Lodgepole Pine and White Spruce Germination: Effects of Stratification and Simulated Aging

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Abstract

The effects of seed pre-treatment (stratification/pre-chilling) and simulated aging on germination parameters (germination capacity, speed and value and peak value) were evaluated for several seedlots originating from seed orchard clones of lodgepole pine (*Pinus contorta* var. *latifolia* DOUGL. ex LOUD.) and white spruce (*Picea glauca* (MOENCH) VOSS). Region of origin and stratification had little effect on white spruce, while stratification enhanced germination speed and completeness of lodgepole pine. Broad-sense heritability for germination parameters ranged from 70 to 97% (unstratified) and from 81 to 96% (stratified) for pine, and from 95 to 97% (unstratified) and from 93 to 97% (stratified) for spruce. Simulated aging (short-term storage at high temperature and relative humidity, approximating the physiological effects of long-term storage) resulted in rapid deterioration of white spruce, with very little germination after six days of aging. Lodgepole pine germination increased during the first several aging treatments relative to the control, but germination capacity decreased following twelve days of aging, and was very low after 18 days. White spruce was non-dormant and responded primarily to moisture conditions, whereas pine was strongly influenced by maternal effects. These results can be incorporated for more efficacious nursery production practices for commercial reforestation seedling production as well as ex-situ gene conservation strategies.

Key words: germination, *Pinus contorta*, *Picea glauca*, simulated aging, dormancy, stratification, broad-sense heritability.

Introduction

Lodgepole pine (*Pinus contorta* var. *latifolia* DOUGL. ex LOUD.) and white spruce (*Picea glauca* [MOENCH] VOSS) are the two predominant species throughout the interior of British Columbia (B.C.) used for reforestation. Currently, 90.5 million, or 45% of total seedlings planted on B.C. public lands were lodgepole pine, while 33% were either pure or a hybrid of white spruce (B.C. MINISTRY OF FORESTS, 2002). With the advent of readily available genetically improved planting stock, increasing areas of interior B.C. are being planted with these two species (BRITISH COLUMBIA MINISTRY OF FORESTS, 2002).

Commercial processing and storage of high-quality seed can have ramifications for the future health and survival of the planting stock. Treatments such as stratification and storage conditions can affect the performance and germinability of seedlots (EDWARDS and EL-KASSABY, 1995). Individual genotypes may have differential responses to these treatments (KUENEMAN, 1983), and it is important to determine both optimal pre-treatment protocols prior to seed germination in order to ensure maximum germination, as well as any potential detrimental effects of long-term seed storage on seed viability and individual genotype representation.

Seeds have varying dormancy mechanisms and a corresponding variety of means to overcome these mechanisms in order to stimulate synchronized germination. It has been hypothesized, based on experiments on excision of embryos and their germination and growth on media, that most conifers do not exhibit physiological dormancy, but have mechanical dormancy that is mainly caused by the seed-coat and/or megagametophyte (SCHNEIDER and GIFFORD, 1994; DOWNIE and BEWLEY, 1996; LEINONEN, 1997; GOSLING, 2000). Specific environmental cues, such as seed coat moisture content, temperature or biochemical changes or a combination of these factors may trigger germination (WANG and BERJAK, 2000). Maximizing efficiency in commercial seed production facilities can only be achieved by elucidating critical factors leading to germination and assessing the normal range of germination parameters that can be expected from seedlots. Stratification (a period of moist chilling prior to seed germination) may stimulate physiological changes in certain genotypes so that germination is more rapid or more uniform (DOWNIE et al., 1998; GOSLING, 2000; WANG and BERJAK, 2000).

White spruce is a boreal species found throughout northern Canada and Alaska. It is typically found in mid- to late-successional forests, reproducing on organic seedbeds. The seeds are minute ($500{,}000 \cdot kg^{-1}$), and require abundant moisture to germinate and grow (NIENSTAEDT and ZASADA, 1990). Spruce seed is highly sensitive to environmental conditions, and seeds deteriorate rapidly. Regeneration is contingent upon annual seedfall, not a stored seed bank (NIENSTAEDT and ZASADA, 1990). Lodgepole pine, on the other hand, is an early seral species which exhibits prolific postfire regeneration. Typically serotinous cones, an adaptation to relatively frequent wildfires, ensure that seeds remain dormant until suitable conditions occur, e.g., a wildfire exposes a mineral seedbed. Seeds can remain viable for many years inside the cones, both on the tree and on the ground (LOTAN and CRITCHFIELD, 1990).

