PLUS-TREE SELECTION IN HARDWOODS: A WASTE OF TIME?

Terry L. Robison[1]

Abstract. Progeny test data for several hardwood species suggests that little or no gain results from plus-tree selection in natural stands. Constraints on effective mass selection are the likely causes. Therefore, short-term genetic improvement through natural regeneration is unlikely. Long term improvement through mass selection seems possible. Suggestions for selection in natural hardwood stands are given.

Additional Keywords: Tree improvement, forest genetics, natural regeneration.

The question of whether genetic improvement can occur through natural regeneration has been discussed for years. Arguments advocating plus-tree selection in natural stands have been made (e.g. Smith 1962; Zobel and Talbert 1984), as well as comments down-playing the role (Steiner 1985, Farmer 1980). Textbooks and countless silviculture and tree improvement classes have expounded the harms that high-grading causes to forests.

When the best stems are removed over time, poorer quality stands result. Long term observations in Europe and the United States support this contention (Zobel and Talbert 1984), but no data exists on what role phenotypic mass selection, when practiced at the silvicultural "Paint-Gun" level, plays in genetically enhancing forest stands. After considering available test data and the biological constraints of hardwood ecosystems, some comments and recommendations can be made.

SELECTION EXAMPLES

There is evidence from progeny tests on the performance of natural stand selections. However, there are limitations with much of this data. Many of the progeny and provenance tests utilized little or pseudo-random selection of parents from widely dispersed stands. Most tests had no check lots on which to base gain. Lastly, several of the species discussed have little potential for natural regeneration. Even with the limitations, these studies help elucidate the role of tree improvement in natural regeneration.

[1] Genetics and Reforestation Specialist, Missouri Department of Conservation, Jefferson City, MO.

Populus spp.

Plus-tree selection in natural stands has had little success. Heilman and Stettler (1985) selected black cottonwood (P. *trichocarpa* Torr. and Gray) ortets based on growth rate and form, but they found very poor as well as very good clones when ramets were tested in a common environment. Exact genetic copies of selected parents were tested, yet performance was less than expected. Their recommendation was to select in the plantation environment for which the clones are intended.

In studies by the University of Kentucky and Westvaco (R. Rousseau, Westvaco, Wickliffe, Kentucky), selection for growth traits in eastern cottonwood (P. deltoides Bartr.) has been met with similar poor success. Disease and wood quality evaluation have yielded some superior clones in test situations.

Other eastern cottonwood studies of trees selected at random in natural stands (e.g. Mohn and Randall 1971; Foster 1986), indicate wide variation in volume, diameter and height. A casual observation by the author indicates a wider range of progeny values obtained from random selections versus phenotypic selections (e.g. Randall and Cooper 1973; Olson et al. 1985). Selection may be modifying the variance of populations, but its effect on the mean is neutral.

Northern Red Oak

Much of the work on red oak (Quercus *rubra* L.) has been under the auspices of the NC-99 regional treeimprovement project (Kriebel et al. 1976). Selection was for average or better trees with the strongest pressure probably applied for fecundity. Again, significant variation was identified, but there is no way to evaluate any gain from selection efforts.

A subsequent study of Tennessee Valley red oak identified plus-trees on the basis of form and vigor (Houston 1987). Among family variation was high with progeny from the same parent tree ranking in the top and bottom 10% for tenth year height growth. A similar study by Farmer (1980) concluded that phenotypic selection in natural stands is not effective for growth traits, whereas selection in progeny tests or seedling seed orchards appears to be quite effective (LaFarge and Lewis 1987).

Yellow Birch

Progeny from yellow birch (*Betula alleghaniensis* Britton) plus-trees selected for height growth and form were evaluated at age 5 (Genys 1981). Growth traits were highly variable, and over 50% of the progeny had forked stems. Genys recommends progeny testing to take full advantage of the tree improvement effort.

