



Winter conditions – not summer temperature – influence establishment of seedlings at white spruce alpine treeline in Eastern Quebec

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Keywords

Alpine treeline ecotone; Climate change; Eastern Quebec; Facilitation; Krummholz; *Picea glauca*; Seedling establishment; Snow cover; Tree islands; Treeline position; White spruce

Abbreviations

DD = sum of degree days; CI = confidence interval; SGH = stress gradient hypothesis.

Nomenclature

Marie-Victorin et al. (2002)

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Introduction

On a global scale, alpine and arctic treelines are controlled by heat deficiency during the growing season, principally because of the physiological constraints of cold tempera-

Abstract

Aims: While treeline positions are globally correlated to growing season temperatures, seedling establishment, an important process of alpine treeline dynamics, is additionally controlled by regional-scale factors such as snow cover duration, desiccating winds and biotic interactions. Knowing that alpine treelines have shown contrasting responses to climate change, we determined the relative importance of key abiotic and biotic factors involved in seedling survival and growth.

Location: McGerrigle Mountains, Parc National de la Gaspésie, Appalachian Range, eastern Quebec, Canada.

Methods: In two white spruce (*Picea glauca*) treeline sites, we used the microclimate in the vicinity of tree islands, densely packed clusters of trees isolated from each other by alpine tundra vegetation, to assess the effects of abiotic variables (sum of degree days [DD], snowpack duration and a wind exposure index) as well as the effects of biotic interactions with neighbouring vegetation on the survival and growth of transplanted white spruce seedlings. For 3 yr, we surveyed seedling survival twice a year to discriminate between winter and summer survival, and measured seedling growth at the end of each growing season. We used Bayesian hierarchical models to estimate the relative effects of covariates on survival and growth.

Results: Survival probability decreased in microsites where winter DD was high, and increased in microsites with longer snowpack duration. In wind-exposed microsites, seedling survival increased when neighbouring vegetation was present, indicating facilitative mechanisms. Seedling growth was positively affected by the duration of snow cover and tended to increase with higher DD during the previous year. In wind-sheltered microsites, seedling growth tended to be negatively affected by neighbouring vegetation, indicating competitive mechanisms.

Conclusions: Our study demonstrates that seedling establishment is more sensitive to winter conditions, notably to the length of snow cover (which protects seedlings from frost and desiccation), than to summer temperature. Biotic interactions increased seedling establishment when environmental stresses were higher. We suggest that regional-scale factors such as winter climate and biotic interactions should be included in modelling exercises to improve future treeline location forecasts.

ture on tree growth (Malanson et al. 2011; Körner 2012). However, at finer scales, numerous regional abiotic factors such as wind (Holtmeier & Broll 2010), snow (Kreyling 2010), water availability (Lloyd & Graumlich 1997) and topography (Macias-Fauria & Johnson 2013), or biotic

factors, e.g. competition (Wilson 1993), modulate the importance temperature has on controlling treeline position (Holtmeier 2003; Malanson et al. 2011). These factors may explain why treeline responses to the recent increase of global temperatures have not been similar globally (Harsch et al. 2009). Since seedling recruitment is a crucial process of treeline formation and persistence (Smith et al. 2003), regional-scale factors can induce a migratory lag due to a lack of regeneration (Fajardo & McIntire 2012) and even a recession of the treeline (Luckman & Kavanagh 1998). Few studies, however, have successfully measured the relative effects of regional-scale factors on seedling recruitment (Danby & Hik 2007; Barbeito et al. 2012).

Microsite conditions are determinant for seedling recruitment at treeline (Resler 2006). In turn, microclimatic conditions are strongly affected by wind and snow, which may ultimately influence the local position of treelines (Sullivan & Sveinbjörnsson 2010). Because of their small size, seedlings are much more affected by soil temperature and microsite conditions than by free-air temperature (Fajardo & Piper 2014). Strong winds during summer have direct negative effects on seedlings through desiccation (Fajardo & McIntire 2011), thus surrounding micro-relief can have an important wind shelter effect on seedling survival and growth. In winter time, seedlings are generally covered by snow, which acts as an insulation layer and a protection from desiccating winds, destructive snow blasts (Wipf et al. 2009), xylem embolism (Mamet & Kershaw 2013) and frost (Mayr et al. 2006). Later, in early spring, radiative stresses, notably photoinhibition, can irreversibly damage seedlings, jeopardizing their survival (Germino et al. 2002). When snow cover persists for a prolonged period of time, seedling survival may decrease because of fungi infections (Barbeito et al. 2013), and seedling growth can decrease as a result of a shortened growing season (Körner 2012). During summer months, warmer temperatures promote survival and growth at the treeline (Danby & Hik 2007), even though water stress associated with high temperatures can hinder seedling survival (Piper et al. 2013), resulting in a hump-shaped response of seedlings survival and growth to temperature (Loehle 2000). Coupled with temperature, the length of the growing season is an important factor that influences seedling survival and growth, notably because it allows adequate resource accumulation and preparation for winter hardening (Stevens & Fox 1991).

