

# Temperature thresholds of shoot elongation in provenances of *Pinus contorta*

Isabelle Chuine, Sally N. Aitken, and Cheng C. Ying

**Abstract:** Periodicity of shoot elongation in seedlings of *Pinus contorta* Dougl. ex Loud. was assessed during one growing season in two extremely different environments (Cowichan Lake, and Red Rock, British Columbia) for 109 provenances sampled range wide. Analysis of variance of total elongation and growth parameters showed significant differences among geographic regions and among provenances within each region. Our study also revealed tremendous genotype-by-environment interaction for growth and phenological traits. The response of growth to temperature of each provenance was assessed from their growth curve using an original methodology. The estimated temperature threshold of the provenance growth responses (i.e., the temperature for which the response reaches half of its maximum) varied between 4.1 and 6.5°C among regions. Threshold temperatures showed less variation than total elongation, and only the northern provenances showed thresholds significantly different from the other regions. Our results show that, across highly contrasting environments, relationship between phenology and growth may not be as important as the relationship between growth and number of internode primordia. This tempers the results of studies, carried out in one or few similar environments, that have shown that phenological differences were important in determining total height growth in lodgepole pine.

**Résumé :** La périodicité de l'élargissement de l'épicotyle de semis de *Pinus contorta* Dougl. ex Loud. a été suivie pendant une année de croissance dans deux environnements extrêmement différents (Cowichan Lake et Red Rock, en Colombie-Britannique) chez 109 provenances échantillonnées sur l'ensemble de l'aire de répartition de l'espèce. L'analyse de variance de l'élargissement totale et des paramètres de croissance montre des différences significatives entre régions géographiques et entre provenances d'une même région. Notre étude révèle également de fortes interactions génotype × environnement pour la croissance et les caractères phénologiques. La réponse de la croissance à la température de chaque provenance a été estimée à partir de leur courbe de croissance et d'un modèle original présenté ici. Le seuil thermique estimé pour la réponse de la croissance de chaque provenance (i.e., la température pour laquelle 50% de l'activité maximale est atteint) varie entre 4,1 et 6,5°C selon la région. Les seuils thermiques sont moins variables que l'élargissement totale et seules les provenances de la région nord ont un seuil thermique significativement différent des autres provenances. Nos résultats montrent, qu'à travers des environnements très contrastés, la relation entre la phénologie et la croissance n'est pas aussi importante que celle entre la croissance et le nombre d'entre-nœuds. Ceci tempère les résultats des études réalisées dans un seul environnement ou quelques environnements similaires, qui ont montré que la phénologie était un facteur déterminant dans la croissance totale en hauteur chez *P. contorta*.

## Introduction

Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) is one of the most widespread conifers in North America, with populations occupying a wide range of environmental conditions. It grows throughout the Rocky Mountains and Pacific coast regions from the Yukon Territory (64°N) in the north

to Baja California (31°N) in the south and the Black Hills of South Dakota in the east (USDA 1965). Four subspecies have been recognised based on morphological and isozyme differences: *Pinus contorta* ssp. *contorta* (Dougl. ex Loud.) Critchfield with a coastal distribution; *Pinus contorta* ssp. *boleri* (Parl.) Critchfield, endemic to the Mendocino County White Plains of California; *Pinus contorta* ssp. *murrayana* (Grev. & Balf.) Critchfield, in the Sierra Nevada; and *Pinus contorta* ssp. *latifolia* (Engelm.) Critchfield, which covers the rest of inland portion of the range (Critchfield 1957; Wheeler and Guries 1982b).

A critical adaptation for populations is optimal utilization of the local growing season, i.e., utilizing the period during which growth is possible without unduly increasing the risk of frost or drought injuries. Comparison of growth, phenology, and adaptation in relation to climate of both provenance origin and growing environment has not previously been conducted rangewide for this species but on provenances from a more restricted geographic area (Cannell and Willet 1975; Cannell et al. 1981; Rehfeldt and Wykoff 1981; Rehfeldt 1987; O'Reilly and Owens 1989), although

Received November 3, 2000. Accepted April 5, 2001.  
Published on the NRC Research Press Web site at  
<http://cjfr.nrc.ca> on August 2, 2001.

**I. Chuine<sup>1</sup> and S.N. Aitken.<sup>2</sup>** Department of Forest Sciences, 3041-2424 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

**C.C. Ying.** Research Branch, British Columbia Ministry of Forests, Victoria, BC V8W 9C2, Canada.

<sup>1</sup>Present address: Paléoenvironnements et Palynologie, ISEM, case 61, Université Montpellier II, place E. Bataillon, 34095 Montpellier CEDEX 5, France (e-mail: chuine@isem.univ-montp2.fr).

<sup>2</sup>Corresponding author (e-mail: aitken@interchg.ubc.ca).

total height growth in long-term field trials in relation to climate has been assessed (Rehfeldt et al. 1999). Here we analyse growth patterns of *P. contorta* seedlings from 109 provenances covering the entire species range. In addition to the analysis of growth patterns, a methodology for assessing the response of growth to temperature from growth curves fitted to a rational growth function and temperature regime is presented. Mathematical growth functions enable the decomposition of growth components and thus help the examination of the underlying processes and mechanisms (Savageau 1979). The objectives of this analysis were to (i) explain the differences observed among regions in growth patterns, in particular the relationship between growth and phenology, (ii) identify regions that differ significantly for growth phenology and temperature response, and (iii) compare our results with those from long-term field tests for this species.

## Materials and methods

Thirty seedlings each of 109 provenances of *P. contorta* from throughout the natural range of the species (Fig. 1) were planted in 1969 at the B.C. Ministry of Forest Cowichan Lake Research Station, (53.7°N, 122.7°W) and Red Rock, British Columbia (48.8°N, 124.1°W), nurseries. The experiment was laid out in a randomized complete block design with three replications of five-seedling row plots per test site. The 109 provenances were grouped into five regions for the result analyses: coastal (ssp. *contorta*), interior (ssp. *latifolia*), transition (ssp. *latifolia* with a ssp. *contorta* influence), Sierra (ssp. *murrayana*), and northern (ssp. *latifolia* in the Yukon Territory).

Seedling culture followed the normal nursery procedure of bare root seedling production at both nurseries, with regular weed control, fertilization, and irrigation if needed to avoid drought stress. Fertilization was more frequent at Red Rock, because the nursery bed was newly built and the soil was very sandy. During the second growing season (1970), weekly shoot growth increments were measured at both nurseries on 15 individuals per provenance up to October.

### Growth curve analysis

Pines, including *P. contorta*, do not have a well-defined point of bud break like other determinate conifers, but shoots in compound buds just start elongating. Phenological parameters are thus best derived from growth curves rather than assessed visually as discrete events. To analyse the differences in maximum growth rate, linear growth duration, and total linear growth among provenances, average growth curves for each provenance were fitted to the model:

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

where  $t$  is the time in days,  $G_{\min}$  is the height 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 (negative), and  $c$  is the date on which half of the total elongation is completed (Fig. 2). Curves were fitted to provenance means rather than individual seedlings, since our main interest is to compare the growth curves of provenances. The maximum growth rate is calculated as  $G_{\text{rate}} = G'(t)_{t=c} = -ab/4$ . The linear growth period can be estimated by the period for which  $G(t) - D(t)$  is within  $\pm 0.005a$  (i.e., around 0.5 mm on average),  $D(t)$  being the tangent to the growth curve at the inflection point (see Fig. 2). The definition of this period is mathematical (linear part of the sigmoid growth curve) but corresponds from a biological point of view to the period when the growth rate

is maximal and remains constant. Linear growth duration is also highly correlated with total growth duration, i.e., the period between the initiation of growth and the cessation of growth during which trees are susceptible to frost injury but is easier to estimate.

Genetic variability in phenology is well known in conifers (e.g., Rehfeldt 1992; El-Kassaby and Park 1993; Aitken and Adams 1997; Hannerz et al. 1999), but the extent to which phenology affects variability in height growth across different environments is still poorly understood. To examine this question, the response of growth to temperature that triggers vegetative phenology was determined for each provenance.

### Formalization of the response of growth to temperature

The response of growth to temperature was assessed for each provenance. The response of growth to temperature is commonly formalized by the so-called forcing unit function, FU, which is a sigmoid type function commonly used in phenological models (Sarvas 1974; Hänninen 1990; Kramer 1994):

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

where  $x_t$  is the mean temperature of day  $t$ ,  $w$  determines the slope of the response, and  $z$  is the temperature for which  $FU = 0.5$ . FU varies from 0 to 1. The threshold temperature, which characterizes the adaptive response of individual provenances to local climate of their native habitats, is constant and can be estimated (Chuine et al. 2000). For some values of the parameter set ( $w, z$ ), FU shows a very steep slope, and then  $z$  becomes a threshold temperature below which no response occurs and above which the response is maximum, or a smooth slope and FU looks like a typical sigmoid curve. Thus, we will call  $z$  the "threshold temperature". Fitting the response of growth to temperature (FU) using the growth curves of each provenance observed at both nurseries increases the robustness of the fit. There was no evidence from the weather records at either nursery to suggest a lack of chilling in early winter, which would reduce response to temperature.

