Growth, morphology, and cold hardiness of *Chamaecyparis nootkatensis* seedlings originating from an abbreviated reproductive cycle

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Abstract: A common garden study investigated growth, morphology, and cold hardiness of yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) seedlings originating from seed that had matured at an accelerated rate. This early maturing seed, produced at a low-elevation southern Vancouver Island seed orchard, was known to have similar germinability and seedling morphology as high-elevation normally maturing seeds. Population differences in 3-year-old seedlings were evident only in shoot harvest index (ratio of stem/shoot dry weight). The amount of stem elongation that occurred prior to the formation of secondary foliage (juvenile height) and harvest index were weakly correlated with source elevation at which maternal parents were developed. Traits that exhibited no discernable differences between progeny from early maturing seed and the control normally maturing seed included midwinter cold hardiness testing and selected measures of shoot morphology and growth. The control seedlings had significantly less height growth prior to the transition of primary foliage to secondary foliage formation than did the seedlings originating from early maturing seed.

Résumé : Une étude réalisée en plantation a porté sur la croissance, la morphologie et la tolérance au froid de semis de faux-cyprès de Nootka (*Chamaecyparis nootkatensis* (D. Don) Spach) provenant de graines arrivées à maturité de façon accélérée. Ces graines à maturité hâtive, produites dans un verger à graines situé à faible altitude au sud de l'île de Vancouver, sont réputées avoir la même faculté germinative et donner des semis dont la morphologie est semblable à celle des semis issus de graines à maturation normale produites à haute altitude. Les différences entre les populations de semis âgés de 3 ans étaient évidentes seulement pour l'indice de récolte (rapport du poids sec de la tige sur celui des pousses). La proportion d'élongation de la tige qui survenait avant la formation des feuilles secondaires (hauteur juvénile) et l'indice de récolte étaient faiblement corrélés avec l'altitude à laquelle croissaient les parents maternels. Les caractères qui n'ont montré aucune différence discernable entre les descendances provenant de graines à maturation hâtive et les descendances témoins provenant de graines à maturation normale incluaient la tolérance au froid testée au milieu de l'hiver et des mesures de la morphologie des pousses et de la croissance qui avaient été retenues. Les semis témoins avaient une croissance en hauteur significativement plus faible avant la transition entre la formation du feuillage primaire et celle du feuillage secondaire que les semis issus de graines à maturation hâtive.

[Traduit par la Rédaction]

Introduction

Although the rate of embryo development in yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) is extremely variable among sites, mature seeds are normally shed between 17 and 21 months after pollination (Owens and Molder 1975). Pollination takes place in the spring following the year in which pollen and seed cone buds are initiated. On a typical high-elevation site, seeds only partially develop during the year in which pollination takes place, with subsequent embryo development resuming the following spring. Owens and Blake (1985) hypothesized that the 2-year period for seeds of this species to mature following fertilization may be an adaptation to short growing seasons, which occur at the high elevations where yellow-cedar is most prevalent. Owens and Molder (1975) suggested that embryo development is dependent on temperature and will continue as long as temperatures do not drop prohibitively low (coinciding at lower elevations with average minimum temperatures just below freezing).

When yellow-cedar progeny are grown in low-elevation seed orchards in mild and relatively drier climates such as those found on the Saanich Peninsula on southernmost Vancouver Island, seeds sometimes develop at an accelerated rate and may be shed as early as 8 months following pollination (El-Kassaby et al. 1991), thus exhibiting a plastic behavior in the length of time needed for reproductive maturation. Concerns about the viability and quality of early maturing seed were addressed by El-Kassaby et al. (1991) and El-Kassaby (1995), who found no adverse effects of an abbreviated reproductive cycle on seed germination or embryo morphology.

A further concern is the possibility of environmental preconditioning of seed or the influence of the maternal parent,

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which might affect subsequent seedling development. Numerous examples of maternal effects in plant species, where the maternal parent exerts a greater influence on its progeny than expected under the assumption of equal chromosomal contributions by each parent, have been described (e.g., Roach and Wulff 1987; Gutterman 1992; Rowe 1964; Farmer 1997); most investigations involved crop or herbaceous species, and most were concerned only with observed effects in seeds.

