could result from selection for higher wood specific gravity, based on clonal means and individual ramets, respectively.

If clonal selection is based on the performance of individual ramets, selection for more stems or branches, or higher moisture content is 8% to 16% more efficient than direct selection for biomass (*Table 4*), although the gain in biomass may still not be significant. Therefore, number of stems, number of branches and moisture content should be identified as potential secondary characters in indirect selection for willow biomass.

Indirect selection for biomass may be of practical advantage even though gains are not as large as those predicted for direct selection. In order to assess biomass, the trees must be harvested, and both green weight and moisture content measured to calculate oven-dry weight. It is therefore more difficult to measure biomass with precision than to count the number of stems or branches. Furthermore, harvesting the trials is not always an option since a genetic test usually serves multiple purposes. Selection for more stems or branches or higher wood moisture content based on clonal means will result in slightly less improvement in biomass than direct selection, but still be a potential alternative in a willow breeding program.

Conclusions

Many characters examined in this paper are correlated phenotypically, but are not necessarily correlated genetically. Only significant genetic correlations can readily be utilized in indirect selection for the characters important to willow biomass production. For number of stems, wood moisture content, and wood specific gravity, direct selection is better than indirect selection. For biomass, however, more rapid improvement can be achieved through indirect selection on individual ramets for more stems or branches, or higher wood moisture content.

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Temporal Variation in the Outcrossing Rate in a Natural Stand of Western White Pine

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Abstract

Population and individual-tree multilocus outcrossing rates were estimated for three successive pollination years (1983 to 1985) in a natural stand of white pine (*Pinus monticola*) using allozyme variation at 6 loci. Population outcrossing rate estimates were nearly static and did not differ significantly over the three years studied. Individual-tree outcrossing rate estimates were dynamic and varied within and among years. Some consistent "inbreeders" and "outcrossers" were identified, however, the outcrossing rate of most trees varied, indicating that these variations were caused by the pollination biology, phenology, or ecology. Our results parallel those reported in most conifer outcrossing-rate studies and support the hypothesis that outcrossing rate is under genetic control and that the among-tree temporal variation is mainly environmental. The observed fluctuation of individual-tree outcrossing-rate estimates indicates that parental ranking using wind-pollinated seeds requires statistical adjestment on the individual tree within a crop year.

Key words: Pinus monticola, mating system, temporal variation, outcrossing, selfing.

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Introduction

Outcrossing rates of coniferous species have been studied extensively at the population level (see Adams and Birkes, 1991; Mitton, 1992, for reviews). Most of these studies have produced a static description of the mating system and little is known of the temporal variation in population outcrossing rate or its dynamics within populations. Temporal fluctuation in outcrossing rate is important due to its potential to affect the filial population's genetic structure. Cheliak *et al.* (1985) and Snyder *et al.* (1985) reported temporal variation in outcrossing rate in jack pine (*Pinus banksiana* Lamb.) and provided a plausible hypothesis on the operating force responsible for this variation.

Most outcrossing-rate estimation methods use the mixed-mating model procedure of Fyfe and Bailey (1951). That procedure assumes that outcrossed individuals in each progeny array are derived independently from a homogenous pollen pool and that all individuals in the population have identical mating systems (Clegg, 1980). These assumptions are often violated in natural populations as a result of ecological, demographic, and genetic factors (Clegg, 1980) and, consequently, variation in the outcrossing rate among individuals is expected. Variation among the outcrossing rates of individual trees has been reported for a few species (Shaw and Allard, 1987; Ritland and El-Kassaby, 1985; El-Kassaby *et al.*, 1986, 1987; Perry and Dancik, 1986; Perry and Knowles, 1990).