### Fit of the response to temperature

The parameter set ( $w, z$ ) was fitted to the growth and temperature records of each provenance at Red Rock and Cowichan Lake using the least-squares method. The least-squares function was

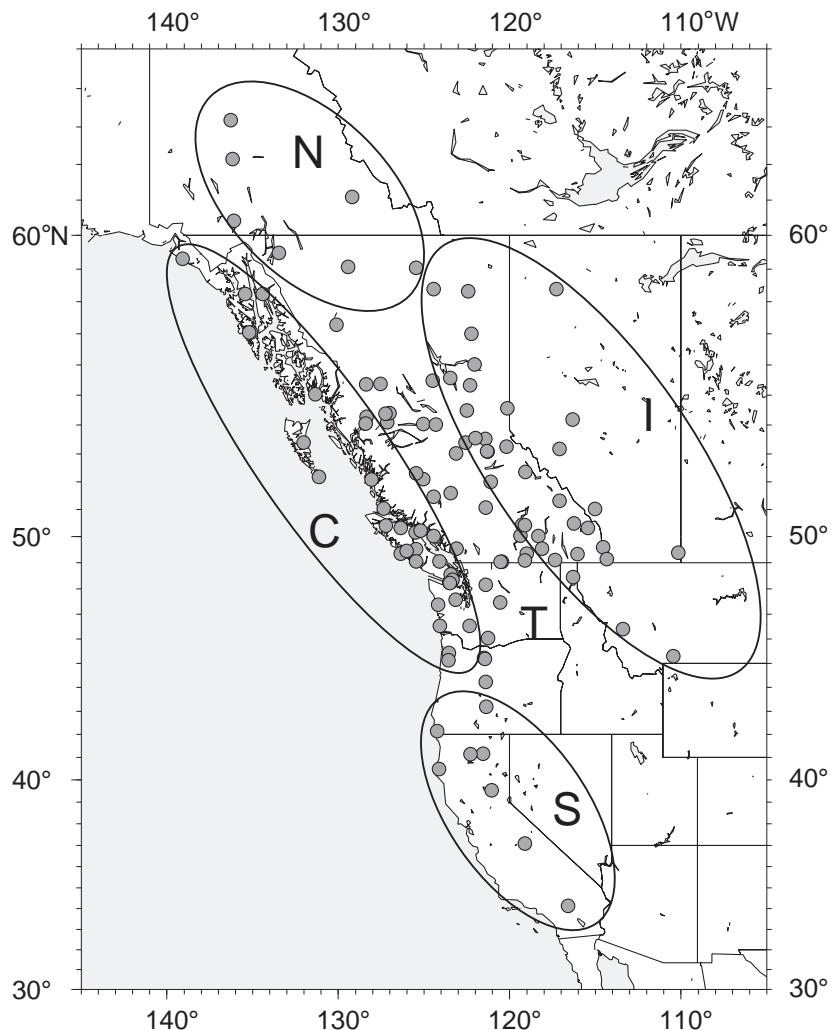
$$[3] \quad LS(w, z) = \sum_{t_0}^{t_1} f + \sum_{t_2}^{t_3} f + \sum_{t_0}^{t'_1} f + \sum_{t'_2}^{t'_3} f$$

where  $t_0$  is 1 January;  $t_1$  is the day when 0.1% of the total elongation is achieved;  $t_2$  is the day when linear growth begins; and  $t_3$  is the day when linear growth ceases at Cowichan Lake;  $t'_1$ ,  $t'_2$ , and  $t'_3$  are the same variables recorded at Red Rock; and

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

The function  $(-ab/4)FU(x_t)$  represents the elongation that can be achieved in 1 day and is equal to the maximum growth rate ( $-ab/4$ ) when the response to temperature is maximum and zero when the response is null. Since even at a constant high temperature primary growth remains sigmoidal rather than linear, we know that the sigmoidal shape of a growth curve is not due to an intermediate response of growth to temperature (i.e.,  $0 < FU < 1$ ). The sigmoidal shape of a growth curve is likely due to asynchronous initiation and cessation of elongation of all internodes. Thus, to fit the response function of growth to temperature using the growth curve and the temperature regime, we have to consider the periods when the elongation is unambiguously directly related to temperature only. They are the period when growth has not yet begun ( $\Delta G = 0$ ),

**Fig. 1.** Location of the 109 sampled populations of *Pinus contorta*. Regions defined for the study are shown: C, coastal; I, interior; T, transition; N, northern; S, Sierra.



i.e.,  $(t_0, t_1)$  or  $(t'_0, t'_1)$ , during which FU should be minimal or null, and the period when growth is maximal ( $\Delta g = -ab/4$ ), i.e.,  $(t_2, t_3)$  or  $(t'_2, t'_3)$ , during which FU should be maximal (Fig. 2). We also calculated the time of initiation and cessation of elongation by the day when 1% of total elongation is reached and the day when 90% of total elongation has occurred, respectively.

The optimization of the least square function was achieved with a simulating annealing algorithm called METROPOLIS (Metropolis et al. 1953), modified to fit phenological models (Chuine 2000). The name "simulated annealing" derives from a thermodynamic principle on the manner in which metals cool and anneal or liquids freeze and crystallize. This principle is described by the Boltzmann probability distribution,  $\text{Prob}(E) \approx e^{-E/kT}$ : a system in thermal equilibrium at temperature  $T$  has its energy probabilistically distributed among energy states ( $E$ ). Metropolis et al. (1953) first used this principle for numerical calculations and optimization algorithms. Considering that a set of parameter values is analogous to a thermodynamic state ( $S$ ) of a system, and the sum of squares is analogous to the energy ( $E$ ) of that system, the range of possible states ( $S$ ) is explored by randomly changing from  $S_1$  to  $S_2$  according to the following rule. The probability of transition from  $S_1$  to  $S_2$  is 1 if  $S_2 < S_1$ , and equals  $e^{-(S_2 - S_1)/kT}$  if  $S_2 > S_1$ , with  $r$  and  $T$  parameters of the procedure decreasing with the number of steps. An infinite decrease of  $T$  leads to the convergence of the system towards its state of minimum energy (Press et al. 1989). The first set of pa-

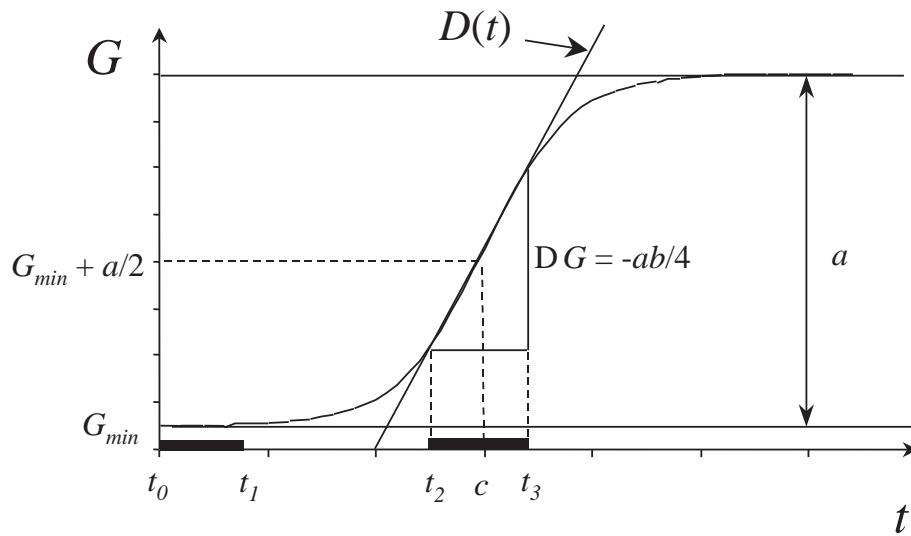
rameters is arbitrary, and then all the parameters are changed by a random amount. The Marsaglia procedure (Marsaglia et al. 1990) was used as the generator of random changes. This generates a random walk, which tends to avoid local minima and converge toward the global minimum. Since the number of local minima of the least-squares function of phenological models is very high, global searches were performed several thousands times with few iterations and beginning each time with random parameter values in the parameter ranges, so that the initial conditions did not influence the search of the global minimum. Then, a classical global search was performed starting at the best point found so far with more iterations than previous searches.

