GENETICS OF AIR POLLUTION TOLERANCE OF TREES IN THE NORTHEASTERN UNITED STATES

by David F. Karnosky, forest geneticist,
Cary Arboretum
Millbrook, N.Y. 12545

and

Daniel B. Houston, associate professor
of forest genetics, Department Forestry
Ohio AgriculturalResearch and Development Center
Wooster, Ohio 44691

ABSTRACT.--Air pollution is an important stress factor on trees growing in the northeastern United States. Because of the complexity of the air pollution problem, this area faces damaging levels of air pollution for many decades to come. Selecting and breeding for air pollution tolerant trees can be justified as a component of an overall air pollution mitigation strategy which centers on control of emissions. Studies of genetic variation in response of trees to air pollutants and of the genetic control of this response suggest that selecting and breeding for air pollution tolerance should be successful in several species of trees. Species which continue to be damaged by air pollution and for which tree improvement programs are needed to increase pollution tolerance include eastern white pine, Scotch pine, trembling aspen, green ash, and white ash. A summary is presented of programs in the Northeast that involved screening trees for air pollution tolerance and/or in selecting and breeding air pollution tolerant trees.

AIR POLLUTION IN THE NORTHEAST

Air pollution continues to be an important stress factor in the northeastern United States. Concentrations of suspended particulates, sulfur dioxide (SO2) and oxidants (primarily ozone (O_3)) frequently exceed federal air quality standards in much of the Northeast (Goldsmith and Mahoney, 1978). The complexity of the air pollution problem is demonstrated by the fact that rural as well as urban areas throughout the Northeast commonly have air pollution levels exceeding federal standards (Hosein et al., 1977; Stasiuk and Coffey, 1974). High levels of oxidant pollution in rural areas have been attributed to long-distance transport of oxidants or their precursors from urban areas (Cleveland et al., 1976, 1977; Hayes et al., 1977; Wolff et al., 1977) and to natural phenomena such as photochemical generation from naturally occurring precursors or transport of 03 from the upper to lower atmosphere (Stasiuk and Coffey, 1974). Long distance sulfur oxides transport from urban to rural areas has also been demonstrated (Altshuller, 1976).

The most damaging components of air pollution in the northeastern United States are oxidants, sulfur oxides and particulates. Sulfur dioxide and oxidants (primarily 03) probably cause more damage to woody plants than all other pollutants combined (Davis and Gerhold, 1976). It is relatively certain that the major air pollutants will continue to exert an influence on forest ecosystems in the Northeast for decades to come. Because of our continued extensive usage of the automobile with its related oxidant pollution and because of our need to increase usage of high-sulfur coal with its related SO_2 pollution, it is unlikely that substantial reductions in either oxidant or SO_2 pollution will occur in the Northeast for the remainder of the twentieth century. Smil (1975) speculated that sulfur oxides standards in the United States will not be met for the next 20 years.

Public reluctance to conserve or to participate in the costs of clean production of energy, as typified by the recent refusal of one Midwestern state government to comply with federal clean air standards, underscores the problem. Technology for scrubbing sulfur oxides from coal-burning industries has not progressed as rapidly as expected. Stack scrubbers are inefficient, expensive and unreliable for cleaning sulfur oxides. As a result, coal-burning power plants have turned to constructing higher stacks for dispersing wastes over wider expanses of land, thereby lowering ground level concentrations in the immediate vicinity of the power plants but doing little to lessen the overall sulfur oxides pollution problem in the Northeast.

TREES WITH AIR POLLUTION PROBLEMS IN THE NORTHEAST AND FOR WHICH IMPROVEMENT PROGRAMS ARE NEEDED

Eastern white pine (*Pinus strobus* L.) probably is subject to more air pollution injury than any other tree species native to eastern North America (Gerhold, 1977). Acute air pollution damage to eastern white pine was first found in the United States in stands covering thousands of acres near copper smelters in the "Copper Basin" of Tennessee. Severe air pollution injury was more recently reported near a munitions plant in Virginia (Skelly et al., 1972). Less dramatic but still important have been the pollutant effects on eastern white pine in both urban and rural areas throughout the Northeast. For example, an aerial survey of two counties of North Carolina revealed that eastern white pine foliage was injured over an area of about 112,640 acres with about 100 trees affected per square mile (Landgraf et al. 1969). Approximately ten percent of the eastern white pine trees throughout Pennsylvania were injured by one air pollution episode in 1972 (Nichols, 1972). A 1959 survey showed air pollution symptons occurring on about seven percent of the trees in 43 eastern white pine plantations in Ohio (Dochinger, 1960). Similar results were reported in Wisconsin (Prey, 1968), Virginia (Morris, 1973), Connecticut, Maine, Massachusetts, and New York (Lautz, 1977).

