# GENETIC VARIATION FOR AIR POLLUTION TOLERANCE

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Abstract.--Evidence of natural selection for air pollution tolerance can indicate that populations of plants are being affected by air quality. Data suggesting that ambient levels of sulfur dioxide resulted in natural selection for tolerance to this pollutant were published in the 1970s, but evidence for a similar effect by ozone has been lacking. We have demonstrated differences in apparent susceptibility to ozone among populations of quaking aspen from areas that differ in air quality. In several of our chamber fumigation studies, populations from areas with relatively high concentrations of ozone tended to show less injury than those from areas with relatively low concentrations of ozone. Subsequent field studies indicated that the clones with the most visible injury grew slowest at doses of ozone typical of relatively polluted areas. Quaking aspen is very intolerant of shade which suggests that ambient levels of ozone in conjunction with intraspecific competition is eliminating ozone-sensitive clones in areas with relatively high levels of ozone.

## INTRODUCTION

Man's activities are changing the chemical composition of the atmosphere and will continue to do so in the future. These changes have the potential to affect the growth and development of plants. Some of these changes can be expected to result in natural selection for traits that confer resistance to stresses they cause. We have chosen to restrict the scope of this discussion to the effects of changes in sulfur dioxide and ozone concentrations. These gases have always existed in the troposphere at some concentration, but their levels today are determined largely by man's activities. These two gases differ markedly in the pattern of changes in their concentration, in their effects on the physiological processes, and in the scale at which they are important.

## SULFUR DIOXIDE
## A HISTORICALLY IMPORTANT LOCAL POLLUTANT IN THE UNITED STATES

Smelters are the major source of sulfur dioxide, but coal-burning electrical-generating facilities also produce significant quantities of this pollutant (Heck 1984). Emissions of this pollutant in the United States more than doubled between 1900 and the late 1930s and tripled by 1970. In 1970

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the U.S. Congress passed the original version of the Clean Air Act which initiated a major decrease in sulfur dioxide emissions. This decrease has been sustained for more than 20 years in spite of continued increases in coal consumption (NAPAP 1987).

Sulfur dioxide enters leaves of plants primarily through stomata. This pollutant causes relatively little damage as it passes through cell membranes (Mudd et al. 1984) and it is assumed that the primary mode of injury is through its affect on metabolic pathways inside the cell. There is no doubt that sulfur dioxide can reduce photosynthetic rates, but there is some question about the mechanism of this response (Hallgren 1984). Exposure to low concentrations of sulfur dioxide for a long time can have as much effect as exposure to a high concentration for a short time. Thus, evaluating the effects of an exposure to this, or any other pollutant requires knowing at least the concentration of the pollutant and the duration of the exposure. However, it is generally recognized that the exposures to sulfur dioxide that are required to cause foliar symptoms (e.g. Karnosky 1976) or growth reductions (e.g. Jensen and Dochinger 1979) in trees are considerably higher than those that occur in most rural parts of the United States today.

Primitive smelters once emitted large concentrations of sulfur dioxide close to the ground and caused catastrophic damage to natural populations. Early studies showed ecosystem impacts near these sources (Gordon and Gorham 1963, Scheffer and Hedgcock 1955), but smelters of this type have not existed in this country for many years. Up until the 1970s, a number of smaller point sources of sulfur dioxide existed in this country that, while they are not large enough to devastate the landscape, were large enough to cause foliar injury and reduced growth on some plants in their vicinity. Since the concentrations of sulfur dioxide being produced in the United States are now lower and spread over a much broader area, phytotoxic concentrations of this pollutant in its gaseous form are rare today. However, some excellent research was done on the genecological effects of sulfur dioxide in this country in the past and is still being conducted in some European countries today. In many cases comparable studies have not been conducted with ozone, so this work should be included in any discussion of the genecological effects of air pollutants.

If natural selection for air pollution tolerance has been occurring, populations in areas exposed to elevated levels of the pollutant should be more tolerant than populations in pristine areas. There is ample evidence to suggest that this is the case for herbaceous plants and sulfur dioxide tolerance. Taylor and Murdy (1975) showed that Carolina cranesbill (*Geranium carolinianum* L.) collected from populations within a kilometer of a large coal-fired electrical facility in Georgia were more tolerant of sulfur dioxide than plants collected from populations that were further away. Horsman et al. (1978) showed that perennial ryegrass (*Lolium perenne* L.) collected from populations in parts of the United Kingdom with high concentrations of sulfur dioxide were more tolerant of this pollutant than plants collected from populations in areas with lower concentrations of sulfur dioxide. Bell et al. (1982) obtained similar results for the effects of ambient levels of sulfur dioxide on a variety of grasses.

