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## Variation in Fruitfulness in a Douglas-fir Seed Orchard and its Effect on Crop-Management Decisions

By Y. A. EL-KASSABY<sup>1)</sup>, A. M. K. FASHLER<sup>2)</sup> and M. CROWN<sup>3)</sup>

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### Abstract

Genetic variation in seed-cone production among 37 open-pollinated families and 63 clones was studied in a coastal clonal/seedling Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] seed orchard. Individual-tree (seedling or ramet) cone counts collected for a period of eight years (1976 to 1983) were analyzed to assess the variation and to

provide information for comparisons between clonal and seedling trees. The seedling trees' cone crops surpassed those of the clonal trees in spite of the physiological maturity of the latter. Open-pollinated families and clones varied in their seed cone production rhythms and were classified as good, poor, and inconsistent cone producers. Parental balance in the resultant cone crop was greatly affected by the size of the crop. Clonal crops in good and poor cone years showed consistent parental imbalance when compared to the seedling cone crops. Heritability estimates for cone production varied among years and, contrary to expectations, the seedlings gave higher estimates than the clones. Several managerial options are proposed to alleviate the variation in cone crop production and produce seed crops with similar representation of all parents.

<sup>1)</sup> Canadian Pacific Forest Products Limited, Tahsis Pacific Region, Saanich Forestry Centre, 8067 E. Saanich Rd., RR #1, Saanichton, B.C., Canada V0S 1M0

<sup>2)</sup> Faculty of Forestry, University of British Columbia, Vancouver, B.C., Canada V6T 1W5

<sup>3)</sup> Forest Consultant, 2188 West 46th Avenue, Vancouver, B.C., Canada V6M 2L1

<sup>4)</sup> Ministry of Forests, Silviculture Branch, Coastal Seed Orchards, Box 816, Duncan, B. C., Canada V9L 3Y2

**Key words:** *Pseudotsuga menziesii*, seed orchards, clones, open-pollinated families, parental balance.

### Introduction

The main function of a seed orchard is to produce seed of improved quality on a regular and sustained basis (SWEET, 1975). If the genetic variation of the seed crop is to be maximized, equality of seed production and pollen fertilization among trees is essential (ERIKSSON *et al.*, 1973; ADAMS, 1982).

The quantity of seed and pollen produced among trees in seed orchards has been reported to differ in several coniferous species (ERIKSSON *et al.*, 1973; JONSSON *et al.*, 1976; O'REILLY *et al.*, 1983; GRIFFIN, 1982; SCHMIDLING, 1983; BYRAM *et al.*, 1986; SCHOEN *et al.*, 1986). Since the relative production of seed and pollen of trees is dissimilar, estimates of these parameters are needed when making management decisions in present orchards and the establishment of new ones. Panmictic equilibrium in seed orchards is dependent upon several factors (WOESSNER and FRANKLIN, 1973). If all the required factors are met, unbalanced strobilus production among the orchard trees alone could constitute a major obstacle to attaining this equilibrium.

ADAMS (1982) found genetic variation in pollen-related characteristics of Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] clones but concluded that the observed differences were relatively small. He indicated also that if balanced clonal representation in pollen mixes is desired, equal weights of pollen would probably suffice for most practical breeding applications (but see MORAN and GRIFFIN, 1985).

As part of an ongoing investigation of the genetics of Douglas-fir seed orchards, we report on the phenotypic and genetic variation in seed-cone production among 37 open-pollinated families and 63 clones in a coastal seed orchard in British Columbia. The actual cone production of every tree in this orchard for a period of eight years (1976 to 1983) is analysed and a comparison between seed-cone production of clonal and seedling trees is presented. The effect of cone production by individual tree or genetic class (clone or open-pollinated family) on the resultant crop and management options are discussed.

### Materials and Methods

This study was conducted at the Canadian Pacific Forest Products Limited, Tahsis Pacific Region, 3.4-ha, high-elevation Douglas-fir seed orchard, in Saanichton, British Columbia, Canada (lat. 48°35' N; long. 123°24' W; alt. 50 m). The orchard consists of a combined clonal/seedling breeding population with 63 clones and 37 open-pollinated (OP) families derived from selected ortets *in situ*. Ortets were located between 450 m to 1,000 m, latitude 48°50' to 49°54' and longitude 121°34' to 125°58', on southern Vancouver Island and the south coastal mainland of British Columbia. The average numbers of seedlings within OP family and ramets within clone are 15.7 (range 3 to 16) and 8.5 (range 11 to 27), respectively. Trees were planted in a randomized incomplete block design replicated 16 times (blocks). The ages of the seedlings and clonal propagules in 1987 are 18 and 21 years, respectively. Trees were planted at 4 × 8 m spacing and attained a maximum height of 8 m before being topped to maintain accessible crowns.

