Genetic Control of Seed Size and Germination in Sitka Spruce[1])

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Abstract

The genetic control of seed size and germinative parameters (germination capacity, peak value, and germination value) in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) were studied using wind-pollination seeds from 18 seed-orchard clones. Broad-sense heritabilities of seed size and germinative parameters were moderate (0.36) and high (0.74 to 0.79), respectively. It was concluded that seed pretreatment (i. e., stratification) is essential for uniform germination, and that the observed differences in seed size, although significant, were not operationally important.

Key words: Sitka spruce, genetics of germination parameters, seed size.

Introduction

Germination is routinely used to estimate viability and germinative energy of seeds. The pattern of seed germination verifies quality with reference to seed source (Association of Official Seed Analysts, 1970). Although the natural environment in which seeds will be sown is unstable, even in the greenhouse, a standard germination test normally is conducted using uniform conditions. Thus, the germination tests often over-estimate field performance of seeds.

The pattern of seed germination in a species varies according to seed source (Allen, 1961), family (Bramlett et al., 1983; El-Kassaby et al., 1992), parental nutrition (Allen, 1960), pretreatments (Kozlowski and Gentle, 1959; De Matos Malavasi et al., 1985; Pitel and Wang, 1985), seed maturity (Allen, 1958a and b; Edwards, 1980; Edwards and El-Kassaby, 1988), environmental preconditioning during seed development (Koller, 1962; Sawhney and Naylor, 1979; Sawhney and Naylor, 1980; Naylor, 1983), and seed size (Spurr, 1944; Shoulders, 1961; Burgar, 1964; Wulff, 1972; Dunlap and Barnett, 1983; Hellum, 1990).

Seed size has been found to be under strong genetic influence (Hellum, 1976; Silen and Osterhaus, 1979; Lindgren, 1982; Wulff, 1986; Bagchi et al., 1990) that is mainly maternal (Perry, 1976; Roach and Wulff, 1987; Tyson, 1989). Geographic variation also influences seed size. Within a species, seed size is correlated with dryness of the site, i. e., as dryness increases, seed size increases (Baker, 1972). In addition, temporal variation in seed size has been observed in noble fir (*Abies procera* Rehd.) (Sorensen and Franklin, 1977) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Silen and Osterhaus, 1979). Within a plant, variation in seed size may be caused by position of seeds in the plant inflorescence (Cavers and Harper, 1966; Datta et al., 1970), or fruit (Linck, 1961; Schaal, 1980). In conifers, the biggest seeds usually occur in the middle portion of the cone.

The relationship between seed size and germination can be variable. Seed size had little effect on the germination pattern in loblolly pine (*Pinus taeda* L.) (Dunlap and Barnett, 1983), Norway spruce (*Picea abies* L. Karst.) (Andersson, 1965), and Japanese red pine (*Pinus densiflora* Sieb. and Zucc.) (Choi and Kim, 1969), but significant effects were observed in slash pine (*Pinus elliottii* Engelm.) (Shoulders, 1961) and white spruce (*Picea glauca* (Moench) Voss) (Ackerman and Gorman, 1969).

In this study, the effects of clones, seed size and seed pretreatment on germination of orchard-produced Sitka spruce seeds are reported.

Materials and Methods

Canadian Pacific Forest Products Ltd. provided the seeds for this study from the Sitka spruce seed orchard located in Saanichton, British Columbia (latitude 48°35'N, longitude 123°24'W). The orchard consists of 139 clones (averaging 9.3 ramets per clones) selected from elevations between 0 m and 415 m on western Vancouver Island, Washington and Oregon. The orchard was established in 1971 in a random single-tree mix over three unequal blocks. Due to mortality, newly grafted trees have been planted for replacement. Trees are spaced 3 m apart and kept approximately 4 m high by top-pruning.

In September 1990, wind-pollination seeds were collected from 18 clones. The clonal identities of the seeds were maintained during seed extraction. Seeds from each clone were divided into two portions, one of which was sorted into two size classes, large ($>$ 1.41 mm.) and small ($<$ 1.41 mm.) using a 14-mesh screen, while the other was kept unsorted. Both unsorted and sorted seed portions were kept at 2° C until used.

Size and weight are the main parameters used in seed sorting, and these parameters are highly correlated in Douglas-fir (Silen and Osterhaus, 1979). Whereas sizing is less time consuming when sorting a seedlot, weighing is more accurate for individual seed-size determinations. In this study, weighing and sizing were used.