Although air pollution resistant genotypes can outcompete sensitive genotypes in a relatively polluted environment, they may be at a competitive disadvantage in a pristine environment. Wilson and Bell (1985) found that the frequency of sulfur dioxide-resistant genotypes in grasses increased significantly within four years after exposure to high concentrations of this pollutant were initiated. However, they also found that the frequency of sulfur dioxide-resistant genotypes started to decrease within three years of the time improvements were made in ambient air quality. Other researchers (Horsman etal. 1978) have not been able to verify these results.

The length of time between generations suggests that populations of trees would require more time to respond to air pollutants than populations of herbaceous plants. There are numerous reports that indicate there is substantial genetic variation for sulfur dioxide tolerance within populations of tree species (e.g. Bergman and Scholz 1985, Geburek et al. 1987, Karnosky 1977, and Karnosky and Steiner 1981). It is not unusual for researchers working with visible symptoms of sulfur dioxide injury to report that one clone or family shows five to ten times as much injury when exposed to the same amount of this pollutant as another clone or family from the same provenance. The large amount of genetic variation within populations coupled with the variation in ambient concentrations of sulfur dioxide around point sources suggests that there is potential for natural selection for sulfur dioxide tolerance in trees.

There is also a great deal of evidence to indicate that substantial genetic variation in sulfur dioxide tolerance exists among populations of tree species (e.g. Karnosky and Steiner 1981, Karpen 1970, Larsen et al. 1988, Oleksyn 1988, Vogl 1970). In spite of the extensive documentation of genetic variation for this trait, only a few researchers working with trees have reported evidence that suggests an association between sulfur dioxide tolerance of populations and ambient levels of this pollutant. Thor and Gall (1970) reported that when white pine Pinus strobus L. grown from seed collected near coal-burning steam plants were planted near point sources of sulfur dioxide, they appeared greener than those collected from other areas. Kriebel and Leben (1981) reported that white pine grown from seed collected in parts of the midwestern United States with presumably low levels of sulfur dioxide showed less injury than those collected in the eastern portions of the country when planted in polluted areas in Ohio.

A number of European researchers have evaluated genetic differences between sulfur dioxide resistant and sensitive individuals within tree species using isozyme analysis. Geburek et al (1987) found that within a single population of Scots pine (Pinus sylvestris L.), resistant individuals tended to be more heterozygous at a suite of nine electrophoretically detectable gene loci. Muller-Stark (1985) reported similar data for a population of European beech (Fagus sylvatica L.) showing extensive damage from an unknown stress. Bergman and Scholz (1985) reported that several alleles were rare, or in one case missing, from sulfur dioxide resistant individuals of Norway spruce (Picea abies (L.) Karst.) and suggested that certain rare alleles are being eliminated from natural populations by air pollutants.

# OZONE
## A REGIONAL POLLUTANT THAT AFFECTS PLANTS AT AMBIENT CONCENTRATIONS

Tropospheric ozone is a secondary pollutant. This means that it is not emitted directly by man's activities, but instead is formed in the lower atmosphere from other pollutants. Formation of this pollutant is a complex process, but involves nitrogen oxides and hydrocarbons reacting in the presence of sunlight to form ozone (Grennfelt and Schjoldager 1984). Nitrogen dioxides are produced primarily by electrical generating facilities and motor vehicles. The major man-made sources of hydrocarbons are transportation related (Heck 1984), but biogenic sources of these compounds, particularly conifers, produce two to three times as much hydrocarbons as anthropogenic sources in the United States. This has made it especially difficult to decrease ambient levels of ozone in the Southeast (Chameides 1988) where high temperatures, long growing seasons, and extensive pine forests predominate.

Because of the way ozone is formed, its spatial and temporal distribution is much different than that of sulfur dioxide. Since it is a secondary pollutant it is often formed some distance from where the primary pollutants are emitted. This tends to make ozone a problem in rural as well as urban areas (Lefohn and Jones 1986). Nationally, the highest concentrations of ozone are found in southern California, but elevated concentrations of ozone exist throughout much of the eastern United States (Vukovich et al. 1985). One consequence of the regional nature of this pollutant is that sites that differ significantly in ozone exposure are separated by long distances.

