

An effort by Ensing et al. (1986) to assess the impact of O₃ on yield of peanut in Ontario found that year-to-year variation was greater than that they could account for either by correlation of O₃ concentration with yield of test plots or by EDU treatment. They conclude that a correlative approach to assessing losses due to O₃ will not work.

Finally, a 4-year study of black cherry using EDU as a protectant was conducted by Long and Davis (1991). They found significant effects with a 47% reduction in aboveground biomass compared to EDU-treated trees. The authors do not believe the difference was due to a stimulation in growth due to nitrogen in the EDU, but they did not conduct studies, as recommended by Kostka-Rick and Manning, to characterize the EDU system for black cherry.

In summary, the EDU method for assessing the impact of O₃ is promising, particularly for remote areas or as a validation tool for existing crop-loss models. The system must be carefully characterized, however, as pointed out by many of its users.

It should be noted that, in spite of the promise shown by EDU as a field protectant over many years, it has not been developed commercially and, until recently, was unavailable for further experimentation.

5.6.6 Summary

Several conclusions were drawn from the various approaches used to estimate crop yield loss. In 1986, U.S. Environmental Protection Agency (1986) established that 7-h/day growing season mean exposures to O₃ concentrations above 0.05 ppm were likely to cause measurable yield loss in agricultural crops. At that time, few conclusions could be drawn about the response of deciduous or evergreen trees or shrubs because of the lack of information about the response of such plants to season-long exposures to O₃ concentrations of 0.04 to 0.06 ppm and above. However, the 1978 and 1986 criteria documents (U.S. Environmental Protection Agency, 1986) indicate that the limiting values for foliar injury to trees and shrubs was 0.06 to 0.10 ppm for 4 h. Since 1986, considerable research has been conducted, and the sensitivity of many tree species has been established.

Based on research published since U.S. Environmental Protection Agency (1986), a number of conclusions can be drawn.

- (1) An analysis of 10 years of monitoring data from more than 80 to almost 200 nonurban sites in the United States established ambient 7-h growing season average concentrations of O₃ for 3 or 5 mo of 0.051 to 0.060 ppm and 0.047 to 0.054 ppm, respectively. The SUM06 exposures ranged from 24.8 to 45.2 ppm-h for 3 mo, and 32.7 to 58.0 ppm-h for 5 mo (Tingey et al., 1991).
- (2) The results of OTC studies that compare yields at ambient O₃ exposures with those in filtered air and retrospective analyses of crop data summarized in this section establish that the current ambient (0.04 to 0.05 ppm) concentrations of O₃ at some sites are sufficient to reduce the yield of major crops in the United States. The results of research since 1978 do not invalidate the conclusions of the U.S. Environmental Protection Agency (1978, 1986) that visible injury due to O₃ exposures reduces the market value of certain crops and ornamentals where leaves are the product (spinach [*Spinacea oleracea*], petunia, geranium [*Pelargonium hotortorum*], and poinsettia [*Euphorbia pulcherrima*] for

instance), and that such injury occurs at O₃ concentrations (0.04 to 0.10 ppm) that presently occur in the United States.

- (3) A growing season SUM06 exposure of 26.4 ppm·h, corresponding to a 7-h growing season mean of 0.049 ppm and a 2HDM of 0.094 ppm may prevent a 10% loss in 50% of the 54 experimental cases analyzed by Tingey et al. (1991) and Lee et al. (1994a,b). A 12-h growing season mean of 0.045 should restrict yield losses to 10% in major crop species (Lesser et al., 1990).
- (4) Concentrations of O₃ and SUM06 exposures, depending on duration, that occur at present in the United States are sufficient to affect the growth of a number of trees species. Given the fact that multiple-year exposures may cause a cumulative effect on the growth of some trees (Simini et al., 1992; Temple et al., 1992), it is likely that a number of species currently are being impacted, even at ambient exposures (0.04 to 0.05 ppm).
- (5) Exposure-response functions for 51 cases of seedling response to O₃ (Hogsett et al., 1995), including 11 species representing deciduous and evergreen growth habits, suggest that a SUM06 exposure for 5 mo of 31.5 ppm·h would protect hardwoods from a 10% growth loss in 50% of the cases studied. A SUM06 exposure of 42.6 ppm·h should provide the same level of protection for evergreen seedlings. It should be noted that these conclusions do not take into the account the possibility of effects on growth in subsequent years, an important consideration in the case of long-lived species.
- (6) Studies of the response of trees to O₃ have established that, in some cases poplars (*Populus*) and black cherry, for instance, trees are as sensitive to O₃ as are annual plants, in spite of the fact that trees are longer lived and have lower rates of gas exchange, and, therefore, a lower uptake of O₃.
- (7) The use of the chemical protectant, EDU is of value to establish O₃-related losses in crop yield and tree growth, providing care is exercised in establishing the appropriate dosage of the compound to protect the plants without affecting growth. Ethylene diurea cannot be used to predict the response of plants at concentrations greater than those that exist in ambient air.

5.7 Effects of Ozone on Natural Ecosystems

5.7.1 Introduction

Ozone is a regionally distributed phytotoxic air pollutant capable of changing the chemical environment of forests. It is the only gaseous air pollutant capable of exposing a large region without a leaving a permanent trace of its presence. Ozone molecules are ephemeral. They decompose rapidly to oxygen and free radicals and leave no residuals; therefore, O₃-caused stresses are frequently difficult to determine (Taylor and Norby, 1985; Garner, 1991).

Ozone stresses can be acute, chronic, or both. Trees may experience O₃ exposures for minutes, hours, a few days, or weeks. In addition, exposures usually occur more than once during a growing season. During an episode, O₃ trajectories may cover very large areas. Concentrations can increase as the air trajectories move across the country and pass over new sources of O₃ (Wolff et al., 1977a,b,c, 1980; Wolff and Lioy, 1980). Acute episodic exposures (short-term high concentrations) may be experienced several times in a year.

During chronic exposures, low concentrations may be experienced continuously for a major portion of the life of a plant. Forest trees, shrubs, and other perennial plants must cope with the cumulative effects of several acute episodes; chronic, long-term exposures; or both. Trees may respond rapidly; for example, the needles of sensitive eastern white pine exhibit visible injury symptoms within days after exposure to high O₃ concentrations (Garner, 1991). In most instances, however, responses are subtle and not observable for many years because trees adapt and respond to cumulative stresses by differential growth, which is the result of altered carbon allocation (Waring and Schlesinger, 1985). Trees usually can recover when the stresses are removed, depending on the length of exposure.

Ozone concentrations and the effects, past and present, of exposure to O₃ on ecosystems in the San Bernardino Mountains and the Sierra Nevada Mountains of California and in the Appalachians Mountains of the eastern United States are presented in the pages that follow. The final section relates known ecosystem responses to stress and presents possible reasons why the effects on the ecosystem components in the two regions resulted in different responses. How plants respond to O₃ exposures and may compensate for stresses has been pointed out in the section on mode of action (Section 5.3). The importance of genetic variability in plant response and plant competition, as well as the multiple biological and physical factors that may modify plant response and, in some cases, cause stress, have been discussed in factors that modify plant response (Section 5.4). The discussion regarding modifying factors is of particular importance in understanding ecosystem response to stresses because they are much more likely to be encountered by plants growing in their natural habitats. Figure 5-30 outlines how plant response can lead to ecosystem response.

The responses to a variety of O₃ concentrations and exposure durations of various species of deciduous trees and shrubs (Table 5-27) and evergreen trees (Table 5-30) under experimental conditions have been presented in the previous section. The studies cited in the tables in the previous section, whether conducted in chambers, greenhouses, or OTCs, suggest that all sensitive plants will respond within hours to O₃ concentrations above 0.06 ppm. In general, depending on the length of exposure, the number and height of peaks, and the sensitivity of the vegetation, data from the field supports this contention. This section places the response of the individual trees, shrubs, and other perennial plants in the ecosystem context. The responses of forest ecosystems to pollutant exposure have received more study than unmanaged ecosystems of other biomes (grasslands, shrublands, or deserts), therefore, the following discussion relies mainly on forest ecosystems for examples.

5.7.2 Ecosystem Characteristics

Ecosystems are composed of populations of "self-supporting" and "self-maintaining" living plants, animals, and microorganisms (producers, consumers, and decomposers) interacting with one another and with the nonliving chemical and physical environment within which they exist (Odum, 1989; U.S. Environmental Protection Agency, 1993). Ecosystems respond to stresses through their constituent organisms. The response of plant species and populations to environmental perturbations depends on their genetic constitution (genotype), their life cycles, and the microhabitats in which they are growing. Stresses such as the changes in the physical and chemical environment of plant populations apply new and additional selection pressures on individual organisms (Treshow, 1980). The

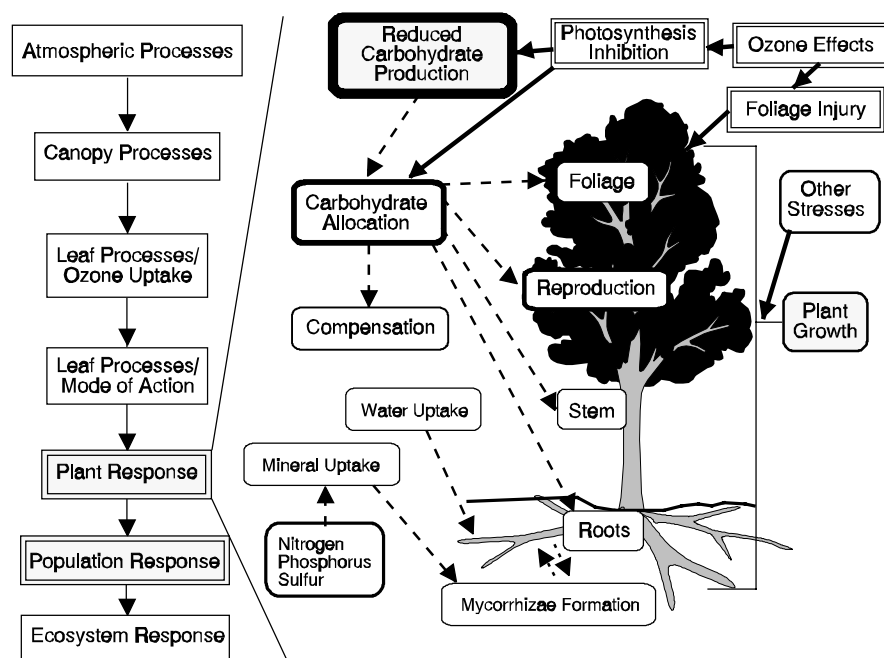


Figure 5-30. Effects of ozone (O_3) on plant function and growth. Reduced carbohydrate production decreases allocation and resources needed for plant growth processes. Individual plant responses must be propagated hierarchically through the more integrative levels of population and community to produce an ecosystem response. Solid black arrows indicate the effects of O_3 absorption; stippled arrows indicate affects on plant functions. Double border indicates site of response; darkened border indicates site of impact.

changes that occur within plant communities reflect these new and different pressures. A common response in a community under stress is the elimination of the more sensitive populations and an increase in abundance of species that tolerate or are favored by the stress (Woodwell, 1970; Guderian et al., 1985).

Ecosystems usually have definable limits within which the integrated functions of energy flow, nutrient cycling, and water flux are maintained (Odum, 1993). Their boundaries, and the organisms that live within them, are determined by the environmental conditions of that particular habitat, area, or region. Structurally complex communities, they are held in an oscillating steady state by the operation of a particular combination of biotic and abiotic factors. They may be large or small (e.g., fallen logs, forests, grasslands, meadows, old uncultivated fields, ponds, lakes or rivers, estuaries, oceans, the earth) (Odum, 1971). Together, the environment, the organisms, and the physiological processes resulting from their interactions form the life-support systems that are essential for the existence of any species on earth, including man (Odum, 1993).

Human existence on this planet is dependent on ecological systems and processes. Natural ecosystems traditionally are spoken of in terms of their structure and functions. Ecosystem structure includes the species (richness and abundance) and their mass and arrangement in an ecosystem. This is termed an ecosystem's standing stock—nature's free

"goods" (Westman, 1977; U.S. Environmental Protection Agency, 1978, 1986, 1993). Society reaps two kinds of benefits from the structural aspects of an ecosystem: (1) products with market value such as fish, minerals, forest products and pharmaceuticals, and genetic resources of valuable species (e.g., plants for crops and timber and animals for domestication); and (2) the use and appreciation of ecosystems for recreation, aesthetic enjoyment, and study (Westman, 1977; U.S. Environmental Protection Agency, 1978, 1986, 1993).

More difficult to comprehend, but of equal or greater importance are the functional aspects of an ecosystem. Ecosystem functions are characterized by the way in which components interact. They are the dynamics of ecosystems—nature's free "services". The benefits imparted to society include absorption and breakdown of pollutants, cycling of nutrients, binding of soil, degradation of organic waste, maintenance of a balance of gases in the air, regulation of radiation balance, climate, and the fixation of solar energy. These, in short, are the functions that maintain clean air pure water, a green earth, and a balance of creatures, the functions that enable humans to obtain the food, fiber, energy, and other materials for survival (Westman, 1977). The majority of the free services are performed by the microorganisms that constitute as many as half of all living creatures on the earth but are seldom recognized.

The term "ecological risk" highlights the importance of ecosystems to human existence. Ecosystems change dramatically throughout time, have no optimal condition, and are only healthy when compared to some desired state specified by humans (Lackey, 1994). The importance of ecosystems to human existence is presented in more detail in the nitrogen oxides (NO_x) criteria document (U.S. Environmental Protection Agency, 1993).

5.7.3 Effects of Exposure to Ozone on Natural Ecosystems

5.7.3.1 The San Bernardino Forest Ecosystem—Before 1986

The mixed-conifer forest ecosystem in the San Bernardino Mountains of Southern California is one of the most thoroughly studied ecosystems in the United States. Chronic O₃ exposures over a period of 50 or more years has resulted in major changes in the San Bernardino National Forest ecosystem. The primary effect was on the more susceptible members of the forest community, individuals of ponderosa and Jeffrey pine, such that they were no longer able to compete effectively for essential nutrients, water, light, and space. As a consequence of altered competitive conditions in the community, there was a decline in the sensitive species, permitting the enhanced growth of more tolerant species (Miller et al., 1982; U.S. Environmental Protection Agency, 1978, 1986). The results of the studies of the San Bernardino Forest ecosystem were reported in both the 1978 and 1986 criteria documents (U.S. Environmental Protection Agency, 1978, 1986). The information summarized below is from these two documents.

An inventory of the forest was begun in 1968 and conducted through 1972 to determine the results of more than 30 years of exposure to O₃. Based on that inventory and accompanying studies, the conclusions reached are presented in Table 5-32. Data from the inventory indicated that, during 5 mo/year from 1968 through 1972, trees were exposed to O₃ concentrations greater than 0.08 ppm for more than 1,300 h. Concentrations rarely fell below 0.05 ppm at night near the crest of the mountain slope (elevation approximately 5,500 ft [Miller, 1973]). The importance of altitude in plant response was discussed in the

Table 5-32. San Bernardino Forest—Status 1972

1. Ponderosa and Jeffrey pine suffered the most injury. Mortality of one population of ponderosa pine ($n = 160$) was 8% between 1969 and 1971 ($p = 0.01$); in a second population ($n = 40$), mortality was 10% between 1968 and 1972. White fir populations suffered slight damage, with scattered individual trees showing severe symptoms. Sugar pine, incense cedar, and black oak exhibited only slight foliar injury from oxidant exposure.
2. A substantial shift occurred in ponderosa pines from the "slight injury" category in 1969 to the "moderate injury" category in 1971, indicating that there was continuing oxidant stress and that the selective death of ponderosa pines was occurring.
3. Suppression of photosynthesis in seedlings was observed (Miller et al., 1969). In ponderosa pine saplings, needles shortened by exposure to oxidants returned to normal length when the seedlings were moved to O_3 -free air from 1968 to 1973 (Miller and Elderman, 1977).
4. Bark beetles were judged to be responsible for the death of weakened trees in the majority of cases. Elimination of ponderosa pine from the mixed-conifer forest was postulated to occur in the future if the rate of bark beetle attack were to continue unabated (Cobb and Stark, 1970).
5. Aerial portions of O_3 -injured pine trees showed a decrease in vigor that was associated with deterioration of the feeder root system (Parmeter et al., 1962).
6. Seed production was decreased in injured pines. Ordinarily, trees 25 to 50 in. diameter at breast height produce the most cones, but they were also the most sensitive to oxidants (Luck, 1980).
7. Under-story plant species sensitive to oxidant pollution may already have been removed by air pollution stress at the time of these early studies (Miller and Elderman, 1977).

Source: U.S. Environmental Protection Agency (1986).

1986 criteria document (U.S. Environmental Protection Agency, 1986) and also is discussed in Chapter 4 of this document. The monthly averages of the daily maxima of total oxidant concentrations for the 5 years of the study are given in Figure 5-31. The highest single daily maximum oxidant concentration of 0.58 ppm occurred in June 1970 between 4:00 and 9:00 p.m., PST (Miller, 1973).

The survey cited above indicated the need for further information. To more accurately determine the effects of the 30 years of exposure to O_3 of the San Bernardino Forest ecosystem, an interdisciplinary research team designed a study to answer the following questions: how do organisms and biological processes of the conifer forest respond to different levels of chronic oxidant exposure? and how can these responses be interpreted within an ecosystem context?

Included in the study plan were the following ecosystem processes: carbon (energy) flow (the movement of CO_2 into the plants, its incorporation into carbohydrates, and then its partitioning among consumers, decomposers, litter, and soil); the movement of water in the soil-plant-atmosphere continuum; mineral nutrient flow through the green plant, litter, and soil-water compartments; and the shift in diversity patterns in time and space, as represented by changes in age, structure, and density in the composition of tree species in communities.

The major abiotic components studied were water (precipitation), temperature, light, mineral nutrients (soil substrate), and oxidant pollution. The biotic components studied

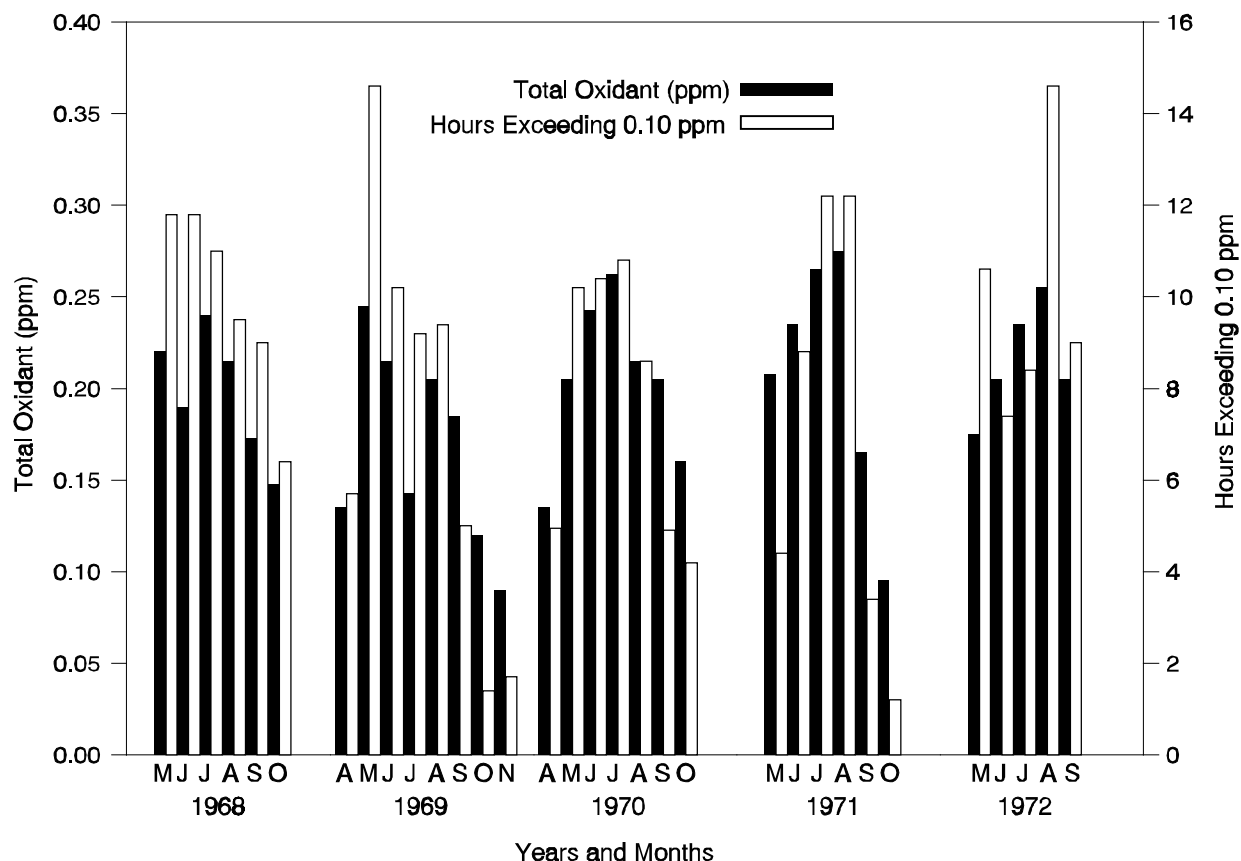


Figure 5-31. Total oxidant concentrations at Rim Forest (5,640 ft) in Southern California during May through September, 1968 through 1972. Values of total oxidant are averages of daily maxima for a month. The number of hours in which total oxidant exceeded 0.10 ppm also was recorded for the 5-year period.

