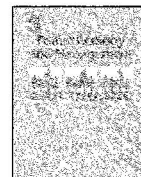




Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Establishment and growth of white spruce on a boreal forest floodplain: Interactions between microclimate and mammalian herbivory

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ARTICLE INFO

Article history:

Received 1 May 2009

Received in revised form 19 August 2009

Accepted 25 August 2009

Keywords:

Alaska

Boreal forest

Ecophysiology

Herbivory

Microclimate

White spruce

ABSTRACT

White spruce (*Picea glauca* (Moench) Voss) is a dominant species in late-successional ecosystems along the Tanana River, interior Alaska, and the most important commercial timber species in these boreal floodplain forests. Whereas white spruce commonly seed in on young terraces in early primary succession, the species does not become a conspicuous component of the vegetation until after 60–80 years. To address what abiotic and/or biotic factors may explain the paucity of spruce in earlier stages of succession, we examined germination and growth of planted white spruce seedlings across an environmental gradient that included variation in soil physico-chemical properties in the presence and absence of mammal browsing. The effect of browsing pressure over the first four years after planting was most noticeable on the older terraces. Likewise, direct effects of hare browsing on spruce seedling mortality were only manifested at the oldest sites. Spruce germination and survival was inversely proportional to soil cation concentrations, which was largely controlled by temperature-driven evapotranspiration. High light intensities and high air temperatures significantly reduced seedling growth, whereas variation in soil moisture only explained a significant amount of variation in seedling survival. Temperatures within the needle clusters on terminal shoots reached values that adversely affect photosynthesis (>32°C) on multiple occasions over the growing season. We conclude that the direct (temperature) and indirect (soil chemistry) effects of high insolation are major factors constraining spruce performance on early successional terraces, and that these effects can be significantly exacerbated by mammal browsing on associated deciduous vegetation.

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1. Introduction

The Tanana River floodplain is one of the most productive environments for white spruce in Alaska's boreal forest due to relatively long growing season, lack of permafrost, and deep alluvial soils (Van Cleve et al., 1993a). New terraces are formed by deposited alluvium of glacial origin which is low in nitrogen and carbon (Viereck et al., 1993). The youngest terraces are prime sites for plant colonization due to high light intensities producing warmer soils. However, young sites on the floodplain are also prone to extreme drought early in the growing season followed by periodic flood events from glacier melt and rainfall events. Because annual evapotranspiration is nearly twice as high as rainfall on these young terraces (Viereck et al., 1993), capillary draw of water to the soil surface results in the formation of a salt crust (Dymess and Van Cleve, 1993; Marion et al., 1993; Van Cleve et al., 1993b). The combination of low macro nutrients and high cation concen-

trations influences which plants are capable of colonizing these young terraces (Chapin and Walker, 1993).

Stands of deciduous shrubs on the Tanana River are favorable feeding habitats for moose due to the high productivity of preferred willow browse species (Kielland and Bryant, 1998; Butler and Kielland, 2008). However, moose browsing alters community structure, species composition and affect soil nutrient regimes (Bryant and Kuropat, 1980; Bryant and Chapin, 1986; Bryant et al., 1991; Pastor and Naiman, 1992; Kielland et al., 1997; Kielland and Bryant, 1998; Persson et al., 2000, 2005; Stolter et al., 2005). Moreover, moose browsing influences microclimate during the summer through decreased canopy cover, increased light and soil temperature, and decreased soil moisture and relative humidity (Kielland and Bryant, 1998). All of these factors may influence plant development and potential successional. Although plant growth is likely to respond positively to increased light and soil nitrogen, moose disturbance may also result in negative effects on plants depending on the magnitude of changes in microclimate (e.g., excess light and temperature) leading to a more stressful habitat for young spruce seedlings. Moreover, moose browsing may increase concentrations of calcium carbonate, potassium, and

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magnesium within the top layer of soil (i.e., increase salt crust development) (Kielland and Bryant, 1998). Such increases in soil salinity have negative effects on seed germination and seedling survivorship on non-halophytic species through increased osmotic stress, cation toxicity after the embryo emerges, and altered radicle growth (Croser et al., 2001; Tobe et al., 2003).

This study examined the relationships between germination, survivorship, and growth of planted white spruce seedlings and sown seeds in the presence and absence of moose browsing. Seedling performance was assessed along a chronosequence (stands aged approximately 4–40 years across 12 terraces) which included numerous changes in physical and chemical parameters as a function of the degree of vegetation development. Our central hypothesis was that moose browsing on deciduous vegetation would have negative effects on white spruce seedling performance. In particular, we predicted that moose browsing would decrease canopy cover, resulting in increased radiation, needle temperature, and soil cation concentrations, which would decrease germination, seedling survivorship, and seedling growth.

