

5. Interacting Effects of Multiple Stresses on Growth and Physiological Processes in Northern Forest Trees

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Global climate change is a complex and controversial subject, both technically and politically. Recently, the Intergovernmental Panel on Climate Change (IPCC) of the United Nations concluded that “the balance of evidence suggests a discernible human influence on global climate,” and that “further accumulation of greenhouse gases will commit the earth irreversibly to global climate change with its consequent ecological, economic, and social disruption” (Houghton et al., 1996; Brown et al., 1997; Kerr, 1997). One of the concerns is that changing climate will have major effects on future forest composition, productivity, sustainability, and biological as well as genetic diversity (Houghton et al., 1996).

Two pollutants that are generally considered to have the greatest impacts on plant growth and are indisputably increasing concomitantly in the atmosphere as a consequence of human activity are carbon dioxide (CO₂) (Keeling et al., 1995) and tropospheric ozone (O₃) (Taylor et al., 1994; Chameides et al., 1997). Both pollutants are increasing concurrently, and are expected in rural agricultural and forested areas to have the greatest impacts on plant growth. Increasing CO₂ typically enhances plant growth (Kimball et al., 1990; Koch and Mooney, 1996), while O₃ has

a deleterious affect on plant growth (Adams et al., 1989; Yunus and Iqbal, 1996). Less is known about the responses of plant growth to the interaction of concomitant increasing CO₂ and O₃ (Allen, 1990; Krupa and Kickert, 1993). Similarly, little is known about the interacting effects of elevated CO₂ and O₃ on forest trees and forest ecosystems, but overall responses in trees to elevated CO₂ (Ceulemans and Mousseau, 1994) and O₃ (Raineer et al., 1993; Taylor et al., 1994) are similar to that of other plants. As with crop plants, it is known that inherent differences exist among and within forest tree species in their response to certain atmospheric stressors (Kozlowski and Constantinidou, 1986a,b; Taylor, 1994; Karnosky et al., 1996; Hogsett et al., 1997).

The literature is exhaustive on the subject of single factor effects of CO₂, O₃, and other stressors on plants. Thus, it is beyond the scope of this chapter to review all these contributions. Anyone seeking more information on CO₂ effects on plants should consult references by Strain (1987), Kimball et al. (1990), Koch and Mooney (1996), and Yunus and Iqbal (1996); and for effects on woody plants, Ceulemans and Mosseau (1994), Curtis (1996), Wullschlegel et al. (1997) and Mickler and Fox (1998). For information on O₃ effects on plants, the reader should refer to Adams et al. (1989), Mooney et al. (1991), Krupa and Kickert (1993), and Yunus and Iqbal (1996); and for effects on woody plants and forest ecosystems, Taylor et al. (1994), Taylor (1994), Fox and Mickler (1996), and Hogsett et al. (1997).

Multiple Stress Effects

Plant responses to CO₂ and O₃ become even more complex when other known stressors such as nitrogen availability, temperature and water extremes, and pests, are combined with the effects of CO₂ and O₃ (Allen, 1990). Traditionally, research on the effects of air pollutant stresses on agricultural crops and forest trees examined one or at most two stresses at the same time with a single plant species. This approach is not surprising given the logistic problems and expense of multiple-factor experiments. However, these single and occasionally multiple-factor experiments have not been very helpful for understanding the long-term response of a single species under natural conditions, much less long-term community or ecosystem responses. Given the strong genetic component of response (Taylor, 1994; Karnosky et al., 1997), and that essentially every biotic and abiotic factor measurable in the environment modifies the responses to air pollutants, and that these responses change with time as trees acclimate to these variable stresses, it is impossible to experimentally determine future stands or community dynamics. However, single- or multiple-factor experiments with as many other environmental factors as possible held constant or increased in response to plant demand, are still necessary to

provide biological and mechanistic input into process-based models (Taylor et al., 1994; Lee and Jarvis, 1995; Lloyd and Farquhar, 1996; Thornley and Cannell, 1996). In this chapter we focus our discussion on the responses of aspen (*Populus tremuloides* Michx.), yellow poplar (*Liriodendron tulipifera* L.), and white pine (*Pinus strobus* L.) to ozone (O_3), carbon dioxide (CO_2), their interactions ($O_3 \times CO_2$), and the interactions with water and nitrogen (N) availability, and with pests. Responses of other tree species may also be included when information is limited.

In general, increasing atmospheric CO_2 concentrations will increase photosynthetic rates, leaf production, height growth, and dry weight production. In contrast, increasing atmospheric concentrations of O_3 will decrease photosynthetic rates, increase leaf senescence, and decrease dry weight production. The amount of change, however, depends on many internal plant factors (e.g., plant and tissue age, plant growth strategy, genotypic response, ability to adapt to changing environmental conditions, etc.) and external environmental factors (e.g., light, nutrients, water, temperature, magnitude and duration of exposure, etc.) (Miller et al., 1997). Because elevated CO_2 concentrations impact many metabolic processes and usually increase growth, higher CO_2 concentrations may also compensate for other environmental stresses (Allen, 1990; Ceulemans and Mousseau, 1994). Compensation may work primarily through an increase in the efficient use of other limiting resources. Such increased efficiency is commonly found in CO_2 –water use interactions (Eamus and Jarvis, 1989; Eamus, 1991; Bowes, 1993; Lee and Jarvis, 1995; Anderson and Tomlinson, 1998; Tomlinson and Anderson, 1998). An increase in CO_2 concentration commonly increases photosynthetic rate and decreases stomatal conductance and transpiration rates. Increased carbon fixation and decreased water use leads to an increase in water use efficiency. This decrease in water use may be beneficial during short periods of water stress. However, high CO_2 concentrations also often increase total leaf area such that improved water use per unit area is offset by increased leaf area. Thus, total water use during drought may be greater, increasing total water stress (Kerstiens et al., 1995; Beerling et al., 1996).

The interactions of CO_2 and nutrients have important implications for plant growth. The lack of consideration or lack of adequate control of nutrient supply is probably a major factor in much of the conflicting experimental results of growth responses to increased CO_2 (Curtis, 1996; Pettersson et al., 1993; Wullschleger et al., 1997). Even when several levels of nutrients are supplied initially, plant growth constantly changes the ratio of supply to internal demand. Ideally, nutrients should increase exponentially to maintain a constant relative growth rate (Ingestad and Ågren, 1995; Coleman et al., 1998). Most studies show that CO_2 enrichment increases growth even though light and/or nutrients are limiting growth (Conroy and Hocking, 1993). A common assumption is that response to CO_2 will be less if light or nutrients are limiting (law of

the minimum). This response is often true if absolute growth increases are considered (low N plants plus CO₂—low N plants). However, the proportional or percent growth increase in response to CO₂ in N-limited plants is often equal to or greater than that found in nonlimited plants (Bowes, 1993; Lloyd and Farquhar, 1996). However, the opposite response is also frequently found (Curtis et al., 1995; Gebauer et al., 1996). Response seems to be strongly controlled by plant life history and the relative allocation of carbon (C) and N to leaf and root growth (Bazzaz and Miao, 1993; Laurence et al., 1994; Lloyd and Farquhar, 1996). A common response to CO₂ enrichment is a greater increase in C fixation rate than N uptake rate. If much of this C is used in leaf growth rather than root growth and N uptake, leaf N concentration will decrease (based on area or dry weight). The increase in total leaf area, however, even if N uptake rate decreases, results in greater total plant N content (Idso et al., 1996; Tissue et al., 1997).

Trees growing in the field are seldom exposed to a single environmental stress. With increasing atmospheric pollutants (e.g., CO₂, O₃, N deposition), trees must respond to these new stresses in addition to more common stresses, such as drought, low light, and nutrient deficiencies. Carbon dioxide enrichment may partially or totally ameliorate growth decreases in response to these common stresses. However, the addition of O₃ stress is often additive to growth impacts of these other common stresses (Greitner et al., 1994), and CO₂ may or may not compensate (Volin et al., 1998). Ozone damage is often greater in fast-growing plants that are watered and fertilized (Winner, 1994; Dickson et al., 1998), or the converse, slow-growing, stressed plants are less sensitive to O₃ damage, particularly if water-stressed (Tingey and Hogsett, 1985). Published results are contradictory. For example, N fertilization had no effect on O₃-induced decreases in growth and leaf senescence of hybrid poplar (Gunthardt-Goerg et al., 1996); however, N fertilization increased O₃ impact on growth of Norway spruce (*Picea abies* [L.] Karsten) (Lippert et al., 1996) and radish (*Raphanus sativus* L.) (Pell et al., 1990); but decreased growth in aspen (Karnosky et al., 1992a,b) and birch (*Betula* spp.) (Pääkkönen and Holopainen, 1995). These differences in response reflect differences in experimental protocols, plant growth strategy, and C allocation patterns. Large differences in response are also found between species (Tjoelker et al., 1993) and among clones or genotypes within species (Taylor, 1994; Karnosky et al., 1996; Dickson et al., 1998).