Seeds often deteriorate during storage. Despite periodic viability testing, there is no foolproof means to accurately assay the nature and speed of seed deterioration in storage. One simple and rapid test which has been developed is the simulated aging technique

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(DELOUCHE and BASKIN, 1973). Exposing seeds to short periods of high temperature and humidity is purported to simulate the stress that can impact seeds over long durations of storage. While the quantitative correlation between simulated aging and actual long-term seed storage has not been measured in conifers, very high correlations have been found in agricultural seeds (DELOUCHE and BASKIN, 1973).

The objectives of this study were to quantify the effects of stratification and simulated aging on lodgepole pine and white spruce seed germination and associated genetic parameters, and to evaluate their applicability for operational applications in these two species.

Materials and Methods

Germination

Seed from 21 seed orchard clones (genotypes) were tested for spruce and pine. The clones were grown in two seed orchards in the British Columbia Ministry of Forests Kalamalka Research Station, Vernon, B.C. The spruce clones represented three geographic regions: East Kootenay (southeast), Prince George (central) and Prince Rupert (northwest) with each contributing seven clones while the pine clones were representatives of one breeding zone. Seed were extracted following standard procedures and were stored at 4 °C until further use. Within each germination test (paired germination tests: chilled (stratified) vs. un-chilled (un-stratified)), every clone was represented by four replications of one hundred seeds each. Germination was conducted following the protocols outlined by the International Seed Testing Association (ISTA, 1993). For complete description of the germination test see EDWARDS and EL-KASSABY (1995).

Simulated aging

Two simulated aging trials were conducted for the pine and spruce. Both species were represented by twelve clones (genotypes). The twelve spruce clones represented the three geographic regions listed above with four clones. A similar simulated aging protocol was implemented for both species and was followed by germination tests as outlined in the germination experiment above. The optimum aging temperature for each species was determined following a brief pilot study (data not shown). Pine and spruce seeds were aged at 42 and 40 °C, respectively. Spruce was subjected to seven aging treatments (zero days = control, three days, six, nine, 12, 15, and 18 days) while pine was subjected to eight aging treatments (similar to that of spruce with an additional aging level of 21 days). Aging treatments were organized chronologically so that treatments with the longest aging began first, followed every three days by the next shortest aging treatment. All aging treatments began germination assays on the same date. Unstratified seeds were placed into cold storage prior to germination; stratified seeds were imbibed for 24 hours prior to germination. For each day, the number of germinants (radicle > 5 mm) per tray was counted, and cumulative totals were determined over a 21-day germination test period.

Germination parameters

Germination was quantified using four separate variables based on different portions of the germination curve: germination speed (R_{50}'), the number of days taken for 50 % of living seeds to germinate (THOMSON and EL-KASSABY, 1993); germination capacity (GC), percentage of seeds germinated by the conclusion of the experiment; peak value (PV), mean daily number of germinants of the most vigorous seeds; and germination value (GV), a combined index of germination speed and completeness, equivalent to PV multiplied by mean daily germination over the entire experiment (CZABATOR, 1962).

Statistical analyses

Germination and aging data analyses were conducted using PROC MIXED procedure (SAS INSTITUTE Cary, NC, USA). This technique was developed for complex, untransformed, unbalanced data sets that deviate from the common statistical assumptions of normality and homoscedasticity, thereby facilitating interpretation of actual values. Region (for spruce), treatment and aging were fixed; clone, clone nested within region (for spruce) and replication were random. Components of variance were calculated by SAS using the REML maximum likelihood iterative method. Outlying data was discarded by comparing germination curves: where one replication varied by more than 25 % from the others, it was dropped from the analysis. This was done to remove variation caused by any defective germination trays. Aging treatments were analyzed separately to highlight effects of aging duration on germination parameters. Control and stratified treatments were analyzed together and separately to quantify the effects of pretreatment on germination. Since no spruce seeds germinated after more than 12 days of aging (i.e., reached total kill), only the first five aging treatments were retained in the analysis. The threshold for statistical significance was always $p = 0.05$.