2. Materials and methods

In 2002, 12 moose-proof enclosures (6.1 m × 6.1 m) were set up on a 30-year chronosequence of willow-dominated terraces along the Tanana River Floodplain about 20 km southwest of Fairbanks, Alaska near the Bonanza Creek Long-Term Ecological Research (LTER) sites (64°N, 148°W). White spruce (*Picea glauca*) seedlings (n = 1152) were planted with a 60 cm spacing in September 2002 (49 seedlings in each of the 12 treatment × control plots). White spruce seeds were sown between the planted seedlings to assess germination. All of the seeds (and seedlings) were from a local seed source and cold stratified prior to being sown. Across this chronosequence we measured seedling germination, growth and survival. Fieldwork was carried out during summer 2006, i.e., during the fourth growing season after the seedlings had been planted.

The climate of interior Alaska is characterized by a broad temperature range from -50°C to 35°C coupled with low annual precipitation (270 mm), which can result in hot and dry summers (Viereck et al., 1993). The soil of the Tanana River is alluvium of glacial origin that is low in soil carbon and nitrogen (Viereck et al., 1993).

2.1. Weather stations

Weather stations were installed at 6 of the 12 control and treatment pairs along the chronosequence, consisting of HOBO Microstations (Onset Corp., Pocasset, MA, USA) recording hourly photosynthetically active radiation (PAR, $\mu\text{E m}^{-2} \text{ s}^{-1}$), temperature (°C), relative humidity (RH, %), and volumetric soil moisture (%) throughout the summer (May–August, 2006). PAR sensors were placed 30 cm from the ground corresponding to the average seedling height. Daily low values for relative humidity were averaged producing a seasonal low relative humidity. The low humidity was chosen to represent the extreme end of moisture stress caused by a high transpiration. PAR values greater than $500 \mu\text{E m}^{-2} \text{ s}^{-1}$ were used to capture the magnitude of excess radiation experienced by the spruce seedlings, because it is the approximate light saturation point for white spruce photosynthesis (Doran et al., 2001).

2.2. Willow growth and consumption by moose

At each enclosure and control plot, heights of 10 tagged individual willow (*Salix interior* Rowlee and *Salix alaxensis* Anders.

Cov.) plants were measured at the beginning of each growing season prior to bud break (~June 5th). Biomass consumed by moose was estimated from measurements of current annual growth (CAG, mm) and diameter point browse (DPB mm) using known biomass-diameter relationships (Kielland and Osborne, 1998).

2.3. Canopy cover

Deciduous canopy cover was estimated using the line intercept method (Canfield, 1941). Transects were placed along each row of planted seedlings to determine the canopy cover directly over each spruce seedling. All shrubs and herbs were identified to species with the exception of mosses and horsetails (*Equisetum* spp.).

2.4. Spruce seedling growth and ecophysiology

Height and basal diameter measurements were recorded on all planted white spruce seedlings. The ratio of height to basal diameter (cm mm^{-1}) was used as an index of shifts in growth from basal (radial) growth to vertical (height) growth. Cumulative germination and survivorship (since 2002) was determined as the proportion of germinants and seedlings that were still alive after the 2006 growing season, respectively.

The thermal environment of needles on the seedlings was measured to examine the prediction that spruce seedlings are experiencing a hotter environment than the ambient air, particularly on sunny, warm days. The thermal environment was measured using 2-mm diameter thermistors (HOBO TMC6-1, Onset Co., Pocasset, MA, USA) at three sites spanning the terrace age gradient at sites 5, 8, and 12. The thermistors were painted spruce green and affixed to the terminal shoot of the seedlings using floral wire. At each treatment or control plot, thermistors were affixed onto three different seedlings, and the fourth thermistor was placed 30 cm from the ground on a nearby pole as an air sensor. High temperatures experienced by the needles was defined as temperatures in excess of 32°C, as it is the maximum temperature for white spruce photosynthesis (Man and Liefers, 1997). All temperature events greater than 32°C were tallied to obtain the number of events in excess of the maximum temperature for optimal photosynthesis.

Spruce seedling response to changes in light intensities across the chronosequence and between browse treatments was assessed by measuring the needle angle of seedlings (Germino and Smith, 1999) using digital photos taken of 3 lateral branches on 5 different seedlings at each enclosure and control site during mid-July.

2.5. Needle chemistry

Spruce foliage was collected for stable isotope analysis of carbon and nitrogen, as well as cation (Ca, Mg, K) concentrations. Nitrogen isotope analysis was performed to examine possible changes in nitrogen sources along the terrace age gradient (Schulze et al., 1994). Ten needles were randomly sampled from 10 plants inside and outside of each enclosure, except at site 7 (excluded due to low seedling survival). Needles were ground in a ball mill and 10 mg and 7 mg subsamples taken for carbon and nitrogen stable isotope analysis, respectively. Isotope analysis was performed on a continuous flow isotope ratio mass spectrometer (PDZ EuropaGeo 20/20, Cheshire, UK) at the Forest Soils Laboratory University of Alaska.

