EFFECTS OF OZONE ON PLANTS

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I. Introduction

Ozone, among gaseous pollutants, is considered to have the greatest harmful effect on plants throughout the world. Although early air pollution research focused on foliar symptoms (Yang et al., 1983a), it now is well known that ozone can alter plant growth and yield without causing any visible symptoms (Duchelle et al., 1982, 1983; Reich and Amundson, 1985; Shafer et al., 1987). Ozone-induced growth reductions in plants have been explained through inhibition of photosynthesis (Miller et al., 1969; Barnes, 1972; Yang et al.,1982, 1983a, b; Reich et al., 1983, 1986, 1987) and through changes in photosynthate allocation (McLaughlin and McConathy, 1983; McLaughlin et al., 1982). However, the responses of plants to ozone is quite variable due to differences in environmental conditions and genetic variation.

II. Effects on Plant Growth

Ozone effects originate with initial injury at the cellular level and manifest themselves as reductions in growth. Early literature pertaining to O_3 effects on plants reported response based on visible foliar injury (Davis and Wilhour, 1976). Foliar injury, however, is not directly related to growth reductions in plants exposed to long-term ambient or near-ambient concentrations of O_3, with the exception of certain areas of the western U.S. that are exposed to unusually high concentrations of O_3 (Miller, 1983; Reich and Amundson, 1985; Chappelka et al., 1985, 1986). In a recent review article, Pye(1988) states the probable reason for this occurrence. Visible foliar injury indicates lost photosynthetic area following a failure of cellular homeostasis. This type of injury occurs most commonly during acute exposures. Relatively low-concentrations of O_3 can reduce photosynthetic efficiency and increase respiration without the loss of homeostasis. Because short-duration, low-concentration exposures cause minimal effects on photosynthesis,

subtle injuries are observed as a cumulative result of longer-term exposures. Since trees are perennials and are exposed to some amount of O_3 continuously, primary interest has involved the study of alterations in growth and productivity under chronic O_3 exposure regimes, irrespective of visible symptom expression.

Kress (1978) conducted screening tests for 23 full-sib families of loblolly pine. Three to four and fourteen to sixteen-week-old pine seedlings were exposed to ozone at 0.10, 0.15, 0.20, 0.25 or 0.30 ppm for eight hours. Family 6-13×2-8 showed the most severe foliar symptoms across all ozone concentrations with the exception of 0.1 ppm ozone. No foliar symptoms were found on seedlings for any family following exposure to 0.1 ppm ozone. Family 540×504 was most tolerant to ozone. The author concluded there were many variations among families of loblolly pine that might be useful for breeding programs. Kress (1978) also examined the long-term effect of ozone on growth of loblolly pine seedlings. One to two-week-old seedlings were exposed to 0.05 ppm ozone, six hours a day for 28 or 56 consecutive days. Height growth was significantly suppressed in the sensitive family.

Kress and Skelly (1982) examined the growth response often tree species including a wild type and a 6-13×2.3 full-sib family of loblolly pine. Four-week-old seedlings were exposed to ozone at 0.0, 0.05, 0.10, or 0.15 ppm, six hours a day, for 28 consecutive days. Only the wild type loblolly pine seedlings showed a significant reduction in height growth with the 0.05 and 0.10 ppm ozone treatment. However, the 0.15 ppm ozone treatment significantly reduced height growth in both the wild type and full-sib family. Shoot and total plant dry weight of loblolly pine seedlings were not significantly changed by any treatments of ozone. In the second experiment, the reseachers selected seven of the ten species used in the first study, utilizing the same treatments as the first study. Only the 6-13×2-8 family of loblolly pine seedlings showed a significant reduction in height growth with the 0.1 ppm ozone treatment.

III. Effects on Biomass Partitioning

Ozone, in addition to causing reductions in the amount of dry matter produced, can alter partitioning of carbon in tree seedings (Tingey et al., 1976; Jensen, 1981) and in mature trees (McLaughlin et al., 1982).

Jensen (1981) studied the root carbohydrate content and above-ground biomass of one-year-okd green ash exposed to 0.50 $\mu l \Gamma^1$ O_3, 8 h d^{-1}, 5 d week^{-1} for up to 6 weeks. Ozone-treated seedlings exhibited significantly less stem and leaf dry weight, less

root starch, and reduced sugar content. Lower root reserves were hypothesized to contribute less above-ground biomass.