Maternal effects may be caused by cytoplasmic inheritance (Roach and Wulff 1987). However, in a number of gymnosperms studied, including some members of the Cupressaceae, cytoplasmic inheritance is paternal (Wagner 1992). The haploid megagametophyte tissue, containing stored nutrient materials, and seed coat (in particular, its structure or permeability characteristics), which both originate from the maternal parent alone, may affect a number of traits such as seed size and subsequent seedling size, seed dormancy, and germination. The environment or genotype (or the interaction between genotype and environment) of the maternal parent may influence the structure or physiology of its progeny (Roach and Wulff 1987).

Environmental factors acting on the maternal parent known to cause after-effects in seeds include temperature, nutrition, photoperiod, exogenous hormonal treatments, drought stress, and elevation (Johnsen 1988; Roach and Wulff 1987; Gutterman 1992; Dorne 1981). Noland (1984) and Farmer (1997) described examples of environmental influences on seed dormancy of coniferous species. Seedling and adult stage phenotypes that may be altered by maternal effects include various leaf habit and seedling growth measures (Roach and Wulff 1987). Rowe (1964) discussed numerous examples that gave evidence of the effects of seed preconditioning on subsequent plant growth, including seedling vigour and earliness of flowering in progeny. He suggested that environmental preconditioning may be at play in a forestry context when moving seed sources to distant seed orchards and provenance-testing nonlocal sources.

Genetic changes induced by environmental stresses imposed on the parent, although rare, have been described for a few crop species (e.g., Durrant 1971; Highkin 1960; Perkins et al. 1971). Genetic changes could occur either before or during meiosis, by a transposition event or through changes in the repetitive DNA, or after meiosis, where gamete or embryo selection may occur at one of several stages (Johnsen 1988). While both nuclear genetic and cytoplasmic genetic maternal effects would be expected to persist throughout an organism's lifetime and beyond to further generations, nongenetic effects, including correlations between seed size and subsequent seedling size, are expected to be transient, declining over time.

Johnsen (1988, 1989*a*, 1989*b*) and Johnsen et al. (1989) found differences in a number of seedling growth and adaptability traits among Norway spruce (*Picea abies* (L.) Karst.) progeny grown from seed collected in northern Norway and progeny derived from seed from the same parental sources but produced in a southern seed orchard. These differences were observed for at least 7 years. Similar effects were noted when progeny of Norway spruce from high elevations were compared with the same sources grown at a low-elevation seed orchard. The authors proposed that the parental environment in the southern seed orchard may have altered genetic performance of the progeny, which behaved more like southern provenances.

Rowe (1964) suggested the possibility of developing customized seed sources using preadaptation, by manipulating controlled environments, to shape a plant for a particular locale. Sorensen and Campbell (1985) obtained increases in seed weight by increasing microclimate temperature of female strobili within pollination bags; seedlings grown from the bagged seeds had an increased volume of 12.5% 2 years after germination than seeds originating from unbagged strobili. The implication of preconditioning observed in seed orchards would be a need for detailed examination of common seed orchard management practices such as applying growth hormones to stimulate reproductive bud formation and fertilizer and watering regimes.

The purpose of this study was to compare the growth, morphology, and cold hardiness of seedlings grown from yellow-cedar seed that matured during an abbreviated reproductive cycle in a low-elevation seed orchard having a mild climate with high-elevation seedlings grown from normally maturing seed. This study is a continuation of the investigation into seed properties of accelerated-grown seeds of this species (El-Kassaby et al. 1991) to describe potential phenotypic effects at the seedling stage.

Materials and methods

Methods

The six yellow-cedar sources for this study (Table 1) originated from wild seedlings of an unspecified age from a number of high-elevation southern Vancouver Island sites. The seedlings were excavated and transplanted in May 1974 to the yellow-cedar seed production area of the former Pacific Forest Products Ltd. at the Saanichton Seed Orchard on southern Vancouver Island (48°35′N, 123°24′W, 50 m elevation). During March 1989, trees were pollinated with bulked pollen composed of eight male contributers from the seed production area. Sources for the pollen mix were from the same provenances as the female parents (Table 1), but all pollen came from individuals not included as a maternal parent in this study. One additional provenance (Walker, 48°31.11′N, 123°58.29′W, 700 m elevation) was included as a pollen source in the polymix. Subsequent cone collection occurred in January 1990 after a maturation period of 10 months, when cones were first observed to be opening. Control seeds, which had matured in the wild under a normal length of time for this species, were collected from trees of a stand at West Leech River, the only provenance of the seed production area trees from which naturally produced seed was available.