Seed-cone count was recorded during harvest for every tree in the orchard (seedling or ramet) for a period of eight

years (1976 to 1983). Two and one-way ANOVAs were used to analyse the cone count data over the eight years and for each year for the clonal and seedling trees separately (Tables 4 and 5). Broad- and narrow-sense heritabilities were estimated for the clonal and seedling trees, respectively, following methods reported in FALCONER (1960). All cone-count data were transformed to  $\log(\text{count} + 1)$  to fulfil the homogeneity-of-variance test (STEEL and TORRIE, 1980, p. 235). The two-way ANOVAs demonstrated significant interaction for families × years and clones × years. Due to the observed significant interaction, presentation of genetic variation in cone production is valid for only the one-way ANOVA (STEEL and TORRIE, 1980, p. 341).

The relationship between OP families and clone cone crops of the eight years were assessed using Pearson's product-moment correlation and Spearman's rank correlation (SOKAL and ROHLF, 1969).

### Results and Discussion

The average number of cones per tree showed considerable annual variation for both clonal and OP trees (Fig. 1). The OP trees, although 3 years younger, out-produced the "physiologically mature" clonal trees. An opposite and predictable trend was observed by VARNELL *et al.* (1967) in slash pine (*Pinus elliottii* ENGELM. var. *elliottii*) and by SCHMIDLING (1981) in loblolly pine (*Pinus taeda* L.). In spite of the considerable variation among years, both clonal and seedling trees followed the same trend in their annual cone crop ( $r = 0.897$ ,  $P < 0.01$ ,  $n = 8$ ) (Fig. 1). Periodicity in cone production seems to be the norm for Douglas-fir.

The average number of cones per family or clone also varied considerably among and within the eight-year period. Figure 2 represents the annual fluctuation for families' cone count over the eight-year period. Large family differences were observed indicating that few families

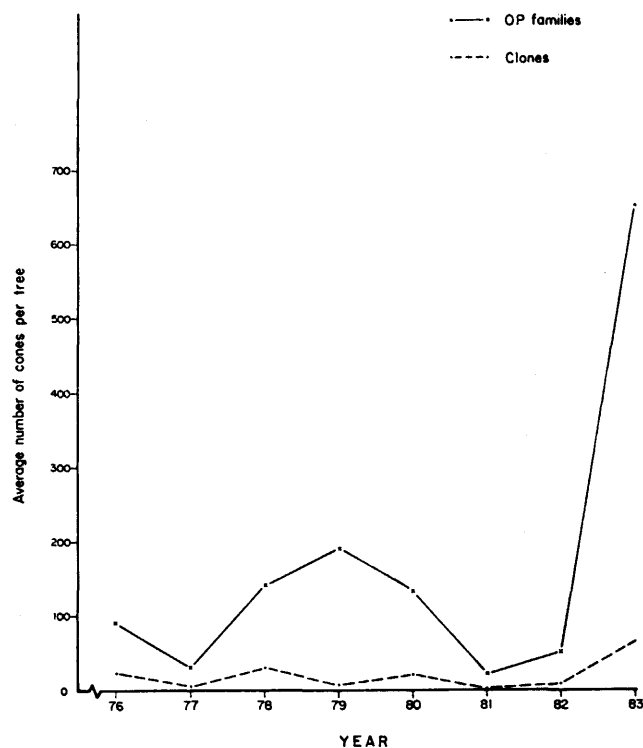


Figure 1. — Development of annual seed-cone production averages for clones and OP families for a period of eight years (1976 to 1983).