### Statistical analyses

An analysis of variance (VARCOMP procedure; SAS Institute Inc. 1990) was performed on the total elongation achieved in the growing season and growth parameters (linear growth duration and amount, maximum growth rate, and duration) to test the nursery (2 test sites), block (3 blocks per test site), region (5 regions), and provenance (109 provenances) effects according to the linear model:

$$Y_{ijklm} = a + S_i + R_j + SR_{ij} + B_{k(i)} + BR_{jk(i)} \\ + P_{l(j)} + SP_{il(j)} + \epsilon_{ijklm}$$

**Fig. 2.** Fitted growth curve parameters.  $G(t) = G_{\min} + a/(1 + e^{b(t-c)})$ ,  $D(t) = ab/4t + G_{\min} + a/2(1 - bc/2)$ , where  $t_0$  is 1 January,  $t_1$  is the day when 0.1% of elongation is achieved,  $t_2$  is the day when linear growth begins, and  $t_3$  is the day when linear growth ceases.



where  $Y_{ijklm}$  is the observed elongation for the  $m$ th seedling in the  $l$ th provenance ( $P$ ) in the  $j$ th geographic region ( $R$ ) in the  $k$ th block ( $B$ ) at the  $i$ th nursery site ( $S$ ). The significance of main effects was tested using the appropriate interaction mean squares as the error term. Because interactions between nurseries and regions or provenances were strong and significant, the region and provenance effects were tested at each site using the "simple main effect procedure" of SAS. This procedure tests the effect of one factor for each level of another factor without physically slicing the data for this second factor. The estimated growth parameters for each provenance (total growth ( $a$ ), maximum growth rate ( $-ab/4$ ), linear growth amount, and linear growth duration) were subjected to a similar analysis of variance with a reduced model with all terms involving provenance removed. To determine the relative magnitude of effects, variance components (expressed as percentage of the total) were estimated for each effect and their interactions for total elongation and for growth parameters using the restricted maximum likelihood method of the SAS VARCOMP procedure (SAS Institute Inc. 1990).

A multiple regression analysis was also conducted on total elongation, linear growth duration, maximum growth rate, and threshold temperature, with climatic variables and their two-way of the provenance interactions as independent variables. Climatic variables (mean annual temperature, mean temperature of the coldest and warmest month, annual precipitation, aridity index, and frost-free period) were derived from the climatic model of Rehfeldt et al. (1999) developed for British Columbia for the geographic range 48.5–62.0°N and 114.0–137.0°W. Outside this range, i.e., for 20 of the 109 provenances, variables were obtained from CLIMAT (version 1.9, 1996; Meteo-France, Paris) that provides monthly maximum and minimum temperatures and precipitation records averaged over the last 50 years for weather stations around the world. Among the 20 provenances, 10 high-elevation or remote provenances for which no meteorological data exist were excluded to avoid extrapolation. So climate variables were available for 99 of the 109 provenances for the multiple regression analysis.

Genetic differentiation of the response of growth to temperature was assessed using the method described in (Chuine et al. 2000). First, the response to temperature was fitted using the data of all populations together or all populations from one region (model A). Second the response to temperature was fitted using the data for each population separately (model B). Both models, A and B, are

nested, since model B considers in addition to model A the interaction between the temperature and the site. The percentage of differentiation between sites is defined as

$$100 \times \frac{(SS_A - SS_B)/df_A - df_B}{SS_{TOT}/df_{TOT}}$$

where  $SS_A$  and  $SS_B$  are the residual sum of squares of models A and B, respectively;  $SS_{TOT}$  is the total variance;  $df_A$  and  $df_B$  are the degrees of freedom of models A and B, respectively; and  $df_{TOT}$  is the total degrees of freedom. The population effect was significant if

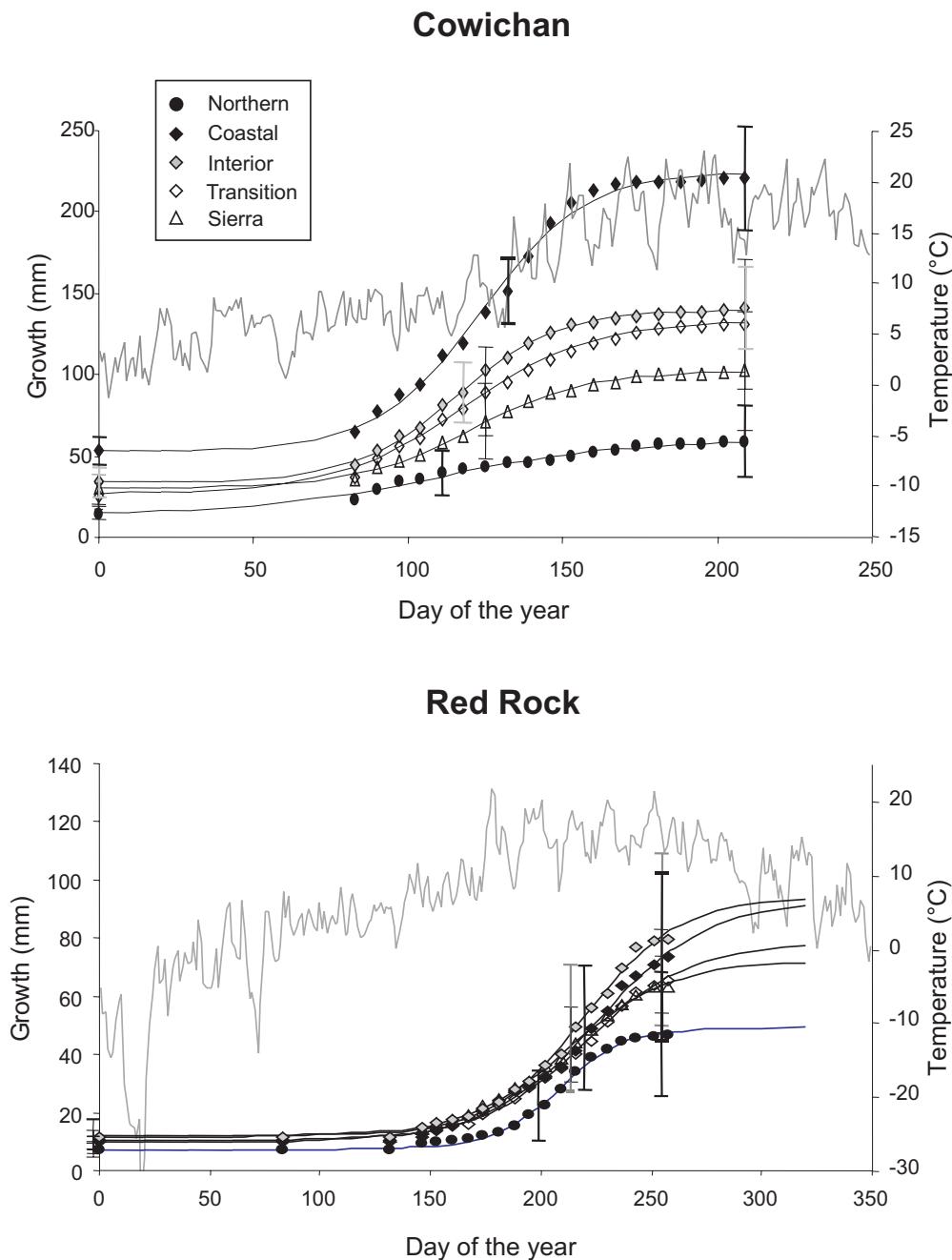
$$F = \frac{(SS_A - SS_B)/df_A - df_B}{SS_B/df_{TOT} - df_B}$$

was significantly higher than  $F(df_A - df_B, df_{TOT} - df_B)$ . Whenever genetic differentiation among all populations was significant, differentiation between particular groups of populations was investigated.

## Results

The curves fitted to the average growth data of each provenance explained 98.4–99.9% (mean 99.4%) of the variation for each provenance at Red Rock and 98.7–99.9% (mean 99.7%) of the variation at Cowichan (Fig. 3). The fitted parameter set ( $w, z$ ) of the response of growth to temperature revealed that the responses were of the threshold type and not of the sigmoid type, i.e.,  $FU = 0$  if  $x_t < z$ , i.e., when the temperature is below the threshold,  $FU = 0.5$  if  $x_t = z$ , and  $FU = 1$  if  $x_t > z$ . The threshold temperature ( $z$ ) fitted for each provenance varied between 4.1 and 6.8°C with an average of 5.1°C for the coastal and interior regions, 5.0°C for the Sierra region, 5.6°C for the transition region, and 6.5°C for the northern region. The confidence interval, i.e., interval between the lower and upper 95% confidence limits, for this parameter varied between 0.1 and 2°C with an average of 0.7°C, which testify the accuracy of fit of this parameter. The confidence intervals for each region are the following: coastal [4.75 to 5.42°C], interior [4.64 to 5.5°C], northern

**Fig. 3.** Growth curves observed at Cowichan Lake and Red Rock (symbols) and predicted by the model (eq. 1) (lines) for one representative provenance of each region (i.e., for which growth curve is the most similar to the mean growth curve of the provenances of that region), and daily temperatures at both nurseries. Standard deviations of elongation within regions are given for  $G = G_{\min}$ ,  $G = G_{\min} + a/2$ , and  $G = G_{\min} + a$ .



