

Genetics and Breeding of Five-Needle Pines in the Eastern United States

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Abstract—Research and breeding of five-needle pines in the eastern USA has been concerned mainly with eastern white pine (*Pinus strobus* L.), which has been found to be a highly variable species. Principal attention has been given to the inheritance of growth traits within and among stands and among provenances. Growth of trees of Tennessee, North Carolina and Georgia provenances exceeds that of other origins in many areas of the US and even in other countries. Research basic to breeding indicates that the genetic barrier to species crossability in the soft pines is embryo failure, whereas in hard pines it is pollen tube incompatibility. Patterns of premature cone drop in relation to genetic affinity have also been determined; cone retention is not closely related to capacity to produce viable seed. The expression of inbreeding after selfing in young plantations of *P. strobus* varies with the parents and the site, but the species is more tolerant of inbreeding than most other species of pines. Eastern white pine population studies show that genetic variability may be maintained even in small isolated stands and in the next generation after heavy thinning, although gene pool deterioration may follow cutting if silviculture disregards gene pool conservation. A genetic gain in volume of about 22 percent has been obtained in *P. strobus* from age 13 family selections in first-generation progeny tests. Potentially useful species crosses are eastern white pine x Himalayan pine and eastern white pine x western white pine. The best hybrid families of the eastern white pine x Himalayan cross have been found to exceed *P. strobus* in volume by 22 to 44 percent at ages 17-22 in progeny tests. These two hybrids also exceed *P. strobus* in wood specific gravity. Selection and breeding of *P. strobus* for blister rust resistance has been difficult and has not yet yielded commercially useful resistant genotypes, nor has selection and breeding for white pine weevil resistance been successful. However, new approaches may overcome these problems. Air pollution tolerance varies widely in *P. strobus*; natural selection in native stands has yielded highly tolerant progenies while eliminating the most sensitive genotypes from the gene pool. Future research directions are suggested.

Key words: Five-needle pines, eastern white pine, breeding, species incompatibility, genetic variability, growth rate, species hybrids, resistance, white pine weevil, white pine blister rust, air pollution tolerance.

Introduction

Research on the genetics and breeding of five-needle pines in the eastern USA began about 1950 with species hybridization experiments and early tests for resistance to the white pine weevil (*Pissodes strobi* Peck) and the white pine blister rust (*Cronartium ribicola* J.C. Fischer). During the subsequent 30-year period, eastern white pine (*Pinus strobus* L.) was probably the subject of more extensive cooperative tree improvement research over the eastern half of the USA and eastern Canada than was any other forest tree species, with the exception of the southern pines. The greatest effort was applied to the study of geographic variation over the entire species distribution by replicated provenance tests, first using seed collections made at the range-wide level, then concentrating on the southern Appalachian part of the species range. The results of this work by numerous state university research stations, the USDA Forest Service and Canadian research centers were combined in joint publications issued at various ages. They provide a very useful knowledge base, especially on adaptability and growth traits as related to seed origin interacting with plantation location. These results have now been put into practice in the commercial planting of eastern white pine.

Studies also provided some measure of stand-to-stand and within-stand variation. Controlled breeding research, although not as extensive as the common-garden testing of open-pollinated seed, has provided estimates of the inheritance of growth rate and the potential for genetic gain from half-sib and full-sib families. Efforts to develop weevil and blister rust resistant eastern white pine have, on the other hand, not yet been successful, although work continues. Research on other species of five-needle pines has been primarily limited to investigations of the potential usefulness of some of the more adaptable species and their hybrids as a source of resistance to the weevil and blister rust. A later research effort was the study of the genetic aspects of air pollution tolerance in *P. strobus*, which was, prior to natural selection for tolerance, highly sensitive to sulfur dioxide and ozone, both major pollutants over much of the natural range of the species.

