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Review article

Genetic improvement of oaks in North America

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Summary —The resource and silvicultural contexts of oak tree improvement in North America are described briefly, and the methods, species, locations, and objectives of specific projects are summarized. Brief descriptions are provided of two projects that differ markedly in scope. Past experience suggests that few of the existing projects will ultimately be successful unless project leaders take deliberate steps to transfer genetic gains from seed orchard to operational plantations.

***Quercus* / genetic improvement / North america / review**

Résumé — Amélioration génétique des espèces nord-américaines. *Le contexte de la ressource et de la sylviculture des chênes est tout d'abord brièvement décrit dans le cadre des programmes d'amélioration de ces espèces. Une revue des espèces concernées, des régions où ces programmes sont menés, des objectifs affichés et des méthodes utilisées est ensuite faite. Deux programmes, dont les ambitions sont différentes, sont plus particulièrement décrits. L'expérience passée montre que peu de projets seront couronnés de succès, à moins que leurs responsables ne prennent des initiatives fermes pour transférer les gains génétiques obtenus dans les vergers à graines vers le reboisement.*

Quercus / *amélioration génétique / Amérique du Nord / synthèse*

INTRODUCTION

There are many oak improvement programs in North America, and they are directed at a rather large number of species. Naturally, the methods and objectives of these programs differ considerably, and a comprehensive coverage of them would involve excessive detail. Instead, this paper gives a general overview of oak improvement with, in addition, some attention to peripheral matters that I think are important to those engaged in this activity in North America. The information regarding specific projects is based upon correspondence with approximately 60 forest geneticists, and I think that it includes all (or very nearly all) existing projects.

THE OAK RESOURCE IN NORTH AMERICA

A rough statistical summary of the oak resource in North America (exclusive of Mexico) will help us to circumscribe the subject. Little (1979) accepts 58 native species of tree-sized *Quercus* in the United States. Ten of these also occur in a small portion of Canada. Oaks are native to 47 of the 48 contiguous states, but 62% of the species occur only east of about longitude 97° (or longitude 105° in the south, Texas and Oklahoma). One important northern species, *Q macrocarpa*, also extends west to 105°. Longitude 97°, which lies roughly along the eastern edge of the Great Plains region in figure 1, is approximately the western limit of the eastern deciduous forest. This area, where most oak species are found, occupies only about half of the US (exclusive of Alaska), but it contains 94% of all oak growing stock by volume (Waddell *et al*, 1989).

Of course, it is difficult to assign a land area to the oak resource because oaks occur in mixtures with other species. 'Oak-hickory' is the most extensive (but not the only) forest type containing a large component of oak, and the area of this type is estimated to be 448,429 km^2 (Anonymous, 1978). To express this area in meaningful terms, it is very nearly equal to the combined land areas of Germany, Denmark, Belgium and the Netherlands. It is about 10 times the area of all oak forest and woodlots in France (Anonymous, 1989).

OAK PLANTING IN THE UNITED STATES

Given the size of the oak resource in the US, the practice of planting to regenerate stands after harvesting is almost inconsequential. No one has compiled statistics on