Seed Weight

Individual seeds from random samples of 100 unsorted seeds, and 50 large and small sorted seeds, from each of the 18 clones, were weighed to the nearest 0.01 mg to determine patterns of weight distribution among clones and of sizes within clones. Filled seeds (determined by X-ray analysis) only were used.

Germination Test

Eight random samples of 100 seeds each were taken from unsorted and sorted (large and small) seeds of each clone and subjected to a standard germination test. Four of the eight samples were soaked in water for 24 h,

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drained, and stratified (prechilled) for 21 days at 2° C. Stratified and unstratified samples were germinated simultaneously. For germination, seed samples were spread in tightly-lidded, clear plastic germination boxes lined with moistened cellulose wadding (Kimpak) and filter paper, and placed in a germinator set at an alternating temperature of 30° C for 8 h followed by 20° C for 16 h. Light at approximately 1,000 lux was provided during the high-temperature period by means of cool-white fluorescent tubes. Germinants were counted every day for 21 days and classified as normal or abnormal according to the ISTA (International Seed Testing Association, 1985) rules. Results were expressed as (i) germination capacity (GC), the percentage of seeds that had germinated at the end of the test; (ii) peak value (PV), the maximum quotient derived by dividing daily the accumulated number of germinants by the corresponding number of days, which is the mean daily germination of the most vigorous components of a seedlot (CZABATOR, 1962), and (iii) germination value (GV), the combination of speed and completeness of germination into a single index (CZABATOR, 1962).

Statistical Analysis

Data transformations were conducted using an ad-hoc procedure for finding appropriate transformations to normalize the calculated response variables and achieve homogeneity of variances. The germination parameters (GC, PV, and GV) were then analyzed using analysis of variance (ANOVA).

Analyses were separated into 2 parts:

(1) Simple one-way ANOVA was used to estimate genetic components of seed weight (*Table 1*) and germina-

Table 1. — Estimation of variance components, significance level, and broad-sense heritabilities (h^2_b) for individual seed weight of 18 Sitka spruce clones.

Source of Variation	df	Expected[1] Means Square	Variance Component of Seed Weight
Among Clones	(C-1) = 17	$\sigma_e^2 + 100\sigma_c^2$	36.18**
Within Clones	C(N-1) = 1782	σ_e^2	63.82
h_b^2			0.36

[1]) σ^2_c = variance among clones; σ^2_e = variance within clones.

