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Physiological/Ecological Interactions Between Ozone and Nitrogen Deposition in Forest Ecosystems

By

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Summary

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Ozone (O₃) is considered as the main factor in the air pollution-related decline of forests in North America and Europe. Decline of ponderosa and Jeffrey pines in the San Bernardino Mountains of southern California and pronounced foliar injury of these species in the Sierra Nevada Mountains of central California are well-known examples of the O₃ effects. Other components of photochemical smog, especially nitrogenous (N) compounds, may also play an important role in the observed changes in forests and other ecosystems. Although direct effects of HNO₃ vapor and peroxyacetyl nitrate (PAN) have not been observed in field conditions, these pollutants have a potential for causing foliar injury of sensitive plants at elevated concentrations. In addition, long-term dry deposition of N gases and particles as well as wet deposition of NO₃⁻ and NH₄⁺ can significantly change plant N status. Below critical load (threshold) values of N deposition, changes in phenology of plants, higher rates of physiological processes, changed chemical composition, altered biochemical processes and improved growth of plants may occur. At levels exceeding N critical load, nutrient deficiencies and other negative effects may lead to decreased growth of trees and changes in species composition. Possible biochemical, physiological, and ecological effects of O₃ and N deposition singly and in combination, mainly based on results of studies performed in mixed conifer forest of California, are discussed.

Introduction

Emissions of sulfur oxides and industrial dust have been declining in North America and Europe since the 1980s (KRUPA 1997). However, concentrations of

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ozone (O_3) in the Northern Hemisphere have been increasing by 1 to 2% each year and are currently estimated to be 2 to 3 times higher than at the beginning of the 20th century (ROSEMAN & al. 1991). In general, the area of forests experiencing potentially phytotoxic concentrations of O_3 has been growing in many nonurban locations of the United States and Europe (KRUPA & MANNING 1988, BUSSOTTI & FERRETTI 1998). Although significant reductions of emissions of nitrogen oxides (NO_x) and volatile organic compounds (VOCs) occurred in the 1990s in most of Europe, at present, due to a steady increase of number of motor vehicles, and despite more efficient and cleaner combustion engines, concentrations of NO_x and VOCs in Central and Eastern Europe will not decrease until 2010 (ELVINGSON 2001). Consequently, concentrations of O_3 , and other products of photochemical reactions of VOCs with NO_x , such as gaseous nitric acid (HNO_3), in Europe are expected to remain high. In addition, no decline in emissions of ammonia (NH_3) and ammonium (NH_4^+), originating mainly from agricultural activities, is foreseen in Europe in the near future (BARTNICKI & ALCAMO 1989, ELVINGSON 2001). As a result, elevated levels of N deposition have been and will continue to be observed in large parts of Europe. Most evidence of increasing concentrations of O_3 and N air pollutants comes from Europe and North America (FOWLER & al. 1999), however, elevated levels of O_3 and N deposition can also be expected in other parts of the World, especially in southeastern Asia, and parts of Latin America and central Africa (GALLOWAY 1998).

For predictions of the future status of forests and other ecosystems, both direct phytotoxic effects of O_3 and N pollutants and effects of N deposition should be considered. In order to understand potential ecological changes caused by air pollutants, mechanisms of their effects should be known (HEATH 1999). However, biochemical and physiological mechanisms of air pollution effects, even for single pollutants, are still poorly understood (POLLE 1998). Since the chemistry of ambient air pollution is complex and dynamically changing in time and space (SEINFELD & PANDIS 1998), various interactions between air pollution compounds at biochemical and physiological levels occur (BARNES & WELLBURN 1998). Such interactions are additionally modified by abiotic and biotic factors. Although numerous experiments have been performed in order to understand the mechanisms of single air pollutants effects on plants, only limited number of studies where plants have been exposed to mixtures of pollutants have been performed mainly due to various technical and economical limitations. It seems that the best understanding of air pollution effects on vegetation may be accomplished by combining knowledge from short-to-medium term controlled experiments (exposures to single pollutants or ambient air vs. clean air in open-top chambers, branch chambers, or free-air pollution systems) where effects at the cell, organ, or single plant levels are studied, with long-term experiments in which responses of individual trees and forest stands to air pollutants on their "natural" gradients are investigated.

