Sitka Alder (*Alnus sinuata* RYDB.) Genetic Diversity in Germination, Frost Hardiness and Growth Attributes

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(Received 17th January 2000)

Abstract

Patterns of genetic variation in adaptive and quantitative attributes of Sitka alder (*Alnus sinuata* RYDB.) were examined at the population level to provide baseline information on genetic diversity of this species. The studied traits were related to germination, growth and frost hardiness. A total of 28 populations were studied covering the species range in British Columbia. An additional population from California was included to provide an outlier source. There were large genetic differences among the populations in all measured traits except for spring frost hardiness. Inter-population variations accounted for 78% to 97%, 37% to 65% and 26% to 61% of the total variance for variables related to germination, fall and winter frost hardiness, and biomass, respectively. For frost hardiness, the differences among populations were less pronounced in winter (maximum frost hardiness) than were found in fall indicating that the onset of frost hardiness is different among populations. Variations related to geography were particularly strong in fall frost hardiness, shoot dry weight, growth rate in July and ratio of root dry weight to total dry weight. Most of the geographic variation was due to latitude and distance from the coast. Plants generated from northern seed sources were in general more frost hardy, smaller and allocated more carbon to roots compared to shoots. Plants from the interior wet belt were grouped together with coastal plants in cluster analysis based on frost hardiness measurements suggesting that snow cover plays a role in Sitka alder adaptation to low temperatures. Speed of germination did not affect the plant size after one growing season and was independent from germination completeness. Strong positive correlation was found between timing of frost hardiness development and spring bud break. The observed patterns of large genetic variation among Sitka alder populations have significant implications for the management of the species.

Key words: Sitka alder, adaptive and quantitative attributes, genetic variation, geographic pattern.

Introduction

Conservation and responsible use of genetic resources is dependent upon the knowledge of the extent and pattern of intra-specific variation. Population/provenance testing has been established for many commercially important tree species to provide information on the extent of genetic variability and adaptation; however, less attention has been paid to species with no timber value. These species are often essential components of healthy ecosystems and are valued for their role in watershed protection and providing wildlife habitat. Additionally, these species can impact crop trees and can have potential economic uses that are not related to wood production. Sitka alder (*Alnus sinuata* RYDB.) is a good example of such a species. It is a small, deciduous tree or a tall bush occurring at middle to higher elevations in cool and moist climates. In British Columbia it occurs throughout the province with the exception of the northeast corner (FARRAR, 1995). Sitka alder is recognized for its important role in slope stabilization, road deactivation and erosion control and it is commercially produced for that purpose in British Columbia. This nitrogen-fixing species also improves site conditions for more valuable trees by adding nitrogen and organic matter to the soil. BINKLEY (1984) reported elevated levels of total and available nitrogen in Sitka alder stands. Due to its short stature, Sitka alder has minimal importance as a competitor in comparison with other alders of coastal British Columbia, and therefore it may be more desirable for inter-planting with conifers. Beneficial effects of Sitka alder on Sitka spruce (*Picea sitchensis* (BONG.) CARR.) and Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) grown on nitrogen poor sites have been observed (VIERECK and LITTLE, 1972; BINKLEY, 1984). Because of its growth characteristics, this species can also be used to rehabilitate power and telephone line right-of-ways.

At present, no information is available about the extent of genetic variability of Sitka alder. In this paper we report the findings of a Sitka alder common garden trial. The population sampling covered much of the species' natural range in British Columbia. The objectives of the study were to examine the structure and patterns of genetic variation in Sitka alder adaptive (germination and frost hardiness) and quantitative (biomass allocation) attributes.

Materials and Methods

Plant material

Bulk, open-pollinated winged nutlets (hereafter referred to as "seeds") of Sitka alder were collected from 27 wild populations in British Columbia (*Table 1* and *Figure 1*). The collection also included one population from Arcata, northern California (*Table 1*). The seeds were sown at three seeds per cavity in styroblocks (PSB313B®, cavity volume 65 mL) in April, 1996 in a commercial nursery located on the Saanich Peninsula of Vancouver Island, British Columbia (latitude 48° 35', longitude 123° 24', elevation 50 m). A total of 1958 seedlings (39 to 80 per population) were potted in October 1996 into plastic containers (volume 2650 mL) and left for a second growing season. Not all of the 28 populations were used in every experiment due to the limited number of seedlings from some locations.

Germination

Four replications per population of at least 100 unstratified, pure and undamaged seeds were used in the germination study. Seeds were hydrated for 24 h at room temperature, drained, lightly surface dried and were spread in 10 x 10 x 4 cm tightly-lidded clear-plastic boxes lined with one layer of Kimpak® (cellulose wadding) overlain by three layers of What-

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Table 1. – Geographic origin of the studied Sitka alder populations.

