GENETIC AND ECONOMIC CONSEQUENCES OF POLLEN CONTAMINATION IN SEED ORCHARDS

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Abstract. Pollen contamination can be a serious obstacle to achieving maximum genetic gains from seed orchards. In the future, the problem will be greater as early-flowering techniques speed up the generation turnover time and advanced-generation seed orchards cane into full production. This will lead to a larger gene frequency differential between orchard and nonorchard clones than occurs in first-generation seed orchards. Economic analyses indicate that the corrective measures available depend upon the number of acres an organization will be planting, the amount of pollen contamination and the gene frequency differential between advanced-generation orchards and the source of pollen contamination. More research is needed to determine how much pollen contamination occurs in seed orchards and the effectiveness of various corrective measures.

Additional keywords: Pollen dilution zone, advanced-generation seed orchards.

INTRODUCTION

The objective of seed orchards is to produce sufficient seed of good genetic quality to meet all of an organization's regeneration needs. Most members of the North Carolina State University - Industry Tree Improvement Cooperative are now meeting this need with their genetically rogued first-generation seed orchards. In addition, Cooperative members have established or are in the process of establishing second-generation orchards.

Predicted gains in volume from loblolly pine plantations established from seed orchard seed over nonimproved plantations is 15 percent from rogued first-generation orchards and 35 percent from second-generation orchards (Weir 1977). However, this expected gain will be achieved only if several assumptions hold. Two major assumptions are that self-fertilization is not great and that the amount of contamination by nonorchard pollen is not significant.

Recent evidence indicates that the proportion of progeny arising from self-fertilization in loblolly pine seed orchards is probably less than 2 percent (Adams and July 1980, Freidman and Adams 1981). Thus, it will not be discussed further in this paper.

Empirical estimates of the amount of wild pollen fertilizing ovules in seed orchards is scarce. In a recent review, Squillace and Long (1981) indicated

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that -- based upon pollen flight patterns, measurements of background pollen, and other factors -- pollen contamination may be extensive in some cases.

To minimize pollen contamination, the policy of the NCSU-Industry Tree Improvement Cooperative is to recommend that each seed orchard have at least a 400-foot pollen dilution zone surrounding it. This dilution zone is expected to significantly reduce pollen contamination in seed orchards.

Until recently, only a few Cooperative members were obtaining sufficient seed to meet their annual regeneration needs. Therefore, seed orchard management practices emphasized increasing the overall yield of cones rather than assuring that the seed obtained was of the best genetic constitution (Woessner and Franklin 1973). Now that many orchards are meeting or exceeding their regeneration needs, emphasis can be shifted to improving the genetic quality of the seed obtained.

DISCUSSION AND ANALYSES

Genetic Consequences and Considerations

Maximum expected genetic gain from plantations established with seed orchard seed can only be obtained if there is no pollen. contamination. The clones selected for use in a seed orchard have undergone intensive selection for several traits. Through selection and establishment of seed orchards, tree breeders are creating new populations where the average frequency of favorable alleles for the traits under selection is higher than in the base population from which the trees were selected.

It is this increase in the frequency of favorable alleles that is responsible for the realized genetic gains observed in plantations and progeny tests. This gain can be a maximum only if there is no migration of pollen into the orchard. If migration occurs, the frequency of the favorable allele(s) in the seed orchard progeny is reduced. The change in average allele frequency in progenies from seed orchards due to pollen contamination, Δp_o, is

$$\Delta p_o = m(p_o - p_f) \qquad \text{(Wright 1976)}$$

where

m = ratio of outside pollen / (2) (outside + orchard) pollen
p_f = frequency of an allele "a" in the pollen coming from outside the orchard
p_0 = frequency of the same allele "a" in the seed orchard

It can be seen from this formula that both the amount of migration and the gene frequency differential between the two populations influence how much the expected gain will be diminished. The effects of pollen contamination on gene frequencies is illustrated in Table 1. For example, with a differential gene frequency between a seed orchard and source of contamination. of .10 and 40 percent pollen contamination, the effective gain in frequency of a favorable allele is .08 versus .10 when there is no pollen contamination.