Source: Miller (1973).

included producers (an assortment of tree species and lichens), consumers (wildlife, insects, and disease organisms), and decomposers, (populations of saprophytic fungi responsible for the decay of leaf and woody litter) (U.S. Environmental Protection Agency, 1978, 1986).

During the period of the study, 1973 to 1978, average 24-h O_3 concentrations ranged from a background of 0.03 to 0.04 ppm in the eastern part of the San Bernardino Mountains to a maximum of 0.10 to 0.12 ppm in the western part during May through September. Hourly average concentrations for 1975 (measured by ultraviolet [UV]) indicated that O_3 buildup began around 10 a.m. and reached a maximum at all six monitoring stations in all months (May through September) at around 4 p.m. For example, at the Rim Forest-Sky station, where the highest concentrations usually were recorded, the 1-mo average of hourly values ranged from 0.07 to 0.10 ppm at 10 a.m. and from 0.15 to 0.22 at 4 p.m. The highest concentrations occurred in June, July, and August, and the lowest were observed in September. The total number of hours with concentrations of 0.08 ppm or more during June through September was never less than 1,300 h per season during the first 7 years (1968

through 1974) of the study (Miller and Elderman, 1977). In addition to total oxidant, PAN and NO₂ concentrations were measured. Peroxyacetyl nitrate injury symptoms could not be distinguished from O₃ symptoms on herb-layer plant species while NO₂ remained at nontoxic concentrations (Miller et al., 1982; U.S. Environmental Protection Agency, 1978, 1986).

The study indicated that the major changes in the ecosystem began with injury to ponderosa and Jeffrey pine. Ponderosa pine was the most sensitive of the trees to O₃, with Jeffrey pine, white fir, California black oak (*Quercus kelloggii*), incense cedar (*Calocedrus decurrens*), and sugar pine (*Pinus lambertiana*) following in decreasing order of sensitivity. Foliar injury on sensitive ponderosa and Jeffrey pine was observed when the 24-h average O₃ concentrations were 0.05 to 0.06 ppm (Miller et al., 1982). Foliar injury, premature senescence, and needle fall decreased the photosynthetic performance of stressed pines and reduced the production of carbohydrates needed for use in growth and reproduction by the trees. Nutrient availability to the trees also was reduced by the trees retention of smaller amounts of green foliage (Miller et al., 1982). Decreased carbohydrate resulted in a decrease in radial growth and height of stressed trees (McBride et al., 1975; Miller and Elderman, 1977).

A reduction in available carbohydrate also influenced tree reproduction. Injured ponderosa and Jeffrey pines older than 130 years produced significantly fewer cones per tree than uninjured trees of the same age (Luck, 1980). Tree-ring analysis indicated declines in ring-width indices for many trees. Stand thinning, however, reversed the trend (Miller et al., 1982).

Summarized, the responses of individual conifers sensitive to O₃ include visible foliar injury; premature needle senescence; reduced photosynthesis; reduced carbohydrate production and allocation; reduced plant vigor; and reduced growth or reproduction, or both (Miller et al., 1982).

The ecosystem components most directly affected by O₃ exposure were tree species, the fungal microflora of conifer needles, and the foliose lichens growing on tree bark. Injury to or changes in the functioning of other living ecosystem components affected, either directly or indirectly, the processes of carbon (energy) flow, mineral nutrient cycling, water movement, and changed vegetational community patterns (Miller et al., 1982). Early senescence and abscission resulted in accumulation of pine needles into a thick layer under the stands of O₃ injured trees and changed decomposition patterns, which changed successional patterns of the fungal microflora as well. Altering the taxonomic diversity and population density of the microflora that normally develop on needles while they are on the tree influenced the relationship of the microflora with the decomposer community. Change in the type of fungi on needles weakened the decomposer community and slowed the rate of decomposition (Bruhn, 1980). Nutrient availability was influenced by the carbon and mineral nutrients accumulated in the heavy litter and thick needle layer under stands with the most severe needle injury and defoliation.

A comparison of species of lichens found on conifers during the years 1976 to 1979 with collections from the early 1900s indicated a 50% reduction in species in the more recent period. Marked morphological deterioration of the common species *Hypogymnia enteromorpha* was documented in areas of high oxidant concentrations (Sigal and Nash, 1983).

Biotic interactions associated with predators, pathogens, and symbionts were influenced by changes in the energy available to the trees. The decrease in vigor and lack of ability to recover from O₃ injury associated with reduced carbohydrates made the ponderosa

pinus more susceptible to attack by predators and pathogens (Stark and Cobb, 1969). Dahlsten and Rowney (1980) have pointed out that oxidant-weakened pinus can be killed by fewer western pine beetles than are required to kill healthier trees. In stands with a high proportion of O₃-injured trees, a given population of western pine beetles therefore could kill more trees. James et al. (1980a,b) observed that the root rot fungus, *Heterobasidium annosum*, increased more rapidly because freshly cut stumps and roots of weakened trees were more vulnerable to attack (U.S. Environmental Protection Agency, 1986).

Changes in the plant populations that alter communities and forest stands also can affect the animal populations. Production of fewer cones, seeds, and fruits reduces the food available to small vertebrates living in the ecosystem (U.S. Environmental Protection Agency, 1978). The continuum of ecosystem responses associated with increasing pollutant stress (presented in Table 5-33) are reflected in the response of the San Bernardino mixed forest ecosystem (Garner et al., 1989; U.S. Environmental Protection Agency, 1986). The influence of pollutants on the processes of carbon production and allocation are presented in continuum Stage II, Table 5-33.

Table 5-33. Ecosystem Response to Pollutant Stress

	Continuum of Vegetation Responses	Continuum of Ecosystem Responses
0	Anthropogenic pollutants insignificant.	Unaffected; systems pristine.
I	Pollutant concentrations low; no measurable physiological response.	Ecosystem functions unaffected; pollutants transferred from atmosphere to organic or available nutrient compartments.
II	Pollutant concentrations injurious to sensitive species: (1) Reduced photosynthesis, altered carbon allocation, and reduced growth and vigor; (2) Reduced reproduction; (3) Predisposition to entomological or microbiological stress.	Altered species composition; populations of sensitive species decline; some individuals are lost. Their effectiveness as functional ecosystem members diminishes; they could be lost from the system. Ecosystem reverts to an earlier stage.
III	Severe pollution stress. Large plants of sensitive species die. Forest layers are peeled off; first trees and tall shrubs, then, under the most severe conditions, short shrubs and herbs.	(1) Simplification, basic ecosystem structure changes, becomes dominated by weedy species not previously present. (2) Reduced stability and productivity; loss of capability for repairing itself. Runoff increases and nutrient loss and erosion accelerates; a barren zone results. Ecosystem collapses.

Source: Garner et al. (1989); adapted from Bormann (1985); Kozlowski (1985); Smith (1974).

5.7.3.2 The San Bernardino Forest Ecosystem—Since 1986

Monitoring of O₃ trends in the South Coast Air Basin of Southern California, the source of pollutants transported to the mixed-conifer forests of the San Bernardino Mountains, resulted in the conclusion that the air quality had improved substantially between 1976 and 1984.

Between 1976 and 1991 the weather-adjusted O₃ data for the May through October "smog season" indicates that the number of Basin days exceeding 0.12 ppm, 1-h average, have declined at an average annual rate of 2.27 days/year, whereas the number of days with episodes greater than 0.2 ppm, 1-h average, have declined at an average annual rate of 4.70 days/year over the same period. The total days per year with concentrations greater than 0.12 ppm was as high as 159 in 1978, with the lowest number being 105 days in 1990 (Davidson, 1993). The 1974 to 1988 trends of the May through October hourly average and the average of monthly maximum O₃ concentrations for Lake Gregory, a forested area in the western section of the San Bernardino Mountains, also have shown a gradual decline (Miller et al., 1989a). Similarly, for the same period, there was an improvement shown in the injury index used to describe chronic injury to the crowns of ponderosa and Jeffrey pines in 13 of 15 plots located on the gradient of decreasing O₃ exposure in the San Bernardino Mountains (Miller et al., 1989a). The two exceptions were plots located at the highest exposure end of the gradient. The basal area increase of ponderosa pines was generally less than competing species at 12 of the 13 plots evaluated. The total basal area for each species as a percent of the total basal area for all species indicates that ponderosa and Jeffrey pines in plots with slight to severe crown injury lost basal area in relation to competing species that are more tolerant to O₃, namely, white fir, incense cedar, sugar pine, and California black oak (Figure 5-32).

In effect, stand development had been reversed (i.e., the development of the normal fire climax mixture dominated by fire-tolerant ponderosa and Jeffrey pines was altered). The accumulation in the understory of a greater number of stems of more O₃-tolerant species resulted in the formation of a fuel ladder that jeopardized the remaining overstory trees in the event of a catastrophic fire. The O₃-tolerant species, because of thinner bark and branches growing close to the ground, are inherently more susceptible to fire injury. The important question for the future at that time was whether the declining O₃ exposure eventually would allow ponderosa and Jeffrey pine to resume dominance in basal area.

The possible interactive effects of nitrogen and O₃ on the forests of the San Bernardino Mountains has come under consideration more recently. For some time, there has been a concern that O₃ is not the only pollutant in the photochemical mixture that may be causing lasting changes in the mixed-conifer forest ecosystem. A multidisciplinary study to investigate the possibility of the combined impacts on ecosystem processes from chronic O₃ injury and both wet and dry deposition of acidic nitrogen compounds has been under way since 1991 at Barton Flats in the San Bernardino Mountains. The database includes frequent measurements of stomatal conductance in relation to weather and O₃ exposure.

The NO_x criteria document (U.S. Environmental Protection Agency, 1993) explored the possible effects of increased nitrogen on litter content and decomposition. That discussion is presented here.

Increases in the nitrogen litter content and in litter decomposition rates and an alteration in nitrogen cycling have been observed in the more highly polluted areas when compared with moderately polluted and low-polluted areas of the San Bernardino Mountains

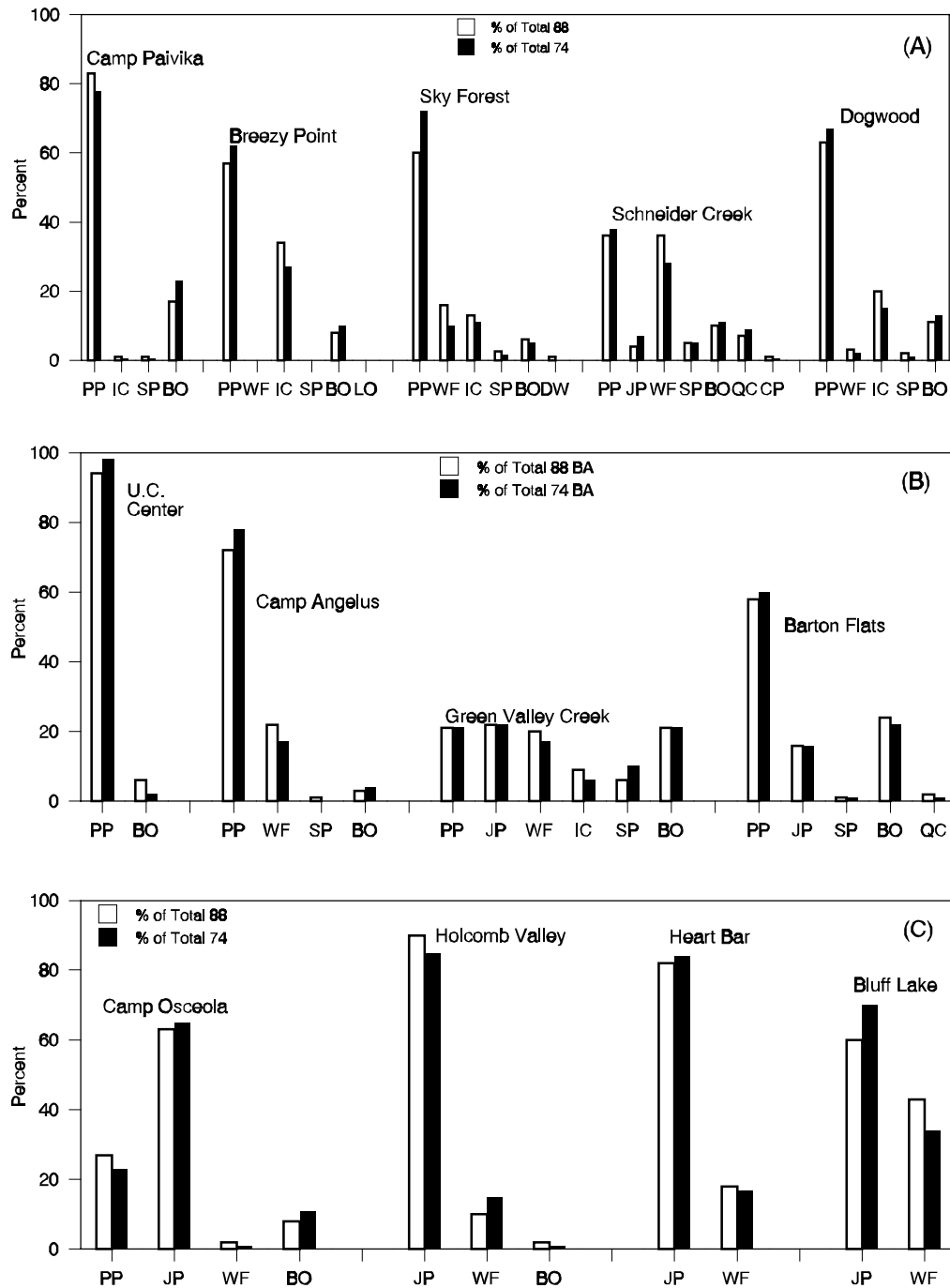


Figure 5-32. Total basal area for each species as a percent of the total basal area for all species in 1974 and 1988 on (A) plots with severe to moderate damage, (B) plots with slight damage, and (C) plots with very slight damage or no visible symptoms. PP = Ponderosa pine, IC = Incense cedar, SP = Sugar pine, BO = Black oak, WF = White fir, LD = Libocedrus decurrens, DW = Dogwood, QC = Quercus chrysolepis, CP = Coulter pine, and JP = Jeffrey pine.

Source: Miller et al. (1991).

(Fenn and Dunn, 1989). A pollutant concentration gradient was observed to exist, with 24-h O_3 concentrations at the high sites in the west averaging 0.1 ppm or more, moderate sites ranging from 0.06 to 0.08 ppm, and low sites in the east averaging 0.05 ppm or less (Fenn, 1991). Nitrogen and sulfur compounds also occur in the pollutant mixture to which the mountains downwind of the Los Angeles Basin are exposed (Bytnerowicz et al., 1987a,b; Solomon et al., 1992). A nitrogen deposition gradient from west to east parallels the decreasing O_3 gradient. Deposition of nitrogen exceeds that of sulfur (Fenn and Bytnerowicz, 1993). Annual average HNO_3 concentrations in 1986 ranged from 1.2 ppb near the Southern California coast to 2.7 ppb in the San Gabriel Mountains (Solomon et al., 1992).

The litter layers under trees severely injured by O_3 are deeper than those under trees less severely injured (Fenn and Dunn, 1989). A comparison study of decomposition rates of the undecomposed surface layer of needle litter indicates that litter in the more polluted areas in the west decomposed at a significantly ($p = 0.01$) faster rate than did litter from moderate to low pollution levels (Fenn and Dunn, 1989; Fenn, 1991). Nitrogen content of litter was greatest at the high pollution sites and was positively correlated with the litter decomposition rate. The higher nitrogen and lower calcium contents of the litter suggest that litter in the western plots originated from younger needles than those at the less polluted sites, possibly due to O_3 -induced needle abscission. Fungal diversity was also greater in the litter from the western San Bernardino Mountains (Fenn and Dunn, 1989).

When the factors associated with enhanced litter decomposition were investigated, it was found that nitrogen concentrations of soil, foliage, and litter of ponderosa and Jeffrey pine were greater in the plots where pollution concentrations were high than in moderately polluted or low-pollution sites. This was also true for sugar pine and for incense cedar, two O_3 -tolerant species. The rate of litter decomposition for sugar pine, incense cedar, and Ponderosa pine species was greatest at the high-pollution sites. Therefore, the increased rate of litter decomposition in the high-pollution plots does not appear to be related to O_3 sensitivity or premature needle abscission, but, instead, it is associated with higher levels of nitrogen in the soils (Fenn, 1991). Foliage and litter nitrogen is higher in high-pollution sites when compared with moderate- or low-pollution sites.

At the present time, data dealing with the response of trees or other vegetation to the combined stresses of O_3 exposure above ground and nitrate deposition through the soil are sparse. Tjoelker and Luxmoore (1991), however, have assessed the effects of soil nitrogen availability and chronic O_3 stress on carbon and nutrient economy in 1-year-old seedlings of loblolly pine and yellow poplar. Elevated O_3 concentrations altered biomass partitioning to needles of the current year. Ozone concentrations of 0.108 ppm reduced the biomass of current-year needles in loblolly pine seedlings grown at the highest (172 $\mu\text{g/g}$) nitrogen supply by 20%, but not those grown with a low (59 $\mu\text{g/g}$) supply of nitrogen. The interaction between O_3 and nitrogen suggests that plants grown with a high nitrogen supply are more sensitive to chronic O_3 stress in terms of biomass reduction (Tjoelker and Luxmoore, 1991). Similar results in the growth of domestic radish were obtained by Pell et al. (1990). Brewer et al. (1961) and Harkov and Brennan (1980) observed increased foliar injury when plants were grown with an adequate nitrogen supply (U.S. Environmental Protection Agency, 1986).