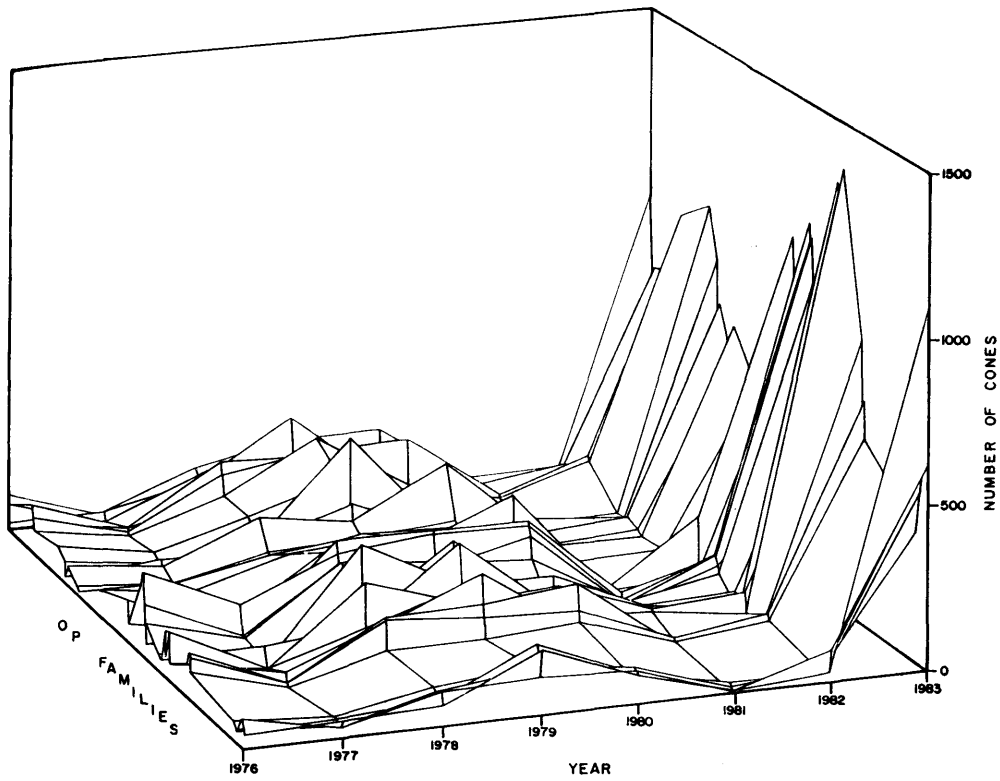


Figure 2. — Three dimensional plot of the average number of seed-cones per OP family for a period of eight years (1976 to 1983).

contribute the most to the resultant cone crop and, consequently, an over- and under- representation of specific families is inevitable in the seed crop. Differences among the clonal material also were observed and a similar situation to that of the OP family cone crop was repeated

(Fig. 3). In general, clonal material showed less variation than those observed for the OP families (Fig. 2).

With the exception of 1982 to 1983, the relationship between cone production of the OP families for any two consecutive years (i.e., 1976 to 1977, 1977 to 1978, . . . 1981 to

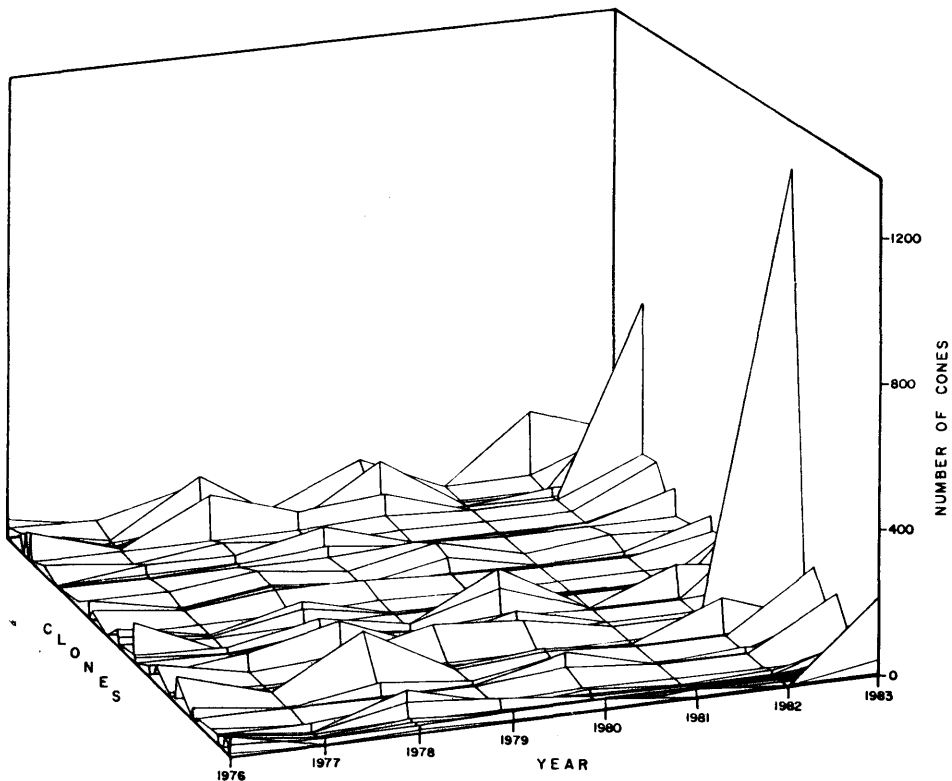


Figure 3. — Three dimensional plot of the average number of seed-cones per clone for a period of eight years (1976 to 1983).

1982) was not significant, indicating that the size of cone crop for one year is not affecting that of the following year (Table 1, above the diagonal). On the other hand, a significant positive correlation was detected between biennial years (i.e., 1976 to 1978, 1977 to 1979, . . . 1981 to 1983) indicating the presence of a carry-over effect (i.e., good or poor cone crop for any one year is followed by a similar crop after two years). The rank correlations (Table 1, below the diagonal), also showed a similar trend. No significant rank correlation was detected between any two consecutive years, indicating the presence of constantly good and poor cone producing OP families. Rank correlations observed between biennial years were significant (five out of six possible combinations), indicating that the rank has been changed due to the presence of an inconsistent group of OP families. Similar trends for both correlation and the rank correlation analyses were detected between cone crops separated by three and four years to those observed between consecutive and biennial years, respectively (Table 1). The correlation coefficients for clonal cone production were similar to those obtained for OP families (Table 2), but 68% (19 out of 28 possible combinations) of the rank correlations gave significant coefficients indi-

cating that the clonal performance was mainly inconsistent (Table 2).

