

Light and temperature differentially colimit subalpine fir and Engelmann spruce seedling growth in partial-cut subalpine forests

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Abstract: We compared the relative impacts of light, soil N, and soil temperature on Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) seedling growth by quantifying (i) microsite environment–growth relationships for N-fertilized and unfertilized planted seedlings in shelterwood, patch cut, and clearcut harvest treatments and (ii) growth, photosynthesis, and biomass allocation for greenhouse-grown seedlings at 5, 10, and 15 °C soil temperatures. Fertilization did not affect seedling growth. Furthermore, soil N availability did not vary among harvest treatments. In contrast, clearcut compared with shelterwood seedlings had greater mass (fivefold), light availability (twofold), and soil temperatures (1.6 °C). Across harvest treatments, spruce and fir mass increased linearly to 100% open-sky light ($R^2 = 0.51$ and 0.57 , respectively), and temperature and light combined explained more variation in mass than light alone (adjusted $R^2 = 0.58$ for both species). Spruce growth was more sensitive to temperature than fir in both field and greenhouse experiments. Diminished growth at low soil temperature was associated with lower photosynthesis and not lower leaf fraction. Thus, soil temperature and light colimit seedling growth in subalpine forests, but responses were species-specific and consistent with microenvironment differences in spruce and fir regeneration niches.

Résumé : Nous avons comparé l'impact relatif de la lumière, de l'azote du sol (N) et de la température du sol sur la croissance de semis d'épinette (*Picea engelmannii* Parry ex Engelm.) et de sapin (*Abies lasiocarpa* (Hook.) Nutt.) en quantifiant : (i) les relations environnement-croissance à l'échelle du microsite pour des semis fertilisés ou non en N dans des traitements de récolte par coupe progressive, par coupe par trouées et par coupe totale et (ii) la croissance, la photosynthèse et l'allocation de la biomasse pour des semis élevés en serre à des températures du sol de 5, 10 et 15 °C. La fertilisation n'a pas affecté la croissance des semis. De plus, la disponibilité en N du sol n'a pas varié entre les traitements de récolte. Par contre, les semis de la coupe à blanc, comparés à ceux de la coupe progressive, avaient une plus grande masse (cinq fois), une plus forte disponibilité en lumière (deux fois) et des températures du sol plus élevées (1,6 °C). La masse de l'épinette et du sapin augmentait linéairement jusqu'à une intensité lumineuse correspondant à 100 % de la lumière à découvert ($R^2 = 0,51$ et $0,57$ respectivement) pour tous les traitements de récolte confondus. La combinaison lumière-température expliquait une plus grande part de la variation de la masse que la lumière seule (R^2 ajusté = 0,58 pour les deux espèces). La croissance de l'épinette était plus sensible à la température que celle du sapin dans les traitements au champ et en serre. Une croissance réduite due à une température basse du sol était associée avec une photosynthèse plus faible mais pas à une plus faible fraction du feuillage. Ainsi, la température du sol et la lumière contribuent ensemble à la croissance des semis dans les forêts subalpines, mais les réponses sont spécifiques et conformes aux différences micro-environnementales entre les niches de régénération de l'épinette et du sapin.

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Introduction

Residual trees left following partial harvest may decrease tree regeneration growth by decreasing light availability (Wright et al. 1998). However, in subalpine forests, their effects on seedling growth may involve more than light effects alone, since light may covary with other limiting factors such as soil temperature and nutrients. Growing season soil temperatures in subalpine forests are often in the range (about 5–15 °C) that can limit growth (Karlsson and Nordell 1996; Lyr 1996; Körner 1998), and temperatures can be 2–7 °C cooler beneath closed forest canopies than in clearcuts (Hungerford 1979; Goldstein and Trowbridge 1985; Junttila and Nilsen 1993; Jull and Stevenson 2001). In other cold ecosystems, fertilization experiments have demonstrated N-

limited productivity in some cases (e.g., alpine vegetation, Bowman et al. 1993; sub-boreal spruce plantations, Swift and Brockley 1994; sub-boreal pine plantations, Brockley 1989) but not others (alpine meadow, Ram et al. 1991; alpine shrub community, Paal et al. 1997), and little is known about nutrient limitations in the subalpine spruce–fir forests of western North America. However, organic matter decomposition and mineralization rates are temperature-limited processes, and trees retained in partial harvests could decrease N mineralization, and thus N supply to seedlings, relative to clearcuts, in part by decreasing temperature (Van Cleve et al. 1983; Nadelhoffer et al. 1991; Fisk and Schmidt 1995; Weih and Karlsson 1999).

Thus, fragmentary information suggests that tree seedlings in subalpine forests are limited by multiple environmental factors and these limitations may be greater in partial harvests than in clearcuts and greater than in forests at lower elevations and latitudes. However, the overall magnitude of these limitations and the relative contributions of N, temperature, and light to growth limitation are unknown. This study was undertaken to address these issues. Our specific objectives were to (i) compare seedling microsite soil temperatures, light, soil N availability, and growth of N-fertilized and unfertilized planted Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) seedlings among shelterwood, patch cut, and clearcut harvest treatments, (ii) quantify the factors contributing to growth limitations by examining relationships of environmental factors with seedling growth for individuals without regard to harvest treatments, and (iii) isolate the effects of temperature on growth and associated physiology and morphology by comparing growth, photosynthesis, and biomass allocation patterns for first-year seedlings of the same species grown at three root temperatures spanning the range of growing season field temperatures (5, 10, and 15 °C).

We accomplished these objectives with complementary greenhouse and field experiments. Objectives (i) and (ii) were addressed in the field at Lucille Mountain Silvicultural Systems Project using experimental shelterwood, patch cut, and clearcut treatments planted with spruce and fir seedlings 6 years prior to this study. Objective (iii) was addressed in a greenhouse experiment because we expected that light, soil temperature, water, and N availability would strongly covary in the field, making it difficult to isolate the independent effects of temperature on seedling performance.

Materials and methods

Field study

Study site and seedlings

The study area and harvest treatments are described in detail in Jull and Stevenson (2001). In brief, the field study area is located in the moist, mild, Engelmann Spruce – Subalpine Fir biogeoclimatic subzone (ESSFmm1) (Coupé et al. 1991) on Lucille Mountain in north-central British Columbia, Canada (53°18'N, 120°14'W). The study area's aspect is north to northeast, with elevations ranging from 1340 to 1585 m above sea level and slope gradients of 15%–40%. The climate of the area is moist and cool, with infrequent

growing season frosts. Snowpacks usually develop by mid-October and last to mid-June.

The soils are poorly sorted, noncompacted glacial tills overlying metamorphic (phyllite and schist) bedrock at depths below 1 m. The uncut forests are multiaged and multistoried and are dominated by subalpine fir (80% by basal area) and Engelmann spruce (20% by basal area). A well-represented shrub layer is dominated by white flowered rhododendron (*Rhododendron albiflorum* Hook.), false azalea (*Menziesii ferruginea* Smith), and black huckleberry (*Vaccinium* spp.).