Population	Code	Latitude	Longitude	Elevation (m)	Distance from the coast (km)
Adam's Plateau	AD	51° 06′	119° 33′	1280	330
Arcata (USA)	AR	40° 54′	124° 05′	1500	2
Bella Coola	BE	52° 19′	126° 46′	800	90
Bute Inlet	BU	50° 56′	125° 05′	960	76
Chine Nose Summit	CH	54° 27′	126° 08′	1430	260
Cold Creek	CO	50° 49′	120° 07′	1310	290
Cranbrook	CR	49° 35′	117° 05′	640	420
Cypress Park	CY	49° 22′	123° 12′	980	6
Dease Lake	DE	58° 45′	130° 03′	869	250
Glena Bay	GL	50° 35′	117° 52′	607	400
Golden	GO	51° 30′	117° 20′	Unknown	490
Green Mountain	GR	49° 03′	124° 21′	1100	20
Hemlock Valley	HE	49° 23′	121° 56′	1013	80
Hope Slide	HO	49° 16′	121° 15′	762	120
Kimsquit River	KIM	52° 53′	127° 10′	800	110
Kitlope River	KIT	53° 03′	127° 36′	820	100
Knight Inlet	KN	51° 06′	125° 48′	790	70
McKay Lake	MC	49° 45′	125° 17′	914	10
McKendrick Pass	MK	54° 50′	126° 45′	1190	250
Owikeno Lake	OW	51° 34′	126° 31′	1080	84
Phoenix	PH	49° 05′	118° 35′	1219	310
Powell River	PO	49° 59′	124° 39′	660	10
Roberts Lake	ROB	50° 13′	125° 30′	366	10
Roger's Pass	ROG	51° 19′	117° 34′	1219	460
Sproat Lake	SP	49° 18′	125° 04′	640	30
Stikine River	ST	58° 00′	130° 02′	915	210
Valemount	VL	52° 50′	119° 15′	850	490
Vanderhoof	VN	53° 56′	123° 49′	1287	370

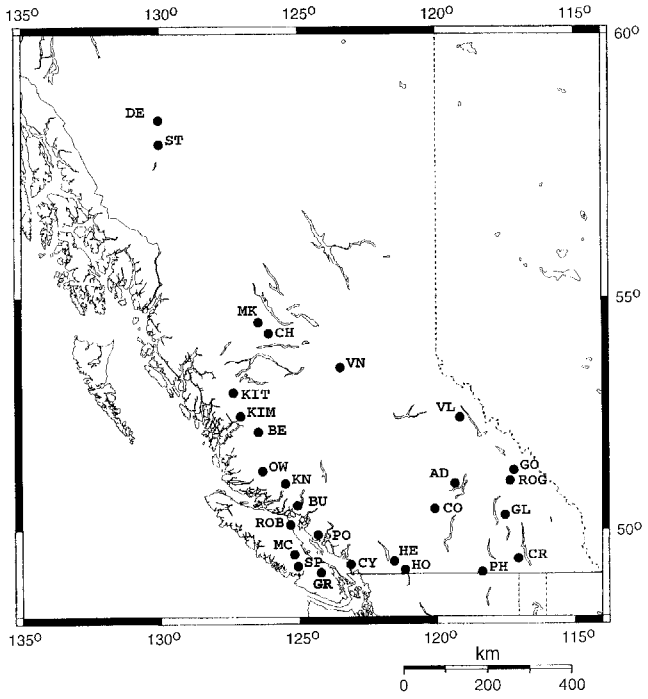

Figure 1. – Locations of the sampled Sitka alder populations from British Columbia.

man® no. 1 filter paper, moistened with 50 ml of distilled water. Boxes were placed in randomly-assigned positions in a germinator with an 8 h photoperiod, 30 °C / 20 °C day/night temperature. After seven days, germinants were counted every day for 21 days and assessed according to International Seed Testing Association (1985) rules.

The following parameters were determined: GC (germination capacity), R_{50} and R'_{50} (germination speed), PV (peak value), GV (germination value) and GU (germination uniformity). GC is the percentage of total germinated seeds; R_{50} is the number of days required to reach 50% germination of all seeds (CHING, 1959); R'_{50} is the number of days required to reach 50% germination of the viable (and non-dormant) seeds (THOMSON and EL-KASSABY, 1993). In order to estimate PV, the accumulated number of germinants was divided daily by the number of corresponding days. The maximum value obtained (PV) represents the mean daily germination of the most vigorous seeds (CZABATOR, 1962). GV was computed by multiplying PV by mean daily germination for the entire testing period and it represents germination speed and/or germination completeness (CZABATOR, 1962). A parameter describing germination uniformity (GU) was devised as a sum of the highest daily germination rates for three consecutive days and it was expressed as a proportion of the total viable seeds.