The following additive linear models represent the various analyses for the two species for the germination and aging experiments (*Table 1*). When a term was not statistically significant in the model, the model was compressed then reanalyzed without that term in order more accurately assess the effects of significant parameters on broad-sense heritability (i.e., the proportion of random model variation explained by genetic effects). For example, if region was excluded from the analysis, then that fixed term would not be included as a primary factor and the clone term would then no longer be nested within regions (*Table 1*).

Table 1. – General linear models for analysis of variance of germination and aging experiments.

Species	Equation[1)]
Pine	[1] $y_{tcp} = \mu + T_t + C_c + TC_{tc} + \varepsilon_{(tc)p}$
Spruce	[2] $y_{rtcp} = \mu + R_r + T_t + C(R)_{c(r)} + R^*T_{rt} + TC(R)_{tc(r)} + \varepsilon_{(rtc)p}$
Spruce (no regions)	[3] $y_{tcp} = \mu + T_t + C_c + TC_{tc} + \varepsilon_{(tc)p}$

[1)] y_{tcp} represents germination parameter y, for the t^{th} treatment (T), the c^{th} clone (C), the p^{th} replicate; μ is the grand mean; $C(R)_{c(r)}$ is the c^{th} clone nested within the r^{th} region (R).

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Table 2. – ANOVA models used in analyzing germination and aging for pine and spruce (subscripts and notation as in *Table 1*).

Source	df[1)]	Germination EMS[2)]	Aging EMS
Combined (Unstratified + Stratified)			
Treatment	j-1	$84\,\sigma^2_T + 4\,\sigma^2_{tc} + \sigma^2_\varepsilon$	$48\,\sigma^2_T + 4\,\sigma^2_{tc} + \sigma^2_\varepsilon$
Clone	k-1	$8\,\sigma^2_C + \sigma^2_\varepsilon$	$8\,\sigma^2_C + \sigma^2_\varepsilon$
TxC	(j-1)(k-1)	$4\,\sigma^2_{TC} + \sigma^2_\varepsilon$	$4\,\sigma^2_{TC} + \sigma^2_\varepsilon$
Residual	jk(l-1)	σ^2_ε	σ^2_ε
Unstratified or Stratified treatments individually			
Clone	k-1	$4\,\sigma^2_C + \sigma^2_\varepsilon$	$4\,\sigma^2_C + \sigma^2_\varepsilon$
Residual	k(l-1)	σ^2_ε	σ^2_ε

[1)] For germination j = 2, k = 21, and l = 4; for aging j = 2, k = 12, and l = 4.
[2)] σ is the residual error term.

Results

Germination

Germination courses, represented by cumulative germination over time curves, were highly consistent with no outlying data and thus the analyses were conducted on the complete data set. For spruce, neither regions nor the region by treatment interaction were significant (data not shown), thus the "Region" term was removed from the model and both species' germination data were analyzed using the model presented in *Table 2*. Overall, the stratification treatment was significant ($p < 0.01$) for all germination parameters, for both species (data not shown). However, the effect of stratification on pine germination was marginally stronger than on spruce, shown by the effects on germination parameters when the stratification terms was removed from the analysis by analyzing stratified and unstratified seed separately. This also quantified the impact of genetics on germination parameters, which would otherwise be masked by strong treatment (stratification) effects.

Pine

Stratification significantly increased the mean values and heritabilities of all germination parameters. The most pronounced effects were on GV, where the mean increased from 12 to 47, and on PV where the mean increased from four to 14. Clones differed from one another for the various dependent variables, although differences were not systematic. Stratification facilitated more rapid and uniform germination of seeds, and clones reached peak germination values more rapidly (*Figure 1A*, *B*). The variation among clones in the control (unstratified) treatment implies that clones are extremely variable in their dormancy breaking requirements.

Table 3. – Pine germination parameters mean values, standard errors and their heritabilities (h^2, %) estimates (different superscripts indicate treatment means are significantly different, Tukey's HSD).

