CONTINUED RELIANCE ON WIND-POLLINATED SOUTHERN PINE SEED ORCHARDS - IS IT REASONABLE?

R.A.Woessner and E.C. Franklin[1/]

Abstract.--During the past 15 years a tremendous amount of individual and organizational energy has been devoted to successfully establishing southern pine seed orchards. Many orchard management techniques have been perfected. A review of the current status of the orchards indicates that a system such as mass dusting of orchard ramets with pollen could serve several useful purposes. Whether supplemental pollination will prove to be economical remains to be seen. However, the potential gains to be made in this direction and the reduced gains if the wind-pollinated orchards performed at their worst certainly indicate that more thought and research effort should be given to this particular aspect of seed orchard management.

Additional keywords: Supplemental pollination, mass-artificial pollination, Pinus taeda, Pinus elliottii, Pinus echinata.

The successful operation of southern pine seed orchards is based upon a number of biological principles and assumptions. To the extent that these are not fully satisfied, or are only partially satisfied, the orchards will not produce seed of the most desired genetic constitution. With all factors considered relating research results and observed performance of the orchards to date, it appears that a supplemental pollination system is needed, such as mass dusting of orchard ramets, as described by Wakeley et al. (1966) whereby the pollination process in the seed orchards is controlled to a greater degree than with wind-pollination.

WHAT ARE THE PROBLEMS WITH THE WIND-POLLINATED ORCHARD

To have maximum efficiency, the "ideal" wind-pollinated, general combining-ability seed orchard relies on the following: (1) the orchard ramets of each select tree will be more or less completely isolated from surrounding unselected trees; (2) ramets will be equally productive of male and female flowers; (3) ramet pollen flight and female flower receptivity will coincide; (4) crosses among clones will be equally compatible; (5) natural self-fertilization will occur at insignificant rates. It appears that not all of the above conditions are being completely realized in practice in a large number of orchards.

Contamination by Foreign Pollen

When wind-pollinated species are established in seed orchards, dilution zones are usually established to prevent contamination from outside sources of pollen. This is understandable because expected genetic gain from seed produced on orchard ramets pollinated by unselected trees is one half that expected if both parents were in the orchard. Seed by contaminating pollen is genetically equivalent to open-pollinated seed from the selected ortets in the woods.

[1/]Authors from Texas Forest Service, College Station, Texas and Southeastern Forest Experiment Station, USDA Forest Service, Olustee, Florida, respectively.

The frequency of such seed is dependent on the availability of foreign pollen. This is especially important in the south because of the difficulty in establishing a seed orchard that is suitably isolated from the vast acreages of natural and artificial pine stands.

Considerable research in this country and in Europe has been devoted to the study of pollen dispersion; for example, Wright (1953) has shown that the amount of contamination for any given ramet depends on factors such as the size and age of the orchard, the location of the ramet within the orchard and the size and type of dilution zone. Dilution zones with a minimum of 500 feet were recommended for southern pines based on data that indicated only 5 percent of pollen from a particular tree will travel 500 feet or more (McElwee 1960, Wang et al. 1960). In Europe, Andersson (1955) estimated as much as 30 percent contamination from studies with Norway spruce (*Picea abies* L.) and Scots pine (*Pinus sylvestris* L.) at dilution zone distances up to sixteen times greater than the minimum recommended for southern pines. Wang et al. (1960) quoted the minimum width of 500 feet to be satisfactory as follows: "The percentage of extraneous pollen, therefore, would be negligible when the trees in the seed orchard begin to produce pollen in quantity as they reach seed production age. Turbulence and unusual weather, however, can make an isolation strip adequate one year and inadequate the next." McElwee (1960) states quite the same: "Distances which prove to be effective barriers in one year will be insufficient in another." A publication by Lanner (1966), mainly a synthesis of research by others, points out that weather conditions which favor pollen shed promote the formation of strong thermal shells (the normal mechanism by which warm or moistened air rises) and suggests that these shells may provide for uplift and transfer of pollen long distances. He feels that the practical isolation of open-pollinated seed orchards seems even riskier than presently thought and they will be subject to erratic and perhaps unpredictable meteorological forces. The interesting point here is that a weather condition which is conducive to maximum pollen shed in the orchard (warm dry air) could also increase the amount of pollen reaching the orchard from outside, unselected sources.

