



Cone and Seed Improvement Program BCMof Tree Seed Centre

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Differences in Seed and Seedling Attributes Between Select (orchard produced) and Standard (wild stand) Seedlots

The topic I will attempt to cover is one that has received a great deal of attention, but has persistently resulted in contrary conclusions on whether differences exist between select and standard seed sources. I will mainly discuss differences in seed attributes, but some individuals have forwarded information on seedling performance and I will also present this data. I would like to initially discuss a few concepts before proceeding with a discussion of evidence available in the literature and new data.

When we speak of differences, we are referring to a specific trait and this trait can be something tangible like seed size (in mm or seeds per gram, for example) or something less tangible like seed dormancy. The trait can be thought of as an expression of the genes that an organism possesses as well as the environment in which it is exposed to. The phenotype (P) of an organism is the 'observable' characteristics of an organism and is a product of the influences of genes (G), the environment (E) and possibly an interaction between the genes and the environment (G * E):

$$P = G + E + G * E$$

Most attributes have some degree of genetic control and the ratio between amount of variability accounted for by genes (G) relative to total variation (G + E + G * E) is referred to as the heritability of a character. Heritability estimates are useful as they indicate to what degree genetics or the environmental conditions, which the organism encounters, will influence a character. For example, a trait with a heritability of 0.8 is considered to be under strong genetic control and 80% of the variation in the phenotype is due to genetics. A trait with a heritability of 0.2 will have weak genetic control and will have 80% of the variability explained by the environment and the G * E interaction. Traits with low heritabilities are largely influenced by the environmental conditions applied to them during formation or expression. This is a very simplified view of heritability, but it should be sufficient for an appreciation of this discussion.

My second tangent refers to 'statistically significant' as it turns up in the literature. This return to STATS 101 may be painful, but important in the use of results from research in an operational setting. Significance is usually describing statistical significance often specified by the value of $\alpha = \infty$. This is the probability of incorrectly declaring when responses or attributes (i.e. seed size) are different when the difference is actually due to chance. The alpha level is almost always set at 0.05 or 5% by default and information deemed not significant is often not published, resulting in less information available to make decisions with. Problems with statistical significance are that 1) they do not specifically take into account attribute 'value', so that significant differences may have no practical (operational) value or vice versa and 2) the level of 0.05 is conservative and does not allow readers to introduce their own risk assessment attitude. The ideas for this concept come from a paper by Marini (1999) and his example sheds light on a practical use of statistics: "as an extension specialist I am willing to recommend a new

inexpensive practice that increases yield by 15% even when there is a 20% probability that the yield increase was not due to the new practice". This may seem like statistical nonsense, but if you are wanting to integrate the results of trial work in your operations it is beneficial to look at the details of the research rather than the abstract to decide what is applicable to your situation. For research results to be implementable we need movement from researchers to make their research more practical, but practitioners can benefit by better understanding the jargon of scientists which includes a frustrating language called statistics. You may want a black and white answer on whether a new practice is beneficial or cost-effective, but few novel practices will be so clear-cut. Increased application of your grey matter in differentiating between the good, bad and ugly in research (apologies to Chris Hawkins) will allow you to better fine-tune your facility and its practices. I'll move on to the actual topic of my talk after pointing out some 'things' you should look at when trying to incorporate the results of research into your facility.

- 1) What is the sample size? How many seedlots were used? How are the origins of these seedlots distributed? How many seeds or seedlings were used in each treatment?
- 2) Are the methods used equivalent to what you are currently doing? Results on bareroot seedling growth may have little practical value to greenhouse grown crops.
- 3) Results from angiosperm species may have no relevance to conifer seedling production. How close are the species? I generally would accept data on Scots pine and Norway spruce to be applicable to lodgepole pine and white spruce, respectively, but would not try to extend the results to *Abies* spp., for example, without further testing.

I have divided the remainder of my talk into sections, which illustrate environmental, genetic and phenotypic differences between select and standard seed, briefly discuss the provided seedling information and provide a brief discussion of the importance of these differences.

Environmental Differences

I would like to first present what I perceive to be the differences between select and standard seed in terms of the seed production environment. The seed orchard environment may be quite different from the natural habitat of a species and the reproductive biology may be impacted resulting in poor seed set and/or germination. A good example of this is yellow-cedar which has an average **standard** germination capacity (GC) of 35%, but an average **select** GC of 8%.

Yellow-cedar seed orchards are generally not in areas where yellow-cedar naturally occurs, but in areas considered good for cone and seed production (i.e. Saanich peninsula). The mechanism for this difference is unclear, but probably relates to interactions between the deep dormancy and the reproductive plasticity (El-Kassaby 1995) found in this species. Heritabilities for germination parameters are also lower than other species studied (El-Kassaby *et al.* 1993) corroborating the importance of the environment. Tree improvement in yellow-cedar is continuing, but with vegetative propagation as the main system of delivery to obtain sufficient quantities of propagules and have much higher genetic gain than with seedlings.

