GENETIC CONSIDERATIONS IN THE OPERATIONAL PRODUCTION OF HARDWOOD NURSERY STOCK IN THE EASTERN UNITED STATES

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ABSTRACT

A recent survey of forest tree nurseries in the eastern US indicated that hardwood tree improvement is not extensively practiced at an operational level, with only 6.8% of hardwood seedlings produced from improved materials (compared to 36% for conifer seedlings at those nurseries that produce both). Fine hardwoods represent less than 20% of improved hardwood seedling production. Most respondents indicated that the use of genetically improved materials would benefit forestry in their region; however, less than 40% have germplasm of hardwood species in improvement programs. Because most respondents stated their intention to use more genetically improved hardwood material in seedling production over the next 10 y, availability of improved materials will likely limit future use. More integration of research involving genetic improvement into operational nursery production will help sustain the future value and supply of our hardwood forest resource.

KEY WORDS

tree improvement, seed zones, seed orchards, forestry, timber production, restoration

NOMENCLATURE

USDA NRCS (2004)

A high-value black walnut (*Juglans nigra*) tree exhibiting desirable timber form.

Photo by Douglass F Jacobs

Successful plantation establishment depends on many factors. Using quality seedlings on the appropriate site and employing necessary silvicultural practices each influence establishment success. Low-quality seedlings are less likely to survive outplanting, and those that do survive often perform poorly. Both morphological and physiological factors can affect seedling quality. These factors can be influenced by nursery culture (for example, growing conditions, fertilization, and root system modification), over-winter storage, and handling (Jacobs 2003). Given the tremendous genetic variation inherent in forest tree species (Zobel and Talbert 1984), the origin of plant material is another important factor in determining seedling quality.

Tree improvement in conifer seedling culture, and in production of hardwood species grown for fiber and energy, is frequently employed in present-day forestry; however, the degree to which nurseries incorporate this technology into operational seedling production of high-quality hardwood species in the eastern US is uncertain. The focus of this paper is on tree improvement practices related to native hardwood species, particularly those grown for timber and veneer products. Our objectives are to: 1) outline some common and potential hardwood tree improvement practices in the eastern US; and 2) identify the degree to which tree improvement is being practiced at an operational level in hardwood forest and conservation nurseries in the eastern US.

TREE IMPROVEMENT

Tree improvement has been defined as "tree selection, evaluation and breeding for more desirable characteristics" (Ordre des ingénieurs forestiers du Québec 2003). Zobel and Talbert (1984) describe tree improvement as an additional silvicultural tool available to foresters and note that its effectiveness is maximized only when used in conjunction with other silvicultural practices. To many, the goal of tree improvement is to produce plantations that are well-stocked and homogenous with respect to growth rate, form, and quality. Tree improvement is achieved through the selection of superior performing individuals that exhibit specific desirable traits (for example, exceptional growth rate, form, or wood quality). Realizing genetic gains at the operational level depends on availability of improved plant materials. Early seed orchards were established using seeds from "superior" selected mother trees. Orchards can then be thinned of weaker specimens and their offspring undergo another round of selection to yield additional genetic gain for particular traits.

Timber and Carbon Gains

Conifer tree improvement in the US has significantly improved plantation productivity through faster growth rates and enhanced tree form, wood quality, and pathogen resistance (Li and others 1999; Schultz 1999). Most loblolly pine (*Pinus taeda* L. [Pinaceae]) plantations established in the southern US use genetically improved seeds from seed orchards (Li and others 1999; Schultz 1999). Plantations established with second generation improved loblolly pine are expected to yield stands with up to 32% greater financial value than those established with unimproved seedlings (Schultz 1999). The advent of biotechnology offers new opportunities for tree improvement. For instance, the introduction of desirable traits into Monterey pine (*Pinus radiata* D. Don [Pinaceae]) is possible through a number of techniques (Walter and others 1998). Genes that control the expression of specific traits are widely available, and successful incorporation and expression is commonplace (Meilan and others 2004). Genetic gains may extend beyond timber productivity, allowing for alternative management objectives. For instance, dry matter production of Monterey pine may be increased by up to 22%, thereby enhancing carbon sequestration rates (Jayawickrama 2001).

