

Adaptive strategies in seedlings of three co-occurring, ecologically distinct northern coniferous tree species across an elevational gradient

D. Scott Green

Abstract: The inherent clinal responses of four quantitative traits thought to be adaptive for trees in cold-limited environments (i.e., height-growth cessation, growth rate, resource allocation to aboveground and belowground tissues, and resource allocation to photosynthetic and nonphotosynthetic tissues in the shoot) were characterized under nonlimiting conditions in a controlled glasshouse study for seedlings of three ecologically distinct and co-occurring northern tree species (*Pinus contorta* Dougl. var. *latifolia* Engelm. (lodgepole pine), *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm. (interior spruce), and *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir)). For each species, clinal trends were quantified among populations adapted to increasingly cold-limited climates across an elevation gradient approaching the tree line. In subalpine fir seedlings, strong clinal variation for all the quantitative traits indicated an increasingly conservative response to climate moving toward harsher conditions. Variation in lodgepole pine and interior spruce seedlings suggested a more plastic strategy, favoring competitive traits across a wide range of climate conditions. Study findings suggest that ecologically distinct species may exhibit different strategies in adapting to local climates.

Résumé : Les réponses clinales inhérentes à quatre caractères quantitatifs que l'on pense être adaptatifs chez les arbres dans les milieux où le froid est un facteur limitant (c.-à-d., l'arrêt de la croissance en hauteur, le taux de croissance, l'allocation aux tissus aériens vs souterrains, l'allocation aux tissus photosynthétiques vs non photosynthétiques dans les pousses) ont été caractérisées sous des conditions non limitantes dans une étude en serre avec des semis de trois espèces nordiques, écologiquement distinctes et sympatriques (*Pinus contorta* Dougl. var. *latifolia* Engelm. (pin tordu latifolié), *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm. (épinette de l'intérieur) et *Abies lasiocarpa* (Hook.) Nutt. (sapin subalpin)). Pour chaque espèce, les tendances clinales ont été quantifiées dans des populations adaptées à un climat de plus en plus froid le long d'un gradient altitudinal atteignant presque la limite des arbres. Chez les semis de sapin subalpin, une forte variation clinale pour tous les caractères quantitatifs indiquait une réponse de plus en plus conservatrice à mesure que les conditions climatiques devenaient plus rudes. Chez les semis de pin tordu latifolié et d'épinette de l'intérieur, la variation suggérait une stratégie plus plastique, favorisant les caractères compétitifs à travers un grand éventail de conditions climatiques. Les résultats de l'étude suggèrent que les espèces écologiquement distinctes peuvent adopter différentes stratégies pour s'adapter au climat local.

[Traduit par la Rédaction]

Introduction

In cold-limited regions (i.e., high latitude and high elevation), adaptive strategies of balancing competitive and survival capacities employed by different species and populations may directly govern their responses to future climate change. Numerous authors (Rehfeldt 1983, 1984; Woodward 1987; Brown and Gibson 1998; Loehle 1998; Rehfeldt et al. 1999; Vetaas 2001) have observed that the adaptation of woody plants to their local environments in cold-limited regions entails a trade-off between competitive capacity (e.g., annual growth) and survival capacity (e.g., cold-tolerance traits). In the adaptation process, links between the environment and plant

response traits that favor one strategy (i.e., competitive capacity or survival capacity) generally entail a cost to the other strategy (Loehle 1998; Thompson 1998; Aitken and Hannerz 2001). For instance, phenology in growth initiation or cessation mediates a trade-off between a long growing period and protection from early or late frosts in cold climates. Resource partitioning to aboveground and belowground plant tissues mediates a trade-off between photosynthetic productivity and acquisition of edaphic resources in limiting environments.

Although categorizing plant traits as conferring competitive or survival capacity may not always be straightforward, this distinction could provide a useful means to delineate unique adaptive strategies in ecologically different species. The expression of competitive versus survival traits in a given environment likely varies between ecologically distinct species; these differences remain poorly understood (Singh and Wheaton 1991; Peterson et al. 2002). Furthermore, unique adaptive strategies in ecologically distinct and co-occurring species may be mediated by different environmental cues

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(Braekke and Kozlowski 1975; Rehfeldt 1984, 1985; Singh and Wheaton 1991; Thompson 1998; Peterson et al. 2002), some of which will vary with climate change in a given location (e.g., air or soil temperature, soil moisture, duration of snow cover) and some of which will not (e.g., photoperiod). Consequently, distinct ecological trade-offs among co-occurring species in a changing climate may alter the balance between competitive capacity and survival capacity for either migrating populations or extant populations undergoing in situ adaptation (e.g., phenotypic plasticity, regeneration) (de Groot et al. 1995; Asselin et al. 2003).

