Tree Physiology 19, 131–136
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Variation in lateral shoot elongation patterns and hybrid vigor in full-sib families and interspecific hybrids of larch

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Received March 31, 1998

Summary Time of shoot initiation and cessation, and rate and duration of lateral shoot elongation of full-sib families of *Larix decidua* Mill., *L. laricina* (Du Roi) C. Koch, and interspecific hybrids between *L. decidua* and *L. kaempferi* (Lamb.) Carrière, *L. kaempferi* × *decidua*, *L. laricina* × *decidua*, and *L. laricina* × *kaempferi* were explored in relation to hybrid vigor determined by height growth after 5 years. Height growth of *L. laricina* and *L. decidua* families was significantly less than height growth of the interspecific hybrids. Differences were observed for all lateral shoot elongation traits among *L. laricina*, *L. decidua*, and the interspecific hybrids. Lateral shoots of *L. laricina* families were the first to both initiate and cease elongation, and grew for the shortest period of time. Overall, the length of the shoot elongation period and date of cessation of shoot growth were significantly correlated with total height growth after 5 years, but the time of shoot initiation was not. Rate of elongation of lateral shoots was strongly correlated with growth increment in 1996, but was weakly correlated with total height growth after 5 years. Hybrid vigor in *Larix* seems to be partly a function of late cessation or increased duration of shoot elongation, or both.

Keywords: heterosis, hybrid larch, Larix decidua, L. decidua × kaempferi, L. kaempferi × decidua, L. laricina, L. laricina × decidua, L. laricina × kaempferi.

Introduction

Hybrid vigor is well documented for larch (Miller and Thulin 1967, Carter et al. 1981, Riemenschneider and Nienstaedt 1983, Einspahr et al. 1984, Carter and Selin 1987, Matyssek and Schulze 1987, Paques 1992). We recently reported that three species of larch and their hybrids exhibited significant differences among families in height growth, and hybrid vigor was evident (Baltunis et al. 1998). Seventeen out of the top 20 families were interspecific hybrids that exhibited both greater height and volume growth than intraspecific crosses involving their parents. This increase in vigor may have many components including carbon allocation patterns, water and nutrient use efficiency, and shoot growth phenology.

Variation in shoot elongation patterns affects height growth, and genetic variation in these patterns can be used to select trees for desirable shoot growth characteristics (Cannell 1974). Shoot elongation patterns have been studied for many conifers including *Larix occidentalis* Nutt. (Rehfeldt 1992*a*), *Picea abies* (L.) Karst. (Skroppa and Magnussen 1993), *Picea glauca* (Moench) Voss (Owens et al. 1977), *Pinus ponderosa* Dougl. *ex* Laws. (Rehfeldt 1991, 1992*b*), *Pinus taeda* L. (Bridgewater 1990), *Pinus rigida* Mill. × *taeda* hybrids (Bailey and Feret 1982), and *Calocedrus decurrens* (Torr.) Florin (Harry 1987), and for hardwoods such as *Betula pendula* Roth (Wang and Tigerstedt 1996), *Populus nigra* L. cv. Italica (Pichot and Teissier du Cros 1988), and other *Populus* hybrids (Ceulemans et al. 1992). For example, significant differences were detected for cessation, duration, and rate of shoot elongation among populations of *Pinus ponderosa* (Rehfeldt 1992*b*). Similarly, Wang and Tigerstedt (1996) reported significant differences in initiation, cessation, and duration of shoot growth between fast- and slow-growing full-sib families of *Betula pendula* with fast-growing families exhibiting higher rates of elongation, as well as earlier growth initiation in spring and delayed growth cessation in fall.