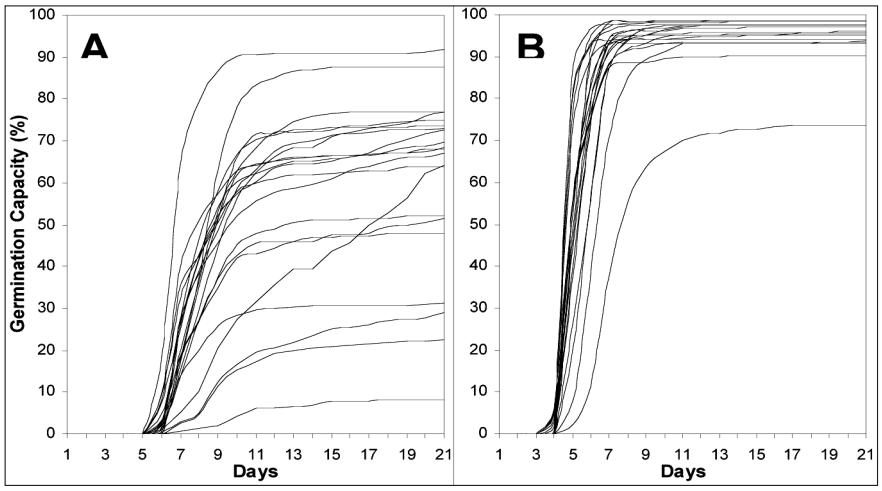
Parameter	Combined	Unstratified			Stratified		
	h^2	Mean	SE	h^2	Mean	SE	h^2
R_{50}'	21.27	8.79^a	0.34	70.42	5.11^b	0.34	95.91
GC	32.77	68.86^a	3.45	97.31	94.86^b	3.45	81.48
PV	35.91	4.18^a	0.51	84.96	13.76^b	0.51	88.09
GV	39.19	11.60^a	1.88	89.12	46.93^b	1.88	87.38

For all germination parameters, heritability more than doubled when the effect of treatments was removed and the data were analyzed separately (*Table 3*). This effect was caused by different partitioning of model variation where stratification (a fixed effect) masked the effect of clone (a random effect) in the combined analysis, or effects were confounded by their interaction.

Treatment was by far the dominant factor, determined by the large effects on heritability when it was removed from the model (*Equation [1]*, *Table 3*). When stratified and unstratified treatments were analyzed separately, the variation attributed to clone ranged from 93 to 97% in unstratified seeds, and from 93 to 96% in stratified seeds for the four germination parameters. Heritabilities were relatively uniform for germination parameters between stratified and control treatments (*Table 3*).

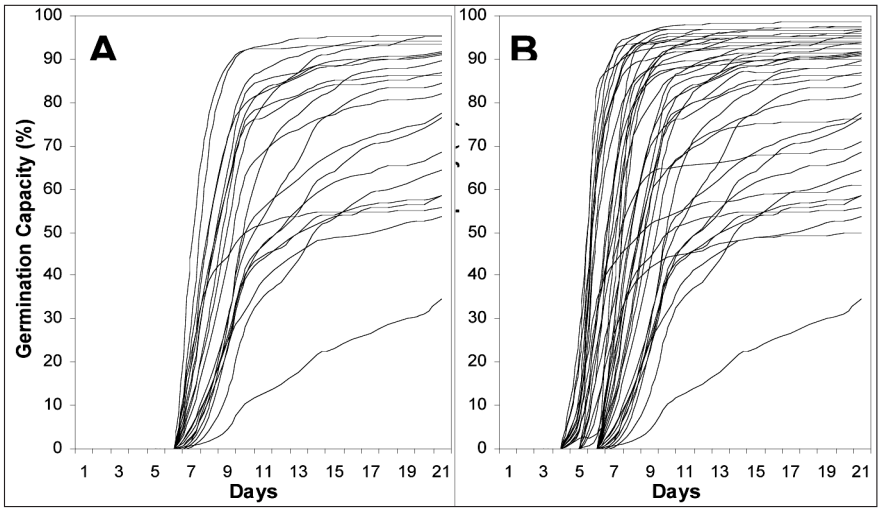
Spruce

Stratification was statistically significant in the model for all germination parameters (*Equation [2]*, *Table 2*),



Figures 1A (unstratified) and B (stratified). – Effects of stratification treatment on germination capacity of pine clones.