Eastern Black Walnut

Black walnut (Juglans nigra L.) is one species in which intensive phenotypic selection has been used in natural stands. Comparison trees, intensive measurements and lots of time have been used to locate plus-trees. Three examples can illustrate the outcome of these practices.

Stelzer et al. (1983) evaluated 36, half-sib families in two progeny tests at age 5. The parent trees were scored mostly on form, although comparison trees were used when available to evaluate height and diameter growth. No significant differences were found among families for form. Height and diameter growth variation was significant among families. However, even the best 20 progeny out of 1440 trees in the two progeny tests exceeded the check lots by only 6, 13 and 30% for height, DBH. and volume respectively. Many progeny in the test were similar or inferior to the check lots.

The same parental selection criteria were used in the second example (M. Coggeshall, Indiana Division of Natural Resources, Vallonia, Indiana). Thirty-seven half-sib families were analyzed for height and form at age 7. The analyses were based on 5 randomized complete blocks with single-tree plots that resulted from thinning to the best tree of a 4-tree row plot. The check lot ranked fourteenth for height and tenth for diameter. When progeny and parent tree form ratings were compared, very low, non-significant correlations resulted (Table 1).

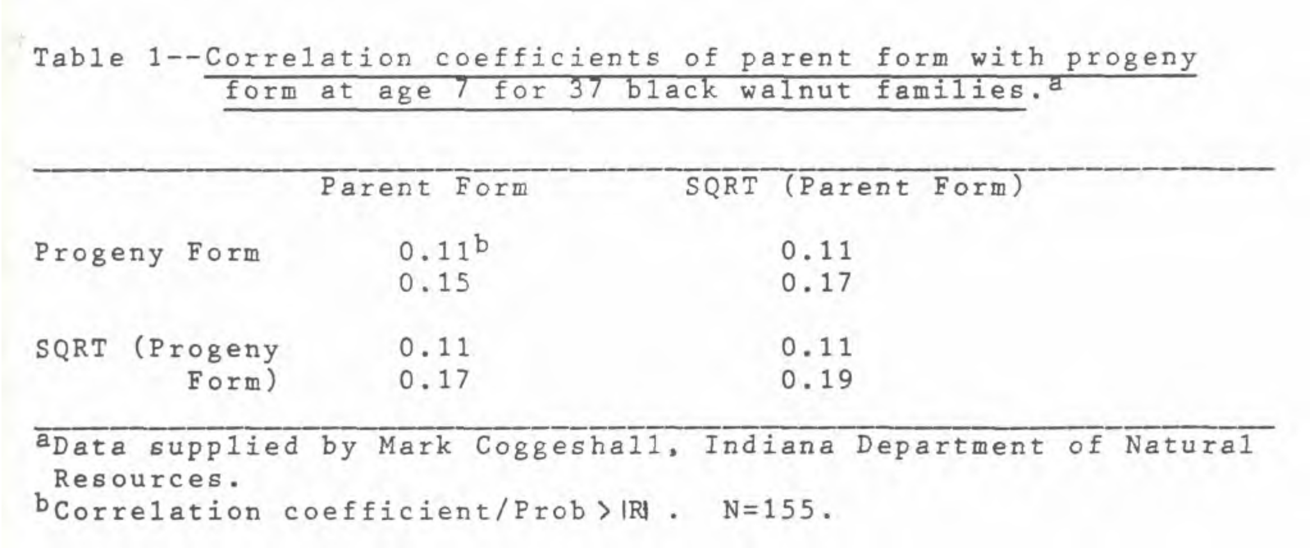


Table 1--Correlation coefficients of parent form with progeny form at age 7 for 37 black walnut families.[a]

	Parent Form	SQRT (Parent Form)
Progeny Form	0.11[b] 0.15	0.11 0.17
SQRT (Progeny Form)	0.11 0.17	0.11 0.19

[a] Data supplied by Mark Coggeshall, Indiana Department of Natural Resources.