**) Significant at $P < 0.01$.

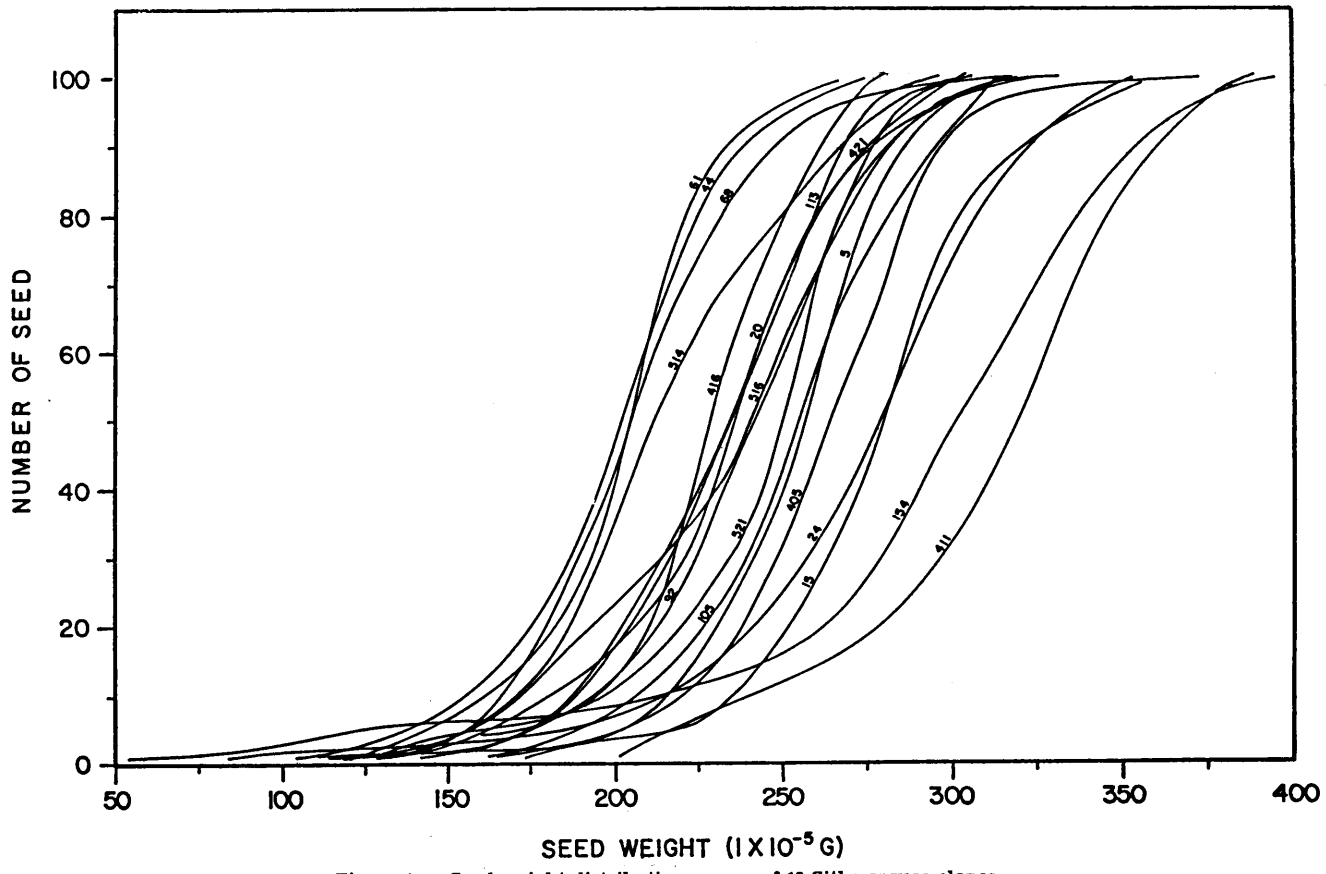

Figure 1. — Seed weight distribution curves of 18 Sitka spruce clones.