Damage to eastern white pine from air pollution includes foliar injury, growth reduction, and, in severe cases, death. The suitability of the species for Christmas trees, in particular, suffers, as the readily visible foliar injury reduces market value (Dochinger, 1973). An out-of-court settlement of nearly $450,000 was paid to Christmas tree growers in 1972 for white pine damage alleged to have been caused by air pollutants from a power generating station (Edwards, 1972) and litigation is pending in additional cases (Gerhold, 1977). Clearly, pollutant injury to eastern white pine has very substantial economic implications for the air-pollution-emitting industries in the Northeast and for the nation's economy as a whole.

While air pollution damage to eastern white pine has been more prevalent than damage to any other tree species, significant air pollution problems have been found with other species as well (e.g., Scotch pine). Broad-leaved trees are, in general, more tolerant of air pollution than are evergreen trees. However, there are some exceptions such as trembling aspen (*Populus tremuloides* Michx.) which is very susceptible to both O_3 and SO_2 (Davis and Wilhour, 1976; Karnosky, 1976) and green ash (*Fraxinus pennsylvanica* var. *lanceolata* (Borkh.) Sarg.) and white ash (*Fraxinus americana* L.) which are highly susceptible to O_3 (Davis and Wilhour, 1976; Wilhour, 1970). Injury to these and other broad-leaved trees has been reported near oil refineries (Linzon, 1965), smelters (Gordon and Gorham, 1963; Scheffer and Hedgcock, 1955), and paper mills (Linzon *et* al., 1973). In addition, considerable concern has arisen regarding the effects of air pollutants on trees growing in urban areas. Townsend and Dochinger (1974) have stated that air pollution damage to shade trees is widespread and increasing in economic and biological importance. A recent survey by Brennan and Rhoads (1976) was conducted to examine the effects of air pollutants on trees in New Jersey. Damage to many species by hydrogen fluoride, oxidants, and particulates was found.

GENETIC CONTROL OF AIR POLLUTION TOLERANCE

Evidence from field observations in highly polluted areas as well as from controlled-environment fumigation studies suggests that there is substantial variation in response of forest trees to air pollutants. Reports of inter- and intraspecific variation in response of trees to air pollutants have been summarized by Gerhold (1977), Houston (1976), and Karnosky (1974). This variation appears to have a strong genetic component. Dochinger and Seliskar (1965), Costonis (1970), and Houston (1974) have all shown that selections for air pollution tolerance in eastern white pine retain their relative tolerance or sensitivity when grafted onto nursery rootstock. These responses suggest that tree-to-tree variation in air pollution sensitivity is controlled by inherited factors.

The extent of genetic control of variation in response to air pollutants has been quantitatively estimated for only a few species. Houston and Stairs (1973) obtained clonal repeatability estimates of 0.51 to 0.82, demonstrating that the response to SO_2 plus O_3 exposures is under strong genetic control in eastern white pines.

Thor and Gall (1976) reported narrow-sense heritabilities of 0.64 for needle color and 0.32 for needle length in eastern white pine progeny tests in the vicinity of SO_2-emitting power plants in Tennessee. Trees from seed collected in stands located in high-SO_2 areas grew faster, had less needle discoloration, and had longer needles than did trees from seed collected in nonpolluted areas. North Carolina State University's fume damage studies indicated narrow-sense heritabilities as high as .27 for susceptibility of loblolly pine (*Pinus taeda* L.) to O_3 (Weir, 1976). Substantial dominance type genetic variance was also found to exist. Demeritt and Gerhold (Unpublished manuscript) found narrow-sense heritabilities in the range of .1 to .3 for O_3 tolerance of Scotch pine as calculated on an individual tree basis. In one of few studies dealing with hardwoods, Karnosky (1977) found clonal repeatability estimates of 0.46 to 0.64 for response to fumigations with SO_2 and O_3, alone and in combination. These studies all suggest that there is strong genetic control of air pollution tolerance and that selection and breeding efforts to develop air pollution tolerant trees will be effective.