[b] Correlation coefficient/Prob > |R| . N=155.

The author's personal experience with black walnut progeny testing in Missouri has indicated little benefit from rigorous selection for height growth, diameter growth or form. Half-sibs may rank in the top and bottom 10% of tests. Check lots consistently rank in the top 50% for all traits and occasionally rank first. To further complicate matters, parent trees selected solely on the basis of nut characteristics have performed well in some tests. Progeny from one of these ranks in the top 20% for height growth at 3 different test locations. The parent tree is growing on a field edge in a railroad right-of-way and possesses poor form and sub-par height.

TREE IMPROVEMENT CONSIDERATIONS

The lack of success of plus-tree selection in hardwood natural stands has a basis in genetics and ecology. DeHayes (1983) discussed several limitations of phenotypic selection (plus-tree selection) in screening trees for insect resistance. These limitations and others apply to selection for other characteristics as well.

Number of Traits

Plus-trees are delineated on the basis of height, diameter and form, which includes stem and crown characteristics. Traits such as specific gravity and pest resistance occasionally are added. An example of this is selection "on the basis of outstanding height growth, stem straightness, branch angle, etc." (Gent's 1981) (underlining added by author for emphasis). Grouping of traits makes gain from selection more difficult. The probability of successfully locating individuals meeting selection criteria decreases with each additional trait screened.

