Integrating Tree Improvement with Hardwood Seedling Production

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Abstract. The genetic improvement of high-value hardwoods is impeded by long rotations, low acreage planted, high costs of seed production, and certain biological difficulties. Under the circumstances, any sort of conventional approach to improvement is financially unattractive. However, there are still opportunities to make clever and profitable use of the large amount of genetic variability that many of these species exhibit. One such opportunity for northern red oak is outlined as an example, a low cost, "low-tech" improvement program that capitalizes on genetic variation in juvenile growth rate.

Introduction

There have been many, often short-lived attempts at hardwood tree improvement in the Northeast over the past 35 years. Without indulging in case histories, and there are some notable exceptions, the overall impact of hardwood tree improvement on silvicultural practice has been minimal in not only this region but the entire U.S. For most hardwood species, tree improvement is economically unappealing because of long rotations, low acreage planted, and high costs of seed production (see for example the analysis by Marquis 1973). In many cases, biological difficulties associated with controlled pollination and vegetative propagation intervene as well.

Nevertheless, it is wrong to conclude that there is no role, no future, for hardwood tree improvement in the Northeast. I believe that there ***must*** be such a role if the quality of the hardwood resource is to be enhanced or even maintained.

My vision of this future involves close cooperation between silviculturists, geneticists, and nursery managers in solving problems of mutual concern. It also involves tree improvement methodologies that are appropriate to the species in question, rather than blind use of some textbook model for tree improvement, and it involves investments that are proportionate to expected returns. I believe that these things are possible with hardwoods, and that nursery managers and silviculturists should endeavor to make wise and clever use of the kinds of genetic variability that have been so useful with other species in other regions.

A Role for Hardwood Tree Improvement

Opportunities in hardwood tree improvement are overlooked by supposing that improvement should be directed only toward productivity gains ***at harvest,*** the classic goal of almost all plant breeders. There is one very obvious difficulty with this improvement goal in the case of high-value hardwoods such as northern red oak, white ash, black walnut, and black cherry: their rotations are so long that genetic selection in progeny tests must be delayed for many years before reliable estimates of end-of-rotation performance can be obtained.

This difficulty can be illustrated in concrete terms using Lambeth's (1980) analysis of age-age correlations in the Pinaceae, a group for which many data are available. His data indicate that a breeder must select as late as one-fourth of the rotation length in order to get even the rather modest age-age correlation of $r = 0.6$. Extrapolating from this data set, for a species with an expected rotation of 80 years, this would mean delaying selection until age 20. The resulting rather tedious rate of progress would almost certainly be disasterous for an improvement program.

Another, and equally important, difficulty with this goal has to do with the fact that high-value hardwoods are usually regenerated *naturally* in stands of *mixed species* composition. For such species, the silviculturist is normally more concerned with getting adequate regeneration of desired species than he is with end-of-rotation productivity on a per-tree basis, and any tree improvement program must accommodate this fact. With species that are often difficult to regenerate, such as northern red oak, common sense tells us that preventing regeneration failures and enhancing stand composition is much more economically attractive than the opportunity of gaining a few percentage points in volume or form improvement on the trees that are harvested.

Under these circumstances, tree breeders can make their greatest contribution by focusing attention on the needs of the nursery manager and the difficulty of enhancing stand composition through seeding or planting. For example, Gall and Taft (1973), McGee (1968), and Russell (1971) have all suggested that genetic selection in oaks can help solve the problem of poor planting success with those species. Even a partial solution to these problems would help make hardwood planting a viable option to the silviculturist whose goal is to achieve rapid, well-distributed regeneration of desirable species. This may prove to be the most rewarding role for tree improvement with long-rotation, high-value hardwoods.

As has been discussed by others at this conference, nursery stock quality is a major determinant of plantation success. In general, good quality seedlings are those that are reasonably large and uniform in size, and have proper morphology of shoots and roots, proper stress preconditioning, proper state of dormancy for scheduled activities, and sufficient carbohydrate reserves to resume growth vigorously after planting.

These characteristics are usually achieved through a combination of cultural treatments such as fertilization and control of spacing and duration of growth before sale. The main point I wish to make in this presentation is that seedling response to these cultural treatments can sometimes be matched through simple forms of genetic selection. This is especially true where the objective is a large and vigorous seedling with a proper balance between shoot and root systems. Genetic selection cannot substitute for good nursery management, but it can play a complementary role in the production of high quality seedlings.