In this review, the effects of O_3 and N pollutants, and N deposition, singly and in combination, on forest vegetation will be discussed. The author understands that insufficient scientific evidence does not allow for a comprehensive review of complex changes taking place in natural ecosystems. However, studies in progress

in Europe and North America continuously provide new information on the subject. In this review, an attempt has been made to bring to the reader the author's current understanding of the discussed effects, mainly by using California forests as an example.

Ozone Effects

Ozone is considered one of the main factors contributing to forest decline in North America and Europe. Probably the best-documented example of O₃-related effects on forests is the decline of ponderosa (*Pinus ponderosa*) and Jeffrey (*P. jeffreyi*) pine stands in the San Bernardino Mountains of southern California (MILLER & MILLECAN 1971, MILLER 1992, ARBAUGH & al. 1999). Exposures of ponderosa pine seedlings and mature tree branches to ambient air, filtered air with O₃ added, and filtered air, demonstrated that the observed chlorotic mottle symptoms and growth reduction were caused by O₃ (MILLER & al. 1963, MILLER 1992). Ozone injury to trees was almost non-detectable when 24-h average concentrations were between 50 and 60 ppb, whereas the high level of injury was associated with averages of 100 - 120 ppb (MILLER & al. 1982). The records for 1974 through 1987 show a gradual decline in monthly average hourly maximum O₃ concentrations (MILLER & MCBRIDE 1989) and the corresponding significant improvement of crown injury of ponderosa pines in the San Bernardino Mountains (MILLER & al. 1989). In a western Sierra Nevada location, exposure of the seedlings for one season to ambient O₃ concentrations (seasonal 24-h mean 54 ppb; 1-h maximum mean 108 ppb) added to clean air did not produce any significant effects, while at the doubled ambient levels (seasonal 24-h mean 96 ppb; 1-h maximum mean 213 ppb) only the accelerated senescence of the oldest foliage was found. During the second season, at similar exposure regimes, physiological and biochemical changes, including a decrease of pigment concentrations in needles and reduction of growth became evident (TAKEMOTO & al. 1997). That study clearly showed that phytotoxic effects of O₃ in ponderosa pine seedlings are cumulative and progress in time.

Ozone, after entering leaves through stomata, moves into the intercellular spaces, and then passes through a thin layer of water surrounding individual cells. It is believed that reactions of O₃ and its effects start taking place in this region of plant tissue. Ozone may form toxic hydrogen peroxide or free oxygen radicals that may affect cell integrity (HEATH 1975, 1988, 1999, KRUPA & MANNING 1988). In healthy cells, calcium concentrations are maintained at low levels compared with concentrations outside of the cells. A disruption of that difference caused by O₃ alteration of cell membranes could be responsible for the observed phytotoxic changes (MUDD 1998). Comprehensive reviews of biochemical and physiological changes in crops caused by O₃ (RUNECKLES & CHEVONE 1992), and in forest trees (CHAPPELKA & CHEVONE 1992) are available. POLLE 1998 eloquently discussed biochemical changes and detoxification mechanisms in plants in response to photochemical oxidant exposures.