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Figures 2A (unstratified) and B (stratified). – Effects of stratification on germination capacity of spruce clones.

although its effects on GC were not as pronounced as for pine (*Figure 2A*, *B*). Germination of stratified seed was generally more complete and uniform, and tended to begin slightly earlier, although at least one clone had poorer germination after stratification (*Figure 2A*, *B*). The region term was not significant, even when stratified and unstratified treatments were analyzed separately (data not shown), nor was the region by stratification interaction significant: the data were reanalyzed without this term, and results presented are based on this modified model (*Equation [3]*, *Table 2*). The clonal proportion of variation (h^2) for all germination parameters was very high when treatment effects were excluded by analyzing stratified and control seed separately (*Table 4*). The relative increase in heritability when treatments were analyzed separately was not as pronounced in spruce as in pine.

Table 4. – Spruce germination parameters mean values, standard errors and their heritability (h^2, %) estimates (different superscripts indicate treatment means are significantly different, Tukey's HSD).

Parameter	Combined	Unstratified			Stratified		
	h^2	Mean	SE	h^2	Mean	SE	h^2
R_{50}'	52.42	8.94[a]	0.23	94.66	6.38[b]	0.23	96.90
GC	53.86	77.61[a]	3.35	94.71	88.83[b]	3.35	92.63
PV	66.16	6.05[a]	0.53	96.50	10.14[b]	0.53	93.71
GV	66.76	23.98[a]	3.00	96.66	44.22[b]	3.00	94.98

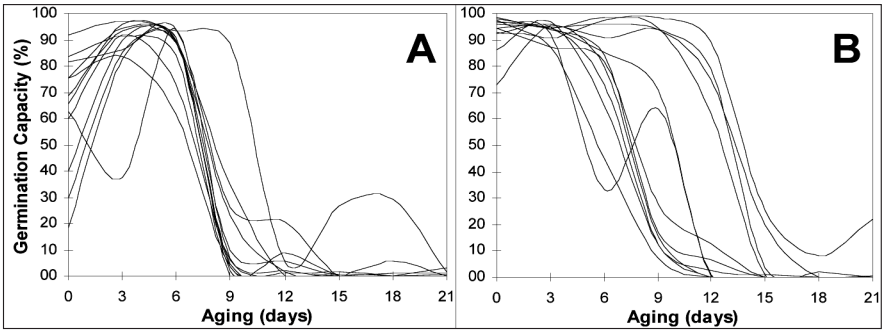
Simulated aging

Each level of aging was analyzed separately in order to highlight effects which may be obscured by the complex experimental design. The relative effects at each level of simulated aging could then be assessed separately, instead of examining overall effects of the aging treatments. Each species responded differently to aging treatments, and the interactions between aging and stratification levels also were significant in many cases. Pine appeared to be less detrimentally affected by aging (*Figure 3A*, *B*), and even appeared to beneficial relative to the control, while spruce germination declined rapidly as aging treatments progressed (*Figure 4A*, *B*).

Pine

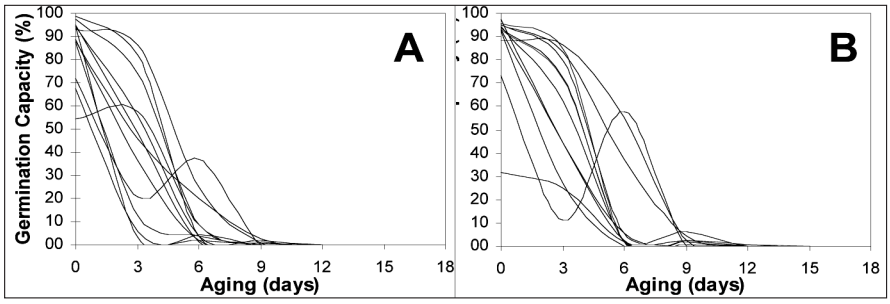
Stratification had a statistically significant effect following zero, three, nine and 12 days of simulated aging (*Table 5*). The impacts of aging on R_{50}' varied somewhat from the other parameters: there was no significant effect of stratification after more than six days of simulated aging.