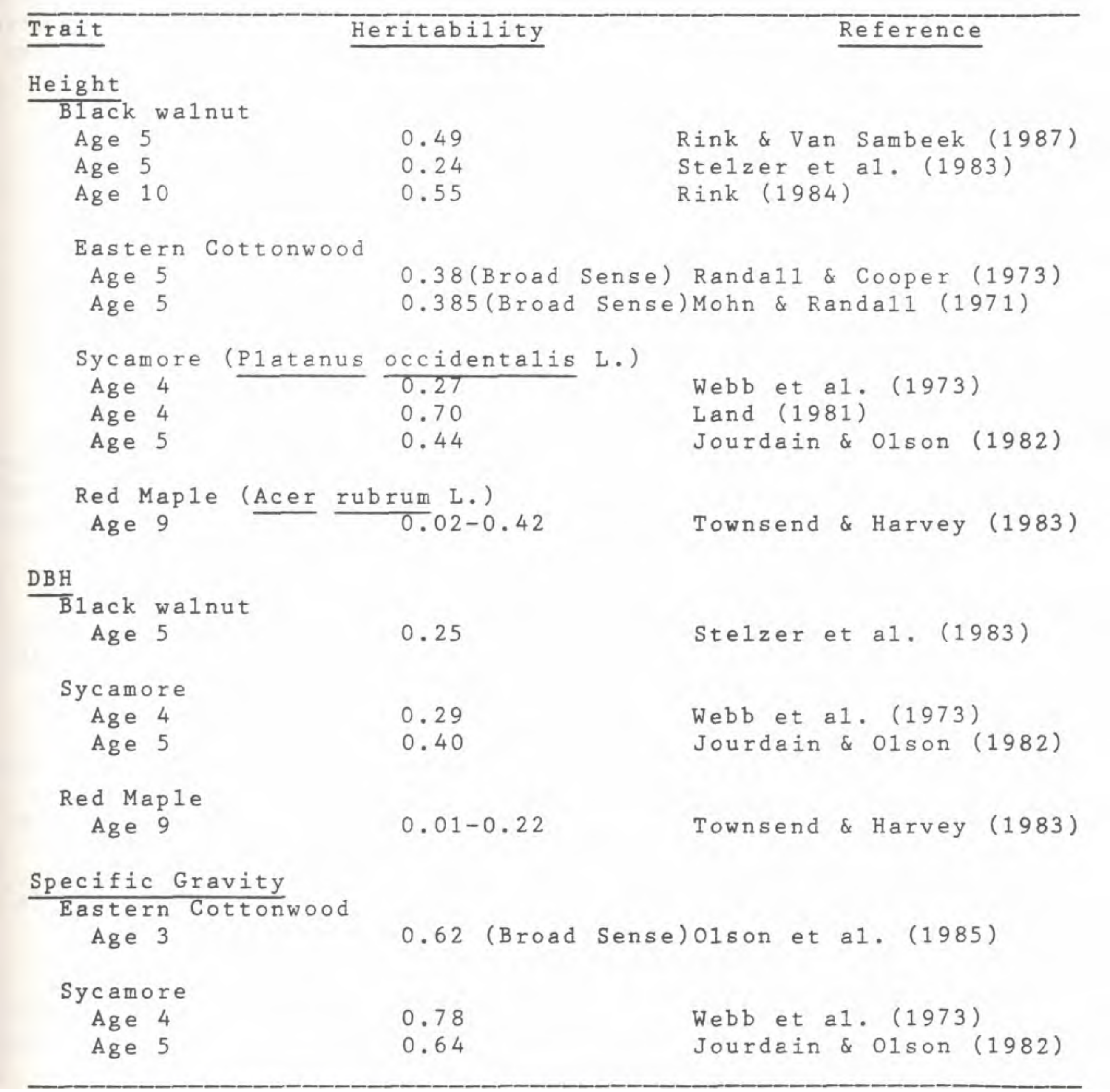
Selection Differential

To attain the highest gain from plus-tree selection, many trees should be screened in a highly variable population with only the best trees retained as parents. The product of the controlling factors (phenotypic standard deviation and selection intensity) is the selection differential. This product varies with population size, the trait, and variability of the trait in the population. On a stand basis, variability is often great, but population size can be restricted by the size of stand to be regenerated and the frequency of the species in question. For example, Appalachian hardwood stands tend to have many species occurring in low to moderate frequencies (Steiner 1985). The selection differential will not be high when considering a naturally regenerated stand.

Heritability

Heritability estimates in hardwoods are apparently high enough to facilitate mass selection (Table 2). However, heritabilities apply only to the population and test site from which they were derived. Estimates to date apply to single tests

Table 2--Individual tree heritabilities for selected hardwoods.



Trait	Heritability	Reference
Height		
Black walnut		
Age 5	0.49	Rink & Van Sambeek (1987)
Age 5	0.24	Stelzer et al. (1983)
Age 10	0.55	Rink (1984)
Eastern Cottonwood		
Age 5	0.38(Broad Sense)	Randall & Cooper (1973)
Age 5	0.385(Broad Sense)	Mohn & Randall (1971)
Sycamore (*Platanus occidentalis* L.)		
Age 4	0.27	Webb et al. (1973)
Age 4	0.70	Land (1981)
Age 5	0.44	Jourdain & Olson (1982)
Red Maple (*Acer rubrum* L.)		
Age 9	0.02-0.42	Townsend & Harvey (1983)
DBH		
Black walnut		
Age 5	0.25	Stelzer et al. (1983)
Sycamore		
Age 4	0.29	Webb et al. (1973)
Age 5	0.40	Jourdain & Olson (1982)
Red Maple		
Age 9	0.01-0.22	Townsend & Harvey (1983)
Specific Gravity		
Eastern Cottonwood		
Age 3	0.62 (Broad Sense)	Olson et al. (1985)
Sycamore		
Age 4	0.78	Webb et al. (1973)
Age 5	0.64	Jourdain & Olson (1982)

of geographically diverse sources. These conditions apply more to plantations than to hardwood stands that will be regenerated naturally. If interactions between genotypes and locations are important, as they likely are in site sensitive hardwoods, heritability estimates will be inflated.

Site variability

By walking a few steps from a northwest to north facing aspect in an Ozark oak-hickory forest, noticeable "superiority" is evident in oak form and growth. It is doubtful that the better phenotypes have genetic superiority. Because of wide site variation in natural stands, any seed would have similar chances of finding poor microsites as good ones, and good genotypes may not be expressed.