[6.32 to 7.4°C], Sierra [4.51 to 5.48°C], and transition [5.39 to 5.83°C]. The higher temperature threshold of the northern provenances is significantly different from the other regions ( $p < 0.0001$ ). The responses to temperature (i.e., parameter set ( $w$ ,  $z$ )) varied significantly among provenances within each region, but the regional effects were extremely weak ( $R^2 < 0.0001$  on average).

The response to temperature showed less variation than total elongation, with coefficient of variation of 19.0% for the threshold temperature and 28.5% for total elongation on

average over both nurseries. In particular, the Sierra provenances did not have a significantly different threshold temperature from the coastal or transition provenances but grew much less in height than these sources (Table 1).

Provenances from the coastal region elongated most rapidly, followed by those from the transition, interior, Sierra, and northern regions in that order at Cowichan Lake, but at Red Rock the transition provenances elongated more rapidly than the coastal provenances (Fig. 3). The correlation between total elongation and maximum growth rate was very

**Table 1.** Mean and SE (in parentheses) of the (A) growth variables at both test sites within each region and (B) parameters of the response to temperature ( $w$  and  $z$  values).

| (A) Growth variables. |              | $t_{1\%}$   | $t_2$       | $t_3$        | $t_{90\%}$ | TLG        | LGD          | $a$             | $b$           | $c$           | MGR |
|-----------------------|--------------|-------------|-------------|--------------|------------|------------|--------------|-----------------|---------------|---------------|-----|
| <b>Cowichan</b>       |              |             |             |              |            |            |              |                 |               |               |     |
| Coastal               | 48.2 (5.2)   | 111.8 (2.5) | 132.3 (3.0) | 158.0 (4.6)  | 37.9 (7.9) | 20.4 (1.8) | 125.2 (25.2) | -0.062 (0.0047) | 121.59 (2.59) | 1.91 (0.333)  |     |
| Interior              | 36.9 (5.5)   | 105.0 (2.0) | 128.2 (2.7) | 157.4 (5.9)  | 31.6 (6.2) | 23.2 (2.5) | 103.4 (20.5) | -0.055 (0.0050) | 116.08 (2.11) | 1.44 (0.363)  |     |
| Sierra                | 33.5 (8.2)   | 108.0 (4.2) | 133.7 (8.6) | 166.3 (16.9) | 24.8 (5.9) | 25.7 (5.4) | 81.3 (19.5)  | -0.051 (0.0087) | 120.19 (6.23) | 1.07 (0.386)  |     |
| Northern              | 17.6 (5.1)   | 106.0 (7.5) | 141.9 (8.5) | 192.7 (12.7) | 20.5 (3.6) | 35.7 (3.8) | 68.0 (12.2)  | -0.035 (0.0040) | 123.46 (7.77) | 0.61 (0.148)  |     |
| Transition            | 44.0 (7.4)   | 108.3 (5.6) | 129.3 (5.2) | 156.7 (4.9)  | 35.0 (8.6) | 21.0 (1.5) | 114.7 (28.1) | -0.060 (0.0038) | 118.45 (5.30) | 1.73 (0.467)  |     |
| <b>Red Rock</b>       |              |             |             |              |            |            |              |                 |               |               |     |
| Coastal               | 109.5 (11.4) | 204.3 (7.4) | 234.5 (8.1) | 272.2 (10.2) | 21.7 (7.2) | 30.3 (3.0) | 71.1 (23.6)  | -0.042 (0.0044) | 218.94 (7.54) | 0.751 (0.270) |     |
| Interior              | 114.1 (13.4) | 205.9 (5.4) | 235.1 (8.5) | 271.8 (13.6) | 20.0 (4.8) | 29.1 (4.8) | 65.9 (15.8)  | -0.044 (0.0073) | 220.04 (6.63) | 0.714 (0.151) |     |
| Sierra                | 110.2 (11.6) | 197.0 (7.5) | 224.5 (6.8) | 259.2 (7.0)  | 20.1 (4.6) | 27.5 (2.1) | 66.4 (15.2)  | -0.046 (0.0036) | 210.40 (7.08) | 0.760 (0.175) |     |
| North                 | 138.0 (6.6)  | 199.1 (4.6) | 218.3 (6.5) | 242.7 (9.2)  | 12.4 (2.5) | 19.1 (2.7) | 41.1 (8.4)   | -0.066 (0.0080) | 208.25 (5.31) | 0.668 (0.109) |     |
| Transition            | 121.4 (9.9)  | 206.8 (3.3) | 234.1 (4.2) | 267.6 (7.0)  | 24.4 (7.2) | 27.3 (2.7) | 79.8 (24.6)  | -0.047 (0.0050) | 219.96 (3.52) | 0.919 (0.224) |     |

(B)  $w$  and  $z$  values.

|            | $w$       | $z$         |
|------------|-----------|-------------|
| Coastal    | -20 (0.0) | 5.07 (0.58) |
| Interior   | -20 (0.0) | 5.09 (0.65) |
| Sierra     | -20 (0.0) | 5.00 (0.84) |
| North      | -20 (0.0) | 6.48 (0.77) |
| Transition | -20 (0.0) | 5.56 (0.61) |

Note: TLG, total linear growth; LGD, linear growth duration; MGR, maximum growth rate;  $a$ ,  $b$ , and  $c$ , parameters of the growth curve;  $t_{1\%}$ , day of initiation of linear growth;  $t_{90\%}$ , day of cessation of linear growth;  $t_2$ , day of initiation of linear growth;  $t_3$ , day of cessation of linear growth.

high (0.95 at Cowichan and 0.86 at Red Rock) but the correlation between total elongation and linear growth duration was very weak and actually inverse at the two nurseries (Figs. 4a and 4b). At Cowichan Lake the slow-growing provenances (northern provenances) grew much longer than the others (Table 1), but there was no clear relationship between linear growth duration and elongation among the other provenances (Fig. 4c). On the contrary, at Red Rock there was a positive relationship ( $R^2 = 0.15$ ) between elongation and linear growth duration, with the slow-growing northern provenances completing linear growth earlier than the others (Table 1, Fig. 4d).

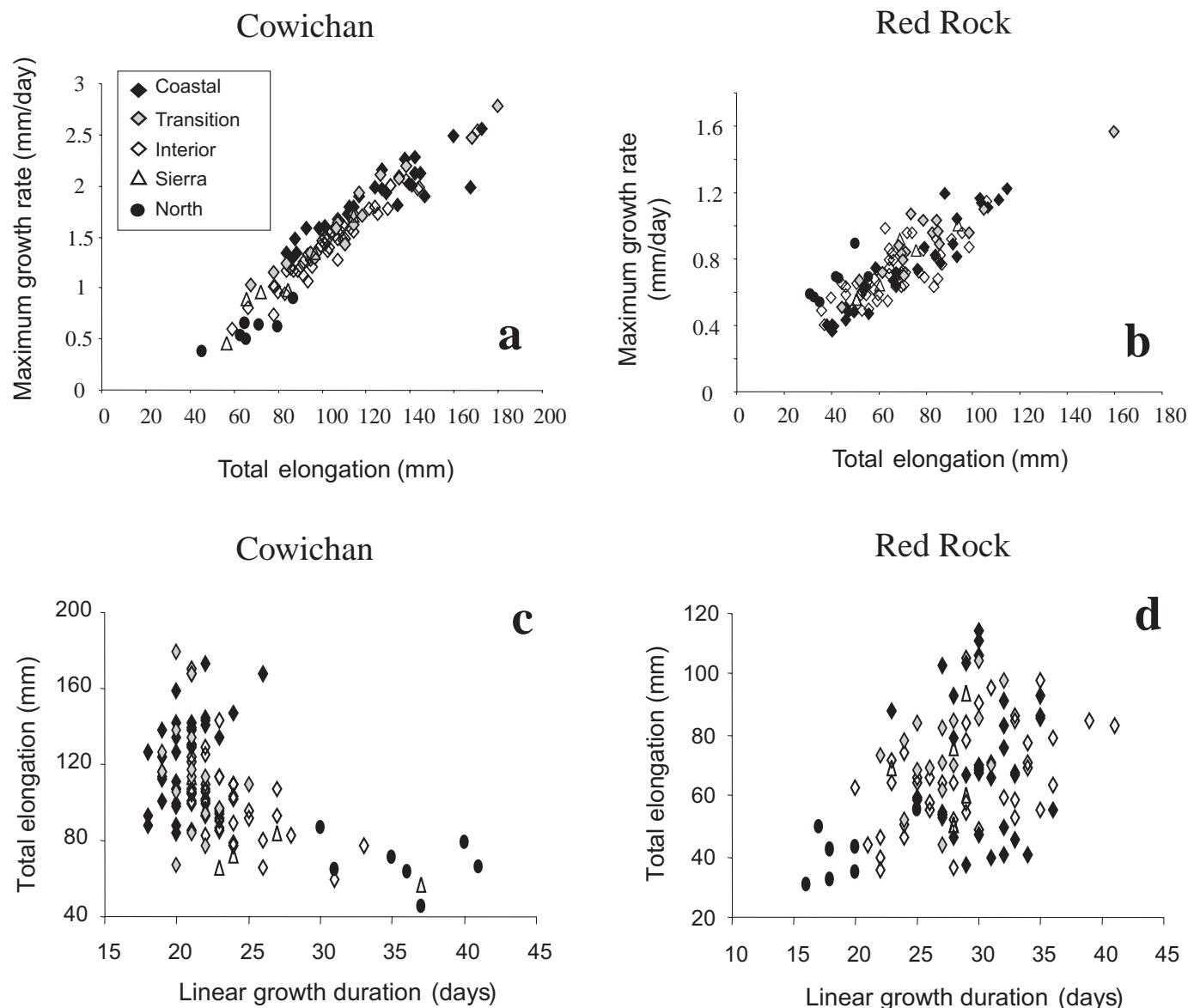
Timing of growth initiation and cessation were strongly correlated to the timing of initiation and cessation of linear growth ( $t_2$  and  $t_3$ ), respectively, the day of initiation and cessation of linear growth, except for cessation of growth at Red Rock (0.77 and 0.93 for initiation and cessation at Cowichan, respectively; 0.95 and 0.17 for initiation and cessation at Red Rock, respectively).