Seed was extracted after air-drying cones at room temperature and stratified using the following regime: 1 week soak at room temperature, then 1 month warm (20°C) stratification followed by 3 months cold (1–3°C) stratification. Further details regarding pollination and germination methodology are provided in El-Kassaby et al. (1991). Control and accelerated-grown seed was sown in the spring of 1991 into Styroblock 415-D® containers (cavity: depth 152 mm, diam-

Table 1. Population origins and measured growth and shoot morphology traits of seedlings grown in a common environment.

	Population						
Variable[a]	Control	West Leech River	Weeks Lake	Roach	Lens Mountain	Muir Mountain	Mount Brenton
Elevation (m)	675	675	550	650	700	885	1100
Latitude (N)	48°34.49′	48°34.49′	48°35.04′	48°44.49′	48°32.36′	48°28.25′	48°54.06′
Longitude (W)	123°50.45′	123°50.45′	123°51.18′	124°03.40′	123°55.58′	123°51.59′	123°50.29′
LLB (cm)	33.9 (1.89)	32.6 (1.32)	32.2 (1.32)	34.4 (1.50)	30.8 (1.71)	31.2 (1.84)	33.5 (2.12)
LTB (cm)	4.2 (0.25)	4.3 (0.28)	3.6 (0.41)	3.4 (0.25)	3.6 (0.29)	4.3 (0.34)	4.0 (0.27)
JHt (cm)	9.5 (0.40)	11.5 (0.47)	9.5 (0.35)	11.2 (0.47)	10.6 (0.46)	11.1 (0.35)	12.1 (0.37)
HtLB (cm)	24.4 (1.69)	24.9 (2.03)	18.8 (1.43)	27.6 (1.92)	22.6 (1.53)	23.8 (2.12)	25.4 (1.76)
HtTB (cm)	66.4 (3.06)	70.1 (2.27)	67.5 (2.70)	76.1 (2.89)	65.7 (2.61)	65.2 (4.04)	75.8 (2.65)
Ht (cm)	71.6 (3.19)	74.0 (2.24)	71.4 (2.75)	80.3 (2.90)	69.6 (2.71)	69.2 (4.11)	80.2 (2.90)
RCD (mm)	11.0 (0.35)	12.0 (0.38)	12.0 (0.46)	12.7 (0.59)	11.2 (0.43)	11.7 (0.64)	13.1 (0.56)
ShDW (g)	59.6 (4.31)	59.5 (3.54)	57.0 (4.44)	68.8 (8.09)	50.6 (4.09)	57.1 (7.04)	69.4 (6.48)
SDW (g)	12.4 (1.11)	12.7 (0.97)	12.1 (1.06)	17.0 (2.31)	10.8 (1.06)	12.7 (2.16)	17.1 (1.57)
BDW (g)	47.2 (3.33)	46.8 (2.61)	44.9 (3.53)	51.8 (5.87)	39.8 (3.16)	44.4 (4.97)	52.4 (5.05)
HI	0.206 (0.008)	0.211 (0.005)	0.210 (0.008)	0.246 (0.008)	0.212 (0.008)	0.209 (0.009)	0.245 (0.007)

Note: Values are means with SE given in parentheses.

[a]LLB, length of longest lateral branch; LTB, length of terminal branch; JHt, juvenile height; HtLB height to longest lateral branch; HtTB, height to base of terminal branch; Ht, total height; RCD, root collar diameter; ShDW, shoot dry weight; SDW, stem dry weight; BDW, branch dry weight; HI, harvest index (= SDW/ShDW).

eter 42 mm, volume 170 mL with 364 plants/m^2 density) and grown for one season as container stock. In the fall of 1991, seedlings were transplanted into a common garden at the Saanichton site in a completely randomized design, with four five-tree row plots per provenance. Trees were not fertilized and were watered only when necessary to prevent serious drought stress.

During the winter of 1992–1993, after seedlings had spent one growing season in the field, frost hardiness measurements were made on four of the accelerated-grown populations plus the control population; equipment constraints prevented the testing of all populations. Testing was conducted on four test dates between early winter and spring, with four test temperatures per date: –18, –24, –30, and –36°C on December 8; –25, –31, –37, and –43°C on January 12; –25, –33, –41, and –49°C on February 9; and –6, –12, –18, and –24°C on March 23.

Frost testing was performed using the electrical conductivity test based on the methods of Glerum (1985). On each test date, branch samples from four trees per population were collected. Five rinsed foliage samples, about 5 mm in length, from a single tree were placed into each of five 20-mL glass scintillation vials, one per test temperature. The test jars were immediately placed into a portable cooler containing freezer packs and brought to the University of British Columbia in Vancouver for testing.