Foliar calcium, magnesium, and potassium were extracted using a perchloric acid digest on 100 mg ground needle samples (Kuo, 1996). Calcium was of particular interest because calcium is immobile in the phloem and can accumulate in plant tissue as calcium oxalate (White, 2001). Due to limited foliage material,

foliar samples were pooled by each gradient site with roughly equal portions of the sample coming from the foliage of treatment and control seedlings at the site. In addition, sites that exhibited poor seedling health (sites 4 and 5, and 7 and 8) tended to be in close proximity and were pooled to provide enough material for analysis. Samples were digested using perchloric acid and analyzed for Ca and Mg, using a direct-current plasma analyzer (Iris DCP Thermo Elemental, Cheshire, UK) and K using atomic absorption spectrophotometry.

2.6. Soil sampling and analysis

Soil samples for cation analysis, total nitrogen, and total carbon analysis were obtained using a 2.5 cm soil corer. Five 5 cm deep soil cores were taken randomly at each exclosure and control plot where the seedlings were planted. Soil cores were pooled within a site by treatment and dried at 65°C for 48 h. Samples were then sifted through a 2 mm mesh screen, and a 10.0 g subsample for each treatment and control ground in a ball mill. Soil C and N concentrations were analyzed on the LECO CNS-autoanalyzer (LECO, USA). We assessed salt crust formation by performing an ammonium acetate extraction to determine the extractable calcium, potassium, and magnesium cations in the top 5 cm of the soil profile. Extraction filtrate was diluted using 5 mL extract and 5 mL ammonium acetate and then analyzed for Ca, Mg and K as described above.

2.7. Principle components analysis

We conducted a principle components analysis (PCA) to condense the extensive amounts of weather data into a pair of derived variables that were biologically meaningful. The PCA was run in SAS (SAS 9.1, SAS Institute, USA) using mean summer values for temperature, summed PAR greater than 500 $\mu\text{Em}^{-2} \text{ s}^{-1}$, soil moisture, low relative humidity (RH), total cover, and shrub cover.

2.8. Statistical analysis

Linear and polynomial regressions were performed in SAS (PROC GLM and ANCOVAs) using the principle component variables and browsing or growth parameters of spruce seedlings. Across the chronosequence alone, data were analyzed using a Spearman Rank correlation test. Percentages were arc-sin transformed prior to analysis, and analyses were tested for normality and homogeneity of variance using Shapiro-Wilks tests and residual plots. Outliers were determined using PROC UNIVARIATE stem-and-leaf plots and three influence statistics (Cook's Distribution, DFFITS, and leverage). Effects were considered significant at ($\alpha = 0.05$).

3. Results

3.1. Microhabitat

Air temperatures were slightly cooler inside the exclosures and light intensities along the chronosequence decreased in relation to increased cover by deciduous vegetation. A major increase in river discharge and soil moisture during the 2006 field season coincided with the mid to late June flush of vegetation following spring snowmelt. This event caused the control plots at sites 7 and 8 to be completely flooded for over 2 weeks with saturated soils persisting for the rest of the growing season. Volumetric soil moisture was significantly higher inside the exclosures (25–35% than control plots (10–27%) suggesting that soil moisture varies markedly even over small (50 m) areas on the Tanana River.

3.2. Microhabitat principle components

The first principle component from the PCA included light, temperature, and cover (PCA_1 (LTC)). The second principle component comprised a soil moisture and RH vector (PCA_2 (MOI)). These two principle components explained 84% of the environmental variability across the chronosequence (PCA_1 (LTC)–59%, PCA_2 (MOI)–25%). Positive PCA_1 (LTC) scores corresponded to younger terraces with decreased cover, increased solar loading, and warmer temperatures. A positive PCA_2 (MOI) score reflected higher soil moisture and increased RH. Further, strongly negative PCA_2 (MOI) loadings represented terraces prone to spring drought, decreased RH, and lower soil moisture.

3.3. Willow growth

All willows exhibited a broomed architecture with upwards of 70% of current annual twigs showing evidence of moose browsing. Browsing reduced the willow canopy height approximately 30% at site where browsing occurred (Fig. 1), and overall there was a significant moose browsing effect on willows ($P = 0.0085$). Sites that showed insignificant effects of browsing were either young sites with sparse willow vegetation (sites 2 and 3) or older sites dominated by a less favored willow species such as *S. brachycarpa* (sites 10 and 12). Moreover, the oldest willow plants at the end of the chronosequence were nearly twice as high as the plants occupying the youngest sites. Moose browsed on average 38% of the current annual growth of tagged willows (range 7–64%) with heaviest browsing occurring on more productive sites dominated by both *S. alaxensis* and *S. interior*.

