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Impact of Crop Management Practices on the Seed Crop Genetic Quality in a Douglas-fir Seed Orchard

By Y. A. El-Kassaby[1], [2]) and R. Davidson[2])

Abstract

The impact of two crop management practices, supplemental-mass-pollination (SMP) and overhead cooling, on levels of pollen contamination and outcrossing was assessed in a 13-year-old seedling Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] seed orchard with the aid of six allozyme loci. A 2 X 2 factorial arrangement of SMP/no SMP and cooling/no cooling was applied to four genetically similar blocks of trees. The four treatment combinations used were spatially and temporally isolated by buffer blocks and nine-day reproductive bud phenology delay, respectively. The study revealed the following conclusions: 1) no contamination was obtained when cooling and/or SMP was used, 2) no inbreeding was observed when cooling and SMP were used concurrently, and 3) SMP was effective in reducing consanguineous mating, but not to the level attained from cooling and SMP combined. In addition, the results obtained from the control block (i.e., no cooling and no SMP) indicate: 1) the effectiveness of isolation zones in reducing contamination and 2) randomization of trees within orchard blocks is associated with a high outcrossing rate.

Key words: Douglas-fir, seed orchards, supplemental-mass-pollination, overhead cooling, contamination, outcrossing rate.

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Introduction

The mating system, the union of male and female gametes and their genetic relationship, plays a crucial part in determining subsequent population structure and on the way genetic information is being transmitted and distributed from one generation to another. Forest trees, conifers in particular, are wind-pollinated and have been characterized as predominantly outcrossing (t > 0.9: Adams and Birkes, 1990, for review), among the most genetically heterozygous of plants (Mitton, 1983), and often displaying a significant level of inbreeding depression (Franklin, 1970).

To date, seed orchards are becoming an important source for the production of seed for most of the economically important conifer species' reforestation programs. These programs rely on non-competitive plantings in both seedling-production (i.e., nursery) and plantation-establishment phases. The presence of inbred or mildly inbred seeds or seedlings produced by inbreeding (selfing or consanguineous matings) may survive past the nursery stage, but likely would suffer from inbreeding depression, which may lead to inferior growth and vigour as mature trees.

In order to maximize the genetic efficiency (i.e., high genetic quality and broad genetic variability) in wind-pollinated seed orchards, forest geneticists rely on several methods to control the mating system of orchard trees.

These methods include: random planting arrangements (BELL and FLETCHER, 1975), supplemental-mass-pollination (SMP) (i.e., the broadcast application of viable pollen to non-isolated receptive strobili) (WAKELEY et al., 1966), and over-head water spray cooling treatment to delay reproductive development and thereby reduce pollen contamination (i.e., migration) from external sources (FASHLER and DEVITT, 1980; EL-KASSABY and RITLAND, (1986a) and improve panmixis by shortening the pollination period (FASHLER and EL-KASSABY, 1987; EL-KASSABY et al., 1986a, 1988).

The impact of seed orchard crop management practices (i.e., SMP and/or cooling) on the genetic quality of seed crops has not been studied under controlled conditions previously due to the lack of seed orchard blocks with the same planting arrangement, genetic material, location, and to the high cost of installing the cooling system. In this paper, the impact of SMP and cooling on the apparent outcrossing rate and degree of contamination (i.e., pollen migration to the orchard) is studied in a full-sib, seedling Douglas-fir [Pseudotsuga menziesii (MIRB.) FRANco] seed orchard. This orchard provided a unique opportunity to conduct such a study. The orchard consists of 14 blocks, each with the same planting arrangement (i.e., systematic), spacing, and age. In addition, only one-half of the orchard is equipped with an overhead cooling system. In 1986, a factorial arrangement (2 × 2) of cooling /no cooling and SMP/no SMP was applied to four blocks. The rate of outcrossing and contamination in the seed crop was estimated using data obtained form electrophoretic analysis of 5,964 seeds representing 325 trees.