NORTHERN RED OAK AS AN EXAMPLE

Northern red oak provides an example of the gains to be made in seedling and sapling performance through selection of seed parents. Several studies have documented provenance variation in growth rate for this species, and as expected, the variation is substantial (Farmer et al. 1981, Gall and Taft 1973, Kriebel 1965, Kriebel et al. 1976, Kriebel et al. 1985, Schlarbaum and Bagley 1981). However, where data on individual family performance is available, results suggest that selection of wild seed parents within even rather small geographic areas can result in considerable genetic gain. In fact, progenies from even the same stand can be extremely variable in juvenile growth rates:

* *Kriebel (1965) studied first-year growth of 191 families representing 31 nearly range-wide provenances. No actual family data were presented, but the family-within-stand variance component for growth was a very large part of total genetic variance, especially when slow-growing provenances from the edges of the species' range were excluded.

* *Farmer (1979) grew progenies of 20 southern Appalachian seed parents for 5 years under fertilized and control conditions. The best family grew 28% faster than the mean for all families. Fertilization improved growth rates by 47%.

* *McGee (1968) grew progenies of 3 southern Appalachian seed parents native to different elevations. At age 1 from seed, progenies from the lowest elevation parent were 68% taller than those from the highest, though part of the difference may have been due to initial seed weight.

* *In a similar study, McGee (1974) grew progenies from 4 elevational provenances. At a low elevation planting site, the best elevational provenance was 31% taller than the overall mean after 2 growing seasons.

* *Gall and Taft (1973) and later Farmer et al. (1981) reported on the juvenile growth of progenies of 55 seed parents representing 5 stands in the Tennessee River Valley and one stand in central Ohio. The tallest provenance was 15% taller than the mean of all provenances at age 2 from seed, and 25% taller at age 11. ***Within*** each stand, the tallest family was 7-53% taller than the stand average at age 11.

* *In a study that is still in progress, we have found large differences in first-year growth associated with seed parent. For progenies of 5 wild parents located no more than 5 miles apart in central Pennsylvania, the largest family was 28% taller than the mean of all. Two seed parents located with within 200 feet of one another yielded progenies with significantly different mean heights of 13.4 and 8.6 inches. The larger had 78% greater dry weight of stem and roots than the other.

These examples of genetic variation pertain only to morphological aspects of stock quality. However, if northern red oak is like other species we will probably find that even the more subtle aspects of seedling physiology are as genetically variable as growth rate. Unfortunately, we presently know little about genetic control of physiological responses of hardwoods to nursery cultural treatments.

The percentage differences cited above translate into a few inches in height or a few grams in weight for one-year-old seedlings. Such absolute differences seem small, but they can be economically important if they result in fewer cull seedlings, larger percentages of "Grade 1" seedlings, or production of plantable seedlings in one year rather than two.

Using an example from our study mentioned above, and using Stroempl's (1985) grades for red oak, one family had 60 percent best-grade seedlings and no culls, while another from a nearby wild parent had only 21 percent best-grade seedlings and 26 percent culls. Although our seedlings were not growing under nursery production conditions, this comparison does illustrate family differences in practical terms. Pennsylvania Bureau of Forestry personnel have seen even larger differences in grade between red oak seedlots growing under apparently similar environments.

GENETIC GAINS AFTER PLANTING

For northern red oak and other oaks, planting failures are primarily due to the slow growth of planted trees (Johnson 1981). Because it affects growth rate, stock size can markedly affect the probability that a planted seedling will become a component of the stand, as Johnson's (1984) statistics show very lucidly, and as many other studies have indicated as well (Foster and Farmer 1970, Larson 1977, Loftis 1979, Wendel 1979).

Seedlings that are large because they have the genetic potential for faster growth, and not merely because they were grown under optimal nursery conditions, have the further advantage that their superiority will continue past field planting. Those who plant northern red oak frequently note that, while average growth is usually very slow, many individual trees show acceptable and even exceptional growth (Johnson 1979, Olson and Hooper 1972). Our studies of juvenile growth of families and clones of this species suggest that genetics may play a major role in such variation. Genetic selection could increase the proportion of such individuals in the plantation and enhance the probability that a planting will be successful.

A REALISTIC IMPROVEMENT STRATEGY

What would be a suitable design for a tree improvement program with this objective? First of all, we must be realistic — the annual production of northern red oak seedlings by state nurseries in the whole of the 20-state Northeastern Area is only about one million seedlings, and no state produces more than a few hundred thousand (Scholtes 1985). Clearly, the investment by any one state agency in red oak improvement must be very small in order to be economically sound.