Most studies to date have dealt exclusively with variation in terminal shoot growth patterns for describing differences in height. We postulated that, on trees that are too large for accurate, repeated measure of the terminal shoot, lateral shoot growth behavior reflects differences in height among inter- and intraspecific hybrid families. We also tested the hypotheses that hybrid vigor in *Larix* is a function of more rapid height growth attributable to: (1) earlier shoot growth initiation; (2) later shoot growth cessation; (3) a longer period of shoot elongation; or (4) a faster rate of shoot elongation. Specifically, we compared the timing of onset and cessation of lateral shoot elongation among a highly variable group of larch families, including intraspecific crosses among *Larix decidua* Mill. and *L. laricina* (Du Roi) C. Koch and four interspecific hybrid crosses including *L. decidua* × *kaempferi* (Lamb.) Carrière, *L. kaempferi* × *decidua*, *L. laricina* × *decidua*, and *L. laricina* × *kaempferi*. Finally, we attempted to explain the variation in height growth among families, including those that show hybrid vigor, in terms of shoot growth phenology.

Materials and methods

The families chosen for study are present in a hybrid larch progeny test in Johnson Mountain, Maine. The test was planted at a 2.3 by 2.3 m spacing in a randomized complete block design in May 1992 with 6-month-old seedlings that were produced in an indoor breeding orchard as described by Eysteinsson et al. (1993). The progeny test included intraspecific crosses including nine full-sib families among *L. laricina*, seven among *L. decidua*, and seven among *L. kaempferi*, and interspecific hybrids including seven full-sib families of *L. decidua* × *kaempferi*, nine of *L. kaempferi* × *decidua*, six of *L. laricina* × *decidua*, and two half-sib families between *L. laricina* × *kaempferi*. Hybridization between *L. laricina* and *L. kaempferi* generally results in low seed-set (Paques 1992, Eysteinsson et al. 1993), so seed from full-sib crosses involving two *L. laricina* parents pollinated with 3–4 different *L. kaempferi* pollen donors were pooled to create the two half-sib *L. laricina* × *kaempferi* families. A check lot consisting of an *L. decidua* × *kaempferi* half-sib family produced in Europe was also included in the study because of its relatively slow growth.

Families exhibiting contrasting height growth were selected based on 1995 total height ranking. The two top and two bottom ranking families were selected from crosses between *L. decidua* × *decidua*, *L. laricina* × *laricina*, *L. decidua* × *kaempferi*, *L. kaempferi* × *decidua*, and *L. laricina* × *decidua*. The two half-sib families from *L. laricina* × *kaempferi* (which grew well) and the *L. decidua* × *kaempferi* check (which grew poorly) were also included. One of the slowest growing *L. kaempferi* × *decidua* families was not included because four of the six selected trees were damaged during the study. Shoots of *L. kaempferi* families were damaged by spring frosts and could not be included in this study because of severe annual dieback of leaders.

Three vigorous lateral shoots were selected at about breast height on each of five to seven individuals per family and measured throughout the 1996 growing season. On each tree the branches were roughly 120° apart, and were not competing for light with adjacent trees or vegetation because crown closure had not occurred. The heights of the trees selected for measurement ranged from 3 to 4 m at the end of the 1996 growing season. Dates of measurement were June 11, 20, 30, July 10, 20, 30, August 10, 20, and September 7 and 24. Shoot elongation had not begun by May 25, so this date was set as Day 0 for estimating the following variables (Rehfeldt 1992*a*): GI = growth initiation, the day by which 20 mm of growth had occurred; GS = start of linear growth, the day by which 80 mm of growth had occurred; GC = growth cessation, the day by which all but 20 mm of growth had occurred; GD = growth duration, the number of days between initiation and cessation; and RE = rate of elongation, elongation per day during the period of most rapid elongation, defined as the period between 20 and 80% of total elongation.

Measurements (in mm) were made from a fixed base point (bud scar from last year's growth) to the tip of the shoot. The mean of each variable from the three sample branches of each tree was used in the statistical analysis. The times of growth initiation, the start of linear growth and cessation were extrapolated from plots of shoot elongation such as those shown in Figure 1.