Germination parameters did not decline noticeably following three days of aging, and parameters for unstratified treatments tended to increase following three and six days of aging. Stratified treatments tend-



Figures 3A (unstratified) and B (stratified). – Effects of simulated aging and stratification on pine clone germination.

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Figures 4A (unstratified) and B (stratified). – Effects of simulated aging and stratification on spruce clone germination.

ed to decline after three days of aging (*Table 5*). Unstratified treatments experienced more gradual declines in the mean values of germination parameters following aging treatments, while the stratified treatments dropped sharply after six days, except for R_{50}', which was more stable (*Table 5*).

Spruce

Stratification combined with aging did not significantly impact the percentage of seed germinated (GC) for spruce clones (*Figure 4A*, *B*). This effect was primarily due to the strong interaction between stratification and clone, which accounted for nearly all of the variation in all parameters in the combined model for control seed; values then declined to 30–50% after three days of aging, increased to 64–80% (except R_{50}', 13%) after six days, and subsequently diminished (data not shown). The lower ranks of spruce clones were negatively impacted: some clones germinated more slowly and less completely. The upper ranks of clones experienced little change following stratification, although stratified seed were still able to germinate more consistently after three days of aging, declining to almost no germination after six days (*Figure 4B*). The mean GC for all clones revealed a 10% increase in germination after three days of simulated aging. No seed germinated after 12 days of aging, so only the first five levels of simulated aging were retained in the analysis (*Table 6*).

No consistent regional differentiation was found, as the same regions did not always differ from each other. Regions were only statistically significant in one treatment for one aging level, so the model was compressed to exclude this term in subsequent analyses. Stratification was not statistically significant for any germination parameters, with the exception of R_{50}' after 12 days of aging. When treatment levels were reanalyzed after excluding the region term, stratification for combined stratified and unstratified treatments was only significant after 12 days of simulated aging. This implies that stratification did not have a pronounced effect on spruce germination. The interaction between stratification and clone, however, accounted for most of the variation attributed to random model factors for the first two aging levels.

All mean values of germination parameters for spruce declined following even three days of simulated aging (relative to the control, zero days of aging), except for R_{50}', which increased slightly up to 6 days of aging. GC showed the most precipitous decline, followed by PV. There was generally less than 10% difference between stratified and unstratified treatments, although statistically the differences were not significant (*Table 6*).

Discussion

As anticipated from their differing physiologies and life histories, spruce and pine had different responses to the stratification and aging treatments, and among-clone variance for germination parameters were partitioned differently among treatment and genetic factors. Spruce seeds deteriorated rapidly under simulated aging conditions: following three days of aging, germination speed and quantity dropped off sharply. This may be analogous to reported viability losses following one to two years in storage (NIENSTAEDT and ZASADA, 1990). Pine seeds were more robust: under the same conditions, pine seeds continued to germinate in similar proportions and speeds up to nine days of aging; simulated aging up to nine days even increased germination in some clones.

Stratification did not impact overall germination percentage of spruce seeds, but it did initiate more rapid germination and reduce variability among clones. This response likely reflects the variability in dormancy found among individuals and natural populations (NIENSTAEDT and ZASADA, 1990; DOWNIE and BEWLEY, 1996). Stratification did enhance pine germination of unaged (control) seed, and simulated deterioration of pine seed subject to aging. While LOTAN and CRITCHFIELD (1990) maintained that stratification is generally not required for lodgepole pine germination, there were substantial benefits in terms of germination completeness, uniformity and speed which could have applications for commercial seedling production and testing.

Individual genotypes did have different responses to stratification and aging treatments, as well as their interaction, as has been found in other studies (KUENEMAN, 1983; CHAISURISRI et al., 1993; EDWARDS and EL-KASSABY, 1995; EL-KASSABY and EDWARDS, 1998). In the case of spruce, clonal differences were the most significant factor, as there were no significant differences among regions for any germination parameter. Most clonal (among genotypes) differences were indistinguishable following six days of simulated aging in spruce and 12 days in pine. Some clones continued to germinate after longer aging treatments. Germination response to each aging level was not consistent among clones, which likely reflects inherent variability among clones, which

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Table 5. – Pine germination parameters mean values and their standard errors as affected by the aging treatment (different superscripts indicate treatment means are significantly different, Tukey's HSD).

