

Improvement of Yellow Poplar

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The process of compiling information about a species on which you have been working for the past six years can be very educational. Although a person constantly tries to keep up his reference file and attempts to stay in contact with other workers in the field, it is difficult to maintain a complete picture of what is becoming known.

There is considerable knowledge about some aspects of the silviculture of yellow-poplar (Liriodendron tulipifera). In recent times, methods have been developed so that the species can be propagated successfully, but knowledge related to the genetics of yellow-poplar is severely lacking. This should not be discouraging because even less is known about most other hardwoods, with the exception of Populus.

In many respects the present state of our knowledge and research effort with yellow-poplar may be compared with that of loblolly pine ten years ago. During the past decade an ever-increasing number of research projects have contributed to our knowledge about loblolly pine. It remains to be seen if similar progress will be made over the next ten years with yellow-poplar. Undoubtedly, the support for yellow-poplar breeding projects will be less than that for the southern pines. However, many accomplishments of the pine breeders, related to principles and development of methodology, will be of great value to those of us interested in hardwoods in general and yellow-poplar in particular.

Tree improvement must be an integral part of silviculture but it is sometimes difficult to determine just what segment of this discipline tree improvement covers. Since regeneration and vegetative propagation have already been discussed for hardwoods in general I will only touch upon propagation as it concerns the development of seed orchards. Other phases of the biology of yellow-poplar of interest to the breeder are flowering and seed production, variation in natural stands, seed, source tests, hybridization, and the heritability of important characteristics with the ultimate objective being the gains that can be achieved.

General information on the silvical characteristics, growth and management of yellow-poplar has been summarized by McCarthy (1933) and Renshaw and Doolittle (1958). Characteristics and variation of wood, properties have been discussed by Luxford and Wood (1944), Barefoot (1958), Thorbjornsen (1961) and Taylor (1963, 1964).

FLOWERING AND POLLINATION

Yellow-poplar trees may start flowering as early as 15 years of age, but these small trees have few flowers. As is true for other forest tree species, there is a relatively good relationship between dbh and flower production. By grafting material from the top of the crown of older trees to seedling understocks, we would expect early flowering. This seems to be the case in a yellow-poplar seed orchard near Knoxville, Tennessee, in which a few flowers have been produced two years after grafting.

Flowering may occur from late March to June, depending on geographic location and weather conditions. There is much variation in time of flowering among individual trees within a stand. Fortunately for the tree breeder, all the flowers on a single tree are not receptive at the same time and the flowering period for individual trees may vary from two to six weeks, thus affording the breeder an opportunity to make his crosses. Techniques for controlled pollinations have been developed by Carpenter and Guard (1950), Wright (1953) and Taft (1962).

The large, showy yellow-poplar flowers are bi-sexual. Nectaries are located on orange spots near the base of the petals. Insects - especially honey bees - get pollen on their bodies when collecting nectar and brush against the stigmas. Apparently, insects often move from flower to flower within the same tree; such a pattern could produce a considerable amount of self-pollination.

The low viability of yellow-poplar seed may be partially due to lack of fertilization which again is the result of ineffective pollination. Self-incompatibility is rather common in yellow-poplar. Boyce and Kaeiser (1961) obtained less than 2 filled seeds per

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100 samaras for all their controlled self-pollinations. Taft's ^{2/} selfings resulted in a seed set varying from zero to nine percent filled seed, and Thor (unpublished) obtained from zero to one percent germination from controlled self-pollinations. Similar effects of selfing in yellow-poplar have been reported by Carpenter and Guard (1950) and Guard (1943).

In addition to self-incompatibilities, there is also good evidence that certain trees may also be cross-incompatible. Kaeiser and Boyce (1962) found that widely separated trees usually had better seed set than those in the same stand. It is to be expected that trees of the same stand may be closely related and thus be less compatible than the wider crosses.

Controlled cross-pollinations usually result in higher percentages of filled seed than open or self-pollinations (Carpenter and Guard 1950; Boyce and Kaeiser 1961). Taft obtained twice as many filled samaras from controlled crosses as from open-pollinated flowers. In another study (Thor, unpubl.) open-pollinated seed germinated at a rate of from one to six percent while controlled out-crossing of the same trees resulted in germination percentages ranging from 6 to 36 percent.

SEED PRODUCTION

The yellow-poplar fruit is an erect conelike aggregate of samaras. The samaras ripen in the early fall and may contain two, one or no seed. The basal-most samaras are sterile (Boyce and Kaeiser 1961). Wean and Guard (1940) report that the middle portion of the "cone" has the highest proportion of filled seed, averaging about 20 percent. Size of cone and position in crown have little or no effect on seed viability (Perry and Coover 1933).