The families or clones could be grouped into three major categories according to their annual cone production. The first is high cone producers whose cone crops consistently exceeded the yearly average. The second group includes low cone producers, who consistently produced a cone crop below the yearly average or did not produce any cones in most years. The third group included clones or families with inconsistent cone crop production over years (i.e., good cone producers in one year and poor producers in other years irrespective of the year's average). This performance of both families and clones in spite of the observed periodicity, is an indirect indication that both genetic and environmental factors control cone production. Good or poor cone-producing clones or families have been observed for several coniferous species (VARNELL *et al.*, 1967; GRIFFIN, 1982; SCHMIDTLING, 1983; YING *et al.*, 1985; BYRAM *et al.*, 1986; SCHOEN *et al.*, 1986).

Close inspection of the data shows that the magnitude of cone production variation is greater within clones and within OP families than among clones or OP families. Means and ranges of single good and poor cone producing

Table 1. — PEARSON correlation coefficients (above the diagonal) and SPEARMAN rank correlation coefficients (below the diagonal) between cone crop production for the period 1976 to 1983 for 37 open-pollinated families

Year	1976	1977	1978	1979	1980	1981	1982	1983
1976	--	0.288	0.857**	0.257	0.749**	0.124	0.530**	0.554**
1977	0.038	--	0.070	0.369*	0.121	-0.066	0.176	-0.011
1978	0.879**	0.007	--	0.198	0.747**	0.259	0.516**	0.597**
1979	0.259	0.377*	0.242	--	0.054	0.549**	0.290	0.327*
1980	0.755**	-0.058	0.811**	-0.001	--	-0.065	0.671**	0.465**
1981	0.191	0.066	0.207	0.549**	0.005	--	0.002	0.368*
1982	0.534**	0.039	0.593**	0.319	0.557	0.186	--	0.344*
1983	0.606**	-0.109	0.598**	0.405*	0.437**	0.358*	0.373*	--

\*) significant at 0.05 probability level

\*\*) significant at 0.01 probability level

Table 2. — PEARSON correlation coefficient (above the diagonal) and SPEARMAN rank correlation coefficients (below the diagonal) between cone crop production for the period 1976 to 1983 for 63 clones.

Year	1976	1977	1978	1979	1980	1981	1982	1983
1976	--	0.045	0.590**	0.235	0.604**	0.047	0.191	0.447**
1977	0.200	--	0.372**	0.277*	0.233	-0.024	0.141	0.058
1978	0.613**	0.403	--	0.185	0.383**	0.018	0.166	0.277*
1979	0.334*	0.301*	0.418**	--	0.161	-0.054	0.020	0.604**
1980	0.457**	0.318*	0.640**	0.262*	--	-0.025	0.217	0.286*
1981	0.332**	-0.051	0.204	0.073	-0.004	--	-0.021	-0.008
1982	0.348**	0.384**	0.384**	0.235	0.420**	0.174	--	0.009
1983	0.540**	0.122	0.476**	0.258*	0.506**	0.155	0.314	--

\*) significant at 0.05 probability level

\*\*) significant at 0.01 probability level

Table 3. — Averages, ranges, and sample size (n) of cone count per tree for a good and poor cone-producing family and clone for the period 1976 to 1983. The yearly overall average and range for the same period also are included.

Year		Open-Pollinated Family			Clone		
		Good (200)	Poor (335)	Year Ave.	Good (393)	Poor (399)	Year Ave.
1976	$\bar{x}$ +S.D.	220+293.3	51+63.4	89+136.5	82+181.5	0	23+48.8
	range	0-1000	0-175	0-1054	0-491	-	0-491
	n	19	15	642	7	8	535
1977	$\bar{x}$ +S.D.	17+35.2	10+18.7	31+73.5	6+14.7	0	4+30.2
	range	0-111	0-62	0-564	0-39	-	0-544
	n	19	15	642	7	8	535
1978	$\bar{x}$ +S.D.	288+448.1	73+78.4	139+206.5	134+102.2	0	31+87.3
	range	0-1770	0-197	0-2217	4-270	-	0-1229
	n	19	14	640	7	8	535
1979	$\bar{x}$ +S.D.	284+306.2	163+185.4	191+237.0	54+130.8	0	7+40.0
	range	0-979	0-577	0-1468	0-350	-	0-610
	n	18	14	637	7	8	535
1980	$\bar{x}$ +S.D.	285+479.1	55+77.2	133+202.3	76+80.6	18+25.5	23+73.5
	range	0-1922	1-288	0-1952	0-200	0-36	0-879
	n	18	13	612	7	8	535
1981	$\bar{x}$ +S.D.	36+63.0	4+10.1	20+70.3	0.4+1.1	0	0.8+8.4
	range	0-182	0-33	0-916	0-3	-	0-186
	n	18	13	593	7	8	535
1982	$\bar{x}$ +S.D.	112+324.0	20+63.1	55+121.9	0	0	9+75.4
	range	0-1307	0-229	0-1307	-	-	0-1346
	n	16	13	583	7	8	535
1983	$\bar{x}$ +S.D.	1131+877.9	426+408.3	762+464.3	563.9+768.4	17+23.3	65+218.7
	range	0-2669	25-1250	0-5889	0-2106	0-33	0-2613
	n	16	13	581	7	8	535