Knowledge about the combined impacts of chronically elevated CO₂ and O₃ on ecosystems remains limited and largely speculative. It has been shown that litter decomposition exposed to elevated CO₂ and/or O₃ is significantly decreased, suggesting nutrient cycling within ecosystems may be impacted (Boerner and Rebbbeck, 1995; Scherzer et al., 1998). Insect herbivory and other impacts on plants are also significant factors in ecosystem responses to environmental stresses. There is sufficient prelim-

inary data to predict with confidence that both CO_2 and O_3 will significantly affect fundamental plant processes, which will translate into altered tree susceptibility to all major guilds of plant-feeding insects (i.e., folivores, phloem and xylem sappers, phloeo- and xylophages, and rhizophages). Under some circumstances, this may precipitate rapid, substantive changes in plant competitive abilities and thereby drastically alter the normal compositional and successional trajectories of plant communities (Maron, 1998). Elevated CO_2 decreases leaf N levels and increases starch content, fiber, leaf temperatures, and concentrations of phenolics and tannins (Mooney et al., 1991; Bazzaz and Fajer, 1992; Lincoln et al., 1993; Trier et al., 1996). Responses for most insect folivores are typically increased leaf consumption, coupled with decreased growth, survival, and fecundity (Lincoln et al., 1993). However, this research applies primarily to external folivores. No one has yet investigated the responses of leaf miners or those of stem and root borers. Miners typically selectively feed on mesophyll and parenchyma tissues and may be able to avoid serious CO_2 -induced nutrient dilutions and increases in raw fiber (Trier and Mattson, 1997). No one knows how the biochemical micro-environment of stem borers is likely to change, and how borers may respond. Carbon dioxide-induced increases in cambial growth may enhance rapid callus formation and thus more certain containment and death of stem-invading larvae. Theory also predicts that the standard hypersensitive or rapid induced (secondary chemical based) resistance (RIR) in stem tissues to foreign invasions may be enhanced given the fact that RIR and plant growth are usually positively linked (Herms and Mattson, 1992).

Under elevated ozone, decreasing whole plant growth and module longevity are typical responses (Pye, 1988). This decrease is due to the phytotoxic effects of elevated O_3 , which typically decreases Rubisco (Brendley and Pell, 1998), lowers rates of photosynthesis and decreases leaf surface area due to premature leaf abscission (especially in sensitive species). Ozone enrichment also generally diminishes branch growth and longevity of short shoots (Matyssek et al., 1993), leading to weakened radial growth and diminished growth and maintenance of fine roots (Coleman et al., 1996). In their seedling and sapling stages, many indeterminately growing tree species produce large populations of leaves, which are strong sinks throughout the growing season. As older source leaves continually abscise with O_3 stress, total C fixation decreases, resulting in new leaf growth at the expense of allocation to fine roots and storage. Shoot growth in the next season may subsequently be affected (Andersen and Rygielwicz, 1991). Ozone fumigation of plants has resulted in increased plant susceptibility to many species of herbivores (Herms et al., 1996). However, there have been no long-term investigations comparing many different guilds of insects. Herms et al. (1996) found that growth of four species of leaf feeders was enhanced by O_3 treatment

of trembling aspen plants. It is likely that other guilds, such as leaf miners and stem borers, will also be enhanced. This enhancement is likely because high levels of O_3 may interfere with the various local and system signal transduction pathways that plants have evolved to produce both generalized and specific defenses against pathogens and insects (e.g., widespread cell membrane damage, stressed C budgets, etc.).

This chapter focuses on the effects of interacting multiple stresses on growth and physiological processes of northern forest trees with emphasis on the investigations conducted as part of the United States Department of Agriculture (USDA) Forest Service's Northern Global Change Research Program. In our portion of that program, parallel studies of the effects of interacting CO_2 and O_3 on forest trees were conducted on plants in pots in controlled environments and in open top chambers, and in the ground in open top chambers, in a cooperative study at Delaware, OH (USDA Forest Service, Northeastern Research Station), Rhinelander, WI (USDA Forest Service, North Central Research Station), and Alberta, Michigan (Michigan Technological University). Emphasis was on trembling aspen at Rhinelander and Alberta, yellow poplar at Delaware, and on common seed sources of white pine at Delaware and Alberta. Because different responses were observed among species and locations, results are presented here on a species basis.

Trembling Aspen

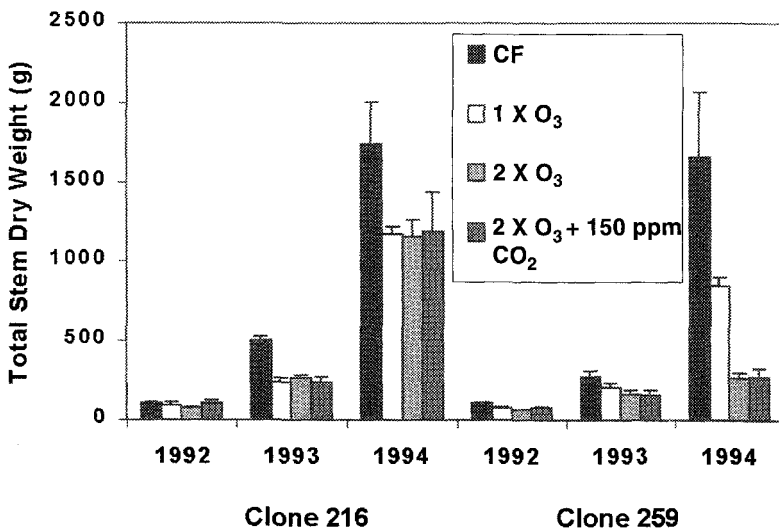
Trembling aspen is the most widely distributed tree species in North America and is a significant ecological and commercial species for the eastern deciduous, boreal, and Rocky Mountain forest biomes (Barrett, 1980; Powell et al., 1992; Hackett and Piva, 1994). It is highly responsive to most stresses and has a high degree of natural genetic variability. Aspen is highly responsive to CO_2 (Brown, 1991; Sharkey et al., 1991), O_3 (Karnosky, 1976; Karnosky et al., 1996; Wang et al., 1986; Berrang et al., 1986, 1989, 1991; Karnosky et al., 1992a,b, 1996), nitrogen (Coleman et al., 1998), water stress (Griffin et al., 1991), and herbivores (Lindroth et al., 1993). The ease of cloning aspen is also an important aspect of this species because various clones can be propagated for use in physiological and molecular studies in which replication is often limited and natural genetic variability of seedling experimental material may mask responses. Karnosky et al. (1996) showed a decrease of 30 to 40% in coefficients of variation for O_3 responses of clones vs. seedlings. This finding was especially striking as the clonal comparisons had only about half as many plants as the seedling studies. By selecting clones with a range of stress tolerances (Table 5.1), the range of natural variability found in seedlings can be mimicked (Karnosky et al., 1996) and the ease of detecting treatment effects is greatly enhanced.

Table 5.1. Origin and Background Ozone-Sensitivity Information of the *Populus Tremuloides* Plants in This Chapter (Karnosky et al., 1996)

Plants	Origin (County)	Foliar Ozone Sensitivity	Growth Ozone Sensitivity
Clone 216	Wisconsin (Bayfield)	Tolerant	Tolerant
Clone 253	Michigan (Leelanau)	Sensitive	Sensitive
Clone 259	Indiana (Porter)	Sensitive	Sensitive
Clone 271	Indiana (Porter)	Intermediate	Intermediate
Seedlings	Michigan (Houghton)	Untested	Untested

Tropospheric Ozone

It is well known that O_3 can affect aspen growth and that this impact varies considerably with genotype (see Fig. 5.1 color insert). Wang et al. (1986) showed an 18 to 20% decrease in aspen growth in nonfiltered vs. filtered air in Dutchess County, New York. In contrast, Karnosky et al. (1992a) found decreases of stem biomass following single season exposures of 80 ppb O_3 varying from 0 to 74%, depending on clone. For the highest seasonal doses (similar to those in the lower Great Lakes region), decreases of 43, 21, and 33%, respectively, were found in leaf, stem, and root biomass across all clones tested. Single season responses may compound with further exposures, particularly in the more sensitive clones such as 259 (Fig. 5.2). Ozone also affected crown architecture by influencing the ratio of long and short shoots retained and by affecting

**Figure 5.2.** Changes in total stem dry weight of aspen clones exposed to elevated O_3 and $O_3 + CO_2$ for 3 years in open-top chambers.

stem and branch diameter and length/weight ratios. Carbon allocation was also impacted (Coleman et al., 1995b). Because the lower leaves of aspen that supply photosynthates to roots senesce prematurely with exposure to O_3 , root growth appears to be particularly sensitive to O_3 (Coleman et al., 1996).

