TB131: Tree Improvement in the Northeast: Interim Summary and Recommendations for Selected Species

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TREE IMPROVEMENT IN THE NORTHEAST:
Interim Summary and Recommendations for Selected Species


Maine Agricultural Experiment Station
University of Maine

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TREE IMPROVEMENT IN THE NORTHEAST: Interim Summary and Recommendations for Selected Species

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Maine Agricultural Experiment Station
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INTRODUCTION

This publication of the regional research project NE-27, Genetics and Improvement of Northeastern Trees, is intended to provide an overview of current knowledge regarding genetic variation and tree improvement practices for eleven common tree species in the Northeast. The authors have attempted to summarize the information that will be most useful to forest managers, administrators, and field foresters in this region. Our intent is to be informative, not exhaustive. Readers who wish to obtain more detailed information should consult the bibliography at the end of each species section.

Tree species treated in this publication have been the focus of NE-27 research during most of the project’s duration, and we have emphasized research that is particularly directed toward application within the region. This publication constitutes a report of the Northeast regional genetics project NE-27. The project’s technical committee is composed of employees of most of the Agricultural Experiment Stations in the northeastern United States, and of the USDA Forest Service. The current technical committee is listed on the inside front cover of this publication.
European black alder is native to the Old World and naturalized to a limited degree in North America. The species has an unusually large native range that occupies almost all of Europe plus parts of northern Africa and Asia east to Iran and western Siberia. Over most of its range the species inhabits climates that are moderate in both temperature and precipitation, but in the extreme it grows wild in regions with as little as 51 cm (20 inches) of annual precipitation or with January normal mean temperatures as low as $-12 ^\circ C (10 ^\circ F)$ (similar to the coldest portions of New England and the upper Midwest).

The naturalized range of the species in North America extends from Newfoundland south to Delaware and west to Illinois and Michigan (Furlow 1979, Little 1979). Its native distribution suggests a greater potential naturalized range than exists in the U.S., but the genetic adaptability of the species is probably limited here by the provenances of the original introductions.

Natural regeneration of black alder is mostly limited to sunny areas and recent alluvia or soils with impeded drainage (Furlow 1979). The species prefers a high water table and seldom occurs away from standing or running water except when planted. However, a two-tiered system of shallow (nodule-bearing) and deep roots enables it to grow under a range of moisture conditions and survive limited periods of drought (McVean 1956).

Black alder is symbiotic with nitrogen-fixing bacteria, and this characteristic plays an important role in its ecology. The species grows best on deep, fertile soils with pH values between 5.5 and 6.5, but it will tolerate compact clays and in fact survives better than most on some of the poorest of mine spoils. Juvenile growth is very rapid on good sites, and annual height increments of 90 cm (3 feet) or more are easily achieved.

Black alder is one of the largest of the alders (to 115 feet tall according to Ehrenberg 1979), and it is certainly the largest alder capable of growing in the eastern U.S. Maximum age is about 120 years. In its native range the species is used as a source of stock for processed wood (pulp, chipboard, etc.)
and specialty items such as wooden shoes. Most plantings of black alder in the U.S. are for mine spoil reclamation.

More recently there has been considerable interest in using the species as a nurse crop in interplantings with other species (Dale 1963, Hansen and Dawson 1982, Plass 1977) and as a short-rotation fiber crop (Franklin 1978, Hall et al. 1983, Phares et al. 1975). The species has proven to be inferior in growth to other bottomland hardwoods in the Southeast (North Carolina State University 1984), but its rapid growth and nitrogen-fixing capabilities may provide it with a special silvicultural role in the Northeast and Midwest.

For best results, planting should be done on deep, moist soils with good control of competing vegetation. As mentioned, black alder will grow on poorer sites, but stem cankering and dieback can be severe problems with this species, and they seem to be aggravated by environmental stresses (Goncalves and Kellison 1980, Steiner 1983). Weed control by cultivation in young plantations is tricky because of the ease with which the shallow roots can be damaged (Saucier 1977). Chemical weed control with a pre-planting application of glyphosate and later applications of the pre-emergence herbicides oxadiazon, oxyfluorfen, napropamide, oryzalin, or metolachlor (at recommended rates) resulted in no adverse effects on growth of black alder in the first year (Hall et al. 1986).

GENETICS AND TREE IMPROVEMENT

 Genetic evaluations of black alder in the U.S. began with a study by Funk (1973) of 15 provenances planted on an Ohio coal mine spoil. The tallest trees after six years in the field were from West Germany (provenances from Belgium, Denmark, and Sweden were also included in the study). The tallest provenance at age six was still the tallest at age 16 (Funk 1979), but the second-tallest had fallen off dramatically in growth. The ten-year height increment of most West German provenances was good regardless of geographic origin.

 A second study was begun in 1976 jointly by NC-99 and NE-27 to augment the data from Funk's test. Collections from 48 provenances were arranged by R.B. Hall (NC-99) and established in several locations in the Midwest and Northeast. Results from plantations in Pennsylvania, New Brunswick, Iowa, Wisconsin, and Illinois have been published by DeWald (1982), DeWald et al. (1983), DeWald and Steiner (1986), Hall et al. (1983), and Maynard and Hall (1981).

 Provenance performance has varied according to plantation. Provenances from northern and eastern Europe (e.g., Poland, Czechoslovakia, Baltic
States) were the tallest in Wisconsin at age 4 from seed (Hall et al. 1983). The same was generally true in New Brunswick at age 2, though the pattern was less clear-cut because some Italian provenances also grew well (DeWald et al. 1983). In contrast, provenances from central Europe have generally grown fastest in the more southern Pennsylvania and Iowa plantations. Of the seven tallest provenances (best 15 percent) in Iowa at age 4 (Hall et al. 1983), four were also among the tallest seven in Pennsylvania at age 5 (unpublished data). These were native to Denmark, West Germany, and Hungary.

DeWald (1982), DeWald et al. (1983), DeWald and Steiner (1986), and Maynard and Hall (1981) have described provenance variation in apical dominance, branch angle, phenology, cold injury, Japanese beetle resistance, and leaf morphology. Relatively strong apical dominance, low cold injury, and early budset are associated with more northern geographic origins. Other characters show complex patterns of geographic variation. Based on an analysis of growth, phenology, and cold tolerance, DeWald and Steiner (1986) identified eight provenances from central Europe as potentially useful for Pennsylvania and noted that several other initially fast-growing provenances appeared to be climatically unsuited to the test area.

Important selection criteria are growth rate, form, and resistance to cankering and dieback (see Oak and Dorset 1983). There was a weak tendency in Funk's (1973) provenance test for the tallest trees to have the fewest stems at age 6, but the correlation between height and apical dominance (a measure of lateral versus terminal shoot growth) at age 2 was non-significant (DeWald 1982). Based upon stem analysis of growth in 17-year-old trees, Hall et al. (1983) recommended selection at one-half to two-thirds of the planned rotation age. Age-age correlations were generally better for diameter than for height. There is concern that seed orchard trees may be inadvertently selected for precocity and later exhibit growth rate declines. However, the 8 percent of trees that were flowering in the Pennsylvania provenance plantation at age 3 were 24 percent taller at age 5 than non-flowering trees.

Robison and Hall (1981) recommended seedling seed orchards rather than clonal seed orchards for black alder. The reasons for this are the earliness with which black alder reaches sexual maturity, the fact that clonal propagation is not yet routine, and the unknown time delay for ramets to resume flowering. Seed production begins on many trees by age 2 or 3 from seed and can be heavy by age 6, though most trees in the Pennsylvania provenance test had not yet flowered by that age. Sexually mature trees that are 7.6 m (25 feet) tall should bear several hundred strobili, each with an average of 60 seeds (McVean 1953). Seed crops in the eastern United States
vary from year to year, but are generally fairly heavy (Funk, unpublished manuscript). White (1981) has described artificial pollination techniques for the species.

CONCLUSIONS AND RECOMMENDATIONS

The impressive growth capabilities and special ecological characteristics of black alder suggest considerable silvicultural merit. However, the economic potential of the species is still unclear, and the sites on which it grows best are limited in extent. Mounting experience suggests that off-site plantings increase the risk of canker-related dieback. If that is true, the risk could be reduced by planting genetic stock that is best adapted to the region.