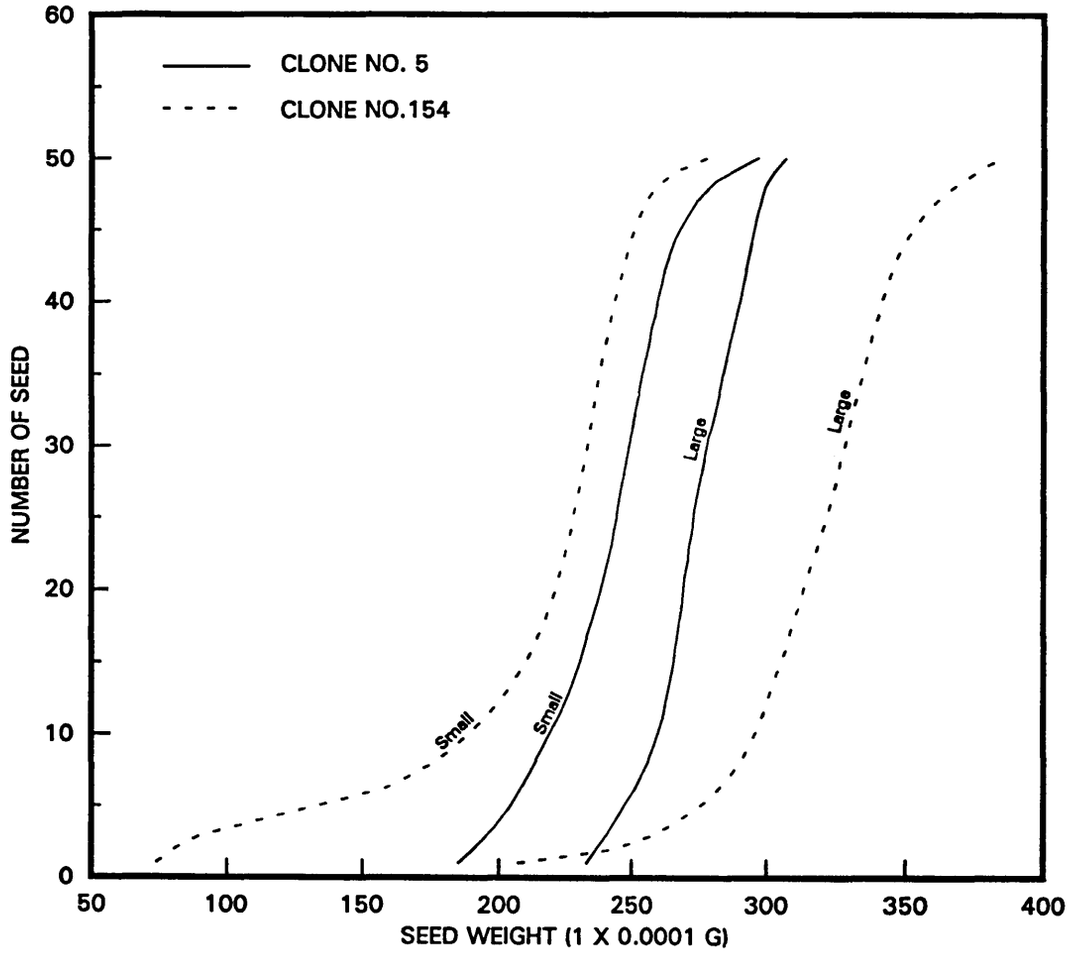

Figure 2. — Differences in seed weight of small and large sorted seeds from clone nos. 5 and 154.

tion parameters of unsorted Sitka spruce seeds (*Table 3*). Broad-sense heritabilities of these parameters were determined using the multiple-measurements concept of animal breeders (FALCONER, 1986, p. 127). Replications were used as multiple measurements per clone.

(2) A factorial experiment with 3 levels, (i) seed size (S; 2 classes plus unsorted seeds), (ii) clone (C; 18 clones), and (iii) pretreatments (P; 2 treatments), was used to assess the effect of seed size on germination parameters. The model for this ANOVA is as follows:

$$Y_{ijkl} = \mu + S_i + C_j + SC_{ij} + P_k + CP_{jk} + SP_{ik} + SCP_{ijk} + \varepsilon_{(ijk)l}$$

where μ = overall means

S_i = effect of seed size (fixed effect), i = 1 to 3,

C_j = clone effect (random effect), j = 1 to 18,

P_k = pretreatment effect (fixed effect), k = 1 to 2,

SC_{ij} = effect of interaction between seed size and clone,

PC_{jk} = effect of interaction between pretreatment and clone,

SP_{ik} = effect of interaction between seed size and pretreatment (fixed effect),

SCP_{ijk} = the effect of interaction among seed size, clone and pretreatment,

and $\varepsilon_{(ijk)l}$ = residual term.

Results and Discussion

The difference between the largest and smallest seeds is small (range 0.0200 mg to 0.0313 mg in seed weight) (*Figure 1*). However, this variation is highly significant ($P < 0.01$) and accounted for 36.18% of total variation (*Table 1*). The largest amount of total variation, 63.82%, is due to differences within clones. When seeds from each clone were sorted into 2 size classes, weight differences between small and large varied considerably from clone to clone. Clone no.5 has the smallest difference in seed weight, while clone no. 154 has the largest difference (*Figure 2*). The estimated broad-sense heritability for Sitka spruce seed weight is moderate ($h^2_b = 0.36$).

Variation in germination of unsorted seeds is highly significant ($P < 0.01$) for pretreatment, clone, and their interaction (*Table 2*). Seed pretreatments account for the largest proportion of variation (range 74.12% to 93.85%), while clonal variation accounts only for a small proportion of total variation (range 3.07% to 5.91%). The interaction between seed pretreatment and clone accounts for 1.85% to 14.06% of total variation.

To make the clonal effect more discernible, complementary analyses were calculated for unstratified and stratified seeds (*Table 3*). For unstratified seeds, clonal differences in germination parameters are highly significant ($P < 0.01$) with estimates of broad-sense heritability (h^2_b) of all parameters ranging from 0.76 to 0.79 (*Table 3*). For stratified seeds, clonal differences remain highly significant ($P < 0.01$), with broad-sense heritability estimates ranging from 0.74 to 0.78 (*Table 3*). These differences in the heritability estimates for unstratified and stratified seeds are considered minimal in this range.

Table 2. — Estimation of variance components, and significance level for germination parameters of 18 Sitka spruce clones.