Orchard location has also been implicated in the relatively poor seed set found with Lodgepole pine in the Vernon area. The hot, dry area, which has no lodgepole pine naturally occurring, produces abundant cones, but seed set has been disappointing. Due to the importance of lodgepole pine to the provincial planting program and the shortage of select seed an extensive set of studies looking at reproductive biology and *Leptoglossus* spp. damage in the Vernon area have been initiated. Initial comments on reproductive problems suggest that the very low humidity at pollination in Vernon is reducing the size of the pollen drop and causing premature withering of

the micropylar arms greatly reducing the amount of pollen making contact with the ovule (John Owens pers. comm.).

The seed orchard environment has attracted a great deal of attention in Scandinavia as studies showed the origin of seed development influenced the adaptive characteristics of seedlings. The persistent effect that the environment during seed development has on performance has been termed 'after-effects'. Johnsen *et al.* (1996) state 'results indicate that some stage in reproduction during female flowering, such as female meiosis, pollen tube growth, fertilization, early embryogenesis and embryo competition may be sensitive to temperature and/or photoperiodic signals which can be transmitted to the progeny'. The suspected explanation is that the 'new' environment activates a regulatory mechanism affecting the genes controlling adaptive traits (Johnsen *et al.* 1996). A **possible** consequence of this relationship is that a warm seed year with early flowering could be less hardy than seed produced in a cool year with later flowering (Johnsen & Skrøppa 1996).

In British Columbia, after-effects have been found in white spruce families for germination traits, number of needle primordia, height and frost hardiness, although the after-effects for height diminished in the second field season (Stoehr *et al.* 1998). In Douglas-fir, the use of isolation bags for controlled crossing resulted in an increase in seed weight by 10%, presumably by changing the microclimate around the developing cone (Sorenson & Campbell 1985) illustrating a non-geographic environmental influence on seed attributes. The impact of after-effects is an area that requires further work to ensure the adaptability of seed produced from seed orchards. Currently the BCMOF Research branch is continuing to investigate after-effects in interior spruce.

Family processing was performed on the same half-sib families (open-pollinated collections from the same clone) in consecutive years for coastal Douglas-fir, interior spruce, and interior lodgepole pine. The year-to-year variability in seed size for the same family was quite large (Figure 1). Since we are dealing with families and seed attributes which are mainly under maternal (*mother plant*) control (El-Kassaby *et al.* 1993) the variability in seed size is probably a result of the environmental conditions occurring during cone and seed development. This year-to-year variation cannot be ignored and in some cases may be greater than the variation between families in any one year.

Variability was also observed in the degree of dormancy exhibited by families in different years. Dormancy will be quantified using the results of a soak-only (W1 test) and a soak and stratify test (G20 for lodgepole pine). The equation used to quantify dormancy is:

$$\text{Dormancy} = (\text{Strat. result} / \text{Soak result}) - 1 * 100$$

For interior lodgepole pine the degree of dormancy varied from year-to-year and the pattern was not consistent across families. Some families were more dormant in 1996 while others more dormant in 1997 and this is one example of a G*E interaction – families not performing consistently across different environments, in this case the environmental conditions provided in two consecutive years. (Figure 2).

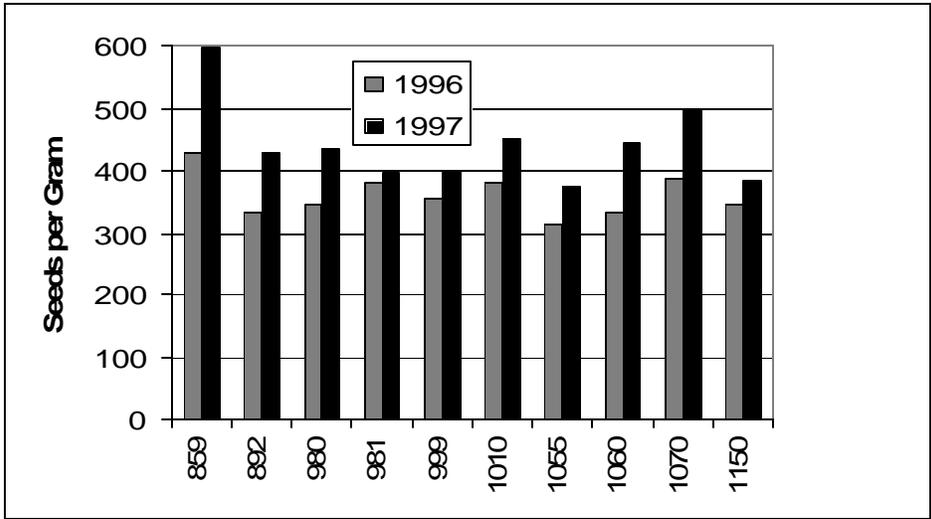


Figure 1. Variation in seeds per gram for family seedlots of interior spruce (Sx) produced in 1996 and 1997.