Materials and Methods

Seed Orchard Description

Material for this study was obtained from Canadian Pacific Forest Product Limited's 6-ha, full-sib Douglas-fir seed orchard located in Saanichton, B.C. (latitude 48°35'N; longitude 123°24'W; elevation 50 m). The orchard production population consists of 110 full-sib families originating from controlled crosses conducted among grafts of 67 plus trees selected from natural stands on sites ranging from 300 m to 1000 m (elevation) in Vancouver Island and SW British Columbia (latitude 48°28' to 49°54'N and longitude 121°34' to 125°58'W). Trees within the orchard's 14 blocks were planted in 1975 as 2-year-old seedlings in a systematic design (i.e., each family appears in the same position relative to other families within every block) using 4 m × 6 m spacing.

A special feature of this orchard is the availability of a solid-set overhead irrigation system in only seven blocks (1 to 7) (Fig. 1). A complete description of the system is reported elsewhere by FASHLER and DEVITT (1980). The overhead irrigation system (i.e., cooling system) is used to delay reproductive phenology development, thereby reducing pollen contamination (FASHLER and DEVITT, 1980; EL-KASSABY and RITLAND, 1986a). The cooling treatment also compacts the pollination period, thus improving panmixis in the orchard (FASHLER and EL-KASSABY, 1987; EL-KASSABY et al., 1986a, 1988).

The orchard is located in close proximity to small mixed natural stand of Douglas-fir, grand fir [Abies grandis (DOUGL.) LINDL.], and western red cedar (Thuja
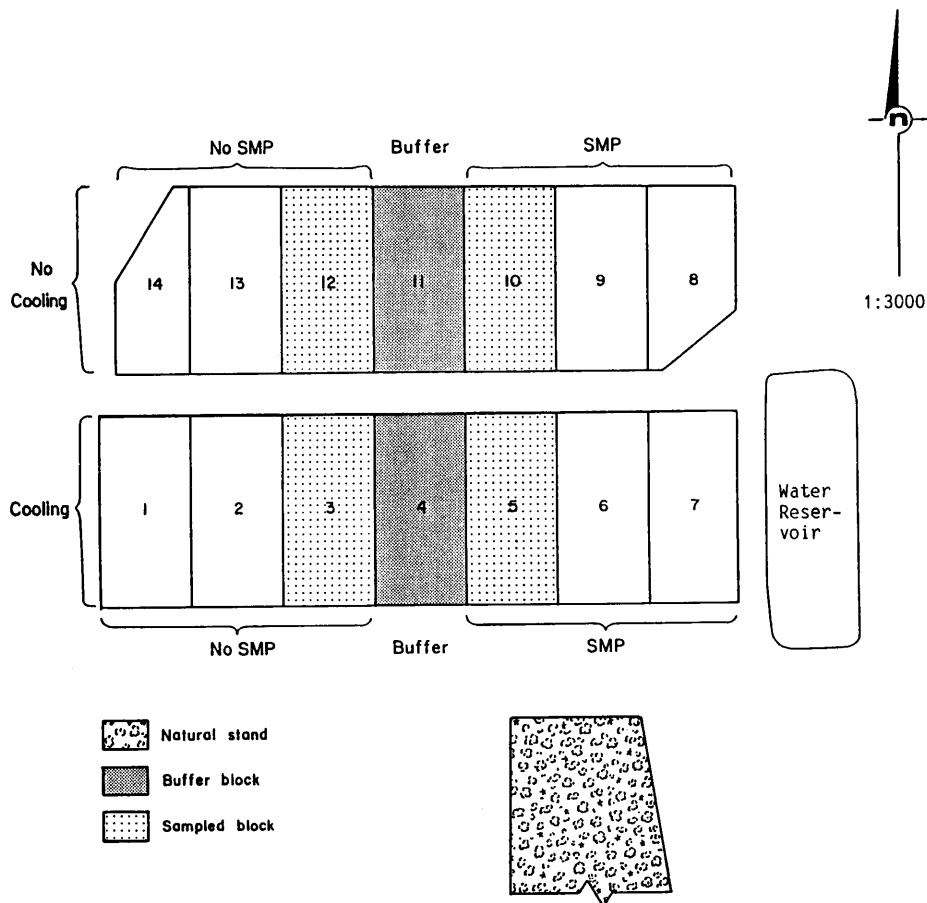