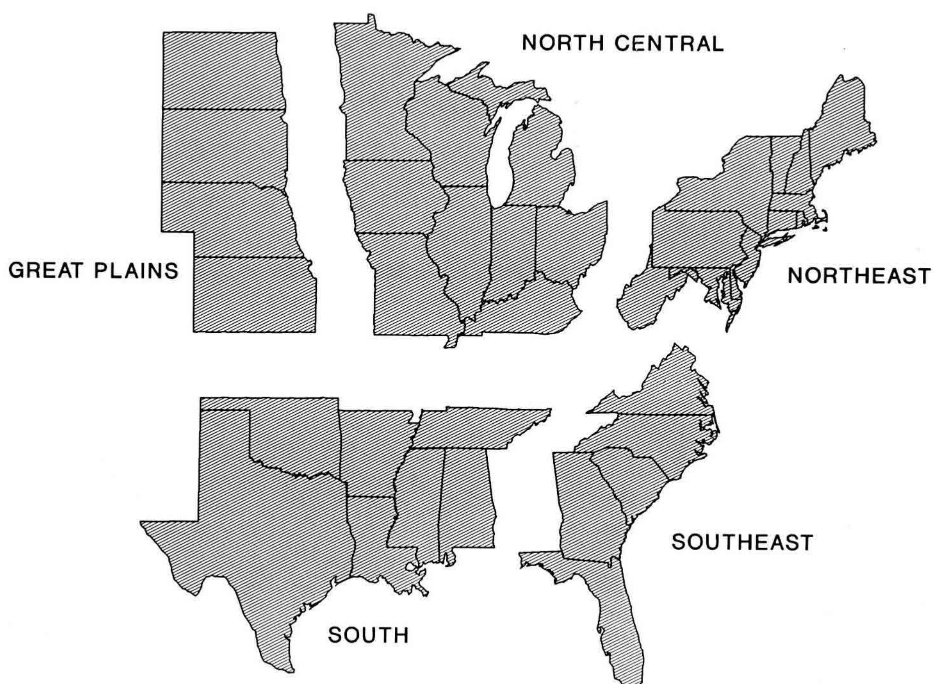

Fig 1. Regions of the eastern United States referred to in the text.

oak planting, but statistics for nursery shipments can provide an indirect measure of planting activity. Table I shows 1990 shipments of oak seedlings from forest tree nurseries (for reforestation only) in the eastern US *. The regions referred to in table I are delineated in figure 1. I do not have similar figures for Canada, but I am sure they would add only marginally to the totals in table I.

Shipments for 1990 totaled 13.8 million seedlings. *Q rubra* was the most commonly grown species (39% of total), and *Q alba* was the second most common (15%). These 2 species occur in great abundance, and they produce finer timber than most other oaks. *Q rubra* is faster growing than *Q alba*, and that explains why it is planted in larger numbers. In addition to those species listed, nurseries grew at least 18 other species for reforestation. Among these species not listed separately in table I, *Q velutina* and *Q palustris* were grown in greatest quantity, each accounting for about 5% of total production.

A surprising revelation of the nursery survey is a disparity between regions in seedling production: the North Central region was responsible for 64% of all US production and the Northeast only 4%.

Table I. Number of oak seedlings shipped in 1990 from US nurseries for reforestation purposes.

Species	*Region* [a]					
	North central	*Northeast*	*Southeast*	*South*	*Great Plains*	*Total*
			thousands of seedlings			
Q alba	1 936	1	72	124	0	2 133
Q falcata	26	0	45	314	0	385
Q macrocarpa	292	0	0	92	57	441
Q nigra	362	0	100	1 067	0	1 529
Q phellos	0	0	103	561	0	664
Q rubra	4 933	277	10	141	0	5 361
Other oaks [c]	1 329	223	497	1 246	0	3 295
Total	8 878	501	827	3 545	57	13 808

[a] North central: Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio and Wisconsin; northeast: Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont and West Virginia; southeast: Florida, Georgia, North Carolina, South Carolina, and Virginia; south: Alabama, Arkansas, Louisiana, Mississippi, Oklahoma, Tennessee and Texas; Great Plains: Kansas, Nebraska, North Dakota and South Dakota. [b] Includes also *Q falcata* var *pagodifolia* (= *Q pagoda*). [c] Predominantly *Q velutina* (23%), *Q palustris* (19%), *Q acutissima* (14%) and *Q virginiana* (9%).

* Questionnaires were sent to all forest tree nurseries in the region (Anonymous, 1987). After responses were received from 57% of the nurseries, non-respondents were divided into 2 categories according to whether they were, or were not, likely to produce oaks. All members of the first group and 28% of the second group were subsequently polled by telephone.

Since the vast majority of oak seedlings are produced by state-owned nurseries, which are not permitted to distribute across state boundaries, regional production figures are indicative of regional planting activity. This disparity is not accounted for by the relative importance of the oak resource. Oak timber is fully as abundant in the Northeast, Southeast and South as it is in the North Central region (Waddell *et al*, 1989). Ownership patterns, topography, silvicultural traditions, and (in the southern states) a preference for planting pine in place of oak may all contribute to these regional differences. However, the disparity cannot be understood as a simple consequence of resource economics.

Even with liberal assumptions, 13,8 million seedlings could be used to regenerate no more than a few percent of the annual harvest of oak stands. This underutilization of artificial regeneration suggests little opportunity for real achievements in oak tree improvement, since planting is the means by which genetic gains are realized. It is illuminating to contrast oaks with the southern pines (primarily *Pinus taeda),* for which tree improvement programs are well-advanced. The US has only about half the area of southern pine forest as it does oak–hickory forest, but we plant over 100 times as many southern pines as oaks (McDonald and Krugman, 1986). As we shall see, the somewhat dismal figures for oak planting are not mirrored by a similarly low level of tree improvement. I shall return to the implications of this paradox.