The test site effect was strong and significant, with the duration of linear growth being on average 5.4 days longer at Red Rock than at Cowichan Lake, and the maximum growth rate twice as high at Cowichan Lake than at Red Rock (Table 1). The response observed at Cowichan Lake was somewhat unexpected. While the coastal provenances had the shortest linear growth duration but the highest growth rate, the Sierra and northern provenances had the longest growth duration but the lowest growth rate (Table 1, Fig. 4e). The transition and interior provenances were intermediate in both growth rate and duration. No such patterns were observed at Red Rock (Table 1, Fig. 4f). Unlike the others, the northern provenances had a higher average growth rate in Red Rock than at Cowichan, but total elongation was less at Red Rock because of a shorter growth duration (Table 1). Linear growth duration explains very poorly the differences in total elongation among regions and provenances (Figs. 4e and 4f), contrary to maximum growth rate, which is highly correlated to total elongation especially at Cowichan (Cowichan:  $r = 0.95$ , Red Rock:  $r = 0.86$ ) (Figs. 4a and 4b).

Analyses of variance revealed that the site effect accounted for most of the variance in total elongation achieved (Table 2). Differences among regions and among provenances within the regions were highly significant within each site, but only differences among provenances were significant across sites. The fact that differences among regions are not significant across sites, but only within sites, is due to the strong interactions between regions and sites. The provenance by site interaction was also significant although less important (Table 2), with northern, Sierra, and interior provenances showing much more conservative growth patterns at both nurseries compared with the coastal and transition provenances, which showed the greatest variance between the two nurseries (Table 1, Fig. 3). Among regions, the differences in maximum growth rate of each provenance were highly significant only at Cowichan Lake, whereas the differences in duration and amount of linear growth were highly significant at both sites (Table 2B).

The multiple regression analysis of growth components (i.e., elongation, linear growth duration, and amount of linear growth) on climate variables at provenance origins revealed a strong dependency of growth on both the mean

**Fig. 4.** Relationships between total elongation and maximum growth rate of each provenance at Cowichan Lake (a) and Red Rock (b), total elongation and linear growth duration of each provenance at Cowichan Lake (c) and Red Rock (d), maximum growth rate and linear growth duration of each provenance at Cowichan Lake (e) and Red Rock (f), linear growth duration for each provenance at Cowichan Lake and Red Rock (g), and maximum growth rate for each provenance at Cowichan Lake and Red Rock (h).



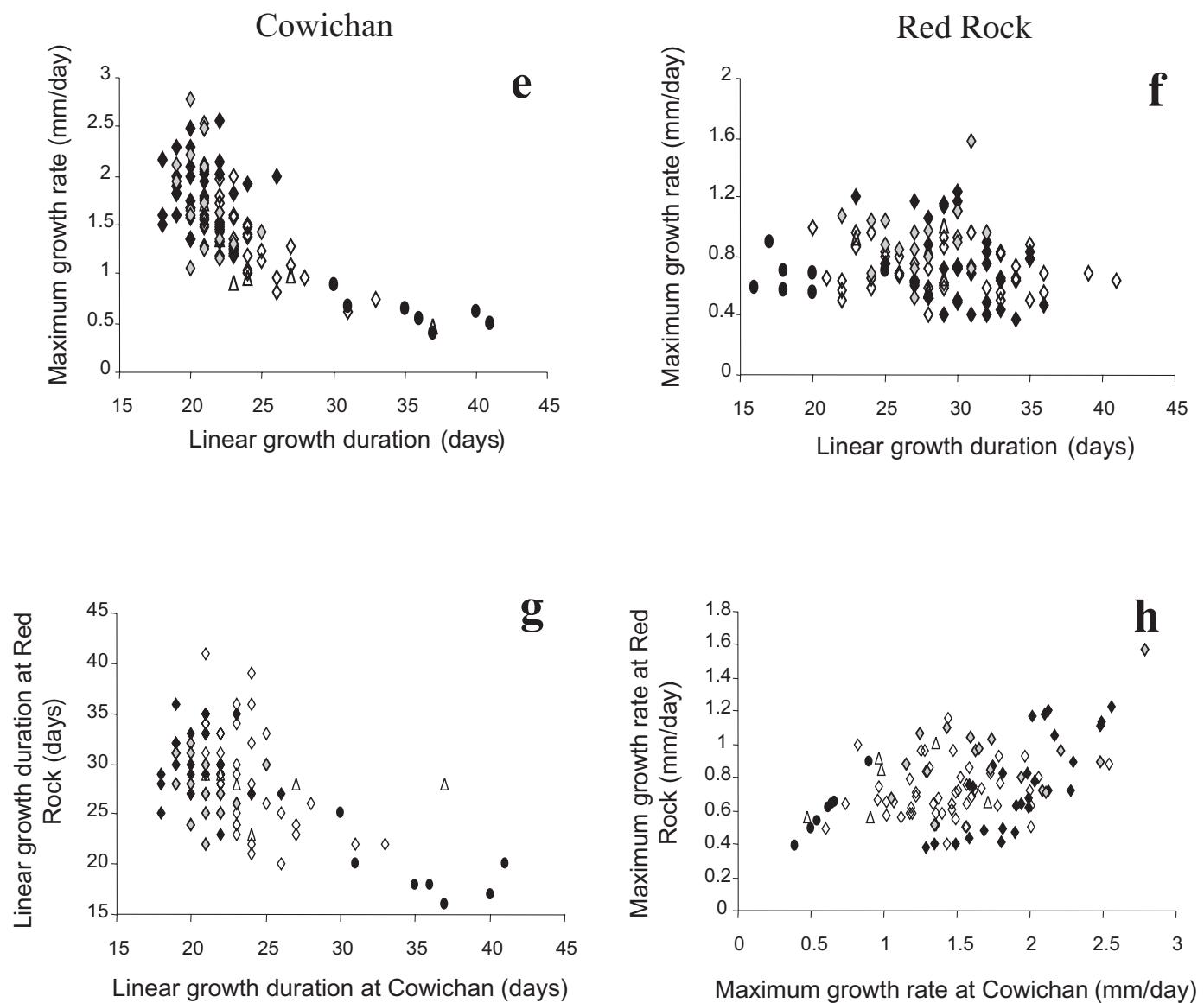
annual temperature and temperature of the warmest month at Cowichan (Tables 3 and 4). However, at Red Rock we observed a weaker relationship between the same growth variables and climatic variables (Table 3). This is likely because expressed differences among provenances are reduced in this continental climate, which has a much shorter growing season length and is more arid. Within each region except for the interior, linear relationships between provenance mean growth variables and both latitude and elevation were also observed (Fig. 5). Variation in threshold temperature is poorly explained by climatic variables compared with the other growth variables, although it is still significant because its relationship with growth is weak (Tables 3 and 4). As the main pattern of variation of the threshold temperature is

higher threshold in the north and lower elsewhere, it is mainly explained by the annual temperature (Tables 3 and 4).

