

Introduction:

White spruce (*Picea glauca* (Moench) Voss) is a widely distributed late-successional conifer in the boreal forests of Alaska ranging from the Bering Sea to Cook Inlet and has been documented as far north as latitude 69°N (Nienstaedt and Zasada, 1990). White spruce tolerates a wide range of climate and soil environments, which accounts for its broad distribution (Nienstaedt and Zasada, 1990). Despite this high tolerance, white spruce has several specific requirements for germination and establishment, such as seed stratification, adequate initial water for root initiation, and a photoperiod greater than 14 hours (Nienstaedt and Zasada, 1990). The environment of the Tanana River floodplain meets requirements for both photoperiod and stratification. However, the distribution and establishment of white spruce are influenced by its slow growth rate and distance to seed source (Walker 1985, Walker and Chapin, 1986, Walker et al., 1986). Observations of planted spruce seedlings established as part of the Bonanza Creek LTER project demonstrated that spruce grew very slowly on early terraces (mean height \approx 40cm after 15 years, F.S. Chapin *unpublished*), while seedlings planted at the same time on an agricultural field at the University of Alaska at Fairbanks grew to be over 4m tall (T. Wurtz, *personal communication*). Although these differences are exacerbated by greatly different soil nutrient conditions between the floodplain soils and the farm fields, nutrient differences alone can not explain the low growth rate of spruce on the floodplain. Deciduous shrub species, which arguably have a greater nutrient demand than spruce, exhibit substantially higher growth rates under the same edaphic conditions. In light of previous studies (e.g., Kielland and Bryant, 1998) showing how moose browsing on

willows (*Salix* spp.) can alter the canopy cover and a suite of microclimate factors (temperature, photosynthetically active radiation (PAR), relative humidity (RH), soil moisture, soil chemistry), mammalian herbivory could have strong indirect effects on regeneration and growth of white spruce early in succession. In particular, if germination and growth of spruce seedlings are limited by physico-chemical conditions pertaining to high temperatures, low soil moisture, and high salt concentrations in the soil (Ronco, 1970, Nienstadt and Zasada, 1990, Croser et al, 2001), then herbivory on deciduous shrubs could be an important ecological factor controlling successional processes on young river terraces.

White spruce seedlings exhibit altered needle morphology, chlorosis (yellowing of the needles), and decreased photosynthesis under high irradiance conditions (Ronco, 1970, Niinemets and Kull, 1995). Optimal light conditions for seedlings are between 40-80% of total sky exposure (Germino and Smith, 1999, Groot, 1999). Partial shading creates a more favorable environment for seedlings, as air and needle temperatures are moderated. However, seedlings can respond to changing light conditions by modifying their needle angle (Germino and Smith, 1999, Groot, 1999). Further, photosynthesis of white spruce plateaus after light intensities reach values greater than $500\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Photosynthesis begins to decline at temperatures greater than 30°C , due to the denaturing of RUBISCO (Man and Lieffers, 1997, Doran et al., 2001). Thus, it is not surprising that higher rates of photosynthesis have been observed in spruce seedlings growing under a canopy than in seedlings growing in the open (Man and Lieffers, 1997, Doran et al., 2001).

The Tanana River floodplain is one of the most productive environments for white spruce in Alaska's boreal forest due to relatively high nutrient availability, lack of permafrost, and deep alluvial soils (Van Cleve et al., 1993a). Early successional communities cause significant shifts in microclimate as a result of vegetation development and increasing age of the terrace. Despite its high latitude, the Tanana River floodplain can be a hot and dry environment during the summer. The youngest terraces are prime sites for plant colonization due to the high light intensities in excess of $1500\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ producing warmer soils. However, young sites on the floodplain are also prone to extreme drought at the beginning of the growing season followed by periodic flood events from snowmelt, glacier melt, and rainfall events. Because annual evapotranspiration is nearly twice as high as rainfall on these young terraces (Viereck et al., 1993a), capillary draw of water to the soil surface and the strong evaporative gradient allow for the formation of a salt crust. This soil crust is composed primarily of calcium carbonate and magnesium sulfate (Dyrness and Van Cleve, 1993, Marion et al., 1993, Van Cleve et al., 1993b). New terraces are mineral soils composed of deposited alluvium of glacial origin that is low in nitrogen and carbon (Viereck et al., 1993a). The combination of low macronutrients and high cation concentrations influences which plants are capable of colonizing these young terraces.

The primary succession sequence from open sand bars to black spruce bog has been extensively studied on the Tanana River (Walker, 1985, Walker et al., 1986, Walker and Chapin, 1986, Van Cleve et al., 1993a, Van Cleve et al., 1993b, Viereck et al., 1993b). The first species to colonize bare terraces are willows (*Salix* spp.) and horsetails

(*Equisetum* spp.). With an increase in terrace age, a more diverse community emerges that includes numerous willow species, alder (*Alnus tenuifolia* Nutt.), and seedlings of balsam poplar (*Populus balsamifera* L.) and white spruce (*Picea glauca*) (Wolff and Zasada, 1979, Walker et al., 1986, Viereck et al., 1993b). After the alder stage, balsam poplar forests are mixed with young white spruce (Viereck et al., 1993b). White spruce becomes a dominant tree species in the mid to later succession stages marking a shift from a deciduous to evergreen community, and this stage may be followed by forests of black spruce (*Picea mariana* (P. Mill.) B.S.P.) (Wolff and Zasada, 1979, Van Cleve and Alexander, 1981, Viereck et al., 1993b). This primary successional sequence is driven mainly by life history traits of each species and cumulative effects of increased vegetation leading to a shady, cooler, and moister habitat resulting in a conifer-dominated forest.

A vegetation successional sequence occurs on the Tanana floodplain as a result of seed dispersal, the physiological ecology of these species, and stochastic river events that influence germination and establishment (Walker, 1985, Walker et al., 1986, Walker and Chapin, 1986). Seedlings of all tree species are present on early terraces of the Tanana River floodplain, however this does not result in an even-aged mixed forest resembling traditional facilitative succession (Slatyer, 1977). Instead, a form of tolerance-based succession occurs on the floodplain (Slatyer, 1977). Willows are the first major species to colonize the youngest terraces; however, they do not appear to improve the habitat for late successional species. Moose browsing of willows appears to facilitate succession allowing for alder and balsam poplar to dominate sooner on young to mid-aged terraces

(Kielland and Bryant, 1998). White spruce is present on all terraces; however, it does not become a dominant species until later in succession because of its slow growth rate and intolerance to direct sunlight and high temperatures.

In interior Alaska, the Tanana River is the source of major abiotic disturbances to the local habitat through flooding, erosion, and sediment deposition. Depending on the flow of the river, these events lead to the erosion of established forests on one side of the river and the formation of bare alluvial terraces on the opposite side. Willows rapidly colonize the bare terraces due to their effective wind-dispersed seeds, fast relative growth rate, and their ability to reproduce vegetatively (Walker, 1985, Walker and Chapin, 1986). Further, succession on the Tanana River floodplain is also partially a result of the nitrogen fixing symbiosis of thin-leaf alder and *Frankia* that favors rapid deciduous tree growth during early and mid-succession. The persistence and slow growth rate of spruce seedlings in the under-story allows for their eventual domination during late succession (Walker, 1985, Walker et al., 1986, Walker and Chapin, 1986).

Stands of deciduous shrubs on the Tanana River represent favorable feeding habitats for moose due to the high productivity of preferred willow browse species (Kielland and Bryant, 1998, Butler et al., *in press*). However, moose can disturb community structure directly through selective browsing of vegetation, decreasing the canopy cover, defecating, and urinating (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, Persson et al., 2005, Stolter et al., 2005). Moose browsing may also induce shifts in plant chemical composition (Bryant and Kuropat, 1980, Bryant and

Chapin, 1986, Bryant et al., 1991). Moreover, as a result of decreasing canopy cover, moose browsing can also have indirect effects on microclimate during the summer through increasing light, increasing soil temperature, decreasing soil moisture, and decreasing relative humidity (Kielland and Bryant, 1998). All of these factors may influence plant development and potential successional interactions by causing patches of nutrients, changing moisture regimes, and increasing temperature and light. Although plant growth is likely to respond positively to increased nutrient cycling, light, and increased soil nitrogen, moose disturbance may also produce 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 seedlings. One such effect involves the salt crust on young floodplain terraces, which potentially confers osmotic stress for young spruce seedlings (Croser et al., 2001). Kielland and Bryant (1998) showed that moose browsing increased the proportion of calcium carbonate in total soil carbon pools on the Tanana River. They also demonstrated that in browsed plots there were higher soil concentrations of potassium, magnesium, and carbonate (in the form of calcium carbonate), i.e., an increase in salt crust development. Generally, soil salinity has a negative effect 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). Increases in soil salinity can decrease and delay germination in white spruce (Croser et al., 2001). It is therefore likely that increased salt crust formation on browsed terraces could result in poorer rates of spruce germination. Croser et al. (2001) hypothesized that increased soil salt

concentrations coupled with seedling dependency on current photosynthesis for energy, as opposed to stored reserves, would lead to high rates of transpiration. Increased transpiration causes an increase in general ion uptake with water, which could potentially lead to salt accumulation and mortality (Croser et al., 2001).

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. My fieldwork was carried out during summer (May-Sept) 2006, i.e., only 3 years after the start of the study. In conjunction with the browsing treatment, seedling performance was assessed along a natural gradient of terrace age that included numerous changes in physical and chemical parameters as a function of the degree of vegetation development. My central hypothesis was that moose browsing on deciduous vegetation would have negative effects on white spruce seedling performance. In particular, I 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. Coupled with browsing effects, I hypothesized that spruce survivorship would be positively correlated with an increase in terrace age due to a decrease in flooding. By examining local climatic and soil factors, browsing pressure on willows, vegetative community, and seedling growth, chemistry, survival, and germination, I sought to evaluate the effect of large ungulate herbivory on spruce seedling establishment and growth on early successional floodplain terraces.

Materials and Methods:

In 2003, 12 moose-proof exclosures (6.1m×6.1m) were set up on willow-dominated terraces along the Tanana River Floodplain about 20km southwest of Fairbanks, Alaska near the Bonanza Creek Long-Term Ecological Research (LTER) sites (64°N, 148°W). The exclosures and adjacent control plots were located on a natural age gradient ranging from young (2-5yr) floodplain terraces to older terraces (25-30yr) within the willow successional stage. Using vegetation cover, plant ages, and knowledge about the site's history, a ranked terrace age gradient was created to represent an increase in age from the youngest floodplain sites (terrace age 1) to the oldest sites within our study (terrace age 12) (Table 1). In the event of terraces of similar ages, the site with the higher canopy cover estimate was considered to be older. The ranked terrace age gradient was used to address seedling responses along the natural gradient as well as interactions between moose browsing and the natural development of vegetation on the early willow-dominated terraces. The climate of interior Alaska is characterized by a broad temperature range from -50°C to 35°C coupled with low annual precipitation (270mm) resulting in an arid environment (Viereck et al., 1993a). The soil of the Tanana River is alluvium of glacial origin that is low in soil carbon and nitrogen (Viereck et al., 1993a).

A total of 1152 white spruce (*Picea glauca*) seedlings was planted in 2003 with 48 seedlings planted at each of the 12 treatment and control plots (K. Kielland and T. Wurtz, *personal comm.*). White spruce seeds were sown between the planted seedlings to assess germination. All of the seeds were from a local seed source and cold stratified prior to being sown (T. Wurtz, *personal comm.*). The seed viability for the sown spruce seeds

was 75% based on germination trials (T. Wurtz, *personal comm.*), which negates problems related to seed quality.

Weather Stations:

Weather stations were installed at 7 of the 12 control and treatment pairs along the terrace age gradient. Weather stations consisted of HOBO Microstations (Onset Corp., Pocasset, MA USA) recording hourly photosynthetically active radiation (PAR, $\mu\text{E}\cdot\text{m}^{-2}\text{s}^{-1}$), temperature ($^{\circ}\text{C}$), relative humidity (RH, %), and volumetric soil moisture (%) throughout the summer (May 27, 2006-August 30, 2006). PAR sensors were placed about 30 cm from the ground and oriented south facing to maximize the PAR levels due to low sun angles. Temperature and relative humidity sensors were located inside radiation shields to prevent bias due to direct heating to the sensor.

Hourly temperature and soil moisture data were averaged by week over the summer and by terrace age gradient. The 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. For the PAR data, I used all values greater than $500\mu\text{E}\cdot\text{m}^{-2}\text{s}^{-1}$ to capture the magnitude of excessive radiation experienced by the spruce seedlings. This threshold was used because it is the approximate light saturation point for white spruce photosynthesis (Doran et al., 2001), and I was interested in the light intensities experienced by seedlings in excess of their photosynthetic requirements. I summed these daily PAR values to produce a cumulative daily index ($\sum\text{PAR}>500\mu\text{E}\cdot\text{m}^{-2}\text{s}^{-1}/\text{day}$) of excess solar radiation.

Willow Growth and Consumption by Moose:

In each enclosure and control plot, willow heights were measured to determine the direct effect of moose browsing on the associated vegetation around the spruce seedlings. In 2003, 10 willow plants, predominately *Salix interior* and *Salix alaxensis*, were tagged inside and outside of each enclosure to monitor yearly height growth. Yearly height measurements were taken on each willow at the beginning of each growing season prior to bud break (~June 5th). To provide an index of the amount of biomass consumed by moose, measurements of current annual growth (CAG, mm) and diameter point browse (DPB, mm) were obtained for all of the tagged willows using calipers in May 2006. A willow biomass regression was determined for *S. interior* and *S. alaxensis* using mass:diameter relationships of current annual twigs. The willow regression for *S. interior* was: $\text{Biomass (g)} = 0.3062(\text{CAG})^2 - 0.3969(\text{CAG})$. The regression for *S. alaxensis* was: $\text{Biomass (g)} = 0.55 - 0.34(\text{CAG}) + 0.03(\text{CAG})^3$ and obtained from previous research (Kielland, *unpublished*). Biomass estimates were calculated only for twigs greater than 1.5mm diameter on the tagged *S. interior* and *S. alaxensis* plants, due to moose rarely browsing twigs smaller than this size, and summed over the 10 tagged plants at each site.

Canopy Cover:

Canopy cover over the spruce seedlings was estimated using the line intercept method (Canfield, 1941) to determine if there were any vegetation shifts or an increase in species richness along the terrace age gradient. 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). Cover data from each transect were summed per plot by species to produce a total cover estimate (%) for each enclosure and control plot (*Appendix 1*). The frequency for each species was also calculated by site and separately for herb and shrub species (*Appendix 1*).

Spruce Seedling Growth and Ecophysiology:

Yearly height measurements were performed on all planted white spruce seedlings. In 2006, basal diameter measurements of all seedlings supplemented height growth measurements. Mean height and basal diameter were calculated for each enclosure and control. The ratio of height to basal diameter ($\text{cm}\cdot\text{mm}^{-1}$) was calculated as an index of shifts in growth from basal (radial) growth to vertical (height) growth.

Differences in survivorship and germination rates were assessed along the terrace age gradient and between enclosure and control plots. Survivorship was determined as the percentage of seedlings that were still alive after the 2006 growing-season. A germination assessment, of the seeds sown in 2003, was conducted in August 2006.

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, hot 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. HOBO8 loggers were deployed at the end of June with four thermistors per logger. The thermistors were painted spruce green and affixed on the south-facing side of 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 30cm from the ground on a nearby pole as an air sensor. I chose healthy seedlings distributed to allow reach of the 1.8m thermistor strings from a centrally located data logger in each plot. When assessing high temperatures experienced by the needles, I used the temperature cut-off of 32°C because it was the maximum temperature for white spruce photosynthesis (Man and Lieffers, 1997). All values in excess of 32°C were counted to obtain a cumulative number of events in excess of the maximum temperature for optimal photosynthesis.

It has been demonstrated that spruce can modify their needle angle relative to the stem in response to varying light regimes (Germino and Smith, 1999). To examine seedling response to changes in light intensities across the terrace age gradient and between browse treatments, the needle angle of spruce seedlings was obtained using digital photos taken of 3 lateral branches on 5 different seedlings at each enclosure and control site during mid-July. I defined needle angle as the angle at which the needle was oriented to the stem. Perpendicular orientation was determined using the needles that were in focus in the plane of the photograph. Needle angle was then assessed by measuring five needles oriented perpendicular to the stem in the center 4-5cm of the branch with a modified clear protractor.

Needle Chemistry:

Spruce foliage was collected for stable isotope analysis of carbon and nitrogen, as well as cation and phosphate concentrations. Carbon stable isotope analysis was performed to assess any enrichment due to water stress (Sun et al., 1996) and nitrogen isotope analysis

to examine possible changes in nitrogen sources along the terrace age gradient (Schulze et al., 1994). I hypothesized that younger terraces would show less depleted carbon signatures because of water stress from two sources: 1) decreased soil water potential due to increased soil salts, and 2) stomatal closure to prevent transpiration caused by high temperatures, thus decreasing the selectivity of RUBISCO for carbon. Ten needles were randomly sampled from 10 plants inside and outside of each enclosure, except at site 7. Site 7 was excluded due to low seedling survivorship. Needle length was measured prior to drying at 60°C for 48h. Needles were ground in a ball-mill and 10mg and 7mg 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 University of Alaska at Fairbanks Forest Soils Laboratory.