Figure 1. — Map of the seed orchard and the natural stand

plicata DONN) that ranges from 50 years to 100 years old and from 20 m to 30 m in height (*Fig. 1*). The distance from this natural stand to the edge of the orchard is 50 m (*Fig. 1*). In general, the orchard is well-isolated from major contamination sources.

Treatments and Experimental Design

A 2 × 2 factorial arrangement of cooling/no cooling and SMP/no SMP treatments was applied during the 1986 pollination season with three orchard blocks per treatment conbination. Blocss 1 to 7 were subjected to the cooling treatment (FASHLER and DEVITT, 1980), while blocks 8 to 14 were left to develop naturally. This cooling treatment 1) delayed flowering until after the local pollen flush, and 2) apparently helped synchronize reproduction, because flowering occurred rapidly in all trees following cessation of the treatment. In addition, the seven blocks in each of the cooling and no cooling treatments were divided into two sets of three blocks separated by one block as buffer (*Fig. 1*). SMP treatment was applied to one set in each of the cooling and no cooling portions of the seed orchard (*Fig. 1*). The four treatment combinations were spatially separated by two buffer blocks and a 20-m space between the sets (*Fig. 1*) and temporally by nine days reproductive phenology delay between the cooled and uncooled blocks.

The SMP treatment was applied to receptive female strobili in the designated blocks following a reproductive phenology survey that was conducted every second day throughout the pollination period to identify receptive trees. SMP treatment was applied to every cone-bearing tree within the six treated blocks. To account for within-tree variation, receptive trees were pollinated up to three times. SMP was applied at two crown levels (the upper crown, reached by manlift and the lower crown, reached by ground crews). A total of 15 fresh pollen undiluted mixes were used. The number of pollen parents per mix ranged between 7 and 20.

Cone Collections

In the fall of 1986 (a good cone crop year), cone samples were collected from every cone-bearing tree within four blocks representing the four treatment combinations, i.e., 3, 5, 10 and 12 (*Fig. 1*). A total of 325 trees were sampled; the number of trees sampled per block ranged between 79 and 85. For each sampled tree, the crown was divided into four sections prior to cone collection: north and south aspects and upper and lower crown, and cone samples were collected from each section. In addition, cone collection was made by helicopter from the upper crown of 30 Douglas-fir trees from the natural stand adjacent to the orchard (*Fig. 1*). The identity of all cone lots and subsequent seedlots was retained for each tree within every block and for each tree in the natural stand. Cones were air dried at room temperature, seeds were extracted and cleaned by hand, and stored at 3 °C.

Electrophoretic Methods

Electrophoretic procedures, staining recipes, and enzyme nomenclature used followed methods reported by EL-KASSABY et al. (1982b) The enzyme systems studied were: glucose-6-phosphate dehydrogenase (G6PD) E.C.1.1.1.49; isocitrate dehydrogenase (IDH) E.C.1.1.1.42; phosphoglucomutase (PGM) E.C.2.7.5.1; 6-phosphogluconic dehydrogenase (6PGD) E.C.1.1.1.44: glucose-6-phosphogluco-isomerase (PGI) E.C.5.3.1.9; and malate dehydrogenase (MDH) E.C.1.1.1.37. The genotype of each tree