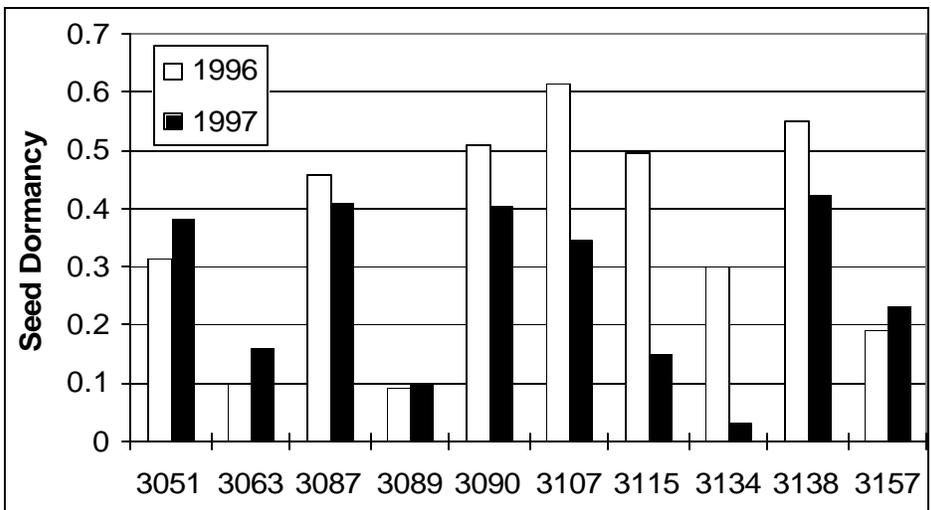


Figure 2. Variation in dormancy for family seedlots of interior lodgepole pine (Pli) produced in 1996 and 1997.

In a review of a wide variety of angiosperm species it was found that the growing conditions of the parent plant might affect the degree of seed dormancy. Lower dormancy was associated with high temperatures, short days, red light, drought and high nitrogen levels during seed development (Fenner 1991). Although these associations have not been confirmed with conifers it provides a hint of areas to explore in better understanding after-effects and their causes.

Genetic Differences

Select seed is produced from parent trees that have been selected for superior characteristics. The evaluation of superiority, or determination of whether the superior tree is a result of good genetics or a good environment, is accomplished through progeny tests which track the performance of a particular tree, or its offspring, across a wide range of environmental conditions. The main

character of interest is volume growth, but pest resistance is also very important for some species. Several copies of each selected parent are grafted and positioned in the orchard to try and minimize self-pollination. There has been some work on the genetic control of germination patterns and these will be discussed below with an emphasis on BC species, although other species have also received a great deal of attention (i.e. pines of the Southern US)

In studies on Sitka spruce it was determined that seed weight had a relatively low heritability (0.36) indicating only 36% of the variation in seed weight is explained by genetics. Germination variables had heritabilities of between 0.74 to 0.78 for GC, germination value (GV) and peak value (PV) as an estimate of germination rate, of stratified seed (Chaisurrisri *et al.* 1992). When Sitka spruce seed was sorted into two classes (> and < 1.41 mm) using a mesh screen there was no impact of seed size on 8-month old seedling height, diameter, shoot and root dry-weight or the shoot-root ratio (Chaisurrisri *et al.* 1994). These results indicate that sizing is not a 'worthwhile' practice in Sitka spruce, at least with the two size classes examined in the studies above.

In Douglas-fir, heritability estimates for GC, GV and PV ranged from 0.91 to 0.93 indicating a very strong genetic component to these variables. No significant correlations between seed weight and GC, PV or GV were found in coastal Douglas-fir from British Columbia (El-Kassaby *et al.* 1992). In coastal Douglas-fir from Oregon it was shown that families differed significantly in seed weight, total percent emergence and rate of emergence (under bareroot conditions). Correlations of emergence with seed weight were low and correlations between seed weight and height diminished from year one to two in the nursery (St. Clair and Adams 1991).

In a study on Interior spruce (*Picea glauca X engelmannii* Perry ex Engelm.) seven half sib families were sized into four fractions (<1.37 mm; 1.37 to 1.54mm; 1.55 to 1.73 mm; and > 1.73 mm). As can be seen in Figures 3 and 4, family 859 appears quite different from the remaining families. When this family is included in the analysis the family term accounts for 71% of the variation in GC and 61% for PV, while the effect of seed size accounts for 7% of the variation in GC and 20% for PV. When family 859 was excluded from the analysis the amount of variability accounted for by family was only 2% for GC and 42% for PV, while the effect of seed size was now 53% for GC and 36% for PV. Sampling of genotypes is important and one 'aberrant' clone can distort the results (especially with small sample sizes). As we move more into family processing it becomes obvious that aberrant clones may not be that rare and tough decisions will need to be made on whether to use this clone in a seedlot and/or the orchard based on its relatively poor germination characteristics.

Whether family 859 was included or excluded the smallest seeds (<1.37 mm) had a significantly lower germination capacity than the other fractions (\approx 6%). The four fractions were not significantly different in PV, but the trend was for the larger seeds to germinate fastest (Figure 4). It may be possible to remove the smallest seeds and obtain a more uniform crop without losing diversity as this fraction only accounted for between 0.2 and 3.9% of each family. It should be emphasized that the removal of seed from within a family (the smallest seeds) is much different than the possible removal of families through inadvertent selection through differential germination, thinning or culling (El-Kassaby & Thompson 1996).