clones and OP families are presented in Table 3. Although each clone or family has its own cone-production rhythm, one would expect to see less difference among trees in good cone years. Family 200 is one of the best cone-producing families, but the amount of variation among trees within this family in 1983 (good cone year) is very large and individual-tree cone production varied between 0 and 2669 cones (Table 3). A similar situation was observed for clone 393, where cone production varied between 0 and 2106 cones (Table 3). Poor cone-producing trees, on the other hand, showed some within-genetic-class variation in their cone production, but the magnitude was smaller than that observed for good cone producers, even in good cone years (Table 3). The within-genetic-class variation in cone production is the result of different production rhythms amongst the class's individuals (i.e., not all trees within OP family or ramets within clone are in production phase).

Significant interactions ( $P < 0.01$ ) were observed between both of the genetic classes (clones or families) and years (Table 4). These significant interactions were expected due to the confounding effect of tree size and climate over the eight-year period. The observed interactions imply some doubt about the statistical validity of the 2-way ANOVAs (STEEL and TORRIE, 1980), therefore 1-way ANOVAs are used to assess among clone and family differences. This large and significant variability has a very useful biological effect. Fluctuation in cone production over years has a selective advantage by maintaining the insect population low over years, thus reducing the intensity of predation (FORCELLA, 1980). In addition, the build-up of nutrients in

trees during low cone years helps to increase vegetative growth and subsequently increases the potential crop in the following years (i.e., more cone-bearing sites are produced).

The variation among families and clones in their annual cone production is evident from the one-way ANOVAs conducted on yearly data (Table 5). With the exception of the 1977 clonal results, all years showed significant differences, confirming that the cone production differs among clones and OP families. Heritability estimates for cone production (narrow- and broad-sense for OP families and clones, respectively) varied and ranged from 0.11 to 0.50, averaging  $0.27 \pm 0.13$  for OP families and from 0.03 to 0.23, averaging  $0.13 \pm 0.07$  for clones. With the exception of 1983, the broad-sense heritability estimates obtained for the clonal material were lower than those estimated for OP families (narrow-sense). Although the heritability estimates are the property of the populations from which they were obtained (FALCONER, 1960; HANSON, 1963), we expected that broad-sense values should exceed the narrow-sense values. Two factors could explain this observed discrepancy. Firstly, estimates of outcrossing rate obtained from natural stands (EL-KASSABY *et al.*, 1981; SHAW and ALLARD, 1982; NEALE, 1985) and seed orchards (SHAW and ALLARD, 1982; RITLAND and EL-KASSABY, 1985) of Douglas-fir have indicated that selfing and other types of consanguineous matings are common. Therefore, progeny obtained from OP families could contain mixtures of half-sib, full-sib and, possibly, selfed individuals. Then, it is not reasonable to expect that the covariance among OP families will estimate 0.25 of the additive genetic variance (GHAI, 1982;

Table 4. — Analyses of variance of seed cone count for the two genetic classes (clones and OP families) over the eight-year (1976 to 1983) period.

Source of Variation	d.f. 1/	Expected Mean Squares 2/	Clonal		OP families	
			d.f.	M.S.	d.f.	M.S.
Genetic Class	C-1	$\sigma_e^2 + K_1 \sigma_{cy}^2 + K_2 \sigma_c^2$	62	3.374	36	5.284
Years	Y-1	$\sigma_e^2 + K_1 \sigma_{cy}^2 + K_3 \sigma_y^2$	7	40.710	7	255.370
Genetic Class x Years	(C-1)(Y-1)	$\sigma_e^2 + K_1 \sigma_{cy}^2$	434	0.590**	252	0.993**
Residual	CY(n <sub>i</sub> -1)	$\sigma_e^2$	3776	0.347	4856	0.706

\*\* Significant at the 0.01 probability level.

1/ C = the number of genetic classes (i.e., 63 clones or 37 OP families); Y = number of years = 8; n<sub>i</sub> = the harmonic mean of the number of ramets within clones or number of seedlings within OP families.

2/  $\sigma_e^2$  = variance due to differences among ramets within the same clone or seedlings within OP family;  $\sigma_{cy}^2$  = variance due to interaction between genetic group (clones or OP families) and year effect;  $\sigma_y^2$  = variance due to year-to-year effect;  $\sigma_c^2$  = variance among individuals within genetic group (i.e., among clones or OP families); K<sub>1</sub>—K<sub>3</sub> = coefficient of variance components.

Table 5. — Analyses of variance of seed cone count for each of the eight years, 1976 to 1983.