Source of Variation	df	Expected[1] Mean Squares	Germination Parameters[2]		
			GC	*PV*	*GV*
Pretreatment (P)	(P-1) = 1	$\sigma_e^2 + 4\sigma_{cp}^2 + 72\phi_p$	74.12**	93.85**	92.17**
Clone (C)	(C-1) = 17	$\sigma_e^2 + 8\sigma_c^2$	5.91**	3.07**	3.23**
C x P	(P-1)(C-1) = 17	$\sigma_e^2 + 4\sigma_{cp}^2$	14.06**	1.85**	3.05**
Residual	PC(N-1) = 108	σ_e^2	5.91	1.23	1.55

[1]) ϕ_p = variance among pretreatment; σ^2_c = variance among clones; σ^2_{cp} = variance due to interaction between pretreatment and clone; σ^2_e = variance within pretreatment within clones.
[2]) GC = Germination Capacity, the percentage of seeds that had germinated at the end of the test (Arcsin).
PV = Peak Value, a mathematical expression of the break of a sigmoid curve representing a typical course of germination (square root (X + 0.5)).
GV = Germination Value (Czabator, 1962), (no transformation).
**) Significant at P $\leq$ 0.01.

Table 3. — Estimation of variance components, significance level, and broad-sense heritabilities (h^2_b) for germination parameters using unsorted seeds of 18 Sitka spruce clones.

Source of Variation	df	Expected[1] Mean Squares	Unstratified			Stratified		
			[2]*GC*	*PV*	*GV*	*GC*	*PV*	*GV*
Among Clones	(C-1) = 17	$\sigma_e^2 + 4\sigma_c^2$	78.87**	76.13**	77.22**	74.14**	77.71**	74.34**
Within Clones	C(N-1) = 54	σ_e^2	21.13	23.87	22.78	25.86	22.29	25.66
h_b^2			0.79	0.76	0.77	0.74	0.78	0.74

[1]) σ^2_c = variance among clones; σ^2_e = variance within clones.
[2]) GC = Germination Capacity, the percentage of seeds that had germinated at the end of the test (Arcsin).
PV = Peak Value, a mathematical expression of the break of a sigmoid curve representing a typical course of germination (no transformation).
GV = Germination Value (Czabator, 1962), (no transformation).
**) Significant at P $\leq$ 0.01.

For unstratified seeds, germination of unsorted seeds was incomplete within the duration of these tests (*Figure 3*). Clonal differences in germination capacity are substantial (range 45.75% to 98.00%). When seeds were stratified (*Figure 4*), variation in germination is greatly reduced (range 90.00% to 98.50%), since stratification enhanced germination rate for all 18 clones. Traditionally, stratification has been used to overcome seed dormancy for temperate species (Edwards, 1980); the response of seeds to stratification indicates "dormancy". Clonal differences in germination patterns between unstratified and stratified seeds indicate the presence of some degree of dormancy (*Figure 3* and *Figure 4*). When germination of unstratified and stratified seeds were compared for individual clones, it was found that dormancy level varied among clones (*Figure 5*).

Seed-size accounts for 0.09% to 1.39% of total variation in germination, while clonal differences account for 2.94%

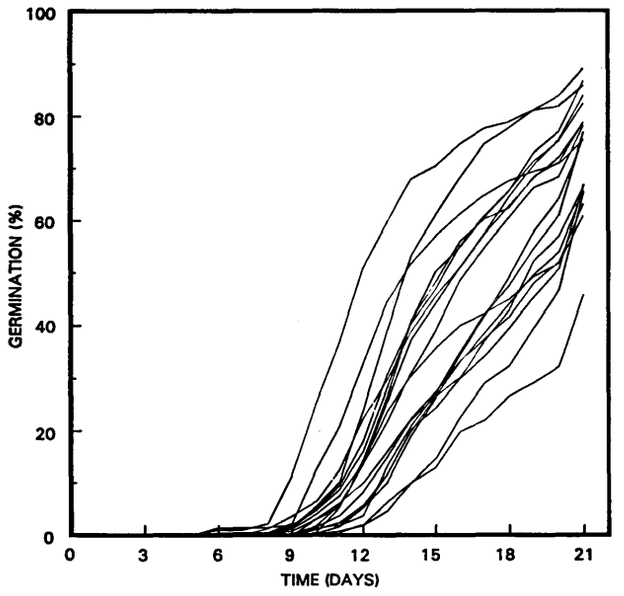

Figure 3. — Germination curves for unsorted-unstratified seeds of 18 Sitka spruce clones.

