MATING PATTERNS IN SEED ORCHARDS

W. T. Adams and D. S. Birkes[1,2]

Abstract.--Pollen contributing to the production of viable orchard seed comes from three sources: self-fertilization, gene flow from surrounding stands (contamination), and cross-fertilization with mates within the orchard. Understanding the relative contributions of each of these sources is critical to the development of orchard designs and management regimes that will maximize the genetic efficiency of orchard crops. In this paper, methods of evaluating mating patterns from the segregation of isozyme genetic markers in the seed of individual mother trees are briefly described and empirical results for conifer orchards reviewed. Self-fertilization accounts, on average, for less than 10% of orchard offspring, but the proportion of self progeny can vary substantially among individual clones. Pollen contamination can be responsible for as much as 50% of orchard seed and is probably the most serious impediment to the genetic quality of orchard crops. The limited data currently available on patterns of cross-fertilization within orchards suggest that near neighbors account for only a small percentage of the offspring produced by an individual ramet, and with low pollen contamination, cross-fertilization among clones may be extensive.

Keywords: Mating patterns, seed orchard, isozyme, pollen contamination, selfing, cross-fertilization.

INIRODUCTION

Patterns of mating in seed orchards determine the parentage of crosses and thus, the genetic quality and variability of seed that is produced. Pollen successful in fertilizing the offspring of any individual mother tree or ramet can be attributed to three sources: self-fertilization, migrant pollen from outside the orchard (gene flow or pollen contamination), or cross-fertilization with other males in the orchard.

[1] Associate Professors, Department of Forest Science and Department of Statistics, respectively, Oregon State University, Corvallis, Oregon.

[2] Paper 2565 of the Forest Research Laboratory, Oregon State University.

The proportion of seed due to selling is significant because of the usual poor survival and growth of selfed offspring (Franklin 1970, Sorensen and Miles 1982). Although the proportion of selfed offspring generally appears to be low (<10%) in natural stands (Adams and Birkes 1989), it might be expected to be higher in seed orchards due to the wide spacing of individuals; and in clonal orchards, due to "effective selfing" resulting from crosses among ramets of the same clone.

Levels of pollen contamination are of concern because seed resulting from fertilization by non-orchard pollen is expected to have only one half the genetic gain of seed fertilized by orchard parents. Reduction in gain may even be worse if contaminant pollen comes from trees poorly adapted to the intended planting sites of orchard seed.

Patterns of cross-fertilization among orchard parents are important in determining the amount of genetic variability produced in seed crops. In addition, the relationship between mating success and distance between mates must be known so that minimum distances needed to prevent mating between related individuals can be incorporated into orchard designs (Marsh 1985). Rapid reduction in the amount of pollen dispersed from individual trees with increasing distance (Levin and Kerster 1974), suggests that most mating in seed orchards may be between near neighbors. Large inferences among clones in pollen fecundity and in the timing of pollen shedding, however, may override distance as factors influencing mating success (Shen et al. 1981, Erickson and Adams 1989).

The ability to study mating patterns in plants has been enhanced in recent years by the availability of isozyme genetic markers (Brown et al. 1985, Adam, and Birkes 1989). Segregation of these markers in the offspring of mother trees with known genotype reflects actual patterns of mating in the previous generation. Mating models developed to account for the genotypic segregation in progeny can be applied to observed offspring arrays and the parameters from the models estimated. Conifers are particularly amenable to mating model studies, because by assaying both the haploid megagametophyte and diploid embryo of a seed, the isozyme genotype of the pollen gamete which fertilized that seed can be determined (Adams 1983).

In this paper, we review results of mating parameter estimation in conifer seed orchards that are wind-pollinated and have been subjected to a minimum of pollen management, other than the possible presence of a pollen dilution zone surrounding the orchard. In practice, the three components of mating mentioned above have been studied using simplified models that address each component separately. Statistical procedures for estimating levels of selling and pollen contamination are adequately described in the literature, so for these two components of mating, we will emphasize the results of parameter estimation. Little data is yet available on cross-fertilization patterns in seed orchards. For this aspect of the breeding system, more effort will be devoted to describing models and estimation procedures.