Much of the O_3 response in aspen appears to be controlled by the photosynthetic apparatus. Clonal tolerances to O_3 as determined by previous studies were highly correlated to photosynthetic responses (Coleman et al., 1995a). The seasonal decrease in biomass attributable to O_3 in aspen can be largely explained by decreases in whole-tree photosynthesis estimated for different leaf categories in combination with total leaf area per each category (Coleman et al., 1995a). Premature leaf senescence (Fig. 5.3) plays an important part in the decrease in whole-tree photosynthesis by eliminating photosynthesizing lower leaves (Coleman et al., 1996). Although some photosynthetic compensation occurs in the upper leaves under O_3 exposure, it is not enough to make up for the lost leaf surface area.

The differences in the tolerance of the clones examined in our studies (Karnosky et al., 1992a,b, 1996, 1997) cannot simply be explained by differences in photosynthesis (Ps) rates or stomatal conductance (Coleman et al., 1995a) that would lead to differing internal O_3 doses as predicted by Reich (1987). Sheng et al. (1997) found increased superoxide dismutase (SOD) activity in our O_3 -tolerant aspen clones as compared with O_3 -sensitive clones during long-term O_3 exposures (Fig. 5.4). In particular, the manganese (Mn) SOD and the copper/zinc (Cu/Zn) SOD were simultaneously elevated in an O_3 -tolerant aspen clone (271) following both long-term and short-term exposures. Because plants have evolved with numerous oxidative stress tolerance mechanisms, it seems likely that multiple mechanisms are involved in determining differences in O_3 tolerance. However, the molecular and biochemical mechanisms controlling the physiological differences in O_3 sensitivity of various trembling aspen genotypes remain largely unknown.

Most O_3 exposure research with aspen used open-top chambers (OTCs) as first described by Heagle et al. (1973). While these chambers are closer to outdoor environmental conditions than indoor chambers, there is still a large chamber effect on aspen growth (Hendrey and Kimball, 1994; Karnosky et al., 1996). For example, following three years of growth in the ground, our nonchambered open-plot aspen trees were some 40% less in height and stem biomass than the $1\times$ ambient O_3 chamber trees and 65% less than the charcoal-filtered trees. Characterizing O_3 risks to forests based on OTC studies (see Hogsett et al., 1997) remains speculative because of the large chamber effects found with trees. It is still unclear as to whether these chamber effects actually alter response to O_3 . Future experiments must address this question (McLeod and Long, 1999). Additional approaches are needed to examine the impact of O_3 on forests

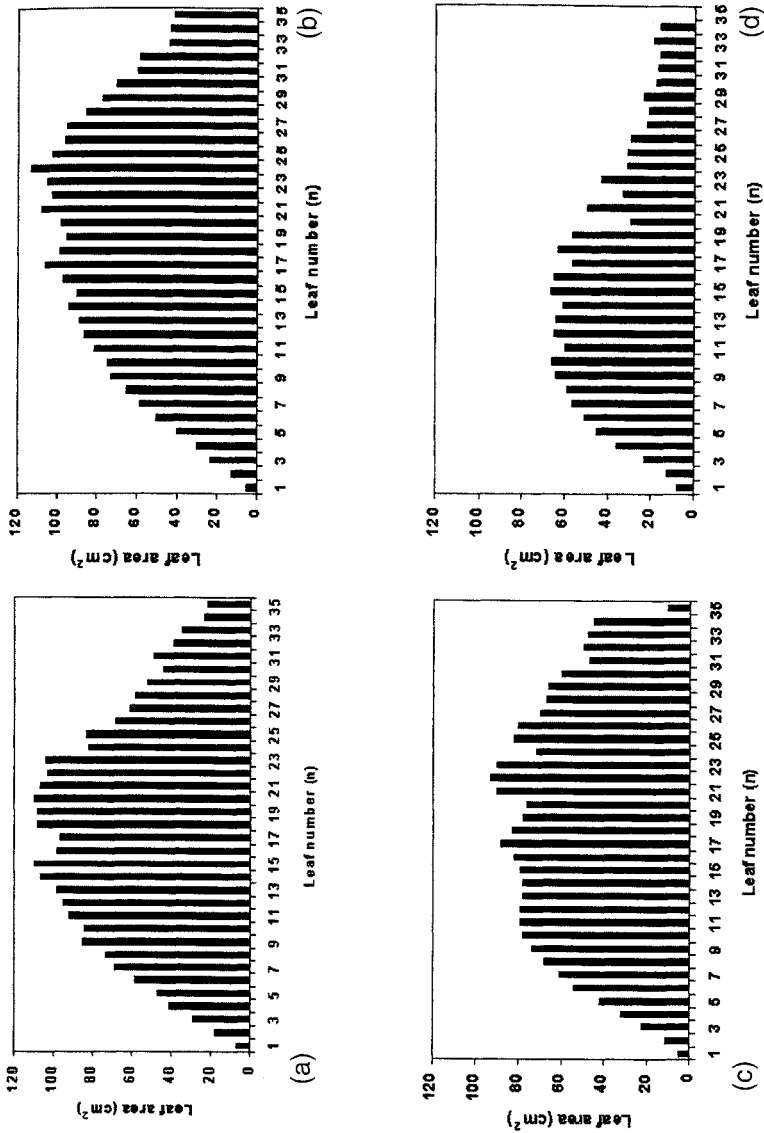


Figure 5.3. Differences in total leaf area (cm²) of aspen clone 216 exposed to (a) CO₂, (b) charcoal-filtered air, (c) O₃, and (d) CO₂ + O₃ for one growing season. Leaves are numbered from the top of the plant.

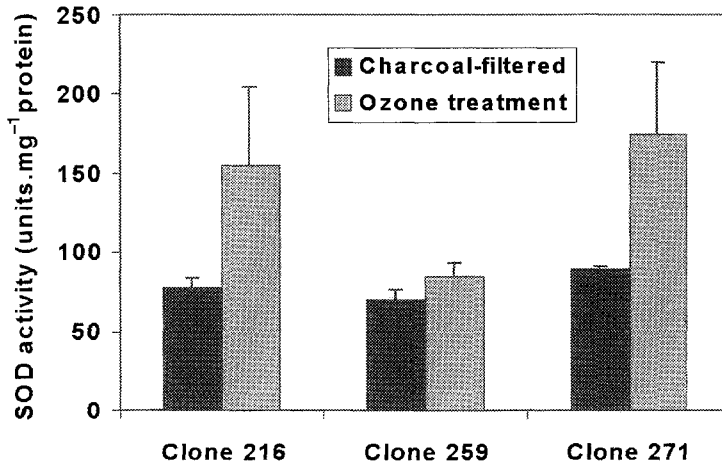


Figure 5.4. Superoxide dismutase (SOD) activity for three aspen clones (216, 259, 271) grown in charcoal-filtered air and O₃ treatment (From Sheng et al., 1997).

and to examine larger-scale forest community and ecosystem-level responses that are impossible to determine in OTCs. For example, to determine the relative growth rates of selected O₃-sensitive and O₃-tolerant clones, trees are grown in pots along a gradient from low to high O₃ in southern Wisconsin. With low O₃ levels, the sensitive and tolerant clones generally grow at about the same rate. However, under elevated O₃, as in southeastern Wisconsin, growth is severely restricted for sensitive clones compared with tolerant clones.

In another study, clones varying in O₃ sensitivity were planted in the field in similarly arranged plantations at areas of high, medium and low O₃ in the Great Lakes region. Ozone bioindication plots, competitive interaction plots, and growth and yield plots were established at each of the sites with identical sets of aspen clones. Preliminary results have shown large clonal growth differences related to O₃ sensitivity.