Three harvest treatments were implemented in the winter of 1991–1992. These were one 32-ha clearcut, fourteen 0.2-ha (45 m × 45 m) patch cuts dispersed in a checkerboard pattern in an approximately 5.6-ha treatment area, and one 15-ha irregular shelterwood (47% volume removal). In summer 1992, several 40 m × 40 m research plots were established in the harvest treatments and planted at 1-m spacing in alternating east–west oriented rows with summer lifted spruce (2 + 0, grown in PSB 313B styroblocks) and fir (2 + 1 bare-root transplants after 2 years in PSB 415B styroblocks) seedlings. The remainder of the trial was operationally planted in spring 1994.

In early June 1997, 5 years after planting, eight 40 m × 40 m seedling research plots were chosen for study. Three plots were randomly chosen in the shelterwood treatment. Three plots were randomly chosen in the patch cut site, each in a separate 0.2-ha patch. The only two plots in the clearcut, which were 100 m apart, were used. About 30 seedlings per species were sampled in each of four randomly selected rows in each plot. We fertilized every second sampled seedling in each row in early June 1997 and 1998 with 25 g of 20:6:12 N–P–K with complete essential micronutrients, applied within a perimeter that was 50% greater than the seedling crown. This amount corresponded to about 200 kg N·ha⁻¹·year⁻¹ for a seedling of average size. The distance between seedlings that we chose for the study was always ≥2 m to provide sufficient distance to prevent lateral movement of fertilizer between fertilized and unfertilized seedlings.

Environmental characteristics of seedling microsites

Soil temperatures were measured on every seedling microsite at 7.5 and 15 cm depth with a handheld thermocouple thermometer (HH-KC; Omega, Laval, Que.) and utility probe (KHSS-14G-RSC-12-NP; Omega). These depths encompassed the distribution of most seedling roots, as determined from a small number of excavated seedlings. Measurements were taken between 1300 and 1500 seven times over the growing season in 1998.

Light availability was estimated by analyzing hemispherical photographs taken above each seedling in summer. Gap light index (GLI), an index of growing season light availability, was computed from each photograph using GLI/C 2.0 software following Canham (1988). A competition index (CI) was also determined for each seedling as $CI = \sum(\text{basal area}/\text{distance})$, where CI is the sum of the basal areas of each tree ≥2 m tall, within 10 m of the subject seedling, weighted by the inverse of each tree's distance to the subject seedling (Lorimer 1983). Acronyms and units for these and other metrics are summarized in Table 1.

Table 1. Abbreviation, full name, and units for environmental variables and growth analysis terms used in this paper.

Variable abbreviation	Variable name	Units
GLI	Gap light index	% of available light
CI	Competition index ($\sum(\text{basal area}/\text{distance})$)	$\text{cm}^2 \cdot \text{m}^{-1}$
LMR	Leaf mass ratio (mass leaves/total plant mass)	$\text{g} \cdot \text{g}^{-1}$
RMR	Root mass ratio (mass roots/total plant mass)	$\text{g} \cdot \text{g}^{-1}$
RGR	Relative growth rate	$\text{mg} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$
A_{max}	Light saturated photosynthetic rate	$\text{nmol CO}_2 \cdot \text{g}^{-1} \cdot \text{s}^{-1}$

Nitrogen mineralization rates were determined by in situ incubation of soil cores (for details, see Rees et al. 1994) for two incubation periods, 30 May – 30 June and 28 July – 28 August 1998. Soil N was not determined for each seedling because of cost and sampling limitations. Instead, in patch cut plots, four transects perpendicular to each side of the opening were established with N sample points at –8 m (into the intact forest), 0 m (at the harvest edge), +8 m, and +16 m (from the harvest edge into the patch cut). In shelterwood plots, the three parallel transects had sample points at –8, 0, +8, +16, and +24 m. For the clearcut, one transect was established in each seedling plot and four sample points were located at 8-m intervals. This sampling design was established to both provide representative values for each harvest treatment and to characterize the effects of variation in overstory tree density on N dynamics.

At each sample point, ten 5.08 cm diameter \times 20.0 cm deep soil cores were taken using PVC tubes. Five of the cores were left in place, in the tube, covered with loose-fitting plastic cups to prevent leaching and allowed to incubate for 30 days. The other five were bulked in the field, transported to the University of Northern British Columbia, and stored at 4 °C for <48 h. Soils were then sieved to exclude the >5 mm fraction, water content was determined, and initial 1 mol/L KCl extractable pools of NH_4^+ -N and NO_3^- -N were analyzed colorimetrically by the Renewable Resources Department, University of Alberta, Edmonton, Alta. The differences in NO_3^- -N and NH_4^+ -N between initial and incubated samples were used to calculate net rates of nitrification and ammonification. Extractable pools and net rates of dissolved organic N (DON) production were determined for the same cores that were used for mineral N, but only for the 30 July – 30 August incubation period, on two of the transects in each patch cut and shelterwood plot and the two clearcut transects. The protocol was similar to that for mineral N except samples were extracted with deionized water and were filtered (0.2- μm opening) to remove microbes. Each sample was subsampled and analyzed for total N following persulfate digestion and for mineral N (as described above). DON was calculated as total N minus mineral N.

Seedling characteristics

All 512 experimental seedlings were harvested in autumn 1998. Height was measured before a stem segment was removed from the base of each seedling. Segments were air-dried and finely sanded and annual ring widths were measured on three radii, excluding bark, with a digital image analysis system (WinDendroTM, Regent Instruments Inc.,

Blain, Que.). From these measurements, average ring width growth rates and total diameter inside bark were calculated.

As a subset of the 512 seedlings, three to six unfertilized whole seedlings of each species were excavated from three locations: clearcut, <2 m from the bole of a large tree in a shelterwood, and >2 and <5 m from the bole of a large tree in a shelterwood. These strata were chosen to obtain a broad range of seedling sizes. In another subset, total aboveground portions were harvested for 10 seedlings per species per plot in the partial-cut treatments and 20 seedlings per species per plot in the clearcut ($n = 190$ seedlings total). Harvested plants were separated into needles, stems, and, if harvested, roots, oven-dried at 70 °C, and weighed. Foliage N was measured on all seedlings in the aboveground harvest subset with a CHN analyzer (Carlo-Erba, Milan, Italy) at the Department of Forestry, Michigan State University, East Lansing, Mich.

Statistical analyses

For analyses of the effects of harvest treatments on environmental and seedling variables, treatment replicates were considered the experimental units and individual seedlings and environmental characteristics measured on individual microsites were considered subsamples. Two-way analysis of variance (ANOVA) was used to test species and harvest treatment effects. For significant effects ($\alpha < 0.05$), Tukey–Kramer HSD tests were used to identify significantly different means among harvest treatments within species, and Student's *t* test was used to identify significant differences among species means within harvest treatments. For treatment effects on standing pools and production rates of mineral and organic N, we included only data from treatment interior sample points (i.e., 8 and 16 m in patch cuts; 8, 16, and 24 m in shelterwoods; and all points in clearcuts). Nitrogen data were not normally distributed, and transformations did not markedly improve distributions (Shapiro–Wilk *W* test, $P < 0.001$ in all cases). Thus, nonparametric Kruskal–Wallis tests were used to identify significant differences in soil N characteristics among harvest treatments.