SELFING VERSUS OUTCROSSING

The greatest emphasis in mating pattern studies has been in determining the proportion of viable progeny produced by selfing versus outcrossing. A variety of estimation procedures, utilizing either single-locus or multilocus progeny arrays have been employed, but they are all based on the same simple model, the mixed-mating model (Brown et al. 1985). This model assumes that all offspring are the result of either selfing (with probability s) or random outcrossing to other trees in the population (t=1-s). Results are usually reported in terms of estimated rates of outcrossing, t.

Current orchard designs emphasizing large numbers of clones (i.e., >25), and physical separation between ramets of the same clone, appear to be effective in generally limiting the frequency of viable selfs. On average, proportions of outcrossed progeny in clonal seed orchards have been found to be high (Table 1), usually greater than 0.90, and no lower than observed in natural stands of the same species.

Table 1. Estimated proportions of progeny in clonal seed orchards resulting from outcrossing (t)

Species	Location	Loci[a]	t	SE(t)	Reference
black spruce	Ontario	5	.837	.037	Barrett et al. 1987
Douglas-fir	Oregon		.910	.020	Shaw and Allard 1982
	Oregon	10	.936	.026	Omi and Adams 1986
loblolly pine	South Carolina	7	.987[c]	.008	Friedman and Adams 1985a
Monterey pine	Australia	4	.900	.040	Moran et al. 1980
Scots pine	Sweden	7	.95/	.004	El-Kassaby et al. 1989
	Sweden	7	.961	.003	" "
	Finland	7	.976	.017	Muona and Harju 1989
	Finland	7	.978	.017	" "

[a] Number of polymorphic loci used in estimating t.

[b] All estimates except for Monterey pine are based on multilocus estimation procedures. The estimate for Monterey pine is an average of single-locus estimates of t.

[c] Unweighted mean over two orchard blocks and two crop years.

[d] Unweighted mean over three crop years.

Considerable variation in t, however, can occur among individual ramets or clones. In Douglas-fir orchards, individual outcrossing rates as low as 0.50 have been observed (Shaw and Allard 1982, Erickson 1987). Two main factors are responsible for variation among individual trees in t. The first is the relative availability of self versus outcross pollen at the time of fertilization. Extremely early or late flowering clones, or particularly heavy pollen producers, might be expected to have higher proportions of self-pollen when female strobili are receptive, and thus, have lower frequencies of outcrossed progeny (El-Kassaby et al. 1988, Erickson 1981). Clones also differ in the ability to produce viable embryos after selfing (i.e., self-fertility), mostly as a function of the number of lethal--gene equivalents they possess (Sorensen 1969). Normally, self--fertility is quite low in conifers (Franklin 1970), but it can range extensively among individuals. For example, in a study of 35 Douglas-fir trees, Sorensen (1971) found self-fertility to range from 0.1 to 45 percent. With equivalent frequencies of self-fertilization, proportions of viable self progeny will be highest in clones with the highest self-fertilities.

POLLEN CONTAMINATION

The use of single-gene markers to identify seeds fertilized by non-orchard pollen sources is limited because allele frequency differences between orchards and background stands are usually small. A multilocus method of estimating gene flow, however, can be applied in clonal orchards (Smith and Adams 1983, Friedman and Adams 1985b). This procedure takes advantage of the fact that clonal orchards have a limited number of multilocus genotypes relative to background stands. Thus, background pollen sources are expected to produce a much greater variety of multilocus gametes which collectively can be used to identify migrant pollen. Pollen gametes observed in orchard offspring which have multilocus genotypes different from any that can be produced by the orchard clones are called detectable contaminants. The proportion of detectable contaminants (b) in an offspring sample provides a minimum estimate of pollen contamination, since not all migrants will be detectable genetically. To obtain an estimate closer to the true value, b must be divided by the probability that a migrant pollen grain will have a detectable genotype (i.e., the detection probability). The detection probability can be estimated from allele frequencies of trees sampled in background stands (Smith and Adams 1983).