Applied genetic research directed toward improved planting stock of five-needle pines has declined in the eastern USA during the last 20 years as part of the general curtailment of public funding for tree improvement research and low level of support from other sources. Thus available new genetic information on five-needle pines published during the last two decades is mainly concerned with 1) biochemical and molecular analysis of variability in natural stands, and 2) continuing efforts to develop rust-resistant strains of eastern white pine and to apply molecular technology to the weevil resistance problem. This paper covers principal results of five-needle pine breeding and improvement

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research in the USA; results of Canadian studies of stand and provenance variation in field trials and the long-term Canadian efforts to develop blister-rust resistant eastern white pine are reported in the paper by Daoust and Beaulieu in these proceedings.

Variability in Eastern White Pine _____

Geographic Variation in Growth Rate in Test Plantations

Extensive range-wide provenance testing has shown that *P. strobus* is a highly variable species, as compared, for example, with the more range-restricted species *Pinus resinosa* Ait. (Fowler 1965). Of particular importance for tree improvement, eastern white pine includes a wide range of genotypes with respect to rate of growth in height, diameter and stem volume, while at the same time retaining the capacity for adaptation to a broad range of environmental conditions. These conclusions are based on statistical analysis of the performance of trees in widely replicated range-wide seed source trials (Wright 1970). In trials at mid-latitudes within the species distribution (Pennsylvania, Maryland, Tennessee, Indiana, Ohio, southern Michigan, Illinois, West Virginia, Nebraska), genotypes of western North Carolina, Tennessee and northern Georgia origin outgrew those of all other provenances by 70 to 80 percent in tree height growth rate by the end of the first decade. The same growth pattern was found in trials in Australia and New Zealand. After the first decade, absolute differences between fast-growing southern and slow-growing northern seedlots increased but relative differences decreased. Diameter growth differences persisted, sustaining large differences in volume during the second decade (Funk 1979, Kriebel 1982). Later trials concentrating on southern Appalachian seed origins confirmed the growth superiority, in all tests, of seed sources in North Carolina, Tennessee and Georgia over those from Virginia, West Virginia and Maryland. The fastest-growing seedlots commonly grew 40 percent faster than the slowest ones, translating into a 2 to 1 superiority in rate of volume growth (Wright and others 1979).

Population Structure

Progeny tests have shown that family differences in height growth rate are commonly large within stands of eastern white pine, the variance component for general combining ability on a family mean basis averaging over several trials about 25 percent of the mean variance over all plots (De Vecchi Pellati 1967, Wright 1970, Kriebel 1978, Thor and Gall 1978). This evidence of high genetic variability is supported by more recent studies of gene diversity in natural stands before and after thinning, facilitated by new technology, using isozyme and DNA analysis. In Wisconsin, using simple sequence repeated satellite DNA markers, Echt (2000) found that genetic diversity in eastern white pine was the same in both 160-year-old trees and their natural regeneration after a shelterwood thinning that removed most trees. Likewise, in Newfoundland, Rajora and others (1998) were unable to show that genetic diversity had declined in

P. strobus populations, even after a century of decline in population size. Allelic diversity in heavily thinned stands was as high as it was in unthinned stands. In fact, the Newfoundland populations were as genetically variable as those from Ontario, near the center of the species range. On the other hand, isozyme and microsatellite DNA analyses of diversity in two old-growth Ontario stands showed that harvesting caused a loss in genetic diversity (Buchert and others 1997, Rajora and others 2000). Differences in silvicultural treatment of the old-growth stands may explain the differences between the Wisconsin and Ontario results; the forestry program on the Menominee Indian Reservation in Wisconsin area is considered by many to be the finest example of sustainable management of eastern white pine on the continent (Echt 2000).