Nature of Genetic Control

The amount of gain possible from plus-tree selection is related to the genetic control governing the trait. A trait controlled by a specific set of non-additive genes cannot be expected with much regularity in the next generation (DeHayes 1983). Similarly, improvement of a quantitative trait can be difficult if parents with high growth capacity have similar alleles for the trait (Fehr 1987).

Developmental and Age Variation Within a Stand

Zobel and Talbert (1984) state that gain can be accomplished through mass selection especially in even aged stands. They add that natural stands containing a conglomerate of tree sizes and shapes are mostly even aged. This may appear true on the "surface" because catastrophic events such as fire and timber harvesting result in fairly even aged above ground biomass. However, it has been found that root systems of small diameter advanced regeneration can vary in age from 1 to 70 years in white oak and 1 to 10 years in red oak (R. McQuilken, U.S.F.S., Columbia, Missouri). Phenotypes could be affected in stands regenerated from seedlings and sprouts of various root age. Sprouts from larger root systems often exhibit fast growth rates and spreading crowns while seedlings or young sprouts may lag behind. The trees of younger (below ground) origin eventually may reach a dominant position in the canopy with the trees originating from older roots. The "younger" trees will have better form while the "older" ones exhibit forks. The form in this case is controlled by competition and not genetics.

From a pest stand point, developmental stage rather than the genetic component could determine susceptibility (DeHayes 1983). For example, the smooth bark on young American chestnut sprouts (Castanea *dentata* (Marsh.) Borkh.) apparently prevents colonization by *Endothia parasitica* (Murr.).

Silvics and Silviculture of the Species

Hardwood species can be found in fairly pure stands, but most stands are extremely heterogenous (Steiner 1985). Density may range from one to thousands of trees per acre depending on the species. Seed production can vary from a few to thousands depending on the species and year. In species that regenerate primarily from sprouts (e.g. *Populus tremuloides* Michx.), there is little chance for improvement from the start (Zobel and Talbert 1984). In species that have seed that stays viable in the forest floor for years (e.g. Liriodendron *tulipifera* L.) or travels great distances (e.g. Betula spp.), phenotypically superior seed trees left behind too little to enhance regeneration (Zobel and Talbert 1984). Other factors such as relatedness of trees in the stand and the silvicultural system of regeneration could limit genetic gain.

CONCLUSIONS AND RECOMMENDATIONS

What role does plus-tree selection play in natural regeneration? First, the emphasis on genetic gain through natural regeneration should be on the long term. Several generations of mass selection can cause changes in gene frequencies and population structure, but short term selection is unpredictable at best (Figure 1) (Falconer 1960). Changes can occur in either direction, hence the effects of high-grading.