At treeline, not only abiotic microclimatic conditions, but biotic interactions also have a modulating effect on seedling establishment (Alftine & Malanson 2004). However, biotic interactions are context-dependent, and according to the Stress Gradient Hypothesis (SGH; Bertness & Callaway 1994), positive plant–plant interactions should be more important than competition where stress on plants

is more prevalent, e.g. at treeline elevation (Callaway et al. 2002; McIntire & Fajardo 2014). At the benign end of any stress gradient, neighbouring plants can limit seedling establishment through competition – commonly for light – (Cranston & Hermanutz 2013), while at the stressful end of the gradient, neighbouring plants can increase the seedling establishment of other (or the same) species through facilitation, e.g. via wind barrier (Fajardo & McIntire 2011). For instance, Batllori et al. (2009) showed that conifer seedlings survived and grew better when positioned leeward of mature trees because of the effect these trees had on the snow distribution in their immediate vicinity.

White spruce (*Picea glauca* [Moench] Voss) is a major treeline species in North America, which has shown contrasting responses to climate change, encroaching or receding in some places (Payette 2007) or being stable in other places (Szeicz & Macdonald 1995). At treeline elevation, white spruce, as many other conifer treeline species in the Northern Hemisphere, generally forms tree islands, clusters of densely packed stems and shrub-like trees called krummholz, isolated by alpine vegetation. These islands have a strong impact on seedling recruitment because they modify the microclimate. Compared to the surrounding alpine tundra environment, during the day, soil temperature is colder in the shade of tree islands while at night it is warmer because of the reduction of radiative heat loss (Körner 2012). Furthermore, snow cover is deeper on the leeward side of the tree island because of its effect on wind flow (Batllori et al. 2009). On this sheltered side, wind speed decreases, which reduces the direct effect of wind on plant tissues (Grace 2006). Because of the role they play in modifying microclimates, tree islands are an important component of treeline dynamics (Smith et al. 2003).

In this study, we measured the relative effects of key abiotic drivers and plant interactions on seedling establishment at white spruce treelines in eastern Canada. We used a transplant experiment and a vegetation removal treatment to measure the effects of temperature, snow cover, wind, competition and facilitation on the survival and growth of white spruce seedlings. For 3 yr, we surveyed seedling development at the end of each winter season (mid-June) and summer season (mid-September) to discriminate between winter and summer effects on survival. We also measured vertical shoot growth at the end of each summer season. First, we expected higher seedling survival and growth in warmer microsites with longer snow cover. Second, we expected to observe a positive lag effect of temperature and snow on seedling survival and growth, notably because white spruce growth is partly defined by the conditions of the previous year (Grossnickle 2000). Third, based on the SGH, we expected neighbouring alpine vegetation to increase survival and growth in wind-exposed microsites, while decreasing them in wind-sheltered

microsites. Our study aims to reveal the importance of winter conditions – a commonly forgotten component of treeline dynamics – on the seedling establishment process at treeline elevation.

Methods

Study area

Our study took place in the McGerrigle Mountains, which are part of the Appalachian Range of eastern Quebec, Canada (Fig. 1, top right panel). The McGerrigles are located in the Parc National de la Gaspésie; here the alpine treeline has been subjected to very little human impact. This region is characterized by steeply rising mountains with flat summits (Jones et al. 2012). White spruce is the dominant tree species at treeline, occasionally accompanied by balsam fir (*Abies balsamea*, Mill.) and black spruce (*Picea mariana*, Mill.). Climate in the area is boreal, with a strong maritime influence; the mean annual temperature is -3 to -5 °C, and the mean annual precipitation is 1600 mm, of which two-thirds fall as snow (Gray & Brown 1982; Fortin & Héту 2014). Wind speed at the summits of the McGerrigles is $24 \text{ km}\cdot\text{h}^{-1}$ on average and can gust up to $250 \text{ km}\cdot\text{h}^{-1}$ (Gaspé Avalanche Center, unpubl. data). On average, mean annual air temperature in the region has increased by 1.3 °C since 1961 (Sainte Anne des Monts weather station, MDDELCC 2014).

The alpine treeline found in the McGerrigles forms an ecotone that gradually changes from a closed canopy forest to a krummholz zone with severely stunted and deformed trees (Payette & Boudreau 1984). At the upper treeline, trees typically grow in densely packed clusters of small trees and krummholz isolated by alpine vegetation, denominated ‘tree islands’. Alpine vegetation is dominated by typical Appalachian alpine vegetation such as *Carex bigelowii* (Torr. ex Schwein.), *Diapensia lapponica* (L.) and *Empetrum nigrum* (L.) (Jones et al. 2012). At the bottom-most part of the treeline ecotone, vegetation is composed of species typical of the boreal system, such as ericaceous shrubs (*Vaccinum* spp.) and feathermosses (*Pleurozium schreberi* [Brid.] Mitt.). Based on an analysis of multi-date aerial pictures, Fortin & Pilote (2006) illustrated that the treeline of the McGerrigles has not advanced since 1974, although the krummholz zone has undergone some densification. Alpine tundra here is used by a small herd of woodland caribou, but it is not known to impact white spruce regeneration (Crête et al. 2001).