Ion extractions of spruce needles were performed to determine any potential changes in uptake along the terrace age gradient and relationships with soil ion concentrations. Calcium was of particular interest because calcium is immobile in the phloem and can accumulate in plant tissue as calcium oxalate (White, 2001). On the youngest terraces, I hypothesized that there would be increased calcium immobilization as a result of high calcium carbonate concentrations in the soil. Foliar calcium, magnesium, phosphate, and potassium were extracted using a perchloric acid digest on 100mg ground needle samples (Kuo, 1996). 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

(gradient sites 4&5, and 7&8) that exhibited poor seedling health tended to be in close proximity and were pooled to provide enough material for analysis. Products from the perchloric acid digest were then analyzed for calcium, potassium, magnesium, and phosphate using a direct-current plasma analyzer (Iris DCP Thermo Elemental, Cheshire, UK).

Soil Sampling and Analysis:

Soil samples were collected for cation analysis, phosphate, total nitrogen, and total carbon inside and outside of all of the exclosures in July 2006. Soil nitrogen and carbon analysis was performed to provide a general description of the amounts of nitrogen and carbon in the soil on early terraces. Calcium, potassium, magnesium, and phosphate were extracted to examine the degree of salt crust formation along the age gradient, as well as in the presence or absence of browsing. Using a 2.5cm soil corer, five 5cm deep soil cores were taken randomly at each exclosure and control plot where the seedlings were planted. Soil cores were pooled by treatment along the age gradient, dried at 60°C for 2 days, and reweighed to determine percent soil moisture at all sites. Samples were then sifted through a 2mm mesh screen, and a 10.0g subsample for each treatment and control ground in a ball mill.

Soil total carbon and nitrogen values were determined using ground soil samples that were weighed (0.01g) and prepared for analysis on the LECO CNS-autoanalyzer (LECO, USA). I assessed salt crust formation by performing an ammonium acetate extraction to determine the extractable calcium, potassium, and magnesium cations in the top 5cm of our floodplain soil samples. Extraction filtrate was diluted using 5mL extract and 5mL

ammonium acetate and then analyzed on a DCP. A water extraction was not performed simultaneously because I was interested in the total concentration of these cations and how they might affect osmotic water potential as opposed to nutrient availability for the spruce seedlings. Soil phosphorous concentrations were obtained using a perchloric acid digest followed by analysis on a DCP (Kuo, 1996).

Principle Components Analysis

A principle components analysis (PCA) was conducted 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 $500\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, soil moisture, low relative humidity (RH), total cover, and shrub cover.

Statistical Analysis

Following PCA, most analyses involved linear or polynomial regressions, performed in SAS, using the principle component variables and browsing or growth parameters of spruce seedlings. All spruce seedling and soil chemistry averages were run in PROC GLM using analyses of covariance (ANCOVAs) that included the browsing treatments, the ranking of terrace ages, and the interaction between these covariants. Across the terrace age gradient alone, data were analyzed using a Spearman Rank correlation test. A student's t-test was used to compare seasonal means of soil moisture. 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. Effects were considered significant at $\alpha = 0.05$.

Results:

Microhabitat

Air temperatures, at the level of the spruce seedlings, were variable along the terrace age gradient and appeared to be slightly cooler inside the exclosures (Table 2). Light intensities along the terrace gradient decreased as terrace age increased in relation to cover development (Table 2). Seasonal mean PAR ranged from $387\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the youngest site to $147\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ inside the oldest site (Table 2). The average low relative humidity was highest on the site that flooded (site 8, Table 2, Table 3). Flooding was determined using both field observations and soil moisture probe values greater than 38%. This value is just below the calibrated value of 40% for the sensor in pure water. The first major increase in river height and soil moisture during the 2006 field season coincided with the mid to late June flush of vegetation following spring snowmelt on these young terraces (Fig. 1). This event caused the control plots at gradient sites 7 and 8 to be completely flooded with river water for over 2 weeks. Saturated soils persisted through the rest of the season at these sites and were maintained by another brief flooding event in late August (Fig.1). Soil moisture was significantly different at most sites between exclosure and control plots suggesting that soil moisture varied markedly even over small (<200 ft) areas on the Tanana River (Table 2).

Microhabitat Principle Components

The first principle component from the PCA was a light (PAR), temperature, and cover vector ($PCA_1(LTC)$), and the second principle component was a soil moisture and RH vector ($PCA_2(MOI)$). These two principle components explained 84% of the environmental variability on my willow-dominated terraces (Table 4). As the name indicates, light, temperature, and cover were the strongest eigenvectors in $PCA_1(LTC)$ (Table 5). Low values of the light, temperature, and cover principle component ($PCA_1(LTC)$) represented older terraces with increased cover, decreased light, and cooler temperatures. Positive $PCA_1(LTC)$ scores corresponded to younger terraces and decreased cover, increased solar loading, and warmer temperatures. $PCA_2(MOI)$ was driven by relative humidity and soil moisture (Table 5). A positive moisture principle component ($PCA_2(MOI)$) score corresponded with higher summer soil moisture and increased seasonal low RH. Further, a strongly negative $PCA_2(MOI)$ loading represented terraces prone to spring drought, decreased seasonal low RH, and lower seasonal soil moisture.

Willow Growth

All willows that were sampled exhibited a broomed architecture with upwards of 70% of current annual growth being browsed by moose. Browsing significantly reduced the willow canopy height at eight of the twelve sites, and overall there was a significant moose browsing effect on willows ($F_{1,24}=8.44$, $P=0.0085$, Fig. 2). Sites that were not statistically different were either young sites with sparse willow vegetation (sites 2 and 3) or older sites dominated by a less favored willow, *S. brachycarpa* (sites 10 and 12).

Willow height increased significantly along the terrace age gradient ($F_{1,24}=22.43$, $P<0.0001$); however, there was no significant interaction between moose browsing and terrace age ($F_{1,24}=0.61$, $P=0.44$). Along the terrace age gradient, the similar browse heights (~60cm) outside of the exclosures represented *S. interior* shrubs browsed to the approximate snow level each year by moose. Across the terrace age gradient, 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* (Fig. 3).

Canopy Cover

The vegetation on the youngest terraces was primarily composed of *S. interior* and *Equisetum* species. The youngest terrace in the gradient was more diverse than other young sites because it was bordered on either side by dense alder thickets (Table 6). At older sites, the willow community shifted from *S. interior*-dominated to a more diverse willow community comprised of *S. alaxensis*, *S. brachycarpa*, *S. novae-angilae*, and *S. lasiandra* (Table 6). This community shift was accompanied by increases in the cover and frequency of *Alnus tenuifolia*, *Populus balsamifera*, as well as herbaceous species (Table 6, Fig. 4, Fig. 5). Shrub cover significantly increased along the terrace age gradient (Shrub: $F_{1,24}=17.76$, $P=0.0004$), but interestingly there was no browsing effect or gradient-browse interaction due to the increased presence of non-willow species on older terraces ($F_{1,24}=0.14$, $P=0.72$; $F_{1,24}=0.03$, $P=0.87$, respectively).

Soil Chemistry

Concentrations of total carbon and nitrogen were low across the entire terrace age gradient (Fig. 6). Average carbon concentrations in the soil were 1.03% (range 0.042-1.78%), and nitrogen concentrations averaged 0.045% (range 0.005-0.078%). Total soil carbon and nitrogen were positively correlated with each other ($Rho=0.89$, $P=0.0001$). There was no significant treatment effect on the soil C:N relationship. Soil phosphorous concentrations did not exhibit any significant trends along the terrace age gradient, between treatments, or any gradient*browse interaction ($F_{1,24}=2.93$, $P=0.10$; $F_{1,24}=2.00$, $P=0.17$; $F_{1,24}=1.87$, $P=0.19$, respectively). There was no significant relationship between soil nitrogen and phosphorous, and there was an average soil N:P ratio of 0.63 ($F_{1,24}=1.18$, $P=0.29$).

The main cations associated with salt crust formation were calcium, magnesium, and potassium. Soil cations were not significantly correlated (K:Ca $Rho=0.09$, $P=0.8$; K:Mg $Rho=-0.04$, $P=0.88$; Ca:Mg $Rho=0.28$, $P=0.37$). Whereas soil potassium exhibited no significant treatment effects or trends along the terrace gradient, concentrations of calcium and magnesium declined significantly (K $Rho=0.032$, $df=24$, $P=0.82$; Ca $Rho=-0.44$, $df=24$, $P=0.047$; Mg $Rho=-0.74$, $df=24$, $P<0.0001$, Fig. 7). Magnesium and calcium concentrations were not significantly different between browsing treatments. Further, soil magnesium was positively correlated with the $PCA_1(LTC)$ ($F_{1,12}=25.26$, $P=0.0005$, Fig. 8), whereas calcium and potassium did not exhibit any trend in relationship to this variable. Instead, both soil potassium and calcium increased weakly

with an increase in the moisture principle component ($F_{1,12}=2.82$, $P=0.12$; $F_{1,12}=3.75$, $P=0.08$, respectively).

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 (Fig. 9). Germination showed no significant trends along the terrace age gradient, between browsing treatments, or any significant gradient-browse interaction ($F_{1,24}=0.51$, $P=0.48$; $F_{1,24}=0.02$, $P=0.9$; $F_{1,24}=0.07$, $P=0.79$, respectively, Fig. 9). Site 6 (control) was an outlier in the data set and was removed in further analyses to determine any potential factors driving germination rates. The weighting towards 0% germination also skewed most germination analyses. Germination decreased with an increase in $PCA_1(LTC)$, i.e., it was lower on warmer and drier sites ($F_{1,11}=10.22$, $P=0.0109$, Fig. 10). However, seedling establishment did not exhibit a clear trend with the moisture principle component. Spruce germination significantly decreased with increasing soil magnesium concentrations ($F_{1,11}=11.59$, $P=0.0078$, Fig. 11). These results suggest that high magnesium concentrations in conjunction with hot and dry sites may be factors inhibiting spruce seed germination. By contrast, germination rates did not exhibit any such relationship with calcium and potassium concentrations.

Survivorship of spruce seedlings was nearly 100% at most of the sites (Fig. 12). Sites 7 and 8 in the gradient represent the sites that experienced the most flooding. The control plots at sites 7 and 8 were slightly lower in terrace height and thus experienced flooding for an extended period of time relative to the exclosures. Survivorship did not vary significantly along the terrace age gradient or between browsing treatments

($F_{1,24}=1.37$, $P=0.26$; $F_{1,24}=0.02$, $P=0.89$, respectively). The interaction was not significant between the gradient and browse covariants ($F_{1,24}=0.45$, $P=0.51$). Spruce seedling survival was significantly correlated with the PCA_2 (MOI) in a curvilinear manner (PCA_2 : $t=-0.78$, $P=0.45$, $(PCA_2)^2$: $t=-3.61$, $P=0.0056$, Fig. 13). Seedlings experienced the highest rates of survivorship at moderately moist sites, as opposed to frequent flooding sites (positive score) or sites that experienced prolonged drought during the spring (negative score) (Fig. 13). This suggests that white spruce seedlings are sensitive to excessive moisture conditions on the Tanana River and are only able to persist on intermediate moisture terraces. Seedling survival also declined marginally with increased soil calcium concentrations ($F_{1,24}=4.50$, $P=0.047$, Fig. 14), possibly due to osmotic stress; however, survivorship was not related to soil magnesium or potassium concentrations. In regards to natural spruce regeneration, spruce recruitment was only observed at the site 6, which was close to a white spruce seed source, and at older terraces (Sites 6 and 11, Table 6).

Spruce Seedling Growth

White spruce seedlings grew well the first year following planting, after which growth was minimal (Fig. 15). Mean spruce seedling heights did not vary significantly between browsing treatments ($F_{1,24}=0.12$, $P=0.73$, Fig. 17, Fig. 16), but seedling height did increase with increasing terrace age ($F_{1,24}=5.35$, $P=0.032$). There was no significant browse*gradient interaction ($F=0$, $P=1$). Shifts in carbon allocation between vertical growth and woody basal growth were determined using an index of height to basal diameter (Ht:BD). Height to basal diameter ratios ranged from $3.4\text{cm}\cdot\text{mm}^{-1}$ to $4.4\text{cm}\cdot\text{mm}^{-1}$ and increased significantly with an increase in terrace age ($F_{1,24}=13.84$,

$P=0.0014$) (Fig. 17). Moose browsing did not significantly affect the Ht:BD ratio ($F_{1,24}=1.20$, $P=0.29$), and there was no significant browse*gradient interaction ($F_{1,24}=0.21$, $P=0.65$, Fig. 17).

Seedling heights significantly decreased with an increase in $PCA_1(LTC)$ on unbrowsed plots ($F_{1,6}=10.22$, $P=0.033$, Fig. 18). Seedling height to basal diameter ratio exhibited a similar trend with increasing $PCA_1(LTC)$ ($F_{1,6}=8.48$, $P=0.044$, Fig. 19). On control plots, the relationships between seedling heights and $PCA_1(LTC)$ and Ht:BD ratio and $PCA_1(LTC)$ were both non significant, reflecting differences in associated vegetation biomass (willow heights) (Ht: $F_{1,6}=3.11$, $P=0.15$; Ht:BD: $F_{1,6}=2.28$, $P=0.21$, Fig. 18, Fig. 19). Both seedling height and height to basal diameter ratios showed no relationship with the moisture principle component ($PCA_2(MOI)$) ($F_{1,12}=0.79$, $P=0.4$, $F_{1,12}=0.55$, $P=0.48$, respectively) suggesting that soil moisture, despite flooding at certain sites, and relative humidity are not critical environmental factors driving spruce seedling growth responses.

Spruce Seedling Growth in Relation to Willow Abundance

Spruce seedling Ht:BD ratio increased with an increase in total biomass produced for the 10 tagged willows at browsed plots ($F_{1,12}=13.37$, $P=0.0053$, Fig. 20). Spruce seedling heights showed a comparable positive relationship with willow CAG biomass produced at control plots ($F_{1,12}=9.15$, $P=0.014$). Since shrub CAG estimates were only performed on control plots, I was unable to determine the interaction between the age gradient and moose browsing. These results suggest, however, that with increased shading, due to an

increase of willow CAG biomass, spruce seedlings shifted allocation from basal growth to vertical growth.

Spruce Needle Temperature and Angle

The maximum temperature experienced by seedlings was 48°C outside of site 5 compared with an air temperature of 32°C at that same time. Man and Lieffers (1997) demonstrated that photosynthetic activity in white spruce begins to decline when air temperatures exceeded 32°C. The number of temperature events greater than 32°C were significantly higher in seedlings versus the air ($F_{1,12}=7.60$, $P=0.018$). Seedlings experienced more events greater than 32°C than the ambient air for all terraces and treatments (Table 8). Mean cumulative daily temperatures (degree hours) were consistently higher on the younger terrace (site 5) than on the older terrace (e.g., site 12, Fig. 21). Generally, seedlings experienced higher cumulative daily temperatures than air most of the time at both enclosure and control plots, however, air temperatures could rise above seedling temperatures on the older terraces (Fig. 21). With the exception of particularly sunny, warm days, there were negligible differences in temperature throughout most of the season (Fig. 21). Over the course of a single day, needle temperatures on older, unbrowsed plots could exceed those on control plots by 11°C due to decreased transport of heat by wind in denser vegetation (Fig. 22). Although total seasonal means were not significantly different between seedlings and air temperatures, the extreme high temperature events likely had biological repercussions through protein degradation and down-regulation of photosynthesis.

Extreme events of high air temperature were tightly correlated with the PCA₁(LTC) (Fig. 23). Due to the limited number of exclosures sampled (n=3) and low germination rates, no estimate of the relationships between needle temperature and spruce seedling survivorship could be made.

Needle angle of spruce seedlings increased significantly along the terrace age gradient ($F_{1,12}=12.32$, $P=0.0027$, Fig. 24). This relationship suggests that the seedlings attempt to compensate for reduced light with increased cover and shading across the terrace gradient by increasing the leaf area exposed to incoming radiation. Alternatively, spruce needles on the youngest terraces could be decreasing the angle of their needles to decrease solar loading. There was no significant browsing effect or gradient-browse interaction ($F=0$, $P=0.97$; $F=0.01$, $P=0.93$, respectively).