Provenance tests are the first step in defining the regional adaptability of an introduced species. So-called "land races" from naturalized populations in the United States are not necessarily superior because original introductions had limited variability. New first-generation seed orchards of black alder should employ material from existing provenance tests or material from new seed collections in promising regions of Europe. An effective improvement strategy would employ progeny tests of parents in superior provenances, later converted to breeding arboreta and seed orchards by roguing and tree-spading based on family and within-family selection. Seed production from even fairly small orchards would satisfy the planting needs of most agencies.

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GREEN ASH

(\textit{Fraxinus pennsylvanica} Marsh.)

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SILVICULTURAL BACKGROUND

The name green ash, formerly restricted to the variety \textit{subintegerrima} (\textit{= lanceolata}), is now commonly applied to the entire species, and most modern authors of taxonomic manuals no longer recognize varieties for this species. Green ash has an exceedingly large natural distribution that spans 25° of latitude and 50° of longitude. The range of climatic conditions under which it grows is large: 38 to 152 cm (15 to 60 inches) of annual precipitation, -18°C to 13°C (0°F to 55°F) average January temperature, 65°F to 80°F average July temperature, and 120 to 280 days of frost-free growing conditions (Fowells 1965).

Under natural conditions, the species grows almost exclusively on bottomland sites that are occasionally flooded (not swamps), but it grows well when planted on uplands. In the western portions of its range, green ash grows along streams in close association with cacti, ponderosa pine, and other notably drought tolerant species. In Michigan it can invade upland fields as vigorously as white ash (Taylor 1972). Green ash is relatively tolerant of seasonal flooding (Gill 1970), a characteristic which probably lends to its widespread use in the poorly aerated soils common in urban environments.

The species is most commonly planted as a forest crop in shelterbelts (about 1.25 million trees per year), where growth rate, crown density, tolerance to cold and drought, and resistance to insects (primarily ash borer and carpenterworm) are the most important characteristics; and in southern bottomlands (about 2,500 acres per year), where growth rate and stem form are most important. Forest plantations of this species in the Northeast are uncommon, although it would appear to have potential in short rotation systems on many sites.

Green ash is the major ash species used in urban forestry plantings in the East and Midwest. Important characteristics are growth rate, crown form, tolerance of cold and drought, and resistance to the ash borer, verticillium wilt, and air pollution. Santamour and McArdle (1983) list 20 valid cultivar names for the species, though only a very few are readily available from nurseries. The newer cultivar selections have stressed growth rate, trunk
straightness, dark green foliage, symmetric crowns, and fruitlessness (male trees).

Shelterbelt plantings are most successful on relatively fine textured, deep soils with good moisture relations. Planting in the South is confined to stream or river bottoms in the Piedmont and rich river terraces or somewhat wet clays in the Coastal Plain. In all situations, green ash plantations should be established using large stock on well-prepared sites, and weed control with herbicides or clean cultivation should be continued for 2 to 3 years.

GENETICS AND TREE IMPROVEMENT

Tree improvement activity with green ash began in the Great Plains in the 1930’s and focused on its use in the shelterbelts. At the present time, at least six agencies and organizations in Montana, North Dakota, South Dakota, and Nebraska are working with green ash in programs involving provenance tests and seed orchards (Cunningham 1981). Tree improvement activity in the South is more recent. The Texas Forest Service and North Carolina State University have established progeny tests or seed orchards from plus-tree selections, and the Southern Forest Experiment Station has a progeny test of open-pollinated families from nine seed source areas in the South.

Improvement of green ash in the Northeast was initiated by NE-27 in 1975 (Steiner 1983, Steiner et al. 1987). Plantations of progenies of up to 60 range-wide populations were established in ten northern states as far west as Nebraska in 1978. Although objectives differ among cooperators, the rationale for the study was to learn about the climatic and edaphic requirements of provenances of this species, which is often moved around somewhat indiscriminately in the nursery trade. Plans at Penn State are to compare the best selections with standard cultivars of the species.

In the earliest common garden study of the species, Meuli and Shirley (1937) found that drought resistance at age 1 increased with both the latitude and longitude of origin of 83 seed parents located in the Great Plains. Variation in such characters as phenology, response to photoperiod, winter injury, petiole color, air pollution resistance, and twig pubescence has been demonstrated in small progeny tests by several authors (Pollard and Logan 1980, Steiner and Davis 1979, Vaartaja 1959, Wright 1944, Ying and Bagley 1976).

Variation in growth rate in provenance tests has often been substantial. In the NE-27 study, provenances differed in height after four years in the field by ratios of 2:1 to 4:1 depending upon plantation. Provenances from south of the Ohio River were generally below average in height; many of
these trees had been winter injured. Provenances from southern Ontario were relatively fast-growing at most locations, but other provenances from the northeastern portion of the species' range were usually below average. For trees from the prairie region of the U.S. and Canada, growth rate tended to decrease with increasing latitude of provenance origin. Trees from the central portion of this region, from Missouri to eastern Nebraska, were the tallest of all provenances at most locations.

Nearly all of the NE-27 plantations experienced some winter injury within the first few years. At most plantations, 95% or more of the injury was confined to populations native at least 140 miles south of the plantation site. However, Williams' (1984) more detailed analysis of these and other winter injury data support a conclusion that any northward transfer of a provenance in this species is attended by some risk. Williams also made laboratory determinations of freezing tolerance of some two dozen of the provenances planted in Pennsylvania. Mid-winter differences amounted to as much as 15° C (34°F) between Tennessee and Manitoba trees.

Flowering began at age 5 in some NE-27 plantations. At the three plantations for which we have data, provenances that flowered at the youngest ages were predominantly native to the former prairie region of the central U.S.

Single-tree progenies from 59 seed parents in 16 populations varied significantly in tolerance to ozone and sulfur dioxide in controlled fumigations (Karnosky and Steiner 1981). Variation was greater among populations than within populations for tolerance to ozone, but vice versa for tolerance to sulfur dioxide. Trees from southern populations were generally more tolerant to both pollutants than those from northern populations.

There are no plans to convert the NE-27 experimental plantations to seed orchards because their purpose is primarily informational and because of the low demand for planting stock of the species within the Northeast. Plant material for urban forestry use is primarily of asexually propagated cultivar origin, so clonal selection would be the most profitable method of improvement for such purposes.

Seed orchards have been established in other regions (Anonymous 1979; Cunningham 1974, 1981; North Carolina State University 1984), and both clonal (grafted) and seedling seed orchards have been used. The effectiveness of plus-tree selection in green ash has not been demonstrated. If it is low, as is likely, then seedling seed orchards converted from progeny tests of wild trees would be the least expensive route to effective improvement. However, clonal orchards have the advantage of affording control over the arrangement and proportion of male and female trees, although almost nothing is known about seed orchard design with dioecious species such as this.
For optimum seed production, no more males should be used than are necessary to pollinate the females. A ratio of 1:3 has been used.

CONCLUSIONS AND RECOMMENDATIONS

Northeastern provenances have performed almost uniformly poorly in NE-27 tests. When green ash is planted in the Northeast, it is usually planted on sites to which it is not native. There is no reason to presuppose any provenance to be best adapted to such sites, so we have little hesitancy in recommending provenances of non-local origin. Nevertheless, the NE-27 tests are relatively young, and performance can change with time. The early sexual maturity of Great Plains stock may presage a decline in the relative vegetative vigor of those trees.

The NE-27 plantations contain as many as six provenances of white ash planted randomly among the green ash. The limited comparisons afforded by this material, as well as ecological observations by Taylor (1972), indicate that green ash has the more rapid juvenile growth of the two species even on upland sites. Green ash should probably not be operationally planted in place of white ash, but green ash may be preferable for special-purpose plantations such as short-rotation-intensive-culture. The species should be nearly as productive in bottomland plantations as it is in the South, where it is planted commercially. Annual increments of 90 to 180 cm (3 to 6 feet) in height and 1 to 2 cm (0.4 to 0.8 inches) in diameter should be possible with good site selection, site preparation, genetic stock, and plantation maintenance.