Experimental design

We selected 16 tree islands on three adjacent mountains (six on Mont Jacques Cartier, five on Mont Dos de la Baleine and five on Mont De la Passe; Fig. 1 left panel, Table 1). Using the summit as a starting point and going in

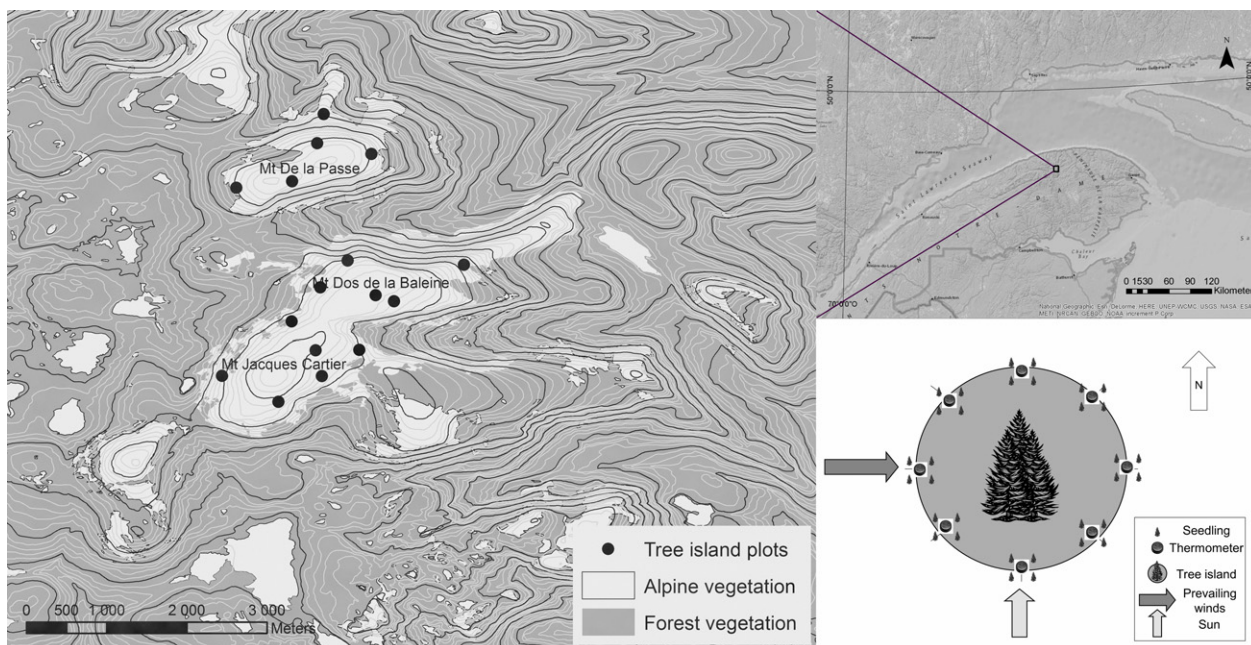


Fig. 1. Top right: map of study's area. Left: locations of the 16 tree islands used as experimental plots in the McGerrigle Mountains alpine treeline (Quebec, Canada). Bottom right: experimental design of white spruce seedling transplantation. Two white spruce seedlings were transplanted per cohort (208 in 2010 and 288 in 2011). For one out of two seedlings per location we removed neighbour vegetation as a treatment effect. Numbers indicate the orientation index based on the prevailing wind effect: -1 = wind-exposed locations, and 1 wind-sheltered locations.

each cardinal direction, we selected the first tree island that had at least one tree with a vertical stem ≥ 1.3 m tall. We also selected the uppermost tree island of each mountain using this height criterion (JCS6, MBS5, MPS5; Table 1), plus one tree island on the southeast aspect of Mont Jacques Cartier in the lower treeline to increase our micro-climatic conditions gradient (JCS1; Table 1). Our study sites spanned elevations from 1098 to 1261 m a.s.l. (Table 1). Tree islands were 1.35 to 3.00 m tall and encompassed areas ranging from 6 to 80 m² (estimated by measuring the edges of each tree island). Based on stem and branch damage, prevailing winds were found to blow eastward, with an average azimuth of 85.07° (Table 1).

To test the effect of abiotic and biotic factors on seedling survival, we transplanted natural white spruce seedlings collected haphazardly from a nearby source located at 600 m a.s.l. and transported to the tree islands at dawn to avoid desiccation. We conducted the transplanting during autumn to minimize drought risks. We selected seedlings based on age (1 or 2 yr old), which we determined by the number of annual growth nodes (one or two) and height (range: 2.4–12.4 cm). To reduce the effect of year of transplant, we transplanted two separate cohorts: the first cohort was transplanted in Sept 2010, 16 around each of 13 tree islands ($N = 208$; Fig. 1, Table 1). The second cohort was transplanted in Sept 2011, 16 seedlings at 12 of the original 13 tree islands ($N = 192$; one tree island set aside for logistical reasons) plus 32 seedlings at three new uppermost tree islands ($N = 96$, total $N = 496$). Thus, we transplanted four seedlings at each cardinal and ordinal

direction (Fig. 1, bottom right panel) of all but one tree island. The distance between each transplanting location around the tree island depended on the tree island size, varying from 0.5 to 5.0 m. At each location, seedlings were planted 20 cm apart under the outermost part of the lowest branches of the tree island.