5.7.3.3 The Sierra Nevada Mountains

The continued presence over the years of O₃ concentrations injurious to trees in the San Bernardino Mountain forests and the knowledge that O₃ is a regionally dispersed gaseous air pollutant led to concern that other forests in California, and possibly other western states as well, were being exposed to injurious concentrations. Summary statistics for the 1980 to 1988 growing season (May through October), using data from O₃-monitoring sites in or near Western forests, substantiated the concern. Growing season (May through October) means, percentiles and percent occurrence of hourly O₃ concentrations above 0.06, 0.08, 0.10, and 0.120 ppm for all O₃ sites near Western forests are presented in Table 5-34 (Böhm, 1992). The lowest O₃ concentrations with little hourly variation were experienced at sites far from urban or point sources. Sites on the fringe of urbanized centers or valleys, on the other hand, experienced patterns with some variation in hourly concentrations; the higher concentrations usually occurred during the late afternoon. Forests located on the rims of valleys with large urban areas experienced O₃ concentrations >0.10 ppm. Yosemite and Sequoia National Parks, which receive pollutants transported from highly urbanized areas, had 24-h means ranging from 0.036 to 0.085 ppm on 75% of summer days, whereas Lake Gregory had a growing season mean of 0.073 ppm. During 49% of the summer days, means of diurnal patterns ranged from 0.085 to 0.100 ppm, decreasing with altitude and distance from the source (Böhm, 1992). The San Bernardino National Forest was exposed to O₃ levels >0.10 ppm during all seasons. Ozone concentrations tended to decrease with altitude and distance from the source.

There is little evidence of O₃ injury in forests in the western United States outside of California, even near urban sites. Growing season means near forests ranged between 0.012 and 0.022 ppm in Washington, between 0.028 and 0.037 ppm in Utah, and between 0.032 and 0.058 ppm in Colorado (Table 5-34; Böhm, 1992; Böhm et al., 1995).

The Sierra Nevada, the largest forested area in the world documented to have visible injury from high O₃ exposures, is an area approximately 300 miles long (Peterson and Arbaugh, 1992). Since 1991, there has been an annual survey of the amount of crown injury by O₃ to the same trees in approximately 33 sample plots located in the Sierra Nevada. These include Tahoe, Eldorado, Stanislaus, Yosemite, Sierra, Sequoia, and San Bernardino National Forests and Yosemite and Sequoia-Kings Canyon National Parks.

Dominant tree species in the area are ponderosa and Jeffrey pine, white fir, sugar pine, incense cedar, Douglas fir, and California black oak, and the giant sequoia (*Sequoiadendron giganteum*) is locally common (Peterson and Arbaugh, 1992).

Foliar O₃ injury to ponderosa and Jeffrey pine was first documented in the Sierra Nevada Mountains of California in the early 1970s (Miller and Millecan, 1971). Monitoring of visible injury to ponderosa pine on national forest land in the western Sierra Nevada, however, was not begun until 1975 (Duriscoe and Stolte, 1989). Results of the monitoring in the Sierra and Sequoia National Forests showed that there was an increase in chlorotic mottle of pines in the plots from approximately 20% in 1977 to approximately 55% in 1988, and an increase in severity of injury was observed as well.

In general, the results of this study document the regional nature of the O₃ pollution problem originating primarily from the San Joaquin Valley Air Basin, as well as from the San Francisco Bay Air Basin further to the west. Oxidant air pollution is transported southward in the San Joaquin Valley Air Basin until it reaches the southern boundary of the air basin, the Tehachapi Mountains. Because of this barrier, polluted air

**Table 5-34. Growing Season (May Through October) Summary Statistics for Ozone Monitoring
Sites in or Near Forests for the Period 1980 through 1988
(Percentiles and means were generated using the entire data set [1980 through 1988; May through October].)**

Site ^b	Elevation (m)	Percent Data Capture	Percentiles (ppb)								Percent Hours ^a			
			5	10	25	50	Mean \pm SD ^c	75	90	95	≥ 60	≥ 80	≥ 100	≥ 120
Aptos, CA	78	100	0	10	10	20	25.1 \pm 15	30	40	50	3	0	0	0
Ash Mountain, CA (AIRS)	526	50	20	30	50	60	64.1 \pm 26	80	100	110	64	36	12	2
Ash Mountain, CA (NPS)	610	57	20	30	47	61	62.9 \pm 24	80	93	100	59	29	8	1
Azusa, CA	185	93	0	0	0	20	43.3 \pm 56	70	130	160	28	22	17	12
Banning, CA	722	98	10	10	20	40	49.6 \pm 35	70	100	120	35	19	11	6
Bishop, CA	1,260	84	0	10	20	30	31.5 \pm 16	40	50	60	7	0	0	0
Burbank, CA	170	95	0	0	0	20	36.3 \pm 45	50	100	130	25	18	12	8
Camp Mather, CA	1,432	33	22	26	36	46	47.5 \pm 16	59	70	76	24	3	0	0
Carmel Valley, CA	131	86	10	10	20	30	28.4 \pm 14	40	50	50	4	1	0	0
Fresno County, CA	1,723	85	20	20	30	40	44.9 \pm 17	60	70	80	26	5	0	0
Lake Gregory, CA	1,397	93	10	20	40	60	72.5 \pm 49	100	140	170	55	37	26	18
Lassen NP, CA	1,788	36	17	21	28	36	37.8 \pm 14	46	58	64	9	0	0	0
Kaweah, CA (AIRS)	1,901	35	10	20	40	60	59.7 \pm 26	80	90	100	57	32	8	1
Kaweah, CA (NPS)	1,890	58	21	30	41	56	56.3 \pm 21	71	83	90	44	15	2	0
Mammoth Lakes, CA	2,395	92	20	30	40	50	46.6 \pm 16	60	70	70	30	5	0	0
Monterey, CA	23	86	10	10	20	30	27.3 \pm 12	30	40	50	1	0	0	0
Ojao, CA	233	87	10	10	20	40	42.3 \pm 26	60	80	90	30	12	3	1
Pasadena, CA	255	89	0	0	10	20	47.8 \pm 58	70	130	170	30	24	18	14
Pinnacles NM, CA	355	66	10	16	26	41	42.8 \pm 22	58	72	80	22	5	1	0
Redwood NP, CA	233	49	8	10	15	22	22.0 \pm 0.09	28	34	39	0	0	0	0
San Bernardino, CA	320	80	0	0	0	30	50.2 \pm 57	80	140	170	35	28	21	15
Santa Barbara, CA	25	96	0	10	20	30	32.2 \pm 19	40	60	60	11	2	0	0
Santa Barbara County, CA	12	96	0	10	20	30	31.5 \pm 20	40	60	70	13	2	1	0
Santa Monica Mountains, CA	191	55	0	2	10	30	39.6 \pm 35	59	86	110	25	13	7	4
Scotts Valley, CA	171	79	0	0	10	20	22.4 \pm 18	30	50	50	5	1	0	0
South Lake Tahoe, CA	1,907	88	10	20	20	40	37.8 \pm 17	50	60	60	18	1	0	0
Ventura County, CA	1,600	83	0	10	20	40	36.2 \pm 22	50	60	70	18	5	1	0
Wawona Valley, CA	1,280	66	9	15	27	42	44.0 \pm 23	61	76	83	26	7	1	0

**Table 5-34 (cont'd). Growing Season (May Through October) Summary Statistics for Ozone Monitoring
Sites in or Near Forests for the Period 1980 through 1988
(Percentiles and means were generated using the entire data set [1980 through 1988; May through October].)**

Site ^b	Elevation (m)	Percent Data Capture	Percentiles (ppb)								Percent Hours ^a			
			5	10	25	50	Mean ± SD ^c	75	90	95	≥60	≥80	≥100	≥120
Yreka, CA	809	80	0	0	10	20	25.9 ± 18	40	50	60	6	0	0	0
Clackamas County, OR	174	94	4	8	14	23	25.3 ± 16	33	45	55	4	1	0	0
Columbia County, OR	6	88	1	4	11	20	21.3 ± 14	29	39	46	2	0	0	0
Crook County, OR	1,372	90	20	25	30	35	36.5 ± 0.09	40	50	55	2	0	0	0
Eugene, OR	187	77	1	3	9	18	21.4 ± 17	30	42	52	3	1	0	0
Marion County, OR	102	94	1	1	7	18	20.3 ± 16	30	41	50	3	1	0	0
Medford, OR	503	93	1	3	9	22	24.8 ± 18	37	50	59	5	1	0	0
Cedar River, WA	210	82	11	14	19	28	31.4 ± 17	39	53	64	7	2	0	0
King County, WA	22	90	0	0	0	10	14.9 ± 17	20	40	50	3	1	0	0
Olympic NP, WA (DOE)	100	85	0	0	10	20	16.3 ± 11	20	30	40	0	0	0	0
Olympic NP, WA (NPS)	125	26	0	1	1	2	4.8 ± 0.07	3	17	23	0	0	0	0
Pack Forest, WA	24	80	10	10	20	30	30.0 ± 18	40	50	70	8	3	1	0
Pierce County, WA	14	85	0	0	0	10	15.1 ± 16	20	40	40	2	0	0	0
Port Angeles, WA	30	71	0	0	1	2	8.4 ± 10	10	20	30	0	0	0	0
Snohomish County, WA	120	83	0	0	0	10	17.0 ± 15	30	40	40	2	0	0	0
Spokane, WA	584	74	0	0	10	20	20.9 ± 16	30	40	50	20	0	0	0
Stampede Pass, WA	1,217	80	20	20	30	30	35.2 ± 14	40	50	60	7	0	0	0
Apache-Sitgreaves, AZ	2,462	94	25	30	35	40	42.3 ± 12	50	60	65	12	1	0	0
Cochise County, AZ	1,401	56	13	17	26	37	37.4 ± 15	49	58	63	8	0	0	0
Flagstaff, AZ	2,117	77	17	24	34	44	43.7 ± 15	53	62	67	13	1	0	0
Grand Canyon NP, AZ	2,073	56	17	20	23	27	29.4 ± 0.09	33	43	46	0	0	0	0
Pima County, AZ	695	86	1	2	10	28	29.8 ± 22	46	60	68	10	1	0	0
Prescott, AZ	1,673	69	5	9	16	30	29.9 ± 16	43	52	55	2	0	0	0
Saguaro NM, AZ	933	66	19	22	30	38	38.8 ± 14	47	57	63	8	1	0	0
Douglas County, NV	1,951	60	6	11	20	35	35.5 ± 19	49	62	69	12	1	0	0
Reno, NV	1,280	92	0	0	10	30	28.4 ± 20	40	50	60	10	1	0	0
Boulder County, CO	1,635	95	8	14	24	35	36.0 ± 18	47	60	69	11	2	0	0
Colorado Springs, CO	1,842	88	0	2	10	25	26.3 ± 18	40	51	57	4	0	0	0

Table 5-34 (cont'd). Growing Season (May Through October) Summary Statistics for Ozone Monitoring Sites in or Near Forests for the Period 1980 through 1988
(Percentiles and means were generated using the entire data set [1980 through 1988; May through October].)

Site ^b	Elevation (m)	Percent Data Capture	Percentiles (ppb)								Percent Hours ^a			
			5	10	25	50	Mean ± SD ^c	75	90	95	≥60	≥80	≥100	≥120
Colordao NM, CO	1,750	30	30	32	37	42	44.1 ± 14	48	54	57	2	0	0	0
Denver, CO	1,591	96	0	2	7	19	21.9 ± 18	33	47	55	3	1	0	0
Great Sand Dunes, CO	2,487	54	24	27	33	39	38.4 ± 0.09	44	49	52	1	0	0	0
Larimer Country, CO	1,522	90	1	4	14	27	27.9 ± 18	40	52	59	5	0	0	0
Rocky Mountains NP, CO	2,743	49	25	31	38	46	46.0 ± 12	54	60	65	10	1	0	0
Arches NP, UT	1,567	32	28	31	36	43	42.8 ± 0.09	49	54	58	4	0	0	0
Bountiful, UT	1,335	87	8	14	25	38	38.3 ± 20	49	62	72	12	3	1	0
Logan, UT	1,382	45	8	12	20	32	32.5 ± 15	45	52	58	4	0	0	0
Ogden, UT	1,314	97	0	1	9	30	29.8 ± 22	46	58	65	8	1	0	0
Provo, UT	1,402	72	2	5	14	29	32.1 ± 22	49	62	68	12	2	0	0
Salt Lake, UT	1,305	87	2	4	11	28	30.4 ± 22	45	59	70	10	3	1	0
Albuquerque, NM	1,585	89	1	5	15	29	29.8 ± 19	43	55	61	6	1	0	0
Yellowstone NP, WY	2,484	58	15	19	27	36	35.4 ± 12	44	51	55	2	0	0	0

^aPercent hours are normalized to represent the average occurrence of ozone levels during May through October. Percent data capture = number of valid hours/4,416 × 100, where 4,416 is the total number of hours during the period May through October.

^bSite abbreviations: NPS = National Park Service, NM = National Monument, DOE = Department of Energy.

^cSD = Standard deviation.

Source: Modified from Böhm (1992).

masses circulate back northward. This circulation cell causes higher O₃ levels to be advected to the southernmost sites, the Sequoia National Forest and the Sequoia-Kings Canyon National Park. Mean hourly average concentrations in the Sierra Nevada during 1987 ranged from 0.018 to 0.076 ppm, with annual hourly maxima of 0.11 to 0.17 ppm. An O₃ exposure gradient with highest concentrations in the south and lowest in the north was observed. Associated with the gradient, injury is most severe at the southern end of the range and least severe in the north (Peterson et al., 1991).

The studies cited above reported visible O₃ injury only to the trees in the Sierra Nevada forests. To evaluate growth changes in O₃-stressed ponderosa and Jeffrey pine, Peterson and his coworkers, beginning in 1985, conducted the largest investigation of regional tree growth in the western United States (Peterson et al., 1987; Peterson and Arbaugh, 1988, 1992; Peterson et al., 1991). Using cores to determine whether growth reductions had occurred, they randomly sampled both trees with visible O₃ injury symptoms and asymptomatic trees. Major decreases in growth occurred for both symptomatic and asymptomatic trees during the 1950s and 1960s. The percentage of trees exhibiting growth decreases at any given site never exceeded 25% in a given decade (Peterson et al., 1991). The mean annual radial increment of trees with symptoms of O₃ injury was 11% less than trees at sites without O₃ injury. Trees larger than 40 cm in diameter and trees older than 100 years showed greater decreases in growth than did smaller and younger trees. Differences in growth between injured and uninjured trees were prominent after 1965 (Peterson et al., 1987).

The region-wide survey (Peterson et al., 1991) of ponderosa pine provides a useful backdrop for reporting a number of other studies or surveys in the Sierra Nevada that were more narrowly focused. Another tree ring analysis and crown injury study concentrated on Jeffrey pines in Sequoia-Kings Canyon National Park (Peterson et al., 1989). This study suggested that decreases of radial growth of large, dominant Jeffrey pines growing on thin soils with low moisture holding capacity and direct exposure to upslope transport of O₃ amounted to as much as 11% in recent years when compared with similar trees without symptoms.

Both a network of permanent plots established in 1980 and cruise surveys have been employed in Sequoia-Kings Canyon and Yosemite National Parks to determine the spatial distribution and temporal changes of injury to ponderosa and Jeffrey pine within the parks (Duriscoe and Stolte, 1989). In Sequoia-Kings Canyon, O₃ injury to individual trees and the mean number of trees injured in each plot increased from 47% for 1980 to 1982 to 79% for 1984 to 1985. Foliar injury was the most common response among the 28 plots studied. Ozone injury tends to decrease with the increasing elevation of plots. The O₃ concentrations associated with the highest levels of tree injury in the Marble Fork drainage of the Kaweah River, at approximately 1,800 m elevation, are hourly averages peaking frequently at 80 to 100 ppb but seldom exceeding 120 ppb.

During a cruise survey in 1986 (Duriscoe and Stolte, 1989) to identify the partial distribution of injury, there were 3,120 ponderosa or Jeffrey pines evaluated for O₃ injury in Sequoia-Kings Canyon and Yosemite National Parks. Approximately one-third of this number were found to have some level of chlorotic mottle. At Sequoia-Kings Canyon, symptomatic trees comprised 39% of the sample (574 of 1,470), and, at Yosemite, they comprised 29% (479 of 1,650). Ponderosa pines generally were injured more severely than Jeffrey pines.

In Sequoia-Kings Canyon, observations at field plots showed that giant sequoia seedlings developed O₃ injury symptoms at both ambient O₃ concentrations and 1.5 × ambient O₃ (0.08- to 0.1-ppm hourly peaks) in OTCs during the 8 to 10 weeks following germination (Miller et al., 1994). Field-plot observations of seedling health and mortality in natural giant sequoia groves over a 4-year period showed that seedling numbers were reduced drastically from drought and other abiotic factors. Any variable, such as O₃, that could stress seedlings sufficiently to reduce root growth immediately after germination could increase vulnerability to late summer drought. Significant differences in light-compensation point, net assimilation at light saturation, and dark respiration were found between seedlings in CF air treatments and 1.5 × ambient O₃ treatments (0.08- to 0.1-ppm hourly peaks) (Grulke et al., 1989). One interpretation of these results is that O₃ could be a new selection pressure during the regeneration phase of giant sequoia, possibly reducing genetic diversity.

The Lake Tahoe Basin is located at the northern end of the Sierra Nevada (near Eldorado National Forest) (Peterson et al., 1991). Because it is an air basin unto itself, the air quality situation is distinct from other Sierra Nevada sites. Ozone injury was first reported for the area in the late 1970s. In 1987, a survey of 24 randomly selected plots in the basin included a total of 360 trees, of which 105 (29.2%) had some level of foliar injury (Pedersen, 1989).

The radial growth response of big cone Douglas firs (*Pseudotsuga macrocarpa*) to long-term O₃ exposure was studied throughout the range of these firs in the San Bernardino Mountains of Southern California. Big cone Douglas fir is found in the mountain ranges of Southern California and northern Baja California, Mexico. In the San Bernardino Mountains, the species grows in canyons and on dry slopes at elevations from 700 to 2,200 m and, in association with canyon live oak (*Quercus chrysolepis*), throughout the chaparral and lower elevation mixed-forest communities. Big cone Douglas fir is usually rated as less sensitive than ponderosa or Jeffrey pine; however, injury symptoms resulting from elevated O₃ exposures have been seen (Peterson et al., 1995).

Dendroecological analyses indicate that growth rates have decreased considerably since 1950 (Peterson et al., 1995). Differences in basal area indices for 1913 to 1950 were compared with those for 1951 to 1988 to determine whether there were growth changes associated with increased air pollution during the latter period. More than 80% of all trees had reduced growth. Trees growing in regions of high O₃ exposure had the largest growth decreases, with approximately 30% of those growing under these conditions having reductions greater than 50%, and 60% having reductions greater than 20%. Fewer than 10% of the trees in any O₃ exposure area had growth increases greater than 25%. Based on their study, the authors conclude that, although O₃ does not have the same level of impact on these trees as it does on ponderosa and Jeffrey pine, reduced needle retention and lower recent growth rates could indicate increased O₃ stress (or O₃ stress mediated by climate) in big cone Douglas fir. Long-term monitoring of this species could provide an early warning of additional injury caused by air pollution in forest ecosystems of Southern California (Peterson et al., 1995).

Site Variables Affecting Ozone Response in the California Ecosystems

Structural changes in forest stands are highly related to their position or site on the landscape. Site variables can be defined at regional and local levels. For example, the regional level is defined in California by the location of forested mountain slopes and summits in relation to polluted urban air basins. In both the Sierra Nevada and the San Bernardino Mountains in California the greatest tree injury is found on ridges that

overlook the polluted air basins. The polluted air masses are transported up-slope or up-canyon in terrain that is usually sunlit in the afternoon and early evening, thus the thermal convection on warm slopes is a major means by which O₃ and associated pollutants are delivered to the first forested ridges. Both vertical mixing and horizontal diffusion into cleaner air results in a distinct gradient of decreasing O₃ concentration in more distant forest stands. Two such gradients have been described in the San Bernardino Mountains (Miller et al., 1986). Along the longer, west-to-east orientation axis of the mountain range, 24-h average O₃ concentrations for the highest summer months ranged from 0.09 to 0.140 ppm nearest the polluted South Coast Air Basin to 0.04 to 0.05 ppm at a downwind distance of 35 to 40 km. In the more narrow, south-to-north direction, the same concentration gradient is seen over a much shorter distance of 5 to 8 km because of a more rapid transition to the warm desert influence, which causes mixing and dilution (Miller et al., 1972). Accordingly, O₃ injury to sensitive vegetation ranges from severe to none over these distances.