Ozone concentrations fluctuate annually and tend to be highest during the summer (Lefohn and Jones 1986). This is because more natural hydrocarbons are produced during the growing season and because temperatures are higher and sunlight is more intense. Ozone levels differ from day to day at any one location with the highest concentrations occurring when there are several consecutive days with high temperatures, intense sunlight, and stagnant air masses. At low elevations there is a great deal of diurnal fluctuation in ozone concentrations. Concentrations are relatively low in the morning, increase by a factor of three (or more) in early afternoon, and decrease gradually during the evening and night. These diurnal fluctuations are diminished at high elevations where ozone concentrations can remain high throughout the night (Berry 1964).

The degree of temporal fluctuation in ambient ozone concentrations makes it difficult characterize the amount of ozone that populations in different areas receive. The traditional method for describing ambient ozone levels is the growing season mean measured during either 7 hour (e.g. Heck et al 1984) or 12 hour days (e.g. Heagle et al. 1988). There is a limited amount of data (Musselman et al. 1983) that suggests the occasional high concentrations are more important in determining the response of plants to ozone than the seasonal mean concentration. For these reasons researchers often provide a measure of acute exposure to ozone; for example, the highest hourly average or the highest daily average (e.g. Heagle et al. 1988). More recently, Lefohn etal. (1988) have advocated the use of several other parameters such as the number of occurrences above some critical concentration (e.g. 8 ppb), the total of ppm x hours for all concentrations above some critical concentration, or the sum of ppm x hours for all concentrations after weighting by a sigmoidal function that gives greater weights to the higher concentrations.

Since ozone enters leaves almost entirely through the stomata, stomatal conductance determines its rate of uptake (Reich 1987). The membranes of plant cells are one of the first sites of injury. Ozone has been shown to increase the permeability of both the plasma membrane and chloroplast membranes (Mudd et al. 1984). One of the first measurable responses to small increases in ozone levels are reductions in photosynthesis. Reich and Amundson (1985) reported decreases in rates of photosynthesis in several species of northern hardwoods and white pine. Sasek and Richardson (1989) have reported that rates of photosynthesis are also reduced in loblolly pine at twice the ambient concentrations of ozone in North Carolina. Dougherty and Teskey (personal communication from Phil Dougherty and Robert Teskey of the Un. of Georgia in 1990) have found reductions in photosynthesis in loblolly pine after two years exposure to ambient levels of ozone in Georgia.

These differences in photosynthesis can result in measurable decreases in growth, even under field conditions. Shafer and Heagle (1989) predicted using models constructed from data collected on loblolly pine (Pinus taeda L.) that the ambient levels of ozone in North Carolina would reduce growth rates by about 10% after two to three seasons of exposure. Wang et al. (1986) reported similar reductions in biomass of quaking aspen (Populus tremuloides Michx.) after three years exposure to ambient levels of ozone in New York State. In some cases the effect of ozone on the growth of plants is more evident on the root system than it is on the above-ground portion of the plant. This effect is especially important in perennial plants like trees (Cooley and Manning 1987).

The small size of some herbaceous plants makes it possible to expose entire communities to controlled doses of ozone. Researchers working with these plants have demonstrated that ambient levels of ozone can alter the species composition of communities. Rebbeck et al. (1988) showed that while clover (Trifolium repens L. c.v. Regal) dominated a field-grown pasture in North Carolina that was exposed to charcoal-filtered air, tall fescue (Fescue arundinacea Schreb. c.v. Kentucky 31) dominated the same pasture when it was exposed to ambient and above-ambient levels of ozone. Bennett and Runeckles (1977) reported similar results for a pasture in California. Demonstrating an ecological effect of ozone is considerably more difficult in forests because of the large size and perennial nature of the individual plants. The classic example of an ozone-induced ecological change in forests is the shift from ponderosa pine to white fir (Abies concolor Lindl. and Gord.) in southern California. Miller (1973) was able to document these effects, in part, because extremely high concentrations of ozone made visible symptoms of injury obvious. On some occasions the concentrations of ozone in these forests were more than four times the current National Ambient Air Quality Standard of 120 ppb. It has turned out to be considerably more difficult to demonstrate community-level changes in forests in other parts of the country where concentrations of ozone are much lower.

Ozone tolerance is known to be genetically controlled within a number of tree species. Karnosky (1977) demonstrated genetic differences in tolerance within populations of quaking aspen and Karnosky and Steiner (1981) reported differences within and among populations of green and white ash for this trait as well. A number of researchers have shown that ozone sensitivity is genetically controlled in loblolly pine (Adams et al. 1988, Horton et al. 1990, and Kress et al. 1982) and white pine (Berry 1973 and Houston and Stairs 1973).