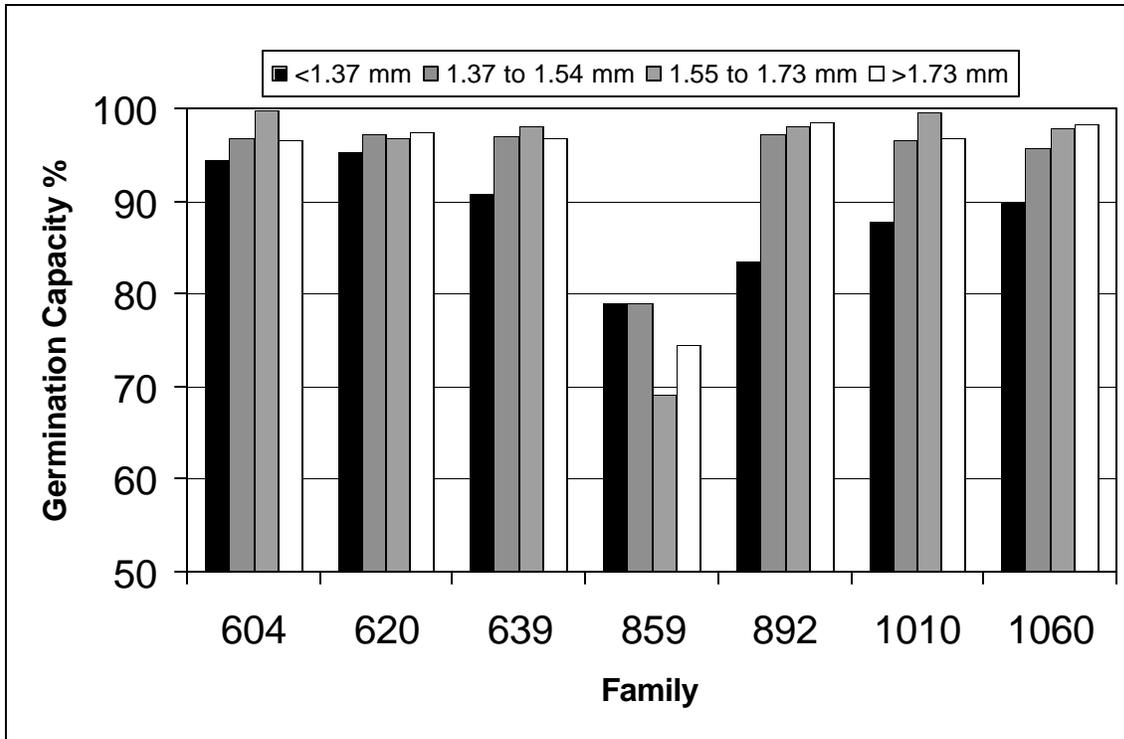


Figure 3. The germination capacity of seven half-sib families of interior spruce (Sx) sized into four fractions based on seed size (Perkins 1998).