was inferred for six allozyme loci (G6PD, IDH, PGM, 6PGD-1, PGI-2 and MDH-3) by electrophoretic assay of the haploid megagametophyte of 20 seeds per tree with equal numbers (10) from each aspect. Given family size K, the probability of inference of homozygous maternal parentage given the parent is actually a heterozygote is $(1/2)^{K-1}$. With this large number of seeds per tree, the probability of misclassifying a heterozygote is close to zero. The genotypes of the corresponding diploid embryos of the 20 seeds per tree were simultaneously derived. Because the haploid genotype of the megagametophyte determines the maternal contribution to the embryo, it was possible to infer the genotype of the pollen gamete based upon the genotype of the embryo. The genotype of the natural stand trees were determined using a sample of 12 megagametophytes for five loci (G6PD, IDH, PGM, 6PGD-1, and PGI-2). The mode of inheritance and lack of linkage of these loci are reported by EL-KASSABY (1981), EL-KASSABY et al. (1982a,b), and NEALE et al. (1984).

Data Analysis

Single and multilocus estimates of outcrossing rate (t) and outcrossing pollen gene frequencies (p) were estimated using the multilocus mixed mating model for megagametophytic conifer data of RITLAND and EL-KASSABY (1985).

The proportion of pollen contamination (m) from the adjacent natural stand was estimated following the method developed by EL-KASSABY and RITLAND (1986a).

Results and Discussion

The cooling treatment produced a 9-day temporal isolation between the cooled and the uncooled parts of the orchard confirming previous observations on cooled orchards and uncooled orchards during cool springs (EL-KASSABY et al., 1984, 1986a; ASKEW, 1986; FASHLER and EL-KASSABY, 1987). The pollination season was relatively damp and was characterized by the presence of intermittent periods of rainy, sunny and overcast days.

Prior to estimating the outcrossing rate and contamination level for the four studied blocks, the chi-square contingency test (SPIESS, 1977) was conducted to assess the variability among each of the maternal (ovule) and pollen (outcrossing pollen) gene pools. Complete block sampling was necessary in order to obtain an accurate estimate of the outcrossing pollen pool required for the contamination assessment. Although the number of trees sampled from the four blocks varied slightly (79 to 85), the four maternal gene pools did not differ significantly (P<0.05) for the six loci studied (*Table 1*). This observed lack of significant differences among the four studied blocks indicated that the full-sib material used in this study was useful in eliminating the block-to-block variation that is commonly observed among seed-orchard blocks (SMITH and ADAMS, 1983; EL-KASSABY and RITLAND, 1986a; SCHOEN and STEWART, 1987).

By contrast, significant differences (P<0.01) among the four outcrossing pollen pools, estimated from the mixed-mating model, were obtained for three out of the six loci studied (*Table 2*). These differences were expected due to the cooling-SMP treatments that were imposed on these four blocks and the possibility of differential pollen migration from outside sources (i.e., contamination) or variation in male fertilities among blocks (SCHOEN and STEWART, 1986, 1987).

Table 1. — Comparison of allelic frequencies in the ovule pool among cooling:SMP treatment combinations (see Table 3 for sample size).

Locus	Allele	Treatment[1/]				Chi-square
		C/SMP	C/NSMP	NC/SMP	NC/NSMP	
G6PD	1	0.506	0.476	0.471	0.481	0.779^{ns}
	2	0.443	0.470	0.459	0.443	
	3	0.051	0.054	0.070	0.076	
IDH	1	0.816	0.756	0.800	0.810	2.559^{ns}
	2	0.076	0.116	0.106	0.120	
	3	0.108	0.128	0.094	0.070	
PGM	1	0.848	0.835	0.853	0.892	1.424^{ns}
	2	0.038	0.055	0.041	0.032	
	3	0.114	0.110	0.106	0.076	
6PGD-1	1	0.943	0.933	0.918	0.911	2.181^{ns}
	2	0.013	0.018	0.041	0.044	
	3	0.044	0.049	0.041	0.045	
PGI-2	1	0.937	0.957	0.912	0.930	1.399^{ns}
	2	0.063	0.043	0.088	0.070	
MDH-3	1	0.848	0.817	0.841	0.892	2.723^{ns}
	2	0.013	0.030	0.018	0.025	
	3	0.139	0.153	0.141	0.083	

[ns]) Not significant at 5% probability level.
[1/] C = cooling, NC = no cooling, SMP = supplemental mass pollination, NSMP = no supplemental mass pollination.