Lateral shoot elongation increment curves for each tree were fitted based on a variation of the Weibull-type sigmoidal growth curve (Weibull 1951, Hoerl 1954):

$$Y = a(1 - \exp(-cX^{2.5})), \tag{1}$$

where Y is the total length achieved by day X, and a and c are regression coefficients. Individual estimates of a and c were calculated for each tree by the nonlinear regression model using Systat (SYSTAT, Inc., Evanston, IL).

An analysis of variance was performed for the five elongation variables and total height based on the following model:

$$Y_{ijk} = \mu + H_i + F_j(H_i) + \in_{ijk}, \tag{2}$$

where Y_{ijk} is the variable mean value of the jth family (F) in the ith hybrid group (H), μ is a constant, and $\in$ is the error term. Growth initiation and start of linear growth were analyzed by weighted least squares to account for nonconstancy of the error variances. The weight used was one standard deviation for each family. Tukey multiple range tests were used for the means of hybrid groups (SYSTAT, Inc.). Correlations between the five elongation variables and total height were analyzed based on family means (5–7 individuals per family).

Results

The Weibull nonlinear growth curve model fit our measured data well, with r^2 ranging from 0.9854 to 0.9996 (Figure 1). Highly significant differences among family groups were observed for all lateral shoot elongation traits (Tables 1 and 2). Families with *L. laricina* parents tended to initiate growth sooner. Time until growth cessation and duration of growth were highly variable among families, but interspecific hybrids tended to exhibit a longer period of growth than intraspecific families.

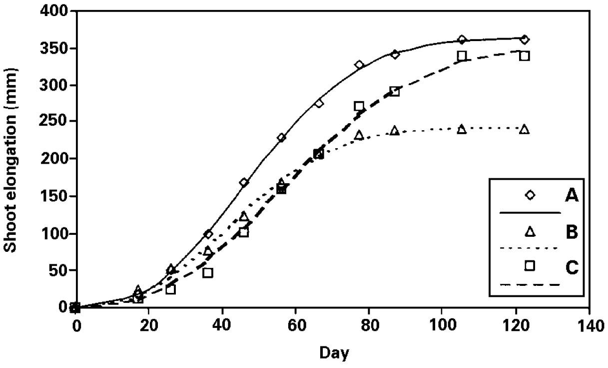

Figure 1. Examples of fitted curves for elongation of lateral shoots from three trees, A, B and C. Values of r^2 were: A = 0.9996; B = 0.9854; and C = 0.9967.

Table 1. Means for *Larix* hybrid groups for 1996 height (HT96), growth initiation (GI), start of growth (GS), cessation (GC), duration (GD), and rate of elongation (RE), ± standard error.

Hybrid	HT96 (cm)	GI (days)	GS (days)	GC (days)	GD (days)	RE (mm day^{-1})
L. decidua × *decidua*	358 ± 10	19 ± 0.3	35 ± 0.6	81 ± 1.3	62 ± 1.2	5.1 ± 0.2
L. decidua × *kaempferi*	417 ± 10	19 ± 0.3	36 ± 0.6	86 ± 1.8	66 ± 1.9	5.1 ± 0.2
L. kaempferi × *decidua*	409 ± 9	19 ± 0.3	35 ± 0.6	85 ± 1.6	66 ± 1.5	5.2 ± 0.2
L. laricina × *decidua*	409 ± 9	17 ± 0.4	30 ± 0.8	83 ± 1.4	66 ± 1.4	7.2 ± 0.3
L. laricina × *kaempferi*	408 ± 12	18 ± 0.3	33 ± 0.6	90 ± 1.3	72 ± 1.3	6.1 ± 0.3
L. laricina × *laricina*	370 ± 8	16 ± 0.4	30 ± 0.8	77 ± 1.6	61 ± 1.6	6.5 ± 0.3
Check	322 ± 22	20 ± 1.1	38 ± 2.4	78 ± 4.3	58 ± 4.4	4.5 ± 0.6

Table 2. Analyses of variance (*P*-values of *F*-tests) for differences among *Larix* hybrid groups and individual full-sib families within hybrid groups. Abbreviations: 1996 height (HT96); growth initiation (GI); start of growth (GS); cessation (GC); duration (GD); and rate of elongation (RE).