LOCATION AND ADMINISTRATION OF OAK IMPROVEMENT PROJECTS

Table II shows the geographic distribution of tree improvement projects and the species at which they are directed. For reasons already made clear, oak improvement is concentrated in the eastern half of the continent. In fact, there appear to be no oak improvement programs west of Texas or the Dakotas. Only 2 Canadian projects emerged in my survey, but of course Canada lies north of most of the oak range.

Nearly half of the 27 projects listed in table II are 5 years old or younger. This may partly reflect the increasingly shorter 'half-life' of forestry research projects in general. However, I tend to think it is indicative of a response by forest geneticists to increasing interest in the oak resource and, especially, in planting oak. Although no concrete data are available, the production of oak nursery stock appears to be increasing annually at a fairly rapid rate.

Oak improvement in the United States and Canada is performed mainly by public agencies and institutions. Only 3 of the projects in table II are run by industry or with full financial support from industry (North Carolina State University's cooperative). Some other university projects may be supplemented with funds from the private sector. Most (17) of the projects are state-level projects, run either by state agencies or by universities that house state agricultural experiment stations. Europeans may wonder about the redundancy of 19 projects on the genetic improvement of *Q rubra* (of which only 5.4 million seedlings were planted in 1990). This is a consequence of our federal system of government. Theoretically, Washington could play the role of coordinator, since most of these state-level programs are funded in part with federal tax monies. However, recalling that the United States began as a federation, it is still true that states behave semi-autonomously.

This is not to say that there is no cooperation among projects, because material and information are freely exchanged. For example, several projects in table II have

Table II. North American projects in genetic improvement of oaks for reforestation purposes, by agency and species.

Agency (project age in yr)	*Species* [a]								
	alb	*fal*	*mac*	*nig*	*phe*	*pri*	*rob*	*rub*	*vel*
North central region									
Illinois Dept of Conservation (1)	–	–	–	–	–	–	–	X	–
Indiana Dept of Natural Resources (10)	X	X	–	–	–	–	X	X	–
University of Kentucky (19)	–	-	–	–	–	–	–	X	–
Michigan State University (15)	-	–	–	–	–	–	X	X	–
Michigan Dept of Natural Resources (1)	–	–	–	–	–	–	–	X	–
Minnesota Dept of Natural Resources (2)	–	–	–	–	–	–	–	X	–
Missouri Dept of Conservation (3)	–	–	–	–	–	–	–	X	–
Ohio State University (Columbus) (5)	–	-	-	-	–	–	–	X	–
Ohio State University (Wooster) (31)	–	–	–	–	-	-	–	X	–
US For Serv Eastern Region (15)	–	–	-	-	–	-	–	X	–
US For Serv NC Exp Station (IL) (18)	X	–	–	–	–	–	X	X	–
US For Serv, NC Exp Station (Wisconsin) (9)	–	–	–	–	–	–	–	X	–
Westvaco (industry) (5)	–	X	–	–	–	–	–	–	–
Wisconsin Dep of Natural Resources (4)	–	–	–	–	–	–	–	X	–
Sum by species and region	2	2	0	0	0	0	3	13	0
Northeastern region									
Pennsylvania State University (11)	–	–	–	–	-	–	–	X	–
Pennsylvania Bureau of Forestry (4)	–	–	–	–	–	–	–	X	–
Quebec Ministry of Forests (1)	–	–	–	–	–	–	–	X	–
Sum by species and region	0	0	0	0	0	0	0	3	0
Southeastern region									
N Carolina State Univ Hardwood Coop (20)	–	–	–	X	X	–	–	–	–
South Carolina Forestry Commission (1)	X	X	–	X	–	–	–	X	X
US Forest Service, Southern Region (6)	X	–	–	–	–	X	–	X	X
Sum by species and region	2	1	0	2	1	1	0	2	2
Southern region									
Louisiana Tech University (10)	–	–	–	X	–	–	–	–	–
Mississippi State University (13)	–	–	–	X	–	–	–	–	–
Scott Paper Company (industry) (10)	–	–	–	X	X	–	–	-	–
Texas Forest Service (16)	–	X	–	X	X	–	–	–	-
Univ of Tennessee & Div of Forestry (20)	X	X	–	–	–	X	–	X	–
Sum by species and region	1	2	0	4	2	1	0	1	0
Great Plains region									
Agriculture Canada (PFRA) (1)	–	–	X	–	–	–	–	–	–
US Dept Agriculture Research Service (1)	–	–	X	–	–	–	–	–	–
Sum by species and region	0	0	2	0	0	0	0	0	0
Total of all programs by species	5	5	2	6	3	2	3	19	2