Frost hardiness and bud break

Depth and induction of frost hardiness was measured five times between 15 October, 1996 and 9 March, 1997 on 23 populations. Frost hardiness of five plants per population was evaluated by the measurement of electrolyte leakage from tissues exposed to sub-freezing temperatures (GLERUM, 1985). Roots, buds and leaves were cut off and the stems were washed in deionized water before they were cut into 5 mm long sections, 16 sections per plant. Equal numbers of sections (four) were put in four 7-mL polyethylene scintillation vials and 0.2 mL of deionized water was added. One vial per plant was kept in the refrigerator at 4 °C as control. The remaining three samples from each plant were placed in a programmable freezer (Forma Scientific) and each was exposed to a different subfreezing temperature. The temperatures were selected based on the results of a pilot study and the previous test (i.e., temperature used for time 1 is based on that of time 0 and so on) and varied from –6 °C to –50 °C depending on the level of frost resistance developed by Sitka alder at the particular time. The samples were cooled at the rate of 4 °C per hour and kept in each test temperature for one hour. After that time, the vials were removed from the freezer and thawed slowly for at least 2 hours at 4 °C. Next, 3.3 mL of deionized water was added to the control and test vials and the samples were allowed to equilibrate at room temperature for 18 hours. The conductivity of the tissue solution was measured with a digital conductivity meter (model 1481-60, Cole Parmer) with a gold plated dip cell (model 1481-62, Cole Parmer). Following the conductivity measurements the tissues were killed in a water bath (90 °C for one hour) and left for 18 hours before the second conductivity measurement. Frost injury index (FII) was calculated following GLERUM (1985). Population mean lethal temperature that kills 50% of the tissues (LT_{50}) was determined by regressing population mean FII on treatment temperatures. The approximate date by which each population LT_{50} was equal to –18 °C was also determined ($DATE_{LT50(-18)}$).

Date when 50% of the population seedlings flushed was estimated. The emergence of the first leaf from the terminal bud was used as a criterion for bud burst. Seedlings starting to grow were counted and expressed as a percentage of the total number of plants in each population.

Quantitative attributes

Height of 25 plants per population from all 28 populations was measured after the first growing season (H1) and after the second growing season (H2). In addition, height was measured monthly during the second growing season from 30 March to 25 September 1997 and absolute height growth rates were calculated for each month. In November 1997, the same 25 plants per population were destructively sampled. The following biomass allocation parameters and plant architecture traits were measured: shoot dry weight (SDW), root dry weight

(RDW), main stem diameter (DIAM) and number of primary and secondary stems or branches within the first 6 cm from the shoot-root transition zone that had diameter greater than 4 mm (STEMS). Root weight ratio (RWR) was calculated by dividing RDW by total dry weight (sum of SDW and RDW).

Statistical analysis

The data were subject to one-way analysis of variance (ANOVA). Where needed, appropriate transformations were found to satisfy the assumptions of normality and homoscedasticity. The GLM procedure of SAS was employed for ANOVA along with the VARCOMP procedure using the restricted maximum-likelihood method of estimation to calculate variances (SAS, 1988). Multiple linear regression, with latitude (LAT), longitude (LONG), elevation (ELEV) and distance from the coast (COAST), was conducted on population means using the REG procedure of SAS (SAS, 1988). PEARSON product-moment correlations were calculated for population means. The probabilities of the observed values for the coefficients of correlation were adjusted for the number of pairs of variables in each test using BONFERONNI's procedure (SYSTAT, 1997).

Hierarchical cluster analysis was conducted to group similar populations together based on frost hardiness data. Population means were subjected to a clustering procedure using the average linkage algorithm (SYSTAT, 1997). The Euclidean distance was used as a measure of distance between the clusters. In the average linkage method the distance is defined as the average distance between all pairs of points (DILLON and GOLDSTEIN, 1984).

Results

Germination

Significant differences ($P<0.05$) among the populations were detected for every germination parameter and most of the total variance was due to the population effect (*Table 2*). Population mean GC varied from 11.8% to 87.2% (*Figure 2*). Since many populations had GC below 50%, germination speed expressed as R_{50} was not calculated (THOMSON and EL-KASSABY, 1993). Speed of germination expressed as R'_{50} varied from 7 to 14 days and was not significantly correlated with GC ($r = -0.27$, $P>0.1$). Germination parameters GC, PV and GV were all highly correlated (r values >0.93). Fast germinating populations were more uniform in germination ($r = -0.88$ between GU and R'_{50}). Based on linear regression analysis, GU did not show any relationship with population geographic location. Very weak north-south trends were observed for the remaining germination parameters. The strongest regression was found for R'_{50} (high latitude populations had higher speed of germination) but latitude could explain only 28% of the variation in R'_{50} ($P<0.01$). Speed of germination and seedling height after the first growing season were not significantly correlated.