Variable	Hybrid	Family (Hybrid)
HT96	0.0001	0.0001
GI	< 0.0001	< 0.0001
GS	< 0.0001	< 0.0001
GC	< 0.0001	0.2651
GD	0.0005	0.3886
RE	< 0.0001	0.0084

Larix laricina families initiated growth significantly earlier than *L. decidua*, *L. decidua* × *kaempferi*, *L. kaempferi* × *decidua* ($P < 0.0001$), and *L. laricina* × *kaempferi* ($P = 0.011$). *Larix laricina* × *decidua* hybrids also initiated growth significantly earlier than *L. decidua*, *L. decidua* × *kaempferi*, and *L. kaempferi* × *decidua* ($P < 0.0001$), and *L. laricina* × *kaempferi* ($P = 0.03$). *Larix laricina* × *kaempferi* hybrids initiated growth significantly earlier than *L. decidua* × *kaempferi* ($P = 0.016$). *Larix laricina* and *L. laricina* × *decidua* hybrids reached 80 mm of growth significantly earlier than *L. decidua*, and *L. decidua* × *kaempferi* and *L. kaempferi* × *decidua* hybrids ($P < 0.0001$). *Larix laricina* also stopped growing significantly earlier than all other family groups with the exception of *L. decidua*. *Larix laricina* × *kaempferi* hybrids stopped growing significantly later than *L. decidua* ($P = 0.007$). Rates of elongation between 20 and 80% of total growth for *L. laricina* and *L. laricina* × *decidua* hybrids were significantly greater than for *L. decidua*, *L. decidua* × *kaempferi*, and *L. kaempferi* × *decidua* hybrids ($P < 0.005$).

Significant differences were also detected among families within hybrid groups for growth initiation, start of linear growth, and rate of elongation, but not for growth cessation and growth duration (Table 2). The range of family means within hybrid groups averaged about 2 days for initiation, 4 days for the start, 6 days for the cessation, 5 days for the duration, and 1.2 mm day^{-1} for the rate of elongation (see Table 1).

Total height in 1996 was strongly and positively correlated with growth cessation and duration (Figures 2 and 3, Table 3). Growth initiation was positively correlated with growth cessation, and negatively correlated with the rate of elongation. The start of linear growth was also negatively correlated with the rate of elongation. Cessation was highly correlated with duration of growth.

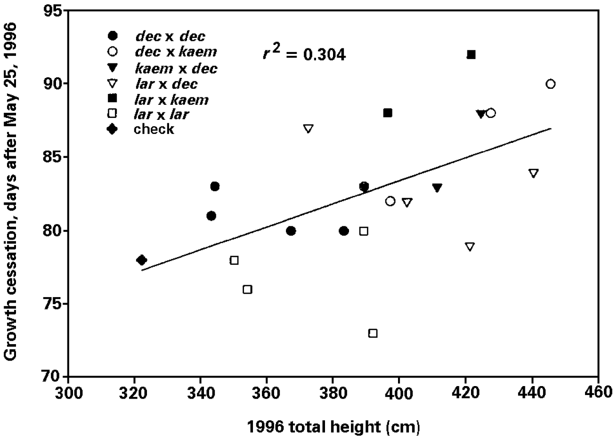

Figure 2. Plot of 1996 total height against growth cessation of individual *Larix* families. Values represent individual family means for the crosses indicated in the legend.