NEEDS FOR DEVELOPING AIR POLLUTION TOLERANT TREES

In his recent EPA-sponsored review of the effects of air pollution on eastern white pine, Gerhold (1977) emphasized that research should shift from extending knowledge about pathological effects of air pollutants to actually protecting trees from excess damage through development of pollution tolerant trees. Among tree breeders this is a controversial issue because many researchers feel that we should concentrate on cleaning up the sources of pollution rather than on breeding pollution tolerant plants. However, given the (1) increasing energy demands, (2) intensifying energy crisis and the concomitant increasing dependence on high-sulfur coal, (3) tremendous costs and technological difficulties involved in abating air pollution at its sources, and (4) public reluctance to conserve energy or to assume the costs of reducing or abating pollutants in the production of energy, it is likely that the major air pollutants will continue to damage large numbers of trees in this country for many decades to come. Selecting and breeding varieties with improved air pollution tolerance cannot substitute for controlling emissions, but they can be justified as components of an overall air pollution mitigation strategy (Gerhold, 1977). In fact, controlling emissions of pollutants and breeding resistant trees may be the two best simultaneously compatible means to protect air pollution sensitive trees such as white pine from air pollution damage.

The Europeans have long recognized the value of breeding air pollution tolerant trees. Selection and breeding programs were started in West Germany some 20 years ago for Norway spruce *(Picea abies* (L.) Karst.) and Scotch pine (Rohmeder and von Schonborn, 1965; Wentzel, 1967) and in East Germany for larches and other species (Polster et al., 1965).

There are needs for selection and breeding work to develop air pollution tolerant trees in several tree species in the United States. For example, given (1) the economic importance of eastern white pine to the forest, landscape, and Christmas tree industries in the Northeast, (2) the extent of damage to the species caused by air pollutants, and (3) the large amount of intraspecific variation in eastern white pine's response to air pollutants, eastern white pine warrants a program of selection and breeding for air pollution tolerance.

There is also a need to preserve specimens of the eastern white pine population which are sensitive to air pollution. These individuals make up anywhere from 5 to 25% of the population and this significant proportion of the population will be lost without a concerted effort to save these genotypes. These sensitive trees are rapidly being lost from native populations because they cannot compete with faster-growing, pollution-tolerant trees which dominate eastern white pine stands. Sensitive trees have value as bioindicators of air pollution, and they may also contain valuable genes for pest resistance, growth rate (given clean-air conditions), form, or wood properties.

Selection and breeding for air pollution tolerance can also be justified in species such as trembling aspen, white ash, and green ash which are known to be very air pollution sensitive. In addition, there is a need to provide additional information as to the relative pollution tolerances of the most commonly planted urban trees. This point was highlighted in a recent survey by Gerhold and Steiner (1976). Arborists rated information on air pollution resistance over increased information on survival, tolerances to deicing salts, maintenance problems, and several other tree problems as their greatest need.

PROCEDURES FOR DEVELOPING AIR POLLUTION TOLERANT TREES

Procedures for developing varieties of pollution tolerant forest trees have been proposed by several authors in recent papers (Ryder, 1973; Karnosky, 1974; Gerhold, 1977). Houston (1976) and others have suggested utilizing existing tree genetics and improvement programs as a basis for such programs. Parent populations from which selections could be made are already in existence in the form of numerous progeny and provenance tests. These tests, as well as thousands of acres of Christmas tree plantations for a number of conifer species, provide favorable conditions of even age and site uniformity under which performance of individuals, families, and populations may be judged.

Selection may be accomplished in many ways, and depends on the ability to distinguish between tolerant and sensitive genotypes. While the safest technique may be to select healthy-appearing trees which have been subjected to repeated pollution exposures in the field, this approach has limitations. In most instances, trees are subjected to a mix of pollutants, rather than a single gas, some of which may mimic symptoms of the pollutant(s) of primary interest. In addition, Berry (1973) has demonstrated that trees tolerant to one pollutant may be sensitive to another. Without long-term, on-site monitoring of air pollutants, testing of selections in subsequent fumigation trials using clonal materials, needle fascicles, leaf discs, etc., appears necessary to verify tolerance under controlled conditions.

Improved methods are needed to increase the efficiency and reliability of selection techniques if improvement programs are to deal with the large numbers of individuals necessary for the development of tolerant populations. Fumigation of large numbers of seedlings in nursery beds or greenhouse chambers offers one solution to this requirement for maintaining a broad genetic base in such a program. High selection intensities could be achieved by this method, and hopefully an increased rate of genetic gain in tolerance realized. The uncertainty inherent in this approach is that it presupposes that tolerance will not vary with tree age. This assumption has not been adequately tested. Short-term fumigation tests followed by long-term field tests in areas with known air pollution problems are needed. These comparison tests are necessary to determine if

(1) the use of short-term selection tests in nursery beds or greenhouse chambers are adequate for selecting pollution tolerant individuals and (2) if the early-age testing is a valid indication of a tree's response to air pollution in later years.