In the Sierra Nevada Mountains, a gradient of decreasing injury is observed from west to east and south to north (Peterson and Arbaugh, 1992). But the worst level of chronic injury is generally much less than observed in the San Bernardino Mountains.

With respect to localized site variables, there is evidence from repeated surveys in Sequoia-Kings Canyon National Parks that the percent of trees injured and the severity of foliar injury both increased with decreasing elevation in the 1,500- to 2,500-m zone on generally west-facing slopes adjacent to the polluted San Joaquin Valley Air Basin (Stolte et al., 1992). In Sequoia-Kings Canyon National Parks, radial growth reductions in Jeffrey pine with foliar injury by O₃ were documented only for large, dominant trees growing on shallow soils (Peterson et al., 1987). Soil moisture availability is generally lower on such sites. One hypothesis for explaining radial growth decline on these sites and not on more favorable sites with greater moisture-holding capacity is that O₃ defoliation in favorable moisture years and water stress in dry years integrate sequentially to suppress growth.

In the San Bernardino Mountains, radial growth of ponderosa and Jeffrey pines in plots along the decreasing O₃ gradient was not well correlated with level of chronic injury but was better correlated with soil-moisture-holding capacity. Within a single plot with relatively uniform moisture availability there was a good correlation between increased radial growth and a decreasing level of chronic O₃ visible injury to crowns.

5.7.3.4 The Appalachian Mountains—Before 1986

Oxidant-induced injury on vegetation in the Appalachian Mountains has been observed for many years but has not produced the same ecosystem responses as vegetational injury in the San Bernardino Mountains. Results of studies in the eastern United States were reported in the 1986 criteria document and are summarized in the following passages (U.S. Environmental Protection Agency, 1986). Needle blight of eastern white pine was first reported in the early 1900s, but it was not known until 1963 that the needle blight was the result of acute and chronic O₃ exposure (Berry and Ripperton, 1963). In the 1950s, the U.S. Forest Service studied the decline of eastern white pine in an area covering several hundred square miles on the Cumberland Plateau in Tennessee and concluded that atmospheric constituents were the causes of this decline (Berry and Hepting, 1964; Garner et al., 1989; Garner, 1991).

Growth reductions in trees growing on the Cumberland Plateau of eastern Tennessee were studied by Mann et al. (1980) and McLaughlin et al. (1982). A steady growth decline in annual-ring increment was observed during the years 1962 through 1979.

Reductions of 70% in average annual growth and of 90% in average bole growth were observed in sensitive trees, when compared to the growth of tolerant and intermediate trees. Tolerant trees, when compared to trees of intermediate sensitivity, consistently showed a higher growth rate (from 5 to 15%) than did intermediate trees for the 1960 to 1968 interval, similar growth rate from 1969 through 1975, and a reduction in growth (5 to 15%) for the period 1976 through 1979. The decline was attributed to chronic O₃, which frequently exceeded 1-h average concentrations of 0.08 ppm. Maximum 1-h concentrations ranged from 0.12 to 0.30 ppm for the years 1975 to 1979 (U.S. Environmental Protection Agency, 1986).

McLaughlin et al. (1982) observed that the decline in vigor and the reduction in growth in trees and the production of carbohydrates (carbon flow) were associated with the following sequence of events and conditions: premature senescence of mature needles at the end of the growing season; reduced carbohydrate storage capacity in the fall and reduced resupply capacity in the spring to support new needle growth; increased reliance of new needles on self-support during growth; shorter new needles, resulting in lower gross photosynthetic productivity; and higher retention of current photosynthate (carbohydrate) by foliage, resulting in reduced availability for transport for external use, including repair of chronically stressed tissues of older needles (U.S. Environmental Protection Agency, 1986).

Despite the early field observations of Berry (1961) and Berry and Ripperton (1963), no concerted effort was made to determine the effects of O₃ on vegetation in the Appalachian Mountains until the 1970s, when, between April 1975 and March 1976, Skelly and his coworkers began monitoring total oxidant concentrations and recording associated injury to eastern white pine in three rural Virginia sites. Injury was observed in the Jefferson and George Washington National Forests and throughout the Blue Ridge Mountains, including areas in the Shenandoah National Park and along the Blue Ridge Parkway in Virginia and North Carolina (Hayes and Skelly, 1977; Skelly et al., 1984). Taylor and Norby (1985), in their analysis of the 4-year monitoring data of Skelly et al. (1984), point out that there were an average of five episodes (any day with a 1-h mean O₃ concentration >0.08 ppm) during the growing season in this area. Episodes lasted from 1 to 3 days.

In studies conducted in the Blue Ridge Mountains of Virginia, Benoit et al. (1982) used annual-ring increments to evaluate the possible effects of oxidant air pollution on the long-term growth on eastern white pine of reproducing age. Reductions in overall growth of eastern white pine trees classified as tolerant, intermediate, and sensitive to O₃ exposure were observed. Comparison of growth from 1974 to 1978 with that for 1955 to 1959 indicated decreases of 26, 37, and 51% for tolerant, intermediate, and sensitive trees, respectively. No significant changes in seasonal precipitation had occurred during the 1955 to 1963 period or the 1963 to 1978 period; therefore, the significant reduction in radial growth was assumed by the authors to be the result of cumulative O₃ stress and reduced photosynthetic performance due to oxidant injury. Monitoring of O₃ indicated monthly average concentrations of 0.05 to 0.07 ppm on a recurring basis, with episodic 1-h peaks frequently in excess of 0.12 ppm for the latter time period (Benoit et al., 1982; U.S. Environmental Protection Agency, 1986). Duchelle et al. (1982), monitoring in the same area, reported peak hourly averages >0.08 ppm for the months of April through September in 1979 and 1980. As early as 1979, Skelly (1980) concluded that the most sensitive eastern white pines were injured so severely by oxidant exposure that they probably were being removed from the population. It was estimated that, of the population, 22% were tolerant, 67% were intermediate, and 11% were sensitive.

In the previous O₃ document (U.S. Environmental Protection Agency, 1986), Duchelle et al. (1982, 1983) reported that exposing native tree seedlings and herbaceous vegetation in the Big Meadows area of the Shenandoah National Park in the Blue Ridge Mountains of Virginia to ambient O₃ reduced both the growth of the native trees other than eastern white pine and the productivity of the native herbaceous vegetation found growing in forested areas. Comparison of growth of seedlings in open plots or OTCs with CF air revealed that growth was suppressed in wild-type seedlings of tulip poplar, green ash, sweet gum (*Liquidambar styraciflua*), black locust (*Robinia pseudoacacia*), eastern hemlock (*Tsuga canadensis*), Table Mountain pine (*Pinus pungens*), Virginia pine (*Pinus virginiana*), and pitch pine, usually without visible foliar injury symptoms. Open-top chambers were operated continuously from May 9 until October 9 during 1979 and from April 24 until September 15 in 1980 (U.S. Environmental Protection Agency, 1986). Common milkweed and common blackberry (*Rubus allegheniensis*) were two species of native vegetation that exhibited visible injury symptoms (Duchelle and Skelly, 1981). Monthly 8-h average O₃ concentrations ranged from 0.035 to 0.065 ppm, and peak hourly concentrations from 0.08 to 0.13 ppm (Skelly et al., 1984; U.S. Environmental Protection Agency, 1986). Common milkweed and common blackberry represented natural vegetation sensitive to O₃ exposure (Duchelle and Skelly, 1981; U.S. Environmental Protection Agency, 1986).

Forest ecosystems at high altitudes experience higher total exposures because of the prolonged duration of elevated O₃ at high altitudes (see Section 5.4; Wolff et al., 1987; Winner et al., 1989; U.S. Environmental Protection Agency, 1986). Although daily maximum and mid-day O₃ concentrations are similar at different altitudes, the dosage increases with height. Ozone is depleted rapidly at night near the earth's surface below the nocturnal inversion layer; however, mountainous sites above the nocturnal inversion layer do not experience this depletion. Therefore, the total exposure to O₃ in mountainous areas can be much higher than that in nearby valleys (Berry, 1964; Garner et al., 1989). Maximum O₃ concentrations observed at elevated mountain sites often occur at night; in addition, higher elevations are often exposed to sustained or multiple peak concentrations of O₃ within a given 24-h period. High morning concentrations occur at a time when stomatal conductance is high and photosynthetic activity is greatest. The cumulative effects of O₃ uptake, therefore, could be severe. These considerations need to be taken into account when assessing the exposure-response relationships of forest ecosystems at high altitudes (Wolff et al., 1987; Garner et al., 1989; Garner, 1991).

The field observations cited above indicate that oxidant-induced injury to vegetation has been occurring in the Appalachian Mountains for many years. By the time intensive studies were begun in Pocahontas County, WV, in 1957, to determine the cause of "emergence tipburn", many people living in the area had been reporting casual observations of the phenomenon for over 20 years. Emergence tipburn, also known as needle blight, of eastern white pine was observed first in the early 1900s, however it was not shown to be the result of acute or chronic O₃ exposure until 1963 (Berry and Ripperton, 1963).

Although vegetation injury resulting from O₃ exposure had been observed in New Jersey in the 1940s, its cause was not recognized until 1960 (Daines et al., 1960). Ozone was first recognized as a causal factor of foliar injury when Heggestad and Middleton (1959) reported that weatherfleck of tobacco was the result of O₃ exposures. Concentrations of 0.38, 0.43, and 0.5 ppm were measured at Beltsville by newly developed Mast meters during 1958. (The concentrations cited are approximately 0.1 ppm higher than those measured more recently. Calibration of the then new Mast meters was sometimes a problem [Garner, 1991]).

Regular oxidant monitoring stations were first established east of the Mississippi River in 1962. Valid oxidant data, however, was not available until 1964, and then only for the cities of Chicago, Cincinnati, St. Louis, Philadelphia, Washington, DC, and Denver (National Air Pollution Control Administration, 1968). Maximum oxidant concentrations recorded between 1964 and 1967 indicated that Cincinnati had 10 days >0.15 ppm; Philadelphia, 60 days >0.06 and 13 days >0.15 ppm; and Washington, DC, 65 days >0.10 ppm and 7 days >0.15 ppm (U.S. Environmental Protection Agency, 1986). Berry and Ripperton (1963) reported the presence of oxidant concentrations above 0.10 ppm during 1961 and 1962 in West Virginia and in North Carolina as far east as Raleigh. These data indicate that O_3 concentrations sufficient to injure vegetation regularly were present from the Midwest to the east coast (Garner et al., 1989; Garner, 1991).

In retrospect, it is apparent that O_3 episodes in the eastern United States have not been unusual. Taylor and Norby (1985) analyzed the 4-year monitoring data of Skelly et al. (1984) and concluded that episodes in which the 1-h O_3 concentration was >0.08 ppm were experienced, on average, five times during the growing season. Episodes when peak O_3 concentrations exceeded 0.10 ppm in the southern Appalachian Mountains were recorded during 1975 (Hayes and Skelly, 1977) and 1979 through 1982 (Skelly, 1980). Injury to eastern white pine at three rural sites in Virginia from July 1 to 5, 1975, was associated with a high pressure over the Great Lakes and a low, Hurricane Amy, off the Atlantic coast. Air parcels bearing O_3 moved in from the Northeast and Midwest into Virginia. The episode dissipated when the cold from the Midwest moved across Virginia into the Atlantic Ocean (Hayes and Skelly, 1977). More recent O_3 episodes in the same area have been associated with meteorological phenomena similar to the one mentioned above (Skelly et al., 1984; Garner et al., 1989).

Ozone episodes for the eastern United States also were recorded during 1976 and 1977. Typical episodes were associated with high-pressure systems that originated in Canada, moved southeastward into the Midwest, and then eastward to the Atlantic coast. For example, an episode covering most of a 20-state area occurred April 12 to 23, 1976. During this episode, O_3 concentrations in excess of 0.08 ppm occurred simultaneously from the Midwest to the Atlantic coast and into the northeastern United States. Ozone trajectories extended from Ohio to New Jersey (Wolff et al., 1977a,b,c; Garner, 1991). Additional studies indicated that two other episodes exhibiting trajectories similar to the one described above took place in August 1976. These episodes included an area extending from West Virginia across Virginia in the south and north to Maine. Maximum concentrations measured in the trajectories during the two August episodes were 0.20 ppm (Wolff et al., 1980; Garner, 1991).

In 1977, there were three episodes: (1) July 12 to 21, (2) July 21 to 24, and (3) July 26 to 30 (Wolff et al., 1980). The first episode, unlike the ones the previous year, originated in the Texas-Louisiana area. Air parcels traveled northeastward to the lower Midwest and then to the Atlantic coast, extending an "ozone river" from the gulf coast of Texas to Louisiana to the northeast Atlantic coast, exposing the entire area to concentrations averaging 0.12 to 0.13 ppm. The second and third episodes, like the 1976 episodes, originated in Canada. Because the southern part of the first episode persisted at the time the second and third episodes began, O_3 from the south was pulled into the Midwest, and the region from the Texas gulf coast eastward to the Atlantic coast continued to be exposed to the high concentrations. These episodes simultaneously exposed nearly two-thirds of the United States (Wolff and Liou, 1980; Garner, 1991).

Long-range transport of O₃ need not begin in Canada, the Midwest or Texas. Fankhauser (1976) reported the transport of O₃ in a giant loop stretching from New York City, Philadelphia, Baltimore, and Washington, DC, west through Virginia and Ohio and back to Wheeling, WV, to the Pittsburgh, PA, area. This path continued for 4 to 5 days in September, 1972. Earlier, in May 1972, a stagnant high and a slow-moving low transported air parcels from the Chicago and Pittsburgh areas to Miami, FL (Garner et al., 1989; Garner, 1991).

The foregoing discussion not only depicts the episodic nature of O₃ exposures, but also points out the fact that the major portion of the United States east of the Mississippi River has been exposed frequently to phytotoxic O₃ concentrations. Taylor and Norby (1985) estimate the probability is 80% that any given O₃ episode in the Shenandoah forest will persist for at least 3 days. This information concerning the effects of O₃ exposure is summarized from the 1986 criteria document (U.S. Environmental Protection Agency, 1986).

5.7.3.5 The Appalachian Mountains and the Eastern United States—Since 1986

Changes in growth, decline, and mortality of certain tree species have been reported for high-elevation forest ecosystems from Maine, New Hampshire, Vermont, and New York, south to North Carolina and Tennessee. Studies indicate that the decrease in growth of forest trees began during the late 1950s or early 1960s (Adams et al., 1985; Benoit et al., 1982; Johnson et al., 1984; Phipps and Whiton, 1988; Garner et al., 1989; Garner, 1991). The extent of decrease in growth and of dieback and mortality, and the factors that precipitated them, are subject to controversy (Garner, 1991; Garner et al., 1989; Taylor and Norby, 1985). Many hypotheses, including O₃ exposure, have been advanced as possible causes. The problem, as pointed out by Woodman and Cowling (1987), is establishing causation. Rigorous proof is needed, but only circumstantial evidence is available. Because the growth reductions began so many years ago, long-term historical data regarding forest structure and composition is lacking (Garner, 1991; Garner et al., 1989). An additional factor that makes causation difficult to determine is that mature ecosystems are not completely stable, but maintain themselves in an oscillating steady state (Kozlowski, 1985). No long-term studies of the effects of tree decline and mortality on ecosystems similar to those dealing with the exposure and response of the San Bernardino mixed-forest ecosystem in California have been made in the East.

Surveys made in 1982, but mentioned only briefly in the previous criteria document (U.S. Environmental Protection Agency, 1986) give quantitative evidence of a marked dieback and large reductions in basal area and in density of red spruce in the high-elevation forests of New York, Vermont, and New Hampshire (Johnson and Siccama, 1983). Red spruce is the most characteristic species of subalpine forests that occupy the higher peaks and ridges of the Appalachian Mountains from Maine to North Carolina and Tennessee. A co-dominant species in the North is balsam fir (*Abies balsamea*), whereas Fraser fir, a closely related species, is co-dominant in the South (Adams et al., 1985). A detailed description of the red spruce decline in the eastern United States and possible causes and studies conducted to determine the causes can be found in Eager and Adams (1992). In the summary chapter of that text, Johnson et al. (1992) write that they "are in a position to state and support with field and laboratory data that regional scale air pollution has played a significant role in the decline of red spruce in the eastern United States." Ozone usually is considered the only regional air pollutant. In this instance, however, the authors are referring to NO_x and SO_x, the precursors of acidic deposition. Studies evaluating the

direct effects of O₃ on red spruce have found little evidence for a significant effect (McLaughlin and Kohut, 1992). Recent studies evaluating the responses of red spruce and loblolly pine to acidic precipitation and O₃ indicate that high-elevation red spruce forests could be impacted by acidic deposition enhancing soil acidification, mobilization of aluminum ions (Al³⁺), and reducing the availability of important base cations (Edwards et al., 1995).

In the Southeast, the decline and mortality of Fraser fir in the Great Smoky Mountains National Park, and, in North Carolina, the Plott Balsam Mountains and the Black Mountains, which include Mt. Mitchell, have been attributed to infestation by the balsam wooly adelgid (Hain and Arthur, 1985). The west-facing slope of Mt. Mitchell showed the greatest injury. During a 20-year experimental study of Fraser fir growing in the Smoky Mountains National Park, balsam wooly adelgids killed almost all of the canopy trees and reduced the basal area in two plots established in the 1960s. Red spruce basal area in these plots remained about the same for the same period. The report does not mention whether atmospheric pollutants were monitored, nor does it discuss possible pollutant-pathogen interaction or possible predisposition (Busing et al., 1988).

Other studies on Mt. Mitchell, however, do not attribute the death of Fraser fir solely to the balsam wooly adelgid, but suggest that atmospheric deposition and multiple pollutant stresses also had a role in tree mortality. These studies cite exposure to gaseous air pollutants, particularly O₃, and cloud-water deposition of acidic substances among possible stresses that have increased host susceptibility to attack by the balsam wooly adelgid (Hain and Arthur, 1985; Aneja et al., 1992). Ozone levels for the area have ranged from 0.01 to 0.150 ppm, with the highest concentrations occurring early in the summer (Aneja et al., 1992).

Other than the studies of tree death in the specific regions cited above, the studies in the Appalachian Mountains have been field surveys made to identify possible O₃-related foliar injury symptoms on native vegetation and experimental exposures to verify the symptoms and to determine O₃ response of individual forest tree species and other native vegetation, usually using OTCs. Unfortunately, some of the studies exposing individual forest tree species cannot be used because the concentrations at which exposure occurred are given as ambient plus 1, plus 1.5, or plus 2, etc. The actual ambient concentration at the time of exposure is never mentioned in the paper. A few studies use an index, again without stating the O₃ concentration and duration of exposure from which the index was derived. These papers are of little scientific value in this discussion because the actual concentrations and duration of exposures at which vegetational injury occurred cannot be determined.

Data from the Forest Inventory Analysis timber inventory taken between 1972 and 1982, revealed that the annual growth rate of most southern yellow pines (loblolly, pitch, shortleaf, and slash) under 16 in. in diameter had declined by 30 to 50% throughout the Piedmont and mountain areas of the Southeast since measurements were made during the survey of 1957 to 1966 (Sheffield et al., 1985). Ozone has been suggested as a possible cause; however, verification of growth effects on mature trees has been lacking (McLaughlin and Downing, 1995).

Additional studies of the forest condition were conducted by the United States Forest Service. Millers et al. (1989) reviewed the information on tree mortality that has occurred in the eastern hardwood forest during the last century to determine whether a relationship exists between the patterns of mortality and the patterns of atmospheric pollution. The authors suggest "that the apparent increase in the decline and mortality of many hardwood species during the last few decades may be due to intensification of reporting and

to the maturation of the forest itself." Most of the mortality observed was attributed to abiotic and biotic stress factors such as weather, silviculture, and injury by insects and diseases. Although there is evidence of injury to hardwoods from point-source pollutants such as smelters and to eastern white pine from O_3 , there is no conclusive evidence of an association between patterns of hardwood mortality and regional atmospheric pollution (Millers et al., 1989). Millers et al. (1989) point out, however, that historical data on atmospheric deposition are not readily available to compare with historical data on mortality.