The major use for green ash in the Northeast will continue to be for amenity purposes. Our results to date have clearly indicated the importance of climatic adaptation in the transfer of provenances. The significance of this to city arborists is suggested by the fact that the most popular cultivar of the species was selected in Utah from material that probably originated in Nebraska and may be grown in New Jersey for sale eventually to a client in New York.

The NE-27 results suggest that new cultivars for the Northeast should originate from the Great Plains portion of the species' range in the U.S. It is probably significant that over 90% of the green ash cultivars offered by U.S. nurseries within the past 30 years appear to have originated in the northern prairie states (Santamour and McArdle 1983). Our results also suggest that southern Ontario is a likely source for superior selections, a fact that was not previously known.


Paper birch has a transcontinental range in the U.S. and Canada. In the Northeast it is a common forest species and is often found as a pioneer on burned or disturbed areas. Paper birch is an intolerant, fast-growing, relatively short-lived species. The best trees are most commonly used for veneer and specialty products.

Paper birch is not often planted because, like most other hardwoods, young seedlings require protection from deer and competing vegetation to become well established. It is possible, however, to establish successful plantations on old field sites that have been plowed and harrowed prior to planting (Higgs 1981), or on cutover forest sites (Hoyle 1984). Paper birch will tolerate a wide variety of soil pH and moisture, but grows best on fertile, well-drained sites. Under optimum conditions plantation-grown paper birch is capable of good survival and height growth of 36 to 52 cm (1.2 to 1.7 feet) per year. Hoyle (1984) estimated that this rate of growth should produce sawlog-sized trees on a 30-year rotation. Marquis (1973) identified paper birch as an attractive candidate for tree improvement, based on economic analyses.

GENETICS AND TREE IMPROVEMENT

Although paper birch is a widely distributed and relatively valuable species, information about genetic variation is limited. A five-year-old Maine provenance test of 68 seed sources of paper birch revealed a negative correlation ($r = -.53$, sig. 1% level) between height and latitude of seed origin. Best survival and growth rates were found in provenances from Connecticut, Vermont, the Lake States, and southeastern Ontario (Carter 1982). Trees from these provenances exceeded the plantation mean height by 20% or more, at age five. Variation also exists among stands within regions.

Genetic control of height and diameter growth in paper birch is moderate, with an estimated heritability of $h^2 = 0.3$ (Klein 1967). Studies assessing the efficiency of comparison-tree selection methods to identify plus-trees in the field revealed no significant differences in growth rate among
17-week-old progeny of selected trees and controls, indicating that some other method such as family selection in progeny tests may be preferred for this species (Stanton 1979; Stanton and Canavera 1983). Ricard and Eckert (1981), however, reported significant differences in height and diameter for 12-week-old seedlings of average and plus-tree progeny selected by the U.S. Forest Service in Michigan and New England. Further research is needed to identify the most effective plus-tree selection techniques for paper birch.

Paper birch begins seed production at age 10 to 15 and produces regular seed crops with little yearly fluctuation. Either seedling or clonal seed orchards of this species are feasible. Because paper birch is such a prolific seed producer, six acres of seed orchard are estimated to provide enough seed to regenerate an area equivalent to 1/3 of the annual paper birch harvest (Marquis 1973).

In Finland, birch seed orchards are maintained in greenhouses that stimulate seed production on seedlings only 3 to 4 years old. At that age, 24 seedlings produced 4.5 million seeds in the greenhouse orchard (Lepisto 1973). Finland expects growth gains resulting from its selection and breeding program to be as great as 40%. If paper birch became more widely planted in the U.S., indoor seed orchards could be a productive means of stimulating seed production and reducing generation time.

CONCLUSIONS AND RECOMMENDATIONS

At the present time paper birch is not a popular species for plantation establishment. If in the future there is an increased demand for planting stock, there appears to be sufficient genetic variability in paper birch to justify some level of selection among provenances and/or individual trees. Birch is a prolific seed producer and a good candidate for the establishment of indoor seed orchards.

BIBLIOGRAPHY


HYBRID POPLAR

(\textit{Populus})

Maurice F. Demeritt, Jr.
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SILVICULTURAL BACKGROUND

\textit{Populus} hybrids occur naturally in the Northeastern United States where the natural range of \textit{Populus} species overlap. The Jackii poplar is a natural hybrid between \textit{P. balsamifera} females and \textit{P. deltoides} males. \textit{Populus x Smithii} is a natural hybrid between \textit{P. tremuloides} and \textit{P. grandidentata}. However, the majority of \textit{Populus} hybrids result from artificial hybridizations and subsequent planting of seedlings, rooted cuttings, or dormant cuttings. Also, an unknown number of hybrids form from natural hybridization between the native species and introduced clones, cultivars, and species. \textit{Populus} hybrids grow throughout the United States, but most grow and do well above latitude 35°N.

In general, hybrid poplars grow best on humid and microthermal areas with adequate moisture during all seasons of the year. They are rarely found in areas that have temperatures which reach -46°C (-50°F) or that have summer temperatures over 38°C (100°F) during the day for more than a week.

\textit{Populus} hybrids grow best where soils are at least 1 meter (3.3 feet) in depth to interrupted bedrock. Also, the water table and porous or gravel layers should be at least 1 meter below the soil surface. Optimum pH ranges from 6.0 to 7.0, though some hybrids tolerate high or low pH conditions. Hybrids grow well on upland and bottomland soils, if the soils have good moisture holding capacities and are of medium texture. Hybrids show extreme variation in tolerance to adverse site conditions.

Hybrid poplars are dioecious and first flower at about 8 years of age. The flowers are borne in catkins in the spring before leafing. \textit{Populus} flower between February and May and disperse seed between April and June of the same year. Many hybrid poplars have never produced flowers and thus are thought to be sterile. Fruits are one-celled capsules borne in long pendulous clusters, and each capsule is surrounded by tufts of long, white silky hairs attached to the short stalks of the seed that promotes wind dispersion over great distances.

Hybrid poplars generally are prolific annual seed producers. Seed germi-
nates and seedlings develop best on moist mineral soils where competing vegetation is minimal for 1 or 2 years after establishment.

*Populus* hybrids reproduce vegetatively by natural and artificial means. *Leuce* (aspen-type) hybrids root best from root sections, though some selections root adequately from dormant stem cuttings. *Aigeiros* (cottonwood-type) hybrids reproduce well from either greenwood or dormant stem cuttings, although most hybrids are reproduced from dormant cuttings.

Hybrid poplars are not strong competitors and thus must be planted on sites kept free of other trees, brush, weeds, and grass. Herbicides such as glyphosate may be applied to the site to kill vegetation before site preparation. For best results, the planting site must be plowed and disced or rototilled to loosen the soil to the extent it could be used for row crops. If stumps and brush must be removed, exercise extreme care so top soil remains.

Cuttings, seedlings, or rooted trees can be machine or hand planted. Cuttings should be soaked in 60°F water for 6 to 8 days prior to planting for best results. Spacing is often determined by the productivity of the site and the purpose of the planting. For most purposes, spacing should be no less than 3 x 3 feet nor greater than 15 x 15 feet. With close initial spacing, the crowns will close early and extensive cultivation can be terminated because crowns will shade out grass and weeds.

Cultivation is essential to control weeds and grass, at least for the first two growing seasons on most sites. Cultivation should be only deep enough to expose grass and weed roots but not deep enough to disturb tree roots. Chemical weed and grass control can be effective if applied correctly.

**GENETICS AND TREE IMPROVEMENT**

*Populus* breeding was initiated in the Northeast in 1925 by Drs. A.B. Stout and E.J. Schreiner. An intensive hybridization and breeding program was undertaken during the years 1925 and 1926 at the New York Botanical Gardens and at Highland Park, Rochester, New York under the control of the Oxford Paper Company, Rumford, Maine. Approximately 13,000 seedlings were produced from 99 full-sib crosses among 34 different poplar species and cultivars. Between 1931 and 1936, the Oxford Paper Company distributed cuttings of clones OP(NE) 1 through 58 to many American and foreign organizations and individuals. In 1936, the Oxford Paper Company transferred all of the poplar hybrids along with Dr. Schreiner to the U.S. Forest Service, Northeastern Forest Experiment Station. A total of 249 individual trees has been selected since 1925 for propagation and distribution from the initial breeding effort.

