

Reproductive Phenology and Precocity as Factors in Seed Orchard Development

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Although in wide use, seed orchards in concept and in practice are still new. Developmental techniques have only begun to evolve. Much diversified experimentation, accompanied by close and sustained observations requiring a cooperative effort by many workers in many places, must be continued before we can turn to our advantage some of the unfolding complexities of the over-all problem.

It seems appropriate to consider reproductive phenology and precocity in forest trees in terms of seed orchards in particular. Why? For reasons already advanced by Zobel and McElwee (21), seed orchards hold great promise in producing in the shortest possible time large commercial quantities of genetically improved seeds for forestation. The consequence is that public and private agencies are increasingly active with seed orchard programs in those parts of the world where forestry is being practiced most intensively.

In seed orchards, most of what we do or fail to do—wittingly or unwittingly—has genetic consequences. For example, almost constant concern has been given to the question of what constitutes an adequate number of clones or families in a seed orchard. Seemingly, however, relatively little consideration has been given to the adverse effects which differences in flowering time can have on the basic need for unrestricted pollen exchange between the selected genotypes in the orchard.

Namkoong *et al* (11) point out that free mating (panmixia) is assumed as a basis for the theoretical gain estimates made for various breeding systems. Marked divergences from panmixia can result through differences in fecundity between genotypes. A further deviation from unrestricted mating occurs when the various participating genotypes are out of cycle in their reproductive phenology (i.e., in the calendar timing of the sexual process). It is not difficult to imagine that the cumulative effects of these departures

from panmixia can be serious enough to place a breeding scheme in jeopardy.

The fact of large differences in fecundity between clones and among young trees is rapidly becoming more evident (3, 4, 8). Field observations and results obtained in breeding or testing cause some workers to select for early seeding trees, either as a matter of expediency or with the stated objective of developing precocious seed orchards. Conversely, selection against early seeding trees is a practice in Russian silviculture (12). This is based on observations that precocious numbers of natural stands commonly mature at an early age. Not only do they fail to attain a normal size but characteristically they are crooked and excessively limby.

Recent observations in an 8-year-old Scotch pine (*Pinus sylvestris* L.) provenance study provide a basis for further consideration of reproductive phenology and precocity as they relate to seed orchard development.

STAND DESCRIPTION AND PROCEDURE

The subject plantation is part of a broad Scotch pine provenance experiment initiated by Dr. Jonathan W. Wright at Michigan State University. He produced and distributed 2-0 planting stock to various participating stations. Wright and Bull (19) have described results obtained in the nursery phase of this work. Wright *et al* (20) later reported on the performances of the stocks from different provenances after 4 years in the field (6 years from seed), as recorded under a wide range of site conditions in the North Central states.

There has been surprisingly little site-origin interaction. In general, seedlings from origins which have given good results in Missouri have performed well in other states and vice versa.

Also, there is a strongly positive relationship between nursery performance and results obtained after several years in the field in terms of such traits as

needle length, winter color of foliage, and growth rate. Now in their 8th year from seed and after 6 seasons in the field, color and height contrasts observed in the nursery seem to have been even further accentuated with each succeeding year.

In the planting studied as a basis for this paper, average heights of trees from the different geographic sources are ranging between extremes of 9 feet and less than 2 feet. Differences in crown volume, of course, are correspondingly much greater. Other things being equal, the amount of crown greatly influences the abundance of coning. Other things are not always equal, however, and some small trees were observed to have a reproductive proclivity while some of the largest trees were remaining strictly vegetative. This lack of a consistent relationship between size and degree of reproductivity was found within as well as between origins.

Not until the outset of the 8th season from seed (1966) was it possible to make meaningful comparisons within and between sources as to the dates of pollen shedding and relative abundance of reproductive structures. There had been a low and slowly increasing level of ovulate development since 1963, restricted to certain trees within only a few origins. Slight amounts of pollen were produced as early as 1964 but it was not until 1966 that structures of both sexes were present in abundance.

