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POPULATION CHANGES IN EASTERN HARDWOODS CAUSED BY AIR POLLUTION

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Abstract -- Evolution of ozone tolerance can provide indirect evidence that air pollution is reducing growth of forest trees. Acer rubrum from natural populations in nine national parks and Populus tremuloides from natural populations in five national parks were fumigated to determine ozone tolerances. Ozone tolerances of P. tremuloides populations from high and intermediate ozone areas were greater than ones from low ozone areas. A. rubrum populations from areas with historically high ozone concentrations showed more tolerance than those from low or historically low ozone areas. These results suggest air pollution is reducing the reproductive fitness of some individuals in relatively polluted areas.

Air pollution has been implicated in reduction of growth of several tree species in the eastern United States (Jensen 1982, Wang et al. 1986). Ozone is the most widely distributed of all air pollutants at known phytotoxic concentrations (Heck 1984). Eastern hardwoods are exposed, in parts of their ranges, to higher than natural background levels of ozone and are a likely candidate for ozone-induced changes in the genetic makeup of natural populations.

Genetic variation in ozone tolerance would be a prerequisite for an ozone-induced population change. Variation in this trait has been shown to exist within one population of quaking aspen, Populus tremuloides Michx., (Karnosky 1977) and within and among many populations of green and white ash, Fraxinus pennsylvanica Marsh. and F. americana L. (Karnosky and Steiner 1981). One objective of this study was to test populations from each of several additional species of eastern hardwoods to determine whether genetic variation for ozone tolerance is common among eastern hardwood tree species.

There should be a gradual increase in the average ozone tolerance of populations of trees in areas with high concentrations of ambient ozone if variation in ozone tolerance is indicative of differences in reproductive fitness in the presence of ozone. Data that indicate populations from high ozone areas are more tolerant than populations from low ozone areas when grown in a common environment can provide indirect evidence that this pollutant has already adversely affected some populations of trees. A second objective of this study was to examine this sort of evidence for several species of eastern hardwoods.

MATERIALS AND METHODS

Four to 14 individuals from each of five populations of quaking aspen and nine populations of red maple (Acer rubrum L.) growing in national parks that differed considerably in air quality (Table 1) were sampled for this

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Table 1 - Locations of populations from which clones of various eastern hardwoods were collected and the average annual ozone concentrations at those locations.

Population origin	Number of clones of each species propagated at each location				Average annual ozone concentration*
	Populus tremuloides	Acer rubrum	Cornus florida	Prunus serotina	
Cuyahoga Valley National Recreation Area, Ohio	10	4			65 ppb
Shenandoah National Park, Virginia		10	3	11	49
Great Smoky Mountains National Park, Tennessee		14	8	6	47
Mammoth Cave National Park, Kentucky		10	8	5	67
Buffalo National River, Arkansas		8	8	8	53
Saratoga National Historical Park, New York	13	12		5	49
Acadia National Park, Maine	14	8		4	52
Isle Royale National Park, Michigan	12	4			14
Voyageurs National Park, Minnesota	14	7			26

*Annual average of maximum daily one hour averages. For each park, the year data was collected; US EPA SAROAD sitecode, Canadian NAPS station, or location of monitor used; and distance and direction from park are listed.

Cuyahoga: 1983, SAROAD 360060020H01, 3 km SE
Shenandoah: 1984, SAROAD 482890003N05, in park
Gt Smoky Mts: 1983, SAROAD 441190101F03, in park
Mammoth Cave: 1983, SAROAD 183140005F01, 90 km NW
Buffalo River: 1983, Average of SAROAD 041880002F01 and 373020174F03, 130 km S and 247 km W, respectively
Saratoga: 1983, SAROAD 336020003F01, 34 km SW
Acadia: 1983, SAROAD 200010003F05, in park
Voyageurs: 1983, Atikokan, Ontario, 100 km
Isle Royale: 1983, NAPS 60806R, 50 km W

study. In addition, three to eleven individuals from populations of black cherry, Prunus serotina Ehrh., in six national parks and populations of flowering dogwood, Cornus florida L., from four national parks were collected from areas with intermediate or relatively high levels of ozone. All individuals were sampled without regard to size, form, or symptoms of ozone injury and were separated by at least 100 m, but not more than 15 km. These individuals were vegetatively propagated and grown in the greenhouse.