Individual and combined effects of environmental variables on seedling size and growth characteristics were analyzed with least squares simple and multiple linear regressions. For these analyses, seedlings and seedling microsite environmental variables were considered experimental units and analyzed without regard to harvest treatments. Justification for this approach was that (i) substantive theory supports continuous seedling growth versus environmental factor relationships and (ii) for our data, within harvest treatments, seedling diameter was significantly ($P < 0.01$) and positively

related to GLI and soil temperature and negatively related to CI in 50% of all cases (data not shown). For regression modeling, logarithm transformations of seedling size data were required to improve homogeneity of variances. Linear and nonlinear bivariate seedling environment versus seedling size relationships were compared. Nonlinear models did not reduce the sum of squares error to less than that for linear models for any variable pair, so linear models were used. Metrics of size (basal diameter)² × height, aboveground mass, and total mass were all used as dependent variables because they scaled strongly with each other and the size of the data sets varied widely among them.

Greenhouse study

Materials and measurements

Seeds were obtained from British Columbia Ministry of Forests registered seed lots collected from the Lucille Mountain area for spruce from 800 and 1300 m above sea level and for fir from 1100 m. These were the closest available seed lots to the Lucille Mountain study site elevation (1340–1585 m). Two spruce seed lot treatments were used to assure that differences among fir and spruce were not confounded by elevation of seed source collection (species–elevation treatment). This was justified because strong differences in growth responses to temperature have been found between seed sources with modest differences in elevation (e.g., 220 m for the high-latitude, high-altitude species *Betula pubescens*) (Weih and Karlsson 1999). Only one seed lot of fir from an acceptable area–elevation was available.

Three circulating water baths (120 cm × 90 cm × 16.5 cm) were constructed with 1.875 cm thick PVC sheeting. Holes were drilled in the top and bottom sheets and open-ended PVC tubes (6 cm in diameter × 15 cm long) were glued between corresponding top and bottom holes. The sheets were then fitted and sealed with insulated side-walls, creating a closed-circulation bath system around the PVC tubes (72 per bath), which remained open, top and bottom, to drain freely. A meshed screen was glued to the bottom ends to hold the growing medium (2:1 v/v mix of pure silica sand and greenhouse soil) in the tubes. To maintain temperature treatments, water was continuously pumped through a baffle system and back to an insulated holding tank equipped with a heating and cooling unit. The three baths were arranged side by side on raised beds in the middle of a polyurethane-covered greenhouse.

The experiment was performed in 1998 and replicated in 1999 because there was no replication of temperature baths within years. On 15 May 1998 and again on 2 June 1999, stratified seeds of each species–elevation treatment were sown in random sequence (24 tubes per species–elevation treatment per bath). Seeds were regularly misted with water and kept at ambient greenhouse light and temperature conditions. When germination was nearly 100% (9 June in 1998 and 24 June in 1999), each bath was covered with 60% transmittance shade cloth houses and watering (twice daily) and fertilization (weekly with 22 mL of 80 ppm 20:8:20 N–P–K with complete micronutrients) commenced. At this time, seedlings were thinned to one per tube (24 per temperature × species–elevation treatment (elevation for spruce only)). Temperature treatments were allocated at random among the three temperature baths, and water bath tempera-

tures were adjusted to the targeted treatment temperatures of 5, 10, and 15 °C over the course of 5 days. The thinned seedlings were completely excavated and were used to determine initial mass for each species–elevation × temperature treatment. In each treatment, eight seedlings were randomly assigned to each of three harvests at 45, 66, and 93 days (90 days in 1999) from the onset of temperature treatments. At harvest, seedlings were separated into leaves, stems, and roots, dried at 70 °C, and then massed. Total dry mass, leaf mass ratio (LMR) (mass of leaves/total plant mass), root mass ratio (RMR) (mass of roots/total plant mass), and relative growth rates (RGR) (milligrams per gram per day) between harvests of total mass and root and shoot fractions were calculated from these samples (Evans 1972).

Soil temperatures were continuously recorded with a data logger (Campbell Scientific 21X, Ogden, Utah) at 2 and 10 cm soil depths in two randomly chosen tubes in each bath. Mean daily temperatures (±1 SD) at 10 cm depth for the 5, 10, and 15 °C baths were 6.3 ± 0.4, 9.9 ± 0.2, and 14.8 ± 0.1 °C, respectively, in 1998 and 5.7 ± 0.2, 11.5 ± 0.4, and 15.2 ± 0.2 °C, respectively, in 1999. Air temperatures were recorded at 5 cm above the soil surface for a centrally located single tube in the 5 and 10 °C baths to determine if cooler baths influenced air temperatures near seedlings. Average air temperatures (±1 SD) above 5 and 10 °C treatments were 18.7 ± 6.7 and 18.6 ± 6.9 °C, respectively, in 1998 and 17.2 ± 6.6 and 17.7 ± 6.9 °C, respectively, in 1999 and were not different from ambient greenhouse temperatures measured distant from the temperature baths. Thus, air temperatures around the seedling canopies were not influenced by soil temperature treatments.

Light-saturated photosynthesis was measured with a LI-COR 6200 portable photosynthesis system (LI-COR Inc., Lincoln, Nebr.) on entire shoots for three seedlings from each species–elevation × temperature treatment immediately preceding the 45-day harvest in both years. At this point, all seedlings had only their first flush of leaves, as many seedlings added a second cohort of leaves later in the experiment. Measurements were taken between 0800 and 1300 at a photosynthetic photon flux density of 2200 μmol·m⁻²·s⁻¹ using an artificial light source (Qbeam 2001, Barneveld, Wis.). Photon flux densities greater than required for light-saturating photosynthesis of individual spruce needles were used to help ensure that all needles in the often overlapping needles of our seedling canopies were light saturated. Photosynthesis was calculated on a leaf mass (A_{\max} (nanomoles of CO₂ per gram of leaf per second)) and whole-plant mass ($A_{\max} \times \text{LMR}$ (nanomoles of CO₂ per gram of whole plant per second)) basis.

Statistical analyses

The experiment had a split-plot design where temperature treatments were assigned randomly to whole unit temperature baths arranged as randomized complete blocks where years were blocks. Species–elevation treatments were then assigned at random to growing tube subunits within temperature bath whole units. With this design, *F* tests of the effects of temperature and blocks (years) used the temperature × blocks interaction (a random effect) mean squares error in the denominator, and *F* tests of the effects of species and species × temperature interactions used residual experimental mean squares error in the denominator (Steel and

Table 2. Growth characteristics of spruce (8 years old) and fir seedlings (9 years old) in three harvest treatments.