Energy and Fiber Production

Hardwood tree species grown for energy and fiber have benefited from tree improvement programs in a similar manner. Clonal production of genetically improved poplar (*Populus* spp. L. [Salicaceae]) in the Pacific Northwest of the US has led to marked increases in annual growth (Debell and others 1997), as well as drought tolerance and pest resistance (Robison and Raffa 1998). In the southeastern US, investigation into improving success of clonal propagation of sweetgum (*Liquidambar styraciflua* L. [Hamamelidaceae]) could result in genetic gains in terms of fiber quality and growth rate (Rieckermann and others 1999). Expression of specific traits can be controlled through the integration of a transgene into a tree's genome (Meilan and others 2004). Identification of a transgene that increases herbicide tolerance in hybrid poplars should lead to more effective control of competing vegetation (Meilan and others 2002). This, in turn, could increase stand productivity and efficiency of management actions. Advances in tissue culture and somatic embryogenesis have allowed the rapid and effective establishment of new poplar clones (Confalonieri and others 2003).

Species Restoration

Tree improvement may also be used in efforts to help restore important keystone species that have been diminished by exotic pest or pathogen introductions. For instance, American chestnut (*Castanea dentata* (Marsh.) Borkh [Fagaceae]) once dominated the eastern US deciduous forests until introduction of an aggressive diffuse canker disease (Anagnostakis 1987) in the early

1900s virtually eliminated the species throughout its range. Breeding programs have made substantial progress toward producing a blight-resistant hybrid chestnut tree for reintroduction (Burnham and others 1986; Hebard 2002). To accomplish this goal, American chestnut was initially hybridized with blight-resistant Chinese chestnut (*Castanea mollissima* Blume [Fagaceae]) and subsequently backcrossed several times to pure American chestnut. This will produce a hybrid American chestnut tree for reintroduction with moderate to high blight resistance that is approximately 94% American chestnut (Burnham 1981; Hebard 2002). Similar or alternative selection strategies may be useful for restoration efforts of other important native hardwood tree species. Examples include butternut (*Juglans cinerea* L. [Juglandaceae]), a species that is seriously threatened by a fungus that causes lethal cankers (Ostry 1998), and American elm (*Ulmus americana* L. [Ulmaceae]), an important urban and forest tree that was devastated by the introduction of Dutch elm disease (Karnosky 1979).

High Value Hardwoods

Fine hardwoods such as black walnut (*Juglans nigra* L. [Juglandaceae]), northern red oak (*Quercus rubra* L. [Fagaceae]), and black cherry (*Prunus serotina* Ehrh. [Rosaceae]) are some of the most valuable tree species grown for timber and veneer in the eastern US. All are major components of the Central Hardwood Forest Region, one of the few regions in the US where high value hardwood species are a dominant forest management objective. Research with northern red oak has explored the effect of genotype on water relations (Kubiske and Abrams 1992) and provenance on growth rate (Kriebel and others 1988). Studies in black cherry have examined family response to ozone exposure (Lee and others 1999) and influence of genotype on leaf structure (Abrams and others 1992). However, most research into the influence of genotype on performance of fine hardwood species has focused on black walnut. Veneer-grade black walnut logs have historically been, and continue to be, among the most lucrative forest products in the region. Given its high commercial value, much of the research into tree improvement in eastern hardwoods has focused on improving black walnut timber quality rather than increasing fiber production. Identification of superior black walnut phenotypes based on apical dominance, annual growth, branching habit, growth form, and heartwood production has led to the establishment of progeny and provenance trials. Selection for specific traits has resulted in improvement of seedling height growth (Bey and Williams 1975; Bey 1980; Rink 1984; Bresnan and others 1994), diameter growth (Bey and Williams 1975), and survival (Bresnan and others 1994). Likewise, use of improved black walnut nursery stock has also yielded more rapid height and diameter growth and better stem form in established plantations (Beineke 1989).

Early research on variation in performance of different black walnut families indicated that selections could be made to increase seedling competitiveness and resistance to drought stress (Rink and Van Sambeek 1985) and growth (Rink 1984). Phenotypic variation in black walnut limits the likelihood of successful selection of superior performing trees without accompanying progeny testing (Bey 1980). Thus, progeny tests were established and resulted in the development of seed orchards (Beineke 1989).

Management of Genetic Composition

Identification of desirable phenotypic traits and collecting seeds from trees that express them is more selective than many present-day seed collection protocols, which often tend to be conducted in readily accessible locales such as cemeteries, urban parks, and city streets. Seed collection in this manner, while economical, is not likely to yield large and consistent genetic gains.