The relative ozone tolerances of the various clones was determined by exposing them to ozone doses shown to induce a broad range of injury in preliminary fumigations (Table 2). All trees were moved from a cold storage facility to a greenhouse in early March and fumigated in May to avoid extra-fumigation exposure to elevated levels of ambient ozone. A randomized complete block design with non-contiguous plots within replicates was used. Each aspen replicate was fumigated on a separate day, but all replicates of each of the other three species were fumigated together. A 2.4 m tall by 4.6 m diameter plastic chamber located in a greenhouse was used for fumigations. Air was charcoal filtered and passed through a duct where ozone was generated with ultra-violet lamps before it entered the fumigation chamber. Ozone concentrations were continuously monitored with a Dasibi Model 1003 Ozone Analyzer and rarely deviated more than 5% from desired levels. Because we were interested in determining relative amounts of injury among large numbers of genotypes within a short amount of time, ozone response was evaluated by visible injury.

Table 2 - Ozone concentrations used to test populations of four eastern hardwood species for within population variation in ozone tolerance and average injury observed for all populations within each species.

Species tested	Ozone exposure			Average injury class[1]
	pphm ozone	No. hrs/day	No. days	
Populus tremuloides	18	6	1	1.8
Prunus serotina	25	6	1	1.7
Acer rubrum	25	8	3	.5
Cornus florida	25	8	3	.1

[1] Injury class can range from 0 (no injury) to 5 (severe injury on all leaves).

Symptoms were allowed to develop seven days for quaking aspen and black cherry and ten days for red maple and flowering dogwood. Then the percentage of leaves injured and the leaf area injury class of injured leaves (0 = no injury, 1 = 1-20%, ... , 5 = 81-100%) was determined for each tree. The average leaf area injury class for all leaves was calculated for each tree. This is similar to the severity index developed by Davis and Coppolino (1974). Data were analyzed using standard methods of analysis of variance.

RESULTS AND DISCUSSION

Differences in visible injury among the four species corresponded well to published information on their relative ozone sensitivities (Davis et al. 1981, Davis and Gerhold 1976). Quaking aspen, which is generally recognized as ozone sensitive, was exposed to the lowest ozone dose and showed the greatest amount of ozone injury. Red maple and flowering dogwood, both considered ozone tolerant, received the highest ozone dose and showed the lowest amounts of injury. Black cherry received an intermediate ozone dose and displayed intermediate levels of injury (Table 2).

Differences among individuals within populations were sizeable for all four species. In almost every population the percentage of leaves injured on the most sensitive clone was twice that of the most tolerant clone and in some cases the differences in percentage of leaves injured was more than twenty-fold. A wide range of ozone tolerances were observed even in the relatively polluted parks and for the more ozone sensitive species. In all cases that could be tested, variation among clones within a population accounted for a larger portion of the variance than variation among populations.

The primary interest in this study was to determine whether there were differences in ozone tolerance between populations of trees in high ambient ozone areas and low ambient ozone areas. Population samples were obtained from areas that differed in air quality for two species, red maple and quaking aspen (Table 1).

Quaking aspen from the most polluted park sampled were considerably more tolerant of ozone than those from the most pristine parks sampled. Fifty percent more of the leaves on trees from Isle Royale and Voyageurs National Parks showed symptoms of ozone injury than on trees from Cuyahoga Valley National Recreation Area (Table 3). The average leaf area injury class for trees from the most polluted park was about half that of those from the least polluted park (Table 4). The 1983 and 1984 ozone data in Table 1 did not necessarily reflect historical levels of ozone, but the significant correlation ($r = -0.95$ $P=0.013$) between the average leaf area injured and the average annual ozone concentration suggested a close relationship between the two variables. Differences in injury among the five parks, as judged both by percentage of leaves injured and average leaf area injury, were highly statistically significant ($P = 2 \times 10^{-5}$ and 2×15^{-4}, respectively). These results are very similar to those obtained the previous year with the same collection of plant material (Table 5). They are consistent with the hypothesis that natural selection for ozone tolerance has occurred in populations of quaking aspen in polluted areas. Although injury to populations from parks with intermediate levels of ozone were not significantly different from those of either high or low ozone parks, the fact that they were intermediate and the strong correlation between ambient ozone and injury suggests that selection for ozone tolerance may be occurring in these parks as well.