Spruce Needle Chemistry

The average total needle carbon was 45%, and nitrogen concentration was 0.72%. Carbon and nitrogen did not vary significantly between browsing treatments or along the terrace age gradient. Similarly, the natural abundance of ^{13}C and ^{15}N in the needles did not exhibit any significant treatment effects or trends along the age gradient (C: browse: $F_{1,12}=2.46$, $P=0.13$, gradient: $F_{1,12}=0.01$, $P=0.91$, gradient*browse: $F_{1,12}=3.85$, $P=0.065$, Fig. 25) (N: browse: $F_{1,12}=0.01$, $P=0.91$, gradient: $F_{1,12}=0.02$, $P=0.89$, gradient*browse: $F_{1,12}=0.08$, $P=0.78$, Fig. 26). Needles exhibited a rather depleted average $\delta^{13}\text{C}$ signature (Mean= -30.17‰) (Fig. 25). Although not significant, the $\delta^{13}\text{C}$ values showed trends towards depletion inside of the exclosures and enrichment outside of the exclosures ($F_{1,12}=3.85$, $P=0.065$, Fig. 25). Mean needle $\delta^{15}\text{N}$ was slightly depleted at -3.92‰ and

significantly correlated with PCA₂(MOI) ($F_{1,12}=11.66$, $P=0.0066$, Fig. 26). This relationship was driven primarily by flooding events at sites 6 and 7, which showed enriched $\delta^{15}\text{N}$ signatures averaging -0.74‰ (Fig. 26, Fig. 27).

Needle concentrations of cations exhibited a broad range among all of the sites (Table 7). Needle concentrations of calcium and potassium did not exhibit any significant relationship along the terrace age gradient (Ca: $Rho=0.067$, $P=0.85$, K: $Rho=0.44$, $P=0.20$). By contrast, needle magnesium concentrations declined significantly with increase in terrace gradient ($Rho=-0.78$, $P=0.0075$). Since browsing treatments were pooled to provide enough sample for extraction, browsing impacts were undetermined. Needle magnesium concentrations were positively correlated with soil magnesium concentration ($F_{1,10}=355.41$, $p<0.0001$, Fig. 30). There were no correlations between soil calcium and potassium and their respective needle cations.

Discussion:

On these early successional terraces, effects produced by moose browsing on microhabitat and soil chemistry were minimal compared to the effects produced by the natural age gradient. There appear to be important small-scale differences in light, cover, and temperature regimes that are essential for the overall success of spruce seedlings, which are mediated by cover of deciduous vegetation. On the Tanana River, canopy cover generally increases along gradients of terrace age with the transition from an open willow community to a closed alder community (Viereck et al., 1993b). I observed this at the exclosures as they ranged from exclusive *Salix interior* and *Equisetum* spp.

communities to diverse communities with alder, poplar, four species of willow, and numerous vascular and non-vascular herbs at older terraces.

The effects caused by moose browsing were limited to significantly reducing the heights of willows. The consumption of willows and the subsequent changes in willow architecture led to small differences in light penetration to the spruce seedlings. At the youngest sites, the browsing effect on cover was significant due to the preference for *S. interior* twigs. However, the broader effects on the community were rather minor because these sites were already sparsely vegetated. On older terraces, browsing was most prominent at sites where felt-leaf willow (*S. alaxensis*) was the dominant willow species. These shrubs experienced heavy browsing pressure that created a broomed architecture. Sites that were dominated by less favored willow species showed little discrepancy between shrub cover in exclosures and control plots. This suggests that the effects of moose browsing are likely to be strongly dependent upon the vegetative community and the proportion of preferred browse species in the area. Previous work has shown that heavy moose browsing does alter the local climate and vegetative community through changes in browsed species architecture, chemistry, leaf litter production, and cover (Pastor and Naiman, 1992, Kielland and Bryant, 1998, Persson et al., 2000, Persson et al., 2005). The results here suggest that moose browsing has significant effects on willow communities, but the development of the successional sequence and cover effects are driven primarily by the age of floodplain terraces (i.e., time).

The growth of planted spruce seedlings responded positively to increased biomass of associated willow vegetation, which implies that the seedlings are experiencing a more favorable microhabitat under such conditions. The increase of willow biomass showed a marked divide between *S. interior*-dominated plots (biomass <150g) and *S. alaxensis*-dominated sites (biomass >200g). The improved microhabitat under *S. alaxensis* is likely due to the larger size of this willow species resulting in increased shading. Decreases in direct light have been shown to improve spruce seedling photosynthesis and growth (Man and Lieffers, 1997, Groot, 1999, Doran et al., 2001), but opposite findings have also been documented for white spruce (Walker and Chapin, 1986). On bright sunny days, the youngest terraces experienced PAR values greater than $1500\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which is nearly 3-fold greater than the light saturation point for white spruce (Doran et al., 2001). Seedlings on control plots likely did not exhibit as strong of a growth response due to seedlings experiencing hotter and brighter microhabitat conditions, typical of younger terraces, for a longer period of time. Seedlings in enclosure and control plots on the youngest terraces experienced similar light and temperature regimes (PCA₁ values 1 to 2) resulting in no significant difference in growth. However, seedlings planted on older, heavily shaded terraces exhibited a stronger positive response to the decrease in PCA₁(LTC) (PCA₁ values -3 to -2) when compared to seedlings in control plots of comparable shading, which suggests that spruce seedlings prefer more shaded terraces that have more moderated levels of light.

Spruce seedling height increased during the first year of growth, however it leveled off over the next three growing seasons. I suggest that this is a result of several local

weather events that affected the seedlings. Spruce seedlings were planted in 2003 and this year was subsequently followed by one of the hottest and driest summers on record in Fairbanks, Alaska (Bonanza Creek LTER Database: http://www.lter.uaf.edu/clin_search/clin_search_start.cfm). In 2006, the weather was more moderate with increased precipitation and decreased fires. However, an unusual cold spell (-7°C) in early June delayed spring green-up and potentially injured emerging foliar tissues of the spruce seedlings. The poor growth over the past three years could be the result of permanent damage from the first two stressful years growing under hot, dry conditions followed by the exceptional cold spell in June 2006. Spruce seedlings also showed visual indicators of stress such as winter desiccation, needle drop, and chlorosis, particularly at the younger sites. The cumulative effects of these detrimental conditions may have contributed to slower overall growth.

As part of the suite of environmental conditions examined, I also demonstrated how high the temperatures may get in the dense packing of spruce needles of young seedlings. The arrangement and proximity of needles, in concurrence with the high solar radiation on early successional terraces, create hot spots on the seedlings where temperatures may greatly exceed the maximum values for optimal photosynthesis (30°C ; Man and Lieffers, 1997). The localized high temperatures were likely caused by a decrease in wind speed around the needle clusters, resulting in a decrease in forced convective transport of heat away from the needles. On the oldest terrace, increased shading moderated both the maximum temperature experienced in the needle clusters and the frequency of extreme temperature events. Most carbon assimilation in white spruce seedlings takes place on

the youngest needles located at the end of branches. The high temperature experienced by these needle age classes probably resulted in down-regulation of photosynthesis. These results suggest that moose browsing on neighboring vegetation or other processes decreasing deciduous canopy cover may lead to increased needle temperatures with negative effects on young spruce seedlings. The degree of heating of needles on young terraces is mediated by the thickness of the boundary layer surrounding the needles. On young terraces, high temperatures are dissipated by turbulent transport of longwave radiation. On older terraces, the effects produced by increased vegetation outweigh the potential decreases in air movement underneath the canopy. Thus, denser vegetation is beneficial to seedlings because fewer high temperature events occur at the level of the needle.

Another seedling parameter that showed a directional change with increased terrace age was the needle angle. Needle angle, as determined by the number of degrees from the horizontal stem, increased along the terrace gradient, but exhibited no response to moose browsing. Carter and Smith (1985) proposed that conifers respond to decreases in light through decreasing needle angle under shaded conditions to maximize mid-day light interception. However in high latitudes, the decreased elevation angle of the sun requires needles to increase their needle angle to maximize light interception.

Alternatively, the angles of spruce needles decrease on young, open terraces to provide shade for other needles because these needles are not light limited. I propose that this is a physiological response of spruce seedlings to reduced light availability, due to shading, in boreal forest communities. Despite needle angle being a potential mechanism for altering

light interception, branch angles of young seedlings may be more important for long-term modification for coping with variations in light. By altering their needle orientation, spruce seedlings exhibit a degree of plasticity in dealing with variations in their immediate microhabitat.

Another habitat factor that was examined on these early terraces was the prevalence of the salt crust on the soil. High salt concentrations in soils have been shown to increase the osmotic potential of the soil, making water more difficult to acquire by seedlings (Tinus, 1980, Landis, 1988, Dyrness and Van Cleve, 1993). Non-toxic concentrations of calcium in foliage from *Pinus ponderosa* seedlings ranged from 0.20-0.50% (Landis, 1988), and 70% of the spruce seedlings exhibited needle calcium concentrations greater than these levels. 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 the planted seedlings. Although these calcium concentrations are not directly comparable to the requirements of white spruce, seedlings on these early floodplain sites matched the symptoms of high calcium-stressed seedlings.

When incorporating potential browsing effects on salt crust, moose did not have any measurable effect on soil cation concentrations. This is contrary to my original prediction and contradicts other studies, which demonstrated that concentrations of soil cations are typically higher in browsed areas (Kielland and Bryant, 1998). However, along the terrace age gradient, the two dominant cations, calcium and magnesium, declined, suggesting that the evapotranspiration effect responsible for the capillary draw

of soil moisture was being moderated. This was probably due to increased vegetation diminishing wind transport of water vapor and increased leaf litter decreasing the amount of exposed soil surfaces. In contrast to calcium and potassium trends, soil magnesium concentrations did not show any trends with the PCA₂(MOI) suggesting that magnesium might have been more independent with respect to moisture gradients than calcium and potassium. On these early terraces, the soil moisture conditions ranged from dry to flooded and work in concert with the capillary draw of cations to the soil surface posing potential water use efficiency (WUE) problems for white spruce growth and establishment.

A physiological parameter that has been used as an indicator of water stress in plants is the ¹³C natural abundance of foliage ($\delta^{13}\text{C}$). I found no significant enrichment in needle $\delta^{13}\text{C}$, which would indicate water stress, along the terrace gradient. On younger terraces, spruce foliage was less depleted in enclosure plots, which is consistent with my original hypothesis. However, on control plots, there was a trend towards less depleted signatures as terrace age increased. This may be a result of water stress induced by soil moisture being decreased by increased associated vegetation leading to higher temperatures on browsed, older sites. Other studies of *Picea glauca* seedlings have shown enriched carbon signatures as water use efficiency increases with increased water stress (Sun et al., 1996, Silim et al., 2001). Sun et al. (1996) reported a division in $\delta^{13}\text{C}$ values in white spruce between water-stressed seedlings and irrigated seedlings around – 27.5‰ $\delta^{13}\text{C}$ with less depleted signatures indicating water stress. Using this value for

comparison, none of the seedlings showed isotopic values enriched enough to suggest that there was significant osmotic stress on the seedlings.

Because nitrate concentrations are much higher than ammonium concentrations in Tanana River water (Clilverd, 2007), I predicted that spruce seedlings would be isotopically depleted in ^{15}N natural abundance on young, low terraces as a result of increased nitrate availability. However, 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. Studies examining nitrogen uptake capacity and kinetics in white spruce seedlings have shown that spruce preferentially take up ammonium rather than nitrate (Kronzucker et al., 1996, Kronzucker et al., 1997). The absence of isotopic depletion in spruce foliage despite increased nitrate supply may reflect low nitrate uptake due to this strong preference for ammonium (Kronzucker et al., 1997). In addition, spruce seedlings growing on frequently flooded sites are likely having decreased rates of mycorrhizal infection due to lower 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. Thus, the inverse relationship between soil moisture and seedling $\delta^{15}\text{N}$ signatures in my results may reflect a decrease in mycorrhizal associations. Hence, the pattern of ^{15}N enrichment that I observed may be a combination of spruce preferential uptake of ammonium over nitrate and variation in mycorrhizal infection of spruce roots.

In addition to potentially influencing mycorrhizal associations, soil moisture was an important factor controlling the survivorship of spruce seedlings. PCA₂(MOI) was primarily driven by variation in soil moisture as opposed to the mean low relative humidity. Stochastic events, such as flooding and spring drought, strongly influenced the mean summer soil moisture. The polynomial relationship between seedling survivorship and PCA₂(MOI) suggests that moderate moisture regimes are important for conifer establishment, as they promote strong root growth and thus nutrient acquisition. On these willow-dominated terraces, a key variable in determining soil moisture retention is the clay concentration, which is mediated by flooding (Van Cleve et al., 1993*b*). In conjunction with flooding, depth to groundwater and terrace height likely influence the ability of white spruce seeds to germinate and subsequently survive on early floodplain terraces. Flooding could mediate germination and survivorship through sediment deposition, increased burial of trunks and roots, increased salt deposition, and decreases in oxygen diffusion to the rooting zone. All of these factors have consequences for root survival and function in spruce seedlings. The wettest sites experienced saturated soils for the duration of the summer following a 2-week flooding event in late June. However, on a low moisture site, seedlings likely experience increased osmotic stress and cation toxicity (particularly calcium), in addition to general water stress. At most other sites, moisture stress was not a problem. Thus, any transpiration issues, caused by either stomatal closure or osmotic stress, were more a result of high temperature rather than water limitation.

The driving factor behind germination success was less clear as no relationships were evident along the terrace gradient or between browsing treatments. Instead, I found a significant relationship between germination and soil magnesium concentrations. This conclusion may be a product of 0% germination at most sites skewing the relationship or a correlation between PCA₁(LTC) and soil magnesium. The controlling factor of spruce germination rates cannot be determined from the results here as there are likely numerous factors subtly influencing the rates of germination. In general, it has already been demonstrated that 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). These abiotic factors in conjunction with potential cation (Mg) toxicity for seeds (Tobe et al., 2003) on dry early terraces appear to be some of the more prominent factors controlling white spruce germination on the Tanana River.

In conclusion, on these willow-dominated terraces, the overall effect of the terrace age on spruce seedling growth was greater than that of moose herbivory. Moose changed the microclimate for spruce seedlings; however, the sum of effects was close to zero due to changes in the willow community and effects produced by the natural gradient. Contrary to my initial hypothesis, moose browsing had only minor effects on soil chemistry and overall canopy cover. Moose browsing was responsible for significantly altering the heights of willows and increasing needle temperatures of spruce seedlings on older terraces. The natural age gradient of these early successional terraces represented a gradient of light, soil moisture, cover, and soil chemistry that largely overrode the effect of moose browsing. These factors also likely influence the successful development of

other important floodplain tree species. Understanding the factors that promote white spruce germination, survivorship, and growth is also important for determining the regeneration potential of white spruce in relation to its future use as a timber crop.

This research provides evidence that white spruce seedlings experience high needle temperatures and variability in microclimate. On the Tanana River, spruce seedlings experience large annual fluctuations in air temperature (-50°C to $+35^{\circ}\text{C}$), soil moisture (5-50%), and salt stress resulting from high concentrations of calcite and gypsum at the soil surface (Viereck et al., 1993*b*, Kielland and Bryant, 1998). All of these factors have adverse effects for the regeneration potential of white spruce. In addition, other experiments using planted spruce seedlings have shown that seedlings can persist on early terraces for 15+ years but put on little yearly growth (seedling height $\sim 40\text{cm}$, F.S. Chapin *unpublished*). These results suggest that although seedlings can exist and be present on these young terraces, the stressful environment (high light, high needle temperatures, salt crust) is likely impeding the growth and successful establishment of spruce through decreased photosynthesis caused by RUBISCO activase denaturing (Feller et al., 1998), water stress, and high radiation loads. 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 denaturation of photosynthetic enzymes.

Literature Cited:

- Bryant, J.P. & P.J. Kuropat, 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. & F.S. Chapin, III, 1986. Browsing-woody plant interactions during boreal forest plant succession. Pages 213-225 in K. Van Cleve, F.S. Chapin, III, P.W. Flanagan, L.A. Viereck, & C.T. Dyrness (eds.). Forest Ecosystems in the Alaskan Taiga. Springer-Verlag, New York, New York.
- Bryant, J.P., Provenza, F.D., Pastor, J., Reichardt, P.B., Clausen, T.P. & J.T. du Toit, 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., Rupp, T.S., & T.A. Hanley, *In Press*. Interactive controls of herbivory and fluvial dynamics over vegetation patterns along the Tanana River, interior Alaska. DOI: 10.11.1365-2699.2007.01713.
- Canfield, R.H., 1941. Application of the line intercept method in sampling range vegetation. *Journal of Forestry*, 39: 388-394.
- Carter G.A. & W.K. Smith, 1985. Influence of shoot structure on light interception and photosynthesis in conifers. *Plant Physiology*, 79: 1038-1043.
- Clilverd, H., 2007. Surface-subsurface hydrologic exchange and nitrogen dynamics in the hyporheic zone of the Tanana River. M.S. Thesis, University of Alaska, Fairbanks, Alaska, USA.