Species	Harvest	Inner basal diameter (mm)	1992–1998 diameter increment (mm)	Total height (cm)	Aboveground mass (g)
Spruce	Shelterwood	7.5 (0.02)*c	6.2 (0.02)*c	46.8 (0.02)c	22.4 (0.07)b
	Patch cut	10.5 (0.02)*b	9.1 (0.02)b	67.6 (0.02)b	53.7 (0.11)ab
	Clearcut	16.0 (0.01)a	14.1 (0.01)a	87.1 (0.01)a	147.9 (0.06)a
Fir	Shelterwood	9.9 (0.02)*c	7.7 (0.02)*b	50.1 (0.02)c	34.7 (0.06)c
	Patch cut	12.6 (0.02)*b	9.1 (0.02)ab	74.1 (0.01)b	77.7 (0.04)b
	Clearcut	16.5 (0.01)a	11.0 (0.02)a	89.1 (0.01)a	154.9 (0.03)a

Note: Values are means (± 1 SE) of harvest treatment replicates ($n = 3$ for shelterwood and patch cut and $n = 2$ for clearcut). The means are for log-transformed data that were then back-transformed. Standard errors are log-transformed values. The total numbers of seedlings (subsamples) were 260 and 252 for diameter, diameter increment, and height and 94 and 98 for aboveground mass for spruce and fir, respectively. Means within species and columns followed by a common letter are not significantly different (Tukey–Kramer HSD, $P < 0.05$). Significant differences among species and within harvest treatments are indicated with an asterisk (Student's t test, $P < 0.05$).

Table 3. Seedling microsite light and soil temperature for the three harvest treatments during the 1998 growing season.

Characteristic	Shelterwood	Patch cut	Clearcut
Light availability (%)	46.8 (1.6)c	67.4 (1.5)b	97.0 (0.3)a
Soil temperature (7.5 cm depth) ($^{\circ}$ C)	7.4 (0.1)c	8.1 (0.2)b	9.0 (0.2)a

Note: Values are means (± 1 SE) of harvest treatment replicates ($n = 3$ for shelterwood and patch cut and $n = 2$ for clearcut). Means within rows followed by a common letter are not significantly different (Tukey–Kramer HSD, $P < 0.05$).

Torrie 1980). For plant characteristics with significant effects, differences among temperature treatments and species were tested with Tukey–Kramer HSD.

In addition to using ANOVA to analyze biomass fraction data at a common age (i.e., harvest date), we separated the effects of treatments and plant size on biomass fractions in roots and leaves by analyzing treatment (i.e., temperature, species) differences in \ln root (leaf) mass versus \ln total plant mass relationships. In all cases, these relationships appeared curvilinear and the sum of squares error was lower for second-order polynomial fits than for linear fits. These fitted curves were statistically compared using methods described in Potvin et al. (1990).

Results

Field study

Seedling growth and microsite environment responses to harvest treatments

Two years after first applications, N fertilizer resulted in modest increases in leaf N concentration (1.49% fertilized versus 1.31% unfertilized, species pooled, ANOVA, $P = 0.034$), but leaf N was not affected by species, harvest treatments, or their interactions with fertilization (all $P > 0.1$). Furthermore, N fertilization did not affect any seedling size or growth characteristic for either species (ANOVA, all $P > 0.25$). Thus, the remaining analyses were done without regard to fertilizer treatments.

Harvest treatments significantly affected all seedling size and growth characteristics ($P < 0.0001$) (Table 2). Species effects were only significant for stem diameter ($P = 0.002$) and species by harvest interactions were significant only for 1992–1998 diameter growth ($P = 0.0009$). Seedlings of both species were larger in clearcuts than in shelterwoods and

patch cut seedlings were intermediate (Table 2). Stem diameter growth was 129% greater for spruce and 43% greater for fir in clearcuts than in shelterwoods. Aboveground mass was more variable in partial-cut than in clearcut treatments with mean standard deviations for treatment replicates ($n = 3$ or 2) of 0.30, 0.34, and 0.23 (spruce) and 0.23, 0.32, and 0.14 (fir) for shelterwood, patch cut, and clearcut treatments, respectively.

The harvest treatments affected light availability and soil temperature at seedling microsites. Clearcut seedlings received two times more light and had 1.6 $^{\circ}$ C warmer soils than shelterwood seedlings, and patch cut seedlings were intermediate for both light and soil temperature (Table 3). Soil N characteristics did not differ among harvest treatments (data not shown); however, there were patterns worth noting. KCl-extractable pools of NO_3^- were an order of magnitude lower than NH_4^+ pools, and NH_4^+ pools were an order of magnitude lower than DON pools (overall means = 0.3, 13.5, and 72.0 $\mu\text{g N}\cdot(\text{g soil})^{-1}$, respectively). Trends in net production rates among NO_3^- -N, NH_4^+ -N, and DON were similar to trends in extractable pools, but differences were more modest (e.g., 0.2 $\mu\text{g NH}_4^+\cdot\text{N}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ versus 0.4 $\mu\text{g DON}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$). Median values for extractable pools of all N forms were less than 50% of the mean values presented above because of distributions that were strongly skewed to lower values. In addition to harvest treatment averages, soil N characteristics were also analyzed as functions of transect position (i.e., from mature forest to the middle of harvest openings) and CI, but these relationships were insignificant ($P > 0.1$, data not shown). Thus, residual tree density did not affect soil N dynamics.

Seedling growth as functions of seedling microsite environmental variables

Seedling size and growth were highly correlated with light

Table 4. Pearson product moment correlations among microsite variables and (basal diameter)² × height ($d^2 \times h$) of spruce ($n = 215\text{--}221$) and fir seedlings ($n = 230\text{--}247$).

	Mean soil temperature	Light	CI
Light	0.57		
CI	-0.45	-0.78	
Spruce $d^2 \times h$	0.53	0.70	-0.70
Fir $d^2 \times h$	0.50	0.63	-0.67

Note: Data for microsite variables are for individual seedlings with all harvest treatments and species pooled ($n = 444\text{--}470$). All correlations are significant at $P < 0.001$.

availability and soil temperature; however, light and soil temperature were correlated ($GLI = -44.3 + 13.9(\text{soil temperature})$, $R^2 = 0.33$, $P < 0.0001$, $n = 448$) (Table 4). In a mixed model of seedling size–growth as functions of species, light, soil temperature, and their interactions, species main effects and interactions were nearly always significant (data not shown). Thus, to simplify presentation, models were developed for species separately (Table 5; Fig. 1). For both species, soil temperature and light generally explained a large percentage of the variation in size and growth (Table 5). Pratt indices (Thomas et al. 1998) indicated that light contributed more to explained variation in growth and size than soil temperature for both species and that soil temperature was an important (Pratt index >0.25) predictor independent of light for spruce but it was unimportant (Pratt index <0.25) or marginally important for fir. Furthermore, spruce responded more steeply to soil temperature than fir, as indicated by greater standardized beta weights (partial regression coefficients) (Thomas et al. 1998) for spruce (Table 5). Notably, relationships of seedling size and growth with CI and with light were similar in strength (Table 4 and data not shown). This was likely because of the strong relationship between residual tree density (CI) and seedling light environment (CI versus GLI, $R^2 = 0.58$, $P < 0.0001$).