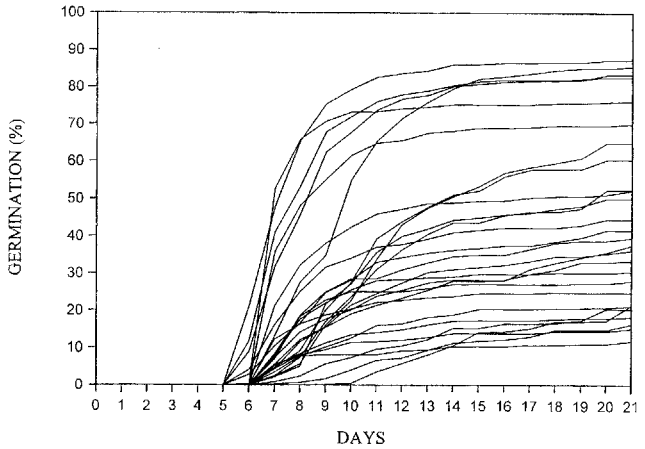

Figure 2. – Germination course of 27 Sitka alder populations.

Frost hardiness and bud break

There were significant differences in FII among the populations at all test dates except for the last test on 9 March (*Table 2*). The least frost hardy populations (AR and RO) reached a LT_{50} of –18 °C 44 and 35 days later, respectively, than the most hardy population (VN). The populations also differed significantly in maximum hardiness. For example, mean LT_{50} calculated for January 20 ranged from –50 °C to –20 °C. The differences in maximum frost resistance were less pronounced than were found for the timing of frost hardiness development. On November 11, 65% of the total variation in FII was explained by population differences, while on December 15, 37% of the total variance was due to the population effect (*Table 2*). Variances were calculated based on data from test temperatures where population differences were most pronounced. In general, populations that started to develop frost hardiness earlier were more frost hardy in the middle of winter, but the correlation was not very strong ($r = -0.6$, $P<0.05$ between January LT_{50} and $DATE_{LT50(-18)}$).

Table 2. – Analysis of variance for attributes related to germination (A), frost hardiness (B) and biomass (C).

Source of Variation	Degrees of Freedom	Components of Variance (%)								Expected Mean Squares
A		**R'50**	**GC**	**PV**	**GV**	**GU**				
Population (P)	26	94.03*	95.85*	78.16*	96.60*	76.86*				$\sigma^2_E + 4\sigma^2_P$
Error (E)	81	5.97	4.15	21.84	3.40	23.14				σ^2_E
B		**FIIoct**[1]	**FIInov**	**FIIdec**	**FIIjan**	**FIImar**				
Population (P)	22	41.46*	65.13*	37.18*	43.63*	4.16				$\sigma^2_E + 5\sigma^2_P$
Error (E)	92	58.54	34.87	62.82	56.37	95.84				σ^2_E
C		**H1**	**H2**	**DIAM**	**SDW**	**RDW**	**RWR**	**GRJL**	**STEMS**	
Population (P)	27	60.96*	45.32*	38.79*	52.09*	39.04*	25.08*	34.83*	30.18*	$\sigma^2_E + 25\sigma^2_P$
Error (E)	672	39.04	54.68	61.21	47.91	60.96	74.92	65.17	69.82	σ^2_E

[1]) FIIoct = Frost injury index for tests conducted in October (oct.). Other months are as follows: November (nov), December (dec), January (jan) and March (mar). All tests are based on the temperature treatment that produced the largest differences among the populations in frost hardiness.
*) significant at $P \leq 0.05$.

Multiple linear regression based on population means detected a clinal trend for population cold hardiness estimated during the time of hardiness development. For example, FII evaluated at –25 °C on November 11 decreased with latitude and the distance from the coast (R^2 = 0.62). On the other hand, only a weak geographic trend was found for population maximum frost hardiness (estimated by January LT_{50}) which increased with latitude (r^2 = 0.31, P<0.01).

Cluster analysis, based on FII population means of all tests, produced four distinguishable divisions among the populations (*Figure 3*): population VN, which was found to be the most frost hardy; population AR, which was found to be the least frost hardy; and two large groups between the two extremes. In one large group, coastal populations were clustered with populations from the southern interior wet belt while northern populations were grouped separately in the second large group with several southern populations from dry interior regions (*Figure 3*).