- Croser, C., Renault, S., Franklin, J., & J. Zwiazek, 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., & T. L. Wurtz, 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.T. & K. Van Cleve, 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.
- Feller, U., Crafts-Brandner, S.J. & M.E. Salvucci, 1998. Moderately high temperatures inhibit ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activase-mediated activation of Rubisco. *Plant Physiology*, 116: 539-546.
- Germino, M.J. & W.K. Smith, 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. & E.A. Hobbie. 2006. ¹⁵N in symbiotic fungi and plants estimates nitrogen and carbon flux in arctic tundra. *Ecology*, 87: 816-822.
- Kielland, K. & J.P. Bryant, 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos*, 82: 377-383.

- Kielland, K., Bryant, J.P., & R.W. Ruess, 1997. Moose herbivory and carbon turnover of early successional stands in interior Alaska. *Oikos*, 80: 25-30.
- Kronzucker, H.J., Siddiqui, M.Y., & A.D.M. Glass, 1996. Kinetics of NH_4^+ influx in spruce. *Plant Physiology*, 110: 773-779.
- Kronzucker, H.J., Siddiqui, M.Y., & A.D.M. Glass, 1997. Conifer root discrimination against soil nitrate and the ecology of forest succession. *Nature*, 385: 59-61.
- Kuo, S., 1996. Phosphorous. Pages 870-872 in: D.J. Sparks (ed.). Methods of Soil Analysis Part III Chemical Methods. SSSA Book Series 5. Soil Science Society of America Inc., Madison, WI.
- Landis, T., 1988. Management of forest nursery soils dominated by calcium salts. *New Forests*, 2: 173-193.
- Man, R. & V.J. Lieffers, 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., & C.H. Black, 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.
- Nienstaedt, H. & J.C. Zasada, 1990. *Picea glauca* (Moench) Voss. Pages 204-226 in: R.M. Burns & B.H. Honkala (eds.). *Silvics of North America*. USDA Forest Services Agricultural Handbook No. 654.

- Niinemets, Ü. & O. Kull, 1995. Effects of light availability and tree size on the architecture of assimilative surface in the canopy of *Picea abies*: variation in needle morphology. *Tree Physiology*, 15: 307-315.
- Pastor, J. & R.J. Naiman, 1992. Selective foraging and ecosystem processes in boreal forests. *The American Naturalist*, 139: 690-705.
- Persson, I-L., Danell, K., & R. Bergström, 2000. Disturbance by large herbivores in boreal forests with special reference to moose. *Annales Zoologici Fennici*, 37: 251-263.
- Persson, I-L., Danell, K., & R. Bergström, 2005. Different moose densities and accompanied changes in tree morphology and browse production. *Ecological Applications*, 15: 1296-1305.
- Ronco, F., 1970. Influence of high light intensity on survival of planted Englemann spruce. *Forest Science*, 16: 331-339.
- Schulze, E.-D., Chapin, F.S., III, & G. Gebauer, 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. *Oecologia*, 100: 406-412.
- Silim, S.N., Guy, R.D., Patterson, T.B., & N.J. Livingston, 2001. Plasticity in water-use efficiency of *Picea sitchensis*, *Picea glauca*, and their natural hybrids. *Oecologia*, 128: 317-325.
- Slatyer, R.O. 1977. Dynamic changes in terrestrial ecosystems: patterns of change, techniques for study and applications to management. *MAB Technical Notes* 4: 9-13. UNESCO, Paris, France.

- Stolter, C., Ganzhorn, J.U., Ball, J.P., Julkunen-Titto, R. & R., Lieberei, 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.
- Sun, Z.J., Livingston, N.J., Guy, R.D., & G.J. Eicher, 1996. Stable carbon isotopes as indicators of increased water use efficiency and productivity in white spruce (*Picea glauca* (Moench) Voss) seedlings. *Plant, Cell, and Environment*, 19: 887-894.
- Tinus, R.W., 1980. Nature and management of soil pH and salinity. pp. 72-86. In: Proceedings North American Forest Tree Nursery Soils Workshop; 1980 July 28 – August 1; Syracuse, NY; Syracuse, NY: State University of New York. College of Environmental Science and Forestry.
- Tobe, K., Zhang, L., & K. Omasa. 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. & V. Alexander. 1981. Nitrogen cycling in tundra and boreal ecosystems. Swedish National Sciences Research Council, Stockholm, Sweden.
- Van Cleve, K., Viereck, L.A., and G.M. Marion, 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., & R. Erickson, 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., & R.E. Schlentner, 1993*a*. Climate of the Tanana River floodplain near Fairbanks, Alaska. *Canadian Journal of Forest Research*, 23: 899-913.
- Viereck, L.A., Dyrness, C.T., & M.J. Foote, 1993*b*. An overview of the vegetation and soils of the floodplain ecosystems of the Tanana River, interior Alaska. *Canadian Journal of Forest Research*, 23: 889-898.
- Walker L.R., 1985. The processes controlling primary succession on an Alaskan flood plain. Ph.D. thesis, University of Alaska, Fairbanks, Alaska, USA.
- Walker, L. R. & F. S. Chapin, III, 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology*, 67: 1508-1523.
- Walker, L.R., Zasada, J.C., & F.S. Chapin, III, 1986. The role of life history processes in primary succession on an Alaskan floodplain. *Ecology*, 67: 1243-1253.
- White, P.J., 2001. The pathways of calcium movement to the xylem. *Journal of Experimental Botany*, 52: 891-899.
- Wolff, J.O. & J.C. Zasada, 1979. Moose habitat and forest succession on the Tanana River floodplain and Yukon-Tanana upland. *North American Moose Conference and Workshop*, 15:213-244.

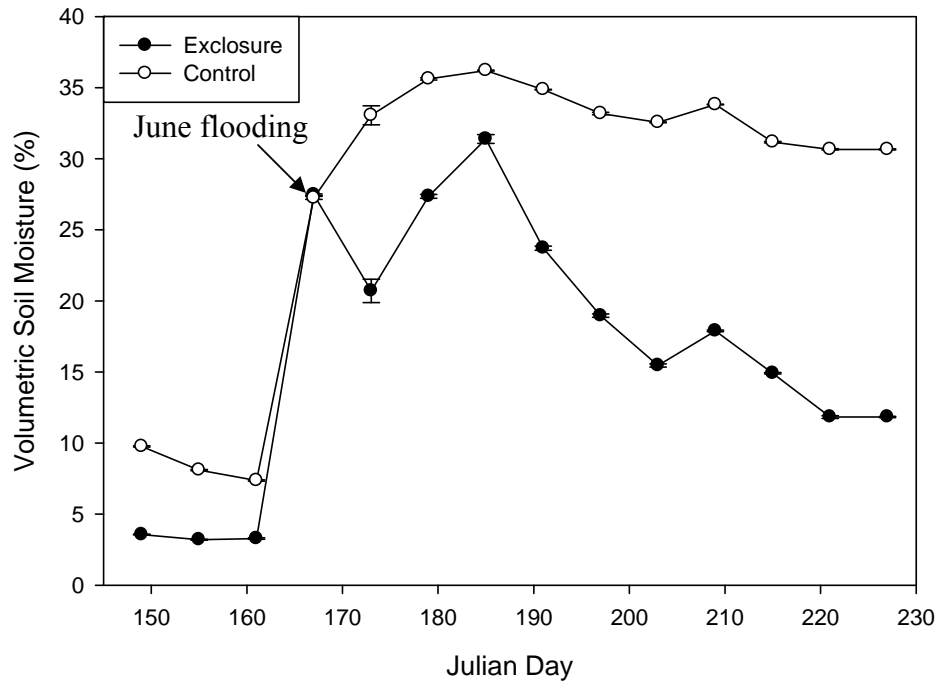


Figure 1: Soil moisture, averaged by week, between the exclosure and control plots at site 6. Flooding in late June is indicated by the arrow. Data presented (Mean \pm SE).

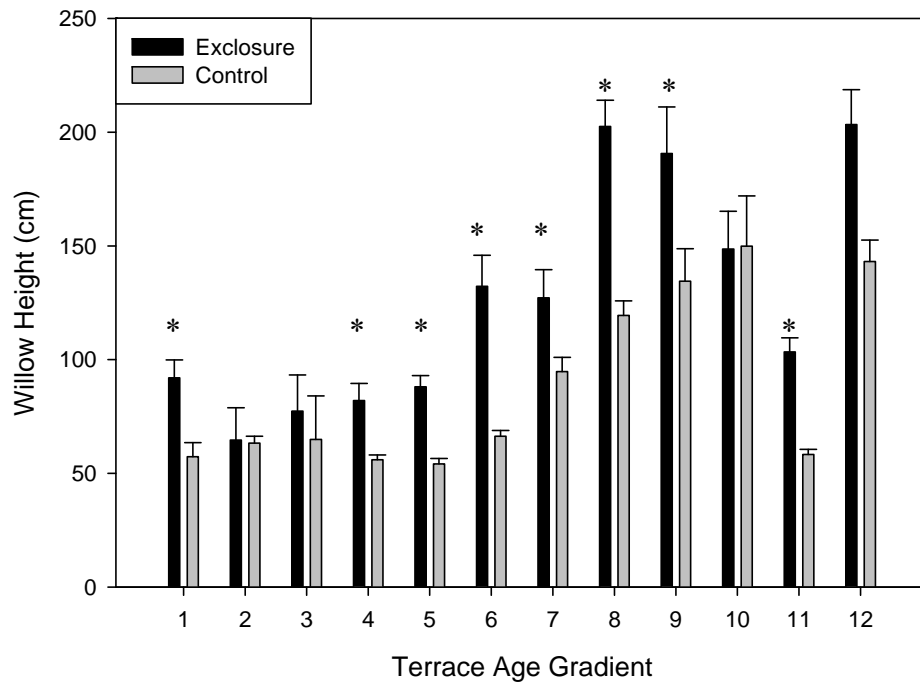


Figure 2: Height of willow plants on exclosure and control plots along the terrace age gradient. Asterisks indicate significant ($P < 0.05$) ANOVA browsing treatment effects by site (Mean \pm SE, $n=10$)

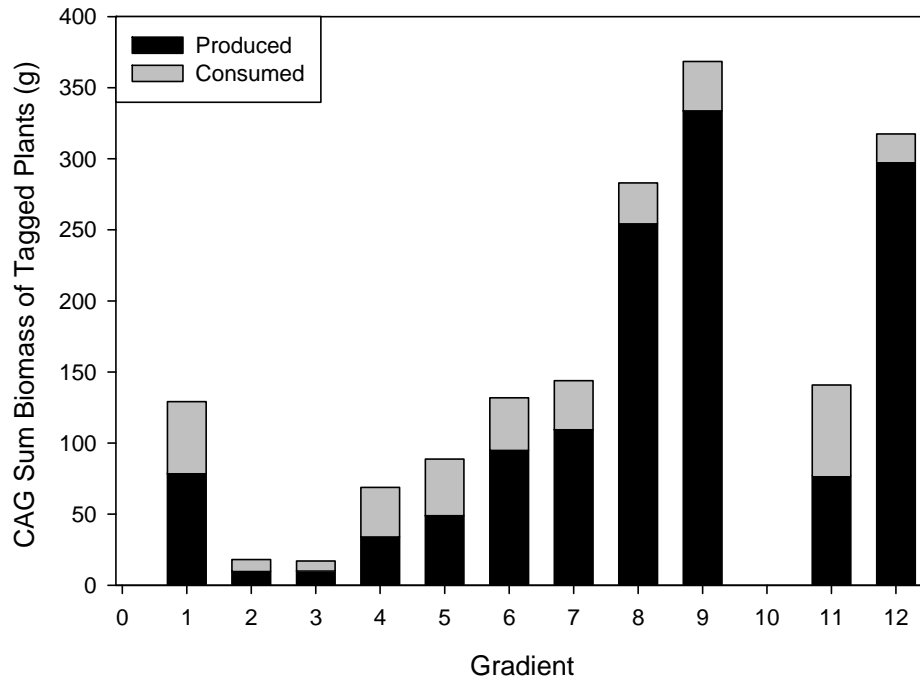


Figure 3: Willow biomass production (sum of the current annual growth produced by the 10 tagged willow plants) and the consumption by moose (amount of CAG biomass consumed) at control plots along the terrace age gradient. Gradient does not include gradient site 10 because it was dominated by a minimally browsed willow species, *S. brachycarpa*.

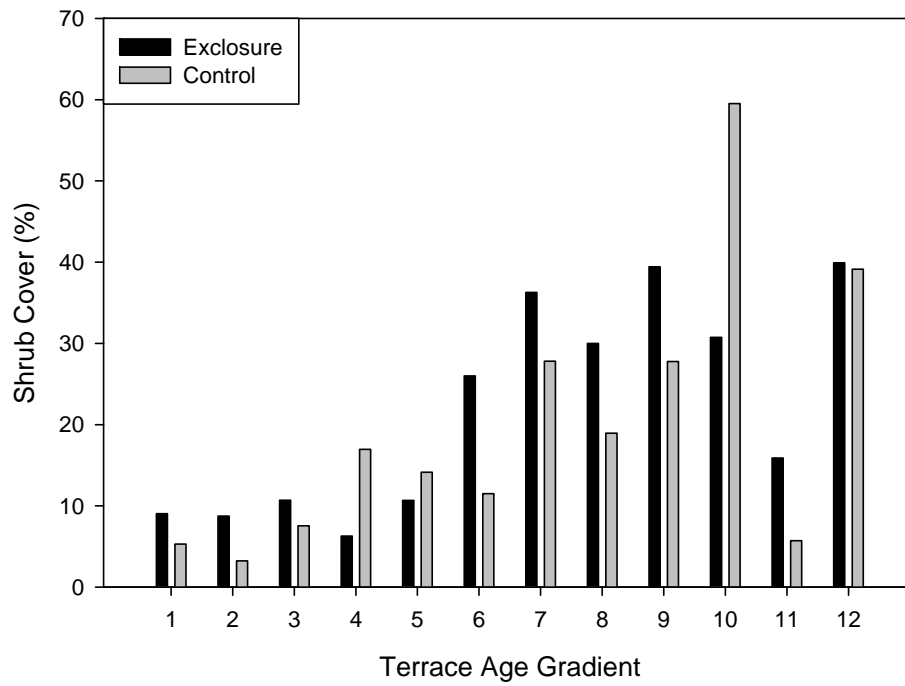


Figure 4: Cover of deciduous shrubs (%) at exclosure and control plots located along a terrace age gradient on the Tanana River.

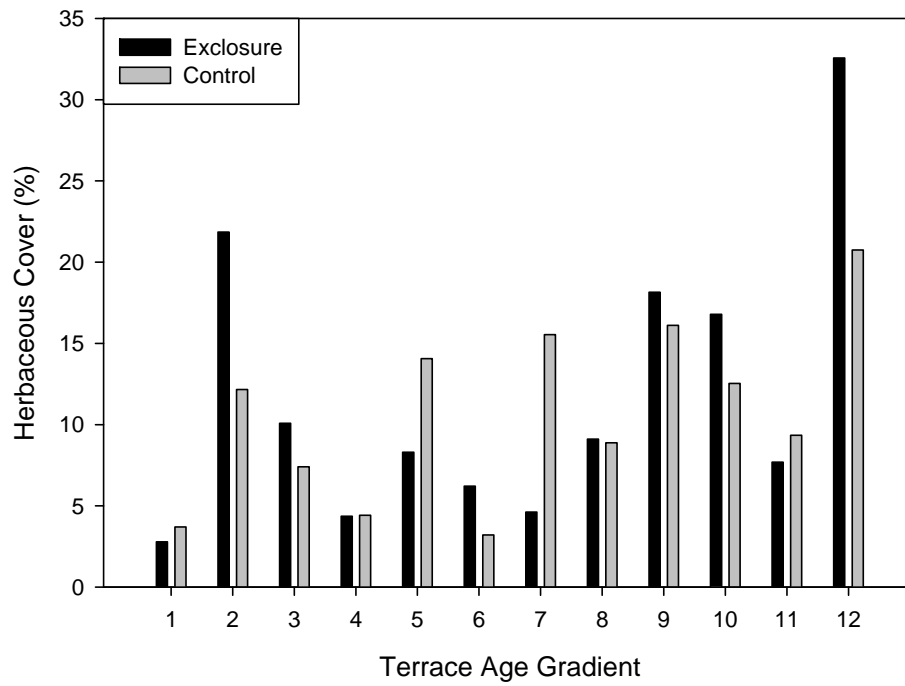


Figure 5: Herbaceous plant cover (%) at exclusion and control plots located along a terrace gradient on the Tanana River.