Table 1. Effective gain in frequency of a favorable allele ($\Delta p'$) in progeny of seed orchards with varying amounts of migration (%) and initial gene frequency differentials, Δp.

		Δp										
		0	.01	.05	.10	.30	.50	.70	.90	.95	.99	1.0
% pollen migration (m)	0	0	.01	.05	.10	.30	.50	.70	.90	.95	.99	1.0
	20	0	.009	.045	.09	.27	.45	.63	.81	.855	.841	0.9
	40	0	.008	.041	.08	.24	.40	.56	.72	.760	.792	0.8
	60	0	.007	.035	.07	.21	.35	.49	.63	.665	.693	0.7
	80	0	.006	.030	.06	.18	.30	.42	.54	.570	.594	0.6
	100	0	.005	.025	.05	.15	.25	.35	.45	.475	.495	0.5

$\Delta p = p_o - p_f$ = differential gene frequency between seed orchard and source of contamination.

m = donor/ 2 (donor + recipient) pollen because the pollen supplies only 1/2 the genes of the tree.

$\Delta p' = \Delta p - \Delta p_o$

$\Delta p_o = m(p_o - p_f)$

Several important points can be noted in Table 1. If there is no pollen contamination then the maximum achievable genetic gain can be realized from the seed orchard. Also, if there is 100 percent pollen contamination the maximum achievable gain in the frequency of the favorable allele is one half of that expected with no pollen contamination. Assuming a completely additive genetic model, this will correspond to an actual gain of one-half of the expected gain. From a practical standpoint, there will always be some contamination unless the seed orchard is located ourside the range of the species or some method is used to speed up or delay the time of flowering in the seed orchard.

A second point illustrated in Table 1 is that pollen contamination has an effect only if there is a difference in average gene frequency, A p between the seed orchard and the source of contamination. Since the clones included in seed orchards will have undergone very intensive selection, a gene frequency differential should always exist between the two sources.

If the seed orchard is surrounded by stands or plantations of poorer genetic quality than the base population from which the clones were selected, the consequences of pollen contamination will be more severe than previously expected. One instance where this will be the case is with advanced-generation orchards. With the emphasis on quick turnover of breeding generations, it is conceivable to have a fourth-generation seed orchard surrounded by plantations originating from genetically nonimproved seeds or seeds from first-generation orchards. Advanced-generation seed orchards will have a larger gene frequency differential between orchard and nonorchard clones than first-generation seed orchards. This means the reduction in expected genetic gains resulting from pollen contamination will be greater than in the first-generation seed orchards. This is illustrated in Table 2, where the average frequency of the favorable allele is .15, .10 and .05 in the seed orchard, in the base population from which the clones in the seed orchard were selected and in the population that is responsible for the pollen contamination, respectively. In this case, the effect of 100 percent pollen contamination from population A would be to reduce the effective gene fre-

Table 2. Influence of percent pollen contamination and source of contamination on effective gene frequency of seed orchard progeny. Assume orchard frequency of allele is p = .15 (see text for explanation).

Pollen Contamination (%)	Population A Base population for clonal selections (p = .10)	Population B Nonbase population (p = .05)
0	.15	.15
20	.145	.140
80	.130	.110
100	.125	.100

quency of seed orchard progeny from .15 to .125 (halfway between the frequency of the allele in the seed orchard and the base population). If in fact the pollen contamination is 100 percent and originates from population B, then the effective gene frequency of the seed orchard progeny would only be .10; or in this example the same as in the base population from which the clones for the seed orchard were selected (population A). Thus, the expected gain due to selection would be nullified and the genetic quality of the seed would be about the same as that expected from the seed orchard of the previous generation in which there was no pollen contamination.

Economic Consequences and Considerations

Pollen contamination reduces the expected genetic gain. Whether or not action can be taken to reduce contamination depends on the cost of the corrective measure and the benefits obtained.