Nitrogenous Air Pollutants Effects

Nitrogenous air pollutants may also affect forest health. Although at presently occurring ambient concentrations, nitrogen oxides (NO_x), nitric acid vapor (HNO_3), peroxyacetyl nitrate (PAN), and ammonia (NH_3) do not affect health of forest vegetation, foliar injury and various physiological and biochemical changes in plants have been found at elevated levels of the pollutant in controlled fumigations (WELLBURN 1988, 1990, BYTNEROWICZ & al. 1999). Nitric oxide (NO) and nitrogen dioxide (NO_2) mainly enter leaves through stomata (SAXE 1986a,b) but transcuticular transport of these pollutants also takes place (LENDZIAN & KERSTIENS 1988). Nitrogen dioxide in leaves dissolves in the extracellular water of the sub-stomatal cavity and forms both nitrite (NO_2^-) and nitrate (NO_3^-). Through a series of enzymatic reactions, NO_2^- and NO_3^- are metabolized to amino acids and proteins (AMUNDSON & MCLEAN 1982). The effectiveness of plants in reducing these ions determines the potential of a plant to detoxify NO_2^- and NO_3^- (WELLBURN 1990). While NO and NO_2 at ambient levels were taken up by Scots pine seedlings with measurable changes in amino acid composition, no significant effects of these exposures on growth, mycorrhizal infection or total N concentrations were detected (NÄSHOLM & al. 1991).

Nitric acid vapor has a very high deposition velocity, readily reacting with plant and other surfaces, and in the photochemical smog affected areas may be a major source of N to forests (HANSON & LINDBERG 1991). Exposures of ponderosa pine and California black oak (*Quercus kelloggii*) to elevated concentrations of HNO_3 vapor caused "microscopic" injury, changes in the chemistry of epicuticular waxes, induced nitrate reductase (NR) activity (KRYWULT & al. 1996a, BYTNEROWICZ & al. 1999), and increased foliar and root concentrations of free amino acids (BYTNEROWICZ & al. 1999). Increased concentrations of major components of the plant antioxidative systems, especially of the ascorbate complex, indicates that impacts of HNO_3 take place mostly on the surfaces of ponderosa pine needles, and possibly in the cell walls of the mesophyll (TAUSZ & al. 2002).

Uptake of NH_3 is almost exclusively through the stomata and is proportional to the ambient concentrations of this pollutant (VAN DER EERDEN 1982, VAN HOVE & al. 1987). Ammonia dissolves in the water film of the mesophyll cells of the substomatal cavity and the resulting ammonium (NH_4^+) ion is assimilated into amino acids and proteins. Assimilation of NH_3 into amino acids plants depends on the availability of carbon skeletons and energy. Toxic effects start occurring when the uptake exceeds the assimilation capacity. Toxicity of NH_3 is caused by: (1) scavenging of electrons leading to uncoupling of electron transport along plant membranes, (2) saturation of membrane lipids leading to membrane dysfunction, and (3) direct etching and necrosis of foliage (FANGMEIER & al. 1994).

In the last few decades, over large areas of Europe and North America, atmospheric deposition of N in gaseous, particulate and wet forms has been increasing. Various effects of the elevated levels of N on forest plants have been reported. In the initial stages, changes in phenology, rates of physiological processes, chemi-

cal composition, altered biochemical processes and improved growth of plants have been seen. Later, as a result of saturation of forests with N, deficiencies of other nutrients may develop (MOHREN & al. 1986, NIHLGARD 1990, DRISCOLL & al. 2001). All these changes, and many others, may lead to higher susceptibility of plants to other stresses such as drought, frost, acidic deposition, UV-B radiation, insect attacks, etc. As a consequence, some serious perturbations of normal growth of forest plants and shifts in species composition may take place (FALKENGREN-GRERUP 1990, FALKENGREN-GRERUP & TYLER 1991). Nitrogen saturation of forest ecosystems can be characterized as a situation where the system cannot retain and process additional inputs of N and when vegetation no longer responds with growth increases. In N saturated forests a persistent loss of excess N in the form of NO_3^- beyond the root zone of plants or into streamwater occurs (STODDARD 1994). Saturation of forest ecosystems with N can also be manifested by elevated emissions of nitrous oxide (N_2O) and nitric oxide (NO) resulting from the soil processes of denitrification and nitrification (ABER & al. 1989). Mixed conifer forests on the extreme western end (closest to the pollution source area) of the San Bernardino Mountains have been saturated with nitrogen for some time. In these forests NO_3^- concentrations in soil solutions are several-fold higher throughout the growing season than in low deposition locations. High N trace gas emissions, and high soil and foliar N concentrations, low C:N ratios in soil, high N:P ratios in foliage, and a lack of a positive foliar biomass growth response to N fertilization have also been observed (FENN & al. 1996). Decomposition of surface litter in the most polluted sites of the San Bernardino Mountains is much higher than in the less polluted sites. A strong correlation between the rate of early stage litter decomposition and litter N concentration has been found (FENN & DUNN 1989). Leaching of NO_3^- below the root zone (FENN & al. 1996), increasing NO_3^- levels in ground water and stream water or release of N trace gases are some of the ultimate consequences of the saturation of forest stands with N (FENN & al. 1998). It has been found that high levels of added N ($\sim 50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) increased bole growth of ponderosa pine and California black oak. Therefore, trees in California mixed conifer forests are less susceptible to the N deposition stress than trees of the more mesic eastern U.S. and European forests (FENN & POTH 2001).