Although such trade-offs may vary at different developmental stages for trees (Brubaker 1986; Stettler and Bradshaw 1994; Hurme et al. 1997; Dunne et al. 2001), seedlings represent a particularly sensitive phase (Campbell 1979; Brubaker 1986; Rehfeldt et al. 1999) because of greater microclimate variation near the ground, high physical stresses (e.g., vegetation and snow press), and lower stress resistance during early establishment. If climate change becomes a forcing factor in northern forests, shifts in the distribution and abundance of tree species will likely be sorted out by ecological trade-offs during this regeneration phase. It is imperative, then, to characterize different adaptive strategies in seedlings of disparate tree species to better predict forest ecosystem responses to future climate change (Peterson et al. 2002; Howe et al. 2003), especially in cold-limited areas where we expect the greatest fluctuations in climate and forest responses in coming decades (Grabherr et al. 1994; Spellerberg and Sawyer 1999; McCarty 2001). Comparing species-specific trade-offs in competition-survival traits across spatial climate gradients (e.g., latitude, elevation, continentality) should provide a systematic basis for characterizing the response strategies of ecologically distinct tree species (Rehfeldt 1984; Loehle 1998).

The primary objective of this study was to compare inherent clinal responses in quantitative traits thought to be adaptive in cold-limited environments in seedling populations of ecologically distinct and co-occurring northern tree species across a severe climate gradient (i.e., elevation) approaching the tree line. Elevation was selected as the climate gradient in this study so that the role of photoperiod in a tree species life history could be examined in geographically close populations adapted to similar daylength conditions.

Assessing real-world adaptive responses to climate is confounded by interactions between genetic expression and environmental acclimation to local conditions. Consequently, the target of this controlled study was to describe the potential (i.e., genetic) expression of quantitative traits in seedlings of different species and climate populations by minimizing environmental limitations. Three co-occurring, northern coniferous tree species were selected for this study: early-successional, shade-intolerant *Pinus contorta* Dougl. var. *latifolia* Engelm. (lodgepole pine), mid-successional, intermediate shade-tolerant *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm. (interior spruce), and late-successional, shade-tolerant *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir). Populations of these species co-occur across the entire elevation gradient at the study site, though in different mixtures. Lodgepole pine dominates at lower elevations; lodgepole pine and interior spruce codominate at mid-elevations; interior spruce and subalpine fir codominate at higher elevations; and subalpine fir dominates at the upper end of the elevational range.

Four quantitative traits were examined to assess trade-offs between competitive and survival capacities among species and climate populations: (1) phenology in the timing of height-growth cessation; (2) average growth rate; (3) resource partitioning to aboveground and belowground tissues; and (4) resource partitioning to photosynthetic and nonphotosynthetic tissues in the shoot.

Although other traits may be important in climate responses (e.g., photosynthetic potential, fecundity, seed dispersal), the target traits in this study may be particularly relevant in cold-limited regions. Phenology in height-growth cessation is a core trait conferring frost resistance in cold-limited regions (Partanen and Beuker 1999). Height-growth cessation typically varies more than height-growth initiation among northern coniferous tree species and populations (Oleksyn et al. 1998; Aitken and Hannerz 2001). Consequently, growing season length is generally more a function of variation in the timing of height-growth cessation than of variation in height-growth initiation (Aitken and Hannerz 2001; Howe et al. 2003). Growing season length and the average growth rate of a tree during that period (either biomass increments or height) should be key determinants of competitive capacity. The combined effect of height-growth cessation and growth rate, then, is of considerable importance in the adaptive responses of tree species to climate change. Differences in resource partitioning have been observed in populations of tree species moving closer to their cold range limits (Giertych 1976; Körner and Renhardt 1987; Oleksyn et al. 1992; Oleksyn et al. 1998). Greater allocation of photosynthetic production to roots (e.g., root/shoot ratios, R/S) should enhance the uptake of mineral substances in environments where edaphic resources can be highly limiting (Oleksyn et al. 1998). Conversely, greater allocation to photosynthetic tissues and less to nonphotosynthetic tissues in the shoot (e.g., foliage/stem ratios) should increase the competitive capacity of a tree.