Identification of biochemical markers and physiological responses which are correlated with tolerance may prove to be a more promising selection approach. Studies by Dr. Daniel B. Houston at the Ohio Agricultural Research & Development Center, as described in the next section, suggest that certain biochemical markers and responses may have utility as selection criteria in programs to improve SO_2 tolerance in eastern white pine.

The apparent strong genetic control of tolerance in several species (Karnosky, 1976, Weir, 1976, Houston and Stairs, 1973) indicates that selection and breeding efforts will be effective. Given the lack of knowledge regarding tolerance inheritance patterns, initial mating schemes should include crosses between proven tolerant x tolerant, tolerant x sensitive, and sensitive x sensitive genotypes, followed by testing of resultant progenies under controlled fumigation regimes and in field plantings. The two latter types of crosses may not be possible in some species (e.g., white pine) as the reduced vigor of very sensitive trees generally precludes flowering. Established seed orchards might be used for such a crossing program. Even if breeding work is not to be done, seed with some degree of improved tolerance could be collected from seed orchard clones selected as tolerant based on biochemical or other criteria.

Depending on program direction, objectives, and species, it may be desirable to emphasize the production of tolerant clones for use in interim planting programs in high risk areas, or even in lieu of sexually reproduced tolerant varieties.

PROGRAMS TO DEVELOP AIR POLLUTION TOLERANT TREES

The forest genetics program at the Cary Arboretum of the New York Botanical Garden has two ongoing research projects aimed at developing air pollution tolerant trees.[1] These projects are under the direction of Dr. David F. Karnosky. The first project is designed to test the relative tolerances of some commonly planted shade tree cultivars (Karnosky, 1978). Thirty-two cultivars of Acer, Fagus, Fraxinus, Ginkgo, Gleditsia, Platanus, and Quercus species have been tested for their response to 7 hr. fumigations with 0.5 ppm O_3 and 1.0 ppm SO_2, alone and in combination. *Platanus acerifolia* (Ait.) Willd. "Bloodgood" and *Fraxinus americana* "Autumn Purple" were sensitive to all three exposures. Cultivars tolerant to all three exposures were *Acer platanoides* L. "Crimson King" and "Summershade", *Acer rubrum* L. "Red Sunset", *Acer saccharum* "Temple's Upright", *Fagus sylvatica* "Rotundifolia", and *Ginkgo biloba* "Sentry". Trees of the same cultivars have been outplanted at four test sites in and around New York City as a follow-up field test of the air pollution tolerances. First-year results from the field test showed that oxidant stipple was the most common type of pollutant injury at each test site. *Platanus acerifolia* "Bloodgood" has been the most sensitive cultivar in the field test.

The second project underway at the Cary Arboretum began recently and involves provenance tests of air pollution tolerance for white ash and green ash. A total of 1000 2-year-old white ash seedlings representing 10 provenances with 5 families per provenance have been tested for their SO_2 and O_3 tolerances. Similarly, some 1300 2-year-old green ash seedlings representing 16 provenances with 4 families per provenance have been tested for their SO_2 and O_3 tolerances. These plants will be fumigated again next year with combinations of the two pollutants. The purpose of this project is to compare the various components of variation in response to air pollutants and to select tolerant individuals, families and/or provenances for further study in follow-up field tests.

Work during the last two years in Dr. Daniel B. Houston's laboratory at the Ohio Agricultural Research and Development Center has investigated the biochemical and physiological responses of eastern white pine to SO_2 in studies examining the mechanisms for intraspecific variation in air pollution tolerance. Some 120 white pine clones selected as being tolerant or sensitive to low concentrations of SO_2 have been studied to date. The initial work has been carried out by Robert T. Eckert and D. B. Houston in cooperation with L. S. Dochinger of the U.S.D.A. Forest Service, Northeastern Forest Experiment Station at Delaware, Ohio. The goals of this study, and additional work with Scotch pine and white ash, are to: (1) investigate the biochemical and physiological mechanisms operative in the tolerance of these species to SO_2, and (2) assess various biochemical parameters for their usefulness as selection criteria for SO_2 tolerance.