Interactions between O_3 and N Air Pollutants

Ozone and N air pollutants commonly co-occur in polluted areas. In general, O_3 does not have any specific effects on stomata, however, it may interact with other gases or stresses and amplify their effects. This is because O_3 affects primarily membranes and their degree of "leakiness" to water and ions. Because stomatal guard cells are sensitive to NO_2 it is very likely that osmotic and ionic disturbances may be part of interactions of this gas with O_3 (WELLBURN 1988). Interactions between O_3 and N air pollutants may be antagonistic, additive or synergistic. Pre-exposure of plants to NO_2 followed by O_3 fumigations gave differing results depending on plant species: synergistic effects on shoot growth of radish

and wheat, reduction of negative effect of O_3 on bean, and no effect on mint. Stomatal conductance of all the studied species did not show any changes attributable to the exposures. Hence, the variations in the effects of NO_2 or response to O_3 reflect differences among the species with respect to biochemical or biophysical effects of NO_2 (RUNECKLES & PALMER 1987). Negative interactions between NO_2 and O_3 commonly occur when plants are exposed to sequential fumigations with these pollutants, while if they are exposed simultaneously, synergistic effects prevail (BARNES & WELLBURN 1998). Sequential exposures to O_3 and NO_2 may result in changes in activities of enzymes linked to the utilization of additional sources of N in leaves which may explain antagonistic interactions between these pollutants (BENDER & al. 1991). It has been found that NO_2 tends to cause partial closure of stomata in corn during the day and inhibit complete stomatal closure at night after daytime fumigations (AMUNDSON & MCLEAN 1982). Ammonia has also been found to inhibit complete stomatal closure in the dark (VAN DER EERDEN & PEREZ-SOBA 1992). These effects could predispose plants to toxic effects of other pollutants present at night, e.g., elevated concentrations of O_3 or SO_2 that may occur in various mountain locations. Toxic effects of other pollutants may also be increased during the day when they are co-occurring with NH_3 , which is thought to indirectly stimulate stomatal conductance (VAN HOVE & al. 1989), and thus the uptake of other pollutants such as SO_2 and O_3 could be higher (VAN HOVE & al. 1989, DUECK & ELDERSON 1992).