Beginning on May 1, when the first pollen flight was observed on a few of the origins, and continuing through the remainder of that month, reproductive phenology was followed closely at 3-day intervals. Stage of development was recorded periodically by sex, as follows:

Female

- 1—buds unopen
- 2—buds opening at tip
- 3—early receptivity
- 4—full receptivity
- 5—scales thickening
- 6—scales closed

Male

- 1—strobili entirely succulent
- 2—initial pollen flight
- 3—full pollen flight
- 4—late pollen flight
- 5—faded

On May 7, three men working together obtained an inventory of pollen structures on all of the 1272 trees now living in the plantation. For each tree, the number of clusters and the total number of staminate strobili were obtained. On a relatively few trees, large numbers of clusters were found. The total

number of strobili on these were estimated, based on random counts of 10 clusters.

Wet and unseasonably cold weather followed the May 7 staminate strobili inventory. A complete tree-by-tree count of the ovulate structures was made on May 12, 13, and 14. This was a slow and tedious task because the female conelets are easily overlooked, especially in the bud stage or on those trees having conelets of an inconspicuous pale color instead of a distinctive pink or red. The procedure was to start at the top of the tree and proceed downward whorl by whorl.

For both sexes, position of the structures was recorded on each tree as top, middle, or low crown or any combination of these.

Seventy geographic origins of stock are included in the plantation. Broadly representative of the extensive natural range of Scotch pine on the Eurasian land mass, these provenances represent an east-west range from Siberia to Scotland and cover a north-south span from Scandinavia and Russia above the 60° N. parallel down to Turkey, Greece, southern Russia, Italy, and Spain.

Plot size is 4 trees in a 1x4 arrangement across contours, using a 7x7-foot spacing. There are five replications in a randomized block design. The topography is gentle, with gradients ranging between 2 and 8 percent. Two of the blocks are located along the top of a low ridge, two downslope with a northeast aspect, and one downslopes to the southwest. Although no significant difference in development, vegetatively or sexually, can yet be attributed to block effects, the trees are somewhat smaller and survival is poorer on the warm and edaphically more severe southwest slope.

The Weldon soil is nutritionally poor. Of light color, it was originally covered by a layer of loess but this has been lost through past agricultural abuses. The remainder is a tight silty clay subsoil a few feet in depth, underlain by limestone.

Preliminary to planting, the area was subsoiled and disked to achieve a greater site uniformity. There has been no subsequent cultivation of the soil but the plantation has been mowed once or twice each growing season to hold down herbaceous cover and sprouts.

The location of this plantation is in southeastern Boone County, central Missouri. One of five such plantings established in Missouri as part of the regional study of Scotch pine provenances, the plantation was especially suitable for this particular study because of its good survival (91 percent), the generally good condition of the trees, and the quick accessibility from the University of Missouri campus at Columbia.

RESULTS AND DISCUSSION

Phenology

Great variation was found between provenances in the dates of reproductive events. Some origins were separated by as much as 3 weeks in their pollination dates, which means complete sexual isolation. From this extreme, differences ranged downward through varying degrees of partial separation to a complete harmony in the timing of pollen exchanges.

In general, there was a phenological gradation among sources from north to south and east to west, with sources from the far north and those from Turkey and Greece being first to "flower." Latest were those origins from Spain, southern France, and Scotland. This relationship lacks clear definition, however, in some of the intervening territory. For example, some origins from northern and central Germany were late in their pollination dates, their male structures being still in the succulent stage on May 7 when certain origins in southwestern Germany and neighboring France were in advanced stages of pollen shedding.

A complex of factors can disrupt the general pattern that suggests a clinal relationship in north-south and east-west directions. Among them are the variations due to continental vs. maritime influences on weather, the effects of topography on local climate, and the uncertain influences of man on patterns of natural adaptation. Seed origin is not known for many of the older planted stands and some apparently indigenous stands may actually have been derived directly or indirectly from plantations.

Add to these variables the further uncertainty of local tree-to-tree variation in phenology. Adaptive relationships between trees of the same species in a locality are often uncertain.

Bingham and Squillace (1) found certain *Pinus monticola* Dougl. individuals to be consistently early or late in their flowering dates, with respect to others, despite an apparently uniform habitat in a valley.

