Controls of growth phenology vary in seedlings of three, co-occurring ecologically distinct northern conifers

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Summary The objective of this study was to investigate the effects of temperature and seed-source elevation on height-growth phenology of three co-occurring and ecologically distinct northern conifers (Pinus contorta Doug. ex Loud. var. latifolia (lodgepole pine), Picea glauca (Moench) Voss × Picea engelmannii Purry ex Engelm. (interior spruce) and Abies lasiocarpa (Hook.) Nutt. (subalpine fir)). Seed from populations of the three indigenous and co-occurring species was collected across an elevational transect on the southwestern slope of McBride Peak, near Prince George, BC. Collection sites were at elevations of 750 to 1850 m, the latter being close to the tree line. In 2003, seeds were germinated and seedlings raised under favorable growing conditions in a temperature-controlled glasshouse. In 2004, seedlings of each population were grown in natural daylengths at a location within 50 km of the seed collection sites both in a temperature-controlled glasshouse and at a nearby field site, and height growth was recorded twice a week throughout the growing season. Species differed in both the date and the accumulated heat sum above 5 °C for the initiation and cessation of shoot extension. Growth durations (which integrate growth initiation and growth cessation) were more similar among species in the field than in the glasshouse. This suggests that different mechanisms of phenological control among co-occurring species can result in adaptive “equivalence” under a particular set of climatic conditions.

Keywords: adaptation, co-occurring tree species, photoperiod, temperature.

Introduction

Northern conifers display marked clinal variation in growth phenology across climatic gradients, suggesting that these traits are highly adaptive and under strong selection pressures (Irgens-Moller 1957, Vaartaja 1959, Campbell and Sugano 1975, Ekberg et al. 1979, Lechowicz 1984, Oleksyn et al. 1992, Howe et al. 2000, Aitken and Hannerz 2001, Johnsen and Skrøppa 2000, Aitken and Hannerz 2001, Chuine and Beaubien 2001, Howe et al. 2003). Photoperiod differences at the seed origin are a confounding factor in common-garden studies in which populations originating from different latitudes are compared (Hänninen et al 2001). To avoid this problem in the present study, growth phenology was compared in populations of ecologically distinct and co-occurring northern tree species originating across a climatic gradient (see Green 2005). 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this way it was possible to assess interactions between temperature and photoperiod on growth phenology among study species and populations.

The study species were early-successional, shade-intolerant Pinus contorta Dougl. ex Loud. var. latifolia (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-occurred at each seed collection site across the elevation transect sampled (see Green 2005).

Materials and methods

Sample populations and treatments

Seed of lodgepole pine, interior spruce and subalpine fir were collected in August–September of 2002 at elevations of 750, 1100, 1400 and ~1850 m along the southwestern slope of McBride Peak (53°21′ N, 122°27′ W) in east-central BC. At the lowest elevation, mean annual temperature and precipitation are 4.4 °C and 680 mm, respectively. Seed was collected, processed, stored and pre-treated for germination according to Koloteloe et al. (2001). Seedlings were grown during spring and summer of 2003 in a temperature-controlled glasshouse (for details, see Green 2005). In early November 2003, seedlings were placed outdoors for winter growth at the University of Northern British Columbia (53°52′ N, 122°49′ W) to ensure that the chilling requirements for dormancy breaking were satisfied and to expose plants to the photoperiod of the native habitat during the dormancy period. In early March, seedlings were moved to cold storage (–2 °C) to prevent any effects of post-dormancy heat-accumulation on growth phenology before study initiation.

In early May 2004, thirty-two randomly selected seedlings of each population were transplanted to 2-liter pots containing 70% peat moss and 30% sand. On May 12, sixteen randomly selected seedlings of each population were placed in a temperature-controlled glasshouse at the University of Northern British Columbia (day/night temperature of 24/20 °C) where they were subject to the natural photoperiod. The remaining 16 trees of each population were taken to a nearby field site (Prince George Tree Improvement Station, elevation 580 m, 53°52′ N, 122°27′ W). Pot exteriors were painted white to minimize solar heating. Seedlings were completely randomized at both locations, and pots were rotated weekly across north–south and east–west directions to minimize the effects of light gradients, temperature gradients and edge effects. A buffer row of pots was maintained around the sample pots. Sample seedlings received regular irrigation and fertilization in both controlled and field conditions (cf. Green 2005) to minimize the potentially confounding effects of water and nutrient limitations (Kramer et al. 2000, Howe et al. 2003, Partanen 2004).

Hourly air temperatures at 25 cm above ground were measured at the field site throughout the study. Cumulative growing degree days (above 5 °C) were calculated for both the glasshouse and the field site. Shoot growth phenology was examined in relation to time from study initiation (date) and heat-sum accumulation.