While alone, at ambient levels, NO_2 is considered as non-injurious. However, when added to the mixture of O_3 and SO_2 , NO_2 caused acceleration of foliar damage. The presence of O_3 and SO_2 could inhibit the activity of N-assimilating enzymes and promote the build-up of NO_2^- ion and other toxic N compounds (GUDERIAN & al. 1989, WELLBURN 1990). High ambient concentrations of NO and NO_2 may also be determining toxicity of O_3 to plants. These two pollutants may enhance the O_3 -mediated leaf injury by initiating the formation of stress ethylene. Reaction of O_3 with small-unsaturated hydrocarbons, such as ethylene, is known to produce various H_2O -soluble highly reactive and phytotoxic free radicals (MEHLHORN & WELLBURN 1987). It is also possible that NO acts as a chain-propagating agent in the O_3 -initiated oxidation of saturated hydrocarbons such as terpenes naturally emitted by plants and generation of $HOO\cdot$ and $ROO\cdot$ radicals. Therefore, it has been postulated that the presence of NO in air >2 ppb is needed for the occurrence of O_3 toxicity (NEIGHBOUR & al. 1990). Fumigations of poplar (*Populus x euroamericana*) seedlings for 12 weeks to 2-fold O_3 ambient concentrations alone and in mixture with 6-fold ambient NO_2 resulted in reduction of total & foliar dry weights and increase in leaf area & stomatal density (GÜNTHARDT-GOERG & al. 1996). The only significant effect of NO_2 alone was a reduced stomatal density. In the combined fumigations the appearance of cell injury of young leaves was enhanced probably because of an increased O_3 uptake due to stomatal widening caused by NO_2 . However, as soon as the visible injury occurred, stomata were narrowed and photosynthesis declined. Further addition of NO_2 to such leaves might slow down the injury process by intensifying repair mechanisms by supplying N for polyamine or stress protein formation. Clearly O_3 effects domi-

nated those of NO_2 despite much lower enhancement of ambient concentrations of O_3 compared to NO_2 (GÜNTHARDT-GOERG & al. 1996).

Potential interactions of O_3 , wet and dry deposition, and soil water availability on ponderosa pine seedlings were studied for 3 years in open-top chambers in a western Sierra Nevada location (TEMPLE & al. 1993). Elevated levels of N pollutants (up to $4.15 \mu\text{g HNO}_3 \text{ m}^{-3}$; up to $3.8 \mu\text{g NO}_3^- \text{ m}^{-3}$ as well as elevated concentrations of NH_3 and NH_4) were present at the study site (BYTNEROWICZ & RIECHERS 1995). For the plants exposed to 150% ambient O_3 concentrations (seasonal 24-h average concentrations 82 - 90 ppb) needle injury was higher at 67% of ambient NO_3^- concentrations than at 36% of ambient NO_3^- (TEMPLE & al. 1992). There is no simple explanation for the different responses, however, predisposition of the needles by gaseous HNO_3 (more than 50% of ambient NO_3^- was in that form) to O_3 toxicity could be suggested. There is also a possibility that HNO_3 may be predisposing needles to O_3 injury considering the previously discussed changes in the epicuticular waxes due to HNO_3 exposure. If these changes occur also in the epistomatal cavity, lowered flexibility of the stomatal apparatus and changes in uptake of O_3 could be imagined.

Nitrate reductase (NR), is a key enzyme in nitrate assimilation that controls NO_3^- reduction to NO_2^- (CRAWFORD & al. 1992). In controlled fumigations, NR activity in ponderosa pine was correlated with the amount of deposited HNO_3 vapor (KRYWULT & al. 1996a). Measurements of NR activity in pine foliage along the air pollution gradient in the San Bernardino Mountains also indicated that intensive N fixation in ponderosa pine foliage was taking place and was correlated with the amount of the airborne NO_3^- intercepted by the foliage. However, high spatial and temporal variability did not allow using NR activity induction as an indicator of N deposition (KRYWULT & al. 1996b). The observed variability could be caused by the differences in nutritional status of individual trees and other environmental factors. However, elevated O_3 concentrations, co-occurring with the elevated N deposition in the San Bernardino Mountains (FENN & BYTNEROWICZ 1993), might also be responsible for the unexpected changes in the activity of the enzyme. Inhibition of NR and nitrite reductase (NiR) activities by O_3 has been reported (TINGEY & al. 1973, GUDERIAN & al. 1989, WELLBURN 1990) and could lead to the prolonged presence of gaseous N pollutant in the intercellular spaces and toxic effects of NO_2^- and nitrous acid (HNO_2) on chloroplasts (WELLBURN 1988). In addition, assimilation of N from stomatal uptake of NO , NO_2 and HNO_3 as well as root and foliar uptake of NH_4^+ and NO_3^- ions could be reduced and lead to disturbances of normal plant development.