Hahn (personal communication) reported phenological differences in flower bud development between clones of a Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) seed orchard. However, the differences in reproductive dates were less striking than for vegetative bud bursting dates, which had a spread of 5 to 6 weeks among the clones. Observations in one season (1966) in this young Douglas-fir orchard showed time of incipient pollen shed to range from April 8 to April 18. Periods of female conelet receptivity ranged between extremes of April 10 to 18 for one clone to April 23 to 30 for another.

Langner (7) reported tree-to-tree differences in the reproductive phenology of a 50-year-old planting

of *Picea omorika* (Pancic) Purkyne, a species considered rather uniform genetically.

Theoretically, there is no reason to believe that all trees of a species within a local population or, more broadly, a geographic race will be reproductively in cycle with each other. The lack of such unison would add to the heterogeneity of the population, which would seem to give the population the advantage of a greater adaptive flexibility in a highly variable habitat, such as mountainous terrain. Apparently, however, considerable tree-to-tree variation in reproductive phenology can be found within locales characterized by a greater uniformity of site.

McLemore and Derr (9), working in central Louisiana, selected for controlled pollination 23 trees, similar in size and age, in a 45-year-old stand of *Pinus palustris* Mill. These trees were examined at 1- to 3-day intervals, and the controlled pollinations were effected at the stage of maximum receptivity. Dates of pollen application ranged from March 2 to 12.

In the present study there was considerably less range in reproductive phenology within sources than between sources. The general finding within origins ranged from a high degree of harmony in sexual cycling to varying degrees of overlap in timing. Within a four-tree plot representing an origin, however, individual trees were occasionally observed to be separated by several stages in their sexual development. For example, one tree of a plot would be at stages 1 and 2 (buds unopen to opening) in the development of female conelets and another in the same plot would be at stages 4 and 5 (full to late receptivity). Inasmuch as there was practically no indication of dichogamy, such trees would not be expected to exchange pollen. Moreover, it seems likely that they would receive pollen from quite different sources.

As still another variable, a crown-position gradient in the development of ovulate conelets was found on individual trees. Buds opened first in the top of the tree and progressed downward through the crown. In extreme cases, where ovulate conelets were found all through a tree crown, as many as four stages in development were found at a given time, e.g., stages 1 through 4, with buds unopened in the low crown and progressing sequentially upward to full receptivity to pollen in the top. This relationship of developmental stage to crown position has been observed in mature Scotch pine stands in Finland by Sarvas (14).

Such a crown-related sequence in development on individual trees was not noted in the case of pollen. The correctness of this observation seems to have support through the findings of Saylor and Smith (15), who reported little correlation between

the sizes of microsporangiate strobili on the same tree and stages of development of pollen mother cells. This is somewhat surprising in that staminate cone size has been observed to vary more with position in a cluster of strobili than with location in the crown. The basal strobili in a cluster are normally larger and appear more mature, becoming progressively smaller in an apical direction.

It is the writer's observation that male strobili on the same tree do vary in time of pollen dispersal. There is variation within a cluster with maturation progressing acropetally. There is also variation between clusters but any possible relationship to position in the crown has not been noted. This needs further study.

What are the implications of these observations on reproductive phenology? Certainly this is a source of variation which can drastically affect tree-to-tree relationships in open pollination. Consequently, the question of phenology should be given careful consideration in commercial breeding schemes. There are probably seed orchards in existence in which the ideal state of free mating among the selected genotypes is far from a reality. Among other things, this is restrictive on the wide range of recombinations of

good germ plasm that might otherwise be expected, thus diminishing the prospective base for future selections. Also, genotypes of clonal or other origin which are either partially or virtually isolated reproductively as a consequence of their phenology will have higher levels of inbreeding and lower seed yields.

What precautions can we undertake as safeguards against such eventualities? One possible but somewhat uncertain measure would be to increase the number of clonal or family selections in the orchard. Stern (16) calculated that, in the case of nearly ideal panmixia, 20 to 30 clones would be adequate but he suggested that 30 to 40 clones would be needed where free mating is restricted. Still a better approach, and seemingly a real advancement in seed orchard technique, would be to make phenological determinations as a basis for assembling genotypes into an orchard.

There may be a good and sufficiently reliable correlation between vegetative and reproductive phenology. In the present study of Scotch pine, a strong relationship was noted between needle development and reproductive events. Origins which were early in their pollination dates were also more advanced in their production of new needles. At stage

TABLE 1.—Reproductive Structures (Male and Female) per Fertile Tree of the 10 Sources Most Productive of Staminate Strobili.