Guard and Wean (1941) found that trees with a dbh above 15 inches had a larger percentage of filled seed than those smaller than 15 inches. Also, a straight line relationship has been established between dbh and the number of viable seeds produced per tree (Carvell and Korstian 1955). In spite of the rather low percentage of viable seed, yellow-poplar usually produces such an abundance of seed that adequate reproduction often is obtained if seed bed conditions are suitable. More than a quarter of a million seeds per acre may be produced from a few seed trees (Carvell and Korstian 1955; Engle 1960).

Individual tree variation in seed viability is large. Limstrom (1959) used tree percents (the ratio of seedlings produced to the number of seed sown) and found wide variations in tree percents among mother trees within each source as well as among sources. Individual tree superiority in seed viability was consistent over a 3-year period. Sluder (1964) and Thor (1965) found that with the same sowing intensity seed-bed density varied strongly by mother trees.

HYBRIDIZATION

Inter-specific hybridization does not offer too great a promise in the genus Liriodendron. In addition to our native yellow-poplar, only one other species is known; the Chinese yellow-poplar (*L. chinense*). The Chinese tree is a small, relatively unimportant forest tree of Central China. Frost has killed back this species in several arboreta in the Northeast, but there is evidence that it may grow successfully in the South. The chromosome number (2N) is 38 for both the Chinese (Li 1954) and American (Whitaker 1933) yellow-poplar.

The outlook for improvement through intra-specific hybridization within the native yellow-poplar is much brighter. Carpenter and Guard (1950) noted that the seedlings produced as a result of cross-pollination tended, to be more vigorous than those resulting from open-pollination. If reduction in vigor goes with inbreeding, we should expect improvement to be obtained in an orchard composed of numerous clones representing many different stands, assuming cross-pollination among trees can be secured.

There is no knowledge available on the result of crosses between trees from different physiographic regions. One breeding orchard has been established in Tennessee to produce intra-specific hybrids from crosses among trees from the same stand, among trees from different stands within the same region, and among trees from different physiographic regions.

VARIATION

Several studies of natural variation in yellow-poplar have been concerned with wood properties such as specific gravity and fiber length. Thorbjornsen (1961) found large among-tree variance components for specific gravity in Tennessee; however, individual trees did

2/ Undated references to Taft indicate personal communications with K. A. Taft, TVA, Norris, Tennessee.

not show as much variation in fiber length. These observations have been supported by Taylor (1964) in North Carolina. Both workers found some differences among stands of geographic areas. A rather large study of variation, including wood properties as well as various morphological properties, has been established by Kellison^{3/} in North Carolina. The Southeastern Forest Experiment Station is planning a large study of wood characteristics; trees will be sampled in Virginia, North Carolina, and Georgia to determine among-tree variation, geographic variation, variation associated with site differences, and changes associated with stand thinning.

When one works with a valuable forest tree which covers a large geographic range, the question of seed source must be considered. Unfortunately, often seed-source testing is not started before artificial reforestation has become an accepted practice and, large areas reforested with poorly adapted sources have shown the need. for such information. This question of provenance in yellow-poplar is a pressing one both in this country and in Europe (Querengasser 1961).

Some of the earliest seed source studies of yellow-poplar were established in 1952 (Limstrom 1955, Lotti 1955). Early results from these tests indicate that seed source has a strong effect on height growth. Sluder (1960) reported large differences in survival and height growth among 16 sources after one growing season. However, after 10 years growth Sluder^{4/} found no significant differences in height among the sources. Limstrom and Finn (1956) found significant differences among six different sources in height of 1-year-old seedlings.

Funk (1958) studied the relationship between seed source and frost damage and found that the extent of dieback was generally related to latitude of the seed source. Trees grown from seed of the southernmost sources were much more severely damaged than those from the more northern sources. Differences in photoperiodic response have been investigated in growth chambers by Vaartaja (1964). The northernmost source (Michigan) grew best under very long days (3-hr. dark periods), while the southernmost source (Georgia) grew best under long days (6-hr. dark periods). Under short day conditions, the Georgia source grew almost twice as much in height as the Michigan source, while the Indiana source was intermediate. There were indications that the variation was gradual and continuous.