Control samples from each population were kept in a darkened cooler at 3°C during the frost test procedure. Test samples were placed into racks that allowed for air flow between vials and put into a programmed biofreezer unit. After stabilizing at 2°C for 1 h, the freezer temperature was decreased at a rate of –5°C/h until the first desired test temperature was reached, held for 1 h, then the first set of samples was removed under dark conditions. These samples were placed in the dark cooler and allowed to thaw gradually overnight at 3°C. The remaining samples in the freezer were cooled at –5°C/h until the second test temperature was reached, held for 1 h, then the next set of samples was removed. This process was repeated until all test temperatures had been reached, and all samples were removed from the freezer and placed into the cooler.

The following day all vials, including those of the unfrozen controls, were removed from the cooler. A volume of 15 mL of distilled, deionized water was added to each jar, and samples were left at room temperature. After 24 h, vials were shaken, and the electrical conductivity was measured. Samples were then completely killed by placing the vials into a 60°C water bath for 45 min. Jars were left at room temperature for a further 24 h; a second conductivity measurement was then taken on each jar.

The amount of injury resulting from freezing to a certain temperature was calculated for each sample using the following formula (Glerum 1985):

$$[1] \qquad I_t = \frac{RC_{frozen} - RC_{control}}{1 - (RC_{control}/100)}$$

where I_t is index of injury (%), RC_{frozen} is the relative conductivity of frozen sample, and $RC_{control}$ is the relative conductivity of control sample:

$$RC_{frozen} = \frac{\text{electrical conductivity of frozen sample}}{\text{electrical conductivity of frozen killed}} \times 100$$

$$RC_{control} = \frac{\text{electrical conductivity of control sample}}{\text{electrical conductivity of control killed}} \times 100$$

The I_t values per tree were plotted against test temperatures. From these graphs, the temperature at which 50% of injury would occur (LT_{50}, lethal temperature for 50% of the population) was estimated for each tree.

Seedling height (Ht), root collar diameter (RCD), and shoot dry weights (ShDW) were measured in the fall of 1993, after three growing seasons, on all seedlings in the common garden. Shoots were separated into stem (SDW, stem dry weight) and branch (BDW, branch dry weight) portions prior to weighing. Root dry weights were not measured because of the difficulty of excavating complete root systems from the soil. The shoot harvest index (HI = SDW/ShDW), an indication of biomass allocation between the stem and the lateral branches including foliage, was estimated.

Various shoot morphology measurements were taken to investigate shoot architecture (Fig. 1). The height of tree from the root collar to the point where primary foliage changes to secondary foliage formation ("juvenile" height, JHt), height from root collar to the longest lateral branch (HtLB), and height from the root collar to the base of the terminal branch (HtTB) were taken. The length of the longest lateral branch (LLB) and length of the terminal branch (LTB) were also measured.

Data analysis

Analysis of variance (ANOVA) was used to analyze the data. The model used for analysis of growth and shoot morphology data was

$$[2] \qquad Y_{ijn} = \mu + P_i + R(P)_{(i)j} + \varepsilon_{(ij)n}$$

where P is population and R is plot.

For all ANOVA, effects were considered to be random. Because of an unbalanced data set, SAS® PROC GLM was performed, using type IV sums of squares. Planned contrasts were made between the normally maturing control population (N) and the accelerated-grown populations to test the following hypothesis:

$$[3] \qquad H_0: 6\mu_N - \mu_1 - \mu_2 - \mu_3 - \mu_4 - \mu_5 - \mu_6 = 0$$

A planned contrast between the control and the accelerated-grown population originating from the same provenance (West Leech River) was also determined, using the following hypothesis:

$$[4] \qquad H_0: \mu_N - \mu_1 = 0$$

Analyses of variance were estimated for frost hardiness parameters on each test date using the following linear models:

$$[5] \qquad I_{t_{ikn}} = \mu + P_i + T_k + PT_{ik} + \varepsilon_{(ik)n}$$

$$[6] \qquad LT_{50_{in}} = \mu + P_i + \varepsilon_{(i)n}$$

where P is population and T is test temperature.