Carbon Dioxide

Increases in photosynthesis, individual leaf area, whole-crown leaf area, leaf area duration, and LAI have been observed in aspen trees grown in elevated CO₂ (Ceulemans and Mousseau, 1994; Ceulemans et al., 1994; Curtis et al., 1995). Trembling aspen response to elevated CO₂ is similar to that found for other aspen species. For example, researchers have found significant increases in whole-leaf photosynthesis in trembling aspen trees grown under twice ambient CO₂, particularly in the lower

canopy. Leaves in the lower canopy transport C to the roots. Therefore, substantial increases in relative below-ground C allocation were found in elevated CO₂ (Zak et al., 1993).

Aspen grown under elevated CO₂ typically have greater tissue C/N ratios than aspen trees grown under ambient CO₂ (Lincoln et al., 1993). In addition, concentrations of phenolic compounds, including simple phenolics, condensed tannins, and hydrolyzable tannins, increase in trees exposed to CO₂ (Roth and Lindroth, 1994; Lindroth et al., 1995). Thus, elevated CO₂ may have a major impact on the herbivory of aspen leaves (Herms et al., 1996).

Ozone and Carbon Dioxide

We know little about the response of forest trees to the interaction of CO₂ and O₃. There are suggestions that increasing CO₂ may ameliorate O₃ damage (Allen, 1990; Taylor et al., 1994). Amelioration is probably valid for some species (Mortensen, 1995). However, our results with 3 years of study with trembling aspen growing in OTCs suggests that CO₂ at the level of 150 ppm over ambient does not compensate for decreases in growth and biomass caused by elevated O₃ (see Fig. 5.2). In fact, elevated CO₂ plus O₃ decreased photosynthetic rates and carboxylation efficiencies in older leaves in some otherwise O₃-tolerant aspen clones (Kull et al., 1996) and decreased overall leaf size compared to CO₂ alone (see Fig. 5.3). The causes of the lack of compensation for O₃ by elevated CO₂ for aspen have not yet been explained. Some authors have shown decreased antioxidant activity in the presence of elevated CO₂ that might counteract increases in antioxidants found in tolerant clones (Sheng et al., 1997), but antioxidant levels were similar for both O₃-treated and O₃ + CO₂-treated aspen plants in one study (Karnosky et al., 1997).

Nitrogen Interaction

Our work with the interactions of CO₂, O₃, and N fertilization on hybrid poplars and aspen clones has shown that CO₂ enrichment may compensate for O₃ impacts on growth, but the degree of compensation has both environmental and genetic components. To examine some of these interactions we tested 5 hybrid poplar clones selected for a range of growth rates in large pots with adequate water and fertilizer in OTCs, and treated with CO₂ + O₃ (Dickson et al., 1998). The decrease in dry weight in response with O₃ compared with controls was greater in the more productive clones (NM-6, 50% and 31.3 g vs. DN-70, 41% and 16.5 g), while the increase in dry weight in response to increased CO₂ (Fig. 5.5) was essentially the same in all clones (NM-6, 36% vs. DN-70,

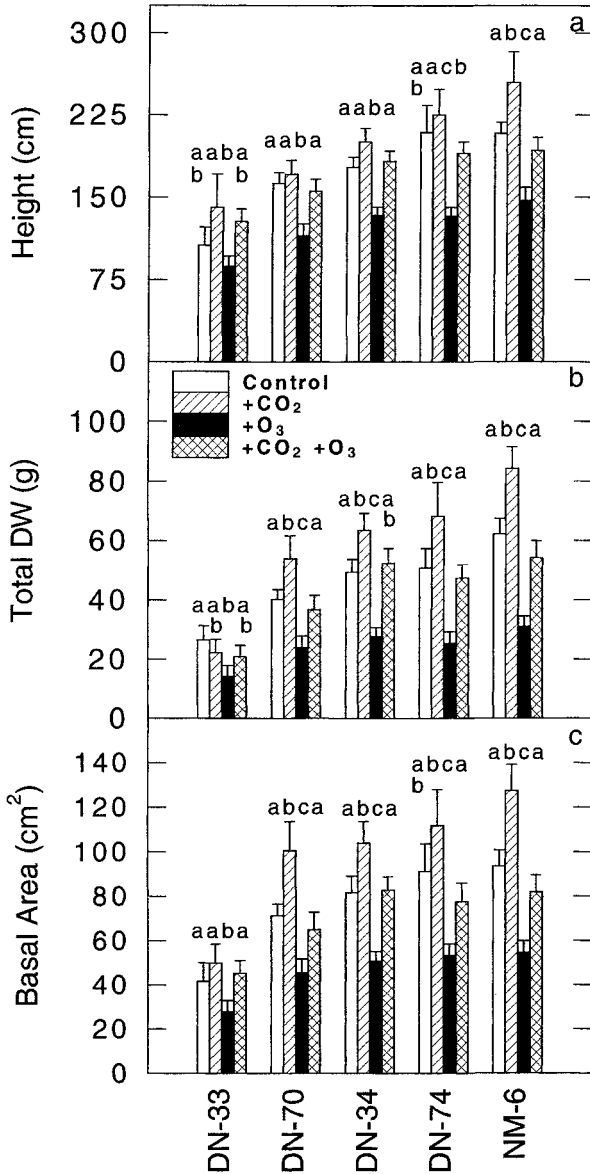


Figure 5.5. (a) Height, (b) total dry weight (DW), and (c) basal area of 5 hybrid poplar clones exposed to CO₂, O₃, and CO₂ + O₃ for one growing season (From Dickson et al., 1998).

34%). In addition, CO₂ exposure alleviated the detrimental response to elevated O₃ (see Fig. 5.5). However, the O₃ exposure also negated the increase in growth from CO₂.

In OTCs, we also tested 3 aspen clones that vary in sensitivity to O_3 . The water and fertilizer regimes were the same as for the poplar hybrids, but the aspen were grown in large pots for unlimited root growth and access to nutrients. Carbon dioxide exposure increased average dry weights 37% and O_3 exposure decreased average dry weight 28%. However, there were large clonal differences in response to CO_2 and O_3 in combination. Carbon dioxide exposure of clone 271 increased total dry weight by 71% compared with controls, while dry weight production from the O_3 - and $CO_2 + O_3$ -exposed plants did not differ. Ozone exposure, however, completely negated the CO_2 response. In contrast, with clone 216 (O_3 -intermediate) and clone 259 (O_3 -sensitive), CO_2 exposure increased total dry weight only 20% while O_3 exposure decreased dry weight 38% (216) and 50% (259), and the addition of CO_2 to the O_3 exposure did not ameliorate yield losses from O_3 .

In another study of the interactions of CO_2 , O_3 , and N availability, the clones 216 and 259 were grown in growth chambers, in large pots and with different N fertilization regimes. In the controlled-access regime, plants were fertilized daily with a complete nutrient solution based on a 3% relative addition rate (RAR) (Ingestad and Lund, 1986). The 3% RAR is designed to maintain these aspen clones at about 2% total plant nitrogen content but limit maximum potential growth rate (Coleman et al., 1998). In the unlimited access regime, plants were fertilized daily with a complete fertilizer solution containing N at a concentration (16 mmol) considerably in excess of maximum growth requirements. When N was limiting growth, there was no response to increased CO_2 by either clone; O_3 decreased total dry weight (216, 10% and 259, 35%), and CO_2 added to the O_3 exposure did not ameliorate the O_3 response (Fig. 5.6). In contrast, when N was

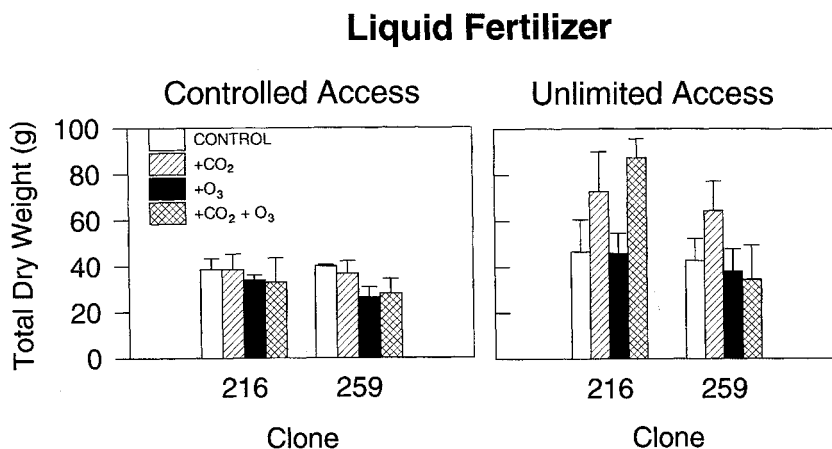


Figure 5.6. Total dry weight of two aspen clones exposed to CO_2 , O_3 , and $CO_2 + O_3$ growing with limiting and excess nitrogen fertilizer (From Coleman et al., 1998).