In an earlier study of the mating system within a stand of white pine (*Pinus monticola* Dougl. ex d. Don) near Ladysmith, B. C. using allozyme markers in a single seed crop (El-Kassaby *et al.*, 1987), evidence of variation in the outcrossing rates among individual trees was presented, suggesting the presence of subpopulation structure (i. e., family structure), limited pollen dispersal (i. e., heterogenous pollen pool for different trees), and differential propensity to inbreed. In addition, adjustment of genetic-variance estimates obtained from progeny produced by wind pollination was proposed. In order to extend our understanding of the breeding pattern in this white pine population, additional cone collections were obtained from the 1984 and 1985 pollination seasons (1985 and 1986 seed crops) from the same trees in the McKay stand to: (1) estimate the temporal variation in outcrossing over the 3 pollination seasons, (2) assess pollen-pool heterogeneity over years, and (3) determine the within-population outcrossing-rate variation.

Materials and Methods

Population description, cone and seed material

Stand location, history and population description, plus cone-harvest and seed-handling procedures, were presented in El-Kassaby *et al.* (1987). Cone collections were conducted in 1985 and 1986 from all of the 30 original trees surviving and bearing cones: 25 in 1985 and 18 in 1986. Forty filled seeds per parent were withdrawn for allozyme analysis.

Electrophoretic procedures

Electrophoretic procedures, staining recipes and enzyme nomenclature used follow those of El-Kassaby *et al.* (1982, 1987). The 6 loci scored were *Aat-3, G6pd, Mdh-3, Pgi-2, Pgm-1, and Pgm-2*. The mode of inheritance of these enzyme loci was reported in El-Kassaby *et al.* (1987).

Genetic analyses

Individual-tree and population multilocus outcrossing rates were estimated for each year using the maximum-likelihood procedures of Ritland and El-Kassaby (1985). The outcrossing pollen pool allelic frequency of each year was estimated jointly with each years' population-outcrossing rate.

The relationship between observed (H) and expected (h) frequencies of heterozygotes in the parental population and their progeny (viable-embryo stage) by seed year was used to measure the extent of gene fixation in both generations. Wright's (1922) fixation index (F) was calculated for each locus and its variance was calculated from the inverted information matrix (Kendall and Stuart, 1979), then a minimum-variance mean was estimated for each filial generation, as well as for the parental population.

Results and Discussion

Estimates of allelic frequencies and their 95% confidence intervals for maternal trees (ovule) and the outcrossing-pollen gene pools of the three pollination years are listed in *table 1*. Differences between any pair of allelic frequencies were checked for significance ($P<0.05$) by comparing bounds of confidence intervals (*Table 1*). Ovule and pollen-pool allelic frequencies of the 3 years (1983 to 1985) did not differ, indicating that the maternal trees are representative of the local population. Significant differences among the three outcrossing pollen pools were observed only between 1983 and 1984 at *Aat-3* and *Pgm-1* (*Table 1*), thus, the outcrossing pollen pool was fairly stable.

The minimum-variance mean of $\bar{\hat{F}}$ for the maternal trees ($\bar{\hat{F}} = -0.105$, El-Kassaby *et al.*, 1987) differed significantly from $\bar{\hat{F}} = 0$, indicating an excess of heterozygotes over those expected from panmixia. This could result from selection favouring heterozygotes during tree establishment and growth (Brown, 1979), leaving an adult population composed mainly of outcrossed individuals. In contrast, $\bar{\hat{F}}$ values for the 3 filial populations (1983 to 1985) were positive and significantly different from $\bar{\hat{F}} = 0$ (*Table 2*), indicating that some form of inbreeding has occurred during the 3 pollination seasons.

Population multilocus outcrossing-rate estimates were high (range 0.977 to 0.988) and did not depart significantly from complete outcrossing ($t = 1.0$) (*Table 2*). On the other hand, estimates of the minimum-variance single-locus means ($\bar{\hat{t}}$) were lower than those obtained from the multilocus estimates (*Table 2*), indicating that some inbreeding has occurred in this population over the three studied years and that, probably, it is due mainly to consanguineous mating. Such matings have been inferred by comparing values from multilocus estimates with those from single-locus averages (Shaw *et al.*, 1981; Ritland and Jain, 1981). Matings among related individuals are expected in natural populations due to the presence of family structure and the possible finite limits to pollen dispersal (Stern and Roche, 1974). The sampled population was characterized by the presence of putative siblings in close proximity (El-Kassaby *et al.*, 1987). The presence of clusters of similar genotypes have been reported also for some natural populations of conifers (Linhart *et al.*, 1981; Neale, 1984; Brunel and Rodolphe, 1985).