Environmental measurements

In order to measure the abiotic conditions experienced by transplanting seedlings, we buried temperature data loggers (Maxim-IC., Ibutton ThermoChron, thermometer DS1921G-F5#, temperature resolution: 0.5 °C) in the soil between the seedlings at a depth of 5 cm (Fig. 1, bottom right panel) at each cardinal and ordinal point around the tree islands. Temperature was recorded every 4 h for the duration of the experiment (3 yr). To test the effect of temperature, we derived the sum of degree days (DD) from the datalogger temperature records for each time period (in winter DD_w and in summer DD_s). DD was defined with a 5 °C threshold, i.e. the sum throughout the season of the daily number of Celsius degrees, where the mean daily temperature was above 5 °C, because that is the approximate temperature at which tree growth stops (Körner 2012). We estimated snowpack duration using the Danby & Hik's (2007) method: three consecutive days of a daily temperature variance of <1 indicates the presence of an overlying snowpack. To derive the snowpack duration ($Snow$), we summed the number of days where we had an indication of snowpack presence.

Table 1. White spruce tree islands characteristics. Aspect is the slope aspect in compass degrees; Slope is the inclination of the slope in degrees; Height is the height of the dominant tree; Size is the projected surface of the tree island; Wind is the direction of prevailing winds in compass degrees based on crown damage; Cohort indicates which cohort of seedlings is transplanted.

Tree Island	Elevation (m)	Aspect (°)	Slope (°)	Height (m)	Size (m ²)	Wind (°)	Cohort
JCS1	1229	110	9	2.80	66	NA	1
JCS2	1224	150	9	3.00	30	87	1–2
JCS3	1216	72	17	2.80	50	88	1–2
JCS4	1239	120	8	2.00	NA	102	1–2
JCS5	1199	276	22	2.20	80	80	1–2
JCS6	1261	122	4	2.00	10	78	2
MBS1	1215	350	30	1.50	6	102	1–2
MBS2	1137	60	14	1.70	50	98	1–2
MBS3	1232	95	7	2.20	50	85	1–2
MBS4	1224	276	10	2.50	30	93	1–2
MBS5	1250	110	3	2.10	15	88	2
MPS1	1098	350	7	1.70	8	80	1–2
MPS2	1205	84	14	1.70	20	70	1–2
MPS3	1239	145	11	1.35	8	75	1–2
MPS4	1204	249	13	1.80	40	72	1–2
MPS5	1191	354	13	3.00	35	78	2
Mean	1210.19	182.69	11.94	2.15	33.16	85.07	NA
SD	41.31	107.25	6.80	0.53	22.76	10.26	NA

Plant measurements

Following the first transplantation event in Sept 2010 until the final measurement in Sept 2013, we visited the experimental plots every mid-June and mid-September to assess winter and summer survival and to retrieve the temperature data from the thermometer logger. A seedling was considered alive when it had at least one green needle. Our surveys provided us with a 3-yr survival history for cohort 1 and a 2-yr survival history for cohort 2. Each year was divided into two periods: 'summer season' (mid-Jun to mid-Sept), which encompassed the peak of the growing season, and 'winter season' (mid-Sept to mid-Jun), which included late autumn, winter and early spring. Each seedling's height was measured at transplantation time (H), to account for the effect of original size on survival, and each following mid-Sept.

To test for the effects of neighbouring vegetation (veg), we removed potential competition from the seedlings' neighbourhood by clipping all vascular vegetation in a 10-cm radius around two randomly assigned seedlings for each group of four seedlings. The other two seedlings were used as controls. Vegetation removal was repeated each mid-June around the same seedlings. To test the effect of wind, we transformed the orientation of seedlings around the tree island into a quantitative variable (ori) to represent the exposure to prevailing westerly winds. We used the sin transformation of the azimuth of location to transform the categorical locations into a circular variable bounded between -1 and $+1$ (Fig. 1, bottom right panel): on the western side of the tree island, where exposure to wind is maximal, values are negative, with West taking a value of -1 . On the sheltered eastern side of the tree island, values are positive, with East taking a value of $+1$, while North and South values are zero.

Data analysis

Tree island effects on environmental covariates

To assess whether the effects of tree islands on microclimatic covariates – DD_w , DD_s and $Snow$ (Appendix S1) – were as assumed, we fitted the data using sinusoidal regressions. Sinusoidal regressions are non-linear models that enable estimation of the phase offset of the sinusoidal model; in our case the angle where the value of the covariate is the larger.

Survival and growth models

We used a Bayesian implementation of a hierarchical, conditional logistic regression model to estimate the relative effects of abiotic and biotic factors on the survival and growth of transplanted seedlings. Prior to this, we had to

deal with missing data, for which we decided the best way to analyse our data set was using the Bayesian hierarchical framework (Gelman & Hill 2006). Due to random thermometer failures, we ended up with time series of temperatures containing missing values, which prevented us from deriving some DD and $snow$ values (4.3% of total possible records were missing). We used Bayesian simulations to infer the missing values from a model of the mean with a random effect on the tree island variable (Appendix S1). The missing data were drawn from a normal distribution, while recorded values fed the estimation of the mean. This allowed us to use the whole data set while carrying over the error attributed to the inferred data. Furthermore, the Bayesian modelling framework allowed the requisite flexibility to account for time-repeated measurements and the conditionality on the previous survival state of the seedling.