## ELIMINATION OF OZONE-SENSITIVE GENOTYPES EVIDENCE OF A LATENT EFFECT?

We feel that in some cases the more obvious ecological effects of ozone; for example, changes in species composition, are being masked by the subtle changes that can occur within populations of a single species. Data that show plants collected from populations in high ozone areas are more tolerant of this pollutant than plants collected from populations in pristine areas provide evidence to support this hypothesis. Dunn (1959) showed that lupine (Lupinus bicolor) grown from seed collected in Los Angeles had less foliar injury when grown in Los Angeles than lupine grown from seed collected in other areas. Although air quality monitoring data was not available for this study, ozone has historically been a major constituent of the smog in this city. We have conducted a series of experiments designed to determine whether this type of relationship exists for quaking aspen. This species was chosen because it is sensitive to ozone (Karnosky 1977), its natural distribution is large enough to include areas that differ in air quality, and it can be clonally propagated.

In 1983 we collected roots from 11 to 14 individuals in each of 5 natural populations of this species. These 5 populations were all in northeastern United States and included areas that differed in ambient ozone levels (Table 1). These root samples were clonally propagated and grown in a single greenhouse. The plants were exposed to 180 ppb ozone for 6 hours using an open-top chamber inside a greenhouse. One week after the fumigation we evaluated each plant for the percentage of leaves showing symptoms of ozone injury and the average surface area of the symptomatic leaves showing symptoms (Berrang et al. 1986).

Differences in ozone sensitivity among clones within populations were highly significant in all five populations. More importantly, there were large differences among populations as well. The average injury for clones was significantly less for the most polluted collection site than for the least polluted collection site and there was a negative correlation ($r = -0.98$) between average injury and ambient ozone levels (Table 1). We suggested that high ambient levels of ozone had eliminated ozone-sensitive clones from the population in the polluted area.

Other researchers offered a number of valid criticisms of this work. First, the ozone concentrations used were higher than those that commonly occur in northeastern United States and might not be relevant to field conditions. Second, since only a few collection sites were involved, the

Table 1 - Ambient ozone levels, average percentage of leaves injured, and ranges of clonal means for five populations of quaking aspen exposed to 180 ppb ozone for 6 hr in a chamber fumigation and to ambient air in a field planting near Millbrook, New York.

| | | Percentage of leaves showing injury | | | |
|---|---|---|---|---|---|
| | | Fumigation | | Field | |
| Population origin | Average ozone concentration | Population means | Range of clones | Population means | Range of clones |
| Cuyahoga Valley NRA<br>Ohio | 65 ppb | $50_{a}$ | 21-63 | $0_{a}$ | 0-2 |
| Saratoga NHP<br>New York | 49 | $58_{ab}$ | 35-83 | $3_{b}$ | 0-12 |
| Acadia NP<br>Maine | 52 | $60_{ab}$ | 22-84 | $4_{b}$ | 0-18 |
| Voyageurs NP<br>Minnesota | 26 | $71_{bc}$ | 60-88 | $22_{c}$ | 2-40 |
| Isle Royale NP<br>Michigan | 14 | $75_{c}$ | 58-88 | $23_{c}$ | 0-48 |

Note: Numbers within columns are not significantly different at $P < 0.05$ as determined by Student-Newman-Keuls test for fumigation data or at $P < 0.1$ as determined by Dunn's non-parametric mean separation procedure for field data.

apparent association between ambient ozone and ozone tolerance might have been spurious. Third, the collection sites were widely separated and differences between sites in rainfall or temperature might be responsible for differences in ozone tolerance. Fourth, we did not show a relationship between visible injury and growth which should exist if ozone can eliminate sensitive clones. We have responded to each of these points in subsequent studies.

We established a plantation of this material about 100 km north of New York City in an area that experiences relatively high levels of ozone. There was considerably less injury in the field than there had been after fumigations, but the relative differences among the populations were the same (Table 1). This study also suggested that variation within populations was affected by ambient ozone. The amount of injury displayed by the least-injured (most tolerant) clone in each population was about equal, but there was a strong negative correlation (r= -0.99) between ozone concentrations at the population collection area and the the amount of injury displayed by the most-injured (least tolerant) clone (Berrang et al. 1989).