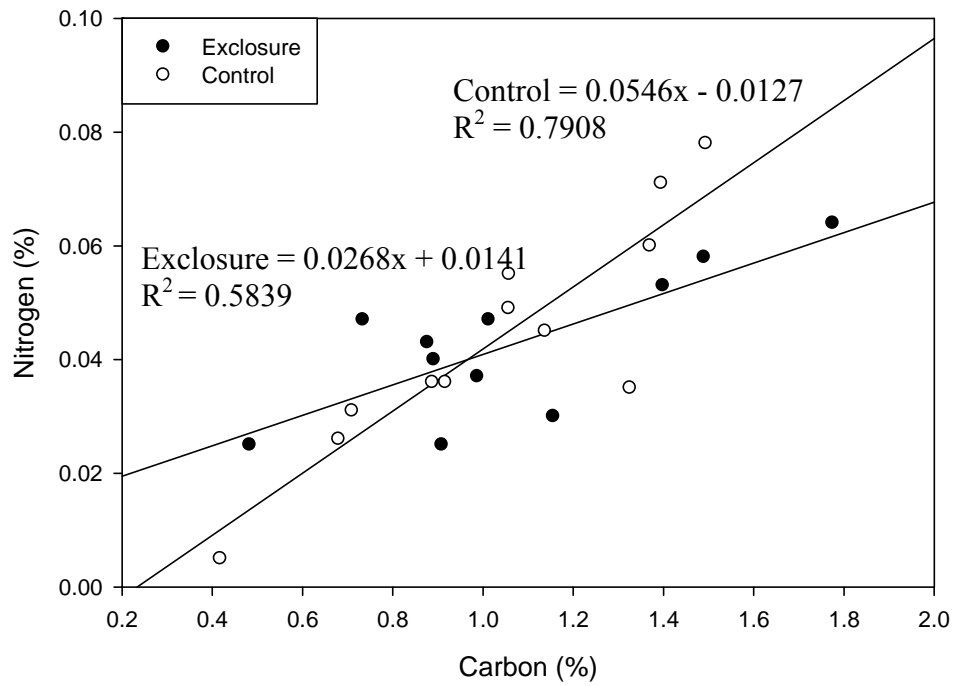


Figure 6: Soil total carbon and nitrogen relationship in the top 5cm of the soil profile on young terraces on the Tanana River.

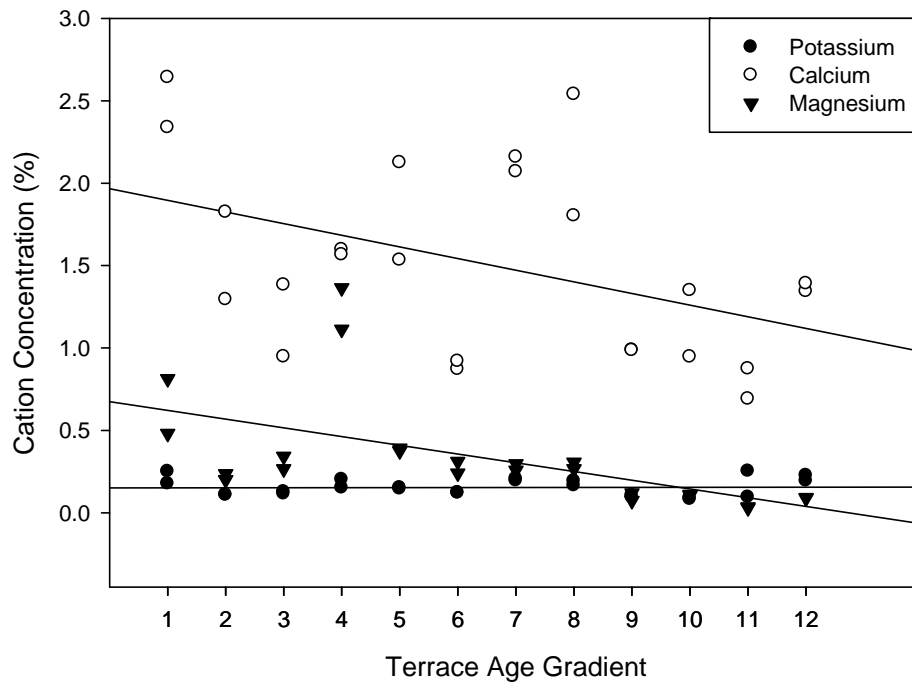


Figure 7: Soil calcium, magnesium, and potassium concentrations along the terrace gradient. (Calcium = $-0.0706x + 1.9663$, $R^2 = 0.1907$, $P=0.032$; Magnesium = $-0.053x + 0.6745$, $R^2 = 0.3222$, $P<0.0001$; Potassium = $0.0003x + 0.1514$, $R^2 = 0.0005$, $p=0.82$)

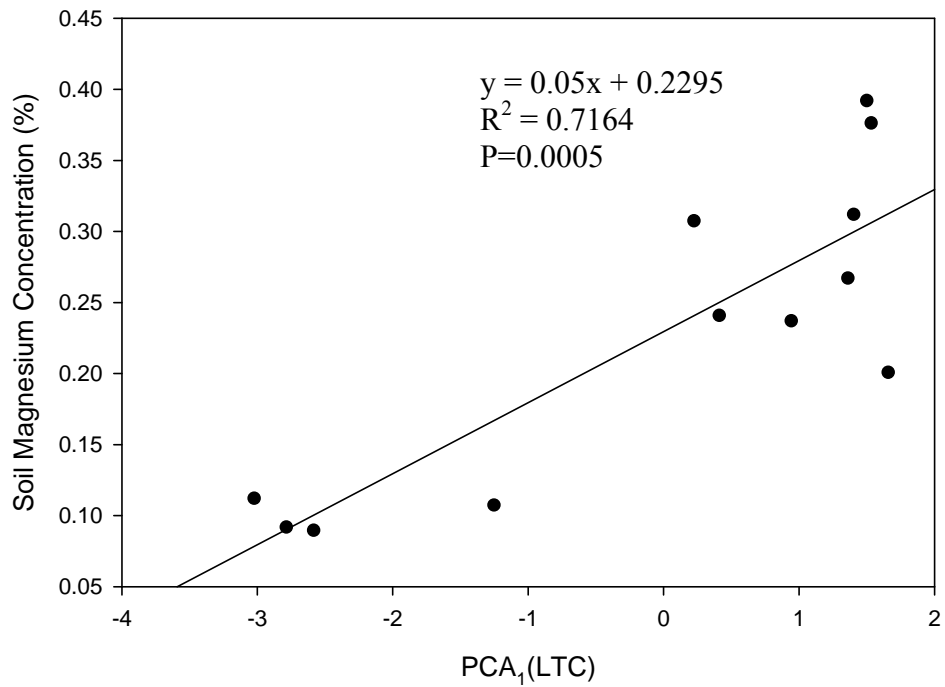


Figure 8: Relationship between soil magnesium concentrations and the light, temperature, and cover principle component (PCA₁(LTC)).

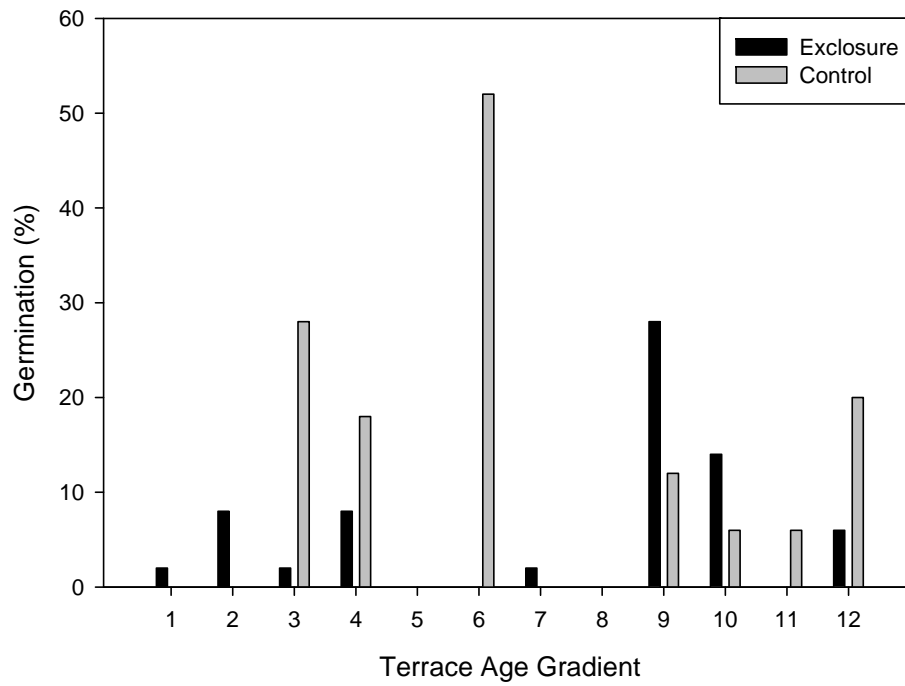


Figure 9: Germination of spruce seeds at exclusion and control plots along the terrace age gradient.

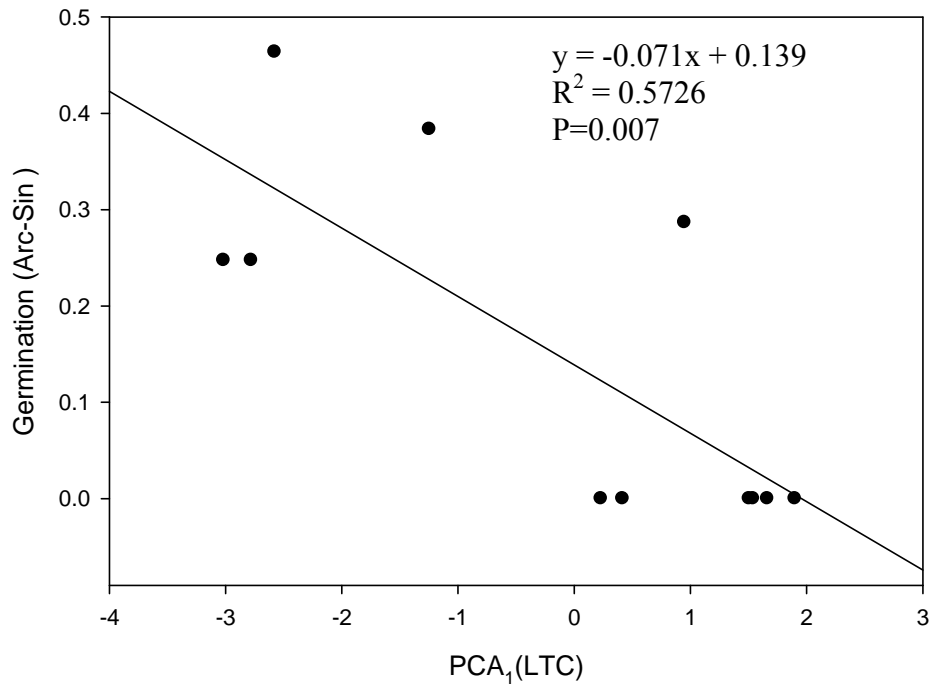


Figure 10: Relationship between the germination of spruce seeds and the light, temperature, and cover principle component (PCA₁(LTC)).

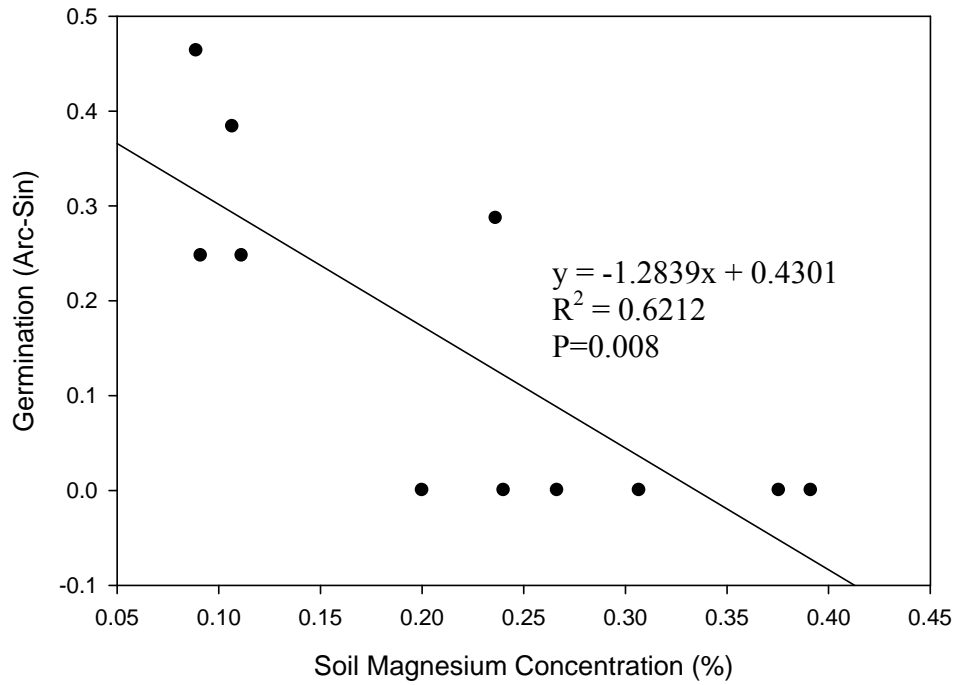


Figure 11: Relationship between spruce germination and soil magnesium concentrations.

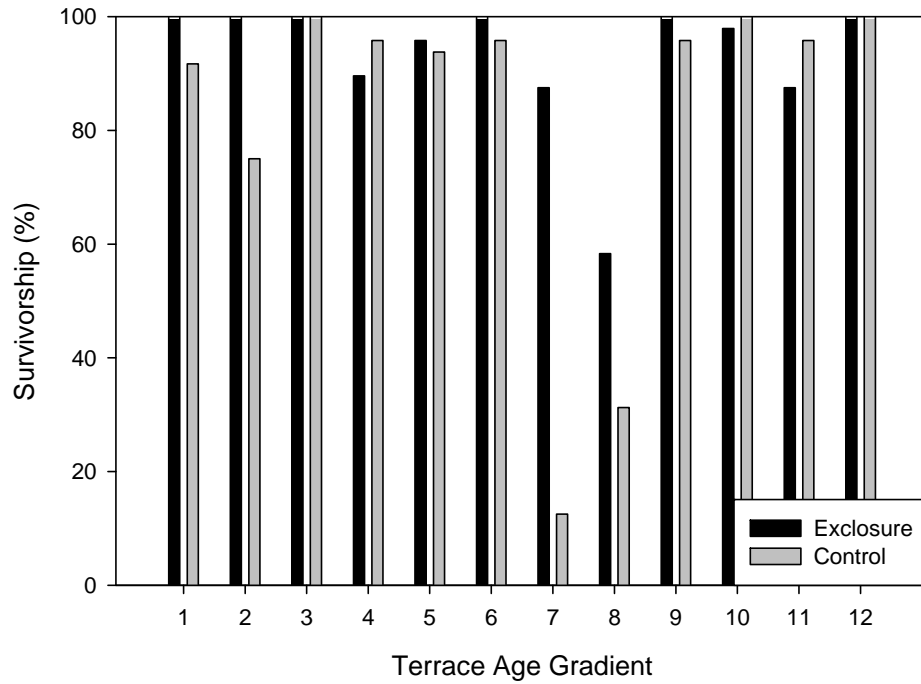


Figure 12: Survivorship of spruce seedlings at exclusion and control plots along the terrace age gradient.

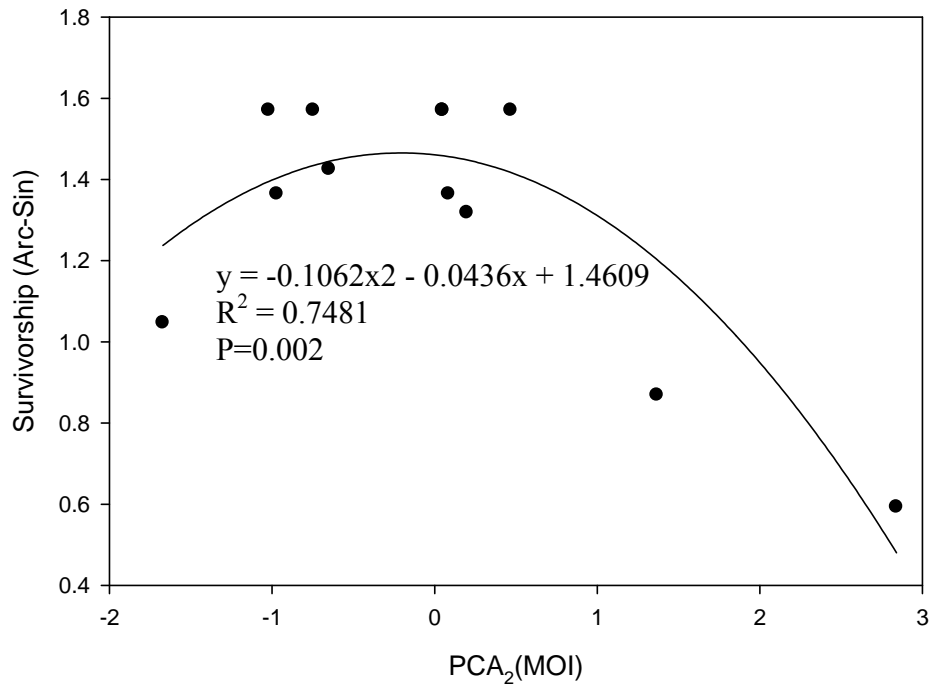


Figure 13: Relationship between the survivorship of white spruce seedlings and the moisture principle component (PCA₂(MOI)).