3.4. Canopy cover

Vegetation on the youngest terraces was primarily composed of *S. interior* and *Equisetum* species. At older sites, the willow community shifted to a more diverse willow community comprised of *S. alaxensis*, *S. brachycarpa*, *S. novae-angliae*, and *S. lasiandra*. This shift was accompanied by increases in the cover and frequency of *Alnus tenuifolia*, *Populus balsamifera*, as well as herbaceous species such as *Achillea borealis*, *Castilleja caudate*, and *Hedysarum boreale*. Shrub cover increased significantly along the chronosequence ($P = 0.0004$) from less than 5% to over 50%, but there was no browsing effect or gradient $\times$ browse interaction due to the increased presence of non-willow species on older terraces.

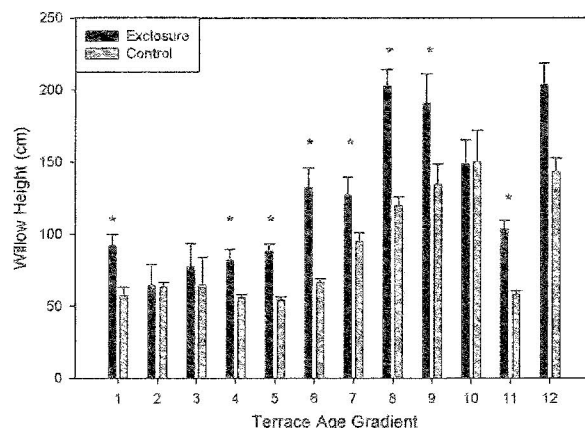


Fig. 1. Height of willow plants on exclosure and control plots along the terrace age gradient. Asterisks indicate significant ($P < 0.05$) ANOVA browsing treatment effects by site (Mean $\pm$ SE, $n = 10$).

Table 1

Germination (%) of spruce seeds and survivorship (%) of spruce seedlings planted at exclosure (Ex) and control plots (Ct) along a terrace age gradient on the Tanana River.

Exclosure	Germination (Ex)	Germination (Ct)	Survivorship (Ex)	Survivorship (Ct)
1	2	0	100	92
2	8	0	100	75
3	2	28	100	100
4	8	18	90	96
5	0	0	96	94
6	0	52	100	96
7	2	0	88	13
8	0	0	58	31
9	28	12	100	96
10	14	6	98	100
11	0	6	88	96
12	6	20	100	100

3.5. Soil chemistry

Soil C and N concentrations were very low (range 0.042–1.78% and 0.005–0.078%, respectively). Total soil carbon and nitrogen were positively correlated with each other ($Rho = 0.89$, $P = 0.0001$), but we found no significant treatment effect on soil C:N ratio.

The main soil cations associated with salt crust formation were calcium, magnesium, and potassium. Concentrations of these ions were not significantly correlated. Concentrations of calcium and magnesium decreased approximately 50% across the chronosequence ($P < 0.05$), but we found no change in potassium concentrations.

3.6. Germination and seedling survivorship

Spruce seed germination rates were low (0–30%) at all of the sites with the exception of the control plot at site 6 (Table 1). Site 6 (control) was an outlier in the data set and was removed in further analyses. Three statistical tools in SAS (Cook's Distribution, Leverage, and DFFITS) were used to justify this decision. Each of these analyses demonstrated disproportional influence and leverage of this data point on the regression analysis. Germination decreased with an increase in $PCA_1(LTC)$, i.e., it was lower on warmer and drier sites ($P = 0.0109$, Fig. 2), but seedling establishment did not exhibit a clear trend in relation to soil moisture availability. Further, germination was inversely related to soil Mg

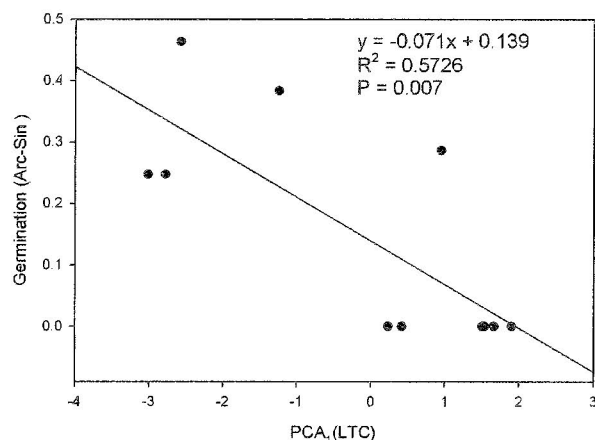


Fig. 2. Relationship between the germination of spruce seeds and the light, temperature, and cover principle component ($PCA_1(LTC)$).