Furthermore, northern red oak presents its own biological constraints for tree improvement: plus-tree (phenotypic) selection in wild stands is of unproven, and in fact doubtful, effectiveness for genetic improvement of growth rate; trees require about 25 years to reach reproductive maturity; annual seed production per area of stand (or seed orchard) is relatively low and erratic; and controlled pollinations are costly for the number of seeds produced. These factors, plus the expense that would be incurred, tend to controvert the use of clonal or seedling seed orchards and any form of actual breeding.

One is reminded of a buzz-word that was popular during the environmental movement of the 1970's, "appropriate technology"—the sophistication of the technology should be appropriate to the circumstances surrounding its use. I think that a very appropriate tree improvement program for northern red oak, and indeed most other quality hardwoods that are planted in small numbers, could involve only the following simple steps (diagrammed in Figure 1):

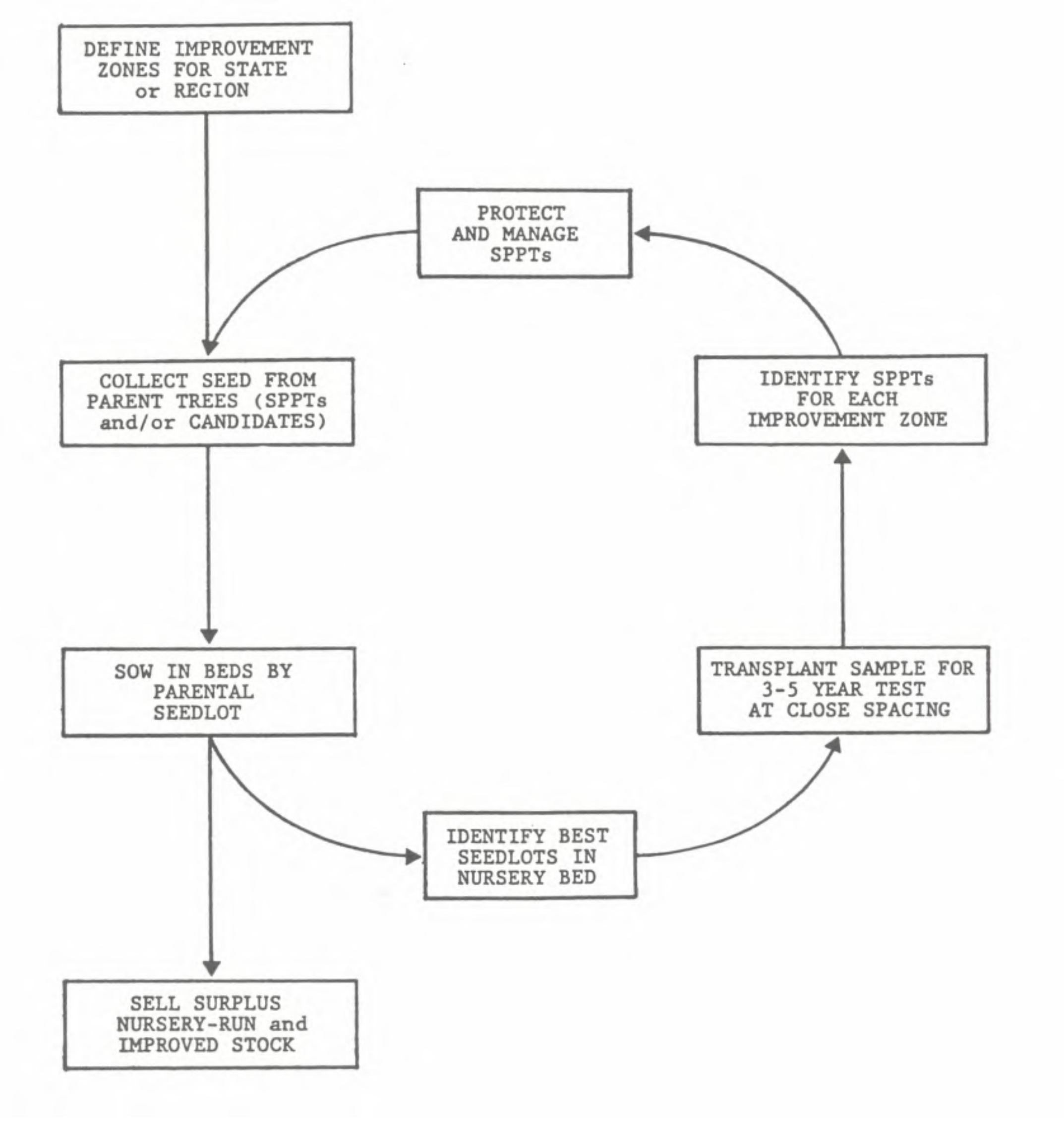

FIGURE 1 - A low-investment scheme for genetically improving juvenile growth rate through the use of in situ Seed Production Plus Trees (SPPTs)