## Discussion

### Comparison with previous studies

Previous studies over a more restricted range on height growth components in *P. contorta* have shown strong genetic variation among populations (Critchfield 1957; Cannell and Willet 1975; Rehfeldt and Wykoff 1981; O'Reilly and Owens 1989), and we confirm this result over the entire range of the species. The results we found for a high number of provenances sampled over the entire range cultivated at two highly contrasted environments bring new insight on the

**Fig. 4 (concluded).**

reaction norms of height growth in *P. contorta* compared with previous studies. As found by Rehfeldt and Wykoff (1981), differences in initiation of shoot elongation were very small within a region (standard deviation among populations: 3.5 days on average, ranging from only 1.2 days among the northern populations to 5.5 days among the transition populations), and differences in growth rate and elongation were significant both along provenances within regions and among regions. Like Critchfield (1957), we found a greater variance in total elongation on average among coastal populations than among interior populations at both nurseries, as well as a greater variance among transition populations (standard deviations in millimetres: 24.8 for coastal, 27.2 for transition, 19.2 for Sierra, 18.6 for interior, 11.1 for northern). However, some studies have shown correlations between phenological parameters and height growth, and we found here that phenology poorly explained differences in elongation between regions. Rehfeldt found a

positive and significant correlation between height growth and growth duration for 3-year-old *latifolia* provenances from Idaho grown in Idaho ( $r = 0.79$ ; Rehfeldt 1987). Here we found that, although differences in phenology did not explain much in differences in height growth among regions and provenances, within a single test site and for all the *latifolia* provenances (not only from Idaho), a significant and positive correlation did exist between linear growth duration and total elongation ( $r = 0.52$ ,  $p < 0.0001$ ). However, this relationship was inverse at Cowichan Lake ( $r = -0.63$ ,  $p < 0.0001$ ). Similarly, whereas Rehfeldt and Wykoff (1981), Cannell and Willet (1975), and O'Reilly and Owens (1989) found a positive correlation between timing of cessation of elongation and total elongation, we found this was the case at Red Rock ( $R^2 = 0.26$ ) but not at Cowichan Lake. This highlights the importance of recording reaction norms of a representative set of *P. contorta* provenances in contrasting environments to assess relationships between height growth

**Table 2.** Results of the analyses of variance of total elongation and the growth model parameters: variance components of (A) total elongation and (B) estimated growth variables estimated using SAS VARCOMP procedure using the restricted maximum likelihood (REML) method.

| (A) Total elongation. |       |        |       |
|-----------------------|-------|--------|-------|
| Source                | F     | P >F   | Var % |
| Site (S)              | 158.5 | 0.0002 | 31    |
| Region (R)            | 3.26  | 0.1397 | 9.3   |
| Cowichan              | 94.67 | 0.0001 |       |
| Red Rock              | 26.98 | 0.0001 |       |
| S × R                 | 47.96 | 0.0001 | 7.4   |
| Block (B)             | 5.56  | 0.0002 | 0.8   |
| B × R                 | 1.4   | 0.1295 | 0.2   |
| Provenance(R) (P(R))  | 4.74  | 0.0001 | 12.3  |
| Cowichan              | 7.88  | 0.0001 |       |
| Red Rock              | 3.83  | 0.0001 |       |
| S × P(R)              | 2.86  | 0.0001 | 4.3   |
| Error                 |       |        | 34.5  |

| (B) Estimated growth variables. |                     |        |       |                     |        |       |                      |        |       |                        |        |       |
|---------------------------------|---------------------|--------|-------|---------------------|--------|-------|----------------------|--------|-------|------------------------|--------|-------|
| Source                          | Total growth amount |        |       | Maximum growth rate |        |       | Linear growth amount |        |       | Linear growth duration |        |       |
|                                 | F                   | P >F   | Var % | F                   | P >F   | Var % | F                    | P >F   | Var % | F                      | P >F   | Var % |
| Site (S)                        | 23.26               | 0.0084 | 44.5  | 7.62                | 0.0509 | 41.8  | 28.6                 | 0.0059 | 45.7  | 1.03                   | 0.3668 | 5.7   |
| Region (R)                      | 4.9                 | 0.0764 | 18.7  | 1.47                | 0.3587 | 7.5   | 5.84                 | 0.0579 | 19.9  | 0.33                   | 0.8449 | 0     |
| Cowichan                        | 13.83               | 0.0001 |       | 34.88               | 0.0001 |       | 12.92                | 0.0001 |       | 42.61                  | 0.0001 |       |
| Red Rock                        | 4.25                | 0.0025 |       | 1.63                | 0.1681 |       | 5.33                 | 0.0004 |       | 8385                   | 0.0001 |       |
| S × R                           | 3.06                | 0.0176 | 4.3   | 14.77               | 0.0001 | 27.1  | 2.67                 | 0.0333 | 3.3   | 38.65                  | 0.0001 | 67.2  |
| Error                           |                     |        | 32.5  |                     |        | 23.6  |                      |        | 31.1  |                        |        | 27.1  |

**Note:** The model for ANOVA on the estimated growth variables is  $Y_{ijk} = a + S_i + R_j + SR_{ij} + \varepsilon_{ijk}$  where  $Y_{ijk}$  is the observation for the  $k$ th provenance of the  $j$ th region ( $R_j$ ) at the  $i$ th site ( $S_i$ ).

**Table 3.** Multiple regression analysis results of growth variables on climatic variables of the origins: best model found by stepwise regression with level of 0.05 for entry and stay in the model.

| Variable               | Model                                   | $R^2$ | p       |
|------------------------|---|-------|---------|
| Threshold temperature  | = AT × CT + AT × PP + AT × AR           | 0.204 | <0.0001 |
| <b>Cowichan</b>        |   |       |         |
| Elongation             | = AT + WT                               | 0.591 | <0.0001 |
| Linear growth duration | = AT + AT × CT + AR + WT × CT + CT + FO | 0.886 | <0.0001 |
| Maximum growth rate    | = AT + WT × CT + CT × PP                | 0.707 | <0.0001 |
| <b>Red Rock</b>        |   |       |         |
| Elongation             | = WT + AT                               | 0.423 | <0.0001 |
| Linear growth duration | = AT × CT + PP × AR + AR                | 0.280 | <0.0001 |
| Maximum growth rate    | = WT × FO + PP × FO                     | 0.256 | <0.0001 |

**Note:** Six climatic variables and their interactions were screened; only the significant ones are shown. AT, mean annual temperature; WT, mean temperature of the warmest month; CT, mean temperature of the coldest month; PP, annual precipitation; FO, frost-free period; AR, aridity index, AR = PP/12/(AT + 10) from Tuhkanen (1980). Variables appear by order of their contribution to the model ( $R^2$ ).

and phenology. Relationships found at a local scale in a restricted environmental gradient clearly cannot be generalized.

Last, growth variables also revealed that two populations classified a priori as interior, Stone Mountain (58.39°N) and Muncho Lake (59.03°N), are more similar to the northern populations. These two populations are near the boundary between the Yukon Territory populations and the other *latifolia* populations (Fig. 1) and are geographically within the area recommended as seed sources for the Yukon by Ying and Illingworth (1986a).

However, our analyses of phenology and growth traits that characterize regional differentiation of populations are consistent with those observed in long-term field tests. The ability of the Yukon and northern interior populations to respond to the long growing season at the maritime nursery environment at Cowichan, contrary to the other populations, is characteristic. Other traits distinguish those populations from the others such as their poor growth (Ying et al. 1985; Ying and Illingworth 1986a; Rehfeldt et al. 1999), their different reproductive capacity (Ying and Illingworth 1986b), and their

susceptibility to needle cast (Hunt et al. 1987) and stem rust (Martinsson 1980). The large variance in total elongation of the transition populations may be a consequence of gene flow from the coastal subspecies (*ssp. contorta*). Poor performance of the Sierra populations (*ssp. murrayana*) at virtually all test environments throughout British Columbia (Ying et al. 1985) is consistent with a low rate of stem elongation (Fig. 3), reflecting their high-elevation origin.

### Relationships between phenology and growth

The fitted responses of growth to temperature help to explain the different growth patterns observed at the two nurseries. The unusually long growth period observed for the northern populations at Cowichan Lake (12 days longer than that of the other populations; Fig. 4a) is explained by their higher threshold temperature. When growth began at Cowichan Lake, daily mean temperatures were higher than the threshold temperature of most of the populations except the northern populations (Fig. 3) so that the maximum growth rate was lower than could have occurred under warmer conditions (0.61 mm/day instead of 0.82 mm/day predicted by the exponential relationship; Fig. 6).

The lack of a significant relationship between elongation and linear growth duration among the coastal, interior, transition, and Sierra populations at Cowichan Lake (Fig. 4c) indicates that the potential growing season on the coast (defined as the period when the temperature is higher than the threshold) is longer than that required by any of these populations to fully elongate the internodes set (Fig. 3). On the contrary, at Red Rock the potential growing season was not as long (Fig. 3) and may have not been sufficiently long for certain populations to completely elongate internodes. The relationship observed at Red Rock between elongation and linear growth duration (Fig. 4d) seems to indicate that, in locations with short growing periods, suboptimal phenology may reduce elongation from the potential maximum achieved in comparison with coastal environments.