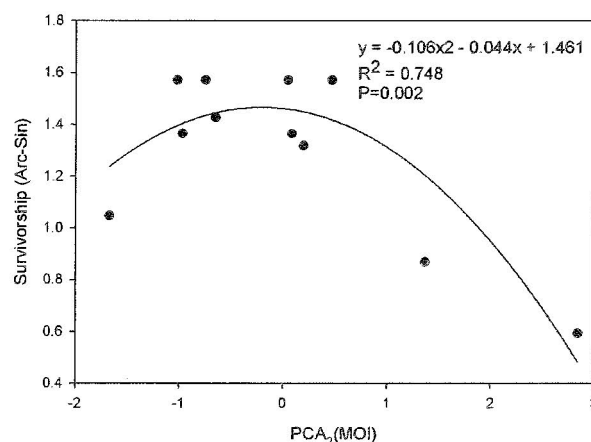


Fig. 3. Relationship between the survivorship of white spruce seedlings and the moisture principle component ($PCA_2(MOI)$).

($r^2 = 0.62$, $P = 0.008$) over a 4-fold increase in soil Mg concentrations.

Survival of spruce seedlings was nearly 100% at most of the sites (Table 1), with the exception of sites 6 and 7 which were flooded for about 10 days in 2003. Survival did not vary significantly along the terrace age gradient or between browsing treatments ($F_{1,24} = 137$, $P = 0.26$; $F_{1,24} = 0.02$, $P = 0.89$, respectively). Spruce seedling survival was significantly correlated with the $PCA_2(MOI)$ in a curvilinear manner (Fig. 3), with the highest rates of survivorship at moderately moist sites. Seedling survival also declined marginally with increased soil calcium concentrations ($P = 0.047$), but was not affected by soil magnesium or potassium concentrations.

3.7. Spruce seedling growth

Seedling height doubled with increasing terrace age ($P = 0.032$), but the combination of variable browsing by hares and individual growth responses resulted in no significant treatment effect. Spruce seedling Ht:BD ratio increased 30% with an increase in total biomass of willows ($P = 0.0053$, Fig. 4), and exhibited a comparable positive relationship with willow CAG biomass ($P = 0.014$). Since shrub CAG estimates were only performed in control plots, we

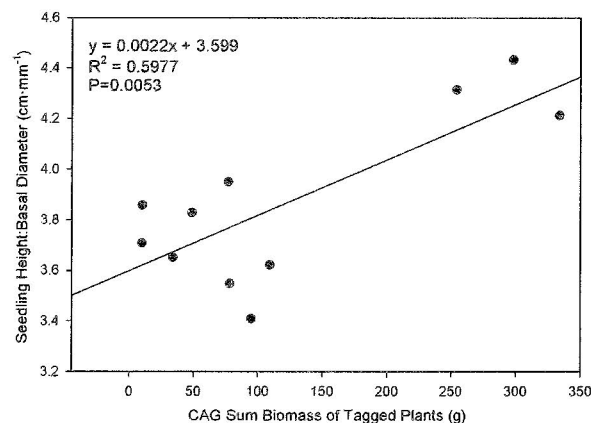


Fig. 4. Relationship between spruce seedling height to basal diameter ratio and the total biomass (sum of CAG for 10 tagged willows) produced by willows at control plots.

Table 2

Average recorded number of temperatures greater than 32 °C experienced by the air and seedlings inside and outside of the exclosures. Terrace ages are relative to the early succession floodplain stage. Measurements were recorded every 15 min.

Terrace Age	Seedling Exclosure	Air Exclosure	Seedling Control	Air Control
Young (Site 5)	60	27	197	25
Middle (Site 9)	51	19	211	24
Older (Site 12)	71	7	46	17

were unable to determine the interaction between the age gradient and moose browsing. These results suggest, however, that with increased shading, due primarily to an increase of willow CAG biomass, spruce seedlings shifted allocation from basal growth to vertical growth,

3.8. Spruce needle temperatures and needle angles

The maximum temperature experienced by seedlings was 48 °C (Site 5-browsed) compared with an air temperature of 32 °C at that same time. The number of temperature events greater than 32 °C was significantly higher in seedling needle clusters (range 46–211) than the air (range 7–27) (Table 2). Over the course of a single day, needle temperatures of seedlings outside the exclosures could reach 40 °C, i.e., upwards of 11 °C warmer than seedlings inside the exclosures (Fig. 5). These extreme high-temperature events likely had biological repercussions through down-regulation of photosynthesis.