Greenhouse study

Soil temperature effects on seedling mass, A_{\max} , and LMR did not differ between the two elevation seed sources for spruce ($P > 0.25$ in all cases); thus, elevation treatments were pooled for all subsequent analyses. Soil temperature effects on seedling mass, A_{\max} , and LMR differed between species (fir versus pooled spruce seed sources) and years (Table 6). Seedling mass increased with soil temperature for spruce in both years, but seedlings were smaller and differences among temperature treatments were smaller in 1999 than in 1998 (Table 7). In contrast with spruce, there was little difference in fir seedling mass among soil temperature treatments in both years (Table 7). At low soil temperature, spruce and fir had similar RGR. However, RGR increased more strongly with temperature for spruce such that fir had lower RGR than spruce at 15 °C (Fig. 2). Despite generally lower RGR, final mass for fir was greater than for spruce in most treatments because seed mass was greater for fir and the seedlings were young (Table 7 and data not shown). In both years, RGR of the shoot and root fraction increased

with soil temperature for spruce, whereas fir root and shoot fractions were less responsive than spruce to temperature (Fig. 2). Both species had positive root and shoot RGR even at 5 °C soil temperature.

LMR and RMR at a common age (45 days after germination) were generally similar among soil temperature treatments for spruce, whereas LMR declined and RMR increased with increasing soil temperature for fir (Table 6). Variation in mass fractions among soil temperature treatments could be a consequence of larger seedlings at higher soil temperature rather than a direct response to soil temperature because mass fractions can change with plant size (e.g., Walters et al. 1993; McConaughay and Coleman 1999). However, using data from all harvests, root or leaf mass versus plant mass relationships indicated that species rankings of LMR and RMR over a broad range of total mass were generally consistent with rankings at age 45 days (data not shown).

Although differences in root and leaf fractions between species and years lack a general pattern, they may be explained by differences in the pattern of leaf growth among treatments and years. Seedlings either flushed a single set of leaves early in the experiment or flushed one set of leaves early and then flushed another, usually between the second and third harvest (45 and 66 days). Patterns of second flushing varied strongly among treatments and years, and these patterns affected biomass fractions and perhaps growth rates. At final harvest, two-flush seedlings for 5 and 15 °C treatments comprised 59% and 92% of all seedlings, respectively, for spruce and 0% and 29% for fir in 1998, and 29% and 79% for spruce and 0% for fir in 1999. Thus, there were less two-flush seedlings at low than at high temperatures for fir than for spruce and in 1999 than in 1998. Higher or similar LMR for two-flush than one-flush seedlings seems logical, as a second leaf flush increases leaf mass, as roots and stems also grow, whereas for one-flush seedlings, mass increases are largely restricted to roots and stems. Consistent with these expectations, treatments with little or no second needle flush, such as fir in both years, had lower LMR and higher RMR.

In contrast with the complex patterns in biomass fractions among treatments, A_{\max} increased strongly with soil temperature for spruce and fir in both years (range 50%–150% greater at 15 °C than at 5 °C) (Table 7). Across temperatures and species, RGR was more strongly correlated with A_{\max} than with LMR, and $LMR \times A_{\max}$ (i.e., whole-plant photosynthetic rate) resulted in, at best, only a marginal improvement in R^2 (Table 8). Although the relationship between A_{\max} and RGR was strong for both years, relationships for the two years had significantly different slopes ($P = 0.0008$) (Fig. 3). Contrary to the expectation of a positive LMR versus RGR relationship, as $RGR = LMR \times NAR$ (Evans 1972), the relationship was negative in 1999. This apparent anomaly can be resolved by the fact that most seedlings had a single leaf flush in 1999 such that seedlings at higher soil temperature, with greater A_{\max} and RGR, accumulated mass primarily in their stem and root fractions and thus had low LMR. Collectively, these results illustrate the importance of temperature effects on photosynthesis and leaf development in limiting growth at low soil temperature.

Table 5. Multiple linear regression summary statistics of seedling size and growth metrics as functions of light and soil temperature (growing season mean soil temperature at 15 cm depth).

Predicted variable	Species	Predictor variable	$P > F$	Beta weight	Pratt index	n	F	MS	Adjusted R^2
$d^2 \times h$	Spruce	Light	<0.0001	0.557	0.69	205	126.6	16.76	0.552
		Soil temperature	<0.0001	0.297	0.31				
	Fir	Light	<0.0001	0.525	0.78	237	85.3	8.10	0.417
		Soil temperature	0.0033	0.188	0.22				
Aboveground mass	Spruce	Light	<0.0001	0.574	0.70	87	59.6	4.72	0.577
		Soil temperature	0.0002	0.307	0.30				
	Fir	GLI	<0.0001	0.663	0.86	92	63.4	3.39	0.578
		Soil temperature	0.0960	0.148	0.14				
Whole mass	Spruce	Light	0.0090	0.549	0.59	16	18.1	5.56	0.695
		Soil temperature	0.0470	0.400	0.41				
	Fir	Light	<0.0001	1.275	1.20	11	29.2	2.72	0.850
		Soil temperature	0.0074	-0.623	-0.20				
1992–1998 diameter increment	Spruce	Light	<0.0001	0.520	0.63	205	132.5	2.40	0.563
		Soil temperature	<0.0001	0.343	0.37				
	Fir	Light	<0.0001	0.351	0.59	237	51.1	0.45	0.299
		Soil temperature	0.0003	0.260	0.41				

Note: Summary statistics for each of the two predictor variables in each whole model are $P > F$, beta weight, and Pratt index. Whole model statistics are n (number of observations), F ratio, MS, and adjusted R^2 .

Discussion

In combination, results from the field and greenhouse experiments indicated that (i) residual canopy cover following harvest decreased growth of planted spruce and fir seedlings compared with clearcuts, (ii) reduced growth was primarily related to the combination of lower light and lower soil temperature, (iii) spruce was more sensitive to soil temperature than fir, and (iv) decreased growth at lower soil temperature was related to lower photosynthesis and not to lower leaf fraction. Each of these points is elaborated upon below.

Residual canopy cover reduces growth of planted seedlings

Harvest treatments differed greatly as environments for seedling growth. These differences may have important implications for regenerating partial-cut systems. Research from other regions has found positive relationships between seedling and sapling growth rates and survival (Kobe and Coates 1997; Walters and Reich 2000; Weih and Karlsson 1999), suggesting that the growth-limiting environments of shelterwoods could lead to unacceptably high rates of mortality there. From the fifth to sixth growing seasons following planting, survival for our study seedlings was high for fir in all harvest treatments (99%), whereas survival for spruce was lower than for fir in all treatments and lower in shelterwoods (88%) than in clearcuts (92%). Compounded over 5 years, annual survival rates of 88% result in nearly 50% mortality. Fir and spruce seedlings in their sixth growing season average only 0.5 m tall in shelterwoods, much less than the height beyond which competition with shrubs is unlikely (i.e., >1.5 m, personal observation). Thus, relatively high rates of mortality may persist for several years for small, slow-growing seedlings because of sustained competition with both residual trees and shrubs and herbs.