Table 1. — Allelic frequencies and their 95% confidence intervals for 6 polymorphic loci in the maternal (1983), and outcrossing (1983 to 1985) pollen pools of *Pinus monticola* at McKAY, B. C.

Locus	Allele	Maternal	Outcrossing pollen		
			1983	1984	1985
Aat-3	1	0.733 ± 0.112	0.769^2 ± 0.025	0.836^2 ± 0.032	0.817 ± 0.040
	2	0.267 ± 0.112	0.231 ± 0.025	0.164 ± 0.032	0.183 ± 0.040
G6pd	1	0.833 ± 0.094	0.807 ± 0.023	0.787 ± 0.035	0.769 ± 0.044
	2^1	0.167 ± 0.094	0.193 ± 0.023	0.213 ± 0.035	0.231 ± 0.044
Mdh-3	1	0.500 ± 0.127	0.490 ± 0.029	0.436 ± 0.043	0.430 ± 0.053
	2	0.500 ± 0.127	0.510 ± 0.029	0.563 ± 0.043	0.570 ± 0.053
Pgi-2	1	0.650 ± 0.121	0.679 ± 0.027	0.698 ± 0.039	0.671 ± 0.049
	2	0.350 ± 0.121	0.321 ± 0.027	0.302 ± 0.039	0.329 ± 0.049
Pgm-1	1	0.783 ± 0.104	0.843^3 ± 0.021	0.775^3 ± 0.036	0.786 ± 0.043
	2^1	0.217 ± 0.104	0.157 ± 0.021	0.225 ± 0.036	0.214 ± 0.043
Pgm-2	1	0.783 ± 0.104	0.689 ± 0.027	0.729 ± 0.038	0.712 ± 0.047
	2	0.217 ± 0.104	0.311 ± 0.027	0.271 ± 0.038	0.288 ± 0.047

1) Synthetic allele (all alleles but the most common were bulked in 1 class).

2,3) Significant differences ($P < 0.05$) between pollen years sharing the same superscript.

Table 2. — Mean single-locus ($\hat{t}$) and multilocus ($\hat{t}_m$) outcrossing-rate estimates and mean fixation-index values (F) and their 95% confidence intervals for progeny from 3 pollination years (1983 to 1985) in a single stand.

Estimate	Year		
	1983	1984	1985
$\bar{t}^1$	0.952 ± 0.056	0.938 ± 0.049	0.927 ± 0.059
$\hat{t}_m$	0.977 ± 0.023	0.982 ± 0.040	0.988 ± 0.050
$\bar{F}$	0.011 ± 0.001	0.058 ± 0.002	0.011 ± 0.002

1) Minimum-variance single-locus mean (see EL-KASSABY *et al.*, 1987)

The present study demonstrated than this population's outcrossing rate did not change over the three pollination seasons studied. Lack of temporal variation in outcrossing rate in a population has been reported for white spruce (*Picea glauca* (MOENCH) VOSS, KING *et al.*, 1984), ENGELMANN spruce (*Picea engelmanni* PARRY, SHEA, 1987), and silver fir (*Abies alba* MILL., SCHROEDER, 1989), while significant variation was reported for jack pine (CHELIAK *et al.*, 1985; SNYDER *et al.*, 1985) and lodgepole pine (*Pinus contorta* DOUGL., HAMRICK; cited in HAMRICK and SCHNABEL, 1984). In these 3 cases, selection against inbred seed during seed storage in serotinous lodgepole and jack pine cones was inferred from the observed linear increase in outcrossing rate with storage time. This relationship was reported for alpine ash (*Eucalyptus delegatensis*, R. T. BAK.; MORAN and BROWN, 1980) also, an angiosperm that retains its seed in fruit clusters on the tree for several years.

The lack of significant variation in outcrossing rate among pollen years indicated that an estimate based on one seed crop is reliable for this stand. Although it is known that the level of outcrossing of a population is under genetic control (CLEGG, 1980), extrapolation beyond this population's estimate is not recommended, due to the fact that the mating system of most plant species is plastic and subject to environmental influences (Clegg, 1980). Therefore, generalizations to the species level should be done with great caution.