Needle angle of spruce seedlings increased significantly from 33° to 62° across the chronosequence ($P = 0.0027$), suggesting that seedlings attempt to compensate for reduced light by increasing the leaf area exposed to incoming radiation. Alternatively, spruce needles on the youngest terraces could have been decreasing the angle of their needles to decrease solar loading,

3.9. Spruce needle chemistry

Average needle carbon and nitrogen concentrations were 45% and 0.72%, respectively. Foliar carbon and nitrogen did not vary significantly between browsing treatments or along the chronosequence. ^{15}N natural abundance of needles did not exhibit any significant treatment effects or trends along the chronosequence. However, needle $\delta^{15}\text{N}$ was positively correlated with moisture conditions ($\text{PCA}_2(\text{MOI})$) ($P = 0.0066$, Fig. 6),

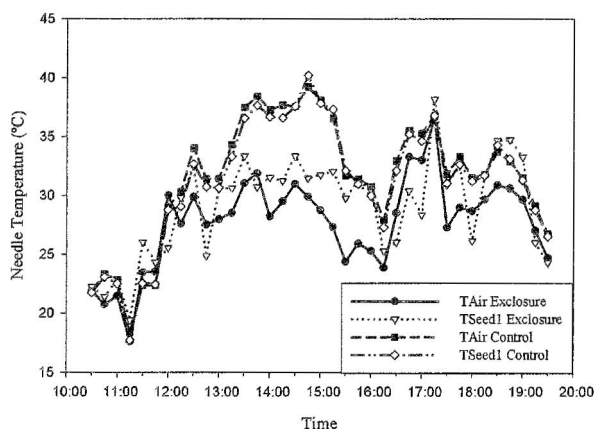


Fig. 5. Example of temperature profiles in air (TAIR) vs. seedling needle clusters (TSeedl) in exclosure and control (site 12 on June 20, 2006 10:00 AM to 7:30 PM).

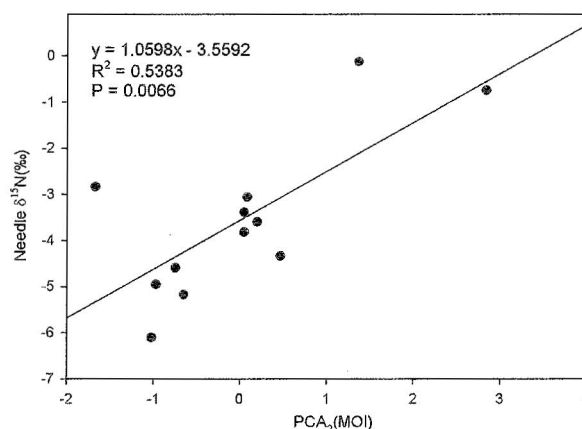


Fig. 6. Relationship between the foliar $\delta^{15}\text{N}$ values of spruce seedlings and the moisture principle component ($\text{PCA}_2(\text{MOI})$).

4. Discussion

Across the chronosequence we observed a number differences in vegetation and biogeochemistry, including a doubling in the height of the willow canopy and large increases in herb and shrub cover, as well as a significant (50%) reduction in soil Ca and Mg concentrations. These changes were associated with higher growth rates of planted spruce seedlings, suggesting that increased canopy cover of associated deciduous vegetation ameliorates conditions to enhance growth of spruce seedlings,

The high survival rates of spruce seedlings reported here (Table 1) is likely a function of the short time since planting. Moreover, our study period (2002–2006) coincided with low over-winter densities of snowshoe hares (Kielland, BNZ LTER http://www.lter.uaf.edu/ascii/files/133_1444_Hare_Data2006.txt). Seedlings were impacted by hare browsing primarily on older sites, which provided good cover from predators due to taller, denser willow stands. Other experiments with planted spruce seedlings on the Tanana River floodplain have similarly shown high initial performance (in association with dense deciduous cover), but nearly zero survival after a decade, largely due to severe browsing by snowshoe hares (Chapin, <http://www.lter.uaf.edu/data>). These observations suggest that the synchrony of masting in white spruce relative to the trajectory of the snowshoe hare cycle can have profound effects on natural generation of white spruce. Moose browsing significantly reduced heights of willows, with subsequent changes in insolation to the spruce seedlings. Spruce seedling growth was positively related to increased biomass of associated willow vegetation, implying a more favorable micro-habitat under such lower light conditions (Man and Lieffers, 1997; Groot, 1999; Doran et al., 2001),

Spruce seedlings were planted in autumn 2002 and thereafter experienced a plethora of disturbances, albeit of unusual magnitude. These disturbances included extended (10 days) flooding during the first growing season after planting, extensive wildfires during the following two years, and a severe freezing event (-7°C) after green-up during the last year of the study. These events may in part explain the poor growth performance of the seedlings. High salt concentrations in soils and the associated increase in osmotic potential makes water uptake more difficult (Tinus, 1980; Landis, 1988; Dyrness and Van Cleve, 1993). Seedlings stressed by high calcium soils show signs of stunted, chlorotic growth with the newest foliage turning yellow (Landis, 1988), which closely matched the appearance of approximately 45% of our planted seedlings.