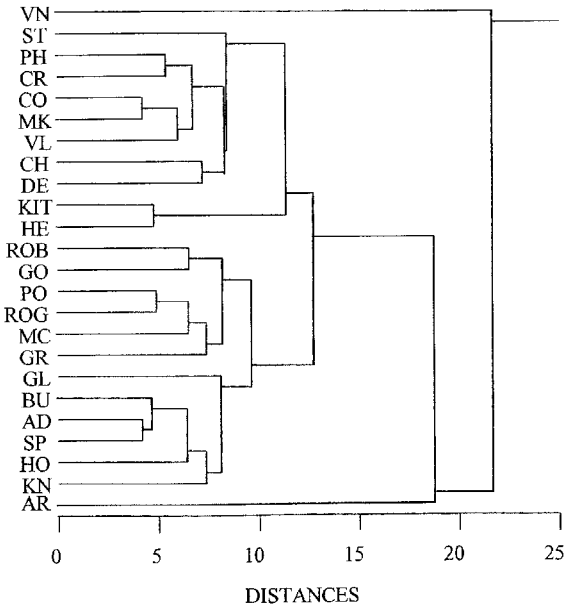

Figure 3. – Dendrogram of cluster analysis showing population grouping based on frost hardiness.

A significant geographic trend was found for spring bud break with northern and interior seed sources having a tendency to flush earlier (R^2 = 0.43). The first population started to grow on March 15 (ST, northern British Columbia) and the last one 25 days later (AR, northern California, high elevation). Differences among British Columbia populations were as large as 23 days. A strong correlation was found for time of bud break and time of frost hardiness development with r = 0.87 between bud flushing date and FII evaluated at –25 °C on November 11 (*Figure 4*). Plants that developed frost hardiness later (i.e., had higher FII in fall) had a tendency towards late bud break in spring.

Quantitative attributes

Significant differences (P<0.01) among the populations were found for all variables related to plant biomass and architecture (*Table 2*). Between 25% (for RWR) and 61% (for H1) of the total variance was explained by population effects (*Table 2*). Most variables related to plant size were highly correlated (SDW, RDW, H2, DIAM; 0.79 <r< 0.98). Absolute height growth rate in July (GRJL) was significantly correlated with SDW

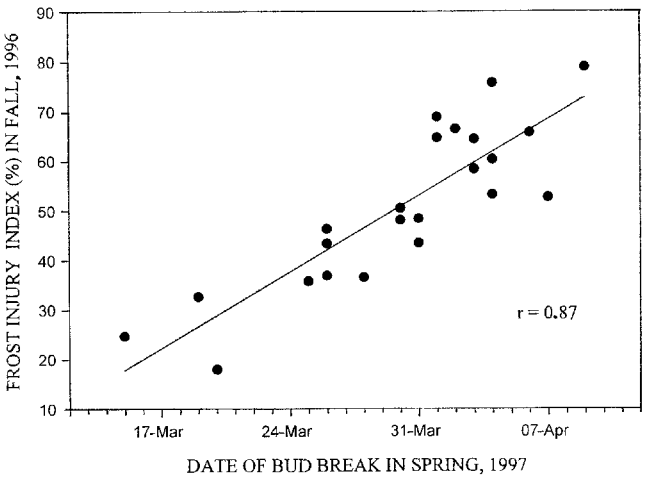

Figure 4. – Correlation between fall frost hardiness estimated by frost injury index and date of spring bud break (r = 0.87, P < 0.01).

(r = 0.73, P<0.01) but not with RDW (r = 0.47, P>0.1). Mean population STEMS ranged from 1.04 to 3.17 and displayed no significant correlation (P>0.1) with any other morphological variable. There was no significant correlation between H1 and H2 (P>0.1).

Height growth rates changed dramatically during the growing season with two distinct peaks: one in the middle of May and the second at the end of July (*Figure 5*). However, the second peak in growth rates was only observed in certain populations that resumed faster growth after slowing down in June while the growth rates of the remaining populations were decreasing. As a result of this contrasting behaviour, the largest differences among the populations in the average growth rates were observed at the end of July.