Twardus et al. (1993) describe forest conditions in twenty states within the Northeastern United States. Information on forest health in this report was obtained from the Cooperative Forest Health Program, from the Forest Inventory and Analysis Surveys conducted by the U.S. Department of Agriculture Forest Service between 1971 and 1993, and from the Northern Forest Health Monitoring Program. They state that "there continues to be no evidence of large, regional-scale declines in forest ecosystem health as determined by observation of visible crown indicators on trees, e.g., crown dieback, crown density, and foliage transparency." Symptoms of exposure to O_3 were noted on sensitive plants on 10 of 98 plots where bioindicator plants were located.

Recently, McLaughlin and Downing (1995) completed a 5-year study of the interactive effects of ambient O_3 and climate on the growth of mature loblolly pines. Ozone, temperature, and moisture stress often correlate well with each other in the southeastern United States because hot, dry years often are associated with air stagnation systems that result in regional O_3 episodes. Tree growth rates, as measured by annual circumference increase per tree for two drier upland sites (16 trees) and a wetter more fertile stand near a stream bottom (18 trees), were compared. Short-term changes in stem circumference of 24 to 34 mature trees were measured at 138 intervals during five growing seasons (May through October) using a sensitive dendrometer band system. During the period of the study, widely variable temperature, rainfall, and O_3 -exposure conditions and growth rates that varied by 75% across the years were observed. Growth rates were consistently influenced by 3-day average O_3 exposures ≥ 40 ppm during the period from 0900 to 2000 hours (9:00 a.m. to 8:00 p.m.). McLaughlin and Downing (1995) stated that their model, which combined 5 years of growth data, suggested that the high-frequency effects of the 0.30 ppm-h increase in mean daily O_3 exposure in the most polluted year (1988), when compared to the cleanest year (1989), would reduce stem growth by approximately 7% in a relatively moist year and by almost 30% in a moderately dry year. They conclude that both episodic and chronic alterations of stem growth in mature trees are associated with ambient levels of O_3 . Episodic reductions are related directly to O_3 exposure, whereas chronic alterations reflect the interaction of O_3 exposures and climatic stresses.

The surveys described below, specifically those made in the Shenandoah National Park, indicate that the injury to native vegetation reported by Hayes and Skelly (1977), Skelly (1980), Benoit et al. (1982), and Duchelle et al. (1982) continues to occur. This is cause for concern because the 48 national parks, including the Great Smoky Mountain and Shenandoah National Parks, are designated as Class I areas under the amended Clean Air Act (U.S. Code, 1991). Air pollution effects on resources in Class I areas constitute an unacceptable adverse impact if such effects diminish the national significance of the area, impair the quality of the visitor experience, or impair the structure and functioning of the ecosystem (Fox et al., 1989; Chappelka et al., 1992). Factors considered in determining if an effect is unacceptable include the frequency, magnitude, duration, location, and reversibility of the impact.

In a survey of eastern white pine stands in the southern Appalachians, 50 white pines were examined for foliar symptoms (chlorotic mottle) believed to be caused by O₃ at each of 201 sites distributed on a 24 × 24-km grid across the natural range of the species in South Carolina, Tennessee, Virginia, North Carolina, Kentucky, and Georgia (Anderson et al., 1988). The survey was conducted from September through November 1985. The percentage of stands with at least one symptomatic tree was highest in Kentucky (77%), followed by Tennessee (31%), and lowest in Georgia (10%). The mean percentage of symptomatic trees per plot for all six states was 27%. The mean volume difference of 48 pairs of symptomatic and nonsymptomatic trees was 49% less for symptomatic trees. Elevation and percent slope were not correlated with occurrence of symptomatic trees, but most symptomatic trees were found on southwest-facing slopes. Plantations had a higher percentage of symptomatic trees than did natural stands. Ozone exposure concentrations were not reported, but it may be possible to make estimates of exposure using data from the nearest O₃ monitoring sites.

Shenandoah and Great Smoky Mountains National Parks are contained within the survey area investigated by Anderson et al. (1988). Winner et al. (1989) surveyed 7 to 10 individuals of five native species at 24 sites in Shenandoah National Park. These species included tulip poplar, wild grape (*Vitis sp.*), black locust, virgin's bower (*Clematis virginiana*), and milkweed. Visible foliar injury due to O₃ was most prevalent on milkweed species (up to 70%), whereas the remaining species had injury approaching 20%. In each case, the level of foliar injury increased with the elevation of the sites. The summer monthly 24-h mean O₃ concentrations at Blacksburg, Rocky Knob, Salt Pond, and Big Meadows did not exceed 0.06 ppm, and foliar injury still was observed.

Another survey made during August to September, 1991, in the Shenandoah National Park included black cherry, yellow poplar, and white ash; and, in the Great Smoky Mountains National Park, black cherry, sassafras (*Sassafras albidum*), and yellow poplar (Chappelka et al., 1992). Black cherry exhibited symptoms in both parks. In the former, the percentage of leaves injured ranged from 18 to 40, whereas, in the latter, the range was 8 to 29% in 1991. Black cherry at Cove Mountain in the Great Smoky Mountains National Park exhibited the highest percentage of symptomatic trees (97%). This site also had the highest number of hours exceeding 0.08 ppm. The majority of occurrences of concentrations exceeding 0.08 ppm occurred during evening hours. Chappelka et al. (1992) suggest that some of the variability in foliar injury response of hardwood species to O₃ in the Shenandoah and Great Smoky Mountains National Parks is due to elevation and microsite conditions, including proximity to streams.

During surveys made in the summers of 1987 through 1990, a total of 95 different plant species, approximately 6% of those growing in Smoky Mountain National Park, exhibited possible foliar injury symptoms attributable to O₃ exposures (Neufeld et al., 1992). Plant species exhibiting foliar injury varied from herbaceous herbs, a grass and a fern, to woody deciduous angiosperms and nine species of evergreens, of which six were conifers. Species exhibiting field symptoms included the native trees (black cherry; sycamore; tulip poplar; black locust; sweet gum; eastern hemlock; and Virginia, Table Mountain, and pitch pines) and herbaceous plants, such as virgin's bower, wild grape, and tall milkweed, all plants previously reported by Duchelle and Skelly (1981) and listed in the previous criteria document (U.S. Environmental Protection Agency, 1986) as being sensitive to O₃ exposures. Ozone concentrations during the period of the surveys did not exceed 0.12 ppm. The observation was made that plants growing at the highest elevations experienced higher maximum and higher minimum concentrations and were exposed to 50% more O₃.

To verify the foliar injury observed in the field as being due to O₃, 39 species, 28 of them with field injury symptoms, had been fumigated experimentally in OTCs at the time of publication. Exposures resulted in injury symptoms on 25 of the 28 species that exhibited injury in the field (Neufeld et al., 1992).

Surveys also were made in a Class I areas in New Hampshire and Vermont during the years 1988 to 1990 (Manning et al. 1991; Lefohn and Manning, 1995). Ozone injury was extensive on vegetation growing in open-top and ambient air experimental plots in both states in 1988, when O₃ concentrations were unusually high. The incidence and intensity of O₃ injury symptoms were considerably less in 1989, whereas, in 1990, injury symptoms were evident on all plants. Based on the studies, it was determined that black cherry, milkweed, white ash, white pine, and two species of blackberry were all reliable biological indicators of ambient O₃ exposure (Manning et al., 1991).

The above surveys indicated that although there has been evidence of widespread injury to native trees and other vegetation from exposure to O₃, the amount of injury has not been great enough for it to be transferred from the tree level to the stand level. Undoubtedly, there has been selection for and removal of the most sensitive tree species of eastern white pine, for example. However, the numbers of sensitive individuals in a stand have not been great enough to make a visible impact on the forest. Simulations suggest that, in forests with mixed species of uneven-aged stands, long-term responses are likely to be shifts in species composition rather than widespread degradation (Taylor and Norby, 1985; U.S. Environmental Protection Agency, 1986).

5.7.3.6 Rhizosphere and Mycorrhizal-Plant Interactions

The importance of the below-ground ecosystem largely has been overlooked when evaluating ecological responses to oxidant exposure. Although the soil system is part of the larger terrestrial ecosystem, it is a system that operates independently and, therefore, is itself an ecosystem (Richards, 1987). Although above-ground components of the terrestrial ecosystem are dominated by producers, the below-ground system is composed primarily of consumers. Thus, the below-ground system is dependent on the above-ground system for inputs of energy-containing substrates. Bacteria, fungi, protozoa, nematodes, microarthropods, earthworms, and enchytraeids all serve various functions in maintaining biological, physical and chemical characteristics of soil, and all are dependent on plant residues for their maintenance. Although the uniqueness of the below-ground ecosystem needs to be recognized, the interdependence between the above- and below-ground systems cannot be over emphasized.

Mycorrhizal fungi are an integral part of the below-ground ecosystem of terrestrial plant communities and are of great importance for vegetational growth. The 1986 criteria document (U.S. Environmental Protection Agency, 1986) discussed mycorrhizae-plant interactions and their importance in some detail. Mycorrhizae are formed on the roots of the vast majority of terrestrial plants and contribute substantially to ecosystem function (Allen, 1991; Harley and Smith, 1983). Fungi invade the roots of terrestrial plants and transform them into mycorrhizae or "fungus roots". The fungus and the host plant live together in an association beneficial to both organisms. Most terrestrial plants cannot adequately take up soil nutrients and water and achieve optimum growth and reproduction without mycorrhizae (Hacskeylo, 1973; Ho and Trappe, 1984; Allen, 1991). Mycorrhizal fungi increase the solubility of minerals, improve the uptake of nutrients for host plants, protect their roots against pathogens, produce plant growth hormones, and transport carbohydrate from one plant

to another (HacsKaylo, 1973). In exchange, the roots of the host plant provide the fungi with simple sugars (HacsKaylo, 1973; Krupa and Fries, 1971). The fungus-plant root relationship is particularly beneficial to plants growing on nutrient-poor soils.

Ozone stress reduces photosynthesis and growth, and roots often are more affected than shoots (Figure 5-33; Winner and Atkinson, 1986; McCool and Menge, 1984; Blum and Tingey, 1977; Manning et al., 1971b; Tingey and Blum, 1973; Hogsett et al., 1985a; Tingey et al., 1976b; Spence et al., 1990; McLaughlin et al., 1982). It has been shown to affect both leaf senescence and root production in plants, thereby disrupting carbon availability for maintenance of the below-ground system (Gorissen et al., 1991b; Andersen and Rygielwicz, 1991), and to alter mycorrhizal colonization and compatibility (Stroo et al., 1988; Reich et al., 1986a; Simmons and Kelly, 1989).

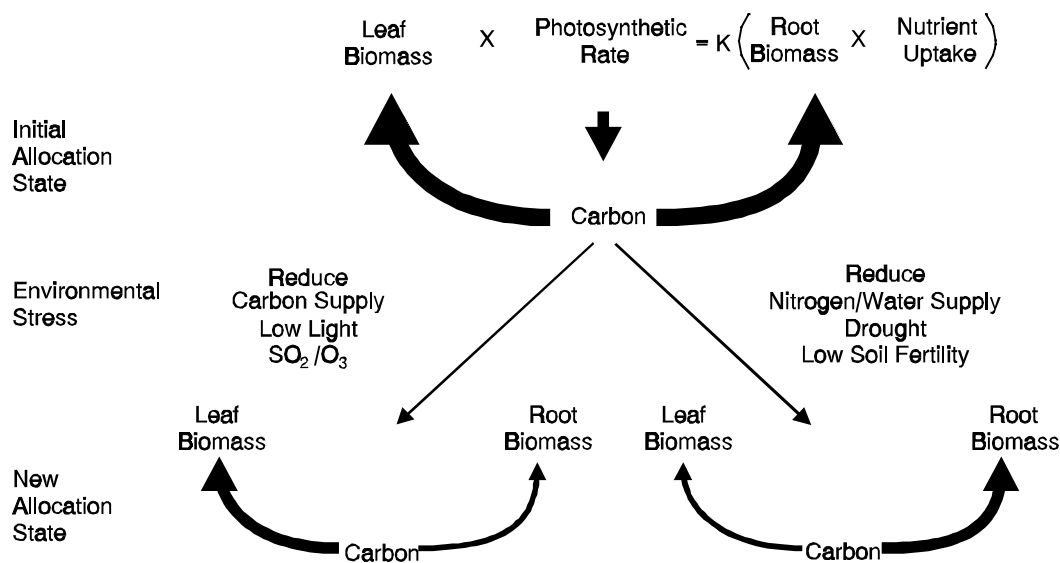


Figure 5-33. *Impact of a reduced supply of carbon to the shoot, or water and nitrogen to the roots, on subsequent allocation of carbon.*

Source: Winner and Atkinson (1986).

Mycorrhizae are sensitive to the capacity of the plant to translocate carbohydrate compounds to the roots. Studies have shown that simple sugars provided by plant roots are utilized readily by mycorrhizae and enhance fungal inoculation (McCool and Menge, 1984; HacsKaylo, 1973). Ozone has the capability of disrupting the association between the mycorrhizal fungi and host plants by inhibiting photosynthesis and reducing the amount of sugars available for transfer from the shoot to the roots (see Figure 5-3). Reduction in the roots of available sugars can reduce mycorrhizal formation and root growth as well (Andersen et al., 1991). Berry (1961) examined the roots of eastern white pine injured by O₃ and observed that healthy trees had almost twice the percentage of living feeder roots as trees with O₃ injury. In the San Bernardino Forest in California, Parmeter et al. (1962) observed

that the feeder roots system of ponderosa pine exposed to O₃ showed marked deterioration (U.S. Environmental Protection Agency, 1986).

Some studies of the effects of O₃ on tree species that include the investigation of the effects on ectomycorrhizal associations and have been discussed in a series of articles (Shafer and Schoeneberger, 1991). Selected studies are summarized in Table 5-35. The understanding of oxidant effects on root symbioses has not changed substantially since 1986 (U.S. Environmental Protection Agency, 1986); however, the understanding of the importance of symbiotic organisms in ecosystem function has improved. The basic hypothesis on mechanisms remains the same (i.e., effects are mediated through host carbohydrate metabolism) because oxidants do not penetrate the soil more than a few centimeters. Most of the research has been conducted on individual plant species, usually as seedlings, in controlled environments. Although the role of mycorrhizae in community structure has been recognized, it has not specifically been addressed experimentally.

Other studies have refined the understanding of oxidant stress effects on roots. In Douglas fir, root/soil respiration was reduced significantly during the first 1 to 2 weeks after exposure to O₃ or SO₂, followed by a recovery period that resulted in similar total respiratory release between treatments and controls (Gorissen and van Veen, 1988; Gorissen et al., 1991a). Total allocation to roots did not appear to be reduced, but O₃ apparently reduced translocation to roots in that respiration of ¹⁴C was suppressed. Edwards (1991) found that root and soil respiration were reduced in loblolly pine seedlings exposed to O₃ levels ranging from 0.07 to 0.11 ppm (7-h mean) compared to seedlings exposed to levels below ambient (0.02 to 0.04 ppm). Nouchi et al. (1991) found that O₃ at 0.1 ppm reduced root respiration by 16% in domestic rice (*Oryza. sativa*) after 1 week of exposure. However, exposure to 3 to 7 weeks of 0.1 ppm O₃ resulted in elevated levels of root respiration.

The effects of O₃ on carbohydrate allocation to roots and subsequent shifts in biomass allocation have been examined (Cooley and Manning, 1987; Kostka-Rick and Manning, 1992a; Karnosky et al., 1992b; De Temmerman et al., 1992; Qui et al., 1992; Sharpe et al., 1989; Gorissen and van Veen, 1988; Gorissen et al., 1991a; Spence et al., 1990). Gorissen et al. (1991b) also studied the effects of O₃ exposure on Douglas fir inoculated with the fungi *Rhizopogon vinicolor* and *Lactarius rufus* and watered with ammonium sulfate. The investigators found greater needle retention of ¹⁴C-labeled compounds in the new needles of O₃-treated plants, and a trend towards fewer ¹⁴C-labeled substrates recovered in roots and root/soil fractions. Short-term transport of ¹¹C-labeled substrates were followed throughout loblolly pine (Spence et al., 1990). A 45% reduction in transport of photosynthates to roots occurred in O₃-treated plants compared to controls. Collectively, the studies have shown a general trend of diversion of carbohydrate from roots and retention in the photosynthetically active portions of plants. A reduction in allocation to roots can be associated with a change in the availability of carbohydrate for maintenance of root symbioses.

Table 5-35. Interactions of Ozone and Forest Tree Ectomycorrhizae^a

Host Plant	Mycorrhizae	Exposure Conditions	Effect of O ₃ on Mycorrhiza	Reference
Loblolly pine	<i>Pisolithus tinctorius</i>	OTC, field	Reduced root infection	Adams and O'Neill (1991)
	Not stated	OTC, field, 3 years	Reduced root infection	Edwards and Kelly (1992)
	Not stated	CEC	No effect	Mahoney et al. (1985)
	Not stated	CSTR	Reduced root infection	Meier et al. (1990)
Scots pine	Ten species	Open air, field, 3 years	No significant effects	Shaw et al. (1992)
White pine	<i>Pisolithus tinctorius</i>	CEC	Reduced root infection	Stroo et al. (1988)
Norway spruce	Six species	Open air, field, 3 years	No significant effects	Shaw et al. (1992)
	Four species	CEC	No consistent effects	Blaschke and Weiss (1990)
Paper birch	<i>Pisolithus tinctorius</i>	CEC	No effects	Keane and Manning (1988)
Red oak	Not stated	CEC and OTC	Significant increase	Reich et al. (1985)

^aSee Appendix A for abbreviations and acronyms.

The effects of O₃ on mycorrhizal colonization have varied depending on the experimental conditions and the species used. Stroo et al. (1988) studied the effects of O₃ on mycorrhizal infection in eastern white pine seedlings grown for 4 mo in several soils. Results varied by soil type and nitrogen availability; however, in several soils, the number of mycorrhizal short roots increased slightly at low O₃ levels and decreased significantly at higher O₃ concentrations. Reich et al. (1986a) found similar results in eastern white pine and red oak and concluded that O₃ may stimulate mycorrhizal infection at low O₃ concentrations. Simmons and Kelly (1989) observed a trend of greater mycorrhizal short roots in loblolly pine seedlings exposed to subambient O₃ treatment than those exposed to ambient or twice ambient O₃ levels, but the results were not statistically significant. In another study with two families of loblolly pine, Adams and O'Neill (1991) found that mycorrhizal colonization tended to increase with O₃ during the first 6 weeks of exposure and decrease with O₃ after 12 weeks of exposure. Meier et al. (1990) found a decrease in ectomycorrhizal root tips and percentage of feeder roots in loblolly pine seedlings. Keane and Manning (1988) found significant interactions among O₃, soil type, and pH; however, the direct effects of O₃ were difficult to elucidate. Collectively, these results suggest that O₃ does impact colonization of roots by mycorrhizal fungi; however, the results illustrate the variability in response due to such factors as soil condition, duration of experiment, and timing of measurements.

Altered root carbohydrate allocation resulting from O₃ exposure can affect host-fungus compatibility (Edwards and Kelly, 1992; Simmons and Kelly, 1989). Combined effects of O₃, rainfall acidity, and soil magnesium status on growth and ectomycorrhizal colonization of loblolly pine has been studied (Simmons and Kelly, 1989). Although variation was high, there was a trend towards altered species composition and reduced mycorrhizal infection in O₃-treated seedlings. Edwards and Kelly (1992) found high variability in morphotype (morphologically different) frequency in response to O₃ treatments in loblolly pine and noted changes in morphotype frequency over the 3-year study that suggested fungal succession had occurred. Fungal succession and the effects of oxidant stress on normal successional patterns are poorly understood. Shaw et al. (1992), using an open-field exposure system, found no differences in morphotype frequency or fruit-body succession in response to O₃ treatments.