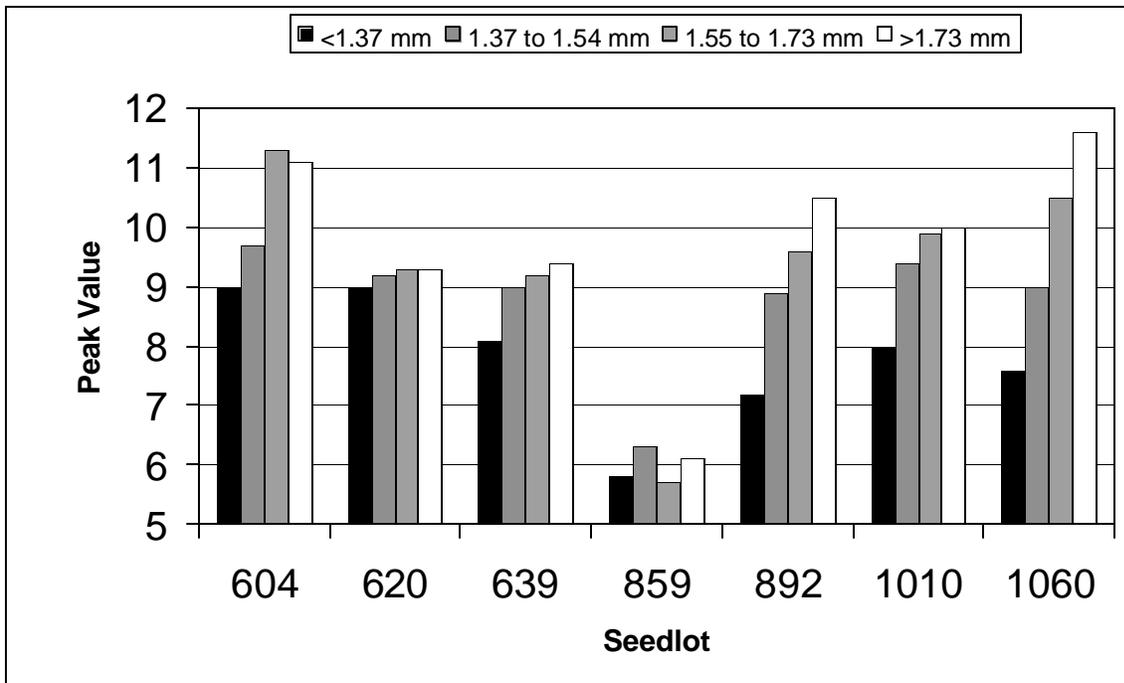


Figure 4. The peak value of seven half-sib families of interior spruce sized into four fractions based on seed size (Perkins 1998)

Phenotypic Differences

This section will discuss phenotypic differences as the proportion of the genetic and environmental influence on a character is not clear. This will revolve more around operational type data, which generally provides a large sample size for a comparison between select and standard seed. Three main characters are expressed in Table 1 illustrating differences in seeds per gram (SPG), GC and PV for all species with productive tree improvement programs in BC.

The most striking difference in seed size appears to be between species in the Cupressaceae (Cw and Yc) and all others in the Pinaceae. A general overall estimate, for the Pinaceae, is that select seed is 15% heavier than standard seed. There appeared to be no practical difference between select and standard seed size for western redcedar and yellow-cedar. I will discuss seeds per gram in more detail below for the four main reforestation species in BC.

Overall, differences in the Pinaceae for GC were practically non-existent, although for coastal Douglas-fir the standard seed has, on average, a 5% advantage. No average is presented for germination parameters in the Cupressaceae as the species differ so widely. This is mainly due to the poor performance of select yellow-cedar seed as was discussed under Environmental Differences. Western red-cedar also appears to have a greater GC from standard seed. Differences in germination rate (PV) were not large and this variable does not seem easily amenable to the adjustment of nursery practices (i.e. other factors – stock type, sowing date, client – are higher priorities for consolidation of requests).

Table 1. Differences in seeds per gram (SPG)[numbers in brackets indicate # of years involved in average], germination capacity (GC) and peak value between select (A) and standard (B) class seed.

Species ¹	Seed per Gram			Germination Capacity		Peak Value	
	SPG A	SPG B	SPG B/A	GC A	GC B	PV A	PV B
Sx	397 [12]	473 [11]	1.19	90	91	7.5	8.8
Pli	264 [13]	343 [13]	1.30	95	93	12.2	12.4
Fdc	85 [13]	97 [8]	1.14	89	94	8.0	10.1
Hw	446 [13]	535 [11]	1.20	92	91	6.1	6.2
SS	397 [12]	425 [9]	1.07	93	93	8.1	8.6
Pw	48 [10]	57 [11]	1.19	89	85	8.5	7.9
Sxs	468 [2]	420 [8]	0.90	87	90	8.2	8.9
Lw	228 [1]	278 [9]	1.22	89	89	9.9	10.6
<i>Pinaceae</i>			1.15	90.5	90.8	8.6	9.2
Yc	231 [4]	220 [9]	0.95	8	35	0.0	2.4
Cw	781 [11]	780 [11]	1.00	78	85	7.2	6.9
<i>Cupressaceae</i>			0.98				

¹ Cw=western redcedar; Fdc=coastal Douglas-fir; Fdi=interior Douglas-fir; Hw=western hemlock; Lw=western larch; ; Pli=interior lodgepole pine; Pw=western white pine; SS=Sitka spruce; Sx=interior spruce; SxS=Sitka X interior spruce hybrid; and Yc=yellow-cedar.

For our four main reforestation species in BC (Pli, Sx, Fdc and Cw) the Seeds per gram (SPG) figures were adjusted for differences in purity and moisture content. The SPG is a measure that uses the average weight of 100 seeds (WT100), using eight replicates, and is adjusted by the purity to give a realistic estimate of the amount of seed one can expect to obtain [SPG = (Purity/WT100)]. Differences in storage moisture contents can also impact seed weight and for the dataset used for Tables 2 and 3 all seedlots have had their SPG figures adjusted to 8% moisture content without a correction for purity (=100%). While SPG estimates in Table 1 were based on a rolling yearly average, this analysis uses all seedlots with data available as presented in Table 2.

Table 2. Differences and ranges of seeds per gram (SPG) estimates adjusted to 100% purity and 8% moisture content for select and standard seedlots of western redcedar (Cw), coastal Douglas-fir (Fdc), interior lodgepole pine (Pli) and interior spruce (Sx).