Presently, there are no direct estimates of the amount of contamination in large commercial orchards. Squillace (1967) in a 5-acre orchard did demonstrate for slash pine (*Pinus elliottii* Engelm.) that if the orchard produced no pollen at all, pollen from outside the orchard was of sufficient abundance to produce normal yields of 50 full seeds per cone.

Equal Productivity

Sizeable variability among clones in production of both female and male flowers has long been evident to anyone working in a seed orchard. Kellison (1971) indicates that the reproductive behavior of second-generation orchard trees is especially important because of the fact that 80 percent of the seed obtained from the first-generation orchards is produced by only 20 percent of the clones. Thus, some of the most productive orchard genotypes are produced in limited numbers because of low fecundity. Kellison (1971) and van Buijtenen (1971) indicate by their discussion that differences also exist among clones in pollen production. Bergman (1968) subjectively rated 15 loblolly clones for their pollen producing ability on a scale from 0 to 5. The poorest clone scored .2 and the best 5.0. He concluded from the data on female and male flowering intensity that 50 percent of the progeny from one orchard would come from the two heaviest cone-producing clones. He also found that clones vary in the number of seed per cone (52 to 122 seeds per cone) and the percentage of unfilled seed. The percentage of unfilled seed varied from 53 to 8 percent. Clones can have low filled seed yields because of natural selfing or because they are out of phase with the other clones in the orchard. Supplemental pollination could alleviate these problems and thus bring about a more equal production from the orchard clones. The age of the orchard and ramet spacing are also recognized factors affecting the percentage of filled seed. In the early years, pollen is quite scarce. Supplemental pollination could alleviate the problem of a pollen shortage in young newly established orchards. Likewise, because of the scarcity of pollen in the formative years of the seed orchard, four times as many grafts are planted than are ultimately desired (Kellison 1971). With supplemental pollination, perhaps fewer grafts would have to be established initially.

Floral Phenology

There is considerable older documented evidence of differences in male flower anthesis and female receptivity (McElwee 1960, Goddard 1964, Jurriaanse 1964, Dorman and Barber 1956). Recently, a report from the Western Gulf Forest Tree Improvement Program indicates that two slash pine orchards flowered well in the spring of 1972, but pollen was not synchronized with female flower receptivity so seed yields were projected to be low in 1973.[1/]

Wasser (1967) did a floral phenological study of seed orchard loblolly pine (*Pinus taeda* L.) and shortleaf pine (*Pinus echinata* Mill.). The female flowers of the clones could differ in maximum receptivity by five days. Pollen of some clones was shed before orchard maximum female receptivity. In other clones, pollen shed lagged behind orchard maximum female receptivity.

A study with shortleaf pine indicated repeatability in fruitfulness and timing of pollen shed. Schmidtling (1971) found that pollen-bearing trees could be predicted from past performance with a fair degree of accuracy. Also there was fairly good agreement in individual trees as to time of shedding from 1969 to 1970 (r - .827).

In order to circumvent the phenology problem, Barber (1964) suggested that adequate numbers of phenologically matched individuals be included within the orchard to yield maximum cross- and minimum self-fertilization. This is an imposing task and it is not sound to use genetic selection to circumvent a problem which might better be handled in another manner. To satisfy the flowering criteria we might be lowering the selection differential for the economically desirable characteristics.

Equal Compatibility among Clones

Incompatibilities among clones are quickly evident to anyone attempting to complete a specific number of crosses for a progeny testing scheme. Seed is obtained in abundance for some crosses whereas other combinations are partially or completely incompatible. Partial incompatibility is indicated by the results of Snyder and Squillace (1966); they report averages of 29 seeds per cone from multi-pollen versus 18 seeds per cone when a single male was used. These values are based on results from a great number of crosses.