The availability of current photosynthate for root growth is reduced under O₃ stress, and maintenance of below-ground processes dependent on roots for their carbon substrates may be affected. Mycorrhizae alter the size, quality, and retention time of carbon-pools below ground. As noted in the previous section, a 45% reduction in transport of photosynthates to roots occurred in O₃-treated loblolly pine (Spence et al., 1990). Ozone reduces concentrations of root carbohydrates (Jensen, 1981; Tingey et al., 1976b; Meier et al., 1990; Andersen et al., 1991). Starch in roots was reduced significantly in ponderosa pine by the end of one growing season of O₃ exposure (Tingey et al., 1976b). Reductions in coarse and fine root starch concentrations persisted over the winter in O₃-treated ponderosa pine and were lower during shoot flush in subsequent years (Andersen et al., 1991). In this study, lower starch concentrations in O₃-treated seedlings were associated with suppressed growth of new roots. The consequences of a reduction in carbon allocation below ground include reduced substrate availability for soil flora and fauna; altered soil physical characteristics, such as total organic matter and aggregation; and altered soil chemical characteristics including cation exchange capacity.

Premature leaf senescence has been observed in plants exposed to O₃ stress (U.S. Environmental Protection Agency, 1986). Premature senescence affects the

belowground ecosystem by reducing canopy photosynthesis and carbon availability for transport to the belowground system and by increasing leaf litter inputs to the forest floor (Miller, 1984; Fenn and Dunn, 1989). The result is increased flux of nutrients, especially nitrogen, below ground, due to oxidant exposure.

The increased flux of nitrogen due to premature needle senescence in oxidant-exposed plants may act to disrupt the nutrient flow of the ecosystem. Allocation of carbon resources throughout a plant is based on a priority scheme that is driven by carbon and nutrient availability (Waring and Schlesinger, 1985). When soil nutrient levels are high, allocation to the shoot is favored over the roots (Figure 5-32). By shifting carbon allocation to organs in this fashion, plants can adjust to shifts in resource availability in their environment. Oxidant stress alters typical allocation schemes and, in the process, may impair the plant's ability to cope with drought or other stresses. In addition, reductions in allocation to roots can alter root-system size, architecture, and spatial arrangement, which, in turn, can influence populations of soil organisms.

Bacteria and fungi are particularly important in nutrient cycles and act to immobilize nitrogen, carbon, phosphorus, and other nutrients in the biomass. The turnover of these nutrient pools is relatively short because bacterial and fungal predators act to release these nutrients. The majority of plant-available nitrogen during the growing season comes from these predatory interactions in the soil (Kuikman et al., 1990; Ingham et al., 1985), emphasizing their importance in the maintenance of terrestrial ecosystems. Currently, there are no data available on the effect of O₃ on soil fauna.

In summary, mycorrhizal fungi are essential for optimal plant growth. Mycorrhizal fungi increase the solubility of minerals, improve the uptake of nutrients for the host plants, and protect plant roots against pathogens. In turn, the plant roots furnish the fungi with simple sugars that readily are utilized by the fungi and enhance their ability to form mycorrhizae. Mycorrhizae are sensitive to the capacity of the plant to translocate these carbohydrates to the roots. Ozone, by inhibiting photosynthesis, reduces the production of sugars available for transport to the roots. Reduction of sugars in the roots can reduce formation of mycorrhizae and root and tree growth as well.

5.7.4 Ecosystem Response to Stress

5.7.4.1 Introduction

Mature forest ecosystems are seldom stable. They are complex, dynamic communities of living and dead trees interacting among themselves; with populations of native forest floor plants; and with an array of microorganisms, insect pests, and environmental, human, and other factors to continuously shape and reshape the community over time (Manion and Lachance, 1992). Forest communities are held in steady state by the operation of a particular combination of biotic and abiotic factors. Stresses that alter or remove any of the factors can alter the community and change the ecosystem (Kozlowski, 1980; Garner et al., 1989).

Growth of new trees and other vegetation requires the expenditure of energy in the form of carbon compounds. Plants accumulate, store, and use carbon compounds to build their structure and to maintain their physiological processes. Carbon dioxide absorbed from the atmosphere is combined in plant leaves with water from the soil to produce the carbon compounds (sugars) that provide the energy utilized by trees for growth and maintenance (Figure 5-34; Waring and Schlesinger, 1985). Patterns of carbon allocation to roots, stems,

and leaves directly influence growth rate. The strategy for carbon allocation changes during the life of a plant, as well as with different environmental conditions (Figure 5-33; Winner and Atkinson, 1986). Mature trees have a higher ratio of respiration to photosynthetic tissue (Cregg et al., 1989). Even small changes in photosynthesis or carbon allocation can profoundly alter the structure of a forest (Waring and Schlesinger, 1985). Impairment of the process of photosynthesis shifts carbon allocation from growth and maintenance to repair and increased respiration and can result in resource imbalances. The significant changes observed in the San Bernardino Forest ecosystem were possible outcomes of the combined influences of O₃ on carbon, water, and nutrient allocation (McLaughlin, 1994).

Intense competition among plants for light, water, nutrients, and space, along with recurrent natural climatic (temperature) and biological (herbivory, disease, or pathogen) stresses, can alter the species composition of communities by eliminating those individuals sensitive to specific stresses, a common response in communities under stress (Woodwell, 1970; Guderian, 1985). Individual organisms within a population vary in their ability to withstand the stress of environmental changes. The range of variability within which these organisms can exist and function determines the ability of the population to survive. Those organisms able to cope with stresses survive and reproduce. Competition among different species results in succession (community change over time) and ultimately produces ecosystems composed of populations of plant species that have a capacity to tolerate the stresses (Kozlowski, 1980). Pollutant stresses, such as those caused by exposure to O₃, are superimposed on the naturally occurring competition stresses mentioned above (see also Section 5.4). Communities, due to the interaction of their populations, respond to pollutant stresses differently from individuals (U.S. Environmental Protection Agency, 1993). Air pollutants are known to alter the diversity and structure of plant communities (Guderian et al., 1985). The extent of change that may occur in a community depends on the condition and type of community, as well as on the pollutant exposure.

The plant processes of photosynthesis, nutrient uptake, respiration, translocation, carbon allocation, and growth are directly related to the two essential ecosystem functions of energy flow and nutrient cycling. Altering the above processes can alter energy flow and nutrient cycling and impact ecosystems (Smith, 1992). Response of forest ecosystems to stress are growth-related processes that begin within individual trees and progress to increasing levels of integration and complexity (Figure 5-35; McLaughlin, 1994). Cytological and biochemical changes within a tree can impact physiological functions and alter the tree's growth and productivity. Plants acclimate to changing environmental stresses through both short- and long-term physiological responses, as well as through structural and morphological modifications (Dickson and Isebrands, 1991). When there are many sensitive individuals, the forest structure is changed. As indicated above, response begins with the interaction of the individual and its environment, progresses to the population and its environment, and then to the biological community and its environment (Billings, 1978).

In unpolluted atmospheres, the number of species in an ecosystem usually increases during succession. Productivity, biomass, community height, and structural complexity increase in the early stages of development. Severe stresses, on the other hand, divert energy from growth and reproduction to maintenance and repair and alter succession (Waring and Schlesinger, 1985). In addition, biomass accumulation and production decrease,

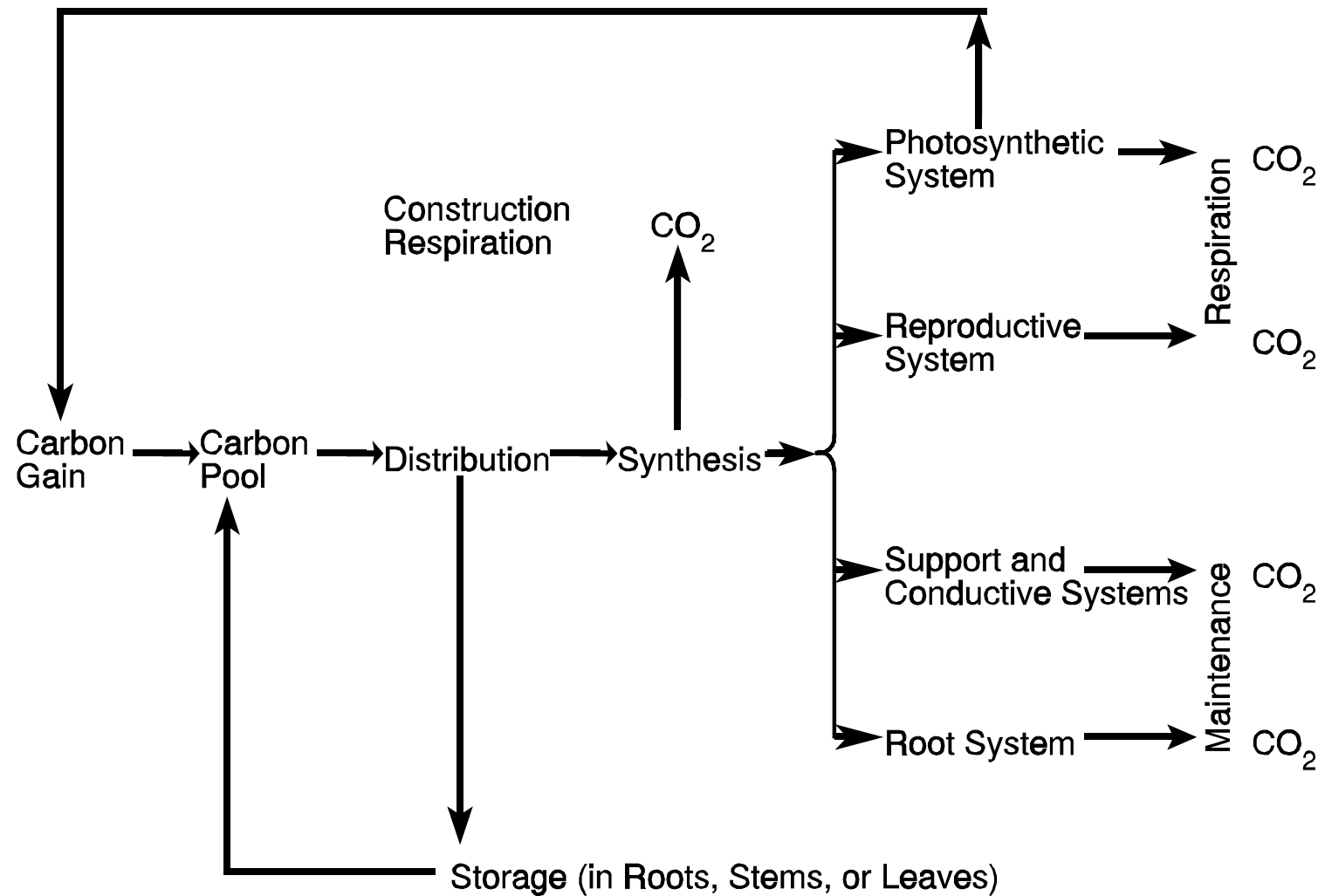


Figure 5-34. Carbon uptake through photosynthesis is made available to a general pool of carbohydrates used in construction and maintenance of various tissues. Carbohydrates may be shifted from one category to another, depending on environmental conditions.

Source: Waring and Schlesinger (1985).

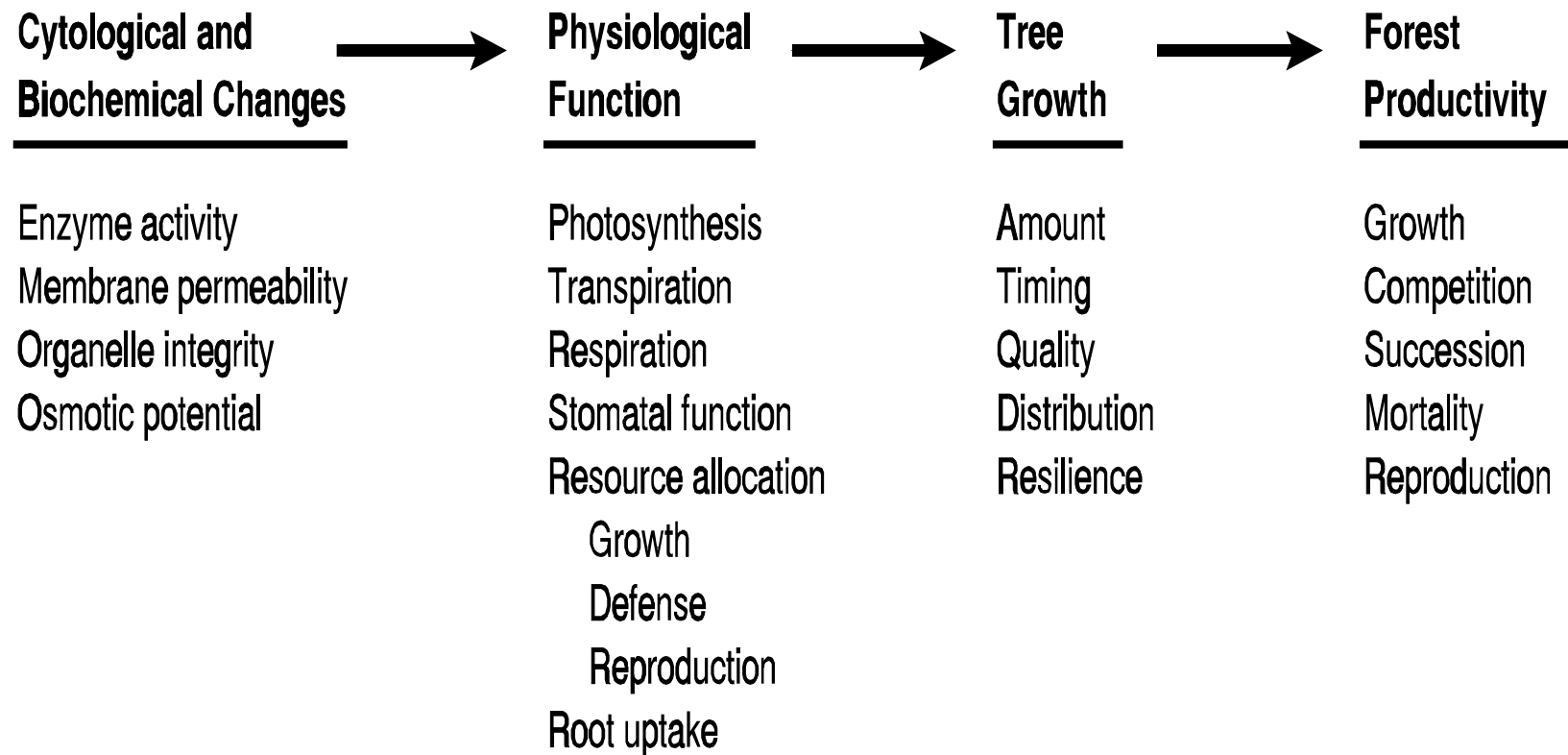


Figure 5-35. Organizational levels at which air pollutants have been shown to affect the growth-related process of forest trees.

Source: McLaughlin (1994).

Table 5-36. Interaction of Air Pollution and Temperate Forest Ecosystems Under Conditions of Intermediate Air Contaminant Load

Forest Soil and Vegetation: Activity and Response	Ecosystem Consequence and Impact
1. Forest tree reproduction, alteration, or inhibition	1. Altered species composition
2. Forest nutrient cycling, alteration <ul style="list-style-type: none"> a. Reduced litter decomposition b. Increased plant and soil leaching and soil weathering c. Disturbance of microbial symbioses 	2. Reduced growth, less biomass
3. Forest metabolism <ul style="list-style-type: none"> a. Decreased photosynthesis b. Increased respiration c. Altered carbon allocation 	3. Reduced growth, less biomass
4. Forest stress, alteration <ul style="list-style-type: none"> a. Phytophagous insects, increased or decreased activity b. Microbial pathogens, increased or decreased activity c. Foliar damage increased by direct air pollution influence 	4. Altered ecosystem stress: increased or decreased insect infestations; increased or decreased disease epidemics; reduced growth, less biomass, altered species composition

Source: Smith (1990).

and structural complexity, biodiversity, environmental modification, and nutrient control are reduced (Bormann, 1985). With maturity, energy utilization in ecosystems shifts from production to maintenance (Odum, 1993) (see Figure 5-34). When catastrophic disturbances or injury, whether from natural (e.g., fire, flood, windstorm) or anthropogenic stresses (e.g., O_3), alter the species composition (biodiversity) of a forest sufficiently to disrupt food chains and to modify rates of energy flow and nutrient cycling, succession reverts to an earlier, less complex stage. The effects of stresses on ecosystems, unless the effects are catastrophic disturbances, are frequently difficult to determine (Kozlowski, 1985; Garner et al., 1989). In a mature forest, a mild disturbance becomes part of the oscillating steady state of the forest community or ecosystem. Responses to catastrophic disturbances, however, as a rule, are readily observable and measurable (Garner, 1994). How changes in plant processes attributed to O_3 exposure affect forest ecosystems is discussed in the following text.

5.7.4.2 Forest Ecosystems

The primary responses of a forest ecosystem to sustained exposure of O_3 are reduced growth and biomass production (Table 5-36; Smith, 1990). Exposure to O_3 inhibits photosynthesis and decreases carbohydrate production and allocation, and, as has been

discussed previously, decreased allocation to the roots interferes with mycorrhizae formation and nutrient uptake (Figure 5-33). The resulting loss in vigor affects the ability of trees to compete for resources and makes them more susceptible to a variety of stresses (Table 5-36; see also Sections 5.3, 5.6.4.2, 5.6.4.3, and 5.7.3.1). Responses of seedlings under experimental conditions indicate that reductions in growth occur at O₃ concentrations of 0.06 ppm or greater (Table 5-30). Cregg et al. (1989) state that information on seedling response must be used with caution. The environments in which seedlings and trees grow are substantially different due to differences in rooting depth and canopy structure. Trees have the potential to significantly alter their environments through shading, whereas seedlings do not. In the San Bernardino Forest, mortality of canopy trees leads to replacement by trees (white fir, incense cedar, sugar pine, and black oak) more tolerant to O₃ and reduced ecosystem structure. Reduction in structure altered nutrient cycling and energy flow and affected the functioning of other ecosystem components (see Section 5.7.3.1). Ozone concentrations capable of causing injury to forest trees and affecting forest processes continue to occur both in the West and the East. Although reports have described the presence of sensitive species in other U.S. forests; only the San Bernardino Forest has been severely impacted by exposure to O₃. Why this is the case is impossible to answer definitively because of the absence of data. Evidence obtained from many studies of a variety of ecosystems over the years indicates that ecosystems, in response to pollution or other disturbances, follow definite patterns that are similar even in different ecosystems (Woodwell, 1970). It is possible, therefore, to predict broadly the basic biotic responses to the disturbance of an ecosystem. These responses are reduction in standing crop (trees), inhibition of growth or reduction in productivity, differential kill (removal of sensitive organisms at the species and subspecies level), food chain disruption, successional setback, and changes in nutrient cycling (U.S. Environmental Protection Agency, 1978).

The effects of the stresses associated with O₃ exposure that have developed over the years in the San Bernardino Forest ecosystem are similar to those listed in the previous paragraph.