Data on two additional seed source tests have not yet been published, but early results have been analyzed. Four seed sources from northern Alabama and Mississippi and, southern Tennessee did not show any significant differences after three years (Southern Forest Experiment Station). Five-year data from a series of seed source tests in Tennessee (University of Tennessee) indicated large differences in mean height among sources, but these differences were only significant at the 10 percent level due to large error terms.

It is, however, interesting to note that the source from West Tennessee had the best height growth in the West Tennessee plantation but did. poorest in the Cumberland Mountains. The Cumberland Mountain source was the best source in the Dumberland. Mountain plantation while it grew poorer than the same sources when tested in West Tennessee.

In future seed source tests, it should be recognized that yellow-poplar is extremely sensitive to relatively minor changes in site conditions. Even large mean differences in height growth will not prove to be statistically significant if care is not exercised in the selection of uniform test areas. While four replications usually give enough accuracy for testing sources of loblolly pine we must probably double this to obtain comparable accuracy in yellow-poplar seed. source tests.

HERITABILITY

Heritability is a term used to express inheritance in a quantitative manner. It is the ratio of the genetic variability to the phenotypic variability. Heritability in the "broad sense" considers total genetic variability, while "narrow sense" heritability considers only the additive portion of the genetic variability. Due to the difficulties in propagating yellow-poplar vegetatively we are mainly interested in determining the "narrow sense" heritabilities for different characteristics.

2/ Undated. references to Kellison indicate personal communications with R. C. Kellison, N. C. State University, Raleigh.

4/ E. R. Sluder, unpublished. progress report, Southeastern. Forest Expt. Station.

Many forest geneticists are busy determining narrow-sense heritabilities for a number of characteristics in various species of pine. The question may be asked as to how this work is useful in tree improvement and if such information should be obtained for yellow-poplar. Since knowledge of heritability is basic to determination of genetic gain and expected improvement, this information is essential to determine which characteristics to work with in a selection program, and to obtain reliable estimates of expected improvement for justification of the expense.

Unfortunately we do not now have any reliable estimates of expected gain for any characteristic of yellow-poplar. There is ample evidence (Limstrom and Finn 1956; Sluder 1964; Thor unpubl.) that one-year-old seedlings differ in size depending upon the mother tree. However, this may be caused by different amounts of self-fertilization (Carpenter and Guard. 1950).

Taft is investigating the inheritance of various characteristics using a diallel test with a total of 78 cross-pollinations. He found indications that heights of seedlings are determined by dominance rather than additive gene action. Leaf shape, however, seems to be determined by additive genes, particularly the ratio of leaf length to leaf width.

In an open-pollinated progeny test in Tennessee, Thor (unpubl.) found large differences in heights among progenies after three growing seasons in the field. In the Cumberland Mountains the four best progenies were from the Cumberland Mountains; in West Tennessee the four best progenies were from West Tennessee. However, even within one provenance there were large differences - in both locations the best and poorest growth was made by progenies from local mother trees.

Sluder/ has established a test to determine the heritability of epicormic sprouting in yellow-poplar. Five heavy-sprouting and five light-sprouting trees have been selected and an open-pollinated. progeny test has been established. Also, Sluder is propagating his selections by grafting to determine "broad sense" heritability for epicormic sprouting. Kellison designed an open-pollinated progeny test involving 108 trees in North Carolina. Outplantings have been made in the Mountains, Piedmont and Coastal Plains.

Results from the heritability studies already established, and others which are still in the planning stage, should yield information which will be of great help in our breeding efforts with yellow-poplar. We should keep in mind that many plants were greatly improved long before we had any knowledge of quantitative genetics and heritabilities. There is no reason for delaying a program of selection and seed orchard establishment because of our present lack of knowledge of heritabilities.

SELECTION

Without knowledge of the inheritance of different characteristics, the breeder has an almost unlimited number of characteristics to choose from. Practical consideration, however, will usually limit his choice to those criteria which have strong economical implications. Secondly, since the amount of gain is based on variation present as well as the heritability, the characteristics chosen for selection should express large phenotypic variation.

Density of yellow-poplar wood is of great economic importance since it is related to most strength characteristics (Luxford. and. Wood. 1953). Also, there is much phenotypic variation present among trees (Thorbjornsen 1961), and relatively little of this among-tree variation appears to be caused by site differences (Thor unpubl.). Other wood properties, like fiber length and extractives, do not show as much promise for selection because of their more limited variation and lesser economic importance.

