Height growth determinants and adaptation to temperature in pines: a case study of *Pinus contorta* and *Pinus monticola*

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Abstract: In this study we aimed to compare and explain the height growth performance of two contrasting pine species: lodgepole pine (*Pinus contorta* Dougl. ex. Loud) and western white pine *(Pinus monticola* Dougl. ex D. Don.). We compiled measurements of total height growth at different ages and shoot elongation phenology realized in several provenance test trials for 109 provenances of lodgepole pine and 54 provenances of western white pine. The response of shoot elongation to temperature was assessed using a phenological model fitted on provenance mean growth curves. Although total height growth followed the same geographic trends in both species, the response of shoot elongation to temperature was different between the two, with few (lodgepole pine) or no differences among provenances (western white pine) from diverse geographic regions. The temperature for which potential cell growth rate is 50% was 10.8 ± 0.13 °C (mean ± standard error) for western white pine compared to 5.26 ± 0.075 °C for lodgepole pine. Phenology did not explain growth performance differences among geographical regions in both species, which instead were explained by differences in the number of internodes set the preceding summer; provenances originating from stressful environments produced the fewest internodes, possibly due to reallocation of carbohydrates to stress resistance.

Résumé : Cette étude avait pour but de comparer et d'expliquer les performances de croissance en hauteur de deux espèces de pins très différentes: pin lodgepole (*Pinus contorta* Dougl. ex. Loud) et pin blanc de l'Ouest (*Pinus monticola* Dougl. ex D. Don.). Nous avons compilé des mesures de croissance en hauteur totale à différents âges ainsi que des mesures de phénologie d'élongation des pousses de l'année, réalisées dans plusieurs tests de provenances pour 109 provenances de lodgepole pine et 54 provenances de pin blanc de l'Ouest. La réponse de l'élongation des pousses à la température a été déterminée à l'aide d'un modèle phénologique ajusté sur les courbes de croissance moyenne des provenances. Alors que la croissance totale en hauteur suivit les mêmes patrons de variations géographiques chez les deux espèces, la réponse de l'élongation des pousses à la température était très différente entre les deux espèces, avec peu (pin lodgepole) ou pas de différences entre les provenances (pin blanc de l'Ouest) des diverses régions géographiques. La température pour laquelle le taux de croissance potentielle des cellules est 50 % était de 10.8 ± 0.13 °C (moyen ± erreur-type) pour pin blanc de l'Ouest et de 5.26 ± 0.075 °C pour pin lodgepole. La phénologie n'expliqua pas les différences de performance de croissance entre les différentes régions géographiques chez les deux espèces, qui étaient davantage expliquées par les différences de nombre d'entre-nœuds produit pendant l'été précédent, les provenances originaires d'environnements stressant produisant moins d'entre-noeuds, possiblement du fait de la réallocation des hydrates de carbone à la résistance aux stresses.

Introduction

Adaptation to environment, and in particular climate, remains one of the most fascinating issues in ecology, especially in the context of global climate change. Identifying those traits of major ecological importance that affect fitness and therefore affect species distribution requires extensive data sets on adaptive traits from populations sampled throughout species ranges. Lodgepole pine (*Pinus contorta* Dougl. ex. Loud) and western white pine (*Pinus monticola* Dougl. ex D. Don) have very different distributions. Lodgepole pine is one of the most widespread conifers in western North America, and, along with the closely related species *Pinus banksiana* Lamb., is one of just two pines represented in the boreal forests of North America (Critchfield 1985). Western white pine occurs along the southern edge of the range of lodgepole pine. These two North American pines not only differ greatly in their geographic distributions, but also in terms of their Holocene and Pleistocene history and population genetic structure. While lodgepole pine is one of the most differentiated conifer species of North America according to both quantitative genetic traits (vegetative or re-

Received 25 August 2005. Accepted 19 November 2005. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 11 April 2006.

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 doi:10.1139/X06-005

Table 1. Summary of the lodgepole pine (*Pinus contorta*) and western white pine (*Pinus monticola*) data used in this study.