Materials and methods

Sample populations

Seedlings of elevational populations of lodgepole pine, interior spruce, and subalpine fir were grown during the spring and summer of 2003 under “nonlimiting” conditions in controlled environments to quantify inherent differences in the clinal expressions of quantitative traits thought to be important in cold-limited forests. Seed from co-occurring, indigenous tree populations of each species was collected in August–September of 2002 across an elevation gradient of about 1100 m (750–1850 m above sea level (a.s.l.)) along the southwestern slope of McBride Peak (53°20'N, 120°07'W) in east-central British Columbia, Canada.

In an effort to adequately sample the variability in quantitative traits within each population, cones for each species were collected from 8–10 trees separated by a minimum distance of 400 m at each source elevation (750, 1100, 1400, and 1700 m a.s.l. (± 50 m at each elevation)). One additional seed source was collected for each species near the upper elevation limit for viable seed, which varied between species. As a result of low abundance of subalpine fir at 750 m a.s.l. and of lodgepole pine above 1700 m a.s.l., cone sampling in

Table 1. Within-species comparisons of quantitative traits across elevations.

Species	Variable	<i>p</i> value	MSD	Seed source elevation (m a.s.l.)				
				750	1100	1400	1700	1800+
Subalpine fir	Average growth	<0.0001	0.81	a	b	c	d	d
Lodgepole pine		<0.0001	1.58	a	ab	b	c	c
Interior spruce		<0.0001	1.49	a	b	bc	bc	c
Subalpine fir	Root/shoot ratio	<0.0001	0.156	b	b	a	a	a
Lodgepole pine		0.0013	0.102	c	bc	ab	ab	a
Interior spruce		<0.0001	0.085	b	a	a	a	a
Subalpine fir	Foliage/stem ratio	<0.0001	0.046	a	a	b	bc	c
Lodgepole pine		0.20						
Interior spruce		<0.0001	0.020	a	ab	c	bc	bc
Subalpine fir	Growth cessation	<0.0001	9.76	a	a	b	b	b
Lodgepole pine		0.02	7.47	a	a	ab	ab	b
Interior spruce		0.11						

Note: All quantitative variables were sampled in the extended photoperiod treatment except growth cessation, which was sampled in the ambient photoperiod treatment. Average growth comparisons are based on aboveground biomass gain. Where overall one-way analysis of variance is significant (indicated by *p*-value column), mean significant differences (MSDs) from Tukey's multiple comparison test are given for within-species comparisons of quantitative traits across elevations. Significant differences ($\alpha = 0.05$) within columns are denoted by letters, with "a" indicating the highest mean value. The highest elevation population is designated 1800+.

those cases was limited to three and six trees, respectively. Seed was collected, processed, stored, and pretreated for germination according to Kolotelo et al. (2001). For each species and elevational population, seed was combined to ensure that each sample tree was equally represented.

Growing conditions

Seed sowing for all populations was done on 28 April 2003 with 615A styroblocs (Beaver Plastics Ltd., Edmonton, Alta.), which provide 336 mL of rooting space per seedling cavity.¹ Each styrobloc contained all elevational populations (three seedlings each) for one species. Twenty-four replications (i.e., styroblocs) of each species were sown in each photoperiod treatment. The growth medium was a typical tree-seedling nursery mixture (70% sphagnum peat, 15% medium-texture perlite, and 15% medium-texture vermiculite), which was used to provide a low-resistance, harvestable substrate. Following seed sowing, seedling cavities were topped with a 3–5 mm forestry-sand cap and irrigated until saturated. Subsequently, styroblocs were irrigated or fertilized when they reached 80% of their saturated mass. Following germination, irrigation was alternated with fertilization with a balanced macronutrient solution (50 ppm N–P–K). After 4 weeks, the fertilization solution was increased to 100 ppm N–P–K. During the study, there were no detectable indications of water or nutrient limitations. Additionally, linear height-growth profiles within populations during the study following initial establishment suggest that water and nutrients were available at fairly constant levels (data not shown).