Genetics of Outbreeding and Inbreeding _____

Genetic Control over Embryo Formation and Cone Set

High yields of viable seed are usually obtained in eastern white pine from both open and controlled crossing with other individuals of the species. Hybrids can be obtained from crosses with several other species of five-needle pines with varying success in terms of seed yield (Wright 1953). Reported histogenetic and serological studies of fertilization and embryogenesis in "soft" pines (Subgenus *Strobus*, Section *Strobus*) have shown that fertilization and early embryogenesis can occur normally in ovules of non-crossable species combinations, i.e. those crosses never reported to yield viable seed, with subsequent post-fertilization breakdown from embryo inviability. In fact, early development of the true embryo has been observed in some of these crosses that do not yield viable seed (Ueda and others 1961, Hagman and Mikkola 1963, Hagman 1967, Kriebel 1972, 1981). In contrast, incomplete pollen tube penetration and failure of ovule fertilization have been the pattern in similar studies of hard pines (McWilliam 1959, Hashizume and Kondo 1962a, 1962b, Chira and Berta 1965). The evidence from these painstaking studies, therefore, usually based on daily or-near daily ovule collections and sectioning over a period of several weeks and some including more than one year's data, suggests a fundamental difference in species isolation mechanisms between the soft and hard pines, the soft pines being characterized by embryo inviability and the hard pines by pollen tube incompatibility.

Soft pines and hard pines also differ in the way in which interspecific hybridization affects cone retention. In soft pines, non-crossable combinations consistently retain first-year cones, whereas in hard pines they often do not. It is possible, for example, to cross *P. strobus* with *P. koraiensis* pollen without first-year cone abscission. Table 1 shows the decrease in maternal control over cone abscission as genetic divergence increases between parent species (left column), for both pine subgenera. Subgenus *Strobus* seed maturation is characteristically blocked by embryo inviability and subgenus *Pinus* by pollen incompatibility. In comparisons of the effect of female parent, pollen species and pollination year on premature cone drop in *P. strobus*,

Table 1—Species isolation mechanism and extent of maternal control over cone abscission in relation to degree of outcrossing in soft and hard pine subgenera (Kriebel 1976b).

Isolation mechanism ⇒ Type of cross	Subgenus <i>Strobus</i>	Subgenus <i>Pinus</i>
	Embryo inviability	Pollen incompatibility
	Degree of maternal control ^b	
Intraspecific, outcross	Strong	Strong
Interspecific, viable seed	Strong	Strong
Interspecific, no viable seed	Strong	Usually weak
Intraspecific, limited pollen ^c	Threshold	Threshold
Unpollinated	Almost nil	Almost nil
The other subgenus	Nil	Nil
Another conifer genus	Nil	Nil

^aSummary constructed from research papers cited in Kriebel (1981), including chronological histogenetic studies of fertilization and embryogenesis, and breeding experiments.

^bStrong = high level of cone retention.

^cDifferent species seem to have different threshold values for the number of collapsed (unpollinated) ovules per cone above which abscission occurs.

extensive histological analysis of developing ovules showed that female parent exercised overriding genetic control in crosses within and between species. Pollen species had no effect on cone abscission, even in the case of a totally non-crossable species combination, nor did year of pollination. The year effect could be significant if, for example, prolonged heavy rain seriously reduced the pollen supply (Kriebel 1981).

Practical Significance of Inbreeding in *P. strobus*

P. strobus is more tolerant to inbreeding than most other species of pines (Fowler 1965). Inbreeding is found in both unmanaged and managed populations, and appears to be a natural characteristic of the species (Echt 2000). Among randomly-selected trees crossed in a small isolated Ohio stand, six of 8 trees manually self-pollinated had no reduction in seed yield; yield of the other two averaged 22 percent of outcross families. Reduction in growth rate in 5-10-year old offspring resulting from controlled self-pollination was variable compared to outcross progenies, averaging 18 percent on a good site and 38 percent on a poor site. Both open- and control-pollinated progenies from this stand were as vigorous as those from larger stands of comparable structure. (Kriebel 1975, 1982).

Growth Improvement in Eastern White Pine

Heritability of Growth Rate

Estimates of narrow sense heritability of height growth have been calculated from several progeny tests of eastern white pine, and from these estimates, genetic gain has been estimated using fixed assumptions. The heritability estimates have been fairly consistent when based either on individual tree means or on family means. Table 2 summarizes early estimates for height growth from open-pollinated (“half-sib”) and control-pollinated (full-sib) progeny tests, and a later estimate of genetic gain in volume at age 13 in Ohio. Height estimates based on individual trees are in general agreement for both half-sibs and full-sibs, as are those with a family mean basis (Adams and Joly 1977, Kriebel and others 1972, Kriebel and others 1974, Thor and Gall 1978).