No. prov.	No. fam.	Site	Block	No. rep.	Year establ.	Measurements	Reference
Pinus contorta							
109(144)	15	Cowichan Lake, British Columbia	3	2	1969	2-year shoot elongation; 3-year height; 15-year height	Illingworth 1969 (Project 657.04 II)
109(144)	15	Red Rock, British Columbia	3	2	1969	2-year shoot elongation; 3-year height; 20-year height	Illingworth 1969 (Project 657.04 II)
Pinus monticola							
58	5	Moscow, Idaho	3	2	1979	3-year shoot elongation; 3-year height	Rehfeldt 1984
58	5	Priest River-Tarlac, Idaho	3	2	1979	3-year shoot elongation; 3-year height	Rehfeldt 1984
58	5	Priest River, Idaho	3	2	1979	3-year height	Rehfeldt 1984
54	3	Moscow, Idaho, greenhouse	3	1	1979	3-year shoot elongation; 3-year height	Rehfeldt 1984
60	15	Whidbey Island, Washington	3	2	1984	11-year height	
21(60)	4(15)	Whidbey Island, Washington	3	1	1984	15-year terminal 4-year-old second-order shoot total elongation and internodes number	

Note: No. prov., number of provenances represented in the trial, when two numbers are indicated, the first one represent the number of provenances measured among the total number of provenances in the test indicated in parentheses. No. fam., number of progenies per provenances represented in the trial, when two numbers are indicated, the first one represent the number of progeny measured among the total number of progenies per provenance indicated in parentheses. Site, name of the test site. Block, number of blocks in the test site. No. rep., number of individuals per progeny per block. Year establ., year of establishment of the test. Measurements, measurements used in this study.

productive) and allozymes (Rehfeldt and Wykoff 1981; Wheeler and Guries 1982; Rehfeldt et al. 1999), western white pine is one of the least differentiated species (Steinhoff et al. 1983; Rehfeldt et al. 1984; Rehfeldt 1997); thus, clines are steep in lodgepole pine and difficult to detect in western white pine. These two species, therefore, are ideal for comparisons involving adaptation to environment in general and to climate in particular.

A critical adaptation to environment in trees of temperate or boreal forests is optimal utilization of the local growing season to assure competitive growth without increasing frost or drought injuries. Many environmental factors and biological variables affect total height so that different strategies of height optimization are possible, and these may differ from one species to another. Identifying such alternate strategies requires interspecific comparisons of the relative performance of environmentally disparate provenances. Here we question whether the geographical patterns in height growth of *P. contorta* and *P. monticola* can be interpreted on the basis of their differences in phenology in relation to temperature. For this purpose we analyzed height growth performance and shoot elongation phenology in relation to temperature for provenances representing the entire species' ranges but grown under common conditions.

Materials and methods

We have assembled and collected data on shoot elongation, height growth, and internode production from short- and long-term provenance trials that had been established for the two species. Table 1 summarizes the information on the different provenance tests and measurements used in this study.