We created the variable DD^2 to test for the quadratic effect of temperature as an index of water stress effects on seedling survival and growth. In general, increasing temperature should increase growth; however, it also increases the probability of water stress as the moisture availability also decreases with increasing temperature. Thus, the probability of water stress increases with increasing temperature. A significant negative quadratic effect would be indirect evidence of a moisture problem; likewise, the absence of a negative quadratic effect of temperature suggests no moisture limitation. We tested this indirect water stress effect because seedlings in the first years are sensitive to drought (Körner 2012), although we did not expect to detect such a negative quadratic effect as the Gaspé Peninsula has abundant precipitation.

We modelled the probability of seedling survival (φ_i) at time t as a Bernoulli random variable conditional on the survival of the seedling (z_i) during previous visit $t-1$ (Eq. 1). Survival probability was estimated for each winter and summer season. The complete model equations are presented in Appendix S1. We used a model with a random intercept $\alpha_{g(i)}$ to account for the variability between tree islands (Eq. 2).

$$z_{i,t} | z_{i,t-1} \sim \text{Bernoulli}(\varphi_{i,t} z_{i,t-1}) \quad (1)$$

$$\text{logit}(\varphi_{i,t}) = \alpha_{g(i)} + \beta_{C1,s(t)} C1_{i,t} + \beta_{C2,s(t)} C2_{i,t} + \dots + \varepsilon_{i,t} \quad (2)$$

where i is the seedling index, g the tree island, t the time step, s the season, and β are the effects of $C1$, $C2$... which are the following explanatory variables: the cumulative degree days and squared cumulative degree days (DD and DD^2), snowpack duration ($Snow$), their lag effects ($lagDD$, $lagDD^2$ and $lagSnow$), the vegetation treatment (veg), orientation around the tree island (ori) and their interaction

(*veg.ori*), and the interaction between *DD* and *ori* (*DD.ori*). We also included elevation (*elev*) and height of seedling at transplantation time (*H*) as covariates, which could be confounding factors (Appendix S1).

We also estimated the effects of the same explanatory variables on seedlings' relative vertical growth using a linear mixed effects model (Appendix S1). We modelled the log-transformed relative growth as $\log(RG_t) = \log\left(\frac{H_t}{H_{t-1}}\right)$, using the same random effect structure as for the survival model. We included *DD*, *DD*², *Snow*, *lagDD*, *lagDD*², *lagSnow*, *veg*, *ori*, *veg.ori*, *DD.ori* and *elev* as explanatory variables of seedling growth. These variables differ from those of the survival model in the sense that they have been compiled on an annual basis to correspond to the growth measurements.

We standardized all continuous variables to facilitate mathematical convergence (Kéry 2010) and to be able to compare the relative effects of explanatory variables on the response variables. We fitted the models using the Markov chain Monte Carlo (MCMC) procedure with WinBUGS from R by the R2WinBUGS library in R3.0.1 (R Core Team, 2014). We used non-informative priors distributions to all parameters while fitting the models to reflect our lack of prior information and to allow the data to drive parameter estimation (Appendix S1; Kéry 2010). We ran the models with three chains of 10 000 iterations using a thinning rate of 0.2 after a burn-in period of 2000 to obtain the posterior distribution for each estimated parameter and derived parameters. We derived the 95% confidence interval (CI) from the posterior distributions. We used the Gelman & Rubin statistic (Gelman & Hill 2006) and visually inspected the plotted chains to assess convergence. We also used a derived measure of Bayesian *P*-value to assess the fit of the models (Kéry 2010).

Results

Microclimate

Microclimatic conditions varied significantly around the tree islands (Appendix S2). Mean degree days during the winter season (*DD_w*) were 327 ± 135 °C (mean \pm SD) and 685 ± 171 °C during the summer season (*DD_s*). Snowpack duration varied between 58 and 261 d. During winter, temperatures showed a maximum on the south-exposed side of the tree islands, with the highest *DD_w* oriented at 202° (south-southwest, *P* = 0.09), while in summer, temperatures were more uniform around the islands and no azimuth presented a significantly larger *DD_s*. Longer snow pack duration was oriented at 97° (east by south, *P* = 0.09). Although snow duration and the orientation index were correlated (Pearson's correlation 0.44, *P* < 0.001), we decided to keep both variables in the subsequent analyses since we were able to separate these two effects using 'season' as an index (Appendix S1).

Survival

Of the 496 transplanted seedlings, 30.6% survived for the duration of the experiment; 37.9% of the first cohort survived 3 yr, and 25.3% of the second cohort survived 2 yr. Survival varied across seasons, ranging from 0.48 to 0.97 (Appendix S3), and between tree islands ($\mu_\alpha = 1.16 \pm 1.01$; $\sigma_\alpha = 0.76 \pm 0.21$). The lowest survival was measured during the summer of 2013 for the second cohort ($\phi = 0.48 \pm 0.05$; Appendix S3).