Modification of O_3 Effects by N Fertilization or Atmospheric Deposition

Phytotoxic O_3 effects depend, among other factors, on the nutritional status of plants (TAYLOR 1974). Obviously, elevated deposition of N, a major plant nutrient, has the potential to modify responses of plants to O_3 . Experiments with trem-

bling aspen (*Populus tremuloides*) seedlings indicated that at levels as low as 10 kg N ha⁻¹ yr⁻¹ a highly significant fertilization effect occurred. Ozone alone (up to 80 ppb for 6 h/day, 3 days/week), induced foliar injury but only a trend toward reduced growth occurred. This trend was lost when 10 - 40 kg N ha⁻¹ yr⁻¹ was added (KARNOSKY & al. 1992). Two years of exposure of ponderosa pine seedlings to ambient levels of photochemical smog (seasonal 24-h O₃ ~ 40 - 60 ppb; 1-h O₃ peaks ~ 170 - 270 ppb; NO₂ < 40 ppb; PAN ~ 20-22 ppb; 12-h daytime HNO₃ vapor ~ 18 ppb, NH₃ < 7 ppb, particulate NO₃⁻ < 22 µg/m³ omrekenen?) in the San Gabriel Mountains at optimal level of N supply in perlite-vermiculate growth medium did not cause significant changes in foliar injury, growth or physiological processes. However, when N supply was reduced to 50%, seedlings from the ambient air treatment showed significantly higher injury of all needles and reduced dry weight of older foliage compared to the clean-air treatment. Reduction of N supply by 50% alone had strong effects on seedlings causing reduction of growth & foliar concentrations of macronutrients, lower stomatal conductance & rates of net photosynthesis, decreased concentrations of foliar pigments and increased starch reserves (BYTNEROWICZ & al. 1990). Reduced leaf size, increased early senescence, increased leaf yellowing, and increased thickness of palisade mesophyll manifested negative effects of elevated levels of ambient O₃ on birch (*Betula pendula*) clones in an experiment performed by PAAKKONEN & HOLOPAINEN 1995. In the same experiment, elevated levels of N supply (up to 150 kg N ha⁻² yr⁻¹) increased leaf size, delayed early foliar senescence, decreased leaf yellowing, increased height & shoot/root ratio, and elevated leaf H₂O content. In that experiment sufficient N supply prevented negative effects of O₃ exposures. PELL & al. 1995 found that leaf and total plant biomass and leaf area of quaking aspen (*Populus tremuloides*) were adversely affected by O₃ only at soil N levels providing optimal plant growth. When growth of plants was slow as a result of N limitations, compensatory responses of plants to O₃ stress (increased shoot/root ratio and accelerated senescence) were sufficient to prevent detectable losses in biomass. The seedlings grown in excess of N (even at toxic levels of N) were less sensitive to O₃. One of the possible explanations of those effects could be that excess N is used to produce secondary metabolites with antioxidizing capacity (PELL & al. 1995). On the other hand, loblolly pine (*Pinus taeda*) current-year needle biomass was reduced at elevated O₃ concentrations (seasonal average 108 ppb) at high levels of N added to the soil. The authors of that study suggested that increased fertility of needles could result in higher levels of 1,5 ribulose biphosphate carboxylase/oxygenase which has been shown as a specific site for O₃ damage and hence more pronounced effects (TJOELKER & LUXMORE 1991). The above examples show that N fertilization may diminish or enhance toxic effects of O₃ in many various ways, depending on plant genetic origin, exposure conditions, and levels of fertilizer applied.