Acquisition No.	Origin	Male		Ovulate Conelets	Fertile Trees of 20	
		Clusters	Strobili		Male	Female
202	Germany 53° N, 10°35' E el. 300 to 400 ft.	71	2,175	13	3	11
318	Belgium 51°15' N, 5°30' E el. unknown	78	1,643	42	8	18
554	Italy 45°59' N, 11°11' E el. 2400 ft	65	1,109	21	3	11
555	Italy 46°20' N, 11°19' E el. 3100 ft.	42	475	34	4	13
236	France 48° N, 2°18' E el. 500 ft.	35	413	15	5	12
221	Turkey 40°30' N, 32°40' E el. 5000 ft.	15	406	3	1	2
239	France 45°18' N, 3°40' E el. 3200 ft.	18	337	13	5	6
528	Germany 50°37' N, 12°01' E el. 1400 ft.	15	164	4	1	9
305	Czechoslovakia 49° N, 14°45' E el. 1300 ft.	7	153	11	2	7
309	Czechoslovakia 50°55' N, 15°5' E el. 2500 ft.	12	152	10	1	11

1 for ovulate cones (buds unopen), needles were still in the pinfeather stage, i.e., the new needles had not emerged through their fascicle sheaths. By stage 6 (conelets closed), needles had grown to approximately half their normal lengths.

According to Vavilov (18), the breeder is likely to realize greater gains through crossing of individuals from widely separated provinces than in utilizing selections from within a restricted range. Prior to observing the unexpectedly great range in the dates of pollen release among the 70 Scotch pine provenances, as described above, the author had contemplated a test orchard in which wide crosses could be effected, utilizing good Christmas tree phenotypes selected at various test sites and brought together on a common area. Hopefully, based on test results, such an assemblage of material would be used eventually as a seed orchard.

In the case of Scotch pine, an assortment of clones of such individuals, representing origins widely separated by geography or perhaps altitude, could serve only as breeding material. Looking ahead, however, there seems to be a very good possibility that judicious crossings could blend genotypes so that Ft generations would be phenologically together in their reproductive processes if there were an intermediacy of offspring between parental extremes.

There is some evidence of this. Pauley and Perry (13) found that progenies obtained in crosses of northern and southern origins of *Populus deltoides* Bartr. had photoperiod responses intermediate between those of the parents. Saylor and Smith (15) report that the time of meiosis is usually intermediate between the two parents in *Pinus* hybrids.

Precocity

Among the 70 Scotch pine provenances, wide variations are also being observed in the earliness and relative abundance of reproductive structures. In general, those sources which produced cones first are now most fecund. This is in accordance with the conclusion of Mergen (10), who reported that once trees start flowering they can continue to do so.

There is no obvious relationship between fecundity and geography. Among the 70 provenances, the 10 most precocious origins, based on their 1966 performance, are from such widely separated sources as Germany, France, Italy, Czechoslovakia, and Turkey (see Table 1).

This should not be surprising. As shown below, there is growing evidence that tree populations have a great potential to respond quickly to selective pressures for precocity. Undoubtedly there have been different degrees in such selective pressures between the parent stands which provided seed for this



Fig. 1.—“Nye Branch” seedling of Scotch pine 1 year after planting as 2-0 stock, with female conelets at top and staminate cone clusters in low crown.

provenance study. Stand-to-stand comparisons are presently impossible, however, because of a lack of information on variation in selection pressure.

In nature there is evidence that precocity is a survival mechanism in habitats where disaster occurs frequently. Such species as *Pinus clausa* (Chapm.) Vasey, *P. banksiana* Lamb., and *P. contorta* Dougl. can persist in fire-ridden environments through the abundant storage of seeds in serotinous cones. Such accumulations of seed begin in very young stands of these species.

As an artificial agent, man can also move tree populations toward precocity. By selecting for early flowering in *Betula verrucosa* Ehrh. through three successive generations, Stern (17) shortened the span between generations to 2 years. In the process, he pro-

duced some extreme individuals which tended toward flower production only instead of a normal seedling vegetative growth.