Clonal propagation allows for greater control over genetic improvement as sexual recombination does not occur (Riemenschneider 1997). In fine hardwood species, which are often difficult to propagate clonally, grafting has long been successfully employed for several species (Beineke 1994; Lee and others 1999). To control the genetic composition of orchards, seedling clones can be used to ensure identical genetic structure to a selected tree. Additionally, clonal propagation can allow for intensive investigation of suitable families for different sites as a means of better defining genotype × environment interactions (St Clair and Kleinschmit 1986). Production-oriented plantations have also been established with grafted seedlings. Even when established with clonal material, however, these seed orchards yield open-pollinated trees and half-sib seed collection allows for increased infiltration of potentially inferior genetic composition into annual seed production, which may limit genetic gain. Mass controlled-pollination of Tasmanian blue gum (*Eucalyptus globulus* Labill. ssp. *globulus* [Myrtaceae]) orchards is presently employed in Chile (Harbard and others 1999) and thus helps maintain genetic gain in seed production. Similar practices are generally not used in orchards for hardwood tree species in the US, and in fact may not be operationally feasible.

SURVEY PROCEDURE

We conducted a survey, in the form of a mail questionnaire, of seedling nurseries in the eastern US to determine the extent to which genetic considerations are incorporated into operational hardwood nursery production. The eastern US was defined as those states that lie on the eastern edge of the prairie, and their longitudinal equivalents (Figure 1). Plant material providers were identified by a comprehensive list produced by the USDA (2003). A letter was addressed to the nursery manager requesting that the questionnaire be completed

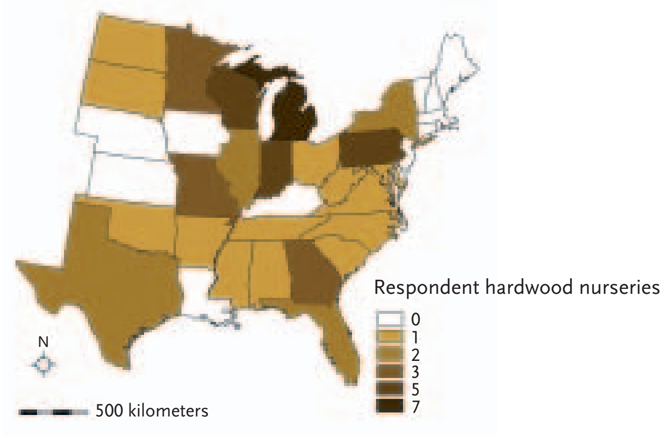

Figure 1. Designation of the eastern US region for survey of operational hardwood tree improvement practices and number of nursery responses by state.

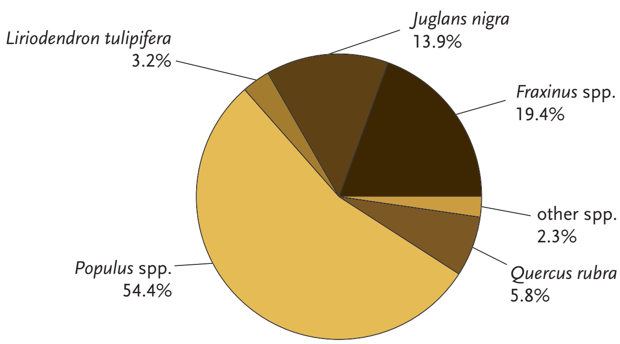

Figure 2. Distribution by species of improved hardwood seedling production in nurseries within the eastern US (n = 40 responses from nurseries to a survey questionnaire).

by the person most aware of the nursery's operations and involved in decision making.

The questionnaire, to which responses were anonymous, requested information on hardwood seedling production for that specific nursery. Questions addressed present and anticipated future incorporation of hardwood tree improvement technology into operational seedling production, the monitoring of hardwood seed sources and their importance to forestry and forest restoration in the region, and an overview of the species, stocktypes, and genetic considerations for plant materials produced at each nursery.

To determine if differences existed by region in the percentage of improvement of hardwood and conifer seedlings, data were analyzed using Analysis of Variance (ANOVA). In the aforementioned case, data analysis was performed using SAS Software (SAS Institute 1999).

RESULTS

A total of 209 questionnaires were mailed to nurseries in the eastern US. Seventeen questionnaires were undeliverable with their current address and 87 nurseries either did not grow tree seedlings for reforestation or conservation purposes or did not grow hardwood seedlings. An additional 21 questionnaires were returned incomplete and excluded from analysis. As 52 were returned completed, the response rate was 51%. These nurseries represented approximately 375 million seedlings, of which more than 69 million consisted of hardwood species. Of those nurseries that responded and met the appropriate criteria, 64% were privately owned and 36% were publicly owned. The average age of private nurseries was 27 ± 3.4 y (mean ± SE), while for public nurseries it was 63 ± 4.0 y. Privately owned nurseries were responsible for producing approximately 37 million hardwood seedlings annually, while annual production of publicly owned nurseries was approximately 32 million seedlings. Responses indicate that approximately 6.8% of hardwood seedlings are from genetically improved materials compared to, at those nurseries that grow both hardwood and conifer species, approximately 36.5% of conifer seedlings that are produced from genetically improved materials. *Populus* spp. represent more than half of the improved hardwood nursery stock produced in the eastern US (Figure 2), followed by ash (primarily green and white ash—*Fraxinus pennsylvanica* Marsh [Oleaceae] and *F. americana* L.) (19.4%), black walnut (13.9%), northern red oak (6.8%), and tulip poplar (*Liriodendron tulipifera* L. [Magnoliaceae]) (3.2%).