A planned contrast was made between the normally maturing control population and the four accelerated-grown populations to test the following hypothesis for both I_t and LT_{50} values:

$$[7] \qquad H_0: 4\mu_N - \mu_1 - \mu_2 - \mu_3 - \mu_4 = 0$$

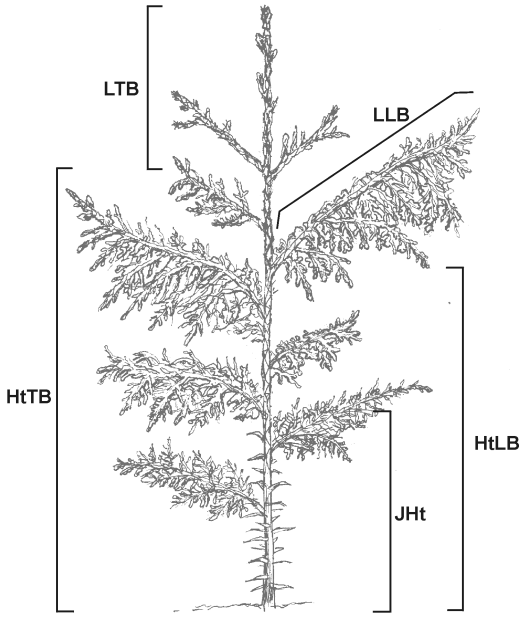
For the I_t values, contrasts were carried out for each test temperature per test date.

A planned contrast between the control and the accelerated-grown population originating from West Leech River was also made for both I_t (by test temperature) and LT_{50} values, using eq. 4.

Simple linear regressions were carried out to detect the influence of elevation on all traits, using the general equation of

$$[8] \qquad Y = \beta_0 + \beta_1(\text{elevation})$$

Fig. 1. Seedling shoot measurements: JHt, juvenile stem height prior to secondary foliage formation; HtLB, stem height to the longest lateral branch; HtTB, stem height to the base of the terminal branch; LLB, length of the longest lateral branch; LTB, length of the terminal branch.



Results

Mean values for various growth and shoot morphology traits are listed in Table 1; Table 2 presents ANOVA results for these traits. Only a single trait, harvest index, differed significantly among populations. Plot effects were evident in most measured traits.

After the 1993 growing season, seedlings from the control population differed significantly from seedlings of the accelerated-grown populations in juvenile height, root collar diameter, and harvest index (Table 2), with the control seedlings having the least amount of stem height growth prior to the transition of primary foliage to secondary foliage formation, the smallest root collar diameter, and the lowest harvest index. Planned contrasts between the control and the corresponding accelerated-grown population from West Leech River also showed a significant difference in juvenile height, with the accelerated-grown West Leech River seedlings having a greater amount of juvenile stem elongation than the control seedlings (Table 2).

The frost index of injury differed significantly among populations on three of four test dates from midwinter to late winter (Table 3), but the control population differed significantly from the accelerated-grown samples and from the West Leech River accelerated-grown population only at the two intermediate test temperatures on December 8, when trees were still in the process of acclimatizing. Significant

Table 2. Analysis of variance and contrasts for measured growth and morphology traits.

Source of variation		LLB	LTB	JHt	HtLB	HtTB	Ht	RCD	SDW	BDW	ShDW	HI
Population	*F*	0.33	1.44	1.86	1.92	1.22	1.23	1.68	1.49	0.71	0.89	4.07
	p	0.911	0.245	0.135	0.123	0.335	0.330	0.174	0.230	0.647	0.522	0.007
Plot(population)	*F*	1.90	1.40	4.73	1.08	2.87	2.64	1.52	2.00	1.72	1.83	1.50
	p	0.019	0.137	0.001	0.379	0.001	0.001	0.087	0.012	0.040	0.025	0.096
N vs. accelerated	*F*	0.38	1.63	19.89	0.10	1.87	0.82	4.60	0.73	0.01	0.03	4.34
	p	0.542	0.205	0.001	0.754	0.174	0.368	0.034	0.396	0.931	0.869	0.040
N vs. West Leech River	*F*	0.17	0.05	21.56	0.03	1.30	0.54	2.39	0.04	0.00	0.00	0.28
	p	0.681	0.824	0.001	0.854	0.257	0.464	0.125	0.835	0.994	0.950	0.601

Note: See Table 1 for trait abbreviations. N, control population.

Table 3. ANOVA and contrasts for frost index of injury on four test dates.