Shoot elongation

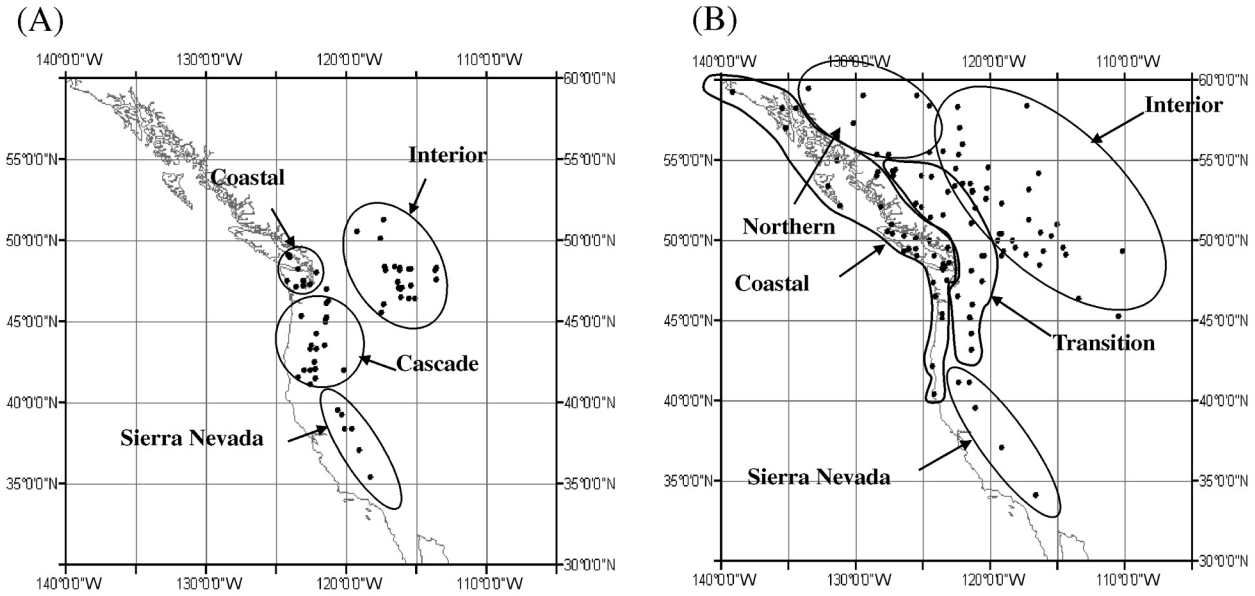
Pinus contorta

We used shoot elongation phenology models previously published by Chuine et al. (2001). These models had been fitted using 2-year shoot elongation of 109 provenances (Fig. 1) grown at the Cowichan Lake Research Station on Vancouver Island, British Columbia (48.8°N, 124.1°W, 180 m a.s.l.), Canada, and at Red Rock Nursery near Prince George, north-central British Columbia (53.8°N, 122.7°W, 614 m a.s.l.), Canada. Each provenance was represented by 15 open-pollinated families and 30 seedlings (2 seedlings per family) per test site. The experiment was a randomized complete block design with three replications of 10-seedling row plots per test site. For further reading concerning the design of tests, provenance variation, and conclusions concerning these research test plantings, see Illingworth (1969) and Ying and Illingworth (1986).

Pinus monticola

We used data from two test sites of the western white pine provenance trial, Moscow, Idaho (48.5°N, 116.7°W) and Priest River Experimental Forest, Idaho, at high elevation (Tarlac site, 48.2°N, 116.9°W, 1475 m a.s.l.). Western white pine was represented by 58 provenances representing the geographic distribution and the ecological amplitude of the species within the Rocky Mountains, the Cascade Range, and the Sierra Nevada. After 1 year of growth in a shade house in Moscow, seedlings were arranged in a randomized complete block design with three replications of 10-seedling row plots per test site. Third-year shoot elongation was measured periodically in 1982 at both sites. Among the 58 provenances, 54 of them (Fig. 1) were also grown in plastic containers for 2 years in a shade house in Moscow. Each of

Fig. 1. Geographic origin of the 109 sampled provenances of *Pinus contorta* (A) and 54 sampled provenances of *Pinus monticola* (B). Geographical regions used in the analyses for both species are shown on the map.



the provenances was represented by three seedlings in each of three blocks. In 1982, these individuals were kept outside until late March, when they were moved into a greenhouse with a temperature regime of 21 °C (light) : 13 °C (dark) to be forced. Shoot elongation was measured periodically until elongation of the preformed bud had ceased. For further details, see Rehfeldt et al. (1984)

Total height

Total height was measured at age 3 and 15 at the Cowichan Lake test site and at age 3 and age 20 at the Red Rock test site for lodgepole pine. Total height was measured at age 3 at the Moscow, Priest River (low elevation), and Tarlac (i.e., Priest River high elevation) test sites for western white pine. The Priest River low-elevation test site had received the same material at the same time as the two other test sites and with the same design. Total height was also measured at age 11 for western white pine in another trial established in a randomized complete block design with three replications of 10-seedling row plots by the Washington State Department of Natural Resources on Whidbey Island, Washington (48.29°N, 122.67°W).

The shoot elongation phenology model

The modeling of shoot elongation phenology according to the temperature of the lodgepole pine provenances was realized in a previous study (Chuine et al. 2001). We followed the same methodology to model shoot elongation phenology according to the temperature of the western white pine provenances.

Shoot elongation was first fitted for each provenance to the model

$$[1] \qquad G(t) = G_{\mathrm{m}} + \frac{a}{1 + \mathrm{e}^{b(t-c)}}$$

where t is time in days; G_{m} is the length of the terminal bud at the end of the previous growing season; a is the total elongation completed in 1 year; b is a component of the maximum growth rate, which is negative; and c is the date on which half of the total elongation is completed (Fig. 2). Maximum growth rate, R, can be calculated as $R = G'(c) = -ab/4$. The period during which growth rate is maximum and steady is determined by the period for which $G(t) - D(t)$ is small, that is, within $\pm 0.005a$ (around 0.5 mm on average), where $D(t)$ is the tangent to the growth curve at the inflexion point (Fig. 2).