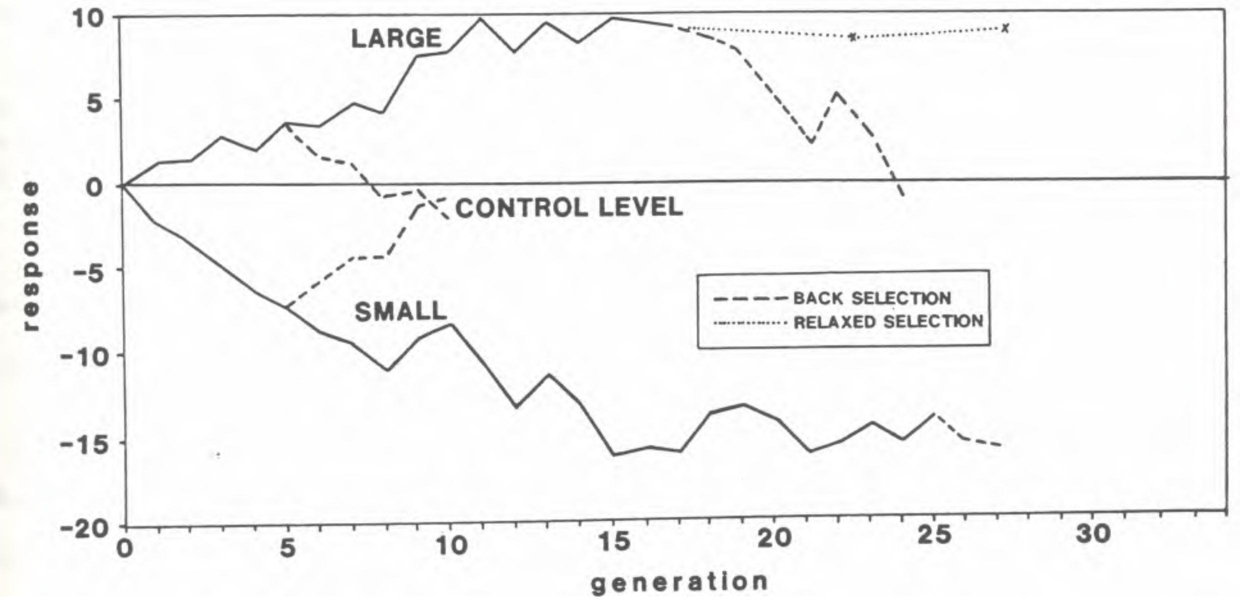


Figure 1--Effects of selection for bristle length in *Drosophila* indicates how long term response is predictable while short term response is variable. (From Falconer 1960, P. 211)

Second, only one or two traits should be screened. Gains from plus-tree selection for growth traits, whether through natural regeneration or untested seed orchards for that matter, seem unlikely because of low heritabilities, large environmental effects, and possibly strong non-additive gene effects (Burdon 1982). Gain in highly heritable traits may be possible. Problem trees should be avoided; those with obvious pest problems, spiral grain or epicormic branching. Disease screening has been successful, but DeHayes (1983) suggests that phenotypic selection for insect resistance in natural stands has great limitations. It may be that pest screening requires strict control of pre- and post-inoculation conditions of plant culture and inoculum (Prakash and Heather 1986). Conditions such as these might be duplicated in test situations, but not regularly in natural stands. Low level selection should at least ensure adaptability of succeeding generations.

Third, the largest influence from selection may be through species changes as opposed to within species genetic improvement. Natural selection has shown that species composition can be altered. Dutch elm disease, chestnut blight, and now gypsy moth and pollution are forces that have caused or possibly will cause significant species changes. Selection applied during thinning operations may provide the best opportunity for changing species composition or for improving specific traits as well (Zobel and Talbert 1984). When thinning is done sufficiently ahead of regeneration cuts, the "superior" trees left may contribute a larger component to the next generation because the cumulative advanced regeneration will have resulted more from the leave trees than from the stand prior to thinning. With selection intensities still rather low (e.g. 100 out of 400), the amount of improvement in one generation will be negligible. Carried over many generations, however, gain should increase. Obviously, long term planning and commitment are needed.

For intensive programs involving the development of seed orchards or seed trees (Steiner 1986), seed production will be very important, and it probably is a highly heritable trait. Rapid juvenile growth will be important to ensure regeneration success, but this trait must be tested because it cannot be selected for in the wild.

Traits with high heritabilities cannot be easily measured in many cases, and samples must be taken and analyzed. These measurements take time, and many trees must be sampled. If the cost of sampling trees is less than the cost of carrying additional families into the program, then rigorous sampling and testing may be warranted.