[a] alb: *Q alba*, fal: *Q falcata* (primarily *Q falcata* var *pagodifolia*), mac: *Q macrocarpa*, nig: *Q nigra*, phe: *Q phellos*, pri: *Q prinus*, rob: *Q robur*, rub: *Q rubra*, vel: *Q velutina*.

plantations of the provenance tests put together by Howard Kriebel at Ohio State University (see Kriebel *et al*, 1988) and Robert Farmer, formerly of Tennessee Valley Authority (see Farmer *et al*, 1981). Also, 7 of the state agencies listed in table II participate in a cooperative tree improvement program for fine hardwoods. Nonetheless, the projects are autonomous projects.

IMPROVEMENT OBJECTIVES AND METHODS

The 27 oak improvement projects are directed at a total of 9 species (table II). Some projects claim effort on as many as 4 or 5 species, but the focus of such projects is usually a single species.

Not surprisingly, *Q rubra* is receiving much more attention than any other species, especially in the Northeastern and North Central regions. The ultimate improvement objective with this species is timber and veneer production, though the near-term objective in one project is improved juvenile growth to enhance plantation success. Improvement activities in the Southern and Southeastern regions are concentrated most heavily on *Q nigra*. In some projects, *Q phellos* is treated along with *Q nigra* and their hybrid as a single species complex. Improvement objectives with these species are either timber or pulp production, depending upon the project. Improvement programs in the Great Plains are focused exclusively on *Q macrocarpa* for use in shelterbelts.

As part of the overall improvement strategy, provenance tests or progeny tests of unselected wild trees are each used in about half of the projects, and two-thirds employ one or the other (table III). Such tests are planned in the other projects, or alternatively, the project leaders are using plus-tree selection to produce a base population for improvement. Actually, plus-tree selection (in wild stands, because we have very few older plantations) is used or contemplated for use in about half of all projects. This is somewhat surprising since there is little evidence that plus-tree selection is indeed effective in hardwood

Table III. Methods and strategies employed by oak tree improvement projects ($n = 27$) in North America.

Method or strategy	*Number of projects using strategy*	
	Currently	*Anticipated*
Seed production areas in untested wild stands	3	2
Provenance testing and selection	14	2
Progeny testing of *in situ* unselected wild trees	15	1
Plus-tree selection (in wild stands)	11	3
Seedling seed orchards	9	3
with half-sib testing	7	4
with full-sib testing	0	2
Clonal seed orchards	7	7
with half-sib testing	2	5
with full-sib testing	0	1
Vegetative propagation	8	5

stands, but of course some programs may be practicing a low-intensity, inexpensive form of selection.

About half of the projects have progressed to seed orchards (seedling, clonal or both) (table III). Clonal seed orchards of oak in North America are largely a recent development, and this is reflected in the fact that progeny tests have not yet been initiated on most of the orchards. No full-sib progeny tests have been implemented in any project and they are being contemplated in only 3 projects. This of course is partly a reflection of the high cost of pollinating oaks artificially.

Two examples

The complexity and, one might say, sophistication of the improvement plan varies considerably among projects. To a degree, this is a function of the emphasis given to oak improvement, relative to other responsibilities, by the various project leaders. However, it is also a function of legitimate differences in opinion over the justification for investments in oak improvement. The full spectrum can be illustrated with 2 examples — one using elaborate and relatively expensive designs and methods, the other simple and inexpensive in design and execution.