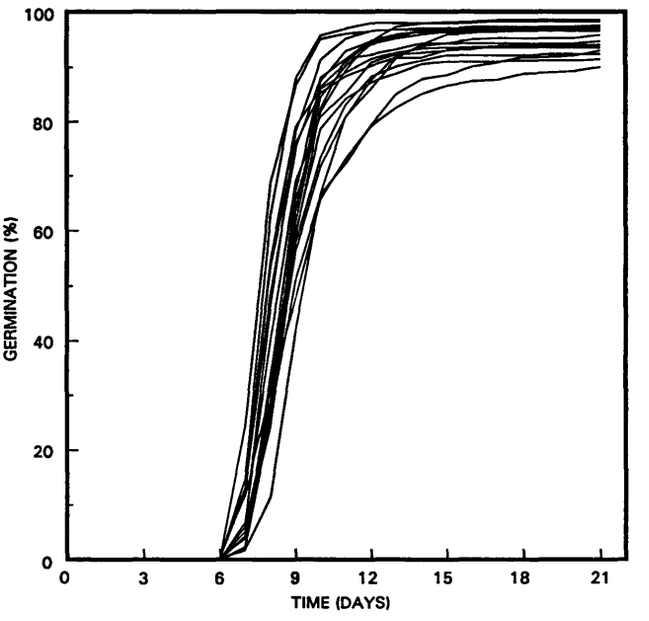

Figure 4. — Germination curves for unsorted-stratified seeds of 18 Sitka spruce clones.

to 5.13% (*Table 4*). However, this small amount of variation in all germination parameters for among seed sizes (except GC) and among clones is highly significant ($P < 0.01$) (*Table 4*). Once again, pretreatment accounted for the largest amount of variation (range: 72.45% to 89.84%) in germination (*Table 4*). To make seed size and clonal effects more discernible, a second, complementary, analysis was conducted separately for unstratified and stratified seeds (*Table 5*). For unstratified seeds, size accounts for a

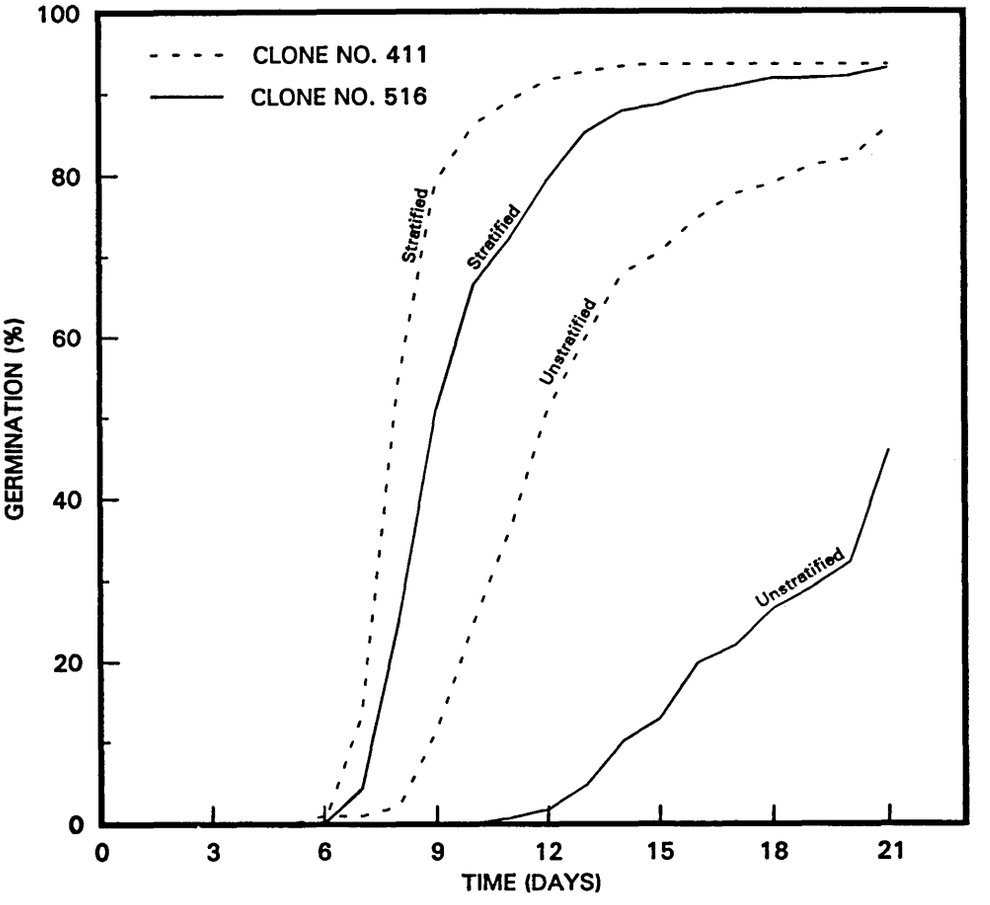

Figure 5. — Differences in germination rate of unstratified and stratified seeds of clone nos. 411 and 516 (low and high dormant seeds, respectively).