Contamination estimates (m) for the four blocks are presented in Table 3. The estimated proportions of contamination varied between —0.121 and 0.005 for the different blocks. A positive contamination value was observed only for the control block (i.e., uncooled — no SMP). The remaining three blocks, in which one or both of the treatments were used, yielded negative contamination values.

El-Kassaby and Ritland (1986a) have indicated that under the migration-model assumptions that were used to estimate contamination, negative values can be caused only by sampling error. In fact, none of the obtained negative values were significantly negative (Table 3). Thus, the contamination level in the control block varied from a maximum of approximately 27.2% to a possible low of zero.

The observed contamination level of the control block is very low in comparison to contamination estimates obtained from other wind-pollinated Douglas-fir seed orchards, however, it is similar to the low 0.2% ±5.7 obtained from another orchard in the same location (El-

Kassaby and Ritland, 1986a). Contamination estimates of 40% and 52% have been reported for two orchards from Oregon (Smith and Adams, 1983) and 44% for an orchard from Washington (Wheeler and Jech, 1986) using a multilocus method and 24% for early- and 18% for late-flowering trees from one orchard in British Columbia using the same analytical method (El-Kassaby and Ritland, 1986b). It is noteworthy that all of the previously stated contamination levels were obtained from orchards located in the middle of continuous mature natural stands (Smith and Adams, 1983), or within a short distance of scattered trees or contiguous stands of Douglas-fir located in the path of prevailing winds (Wheeler and Jech, 1986), or surrounded by three small natural stands (El-Kassaby and Ritland, 1986b). In addition, the among-orchard-block gene flow (i.e., within-orchard sources) could be a significant factor contributing to the high contamination estimates reported. Wheeler an Jech (1986) estimated that 68% of the 44% contamination level could be attributed to pollen flow among blocks. Gene flow between adjacent orchards was reported to be 10% in a Pinus

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| Locus | Allele | Treatment[1] | | | | Chi-square |
		C/SMP	C/NSMP	NC/SMP	NC/NSMP	
G6PD	1	0.495	0.518	0.502	0.515	3.662^{ns}
	2	0.481	0.457	0.476	0.457	
	3	0.024	0.025	0.022	0.028	
IDH	1	0.820	0.809	0.816	0.816	5.507^{ns}
	2	0.079	0.098	0.097	0.093	
	3	0.101	0.093	0.087	0.091	
PGM	1	0.865	0.875	0.876	0.895	32.627^{**}
	2	0.025	0.039	0.031	0.047	
	3	0.110	0.086	0.093	0.059	
6PGD-1	1	0.948	0.945	0.948	0.920	26.061^{**}
	2	0.016	0.027	0.023	0.044	
	3	0.036	0.028	0.029	0.036	
PGI-2	1	0.917	0.922	0.924	0.936	4.053^{ns}
	2	0.083	0.078	0.076	0.064	
MDH-3	1	0.919	0.892	0.919	0.934	21.552^{**}
	2	0.002	0.005	0.002	0.005	
	3	0.079	0.103	0.079	0.061	

ns) Not significant at 5% probability level.
**) Significant at 1% probability level.
[1] C = cooling, NC = no cooling, SMP = supplemental mass pollination, NSMP = no supplemental mass pollination.

taeda orchard (FRIEDMANN and ADAMS, 1985a). In contrast, in this orchard there were no blocks with different genetic material which could contribute to among-orchard block contamination.