Source of Variation	d.f. 1/	E.M.S. 2/	Mean Square						
			1976	1977	1978	1979	1980	1981	1982
<b>Clones</b>									
Among Clones	C-1	$\sigma_e^2 + K \sigma_c^2$	1.440**	0.145 <sup>ns</sup>	1.513**	0.418**	1.484**	0.064**	0.339**
Residual	C(n <sub>i</sub> -1)	$\sigma_e^2$	0.504	0.123	0.545	0.224	0.430	0.045	0.165
<b>OP Families</b>									
Among OP fam.	F-1	$\sigma_e^2 + K \sigma_{op}^2$	1.436**	0.943*	1.780**	1.380**	1.990**	0.858**	2.404**
Residual	F(n <sub>i</sub> -1)	$\sigma_e^2$	0.768	0.637	0.703	0.630	0.709	0.459	0.732

<sup>ns</sup>, not significant; \*, significant at 0.05 probability level; \*\*, significant at 0.01 probability level.

1/ C = number of clones = 63; F = number of OP families = 37; n<sub>i</sub> = the harmonic mean of number of ramets within clones or number of seedlings within OP families.

2/  $\sigma_e^2$  = variance due to differences among ramets within clone or seedlings within OP families  $\sigma_c^2$  and  $\sigma_{op}^2$  = variances due to differences among clones or OP families, respectively; coefficient of variance component [K = 1/a-1(Σn<sub>i</sub> - Σn<sub>i</sub><sup>2</sup>/Σn<sub>i</sub>) where a = number of clones or OP families and n<sub>i</sub> = number of ramets within the i<sup>th</sup> clone or number of seedlings with i<sup>th</sup> OP family].

COCKERHAM and WEIR, 1984). In conclusion, the method adopted for estimating the narrow-sense heritability for the OP families probably has over-estimated the actual value. Secondly, greater variation in cone production was observed among ramets within clones which caused an inflated error (residual) term in spite of the transformation used (see M & M), thus yielding a small among-clone component. This small among-clone value was in turn used to estimate the broad-sense heritability. These variations in cone production among ramets within clones are the results of differences in crown size among grafts due to plagiotropism (branch habit) or grafting incompatibility. SCHMIDLING (1978, 1983) has shown that the within-clone variance is also affected by variation in rootstock and yield lower heritability estimates, even from compatible grafts.

In order to estimate each clone's or family's cone-production contribution to the yearly cone crop, cone-crop curves were developed by calculating the total cone crop

of each genetic class (clones of families) and expressing the contribution of each clone or family as a percentage of the total cone yield of that class. Genetic class members were then ranked in decreasing order of yield, and the cumulative percentage calculations were plotted against the total number of clones or families (Figs. 4 and 5). The cone crop production curves varied between genetic classes and among years. The best case was observed for families in a good cone year (Fig. 4). In that year (1983), the top 18 families (approximately 50%) produced 63% of the total cone crop and the top 33 families (approximately 90%) produced 95% of the total cone crop. This close-to-ideal situation was not observed in poor cone years. In 1981 (a poor cone year), the top 50% of the families produced 83% of the total cone crop. This means that several families did not produce any cones and the remaining ones contributed a very small percentage to the final cone crop.

On the other hand, the clonal material gave a very distorted clonal contribution in both good and poor cone

years (Fig. 5). In 1981 (a poor cone year), 6 clones (10%) produced 80% of the total cone crop, while 10 clones (approximately 16%) produced over 90% of the total cone crop. The 1983 results (a good cone year) also showed a disproportionate contribution among the different clones. A total of 31 clones (approximately 50%) produced 88% of the total cone crop while 56 clones (approximately 90%) produced 100% of the total cone crop. This observed disproportionate contribution among the orchard's OP families or clones to the cone crop is not unique to this orchard. In fact, the so-called "20/80" rule (i.e., 20% of the clones produce 80% of the cone crop) that was reported by the North Carolina State Tree Improvement Co-operative (Anon., 1976) is a very conservative estimate for that orchard and all the previously-studied orchards. A "16/55" ratio was reported for *Picea abies* (ERIKSSON *et al.*, 1973), "23/50" for *Pinus radiata* (GRIFFIN, 1982). "25/50" for *Picea mariana* (O'REILLY *et al.*, 1982) and "22/69" for *Pinus taeda* (SCHMIDTLING, 1983). It was observed in our orchard that the distortion in the families in poor cone years was less than that observed in the clones even in good cone years.

The seedlings (families) have outproduced the grafts (clones) in cone production, but the latter were the first to produce due to their physiological maturity (i.e., no juvenile period). The seedling trees have reached the adult condition after either reaching a certain characteristic age or attaining certain absolute size (i.e., passing through a certain number of seasonal growth cycles, MATHEWS, 1963). It has been observed for Douglas-fir that clonal orchards come into flowering earlier, but that seedling orchards rapidly catch up and soon become much more productive (KONSHI, 1985). This difference in production level could be explained by distinguishing between "maturation", which WAREING (1959) defines as the transition from the juvenile to adult state, and "ageing", which is a loss of vigour during the course of development. Maturation involves a change to a relatively stable condition, whereas ageing involves effects that are readily reversed. Grafts produced cones earlier than seedlings did due to physiological maturity, but were outproduced later, possibly due to the ageing effect.