1) Divide the target area for nursery stock into "improvement zones" based upon physiographic and climatic similarities. In Pennsylvania, for example, these would consist at the minimum of the Allegheny Plateau, the Ridge-and-Valley Province, and the Piedmont.

2) Require seed collectors in each zone to keep seed separated by parent tree, number the seedlots, mark each tree, and retain exact location information keyed to seedlot numbers. It is important that each parent can be relocated. Parent trees should be chosen mainly on their ability to produce seed, but poorly formed individuals should be avoided unless their form has obvious environmental causes.

3) Sow seed in nursery beds as usual for production seedlings, but sow by seedlot in identifiable plots. To avoid environmental biases on growth, lots should preferably be randomized and the whole set planted in two or more replications.

4) During the autumn before lifting, in preparation for new seed collections, identify the seedlots with the largest seedlings and require collectors to return to those respective seed parents plus others that were not collected from previously. This introduces a new cycle of nursery testing, and cycles can be continued annually for as long as necessary to identify enough seed parents which yield superior nursery stock that annual seed requirements can be met by collecting only from those trees. For comparison purposes, it is desirable that there be some annual overlap of previously tested parents.

5) At lifting time, retain a random sample of at least 30 seedlings from each of the selected seedlots, and a random sample of seedlings from a few lots with average-sized seedlings. The latter will serve as checks on the amount of improvement that is actually accomplished. Distribute the bulk of the seedlings through normal production channels as "nursery-run" stock, and plant the samples in replicated transplant beds at close spacing. These small tests, established annualy as the cycle is repeated, will each run for 3 to 5 years and will serve as evaluations of post-planting performance. Final designation of a parent as a genetically superior Seed Production Plus Tree (SPPT) will depend upon the performance of its progeny in these post-planting trials.

6) As superior parents are identified for each improvement zone based upon evaluations in transplant beds, designate these trees as SPPTs and take steps to permanently identify and protect these trees and stimulate their fruitfulness. Seedlings from these trees can be truthfully marketed as improved stock and part of the premium passed on to the seed collectors for their troubles. As long as some semblance of the basic procedure is continued, with accurate records maintained, parents can always be added to or eliminated from the register of SPPTs and further genetic gains can be made almost indefinitely.

These six steps comprise a bare-bones approach to improving seedling growth in the nursery and in the first few years after planting. Possible elaborations include establishing the transplant tests at more than one site, to avoid losses in gain caused by genotype x environment interactions, and moving the best seedlings from the best families in transplant tests to a seed orchard site for future production. The latter option would also permit family selection for growth and form at more advanced ages. These elaborations would add to the cost of the improvement program, but they would also add to the genetic gain. If the improvement program is successful in making planting a more feasible silvicultural alternative, then increased planting could justify further investments in genetic improvement.

Conventional tree improvement is usually directed at the culturally extensive phase of plantation sawlog production, the phase that follows plantation establishment. In this paper, I have shown how tree improvement can also contribute to the culturally intensive, "juvenile" phases involving seedling production and seedling establishment. Where conventional tree improvement directed at long-term productivity is economically impractical, improvement goals can be focused exclusively on juvenile growth rates if it is assumed that juvenile growth is at least not negatively correlated with adult performance.

The improvement plan that I have outlined for northern red oak capitalizes on the large amount of genetic variation in juvenile growth often exhibited by progenies from different wild parents within relatively small geographic areas. It utilizes in situ Seed Production Plus Trees and normal seed procurement channels rather than expensive clonal or seedling seed orchards, although these could be installed at a later date. It could be implemented through relatively simple modifications to existing nursery management practices with minimal assistance from a trained geneticist and without incurring large costs. Genetic selection for juvenile growth rate in a "low-tech", low-investment improvement program such as this can be economically more attractive than conventional improvement because the return on investment can be realized more quickly through better quality seedlings and a lower average cost per successfully established seedling.

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