The observed low level of contamination in the control block could be attributed to the fact that the orchard studied is relatively isolated and that the position of the adjacent natural stand is downwind from the orchard. In addition, the position and size of the cooled section of the orchard acts as a buffer between the natural stand and the control block (*Fig. 1*). The damp/rainy environmental conditions that were observed during the pollination season could also have reduced the pollen flow level.

The intensity of the background pollen is also a major factor contributing to the potential contamination level. The level of background pollen in the Saanich Peninsula area where the orchard is located was very high, low and moderate for 1983, 1984 to 1985, and 1986, respectively. In a study designed to estimate the temporal variation of the mating system over three years (1984 to 1986) (EL-

KASSABY and DAVIDSON, unpublished), the contamination estimates for the control block varied between zero (1984 to 1985) and 0.005±0.267 (1986, the year studied here). Regardless of the observed low level of contamination in this orchard site, all of the cooling and/or SMP treatments have demonstrated to be effective methods for reducing the contamination level in this orchard under "moderate" local pollen load. These results concur with those reported for another, nearby Douglas-fir orchard crop that was managed under cooling (EL-KASSABY and RITLAND, 1986a) or under SMP (EL-KASSABY and RITLAND, 1986b) treatments.

The method used for estimating the contamination level in this study is based upon differences among gene-frequency estimates derived from single-locus outcrossing pollen (male) ovule (female) and outside (natural stand) seed collections (EL-KASSABY and RITLAND, 1986a). The large number of full-sib trees within the orchard blocks necessitated the use of this method. In clonal orchards, where the number of within-orchard genotypes is determined by the number of clones, the method of SMITH and

Locus	Treatment			
	Cooled		Uncooled	
	SMP	No SMP	SMP	No SMP
G6PD	1.003±0.051	0.984±0.053	0.949±0.053	0.975±0.054
IDH	0.975±0.054	0.999±0.051	0.998±0.050	0.974±0.054
PGM	1.083±0.030	0.985±0.061	0.921±0.060[*]	0.975±0.057
6PGD-1	1.010±0.044	0.975±0.060	1.008±0.047	0.974±0.058
PGI-2	1.044±0.063	0.950±0.082	0.974±0.073	0.950±0.083
MDH-3	0.974±0.062	0.921±0.068[*]	0.974±0.058	0.901±0.074[*]
$\underline{t}$[1/]	1.037±0.020	0.975±0.025	0.975±0.023[*]	0.964±0.025[*]
$\underline{t}_m$	1.090±0.002	0.978±0.018[*]	0.970±0.019[*]	0.970±0.019[*]
# of Trees	79	82	85	79
# of Seeds	1462	1487	1574	1441
m	-0.110±0.357	-0.121±0.428	-0.016±0.337	0.005±0.267

*) Rejection of the null hypothesis that $\underline{t}$ = 1.00 at 5% level.

1/ Single-locus minimum variance mean (t) = $[\Sigma \, 1/V_{t_i}]^{-1} \Sigma \, t_i/V_{t_i}$

where

t_i = single-locus estimate, and

V_{t_i} = variance of t_i

ADAMS (1983), which relies on detecting unique multilocus gametes, is recommended.

Single-locus (t) and multilocus (t_m) estimates of outcrossing rates for the four treatment combinations are listed in *Table 3*. With the exception of the cooled-SMP treatment combination, significant departures from complete outcrossing (t = 1.0) were observed at one single-locus estimate for each of the three remaining treatments (*Table 3*). Differences among single-locus outcrossing rate estimates obtained from the same set of embryos are common and have been reported for several coniferous species. This observed variation is an inherent problem of all single-locus estimates due to their sensitivity to violations of the mixed-mating model assumptions (BROWN *et al.*, 1984).