[1/] Texas Forest Service. 1972. 20th Progress Report of the Cooperative Forest Tree Improvement Program. Circular 213.

Self-Fertilization

The detrimental effects of self-fertilization are readily recognized in the southern pines. Studies by Kraus and Squillace (1964) with slash pine and Franklin (1971a) with loblolly pine attest to the high rates of selfing in these two species. Studies of selfing in southern pines have consistently shown drastic reduction in yields of filled seed and moderate to severe reductions in germinability of filled seed and in subsequent height growth of seedlings (Franklin 1969, 1970). High rates of selfing within seed orchards may be one major factor in reducing yields. It has been observed that seed yields in many orchards start out at satisfactory levels for the age of the orchard but then show a relative decrease with increasing orchard age (Franklin 1971b). This result is found because in a young tree the female conelets are borne near the top and the male catkins near the bottom of the crown and selfing is minimal. But the typical result of crown development in orchard trees is that the midcrown becomes an area of intimate association of conelets and catkins. This leads to a tremendous increase in self-pollination in the lower and midcrown areas.

The result of the last four mentioned factors (i.e., equal productivity, phenology, compatibility and selfing) is that we do not actually have equal numbers of progeny from each clone contributing to orchard production. Thus, instead of the orchard being composed of random cross-breeding clones, it consists of a series of specific crosses between the clones in which compatibility, receptivity and pollen anthesis happen to coincide. This specificity of crossing is determined by the individual genetic constitution of the clones, the particular weather conditions prevailing in any given year, and the location of the ramets of various clones within the orchard. Within seed orchards specific limited combinations are being produced, but not on the basis of characteristics of importance to the forest manager, such as increased growth or disease resistance. Combinations are determined purely on the basis of compatibility, receptivity of conelets and availability of pollen.

WHAT IS AN ADEQUATE GENETIC BASE

The superior tree concept along with the rest of forestry is being criticized by the environmentalist faction. The environmentalists question the use of a few genotypes to regenerate large acreages. Nelson (1971) in the 11th SFTIC Keynote address states that we must really work at keeping a broad genetic base and questions whether the base of first-generation-orchards should have been broader. The question is not easily answered. However, it appears that in some cases a lot of acreage could be regenerated with a limited number of genotypes. Assume a 20 clone orchard of 40 acres in size that will have a seed producing life of 25 years. Further assume a regeneration rate of 300 acres per acre year of orchard for the 25 years or a total of 300,000 acres regenerated. Also assume that 80 percent of the seed will come from 20 percent or four of the clones. Over the 25 years, 240,000 acres would be regenerated with 4 maternal parents. Supplemental pollination could help broaden this genetic base by assuring that different male parents were involved. Males chosen for supplemental pollination could be chosen on the basis of superiority so that the overall percentage gain of the orchard would be increased. A striking example of the effect that different male parents can have on progeny rust infection when crossed to a common female is presented by Woessner (1965). Five loblolly males were crossed to a common female (Table 1). The female parent, 11-2, was shown by an open-pollinated test to be 22 percent above average in rust susceptibility whereas the five males averaged 9 percent below their plantations. The full-sib crosses of 11-2 with the five males averaged 37 percent infection while the range was from 11 to 59 percent.

Table 1.--Comparison of percent infection of southern fusiform rust on open- and control-pollinated families; tree 11-2 was the female parent in all the control crosses.

	Open-pollinated		Control-pollinated	
	% infected	Plantation mean	% infected	Plantation mean
11-41	14	34	11	37
11-9	26	34	21	"
11-20	13	19	37	"
7-34	22	27	55	"
11-18	16	19	59	"
11-2	41	19		

THE EFFECTS OF THE ENVIRONMENT ON FLOWER PRODUCTION

Weather conditions can influence orchard performance in ways other than pollen dispersion (Lamb et *al.* 1973). These need not be as drastic as hail or freezing weather which affect both the female and male flowers. Cool, wet weather in the spring can result in the female flowers continuing to develop while the male flowers are retarded. Even if the catkins have reached maturity, rainy, damp weather retards shedding. Climatic and site conditions also influence the male and female flowers differently. On two matched orchards in different areas, Jurriaanse (1966) found that the one getting the lowest rainfall produced the greatest number of female flowers per ramet. Timing of moisture is also important in female flower production (Lamb *et* al. 1973), Dewers and Moehring 1970). Conversely, a positive influence of moisture on pollen production relative to cone production was indicated by the work of Florence and McWilliam (1956). They showed that wild stands on better, more moist sites produced 1.3 times as many cones but 4.2 times as much pollen as the dry site.