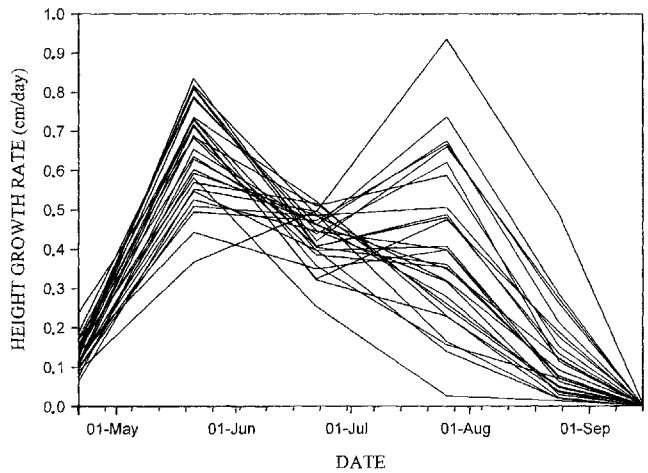

Figure 5. – Changes in mean population height growth rates (cm/day) during the growing season.

Strong geographic trends were found for GRJL (R^2 = 0.70) which decreased with LAT and ELEV and increased with LONG and for RWR (R^2 = 0.67) which increased with LAT and ELEV. Both SDW and RDW were lower in populations from colder regions but the pattern was stronger for SDW (R^2 = 0.64) compared to RDW (R^2 = 0.40) relating to LAT, ELEV and COAST.

Discussion

Germination

The very large differences observed in germination parameters resulted from genetic differentiation of populations and/or genetic-environmental interaction. Both, genetic and environmental factors can affect percentage of viable seeds in the sample, germinability of the viable seeds and seed vigor.

There seems to be a pattern of large variability in seed viability as well as frequent occurrence of low seed viability for *Alnus* spp. based on literature reports for species other than Sitka alder. Percent of viable red alder (*Alnus rubra* BONG.) seeds varied from 7% to over 74% in one germination test (ELLIOTT and TAYLOR, 1981) and from 59% to 87% in another test (RADWAN and DE BELL, 1981). Percent of empty seeds for gray (*Alnus incana* spp. *rugosa* (DU ROI) J. CLAUSEN) and black alder (*Alnus glutinosa* (L.) GAERTN.) was above 40% (SCHALIN, 1968). Large population variation in seed viability (0% to 80%) of black alder was also reported by MCVEAN (1955) and was due mostly to failure of embryo formation. A sampled population of green alder (*Alnus crispa* (AIT.) PURSH.) in Alaska had 40% viable seeds (ZASADA *et al.*, 1983). These studies indicate that the large differences in GC found in the present study are typical of alder species. However, it is not clear what caused the differences: empty seeds, defective embryos, dormancy or population variable requirements with respect to germination conditions.

Percent of viable seeds may be affected by pre-embryonic selection during seed development. Embryo abortion can be caused by high genetic loads from which many outcrossers suffer (WEINS *et al.*, 1987). Genetic load is defined as "relative lowering of the mean fitness of a population compared with the fitness of the best possible genotype" and is a consequence of the presence of mutated harmful recessive alleles (CHARLESWORTH, 1989). Genetic load is readily expressed at various levels of inbreeding leading to the development of defective seeds (PARK and FOWLER, 1984; SORENSEN and CRESS, 1994). Since the rate of mutation to lethal form is not uniform for all locations, the genetic load carried in populations will vary with site (BISHIR and NAMKOONG, 1987). In the case of Sitka alder, inbreeding and site effects on mutation rate could both play a significant role. This supposition follows from the species' wide range and its patchy distribution, its pioneer character that increases the chance of founder effect, and population isolation due to the high elevation habitat.

Large differences in germination parameters among Sitka alder populations suggest that the germination capacity as well as germination speed in this species may be adaptive. Genetic control of germination traits has been indicated for Douglas-fir (EL-KASSABY *et al.*, 1992), Pacific silver fir (*Abies amabilis* (DOUGL.) FORBES) (DAVIDSON *et al.*, 1996), Sitka spruce (CHAISURISRI *et al.*, 1992), palebark Heldreich pine (*Pinus leucodermis* ANTOINE) (GIANNINI and BELLARI, 1995), aspen (*Populus tremula* L. and *P. tremuloides* MICHX.) (GALLO, 1985) and tulip tree (*Liriodendron tulipifera* L.) (BARNETT and FARMER, 1978). Between population differences in germination capacity may result from variable levels of dormancy. Dormancy prevents seed germination in situations that could lower the survival rate of the seedlings; for example, where short periods of warm temperatures are followed by cold weather. There is no information with regards to Sitka alder seed dormancy. In this experiment, some populations had very high GC indicating that they were not dormant and stratification was not needed, at least for these seed sources. It has been suggested that red alder seeds are merely quiescent (i.e. when shed would germinate in favourable conditions) rather than physiologically dormant (KENADY, 1977; RADWAN and DE BELL, 1981). However, ELLIOTT and TAYLOR (1981) showed that while dormancy in red alder seed is not common, it does exist in some populations. The same may be true of Sitka alder.