Estimates of outcrossing rate that exceeded unity were obtained for several single-locus and one multilocus estimate (*Table 3*). The interpretation of these "biologically unreasonable" values is t = 1.0 (BROWN *et al.*, 1984). BROWN *et al.* (1984) recommended the truncation of these values at 1.0 after the estimates are obtained. Any automatic truncation during the estimation procedure, such as with the E. M. algorithm (CHELIAK *et al.*, 1985), will bias the overall estimate of t and its variance downwards, as well

as biasing the estimate of pollen-pool allelic frequencies (BROWN *et al.*, 1984; RITLAND and EL-KASSABY, 1985), and nullify the detection of assortative mating (HAMRICK, 1982; BROWN *et al.*, 1984).

Single-locus outcrossing rates are biased downward by any form of inbreeding in addition to selfing (i.e., consanguineous matings), while multilocus estimates are much less subject to such biases. Thus, comparison of multilocus estimates to the means of single-locus estimates is a means of detecting the presence of inbreeding other than selfing (RITLAND and JAIN, 1981; SHAW *et al.*, 1981). Since the 110 full-sib families in the orchard originated from crosses from 67 plus trees, then sib mating is expected due to the inclusion of some plus trees in more than one cross. The cooled-no SMP and uncooled-no SMP treatment combinations yielded single-locus outcrossing rate estimates lower than those obtained from the multilocus method (*Table 3*). This indicates that the SMP treatment is effective in providing unrelated pollen to receptive strobili. The ability of unrelated pollen to out-compete selfed pollen has been demonstrated for Douglas-fir (WEBBER and YEH, 1987) and *Pinus sylvestris* (LINDGREN and YAZDANI, 1988).

With the exception of that from the cooled-SMP treatment, all the multilocus estimates of outcrossing rate obtained showed a significant departure from complete outcrossing ($t = 1.0$) (*Table 3*). The amount of outcrossing estimated from the cooled no SMP treatment was higher than that obtained for the uncooled-SMP or -no SMP treatments (*Table 3*). The two identical estimates of t_m that were obtained for the two uncooled (SMP and no SMP) treatment combinations should be interpreted with caution. EL-KASSABY and RITLAND (1986b) have demonstrated that estimates of outcrossing rate in seed orchards are inflated due to the confounding effect of combination. High estimates of outcrossing rates were always reported for seed orchards that displayed high contamination levels. Such results are reported in Douglas-fir (EL-KASSABY and RITLAND, 1986b), *Pinus sylvestris* (EL-KASSABY et al., 1989), and *Pinus taeda* (FRIEDMAN and ADAMS, 1985a,b).

Outcrossing rate estimates obtaind from this study and, more specifically, that of the control block, are higher than those reported for natural stands of Douglas-fir. In fact, most mating-system studies conducted in seed orchards give higher estimates of outcrossing rate than those obtained from natural stands (see RUDIN et al., 1986, for example). This suggests that population structure (i.e., the physical arrangement of related and unrelated individuals within a population) has affected the rate of outcrossing. Similar results were obtained empirically by ENNOS and CLEGG (1982) and ELLSTRAD and FOSTER (1983) in experimental settings.

Conclusion

Several findings important to seed-orchard management were revealed in this study: 1) no contamination was obtained when cooling and/or SMP was used, 2) no inbreeding was observed when cooling and SMP were used concurrently, and 3) SMP was effective in reducing consanguineous mating, but not to the level attained from cooling and SMP combined. In addition, the results obtained from the control block indicate: 1) the effectiveness of isolation zones in reducing contamination and 2) randomization of trees within seed orchard blocks is associated with a high outcrossing rate.

Acknowledgements

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Alternative Analyses of Parent-Offspring Correlations for Stem Straightness in Jack Pine

By S. Magnussen[1])

Summary

Parental phenotypes of stem form in jack pine (*Pinus banksiana* Lamb.) explained a highly significant proportion (0.11, P = 0.01) of the variability in stem straightness among their offspring. Overall, the narrow-sense heritability of stem straightness scores was comparatively high (about 0.3) in progenies from 43 assortative matings (mainly positive) of parents with contrasting phenotypic scores. Three statistical procedures (parent-offspring regression, maximum likelihood, and tetrachoric correlations) for calculating parent-offspring correlations in the presence of nonrandom mating, unequal family sizes, and a limited range of straightness scores are compared and discussed. Problems related to using parent-offspring regression for traits with only a few subjective scoring categories dissuade its use. As an alternative, estimating tetrachoric correlations is recommended owing to the computational ease and less restrictive assumptions associated with the procedure.