Tingey *et al.* (1976) exposed 1-week-old ponderosa pine to O_3, 6 h d^{-1} for 20 weeks, to determine metabolite levels in shoots and roots. Ozone-treated plants contained high amounts of free amino acids in the roots. Levels of soluble sugars, starch, and phenolics increased in shoots and decreased in roots of seedlings to which O_3 was applied. The authors attributed their results to metabolite retention in the foliage and disruption in transport to the roots. Several researchers (Kress and Skelly, 1982; Hogsett *et al.*, 1985; Chappelka and Chevone, 1986) have reported that root growth of certain tree species can be depressed more than shoot growth, supporting the findings of Tingey *et al.* (1976).

Adams *et al.* (1990) using ^{14}C found that loblolly pine seedlings exposed to two times ambient O_3 voer one growing season exhibited lower rates of CO_2 assimilation and increased respiration rates, and allocated less photosynthate to fine roots. Spence *et al.* (1990) exposed loblolly pine seedlings to 0.120 μl^{-1} O_3, 7h d^{-1}, 5 d week^{-1} for 12 weeks. Seedlings were labeled with ^{11}C in order to characterize changes in allocation patterns. Ozone-treated seedlings exhibited a 16% reduction in CO_2 assimilation, 11% decrease in the speed of phloem transport, a 40% reduction in the amount of photosynthate in the phloem, and a 45% decrease in photosynthate allocation to the roots.

Ozone is also known to cause shifts in allocation patterns in mature trees. Wilkinson and Barnes (1973) exposed eastern white and loblolly pine branches to 0. 00, 0.10, or 0.20 $\mu l l^{-1}$ O_3 continuously for up to 21 d to study ^{14}C-fixation patterns in response to O_3. The primary changes in ^{14}C distribution due to O_3 exposure were reductions in soluble sugars, increases in sugar phosphates, and an increase in free amino acids. McLaughlin *et al.* (1982), using ^{14}C distribution due to O_3 exposure were reductions in soluble sugars, increases in sugar phosphates, and an increase in free amino acids. McLaughlin *et al.* (1982), using ^{14}C, demonstrated that the foliage and branches of oxidant-sensitibe eastern white pines retained significantly more photosynthate than did intermediate or tolerant trees, indicating that the export of photosynthate to the stems and roots of sensitibe trees was inhibited.

These results indicate that in addition to having an effect on overall plant growth, O_3 can cause alterations in the way biomass is partitioned. Changes induced by ambient O_3 concentrations would therefore be expected to cause reductions in carbohydrate levels, especially in the roots. Depletions in these reserves could cause reduced vigor of the root systems and enhance the susceptibility of trees to other

forms of stress, such as drought and root diseases.

IV. Effects on Gas Exchanges

It is well known that air pollutants affect plants without any visible injury. Ozone can inhibit the rate of carbon assimilation in a variety of conifer and hardwood tree species. Early investigations of O_3 effects on photosynthesis (Miller et al., 1969; Barnes, 1972) distinguished between short- and long-duration fumigations, concentration-dependent changes in CO_2 exchange rate, and variationx in response among genotypes of a particurar species. In later years O_2 inhivition of CO_2 uptake was observed to be modified by numerous environmental variables (light, humicity, ambient CO_2 concentration, other gaseous pollutants) and other biological factors (leafage, plant water status, respiration rate), in addition to the genotype (Reich, 1983; Yang et al., 1983a; Reich and Lassoie, 1984; Lee et al.,1990). These studies have served to emphasize the complexity of interactions involved in O_3 impairment of net photosynthesis in trees.

Miller et al. (1969) fumigated three-year-old ponderosa pines (Pinus ponderosa Laws) with ozone at 0.15, 0.30, or 0.45 ppm for nine hours a day. Photosynthesis declined after 20 days exposure to 0.15 ppm ozone, whereas 0.30 ppm ozone caused a significant reduction in only ten days. At the end of 30 days, photosynthesis rates were reduced by 10, 70, and 85% with exposure of 0.15, 0.30, or 0.45 ppm ozone, respectively.