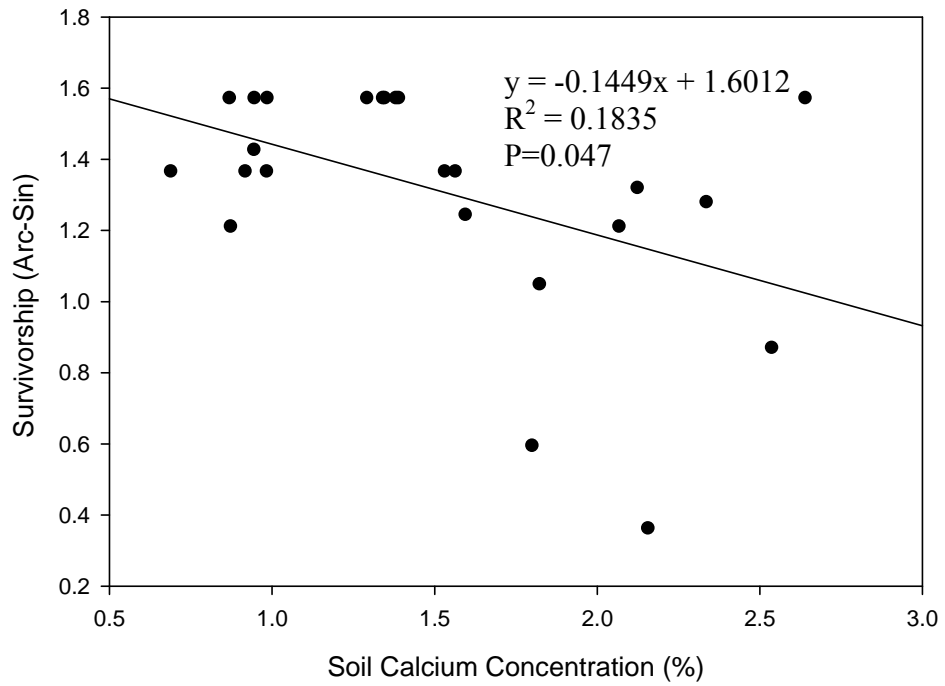


Figure 14: Relationship between seedling survivorship on early terraces and soil calcium concentrations.

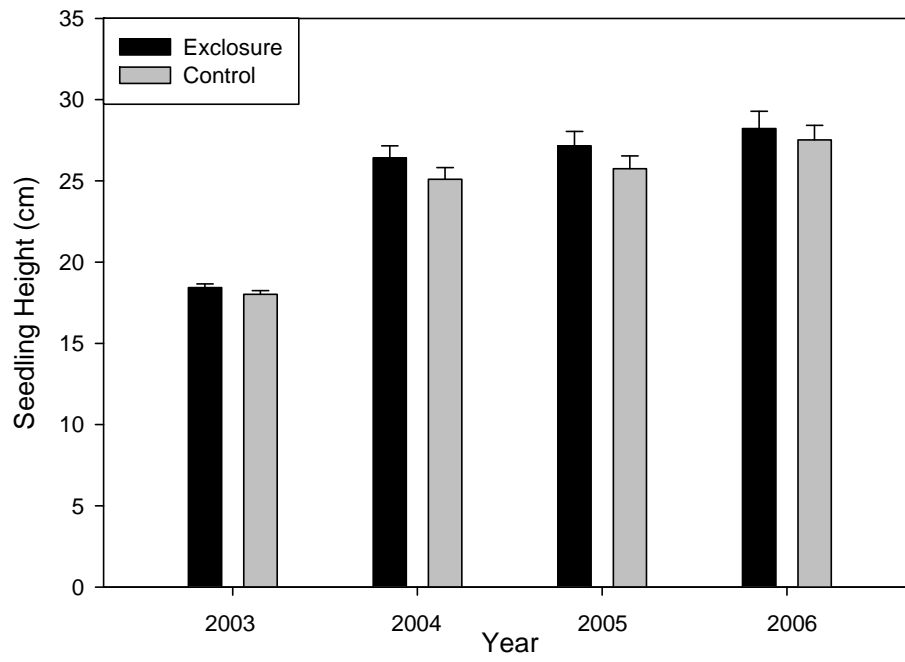


Figure 15: Average spruce seedling heights at exclosure and control plots for the 2003-2006 growing seasons. (Mean \pm SE).

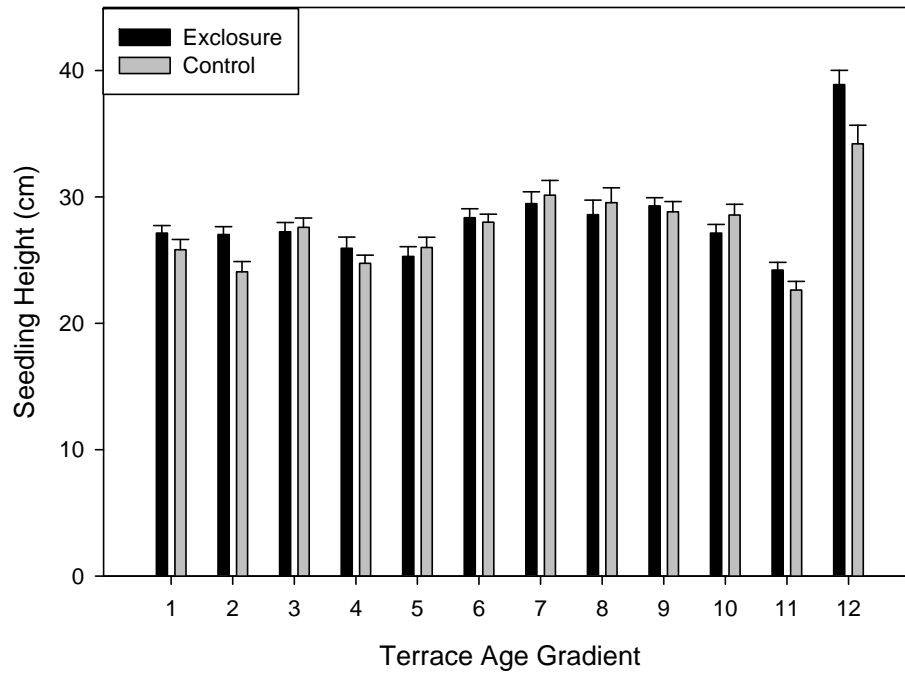


Figure 16: Spruce seedling heights (2006) at exclusion and control plots along the terrace age gradient. (Mean \pm SE).

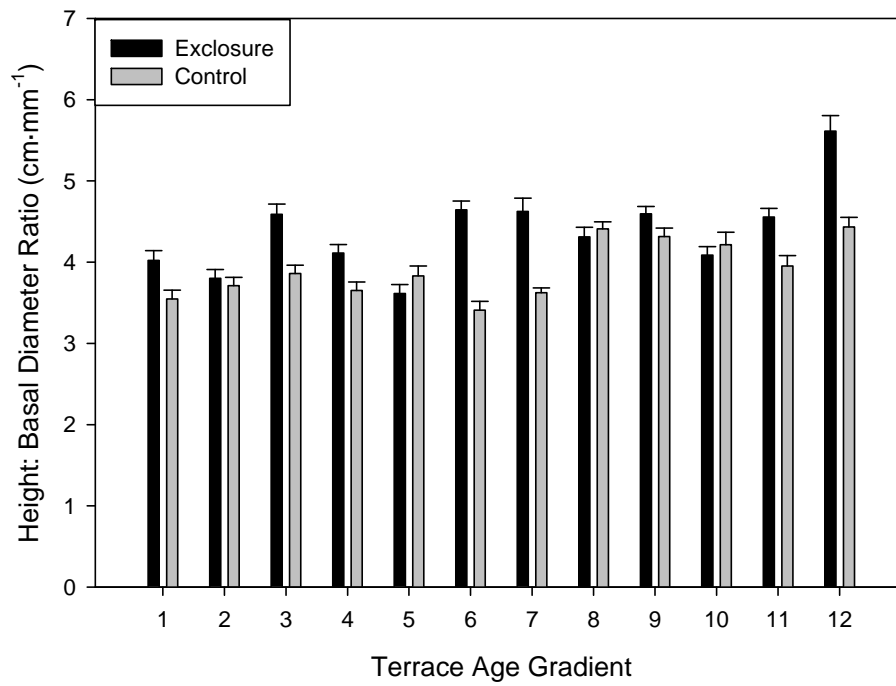


Figure 17: Height to basal diameter ratios of spruce seedlings located at exclosure and control plots along the terrace age gradient. (Mean±SE).

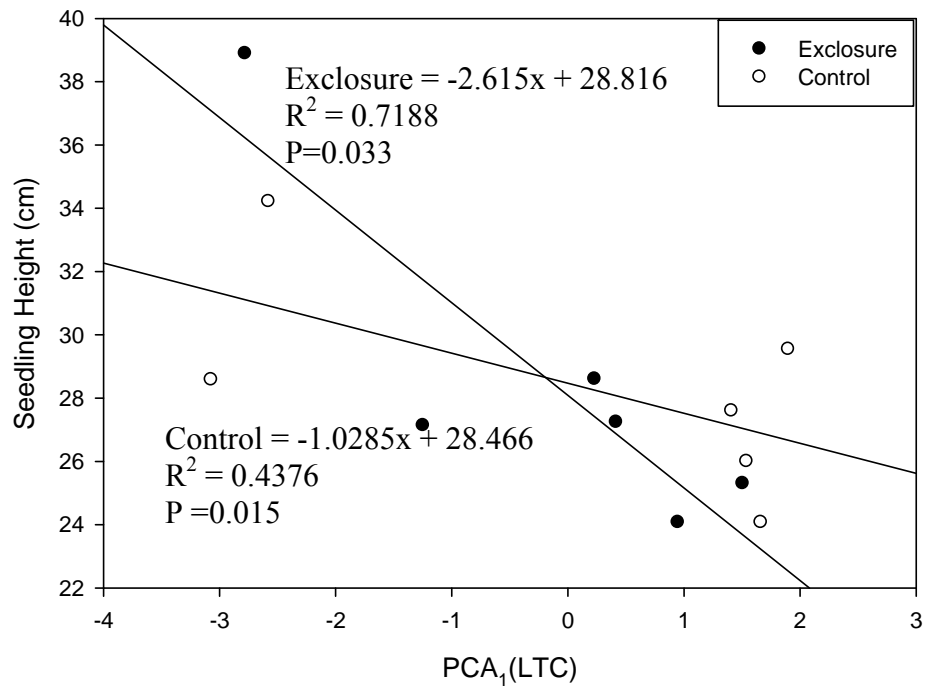


Figure 18: Relationship between average seedling height and the light, temperature, and cover principle component (PCA₁(LTC)) at exclosure and control sites.

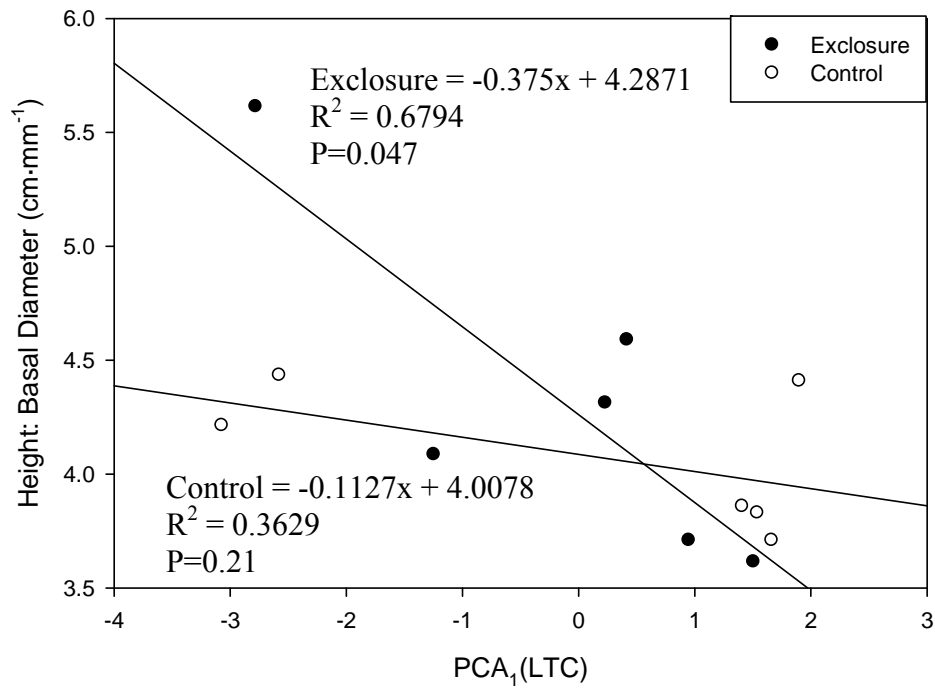


Figure 19: Seedling height to basal diameter ratio in relationship to the light, temperature, and cover principle component (PCA₁(LTC)) at exclosure and control plots.

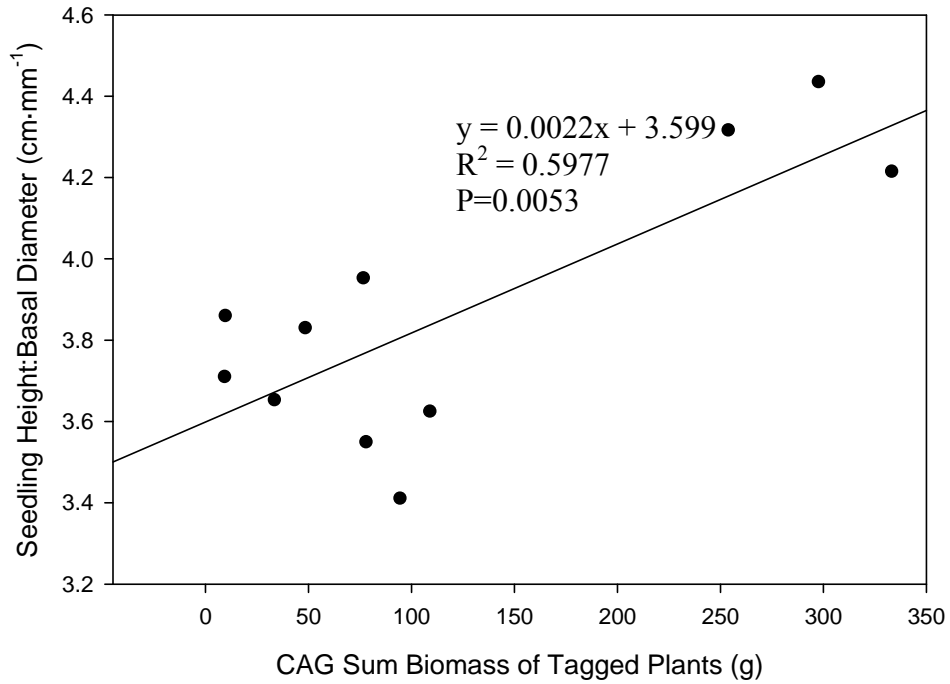


Figure 20: Relationship between spruce seedling height to basal diameter ratio and the total biomass (sum of CAG for 10 tagged willows) produced by willows at control plots.