A comparison of the percentage of improved nursery stock by region (Figure 3) identified that a significantly (P = 0.0008) greater percentage of nursery stock were of improved origin in the southern US (65 ± 3, mean ± SE) than in the mid-western US (20 ± 6), but neither differed significantly from the northeastern

US (33 ± 12.5). No difference ($P = 0.74$) was detected across each region in the percentage of improved hardwood stock.

While more than 75% of respondents thought the use of genetically improved materials would be beneficial to forestry in their region (Table 1), 40% do not presently use any improved hardwood material in seedling production. Although 64% of respondents stated that they intend to use more genetically improved material in the next 10 y, 52% of respondents do not currently have hardwood species in improvement programs that they expect will yield new material in the future (for instance, seed orchards not yet of reproductive age) (Table 1). Most nurseries (82%) have ≤ 10% of their hardwood seedling production as genetically improved materials (Figure 4). In contrast, 46% of nurseries that also produce conifer seedlings have ≥ 10% of their conifer seedling production from genetically improved material (Figure 4).

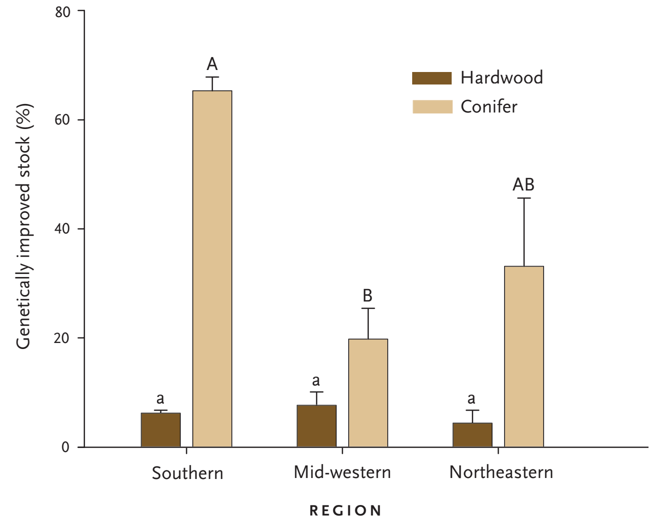

Figure 3. Regional differences in tree improvement in the eastern US. *Southern region*: Alabama, Arkansas, Louisiana, Florida, Georgia, Maryland, Mississippi, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, Virginia, and West Virginia. *Mid-western region*: Illinois, Indiana, Iowa, Kansas, Michigan, Minnesota, Missouri, Nebraska, North Dakota, Ohio, South Dakota, and Wisconsin. *Northeastern region*: Connecticut, Maine, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, and Vermont. Bars are means and error bars are standard errors. Different letters represent significant differences between regions for hardwoods or conifers at $\alpha = 0.05$.

DISCUSSION

Our results indicate that hardwood tree improvement is not extensively practiced at an operational level in the eastern US, with only an estimated 6.8% of seedlings each year being produced from improved plant materials. Despite well-documented gains from tree improvement for black walnut (Beineke 1989), only about one-fifth of the improved hardwood seedlings produced annually are black walnut and northern red oak (combined). The relatively high proportion of improved material in green and white ash is interesting given that these species are considered less valuable than black walnut or northern red oak. Early work to improve growth rates of other hardwood species (such as white oak, *Quercus alba* L. [Fagaceae]) (Rink and Coggeshall 1995) also has not been incorporated into operational practices. The degree to which hardwood tree improvement is operationally practiced in this region is obviously quite far behind that of conifer tree improvement. While this may simply be a result of a large number of species and relatively low production of each species (compared to important conifer species), the potential gains may in time be highly beneficial to hardwood forestry.

Little regional variation in the percentage of improved hardwood material may indicate that familiarity with conifer tree improvement materials and methods does not necessarily increase the likelihood of application of the same technology to hardwood species. For example, in the mid-western US, the percentage of improved conifers produced annually was lower than in the southern US, but there was no difference for hardwoods.