The extent of injury that an ecosystem will experience from O₃ exposure is determined by the severity and extent of individual response. Leaf injury, as has been stated previously, is usually the first visible indication of O₃ exposure. Structural effects develop when physiological processes within individual plants are disrupted severely (see Table 5-37 and Figure 5-35). With ecosystem responses such as those seen in the San Bernardino Forest, four levels of biological organization beginning with the individual organism are altered (see Table 5-37; Sigal and Suter, 1987). Taylor and Norby (1985) discuss the possible effects on ecosystems at the individual population and community levels. Alteration of functional properties (ecosystems functions) results in structural dysfunction. Stresses, whose primary effects occur at the molecular or cellular physiology level in the individual, must be scaled progressively up through more integrative levels of organ physiology (e.g., leaf, branch, root) to whole plant physiology, stand dynamics, and then to the landscape level to produce ecosystem effects (Figure 5-36; Table 5-37). Particularly, this is true if the stress is of low-level because only a small fraction of stresses at the molecular and cellular level become disturbances at the tree, stand, or landscape level. The processes of energy flow and nutrient cycling must be altered if ecosystems are to be affected. Insect defoliation, for example, may reduce severely the growth of one or several branches, whereas the growth of the tree appears not to be affected (Hinckley et al., 1992).

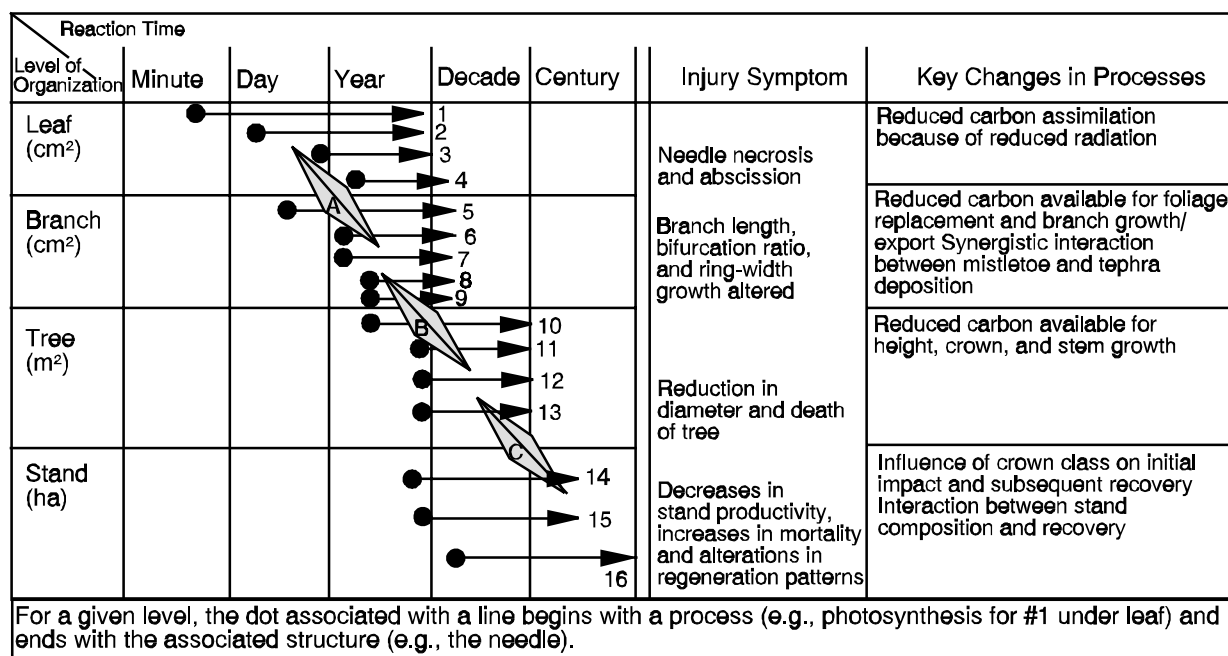
Table 5-37. Properties of Ecological Systems Susceptible to Ozone at Four Levels of Biological Organization

Level of Organization Properties	Structural Properties	Functional Properties
Organism	Leaf area and distribution Biomass and allometry	Photosynthesis, respiration Nutrient uptake and release Carbon allocation
Population	Age and size structure Population density Genetic composition Spatial distribution Dispersion (spatial pattern)	Natality (reproduction, mortality) Competition Productivity
Community	Species composition (diversity) Trophic levels and food webs Physical structure (leaf-area index)	Redundancy and resilience Succession (the integration of all species processes such as competition and predation)
Ecosystem	Biomass Element pools Soil properties	Ecosystem productivity Nutrient cycling Hydrologic cycling Energy flow

Source: Adapted from Sigal and Suter (1987).

Variability and compensation are two properties important in determining the effect a stress at one hierarchical level will have on a higher level of organization (see Sections 5.3 and 5.4). Variability in individual response to stress can be the result of each individual being genetically different (See Section 5.4). Individual trees do not respond equally to O₃ exposure. Ponderosa, Jeffrey, and eastern white pine all have been observed to have sensitive, intermediate, and tolerant varieties based on the degree of response. Variability in exposure-response also can be influenced by the movement of O₃ from the leaf surface through the stomata to the metabolic site of action in the leaf interior (Taylor and Hanson, 1992). The stomatal conductance also influences this action.

Variation in age and stage of growth of the organism also can determine response to O₃ exposure (see Section 5.3). Variability in response between seedlings, saplings, and canopy black cherry trees at a site in north-central Pennsylvania was observed by Frederickson et al. (1994). Physiological, phenological, and morphological differences among seedlings, saplings, and canopy trees were associated with altered O₃ uptake and differential response. Leaves at different crown positions of larger trees exhibited differences in leaf physiology and O₃ uptake. Seedling uptake of O₃ and apparent sensitivity per unit leaf area was greater, based on foliar injury symptoms; however, the relative



Evaluating Impacts Within a Level of Organization

Leaf Level	Carbon exchange-1 Carbon pools-2 Needle number and size-3 Needle retention/abscission-4	Tree Level	Height and diameter growth-10 Crown shape and size-11 Tree vigor-12 Mortality-13
Branch Level	Carbon allocation-5 Branch growth-6 Branch morphology-7 Branch vigor-8 Branch retention-9	Stand Level	Productivity-14 Mortality-15 Species composition-16

Evaluating Interactions Between Different Levels of Organization


	<p>The diagonal arrow indicates the interaction between any two levels of organization. The types of interaction are due to the properties of variability and compensation.</p> <p>A - Refers to the interaction between the leaf and branch levels, where, for example, variability at the branch level determines leaf quantity, and compensation at the leaf level in photosynthesis may compensate for the reduction in foliage amount.</p> <p>B - Refers to the interaction between the branch and the tree, where variability in branches determines initial interception, branch vigor, and branch location in the crown; compensation may be related to increased radiation reaching lower branches.</p> <p>C - Refers to the interaction between the tree and the stand. Both genetic and environmental variability, Inter- and intraspecific compensations, and tree historical and competitive synergisms are involved.</p>
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Figure 5-36. Effects of environmental stress on forest trees are presented on a hierarchical scale for the leaf, branch, tree, and stand levels of organization. The evaluation of impacts within a level of organization are indicated by horizontal arrows. The evaluation of interactions between different levels of organization are indicated by diagonal arrows.

Source: Hinckley et al. (1992).

exposure of seedlings to O₃ was reduced by an indeterminate growth habit because the majority of their leaves were produced after shoot growth had ceased for sapling and canopy trees. Therefore, their relative uptake was reduced on a whole-crown basis over the growing season and cumulative exposure. Lower crown leaves of saplings and canopy trees appear to be more sensitive to O₃ than upper crown leaves, despite lower uptake, which possibly is due to low availability of photosynthate for anti-oxidant defense and repair of injured leaf cell membranes. Shade leaf morphological characteristics also may play a significant role. The above study describes the interaction of multiple factors that determine O₃ uptake and potential response and illustrates the complexity involved in scaling responses from controlled studies of open-grown seedlings to larger forest trees (Fredericksen et al., 1994).

Compensation in response to stress involves the capacity of the individual to adapt to the stress. Some plants compensate physiologically by detoxifying the O₃ entering the leaves. Other plants compensate by altering the root-shoot ratio. They reallocate carbohydrates to the source of injury in the leaves instead of to the roots, as do uninjured trees (see Figure 5-33 and Section 5.1.3). At the stand level, the slower growth of some trees may be compensated for by the relatively faster growth of others that are experiencing reduced competition so that the overall growth of the stand is not affected (Hinckley et al., 1992). These properties, when taken together, will determine the extent and the rate at which stress at one hierarchical level will impact the next highest level. A framework of hierarchical scales (Figure 5-36) was developed by Hinckley et al. (1992) to provide a means by which the effects of the eruption of Mount St. Helens on forest trees could be followed and understood. This framework is also applicable for use when considering O₃ effects and can be used to explain the difference between the response of the San Bernardino Forest ecosystem and the forests in the eastern United States. As pointed out above, variability and compensation determine the severity of the response of the individual.

Variability and compensation also occur at the population level, all populations do not respond equally (Taylor and Pitelka, 1992). Plant populations can respond in four different ways: (1) no response, the individuals are resistant to the stress; (2) mortality of all individuals and local extinction of the extremely sensitive population (the most severe response); (3) physiological accommodation, growth, and reproductive success of individuals are unaffected because the stress is accommodated physiologically; and (4) differential response, members of the population respond differentially, with some individuals exhibiting better growth and reproductive success due to genetically determined traits (Taylor and Pitelka, 1992). Differential response results in the progressive elimination over several generations of the sensitive individuals and a shift in the genetic structure of the population toward greater resistance (microevolution). Physiological accommodation or microevolution, with only the latter affecting biodiversity, are the most likely responses for exposure to chronic stress (i.e., stresses that are of intermediate-to-low intensity and of prolonged duration). The primary effect of O₃ on the more susceptible members of the plant community is that the plants can no longer compete effectively for essential nutrients, water, light, and space, hence are eliminated. The extent of change that can occur in a community depends on the condition and type of community, as well as the exposure (Garner, 1994). Forest stands differ greatly in age, species composition, stability, and capacity to recover from disturbance. For this reason, data dealing with the responses of one forest type may not be applicable to another forest type (Kozlowski, 1980).

In the eastern United States, ecosystem reduction in structure and diversity has never reached the proportions seen in the San Bernardino Mountains. Visible tree decline has

been observed only in the southern Appalachian Mountains, particularly Mt. Mitchell, and on Camel's Hump, VT. The actual cause of decline and mortality of trees in these areas is a matter of question.

Among the hypotheses suggested for the absence of major changes in the eastern forests is a difference in the O₃ exposures experienced by the eastern forests when compared with the San Bernardino Forest, a region noted for high O₃ levels. Lefohn et al. (1994) characterized and compared O₃ concentrations measured from 1988 to 1992 at Bearden Knob and Parsons, located in a remote forested region of north-central West Virginia, with other sites in the region. It was observed that 1988, when compared with 1992, was a year with very high O₃ exposures. At almost all sites in 1992, few hourly concentrations were ≥ 0.10 ppm, whereas in 1988, several sites had 100 or more average concentrations ≥ 0.10 ppm. These concentrations were found at both high- and low-elevation sites. In 1992, Bearden Knob, a high-elevation site, experienced a flat diurnal pattern, whereas Parsons, the nearby low-elevation site, experienced a varying diurnal pattern, an indication that O₃ was being scavenged. Horton Station, a high-elevation site in southwestern Virginia, in 1992, experienced 25 episodes with hourly average concentrations near 0.05 ppm for 8 h or longer, 18 episodes with hourly average concentrations near 0.06 ppm, and three episodes with concentrations at or near 0.07 ppm. For the same period, Bearden Knob experienced 31 episodes of 8 h or longer for average hourly concentrations near 0.05 ppm, 13 episodes at or near 0.06 ppm, and 3 episodes at or near 0.07 ppm.

Maximum hourly average concentrations from April to October during 1988 were 0.145 ppm at or near Horton Station, compared with the 0.29 ppm received by the San Bernardino National Forest. Horton Station was exposed to 2,758 hourly concentrations between 0.05 ppm and 0.087 ppm, whereas the San Bernardino site received 2,027 h. The latter site had more concentrations above 0.10 ppm; therefore, it received fewer exposures between 0.05 and 0.087 ppm. It was suggested that the extreme growth reduction and injury that has been observed in the San Bernardino area over the years, when compared with the absence of such injury in the Horton Station area, could be attributed solely to the higher number of hourly average concentrations exceeding 0.10 ppm at the former site (Lefohn et al., 1994). Factors not considered were differences in sensitivity, stand composition, and the ability to compensate for the stress, as well as site variables.

These factors definitely apply in the Appalachian Mountains and, to a degree, in the Sierra Nevada, where the sensitive individuals and composition of the forests vary from the San Bernardino Mountains. The forests of the Appalachian Mountains are known to be more biologically diverse than western forests. Only in the San Bernardino Forest did the removal of sensitive trees reach the population level. Population dynamics impact the ecosystem functions of energy flow and nutrient cycling.

Eastern white pine responses to O₃ exposures were classified into three sensitivity levels ([1] sensitive, [2] intermediate, and [3] tolerant) by both McLaughlin et al. (1982) and Benoit et al. (1982). Black cherry also has been observed to have three sensitivity levels. None of these trees can be termed canopy dominants. In addition to conifers, the forest canopy includes varieties of oaks that are not as sensitive to O₃ exposures. Species removal, therefore, has not affected the eastern forests as did removal of ponderosa and Jeffrey pine from the San Bernardino Forest. Taylor and Norby (1985) have pointed out that the nature of community dynamics, particularly in mixed species, and stands with trees of uneven age play important roles in forest response. Shifts in species composition are more likely responses to stresses such as O₃ than to community degradation. The removal of the codominant

American chestnut (*Castanea dentata*) in the first half of this century caused no major change in the tree species relationships in the Appalachian forests. The effects of O₃ exposure also will probably not cause major change.

The previous O₃ document (U.S. Environmental Protection Agency, 1986) concluded that none of the tree species shown to be injured by O₃ play a dominant role in the Blue Ridge Mountain ecosystem. Therefore, the removal of any of these species probably would not have the impact that the decline and death of ponderosa and Jeffrey pine have had on the San Bernardino Forest ecosystem. This same conclusion applies today.

5.7.5 Summary

Ecosystems are composed of populations of "self-supporting" and "self-maintaining" living plants, animals, and microorganisms (producers, consumers, and decomposers) interacting with one another and with the nonliving chemical and physical environment within which they exist (Odum, 1989; U.S. Environmental Protection Agency, 1993). Mature ecosystems are seldom stable. Structurally complex communities, they are held in an oscillating steady state by the operation of a particular combination of biotic and abiotic factors, and they must respond and adapt continually to changing environments (Kozlowski, 1985).

Ecosystem response to stress begins with individuals (Figures 5-34, 5-35, and 5-36). Growth of trees and other vegetation requires the expenditure of energy in the form of carbon compounds. Carbon compounds are accumulated, stored, and used by plants to build their structure and maintain their physiological processes (Figure 5-34). Carbon dioxide absorbed from the atmosphere, combined with water from the soil in plant leaves during photosynthesis, provides the energy in the form of carbon compounds (sugars) utilized by trees for growth and maintenance (Figure 5-34; Waring and Schlesinger, 1985). Patterns of carbon allocation to roots, stems, and leaves directly influence growth rate. The strategy for carbon allocation may change during the life of a plant, as well as with different environmental conditions (Figure 5-33; Winner and Atkinson, 1986). Trees acclimate to changing environmental stresses through both short-term and long-term physiological responses and structural and morphological modifications (Dickson and Isebrands, 1991). Even small changes in photosynthesis or carbon allocation can alter profoundly the structure of a forest (Waring and Schlesinger, 1985). Impairment of the processes of photosynthesis shifts carbon allocation from growth and maintenance to repair, increases respiration, and can result in resource imbalances. The significant changes observed in the San Bernardino Forest ecosystem were a possible outcome of the combined influences of O₃ on carbon, water, and nutrient allocation (McLaughlin, 1994).

Mycorrhizae are an extremely important, but unheralded, component of all ecosystems. The majority of plants depend on them for the uptake of mineral nutrients from the soil. Their absence from the roots of plants has been shown to have a detrimental impact on plant growth. Decreased carbohydrate production and reduced allocation to the roots due to O₃ exposure affect the formation of mycorrhizae and impact plant growth. Exposure to O₃, therefore, affects plant growth both above and below ground.

Intense competition among plants for light, water, nutrients, and space, along with recurrent natural climatic (temperature) and biological (herbivory, disease, pathogens) stresses, can alter the species composition of communities by eliminating those individuals sensitive to specific stresses, which is a common response in communities under stress (Woodwell, 1970;

Guderian, 1985). Those organisms able to cope with stresses survive and reproduce. The effects of stresses on ecosystems, unless the effects are catastrophic disturbances, are frequently difficult to determine (Kozlowski, 1985; Garner et al., 1989). In a mature forest, a mild disturbance becomes part of the oscillating steady state of the forest community or ecosystem. Responses to catastrophic disturbances, however, as a rule, are readily observable and measurable and return ecosystems to a less complex stage (Garner, 1994).

Ecosystem responses are hierarchical. The extent of injury that an ecosystem can experience from exposure to O₃ will be determined by the severity of the effect on individual members of a population. Stresses, whose primary effects occur at the molecular or cellular physiology level of an individual, must be propagated progressively through the more integrative levels, from the leaf, branch, or root, to whole plant physiology, to stand dynamics, and, ultimately, to the ecosystem (see Figures 5-35 and 5-36). Only a small fraction of the stresses at the molecular, cellular, or leaf level leads to disturbances at the tree, stand, or ecosystem level. Variability in response to stress at both the individual and the population level and the ability to compensate for the stress determine the hierarchical extent of the response.

The mixed-conifer forest ecosystem in the San Bernardino Mountains of Southern California is one of the most thoroughly studied ecosystems in the United States. The changes observed in the mixed-conifer forest ecosystem exemplify those expected in a severely disturbed ecosystem. Chronic O₃ exposures over a period of 50 or more years resulted in major changes in the San Bernardino National Forest ecosystem by influencing forest processes. The primary effect was on the more susceptible members of the forest community, individuals of ponderosa and Jeffrey pine, in that they were no longer able to produce the energy required to compete effectively for essential nutrients, water, light, and space. As a consequence of altered competitive conditions in the community, there was a decline in the sensitive species, permitting the enhanced growth of more tolerant species (Miller et al., 1982; U.S. Environmental Protection Agency, 1978, 1986). Changes in the function of other ecosystem components directly or indirectly affected the processes of carbon (energy) flow, mineral-nutrient cycling, and water movement and changed community patterns. Biotic interactions associated with predators, pathogens, and symbionts were influenced by changes in available energy. The results of the studies of the San Bernardino Forest ecosystem were reported in both the 1978 and 1986 criteria documents (U.S. Environmental Protection Agency, 1978, 1986). The more recent data from the San Bernardino Forest and from other ecosystems in California indicate that O₃ concentrations capable of injuring forest vegetation continue to occur, but at lower concentrations and with shorter durations. Therefore, vegetational injury has not been as great.

There is some indication from new data that O₃ may not have been the only stress encountered by the San Bernardino Forest ecosystem. Nitrate deposition gradients similar to those measured for O₃ suggest that possible soil-mediated exposures to nitrate could have been and continue to be combined with the foliage-mediated O₃ exposures as an additional stress. Research in this area is continuing.

Ozone concentrations capable of causing injury to trees in the Sierra Nevada Mountains have been occurring for many years. Injury to sensitive trees, however, has never reached the same proportions as in the San Bernardino Forest. Differences in forest stand composition (fewer conifers, more hardwoods), ability to compensate for stress, and site dynamics undoubtedly play roles in the forest response.