The option of establishing seedling orchards or including OP seedlings in the first-generation untested orchards was evaluated; the latter was chosen to insure the production of seeds for the interim period between testing and the attainment of useful seed production from second-generation orchards (C. HEAMAN and W. J. B. DEVITT, personal commu-

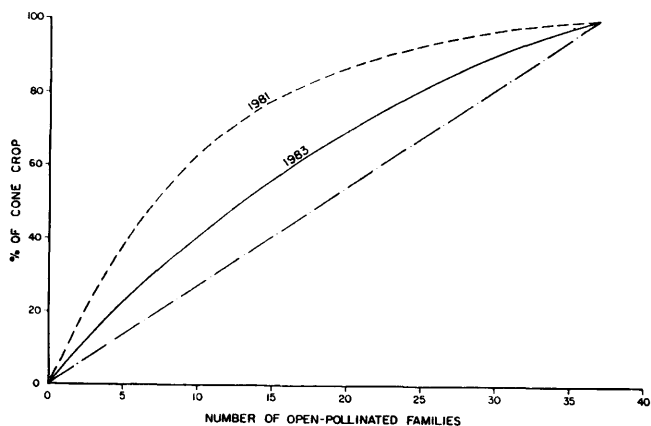


Figure 4. — Cumulative seed-cone production curves for OP families for a good cone year (1983) and poor cone year (1981). Straight line represents equal contribution.

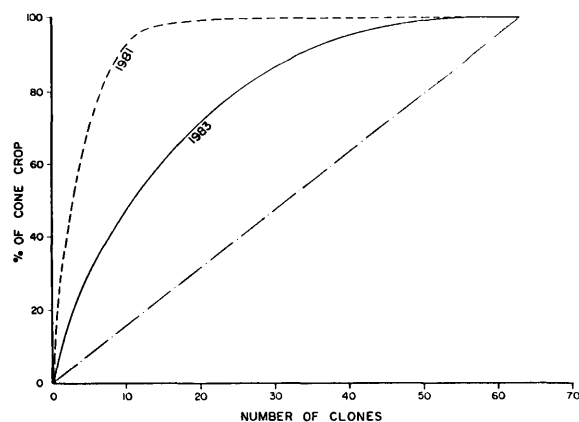


Figure 5. — Cumulative seed cone production curves for clones for a good cone year (1983) and poor cone year (1981). Straight line represents equal contribution.

nication, 1986). The problem of low and/or inconsistent cone production among clones in existing or in future second-generation orchards could be overcome through the use of cultural or hormonal treatments. Such treatments alone or in combination have been shown to increase cone production in Douglas-fir (ROSS, 1978; PHARIS *et al.*, 1980; ROSS *et al.*, 1985; WHEELER *et al.*, 1985). However, clones or families with different inherent fecundity (i.e., poor- and good-flowering histories) have responded differently to the treatment; poor- and good-flowering families have all responded to the treatment and produced seed-cone buds, but the production magnitude between the two groups was a significant 2.25 fold (ROSS *et al.*, 1985). Cultural and hormonal treatments will help in promoting cone production in poor-flowering trees but may not alleviate parental imbalance in the seed crop unless used on a selective basis. It must be emphasized that all effective cultural (water stress, girdling, root-pruning and nitrogen fertilization) and hormonal (exogenous gibberellins) treatments are also stress treatments, and consequently, their repeated application in consecutive years will affect future flowering potential and the development of existing reproductive buds (ROSS and PHARIS, 1985a, b). In addition to that, the unknown, undetected, permanent genetic changes that might be generated in response to stress require thorough evaluation (WILLS, 1984; ANTOLIN and STROBECK, 1985; CULLIS, 1987).

The number of families or clones contributing to the cone crop varies over years with several families or clones entering or dropping out of the breeding pool every year (Table 4, significant family and clone  $\times$  year interactions). Thus, the genetic diversity of the seed crop is reduced over that expected under panmixia and unpredictable gene frequencies in the nursery stock are eminent. Therefore, mixing seed crops from several good and moderate cone years will increase the chance of having a representative sample of most clones and families in the final seed crop. This mixing of different years' crops may also reduce or even eliminate the clone or family  $\times$  year interaction that was observed by LEE (1978).