It is fair to say that the amount of information around the world on North-
eastern (NE) hybrid poplar clones is voluminous. Hybrid poplars developed in the Northeast have been distributed to the 48 contiguous United States and to at least 40 foreign countries.

We know how to plant and care for poplar plantations that have been established by dormant or rooted cuttings. Also, there is information that juvenile-mature growth correlations are low. This necessitates growing clonal tests until at least half rotation age to be able to predict later performance. We also are aware of the many insects and diseases associated with growing *Populus* species or hybrids in general. More study on clone-site relationships are necessary in order to match clones to sites for maximum productivity. We do know that some clones do well on a variety of sites while other clones are quite site specific. Also there is a body of information on the effects of air pollutants and particular heavy metals on survival and growth of certain clones.

**CONCLUSIONS AND RECOMMENDATIONS**

World-wide, poplars are one of the more investigated genera of trees. Scientists and users of NE hybrid poplars in the rest of the world know more about NE hybrids in their countries than we know about NE hybrids where they were developed. Most of the information from other regions of the world can be used in the Northeast with some caution.

Extensive breeding programs with *Populus* have been initiated throughout the world. Selections from these programs should be introduced into the Northeast for testing. With the minimal number of acres planted to hybrid poplars each year in this region, I don't believe we can justify initiation of a local breeding and extensive tree improvement program.

Demonstration areas are needed to show clients the potential of existing hybrid poplar clones for biomass, home fuelwood, and amenity use purposes.

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DOUGLAS-FIR

(Pseudotsuga menziesii (Mirb.) Franco)

Henry D. Gerhold
The Pennsylvania State University

SILVICULTURAL BACKGROUND

Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, is a valuable timber tree of western North America and an important Christmas tree in the northeastern United States. Two main varieties have been named. The coastal or green variety (var. *menziesii*) is a principal component of the Pacific slope forests. The blue variety (var. *glauca*) occurs along the Rocky Mountains from Canada into Mexico; the gray variety, which has no taxonomic legitimacy, is found in British Columbia.

Considerable care is required for successful plantations in the Northeast. The most appropriate sites have well drained soils and good air drainage, necessary for good growth and to avoid late spring frost injury. Seedlings or transplants should come from seed origins that are carefully matched to sites, excluding the coastal variety that is not cold hardy enough. It is very important to control competing vegetation by herbicides and mowing. Shearing is necessary to improve crown shape and density, but its timing and frequency are not as critical as with pines. The most serious disease and insect problems are caused by needlecast and Cooley spruce gall aphid.

Genetic variation is large within and among provenances. Therefore, opportunities are excellent for Christmas tree growers to select superior seeds or seedlings, and for tree breeders to produce improved varieties. Substantial improvements are possible in growth rate, crown form and density, foliage color, and resistance to frost, winter injury, and aphids.

GENETICS AND TREE IMPROVEMENT

In the Northeast and Central states, objectives of tree improvement have focused on characteristics important for Christmas trees in the more winter-hardy inland provenances. In contrast, research in other places has dealt mainly with timber traits of the faster growing coastal provenances. Objectives in the Northeast include:

1. Locate the best seed sources and study patterns of genetic variation through provenance experiments.
2. Select superior trees and evaluate them via progeny or clonal tests, for use in breeding programs or seed orchards.
4. Study methods of promoting flowering to overcome problems of delayed and sporadic seed production in seed orchards.

Provenance studies during the past 30 years have provided extensive information about genetic variation patterns. Furthermore, they have identified superior seed sources that are widely used in nurseries and by tree growers. These are mainly in two regions, one in the vicinity of Shuswap Lake, British Columbia, extending southward into the United States; and the other encompassing portions of southern Colorado, northern New Mexico, and northern Arizona. Trees from the British Columbia region are characterized by greater winter hardiness, dark green foliage, later bud burst, and being nearly immune to aphids. The southern Rocky Mountain provenances display fast growth and blue-green foliage. Provenances from large portions of Montana, Idaho, Wyoming, Utah, and northern Colorado grow too slowly to be of commercial interest.

Beyond the great genetic variation among varieties and races, there is considerable variation within populations in many traits. Many superior trees have been selected that excel in desirable combinations of characteristics, including fast growth, dense and symmetrical crowns, good winter color, and resistance to frost, winter injury, and aphids. Subsequent selection for disease resistance will require development of better techniques. Selected trees are currently being evaluated through progeny tests and clonal tests.

CONCLUSIONS AND RECOMMENDATIONS

The knowledge that has already been gained about genetic variation could be exploited more fully. The simplest, most reliable possibilities are to set up seed production stands in the best western provenances, and to establish seedling seed orchards in the Northeast derived from single, superior provenances. This could be done by individual nurseries or growers, or preferably through a cooperative tree improvement program. Technical advice from experts will be needed, as there are many alternatives to be considered in designing and implementing even these simple improvement methods.

Continuing research, some of it already underway, is needed to determine the most effective improvement strategies and to implement breeding and/or propagation technologies. The more important research topics are:

• obtaining information on heritabilities and genetic gains of important traits, to be used in designing selection and breeding procedures.
• perfecting vegetative propagation methods for commercial production of clones.
• studying genotype - environment interactions in relation to deployment of clones or varieties over a range of sites.
• developing better methods of selecting for resistance to needle cast and frost.

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Balsam fir is a common component of the boreal and montaine forest regions in eastern North America and is an important Christmas tree and pulpwood species in New England and eastern Canada. Balsam fir is distributed over approximately 15° of latitude and 65° of longitude and has the largest natural range of any North American fir species. Although most common throughout eastern Canada and northern New England, maximum development for balsam fir is achieved in the region along the St. Lawrence River (Bakuzis and Hansen 1965).

Within its natural range, the utility and distribution of balsam fir is limited largely by its susceptibility to spruce budworm (Choristoneura fumiferana Clem), a defoliator that can have a devastating impact on balsam fir stands. In milder regions peripheral to its range where balsam fir is planted as a Christmas tree, the utility of the species is limited primarily by its susceptibility to spring frost damage, summer drought, and some locally important pathogens such as the balsam twig aphid (Mindarus abietinus Koch) and the balsam gall midge (Dasineura balsamicola (Lint.))

Genetics and tree improvement research in balsam fir has focused primarily on two areas. Several studies of natural variation have been conducted to examine the taxonomic affiliations between balsam fir and several related taxa within section Balsameae. Those taxa include subalpine fir (Abies lasiocarpa (Hook.) Nutt.) of the west, Fraser fir (Abies fraseri (Pursh) Poir.) of the southern Appalachians, and bracted balsam fir (Abies balsamea var. phanerolepis Fern.) of the central Appalachians and high elevations of New England. In addition to providing information on evolutionary relationships among taxa, these studies have helped elucidate patterns of geographic variation among and within species. A more recent emphasis in balsam fir research has been the selection of individual trees and seed sources for the purpose of genetic improvement of the species. Provenance and progeny tests of balsam fir have been conducted in the Lake States and New England and have documented genetic variation in several economically important characteristics related to both pulp and Christmas tree production.
Studies of the extent and patterns of natural variation among and within section *Balsameae* taxa have described variation in morphological (Lester 1968; Myers and Bormann 1963), anatomical (Robinson and Thor 1969; Roller 1966; Thor and Barnett 1974), and biochemical (Zavarin and Snajberk 1965 and 1972; Zavarin et al. 1970; Lester 1974) characteristics and have provided a forum for speculation about evolutionary relationships among taxa. Balsam, Fraser, and subalpine firs are closely related and morphologically similar species that are distinguishable based on relatively few subtle characteristics, such as cone scale to bract ratios and the concentration of monoterpenes in leaf and twig oleoresins. The so-called bracted balsam fir represents a morphological intermediate between balsam and Fraser firs in the east, and intergrading populations between subalpine and balsam fir exist in central Alberta where the natural ranges of the two species overlap. After assessments of morphological and geographic variation patterns, Boivin (1959) has proposed that subalpine, balsam and bracted balsam firs be considered as subspecies or varieties of *A. balsamea*, and Thor and Barnett (1974) have subdivided the Appalachian firs into varieties rather than separate species. Interestingly, interspecific hybridization studies (Hawley and DeHayes 1985a) have demonstrated nearly complete crossability among fir taxa in section *Balsameae* and reinforce the relative genetic similarity among species in this fir complex.