Our CI generally explained ~40%–50% of the variation in spruce and fir seedling growth and it was related to soil tem-

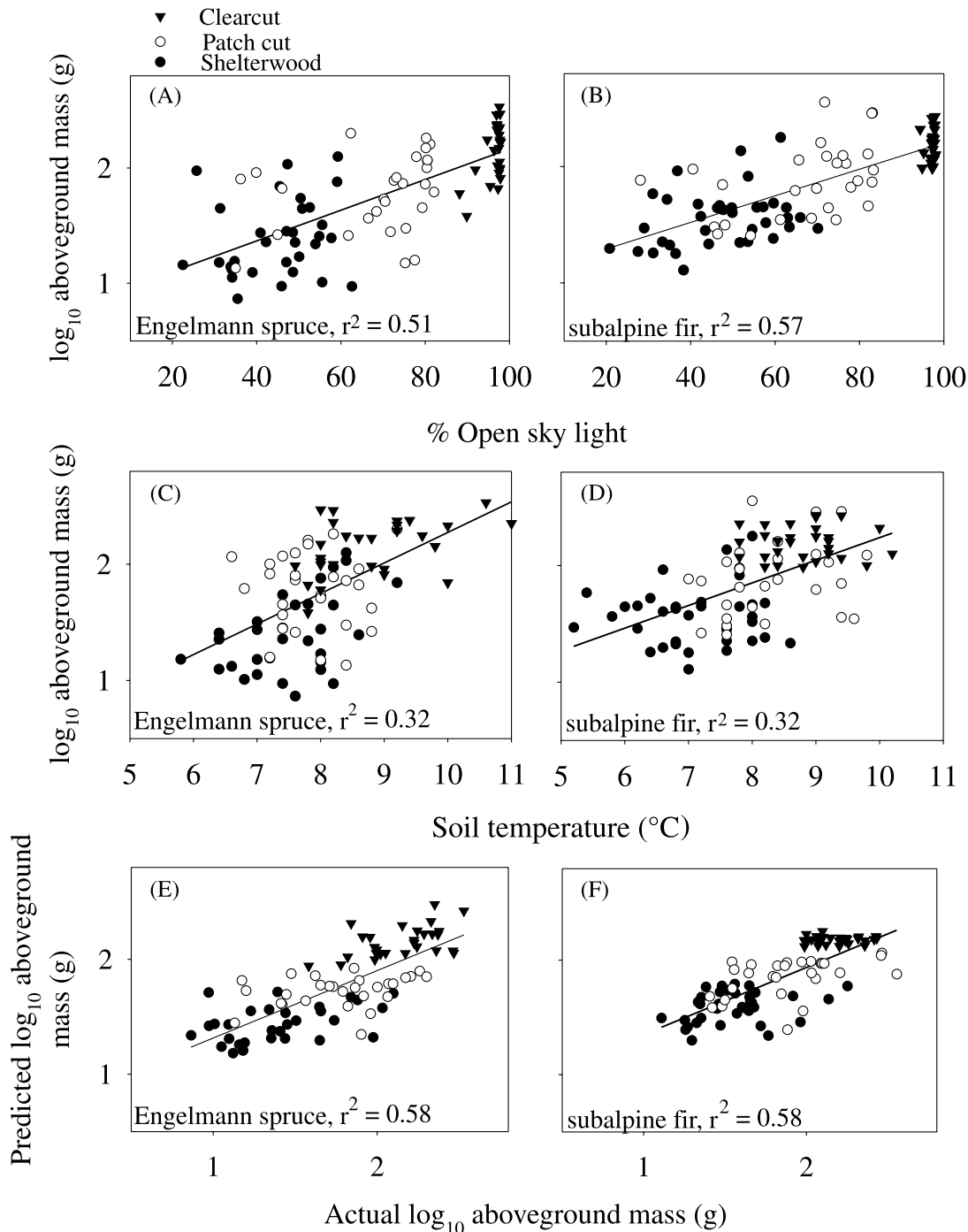
perature and light availability. Thus, simple point indices can effectively integrate the effects of residual tree density on seedling environments and growth. Forest managers could use CI as a tool to more effectively distribute planted seedlings within harvest systems that have spatially variable residual tree densities.

Reduced seedling growth is primarily due to decreased light and soil temperature

The combination of light and soil temperature explained over half of the variation in aboveground mass for both species, suggesting that light and temperature are important determinants of seedling growth in subalpine spruce–fir forests. Yet, nearly half the variation in growth and size was unexplained. Several factors may account for the unexplained variation. These include (i) seedling size metrics integrated environmental effects on growth from 1992 to 1998, but light and temperature were just single-year estimates, and temperature measurements were small samples of values that are likely highly variable over the growing season, and (ii) several unmeasured factors that could affect size and growth, including frost damage (Jull and Stevenson 2001), air temperatures, size of seedlings at planting, genetic variation in growth potential, and variation in the persistence of late-spring snowpack and growing season length (Peterson and Peterson 1994; Peterson et al. 2002).

In this study, growth for both species continued to linearly increase at up to 100% open-sky light. While some studies have found that growth of juvenile trees plateaus at 30%–70% light (Pacala 1993), field-grown conifer seedlings from high latitudes and (or) altitudes have sometimes shown lack of light-saturated growth at 100% open-sky light (Wright et al. 1998). Perhaps the effects of light on soil warming, over and above the light levels required for canopy-level light saturation, result in increased growth benefits. Alternatively, the dense canopy of the older conifer seedlings and saplings

Fig. 1. Linear regression of the base 10 logarithm (\log_{10}) of aboveground mass versus light for (A) spruce and (B) fir, linear regression of \log_{10} aboveground mass versus mean soil temperature for (C) spruce and (D) fir, and actual versus predicted values of \log_{10} aboveground mass from multiple regression with light and mean growing season soil temperature as predictor variables for (E) spruce and (F) fir.



used in this study and some others (e.g., Logan 1966; Wright et al. 1998) may result in a high degree of self-shading and lack of light saturation for canopy interior foliage, even at 100% open-sky light.

In our field study, we could only crudely estimate the effect of soil temperature on seedling growth with multiple regression techniques because of the strong covariation of temperature and light. However, our greenhouse results corroborated our field results by demonstrating that seedling

growth, especially for spruce, was temperature limited over the range of soil temperatures found over the growing season in the field (i.e., 4.7–11.0 $^{\circ}$ C). Notably, in the greenhouse experiment, growth in 1998 increased between 10 and 15 $^{\circ}$ C, suggesting that growth in the field can be temperature limited, even for clearcut seedlings in midsummer.

In a review, Körner (1998) concluded that growing season temperature is likely the most important mechanism establishing the alpine treeline globally. He speculated that low

Table 6. ANOVA of the effects of temperature, year, species, and their interactions on final seedling mass (90 days), A_{\max} (45 days), and LMR (45 days).