Management practices currently used in the majority of orchards appear to be aimed mainly at increasing the overall yield of cones, not assuring that maximum pollination takes place. This situation could arise because of an interaction between irrigation, fertilization and male and female flower production. Studies by van Buijtenen (1965) indicate that mineral fertilization increases the number of female flowers, decreases the number of male flowers, but overall cone production is increased. Bengston (1965) states that irrigation had a significant depressing effect on female flower production, but promoted pollen production. In a seed orchard study combining irrigation and mineral fertilization, Gregory (1968) found that irrigation increases male flower production relatively more than fertilizer alone, while irrigation and fertilization together gave the greatest increase over the control. Fertilizer gave a greater increase of female flowers than irrigation, but both together produced many more cones than the control. But, cone production is only part of the story; also important is the number of germinable sound seed per cone. Sound seed per cone is known to double in years of pollen abundance. (Florence and MoWilliam 1956). Van Buijtenen's data (1965) shows that the control had greater pollen production but 10 percent less sound seed than the fertilized plots in a year which had a normal spring. The next year the control again had the greatest pollen production but due to a freeze which damaged the pollen, the control exceeded the fertilized plots in percentage of sound seed by 38 percent, although having only 49 percent as many total seed. Thus, although fertilizer increased the number of cones and increased yield generally, it appears to have decreased pollen production to the point that it became critical in a poor year. A similar situation was found by Gregory (1968) in that the control and irrigated only plots have a higher percentage of full seed than the fertilized and irrigation plus fertilized plots. There were no data concerning pollen production for this particular seed crop.

Strictly from a viewpoint of orchard management, even if a near randomly breeding, well-isolated orchard composed of self-sterile clones existed, relying wholly on wind-pollination must be considered a weak link in the efficient production of seed. For maximum efficiency, orchards must produce crops annually in spite of the weather. The effects of weather could be overcome considerably if mass artificial pollination is used. It certainly cannot make up for losses in conelets due to hail or freezing weather, but it could assure that the cones that matured would have larger numbers of filled seed per cone. The amount of money spent on orchard maintenance and protection is dependent on the size of the orchard, not on the yield for any given year. It costs just the same to protect, irrigate, and fertilize a tree with 20 cones as the same tree having 120 cones. The same is true whether the cones have many or few sound seed.

IS SUPPLEMENTAL POLLINATION FEASIBLE

Gains from applied breeding programs are not absolute but must be considered in terms of cost per unit of improvement. Up to that point in time when improved seed is available for all the needs of all planting programs, any cultural practice which would increase the total annual seed yields from an orchard should be considered feasible if the cost per pound did not exceed the point at which it was more profitable to plant nursery run seedlings.

Results in certain South African orchards have overwhelmingly proven the ability of artificial hand pollination to increase seed yields. It was conclusively demonstrated that hand pollination more than doubled the yield of filled seeds compared to orchard open-pollination even with abundant pollen production in the orchard (Denison 1971).