The shoot elongation phenology model is as follows. The daily rate of development of buds is triggered by temperature and is mathematically formalized by the so-called forcing unit (FU) function classically used in phenological models (Sarvas 1974; Hänninen 1990; Kramer 1994):

$$[2] \qquad \mathrm{FU}(x_t) = \frac{1}{1 + \mathrm{e}^{w(x_t - z)}}$$

where x_t is the mean temperature of day t; w is the parameter of the slope of the sigmoid; and z is the mid-response temperature, that is, the temperature for which FU = 0.5 (FU varies from zero to one). The parameter set (w, z) was fitted for each provenance using the least square method. The least square function was

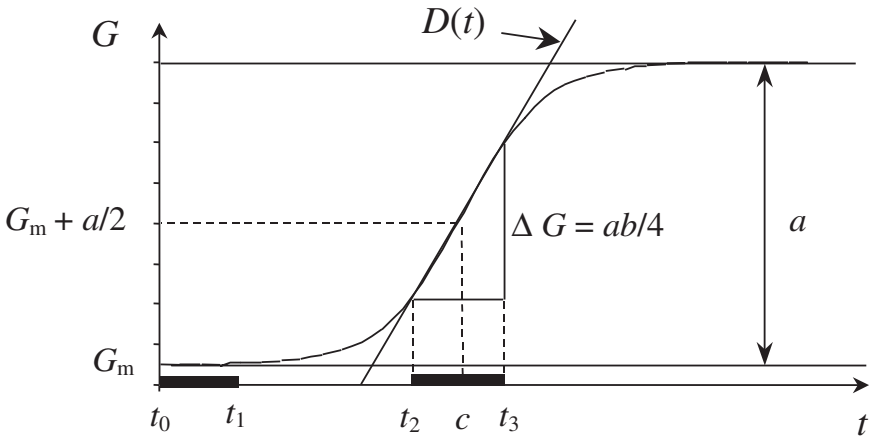
$$[3] \qquad \mathrm{LS}(w, z) = \sum_{t_0}^{t_1} f + \sum_{t_2}^{t_3} f$$

where t_0 is 1 January, t_1 is the day when 0.1% of the total elongation is achieved; t_2 and t_3 are, respectively, the days when maximum growth rate begins and ceases according to the shoot elongation model of each provenance; and

$$[4] \qquad f = \left\{ \Delta \mathrm{G}(t) - \left[\frac{-ab}{4} \mathrm{FU}(x_t) \right] \right\}^2$$

where $(-ab/4)\mathrm{FU}(x_t)$ represents the elongation that can be achieved in 1 day and is equal to the maximum growth rate

Fig. 2. Growth model. Annual growth curves were fitted to the equation $G(t) = G_{min} + \frac{a}{1 + e^{b(t-c)}}$. $D(t)$ is the tangent to the growth curve at the inflection point ($G(t) = G_{min} + a/2$): $D(t) = (ab/4t) + G_{min} + a/2(1 - bc/2)$. t_0 is 1 January; t_1, t_2, t_3 are the days when 0.1% of elongation is achieved, when linear growth begins, and when linear growth ceases, respectively.



($ab/4$) when FU(x_t) = 1 and zero when FU(x_t) = 0; $\Delta G(t)$ is calculated with the shoot elongation model; x_t is the daily temperature at the test sites. The optimization of the least square function was achieved with the simulating annealing algorithm Metropolis (Metropolis et al. 1953).

The response of shoot elongation of western white pine to temperature was fitted for the 54 provenances using conjointly the measurements taken in 1982 at Moscow and at Tarlac as well as shoot elongation measurements done in the greenhouse at Moscow. For this purpose we used the daily temperatures recorded at Moscow in 1982 and adjusted the daily temperatures recorded in 1982 at Priest River for the elevation at Tarlac using Tarlac monthly normals.

Internode number

We sampled terminal shoots of twelve 15-year-old western white pine individuals from each of 21 provenances (four trees per block from three blocks) grown at the Whidbey Island provenance trial. The shoots sampled were 4-year-old second-order shoots from the southern exposure. Shoots were sampled in mid-May when elongation had already started (3 cm on average). The total elongation achieved and the number of nodes (needle fascicle bundles) produced during the preceding growing season were measured for each individual.

Results

Provenance variation in total height

Total height at age 3 was highly correlated with total height at age 15 ($r = 0.89$, $p < 0.001$) and age 20 ($r = 0.64$, $p = 0.0028$) in lodgepole pine. Total height at age 3 was also highly correlated with total height at age 11 ($r = 0.88$, $p < 0.001$) in western white pine. Total height at age 3 on average was higher in Cowichan (142.3 mm ± 3.6) than in Red Rock (78 mm ± 1.66) for lodgepole pine, and total height at age 3 was higher in Moscow (217.9 mm ± 5.6) than in Priest River (171.6 mm ± 3.7) and Tarlac (135.7 mm ± 2.5) for western white pine, following a trend consistent with the mean annual temperature of the sites during the 3 years of cultivation (9.7 °C in Cowichan, 3.8 °C in Red Rock, 8.3 °C in Moscow, 7.1 °C in Priest River, 3.7 °C in Tarlac). Total height at age 3 was also highly correlated between test sites in lodgepole pine ($r = 0.88$) and in western white pine ($0.85 < r < 0.89$).