Barnes (1972b) studied the effects of ozone on photosynthesis and respiration of slash pine (Pinus elliottii), pond pine (P. serotina), white pine (P. strobus), and loblolly pine (P. taeda). Seedlings were exposed to ozone at 0.05 or 0.15 ppm for five to eighteen weeks. Respira tion was significantly stimulated in two-year-old eastern white pine, and eight-month-old slash, and loblolly pine seedlings exposed to 0.15 ppm ozone for 36 days. Net photosynthesis declined in all species with ozone exposure, but was not significant.

Yang et al. (1983b) found similar effects of ozone on net photosynthesis and dark respiration of eastern white pine. Three eastern white pine clones differing in sensitivity to ozone were fumigated with 0.10, 0.20, or 0.30 ppm ozone for four hours. Net photosynthesis was significantly reduced by 7%, 14%, and 19% in all three clones exposed to ozone at 0.1, 0.20, and 0.30 ppm, respectively. Dark respiration significantly increased and light transpiration decreased in ozone-sensitive clone after ozone exposure.

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In a study of effects of long-term exposure to ozone on photosynthesis and dark respiration of eastern white pine, Yang et al. (1983a) found contradictory results regarding dark respiration. In the ozone-sensitive clone, dark respiration was significantly declined and, in the ozone-insensitive and intermediate clone, dark respiration remained unchanged after 50 days exposure (4 hr d^{-1}) with ozone at 0.10, 0.20, or 0.30 ppm. Net photosynthesis was significantly reduced by ozone exposure at all concentra tions in the sensitive clone.

Respiration results of Yang et al. (1983a) support the findings of MacDowell (1965), who found two stages of respirational response in tobacco leaves after ozone fumigation at 0.7 ppm for one hour. Respiration initially decreased, then increased within five hours, accompanied by visible symptoms of ozone damage.

Reich et al. (1986b) studied the effects of low concentrations of ozone on net photosynthesis and chlorophyll concentration of soybean. They fumigated soybean plants with 0.05, 0.09, 0.13 ppm ozone for six or eight hours every day for eight weeks. Net photosynthesis was significantly reduced and linearly correlated with ozone concentration for both individual leaves and for whole plants compared with the control (0.01 ppm ozone). Chlorophyll concentration also declined due to ozone treatments and was correlated with net photosynthesis for both individual leaves and for whole plants. However, there was no significant change in dark respiration.

Reich (1983) examined the effects of low concentrations of ozone on net photosynthesis, dark respiration, and chlorophyll concentrations of hybrid poplar (Populus deltoides×trichocarpa) plants. Plants were exposed to ozone at 0.04, 0.08, or 0.12 ppm, 5.5 hours a day, for 62 days.

There was no immediate effect on photosynthesis regardless of ozone concentration (0.01-0.20 ppm), leaf age, and duration of ozone exposure. However, chronic exposure to ozone decreased net photosynthesis and leaf chlorophyll concentration, and increased dark respiration. The reduction of net photosynthesis was, in part, due to accelerated leaf aging.

Accelerated leaf aging with low concentration of ozone was found in poplar (*Populus euramericana* cv 'Dorskamp' and 'Zeeland') by Mooi (1980). Seedlings were exposed to ozone at 0.04 ppm for 12 hours everyday for 23 weeks. Premature defoliation occurred in about 60% of stems. The impact of ozone on net photosynthesis in oat (*Avena sativa*) and duckweed (*Lemna gibba*) was examined by Forberg et al. (1987). Plants were exposed to ozone at 0.07, 0.18, or 0.25 ppm for two hours. Net photosynthesis was significantly reduced in oat seedlings exposed to concentrations above 0.07 ppm ozone and reduced in duckweed exposed to

concentrations above 0.18 ppm ozone.

V. Effects on Reproduction

Air pollution influences the reproductive capacity of plants by causing reductions in photosynthesis and shifts in the partitioning of photosynthate (Cooley and Manning, 1987). Benoit *et al.* (1983) collected pollen from eastern white pine growing along the Blue Ridge Parkway in Bitginia. Percent germinaion was signifiantly reduced in wet pollen exposed to O_3 (0.15 μll^{-1}, 4h). Dry pollen production and germination was unaffected by O_3 fumigation. peasons for this discrepancy were not explained, but may be related to increased permeability of O_3 in the wet pollen.

