location, we collected soil samples from the vertexes of an equilateral triangle with 8.6-m sides. We collected soil samples from each location three times from June to August 2018, dried them at 105°C, and determined their moisture content gravimetrically. We constructed a generalized additive mixed model to account for changes in moisture over time and used this model to predict average soil moisture at each sampling location for a reference date of 1 July 2018 (Shovon et al. 2020). Soil C and N were measured by combining three soil samples (collected at depths of 5–10 cm) from each sampling location and determining their elemental composition through mass spectrometry. Soil C/N ratio and soil moisture ranged from 12 to 33 (mean 21) and 16–41% (mean 23%), respectively. We assigned the soil moisture and C/N ratio for the closest sampling location to each seedling (mean distance = 39 m). By necessity, this introduced a degree of error because soil measurements were not taken at the seedlings’ exact locations.

For light, we measured canopy openness above each seedling from a north-facing hemispherical photograph taken at a height of 1.5 m in 2016. Canopy openness was calculated from these images using the program Gap Light Analyzer V2 (Frazer et al. 1999). Canopy openness ranged from 19% to 72% (mean 41%).
Statistical analyses

We fit linear hierarchical models to estimate how the effects of removing competition varied with above- and below-ground resource availability (canopy openness, soil moisture, soil C/N ratio). Specifically, we developed a set of 11 candidate models that variously included or excluded responses to a single resource (either light, water, or nitrogen), responses to competition removal, and an interaction between the two (i.e., responses to competition removal depend on levels of either light, water, or nitrogen). All models also included a size term that described changes in seedling growth with either initial diameter or initial height, a year term that described the difference in growth between 2016 and 2017, and a treatment term that described initial growth differences between the control, clipping, and trenching treatments before carrying out any manipulations. A random intercept for each seedling accounted for individual differences in growth rate that were not explained by other terms in the models.

Our set of candidate models included different main effects for environmental variables, and individual models either included or omitted several two- and three-way interaction terms. These models can be divided into five groups: (1) a null model that included only size, year, treatment (before competition removal), and individual effects; (2) a competition removal model, which included all terms in the null model plus a two-way year × treatment interaction; (3) resource availability models, which included all terms in the null model, the main effect of a single resource, and two-way resource × year and resource × treatment (before competition removal) interactions; (4) resource availability plus competition removal models, which included all terms from the previous two groups; and (5) resource availability plus conditional competition removal models, which included all terms from the previous group plus a three-way year × treatment × resource interaction. Groups 3, 4, and 5 all contained three models with a different environmental variable (canopy openness, soil moisture, or C/N ratio) specified in each.

We fit the 11 candidate models with both diameter and height growth as the response variable. Few seedlings died during the experiment, so it was not possible to fit survival models with the full set of predictor variables. Instead, we only fit the null and competition removal models (groups 1 and 2) to seedling survival. Survival observations were binary values (dead/alive), and so these models used a Bernoulli distribution and logit link function to model expected seedling survival rates.

We adopted a Bayesian framework using the R package BRMS 2.6.1 (Bürkner 2017) for data analysis. All model parameters were assigned default, uninformative priors that minimized their influence on posterior estimates. We fit all models using four Markov chain Monte Carlo chains, each of which had 1000 warm-up iterations (which were discarded) and 1000 sampling iterations. All parameters were checked for convergence among chains. We used a leave-one-out (LOO) cross-validation information criterion (Vehtari et al. 2017) to compare the expected predictive accuracy of each of the candidate models. Models with lower LOO were considered to be better models, especially if the difference in LOO was more than twice its standard error. All statistical analyses were conducted in R v.3.5.1 (R Core Team 2018).

As we fit our models in a Bayesian framework, we do not describe results in the context of null-hypothesis significance testing. We focus instead on the presentation of effect sizes, credible intervals on model parameters, and differences in expected predictive ability (as measured by LOO) among models.