Keathley (1977) estimated the heritability of volume growth in an Ohio white pine half sib progeny test at age 13 as h^2 (plot mean basis) = 0.45 ± 0.02 . From this estimate, using a selection differential of 1.3s and assuming family means to be normally distributed around the plantation mean, estimated genetic gain in volume was about 22 percent (Table 3).

Table 2—Estimates of heritability of tree height and stem volume in eastern white pine (Keathley 1977).

Parameters for estimates	TN ^a	OH ^b	NH ^c
Height, half-sib, individual tree	0.27	0.28	0.33
Height, half-sib, family mean	—	0.59	0.59
Height, full-sib, individual tree	—	0.32	—
Height, full-sib, family mean	—	0.54	—
Volume, half-sib, family mean	—	0.45	—

^aAge 7, Tennessee, Thor and Gall 1978

^bAge 13, Ohio, Kriebel 1978

^cAge 3, New Hampshire, Adams and Joly 1977

Table 3—Estimated genetic gain in tree volume after thinning in a half-sib progeny test of eastern white pine (Kriebel 1978).

Parameter	Statistic
Initial spacing	1 m (within rows) x 2 m
Trees per linear plot	4
Plots per family	12
50% thinning to 2 best trees/plot	Age 13 (to 2500 trees/ha)
h^2 for volume (plot mean basis)	0.45 ± 0.02
Mean 2-tree plot volume	0.021 m^3
Standard deviation (s)	0.008 m^3
Selection intensity	6 families out of 48
Final stocking	313 trees/ha
Selection differential	1.3s
Genetic gain (ΔG)	0.223
Realized gain, thinning at age 18	0.40

Actually, thinning was not made until age 18, since selection was a 2-stage process, combining a low-level individual tree selection within family plots with a subsequent high-level family selection. The realized gain in volume at age 18, based on plot means, was about 40 percent (Kriebel 1983).

Species Trials and Species Hybridization

In addition to arboretum plantings of many of the five-needle pines, a number of species have been tested in the eastern United States for their possible economic value as commercial plantation trees. The two species of most interest have been the Himalayan pine (*P. wallichiana* A. B. Jacks., syn. *P. griffithii* McClel.), and western white pine (*P. monticola* Dougl. ex D. Don). Himalayan pine, or blue pine, as it is known in its native region, has been tested on the provenance level, including some families within provenances. It has fast growth and variable cold hardiness, depending on the seed source and planting region. Although it is cold-hardy in parts of the mid-Atlantic coastal plain, in Ohio it suffers from late spring frost damage to new shoots, resulting in deformity with multiple branching. Seed sources in the eastern Himalayas (Nepal) do not survive winters in this region (Kriebel 1976a, Kriebel and Dogra 1986). Tests were made in Tennessee of some of the same provenances tested in Ohio. Survival and height growth were probably affected by a severe drought rather than cold winter temperatures. Families that had a high percentage of survival and good growth at each plantation came from a wide geographic spectrum (Schlarbaum and Cox 1990). Himalayan pine is generally susceptible to the white pine weevil (Heimbürger and Sullivan 1972) and variable in resistance to white pine blister rust (Bingham 1972).

Western white pine has the necessary cold hardiness in the eastern US and Canada, where it has a variable growth rate and good form. It appears to suffer less weevil damage than does eastern white pine, and this is probably its principal value for planting in these regions (Heimbürger and Sullivan 1972). It does not seem to be well adapted to the warmer, drier interior part of the eastern USA within the native range of *P. strobus* and is not recommended for Ohio (Kriebel 1982).

Macedonian white pine (*P. peuce* Griseb.) has been reported to have some resistance to the white pine weevil. It has good form but it has a slower growth rate in the eastern US than eastern white pine (Wright and Gabriel 1959).