No satisfactory estimates of the amount of pollen contamination occurring are available, and it probably varies by orchard and year from less than 5 percent to 20 percent or more. The total cost that would be incurred to reduce pollen contamination will vary depending on whether corrective measures are undertaken each year that the orchard is flowering (e.g. supplemental mass pollination) or whether it is a one-time action, such as increasing initial orchard size or increasing the size of the dilution zone.

In the case where some action would be taken in each year the orchard flowers, the net present value (NPV) of the loss in gain due to one trait such as volume growth is given by the formula:

$$NPV_x = V_n / (1+i)^n \qquad \text{(Duerr 1960)}$$

where

x = age at which treatment is applied
i = interest rate
n = time from treatment until end of rotation (years)
V_n = s x b x r x g" x a = value at rotation age of loss in volume due to pollen contamination
s = stumpage value (\$/cord at time of harvest)
b = base growth rate (cords/acre/year)
a = number of acres planted per year
r = number of years in rotation
$g'' = (g-g') = g(\frac{m}{2})$ = loss in volume gain due to pollen contamination
g = expected gain in volume with no contamination (%)
g' = expected gain in volume with m amount of contamination (%)

The NPV for several levels of genetic gain, stumpage value and base growth when the level of pollen contamination is only 10 percent is shown in Table 3. For a projected gain in volume of 15 percent over nonimproved seed, an interest rate of 8 percent, a rotation age of 25 years, and a base growth rate of 1.0 cord/acre/year a company that plants 15,000 acres per year could spend up to $3,521 each year to reduce pollen contamination by 10 percent even at a moderate stumpage price of $10/cord. This amount increases as the interest rate decreases and as the stumpage value, base growth rate, number of acres planted per year, amount of pollen contamination or expected genetic gain increases. For example, the expected genetic gain in volume from second-generation seed orchards is 35 percent. Under the same conditions as first generation orchards, the amount that can be spent to reduce the level of pollen contamination by 10 percent is more than doubled (Table 3). The NPV in Table 3 represents the break-even cost that could be incurred each year to reduce contamination.

If it proves simpler or more efficient to reduce pollen contamination through a one-time operation such as increasing the size of the isolation zone, then the amount that could be spent can be estimated from the following formulae:

$$NPV_y = V_n \frac{(1+i)^p - 1}{i\,(1+i)^p} \qquad \text{Duerr 1960)}$$

$$NPV_o = \frac{NPV_y}{(1+i)^y}$$

where

NPV_y = value at the year before the first plantation is harvested of volume loss due to pollen contamination of all plantations originating from seed of that orchard.

y = number of years from orchard treatment until one year before the first plantation is harvested.

NPV_o = value at time of orchard establishment of volume loss due to pollen contamination of all plantations originating from seed of that orchard.

V_n = value at harvest time of loss in volume due to pollen contamination

p = number of years of full production of seed orchard

i = interest rate

The NPV at time of orchard establishment for the same conditions given in Table 3 is shown in Table 4. An additional condition, in this example, is that a seed orchard begins to produce enough seed to plant 15,000 acres per year at age 12 and continues to do so for 20 years. The figures in Table 4 represent the amount that could be spent at the time of orchard establishment to reduce pollen contamination by 10 percent under the conditions stated.

Both Table 3 and Table 4 consider volume gain only. If the added value of improvement in straightness, wood quality and other traits were considered, then it will be more profitable to reduce pollen contamination.

Table 3. Present value (at time of yearly treatment) of taking measures aimed at lessening the amount of pollen contamination occurring during a given year for the conditions given. 1/

	Case 1		Case 2	
Expected genetic gain	15%		35%	
Stumpage Value $/cord at time of harvest)	Base Growth (cords/ac/yr)		Base Growth (cords/ac/yr)	
	1.0	2.0	1.0	2.0
6	$ 2,112	$ 4,225	$ 4,929	$ 9,858
10	3,521	7,042	8,215	16,431
15	5,281	10,563	12,323	24,646
20	7,042	14,084	16,431	32,862
30	10,563	21,125	24,646	49,293

1/ Based on 25year rotation, 8% interest rate, 10% pollen contamination and 15,000 acres planted per year.