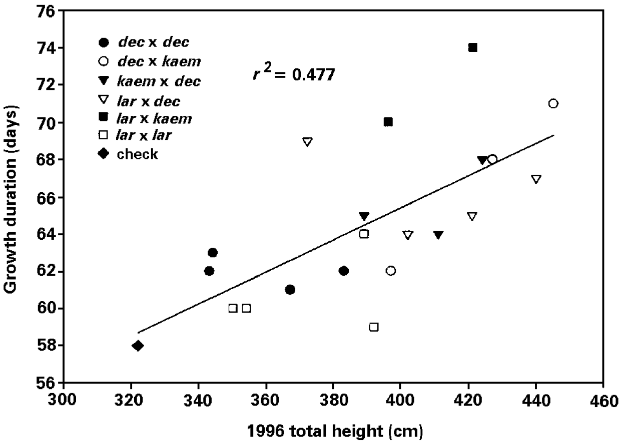

Figure 3. Plot of 1996 total height against growth duration. Values represent individual family means for the crosses indicated in the legend.

Table 3. Correlations among 1996 total height (HT96), growth initiation (GI), start (GS), cessation (GC), duration (GD), and rate of elongation (RE) among selected families among *Larix* hybrid groups. The *P*-values (based on family means) are in parentheses.

	HT96	GI	GS	GC	GD	RE
HT96	–					
GI	−0.1652 (0.4624)	–				
GS	−0.2067 (0.3560)	0.9982 (< 0.0001)	–			
GC	0.5511 (0.0079)	0.4716 (0.0267)	0.4221 (0.0504)	–		
GD	0.6910 (0.0004)	0.1094 (0.6278)	0.0544 (0.8100)	0.9281 (< 0.0001)	–	
RE	0.3558 (0.1041)	−0.9424 (< 0.0001)	−0.9529 (< 0.0001)	−0.2172 (0.3317)	0.1531 (0.4965)	–

Discussion

Parker et al. (1994) reported that phenological variables related to shoot elongation showed little or no variation among 75 seed sources of *Picea mariana* (Mill.) BSP, which they attributed to a poor logistic growth model. The elongation of shoots has been modeled for many tree species based on such functions as a logistic function with a hyperbolic time term (Rehfeldt and Wykoff 1981), Richards' function (Bridgewater 1990), and by the Weibull function (Magnussen and Yeatman 1989, Skroppa and Magnussen 1993). Individual tree measurements of lateral shoot elongation in this study fit the Weibull-type growth curve function extremely well.

Lateral shoot elongation may vary depending on where in the crown the branch is located. Clausen and Kozlowski (1970) found that the lengths of long shoots in *Larix laricina* depend on both shoot vigor and location in the tree. Elongation of primary branches tends to decrease with increasing depth in the crown (Remphrey and Powell 1984). Similarly, in *Pinus resinosa* Ait., *P. strobus* L., *Picea glauca*, and *Picea mariana*, elongation of lateral shoots decreased from the top of the tree downward (Kozlowski and Ward 1961). However, there were no consistent differences in final shoot lengths between lateral shoots from the top third of the crown and those from the middle of the crown for 30-year-old *Picea glauca* (Owens et al. 1977). In *Calocedrus decurrens*, the overall pattern of shoot elongation for branches resembled that of the leaders (Harry 1987). In our study, total elongation of lateral shoots in 1996 was correlated with height increment in 1996 (Pearson $r = 0.52$, $P < 0.0122$). Similarly, Mikola (1985) reported significant positive correlations between mean length of lateral shoots of the uppermost whorl and both total 8-year height and the height increment during the eighth growing season in *Pinus sylvestris* L.

Of the larch families studied, *L. laricina* families exhibited both the earliest initiation and cessation of shoot growth and the shortest duration of elongation. *Larix laricina* families had ceased elongation by August 9, whereas *L. laricina* × *kaempferi* hybrids did not stop elongating until August 22. *Larix laricina* experiences the coldest climate of the three species studied, and a rapid response to warming is a typical response of provenances experiencing short growing seasons (Bey et al. 1971). Similarily, Skroppa and Magnussen (1993) reported that northern provenances of *Picea abies* had both earlier initiation and cessation of shoot growth and a shorter growth period than southern provenances. We conclude that *L. laricina* and *L. decidua* families grew less than their interspecific hybrids because of earlier cessation of growth, a shorter elongation period and slower growth rate compared with the hybrids.