Estimates of pollen contamination (m) based on the multilocus procedure have been made for a variety of species and orchard situations. The estimates in Table 2 are for total contamination, including migrant pollen from natural stands, and from other orchard blocks on the same site. In all cases, the levels of pollen contamination appear to be quite high. In one young Douglas-fir orchard with poor pollen production, m was greater than 90 percent. But even in older orchards, where pollen production is much greater, contamination has been observed to be as high as 40 to 50%. Fortunately, pollen management techniques such as flower stimulation, supplemental mass pollination, and bloom delay (by water cooling) appear to be effective in reducing contamination in seed orchards (El-Kassaby and Ritland 1986, Wheeler and Jech 1986).

Table 2. Estimates of pollen contamination (m) in conifer seed orchards based on multilocus genetic markers.

	Orchard					
Species	Location	Block size(ha)	Age		SE(M)	Reference
Douglas-fir	Oregon	1.8	14	0.52a	0.02	Smith and Adams 1983
	Oregon	2.4	20	0.40b	0.05	
	Oregon	3.3	8-9	0.91b	0.08	Adams, unpublished
	Washington	5.0	15	0.44c	0.04	Wheeler and Jech 1986
loblolly pine	South Carolina	2.0	15	0.46d	0.02	Friedman and Adams 1985b
	Texas	-		0.51b	0.05	Wiselogel 1986
Scots pine	Finland			0.36b		Harju et al. 1987
	Sweden	12.5	17-18	>0.36b,e		El-Kassaby et al. 1989
	Sweden	16	14-18	>0.21b,c		

[a] Mean estimate for 10 orchard blocks in one cone crop year.

[b] Estimate for one orchard block in one cone crop year.

[c] Mean estimate for two orchard blocks in one cone crop year and one orchard block in a second crop year.

[d] Mean estimate for two orchard blocks in three crop years.

[e] A minimum estimate, based only on the proportion of detectable contaminants (see text).

PATTERNS OF CROSS-FERTILIZATION WITHIN ORCHARDS

Two approaches have been employed to investigate cross-fertilization mating patterns in seed orchards using genetic markers. In the rare marker approach, offspring are sampled from mother trees at varying distances and directions around a pollen parent carrying a rare marker allele (Seen et al. 1981, Erickson and Adams 1989). The frequency of the rare marker in the offspring of each mother tree is a measure of the relative mating success of the pollen parent. This is an effective means of measuring cross-fertilization patterns, particularly the relationship between mating success and distance between mates, but is limited in application because of the requirement for individuals with rare markers. In addition, the presence of multiple ramets carrying the same rare marker, can confound the interpretation of results.

In the model_approach, mating parameters are estimated directly from probability models designed to account for the frequencies of multilocus genotypes of pollen gametes in the offspring of individual mother trees. this approach was used by Schoen and Stewart (1986) to investigate male fertilities of clones in a white spruce orchard. A more general model has also been described by Roeder et al. (1989). Both of these models, however, require that populations be isolated from migrant pollen sources.

As is evident from the previous section, it cannot be assumed that orchards are isolated. Thus, there is a need for methods of evaluating cross-fertilization patterns when at least some pollen contamination can be expected. A probability model which can be used under such circumstances is the "Neighborhood Model" described by Adams and Birkes (1989). In this model, a specified area around a mother tree is called its neighborhood. The model states that pollen successful in fertilizing viable offspring of the mother tree is due to three sources: self-fertilization (with probability s); migrant pollen from outside the neighborhood (with probability m); and, cross-fertilization with males within the neighborhood (with probability T-m-s), with the relative mating success of the jth outcross male in the neighborhood being ϕ_j. The probability, therefore, of observing multilocus genotype g_i in the pollen gametes of offspring from the mother tree is

$$P(g_i) = s\ P(g_i|M) + (1-m-s) \sum^{r} \phi_j\ P(g_i|F_j) + m\ P(g_i|B),$$

where P(gi|M) is the probability that the mother tree produces pollen gametes with genotype gi, P(gi|Fj) is the probability that the jth outcross male in the neighborhood produces pollen gametes of this type, and P(gi|B) is the probability that pollen gametes from migrant (background) sources have genotype gi.