The log (3-year mean height) (over the different test sites) showed similar variation with latitude in both species over their common latitudinal range (34°–53°N) (Fig. 3), with provenance height increasing with latitude up to 46°–50°N and decreasing from 50°–63°N. Geographical variation in log (3-year mean height) was compared between the two species over their common range by calculating the average height within all common 1° latitude × 1° longitude grid cells. The log (3-year mean height) of both species was significantly correlated with each other over these grid cells ($r = 0.64$, $p = 0.007$, df = 16).

Provenance variation in the response of shoot elongation to temperature

Western white pine had a response of shoot elongation to temperature characterized by a high mid-response temperature, averaging 10.2 ± 0.15 °C (mean ± standard error) (Fig. 4). There were no significant differences among coastal, interior, Sierra Nevada, and Cascade provenances (ANOVA with region as fixed effect, $F_{[3,50]} = 1.86$, $p = 0.14$, Shapiro–Wilks' W test for non-normality not significant, $p = 0.52$). In contrast, lodgepole pine shoot elongation was characterized by a much lower mid-response temperature, varying between 5.0 and 6.5 °C depending on the region: coastal provenances averaged 5.1 °C (+ 0.32 °C, –0.35 °C), interior 5.1 °C (+0.40 °C, –0.46 °C), northern 6.5 °C (+0.09 °C, –0.18 °C), Sierra 5.0 °C (+0.48 °C, –0.49 °C), and coastal–interior transition 5.6 °C (+0.23 °C, –0.21 °C) (Chuine et al. 2001). Only the most northern provenances were significantly different from other regions for temperature response ($p < 0.0001$, Chuine et al. 2001).

Height growth determinants

Maximum growth rate explained a large part of the total sapling height variance among provenances in both lodge-

Fig. 3. Relationship between log (3-year mean height) and latitude of the origin of the 109 provenances of *Pinus contorta* (LP) grown at Cowichan Lake and Red Rock, British Columbia (open symbols), and 54 provenances of *Pinus monticola* (WP) grown at Moscow, Priest River, and Tarlac, Idaho (filled symbols).

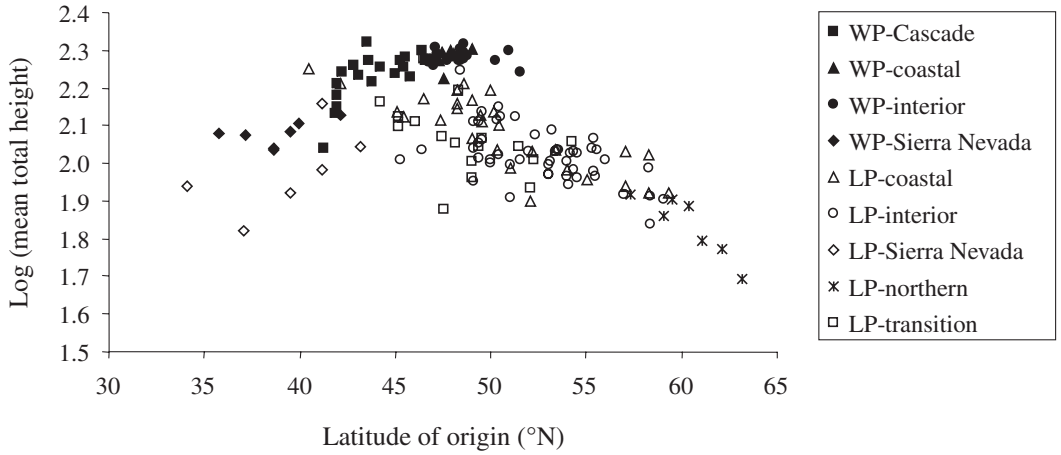
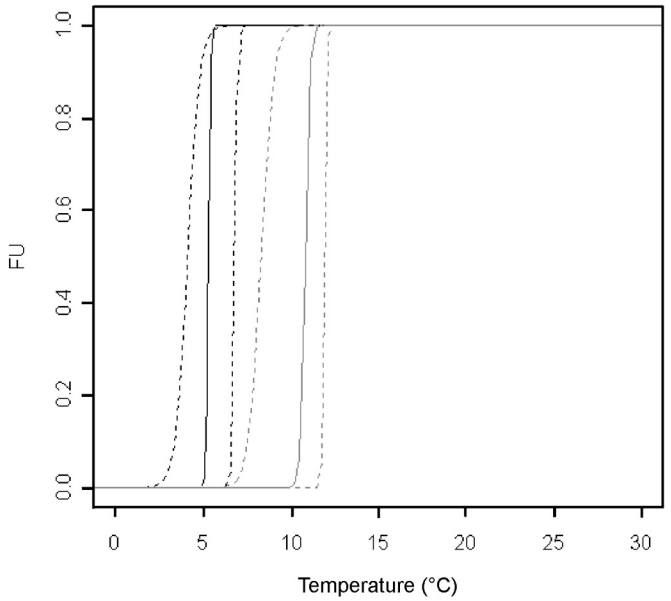