Recent results indicate that the first pollen to reach the female flower has the highest probability of effecting fertilization (Franklin, in press). Therefore, if weather conditions cause the conelets to be receptive before pollen flight from the same tree, either orchard pollen or foreign pollen would have the first opportunity for pollination. If pollen flight and maximum receptivity coincided, much self-pollination and eventual self-fertilization would probably take place because of the high density of self-pollen in the area of receptive, previously unpollinated conelets. If mass-artificial pollination were done as soon as or slightly before conelets reached maximum receptivity, the frequency of self-fertilization as well as fertilization resulting from pollination by non-orchard pollen could be drastically reduced. This would be due to the result of the mechanism of the pollination droplet described by Doyle and O'Leary (1935). The pollen is captured in a droplet of fluid which exudes from the nucellar tissue. When several pollen grains have been captured, the droplet will not exude again. When self and cross pollen grains are captured within the same droplet, all evidence indicated that the self-pollen suffers no disadvantage in accomplishing fertilization (Franklin 1970). But the embryo resulting from self-fertilization would usually be at a disadvantage, especially if it had to compete with an embryo resulting from cross-fertilization (Fowler 1964). Thus, even a mixture of artificially applied cross pollen with native self-pollen would be preferable to self-pollen alone.

Producing more seed is only part of the answer. In looking toward the future, we must consider current trends in forest management and see how mass artificial pollination fits with them. The argument has been presented in the past (McElwee 1960) that we do not need all superior seed because we always harvest fewer trees than we plant. This argument is much less relevant now than originally proposed. Such an argument is reasonable under forest management with a close original spacing and one or two law selective thinnings to remove the poorer trees. Current management practice is dictating short rotations, wider spacing, non-selective row thinnings and uniform tree sizes for mechanical harvesting.

Management is not only demanding uniformity in seed quality, but also seed of a specialized nature--seed that will produce trees suited for special purposes and for special sites. Even now one sees the demand for trees with specific wood properties, high resistance to *Cronartium,* better response to fertilizer, or seed with specific germination properties for direct seeding. What happens when the results of the progeny tests indicate that certain parental combinations are growing faster, and straighter, and are more disease resistant but one of the parents is either a poor cone or pollen producer or is out of phase with the rest of the orchard? Several alternatives are available such as using two-clone orchards, controlled-pollination, mass dusting, or even new selections. The ultimate solution might be two-clone orchards supplemented with mass-artificial pollination. But how are we to supply these needs as quickly as possible? Are the management personnel going to be willing to wait six or seven years for us to re-establish new orchards?

In the meantime, however, in the present orchards, we can increase the percentage of desirable offspring simply by mass dusting with known good combiners. Only a portion of an orchard system might be managed for production of pollen, the remainder managed for production of seed. When rogued, the clones left in the seed production orchard would be judged on general performance of progeny and cone productivity. The former should be given the most weight, but the seed orchard should be managed to give maximum cone production at the expense of pollen production. In order to avoid outside contamination the orchard could be put out of phase with the surrounding area by irrigation[1/]

[1/] Anon. 1966. Tenth Annual Report N.C. State-Industry Cooperative Tree Improvement Program.

(Silen and Keane 1969). Pollen for mass dusting could come from a pollen orchard managed specifically for pollen production, the individuals here judged on the basis of pollen productivity and general performance of progeny. Such pollen orchards might be located several hundred miles south of the cone producing orchard to assure that the pollen would be available before the conelets were receptive.

SUMMARY

A review of the current status of pine seed orchards indicates that (1) some present day orchards are not randomly breeding and clones differ in productivity of pollen, cones, and seed; this can result in a narrowed genetic base, (2) lack of adequate amounts of pollen can result in high proportions pf contaminate pollen or too little pollen for maximum seed set, while large amounts of pollen may cause excessive selfing, (3) weather conditions may drastically affect yields and the seed quality, and (4) current orchard management practices could be altered to favor either male or female flower production as needed.

To offset the above adverse conditions in the seed orchards, mass dusting of ramets with pollen as described by Wakeley, et al. (1966) and Franklin (1971b) could have the following beneficial effects: (1) higher, earlier and more consistent seed yields, (2) less selfing, (3) a greater percent improvement from the established orchards by using highly superior clones as male parents, (4) the genetic base of an already established orchard could be broadened.

Whether supplemental pollination proves economical remains to be seen. However, the potential gains to be made in this direction and the reduced gains if the wind-pollinated orchards performed at their worst certainly indicate that more thought and research effort must be given to this particular aspect of seed orchard management.

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