Most people are not aware of the variation in straightness in yellow-poplar. Compared to most other hardwoods, this species has a good, straight bole; but when one starts looking for superior phenotypes, with straight boles, it is often difficult to find. acceptable trees. Since straightness is of great economic importance and there is surprisingly much variation in this characteristic, it should be one of the most important selection criteria in a breeding program.

High-quality large logs of yellow-poplar command a high price on the veneer market. It is essential that these logs be clear. Selection of trees with small branches, good pruning, and a minimum of epicormic branching may lead to a larger percentage of premium logs.

5/ Personal communication with E. R. Sluder, Southeastern Forest Expt. Station.

Wahlenberg (1950) studied heavy and light sprouters before and after thinning. He found that the heavy sprouters had nearly twice as many sprouts before thinning and nearly three times as many after thinning, suggesting that the trees which are naturally poor in this respect tend to become progressively worse. Large branch diameters are associated with stem rot and poor pruning. The phenotypic variation present for branching characteristics is well illustrated in Limstrom's latest publication (Limstrom 1965).

Although the emphasis probably should be on quality improvement in a selection program for yellow-poplar we cannot afford to sacrifice rate of growth. Selection for growth rate in yellow-poplar phenotypes may be rather ineffective because of the extreme site sensitivity of the species. The best we can do is probably to limit our selections to the largest dominant members of a stand. When the environmental conditions are relatively uniform, the prospect for effective selection in growth rate may be more favorable. Funk (1964) reported that large seedlings selected in the nursery were growing twice as fast as small seedlings; the premium seedlings increased their original advantage during eight years in the field.

Occasionally yellow-poplar trees have an abnormal grain, such as blister grain, which may be of considerable economic value. Bailey (1948) grafted blister-grained yellow-poplar, but the trees did not show any sign of abnormal grain soon after grafting. The trees were examined again this year by Zarger^{6/} and Thor, but no evidence of abnormal grain was found. Obviously, selection and breeding for such characteristics should be delayed until we have more knowledge about their inheritance.

Most breeders of yellow-poplar will probably stress characteristics such as straightness, pruning, branching habit, and, wood density. In some localities two or more organizations may be looking for trees with approximately the same characteristics. To provide for maximum utilization of the best selected phenotypes, the University of Tennessee in cooperation with the Kentucky-Tennessee Section, SAF, has prepared lists of selected trees. The list submitted with his paper should not be considered as a "shopping list" - rather it is a "trading list." If all the organization working with yellow-poplar let other people know what type of breeding material they have available, we could probably make faster progress in both basic work in forest genetics and applied tree breeding.

Agency	Tree #	State	County	Height	DBH	Prun.	Straightn.	Crown	Sp. gr.	Fiber L.
U. T.	1	Tenn.	Sevier	*	**	0	*	0	*	0
U. T.	2	Tenn.	Monroe	*	0	*	**	*	*	-
U. T.	4	Tenn.	Monroe	*	-	0	**	*	*	*
U. T.	6	Ky.	Bell	0	0	*	**	*	0	0
U. T.	7	Ky.	Bell	*	0	*	*	**	**	*
U. T.	10	Tenn.	Coke	0	0	*	**	*	*	0
U. T.	11	Tenn.	Sevier	0	0	*	*	*	*	*
U. T.	12	Tenn.	Sevier	*	0	*	**	*	-	0
U. T.	14	Tenn.	Sevier	*	0	*	**	**	-	0
U. T.	15	Tenn.	Lauderdale	0	-	*	**	*	*	-
U. T.	16	Tenn.	Lauderdale	0	*	*	**	**	-	0
U. T.	17	Tenn.	Lauderdale	0	*	0	*	0	*	0
U. T.	18	Tenn.	Sevier	0	*	*	**	*	*	0
U. T.	20	Tenn.	Obion	0	0	*	*	**	*	0
U. T.	21	Ala.	Lawrence	0	0	*	**	*	*	-
U. T.	23	Tenn.	Madison	0	0	0	*	*	*	*
U. T.	26	Tenn.	Obion	0	0	*	**	*	*	0
U. T.	31	Tenn.	Morgan	0	**	0	**	*	-	0
U. T.	32	Tenn.	Morgan	0	-	*	**	**	0	0
U. T.	34	Tenn.	Morgan	*	*	*	**	0	0	*
U. T.	35	Tenn.	Morgan	*	0	*	**	0	*	0
U. T.	39	Tenn.	Morgan	0	0	*	**	*	0	0
U. T.	40	Tenn.	Morgan	*	0	0	*	*	*	0
U. T.	41	Tenn.	Morgan	0	0	*	**	*	**	0
U. T.	81	Tenn.	Shelby	**	0	0	**	*	-	0

** Excellent
 * Better than average
 0 Average
 - Poorer than average

Figure 1. List of yellow poplar superior phenotypes. Forest Tree Improvement Committee, SAF Kentucky - Tennessee Section, Revised 1965.