We found that *DD_w* had a negative linear effect on seedling winter survival (Fig. 2, Appendix S4, left panel). Seedlings exposed to a longer snow cover period had a higher survival probability ($\beta_{\text{Snow}} = 0.33$, 95% CI = 0.095, 0.56; Fig. 2). Lag effect of *DD_w* on seedling survival during the following summer (*lagDD_w*) was negative with a positive quadratic effect (Fig. 2, Appendix S4 right panel). Lag effect of snow cover on seedling survival was marginally positive ($\beta_{\text{lag Snow}} = 0.20$, 90% CI did not include zero). Microclimatic conditions in summer did not affect seedling survival: CI of *DD_s*, *DD_s*², lag effects of *DD_s* and *DD_{s.ori}* included zero.

Seedling survival probability was lower when neighbouring vegetation was removed, but the effect of the vegetation removal treatment varied with the orientation

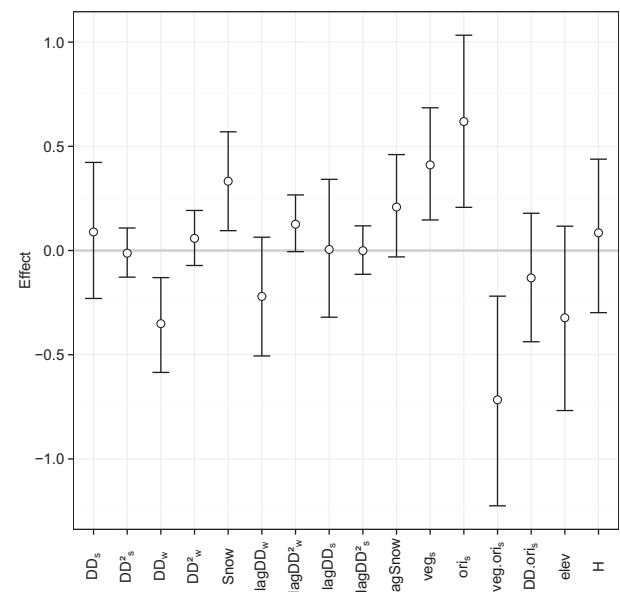


Fig. 2. Median estimates and 95% CI of covariates effect on survival of transplanted white spruce seedlings at alpine treeline. Sum of degree days in summer season and in winter season (*DD_s* and *DD_w*) and quadratic effects (*DD_s*² and *DD_w*²), snow cover duration (*Snow*), lag effects (*lagDD* and *lagDD*² with season indexing, *lagSnow*). Vegetation (*veg*), orientation index (*ori*), interaction of vegetation and orientation during summer (*veg.ori_s*), interaction of *DD* and orientation during summer (*DD.ori_s*), elevation (*elev*) and seedling height at transplantation time (*H*). 95% CI excluding zero value indicates meaningful effect on seedling survival.

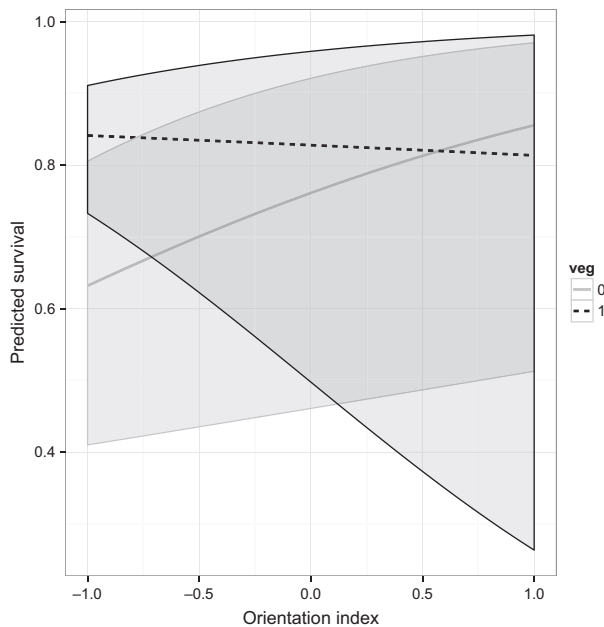


Fig. 3. Effect of wind protection and neighbouring vegetation on transplanted white spruce seedling survival at alpine treeline. Model based predicted survival of seedlings along the orientation index representing wind protection around the tree island (−1 is westward of tree island, 1 is eastward) with or without neighbouring vegetation (Vegetation 1 and 0, respectively)

where seedlings were transplanted. Seedlings transplanted westward of the tree islands had a better survival probability with neighbouring vegetation than without ($ori = -1$; Fig. 3); however there was no effect of vegetation removal on seedlings transplanted eastward of the tree islands ($ori = 1$). Elevation and height at transplant time had no meaningful effect on survival.