not limiting growth, CO₂ increased dry weight production in both clones (216, 60% and 259, 49%); O₃ exposure had little effect on either clone (259 decreased 12%), and CO₂ added to the O₃ exposure completely counteracted the O₃ response in clone 216 (actually increased dry weight production 85% over controls) but did not counteract the O₃ response of clone 259 (see Fig. 5.6). These results indicate that it will be very difficult to predict average species response to increasing concentrations of CO₂ and O₃, other environmental stresses, and their interactions, because genotype has such a large and variable effect on plant responses. Ecological risk assessment based on a limited number of studies of seedling populations (Hogsett et al., 1997) cannot account for the potentially large impact on sensitive genotypes. Risk assessment could be considerably strengthened, however, if information were available on the potential range of genotypic response expected within a species (Taylor, 1994).

Multiple Stresses and Insects

Studies of aspen foliage from plants treated in exposure chambers have shown that increased CO₂ and O₃ alter the chemical composition of the foliage, which in turn influences both its resistance to insect attack and its nutritional value for insect growth. Using plant material from growth chamber experiments, we found that elevated O₃ generally increased insect growth, while elevated CO₂ generally decreased insect growth. However, the increase in foliage volume expected under increased CO₂ may be partially offset by increased insect feeding, thus decreasing the potential increase in tree growth from CO₂ (Herms et al., 1996). Likewise, a decrease in foliage volume from O₃ damage may not decrease plant growth as much if insects consume less foliage from the O₃-damaged trees. Lindroth et al. (1993) demonstrated that light environment affects the dynamics of O₃ interactions with insects. Preliminary results from field studies of aspen show that foliar insect populations increase under O₃ and CO₂ (Mattson et al., unpublished).

Yellow Poplar

Yellow poplar is an ecologically and economically important hardwood species with a wide geographical range (Fowells, 1965). It grows throughout most of the eastern United States from southern New England west through Michigan and southern Ontario. At the northern end of its range, yellow poplar is usually found in stream bottoms and valleys at elevations below 300 m (Beck, 1990). It is a fast-growing shade-intolerant species with an indeterminate growth habit. It thrives on many soil types

but generally grows best on moderately moist, well-drained, and loose-textured soils. It does not grow well in very dry or very wet situations.

Tropospheric Ozone

Because of yellow poplar's wide geographical range, it is potentially exposed to elevated levels of tropospheric ozone (O_3), the most widespread and phytotoxic of the atmospheric pollutants on forest ecosystems (Lefohn and Pinkerton, 1988; Linzon and Chevone, 1988; Simini et al., 1992). Yellow poplar has been rated as O_3 -sensitive based on foliar symptoms and induced leaf abscission and has been used as a bioindicator (Davis and Skelly, 1992a,b). Although considered O_3 -sensitive, Simini et al. (1992) reported foliar stipple injury and premature leaf abscission without any significant negative growth effects for field-planted yellow poplar seedlings exposed to ambient O_3 in OTCs in Pennsylvania. Consistent growth responses to O_3 have not been reported with this species because different studies have shown both decreases and increases in growth (Kress and Skelly, 1982; Mahoney et al., 1984; Jensen, 1985; Chappelka et al., 1988; Jensen and Patton, 1990; Tjoelker and Luxmoore, 1991; Cannon et al., 1993). Most of the O_3 growth and physiological response studies of seedling yellow poplar have used 1-year-old bare root stock in environment-controlled systems, such as greenhouses, growth chambers, or continuously stirred tank reactors (Kress and Skelly, 1982; Chappelka et al., 1988; Roberts, 1990; Jensen and Patton, 1990; Cannon et al., 1993; Cannon and Roberts, 1995). Typical results of such studies are those of Chappelka et al. (1988) who reported decreases in net photosynthesis (P_n) and stomatal conductance (g_s) in seedlings exposed to elevated ozone (100 to 150 ppb O_3) without growth or biomass effects, while Jensen (1985) reported relative growth rate was decreased 35% in seedlings exposed to 100 ppb O_3 for 20 weeks compared with control seedlings.

Results from OTC exposures of potted yellow poplar seedlings have been inconsistent. Tjoelker and Luxmoore (1991) exposed potted yellow poplar seedlings to O_3 ranging from 32 to 108 ppb (7-hour seasonal mean) in OTCs for 18 weeks and reported no significant effect on P_n , water use efficiency or, final whole-plant biomass but did report increased leaf abscission. They hypothesized that the indeterminate growth habit of yellow poplar permitted compensatory leaf growth which could have ameliorated O_3 effects on biomass production. Rebbeck (1996a) reported a stimulation in growth and plant biomass after one season of exposure to $107 \text{ ppm h}^{-1} O_3$ in OTCs, but after two seasons of exposure, root/shoot ratios and leaf area declined with increasing exposure to O_3 (Fig. 5.7). Net photosynthesis of yellow poplar leaves decreased 21 to 42% exposed to 1.7 times ambient O_3 compared with control seedlings, while g_s was generally unaffected (Rebbeck and Loats, 1997) (Figs. 5.8 and 5.9). There may be a

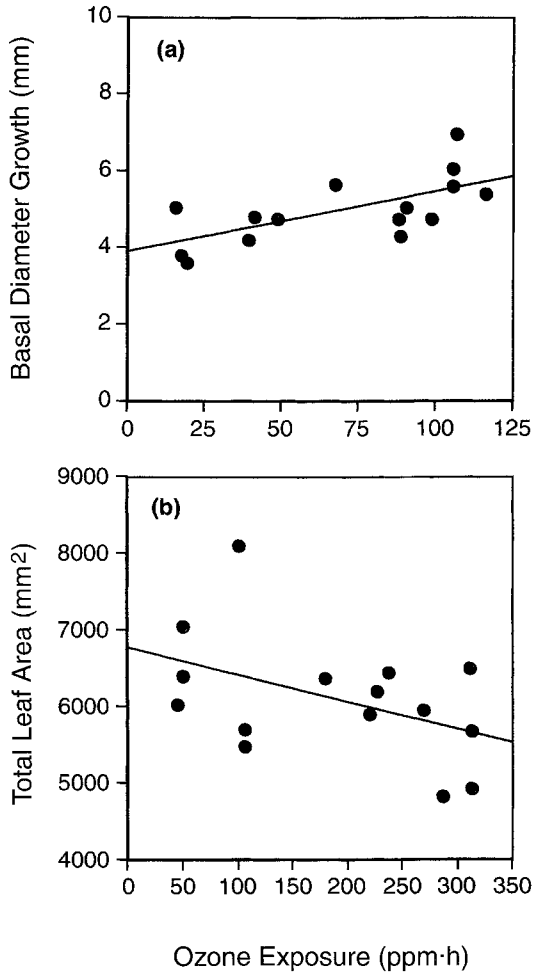


Figure 5.7. The relationship between O₃ exposure (ppm h⁻¹) and yellow-poplar growth: (a) basal diameter growth (mm) in 1990 and (b) total leaf area (mm²) in 1991 (From Rebbeck, 1996a).

significant lag in the expression of growth effects following decreases in C fixation after exposure to elevated O₃. To date, there are no published reports on the response of saplings or mature yellow poplar to gaseous pollutants. Studies are underway to investigate the effects of elevated O₃ plus elevated CO₂ on plantation-grown yellow poplar seedlings over five growing seasons to determine how this species responds as it ages and increases in size. The goal is to extrapolate seedling pollutant response data to saplings and older trees grown under more realistic growing conditions.