Our results show that, across highly contrasted environments, phenology poorly contributed in differences in height growth among regions and provenances, which were rather explained by differences in maximum growth rate, a good estimate of the number of internodes set during the previous growing season (Cannell and Willet 1975; I. Chuine, unpublished data). The studies of Cannell et al. (1981) and Cannell and Willet (1975) have shown that height growth depended strongly on the number of internodes set during the previous growing season in *P. contorta*. The elongation achieved each year is the product of the number of internodes produced during the former growing season and the average final length of the internodes achieved in the current growing season. It can also be expressed as the product of (i) the number of internodes, (ii) their average daily increase in length, and (iii) the duration of elongation, i.e., the product of (i) growth rate and (ii) growth duration. Thus, growth rate in *P. contorta* seems to depend primarily on the number of internodes produced during the former growing season: the more internodes, the higher the potential growth rate and elongation. This result tempers those obtained during experiments in one or few similar environments (Cannell and Willet 1975; Rehfeldt and Wykoff 1981; Rehfeldt 1987;

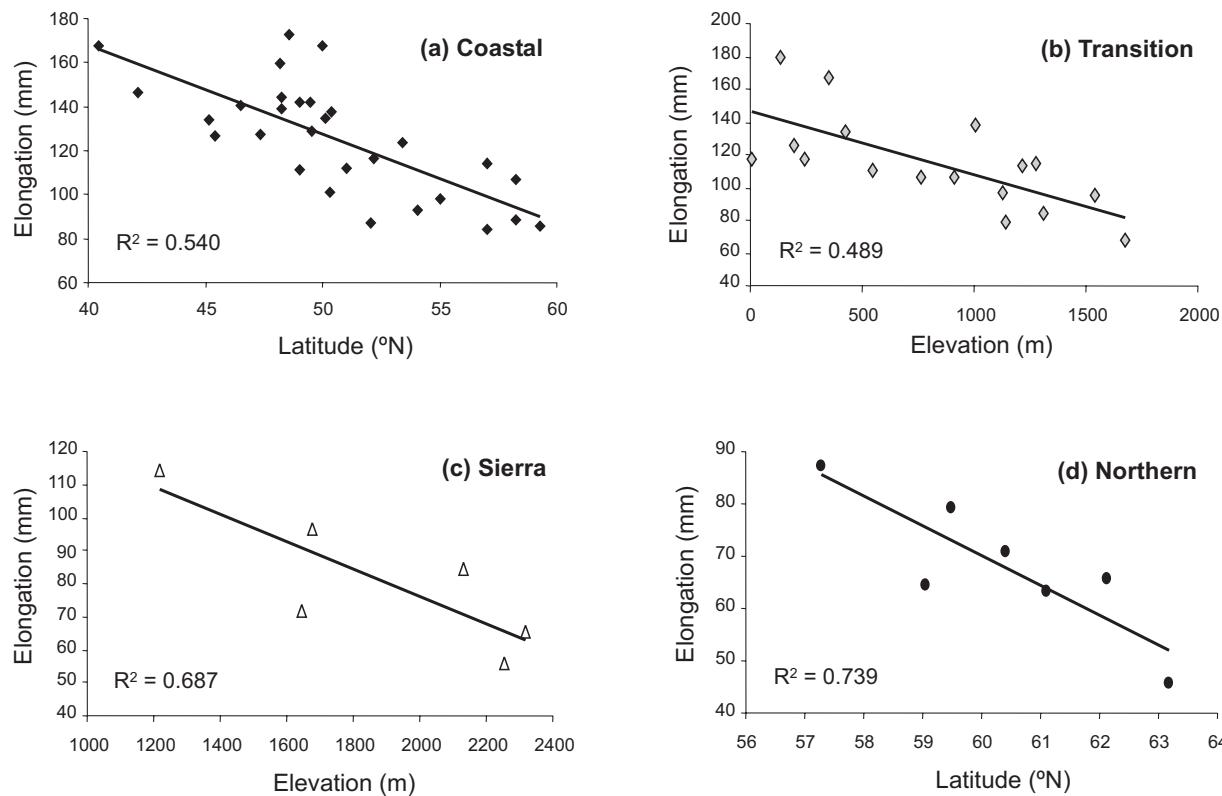
**Table 4.** Correlations between the growth and climate variables.

| Site and variable* | AT     | CT     | WT     | PP     | FO     |
|--------------------|--------|--------|--------|--------|--------|
| <b>Coastal</b>     |        |        |        |        |        |
| Cowichan           |        |        |        |        |        |
| LGD                | -0.223 | -0.120 | -0.348 | 0.000  | -0.164 |
| <i>a</i>           | 0.568  | 0.560  | 0.575  | -0.294 | 0.507  |
| MGR                | 0.490  | 0.450  | 0.561  | -0.173 | 0.420  |
| Red Rock           |        |        |        |        |        |
| LGD                | -0.433 | -0.334 | -0.497 | 0.494  | -0.431 |
| <i>a</i>           | 0.456  | 0.346  | 0.669  | -0.276 | 0.331  |
| MGR                | 0.450  | 0.352  | 0.618  | -0.370 | 0.401  |
| <i>z</i>           | 0.227  | 0.161  | 0.314  | -0.503 | 0.359  |
| <b>Interior</b>    |        |        |        |        |        |
| Cowichan           |        |        |        |        |        |
| LGD                | -0.749 | -0.677 | -0.636 | 0.207  | -0.445 |
| <i>a</i>           | 0.762  | 0.599  | 0.707  | -0.208 | 0.479  |
| MGR                | 0.772  | 0.628  | 0.721  | -0.214 | 0.454  |
| Red Rock           |        |        |        |        |        |
| LGD                | 0.427  | 0.434  | 0.345  | -0.184 | 0.058  |
| <i>a</i>           | 0.681  | 0.563  | 0.649  | -0.220 | 0.427  |
| MGR                | 0.242  | 0.138  | 0.261  | -0.064 | 0.316  |
| <i>z</i>           | -0.464 | -0.438 | -0.463 | 0.162  | -0.082 |
| <b>North</b>       |        |        |        |        |        |
| Cowichan           |        |        |        |        |        |
| LGD                | -0.802 | -0.776 | -0.574 | -0.679 | -0.892 |
| <i>a</i>           | 0.851  | 0.847  | 0.134  | 0.551  | 0.784  |
| MGR                | 0.909  | 0.874  | 0.491  | 0.757  | 0.955  |
| Red Rock           |        |        |        |        |        |
| LGD                | 0.190  | 0.073  | 0.145  | 0.280  | 0.236  |
| <i>a</i>           | 0.969  | 0.962  | 0.285  | 0.571  | 0.934  |
| MGR                | 0.608  | 0.688  | -0.013 | 0.146  | 0.512  |
| <i>z</i>           | 0.277  | 0.374  | -0.209 | -0.322 | 0.176  |
| <b>Transition</b>  |        |        |        |        |        |
| Cowichan           |        |        |        |        |        |
| LGD                | -0.732 | -0.753 | -0.352 | -0.253 | -0.776 |
| <i>a</i>           | 0.704  | 0.762  | 0.468  | 0.164  | 0.662  |
| MGR                | 0.735  | 0.790  | 0.430  | 0.206  | 0.723  |
| Red Rock           |        |        |        |        |        |
| LGD                | 0.185  | 0.269  | 0.188  | 0.209  | 0.151  |
| <i>a</i>           | 0.537  | 0.500  | 0.347  | -0.112 | 0.447  |
| MGR                | 0.329  | 0.268  | 0.182  | -0.167 | 0.279  |
| <i>z</i>           | -0.305 | -0.370 | -0.267 | -0.054 | -0.137 |
| <b>Total</b>       |        |        |        |        |        |
| Cowichan           |        |        |        |        |        |
| LGD                | -0.737 | -0.723 | -0.65  | -0.398 | -0.567 |
| <i>a</i>           | 0.745  | 0.692  | 0.608  | 0.263  | 0.627  |
| MGR                | 0.812  | 0.769  | 0.633  | 0.391  | 0.681  |
| Red Rock           |        |        |        |        |        |
| LGD                | 0.190  | 0.210  | 0.080  | 0.267  | 0.092  |
| <i>a</i>           | 0.531  | 0.458  | 0.623  | 0.021  | 0.345  |
| MGR                | 0.315  | 0.260  | 0.404  | -0.079 | 0.243  |
| <i>z</i>           | -0.246 | -0.23  | -0.257 | -0.183 | -0.072 |

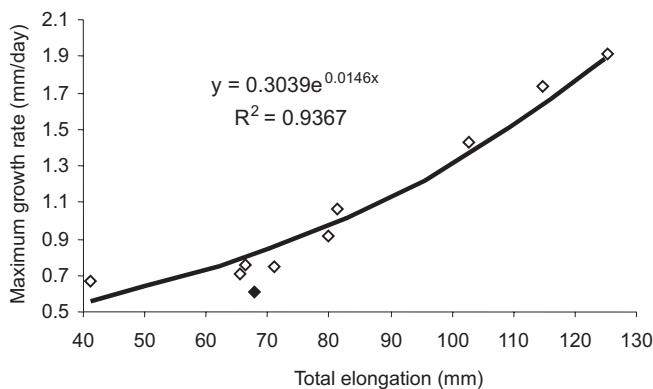
**Note:** Abbreviations for climatic variables are given in Table 3.  $p < 0.0001$  for  $r > 0.365$ ;  $p < 0.01$  for  $r > 0.246$ ;  $p < 0.05$  for  $r > 0.189$ .