Fig. 4. Fitted FU as a function of temperature for *Pinus monticola* (grey) and *Pinus contorta* (black). Solid and broken lines represent the mean response and the extreme responses in both species, respectively.



pole pine and western white pine, in contrast to phenology (Table 2), except for western white pine at Tarlac.

We found a strong relationship between total elongation and number of internodes (R^2 = 0.86, p < 0.001) and between maximum growth rate and the number of internodes (R^2 = 0.83, p < 0.001) (Fig. 5*a*) in the terminal shoot of western white pines in the Whidbey Island, Washington, trial. Internode number exhibited significant clines with both latitude (positive) and elevation (negative) (Fig. 5*b*, 5*c*) in western white pine and differed significantly among the Sierra, coastal, Cascade, and interior regions (F = 21.21, p = 0.00139), but not among provenances within regions (F = 1.14, p = 0.36). However, these differences were due to the Sierra provenances, which differed significantly from the other regions, while the Cascade, coastal, and interior regions did not differ from each other.

Table 2. Multiple regression analyses of population means for total 3-year height in Moscow and Tarlac for *Pinus monticola* and in Cowichan Lake and Red Rock for *Pinus contorta*, against maximum growth rate (R) and date of mid-growth (c); partial and total R^2 are shown.

	P. contorta		*P. monticola*	
Variable	Cowichan Lake	Red Rock	Moscow	Tarlac
R	0.858***	0.492***	0.641***	0.353***
c	0.001ns	0.006ns	0.003ns	0.190***
total	0.859***	0.498***	0.644***	0.543***

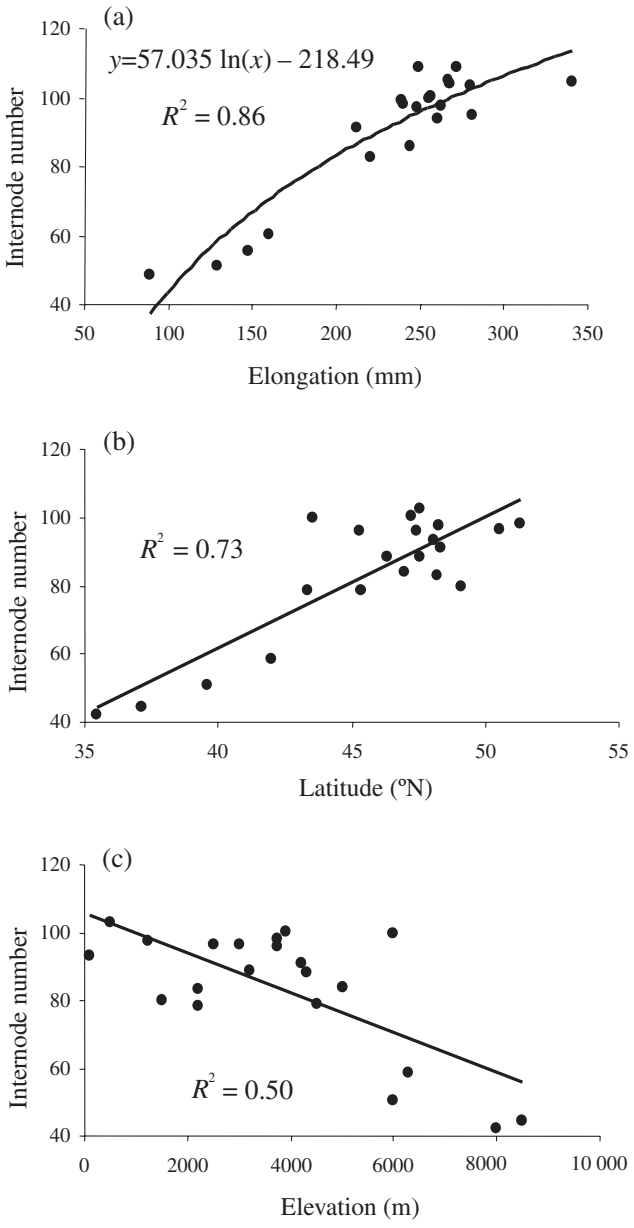
Note: ***, p < 0.0001; ns, p > 0.05.