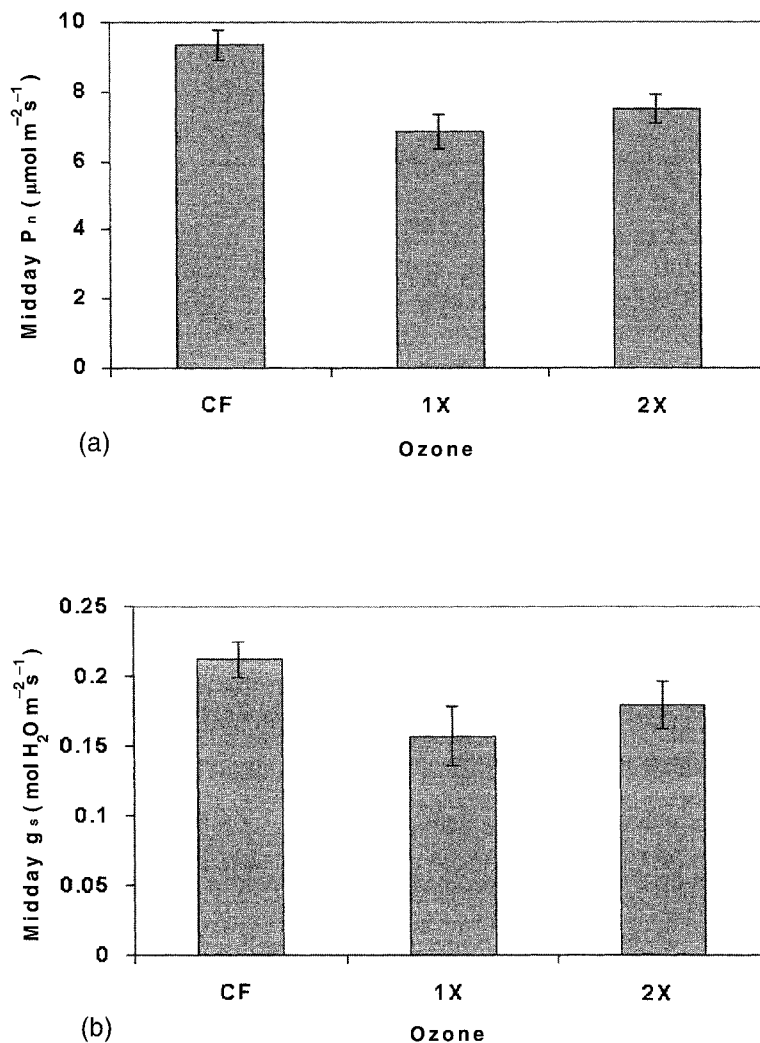


Figure 5.8. Seasonal midday (a) net photosynthesis (P_n) and (b) stomatal conductance (g_s) of yellow-poplar foliage exposed to CF, 1x, and 2x ambient O_3 for two growing seasons (From Rebbeck and Loats, 1997).

Carbon Dioxide

Enhanced growth of seedling yellow poplar exposed to increased concentrations of CO_2 was found by Norby and coworkers in the southeastern United States (O'Neill et al., 1987; Norby and O'Neill, 1991; Norby et al., 1992; Wullschlegel et al., 1992; Gunderson et al., 1993). O'Neill et al. (1987) found that newly germinated yellow poplar seedlings exposed to

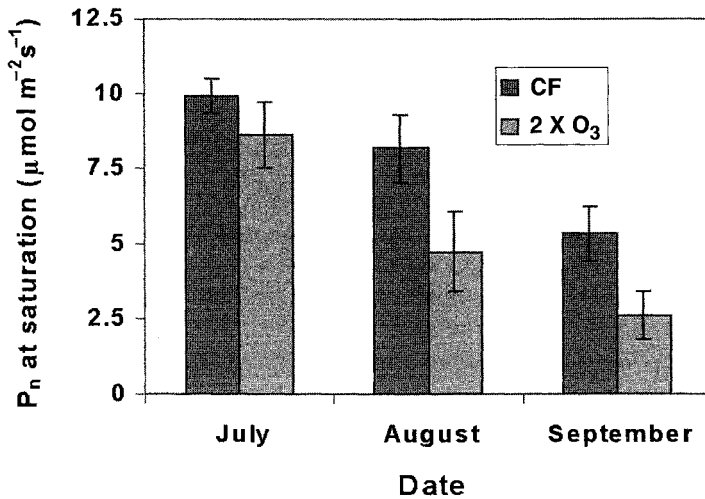


Figure 5.9. Net photosynthesis (P_n) at light saturation calculated from light response curves for leaves of yellow-poplar seedlings exposed to either charcoal-filtered air (CF) or twice ambient ozone ($2\times\text{O}_3$) during the second season of exposure (From Rebbeck and Loats, 1997).

692 ppm CO_2 for 24 weeks in growth chambers had significantly greater root (99%), leaf (69%), stem diameter (20%), and total dry weights (73%) while specific leaf area was significantly less (-21%) than for seedlings grown in ambient CO_2 (367 ppm). Norby and O'Neill (1991) exposed fertilized and unfertilized seedlings to ambient, +150 ppm, or +300 ppm CO_2 for 24 weeks and reported the only increase in dry weight associated with enriched CO_2 occurred in roots (25 to 40%). Leaf area was slightly decreased in elevated CO_2 . Some of the commonly reported physiological and growth responses associated with elevated CO_2 , such as decreased stomatal conductance (g_s) and photosynthetic down-regulation/acclimation were not consistently observed in these studies. In fact, stomatal conductance and P_n increased with increasing CO_2 concentration throughout the study. Nutrient deficiency did not impede growth enhancement in enriched CO_2 . In a subsequent 3-year OTC study of field-planted, unfertilized and unirrigated yellow poplar seedlings exposed to elevated CO_2 , Gunderson et al. (1993) found no photosynthetic down regulation (12 to 144% enhancement) and limited effects on g_s . These responses were consistent across leaf age and canopy position. Foliar total chlorophyll content was decreased 27% in seedlings exposed to +300 $\mu\text{l l}^{-1}$ CO_2 for 24 weeks. Significant decreases in respiration of foliage exposed to elevated CO_2 were also observed (Wullschleger et al., 1992). Despite observed enhancement in leaf-level P_n and lower rates of leaf respiration, whole-plant biomass production did not increase (Norby et al., 1992). They suggested

that the lack of above-ground response resulted from changes in C allocation patterns that decreased leaf production and increased fine root production.

Ozone and Carbon Dioxide

To predict how yellow poplar might respond to future climate changes, a 5-year OTC study to investigate the response to enriched CO₂ in the presence of elevated O₃ was conducted in Delaware, Ohio. It was hypothesized that negative O₃ effects would be ameliorated by exposure to elevated CO₂, and that the response of older trees to these atmospheric gases would be similar to seedlings. Throughout the study, most of the typical enhancement responses observed were associated with exposure to enriched CO₂, with few or no effects associated with exposure to elevated O₃ (Rebbeck, 1996b). After the first season of exposure (20 weeks), no impacts on stem height or basal diameter were observed in seedlings grown in twice ambient O₃ (2×O₃, cumulative exposure of 136 ppm h⁻¹) (Table 5.2). Basal stem diameter of seedlings exposed to twice ambient O₃ + twice ambient CO₂ (2×O₃ + 2×CO₂) increased (13 to 21%) compared with seedlings grown in charcoal-filtered, one times ambient (1×O₃), or 2×O₃-air (Rebbeck, 1993; Rebbeck et al., 1993). Stimulated height and diameter growth of yellow poplar exposed to 2×O₃ + 2×CO₂-air continued for three growing seasons (Rebbeck, 1996b). After two years of exposure, 2×O₃ + 2×CO₂ grown yellow poplar tended to have greater leaf (6%), stem (25%), branch (14%), and root (20%) biomass, and total leaf area (12%) compared with all other treatments. Photosynthetic enhancements (24 to

Table 5.2. Total Stem Height and Diameter of Yellow Poplar Seedlings Exposed to Ambient and Elevated O₃ + Elevated CO₂ in Delaware, Ohio, from 1992 through 1994

Treatment	Total Stem Height (cm)		
	1992	1993	1994
CF	94.85 ± 3.14a	274.97 ± 10.36a	365.9 ± 20.8a
1×O ₃	90.84 ± 4.44a	267.35 ± 8.66a	343.9 ± 20.2a
2×O ₃	96.89 ± 4.08a	285.44 ± 8.43a	382.2 ± 24.3a
2×O ₃ + CO ₂	102.88 ± 5.04b	304.70 ± 10.47b	460.0 ± 11.1b
Treatment	Basal Diameter (mm)		
	1992	1993	1994
CF	9.85 ± 0.5a	13.99 ± 0.78a	45.17 ± 2.73a
1×O ₃	8.93 ± 0.5a	29.24 ± 1.39a	39.46 ± 3.37a
2×O ₃	9.47 ± 0.5a	29.71 ± 1.17a	43.85 ± 2.98a
2×O ₃ + CO ₂	11.33 ± 0.5b	34.41 ± 1.61b	53.94 ± 3.18b

* Each value is a mean of 36 trees ± 1 standard error. Means followed by different letters are significantly different at $P < 0.05$ (Rebbeck, 1996b).