Species Hybrids

At least seven F_1 hybrids and some of their reciprocals frequently outgrow either parent during the first decade (Wright 1959). The two of these hybrids that may have value for forest planting are eastern white pine x Himalayan pine and the reciprocal cross, and eastern white pine x western white pine and its reciprocal (Kriebel 1972). The first of these hybrids has had excellent growth and survival in Ohio (Kriebel 1982). In a 43-family full-sib progeny test, the two eastern white x Himalayan pine families were in the top 10 in volume growth at age 13, and one of these families outranked all others in the plantation. Hybrids with western white pine were more variable in volume growth; among the 43 families, two of the five eastern x western white pine families ranked third and sixth. When wood specific gravity of the hybrids *P. strobus* x *wallichiana* and *P. strobus* x *monticola* was measured in the same test and compared with that of eastern white pine, both hybrids clearly outranked *P. strobus* (Table 4). For the 152 trees tested for specific gravity, the results were:

P. strobus x *strobus*, 120 trees, mean wood specific gravity = 0.266

P. strobus x *wallichiana*, 15 trees, mean wood specific gravity = 0.295

P. strobus x *monticola*, 17 trees, mean wood specific gravity = 0.312

Since eastern white pine wood fiber is now in use at some paper mills, there could be a two-way gain from the use of these two hybrids in plantations, both from wood volume and wood specific gravity (Whitmore, F.W. and Kriebel, H.B., unpublished data).

Weevil Resistance Breeding

Repeated destruction of terminal shoots by the weevil larvae does not affect the health of white pines but it

Table 4—Relative stem volume and wood specific gravity of the hybrids *P. strobus* x *P. wallichiana* and *P. strobus* x *P. monticola*, compared with *P. strobus*; top 10 of 43 families in a full-sib progeny test at age 13 ranked by volume (Kriebel and Whitmore, unpublished, Kriebel 1982).

Hybrid family	Cross ^a	♀ x ♂	Relative stem vol. ^b	Rank ^c	Relative specif. gr.	Rank, sp. gr. ^d	Rank, sp. gr. x vol. ^e
1430	st x wa	1278 x 1213	202	1	110	4	1
1375	st x st	1130 x 1279	171	2	100	4	4
1428	st x mo	1278 x 635	166	3	115	2	2
1408	st x st	1276 x 1277	155	4	93	8	6
1420	st x st	1278 x 1275	148	5	98	5	7
1429	st x mo	1287 x 645	143	6	124	1	3
1424	st x st	1278 x 1280	139	7	97	6	9
1393	st x wa	1275 x 1213	139	8	112	3	5
1448	st x st	1280 x 1279	139	9	94	710	
1373	st x st	1130 x 1277	138	10	98	5	8

^ast = *strobus*, wa = *wallichiana*, mo = *monticola*.

^bMean stem volume in m³ at age 13 from seed, as a percentage of the mean of all 43 family means in the progeny test (0.0337 m³ per tree). The experiment included 33 full-sib *P. strobus* families, 5 *P. strobus* x *monticola* families, 2 *P. strobus* x *wallichiana* families, and 2 *P. strobus* x *peuce* families.

^cRank in volume among the 43 families in the progeny test.

^dMean specific gravity of the stem wood at age 13 from seed, expressed as a percentage of the mean of all 43 family means (266 kg/m³).

^eRank in family mean specific gravity x mean volume.

destroys their commercial value by causing permanent deformities in the main stem. Although significant progress has been made in breeding for superior growth rate in eastern white pine and hybrids, genetic improvement in resistance to the white pine weevil and white pine blister rust has so far been unattainable in eastern North America. In geographic seed source trials, weevil damage was usually heavy in trees from all sources. Although seed sources varied in the degree of weevil injury, there was no total resistance, i.e. complete absence of weevil attack, in trees of any origin (Garrett 1972). However, since a few geographic provenances have been identified that have low susceptibility to repeated weevil attack, selection within stands based on relative degree of susceptibility in provenance tests may be useful as a first step in a selection program (Genys 1981, Wilkinson 1981). Noncrystallization of cortical oleoresins, earlier thought to be a resistance factor (Santamour 1965, Van Buijtenen and Santamour 1972) was subsequently found to be unrelated to weevil susceptibility (Bridgen and others 1979, Wilkinson 1979a, 1979b). Later work indicated that the concentrations of two monoterpenes may be useful as selection criteria for reducing susceptibility to weevil attack (Wilkinson 1980).