Aging	Parameter	Unstratified		Stratified	
(days)		Mean	SE	Mean	SE
0	R_{50}'	8.09[a]	0.22	5.59[b]	0.22
0	GC	62.83[a]	4.81	92.96[b]	4.81
0	PV	5.03[a]	0.79	13.03[b]	0.79
0	GV	17.24[a]	3.99	58.48[b]	3.99
3	R_{50}'	7.84[a]	0.22	5.61[b]	0.22
3	GC	85.75[a]	3.32	93.16[a]	3.31
3	PV	8.19[a]	0.49	12.47[b]	0.49
3	GV	34.76[a]	2.68	55.54[b]	2.66
6	R_{50}'	7.70[a]	0.35	6.97[b]	0.35
6	GC	86.67[a]	4.62	77.53[a]	4.63
6	PV	8.40[a]	0.96	8.85[a]	0.96
6	GV	35.31[a]	5.17	36.40[a]	5.17
9	R_{50}'	7.57[a]	0.97	9.34[a]	0.97
9	GC	17.30[a]	9.34	50.56[b]	9.34
9	PV	1.27[a]	1.20	5.53[b]	1.20
9	GV	3.31[a]	5.72	22.65[b]	5.71
12	R_{50}'	5.96[a]	1.36	6.70[a]	1.34
12	GC	3.72[a]	7.63	27.42[b]	7.62
12	PV	0.26[a]	1.02	3.43[b]	1.02
12	GV	0.25[a]	4.05	12.77[b]	4.04
15	R_{50}'	1.63[a]	0.97	4.06[a]	0.97
15	GC	2.46[a]	2.37	4.34[a]	2.36
15	PV	0.20[a]	0.21	0.39[a]	0.21
15	GV	0.27[a]	0.30	0.46[a]	0.30
18	R_{50}'	2.51[a]	1.30	1.50[a]	1.29
18	GC	2.97[a]	1.76	0.85[a]	1.76
18	PV	0.15[a]	0.09	0.05[a]	0.09
18	GV	0.21[a]	0.14	0.02[a]	0.14
21	R_{50}'	2.54[a]	1.05	1.58[a]	1.04
21	GC	0.55[a]	1.31	1.94[a]	1.31
21	PV	0.03[a]	0.07	0.10[a]	0.07
21	GV	0.01[a]	0.07	0.10[a]	0.07

Table 6. – Spruce germination parameters mean values and their standard errors as affected by the aging treatment (different superscripts indicate treatment means are significantly different, Tukey's HSD).

Aging	Parameter	Unstratified		Stratified	
(days)		Mean	SE	Mean	SE
0	R_{50}'	7.6[a]	0.56	8.4[a]	0.56
0	GC	85.8[a]	4.73	86.9[a]	4.73
0	PV	8.9[a]	0.94	7.6[a]	0.94
0	GV	38.8[a]	4.84	33.3[a]	4.84
3	R_{50}'	8.1[a]	0.52	8.7[a]	0.52
3	GC	43.8[a]	8.00	57.5[a]	7.97
3	PV	3.9[a]	0.78	4.7[a]	0.77
3	GV	12.3[a]	3.45	15.7[a]	3.43
6	R_{50}'	9.1[a]	0.98	7.9[a]	1.00
6	GC	9.9[a]	4.98	14.3[a]	4.98
6	PV	0.5[a]	0.29	0.8[a]	0.29
6	GV	0.6[a]	0.77	1.9[a]	0.77
9	R_{50}'	3.4[a]	1.02	5.1[a]	1.03
9	GC	0.7[a]	0.44	1.8[a]	0.45
9	PV	4.4×10^{-2}[a]	2.3×10^{-2}	0.1[a]	2.4×10^{-2}
9	GV	1.1×10^{-3}[a]	9.9×10^{-3}	0.03[a]	9.9×10^{-3}
12	R_{50}'	0.0[a]	0.60	1.99[b]	0.60
12	GC	0.0[a]	4.7×10^{-2}	0.1[a]	4.7×10^{-2}
12	PV	0.0[a]	2.4×10^{-3}	7.5×10^{-3}[a]	2.4×10^{-3}
12	GV	0.0[a]	2.1×10^{-4}	5.7×10^{-3}[a]	2.1×10^{-4}

is high in the Pinaceae (Lotan and Critchfield, 1990; Nienstaedt and Zasada, 1990).