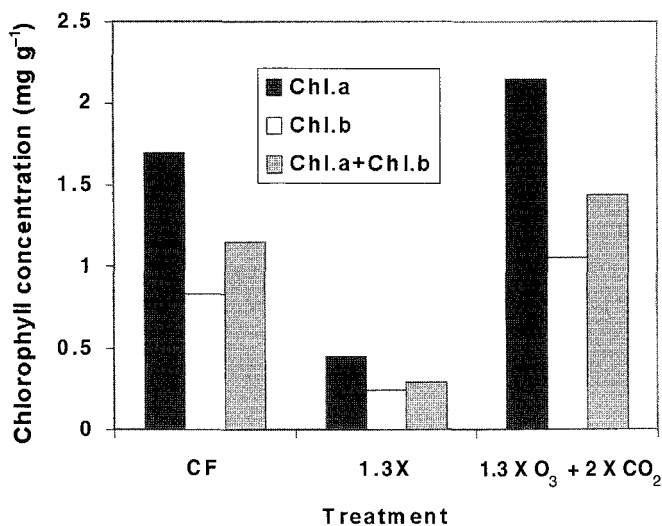


Figure 5.10. Response of mean foliar chlorophyll concentrations of yellow poplar foliage exposed to elevated O₃ (1.3 × ambient ozone) alone or in combination with twice ambient CO₂ (1.3 × O₃ + 2 × CO₂) for one growing season (From Carter et al., 1995).

48%) were observed for seedlings exposed to 2 × O₃ + 2 × CO₂-air for one and two seasons (Rebbeck et al., 1995; Rebbeck, 1996b), while foliar chlorophyll (Fig. 5.10) and N content decreased (Carter et al., 1995; Rebbeck et al., 1995; Scherzer and Rebbeck, 1995). After four seasons of treatment, O₃ alone had no effect on foliar N concentrations; however, 2 × O₃ + 2 × CO₂-air decreased N concentrations by 18 to 40% (Scherzer et al., 1998). Preliminary analyses indicate, after 5 seasons of exposure, continued enhancement of growth and photosynthesis in 2 × O₃ + 2 × CO₂-air. Because there were limited O₃ effects on the growth or physiology of these seedlings, it was difficult to ascertain the ameliorative effects of enriched-CO₂. Most of our enriched-CO₂ responses observed in Ohio were similar to those reported in the southeastern United States (Norby and O'Neill, 1991; Norby et al., 1992; Wullschlegel et al., 1992; Gunderson et al., 1993). These findings suggest that field-planted yellow poplar, when exposed to enriched CO₂ and grown with limited nutrients, limited soil moisture, and ambient or elevated O₃ will display enhanced growth and photosynthetic assimilation.

Nitrogen and Water

Little direct information on the growth and physiology of yellow poplar is available in response to CO₂ and O₃ combined with water stress and

nitrogen stress (limited or excess). However, the influence of water stress on modulating the response of yellow poplar to O_3 has been studied (Roberts, 1990; Cannon et al., 1993; Cannon and Roberts, 1995). In growth chamber studies, water stress significantly decreased P_n , g_s , and transpiration (T_s) (by more than 70%) but O_3 treatments generally had little effect on physiological or growth parameters. The combination of water stress and 70 ppb O_3 significantly decreased root biomass and root/shoot ratio (Cannon et al., 1993). Roberts (1990) reported a significant additive effect of drought and O_3 on xylem water potential. These studies indicate that significant interactions involving low levels of O_3 and short periods of water stress may have considerable effects on stomatal physiology. Tjoelker and Luxmoore (1991) reported that yellow poplar whole-plant dry weight did not respond to either O_3 or N (levels ranging from 58 to 172 $\mu g\ g^{-1}$) but allocation to fine roots did increase in low-N soils.

Eastern White Pine

Eastern white pine is a widely distributed component of the eastern US forest and is the largest of the northeastern conifers (Fowells, 1965). White pine has played an important role throughout our history as the “peace tree” of the Native Americans and as a valuable source of lumber for construction of eastern and midwestern cities. It also is important ecologically because it rapidly invades old fields and is intimately associated with oaks (Stine and Baughman, 1992). White pine has long been known to be sensitive to multiple environmental stresses (Kozlowski, 1979), although there are fewer published works on the interacting stresses on white pine than on aspen and yellow poplar. An exception is the pioneering work of Dochinger et al. in the USDA Forest Service, Northeastern Forest Experiment Station in the 1960s who studied the interactions of sulfur dioxide and tropospheric O_3 as influenced by other environmental factors (Dochinger et al., 1970; Houston, 1974).

Tropospheric Ozone

White pine’s sensitivity to O_3 has been known for many years (Kozlowski and Constantinidou, 1986a). When white pine experiences acute O_3 episodes, its current-year needles develop silver flecks and tip dieback (“tipburn”) (Woodman, 1987). Chronic symptoms include chlorosis and premature needle abscission of older needles. High O_3 levels throughout the southeastern US have been shown to cause extensive damage to white pine on a watershed scale, including premature needle abscission and decreased basal area increment (McLaughlin, 1985; Swank and Vose, 1990). Moreover, McLaughlin et al. (1982) showed that chronic O_3 stress caused declined vigor, increased respiration, and altered C allocation

patterns in field-grown white pine. However, Bennett et al. (1994) in a review of air pollution surveys of white pine found that hypersensitive white pine individuals are no longer present in the forest because they have succumbed to past O_3 exposures. More recent tree-ring studies, in Acadia National Park, Maine, suggest white pine tree-ring growth is affected negatively by O_3 level and duration (Bartholomay et al., 1997).

As in aspen, white pine has a high degree of genetic variability in response to O_3 (Houston and Stairs, 1973). Karnosky (1981) found a higher mortality rate in O_3 -sensitive genotypes of eastern white pine stands in southern Wisconsin. That study indicated that natural selection may have already altered many stands in higher O_3 regions of the Northeast. To examine possible genetic differences between white pine from O_3 selected (sensitive genotypes lost) and nonselected regions, a large cooperative study was initiated by a consortium of scientists from Michigan Technological University; USDA Forest Service, Northeastern Forest Experiment Station, and the USDA Forest Service, North Central Research Station to compare the responses of seedlings from Ohio (where O_3 levels have been historically high) and from northern Michigan (where O_3 levels have been historically quite low). Seedlings from these two locations were exposed to ambient O_3 ($1\times O_3$), twice ambient O_3 ($2\times O_3$) and $2\times O_3$ + elevated CO_2 in OTCs at 2 locations: a clean-air site in the upper peninsula of Michigan and a relatively high O_3 site near Delaware, Ohio.

At the Alberta, Michigan site, we found no significant differences in height, stem, root, or current year needle biomass in response to the O_3 treatments, but there were significant O_3 effects on diameter growth and mature needle retention for the Michigan source but not for the Ohio source. At the Ohio site, O_3 had a small stimulating effect on height growth of white pine in the first year. However, after 3 years, there was no significant effect on height or diameter growth from $2\times O_3$ (Rebbeck, 1996b).

Carbon Dioxide

Little is known about the effects of elevated CO_2 on white pine. In three recent reviews of the CO_2 literature (Ceulemans and Monsseau, 1994; Curtis, 1996; Wullschlegel et al., 1997), only one reference was cited. Bazzaz et al. (1990) reported a 20% increase in biomass growth, a 14% decrease in leaf area, and an 11% increase in root/shoot ratio with elevated CO_2 in a glasshouse experiment with white pine seedlings. Although there is essentially no information on the response of white pine to elevated CO_2 , white pine can be expected to respond like other conifers and C_3 plants with increases in photosynthesis, biomass, and water use efficiency and decreases in N content (Conroy and Hocking, 1993; Ineichen et al., 1995; Wullschlegel et al., 1997).