Multilocus single-tree outcrossing-rate estimates varied among individual trees within and among years, ranging between 0.683 and 1.207 (1983), between 0.843 and 1.240 (1984) and between 0.666 and 1.106 (1985) (*Figure 1*). The highest value (*Figure 2*) was obtained for tree 1 (t_m = 1.240), while the lowest value was t_m = 0.666 for tree 17. Tree 6 displayed the least variation in estimate (t_m ranged from 1.019 to 1.038) while the greatest contrast in outcrossing rate occurred for tree 21, which ranged from 0.683 to 1.118. The multilocus outcrossing-rate estimates in *figure 2* were examined for patterns within or among years. Only 6 trees (numbers 6, 7, 9, 20, 24 and 26) were consistent "outcrossers", although only 2 years' seeds were available for trees 9 and 26, while 5 trees (numbers 16, 17, 18, 29 and 30) were consistent "inbreeders" (values for trees 18 and 29 based on 2 seed crops). No pattern of consistency among years was apparent.

This variation could be attributed to several factors that include population structure (Ellstrand and Foster, 1983; Cheliak *et al.*, 1985; Epperson and Clegg, 1987; Ritland and Ganders, 1987), negative assortative mating caused by phenological differences (Cheliak *et al.*, 1985; El-Kassaby *et al.*, 1988; Golenberg, 1988; Erickson and Adams, 1990), differences in male reproductive output and success (Schoen and Stewart, 1986, 1987; Shea, 1987; Denti and Schoen, 1988), limited pollen flow (Müller, 1976; Shen *et al.*, 1981; Cheliak *et al.*, 1985; Snyder *et al.*, 1985; Erickson and Adams, 1989) and genetic differences among individuals in their selfing ability, specifically in species that exhibit higher self compatibility, like white pine. Bingham and Squillace (1955) reported that seed yield per cone from 32 trees was reduced by selfing to about half (52.7%) of that produced by controlled outcrossing. However, filled seeds per cone from 3 trees were higher than from outcrossing and five more trees equalled or exceeded 75% of the seed yield from outcrossing, making western white pine a good selfer (Franklin, 1970).

Although standard errors around outcrossing estimates derived from seed crops are generally high (see *Table 2*), the position of an estimate relative to complete outcrossing (t_m = 1.00) should not be affected, meaning that temporal variation in the outcrossing rate of individual trees has been detected. Similar genotypes and "full-sib" parental groups (El-Kassaby *et al.*,1987) were checked for similarity of outcrossing estimate and for consistency among years. Of the 5 parental groups identified, only 1 (trees 2, 3 and 4) showed reasonable consistency in outcrossing level; also, trees 3 and 4 showed similar patterns for the same pollination years (1983 and 1984). Conversely, trees 6 and 7, which are not similar in isozyme pattern, were nearly identical in outcrossing rate and were very consistent among pollination years (*Fig. 2*). Judging by this inconsistency between parental genotype and outcrossing rate, other factors are mainly responsible for the variability in outcrossing rate found here among trees and years. Pollination phenology, the varying levels and distribution patterns of pollen within the stand and different weather among the subject years are likely the major causes of differences in the outcrossing rates documented (Cheliak *et al.*, 1985; Snyder *et al.*, 1985). However, it should be emphasized that intra-population variation in outcrossing rate could be partly a reflection of the power of detecting outcrossing events among trees. Seed parents with a low level of heterozygosity permit identification of selfs; however, outcrosses are identified more accurately among their progeny (K. Ritland, Botany Dept., University of Toronto, pers. communication).