Greene (4) reported evidence of progress toward precocious lines in similar selective breeding of *Pinus taeda* L.

Gerhold (2) described how, in the production of a commercial Christmas tree strain of Scotch pine called Nye Branch, nursery personnel unintentionally bred precocity into the strain through the practice of collecting cones in young stands.

Plots of Nye Branch (of the same age but of a different nursery background) were included in the present study in central Missouri. None of the 70 provenances is precocious to the degree of the Nye

Branch stock (Figure 1). It was not unusual to find seedlings abundantly reproductive 1 year following their field planting as 2-0 nursery stock. These trees have continued to reproduce and are yielding increasingly abundant crops of mature cones.

One observation of interest is that pollen production in the low crown may indicate sexual maturity (Figure 2). This trait characterizes older trees in general. In the study area, it characterized the Nye Branch seedlings and the most precocious individuals among the 70 provenances. Conversely, trees which lacked such degrees of precocity were observed to produce their first pollen at the base of the season's flush of growth in the top of the crown. This was the case in more than 80 percent of the trees



Fig. 2.—Apparent relationship between low crown production of pollen and precocity (left) in con-



trast to usual development of relatively few strobili located only at base of top flush of growth (right).

which yielded pollen in the test plantation in 1966, most for the first time.

Ovulate structures were found in 67 of the 70 provenances (96 percent) in 1966 but on only 462 of 1272 trees (36 percent). Pollen was produced in 46 of the 70 sources (66 percent) but on only 122 of the 1272 trees (under 10 percent). These figures, of course, show that there were many infertile trees among those sources showing some sexual activity.

Within-source fertility ranged from 90 percent of all trees downward to 0 for female conelets and from 45 percent to 0 for male strobili. Three sources were completely lacking in structures of either sex. These came from near the borders of the Scotch pine range in northern Russia, Spain, and Greece. There was a great within-plot range in fecundity, especially among the most fertile origins, indicating a potential for precocity through selection.

Is precocity a desirable objective in tree breeding? Perhaps it is in the development of special experimental materials but the author is inclined to support a selection against precocity among commercial trees. The risk of sacrificing potential vegetative energy for early and abundant fruitfulness seems too great. Even if this was not so, we would greatly narrow the selection base for those inherent traits required in commercial stocks—whether they are primarily for timber, windbreaks, Christmas trees, or other purposes—if one of the criteria for selection is precocity.

It seems doubtful that forest geneticists would deliberately breed precocity into their commercial stocks. Unintentional selection, such as that cited in the Nye Branch experience, probably poses a greater danger. In that case the practice was simply to harvest seeds from young stands for use in a commercial nursery. Similar unpurposeful selection could result through the practice of breeding trees in young stands as a means of shortening the span between generations. It is conceivable that the results could be highly deleterious in terms of the real objectives of a breeding program.

Seed production in young orchards—whether for commercial or breeding purposes is a desirable objective. The correct means of accomplishing this, however, would seem to be through environmental rather than genetic manipulations.

The effects of wide spacing and high nutrition in causing otherwise unfruitful young trees to produce seed are well known. The selection of an orchard site in terms of the physical properties of the soil and irrigation offer other possibilities. Based on a recent experience, Ike (6) described the effects of site

factors on early fruiting in *Platanus occidentalis* L., a species which is normally slow to flower.

One problem in an orchard is to obtain a greater balance in sexual participation among the various genotypes. A disproportionate cultural attention in favor of low-yielding trees may offer some solution. In time we shall learn how to accomplish this more effectively. Horticulturists, for example, have found that the kind of rootstock can greatly affect fruit production in graft clones (5). We have only begun to explore the potential of ordering the environmental complex and other cultural techniques toward the achievement of an early and balanced seed production in seed orchards.

SUMMARY

In the seasonal timing of the sexual cycle, trees in an 8-year-old Scotch pine provenance experiment were found to differ greatly among the 70 origins and to a lesser degree within origins. High variation in the abundance of reproductive structures was observed within as well as between sources. The importance of these two variables in seed orchard management is discussed.

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DISCUSSION

Polk: There are two questions, leading out of my discussion, which I would like to raise myself. One is the question of crossing material from extremely different geographic areas, rather than crossing within local populations, in order to increase chances of achieving improvement. The other question is: Should we breed for precocity?