The first example is taken from a consortium of independent projects being carried out by 7 state agencies in the North Central region *. Considering all oak improvement work in North America, this cooperative is unsurpassed for its careful planning and coordination among individual projects. Briefly, this program intends to: 1) delineate breeding zones within the region; 2) make careful plus-tree selections in wild stands; 3) graft ramets into multiple breeding populations (distinct sublines); and 4) conduct half-sib progeny tests to identify: a) the 2 best clones in each subline for regrafting into a production orchard, and b) the best progenies within sublines for creating the next generation of breeding populations. The overall strategy is taken from McKeand and Beineke (1980). Each breeding zone is planned to have 10-12 sublines, each containing 25–30 clones from (in the first iteration) plus-tree selections. The cooperative has made over 300 plus-tree selections and has begun to graft them into subline breeding populations. Among cooperative members, Indiana has made the most progress with *Q rubra*, and Mark Coggeshall has a separate report on this project in these proceedings.

The second example is a plan advanced by Steiner (1986) for the purpose of achieving gains in *planting success* as inexpensively as possible. The strategic goal is to utilize genetic improvement, directed at juvenile growth rate, to further the use of artificial regeneration of oaks, and thereby open avenues for more comprehensive approaches to tree improvement. The underlying philosophy is that the value of any realistic gain in yield, as sought in conventional improvement schemes, is small compared to the economic advantages of enhancing the regeneration of valuable oaks in mixed stands. This can be done by making planting a practical silvicultural alternative. Overall survival in hardwood plantations in the US is appallingly low, 9% in one survey (Hill, 1986), and it is widely considered that success

* The state agencies are those of Illinois, Indiana, Michigan, Minnesota, Missouri, Ohio and Wisconsin (table II). This description is taken from a 7-page unpublished document entitled: North Central Fine Hardwood Tree Improvement Cooperative: Ten-Year Plan (dated 1989), and from the cooperative's 1991 annual report.

with oak plantings would be better if the seedlings could be made to grow faster.

Procedures in this example are simple and can be integrated into the normal nursery production routine with relatively little additional cost. Acorns are obtained from seed collectors in the usual manner, except that collectors maintain detailed origin record by seed parent. A portion of seed from each open-pollinated family is sown separately by replicated plots within the nursery bed. Seedlots with the highest percentage of first-quality nursery stock are identified and transplanted for short-term (3–5-yr) progeny tests. After testing, parents of the best lots are identified as 'seed production plus trees' (SPPTs), steps are taken to protect these trees and seed collectors are required to collect from them in subsequent years. The process is repeated annually until enough SPPTs are identified to supply annual seed requirements, at which point the entire oak production of the nursery would consist of stock with superior potential for producing successful plantations. If resources are available, genetic gains in performance can be increased further by grafting SPPTs into clonal orchards. This plan is in its third year of implementation by the Pennsylvania Bureau of Forestry.

Analysis

Every project leader hopes that his efforts will be fruitful and continued after his inevitable departure. Experience suggests otherwise. Of the 7 oak improvement projects mentioned by Cech (1971), only 1 seems to have survived the last 20 years of 'progress'. Furthermore, it is difficult to detect any evidence that those defunct projects have had a measurable impact on oak siviculture and management. In many cases, the abandoned tests and orchards have been rescued by other projects, but these are projects with new personnel, employed by different agencies or institutions and probably with different plans for the material than those of the original project leaders. This is a clear example of the problem of 'administrative fatigue' in forest tree improvement, as described by Wright (1962): success precluded by the inevitability of personnel turnover.

It seems likely that many, perhaps most, of the current projects on oak improvement will not survive the next 20 years, unless steps are taken to avoid the pitfalls encountered by earlier projects. Indeed, in the several months since the original survey, at least 2 of the projects in table II have become endangered because of budget cuts and personnel departures. Given the rather low (but increasing) level of oak planting in North America, the current number of improvement projects may be excessive. However, I feel certain that there is an opportunity to greatly expand the use of planting through education and training.

Tree breeders should play a role in this if they wish to ensure a market for the fruits of their labors. Historically, tree improvement gains have not been adopted by practioners in the US unless there has been a pre-existing demand. A linkage with planting practice is part of the 'operational' component of tree improvement, which Zobel and Talbert (1984) considered to be crucial to the success of tree improvement projects. Although their financial support tends to be low and uncertain, state agency programs are the most promising of success because the operational component of these projects is usually enhanced by close organizational ties with state-owned nursery systems. University and Forest Service experiment station projects may be less successful because applied tree improvement tends to lie slightly outside their organizational missions, which emphasize research. On the balance, North American progress in oak tree improvement and its application in silviculture will continue to be slow.

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