Following seed sowing, styroblocs were completely randomized in controlled glasshouse rooms (Enhanced Forestry Lab, University of Northern British Columbia, 53°54'N, 122°49'W), and they were rotated weekly across both north–south and east–west directions to minimize the effect of any potential light or temperature gradients. Daytime air temper-

ature for all seedlings was maintained at 25 °C to promote high photosynthetic rates (Medlyn et al. 2002), and night temperature was maintained at 17 °C to minimize growth reductions due to high tissue respiration (Berry and Björkman 1980). Some studies have shown lower photosynthetic temperature optima in high-elevation tree populations (e.g., Fryer and Ledig 1972). However, a temperature–response study conducted in growth chambers on a subsample of populations indicated that greater growth would not be achieved at lower daytime temperatures for high-elevation populations (data not shown).

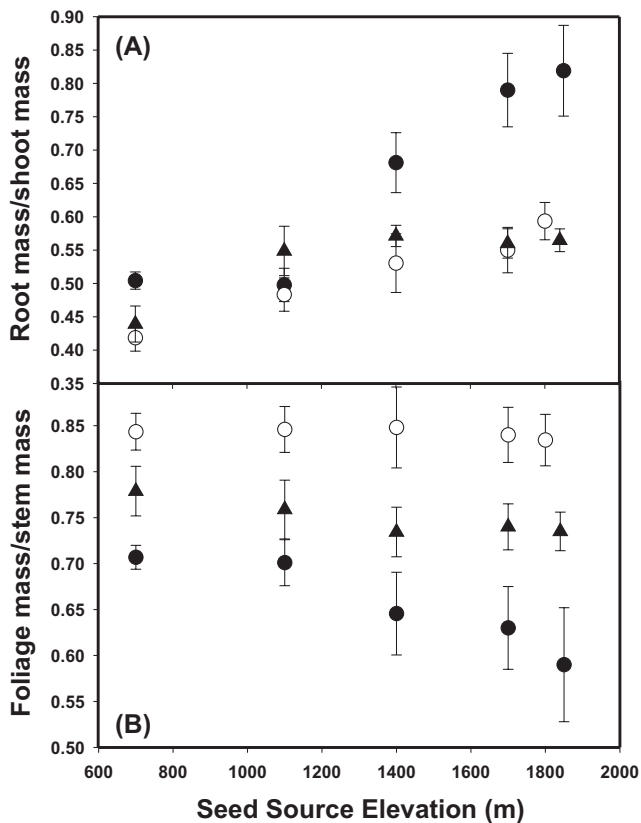
For assessment of the role of photoperiod in height-growth cessation, half the seedlings were grown under the ambient photoperiod, whereas the other half were grown under an extended photoperiod (~18 h), which corresponded to the peak annual daylength at the seed-source latitude. The extended photoperiod irradiance was maintained at about 200 $\mu\text{mol}\cdot\text{m}^{-2}$ photosynthetically active radiation by an array of 400-W high-pressure sodium lights (P.L. Light Systems, Beamsville, Ont.).

Seedling measurements

For quantification of average growth rates and resource partitioning under nonlimiting conditions, seedlings were harvested at two dates in the extended photoperiod treatment only (to avoid the confounding effects of phenology). An initial harvest was done on 21 June 2003 (one randomly chosen seedling per population from each of 12 replications), and a final harvest was done on 29 August 2003 (one randomly chosen seedling per population from all 24 replications). Shoots were cut at the soil line, and roots were carefully extracted from the growth medium. Roots and shoots were individually bagged and dried to a constant mass at 70 °C for quantifying root mass / shoot mass ratios. Foliage was then separated from stems for quantifying foliage mass / stem mass ratios.

¹Roots extracted during harvesting did not appear to be pot bound, which is common in commercially produced seedlings that are grown in smaller cavities (about 25%–50% of the volume of styroblocs used in this study) and over longer durations (6–7 months vs. 4 months). Consequently, it does not appear that the study results reflect growth artifacts related to rooting constraints.

Fig. 1. Elevational trends in biomass allocation between species (\pm SE). Both quantitative variables were sampled in the extended photoperiod treatment. (A) Average allocation to aboveground and belowground plant tissues (root/shoot ratios) as a function of seed source elevation. (B) Average allocation to photosynthetic and nonphotosynthetic plant tissues in the shoot (foliage mass/stem mass) as a function of seed source elevation. Species symbols: open circles, *Pinus contorta* var. *latifolia* (lodgepole pine); filled triangles, *Picea glauca* \times *Picea engelmannii* (interior spruce); filled circles, *Abies lasiocarpa* (subalpine fir).