RESULTS

Out of 11 candidate models, the model that included a three-way year × treatment × canopy openness interaction was ranked highest for height growth, while that which included a two-way year × treatment interaction but no resource effects was ranked highest for diameter growth (Table 1). Models that included effects of soil moisture or C/N ratio did not perform as well as models with canopy openness, although C/N ratio sometimes outperformed models with no resource effects. Our model selection procedure thus indicated that light availability and competition were each important predictor for white spruce seedling growth. Furthermore, the effects of competition removal on seedling height growth appeared to vary with canopy openness.
Differences among years and treatments

There was evidence that height and diameter growth were lower in the dry year (2017) than in the previous wet year (2016). Compared to 2016, height growth was 2.3 (1.4–3.2), 3.1 (1.6–4.5), and 2.9 cm (0.8–5.1) lower in 2017 in the control, trench, and clipping treatments, respectively (Fig. 2a). The intervals on these estimates do not overlap zero, and so the results indicate a clear change in height growth between years. Differences in diameter growth varied among the three treatments. Control seedlings had 0.2 cm (0.1–0.2) lower diameter growth in 2017 than in 2016. The growth difference for seedlings in which competition was removed was much less, with trench and clipping seedlings having 0.1 cm (0.0–0.1) and 0.03 cm (0.0–0.1) lower diameter growth in 2017, respectively (Fig. 2b). The smaller post-treatment difference in 2017 diameter growth rates reflects the effect of our competition removal treatments on diameter growth compared with control seedlings. Since trenching removed above-ground competition and below-ground competition from both close and distant neighbors, its effect was expected to be greater than the clipping treatment in which below-ground competition from distant neighbors was not removed.

Twenty-three out of 372 seedlings died during our experiment. Survival was higher for taller seedlings than shorter ones, with predicted survival increasing from 98% (92–100%) for a 25-cm seedling to 99% (98–100%) for a 50-cm seedling in 2016 (see Appendix S1: Table S1). The predicted probability of seedling survival was 99% (99–100%) in 2016 (before treatments were imposed), but in 2017, the predicted survival probability of control seedlings dropped to 94% (91–97%). The model that included treatment effects performed better than the null model (Table 1). Survival rates for seedlings in the trench and clipping treatments appeared to be somewhat higher than that of control seedlings in 2017, at 96% (90–99%) and 98% (94–100%), respectively (Fig. 2c). With a lower sample size, these survival rates were not clearly different

| Model group | Resource availability§ | Competition removal (treatments)¶ | ΔLOO (± SE)† | ΔLOO (± SE)‡ |
|-------------|------------------------|-----------------------------------|--------------|--------------|
| 1           | None                   | No                                | 0.0          | 0.0          | 0.0          |
| 2           | None                   | Yes                               | 0.99 (±2.43) | −10.04 (±7.77) | −17.9 (1.24) |
| 3a          | Light                  | No                                | −8.92 (±9.66) | 2.04 (±4.49)  |
| 4a          | Light                  | Yes                               | −4.75 (±9.88) | −8.34 (±8.75) |
| 5a          | Light                  | Conditional                       | −11.78       | −6.27 (±8.97) |
| 3b          | Water                  | No                                | 0.84 (±5.35) | 5.56 (±3.72)  |
| 4b          | Water                  | Yes                               | 0.96 (±5.99) | −4.52 (±8.75) |
| 5b          | Water                  | Conditional                       | 8.25 (±5.14) | 0.92 (±9.45)  |
| 3c          | Nitrogen               | No                                | −6.68 (±6.10) | 5.14 (±2.93)  |
| 4c          | Nitrogen               | Yes                               | −5.76 (±6.98) | −5.94 (±8.07) |
| 5c          | Nitrogen               | Conditional                       | −1.60 (±6.83) | −3.65 (±8.73) |

† All models include fixed effects of size (either initial diameter or height), year, and treatment (before competition removal), and a random intercept term for each individual seedling.
‡ Estimated difference in the leave-one-out cross-validation information criterion (ΔLOO) compared with a null model with no effects of resource availability or competition removal. Values less than zero indicate better expected predictive ability on new data than the null model. The smallest value in each column indicates the best model by this measure among those considered.
§ Light, water, and nitrogen correspond to predictor variables for canopy openness, soil moisture, and C/N ratio, respectively.
¶ No: no interaction terms between year and treatment; yes: includes two-way interaction term between year and treatment; conditional: includes three-way interaction term between year, treatment, and resource.
# Only initial height was used in the null model for survival analysis. No random effect of individual seedling was used in survival models.
from that of control seedlings or 2016 survival rates.