In theory, seed orchards are culled on the basis of the breeding value of clones rather than their fecundity. If the seed-cone-production history alone is used as a culling criterion in existing orchards to reduce the number of trees to be managed (DANBURY, 1971) or to select clones for new orchards this is in effect a direct selection for cone production, meaning that some valuable pollen-producing

clones might be eliminated. Negative and no correlations between pollen and seed cones have been reported earlier (SCHULTZ, 1971; STERN and GREGORIOUS, 1972; SCHMIDTLING, 1983). Seedlings with high cone-production potential are definitely not needed for commercial reforestation programs because the majority of managed forest lands in B.C.'s Coastal Douglas-fir zone are being, and will continue to be, replanted artificially. Substantial reduction in growth traits is expected if seedlings with high cone-production potential were used for reforestation due to the known negative genetic correlation between reproductive and vegetative outputs (POLK, 1966; HOLMSGAARD, 1972; SCHMIDTLING, 1981; EL-KASSABY and BARCLAY, unpublished).

During the early phases of the life of an orchard it is important to collect a considerable amount of reproductive and phenological data in order to get to know the parental ordinal influences within the orchard. Successful seed-orchard management should utilize this information and consider the year-to-year variation in cone crop in order to produce seed crops with acceptable high effective population size. The information obtained from reproductive assessment surveys (i.e., estimating the expected size of cone crop for the following year) should be evaluated every year to aid management decisions. The expected cone crop size, the demand for orchard seeds and the economics of management practices should dictate what management options to consider. In poor cone years, aborting the crop seems to be a practical option. The genetic quality of an unbalanced clonal contribution defeats the seed orchard goals. It has been observed also that the rates of contamination and inbreeding were highest in low cone years (EL-KASSABY and RITLAND, 1986) and that filled-seed count was lower due to lack of pollen and to predation (DANIELS, 1978; MILLER, 1983). A practical method for aborting cone crops in Douglas-fir seed orchards has been reported by MILLER (1982). Larger cone crops could be obtained in following years, with added biological and economical advantages. If a good or moderate cone crop is expected, then both reproductive phenology and reproductive output differences among the orchard clones should be dealt with to produce a seed crop with acceptable quality and parental balance. Reproductive phenology differences can be overcome by either the use of supplemental mass pollination (SMP) and/or cooling to improve panmixis (EL-KASSABY *et al.*, 1984; FASHLER and EL-KASSABY, 1987). Reproductive output differences could be adjusted by any of several options: a) increasing cone production from low cone-producing clones using cultural and/or hormonal treatments, b) aborting some ramets of the high-producing clones to reduce their seed contribution in the resultant crop, and c) if seeds are in great demand, employing SMP on high seed-cone producing trees using pollen mixes from low-seed-cone producing trees to adjust the parental balance and obtain all seed possible. Finally, it is necessary to mention that although all of these treatments (i.e., SMP, cooling, aborting and cultural or hormonal treatments) are labour intensive, the production of high genetic quality seeds for reforestation is a worthy return on the investment.

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## Genecological Variation in *Pinus strobus*: Growth Rate, Date of Fall Needle-Shedding, and Second-Winter Needle Retention<sup>1)</sup>

By J. E. KUSER, J. C. EBERHARDT and E. G. BRENNAN

Department of Horticulture and Forestry and Department of Plant Pathology, Cook College, New Jersey Agricultural Experiment Station, Rutgers University, New Brunswick, NJ 08903, USA

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### Summary

At a test site in New Jersey, genecological variation in eastern white pine, *Pinus strobus* L., exists not only in growth rate, but also in the time of fall shedding of old needles, and in percent of needles held on trees through a second winter.

We examined a 57-seedlot progeny and provenance test plantation at New Brunswick, NJ after six growing seasons to determine the extent of variation in these characteristics, and their correlation with latitude of origin. Seedlot differences explained 64% of variation in height, 35% of variation in date of fall yellowing of old needles, and 18% of variation in second-winter needle-holding. Variation in all three responses was significantly associated with latitude of origin of female parent.

*Key words:* genecology, geographic variation, phenology, needle retention, growth, white pine.

### Introduction

In contrast to the many reports on comparative height growth of eastern white pine, *Pinus strobus* L. (GARRETT *et al.*, 1973; WRIGHT *et al.*, 1978), very little information has accumulated on variation in its needle-shedding phenology

and holding of needles through a second winter, characteristics of importance to its value as a Christmas tree. In 1922, Sargent stated that needles mostly turn yellow and fall in September of their second season, or persist until the following June. In 1971, Walters noted that most white pines in winter have needles both from the current year and one past year, but some have needles only from the current year's growth. He found no evidence of partial needle drop on trees holding needles through a second winter, or of white pines with needles from more than two growing seasons in the winter. In 1974 COLLINGWOOD and BRUSH stated that needles remain on white pines from three to five years. In 1979, HARLOW *et al.* agreed with SARGENT, stating that they persist until the end of the second season or the following spring. Despite the contradictions, none of these authors made any reference to genecological variation in the amount of needle holdover through the second winter, or in the timing of fall needle-shedding.

Curious about these sparse and conflicting reports, we studied the genecology of needle shedding and winter needle retention at our 6-year-old 57-seed-source test plot in New Brunswick, NJ. Before examining the plantation, we first made some general observations on white pines in our area. Yellowing and shedding of old needles occurred during September and October, with several days' difference in shedding time among trees in the same stand.

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