The approach was to utilize low concentrations of SO2 (5 pphm for 2 hours) to study response in visibly uninjured tissue. Subsequent comparisons of tolerant and sensitive responses at both pre- and post-sampling times helped to determine the utility of a number of biochemical measures in selecting for tolerance, as well as indicating which parameters would be fruitful for further, more intensive study.

Responses were characterized for the following characters:

1. photosynthesis
2. simple and polyphenolics
3. monoterpenes
4. peroxidase and acid phosphatase isozymes and total activity.

Photosynthesis rates in sensitive clones were depressed to a greater extent ($\bar{x}$ = 36%) than in tolerant clones ($\bar{X}$ = 14%); however, rates in both classes were depressed significantly below control levels. Qualitative differences were found to exist between sensitive and tolerant white pine in both simple and polyphenols. Thin-layer chromatographic patterns of response to fumigation were different for each class in that phenolic compounds influenced by fumigation were located at different R_f positions than those which differed between classes. Differences in frequencies of phenolic compounds and differing patterns of response to fumigation suggest natural selection is effectively producing separate populations within eastern white pine in response to pollution stress.

Monoterpenes (from stem cortical oleoresin) did not discriminate between sensitivity classes or between control and fumigated clones. Needle monoterpenes may prove to be more useful.

Acid phosphatase isozyme and total activity assays of tissue extracts also suggested the existence of population differentiation in response to pollutant stress. Frequencies of three isozymes showed significant dependence on sample time following fumigation, while two isozyme frequencies varied significantly according to sensitivity class. Total activity assays indicated that activity in sensitive foliage is depressed up to 24 hours after fumigation, while such depression does not occur in tolerant foliage. Comparison of peroxidase isozyme frequencies indicated that discrimination of tolerant and sensitive classes is not possible using this parameter. However, total enzyme activity was 63 percent higher in sensitive controls than in tolerant controls, and averaged 29 percent higher in sensitive clones over all sampling times following fumigation. Data trends suggest that the peroxidase system may be induced to a small degree in tolerant trees but not in sensitive trees.

Study of these few biochemical parameters indicates that foliar peroxidase activity and certain simple and polyphenols may be useful for screening materials for tolerance to SO_2 injury. Future studies will concentrate on these and other parameters to verify their utility as tolerance markers, and to elucidate more fully the mechanisms of tolerance to SO_2 in eastern white pine, as well as in Scotch pine and white ash. Finally, reliable indicators will be incorporated into selection functions suitable for use in improvement programs. Additional questions need to be addressed:

(1) What is the relationship between juvenile and mature biochemical responses in forest trees to pollutants of interest.

(2) What are the responses of the tested enzyme systems (as well as others) to low concentrations of other pollutants, especially O_3 and mixtures of O_3 and SO_2.

(3) What are the correlations between markers and other important characters.

(4) What are the implications of depressed photosynthetic rates caused by SO_2 in terms of growth rates and production. We have also found that final needle lengths were reduced by even a two-hour fumigation at 5 pphm SO_2. Differences between control and fumigated needles were not statistically significant, but all fumigated needles were shorter, with the greatest reduction occurring in sensitive clones. Reductions in photosynthetic area coupled with depressed rates of photosynthesis may have great significance when considering wood production on a per acre and ecosystem basis.

There have been several air pollution screening projects at Pennsylvania State University. In one of the first programs aimed at developing pollution tolerant trees in this country, Dr. Henry D. Gerhold's group began screening Scotch pine progenies for tolerance to O_3 and SO_2 over 10 years ago (Gerhold and Palpant, 1968). More recently, Dr. Donald D. Davis' laboratory has studied the relative ozone sensitivities of over 50 species and/or cultivars of trees, shrubs, and vines (Davis and Coppolino, 1974, 1976; Davis and Wood, 1972; Gesalman and Davis, 1976).

Dr. Eyvind Thor's group at the University of Tennessee has been actively involved in selecting and testing for air pollutiontolerance in eastern white pine near TVA's coal-fired power plants. Other air pollution screening projects in the Northeast have been completed by Dr. Alden M. Townsend at the USDA-ARS laboratory in Delaware, Ohio (Townsend, 1974; Townsend and Dochinger, 1974), by Dr. Frank S. Santamour at the U.S. National Arboretum (Santamour, 1969), by Drs. Eileen Brennan and Ida Leone at Rutgers University (Brennan and Leone, 1970), and by Dr. Keith Jensen at the USDA Forest Service Laboratory in Delaware, Ohio (Jensen, 1973; Jensen and Masters, 1975).

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FOOTNOTES

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