The similarity and near complete crossability among section *Balsameae* taxa, coupled with the presence of taxonomically unsettled varieties, suggest relatively recent geographic isolation and genetic differentiation in this group of firs. As a result, selection and breeding efforts designed to improve fir could perhaps incorporate germ plasm that extends across traditional species boundaries.

As expected because of its wide distribution over varied environments, considerable genetic variation in a diversity of characteristics is evident in balsam fir. Provenance tests in the Lake States and New England have revealed substantial genetic variation in growth rate (Lester et al. 1976a; Lowe et al. 1977), leafing-out phenology (Lester et al. 1976a), wood properties (Dery and DeHayes 1978), insect susceptibility (DeHayes 1981), and foliar water relations (DeHayes et al. 1978). For most characteristics examined, a predominantly east to west pattern of geographic variation and a substantial range delineation between the 80th and 84th parallels have been evident.

With respect to growth rate, provenances from the eastern portion of the range are fastest-growing when tested in experiments conducted in both the
Lake States and in New England. In fact, provenances from Vermont (Granville and Ripton), New York (Indian Lake), and Quebec (Cabano) are consistently among the fastest growing of all provenances in a diversity of environments in the northeast. Fraser fir provenances exhibit a slight growth advantage over the best balsam fir provenances in environments slightly warmer and dryer than in the balsam fir range, but are equivalent to average balsam fir provenances in northern test sites.

Genetic differences in leafing-out phenology are especially large in balsam fir. Provenances from relatively mild climates generally flush later than those from cold climates at test plantations in New England and the Lake States. As a result, late-flushing provenances more frequently escape injury from late spring frosts. Provenances from the northern Lower Peninsula of Michigan (Roscommon) are particularly late to break bud in spring and are only infrequently injured by spring frosts. Finally, Fraser fir is extremely late to break bud and may be the best planting alternative in areas with a high frequency of spring frosts. When planted in Vermont, Fraser fir began growth 23 days later than the average of several balsam fir provenances and 12 days later than the latest of 21 balsam fir provenances tested.

Balsam fir provenances also have exhibited striking variation in susceptibility to the balsam twig aphid, an insect that can be damaging to plantation-grown trees in New England and the Maritime Provinces. Provenances from the eastern portion of the range suffered nearly twice the crown injury from this insect than those from the western portion of the range when all were growing in Vermont. Trees grown from seed collected in Minnesota (Isle) were consistently injured less than all other balsam fir provenances, but trees of this provenance are undesirable in most other characteristics. Fraser fir suffered little or no injury and appears to avoid twig aphid attack when planted in the north because it begins growth after the aphid population has peaked.

With respect to characteristics important in pulpwood production, balsam fir has also been shown to vary considerably in specific gravity and tracheid length. Trees from eastern Ontario, Quebec, New York, and New England have the longest tracheids, but relatively low specific gravity. However, the low specific gravity is offset by their rapid growth and associated superiority in volume production. Although trees grown from seed collected in the western Lake States have high specific gravity, wood from these trees has short tracheids and biomass production is low because of their relatively slow growth rate.

In addition to considerable genetic variability among balsam fir provenances, individual trees from the same stands also exhibit considerable genetic variation. Lester et al. (1976b) reported significant genetic variation
in growth rate and leafing-out phenology among half-sib families within several Lake States provenances. In addition, DeHayes et al. (1982) found considerable genetic variation in growth rate and branching characteristics among half-sib families growing in Vermont and Maine. As a result, it appears that considerable improvement in the growth and quality of balsam fir Christmas trees can be expected through family selection. However, poor parent-progeny growth rate correlations and the lack of differences in growth rate between progeny of selected and average parents in that study indicate that phenotypic selection for growth rate in balsam fir using the comparison tree method of selection was ineffective. Although the development of highly sophisticated phenotypic selection methods may improve the efficiency of selection, results to date indicate that casual ocular selection for growth rate among balsam fir trees in the wild will not result in the production of fast-growing offspring.

Although interspecific hybrids are only rarely of importance from a tree improvement perspective, some hybrid combinations of fir are easily produced (Hawley and DeHayes 1985a) and exhibit a desirable combination of characteristics (Hawley and DeHayes 1985b). Fraser X balsam, Fraser X white, and bracted balsam X balsam fir hybrids are growing faster than balsam, Fraser, and white fir seedlings after five growing seasons. Although intermediate between their parents in time of budbreak, Fraser X white and Fraser X balsam fir break bud 8 to 12 days later than their paternal parents, which may provide the hybrids an escape from spring frost damage and insect attack some years. Also, the relatively long needles of these hybrid seedlings may provide an aesthetic advantage over the relatively sparse-crowned Fraser fir typically found in New England plantations. If hybrid performance remains consistent through Christmas tree rotation age, then it would appear that interspecific hybridization has the potential of producing fast-growing, long-needled Christmas trees.

Because it is cultivated as a Christmas tree, there has been considerable localized selection and propagation of balsam fir by commercial growers. A few such selections have performed well over a large geographic area and have been informally designated as strains among the growers and nurseryman. One such strain of balsam fir has been designated as the "Cook' strain and it has performed consistently well across several areas in northern New England. This strain is characterized by faster than average growth, blue-green foliage, and relatively late budbreak.

CONCLUSIONS AND RECOMMENDATIONS

Balsam fir is a genetically variable species and considerable gain in growth
and quality characteristics can be achieved with careful seed source selection. In general, provenances from the eastern portion of the range have exhibited the most desirable combination of growth, budbreak, wood properties, and branching characteristics. In particular, trees grown from seed collected in Ripton and Granville, VT, Indian Lake, NY and Cabano, PQ have performed exceptionally well on a diversity of sites in northern New England. Trees of the so-called “Cook” strain are also recommended for Christmas tree plantations in many parts of New England and the Maritime Provinces. However, trees of these and other eastern provenances are susceptible to the balsam twig aphid. Fraser fir should perhaps be considered as an alternative to balsam in areas with chronic twig aphid infestations. With careful seed source selection and good cultural practices (such as site selection and weed control), it should be possible to produce high quality fir Christmas trees on approximately 7 to 9 year rotations.

Although there is undoubtedly considerable genetic variability among individual balsam fir trees growing within the same stand, little or no gain in growth rate has been achieved by selecting superior individuals in natural stands and propagating them through seed. However, for more highly heritable characteristics such as time of budbreak and foliage color, it may be possible to enhance the quality of balsam fir seedlings through rigorous phenotypic selection. Finally, hybrids between different fir species are exhibiting excellent growth and form characteristics in the juvenile stage and have considerable potential as quality Christmas trees.

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Eastern white pine grows naturally from the Maritime Provinces of Canada west to Manitoba and Minnesota and south along the Appalachians to northern Georgia (Wright 1970). It is the largest of northeastern conifers, and has been a most valuable species since the beginning of logging in the country (Harlow et al. 1979). White pine wood is soft, straight-grained, easily cut, polishes well, and, when seasoned, warps but little. Almost everything from ships’ masts to matches, including doors, flooring, framing, trim, crating, and novelties have been made of this wood.

White pine is the most commonly planted tree within its range. Approximately 40,000,000 seedlings are planted yearly for timber and Christmas tree use. In addition, an estimated 250,000 balled-and-burlapped specimens are planted for windbreaks, screening, and other amenity uses throughout its native range and for some distance to the south and southeast (Kuser et al. 1985).