Species	SPG - A	SPG - B	B/A	Range A	Range B
Cw	789 [86]	839 [353]	1.06	619 to 1022	552 to 1344
Fdc	85 [262]	100 [207]	1.17	70 to 113	71 to 136
Pli	254 [78]	342 [1896]	1.35	196 to 377	216 to 468
Sx	396 [139]	497 [1185]	1.26	300 to 555	267 to 690

The striking aspect of Table 2 is the range that the species display in terms of seeds per gram. Standard interior spruce (Sx) seed has a huge range from 267 to 690 seeds per gram amounting to a range ratio of 2.58 (690/267). The standard seed certainly can be much smaller (more SPG) than select seed, but with the exception of coastal Douglas-fir the standard seed is also larger at the far end of the range. The greater number of seedlots representing standard seed can partly explain the large range. The ratios between select and standard seed become slightly greater when adjusted for purity and moisture content but the ranking remains stable. The greatest difference between select and standard seed is with lodgepole pine (select is 35% heavier) followed by interior spruce, coastal Douglas-fir and finally western redcedar.

Correlations between seeds per gram and environmental variables of seed origin were generally quite low (Table 3). Surprisingly, the highest correlations for standard Pli and Sx were with longitude. This suggests that SPG increases as one goes west or actual seed size decreases as one moves east. The opposite trend (SPG increases eastward) was found for select western redcedar (Cw), although the longitudinal range would be quite limited for orchards of this species. The relationship between longitude and SPG is illustrated in Figure 5 for interior lodgepole pine.

Table 3. Pearson correlation coefficients of seeds per gram, corrected to 100% purity and 8% moisture content, with latitude, longitude, and elevation of seed production location of standard and select seed from western redcedar (Cw), coastal Douglas-fir (Fdc), interior lodgepole pine (Pli) and interior spruce (Sx). [statistically significant r values at 0.05 are indicated by *]

Species	Class	# Seedlots	Latitude	Longitude	Elevation
Cw	Select	86	-0.05	-0.22 *	-0.03
Cw	Standard	353	0.05	-0.04	0.18 *
Fdc	Select	262	-0.16 *	-0.04	0.10
Fdc	Standard	207	0.07	0.10	0.03
Pli	Select	78	-0.10	-0.12	-0.11
Pli	Standard	1896	0.28 *	0.45 *	-0.05
Sx	Select	139	< -0.01	0.01	0.02
Sx	Standard	1185	0.20 *	0.23 *	< 0.01

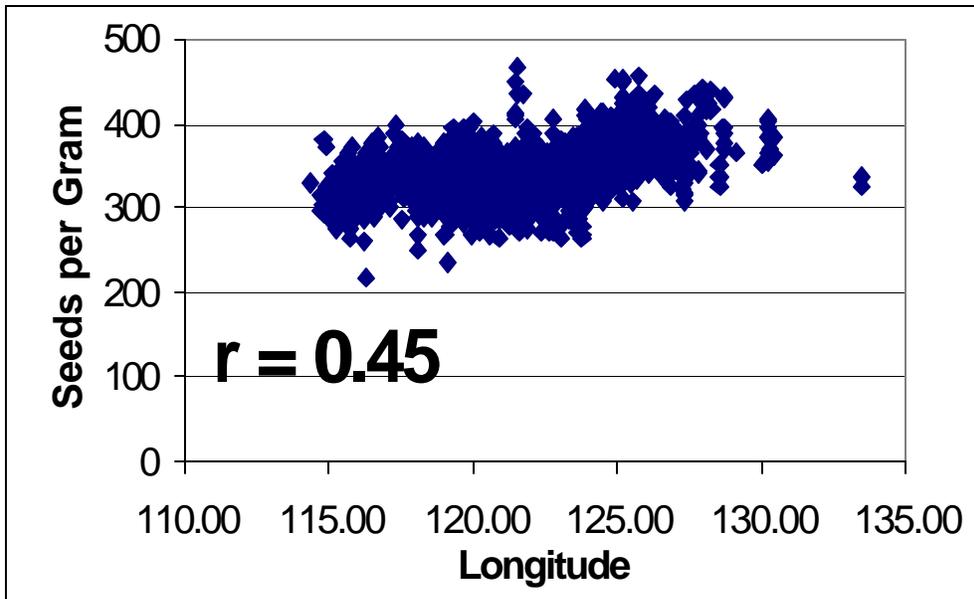


Figure 5. The relationship between seeds per gram and longitude for 1896 standard interior lodgepole pine seedlots.

Using seedlot test data the dormancy of operational seedlots was estimated using the formula previously presented ($\text{Dormancy} = (\text{Strat result} / \text{Soak result}) - 1 * 100$) and the initial tests performed on a seedlot (Table 4). Differences between interior spruce, that possesses almost no dormancy, and lodgepole pine are obvious and correspond to the greater stratification duration required for interior lodgepole pine (4 vs. 3 weeks). Although the Dormancy estimates are low and consistent for interior spruce, lodgepole pine has approximately double the degree of dormancy from select seed. Although average dormancy is not high in either species the max column in Table 4 illustrates that even interior spruce can have 60% of its seeds exhibiting dormancy. The negative values for minimum dormancy indicate that the soak-only test is superior to the soak and stratify test. This is not common and probably results from mechanical damage or fungal infection, which may compromise the usual advantages provided by cold stratification.