Average growth rate (milligrams dry mass per day for both aboveground and total biomass increments) was used as the primary growth indicator. Height growth was not included in the analysis, because of its sensitivity to density effects at this developmental stage. At higher densities, height growth would likely be proportionally greater for faster growing species (i.e., lodgepole pine and interior spruce) than for slower growing species (i.e., subalpine fir), which would have skewed the cross-species comparisons. At the initial harvest, no significant differences in total dry mass were detected between elevational populations for any species. Furthermore, linear height growth between the initial and final harvests suggests that growth was fairly constant over this period (data not shown). Consequently, the average growth rate (i.e., aboveground and total dry mass gain) of each seedling population during the period between the initial and final harvests was calculated as (dry mass)/(68 days) (68 days was the growth period from the initial harvest to the final harvest).

For quantification of phenological responses to photoperiod, the heights of 24 seedlings per elevation population in each photoperiod treatment were measured weekly following the initial harvest. In the ambient photoperiod

treatment, measurements continued until each elevational population reached zero growth. Height-growth cessation for each seedling population was calculated as the average date of growth termination for all sampled individuals. Measurements in the fixed photoperiod treatment were continued until the end of October, when the study ended.

Statistical analyses

Quantitative traits were normally distributed for sample populations of all seedlings (Shapiro–Wilk statistic, SAS Institute 2003). Consequently, population means for each quantitative trait were compared within and between species by one-way analysis of variance (Rehfeldt 1984) (SAS Institute 2003). Where significant differences were found within or between species, pairwise comparisons were conducted with Tukey's multiple comparison test to determine specific differences between seedling populations.

Results

Seedling resource partitioning

In the extended photoperiod treatment, average seedling R/S ratios (grams root dry mass per gram shoot dry mass) within each species showed distinct clinal variation across the climate gradient (Table 1, Fig. 1A). In subalpine fir, populations up to 1100 m a.s.l. displayed little variation, whereas higher elevation populations exhibited large increases in R/S . Conversely, a continuous increase in R/S was observed in lodgepole pine across the range of elevational populations. In interior spruce, the 750-m elevational population displayed lower R/S , whereas all populations at or above 1100 m a.s.l. exhibited little variation in R/S . Between species, seedling clinal variation was most distinct above 1100 m a.s.l. (Table 2, Fig. 1A), where subalpine fir diverged markedly from lodgepole pine and interior spruce.

As with R/S , average seedling foliage/stem ratios (F/s , grams foliar dry mass per gram stem dry mass) within each species showed distinct responses across the climate gradient in the extended photoperiod treatment (See Table 1, Fig. 1B). For subalpine fir, F/s showed little population variation up to 1100 m a.s.l., above which it decreased markedly. Lodgepole pine exhibited no clinal variation in F/s , whereas interior spruce displayed slight decreases in F/s in increasing elevational populations. Between species, seedling F/s responses were more distinct than any other quantitative trait (Table 2, Fig. 1B). At all elevations, lodgepole pine seedlings had the highest average F/s , interior spruce had intermediate F/s , and subalpine fir had the lowest F/s .

Average seedling growth rate

Average seedling aboveground growth rates (milligrams shoot dry mass per day) decreased with increasing elevation for all species in the extended photoperiod treatment (Table 1, Fig. 2B). The degree of variation was much greater in subalpine fir: growth rate decreased by about 82% across the elevation gradient. Lodgepole pine and interior spruce showed smaller decreases (31% and 28%, respectively). When average seedling growth was examined on the basis of total (aboveground and belowground) biomass gain, elevation populations varied in only subalpine fir (subalpine fir: $p < 0.0001$; lodgepole pine: $p = 0.68$; interior spruce: $p = 0.25$).

Table 2. Elevational comparisons of quantitative traits among species.