Provenance variation in shoot growth characteristics has been noted in other tree species, such as *Pinus ponderosa*, where significant provenance differences were detected for cessation, duration, and rate of elongation, but not for initiation (Rehfeldt 1986*a*, 1986*b*, 1992*b*). Only duration of terminal shoot elongation was significantly correlated with total height growth for 8-year-old *Pinus sylvestris* (Mikola 1985). Farmer et al. (1993) concluded that variation in height among provenances of *Larix laricina* mostly resulted from differences in late season elongation. According to Koski and Sievanen (1985), the duration of elongation is one of the main components of total growth. The duration of height growth in young seedlings and height in older trees are usually positively correlated with each other (Nanson 1968 cited in Mikola 1985). In a range-wide provenance test of *Juglans nigra* L., strong correlations between duration and total growth were reported (Bey et al. 1971). Approximately 40% of the variance in height was associated with origin of provenance, with southern trees growing for 134 days and northern trees growing for 93 days.

Rate of shoot elongation has also been correlated with total growth. For example, in *Betula pendula*, large annual growth increments have been attributed to rapid growth rates during a short period of time rather than to an extended growing season (Wang and Tigerstedt 1996). Similarly, the rate of elongation was a better predictor of final within-family shoot length than growth duration for *Pinus banksiana* Lamb., with rate of shoot elongation explaining 59% of the variation in annual height increment versus 41% accounted for by duration (Magnussen and Yeatman 1989). Rehfeldt (1992*a*) observed strong genetic correlations between height and cessation, duration, and rate of shoot elongation for populations of *Larix occidentalis*. Populations that showed the greatest total growth also showed a rapid growth rate and late cessation of elongation (Rehfeldt 1992*a*). We found significant differences in rate of elongation among both hybrid groups and families within hybrid groups, and the rate of lateral shoot elongation was weakly correlated with total height in 1996 ($P < 0.1041$). Rate of elongation was strongly correlated with total elongation of the lateral shoot ($P < 0.0001$), indicating that the rate of elongation of the terminal shoot might be correlated with height increment or total height for hybrid larch families.

The strong correlation of both cessation and duration of elongation with current-year total height implies that superior families of hybrid larch could be identified by selecting for late cessation or long duration of shoot growth. Li et al. (1998) also noted that hybrid vigor in aspen hybrids (*Populus tremuloides* Michx. × *tremula* L.) is associated with delayed bud set resulting in a longer duration of growth. Similar results were reported for *Picea abies* (Skroppa and Magnussen 1993). Provenances that had a long shoot elongation period and late cessation of growth generally had the greatest total shoot length.

We conclude that patterns of lateral shoot elongation of *Larix* species and hybrids can be used to predict height growth. Specifically, cessation and duration of growth were strongly correlated with total height after 5 years. Duration of the elongating period was strongly and positively correlated with total height at age five for interspecific hybrid families. Hybrid vigor in height growth by Larix *laricina* × *decidua* hybrids in this study was a function of time of growth cessation and duration of growth. All interspecific hybrids ceased growth later and grew longer than families of either *L. laricina* or *L. decidua*. Selection of families with a long period of growth should be made cautiously if these families are to be planted in areas with late spring or early fall frosts (Rehfeldt 1992*b*), because they may be poorly adapted to these sites. *Larix kaempferi* shoots were severely damaged by cold weather, and hybrids with *L. kaempferi* as a parent exhibited the longest growth duration and latest growth cessation. A practical application of these results is that lateral shoots may be used instead of the terminal shoot to compare shoot growth behavior for some traits among hybrid families.

Acknowledgments

The authors sincerely acknowledge Dr. William A. Halteman for his statistical assistance with data analysis. Thanks also to Drs. Katherine K. Carter and Robert S. Seymour for their input, the Cooperative Foresty Research Unit, and to Carl Haag and S.D. Warren Co. for providing the progeny test site. Maine Forest and Agricultural Experiment Station Paper 2277.

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