The available literature indicates O_3 has the potential to influence reproduction in trees: directly by affection reproductive structures, or indirectly by altering host metabolism. Much more research is needed, however, in order to determine the overall significance of these effects on forest ecosystems.

VI. Interactions of O_3 and Other

1. Combined Effects of O_3 and Other Gaseous Pollutants

Several research groups have exposed trees to various combinations of O_3 and other phytotoxic gases. Ozone in combination with SO_2 and/or NO_2 generally results in the greatest suppression of growth. These findings are highly variable and are dependent upon the pollutants and concentrations used, the genetic makeup of the material (Kress and Skelly, 1982; Yang *et al.*, 1983a, b), the timing of fumigation (Jensen, 1985), and the species exposed (Kress and Skelly, 1982).

In testing tree response to pollutant mixtures, one of the most important issues is the determination of synergistic or antagonistic effects. Very few studies to date have adequately determined these effects (Chappelka *et al.*, 1985). By definition, synergism is the joint action of different substances in producing an effect greater than the sum of the individual effects of the substances.

Only limited research has been conducted on mechanisms of pollutant interactions (Carlson, 1979; Constantinidou and Kozlowski, 1979; Boyer *et al.*, 1986). All the studies used O_3 alone and in combination with SO_2, and all the studies investigated the effects of these pollutants on net photosynthesis. Two studies used unrealistic concentrations of the pollutants (Carlson, 1979; Constantinidou and Kozlowski,

1979), and these results have to be interpreted with caution. Boyer *et al.* (1986) found the combination of O_3 and SO_2 to depress net photosythesis in easten white pine more than did O_3 alone. However, results were variable. No research to date has investigated the biochemical mechanisms of pollutant interactions in trees, at realistic concentrations and appropriate co-occurrence patterns.

2. Combined Effects of O_3 and Acidic Deposition

Results regarding combined effects of O_3 and acidic depositon on tree growth are not as definitive as those with O_3 in combination with gaseous pollutants and are quite variable and dependent upon the environmental conditions imposed on them.

Growth of yellow poplar (Chappelka *et al.*, 1985), white ash (Chappelka and Chevone, 1986), and paper birch (Keane and Manning, 1989) exposed to O_3 and simulated acidic mist or rain exhibited significant treatment interactions, with growth decreasing as solution acidity increased, except in paper birch (Keane and Manning, 1989). In contrast, no interactive effects occurred on the growth of eastern white pine (Reich *et al.*, 1987), Scots pine (Skeffington and Roberts, 1985), red spruce (Taylor *et al.*, 1986), sugar maple, northern red oak (Reich *et al.*, 1986a), and green and white ash (Elliott *et al.*, 1987), exposed to O_3 and acidic deposition.

Reich and Amundson (1985) examined the impact of ozone and simulated acid rain in four tree species. Sugar maple (Acer saccharum), eastern white pine (Pinus strobus), hybrid poplar (Popullus deltoides×trichocarpa), and northern red oak (Quercus rubra) seedlings were exposed to ozone at the range of 0.02 to 0.14 ppm (maximum doses were less than 30 ppm hour) in combination with simulated acid rain (pH 5.6, 4.0, or 3.0). Ozone induced a linear reduction in net photosynthesis in all species in relation to ozone concentration. However, simulated acid rain have neither significant single effect nor interaction with ozone on net photosynthesis for all species.

Reich *et al.* (1986a) examined the impact of ozone and simulated acid rain on photosynthesis, chlorophyll concentration, and growth in sugar maple and northern red oak seedlings. Two-year-old seedlings were exposed to ozone (0.06, 0.09 or 0.12 ppm, 7 hr d^{-1}, 5 d wk^{-1}) and simulated acid rain (pHs of 5.6, 4.0, or 3.0, 1.25 h wk^{-1}, 2.5 cm wk^{-1}) for six to ten weeks in all possible combinations. Net photosynthesis significantly decreased with increasing ozone concentration compared with control (0.03 ppm ozone) seedlings. Chlorophyll concentration was increased in sugar maple leaves exposed to 0.09 and 0.12 ppm ozone. However, there was no significant effect of simulated acid rain on net photosynthesis and chlorophyll concentration and no

interactions between acid rain and ozone for both species.