	Dependent variable								
	Final seedling mass (g)			A_{\max} (nmol CO ₂ ·g ⁻¹ ·s ⁻¹)			LMR (g·g ⁻¹)		
	SS	F	P >F	SS	F	P >F	SS	F	P >F
Temperature	0.097	2.16	0.317	15 456	20.63	0.046	0.076	7.94	0.112
Year	0.364	16.27	0.056	13 807	36.87	0.026	0.374	78.3	0.013
Temperature × year (random)	0.479	10.71	<0.001	1 082	1.44	0.241	0.027	2.80	0.065
Species	0.651	29.10	<0.001	31 243	83.44	<0.001	0.040	8.45	0.004
Temperature × species	0.675	15.09	<0.001	1 504	2.00	0.141	0.075	7.82	<0.001

Note: Because the experiment was designed as a split plot, temperature and year are tested with temperature × year interactions as the error term (2 df) and species and temperature × species interactions are tested with the residual error term (134 df).

Table 7. Mean (±1 SE) values of seedling mass (mg), A_{\max} (nmol·g⁻¹·s⁻¹), LMR, and RMR.

	1998			1999		
	5°C	10°C	15°C	5°C	10°C	15°C
Mass						
Spruce	36±0.03c	47±0.04b	151±0.03a	16±0.03b	23±0.03a	22±0.02a
Fir	53±0.03a	62±0.03a	52±0.04a	39±0.05a	48±0.01a	46±0.02a
A_{\max}						
Spruce	41±5c	68±5b	96±8a	74±8b	114±7a	136±8a
Fir	27±2b	29±3b	51±3a	37±1c	72±5b	92±8a
LMR						
Spruce	0.74±0.01a	0.71±0.01a	0.73±0.01a	0.55±0.02a	0.42±0.02b	0.44±0.02b
Fir	0.68±0.01a	0.64±0.02a	0.53±0.01b	0.62±0.02a	0.48±0.03b	0.43±0.01b
RMR						
Spruce	0.20±0.01a	0.25±0.01a	0.24±0.01a	0.31±0.02b	0.43±0.02a	0.40±0.02a
Fir	0.22±0.01b	0.26±0.02b	0.39±0.01a	0.22±0.02c	0.36±0.02b	0.45±0.01a

Note: Mass is from final harvest (90 days in 1998, 93 days in 1999); other characteristics are from the harvest at 45 days. Values without common letters within rows and years are significantly different (Tukey–Kramer HSD, $P < 0.05$).

temperatures limit the use of C assimilates in growth and not C assimilation itself, since available evidence indicates substantial photosynthetic rates at air temperatures close to 0 °C. He proposed that root zone temperatures may be most critical and that growth (e.g., cell division and expansion) may approach zero at soil temperatures less than ~3–5 °C. Our data only partially support his assertions. First, we found that root growth was limited, at least for spruce, at soil temperatures typical of high-elevation spruce–fir forests, as root RGR for this species consistently declined with soil temperature. However, root RGR was still positive for both species at 5 °C (range 19–49 mg·g⁻¹·day⁻¹), and it was between 68% and 83% of root RGR at 15 °C. Landhauser et al. (2001) also found positive root growth at 5 °C for the boreal–sub-boreal species *Picea glauca* (Moench) Voss but not for *Populus tremuloides* Michx. Second, on first appearance, our data do not support Körner's (1998) suggestion that growth is not assimilation limited at low soil temperatures. We found that photosynthesis was strongly limited by low soil temperatures and that growth rates were strongly related to photosynthetic rates. However, the cause–effect relationship between photosynthesis and growth is unclear.

For example, low sink activity (i.e., low growth due to low temperatures) could result in high assimilate concentrations and result in feedback inhibition of photosynthesis.

Although the greenhouse experiment clearly showed temperature limitation of growth, our results differed strongly between years, as did patterns of LMR and A_{\max} . The factors responsible for these differences are not clear. Among potential explanations, one is a different environment between years due to the only partially controlled greenhouse conditions and the later start of the experiment in 1999 than in 1998. Compared with 1999, 1998 air temperatures near seedling canopies were 1.6 °C warmer (18.7 versus 17.0 °C), and seedlings received 7% greater total hours of daylight and approximately 10% more hours of direct sunshine (Prince George Weather Station, 10 km distant). The lower slope of the RGR versus A_{\max} relationship for 1999 than for 1998 is consistent with lower light levels in 1999 than in 1998, as (Fig. 3) lower light would result in in situ photosynthesis being a smaller fraction of potential light-saturated photosynthesis. In addition, differences in photoperiod due to the later start of the experiment in 1998 than in 1999 (18 days) could have been responsible for many fewer seed-

Fig. 2. Relationship of root and shoot (stems and leaves) RGRs with temperature by species and temperature treatments for each year.

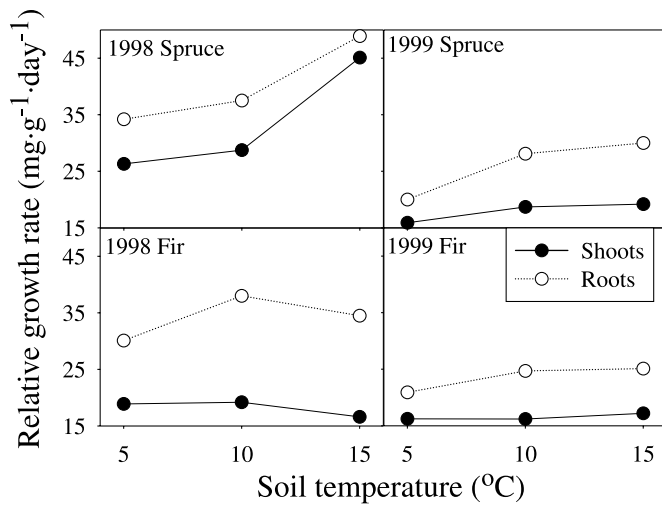
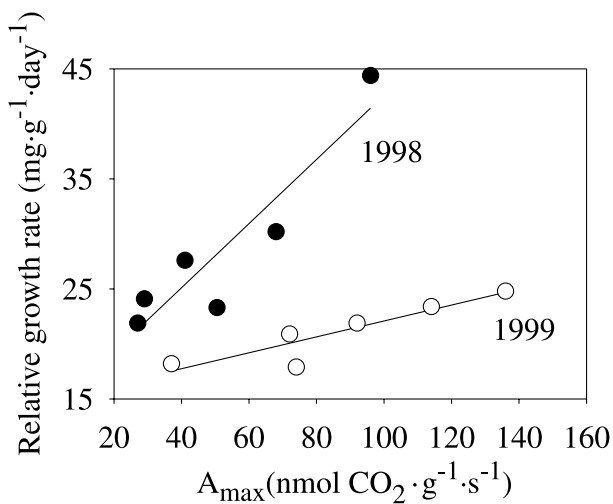


Fig. 3. Relationship of RGR (0–90 days) with A_{\max} for 1998 and 1999. Each datum is a temperature \times species–elevation treatment mean. For 1998, $RGR = 13.5 + 0.29A_{\max}$ ($r^2 = 0.85$, $P = 0.008$); for 1999, $RGR = 14.9 + 0.07A_{\max}$ ($r^2 = 0.82$, $P = 0.0123$).



lings developing a second flush of leaves in 1999. Thus, growth could have been constrained by both leaf development and lower light in 1999 than in 1998.