Table 4. — Estimation of variance components, and significance level for germination parameters using sorted seeds of 18 Sitka spruce clones.

Source of Variation	df	Expected[1] Mean Squares	Germination Parameters[2]		
			GC	*PV*	*GV*
Seed Size (S)	(S-1) = 2	$\sigma_e^2 + 8\sigma_{sc}^2 + 144\phi_s$	0.09^{ns}	1.39**	0.76**
Clone (C)	(C-1) = 17	$\sigma_e^2 + 24\sigma_c^2$	5.13**	2.94**	3.88**
Pretreatment (P)	(P-1) = 1	$\sigma_e^2 + 12\sigma_{cp}^2 + 216\phi_p$	72.45**	89.84**	83.71**
SxC	(S-1)(C-1) = 34	$\sigma_e^2 + 8\sigma_{sc}^2$	0.36*	0.27**	1.03**
SxP	(S-1)(P-1) = 2	$\sigma_e^2 + 72\phi_{sp}$	0.80**	1.81**	0.83**
CxP	(C-1)(P-1) = 17	$\sigma_e^2 + 12\sigma_{cp}^2$	9.83**	2.14**	6.03**
SxCxP	(S-1)(C-1)(P-1)=34	$\sigma_e^2 + 4\sigma_{scp}^2$	7.16*	0.37**	2.58**
Residual	SCP(N-1)=324	σ_e^2	4.17	1.22	1.17

[1]) ϕ_s = variance among seed sizes; σ_c^2 = variance among clones; ϕ_p = variance between seed pretreatments; σ_{sc}^2 = variance of interaction effect between seed size and clone; ϕ_{sp} = variance of interaction effect between seed size and seed pretreatment; σ_{cp}^2 = variance of interaction effect between clone and seed pretreatment; σ_{scp}^2 = variance of interaction effect among seed size, clone and seed pretreatment; σ_e^2 = variance within clones.

[2]) GC = Germination Capacity, the percentage of seeds that had germinated at the end of the test (Arcsin).
PV = Peak Value, a mathematical expression of the break of a sigmoid curve representing a typical course of germination (no transformation).
GV = Germination Value (Czabator, 1962), (no transformation).

ns) Non significant; *) Significant at $P \leq 0.05$; **) Significant at $P \leq 0.01$.

very small, insignificant, proportion of total variation (range 0.89% to 1.16%) (*Table 5*). The largest proportion, 74%, is due to among-clone variation and is highly significant ($P < 0.01$) (*Table 5*). Although the effect of seed size on germination is not significant, the effect of interaction between clone and seed size is highly significant, indicating that germination parameters of different seed sizes differ among the 18 clones.

For stratified seeds, the effects of both seed size and clone on all germination parameters are highly significant (*Table 5*). This indicates that the effect of seed size is significant for the rapidity of Sitka spruce seed germination. Dunlap and Barnett (1983) found a similar influence of seed size in loblolly pine. Under nursery conditions where the germination environment is more variable than the testing environment, this effect might be considerably larger indicating that longer stratification is significant for reducing the clonal-response differences.

Genetic variation in germination in conifers has been reported to be under strong maternal genetic control

Table 5. — Estimation of variance components and significance level for germination parameters of 18 Sitka spruce clones.