Large differences in injury were found among populations of red maple from the nine national parks where this species was collected. The percentage of leaves injured and the average leaf area injury class for trees from the most sensitive population was more than twice that for trees from the most tolerant population (Tables 6 and 7). The three populations

Table 5 - Percentages of leaves showing visible injury for one-year-old clones of quaking aspen from populations in five national parks that were fumigated with 18 pphm ozone for six hours.

Population origin	Population mean	Range of clonal means	No. of clones
Cuyahoga Valley NRA	38%	21 - 62	11
Saratoga NHP	47	15 - 72	14
Acadia NP	49	24 - 73	15
Voyageurs	45	20 - 62	12
Isle Royale	54	27 - 65	15

These results support our hypothesis that natural selection for ozone tolerance is occurring in relatively polluted parks. Because red maple is more tolerant of ozone than quaking aspen it is reasonable to expect that higher levels of ambient ozone and longer periods of time would be required to cause a discernable change in populations. Thus, red maple populations from Shenandoah and Great Smoky Mountains National Parks which have been exposed to phytotoxic concentrations of ozone since at least the 1950s (Berry 1964, Berry and Hepting 1964, Berry and Ripperton 1963), are more tolerant of ozone than one might predict based on present ambient ozone levels. The red maple population from Mammoth Cave National Park which has only recently experienced large increases in ambient ozone (based on nitrogen oxide emissions described by Gschwandtner et al. 1986) is less tolerant of ozone than one would predict based on present ambient ozone levels.

Table 6 - Percentages of leaves showing visible injury for clones of red maple from populations in nine national parks that were fumigated with 25 pphm ozone for eight hours per day on three consecutive days.

Population origin	Population mean*	Range of clonal means	No. of clones
Shenandoah NP	26% c	6 - 49%	10
Cuyahoga Valley NRA	29 bc	0 - 52	4
Great Smoky Mts. NP	32 bc	2 - 67	14
Voyageurs NP	37 abc	14 - 93	7
Isle Royale NP	41 abc	3 - 60	4
Saratoga NHP	44 abc	11 - 78	12
Mammoth Cave NP	48 abc	23 - 81	10
Buffalo NR	50 ab	17 - 81	8
Acadia NP	55 a	26 - 80	8

* Populations followed by the same letter are not significantly different ($P \leq .05$) from each other.

Table 3 - Percentage of leaves showing visible injury for two-year-old clones of quaking aspen from populations in five national parks that were fumigated with 18 pphm ozone for six hours.

Population origin	Population mean*	Range of clonal means	No. of clones
Cuyahoga Valley NRA	50% a	21 - 63%	10
Saratoga NHP	58 ab	35 - 83	13
Acadia NP	60 ab	22 - 84	14
Voyageurs NP	71 bc	60 - 82	14
Isle Royale NP	75 c	58 - 88	12

* Populations followed by the same letter are not significantly different ($P \leq .05$) from each other.

with the lowest percentage of leaves showing visible injury included one from a park with a relatively high level of ozone, Cuyahoga Valley National Recreation Area and two with intermediate levels of ozone, Great Smoky Mountains and Shenandoah National Parks. The population from Cuyahoga Valley National Recreation Area was also relatively ozone tolerant in the quaking aspen study. The relative amounts of injury among the remaining six populations did not appear to be related to differences in ambient ozone at the parks of origin. Differences among the nine populations, as determined by both percentage of leaves injured and average leaf area injury class, were not statistically significant ($P = .102$ and $.157$, respectively) when the effect of clone within park was included in the model, but were highly significant ($P = 2 \times 10^{-6}$ and 5×10^{-5}) when it was dropped from the model.

Table 4 - Average leaf area injury class* for all leaves on two-year-old cuttings of quaking aspen from populations in national parks that were fumigated with 18 pphm ozone for six hours.

Population origin	Population mean**	Range of clonal means	No. of clones
Cuyahoga Valley NRA	1.1 a	0.2 - 2.3	10
Saratoga NHA	1.4 ab	0.5 - 2.9	13
Acadia NP	1.7 ab	0.2 - 3.2	14
Voyageurs	2.3 b	1.0 - 3.8	14
Isle Royale	2.3 b	0.6 - 4.1	12

* Average leaf area injury class could range from 0 (no injury) to 5 (severe injury on all leaves).

** Populations followed by the same letter are not significantly different ($P \leq .05$) from each other.

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