The forests of the Appalachian Mountains have been episodically exposed to O₃ concentrations capable of causing vegetational injury for many years. Visible injury to foliage of eastern white pine and reduction in growth have been associated with the exposures to concentrations >0.06 ppm lasting for several days. Black cherry also has been shown to be sensitive to O₃ exposures. Surveys of various regions, including the Smoky Mountain and Shenandoah National Parks, indicate that visible injury to a variety of different types of vegetation is continuing to occur. Neither eastern white pine nor black cherry are dominant canopy trees. Removal of sensitive individuals and the absence of changes in the population of these species have not resulted in any visible change in the forest ecosystems along the Appalachian Mountains, possibly because no changes in the ecosystem functions of energy flow or nutrient cycling have occurred. Decline and dieback of trees on Mt. Mitchell and Camel's Hump cannot be related solely to O₃ injury. Ongoing research is attempting to better understand the effects of O₃ exposure on individual plants and the effect, if any, on the ecosystems to which the plants belong.

5.8 Effects of Ozone on Agriculture, Forestry, and Ecosystems: Economics

5.8.1 Introduction

Evidence from the plant science literature cited in the 1986 O₃ Criteria Document (U.S. Environmental Protection Agency, 1986) and in the present document is unambiguous with respect to the adverse effects of tropospheric O₃ on some types of vegetation. For example, findings from EPA's multiyear NCLAN program provide rigorous corroboration of at least a decade of previous research that showed that O₃ at ambient levels caused physical damage to important species. Specifically, NCLAN established that ambient O₃ levels resulted in statistically significant reductions in yields for these crops. Literature reviewed in Section 5.6 of this document assesses the state of natural science findings regarding O₃ effects on crops, forests, and other types of vegetation in more detail.

Information on the benefits and costs of alternative policy options or states of the world (such as changes in air pollution) is of use to decision makers in a variety of settings. For example, economic information provides one means by which to choose from alternative policies or public investments. The role of cost-benefit analysis in federal rule making or standard setting was enhanced by President Reagan's Executive Order 12291 (February 19, 1981), which required that such calculations be performed on any rule or regulation promulgated by the federal government. President Clinton's Executive Order 12886 (October 4, 1993) reconfirmed the importance of economic information in the federal regulatory process. These executive orders provided the stimulus for a large increase in the use of economic analysis in evaluating federal actions, including environmental policies. Although the Clean Air Act and its amendments do not allow the use of cost-benefit analysis in the standard-setting process for primary (human health) effects, economic information has been introduced into the discussion of secondary or welfare effects. A number of economic studies addressing vegetation and other welfare effects have been performed in the last decade.

Assessments of the economic consequences of O₃ on vegetation reflect the state of natural science information on each vegetation category. The natural science evidence concerning effects of O₃ on individual tree species or plant communities is less secure than for agricultural crops (see Section 5.6). As a result, most economic assessments focus on

agricultural crops. The economics literature on effects of O₃ and other air pollutants on forest productivity is very sparse; the few assessments are confined to evaluations of assumed or hypothetical changes in output (e.g., board feet of lumber). The economic effects of O₃ on plant communities or ecosystems have not been measured in any systematic fashion.

This section reviews economic assessments across these vegetation categories. The discussion of economic valuation of ecosystem effects is limited to conceptual and methodological issues in performing such assessments, given the absence of empirical analyses in this category.

5.8.2 Agriculture

In view of the importance of U.S. agriculture to both domestic and world consumption of food and fiber, reductions in crop yields could adversely affect human welfare. The plausibility of this premise resulted in numerous attempts to assess, in monetary terms, the losses from ambient O₃ or the benefits of O₃ control to agriculture. Fourteen assessments of the economic effects of O₃ on agriculture were reviewed in the 1986 document (U.S. Environmental Protection Agency, 1986). Since the preparation of the 1986 document, there have been at least nine other studies published in the peer review literature that provide estimates of the economic consequences of O₃ on agriculture.

The 1986 document highlighted key issues in judging the validity of economic assessments that are applicable to post-1986 studies (i.e., how well the biological, aerometric, and economic inputs used in the assessment conform to specific criteria). First, the evidence on crop response to O₃ should reflect how crop yields will respond under actual field conditions. Second, the air quality data used to frame current or hypothetical effects of O₃ on crops should represent actual exposures sustained by crops at individual sites or production areas. Finally, the assessment methodology into which such data are entered should capture the economic behavior of producers and consumers as they adjust to changes in crop yields and prices that may accompany changes in O₃ air quality; should reflect accurately institutional considerations, such as regulatory programs and income support policies (e.g., provisions of federal "Farm Bill" legislation), that may result in market distortions; and use measures of well-being that are consistent with principles of welfare economics.

5.8.2.1 Review of Key Studies from the 1986 Document

Assessments of O₃ damages to agricultural crops reported in the 1986 document displayed a range of procedures for calculating economic losses, from simple monetary calculation procedures to more complex assessment methodologies that conform to some or all of the economic criteria above. As noted in the 1986 document, the simple procedures calculate monetary effects by multiplying predicted changes in yield or production resulting from exposure to O₃ by an assumed constant crop price. By failing to recognize possible crop price changes arising from yield changes and not accounting for potential producer responses, such assessments are flawed, except for highly restricted situations such as localized pollutant events. Conversely, some assessments provide estimates of the economic consequences of O₃ and other air pollutants that reflect producer-consumer decision-making processes, associated market adjustments, and some measure of distributional consequences between affected parties. The distinctions between studies based on naive or simple models and those based on correct procedures is important at the regional and national levels, because the simple procedures may be biased and lead to potentially incorrect policy decisions.

Most (9 of 14) of the economic assessments reviewed in the 1986 document focused on O₃ effects in specific regions, primarily California and the Corn Belt (Illinois, Indiana, Iowa, Ohio, and Missouri). There have been a number of additional regional assessments since the 1986 document; most are non-peer-reviewed reports arising from consulting or contract research. This regional emphasis in the earlier literature may be attributed to the relative abundance of data on crop response and air quality for selected regions, as well as the importance of some agricultural regions, such as California, in the national agricultural economy. Most of the recent state or regional assessments are commissioned by state public utility commissioners or similar regulatory agencies and use variants of the simple "price times yield" approach, where yields are calculated from response functions arising from the NCLAN data. Although perhaps of use to public utility commissioners concerned with effects from single power plants or other localized sources, these studies generally contribute little to the assessment of pollution effects at the national level. (Most local or regional studies abstract from physical and economic interdependencies between regions, which limits their utility in evaluating secondary National Ambient Air Quality Standards [NAAQS].)

National studies that account for economic linkages between groups and regions can overcome some limitations of regional analyses. A proper accounting of these linkages, however, requires additional data and more complex models and frequently poses more difficult analytical problems. Thus, detailed national assessments tend to be more costly to perform. As a result, there are fewer assessments of pollution effects at the national level than at the regional level.

Two national studies reported in the 1986 document were judged to be "adequate" in terms of the three critical areas of data inputs. Together, they provided a reasonably comprehensive estimate of the economic consequences of changes in ambient air O₃ levels on agriculture. Because of their central role in the 1986 document, these two studies are reported in Table 5-38 and are reviewed briefly below.

In the first of these studies, Kopp et al. (1985 [cited as 1984 in the earlier document but subsequently published as a journal article in 1985]) measured the national economic effects of changes in ambient O₃ levels on the production of corn, soybeans, cotton, wheat, and peanuts. In addition to accounting for price effects on producers and consumers, the assessment methodology used is notable in that it placed emphasis on developing producer-level responses to O₃-induced yield changes (from NCLAN data available at the time) in 200 production regions. The results of the Kopp et al. study indicated that a reduction in O₃ from 1978 regional ambient levels to a seasonal 7-h average of approximately 0.04 ppm would result in a \$1.2 billion net benefit in 1978 dollars. Conversely, an increase in O₃ to an assumed ambient concentration of 0.08 ppm (seasonal 7-h average) across all regions produced a net loss of approximately \$3.0 billion.

The second study, by Adams et al. (1986a), was a component of the NCLAN program. The results were derived from an economic model of the U.S. agricultural sector that includes individual farm models for 63 production regions integrated with national supply and demand relationships for a range of crop and livestock activities. Using NCLAN data, the analysis examined yield changes for six major crops (corn, soybeans, wheat, cotton,

Table 5-38. Recent Studies of the Economic Effects of Ozone and Other Pollutants on Agriculture^a

Study	Region	Pollutant and Concentration	Model Features				Results (Annual 1980 U.S. Dollars)			
			Price Changes	Output Substitutions	Input Substitutions	Quality Changes	Crops	Consumer Benefits	Producer Benefits	Total Benefits (Costs)
Garcia et al. (1986)	Illinois	Ozone, 10% increase from 46.5 ppb ^b	No	Yes	Yes	No	Corn, soybeans	None	226×10^6	226×10^6
Adams et al. (1986a) ^d	U.S.	Ozone, 25% reduction from 1980 level for each state ^a	Yes	Yes	Yes	No	Corn, soybeans, cotton, wheat, sorghum, barley	$1,160 \times 10^6$	550×10^6	$1,700 \times 10^6$
Kopp et al. (1985) ^d	U.S.	Ozone, universal reduction from 53 to 40 ppb ^b	Yes	Yes	Yes	No	Corn, soybean, wheat, cotton, peanuts	Not reported	Not reported	$1,300 \times 10^6$
Shortle et al. (1988)	U.S.	Ozone, universal reduction from 53 to 49 ppb ^a	Yes	No	No	Yes	Soybeans	880×10^6	90×10^6	790×10^6
Adams et al. (1986b)	U.S.	Acid deposition, 50% reduction in wet acidic deposition	Yes	Yes	Yes	No	Soybeans	172×10^6	30×10^6	142×10^6
Kopp and Krupnick (1987)	U.S.	Ozone, 10% reduction from annual levels (1986 to 1990) for rural areas. Includes adjustments for 1985 Farm Bill.	Yes	Yes	Yes	No	Corn, cotton, soybeans, wheat	NA	NA	$2,500 \times 10^6$ (sum of discounted values at 5%, 1986 to 1990)
Adams et al. (1989)	U.S.	Ozone, seasonal standard of 50 ppb with 95% compliance ^c ; includes adjustments for 1985 Farm Bill.	Yes	Yes	Yes	No	Corn, soybeans, cotton, wheat, sorghum, rice, hay, barley	905×10^6	769×10^6	$1,674 \times 10^6$
Adams and Rowe (1990)	U.S.	Increased UV-B radiation and associated increase of tropospheric O ₃ (of 16%)	Yes	Yes	Yes	No	Soybeans (for UV-B) and all crops in Adams et al. (1989) for tropospheric O ₃	NA	NA	-830×10^6 (for the increase in tropospheric O ₃ only)

^aAll studies except Garcia et al. (1986) use NCLAN data to generate yield changes due to ozone; see Appendix A for abbreviations and acronyms.

^bSeven-hour growing season geometric mean. Given a log-normal distribution of air pollution events, a 7-h seasonal ozone level of 40 ppb is approximately equal to an hourly standard of 80 ppb, not to be exceeded more than once a year Heck et al. (1982).

^cSeven and 12-h growing season geometric mean. Analysis includes both fixed roll-backs (e.g., 25%) and seasonal standards (with variable compliance rates).

^dReported in the previous criteria document (U.S. Environmental Protection Agency, 1986).

sorghum, and barley) that together account for over 75% of U.S. crop acreage. The estimated annual benefits (in 1980 dollars) from O₃ adjustments are substantial, but make up a relatively small percentage of total agricultural output (about 4%). Specifically, in this analysis, a 25% reduction in O₃ from 1980 ambient levels resulted in benefits of \$1.7 billion. A 25% increase in O₃ resulted in an annual loss (negative benefit) of \$2.4 billion. When adjusted for differences in years and crop coverages, these estimates are close to the Kopp and Krupnick (1987) benefit estimates.

The Kopp et al. (1985) and Adams et al. (1986a) studies indicated that ambient levels of O₃ were imposing substantial economic costs on agriculture. However, both Kopp et al. (1985) and Adams et al. (1986a) were judged to suffer from several sources of uncertainty. These include the issue of exposure dynamics (7-h/day exposures from the NCLAN experiments versus longer exposure periods, such as 12-h exposures) and the lack of environmental interactions, particularly O₃-moisture stress interactions, in many of the response experiments. Also, the O₃ data in both studies are based on a limited set of the monitoring sites in the AIRS system, mainly sites in urban and suburban areas. Although the spatial interpolation process used for obtaining O₃ concentration data (Kriging) resulted in a fairly close correspondence between predicted and actual O₃ levels at selected validation points, validation for rural sites was limited (Lefohn et al., 1987a). The economic models, with their large number of variables and parameters and the underlying data used to derive these values, also were noted as potential sources of uncertainty, including the effects on economic estimates of market-distorting factors such as the federal farm programs. Concern over farm programs stems from the evidence that reductions in O₃ will increase yields and hence total production of some crops. If the crop is covered (eligible for deficiency payments) under the provisions of the farm program, then the total costs to the government (of the farm program) may *increase* as a result of reduced O₃ (McGartland, 1987). Thus, the benefits of the O₃ reduction may not be as great as estimated.

The 1986 criteria document concluded that these possible improvements in future assessments were not likely to alter greatly the range of agricultural benefit estimates for several reasons. First, the studies covered about 75 to 80% of U.S. agricultural crops (by value). For inclusion of the other 20% to change the estimates significantly would require that their sensitivities to O₃ be much greater than for the crops included to date. Second, model sensitivity analyses reported in past studies indicate that changes in plant exposure-response relationships must be substantial to translate into major changes in economic estimates. For example, it was believed unlikely that use of different exposure measures or inclusion of interaction effects would alter greatly the magnitude of the economic estimates. Third, it was believed that there were likely to be countervailing effects that would mitigate against large swings in the estimates (e.g., longer exposure periods may predict greater yield losses), but O₃-water stress tends to dampen or reduce the yield estimates. Finally, the document noted that potential improvements in economic estimates are policy-relevant only to the extent that they alter the relationship between total benefits and total costs of that policy. The possible exception to this generally optimistic assessment of the robustness of the estimates was inclusion of market-distorting factors (i.e., farm programs), an issue that is addressed in some of the post-1986 assessments reviewed below.

5.8.2.2 A Review of Post-1986 Assessments

The previous criteria document (U.S. Environmental Protection Agency, 1986) concluded that the O₃ assessments of economic benefits to agriculture by Kopp et al. (1985)

and Adams et al. (1986a) provided the most defensible evidence in the literature at that time of the general magnitude of such effects. These two studies, in combination with the underlying NCLAN data on yield effects, were judged to be the most comprehensive information available on which to evaluate the economic impact of O₃ on crops.

Seven national assessments performed since the last criteria document are reported in Table 5-38. Of these, all use defensible economic approaches to quantify dollar effects, where "defensible" is measured in terms of conforming to the criteria cited earlier. An evaluation of these studies in terms of the adequacy of critical plant science, aerometric, and economic data is presented in the table, along with estimates of benefits or damages associated with changes in O₃.

The concluding statements in the 1986 document are a benchmark against which to judge these seven national studies published since the last document. Most of the contemporary studies build on either Kopp et al. (1985) or Adams et al. (1986a); indeed, the motivation of some of the more recent studies is to test whether the problems noted above (such as exclusion of farm programs) are sufficient to alter the original estimates in a meaningful manner. A relevant question is whether these new studies provided any "surprises" in terms of magnitude of economic effects. These studies are summarized in Table 5-38.

In discussing these latest evaluations, there are several points that relate to the comparability of the evaluations with those of Kopp et al. (1985) and Adams et al. (1986a). First, all studies use NCLAN response data to generate yield effects (for inclusion in the respective economic models). In most cases, data used in the post-1986 assessments reflect improvements of earlier NCLAN data. Second, these studies may be characterized as second generation assessments. They build on the first generation of studies reported in the 1986 document by refining selected aspects of those earlier studies, including interactions with other stresses; use of aerometric data and assumptions that, in some cases, more closely follow the seasonal and regional characteristics of O₃ exposure (Adams et al., 1989); and effects of O₃ on quality of commodities (Shortle et al., 1988). Several of the studies use updated versions of the economic models in Adams et al. (1986a) and Kopp et al. (1985). In addition, some of the studies model the effects of government programs to judge the potential consequences of such distortions on economic estimates (Kopp and Krupnick, 1987; Adams et al., 1989). Third, there are differences in underlying aerometric assumptions; some studies include both O₃ and other environmental stresses (e.g., acid deposition, ultraviolet-B [UV-B], radiation); others reflect O₃ data for more recent time periods. Because ambient O₃ levels vary across years, the choice of year will influence the yield estimates and ultimately the economic estimates.

Common themes or findings from these (and earlier) O₃ and other air pollution studies have been summarized in two recent synthesis papers (Adams and Crocker, 1989; Segerson, 1991). The results of the post-1986 assessments in Table 5-38 and the recent synthesis papers corroborate the general findings of the 1986 document. Specifically, the agricultural effects of tropospheric O₃ at ambient levels impose economic costs to society (or conversely, that reductions in ambient O₃ result in societal benefits). The magnitude of the economic costs reported in the more recent studies is similar to the estimates in Kopp et al. (1985) and Adams et al. (1986a). Such a similarity is not surprising, given the points noted above concerning use of similar data and economic models.

One important recent finding pertains to farm programs. In each case, the inclusion of farm programs in the economic models resulted in modest changes (reductions)

in the economic benefits of O₃ control (due to increased farm program costs). As Segerson notes, however, it is not clear that these increased costs should be charged against the potential benefits of an O₃ regulatory standard but rather as an additional cost associated with the inefficiencies of the federal farm program. Even with the inclusion of farm programs and other elements, the general magnitude of further effects reported in the 1986 criteria document are reduced only by approximately 20%.

In addition to including farm programs, there are a couple of other notable additions to the assessment literature. One study (Adams et al., 1989) attempts to analyze economic benefits under a regulatory alternative involving a seasonal (crop growing season) O₃ exposure index measured as a 12-h mean, instead of hourly levels or percent changes from ambient reported in earlier studies. Specifically, a seasonal average of 50 ppb O₃ (measured as a 12-h seasonal average), with a 95% compliance level, is reported in Adams et al. (1989). The result (of a \$1.7-billion benefit) is similar to the assumed 25% reduction across all regions reported by Adams et al. (1986a). At least one study also has combined environmental stresses (e.g., O₃, UV-B, radiation) in performing economic assessments. Adams and Rowe (1990), using the same model as Adams et al. (1986a, 1989), report that a 15% depletion of stratospheric O₃ (which results in a 13% increase in tropospheric O₃) caused an economic loss of approximately \$0.8 billion attributed to the tropospheric O₃ increase.

5.8.2.3 Limitations and Future Research Issues

The recent literature (post-1986) on economic effects of O₃ on agriculture supports the general conclusions drawn in the 1986 document. That is, ambient levels of O₃ are imposing economic costs on producers and consumers. As in earlier economic assessments, the validity of this finding is conditional on the quality of the supporting agronomic and aerometric data. In addition, there are at least three issues that are not addressed in the extant literature on the topic. First, the existing assessments do not consider the external costs of changes in agricultural production arising from changes in O₃ exposures (Segerson, 1991). These costs are important if changes in O₃ result in changes in crop mixes or production practices, which in turn result in changes in soil erosion, fertilizer and pesticide runoff, or other agricultural externalities. For example, if reductions in O₃ increase the relative profitability of a crop that uses higher levels of chemical inputs, then some increase in chemical effluent may result. Given that some assessments suggest that such changes in crop mixes and production practices are likely to accompany O₃ changes, these costs/benefits need to be addressed.

A second issue not directly assessed in the current literature is the relationship between climate change and tropospheric O₃ effects. This relationship is important if global warming is expected to increase tropospheric O₃ levels. In addition, research indicates that global climate change will lead to a relocation of crops (Adams et al., 1990d). This relocation may change the vulnerability of crop species to O₃, given the spatial distribution of O₃ across the United States (i.e., increased crop production in areas of relatively low ambient O₃, such as the Pacific Northwest, implies lower O₃ damage).

A third issue involves the institutional setting in which agricultural production occurs. Several recent studies have assessed O₃ effects in the presence of federal farm programs. However, the United States and most industrialized economies are moving away from price supports, production quotas, and import restrictions, the traditional form of government intervention in agriculture. At the same time that these market distortions are