White pine is a slow starter in height growth during the first few years after establishment. After this initial period, the species begins to grow rapidly and thrives best at 50% full sunlight and more. Open grown trees may reach only 1.5 m (5 feet) by age 8 to 10 years but thereafter height growth can reach 1.4 m (4.5 feet) per year. Average annual growth of dominant trees after age 10 is about 0.5 m (1.5 feet) (Fowells 1965). In natural stands where white pine is competing with hardwoods, early growth is suppressed and it is a common understory tree. Growth often persists until white pine reaches codominant and dominant positions in the canopy, at which time it is outgrowing hardwood competitors (Hibbs 1982).

Although white pine can grow on nearly every soil within its range, it can be managed most effectively and economically on those soils having a high proportion of sand (Lancaster 1984). Site selection involves picking pine sites with site index less than 60, and leaving better sites to the hardwoods because the latter are so costly to control on good sites. Hardwood control measures should be started early in the life of the stand. Special considera-
tion must be given to avoiding damage by the white pine weevil, and in consequence two methods are generally used to start white pine. If using natural regeneration, the shelterwood system is best; and if planting, close spacing (1.7 m or 6 ft. square) is preferable (Lancaster 1984).

GENETICS AND TREE IMPROVEMENT

Despite historical interest by silviculturists in the species, genetic experimentation is recent. Nearly all provenance and inheritance data are from experiments after 1955, when the Northeastern Forest Experiment Station concluded that information was urgently needed on racial variation (Garrett et al. 1973). Fowler and Dwight (1964) found a difference in the stratification requirements of seed of northern and southern seedlots, with the latter germinating only 1/10 as well as the former unless stratified. In the Forest Service rangewide provenance test, the growth-rate pattern was similar in 16 central and southern plantations, but very different in four test plantations in the northern Lake States and northern Ontario. At the central and southern plantations, most of the best origins were from south of the planting sites (Wright 1970).

Growth rates of trees from the best seed sources have exceeded those of trees from the poorest sources by 40 to 80%. Trees of southern Appalachian origin have generally grown faster than local seedlings as far north as central Pennsylvania (lat 41°N), at about equal rates between 41° and 44°N, and more slowly than trees from mid-range or local sources north of 45°N (Garrett et al. 1973). These trends continued for 16-year growth results as summarized by Demeritt and Kettlewood (1976). The same tendencies are also manifest in progeny of improved seed orchards (Kuser and Hobbs 1985; Kuser et al. 1985).

Genetic variability in white pine is ample for mass selection. Many plus clones have been selected and most states within white pine's range now have grafted first-generation seed orchards from which progeny test information is beginning to flow. North Carolina has a 23-acre white pine seed orchard and plans more.

Many other studies have been conducted by the U.S. Forest Service and USDA Regional Research project NF-27 cooperators using material from the rangewide study including rooting of cuttings (Kiang and Garrett 1975); resistance to white pine weevil (Wilkinson 1983); and genetic variation in proteins (Ryu and Eckert 1983, Eckert et al. 1981).

Other large scale cooperative projects were established through Michigan State University and USDA Regional Research project NC-51 that detailed population differences in survival, growth rates, winter injury, flowering,
and chemical properties (Funk 1979; Garrett et al. 1973; Genys et al. 1978; Wright 1970, 1976; Wright et al. 1979).

CONCLUSIONS AND RECOMMENDATIONS

The size of the market for white pine and the existence of sufficient genetic variability in wild populations combine to give this species top priority for domestication. Conceivably more than one type of white pine may need to be developed. Breeding could be directed toward 1) a fast-growing forest and amenity tree for central and southern sections of its range, and southeastward; 2) a fast-growing forest tree for the northeastern part of its range; 3) a blister-rust-resistant, fast-growing tree for the northwestern part of its range, and 4) a fast-growing, bushy Christmas tree with internodal branches (as occasionally occur naturally) and good needle color.

It appears possible to achieve genetic gains of approximately 10% to 30% over juvenile growth rates of native populations by mass selection and establishment of first-generation grafted seed orchards followed by roguing (Kuser and Hobbs 1985). While the potential for genetic improvement in white pine is high, the essential support of forest industry and the U.S. Forest Service is currently lacking. Tree improvement in this species will not progress beyond the research level without coordinated support and effort. University researchers should develop “demonstration seed orchards” that use the latest management techniques, such as supplemental mass pollinations and irrigation for controlling timing of flowering. This approach coupled with visits to progeny tests should provide convincing evidence of genetic potentials and industrial scale seed orchard operations. Forest industry should be approached for support, at all stages of development, of a coordinated tree improvement plan for this species.

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Pitch pine (Pinus rigida Mill.) is found from southeastern Ontario to northern Georgia. In the Northeast, it is most commonly found on sandy soils and farther south it is found on shallow soils along the Appalachian Mountains. In some parts of its range, it appears as a pure species; but on better sites, it is a component of other major forest types.

Climate throughout the natural range of pitch pine is humid with annual precipitation between 94 and 142 cm (37 and 56 in) and is well distributed throughout the year. Because of its large north-south distribution, the length of the frost-free season ranges from 212 to 90 days and temperatures range from a low of -40°C in the northern part of the range to a high of over 38°C in most sections.

Pitch pine is usually restricted to less fertile soils. Many of the northern stands occupy sandy outwash plains of glacial origin or sandy and gravelly soils of alluvial and marine origin. In the mountains, it is most common on steep slopes, ridges, and plateaus where soils tend to be shallow. This species is generally found on acid podzol or podzolic soils with a pH between 3.5 and 5.1. In southern New Jersey, pitch pine occurs on excessively drained, imperfectly drained, and poorly drained sands and gravels as well as on peat soils in the white-cedar swamps. Even in the mountain regions, it grows on both well or excessively drained slopes and in swamps. Pitch pine is found growing near sea level as far south as New Jersey and at elevations of 1,370 m (4,500 ft) in the Great Smokey Mountains. At higher elevations, it tends to occupy warmer and drier sites facing south or west.

Open-grown seedlings of pitch pine begin to produce cones between 8 and 12 years, but vigorous basal sprouts begin bearing mature cones at age 3. Pollen production usually occurs several years after cone production as in other conifer species. In southern New Jersey, the staminate flowers are visible by the third week of April; pistillate flowers usually by May 1. Pollen shedding usually occurs during the second or third week of May.

Although pitch pine is reported to bear good cone crops at 3-year intervals, production may be irregular. In parts of New Jersey, good cone crops have occurred at 4- to 9-year intervals. Occasionally poor crops occur in suc-
cessive years, although it is more common for a poor crop to be followed by several years with good crops. Seed dissemination is variable, depending on the length of time cones remain closed after maturity. On some trees, the cones open soon after maturity; at the other extreme, some cones remain closed for many years until the heat of fire opens them or until the trees are cut. Trees of the latter type are characteristic of areas with a long history of wildfire. When cones open at maturity, seed dispersal begins about November 1 in southern New Jersey. Ninety percent of the seed falls within the first two months. Although equipped with large wings, pitch pine seeds usually are not carried very far by wind. In one study, all natural reproduction in an abandoned field occurred within 90 m (300 ft) of the parent trees.

Natural regeneration from seed or sprouts is still the most common method of reproduction with pitch pine. As with most pine species, growth during the first 5 or 6 years is generally quite slow followed by a period of more rapid growth. Growth of open-grown seedlings may reach 20 cm (8 in) at the end of the first growing season on the best sites. After the first several seasons, average height growth may average between 0.4 and 0.7 m (1.5 and 2.2 ft).

With few exceptions, seed for planting stock is still purchased locally on the open market and is obtained from cutting operations or collected from trees of unknown quality. As a consequence, growth figures for planted stock have not exceeded that of naturally seeded stands. In recent years, several mid-Atlantic states and several industries have established seed orchards in an attempt to improve the quality of the seedlings being planted.

Among the conifer species in the East, pitch pine has an outstanding ability to survive serious injury. Even when all of the foliage is killed by fire, dormant buds along the stem will permit the tree to flush again. If the entire stem is killed, sprouts frequently start at the base. Although pitch pine's sprouting ability is an asset that enables trees to survive fire or other injury, it is also a liability from a commercial point of view. Apparently, the form and growth rate of sprouts decrease rapidly with age of the root crown after crown age reaches about 20 years.