Germination parameters had high heritability when the effects of treatment (stratification) were removed by analyzing each treatment separately. Spruce seeds had decreasing heritability for all germination parameters and least-squares means of those parameters as aging duration increased; three days of aging did not impact stratified seed as much as unstratified seed. Stratification did not significantly affect these results. This is likely caused by a low level of dormancy in the seed tested, which would also account for its inability to withstand physiological stress caused by aging treatments.

Interestingly, pine had a completely different response, both in terms of mean values for germination parameters and associated heritabilities when subjected to stratification and aging treatments. The mean values for most germination parameters of stratified seed increased following three and six days of simulated aging. Unstratified seed either maintained the same values as the control (no aging) for three to six days, or gradually decreased.

The increase in germination following the first several simulated aging levels in pine is attributable to the increased moisture content of seeds and raised temperatures increasing metabolic activity (Schneider and Gifford, 1994). This effect did not occur in spruce, which has highly variable dormancy, or may even lack dormancy (Downie and Bewley, 1996, 2000; Nienstaedt and Zasada, 1990). Dormancy in white spruce has been found to vary across trees, collection years, populations, and even among seeds produced from the same tree (Caron et al., 1993; Downie et al., 1998).

The major barrier to germination of white spruce is the physical resistance of the testa, and also to a lesser degree, the megagametophyte, reflecting a strong maternal influence on germination (Downie and Bewley, 1996). Most of the clones tested in this experiment showed no or low seed dormancy, as revealed by the lack of increased germination following stratification, although there was some variation across locations. Pine did exhibit dormancy, although germination is subject to a complex series of physiological and metabolic changes in addition to the moistening of the seed coat. Maternal effects on germination are strong in

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conifers, since the seed coat and megagametophyte are composed entirely of maternal tissue; the paternal genotype is only expressed as one half of the embryonic diploid genome, or 20% of the genomic components of the seed (EL-KASSABY et al., 1993). Responses to various treatments impacting germination can therefore largely be estimated based on maternal characteristics, if these are known.

Based on these results, seedling nursery managers may be able to recover 92 to 93% of early season lodgepole pine seedling losses (based on germination capacity of unaged, prestratified seeds) by subjecting them to three to six days of simulated aging prior to germination. This technique provides a short cut to production of vigorous seedlings without the need for lengthy stratification treatments (CHAISURISRI et al., 1993), although performance is not as uniform across seedlots as for prestratified seed (*Figure 3A*, *B*). Prestratified seed is more vigorous (higher germination parameter values) than unstratified, aged seed, but the inherent time and labour savings may make a slightly lower germination percentage and speed an expedient compromise for commercial seedling producers. The results of this study do not commend the use of simlulated aging for white spruce production, although stratification would increase consistency of germination parameters among families, thereby ensuring more complete representation of selected genotypes in the production population.

Conclusions

Dormancy was overcome largely by stratification in pine, but made no difference for spruce. Simulated aging at high temperature and humidity caused a rapid decline in spruce viability (after six days of aging), but similar effects did not occur until after nine to 12 days in pine. Individual genotypes had differing responses for all germination parameters, and genotype by treatment interaction accounted for a large proportion of model variance. In spruce, those differences were not influenced by area of origin. These results are determined by the differing ecophysiological habits of these species. Pine has a thicker seed coat that can withstand more severe environmental conditions, and seeds of this pioneer species can often lie dormant within unopened serotinous cones for years, whereas spruce seed, used for this experiment, had only mild to no dormancy. White spruce has thin seed coats and seeds typically germinate on organic soils soon after heat sums are reached in its boreal habitat. Moisture imbibition is the major factor responsible for white spruce seed coat weakening and subsequent radicle emergence, while pine seeds must undergo more complex physiological changes subsequent to meeting chilling requirements and heat sums.

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