Date		Population (P)	Temperature (T)	P × T	N vs. accelerated[a]				N vs. West Leech River			
					T_1	T_2	T_3	T_4	T_1	T_2	T_3	T_4
December 8	*F*	6.70	158.72	0.63	1.46	11.31	4.98	2.84	2.67	17.18	7.04	1.88
	p	0.001	0.001	0.804	0.231	0.001	0.029	0.097	0.108	0.001	0.010	0.176
January 12	*F*	11.07	62.84	0.73	3.04	0.78	0.00	0.05	3.24	1.18	0.34	0.47
	p	0.001	0.001	0.714	0.086	0.382	0.944	0.826	0.077	0.282	0.559	0.494
February 9	*F*	5.04	191.81	0.54	0.08	1.24	0.08	0.10	0.80	1.18	1.31	0.09
	p	0.001	0.001	0.879	0.772	0.270	0.774	0.754	0.374	0.282	0.257	0.768
March 23	*F*	0.63	112.01	0.46	0.58	0.53	0.88	0.27	0.43	0.05	0.23	0.72
	p	0.640	0.001	0.932	0.449	0.468	0.353	0.603	0.515	0.829	0.632	0.399

[a]N, control population; T_1, highest of the four test temperatures; T_4, lowest of the four test temperatures.

Table 4. ANOVA and contrasts of frost LT_{50} on four test dates.

	Population		N vs. accelerated[a]		N vs. West Leech River	
Date	*F*	*p*	*F*	*p*	*F*	*p*
December 8	3.12	0.047	8.79	0.010	11.84	0.004
January 12	2.11	0.130	0.10	0.757	0.27	0.613
February 9	2.48	0.089	0.59	0.455	0.86	0.370
March 23	0.35	0.837	0.22	0.649	0.07	0.793

[a]N, control population.

differences among populations and between the control and accelerated-grown trees and control and West Leech River with respect to LT_{50} were noted only for one date, December 8 (Table 4, Fig. 2). Thus, the 2-year-old accelerated-grown progeny showed no detrimental effects in winter cold hardiness levels, at least during the period between midwinter and early spring, from the time just prior to when trees were experiencing maximal hardiness levels, estimated to occur around the end of January (Silim and Lavender 1994), through the period of deacclimation.

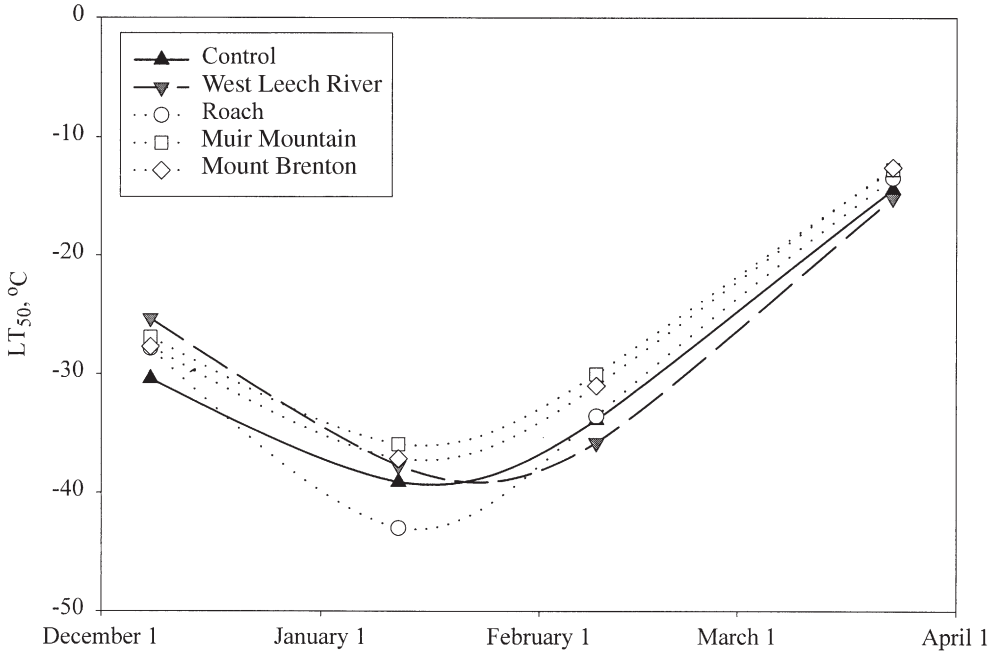
Juvenile height ($r^2 = 0.088$, $p = 0.0004$) and harvest index ($r^2 = 0.045$, $p = 0.016$) increased slightly with increased elevation of the provenance, but these trends were weak.