Correlations between dormancy and geographic variables indicate quite different patterns for lodgepole pine and interior spruce. For standard lodgepole pine seed dormancy it appears that dormancy increases as one moves eastward, southward and upwards in elevation. Although correlations are statistically significant the effect of latitude, for example, only explains 16% of the variation in dormancy for lodgepole pine. Other sources of variability are genetic differences, year-to-year environmental variation and probably some variables that are currently not being considered. Standard interior spruce did not show as strong a relationship and elevation was the only variable significantly correlated with dormancy (greater dormancy at higher elevations). The origin of select interior spruce seed was correlated with all environmental variables, but not as strongly as standard lodgepole pine seedlots.

Table 4. The average, minimum and maximum level of dormancy for interior lodgepole pine (Pli) and interior spruce (Sx) and correlation coefficients with latitude, longitude and elevation.

Sp.	Class	# Seedlots	Dormancy	Min	Max	Latitude	Longitude	Elevation
Pli	Select	73	0.21	-0.04	0.88	-0.05	< 0.01	-0.03
Pli	Standard	1264	0.11	-0.34	0.74	-0.40 *	-0.41 *	0.36 *
Sx	Select	135	0.05	-0.05	0.26	0.27 *	0.20 *	-0.21 *
Sx	Standard	656	0.03	-0.33	0.60	-0.07	0.01	0.14 *

Seedling Data

Concerns with differences between select and standard seed were thoroughly investigated for interior spruce after numerous concerns were lodged against growing seedlings from select seed. A nursery study found a great deal of variation in germination and early growth, but the variability of select seed was within that of standard seed although at the upper end (Hawkins & Krasowski 1993). Changes in seedling production and the 'general' use of blackout treatments to terminate shoot elongation have erased most of the concerns with select seed.

A comparison of recoverable seedlings (% seedlings sold relative to seedlings sown) from select and standard coastal Douglas-fir seed was performed at Surrey nursery for requests sown between 1985 and 1992 and no differences were detected (Woods 1992). When Douglas-fir was sorted into eight treatments using size and density there appeared to be large differences in germination and initial growth, but at time of lifting there were no noticeable differences between treatments and seed sorting was not recommended (Crowder 1991). In Oregon, it was determined that if seed-weight differences were greater than 50% most of the culled seedlings will come from the smaller seed (Figure 6) (Sorensen & Campbell 1985).

Data on plantation survival and performance will become more readily available and scrutinized in the future to validate our anticipated gains. An initial look at plantation survival comparing select and standard seedlots for lodgepole pine and interior spruce was forwarded for inclusion in this presentation (Figure 7). Results indicate very little difference between select and standard seed for survival, although select seed of lodgepole pine performed slightly better than interior spruce in comparison to their standard wild stand counterparts.

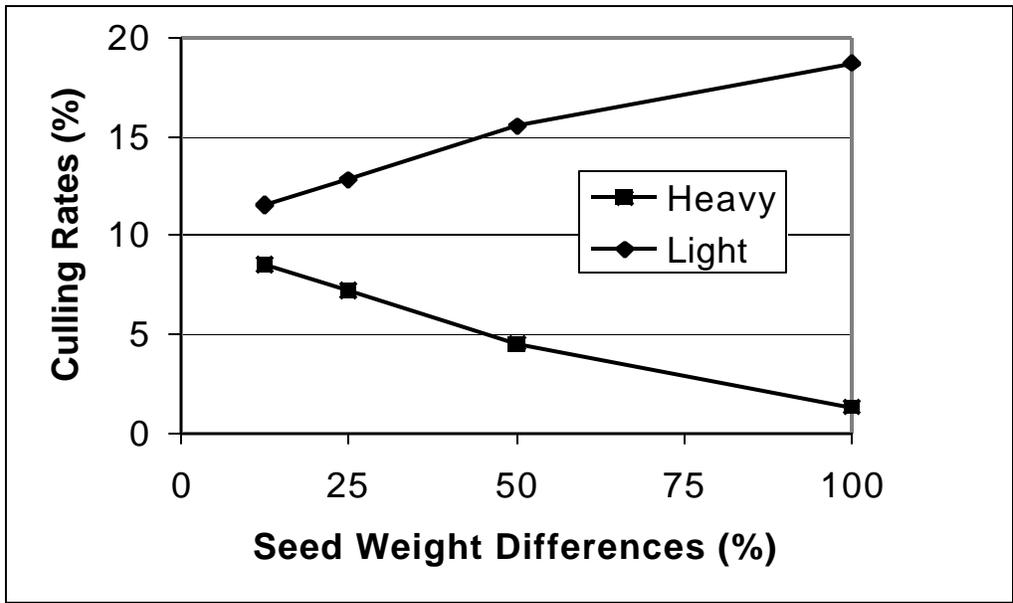


Figure 6. The Effect of seed-weight differences on culling rate at 10% in coastal Douglas-fir (adapted from Sorensen & Campbell 1993)