Northern seed sources of Sitka alder germinated faster than southern sources and this trend is consistent with literature reports for other species: e.g., paper birch (*Betula papyrifera* MARSH.) (BEVINGTON, 1986) and western hemlock (*Tsuga heterophylla* (RAF.) SARG.) (CAMPBELL and RITLAND, 1982). Faster germination in the north may be an adaptive trait since the benefits of extending the length of the growing season by several days may outweigh the risk of exposure to low temperatures.

In addition to genetic factors, local environmental conditions during seed development can strongly affect germination. Stress from low/high temperatures, low/high moisture, limited resources, predation, and competition can all have an impact on seed development (OWENS, 1991). Even very short exposure to adverse environmental conditions can hinder proper seed development by affecting the vigor, viability and quantity of pollen, and can lead to the formation of empty seeds.

Frost hardiness and bud break

Large differences among the populations in fall and winter frost hardiness, which parallel environmental gradients, indicate strong genetic control and the adaptive nature of this attribute. The differences were particularly large during the time of frost hardiness development where over 65% of the total variance was due to the population effect. Greater differences in fall frost hardiness compared to differences in maximum frost resistance are often observed (see SAKAI and LARCHER, 1987). For example, DEANS and HARVEY (1996) found the largest inter-population differences in sessile oak (*Quercus petraea* (MATT.) LIEBL.) frost hardiness in fall and spring and the smallest differences in midwinter. In contrast to the sessile oak study, we found no significant differences for Sitka alder cold resistance during the spring season. Similar results were found in red alder (CANNELL *et al.*, 1987) where northern populations started to develop cold resistance earlier in the fall, but all populations dehardened at about the same time in March.

The geographic trend in Sitka alder frost hardiness is rather unusual. As a group, interior populations tend to be somewhat more frost hardy than coastal populations; however, populations from the interior wet belt of the western side of the Rocky Mountains were similar in frost hardiness to coastal populations. The latitudinal trend in frost hardiness, often reported for other species (FLINT, 1972; JOYCE, 1987), was distinct in Sitka alder but not as strong as might be expected given latitudinal range covered (18 degrees). The trend was more evident in fall frost hardiness than in the maximum cold resistance. The same level of cold hardiness of populations from regions of high snowfall (over 4 m in coastal regions and interior wet belt), relatively low frost resistance of the species as a whole, and its weak geographic trend in midwinter all indicate that snow cover may influence adaptation of Sitka alder to winter temperatures. Important for this hypothesis is the small size of Sitka alder plants that can be as low as 3 meters for mature plants (HAEUSSLER *et al.*, 1990). Snow cover acts as an insulating material. For intermediate latitudes the temperature usually does not decrease below −5 °C beneath snow cover thicker than 20 cm (SAKAI and LARCHER, 1987). Climate change causing reduction in duration and thickness of snow cover may result in more frequent occurrence of frost injury in Sitka alder, within some populations, despite potentially warmer winters.

Strong correlation was observed between fall frost hardiness and date of bud break. Plants that develop frost resistance

earlier also break their buds earlier in spring. It is not possible, based on this study, to determine whether frost hardiness and dormancy are physiologically interdependent or correlated without causal relation in Sitka alder. In general, the relationship between dormancy and cold hardiness is not clear since there are species that do not develop dormancy yet develop frost resistance (SILIM and LAVENDER, 1994), or develop dormancy but not frost resistance (KRAMER and KOZLOWSKI, 1979). On the other hand, frost resistance and dormancy are positively correlated in many species (e.g. FUCHIGAMI *et al.*, 1982; SAKAI and LARCHER, 1987; ERSTAD, 1994).

There may be several reasons for the differences among the populations in time of bud break: different time of dormancy onset, different chilling requirements to break bud dormancy or different heat sum requirements for bud flushing after dormancy is broken. The most likely reason for differences in time of bud break in Sitka alder populations is related to different heat sum requirements. It has been suggested that the chilling requirement plays a role in preventing bud break in fall (BORCHERT, 1991), rather than preventing too early a flush in spring. After chilling requirements are met, the plants must be exposed to warm temperatures for a certain period of time before they start to grow. Different populations may have different heat sum requirements and therefore start to grow at different dates in a common garden experiment. It can be concluded that all Sitka alder populations were not dormant at the beginning of March based on the following: (1) frost hardiness usually correlates with dormancy, (2) there were no differences among populations in frost hardiness in March, and (3) some of the populations were already starting to break buds in early March. Therefore, the likely cause of differences in timing of bud break in Sitka alder is differential heat sum requirements needed by different populations to commence growth. Plants from colder regions would have lower heat sum requirements in accordance with lower spring temperatures in their native habitats and, as a result, would flush earlier in a common garden experiment established in a warmer climate. On the other hand, it is also possible that some populations started to grow before others because they were released from dormancy earlier and were thus able to start accumulating their heat sum earlier.