Table 4. Present value (at time of seed orchard establishment) of reducing the amount of pollen contamination occurring over the productive life of the orchard for the conditions stated. 1/

	Case 1		Case 2	
Expected genetic gain	15%		35%	
Stumpage Value ($/cord at time of harvest)	Base Growth (cords/ac/yr) 1.0	2.0	Base Growth (cords/ac/yr) 1.0	2.0
6	$10,376	$20,752	$24,210	$48,421
10	17,293	34,586	40,351	80,701
15	25,940	51,879	60,526	121,052
20	34,586	68,172	80,701	161,403
30	51,879	103,759	121,052	242,104

1/ Based on 25 year rotation, 8% interest rate, 10% pollen contamination, 15,000 acres planted per year and a productive life of 20 years for the seed orchard.

The use of pollen dilution zones is the primary method of reducing pollen contamination in most seed orchards. To be effective, the dilution zone requires a large amount of land be taken out of timber production. Therefore, maintaining a pollen dilution zone around a seed orchard can be very expensive. However, even a moderate reduction in pollen contamination is sufficient to justify the expense. For example, a 35 acre second-generation seed orchard might require an additional 80 acres to ensure a 500-foot pollen dilution zone. Assuming a land cost of $1,200 per acre, a base growth rate of 1.5 cord/acre/year, a stumpage value at the time of harvest of $15/cord, and an interest rate of 8 percent, the cost of including a 500-foot dilution zone would be about $107,000. To offset this cost (for a second-generation seed orchard) the dilution zone need reduce pollen contamination by less than 20 percent, assuming a base growth rate of 1.0 cord/acre/year, a stumpage value of $15 per cord, and the conditions stated in Table 4. That is, a 20 percent reduction in pollen contamination would give an increased stumpage value of $121,052 for a oampany that planted 15,000 acres per year.

In most cases, the actual cost of the pollen dilution zone will be much less than stated. When the seed orchard is on prime agricultural land (as assumed above) the land can often be leased to farmers for row or forage crops. When the seed orchard is not located on prime agricultural land, the land cost will be much lower than in the above example.

CONCLUSIONS AND RECOMMENDATIONS

Both the genetic and economic cost of contamination may be high and will be greater in the future. Each organization must determine how much pollen contamination it is faced with and must decide on what corrective measures, if any, it wishes to take. Among the options are (Squillace and Long 1981):

1. Increasing the size of the pollen dilution zone.

2. Increasing orchard size.

3. Use of only clones whose flowering times are known to be fairly synchronous.

4. Use of management practices to increase pollen production.

5. Increasing scrutiny to seed orchard site selection. Among the variables to consider are abundance and genetic quality of surrounding stands or plantations. The ideal situation would be to locate an orchard outside the species range or in an area where the flower phenology of the orchard trees would be out-of-phase with those contributing the background pollen.

6. Modification of the environment of the seed orchard so that the trees are out-of-phase with those in the surrounding area.

7. Use of supplemental mass pollination techniques (SMP) to increase the relative level of orchard pollen present at crucial times (Bridgwater and Trew 1981, Woessner and Franklin 1973).

All of the above options have some merit. If it is not possible to locate an orchard in an area with no background pollen, the best choice would probably be to use a combination of several of the options listed.

Use of pollen dilution zones is a standard practice for members of the N. C. State - Industry Tree Improvement Cooperative. The dilution zones are no doubt effective in reducing the level of pollen contamination. However, the precise effectiveness of these dilution zones is really unknown. The two estimates of pollen contamination presently available are 28% in one case and greater than 80% in another case (Friedman and Adams 1981, Squillace and Long 1981, respectively). Both of these studies used small orchards, so the estimates of pollen contamination obtained may be higher than expected in a typical seed orchard. The genetic and economic consequences of pollen contamination will continue to increase as more advanced-generation seed orchards are established. Therefore, more information is needed on the amount of pollen contamination occurring in seed orchards to determine if it is severe enough to warrant additional attention.

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