Source elevation (m a.s.l.)	Variable	<i>p</i> value	MSD	Lodgepole pine	Interior spruce	Subalpine fir
750	Average growth	<0.0001	1.55	a	b	c
1100		<0.0001	1.46	a	b	c
1400		<0.0001	1.72	a	b	c
1700		<0.0001	1.89	a	a	b
1800+		<0.0001	1.27	a	a	b
750	Root/shoot ratio	0.0032	0.062	b	b	a
1100		0.0226	0.087	a	a	a
1400		0.0179	0.110	b	b	a
1700		<0.0001	0.138	b	b	a
1800+		0.0009	0.145	b	b	a
750	Foliage/stem ratio	<0.0001	0.022	a	b	c
1100		<0.0001	0.018	a	b	c
1400		<0.0001	0.032	a	b	c
1700		<0.0001	0.037	a	b	c
1800+		<0.0001	0.045	a	b	c
750	Growth cessation	<0.0001	9.58	a	a	b
1100		<0.0001	8.45	a	a	b
1400		<0.0001	10.39	a	a	b
1700		<0.0001	7.89	a	a	b
1800+		<0.0001	7.97	a	a	b

Note: All quantitative variables were sampled in the extended photoperiod treatment except growth cessation, which was sampled in the ambient photoperiod treatment. Average growth comparisons are based on above-ground biomass gain. Where overall one-way analysis of variance is significant (indicated by *p*-value column), mean significant differences (MSDs) from Tukey's multiple comparison test are given for within-species comparisons of quantitative traits across elevations. Significant differences ($\alpha = 0.05$) within columns are denoted by letters, with "a" indicating the highest mean value. The highest elevation population is designated 1800+.

Between species, subalpine fir seedlings had lower average aboveground growth than lodgepole pine and interior spruce seedlings at all elevations (Table 2, Fig. 2B). Interior spruce seedlings had lower average aboveground growth than lodgepole pine seedlings in all but the higher elevation populations. When average growth was examined on the basis of total (aboveground and belowground) biomass gain, subalpine fir had lower values than lodgepole pine and interior spruce for all elevation populations (data not shown). Lodgepole pine and interior spruce differed only at the two highest elevations, where spruce had lower growth rates.

Seedling height-growth cessation

Seedling height growth was indeterminate in all species and populations in the extended photoperiod treatment up until the termination of the study at the end of October. Conversely, seedling height growth ceased in all populations by the end of the first week in September in the ambient photoperiod treatment (Fig. 2A). Clinal variation in seedling height-growth cessation in ambient photoperiods was distinct between species, with subalpine fir being markedly different from pine and spruce (Table 1, Fig. 2A). Height-growth cessation in subalpine fir seedlings occurred earlier in higher elevation populations than in lower elevation populations, spanning nearly 3 weeks between elevation populations. Similar clinal patterns were observed in lodgepole pine and interior spruce seedlings (i.e., earlier height-growth cessation in higher elevation populations), whereas height-growth cessation varied between populations by only 10 and 6 days, respectively. Significant differences in seedling height-growth cessation were only detected for lodgepole pine in the highest eleva-

tion population, and no differences were found in interior spruce. Between species, seedling height-growth cessation in subalpine fir occurred earlier than in lodgepole pine and interior spruce at all elevations (Table 2, Fig. 2A). Between lodgepole pine and interior spruce, there were no differences in height-growth cessation between seedling populations at any elevation.