Pitch pine trees exceeding 350 years of age and 30 m (100 ft) have been reported, although they seldom exceed 25 m (80 ft) in height or 60 cm (2 ft) in diameter under stand conditions. On the better sites, the species maintains an average annual height growth of 30 cm (1 ft) or more until the trees are 50 to 60 years old. The rate of growth then starts to decline, and the trees add little to their height after age 90 to 100.

In closed stands of seedling origin, pitch pine self-prunes about as well as shortleaf pine, but in understocked stands it tends to produce somewhat larger and more persistent branches than shortleaf. Open-grown trees typi-
cally develop large spreading branches, which contributes to the rough appearance people associate with this species.

Pitch pine is intolerant of shade. On swamp sites, it is less tolerant than Atlantic white-cedar; and on upland sites, it is less tolerant than its common hardwood associates—blackgum, red maple, various oaks and hickories. Because of its relatively lower tolerance to shade and its requirement of mineral soil for germination, pitch pine can best be maintained in stands by even-aged management with seedbed preparation and control of competing hardwoods.

GENETICS AND TREE IMPROVEMENT

Where pitch and shortleaf pines grow together, natural crossing may occasionally occur. Trees with intermediate characteristics have been reported in southern New Jersey and Pennsylvania. Pitch pine has been artificially crossed with shortleaf, pond, table-mountain, and loblolly pine. The largest program of interspecific hybridization of pines has taken place in Korea where millions of pitch x loblolly trees are produced annually. Early field trials in several states showed only slight promise for this Korean hybrid. However, by using carefully selected parent trees and extensive planting trials, the Northeastern Forest Experiment Station and several cooperating agencies produced hybrids with exceptionally fast growth, good form, winter hardiness, and resistance to fusiform rust. At the present time, there are 67 plantings of first and second generation hybrids in 22 states ranging in age from 2 to 15 years. Because pitch and loblolly pine do not flower at the same time, all of these trees were produced by controlled pollination methods. Now that outstanding hybrid combinations and individuals have been identified, the problem is to find a way to mass produce seed. Two techniques that are now being explored are the use of single-clone orchards that will be mass pollinated and the establishment of clonal orchards of the best first-generation hybrid individuals to produce wind pollinated second-generation hybrid seed.

CONCLUSIONS AND RECOMMENDATIONS

The Forest Service, industry, and university programs currently underway in the United States should be continued and expanded. Additional testing needs to be initiated in other countries, including developing nations, with large areas of semi-arid sites. Cooperative programs should be developed between researchers in the United States and other countries to permit the free exchange of plant materials and ideas.
Research priorities should be as follows:
1. Identify additional "select" pitch pine.
2. Evaluate variation within and between provenances of pitch pine.
3. Intraspecific hybridization program with pitch pine to determine heri-
tability of desirable traits.
4. Evaluation of existing progeny tests of pitch x loblolly hybrids.
5. Production and testing of selected hybrid combinations on specific sites
based on performance of existing plantings.
6. Continue to research problems of mass production of first- and second-
generation hybrid seed.
7. Evaluate seed production, seed quality, and growth potential of ad-
vanced generation hybrids.

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SCOTCH PINE

(Pinus sylvestris L.)

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SILVICULTURAL BACKGROUND

Scotch pine, Pinus sylvestris L., has been planted extensively in northern United States for Christmas trees and landscaping. Its natural range extends over vast regions of Europe and Asia, where it is a very important timber species. Many varieties and cultivars have been described, reflecting great genetic variability and adaptation to diverse environments. Scotch pine is easy to grow on many kinds of sites and exhibits rapid juvenile growth. Cultural practices in Christmas tree plantations include weed control by mowing and herbicides, spraying to control various diseases and insects when they become problems, and shearing to improve shape and density of crowns.

Opportunities for genetic improvement are excellent, as there is a wealth of genetic variation in traits that can quickly lead to large economic benefits. These include better crown shape and density, faster growth, straighter stems with smaller butts, greater cold-hardiness, better color, and resistance to various diseases and insects. The early onset, frequency, and quantity of flowering are very favorable for breeding and seed production; but excessive, precocious flowering must be avoided as it can lead to sparse foliage.

GENETICS AND TREE IMPROVEMENT

Objectives for improving Scotch pine in the Northeast have shifted as the research evolved and as results from other investigators become available. Objectives have included:

1. Study genetic variation in important traits among provenances, to find the most useful ones and define their characteristics.
2. Estimate heritabilities of traits and effectiveness of alternative breeding methods, to design strategies of selection and breeding.
3. Select superior trees and evaluate them via progeny tests, for use in breeding programs or seed orchards.
4. Investigate possibilities for clonal propagation of selected trees in commercial production.
5. Arrange for commercial production of improved varieties by seed or as clones.
There is a long history of genetic research with Scotch pine. The first publication on a common-garden study appeared in 1821, and early provenance experiments were planted in 1907 and 1938. Soon after research in Project NE-27 began in 1956, an extensive series of provenance experiments was started in Project NC-51 (now NC-99). These and other studies have produced a large amount of basic information needed for conducting genetic improvement programs. Useful levels of genetic variation have been found in many traits that have economic importance (see summary in Wright 1976, pages 267-281). Only the salient points can be addressed here.

Provenances from Spain and southcentral France have better combinations of characteristics for Christmas trees than most other wild populations, as do several named varieties grown from seed production areas in North America. Valuable genes for fast growth, winter hardiness, and disease resistance may be obtained from other seed sources via hybridization. Selection within Spanish or French provenances to improve these traits is also feasible. There is extensive genetic variation among and within populations. Practical methods have been developed to select for growth rate, crown form, and foliage color; further research is needed on selection for disease resistance.

Several kinds of practical achievements have been stimulated by Scotch pine research in Projects NE-27 and NC-99. Information from provenance experiments has been used by nurserymen to obtain superior seed, and by growers to purchase seedlings best suited to their land and production methods. Heritability and hybridization studies employing extensive controlled matings among trees of diverse provenances have provided knowledge needed for designing breeding and selection methods. The "Pennspanish" variety was created through two generations of selection and breeding, and seed from the seed orchard was released for commercial production in 1984. "Pennspanish" has better crown form and color than other varieties, and grows faster than the Spanish variety from which it was derived. A grafted orchard in Nebraska has been developed through Project NC-99. Advice has been furnished to nurserymen who want to develop their own grafted or seedling orchards.

CONCLUSIONS AND RECOMMENDATIONS

A broad base of information has been assembled which justifies and can guide more active tree improvement programs. Many superior trees have been selected, too. Commercial nurseries have lagged in exploiting these resources, partly because they have lacked the expertise to implement more
than the simplest genetic methods; this situation appears to be changing for the better.

As progress continues in the initial phase of developing commercial varieties from wild populations, many questions worthy of research become increasingly important. The next phase should focus particularly on alternative breeding strategies and associated prospects for genetic gains. Research is needed on

• comparing genetic gains in important traits from selection within populations versus hybridization among provenances.
• exploring possibilities for vegetative propagation to exploit non-additive plus additive genetic variation.
• determining if the narrower genetic variation within families or clones will reduce the range of site adaptability.
• developing methods of selecting for disease resistance.

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BLACK SPRUCE

(Picea mariana (Mill.) B.S.P.)

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SILVICULTURAL BACKGROUND

Although black spruce is a major component of the northern coniferous forests of North America, it was seldom planted on a large scale prior to the 1970's. Recently, however, it has become a major plantation species in eastern Canada and northern New England. It is capable of rapid juvenile growth when competing vegetation is controlled, reaching average heights of 4 to 5 m (13 to 16 feet) ten years after planting on several sites in New Brunswick (van Groenwoud and Ruitenberg 1982). Growth is best on moderately well-drained soils of medium fertility, although black spruce will also grow on poorly drained and less fertile sites.

Black spruce breaks bud later in the spring than does white spruce, and for this reason it is less susceptible to late spring frosts and to damage from the spruce budworm. It has no severe insect or disease problems and is tolerant of herbicide applications except during the period of shoot elongation.