One of the well known effects of O₃ on plants is a reduction in the amount of assimilates (sugars and amino acids) transported to roots and the resulting alteration of mycorrhizal inoculation (MCCOOL & MENGE 1983). Similarly, high N soil levels may influence growth of ectomycorrhizal (ECM) fungi (KOTTKE 1995,

MUNZENBERGER & al. 1995). Long-term N additions may have pronounced effects on below-ground structure of ECM fungal communities. Some of the fungi can be profoundly affected by N inputs while other appear relatively insensitive. Such differences in responses to N additions are likely to strongly influence the relative competitiveness of ECM fungi and shifts in structure of below-ground communities (CAIRNEY & MEHARG 1999). A possibility of severely reduced nutrient uptake by altered ECM associations as a consequence of O₃ exposures and N additions leading to decreased growth of forest trees should be considered. The stimulation of shoot growth by N deposition and O₃-induced premature needle senescence, are responsible for litter layer accumulation in mixed conifer forests at high pollution sites in the San Bernardino Mountains. Thick litter inhibits ponderosa pine seedlings establishment since mineral seedbed and low shade are essential for good germination and survival (GRULKE & BALDUMAN 1998). Litter decomposition rates depend on foliar N content. High N content frequently stimulates the early stages of litter decomposition. At later stages, decomposition of litter has been found to decompose slower when N content was high (BERG 2000). While both phenomena have been found in the mixed conifer forests sites in the San Bernardino Mountains, the latter one seems to dominate resulting in litter accumulation (MARK FENN, personal communication). In summary, various interactive effects on pine seedlings establishment between O₃ and N deposition occur and depend on ratios of O₃ concentrations/N deposition (FENN & DUNN 1989, FENN 1991). Thickness of litter layer will also affect susceptibility of forests to forest fires. At high level of litter (fuel) accumulation, a probability of catastrophic crown fires fire that may result in complete stand composition changes (MINNICH & al. 1994).

Elevated concentrations of O₃ resulting from the transport of photochemical smog from the California Central Valley (MILLER & al. 1972), have been considered as a primary cause of foliar injury of ponderosa and Jeffrey pines in the western Sierra Nevada, including the Sequoia, Kings Canyon and Yosemite National Parks (DURISCOE & STOLTE 1989). Jeffrey pines in the Sierra Nevada showing O₃ injury symptoms had reduced radial increments compared with non-symptomatic trees. However, no significant changes in radial growth could be detected for the O₃-injured ponderosa pines (PETERSON & ARBAUGH 1992). It is possible that the increased levels of the available N, which co-occurs with high O₃ concentrations, compensated plants for growth reduction caused by O₃ exposures. Elevated levels of NH₃, gaseous HNO₃, and particulate NO₃ and NH₄ are found in the mixed conifer stands of the western Sierra Nevada (BYTNEROWICZ & RIECHERS 1995, BYTNEROWICZ & al. 2002). These dry-deposited compounds and wet deposited N from snow, rain and fog may provide enough N for improved growth of trees. In the mixed conifer forest zone of Sequoia National Park, total N deposition has been estimated at 6 - 10 kg N ha⁻¹ yr⁻¹ (CHOROVER & al. 1994). At such levels interactions between elevated levels of O₃ and N deposition seem to be plausible. Such interactions can also be expected in other ecosystems of the western Sierra Nevada, e.g., in sub-alpine ecosystems where in addition to elevated concentrations of O₃ (PEDERSON & CAHILL 1989) depositions of NO₃ and NH₄ were also elevated

Table 1. Potential interactions between O₃, N air pollutants & N deposition.