Source of Variation	df	Expected[1] Mean Squares	Unstratified			Stratified		
			[2]GC	PV	GV	GC	PV	GV
Seed Size (S)	(S-1) = 2	$\sigma_e^2 + 4\sigma_{sc}^2 + 72\phi_s$	0.89^{ns}	1.16^{ns}	1.09^{ns}	9.39**	38.50**	11.89**
Clone (C)	(C-1) = 17	$\sigma_e^2 + 12\sigma_c^2$	74.33**	73.75**	74.30**	38.93**	41.89**	56.23**
S × C	(S-1)(C-1) = 34	$\sigma_e^2 + 4\sigma_{sc}^2$	7.01**	5.89**	6.53**	0.00	5.74**	23.82**
Residual	SC(N-1) = 215	σ_e^2	0.18	19.20	18.08	53.69	13.87	8.06

[1]) ϕ_s = variance among seed sizes; σ_c^2 = variance among clones; σ_{sc}^2 = variance of interaction effect between seed size and clone; σ_e^2 = variance within clones.
[2]) GC = Germination Capacity, the percentage of seeds that had germinated at the end of the test (Arcsin).
PV = Peak Value, a mathematical expression of the break of a sigmoid curve representing a typical course of germination no transformation).
GV = Germination Value (Czabator, 1962), (no transformation).
[ns]) Non significant; [**]) Significant at P $\leq$ 0.01.

(Bramlett et al., 1983; El-Kassaby et al., 1992; Hoff, 1987). Germination is influenced by maternal effects in most plants since a major portion of the seed components (seed coat (2n), endosperm (1n), and half of the embryo (1n)) are maternally contributed (Perry, 1976; Ellner, 1986; El-Kassaby et al., 1992). Variation in seed germination was considered to be an adaptation for survival under extreme environmental conditions (Jain, 1982).

Seed-dormancy mechanisms vary among species, so different seed pretreatments are required. Seed dormancy among families within a species has been reported for western white pine (*Pinus monticola* Dougl.) (Hoff, 1987). In his study, Hoff (1987) also found that improvement in germination varied with duration of stratification. In contrast, Heit (1961) concluded that neither stratification nor chemical pretreatment is required for germination of Sitka spruce seeds. However, the present study demonstrates that stratification is essential for uniform germination in this species. A period of stratification of at least 21 days is recommended to reduce the germination differences due, probably, to differential dormancy (*Figure 3* and *Figure 4*).

Correlations between seed size and germination have been reported in species such as *Hyptis suaveolens* (Wulff, (1972), *Pinus strobus* (Spurr, 1944) and *Acacia holosericea* (Hellum, 1990). In contrast, no significant realized gain in favour of large seeds over small seeds was observed in the germination of many other species (Burgar, 1964; Larson, 1963; Ackerman and Gorman, 1969). Therefore, sowing unsorted seeds is recommended to maximize genetic diversity (Hellum, 1976; Lindgren, 1982; Silen and Osterhaus, 1979). The effect of seed size in Sitka spruce is considered small in comparison to the among- and within-clone variation in germination.

Conclusion

In this study, minimal, yet statistically significant, variation in seed weight was observed among Sitka spruce clones; this variation is believed to be under moderate genetic control. When seeds were sorted into small and large sizes, the same variation in seed weight within size classes within clones was observed. Different clones exhibited markedly differing ranges in variation. The major source of variation in germination for unsorted seeds was seed pretreatment. Complementary analyses to remove the effect of pretreatment indicated that all germination parameters studied were under strong genetic control. Seed-size effects were significant for stratified seeds only. Clonal effects were dominant, and accounted for the majority of variation in germination even when seeds had been sized. This study demonstrates that stratification is essential for achieving germination uniformity in Sitka spruce, and that seed size has little operational importance.

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Genetic Variation for Frost Tolerance in A Breeding Population of Eucalyptus nitens

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Abstract

Patterns of genetic variation for frost tolerance were studied in a first-generation breeding population of *Eucalyptus nitens* (Deane and Maiden) Maiden. Winter hardened seedlings from 198 families, representing 5 provenances were found to differ significantly in their frost tolerance at all three tested temperatures (—5.0° C, —6.5° C and —8.0° C). Provenance effects accounted for between 11% (at —5.0° C) and 29% (at —8.0° C) of the total variation. The most frost tolerant provenance was Northern NSW, with Toorongo being the least tolerant. Significant differences were also found between families within provenances and between seedlings within families. Family effects accounted for 14% to 22% of total variation and seedling effects accounted for between 22% and 26% of the total variation. All five provenances were represented in the top seven ranked families. When each provenance was analysed separately, there were significant differences between families but no strong relationship was found with altitude of origin.

Key words: Frost tolerance, genetic variation, *Eucalyptus nitens.*

Introduction

With increasing areas of eucalypt plantation currently being established in temperate regions of the world, there is a need for detailed examination of frost tolerance in

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