Ozone and Carbon Dioxide

Very little research has been done on the interacting effects of O_3 and CO_2 on white pine. The only available information on the combined effects of O_3 and CO_2 on white pine is from the cooperative OTC experiment in Michigan and Ohio. At the Michigan site, in the first two years after planting, O_3 decreased needle length compared with the charcoal-filtered (CF) treatment, while the needle length in the $O_3 + CO_2$ treatment did not differ from the CF treatment. This result indicates that CO_2 may offset some detrimental effects of O_3 . After four years of growth in the OTCs, O_3 increased the loss of older needles and decreased total plant dry weight. Carbon dioxide in the $O_3 + CO_2$ treatment partially counteracted needle senescence and increased stem dry weight and total plant dry weight compared with both O_3 and the CF treatment.

At the Ohio site, there were no significant growth differences attributable to $O_3 + CO_2$ in the first 4 growing seasons. There was a slight stimulatory effect of $O_3 + CO_2$ in height growth in the first year, but in the second year height was less than the control. In the second year, $O_3 + CO_2$ stimulated photosynthesis compared with the O_3 and control treatments. Chlorophyll content of the older needles was decreased by $O_3 + CO_2$ by 40 to 50% compared with the controls. Despite these physiological differences, no significant growth effects were detected with $O_3 + CO_2$ compared with other treatments (Rebbeck, 1996b).

Nitrogen and Other Multiple-Stress Interactions

There have been few studies of the effect of N on white pine's response to interacting multiple stressors. We would expect low nitrogen availability to limit the effect of CO_2 on white pine as in other plants (Conroy and Hocking, 1993). Moreover, we would expect low nitrogen availability to increase the detrimental effects of O_3 on white pine growth. Eberhardt et al. (1988) found no effect of N fertilizer on the O_3 response in white pine and Reich et al. (1988) found that increased N from acid rain in combination with O_3 had a deleterious effect on white pine growth depending upon soil conditions in a microcosm experiment. In a related study, Stroo et al. (1988) found that acid rain (i.e., lower pH) and O_3 exposure decreased mycorrhizae infection and therefore nutrition in white pine. McLaughlin (1985) reported that the interactions of O_3 and SO_2 atmospheric pollutants were primary causal agents in white pine decline in the eastern US, while genetic variation accounted for a 5-fold difference in the response to the interacting stressors. No reports of the effects of interacting stressors on pest and disease incidence in white pine are currently available. Based upon the research to date, we would expect significant multiple-stress pest interactions in white pine as found in our other species.

Summary and Future Direction

The interacting effects of multiple stresses on growth and physiological processes in northern forest trees are complex, and the mechanisms of sensitivity to the combinations of multiple stressors remain unknown. There are major differences among species and genotypes within species in their responses to various interacting stressors. Aspen is particularly sensitive to elevated O_3 , CO_2 , and their interactions, while hybrid poplars, yellow poplar, and white pine vary in sensitivities. Nutrition has an important effect on the response to multiple stressors, with poorer nutrition usually predisposing plants to the effects of other stressors. Multiple stressors also have an important effect on ecological factors such as insect feeding that deserves more attention.

To date, most studies of multiple-stress interactions in trees have been conducted on small trees growing in pots and/or in controlled environments and OTCs. Such experiments cannot incorporate the host of biotic and abiotic interactions that occur in a forest ecosystem (Koch and Mooney, 1996). Large-scale field experiments are needed in the future to minimize chamber effects and better depict "real world" conditions (Hendrey and Kimball, 1994; McLeod and Long, 1999). To accomplish the goal of studying the interacting effects of multiple stressors on physiological processes and growth of northern temperate forest ecosystems, we have initiated a free air carbon dioxide enrichment (FACE) experiment in Rhinelander, Wisconsin, to examine the interacting effects of elevated CO_2 and O_3 on physiological processes (C and N allocation) growth, survival, and competition of pure and mixed stands of aspen clones, sugar maple (*Acer saccharum* Marsh.), and paper birch (*Betula papyifera* Marsh.) (Karnosky et al., 1999). This study design consists of twelve 30 m FACE rings—a factorial combination of 4 treatments (ambient control; 560 ppm CO_2 ; 80 to 100 ppb O_3 ; and $CO_2 + O_3$) with three replications. The FACE technology features a vertical vent pipe delivery system equipped with baffles as well as a centralized O_3 delivery system. This experiment offers the opportunity for an interdisciplinary team of scientists to study the mechanisms of interacting multiple-stress effects on a larger scale. This approach is expected to lead to a better understanding in the future of forest ecosystem responses to the ever-changing complexities of the environment.

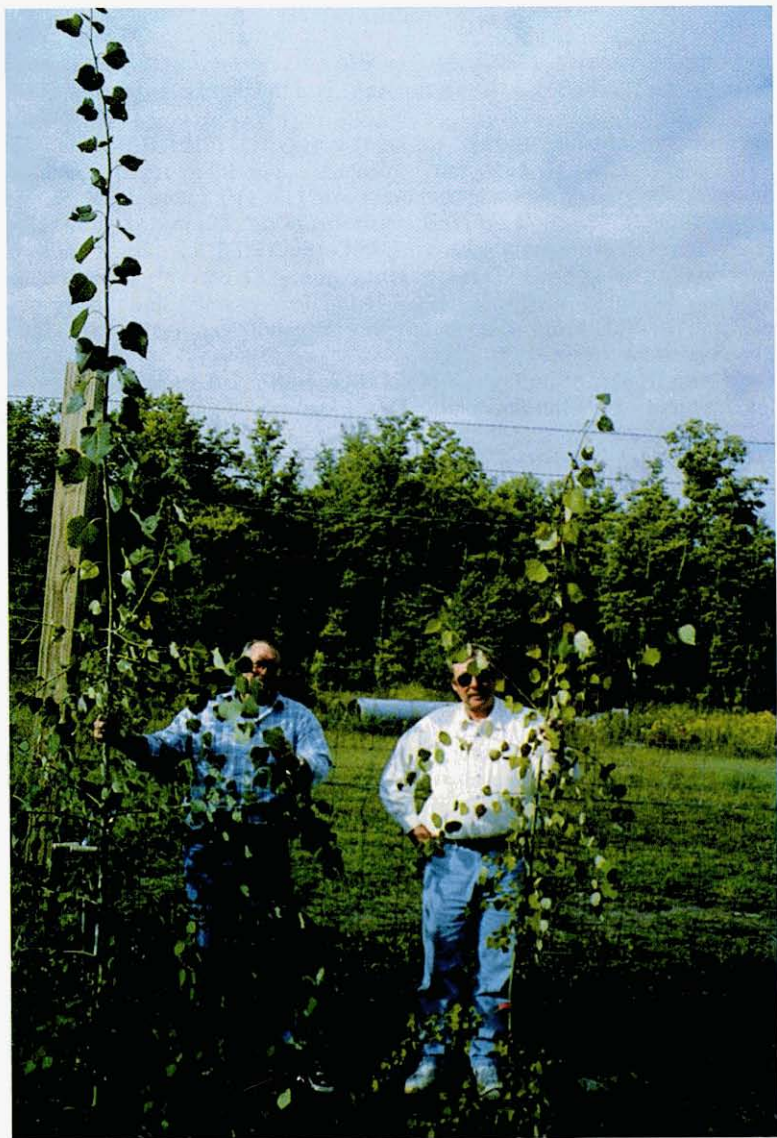


Figure 5.1. Two-year-old aspen trees of clone 259, an ozone-sensitive genotype, grown in open-top chambers at Alberta, MI, charcoal-filtered (right) vs. Milwaukee, WI, O_3 profile (left).

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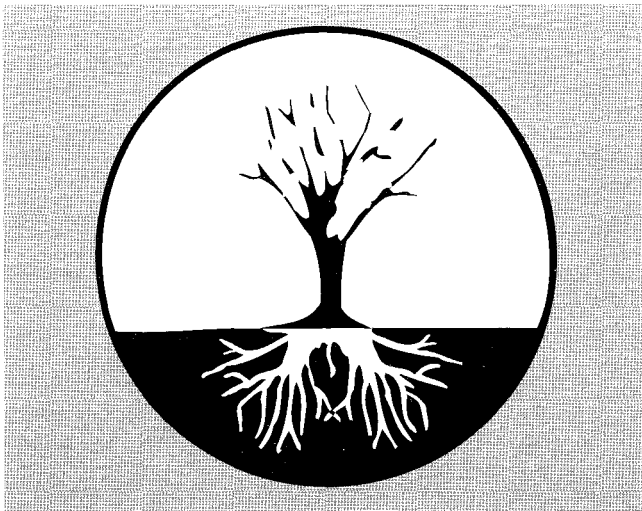
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