One area of potential concern is the disparity between the perceived benefits of using genetically improved seedlings and the future availability of improved material. While most respondents see genetically improved nursery stock as beneficial to forestry in terms of timber and fiber production or eco-

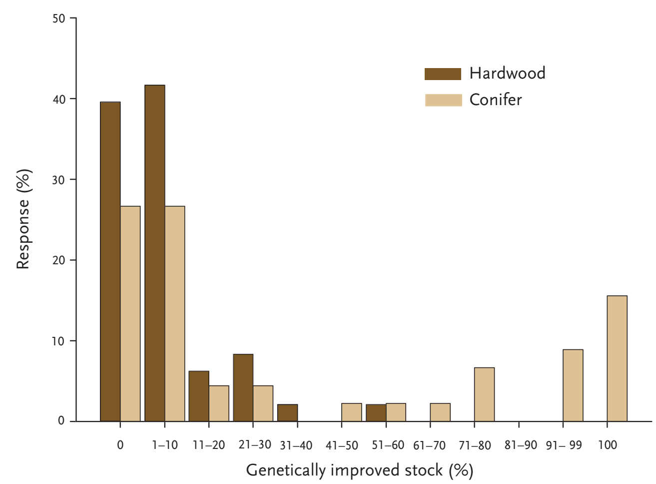

Figure 4. Difference in degree of tree improvement for conifer and hardwood seedlings (conifers, n = 45, hardwoods, n = 47, responses from nurseries to a survey questionnaire).

TABLE 1

Perceptions of nursery managers toward the benefits of genetic improvement and the future production of genetically improved hardwood seedlings (each question lists responses [n] from nurseries to a survey questionnaire).

	Yes, for:			No
	Timber production	Fiber production	Ecological restoration	
	%			
Do you see the use of genetically improved hardwood nursery stock as beneficial to forestry in your region? (n = 48)	77	40	38	10
In the next 10 y, do you foresee increased production of genetically improved hardwood seedlings in your region? (n = 51)	49	24	31	39
Do you have hardwood species in tree improvement programs for which improved material is not yet available? (n = 48)	35	15	17	52
		Yes		No
Do you intend to use more genetically improved hardwood material in the next 10 y? (n = 46)		64		36

TABLE 2

Degree of involvement of nurseries in tree improvement (n = 50 responses from nurseries to a survey questionnaire).

Activity	Degree of involvement (%)
Read scientific literature	3
On-site tree improvement personnel	27
Private tree improvement program	17
Collaborate with:	
Government programs	27
University researchers	33
Cooperative programs	16
Not involved	31

logical restoration in their region, less than half of those nurseries have tree improvement programs from which improved material should become available in the future, and nearly one-third of nurseries are in no way involved with any tree improvement programs. This likely explains why 61% of respondents foresee increased production of genetically improved nursery stock in the next 10 y. Because most nursery managers indicated that they intended to grow more genetically improved hardwood material over the next 10 y, however, effective communication of tree improvement techniques and increased availability of improved material is necessary.

Encouragement of nursery managers and operators to participate in cooperative programs and collaborate with researchers should advance operational hardwood tree improvement. Because one-third of respondents indicated that they are not involved in tree improvement, and only up to one-third indicated that they were collaborating with a research agency, it may be necessary for extension agents to bridge that gap to ensure that nursery managers are aware of the technologies available and the implications of incorporating them in to their nursery production practices (Table 2).

CONCLUSIONS AND FUTURE DIRECTIONS

While benefits of tree improvement are well defined and readily available in conifer production, only a small percentage of the annual hardwood seedling production in the eastern US is of improved origin. Incorporation of such practices into operational seedling production is likely to increase in the future as interest in hardwood tree improvement is apparently high within the nursery industry; however, there appears to be limited supplies of improved fine hardwood plant material available. Presently, the cost of producing genetically improved nursery stock is higher than that for unimproved nursery stock. It is possible that seedling buyers may not be willing to pay a premium for genetically improved nursery stock, which could be a major obstacle in incorporating improved stock into afforestation and reforestation programs.

The development of research cooperatives such as the Hardwood Tree Improvement and Regeneration Center at Purdue University that comprises government and university scientists advised by industrial associates, all levels of government, and interested stakeholders should help spur greater application of tree improvement techniques to fine hardwood species. Management of genetic resources, coupled with increased understanding of genotype × environment interactions, and the use of appropriate silvicultural practices should increase future productivity of fine hardwood plantations. With the constant threat of conversion of forestland to other uses, genetic improvement of hardwood species will be continuously needed to help meet society's increasing demand for hardwood resources, ensure sustained economic viability of hardwood forests, and restore threatened species.

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