The relative mating success of each outcross male in the neighborhood (ϕ_j) is determined by a number of factors including proximity to the mother tree, pollen fecundity relative to other males, and the degree to which the pollen shedding period overlaps with the female receptivity period of the mother tree. To investigate the relationship between mating success and factors expected to influence mating success, ϕ_j can be expressed as a function of these factors. Thus, the parameters to be estimated in the model are s, m, and one or more terms related to mating success within the neighborhood. Maximum likelihood procedures can be used to estimate these parameters when the model is applied to offspring data. In practice, the neighborhood might be an entire orchard block, but in clonal orchards it is necessary to keep neighborhood size relatively small, because as neighborhood size increases, the number of individuals with identical genotypes within the neighborhood increases. The smaller the number of potential males within the neighborhood, the greater the ability to discriminate among them genetically, and between multilocus pollen gametes from within and outside the neighborhood.

We have applied the neighborhood model to offspring data from five ramets in i 20-year-old block of a 25-clone Douglas-fir seed orchard (Adams and Birkes 1989). All pollen producing trees within a 25-m radius (25-26 trees) were considered the neighborhood of each mother tree ramet. Genotypes of all trees in the block were known at 11 loci, and estimates of pollen gamete frequencies in background pollen sources were also available for the same loci. In addition, pollen gamete genotypes were available for samples of 30-40 offspring per mother tree.

First, we were interested in the relationship between mating success (ϕ) of the males in a neighborhood and distance (d) to the mother tree. An exponential function was used to relate ϕ to d (Figure 1). When the distance parameter β is 0, ϕ is unrelated to d, and as β increases in value, near neighbors are increasingly favored in mating. The mating model with three parameters, s, m and β, was applied to the combined offspring data of all five ramets (total = 173), giving maximum likelihood estimates of s = 0.00 (SE=.03), m = 0.69(.06) and β = 0.02(.07). Only $\hat{m}$ was significantly ($P<.05$) different from zero. We conclude from these results that most pollen effective in fertilizing viable offspring came from outside the neighborhoods, that the proportion of viable selfed offspring is low (or zero), and mating success within the neighborhoods is unrelated to distance between mates. The latter result is consistent with earlier seed orchard studies in Douglas-fir (Erickson and Adams 1989) and Scots pine (Shen et al. 1981) using the rare marker approach. These studies indicated that the large pollen fecundity and phenology differences among orchard clones can overwhelm distance as an important determinant of mating success within 20 to 30 m of mother trees; however, when floral synchrony between males and females is high, near neighbors are favored.

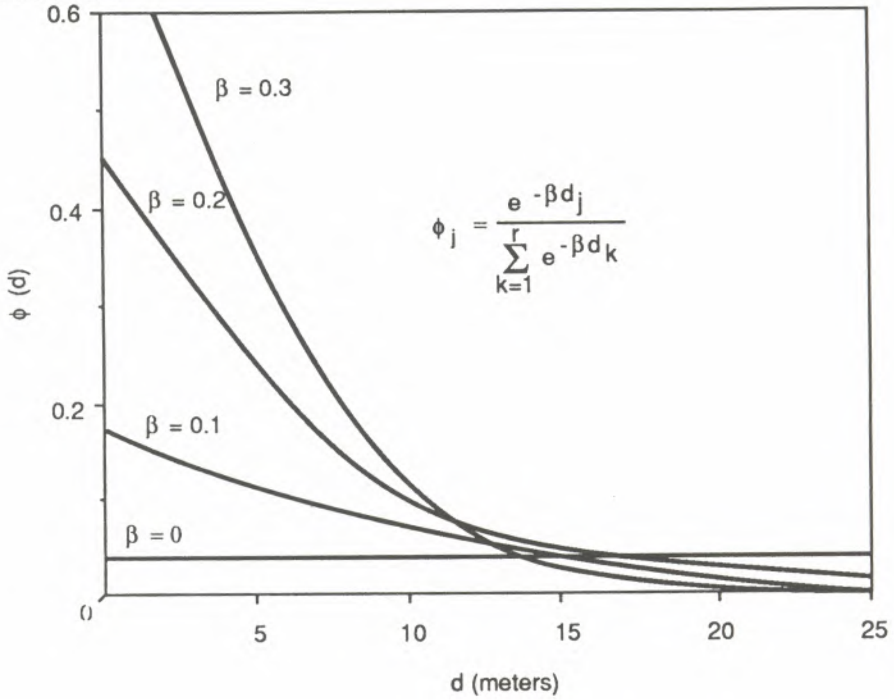

Figure 1. Relationship between mating success of a male (ϕ) and distance to the mother tree (d) for various values of the distance parameter (β). Also given is the formula for computing ϕ for the jth male (ϕ_j), where d_j is the distance the jth male is to the mother tree and r is the number of males in the neighborhood.