In the field, N supply did not appear to limit seedling growth, since N fertilizer applications increased leaf N but not growth; however, some of our data indirectly suggest seedling N limitation. First, leaf N for our unfertilized seedlings (average = 1.3% N) was within the range considered moderately N deficient (Ballard and Carter 1986). Second, although leaf N was not, on average, lower in shelterwood than in clearcut seedlings, there was a negative relationship between CI and leaf N (for unfertilized seedlings, $R^2 = 0.29$, $P < 0.0001$, %N = $1.51 - 0.000772$ CI). Based on this relationship, seedlings growing at high CIs (e.g., >550) had a predicted leaf N of <1.1%. Furthermore, 7 years after planting, excavated seedlings at high CI still had most of their roots in the volume of the original root plug, indicating very

Table 8. Correlations with RGR from 0 to 90 days.

Year	A_{\max} , 45 days (nmol CO ₂ ·g ⁻¹ ·s ⁻¹)	LMR, 45 days (g·g ⁻¹)	$A_{\max} \times$ LMR
1998	0.92***	0.50	0.96***
1999	0.91**	-0.84**	0.82**

Note: Values are temperature by species means ($n = 6$) for each year separately; values are Pearson correlation coefficients. *, $P < 0.10$; **, $P < 0.05$; ***, $P < 0.01$.

poor root growth that might have limited the capacity of the roots for nutrient uptake. Thus, although our results do not indicate N limitation of seedling growth, fertilizer responses in the cold subalpine environment may be slower than the two-growing-seasons response that we measured. Alternatively, seedlings may be uptake limited by cold root zone temperatures and (or) poor root system development and not by N supply.

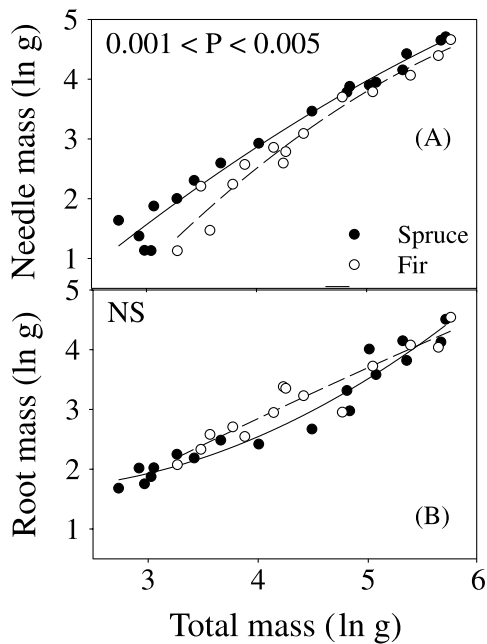
Spruce is more sensitive to temperature than fir

In subalpine forests, it is commonly known that spruce is less shade tolerant than fir. Spruce seedlings are more abundant in canopy openings than in understories, whereas fir seedlings are abundant in openings and understories. The greater temperature sensitivity of spruce than fir is consistent with differences in their natural distribution and supports the notion that shade-tolerant species (e.g., fir) are less responsive to improved environmental conditions than are less tolerant (e.g., spruce) species (Veneklaas and Poorter 1998; Walters and Reich 1999). In open, high-light areas with relatively warm soil temperatures, spruce may outcompete fir for growing space via greater growth rates. In areas with intact forest cover and lower light and soil temperatures, fir does not have a growth rate advantage over spruce, but it has greater survival at low growth rates (Kobe and Coates 1997; this study). More generally, differences between our study species suggest that understory tolerance in subalpine forests is tolerance of both low light and low soil temperatures. Consistent with this suggestion, Landhauser et al. (2001), in a comparison of boreal–subboreal species, found greater low-temperature growth inhibition for early successional, high light adapted *Populus tremuloides* than for the more shade-tolerant *Picea glauca*.

Decreased growth is related to decreased photosynthesis

Seedlings grown at high soil temperatures consistently had higher A_{\max} than seedlings grown at low temperatures, which corroborates data for *Picea engelmannii* seedlings in field conditions (DeLucia and Smith 1987) and other species (e.g., *Andropogon gerardii*, DeLucia et al. 1992; *Populus tremuloides*, King et al. 1999). However, less intuitive and less documented are the responses of biomass fractions that we observed. At low soil temperature, increased water viscosity and decreased root permeability result in reduced root conductance of water (Kaufmann 1975; Running and Reid 1980; Day et al. 1990; Wan et al. 1999), which may reduce stomatal conductance and net photosynthesis. One possible mechanism for overcoming diminished root permeability at lower temperatures is to make more roots and fewer leaves. However, we saw the opposite pattern (i.e., increased RMR and decreased LMR with temperature), and some other stud-

Fig. 4. (A) Leaf mass versus total mass and (B) root mass versus total mass relationships for excavated 8- and 9-year-old seedlings. Seedlings of each species are pooled over clearcut, patch cut, and shelterwood treatments. *P* values are for *F* tests of differences between species.



ies have reported no pattern in the response of biomass fractions to temperature (e.g., DeLucia et al. 1992; King et al. 1999). Thus, given the caveat that we did not measure stomatal conductance, it does not appear that increasing allocation of mass to roots, albeit a crude metric of root function, is an important compensatory mechanism for low specific root conductance at low root temperatures.

Patterns in the variation in LMR and RMR among species and temperatures were complex and difficult to generalize, perhaps because of large variation in patterns of periodic leaf development (i.e., one- versus two-needle flush events) among treatments and years. The degree to which this variation was due to cultural conditions, such as the potential effect of differences in photoperiod and (or) light availability between years, is unknown. Furthermore, potential differences in biomass fractions and photosynthesis beyond the first year cannot be predicted from our greenhouse results. However, a small number of seedlings that we excavated from the field provide some insight into species differences in mass fractions for older seedlings (Fig. 4). Given the caveat that size and environment are confounded, as small seedlings were harvested from cooler soils and lower light microsites, root mass versus plant mass relationships were similar for both species, whereas needle mass was greater for spruce than for fir. Greater leaf fraction for older field grown spruce than for fir could be associated with spruce's higher growth rates in more open environments, as the impact of variation in leaf allocation on growth rates is greatest at high light levels (Walters and Reich 1999).

Conclusions

Combined field and greenhouse data demonstrated that the use of partial-cut harvest treatments with residual tree

cover, or small harvest openings, limits spruce and fir seedling growth. Decreased growth was primarily due to lower light and secondarily to lower soil temperatures. Spruce growth was more sensitive to temperature than fir growth, which is consistent with observed differences in species natural seedling distributions. They also indicate that seedling establishment in partial-cut systems may be more problematic for spruce than for fir. Low temperature limited growth was related to reductions in photosynthetic capacity and not to leaf fraction.

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