In conclusion, I suggest that low-intensity selection be practiced in natural stands: the time spent on selecting a tree should not exceed the time needed to walk around the tree. Steps should be taken to avoid siblings. More trees would be included in testing programs, but experimental designs now allow efficient family discrimination through the use of incomplete blocks (McCutchan et al. 1985), non-contiguous plots (Libby and Cockerham 1980), and the use of clonal replicates in some cases (Shaw and Hood 1985). The inclusion of more genotypes in the first generation will increase the genetic base and help limit inbreeding in advanced generations. Methods such as sublining (McKeand and Beineke 1980; Burdon and Namkoong 1983; Lowe and Van Buijtenen 1986) allow for management of inbreeding and large populations.

Once test plantations, or for that matter, any plantations are established, more rigorous plus-tree selection can be practiced. Plus-tree selection in plantations works much better than in natural stands (Houston 1979; LaFarge and Lewis 1985) because better techniques, uniform sites and ages, and ease of sampling allow better comparisons.

LITERATURE CITED

Burdon, R. D. 1982. Breeding for productivity-Jackpot or Will-o-the wisp? Pp. 35-51 in: B. Thielges, ed. "Physiology and Genetics of Intensive Culture." Proc. 7th North Amer. For. Biol. Workshop. Lexington, KY. July 26-28, 1982.

Burdon, R. D. and G. Namkoong. 1983. Short note: Multiple populations and sublines. Silv. Gen. 32(5/6):221-222.

DeHayes, D. H. 1983. Selection for insect resistance in forest trees. Pp. 9-14 in: Proc. Forest Defoliators-Host Interactions: A comparison between Gypsy Moth and Spruce Bud Worm. New Haven, CT. Apr. 5-7, 1983. U.S.D.A. For. Serv., NE-GTR-85.

Falconer, D. S. 1960. Introduction to Quantitative Genetics. The Ronald Press Company. New York. 365p.

Farmer, R. E. 1980. Progress report. An open-pollinated progeny test in northern red oak (*Quercus rubra* L.). Division of Land and Forest Resources, Tennessee Valley Authority, Norris. TN. (Unpublished; 75p.)(Cited in LaFarge and Lewis 1987).

Fehr, W. R. 1987. Principles of Cultivar Development. Volume 1. Theory and Technique. Macmillan Publishing Company. New York. 536p.

Foster, G. S. 1986. Provenance variation of eastern cottonwood in the lower Mississippi valley. Silv. Gen. 35(1):32-38.

Genys, J. B. 1981. Diversity among progenies of selected phenotypes of yellow birch. Pp. 106-110 in: R. P. Guries, ed. Proc. 2nd North Cent. Tree Improv. Conf. Lincoln, NE. Aug. 5-7, 1981.

Heilman, P. E. and R. F. Stettler. 1985. Genetic variation and productivity of Populus trichocarpa and its hybrids. II. Biomass production in a 4-year plantation. Can. J. For. Res. 15:384-388.

Houston, D. B. 1987. Variation in southern seed sources of northern red oak. Pp. 132-140 in: R. P. Guries, ed. Proc. 5th North Cent. Tree Improv. Conf. Fargo, ND. Aug. 10-12, 1987.

Jourdain, C. J. and J. R. Olson. 1982. Selection for wood quality in five-year-old American sycamore. Pp. 125-130 in: B. Thielges, ed. "Physiology and Genetics of Intensive Culture." Proc. 7th North Amer. For. Biol. Workshop. Lexington, KY. July 26-28, 1982.

Kriebel, H. B., W. T. Bagley, F. J. Deneke, R. W. Finsch, P. Roth, J. J. Jokela, C. Merritt, J. W. Wright, and R. D. Williams. 1976. Geographic variation in Quercus rubra in north central United States plantations. Sim. Gen. 25:118-122

LaFarge, T. and R. A. Lewis. 1987. Phenotypic selection effective in a northern red oak seedling seed orchard. Pp. 200-207 in: B. Bongarten, mod. 19th South. For. Tree Improv. Conf. College Station, TX. June 16-18, 1987.