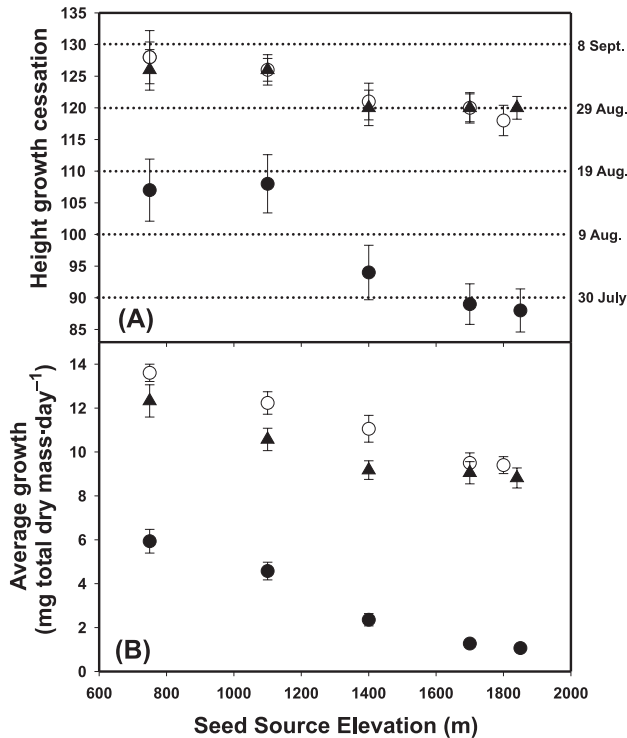
Discussion

Differences in the expression of target quantitative traits across the climate gradient in this study suggest unique response strategies to climate variation in these co-occurring, ecologically distinct northern tree species (at least, at the seedling stage). Overall, lodgepole pine and interior spruce showed similar responses, only exhibiting allocational differences that may reflect ecological priorities of their successional positions. Subalpine fir displayed unique responses in all the quantitative traits examined in this study. These findings suggest that it may be useful to characterize general differences between ecologically distinct species, such as early- and late-successional positions, in predicting forest responses to future climate change.

Potential growth determinants

Potential annual growth in seedlings (a key indicator of competitive capacity) is largely a function of the length of the growing season (i.e., phenology, especially growth cessation) and average growth rate during that period. Study findings suggest that photoperiod was a key trigger of height-growth cessation in all populations, as indicated by the persistent

Fig. 2. Elevational trends in growth determinants between species (\pm SE). (A) Average date of height growth cessation (days from seed sowing) as a function of seed source elevation (m a.s.l.). Height-growth cessation was sampled in the ambient photoperiod treatment. Calendar dates at 10-day intervals are indicated to the right of the figure. (B) Average aboveground growth rate from 21 June to 29 August as a function of seed source elevation (m a.s.l.). Growth rate was sampled in the extended photoperiod treatment. Species symbols: open circles, *Pinus contorta* var. *latifolia* (lodgepole pine); filled triangles, *Picea glauca* \times *Picea engelmannii* (interior spruce); filled circles, *Abies lasiocarpa* (subalpine fir).



height growth in all species and populations in the extended photoperiod treatment. However, the role of photoperiod in growth phenology appeared to be quite distinct in these co-occurring species.

Height-growth cessation in trees is known to respond to both photoperiod and temperature (Koski and Sievanen 1985; Oleksyn et al. 1998; Partanen and Beuker 1999; Heide 2003; Howe et al. 2003). Large temperature variability near the elevation limits of the tree species examined here creates a high risk of frost damage early and late in the growing season. Consequently, we might expect a high sensitivity of height-growth cessation to fixed timing cues (i.e., photoperiod) in species adapted to cold marginal climates to minimize the potential of frost damage (Vaartaja 1959; Partanen and Beuker 1999). Indeed, clinal variation toward increasingly conservative traits has been observed in tree populations moving across climate gradients in cold-limited regions, suggesting that strong selection pressures constrain genetic and quantitative variability within such populations (Stern and Roche 1974; Oleksyn et al. 1998; Hänninen et al. 2001).

Populations of subalpine fir seedlings near the tree line in this study appeared to be highly constrained by photoperiod, strongly favoring survival capacity. Height-growth cessation

of these populations growing under “optimal” conditions in the greenhouse approximately coincided with that of natural populations of saplings near the tree line (as determined with regular field observation), suggesting a limited role of temperature in growth cessation phenology in these populations. In lodgepole pine and interior spruce, height-growth cessation in high-elevation seedling populations in the controlled environment was extended by about a month, compared with natural field populations. This finding suggests an interaction between photoperiod and temperature in triggering growth cessation in lodgepole pine and interior spruce, reflecting a strategy that should favor competitive capacity in a warming climate.

As with phenology, trends in average growth rates of subalpine fir seedlings appeared to be markedly different from those of its associates across the climate gradient. As might be expected, average growth rate was higher in lodgepole pine and interior spruce at all elevations than in subalpine fir (for both aboveground and total biomass production), which reflects their earlier successional position. However, clinal variation was markedly different between species. Average growth rate (both aboveground only and total biomass gain) in seedlings of both lodgepole pine and interior spruce showed less sensitivity to deteriorating conditions, suggesting a more limited trade-off between competitive capacity and survival capacity across the entire climate gradient in this study. Conversely, average growth rate (both aboveground only and total biomass gain) in subalpine fir seedlings was highly sensitive to deteriorating conditions, again suggesting a conservative strategy that would likely result in little growth response to improving conditions in high-elevation populations.