Discussion

Three years after germination, most growth and morphological traits did not differ significantly among yellow-cedar seedlings originating from seed that matured 1 year earlier than the norm for this species in comparison with seedlings originating from a point source representing a normally maturing yellow-cedar seed reproductive cycle. The accelerated-grown seedlings had a greater amount of stem growth prior to exhibiting secondary foliage than trees originating from the normally maturing seed. The amount of juvenile stem growth apparently had no noticeable long-term effect on growth or cold hardiness traits. The accelerated-grown seeds, which developed in the seed production area at a lower elevation and longer growing season than those of the control, may have undergone some type of environmental preconditioning, which affected early growth responses. If the change from primary to secondary foliage formation is associated in some way with a general increase in overall seedling hardiness, the greater amount of juvenile height of the seedlings from accelerated-grown seeds when grown in a mild low-elevation common garden may be associated with an ability to capitalize on a more favourable growing environment.

It is possible that one effect of a shortened seed maturation time could be that certain biochemical or hormonal processes might be altered from those of normally maturing seed; thus, a longer period may be required postgermination for seedlings originating from accelerated-grown seed to approach a similar stage of development as seedlings grown

Fig. 2. Population LT_{50} on four test dates for seedlings originating from early maturing (accelerated) seed and control seedlings.



from normally maturing seed. However, this study showed no support for such a hypothesis. It is unlikely that any long-term effects will appear as the trees mature. These findings do not preclude the possibility that gametic selection at the time of fertilization may be occurring based on environmental conditions prior to or during receptivity.

Seven years after germination, seedling height differences of 15% were observed between Norway spruce seedlings originating from seed of parents from northern Norway transferred to a southern seed orchard and their half-sibs grown in their natural environment (Johnsen 1988). In addition, vegetative shoot phenology and frost hardiness of these trees differed. These differences were interpreted as being too large to be caused by seed mass effects on seedling size and were inferred to be due to genetic changes induced by environmental effects acting on the maternal parent. By contrast, identical controlled crosses were made in three Scots pine (*Pinus sylvestris* L.) replicated clonal archives in Sweden (Johnsen 1988). Resulting progeny exhibited height and, to a lesser extent, frost hardiness differences in 1-year-old seedlings, but by age 2, frost hardiness differences were minimal, leading to the conclusion that differences were temporary and nongenetic. The response in yellow-cedar to transfer appears more similar to the transient nature of Scots pine than to that shown by Norway spruce.

An obvious drawback to the current study was the lack of more than one wild stand population from which normally maturing seed could be obtained. Without another wild stand population to compare with, it is impossible to determine whether the control was representative of other normal wild stands. However, growth of seedlings originating from the control did not appear atypical of seedling growth observed in this species under similar growing conditions. As yellow-cedar is well known for having infrequent seed years and normally does not have heavy seed yields under natural conditions or high seed germination rates, further studies of this nature would be well advised to time the work with years in which wild stand populations are expected to produce good cone crops.

The findings from this experiment concur with others (Russell 1993; Cherry and Lester 1992; El-Kassaby et al. 1991; El-Kassaby 1995) that yellow-cedar displays phenotypic plasticity in a number of traits. The indeterminate nature of shoot growth in this species makes it amenable to plastic growth responses. Our results plus those of El-Kassaby et al. (1991) support the hypothesis of Owens and Molder (1975) that seed development is temperature dependent and has a plastic response to ambient conditions. As suggested by Owens and Blake (1985), yellow-cedar appears to have adapted to shorter growing seasons at high-elevation sites by responding in an opportunistic manner with regard to cone maturation and seedling growth to favourable temperatures.

The results of this study indicate that if any environmental preconditioning has occurred in the accelerated-grown seed, the effects on seedling development are transient only. Hence, if adequate conditions are present, a shortened seed maturation period is sufficient to produce viable seed and normal seedlings. Therefore, these results are encouraging for the production of yellow-cedar seed in favourably located seed orchards, where the length of time to produce a cone crop may be shortened without any evident detrimental effects on seedlings subsequently grown from such crops.

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References

Cherry, M.L., and Lester, D.T. 1992. Genetic variation in *Chamaecyparis nootkatensis* from coastal British Columbia. West. J. Appl. For. **7**: 25–29.

Dorne, C.J. 1981. Variation in seed germination inhibition of *Chenopodium bonus-henricus* in relation to altitude of plant growth. Can. J. Bot. **59**: 1893–1901.