**Interaction between competition and canopy openness**

Canopy openness had a positive effect on height growth, but not on diameter growth (Fig. 3a). For every 10% increase in canopy openness, seedling height growth increased by 0.9 cm (95% credible interval: 0.3–1.6; Appendix S1: Table S2). Although alleviating competition did not have strong overall effects on height growth, there was evidence that the effect of competition removal depended on the level of canopy openness. Our model comparison showed that the height growth model in which effects of competition removal varied with canopy openness performed better than one with no effect of competition removal (Table 1). We quantified these treatment effects (Δ growth) by deducting the predicted height growth of control seedlings in 2017 from the predicted 2017 growth of trench and clipping seedlings. Trenched seedlings were estimated to grow 3.2 cm (−0.5 to 7.0) less than controls under shade (20% canopy openness), but 5.9 cm (1.5–10.6) more than controls under high light conditions (70% canopy openness). The clipping treatment did not produce any clear
differences in growth compared to controls, with these seedlings having just 1.8 cm (−1.4 to 5.0) lower growth at 20% canopy openness, and 0.8 cm (−5.2 to 3.6) higher growth at 70% canopy openness (Fig. 4).

**Influence of below-ground resources**

Height growth increased with a lower C/N ratio (i.e., greater nitrogen availability), although C/N had a weaker effect on growth than canopy openness (model 3a vs. 3c in Table 1; Fig. 3b). Soil moisture did not appear to affect height growth, and neither below-ground resource seemed to influence seedling diameter growth. Neither soil moisture nor nitrogen availability appeared to influence responses to competition removal, as models for both these resources that included the three-way interaction term performed worse than models without it (model 4b vs. 5b and 4c vs. 5c in Table 1).

**DISCUSSION**

Seedlings experience competition from shade cast by neighboring trees, as well as for water and nutrients taken up by both neighboring trees and understory vegetation. We found that effects of removing competition (trenching) on the height growth of white spruce seedlings were greatest under an open canopy but did not vary with below-ground resource levels (Matsushima and Chang 2007). Alleviating competition also compensated for much of the decrease in diameter growth and reduced survival that we observed in seedlings growing with competitors in a dry year (Fig. 2). These results indicate that competition has important effects on seedling performance that may increase with light availability, and which can exacerbate the adverse effects of dry summer conditions on growth and survival.

**Inter-annual differences and competition removal**

The height, diameter growth, and survival rate of control seedlings were lower in the dry post-treatment year than in the wet pre-treatment year (Fig. 2). While it is not possible to determine the cause of these decreases with certainty, we believe that seedling performance was likely reduced by drought stress in the dry year (Collet et al. 1996). White spruce avoids the effects of drought by reducing its physiological activities (stomatal closure, gas exchange, photosynthesis), which slows its growth rate (Grossnickle 2000). We observed lower diameter growth and height growth in the dry summer relative to the previous wet year. Shoot growth of white spruce seedlings might not be affected by changes in soil moisture in just one growing season. Height growth is determined by needle primordia that are formed in the previous year, and so it is influenced by environmental conditions in both the current and previous growing seasons (Grossnickle 2000). As there were two consecutive dry summers after the wet summer of 2016 (Fig. 1), we observed a clear decrease in height growth in our study (Marshall et al. 2000).

Unlike the control seedlings, the diameter growth and survival of treated seedlings in the dry post-treatment year were not clearly less than in the wet pre-treatment year (Fig. 2b). Seedlings usually compete for soil moisture with understory vegetation because small plants also take up water from the upper soil (Kulmatiski and Beard 2013). The removal of competition from nearby understory vegetation, as well as from more distant neighbors in the trenching treatment, increased resource availability (Lindh et al. 2003) and mostly compensated for otherwise adverse conditions in the dry year. Since
diameter growth is more sensitive to resource availability (Grossnickle 2000) and white spruce seedlings growing under dry conditions could obtain sufficient nutrients to maintain carbon assimilation and growth (Livingston et al. 1999), we found trenching affected diameter growth positively.