To investigate the relationship of pollen fecundity and phenology of males to mating success within the neighborhoods, we applied a second model. Both flowering factors were combined into a single measure called effective pollen fecundity (f), which was calculated for each male as its relative pollen production multiplied by the degree to which its pollen shedding period overlapped with the female receptivity period of the mother tree. Estimates of relative pollen production and the flowering periods of each ramet in the study block were derived from observations on flowering in the spring previous to seed collection (Adams, unpublished). The number of ramets per clone in the orchard block ranged from 2 to 29, and the proportion of the pollen crop contributed by each clone ranged from 0.41 to 10.0%. Fifty percent of the clones produced 80% of the pollen crop. The mean date at which each of the clones initiated pollen shedding ranged over two-weeks, although 75% of the mean initiation dates occurred within a five-day period.

As for the distance relationship, we used an exponential function to relate ϕ to f (Figure 2). When the effective fecundity parameter γ is 0, ϕ is unrelated to f, but as γ increases, ϕ increasingly becomes a function of f. Since s was found not to differ significantly from zero in the previous analysis, the mating model with two parameters, m and γ, was applied to the combined offspring data of the five ramets. The maximum likelihood estimates of both parameters, $\hat{m}$ = 0.68(.06) and $\hat{\gamma}$ = 0.34(.15), were significantly different from zero. As with the previous model, migrant pollen from outside the neighborhoods accounted for nearly 70% of the viable offspring of the mother trees. In addition, there appears to be at least a weak relationship between relative mating success of males within the neighborhoods and f. Thus, effective pollen fecundity is more useful for explaining mating success differences among males in the neighborhoods, than is distance to mother trees.

Because distance to the mother tree and effective pollen fecundity appeared to interact in their influence on mating success in earlier seed orchard studies based on rare markers (Erickson and Adams 1989, Shen et al. 1981) we tested a third model, which in addition to m and γ, included a parameter specifying the interaction between d and f. The fit of this model to the combined offspring data was not significantly better than the two parameter (m and γ) model.

The greater γ is, the more skewed will mating success be towards fewer males with higher f, and the less will be the genetic diversity present in pollen gametes produced by outcross males within the neighborhoods. Since ϕ measures the proportional contribution of an individual to the outcross pollen pool within a neighborhood, the influence of differences in f on genetic diversity can be evaluated by examining the variation of $\hat{\phi}$ among males in the neighborhood, where $\hat{\phi}$ is calculated using the exponential function (Figure 2) and $\hat{\gamma}$ is substituted for γ. For each neighborhood, a ϕ for each clone was obtained by summing the $\hat{\phi}$ values of all ramets of the clone that were present. On average, each neighborhood included 15.4 (range 13 to 18) clones. If each clone in a neighborhood contributed equally to the outcross pollen pool, $\hat{\phi}$ would be the same for all clones. In reality, $\hat{\phi}$ may range as much as from 0.01 to 0.26 in any one neighborhood; nevertheless, there were only 4 cases where $\hat{\phi}$ exceeded 0.15. Thus, the outcross pollen gametes produced by males within the neighborhoods, were not dominated by one, or a few, clones.