Quantitative attributes

Average rates of daily height growth showed different patterns from population to population during the growing season, although all the populations except one exhibited a depression of growth rates in June (*Fig. 5*). Since June 1997 was particularly cold and since virtually all populations decreased their growth rate about this time it follows that the growth depression was probably due to an environmental effect. Another explanation for the growth rate pattern might be periodic shoot growth with an intervening period of rest (BORCHERT, 1991). Close examination of the stems did not reveal, however, the presence of more than one set of bud scale scars per year, suggesting that recurrent flushing did not occur. After the growth depression in June, some populations resumed rapid growth while others continued slowing down. As a result, at this time there were the largest differences in growth rate and a strong geographic trend in this trait. Higher growth rates were found in populations from warmer regions indicative of a longer growing season.

Populations were different with respect to plant structure based on STEMS and RWR but only the variation in RWR was related to geography. With the exception of several coastal populations such as CY, KN, and OW, the form of the majority of plants was tree-like (monopodial) rather than bush-like (polypodial). In natural stands, however, the habit of Sitka alder is usually bush-like. Perhaps the growth form changes with time and these plants will become bushier after several years or the bushy habit form results from damage to the main stem in natural stands (e.g. from frost, browsing or insects). In contrast to STEMS, RWR showed a distinct geographic trend by increasing strongly with latitude and less strongly with elevation. Greater allocation of carbon to roots in plants from colder regions is often observed (e.g. SCHULTZ and GATHERUM, 1971; CANNELL and WILLET, 1976; STAHL and PERSSON, 1992). Plants may invest more carbon into roots in conditions of low soil temperatures to compensate for lower nutrient (RUEL *et al.*, 1996) and water uptake (KRAMER and KOZLOWSKI, 1979) or in response to lower soil fertility and/or moisture availability (KEYES and GRIER, 1981).

Large differences found among the populations in quantitative traits important for Sitka alder utilization (STEMS, RDW, SDW and RWR) indicate the possibility to select seed sources most suitable for slope stabilization, road deactivation and inter-planting with conifers. In the case of RDW, the relatively weak geographic trend found for this trait means that it is possible to find populations with high RDW within any given geographic region. For Vancouver Island and the south coastal region of the mainland these include GR, ROB, SP and OW. Since RDW and RWR were not significantly correlated, a different seed source must be selected if small plants with relatively large roots are required rather than plants with large RDW. Populations with large RDW will also have large above-ground biomass which may have undesirable effects on crop species. Because there was only a weak negative correlation between fall frost hardiness and biomass and no correlation with midwinter hardiness, it should also be possible to find populations with superior growth and high frost hardiness if such a trait combination is required.

Conclusions

Large differences among the populations and distinct geographic trends found for some traits indicate that Sitka alder has enough variation in spite of the species population dynamics that is characterized by rapid expansion and contraction that can erode genetic resources. It also indicates that the selection process is rapid in this high elevation species since Sitka alder is an early successional, short-lived pioneer plant. On the other hand, large genetic differences not related to geography (found for several traits) suggest that this species may be subject to random genetic drift or that the location variables did not reflect the selective forces. Differences among neighbouring populations indicate the possibility of significant barriers to gene flow in addition to already mentioned genetic drift and small scale site heterogeneity. The observed patterns of large genetic variation in Sitka alder populations have significant implications for the management and conservation of the species.

Generally, in most common garden experiments, it is assumed that the ecological requirements of various populations are satisfied and variation in performance is mainly based on genetic differences. The results from the present study indicate the possible presence of artifacts caused by the common garden approach. The relatively low level of frost resistance observed among the Sitka alder populations may be due to a higher rate of heat sum accumulation in the common garden location as compared to the temperatures in natural locations (different elevations with the confounding effect of latitude). Higher RWR found in northern populations may have been caused by the continuous growth of roots during fall after their shoot growth

was arrested in response to the common garden local environment (this is commonly observed in container nurseries where root development continues after bud set). The caveats of common garden experiments should be considered in light of the present results.

Acknowledgements

This paper is based on a portion of a dissertation by A.B. submitted in partial fulfillment of the requirements for the M.Sc. degree at the Faculty of Forestry, The University of British Columbia. This study was supported by Forest Renewal British Columbia Grant number HQ96060-RE made to Y.A.E. and a DONALD S. MCPHEE Fellowship awarded to A.B. The procedure for frost hardiness testing was established with help from SILVIA L'HIRONDELLE (British Columbia Ministry of Forests, Research Branch).

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