Land, S. B. Jr. 1981. Genetic variation, heritabilities, and selection strategies for early growth of sycamore in the gulf south. Pp 123-135 in: Proc. 16th South. For. Tree Improv. Conf. Blacksburg, VA.

Libby, W. J. and C. C. Cockerham. 1980. Random non-contiguous plots in interlocking field layouts. Silv. Gen. 29:183-190.

Lowe, W. J. and J. P. van Buijtenen. 1986. The development of a sublining system in an operational tree improvement program. **Pp. 98-106 in:** Proc. IUFRO Conf., Joint Meeting of Working Parties on Breeding Theory, Progeny Testing and Seed Orchards. Williamsburg, VA. Oct. 13-17, 1986.

McCutchan, B. G., J. X. Ou, and G. Namkoong. 1985. A comparison of planned unbalanced designs for estimating heritability in perennial tree crops. TAG 71:536-544.

McKeand, S. E. and W. F. Beineke. 1980. Sublining for half-sib breeding populations of forest trees. Silv. Gen. 29(1):14-17.

Mohn, C. A. and W. K. Randall. 1971. Inheritance and correlation of growth characters in *Populus deltoides*. Silv. Gen. 20(5/6):182-184.

Olson, J. R., C. J. Jourdain, and R. J. Rousseau. 1985. Selection for cellulose content, specific gravity, and volume in young *Populus deltoides* clones. Can. J. For. Res. 15:393-396.

Prakash, Ch. S. and W. A. Heather. 1986. Inheritance of resistance to races of Melampsora *medusae* in *Populus deltoides*. Silv. Gen. 35(2/3):74-77.

Randall, W. K. and D. T. Cooper. 1973. Predicted genotypic gain from cottonwood clonal tests. Silv. Gen. 22(5/6):165-167.

Rink, G. 1984. Trends in genetic control of juvenile black walnut height growth. For. Sci. 30(3):821-827.

Rink, G. and J. W. Van Sambeek. 1987. Seedling sapling growth variation in a southern Illinois black walnut provenance/progeny test. Pp. 156-162 in: R. P. Guries, ed. Proc. 5th North Cent. Tree Improv. Conf. Fargo, ND. Aug. 10-12, 1987.

Shaw, D. V. and J. V. Hood. 1985. Maximizing gain per effort by using clonal replicates in genetic tests. TAG 71:392-399.

Smith, D. M. 1962. The Practice of Silviculture. Seventh Edition. John Wiley & Sons, Inc. New York. 578p.

Steiner, K. C. 1985. Constraints and opportunities for tree improvement in the Appalachian hardwood region. Pp. 203-217 *in:* M. E. Demerritt, Jr., ed. Proc. 29th Northeastern Tree Improv. Conf. Morgantown, WV. July 18-20, 1985.

Steiner, K. C. 1986. Integrating tree improvement with hardwood seedling production. Pp. 24-30 in: Proc. Northeastern Area Nurserymen's Conference. State College, PA. July 14-17, 1986.

Stelzer, H. E., W. F. Beineke, and M. V. Coggeshall. 1983. Fifth-year height, diameter, volume, and form in black walnut open-pollinated families. Unpublished; 14p. Purdue University, West Lafayette, IN.

Townsend, A. M. and W. R. Harvey. 1983. Genetic analyses for height and diameter growth of 9-year-old red maple progenies in five plantations. Pp. 1-13 in: R. P. Guries, ed. Proc. 3rd North Cent. Tree Improv. Conf. Wooster, OH. Aug. 17-19, 1983.

Webb, C. D., R. P. Belanger, and R. G. McAlpine. 1973. Family differences in early growth and wood specific gravity of American sycamore (*Plantanus occidentalis* L.). Pp. 213-227 *in*: Proc. 12th South. For. Tree Improv. Conf. Baton Rouge, LA.

Zobel, B. and J. Talbert. 1984. Applied Forest Tree Improvement. John Wiley & Sons. New York. 505p.