^{6/} The author is indebted to T. G. Zarger, TVA, for his assistance.

SEED ORCHARDS

Basically there are two ways of establishing a yellow-poplar seed orchard - either with seedlings or by clones. Since the advantages of clonal and seedling orchards have been discussed at great length by able men from all over the world (Silvae Genetica Vol. 13. 1964), I shall not attempt to contribute any new arguments. In the South there are only five or six organizations, mostly in North Carolina and Tennessee, working on the establishment of yellow-poplar orchards. To my knowledge all these orchards were established by vegetative propagation, usually grafting.

Rooting of mature yellow-poplar cuttings is a rather difficult task (Huckenpahler 1955). Enright (1957) reported that he was able to root up to 78 percent of his cuttings, but repeated trials with similar techniques have been unsuccessful (McAlpine 1964; Thor unpubl.). McAlpine was, however, able to root cuttings taken from stump sprouts of 7-year-old trees.

Grafting of yellow-poplar is by no means easy, but satisfactory results may be obtained by careful work and, correct timing. After five years of grafting yellow-poplar, we have found that in the Knoxville area best results are obtained by grafting in early April. The scion wood is collected in February and stored in the refrigerator until grafting time. The importance of the relative vegetative stages of stock and scion has been noted by Churchwell (1965). In the most successful series of grafting in Knoxville (April 1964) we obtained 59 percent "takes" on our grafts. Since we usually put on two grafts per tree the percent of successfully grafted trees was boosted to 67 percent. In that same year we established an informal test in two locations to determine the effect of bagging on grafting success. There was no difference in survival between bagged and unbagged grafts we have now discontinued the use of bags and thus reduced, grafting costs considerably.

Bud-grafting of yellow-poplar in the fall has the advantage of extending the propagation season. Funk (1963) reported good early success with budding between 3 and 6 weeks after height growth ended in the woods. Sluder^{7/} had poor results with bud-grafting on potted plants. Thor (unpubl.) had good early success with bud-grafting on sturdy 2-year-old stock in the nursery. When the top of the stock plant was removed 2 weeks after budding, the bud usually broke dormancy; however, the tender new growth formed did not harden off and the majority of the bud-grafts were lost during the winter.

Taft makes a conservative estimate that 20 percent of open-pollinated seed is selfed under natural conditions. Since some trees appear to have high selfing fertility it may be possible to develop selfed lines of high-quality trees. However, most orchards should probably be based on maximum cross-pollination. In order to secure a high proportion of outcrossing and a high germination percent of the seed, we must work with a relatively large number of clones which are well spaced in the orchard. It may be advantageous to pair highly compatible clones, or even graft such clones on the same under-stock.

The first three to four years after establishment there will be very few flowers and the management of the orchard should be directed to obtain as strong growth as possible. At the University of Tennessee we have found that both irrigation and fertilization-especially with nitrogen-are essential for rapid development. Other management practices, such as protection, mowing, mulching are not different from those necessary for any seed orchard.

We do not know when abundant flowering starts in grafted yellow-poplars, but my estimate would be between five and ten years. Problems with regard to maintenance of proper insect populations will have to be solved, before the orchards become fully functional.

SUMMARY

1. A considerable amount of information on flowering, pollination, and seed production in natural stands of yellow-poplar is available. Individual tree variation in seed viability is large. In addition to self-incompatibilities there is also good evidence of cross-incompatibility.

2. Inter-specific hybridization does not offer much promise, but the outlook for improvement through intra-specific hybridization is good.

3. Results from studies of natural populations and provenance tests support the view

^{7/} E. R. Sluder, unpublished. progress report, Southeastern Forest Expt. Station.

that much variation is present for such characteristics as early height growth, frost hardiness, stem form, branching habit, and wood specific gravity.

4. Very little substantial information is available on the heritability of various characteristics in yellow-poplar. However, several studies have been established, and data necessary for prediction of gains in some characteristics will be obtained in the not too distant future.

5. Based on our present knowledge, a selection breeding program - using characteristics such as wood specific gravity, stem straightness, pruning, and, branching characteristics - shows considerable promise.

6. The establishment of clonal seed orchards appears to be one practical solution to the problem of obtaining good quality seed of yellow-poplar.

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