The high temperatures we measured in needle clusters of the spruce seedlings likely resulted in down-regulation of photosynthesis, suggesting that moose browsing on neighboring vegetation may lead to increased needle temperatures that have negative effects on young spruce seedlings. Seedlings appear to respond to high temperatures by reducing needle angle as this varied over 50% across the chronosequence in consort with the abundance of (shading) deciduous shrubs.

Because nitrate concentrations are much higher than ammonium concentrations in Tanana River water (Clilverd et al., 2008), we predicted that spruce seedlings would be isotopically depleted in ^{15}N natural abundance on young terraces as a result of increased nitrate availability. However, current-year spruce needles had an enriched $\delta^{15}\text{N}$ signature on heavily flooded terraces, suggesting that the relationship between nitrate availability and spruce physiology is more complex. The absence of $\delta^{15}\text{N}$ depletion in the spruce foliage, despite increased nitrate supply, may reflect low nitrate uptake due to the strong preference for ammonium by white spruce (Kronzucker et al., 1997). Moreover, spruce seedlings growing on frequently flooded sites are likely having decreased rates of mycorrhizal infection due to low soil oxygen tension. Species that are heavily dependent on mycorrhizae for their N supply have been shown to have significantly depleted $\delta^{15}\text{N}$ values (Hobbie and Hobbie, 2006), as a result of fungal isotopic discrimination. Hence, the pattern of ^{15}N enrichment that we observed may be a combination of spruce preferential uptake of ammonium over nitrate and variation in mycorrhizal infection of spruce roots in response to soil oxygen tension.

The strong, inverse relationship between spruce germination and soil Mg concentrations suggest potential Mg toxicity for seeds (Tobe et al., 2003), and appear to be a factor controlling white spruce germination on the Tanana River. This biological interaction, in addition to physical factors such as seed abundance and potential for burial, due to flooding, are key factors in natural seedling establishment (Walker, 1985; Walker and Chapin, 1986; Walker et al., 1986). Thus, the paucity of spruce seedlings on these early successional, willow-dominated terraces may be the consequence of several interacting factors: low germination and establishment due to high salt concentrations in the soil, low availability of the preferred form of nitrogen for spruce growth, and finally, all of these factors being exacerbated by increased thermal stress and damage to photosynthetic enzymes resulting in reduced plant growth.

Acknowledgements

We would like to thank Dr. Christa Mulder and Dr. John Fox for their technical and statistical review of this manuscript. Special thanks go to Karl Olson and Rachel Lord for their assistance in the field and to Lola Oliver of the UAF Forest Soils Lab for sample analysis. Bonanza Creek Long-Term Ecological Research program (NSF grant DEB-0423442) and USDA Forest Service (Pacific Northwest Research Station (PNW01-JV11261952-231) funded the research.