Growth

Mean relative shoot growth was $1.08 (\pm 0.15)$, no units as it is a ratio of height) and varied little from year to year (Appendix S5). Variability in relative shoot growth amongst tree islands was low ($\mu_{\alpha} = -1 \pm 0.02$; $\sigma_{\alpha} = 0.01 \pm 0.009$). Results of our growth model showed that neither the DD nor the DD^2 of the same year affected relative growth (Fig. 4). However, the previous year's temperature, $lagDD$ and $lagDD^2$, tended to positively affect relative growth (90% CI did not include 0). Seedlings were not affected by previous year DD across a wide range of low DD values, but grew better above 1200 °C DD (Appendix S6). Seedlings with a longer snow cover period had a higher relative growth (Fig. 4). However, snow cover of the previous year tended to decrease relative growth (90% CI: $-0.03, 0.00$). Neighbouring vegetation and its interaction with ori also tended to reduce relative growth (90% CI:

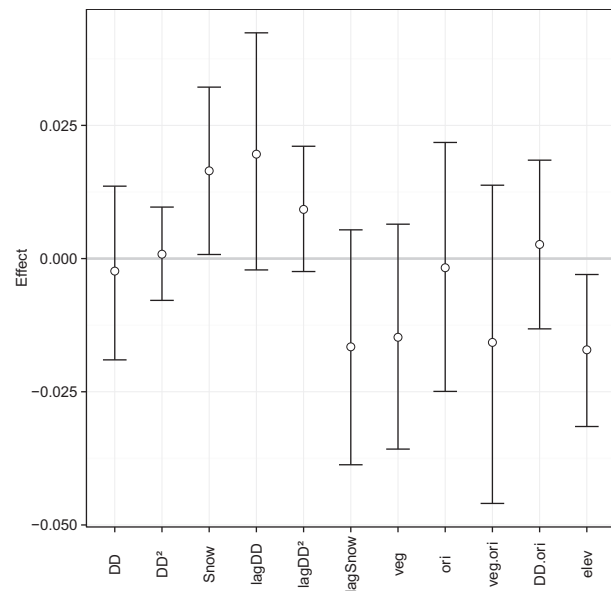


Fig. 4. Median estimates and 95% CI of covariates effect on the relative growth (log transformed) of transplanted white spruce seedlings at alpine treeline. Sum of degree days and quadratic effects (DD and DD^2), snowpack duration ($Snow$) and previous year effects ($lagDD$, $lagDD^2$, $lagSnow$), vegetation (veg), orientation index (ori), interaction of vegetation and orientation ($veg.ori$), interaction of sum of degree days and orientation ($DD.ori$) and elevation ($elev$). 95% CI excluding zero value indicates meaningful effect on seedling relative growth.

$-0.035, 0.00$ and $-0.04, 0.00$, respectively). The interaction term $DD.ori$ did not affect relative growth. Finally, elevation decreased relative growth ($\beta_{Elev} = -0.01$, 95% CI: $-0.03, -0.00$).

Discussion

Our study demonstrates that seedling survival at white spruce alpine treeline in eastern Quebec is largely controlled by winter abiotic conditions (from mid-Sept to mid-Jun), with relatively little effect of the growing season temperatures (from mid-Jun to mid-Sept), as is commonly believed. Our results revealed that warm temperatures in winter had a negative effect on seedling survival, while longer snowpack duration increased survival. Furthermore, during summer, neighbouring vegetation increased seedling survival in wind-exposed locations, indicating facilitative mechanisms. As expected, higher annual temperature during the previous year, and longer snow cover, tended to increase seedling growth. Elevation, independently of temperature, had a negative effect on seedling growth. We did not detect a negative quadratic effect of temperature, providing indirect evidence that water stress did not limit seedling establishment at our sites. Thus, our experimental findings strongly imply that changes affecting winter climatic variables will possibly have a larger

impact on seedling establishment at treeline than changes affecting summer temperature. We believe this assertion can be scaled up to other treelines, at least those with tree island structure.

Effects of abiotic factors: warm temperature in winter and early snowmelt decrease survival

We found that warmer temperatures during the winter period had a negative effect on seedling survival. It is generally accepted that temperature is positively correlated with seedling development, mainly because low temperatures decrease photosynthesis, metabolism (Körner 1998), nitrogen uptake (Weih & Karlsson 2002) and also cause damage through tissue freezing. However, at alpine tree-line elevation, warmer temperatures during winter could lead to premature release of plant winter dormancy, consequently exposing plants to photoinhibition and freeze-thaw cycles (Germino et al. 2002; Taschler & Neuner 2004). Our results are consistent with those of other studies showing that increased temperatures in winter increase seedling sensitivity to frost (Rixen et al. 2012; Mamet & Kershaw 2013). This negative effect of relatively high winter temperatures also affected summer survival through a lag effect. We assert that important winter damage to plant tissues, because of seedlings' exposure to winter harshness, impaired photosynthesis and/or cell division during summer and consequently reduced summer survival. Global predictions of climate change forecast an increase in the frequency of extreme events, such as heatwaves and frost, which could decrease seedling establishment at alpine treelines (Inouye 2000; IPCC 2013).