Seedling measurements

Height growth of all seedlings was measured twice a week. For each individual, dates of growth onset and cessation were determined as the dates on which height growth was 5 and 95% of the seasonal growth increment, respectively (Nilsson 2001). Height-growth duration was the difference between the dates of growth onset and cessation.

Statistical analysis

Times to growth initiation and cessation and growth durations were normally distributed for all sample populations (Shapiro-Wilk Statistic). Consequently, population means for each phenological trait were compared within and between species by one-way analysis of variance (Rehfeldt 1984). Where significant differences were found within or between species, pairwise comparisons were conducted by Tukey’s multiple comparison test to determine specific differences among seedling populations.

Results

Height-growth initiation

Within species, differences with seed-source elevation in the date of onset of shoot extension were absent in both glasshouse- and field-grown lodgepole pine and interior spruce, whether responses were assessed by date or heat-sum accumulations (Table 1, Figure 1). Subalpine fir showed a weak negative trend between the onset of shoot extension and seed-source elevation, whether assessed by date or heat-sum accumulation. For all species and populations, the date of growth initiation was significantly later (P < 0.0001) in the field than in the glasshouse (Figure 1). Conversely, growth initiation based on heat-sum accumulations was significantly delayed (P < 0.0001) in the glasshouse compared with in the field (Figure 1).

Among species, height-growth was initiated first in lodgepole pine, which showed the smallest difference between growth environments in both the date of growth initiation and the heat-sum accumulation preceding the onset of growth (Table 2, Figure 1). In the glasshouse, height-growth initiation occurred almost simultaneously in interior spruce and subalpine fir, except in the treeline populations. In the field, height-growth initiation occurred later and after the accumulation of a greater heat sum in spruce than in fir in populations at all seed-source elevations (Table 3, Figure 1). Overall, variation in the date of height growth onset was greater in the field than in the glasshouse. Conversely, variation in the onset of height growth measured by heat-sum accumulation was greater in the glasshouse than in the field.

Height-growth cessation

In all species, clinal trends were more evident in time of height-growth cessation than in height-growth initiation,
whether phenology was related to date or heat-sum accumulation (Figures 1 and 2). Subalpine fir showed a strong negative trend in date of growth cessation versus seed-source elevation in both the glasshouse and the field, whether phenology was related to date or cumulative heat sum (Table 1, Figure 2). However, the date of height-growth cessation in subalpine fir

Table 1. Seed-source population variation in the dates of growth initiation and cessation and the duration of growth (Temporal assessment) and on the cumulative degree days to the dates of growth initiation and cessation (Heat-sum assessment) in subalpine fir, lodgepole pine and interior spruce grown in a temperature-controlled glasshouse or at a nearby field site. Where the analysis of variance indicated a significant effect ($P < 0.05$), minimum significant differences (MSD) were determined with Tukey’s multiple comparisons test. Significant differences ($\alpha = 0.05$) between seed-source elevations are indicated by different lower case letters.

<table>
<thead>
<tr>
<th>Growth conditions</th>
<th>Species</th>
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<th>Heat-sum assessment</th>
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<td>MSD</td>
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Figure 1. Height-growth initiation ($\pm$ SE) in subalpine fir (●), lodgepole pine (■) and interior spruce (▲) differing in seed-source elevations grown in a temperature-controlled glasshouse (A and C) or the field (B and D) expressed in days from study initiation (A and B) and in relation to heat-sum accumulation (C and D).
differed between temperature treatments only in the population originating at 1100 m, with growth continuing for slightly longer in the field (Table 3, Figure 2). Based on the cumulative heat sum, height-growth cessation of all subalpine fir populations was delayed in the glasshouse compared to in the field. Interior spruce showed weaker negative relationships than subalpine fir between height-growth cessation and seed-source elevation in both the glasshouse and the field (Table 1, Figure 2). The date of growth cessation in interior spruce was slightly later in the low- and mid-elevation populations in the field than in the glasshouse (Table 3, Figure 2). Based on heat-sum accumulation, growth cessation in all interior spruce populations was delayed in the glasshouse compared to in the field.

Only in the field did lodgepole pine show a negative relationship between seed-source elevation and the timing of growth cessation (Table 1, Figure 2). Interior spruce and subalpine fir both exhibited negative clines in height-growth duration in glasshouse and field conditions. Differences in height-growth among species were much greater in the glasshouse than in the field (Table 3, Figure 2), with height-growth cessation occurring much earlier and at smaller heat sums in the field than in the glasshouse. There was convergence among species in the field relative to those in the glasshouse in the date and the cumulative heat sum at the time of growth cessation (Table 3, Figure 2).