\*LGD, linear growth duration; *a*, total elongation; MGR, maximum growth rate; *z*, threshold temperature.

**Fig. 5.** Relationships between elongation and latitude or elevation for the (a) coastal, (b) transition, (c) Sierra, and (d) northern provenances at Cowichan Lake. Relationships were identical at Red Rock but sometimes weaker.



**Fig. 6.** Relationships between maximum growth rate and total elongation of each region at both nurseries (Cowichan Lake and Red Rock); the solid diamond shows the northern provenances at Cowichan Lake.



O'Reilly and Owens 1989) showing that phenology affected height growth.

However, it is probable that, in certain environments where the potential growing period is short, phenology affects height growth by affecting the rate of internode initiation. Total elongation can be affected either by reducing the number of internodes set or by reducing their average length, and phenology may affect either of these components. The initiation of internodes for the subsequent year occurs during the elongation of internodes of the current growing season. Cannell and Willet (1975) have shown that both the period of initiation and the rate of initiation of

internodes of slow-growing populations of *P. contorta* were lower than for fast-growing populations, and those periods were associated with cell division and high metabolic activity. It is probable that, when the temperature decreases below the threshold of a provenance, the metabolic activity is affected and cell division decreases or ceases. It follows that, in locations with short growing periods, such as Red Rock, phenology (largely controlled by the threshold temperature) might affect total elongation of the current growing season not only by reducing the length of internodes but also by reducing the rate and period of internode initiation in the previous growing season.

If the response of growth to temperature does not seem greatly involved in total height growth in *P. contorta*, it may well be important in survival to frost injuries. Lindgren and Nilsson (1992) demonstrated higher frost hardiness in more northern populations of *P. contorta*. Selection for higher threshold temperature results in a delayed initiation of growth and, therefore, a decrease in spring frost injury risk when young leaves or needles are very sensitive to frost. Our results suggest that such selection may have occurred in *P. contorta* for the northern populations, which show significantly higher estimated thresholds temperature (this study) and are potentially exposed to much higher risks of frost injury in situ than all other populations.

## Acknowledgements

The authors are very grateful to Keith Illingworth, who established these nursery trials and the visionary provenance tests that followed. We also thank W. Parker and anonymous

referee for their helpful comments, Leslie McKnight for the technical assistance with the original data sets, Tongli Wang and Sonya Budge for providing input on an earlier version of this manuscript, and G.E. Rehfeldt for his helpful comments. This research was supported by the Natural Sciences and Engineering Research Council Industry Junior Chair in Population Genetics to S.N.A..

## References

- Aitken, S.N., and Adams, W.T. 1997. Spring cold hardiness under strong genetic control in Oregon populations of *Pseudostuga menziesii* var. *menziesii*. *Can. J. For. Res.* **27**: 1773–1780.
- Cannell, M.G.R., and Willet, S.C. 1975. Rates and times at which needles are initiated in buds on differing provenances of *Pinus contorta* and *Picea sitchensis* in Scotland. *Can. J. For. Res.* **5**: 367–380.
- Cannell, M.G.R., Thompson, S., and Lines, R. 1981. Heights of provenances and progenies of *Pinus contorta* in Britain correlated with seedling phenology and the duration of bud development. *Silvae Genet.* **30**: 166–172.
- Chuine, I. 2000. A unified model for the budburst of trees. *J. Theor. Biol.* **207**: 337–347.
- Chuine, I., Mignot, A., and Belmonte, J. A. 2000. A modelling analysis of the genetic variation of phenology between tree populations. *J. Ecol.* **88**: 1–12.
- Critchfield, W.B. 1957. Geographic variation in *Pinus contorta*. Maria Moors Cabot Foundation, Cambridge, Mass.
- El-Kassaby, Y.A., and Park, Y.S. 1993. Genetic variation and correlation in growth, biomass and phenology of Douglas-fir diallel progeny at different spacings. *Silvae Genet.* **42**: 289–297.
- Hannerz, M., Aitken, S.N., King, J., and Budge, S. 1999. Effects of genetic selection for growth on frost hardiness in western hemlock. *Can. J. For. Res.* **29**: 509–516.
- Hänninen, H. 1990. Modeling dormancy release in trees from cool and temperate regions. In *Process modeling of forest growth responses to environmental stress*. Edited by R.K. Dixon, R.S. Meldahl, G.A. Ruark, and W.G. Warren. Timber Press, Portland, Oreg. pp. 159–165.
- Hunt, R.S., Ying, C.C., and Ashbee, D.A. 1987. Variation in susceptibility among *Pinus contorta* provenances to the needle cast *Lophodermella concolor*. *Can. J. For. Res.* **17**: 594–597.
- Kramer, K. 1994. Selecting a model to predict the onset of growth of *Fagus sylvatica*. *J. Appl. Ecol.* **31**: 172–181.
- Lindgren, K., and Nilsson, J.E. 1992. Cold acclimation of *Pinus sylvestris* and *Pinus contorta* provenances as measured by freezing tolerance of detached needles. *Scand. J. For. Res.* **7**: 309–315.
- Marsaglia, G., Zaman, A., and Tsang, W. 1990. Toward a universal random number generator. *Stat. Probab. Lett.* **8**: 35–39.
- Martinsson, O. 1980. Stem rusts in lodgepole pine provenance trials. *Silvae Genet.* **29**: 23–26.
- Metropolis, N., Rosenbluth, A.W., Rosenbluth, M.N., and Teller, A.H. 1953. Equation of state calculations by fast computing machines. *J. Chem. Phys.* **21**: 1087–1093.
- Murray, M.B., Cannell, M.G.R., and Smith, R.I. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. *J. Appl. Ecol.* **26**: 693–700.
- O'Reilly, C., and Owens, J.N. 1989. Shoot, needle and cambial growth phenology and branch tracheid dimensions in provenances of lodgepole pine. *Can. J. For. Res.* **19**: 599–605.
- Press, W.H., Flannery, B.P., Teukolsky, S.A., and Vetterling, W.T. 1989. Numerical recipes in Pascal. Cambridge University Press, Cambridge, U.K.
- Rehfeldt, G.E. 1987. Components of adaptive variation in *Pinus contorta* from the Inland Northwest. *USDA For. Serv. Res. Pap. INT-375*.
- Rehfeldt, G.E. 1992. Early selection in *Pinus ponderosa*: compromises between growth potential and growth rhythm in developing breeding strategies. *For. Sci.* **38**: 661–677.
- Rehfeldt, G.E., and Wykoff, W.R. 1981. Periodicity in shoot elongation among populations in *Pinus contorta* from the northern Rocky Mountains. *Ann. Bot. (London)*, **48**: 371–377.
- Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., and Hamilton, D.A. 1999. Genetic responses to climate for *Pinus contorta* in British Columbia: niche breadth, climate change and reforestation. *Ecol. Monogr.* **69**: 375–407.
- Sarvas, R. 1974. Investigations on the annual cycle of development of forest trees. Autumn dormancy and winter dormancy. *Commun. Inst. For. Fenn.* **84**. pp. 1–101.
- Savageau, M.A. 1979. Growth of complex systems can be related to the properties of their underlying determinants. *Proc. Natl. Acad. Sci. U.S.A.* **76**: 5413–5417.
- U.S. Department of Agriculture (USDA). 1965. Silvics of forest trees of the United States. U.S. Department of Agriculture, Forest Service, Washington, D.C.
- Wheeler, N.C., and Guries, R.P. 1982a. Populations structure, genetic diversity, and morphological variation in *Pinus contorta* Dougl. *Can. J. For. Res.* **12**: 595–607.
- Wheeler, N.C., and Guries, R.P. 1982b. Biogeography of lodgepole pine. *Can. J. Bot.* **60**: 1805–1814.
- Ying, C.C., and Illingworth, K. 1986a. Lodgepole pine provenance research in northwestern Canada with particular reference to the Yukon Territory. The Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology, Umeå, Sweden, Rep. 6. pp. 189–219.
- Ying, C.C., and Illingworth, K. 1986b. Variation in cone and seed production from natural stands, plantations and clonebanks of lodgepole pine. In *Conifer Tree Seed in the Inland Mountain West Symposium*, 1985, Missoula, Mont. Edited by R.C. Shearer. U.S. Dep. Agric. Intermountain Res. Stn., Ogden, Utah, Gen. Tech. Rep. INT-203. pp. 191–199.
- Ying, C.C., Illingworth, K., and Carlson, M. 1985. Geographic variation in lodgepole pine and its implications for tree improvement in British Columbia. In *Proceedings of the Lodgepole Pine: the Species and its Management Symposium*, 8–16 May 1984, Spokane, Wash. and Vancouver, B.C. Edited by D.M. Baumgartner. Washington State University, Pullman. pp. 43–53.