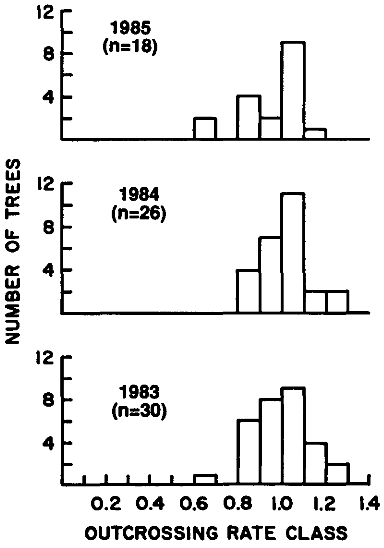

Figure 1. — Frequency distribution of parental multi-locus outcrossing rate by pollination year.

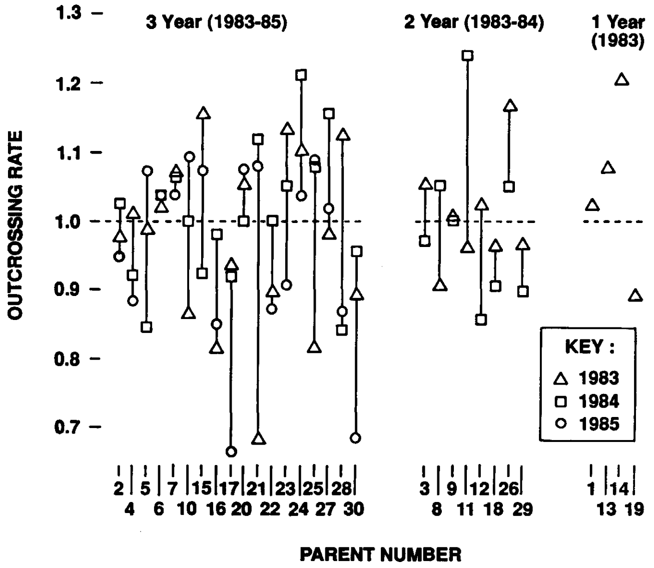

Figure 2. — Multi-locus outcrossing rate by seed parent in pollination year.

Bingham and Squillace (1955) found that selfing of white pine reduced seedling height to age three an average of 21% vs. outcross progeny of the same parents. Furthermore, they found runty seedlings in the progeny of open pollination of the same trees, similar to dwarf seedlings produced by selfing, suggesting that self seedlings were present in those progenies. Field performance of the families produced by Bingham and Squillace were studied by Barnes (1964). Survival to age 12 of the self was 74% to 79% of that of outcross seedlings and height of selfs was only 72% to 85% of that of their outcross counterparts. Thus, despite their relative ease of production in western white pine, self seedlings are at a competitive disadvantage vs. their outcross siblings and likely will be eliminated by competition prior to flowering (see *F* values in *Table 2*). These studies did not include crosses among close relatives, such as might occur from wind pollination also, but it is not unrealistic to assume that such inbreeding would reduce seedling vigour. Woods and Heaman (1989) found a strong reduction in filled-seed set by crossing among relatives in Douglas-fir. Since selfing is known to affect seed set in Douglas-fir more seriously than in western white pine (Orr-Ewing, 1965; Bingham, 1973), the effects of mating among relatives in white pine may be less serious than found in most conifers studied (Franklin, 1970; Bingham, 1973).

Variation in outcrossing rate among individual trees within a population was reported in some conifers (Shaw and Allard, 1982; Ritland and El-Kassaby, 1985; Neale and Adams, 1985; El-Kassaby *et al.*, 1986; Perry and Dancik, 1986; Denti and Schoen, 1988; Schroeder, 1989; Erickson and Adams, 1990; Perry and Knowles, 1990). Squillace (1974) analysed the impact of varying degrees of relatedness among parents and of inbreeding in their progeny on the genetic covariances in families and the effects on estimates of genetic parameters. Evidence of relatedness among the parents and of consanguineous mating among these trees was presented in our earlier paper (El-Kassaby *et al.*, 1987). Thus, estimates of heritability from these seed crops should be reduced to compensate for the bias due to those sources (Squillace, 1974; *Table 9)*.

Progenies of seed collections analysed here are being grown to determine the relationship between seedling dimensions and weights and the estimated outcrossing level. In the meantime, researchers should be prepared to collect seeds from trees more than once if less-biased estimates of parental rankings are desired than implicit in the data presented here.

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