**Height-growth duration**

Clinal variation in height-growth duration differed among species (Figure 3). In lodgepole pine, there was a weak negative relationship between growth duration and seed-source elevation in the field but not the glasshouse (Table 1, Figure 3). Interior spruce and subalpine fir both exhibited negative relationships between height-growth duration and seed-source elevation in both the glasshouse and the field. Differences in height-growth duration among species were greater in the glasshouse relative to the field, primarily because of a large decrease in lodgepole pine height-growth duration in the field relative to the glasshouse (Table 2, Figure 3).

**Table 2. Species differences in growth duration and the date (Temporal assessment) and cumulative degree-days at the time (Heat-sum assessment) of growth initiation and cessation of lodgepole pine (LP), interior spruce (IS) and subalpine fir (SF) grown from seed obtained at different elevations (Seed-source elevation) in a temperature-controlled glasshouse or at a nearby field site. Where the analysis of variance indicated significant differences (P < 0.05), minimum significant differences (MSD) were determined with Tukey’s multiple comparisons test. Significant differences (α = 0.05) between species are indicated by different lower case letters.**

<table>
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<th>Heat-sum assessment</th>
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Table 3. Differences in growth duration and date of growth cessation in subalpine fir, lodgepole pine and interior spruce seedlings differing in seed-source elevation and grown subject to the prevailing photoperiod in either a temperature-controlled glasshouse or at a nearby field site. Significance of one-way analysis of variance between temperature treatments is indicated by $P < 0.05$. All comparisons of height-growth initiation (for both temporal and heat-sum assessments) and height-growth cessation (based on heat-sum accumulations) were significant ($P < 0.0001$).

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<th>Phenology variable</th>
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</tr>
<tr>
<td>Duration</td>
<td>750</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>1100</td>
<td>0.96</td>
</tr>
<tr>
<td></td>
<td>1400</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>1800+</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Discussion

Species-specific growth phenology responses


All species and elevational seed sources showed significant delays in the time to growth initiation in the field compared with in the glasshouse, suggesting a primary role of temperature in early-season phenology. Initiation of height growth was presumably reliant on the accumulation of a minimum heat sum (Cannell and Smith 1983, Hänninen and Pelkonen 1989, Hänninen 1990, Höyhtyä and Hänninen 1991, Hunter and Lechowicz 1992, Howe et al. 2000, Aitken and Hannerz 2001, Hänninen et al. 2001). As such, the divergence in time of growth initiation among species in the field relative to those in the glasshouse suggests that the heat-sum accumulations of seedlings of all species in the field converge because of species differences in bud break delay in the field. However, growth initiation in all species occurred after a smaller heat-sum accumulation in the field than in glasshouse. Thus, there appear to be different consequences of rapid, constant heat accumulation (glasshouse conditions) versus slow, fluctuating heat accumulation (field conditions) on the initiation of height growth.

The study species appeared to have unique mechanisms for processing temperature signals during growth initiation, as indicated by the convergence in heat-sum accumulations, but divergence in the number of days preceding growth onset in the field relative to the glasshouse. Differences were seen between interior spruce and subalpine fir, which began shoot extension growth after the accumulation of a similar heat sum and on almost the same date in the glasshouse, but after substantially different heat-sum accumulations and on different dates in the field.

A closer examination of the species-specific responses to temperature was made by comparing the differences in heat sum at growth initiation between the glasshouse and field populations (Figure 4). The species with the lowest heat-sum differentials for growth initiation, lodgepole pine and interior spruce, exhibited the greatest difference in the date of growth initiation. In lodgepole pine, growth was initiated quickly in both the field and glasshouse after the accumulation of only a small heat sum. The heat-sum accumulations at growth initiation in interior spruce were intermediate between those of lodgepole pine and subalpine fir. In this case, the longest delay in bud break resulted in a “catching up” in heat-sum accumulations for the field populations. Subalpine fir showed the greatest difference between glasshouse and field conditions in the heat-sum accumulation preceding growth initiation, which resulted from intermediate delays in bud break.

Height-growth cessation varied among species in relation to both heat-sum accumulation and photoperiod. Species also differed in responses to growth conditions, suggesting species-specific interactions between temperature and photoperiod. These differences resulted in a convergence among species in both the date of, and the heat-sum accumulation preceding, growth cessation in the field relative to differences in the glasshouse. This pattern is less clear for growth cessation than for growth initiation. Late-season trends are more complex because seedlings may respond to photoperiod and different temperature signals (e.g., low temperatures and temperature fluctuations) (Ekberg et al. 1979, Johnsen and Skrøppa 2000, Partanen 2004).

Ecological implications of interspecific differences

Height-growth duration, which integrates early- and late-sea-
son phenology, may reveal ecological implications of different adaptive mechanisms in co-occurring species (e.g., tradeoffs between competitive and survival capacities). In this study, mean growth durations of the three species were more similar in the field than in the glasshouse. The convergence of growth duration under natural conditions was the result of different times of initiation and cessation of height growth among species, suggesting selection for unique adaptive traits.