Reich *et al.* (1987) submitted white pine seedlings to ozone at 0.02, 0.06, 0.10, and 0.14 ppm in combination with acid rain at pHs of 5.6, 4.0, 3.5, and 3.0, for four months. In general, net photosynthesis significantly increased with increasing rain acidity, whereas the ozone treatment induced a linear reduction in net photosynthesis. The interaction between ozone and rain pH was minimal.

3. Combined effects of $_3$ and physical factors

The ambient environment exerts a profound influence on the physiological status of a plant and, therefore, its response to O_3. Some early studies with agronomic crops indicated that changes in temperature, light, and relative humidity resulted in alterations in response to O_3.

Only a few studies are available that examined the effects of variable temperature, lingt, and humidity on tree response to O_3 (Davis and Wood, 1973). General conclusions from these experiments were that visible injury wasmore seere when plants were exposed to relatively high temperatures (27 to 32°C) and high humidity ($>$ 80%), compared with other treatments.

Jensen and Roberts (1986) studied the effect of ozone on stomatal resistance in yellow poplar (*Liriodendron tulipfera* L.) seedlings at two humidity levels. One-year-old yellow poplar seedlings were exposed to ozone at 0.00 or 0.15 ppm in combination with 40% or 80% humidity for five hours for five consecutive days. No effect of ozone on leaf diffusive resistance was found at 40% humidity. However, at 80% humidity, leaf diffusive resistance was significantly increased by ozone exposure.

Recently, evidence has accumulated in support of an O_3-low-tmperature interaction, leading to visible foliar injury for several tree species, including Norway spruce (Barnes and Davison, 1987), red spruce (Fincher *et al.*, 1989). This could be caused by an impairment of the winter hardening process due to O_3 and is, in part, generally controlled, as exhibitd by a wide range in clonal variation in combined studies with these stress factors (Barnes and Davison, 1987). The mechanism(s) behind this response are unknown.

The decline of mature coniferous trees in the northeastern United States, beginning in the early 1960's, appears to have been initiated by a severe drought (Johnson and Siccama, 1983, 1984). The similar synchronous occurrence between the initiation of growth decline and drought was also reported in mid-Appalachian forests (Adams *et al.*, 1985). A hypothesis has been suggested that acid deposition,

heavy metal inputs, and possibly, ozone stress can impair root growth and root physiology to such an extent that affected trees become highly drought susceptible (Johnson and Siccama, 1984). Although effects of ozone and water stress in combination have been studied (Khatamian et al., 1973; Olszyk and Tibbitts, 1981; Tingey et al., 1982; Tingey and Hogsett, 1985), the effect of drought stress on plants already subjected to ozone and acid rain has not been investigated.

VII. Protective Chemicals

For more than 30 years, many investigators have evaluated diverse groups of chemical compounds, including antioxidants, antisenescence agents, antitranspirants, dusts, grawth regulators, growth retardants, and pesticides, to determime whether these compounds will protect plants from O_3 injury.

While there have been many reports of chemicals that were succesful in preventing ozone injury to plants, most of them are of a preliminary nature, and further experiments need to be conducted. The development of the open-top chamber method in the 1970s also contributed to a decrease in interest in protective chemicals. A great deal of work, however, has been done with the systemic fungicide benomyl, and antioxidant EDU.

EDU(ethylene diurea) is currently the best known systemic antioxdant. It has been used extensively, and many reports are available for many crops and trees (Kostka and Manning, 1992, 1993a, b). EDU was developed specifically as an antioxidant to protect plants (Carnahan et al., 1978). At approptiate concentartions it retards senescence in plants. However, the mode of action is not completely understood. One of the reasons for this is that we do not have a clear understanding of the complete mechanism for O_3 injury at the moleculat level. EDU has excellent potential as a tool for use in research on the mechanisms or the mode of action of O_3.

Carnahan et al. (1978) clearly demonstarted that EDU could protect bean leaves from O_3 injury. A large quantity of EDU was produced by the duPont Chemical Company(U.S.A.) and distributed to many investigators. Many trials showed that EDU could be used to suppress O_3 injury and, most likely, yield depressions (Clarke et al.; 1983).

EDU has a great potential as a chemical protectant to prevent O_3 injury to plant. Some of the other chemical compounds may also have this property, but not much is known about most of them. Continued research and toxicolohy studies with EDU will lead to the development of a valuable verified method for the study of the

effects of ambient, or above ambient concentrations of O_3 on plants.

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