Key words: stem straightness, heritability, parent-offspring correlation, assortative mating, *Pinus banksiana*.

Introduction

The economic value of a softwood bole for sawn construction-grade products depends foremost on size, straightness, wood density, and the amount and distribution of knots (Brown and Miller, 1975; Persson, 1975; Wilkes, 1987). Attempts to isolate the economic value of stem straightness have confirmed a significant relationship between visually assigned scores and the product value (Brown and Miller, 1975; Bridgwater and Stonecypher, 1979; Grant et al., 1984; Chollet and Roman-Amat, 1987). With an economic impetus to improve stem straightness in trees, many tree improvement programs require that candidate trees for breeding must be of superior stem form (Morgenstern et al., 1975; Shelbourne and Low, 1980; Zobel and Talbert, 1984; Bastien and Roman-Amat, 1987; Cotterill et al., 1987). Genetic improvement of stem straightness can be expected to progress fairly rapidly without compromising progress in quantitative traits owing to a combination (Shelbourne and Stonecypher, 1971; Wilcox et al., 1975 Burdon, 1977; Bridgwater and Stonecypher, 1979; Cotterill and Zed, 1980; Shelbourne and Low, 1980; Ledig and Whitmore, 1981; Dean et al., 1986) of comparatively high heritability and a favorable — or at least neutral — genetic correlation with growth traits. Density

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management of forest stands offers additional and immediate tangible ways to improve stem form (Rudolf, 1951; Reukema, 1970; Frömsdorf and Magnussen, 1980; Carter et al., 1986).

Heritability estimates of stem straightness are needed to gauge the potential of genetic gains and to evaluate various breeding strategies (Zobel and Talbert, 1984). This study presents and compares three statistical methods of obtaining this heritability from parent offspring correlations of stem form in 43 jack pine (*Pinus banksiana* Lamb.) parents and their full-sib offspring. The three methods (parent-offspring regression, maximum likelihood, and tetrachoric correlations) are based on different assumptions and derive their estimates from different levels of data aggregation (family, individual, and form category). Problems related to imbalanced mating design, few subjective scoring categories, and unequal family sizes are addressed.

Material and Methods

Stem straightness at age 23 years was assessed in 43 full-sib families of jack pine growing in a randomized complete block design at Sturgeon Lake (Chalk River, Ontario). The full-sib families originated from assortative matings (38 positive and 5 negative) among 48 unrelated trees of contrasting stem form. Parent trees were selected in a local 40-year-old natural jack pine stand. Selected parents were separated by a distance of at least 100 m, which was deemed sufficient to ensure that the trees were unrelated. Matings were completed in 1964, whereas the resulting seed was sown in the spring of 1966. Two-year-old seedlings were outplanted in the spring of 1968 on a former jack pine site of windblown material on alluvial sand. The field design entailed six replicates with five-tree row-plots. Espacement was 1.8 m × 1.8 m. Two surround rows of a local stock were planted along the outside borders. A thinning operation in 1987 removed every third row and all dead, dying, and porcupine damaged trees in the intervening rows. After thinning, the remaining number of trees per family varied from 4 to 22. Tree height at age 23 years averaged 10.7 m, with a diameter of 10.1 cm at 1.3 m above ground level

Assessment of Stem Straightness

A four-point scoring system of stem straightness was used by a single observer to rate the parent trees in 1964. Stems 'with only minor departures from complete straightness (the amplitude of any deviation being less than 2 cm) were assigned a score of 1 ("Good"), whereas