**Direct resource effects**

The height growth of seedlings was positively related to canopy openness (Chen 1997), a surrogate measure of overstory light transmission, and to soil nitrogen availability. Seedlings compete with canopy trees for light, and so seedling growth was lower under shade than under an open canopy (Collet and Chenost 2006). Seedlings have higher rates of photosynthesis under open canopy conditions which often leads to higher height and diameter growth (Grossnickle 2000), although we did not find a clear trend in diameter growth with increasing light. Seedling mortality is also higher under shade than an open canopy (Chen 1997), but because of low mortality during our three-year experiment, we did not test for any effect of shade on seedling survival. Healthy seedlings were found mostly under >20% canopy openness, which suggests that healthy seedlings did not grow under the heaviest shade.

We also found a positive relationship between height growth and soil nitrogen availability (Fig. 3b; Hangs et al. 2004), but did not find any effect of soil moisture on either height or diameter growth. Soil C/N ratio at our sites was largely related to the overstory tree composition, as leaf litter determines the soil nitrogen available to plants (Barbier et al. 2008). Soil moisture varies with micro-topography at the scale of just a few meters (Kuuluvainen 1994), and also over time since it depends on precipitation recharge (McLaren et al. 2004). Our results suggest that temporal variation in precipitation may be more important for seedling growth than spatial variation in soil moisture.

Since we measured gross resource availability at sampling locations 25-50 m away rather than the net resource availability for individual seedlings, it is possible that the water and nitrogen resources that we measured did not accurately represent those experienced by each seedling. This could explain why we did not find any relationship between soil moisture and seedling growth, and only a weak relationship between soil nitrogen availability and height growth.

**Interactions between competition and resource availability**

Our trenching and clipping treatments did not have comparable effects on height growth. Clearing away neighboring stems did not increase growth by itself, but when combined with trenching, it did increase height growth in areas with the greatest light availability (Fig. 4). However, these effects of competition removal were not apparent under shade. Seedling growth was already limited by low light under a closed canopy, and so trenching had no further effect (Barberis and Tanner 2005). In some years, white spruce can continue photosynthesis through the fall, when it can take advantage of aspen’s leafless condition and receive more light (Man and Lieffers 1997). While this strategy could be effective in wetter years, the dry conditions present in late summer of 2017 meant that seedlings did not have sufficient moisture to sustain their growth late into the growing season, even with the removal of competition under a closed canopy. As a result, the benefits of removing competition were limited to those areas with greater light availability throughout the summer.

Trenching can improve soil conditions by removing below-ground competition from more distant plants, including larger trees (Strand et al. 2006). Past studies have likewise found that the positive effects of trenching on seedling growth increase with light availability as seedlings become more limited by below-ground resources (Coomes and Grubb 2000, Carswell et al. 2012). Effects of trenching can also depend on the availability of below-ground resources: Studies have mostly found that positive effects of trenching are limited by soil nutrients and/or soil moisture (Coomes and Grubb 1998, Barberis and Tanner 2005). The effects of competition did not vary with soil moisture or nitrogen availability in our study, and therefore, we cannot infer that higher competition intensity in resource rich areas masked the relationship between growth and below-ground resources (Esch et al. 2018). At the same time, competition for soil nitrogen...
did not appear to be stronger in nitrogen-poor soil (Wilson and Tilman 1993).

**Climate change implications**

The southern range limit of white spruce in western Canada is believed to be controlled by the effects of moisture limitation on regeneration success (Hogg and Schwarz 1997). Future increase in temperatures will produce greater water deficits in this region and have the potential to affect the regional occurrence of this widely distributed species (Erickson et al. 2015). These inferences, however, are largely based on ecophysiological modeling and data from planted spruce in farmyards and other cleared areas (Hogg 1994, Erickson et al. 2015), and do not account for the effects of competition in forested environments. Our results show that competition from neighboring plants can negatively affect the performance of white spruce seedlings during summer drought. Environmental change can alter competition from neighboring plants and in turn alter species performance over time (Grossiord et al. 2018).

In addition to climatic factors, models of white spruce’s future population dynamics may need to take into account the indirect effects of competition under light limitation and drought. Further research is needed to understand how prolonged drought can affect this species at the seedling stage by altering inter-specific competition from existing and novel competitors (Alexander et al. 2015), or by depleting soil moisture and reducing seedling survival directly. A clear understanding of how direct and indirect effects of climate change affect seedling performance will help in predicting range shift dynamics under climate change (Clark et al. 2016, Ettinger and HilleRisLambers 2017).

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