Although some studies have observed relations between initial seed size and conifer seedling growth (Hawkins 1998), other studies have shown no detectable effect of seed size on growth (e.g., Reich et al. (1994) examined Scots pine, and Chaisurisri et al. (1994) examined sitka spruce). In this study, seed size did not appear to be a primary factor in clinal variation in average growth rates for any of the species. Seed mass was only correlated to source elevation for interior spruce (lodgepole pine: $r^2 = 0.62$, $p = 0.11$; interior spruce: $r^2 = 0.79$, $p = 0.04$; subalpine fir: $r^2 = 0.57$, $p = 0.14$). Furthermore, average aboveground seedling growth was not related to seed mass for any species ($p \geq 0.09$ for all species), whereas elevation alone explained most of the variation in average seedling growth for all species (lodgepole pine: $r^2 = 0.97$, $p = 0.002$; interior spruce: $r^2 = 0.87$, $p = 0.02$; subalpine fir: $r^2 = 0.97$, $p = 0.002$). Additionally, seedling size did not vary between populations of any species in the first harvest. Consequently, differences in growth were sorted out after the first 6 weeks, suggesting that the variation was not a function of initial seed size.

Resource partitioning

As with phenology and average growth rate, resource partitioning in subalpine fir seedlings showed a greater sensitivity to climate variation. Across the climate gradient, trade-offs in subalpine fir were observed between aboveground and belowground allocation and between allocation to photosynthetic and nonphotosynthetic tissues in shoots with increasing allocation to the procurement of edaphic resources (i.e., greater relative root mass) and decreasing allocation to photo-

synthetic productivity (i.e., lower foliar mass as a proportion of shoot mass) in colder climates. In lodgepole pine and interior spruce, only trade-offs in aboveground and belowground allocation were observed in seedling populations across the climate gradient. Additionally, clinal variation in pine and spruce seedlings was smaller than in subalpine fir.

Furthermore, F/s was negatively related to R/S in subalpine fir in all seedling samples in the final harvest ($F/s = -0.25R/S + 0.82$, $r^2 = 0.55$, $p < 0.0001$), suggesting a strong ecological shift toward survival traits in increasingly severe climates. No such relations were found for lodgepole pine or interior spruce, both of which exhibited surprisingly consistent allocation to photosynthetic production up to their climate limits. The allocation trends observed in subalpine fir seedlings may indicate a primary adaptation to a true subalpine environment, where belowground resources are extremely limiting and aboveground limitations include physical stresses (snow press, high wind stress, etc.) that would favor shoot strength over photosynthetic productivity. The highly conservative allocational trend observed in subalpine fir appeared to exact a direct cost on competitive capacity.

Of all the quantitative traits examined in this study, allocation to photosynthetic and nonphotosynthetic aboveground tissues most clearly distinguished lodgepole pine and interior spruce seedlings. This trait may best characterize the early-successional, fast-growth habit of lodgepole pine, wherein high allocation to photosynthetic tissues reflects an ecological "commitment" to competitive capacity across its entire climate range. The lack of clinal responses in key competitive traits (height-growth cessation, average growth, F/s) to strong selection pressures across the climate gradient at this site suggests that lodgepole pine seedlings possess a particularly competitive disposition across a wide range of climate conditions.

Summary of species differences

The strong clinal trends observed in late-successional subalpine fir seedlings for all the quantitative traits examined here suggest an increasingly conservative response to climate variation as conditions became harsher. Phenotypic plasticity in traits may be low in subalpine fir populations in cold climates during establishment, and we might expect a limited capacity to express competitive responses to improving growing conditions under a warming climate (Ettl and Peterson 1995). Furthermore, the stronger apparent influence of photoperiod in phenology in subalpine fir (relative to pine and spruce) in this study suggests that this species may respond poorly to geographical transfer, as a result of maladaptation to timing cues in altered photoperiods. "Facilitated migration" strategies in forest management responses to climate change must take into consideration such clear species differences, and a wider assessment of species responses is warranted.

Trends in lodgepole pine and interior spruce suggest a more plastic strategy during establishment at this site. The adaptive strategies in these early- and mid-successional species appear to favor competitive traits across a wide range of climate conditions. For these species, we might expect to see pronounced competitive responses during years with favorable growing conditions, particularly near the cold extreme

in the species climate ranges, where high growth potentials are muted by physiological limitations.

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