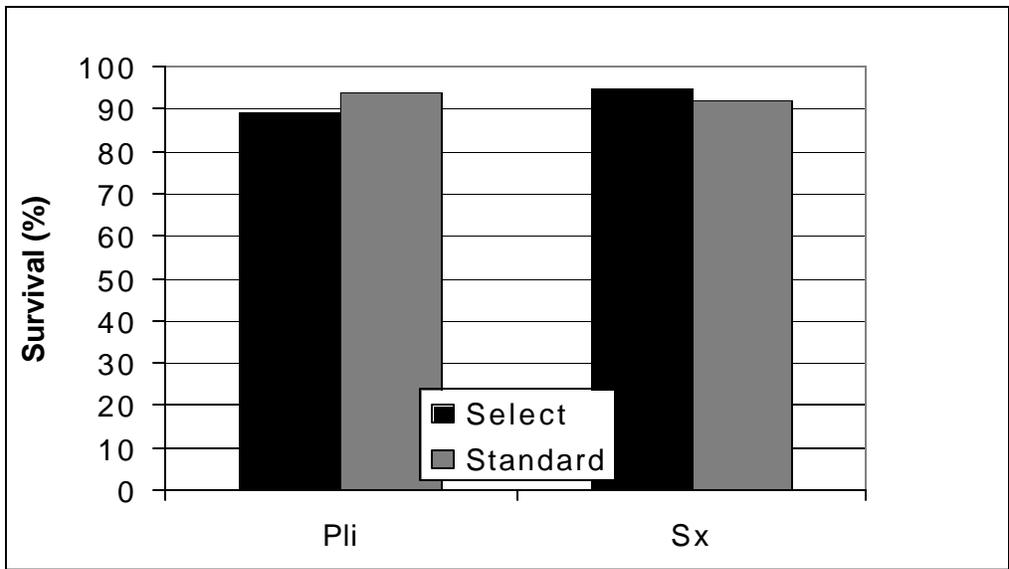


Figure 7. Initial differences in plantation survival for lodgepole pine (Pli) and interior spruce (Sx) from select and standard seed. (Data courtesy of Northern Interior Vegetation Management Association).

Discussion

In discussing differences in seed and seedling attributes I will divide the discussion into the variables presented in this paper.

Seed size

It appears from the evidence that seed size is an attribute that is under fairly weak genetic control. This appears counter-intuitive as we commonly hear about the importance of the maternal parent to seed size? Although trees which produce larger cones will produce larger seeds a variety of other factors influence seed size. Seed size has been shown to vary by year (Figure 1) and

generally select seed is larger than standard seed, especially in the Pinaceae. No strong correlations of seed size with geographic variables were found in the four primary reforestation species in BC (Table 3). Sorensen and Campbell (1985) provide a good synthesis of possible reasons for the inconsistency of results of seed and seedling size which are summarized below.

- 1) Seed size may not reflect embryo size or seed size may not be related to embryo vigor.
- 2) Interactions between seed weight and genetic differences in seedling performance may occur obscuring the relationship between seed and seedling size.
- 3) Influence of the test environment on effects of seed weight on seedling size (i.e. if growth cessation was even partly size related).
- 4) Competitive effects among seedlings. If seed sizes are inter-mixed competition will probably magnify any initial differences in growth.

The use of larger seed provides some advantages to mechanization in the current sowing system. One can expect a higher efficiency from seeders with a larger product, given the same shape of seed. The critical question is whether seed size differences between seedlots or families or years is sufficient to require a grower to adjust their practices. Is there an advantage to sowing different sized seed separately? At present the answer appears to be no – there does not seem to be a strong relationship between seed size and final seedling size. Even if a strong relationship occurs how does it relate to current stock specifications. Seed size appears to be an attribute with a great deal of variability, but not one that provides operational gains through sowing seeds of different sizes.

Germination Parameters

Except yellow-cedar, there are no large differences in germination parameters between select and standard seed. Slight downfalls were observed in select coastal Douglas-fir and western redcedar. This may indicate a need to extend cold stratification in Douglas-fir as recommended by Edwards and El-Kassaby (1995), but **operationally** stratification may already be approaching five weeks prior to sowing. Although stratification does not greatly increase germination capacity it does make germination of the families more uniform.

Dormancy

Differences in dormancy seem present in lodgepole as the degree of dormancy is almost doubled in select seed (Table 4). Differences are not apparent for interior spruce. Differences in seed dormancy are evident between families and between years (Table 4). Yellow-cedar seed is the obvious example of a species with dormancy issues different between select and standard seed. Although data is not available on differences in dormancy for select and standard western white pine this is the only other species in which operational pretreatments are not optimal for the species. All remaining species in tree improvement programs are considered to have seed pretreatment methods which would overcome the dormancy present.

Seedlings

The evidence for BC conifers is not convincing that a difference exists in the performance of select and standard seed. The only area that remains relatively unstudied in BC is the impact of after-effects or the seed orchard location on adaptive characters. Growth (i.e. height) appear to diminish with time in most studies, but the effect of orchard location on frost or drought hardiness should be thoroughly investigated to ensure we are planting material adapted to the planting site.

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