Some literature suggests that growth duration in northern conifers depends more on late-season than early-season phenology, because inter- and intraspecific variation in the time of growth initiation is generally less than that of growth cessation (Oleksyn et al. 1998, Linkosalo 2000, Howe et al. 2000, Aitken and Hannerz 2001, Chuine et al. 2001, Howe et al. 2003). In this study, however, the convergence of growth durations observed among field-grown seedlings occurred as a result of species differences in the degree and direction of phenological responses and in differences in the critical response periods (i.e., early- and late-season).

In lodgepole pine, the much shorter growth duration in the field versus the glasshouse was primarily due to differences in the time of growth cessation. Based on temporal and heat-sum assessments, all elevational populations of lodgepole pine grown in the field ceased growth before those in the glasshouse; the same trend in growth initiation was observed, but with less variation than growth cessation. Conversely, populations of interior spruce and subalpine fir exhibited relatively minor differences in growth duration between growth conditions, but for different reasons. In lodgepole pine, temperature appeared to be important in the control of both early- and late-season phenology. In interior spruce, delays in the date of both the initiation and cessation of growth in the field relative to that in the glasshouse cancelled out differences in growth duration between the glasshouse and field. In early-season phenology, interior spruce exhibited the greatest temperature responses among study species, but in late-season phenology, it exhibited intermediate responses that were directionally opposite to those of lodgepole pine.

In contrast, the small variations in growth duration between treatments for subalpine fir populations appeared to be driven...
late-successional species (lodgepole pine and subalpine fir, re-
duration ranked with successional position, and early- and
(Green 2005). In this study, phenotypic plasticity in growth
early-successional species than in late-successional species
herent sensitivity to climate fluctuations might be expected in
regulation may reflect ecological differences, and greater in-
Links between species ecology and adaptive distinction
Interspecific differences in mechanisms of growth phenology
regulation may reflect ecological differences, and greater in-
Green 2005). In this study, phenotypic plasticity in growth
duration ranked with successional position, and early- and
late-successional species (lodgepole pine and subalpine fir, re-
respectively) showed the most distinct phenological responses.
For any species, a more conservative adaptive strategy (e.g.,
more fixed growth durations) might be expected at the margin
of a species’ range relative to more favorable conditions
(Irgens-Moller 1957, Stern and Roche 1974, Oleksyn et al.
Oleksyn et al. 1998, Bannister and Neuner 2001, Hänninen et al. 2001). Conversely, a more competitive adaptive
strategy (e.g., higher phenotypic plasticity in growth dura-
tions) might be expected in populations originating in the most
favorable environments. Although all field-grown populations
originating from the lowest seed-source elevations (warmest
native environment) had the longest growth durations, and those
from the highest seed-source elevations had the shortest
growth durations, each species expressed unique adaptive
mechanisms across the entire range of climatic conditions,
which was unexpected. All lodgepole pine populations
showed high phenotypic plasticity in growth duration, even in
the case of the tree-line population. Conversely, subalpine fir
showed a relatively fixed growth duration across all seed-
source elevations (suggesting a conservative adaptive strategy,
see Ettl and Peterson 1995), even in the most favorable envi-
Further examination of northern conifers occurring in a
wider range of climatic conditions is necessary before adaptive
mechanisms can be generalized at the species level. Adaptive
mechanisms among populations originating at different
evocations may result from the strength and direction of selec-
tion pressures, or from the amount of gene flow occurring be-
tween populations, or both (Aitken and Hamnerz 2001). Con-
sequently, phenological clinal patterns across latitudinal cli-
mate gradients (which would limit gene flow potential among
climatic populations relative to elevational gradients) may dif-
fer from the phenological clines observed in this study. The
findings of this study, however, suggest that co-occurring tree
species may achieve adaptive “equivalence” at a given site, at-
taining balance through unique mechanisms of processing
local climatic conditions.
In conclusion, unique adaptive strategies were observed
among ecologically distinct and co-occurring tree species in
the regulation of early- and late-season shoot growth phenol-
ogy. All species demonstrated sensitivity to temperature dur-
ing early-season growth phenology, whereas late-season
growth responses to temperature conditions were more com-
plex, varying in magnitude and direction. Among the studied
species, early-successional lodgepole pine expressed high
late-season temperature sensitivity in all populations; con-
versely, late-successional subalpine fir showed low tempera-
ture sensitivity. Further, adaptive strategies within species ap-
peared to be expressed uniformly across the climatic range.
The species-specific adaptive mechanisms observed resulted
in a convergence of growth period duration in the field relative
to the glasshouse. The robustness of such adaptive balances
among co-occurring species in a changing climate remains
largely unknown.

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