Discussion

Western white pine and lodgepole pine showed very different responses of shoot elongation to temperature. It is noteworthy that when the response to temperature is already optimal for lodgepole pine (temperature higher than 7 °C), western white pine still does not respond (Fig. 4). The temperature of 5 °C has long been used as the standard mid-response temperature in tree phenology studies (Wang 1960; Lieth 1974; Cannell and Smith 1983; Murray et al. 1989; Frenguelli and Bricchi 1998). There is now, however, a general consensus that the phenological response to temperature is species specific and could be anywhere between 0 and 20 °C (Hänninen 1990; Hunter and Lechowicz 1992; Kramer 1994; Chuine 2000). The low mid-response temperature of lodgepole pine seems consistent with field observations showing that lodgepole pine growth initiation starts soon after snow has melted, that is, when temperature rises above zero but is still quite low. The higher mid-response temperature of lodgepole pine northern provenances compared to that in other provenances may have been selected to avoid late spring frost that may be more frequent at this time of year in the north than at lower latitudes.

We found no significant relationship between growth and phenology except at the Tarlac test site. However, the relationship found at Tarlac between growth and phenology was mainly due to the Sierra Nevada and southern high-elevation

Fig. 5. Relationship between internode number and (*a*) elongation, (*b*) latitude of origin, and (*c*) elevation of origin for the 21 provenances of *Pinus monticola* grown in Whidbey Island.



Cascade provenances, which achieved mid-elongation earlier than the other provenances, the opposite of what one would customarily expect. The relationship found in Tarlac is probably due to much slower growth (2.5 times slower than in Moscow), exacerbating small differences among provenances in the phenology of shoot elongation, which slightly delayed the date of mid-growth of taller provenances. Thus, higher growth does not seem to be due to either earlier initiation or later cessation.

Total elongation achieved each year in a species with determinant shoot elongation is the product of the number of internodes set during the previous growing season and their average length achieved through elongation in the current year. Growth rate depends primarily on the number of internodes produced during the previous growing season. All else being equal, the higher the number of internodes, the higher the growth rate and the greater the amount of elongation. This relationship between the number of internodes and both total elongation and growth rate has previously been shown experimentally for lodgepole pine by Cannell and Willet (1975) and Cannell et al. (1981). We found the same relationship for western white pine in the present study.

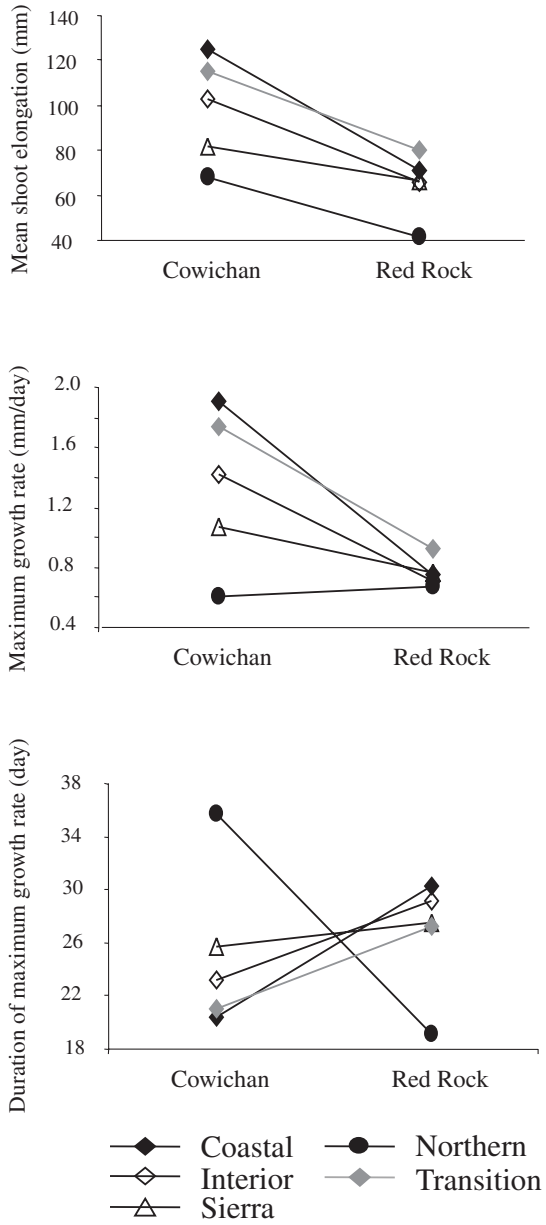
Height growth performance in lodgepole pine and western white pine thus seemed governed by the number of internodes set during the previous growing season, which itself is determined by the rate of node initiation (Cannell and Willet 1975), rather than by the phenology of the elongating shoots in our data (although the two are not independent). This hypothesis finds strong support in the variation observed in internode number and maximum growth rate among lodgepole pine (Chuine et al. 2001) and western white pine provenances in relation to their latitude or longitude of origin.