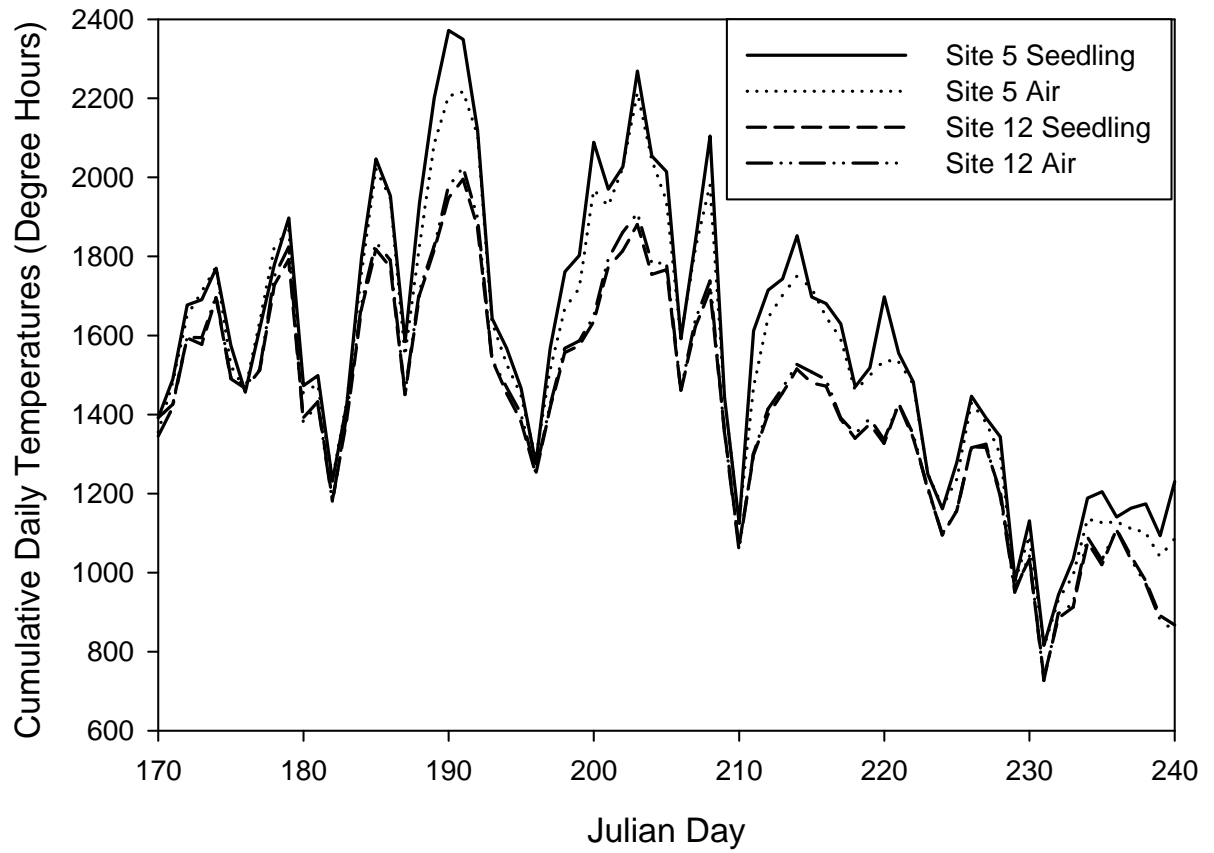


Figure 21: Average cumulative daily temperature (degree hours) measured by thermistors located in needle clusters on seedlings and in the air on June 20, 2006 through August 5, 2006 at site 5 (younger site) and site 12 (oldest site).

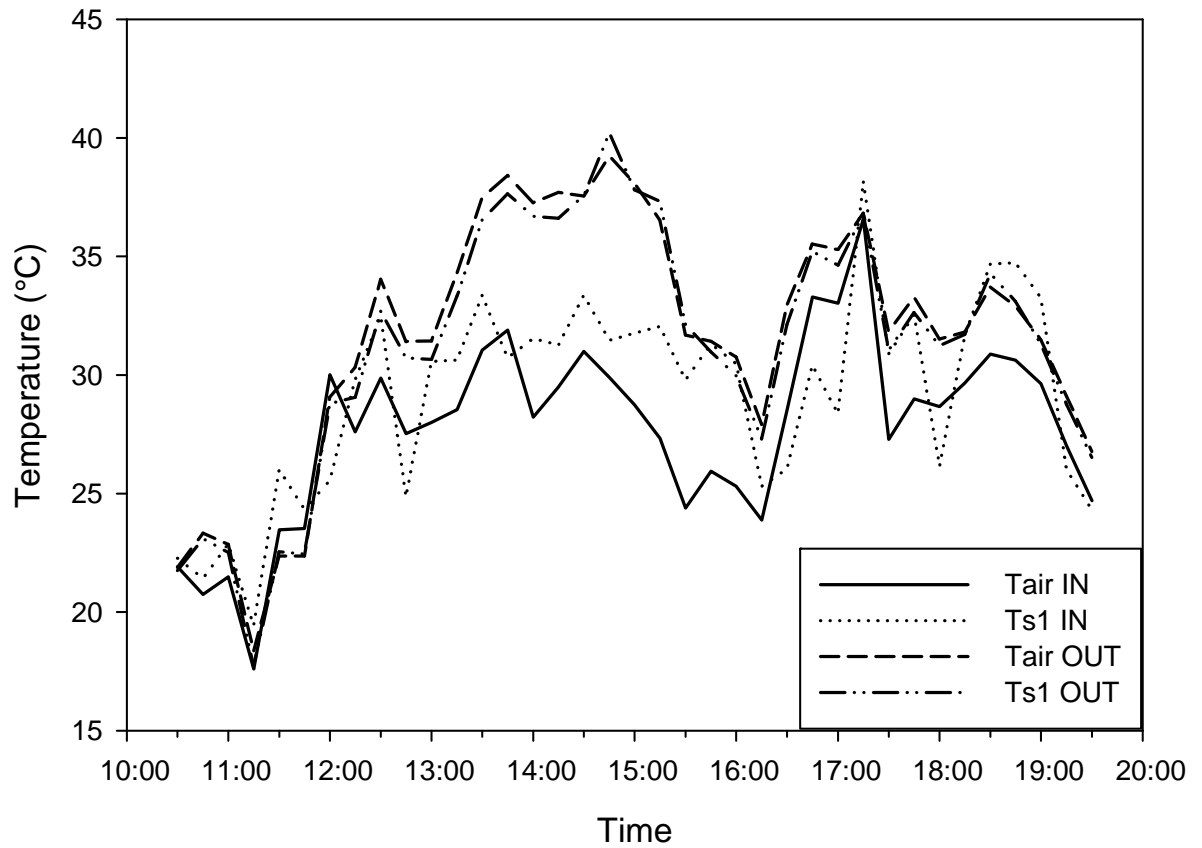


Figure 22: Air (Tair) and seedling (Ts1) temperatures of needle clusters at enclosure and control plots of site 12 on June 20, 2006 between 10:00AM and 7:30PM.

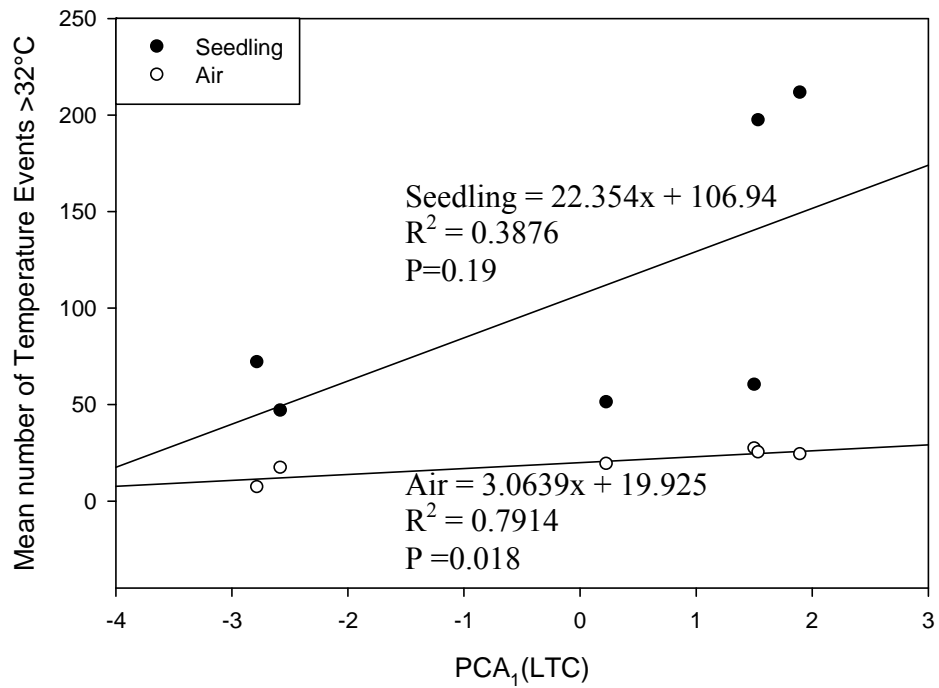


Figure 23: Relationship between the average number of temperature events greater than 32°C experienced by seedling and air thermistors and the light, temperature, and cover principle component (PCA₁(LTC)).

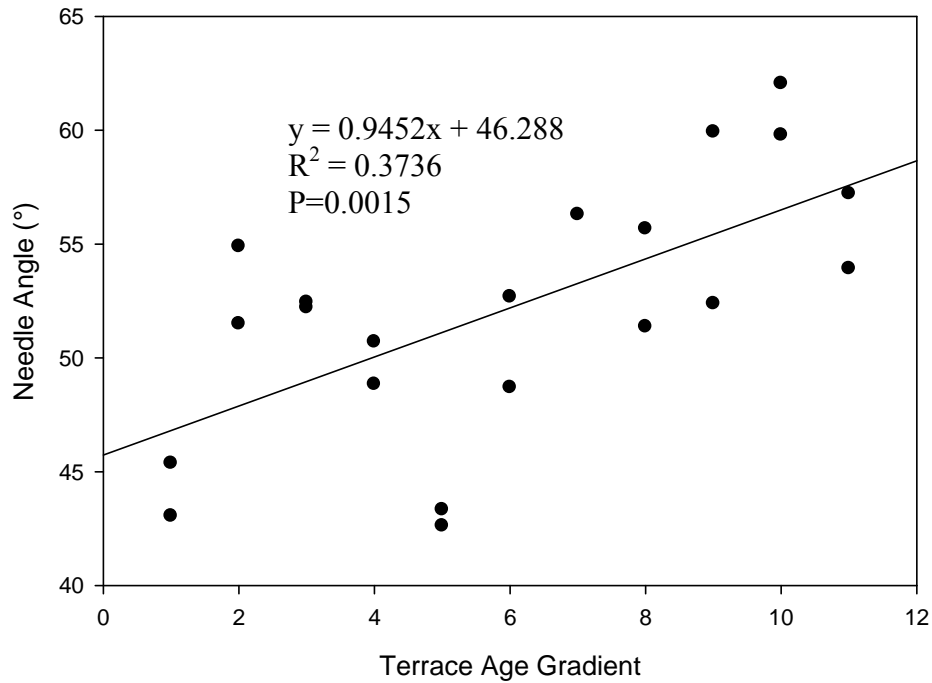


Figure 24: Average needle angle (° from horizontal) of white spruce needles along the terrace age gradient.

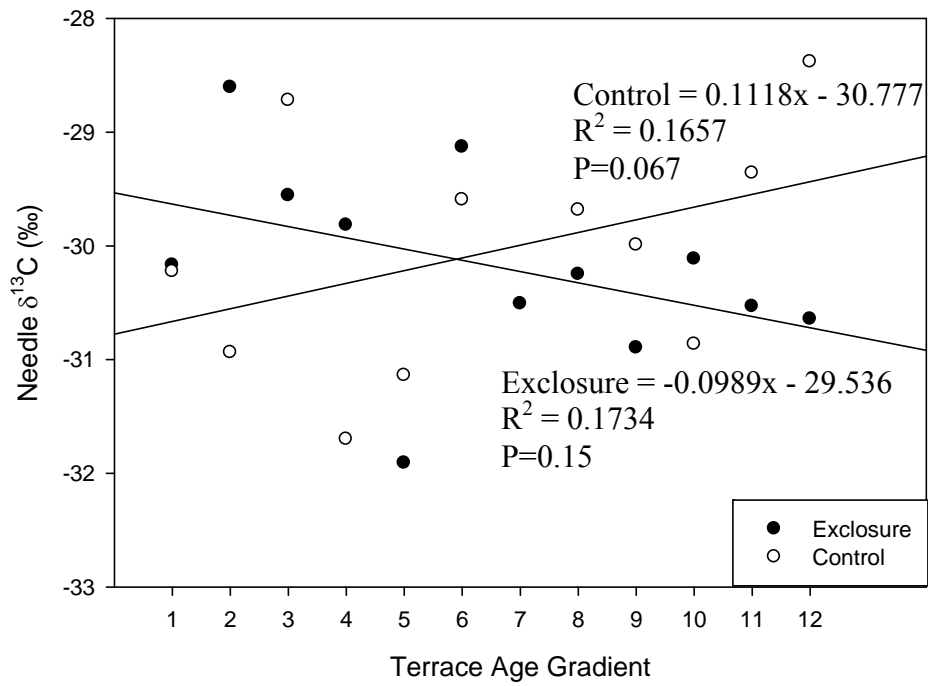


Figure 25: Foliar $\delta^{13}\text{C}$ values of spruce seedlings at exclosure and control sites along the terrace age gradient.

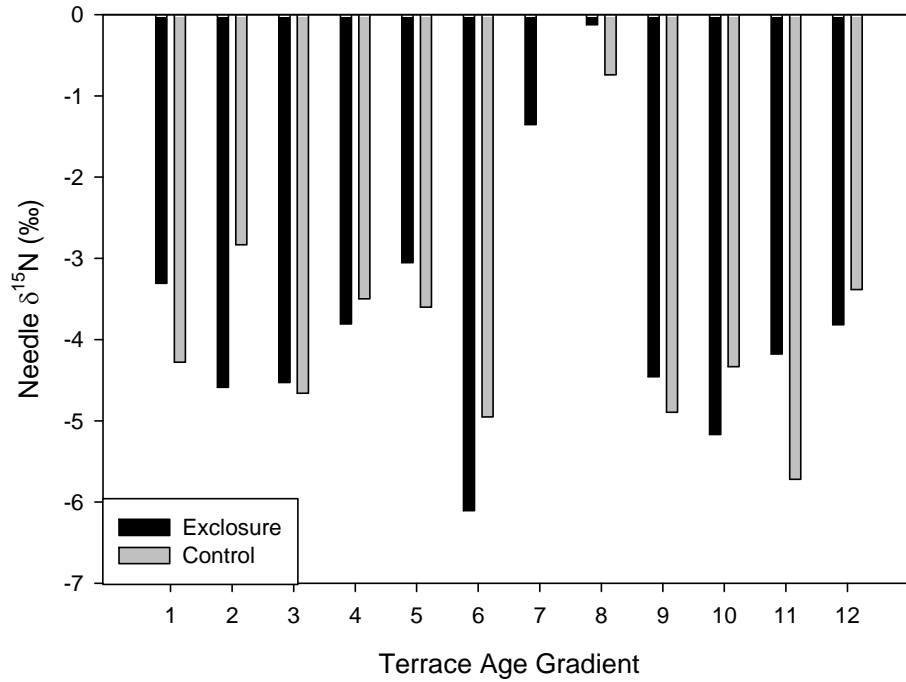


Figure 26: $\delta^{15}\text{N}$ values of spruce needles at exclosure and control sites along the terrace age gradient.

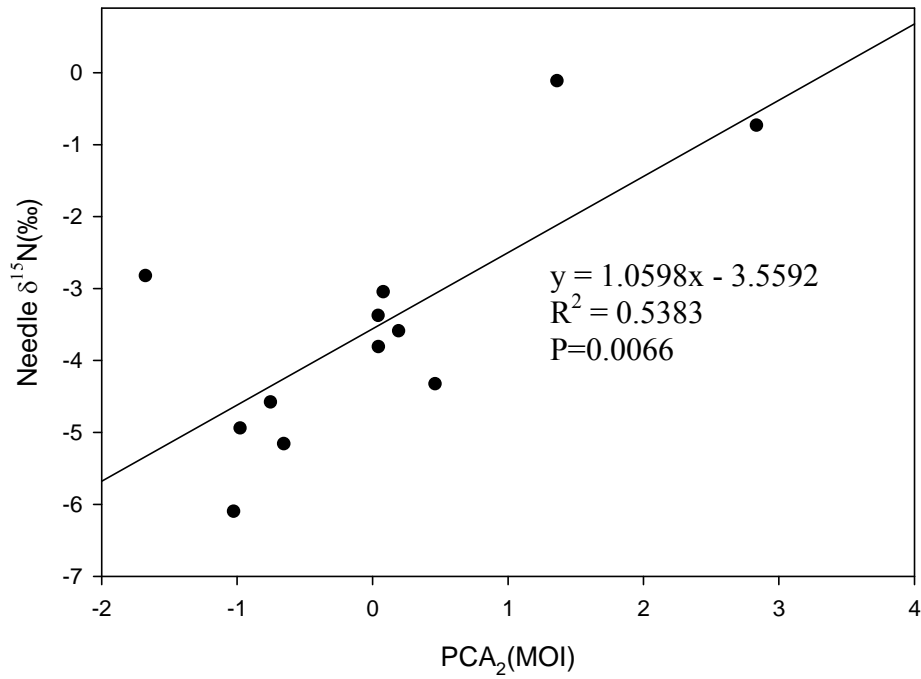


Figure 27: Relationship between the foliar $\delta^{15}\text{N}$ values of spruce seedlings and the moisture principle component (PCA₂(MOI)).