Two other species of five-needle pines have been considered in breeding for resistance to the white pine weevil. One is *P. peuce*, which has variable resistance (Zsuffa 1979). Although it has a moderate growth rate, its weevil resistance and crossability with *P. strobus* suggests its use as the male parent in hybrids for the introduction of resistance into eastern white pine. The hybrids could then be backcrossed to *P. strobus* to improve the growth rate. The long-term nature of this option, with low yields of hybrid seed, makes it impractical. The second species is *P. monticola*, and in this case instead of hybridization the species would be used directly, since *P. monticola* appears to be more weevil-resistant than *P. strobus* (Heimburger 1972). But western white pine varies in vigor and adaptability in the eastern United States, necessitating local progeny testing of trees screened for weevil resistance. Since 1980, no studies have

been undertaken in the eastern USA to explore the feasibility of using hybrids or alternate species for weevil resistance. For a more detailed historical review of weevil resistance breeding, see Kriebel (1982).

Using Silviculture as an Alternative to Breeding

An alternative strategy to minimize weevil damage is particularly suitable for the northeastern and northern Lake States (Michigan, Wisconsin, Minnesota). It integrates genetics with silviculture by the planting of fast-growing selections of eastern white pine in a mixture or under an associated pioneer species such as aspen or birch, to provide partial shade for weevil protection. There are two possibilities. One is to allow the pine to overtop the short-lived aspen or birch, commonly in 20 years or less. The other is to remove the aspen or birch, if economically feasible, after the pine has developed one clear log that is free of weevil damage or nearly so. This is based on the weevil preference for trees growing in full sun over trees under shade or partial shade (MacAloney 1952, Ledig and Smith 1981).

Breeding For Rust Resistance

In the eastern USA, the white pine blister rust is a serious problem primarily in cool, humid regions, especially in the northern Lake States and the northeastern states. The rust is ubiquitous under these conditions and there are no reported unique populations that are threatened. The rust is not a problem in warm and dry localities within these regions and in low-elevation stands in the southern and southwestern parts of the range of *P. strobus*. Resistance appears to be polygenic in nature, thus requiring several generations of breeding to build up a practical level of resistance in offspring (Heimburger 1972). Artificial inoculation of eastern white pine alone does not accurately identify breeding stock suitable for field planting, since

progenies succumbing to high concentrations of inoculum may be tolerant to the levels to which they are actually exposed in the field. Blister rust hazard is not high in all regions of the northeastern US and Canada. In warm zones and in cool zones with large openings to the sky, resistant strains are not essential (Van Arsdell 1972, Zsuffa 1979). Interspecific hybridization with other more rust-resistant species of five-needle pines has so far not been an effective breeding strategy (Zsuffa 1981).

Given these constraints on breeding eastern white pine for resistance to the white pine blister rust, new technology is now being applied to the problem by the US Forest Service in forest genetics and forest pathology projects in the North Central Region. Objectives are: (1) to develop a better understanding of the genetic structure of tree and pathogen populations, using molecular markers; (2) to identify genes for important quantitative traits; (3) to develop micropropagation techniques for production of elite trees; and (4) to develop gene transfer technologies for introduction of novel genetic constructs. Plantations of self- and reciprocal-crosses of eastern white pine progenies are being established for studying the genetics of blister rust resistance. The blister rust program has the objectives of determining rust variation in the Lake States and comparing it with rust variation in the rest of North America, determining whether resistance can be reliably identified in inoculated seedlings at an early age and whether there is a race-specific component in seedling resistance. Although current work involves inoculation of seedlings from clonal parents, diallel crosses and selfs among selected parents have been made for future studies. Sugar pines (*Pinus lambertiana* Dougl.) with and without the MGR gene (Kinloch 2001) have also been included in each inoculation for detection of one form of race-specific virulence. Michler and Pijut have developed improved micropropagation technologies for eastern white pine, and Michler and Davis have isolated eastern white pine chitinase genes with the goal of developing efficient genetic engineering protocols for pines using constructs with pine promoters. Eastern white pine seedlings are currently being tested in greenhouse studies to determine stability of transgene insertion (Michler and Zambino, personal communications).