Durrant, A. 1971. Induction and growth of flax genotrophs. Heredity, **27**: 277–298.

El-Kassaby, Y.A. 1995. The fitness of reproductive-cycle plasticity in yellow-cedar (*Chamaecyparis nootkatensis*). Silvae Genet. **44**: 217–218.

El-Kassaby, Y.A., Maze, J., MacLeod, D.A., and Banerjee, S. 1991. Reproductive-cycle plasticity in yellow-cedar (*Chamaecyparis nootkatensis*). Can. J. For. Res. **21**: 1360–1364.

Farmer, R.E., Jr. 1997. Seed ecophysiology of temperate and boreal zone forest trees. St. Lucie Press, Delray Beach, Fla.

Glerum, C. 1985. Frost hardiness of coniferous seedlings: principles and applications. *In* Evaluating Seedling Quality: Principles, Procedures, and Predictive Abilities of Major Tests. Workshop Proceedings. *Edited by* M.L. Duryea. Oregon State University, Corvallis, Oreg. pp. 107–123.

Gutterman, Y. 1992. Maternal effects on seeds during development. *In* Seeds: the ecology of regeneration in plant communities. *Edited by* M. Fenner. CAB International, Wallingford, U.K. pp. 27–59.

Highkin, H.R. 1960. The effect of constant temperature environments and of continuous light on the growth and development of pea plants. Cold Spring Harbor Symp. Quant. Biol. **25**: 231–237.

Johnsen, Ø. 1988. After-effects on progenies from orchard clones moved to non-native environments. *In* Proceedings, 10th North American Forest Biology Workshop: Physiology and Genetics of Reforestation. *Edited by* J. Worrall, J. Loo-Dinkins, and D.P. Lester. University of British Columbia, Vancouver, B.C. pp. 1–11.

Johnsen, Ø. 1989*a*. Phenotypic changes in progenies of northern clones of *Picea abies* (L.) Karst. grown in a southern seed orchard I. Frost hardiness in a phytotron experiment. Scand. J. For. Res. **4**: 317–330.

Johnsen, Ø. 1989*b*. Phenotypic changes in progenies of northern clones of *Picea abies* (L.) Karst. grown in a southern seed orchard II. Seasonal growth rhythm and height in field trials. Scand. J. For. Res. **4**: 331–341.

Johnsen, Ø., Dietrichson, J., and Skaret, G. 1989. Phenotypic changes in progenies of northern clones of *Picea abies* (L.) Karst. grown in a southern seed orchard III. Climatic damage and growth in a progeny trial. Scand. J. For. Res. **4**: 343–350.

Noland, T.L. 1984. Investigations into the physiological nature of dormancy in sugar pine seeds. Ph.D. thesis, University of Arkansas, Fayetteville, Ark.

Owens, J.N., and Blake, M.D. 1985. Forest tree seed production. Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep. PI-X-53.

Owens, J.N., and Molder, M. 1975. Pollination, female gametophyte, and embryo and seed development in yellow cedar (*Chamaecyparis nootkatensis*). Can. J. Bot. **53**: 186–199.

Perkins, J.M., Eglington, E.G., and Jinks, J.L. 1971. The nature of the inheritance of permanently induced changes in *Nicotiana rustica*. Heredity, **27**: 441–457.

Roach, D.A., and Wulff, R.D. 1987. Maternal effects in plants. Annu. Rev. Ecol. Syst. **18**: 209–235.

Rowe, J.S. 1964. Environmental preconditioning, with special reference to forestry. Ecology, **45**: 399–403.

Russell, J.G. 1993. Genetic architecture, genecology and phenotypic plasticity in seed and seedling traits of yellow-cedar (*Chamaecyparis nootkatensis* [D. Don] Spach). Ph.D. thesis, University of British Columbia, Vancouver, B.C.

Silim, S.N., and Lavender, D.P. 1994. Seasonal patterns and environmental regulation of frost hardiness in shoots of seedlings of *Thuja plicata*, *Chamaecyparis nootkatensis*, and *Picea glauca*. Can. J. Bot. **72**: 309–316.

Sorensen, F.C., and Campbell, R.K., 1985. Effect of seed weight on height growth of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) seedlings in a nursery. Can. J. For. Res. **15**: 1109–1115.

Wagner, D.B. 1992. Nuclear, chloroplast, and mitochondrial DNA polymorphisms as biochemical markers in population genetic analyses of forest trees. New For. **6**: 373–390.