Type of Effect	Description
<i>Biochemical</i>	Activities of NO ₃ ⁻ and NO ₂ ⁻ reductases may be inhibited by O ₃ that would lead to increased toxicity of NO, NO ₂ and HNO ₃ NO and NO ₂ may enhance O ₃ toxicity by initiating formation of stress ethylene which in turn may react with O ₃ producing toxic free radicals NO may act as a chain-propagating agent in the O ₃ -initiated oxidation of saturated hydrocarbons such as terpenes naturally emitted by plants and the generation of phytotoxic HOO [•] and ROO [•] radicals. Presence of NO in air >2 ppb is required for the occurrence of O ₃ toxicity Excess of N may enhance production of secondary metabolites with antioxidative properties that may reduce toxicity of free radicals generated during O ₃ and HNO ₃ exposures
<i>Physiological</i>	HNO ₃ vapor may affect plant cuticles and stomata modifying uptake and responses of plants to O ₃ NO ₂ and NH ₃ may inhibit complete closure of stomata at night allowing for uptake of O ₃ (especially in mountain areas remote from pollution sources)
<i>Ecological</i>	Modifying effects of N on O ₃ toxicity will differ depending on total amount of available N, and such characteristics as ratios of wet/dry deposition, reduced/oxidized compounds, gaseous/particulate forms Within tree canopies the degree of N mitigation of the toxic effects of O ₃ will differ depending on micrometeorological conditions and the physiological activity of foliage Mitigation of O ₃ toxic effects by available N will vary within forest stands due to differences in H ₂ O & nutrient availability, sun exposure, temperature, etc. At the landscape level, diurnal O ₃ profiles and spatial patterns of N deposition may drastically differ with changes in elevation and distance from pollution source areas Increased foliar senescence caused by O ₃ and stimulation of shoot growth by N may result in accumulation of litter. This in turn, may inhibit pine regeneration (pine seedlings require mineral seedbed and thin litter layer for germination and survival) N additions from atmospheric deposition may increase growth of trees and compensate for biomass losses caused by O ₃ (resulting in an apparent lack of negative effects of O ₃ on aboveground tree growth) Both O ₃ and N addition may cause decrease of root growth and mycorrhizal development. Consequences of that may be reduced nutrient uptake, drought stress, shallow roots and sensitivity to wind throw) Both O ₃ and N deposition have a strong potential for changing species composition of forests and other ecosystems. Plants sensitive to O ₃ may be replaced by the O ₃ -tolerant plants, and nitrophilous plants may be favored with high levels of N deposition.

(BYTNEROWICZ & al. 1991, 1992). Effects of elevated N deposition as well as other forms of anthropogenic pressure are considered as possible factors leading to shifts in species composition in coastal sage ecosystems of southern California (ALLEN & al. 1998). Coastal sage ecosystem, as well as other lower elevation ecosystems in southern California, such as chaparral and deserts, is dormant or operating at reduced levels of physiological activities in the high pollu-

tion (May - September) season. Therefore, direct phytotoxic effects of O_3 or N air pollutants as well as their interactive effects with N deposition, are less likely to occur.

A summary of the above-described interactions between O_3 , N air pollutants & N deposition is shown in Table 1.

Conclusions and Recommendations for Futures Research

Much remains to be learned about the mechanisms by which O_3 and N pollutant mixtures effect forest trees. Serious limitations in studies of air pollution mixtures on trees (problems with "scaling" results obtained with seedlings to mature trees; unrealistic, mostly short-term air pollution exposures that do not reflect field conditions; technical difficulties with pollutant mixture fumigations) are the main reasons for our lack of understanding of the effects of pollutant mixtures. Better understanding of air pollution effects on vegetation may be accomplished by comparing knowledge from short-term controlled experiments in which effects at the levels of a cell, organ, or single plant are studied, with long-term field experiments in which responses of individual trees and forest stands to "natural" gradients of air pollutants are investigated.

Implementation of better air pollution control strategies may reduce concentrations of O_3 as observed in the San Bernardino Mountains of southern California. However, at the same time, N emissions and deposition remain high and result in higher amounts of available N in mixed conifer forests in these mountains. Positive effects of N may counter-act any phytotoxic O_3 effects, however, after reaching "critical N level" thresholds various negative environmental changes may take place. Some of the potential changes were discussed above, however, many others are also to be expected. A high probability of serious and non-reversible shifts in species composition (trees and understory species) exists and should be addressed in future studies. Such changes attributed to elevated N deposition have already been observed in other ecosystems of southern California, e.g., coastal sage brush (ALLEN & al. 1998).

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