As expected, we found that a longer period of snow cover increased seedling survival. Snow cover provides insulation from harsh winter conditions as well as protection from freezing events and radiative stress during early spring. Similarly, other studies have demonstrated a positive effect of snow cover on seedling survival (Frey 1983; Battlori et al. 2009) and shrub performance (Wheeler et al. 2014). We also found a positive lag effect of snow on survival during the summer season, which could be attributed to lasting snow providing water resources during potential summer drought (Malanson et al. 2011). We did not find a negative quadratic effect of temperature during summer on seedling survival, suggesting that moisture stress was not a factor at these sites (Moyes et al. 2013). On the other hand, prolonged snow cover can also have a negative effect and reduce seedling survival as it reduces growing season length and promotes snow fungal infections (Holtmeier 2003; Barbeito et al. 2013). We detected a slight negative effect of the previous year's snow cover on growth, which could be attributed to a shorter growing season delaying the development of leaves. Thus seedling

recruitment and snow cover duration might display a non-linear relationship, calling for a more complete understanding of snow–seedling relationships.

Effects of biotic factors: neighbouring vegetation increases survival in wind-exposed microsites

We found that the effect of alpine neighbouring vegetation on seedling survival varied with the orientation around the tree island. In wind-exposed locations, seedlings survived significantly better with neighbours than without, while on the leeward side of tree islands, the neighbour removal treatment had no discernable effect. This positive neighbour effect, *only in the most stressful conditions*, provides a full picture of how and where the SGH is supported (Bertness & Callaway 1994; McIntire & Fajardo 2014). Even within very short distances, i.e. meters, the abiotic stress may be sufficiently strong to elicit a net positive effect of neighbours on survival. Thus, this apparent 'partial' support is really creating a more complete story about how net facilitation varies within an ecosystem. There is a long list of studies that have found support for the SGH in multiple environments that have included stressful extremes (e.g. Pugnaire et al. 2010; McIntire & Fajardo 2014), such as alpine vegetation (Callaway et al. 2002). Although identifying the exact mechanisms involved here was not part of this study, we suspect that reduction of photoinhibition (Germino & Smith 1999), protection from the desiccation effect of wind (Fajardo & McIntire 2011) and reduction of drought stress (Cavieres et al. 2006) could be the three main mechanisms of facilitation by alpine neighbouring vegetation on seedling survival. In wind-sheltered locations, alpine vegetation did not reduce seedling survival, although we detected a slight negative effect of neighbour vegetation on seedling growth, which could indicate competition for a common resource such as light, water or soil nutrients. As the effect of facilitation seems to be very well oriented – wind-exposed locations – this phenomenon may partly explain treeline encroachment and, therefore, treeline dynamics (Alftine & Malanson 2004).

Elevation decreases seedling growth, pointing toward an unmeasured covariate

While elevation did not affect seedling survival, we found that it decreased growth. Elevation is generally used as a proxy of temperature, i.e. higher elevation, lower temperature. However, since we directly measured the temperature at the seedling level and it was not a limiting factor, we therefore infer that the effect of elevation on growth should be attributed to another factor that varies by elevation. We believe that the most likely variable involved in the negative effect of elevation on seedling growth could

be related to the soil. Soil nutrient levels decrease with elevation due to lower microorganism activity and increased cryogenic disturbances, and alpine soils in particular have a tendency to retain less water (Schmid et al. 2009; Thébault et al. 2014). Because of poorer or drier soils at higher elevations, transplanted seedlings either needed to allocate more carbon to root growth than to shoot growth or had less nutrients and water available for growth in general. We suggest that soil quality and drought stress due to low water retention could explain the negative effect of elevation. Soil has been suspected to be the cause of certain types of treeline formations, notably in the Arctic (Sveinbjörnsson et al. 2002), and the impacts of soil on treeline dynamics merit further investigations.

Conclusions

With the recent increase of surface temperatures and the forecasted continuation of that trend (IPCC 2013), much focus has been put on how treeline species will respond to global warming. We demonstrated that regional-scale factors, particularly those associated with winter conditions, are crucial in driving seedling establishment at the white spruce treeline. White spruce treelines are major vegetation formations in North America, they are also comparable with many other treeline formations in the Northern Hemisphere (Körner 2012), including *Pinus cembra* and *Picea abies* in Europe, which gives generality to our results. We propose that more thorough attention to regional factors and winter conditions is necessary to achieve improved forecasting of treeline responses to climate change: since a warmer climate may reduce constraints imposed by temperature, it would leave the control of treeline dynamics to regional-scale factors. In our case, an increase in temperature is unlikely to alleviate the effects of factors controlling seedling establishment associated with winter conditions such as frost, freeze–thaw cycles or winter desiccation (Mayr et al. 2006; Martin et al. 2010). Incorporating snow cover effect on ecological processes such as seedling survival and growth would improve our current forecasts of treeline dynamics in response to a changing climate.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Details of the statistical analyses used to study microclimatic conditions, handling of missing data, description of survival and growth model and description of Bayesian priors distributions.

Appendix S2. Plots of the microclimatic variables data affecting the transplanted seedlings around the tree island experimental plot.

Appendix S3. Plot of the survival distribution of the transplanted seedlings.

Appendix S4. Plot of the effect of winter temperature and lag effect of winter temperature on survival of transplanted seedlings.

Appendix S5. Plot of the relative shoot growth of transplanted seedlings.

Appendix S6. Plot of the effect of sum of degree days of previous year on the relative growth of transplanted seedlings.