Funk: There is another side to this story on precocity and the possibility that trees which flower and fruit at an early age may do so at the expense of vegetative growth. Wareing has worked with larch and has found attainment of a given size necessary for flowering. Therefore, perhaps if you were selecting among the precocious trees, they would be the largest trees in a collection. Have you noticed one way or the other? Are your early flowering trees the big ones or the little ones?

Polk: They are both. Some of the small-tree origins have lots of cones on the trees and some of the larger ones are also bearing quite a few cones. But my question is: If you started breeding within a line for precociousness and greatly stimulated the reproductive process, what would you do to the vegetative process?

Schreiner: The evidence from agricultural breeding indicates that maximum genetic improvement will involve wide crosses. We cannot expect to get maximum genetic improvement through seed orchards; these, as Zobel has pointed out, are really a "crash program." If you are going to use parents from widely separated (intraspecific) sources in seed orchards, this could be hazardous unless the progeny of such wide crosses have been tested for at least half-rotation performance.

Polk: It has been common practice, for example in Sweden, to be careful to work within a particular geographic range and, where you have elevational problems, within an elevational zone for adaptive reasons.

Schreiner: Since I'm not an ardent seed orchard advocate, I am in favor of wide crosses. And I would like to see some of this seed-orchard money spent on research on apomixis to develop practical methods of vegetative propagation to make synthetic multiclonal hybrid varieties possible. In approximately 25 years, they developed a peach which is hardy in New Hampshire. How long would it take to produce a peach combining acceptable market quality and hardiness if they had to use seedlings instead of grafted trees? Admittedly, research on apomixis in the broadest sense, particularly the use of propagules (other than seed), is not genetics. So it's

difficult to spend genetics research money on this problem.

Polk: It's part of genetics, isn't it, if you can get something really good by the process of apomixis?

Schreiner: It is the keystone to maximum improvement. We would be justified in putting a large proportion of our research effort into basic research on apomixis, including all forms of vegetative propagation, such as apospory and propagation by cuttings or other propagules.

Polk: What you said earlier about wide crosses called to mind something I would have reported here in a longer paper. Zobel and McElwee in a recent paper (21) suggested the possibility, as a projection of the seed orchard principle, of taking outstanding clones from different orchards which have been developed over the southeast and bringing them together on a common area. The question is, would this material be in cycle or would we run into a problem similar to the variation in Scotch pine reproductive phenology already discussed. This has to be determined. There is even the possibility of local variation, as in the case of the within-stand differences reported by McLemore and Derr. In this stand, 23 longleaf pines were selected for controlled pollination and, among those 23 trees, some were as far as 2 weeks apart in date of maximum receptivity.

Schreiner: My point is that I wouldn't advocate wide crosses for a crash program. I would definitely advocate wide crosses in hybridization (intra- and interspecific) aimed at maximum improvement. Go as wide as you can for ultimate maximum genetic improvement.

Polk: Even in these crash programs, the breeders reach a point where they want to move along to another stage.

Wright: Is it possible that we in Michigan should think of locating some of our seed orchards down in Missouri? You seem to be getting a much heavier cone production than we do and Ralph Read has had red pine flowering 3 years after planting in Nebraska.

Polk: I really don't know. I think we should compare notes on these things. The only reason I would hesitate to recommend any real effort in Missouri is that we have had rather poor luck in terms of seed production so far. We have some extremely long dry periods down there sometimes and I have found out that water, as you might guess, is a rather critical factor in seed production. We are presently trying to establish a study area which I hope will also be of some value as a seed orchard which we can irrigate. I think we'll do a much better job of seed production under those conditions.

Schreiner: You were referring to planting outside the botanical range of the species. Actually, the most precocious white pines I have seen are down in Maryland, beyond the natural range of white pine. I don't know whether they are genetically precocious or whether they're growing under environmental conditions which are responsible for the early flowering. Agricultural seed is often produced in especially favorable localities. We may find earlier and heavier fruiting in seed orchards outside the natural range of a species.

Polk: In relation to this question, it is my experience that in trying to do breeding work or genetic work you are continually bumping into some physiological problem. I would like to see some physiologists start to work on tree reproduction.