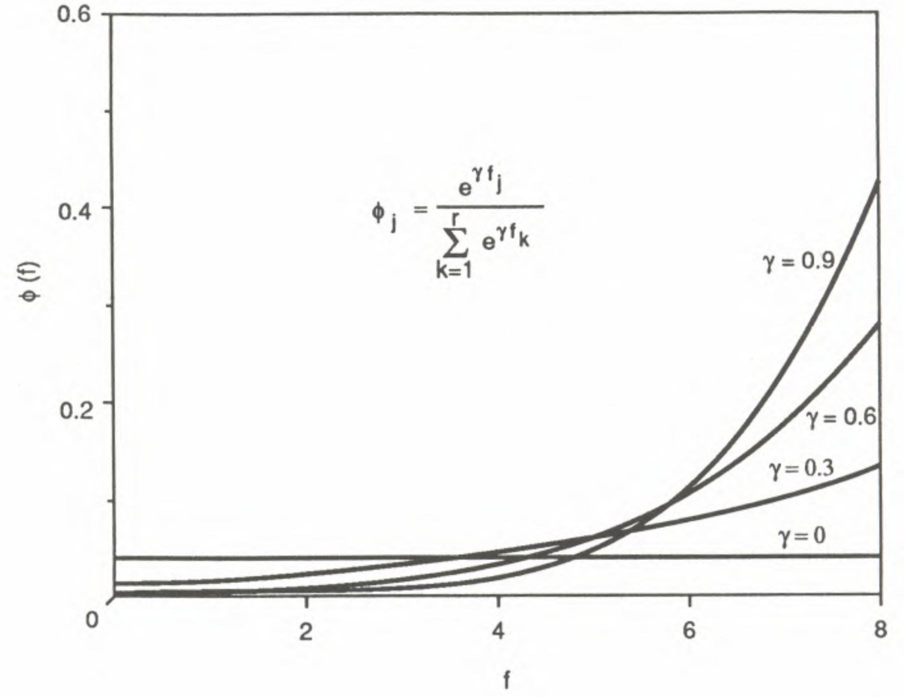

Figure 2. Relationship between mating success of a male (ϕ) and its effective pollen fecundity (f) for various values of the effective fecundity parameter (γ). Also given is the formula for computing ϕ for the jth male (ϕ_j), where f_j is the effective pollen fecundity of the jth male and r is the number of males in the neighborhood.

The effective number of outcross male clones in a neighborhood (N_e) is the theoretical number of males necessary to generate an equivalent amount of genetic diversity in the outcross pollen pool as produced by the actual males in the neighborhood, given that all males in the neighborhood have an equal chance of mating with the mother tree. N_e can be calculated as $1 / \sum \hat{\phi}_j^2$, where $\hat{\phi}_j$ is the estimated mating success of the jth clone, and the summation is over the total number of clones in the neighborhood (Crow and Kimura 1970). N_e averaged 10.1 over the 5 mother trees (range 8.1 -12.8), indicating that despite differences among clones in effective pollen fecundity, considerable cross-fertilization occurred within the neighborhoods.

CONCLUSIONS

Although research on mating patterns in seed orchards has accelerated in recent years with the availability of isozyme genetic markers, most of this work has been directed at estimating proportions of progeny due to selfing. On average, this proportion appears to be low in clonal orchards, but occasionally individual clones have high levels of viable selfed offspring. These clones need to be identified and either rogued from the orchard, or treated by pollen management techniques (e.g., supplemental mass pollination) to reduce the amount of self--fertilization to acceptable levels (El-Kassaby and Ritland 1986, Webber 1987).

In the future, research on the outcrossing component of the breeding system needs to be emphasized since there is little known about this aspect of mating. The high levels of pollen contamination that have been observed in several orchards is particularly disturbing because of the severe negative impact it has on genetic quality of seed crops. We need a better unlerstanding of how various parameters such as orchard size, age, composition, and degree of isolation influence levels of contamination; and the degree to which pollen management techniques are effective in limiting contamination (El -Kassaby and Ritland 1986, Wheeler and Jech 1986). If wind-pollinated seed orchards are to be relied upon in the future, satisfactory solutions to the pollen contamination problem must be realized.

The neighborhood model seems to be promising for studying patterns of cross-fertilization. Estimates of mating parameters in a Douglas fir orchard block based on this model were consistent with previous information on cross-fertilization in seed orchards. In particular, for any one mother tree ramet, crosses with near neighbors appear to account for only r small percentage of the total offspring. In addition, the data suggest that with low pollen contamination, cross-fertilization among clones may be extensive. These conclusions, however, are based on only a few studies and must be considered tentative. In addition to the need for better information on cross-fertilization in orchards not subjected to pollen management, the influence of practices such as flower stimulation and bloom delay on cross-fertilization patterns must be understood. This information is necessary if the influence of orchard designs and management regimes on the genetic efficiency of seed crops is to be adequately assessed (Adams 1983).

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