References

- Bryant, J.P., Kuropat, P.J., 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annual Review of Ecology and Systematics* 11, 261–285.
- Bryant, J.P., Chapin III, F.S., 1986. Browsing-woody plant interactions during boreal forest plant succession. In: Van Cleve, K., Chapin, III, F.S., Flanagan, P.W., Viereck, L.A., Dyrness, C.T. (Eds.), *Forest Ecosystems in the Alaskan Taiga*. Springer-Verlag, New York, New York, pp. 213–225.
- Bryant, J.P., Provenza, F.D., Pastor, J., Reichardt, P.B., Clausen, T.P., du Toit, J.T., 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics* 22, 431–446.
- Butler, L.G., Kielland, K., 2008. Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems. *Journal of Ecology* 96, 136–144.
- Canfield, R.H., 1941. Application of the line intercept method in sampling range vegetation. *Journal of Forestry* 39, 388–394.
- Chapin III, F.S., Walker, L.R., 1993. Direct and indirect effects of calcium sulphate and nitrogen on growth and succession of trees on the Tanana River floodplain, interior Alaska. *Canadian Journal of Forest Research* 23, 995–1000.
- Clilverd, H., Jones, J., Kielland, K., 2008. Nitrogen retention in the hyporheic zone of a glacial river in interior Alaska. *Biogeochemistry* 88, 31–46.
- Croser, C., Renault, S., Franklin, J., Zwiazek, J., 2001. The effect of salinity on the emergence and seedling growth of *Picea mariana*, *Picea glauca*, and *Pinus banksiana*. *Environmental Pollution* 115, 9–16.
- Doran, K., Ruess, R.W., Plumley, F.G., Wurtz, T.L., 2001. Photosynthetic responses of white spruce saplings (*Picea glauca*) to controlled density gradients of spruce and green alder (*Alnus crispa*). *Ecoscience* 8, 76–88.
- Dyrness, C.R., Van Cleve, K., 1993. Control of surface soil chemistry in early-successional floodplain soils along the Tanana River, interior Alaska. *Canadian Journal of Forest Research* 23, 979–994.
- Germino, M.J., Smith, W.K., 1999. Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. *Plant, Cell, and Environment* 22, 407–415.
- Groot, A., 1999. Effects of shelter and competition on the early growth of planted white spruce (*Picea glauca*). *Canadian Journal of Forest Research* 29, 1002–1014.
- Hobbie, J.E., Hobbie, E.A., 2006. ^{15}N in symbiotic fungi and plants estimates nitrogen and carbon flux in arctic tundra. *Ecology* 87, 816–822.
- Kielland, K., Bryant, J.P., Ruess, R.W., 1997. Moose herbivory and carbon turnover of early successional stands in interior Alaska. *Oikos* 80, 25–30.
- Kielland, K., Bryant, J.P., 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos* 82, 377–383.
- Kielland, K., Osborne, T., 1998. Moose browsing on field-leaved willow: optimal foraging in relation to plant morphology and chemistry. *Alees* 34, 149–155.
- Kronzucker, H.J., Siddiqui, M.Y., Glass, A.D.M., 1997. Conifer root discrimination against soil nitrate and the ecology of forest succession. *Nature* 385, 59–61.
- Kuo, S., 1996. Phosphorous. In: Sparks, D.J. (Ed.), *Methods of Soil Analysis Part III Chemical Methods*. SSSA Book Series 5. Soil Science Society of America Inc., Madison, WI, pp. 870–872.
- Landis, T., 1988. Management of forest nursery soils dominated by calcium salts. *New Forests* 2, 173–193.
- Man, R., Lieffers, V.J., 1997. Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open. *Tree Physiology* 17, 437–444.
- Marion, G.M., Van Cleve, K., Dyrness, C.T., Black, C.H., 1993. The soil chemical environment along a forest primary successional sequence on the Tanana River floodplain, interior Alaska. *Canadian Journal of Forest Research* 23, 914–922.
- Pastor, J., Naiman, R.J., 1992. Selective foraging and ecosystem processes in boreal forests. *The American Naturalist* 139, 690–705.
- Persson, I.-L., Danell, K., Bergstrom, R., 2000. Disturbance by large herbivores in boreal forests with special reference to moose, *Annales Zoologici Fennici* 37, 251–263.
- Persson, I.-L., Danell, K., Bergstrom, R., 2005. Different moose densities and accompanied changes in tree morphology and browse production. *Ecological Applications* 15, 1296–1305.
- Schulze, E.-D., Chapin III, F.S., Gebauer, G., 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. *Oecologia* 100, 406–412.
- Stolter, C., Ganzhorn, J.U., Ball, J.P., Julkunen-Titto, R., Lieberei, R., 2005. Winter browsing of moose (*Alces alces*) on two different willow species: food selection in relation to plant chemistry and plant response. *Canadian Journal of Zoology* 83, 807–819.
- Tinus, R.W., 1980. Nature and management of soil pH and salinity. In: *Proceedings North American Forest Tree Nursery Soils Workshop*, 1980 July 28–August 1; Syracuse, NY; State University of New York, College of Environmental Science and Forestry, Syracuse, NY, pp. 72–86.
- Tobe, K., Zhang, L., Omasa, K., 2003. Alleviatory effects of calcium on the toxicity of sodium, potassium, and magnesium chlorides to seed germination on three non-halophytes. *Seed Science* 13, 47–54.
- Van Cleve, K., Viereck, L.A., Marion, G.M., 1993a. Introduction and overview of a study dealing with the role of salt-affected soils in primary succession on the Tanana River floodplain, interior Alaska. *Canadian Journal of Forest Research* 23, 879–888.
- Van Cleve, K., Dyrness, C.T., Marion, G.M., Erickson, R., 1993b. Control of soil development on the Tanana River floodplain, interior Alaska. *Canadian Journal of Forest Research* 23, 941–955.
- Viereck, L.A., Van Cleve, K., Adams, P.C., Schlentner, R.E., 1993. Climate of the Tanana River floodplain near Fairbanks, Alaska. *Canadian Journal of Forest Research* 23, 899–913.
- Walker, L.R., 1985. The processes controlling primary succession on an Alaskan flood plain. PhD. Thesis, University of Alaska, Fairbanks, Alaska, USA.
- Walker, L.R., Zasada, J.C., Chapin III, F.S., 1986. The role of life history processes in primary succession on an Alaskan floodplain. *Ecology* 67, 1243–1253.
- Walker, L.R., Chapin III, F.S., 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology* 67, 1508–1523.
- White, P.J., 2001. The pathways of calcium movement to the xylem. *Journal of Experimental Botany* 52, 891–899.