In both species, rapid growth takes place in provenances originated from the 46°–50°N latitudinal range, either from the coast or the interior, which is in agreement with the results of Rehfeldt et al. (1999) using growth data from the 60 Illingworth test sites. Provenances beyond this latitudinal range tend to have a lower height growth potential. In these peripheral regions, the abiotic environment becomes more harsh in terms of drought, minimum and maximum temperatures, frost occurrence, and growing season length: provenances to the north tend to experience a sub-boreal to boreal climate, while those to the south a sub-alpine to alpine climate (western white pine and lodgepole pine occur only at high elevations in the Cascade and Sierra Nevada ranges).

Although their distributions and phenology differ greatly, height performance of western white pine and lodgepole pine populations seem to have adapted similarly to the abiotic conditions of their origin. Trade-offs between the allocation of resources to survival (resistance to frost and drought) and to growth (competition for light) affect the average performance of each population. In a pattern typical of conifers, provenances from stressful environments exhibit lower growth performance than do provenances from less stressful environments, whatever the environmental conditions they are grown in (Hannerz et al. 1999; Aitken and Hannerz 2000; Cregg and Zhang 2001). The existence of a trade-off between growth and survival in pines is supported by the results of studies on cold hardiness, showing that fast-growing provenances exhibit lower cold hardiness in both species (Rehfeldt et al. 1984; Rehfeldt 1987; Thomas and Lester 1992), and is a general trend across temperate and boreal tree species (Howe et al. 2003). Slower-growing provenances also exhibit greater resistance to drought stress (Cregg and Zhang 2001).

Shoot elongation and maximum growth rate (and thus probably internode number) are plastic traits, as shown by differences in the maximum growth rate and shoot elongation of *P. contorta* among regions between a coastal environment (Cowichan Lake) and a continental environment (Red Rock) (Fig. 6). Surprisingly, northern provenances exhibit a shorter period of maximum growth in Red Rock than in Cowichan Lake, contrary to the other provenances. This is due to the fact that northern provenances exhibit a slightly higher maximum growth rate in Red Rock than in Cowichan Lake contrary to all other provenances, whereas similarly to

Fig. 6. Reaction norm of the mean 2-year shoot elongation, shoot maximum growth rate, and duration of maximum growth rate of the different provenances of *Pinus contorta* grown at Cowichan Lake and Red Rock, British Columbia.



these latter provenances the total elongation achieved is lower at Red Rock. The reaction norm of the number of internodes set also differs among provenances: trees from more abiotically stressful environments (northern, interior, Sierra) exhibit less plasticity among environments than those from more moderate climates (coastal, transition) (Fig. 6). It has been widely argued based on both theoretical and empirical studies that because plasticity is a costly trait, organisms cannot exhibit an optimal phenotype in every environment. Increased fitness in one environment is only achieved at the cost of decreased fitness in other environments (Bradshaw 1965; Via and Lande 1985; Gillespie and Turelli 1989; Van Tienderen 1991; Gomulkiewicz and Kirkpatrick 1992; Sultan 1995; Reboud and Bell 1997). The number of internodes set depends on the length of the growing season and on frost and drought occurrence when internodes are being set. The cost of resistance to drought and frost, and a shorter growing season, may have reduced the plasticity for growth in the interior, transition, Sierra, and northern provenances, in contrast to the coastal provenances, which experience less stressful abiotic conditions. Phenotypic plasticity in height growth in lodgepole pine thus seems to be the product of both different selection regimes and evolutionary constraints, but further investigation involving experiments with family structure would be required to determine how selection and constraints interact to produce the reaction norms observed (Gomulkiewicz and Kirkpatrick 1992).

Acknowledgements

The authors are very grateful to Cheng C. Ying, who provided lodgepole pine growth data, Dean De Bell, Washington State Department of Natural Resources, who permitted access to the western white provenance trial and provided climatic data for Whidbey Island. This research was supported by the Natural Sciences and Engineering Research Council (NSERC) – Industrial Junior Research Chair in Population Genetics (S.N.A.).

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