We conducted another fumigation experiment with clones from 15 populations of quaking aspen that spanned the entire United States (Table 2). The results were similar to our first study. Differences among populations were statistically significant and ozone-tolerant populations were usually found in the areas with the highest maximum daily ozone concentrations. Populations from areas that met the Environmental Protection Agency's Ambient Air Quality Standard for ozone (i.e. had low levels of ozone) had significantly more injury than populations from areas that did not meet this standard. In spite of the close association between maximum daily ozone concentrations and visible injury, there was no relationship between seasonal average ozone concentrations and visible injury. Evaluation of the air quality data revealed that there was also no relationship between seasonal average ozone concentrations and maximum daily ozone concentrations. This suggests that there can be a very close relationship between the type of ozone exposure a population evolves under and the type of ozone exposure to which the population will be resistant (Berrang et al. 1991).

We also found an association between climatic variables and ozone tolerance in this study using rank correlation. Leaf injury was negatively correlated with both minimum annual temperature (r = - 0.66, P = 0.01) and annual precipitation (r = -0.50, P= 0.06). Perhaps the large amount of precipitation at Crater Lake helps explain why this population was more ozone tolerant than would be expected based on the presumably low levels of ambient ozone at its origin. This relationship between climatic variables and injury does not negate the relationship between ozone and injury. Partial correlation revealed there was a significant relationship between ambient ozone and some measures of ozone injury even when the effects of precipitation and temperature are taken into account (Berrang et al. 1991).

There seems to be a good relationship between visible injury determined under our test conditions and growth in the field for this species. Two sensitive clones and one resistant clone from Karnosky's 1977 study of genetic differences in ozone tolerance were established in the same field in New York described earlier. After ten years growth in this high ozone environment, the resistant clones were about twice as as tall as the sensitive clones (Berrang et al. 1989). Eighteen clones identified as sensitive and 18 identified as tolerant based on visible injury were established in open-top chambers in the field in Michigan in 1989. When exposed to chronic levels of ozone (80 ppb for 6 h/day for 3 days/wk) there was no reduction in stem biomass for the ozone-tolerant clones, but the growth of ozone-sensitive clones was reduced by 46%. It is also interesting to note that the sensitive clones outgrew the tolerant clones in charcoal-filtered air, suggesting that there may be a cost associated with ozone tolerance that makes these clones less competitive in a pristine environment (Karnosky and Scholz 1990).

Ambient levels of ozone are probably not high enough to kill even the most ozone-sensitive clones we tested. However, quaking aspen is extremely sensitive to shading (Baker 1949 and Shirley 1941), and differential growth rates caused by ozone in conjunction with competition could result in the elimination of ozone sensitive clones from populations in polluted areas. The correlations we have reported between ambient levels of ozone and ozone tolerance suggests that an early stage of selection, the elimination of sensitive genotypes, has begun to occur in some North American forests.

Table 2 - Ambient ozone levels, average percentage of leaves injured, and range of clonal means for 15 populations of quaking aspen exposed to 150 ppb ozone for 6 hours in a chamber fumigation.

| Population origin | Average ozone concentration | Average maximum daily ozone concentration | Percentage of leaves showing injury | |
|---|---|---|---|---|
| | | | Population mean | Range of clones |
| Apostle Islands NL Wisconsin | na | na | 54 cd | 22-85 |
| Crater Lake NP and Winema NF, Oregon | na | na | 34 a | 10-64 |
| Cuyahoga Valley NRA Ohio | 31 | 118 | 41 abc | 29-65 |
| Delaware Water Gap NRA Pennsylvania | 32 | 136 | 41 abc | 14-65 |
| Glacier NP Montana | na | na | 64 d | 18-91 |
| Indiana Dunes NL Indiana | 31 | 126 | 34 a | 21-57 |
| Monongahela NF and Blackwater Falls SP, West Virginia | 45 | 116 | 43 abc | 23-63 |
| Rocky Mountain NP Colorado | 45 | 83 | 55 cd | 29-82 |
| Saguaro NM and Coronado NF Arizona | 38 | 75 | 35 a | 18-54 |
| Sequoia NP and Sequoia NF California | 48 | 106 | 38 ab | 14-65 |
| Sleeping Bear Dunes NL Michigan | na | na | 41 abc | 14-60 |
| Voyageurs NP Minnesota | 29 | 77 | 51 bcd | 22-80 |
| Wind Cave NP, Mt Rushmore NM, and Blackhills NF South Dakota | 34 | 63 | 53 cd | 20-72 |
| Yellowstone NP Wyoming | 37 | 62 | 59 d | 30-80 |
| Yosemite National Park California | 34 | 94 | 43 abc | 24-68 |

Note: Numbers within columns are not significantly different at $P < 0.05$ as determined by Student-Newman-Keuls test.

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