GENETICS AND TREE IMPROVEMENT

Information on provenance variability in black spruce is available from a large number of rangewide provenance test plantations established in the U.S. and Canada through cooperation with the Petawawa National Forestry Institute of the Canadian Forestry Service. Morgenstern (1978) found that most of the genetic variation in seedling growth characteristics was attributable to differences between geographic areas, with less variability attributable to stands within areas. A general north-south cline is evident in phenology and growth. However, within a restricted geographic area the effect of stand-to-stand genetic variation can be identified.

At age six, results in a Maine plantation of the Petawawa provenance test indicated that the tallest trees, from Canadian and U.S. provenances of the Great Lakes region, were 20% to 30% above the plantation mean (Bihun and Carter 1983). Survival was excellent for all provenances except those from north of 55°N latitude. In ten New Brunswick plantations of the same provenances, 9-year height of southern Ontario and Lake States provenances was frequently above average, as were several provenances from the Mari-
times (Fowler and Park 1982). The Maritime provenances possessed greater stability of performance across planting sites.

Considerable variation in growth rate is evident in half-sib families of black spruce within restricted geographic areas. Morgenstern (1974) examined 20 seedling families through age 9, and found that family height varied from 88% to 112% of the plantation mean. In a larger study of 79 families, Kenlan (1981) observed large differences in family height at age 2, ranging from 130% to 79% of the overall mean. Selection of the ten best families in Kenlan's test lead to a gain of 22% in overall height at age 2.

Overall height correlations for provenances between ages 3 and 12 are high; but when only faster-growing provenances from the southern and central portions of the range are considered, no significant correlations exist between heights at these ages, and correlations among plantations at age 12 are low (Nienstaedt 1984). Overall correlations for height at ages 4 and 9 in New Brunswick plantations ranged from 0.26 to 0.83 (Fowler and Park 1982). Similarly, correlations for half-sib progeny height at ages 4 and 9 are low and testing of 4-year-old progeny on different sites indicated changes in family ranking, presumably due to genotype x site interaction (Morgenstern 1974). Correlations of 5th-year half-sib progeny height in three Maine plantations with first- and second-year heights are low, as are family correlations among sites at age 5 (Carter 1987).

Black spruce and red spruce are known to hybridize readily under some conditions, and the resulting hybrid forms have inferior photosynthetic capacity (Manley and Ledig 1979). Trees that show evidence of hybridization should be avoided in selection and breeding programs.

Individual-tree selection techniques in natural stands appear to be relatively ineffective in black spruce (Kenlan 1981), and most selection and breeding programs have been based on family selection techniques and the establishment of seedling seed orchards. Using this approach, large numbers of trees are selected to serve as seed parents, and their offspring are established in half-sib family tests and seedling seed orchards. Information from the family tests is later used to remove the poorer families from the seed orchard. Gains in height growth from first-generation seed orchards using this approach are expected to reach 10%.

Seedling seed orchards of black spruce should produce seed in quantity by age ten, with an eventual seed production capacity of about 500,000 seed per acre of orchard each year (McPherson et al. 1982). In the Northeast, seedling seed orchards have been established by industrial and state organizations in Maine and Vermont. These orchards should start producing seed in the early 1990's.

Black spruce seedlings can be clonally propagated by the use of rooted
cuttings. The development of this technology may allow for much greater genetic gains in future breeding programs. In addition, as programs move into the second and succeeding generations the use of clonal seed orchards is expected to expand as techniques for identifying superior trees become more reliable.

CONCLUSIONS AND RECOMMENDATIONS

There is sufficient variability among provenances and families of black spruce to justify the establishment of breeding programs in regions where the species is widely planted. The expected genetic gain for first-generation programs is lower than for white spruce due to the low efficiency of mass selection, the potential for genotype x site interaction, and uncertain age-age correlations. As more information accumulates on the genetics of black spruce, however, the levels of gain that can be attained should increase.

BIBLIOGRAPHY

WHITE SPRUCE

(Picea glauca (Moench) Voss)

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SILVICULTURAL BACKGROUND

White spruce is one of the more commonly planted conifers in the Lake States and the Northeastern United States. This species is capable of growth on a variety of soil types, although highest productivity is expected on well-drained loamy soils. It tolerates a wide range of pH values but requires higher fertility levels for good growth than do other commonly planted conifers (Nienstaedt 1982). White spruce can grow on relatively dry sites if other soil factors are favorable, and will tolerate moist soils so long as the soil water is not stagnant.

Young white spruce are susceptible to damage by late spring frosts and planting sites where these are likely to occur should be avoided. Seedlings are tolerant of light competition but heavy competition, particularly from grasses, should be controlled by mechanical or chemical means to ensure optimum survival and growth (Perala 1982).

Because white spruce is a popular plantation species in the Lake States and the Northeast, it was one of the first northern conifers for which tree improvement programs were developed. Analyses of the economics of artificial regeneration in white spruce indicate that the application of selection and breeding programs can have a significant impact on economic returns from white spruce plantations (Carlisle and Teich, 1978; Rensema, 1984).

GENETICS AND TREE IMPROVEMENT

Early research on the genetics of white spruce focussed on geographic variation among provenances. In more recent years information has been obtained regarding family variability, efficiency of plus-tree selection, seed orchard management, and population genetics. This accumulation of knowledge over the past 25 years makes white spruce one of the best understood northern conifers, from a genetic standpoint.

Provenance tests in Ontario during the 1950's demonstrated the existence of substantial variability among seed sources in growth rate and specific gravity (Holst 1960). In 1962, a large rangewide cooperative provenance test was
planted at numerous field locations in the United States and Canada. After 5 years in the field, provenances demonstrated minor differences in survival but large differences in growth rate (Nienstaedt 1969). Rankings of seedling height growth at 14 sites from North Dakota to New Brunswick were similar, and several provenances from the Ottawa River Valley region were among the tallest provenances at each planting site. These trends continue to be evident in plantations measured at 15 years of age, with the Beachburg, Ontario, seed source generally being 20% to 30% above average in height (Radsliff et al. 1983).

Within a single geographic region, variation in height between the offspring of individual trees is large, with the fastest-growing families often being 25% taller than average (Dhir 1976, Mohn et al. 1976, Tebbetts, 1981).

Recognition of high genetic variability in white spruce led to the early establishment of seed orchards. Heritability for growth traits is high in white spruce, so grafted clonal seed orchards are generally preferred over seedling seed orchards in this species. During the 1960's and early 1970's superior trees were selected by the New York State Forest Service and the Maine-New Hampshire Spruce-Fir Committee headed by Clyde Hunt of the U.S. Forest Service. Grafts and seedling offspring of these trees are maintained in seed orchards by several organizations, and some are now producing seed.

Open-pollinated progeny tests of the Spruce-Fir Committee selections indicate that offspring of select trees are superior to nursery-run seedlings (Hale and Canavera 1977; Carter 1985). After 11 years in the field, open-pollinated offspring of 23 select trees averaged 23% taller than New Hampshire nursery-run seedlings, in one Maine progeny test plantation.

Data from grafted seed orchards in Ontario indicate that significant quantities of seed begin to be produced ten years after orchard establishment (McPherson et al. 1982). When in peak production, an acre of white spruce seed orchard is expected to produce 500,000 seeds per year.

Seedling seed orchards of white spruce have been established in a few instances, usually to take advantage of Ottawa River Valley material. Seed production in seedling seed orchards begins at approximately 15 years of age.

It appears that fast-growing white spruce can be reliably identified at a relatively early age, so advanced generation breeding programs could move forward rapidly. The large degree of genetic variability present in white spruce indicates that well-designed breeding programs should be capable of producing continued improvement in desirable characteristics for many generations.
CONCLUSIONS AND RECOMMENDATIONS

White spruce is a genetically variable species and significant gains in growth rate can be made either by the selection of appropriate seed sources for planting stock, or by the establishment of seed orchards. Because inbreeding in natural stands of white spruce is relatively high, Coles and Fowler (1976) suggest using a baseline selection method to identify superior trees. The comparison-tree method is widely used, however, and ocular selection also appears to be effective. In addition to initial gains resulting from provenance or plus-tree selection, seed orchards will result in reduced levels of inbreeding, leading to additional growth gains.

BIBLIOGRAPHY