Integrated Management for Rust and Weevil Control

The feasibility of applying a silvicultural regime integrating management for growth, blister rust and weevil resistance is currently being studied in northern Wisconsin (Ostry 2000). Variables in the study include survival, height, rust infection and weeviling. Treatments include clearcut vs shelterwood, nonselected stock vs selected stock, and no pruning vs pruning. Age 10 analysis, although preliminary, showed that:

1. Height growth was greater in clearcut than in shelterwood plots.
2. Weevil attack was greater in clearcut than in shelterwood plots.
3. Blister rust infection was higher in shelterwood than in clearcut plots.
4. Selected planting stock outgrew nonselected stock.

5. Blister rust infection was higher in nonselected than selected stock.

6. Blister rust infection was higher in unpruned than in pruned trees.

Pruning of lower branches had double benefits, both in correcting stem form for weevil damage, and also by removal of the branches most susceptible to rust infection.

Genetics of Air Pollution Tolerance

Because of inherent sensitivity and geographical distribution in relation to industry, population centers and prevailing winds, eastern white pine has probably been more impacted by air pollution than any other tree species in eastern North America (Gerhold 1977). Karnosky and Houston (1979) reviewed the genetics of air pollution tolerance of eastern white pine in the northeastern US. White pines are sensitive to both SO₂ and O₃, but the interaction of these pollutants has more serious effects than either pollutant alone (Houston 1974). There is significant tree-to-tree variation that has a strong genetic component (Houston and Stairs 1973). The effect of this large genetic component has been natural selection against sensitive trees in native stands over a wide region of eastern North America, with losses to the gene pool that may have included linked genes of unknown biological or commercial value. It was estimated that in northern Ohio stands of *P. strobus*, more than 40 percent of the potential seed-bearing trees had dropped out of the breeding population. Only pollution-tolerant trees survive to produce seed, and progenies from stands in polluted regions were found to be almost totally free of air pollution injury while retaining the vigor of the parent stands (Kriebel and Leben 1981). Similar evidence of the inheritance of pollution tolerance was obtained from the progenies of healthy trees growing in Tennessee for many years under polluted conditions. The progenies had darker green needles than progenies from other southern Appalachian stands and were consistently faster-growing than others in three polluted areas in Tennessee and in Ohio (Thor and Gall 1978, Kriebel 1982).

As a result of this natural elimination of sensitive genotypes throughout the regions where eastern white pine is native and planted, SO₂ is not currently a serious problem. Ozone injury tends to be more localized and is primarily a problem where white pines are planted close to major highways with high emission levels from motor vehicles. However, the future effect of air pollution on eastern white pine is uncertain. Industrial emissions of SO₂ from coal-burning power plants in the midwestern states continue to have an impact on northeastern forest land and waters. Unless the currently inadequate emission controls in the midwestern region of the US are strengthened, increases in coal-burning power plant outputs may further affect the survival and growth of eastern white pine in the northeastern states.

Directions for the Future

The primary goal for future research on the genetics and improvement of five-needle pines in the eastern United

States should be the restoration of the superior position of eastern white pine as a high-quality timber tree. The most promising methods of achieving this goal through genetic research and its applications are the following:

1. Ecology, management and resistance screening can be integrated to achieve the objective of planting pest-free eastern white pine planting stock in regions where white pine blister rust and the white pine weevil are major deterrents to the commercial planting of this valuable native tree.

2. Existing older eastern white pine progeny tests can be converted into seed orchards for rapid gain from the use of open-pollinated seed of known parentage and proven potential. Seedlings from elite trees should be planted in rust-free areas at close initial spacing to minimize weevil damage. This procedure has already been applied in some progeny tests.

3. Weevil resistance should be incorporated into eastern white pine through genetic engineering to incorporate genes for insect resistance into the species. A program has already been initiated to develop the molecular technology that may make possible the introduction of weevil resistance into white pine.

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