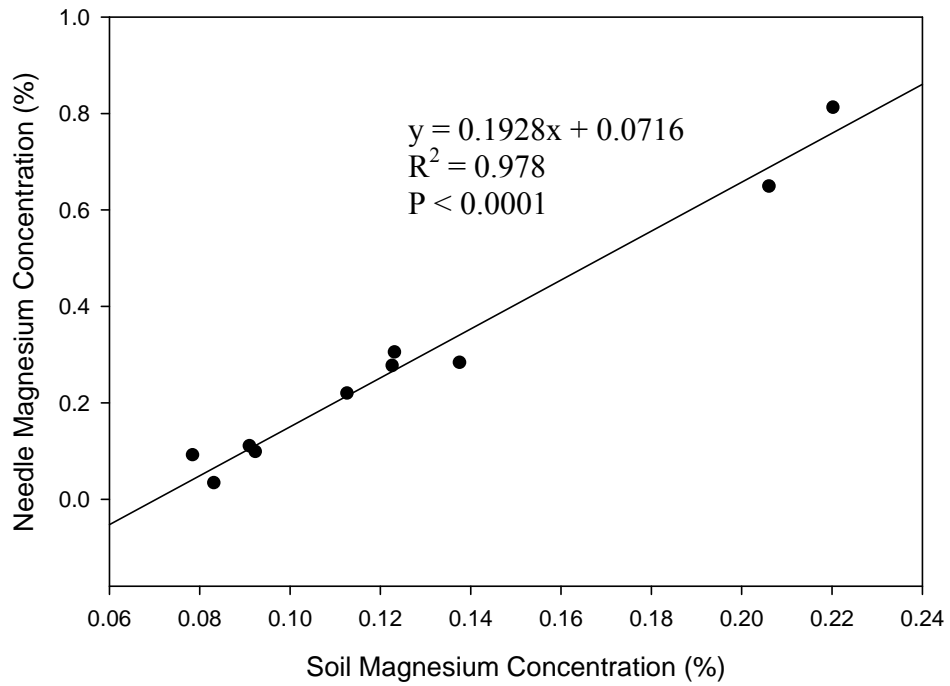


Figure 28: Soil magnesium concentrations versus the magnesium concentrations of needles on spruce seedlings.

Tables:

Table 1: The relationship between the terrace age gradient rankings of enclosure and control plots and their estimated ages.

<i>Terrace Age Gradient Rank</i>	<i>Estimated Terrace Age (yrs)</i>
1	4
2	7
3	7
4	10
5	10
6	12
7	15
8	15
9	20
10	20
11	22
12	26

Table 2: 2006 seasonal mean temperature ($^{\circ}\text{C}$), low daily relative humidity (%), and PAR ($\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at enclosure (Ex) and control (Ct) plots along the terrace gradient.

<i>Gradient #</i>	<i>Ex/Ct</i>	<i>Temperature</i> ($^{\circ}\text{C}$)	<i>Low RH</i> (%)	<i>PAR</i> ($\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
2	Ex	15.62	46.83	322.70
	Ct	15.67	46.45	387.75
5	Ex	15.50	48.34	320.27
	Ct	15.61	47.90	360.06
6	Ex	15.61	48.48	372.53
	Ct	15.79	47.31	335.20
8	Ex	15.24	51.81	230.85
	Ct	15.31	55.82	356.62
10	Ex	14.58	48.50	292.90
	Ct	14.60	47.32	172.78
12	Ex	14.74	47.67	147.25
	Ct	14.09	47.46	286.78

Table 3: Volumetric soil moisture (%) at exclosure and control plots on the Tanana River floodplain (Mean±StD). P-values are from studentized t-tests (1: Gradient 10 only represents soil moisture from May 27 – July 7, 2006 due to sensor damage outside n=6).

<i>Gradient #</i>	<i>Exclosure (%)</i>	<i>Control (%)</i>	<i>p-value</i>
2	21.2 (±11)	15.3 (±7)	0.1
5	32.9 (± 3)	33.7 (±6)	0.61
6	16.0 (± 10)	26.1 (±11)	0.018
8	30.3 (±2)	35.6 (±2)	<0.0001
10 ₁	11.4 (±8)	23.6 (± 5)	0.012
12	24.4 (±1)	22.6 (±3)	0.036

Table 4: Eigenvalues from the principle component analysis showing the amount of variation explained by the principle components.

<i>Principle Component</i>	<i>Eigenvalue</i>	<i>Proportion</i>	<i>Cumulative</i>
1	3.56	0.59	0.59
2	1.45	0.25	0.84
3	0.62	0.10	0.94

Table 5: Eigenvectors showing direction and strength for each environmental measurement as they relate to the two major principle components.

<i>Environmental Variable</i>	<i>Principle Component 1</i>	<i>Principle Component 2</i>
Temperature	0.47	-0.18
Cumulative PAR	0.47	0.10
Soil Moisture	0.21	0.60
Low Relative Humidity	0.14	0.72
Total Cover	-0.51	0.16
Shrub Cover	-0.48	0.23

Table 6: Cover of shrub species (%) over the spruce seedlings, averaged between enclosure and control plots, along the terrace gradient. Species key: SAIN: *Salix interior*, SAAL: *Salix alaxensis*, SABR: *Salix brachycarpa*, SANO: *Salix novae-angilae*, SALA: *Salix lasiandra*, ALTE: *Alnus tenuifolia*, POBA: *Populus balsamifera*, PIGL: *Picea glauca*, SHCA: *Sheperdia canadensis*, and LALA: *Larix laricina*.

Species	Terrace Gradient #											
	1	2	3	4	5	6	7	8	9	10	11	12
	4.09	3.54	5.12	11.31	9.18	13.75	0	2.14	0.31	0.58	8.03	1.25
SAIN	2.02	0	0	0	0	0	25.21	10.68	4.04	0	0	0
SAAL	0.14	0	0	0	0	0	0	2.85	7.03	6.7	0.61	18.7
SABR	0.33	0	0	0	0.26	0	0.3	1.58	5.27	0.23	0	1.87
SANO	0.35	0	0	0	0	0.19	4.29	1.8	1.26	0.77	0	0
SALA	0.23	0	0	0	0.07	0	1.85	4.74	12.32	32.03	0	5.74
ALTE	0	2.43	3.99	0.31	2.89	4.73	0.23	0.67	3.36	4.5	2.01	11.5
POBA	0	0	0	0	0	0.07	0	0	0	0	0.14	0
PIGL	0	0	0	0	0	0	0	0	0	0	0	0.09
SHCA	0	0	0	0	0	0	0	0	0	0	0	0
LALA	0	0	0	0	0	0	0	0	0	0.31	0	0
TOTAL	7.16	5.97	9.11	11.62	12.4	18.74	31.88	24.46	33.59	45.12	10.8	39.2

Table 7: Concentrations of potassium, calcium, magnesium, and phosphorous in spruce needles. Values from exclosure and control plots were pooled. Data presented as mean (\pm SE).

<i>K (%)</i>	<i>Ca (%)</i>	<i>Mg (%)</i>	<i>P (%)</i>
0.52 (\pm 0.027)	0.53 (\pm 0.036)	0.13 (\pm 0.016)	0.11 (\pm 0.0054)

Table 8: 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 minutes.

<i>Terrace Age</i>	<i>Seedling In</i>	<i>Air In</i>	<i>Seedling Out</i>	<i>Air Out</i>
Young (Site 5)	60	27	197	25
Middle (Site 9)	51	19	211	24
Older (Site 12)	71	7	46	17

Appendices:

Appendix 1: Frequency of shrub and herb species at each enclosure and control plot on the Tanana River. Enclosure number (Ex), as opposed to the gradient age number, labels each site. Use enclosure conversion table below to determine the terrace age relative to this study.

Shrub Species Key:Herbaceous Species Key:

<i>Abbreviation</i>	<i>Scientific Name</i>	<i>Abbreviation</i>	<i>Scientific Name</i>
SAIN	<i>Salix interior</i>	EQSP	<i>Equisetum</i> spp.
SAAL	<i>Salix alaxensis</i>	CACA	<i>Castilleja caudata</i>
SABR	<i>Salix brachycarpa</i>	SOCA	<i>Solidago canadensis</i>
SANO	<i>Salix novae-angilae</i>	ANT	<i>Antennaria pulcherrima</i>
SALA	<i>Salix lasiandra</i>	CASP	<i>Carex</i> spp.
POBA	<i>Populus balsamifera</i>	ACBO	<i>Achillea borealis</i>
ALTE	<i>Alnus tenuifolia</i>	TAOF	<i>Taraxacum officinale</i>
PIGL	<i>Picea glauca</i>	CASP	<i>Calamagrostis</i> spp.
SHCA	<i>Sheperdia canadensis</i>	MOSS	Moss
LARIX	<i>Larix laricina</i>	EPAN	<u><i>Epilobium angustifolium</i></u>
		PYAS	<i>Pyrola asarifolia</i>
		PYSE	<i>Pyrola secunda</i>
		LIVE	Liverwort
		HEAL	<i>Hedysarum alpinum</i>

Terrace Age Gradient versus Enclosure Number:

<i>Exclosure</i>	<i>Gradient</i>
1	1
2	11
3	5
4	4
5	12
6	8
7	7
8	10
9	9
10	3
11	6
12	2

Ex 1 In Summary Statistics				Ex 1 In Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	119.0	40.00	4.15	EQSP	20	66.67	0.70
SANO	5.5	12.00	0.19	CACA	10	20.00	0.35
SAAL	106.5	36.00	3.71	SOCA	10	6.67	0.35
SABR	8.0	4.00	0.28	CASP	2	6.67	0.07
SALA	20.0	8.00	0.70	TOTAL	42	100.00	1.46
TOTAL	259.0	100.00	9.03				
Ex 1 Out Summary Statistics				Ex 1 Out Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	115.5	55	4.03	EQSP	99.50	85.71	3.47
SANO	13.5	30	0.47	CACA	4.50	9.52	0.16
SAAL	9.5	5	0.33	CASP	2.00	4.76	0.07
ALTE	13	10	0.45	TOTAL	106.00	100.00	3.70
Ex 2 In Summary Statistics				Ex 2 In Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	310.5	89.19	10.83	TOAF	32.50	12.28	1.13
POBA	110	8.11	3.84	EQSP	79.00	52.63	2.75
SABR	35	2.70	1.22	CASP	14.00	10.53	0.49
TOTAL	455.5	100.00	15.88	MOSS	95.00	24.56	3.31
				TOTAL	220.50	100.00	7.69
Ex 2 Out Summary Statistics				Ex 2 Out Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	150.0	88.89	5.23	EQSP	215.5	85.00	7.51
POBA	5.5	5.56	0.19	MOSS	52.5	15.00	1.83
PIGL	8.0	5.56	0.28	TOTAL	268	100.00	9.34
TOTAL	163.5	100.00	5.70				
Ex 3 In Summary Statistics				Ex 3 In Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	196.0	67.86	6.83	EQSP	169.5	53.13	5.91
POBA	95.0	28.57	3.31	CACA	58.5	37.50	2.04
SANO	15.0	3.57	0.52	PYSE	2	3.13	0.07
TOTAL	306.0	100.00	10.67	MOSS	3	3.13	0.10
				LIVE	5	3.13	0.17
				TOTAL	238	100.00	8.30

Ex 3 Out Summary Statistics				Ex 3 Out Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	330.5	54.55	11.52	EQSP	264.5	50.00	9.22
POBA	70.5	42.42	2.46	CACA	134.5	47.73	4.69
ALTE	4	3.03	0.14	CASP	4	2.27	0.14
TOTAL	405	100.00	14.12	TOTAL	403	100.00	14.05
Ex 4 In Summary Statistics				Ex 4 In Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	180	100.00	6.28	CACA	109	78.57	3.80
TOTAL	180	100.00	6.28	CASP	11	14.29	0.38
				EQSP	5	7.14	0.17
				TOTAL	125	100	4.3584
Ex 4 Out Summary Statistics				Ex 4 Out Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	468.5	84.62	16.34	CACA	51	52.94	1.78
POBA	17.5	15.38	0.61	EQSP	45	41.18	1.57
TOTAL	486	100.00	16.95	HEAL	30.5	5.88	1.06
				TOTAL	126.5	100.00	4.41
Ex 5 In Summary Statistics				Ex 5 In Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	71.5	11.11	2.49	EQSP	620.5	64.52	21.64
SABR	704.5	36.51	24.56	MOSS	279	24.19	9.73
POBA	330.5	44.44	11.52	ANT	23	6.45	0.80
ALTE	7	3.17	0.24	SOCA	9.4	3.23	0.33
SANO	31	4.76	1.08	PYAS	2	1.61	0.07
TOTAL	1145	100.00	39.91	TOTAL	933.9	100.00	32.56
Ex 5 Out Summary Statistics				Ex 5 Out Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SABR	368.5	27.40	12.85	EQSP	55.5	36.49	1.94
POBA	331.5	39.73	11.56	MOSS	514.5	51.35	17.94
SANO	76	6.85	2.65	ACBO	2.5	2.70	0.09
ALTE	322.5	21.92	11.24	SOCA	14.5	5.41	0.51
SAIN	19	2.74	0.66	PYAS	1	1.35	0.03
SHCA	5	1.37	0.17	EPAN	4	1.35	0.14
TOTAL	1123	100.00	39.14	PYSE	3	1.35	0.10
				TOTAL	595	100.00	20.75

Ex 6 In Summary Statistics				Ex 6 In Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	69.5	17.74	2.42	EQSP	176	65.63	6.14
SAAL	483.5	51.61	16.86	CASP	59.5	21.88	2.07
SANO	43.5	6.45	1.52	ACBO	13.5	6.25	0.47
SALA	23	3.23	0.80	CASP	2	1.56	0.07
SABR	8	1.61	0.28	EPAN	10	4.69	0.35
POBA	38.5	4.84	1.34	TOTAL	261	100.00	9.10
ALTE	194	14.52	6.76				
TOTAL	860	100.00	29.99				
Ex 6 Out Summary Statistics				Ex 6 Out Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	53	20.00	1.85	EQSP	198.5	70.77	6.92
SAAL	129	30.00	4.50	CASP	45.5	23.08	1.59
SABR	155.5	15.00	5.42	ACBO	5.5	3.08	0.19
SANO	47	10.00	1.64	EPAN	2.5	1.54	0.09
SALA	80.5	10.00	2.81	ANT	2.5	1.54	0.09
ALTE	78	15.00	2.72	TOTAL	254.5	100.00	8.87
TOTAL	543	100.00	18.93				
Ex 7 In Summary Statistics				Ex 7 In Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAAL	787	85.48	27.44	EQSP	92.5	70.37	3.23
SALA	246	11.29	8.58	CASP	21	14.81	0.73
ALTE	7	3.23	0.24	ACBO	16.5	11.11	0.58
TOTAL	1040	100.00	36.26	ANT	2.5	3.70	0.09
				TOTAL	132.5	100.00	4.62
Ex 7 Out Summary Statistics				Ex 7 Out Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAAL	659	66.67	22.98	EQSP	325	68.35	11.33
SABR	9	5.13	0.31	CASP	65	22.78	2.27
SANO	17	2.56	0.59	MOSS	50	5.06	1.74
ALTE	99	23.08	3.45	ACBO	4.5	2.53	0.16
POBA	13	2.56	0.45	ORCHID	1	1.27	0.03
TOTAL	797	100.00	27.79	TOTAL	445.5	100.00	15.53

Ex 8 In Summary Statistics				Ex 8 In Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	17	4.08	0.59	EQSP	448.5	78.43	15.64
SABR	289.5	22.45	10.09	CASP	7	3.92	0.24
POBA	90.5	16.33	3.16	ANT	15.5	5.88	0.54
ALTE	484.5	57.14	16.89	PYAS	5.5	7.84	0.19
TOTAL	881.5	100.00	30.74	EPAN	5	3.92	0.17
				TOTAL	481.5	100.00	16.79
Ex 8 Out Summary Statistics				Ex 8 Out Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SAIN	16	2.74	0.56	EQSP	293	68.89	10.22
SABR	95	9.59	3.31	CASP	8	4.44	0.28
SALA	44	5.48	1.53	PYAS	14.5	8.89	0.51
SANO	13	1.37	0.45	ANT	21	8.89	0.73
POBA	167.5	13.70	5.84	EPAN	8	2.22	0.28
ALTE	1353	65.75	47.18	MOSS	15	6.67	0.52
LARIX	18	1.37	0.63	TOTAL	359.5	100.00	12.53
TOTAL	1707	100.00	59.50				
Ex 9 In Summary Statistics				Ex 9 In Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SABR	109	16.39	3.80	EQSP	112.97	72.00	3.94
SAAL	143.5	11.48	5.00	MOSS	374	18.00	13.04
SANO	116.5	22.95	4.06	PYAS	12	4.00	0.42
SAIN	18	3.28	0.63	CASP	6	2.00	0.21
POBA	95.5	14.75	3.33	ANT	1.5	2.00	0.05
ALTE	648.5	31.15	22.61	HEAL	14	2.00	0.49
TOTAL	1131	100.00	39.44	TOTAL	520.47	100.00	18.15
Ex 9 Out Summary Statistics				Ex 9 Out Herb Summary Statistics			
Species	Cover	Frequency	% Cover	Species	Cover	Frequency	% Cover
SABR	294.5	39.34	10.27	EQSP	327	65.38	11.40
SAAL	88	6.56	3.07	MOSS	64	7.69	2.23
SANO	186	14.75	6.49	PYAS	65.5	23.08	2.28
SALA	72.5	4.92	2.53	ANT	3	1.92	0.10
POBA	97.5	22.95	3.40	HEAL	2.5	1.92	0.09
ALTE	58	11.48	2.02	TOTAL	462	100.00	16.11
TOTAL	796.5	100.00	27.77				

