

Mature Ponderosa Pine Nutrient Use and Allocation Responses to Air Pollution¹

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Abstract

Current-year needles from mature ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.) were sampled at four sites across the air pollution gradient in the San Bernardino Mountains in southern California. The sites, in order of decreasing air pollution exposure, included: Sky Forest (SF), Conference Center (CC), Camp Angelus (CA) and Heart Bar (HB). Needle nutrients measured were: nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), zinc (Zn), iron (Fe) and aluminum (Al). Concentrations of N in foliage (12.5 g/kg) were significantly higher at SF, the site most exposed to air pollution. This level is similar to concentrations for container-grown seedlings fertilized with nutrient solution. Mature tree needle concentrations of K, Mg, Fe and Al were higher at sites more exposed to air pollution. Mature trees with two annual whorls of needles (more severely injured) had significantly higher current year needle concentrations of P, K, Zn, and Fe at SF than trees with three annual whorls of needles (less severely injured). However, significant differences were not found in foliar nutrient concentrations between trees with different levels of needle retention (injury) at CC, which is also a high pollution site. At Barton Flats (BF), a low to moderate air pollution site in the San Bernardino Mountains, N, K and P were measured in current-year needles and litter fall. The resorption efficiencies (the percent reduction in nutrient concentration upon senescence of leaves or needles) for mature trees at BF were: 45 percent for N, 60 percent for P and 80 percent for K. N resorption proficiency (the concentration a nutrient is reduced to before needle abscission) was high with N reduced to 4.4 g-N/kg (considerably less than the defined threshold of 7g-N/kg). However, P resorption proficiency was very poor with P reduced to 0.59 g-P/kg (higher than the defined threshold of 0.4 g-P/kg). A complete understanding of the changes in tree nutrition associated with air pollution will require more research.

Introduction

Long-term chronic exposure to ozone and other associated air pollutants has a pronounced effect on growth and mortality of ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.). This has been clearly documented (Miller and others 1963, Miller and others 1989) over the last 25 years in the San Bernardino Mountains of southern California. The San Bernardino and San Gabriel Mountains form the transverse ranges, which run from west to east and form the northern boundary of the South Coast Air Basin. The Basin includes Los Angeles and the surrounding communities. Vegetation in the San Bernardino Mountains varies with elevation and aspect. Scrub and chaparral species dominate the lower elevations (1,200-1,600 m) on the western and southern ends of the range, while the pinyon-juniper type is found on the desert-facing eastern and northern extremes of the San Bernardino Mountains. The mixed conifer forest occurs at elevations of about 1,500 to 2,400 m. Ponderosa pine is the dominant pine species of the mixed conifer forest, except on the eastern end of the San Bernardino Mountains where ponderosa pine is replaced by the closely-related Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.). Visible indications of ozone stress in ponderosa pine in the mixed conifer zone include a combination of reduced needle retention, thinning of the lower crown, chlorotic mottle of foliage, the production of shorter needles, and mortality—typically as the result of an insect attack (Miller 1983).

A major research effort in Germany has shown that forest decline in a spruce forest was caused by nutrient imbalances from atmospheric deposition of sulfur (S), and nitrogen (N). (Huettl and others 1990, Schulze 1989). Magnesium (Mg) was retranslocated from old needles to new foliage until luxury levels were reached in the current-year foliage, and Mg deficiency levels occurred in the older and subsequently-chlorotic foliage. Although Mg levels were in excess

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in current-year foliage, N levels in new foliage became deficient, notwithstanding the excessive deposition of N (Schulze 1989). Similarly, given the dramatic effects of ozone and associated air pollutants in the San Bernardino Mountains on foliar injury, growth, and abscission in ponderosa pine (Miller 1983), it is likely that nutrient relations of these ponderosa pine trees are also significantly affected.

Despite the importance of ponderosa pine in western North America, information on ponderosa pine nutrition is scant. Available data are restricted to studies of N fertilization or the responses of seedlings or unique site situations, some of which are thought to define the limits of species range. Rarely is any nutrient other than N and P examined. This is a reflection of the pattern of use for the ponderosa pine resource. Historically, ponderosa pine has been harvested primarily from old-growth stands. Second-growth from natural regeneration can take 80 to 100 years for trees to reach marketable size. Although silviculturalists have successfully developed methods for ponderosa pine regeneration, specific knowledge of nutrient use and requirements remains poor (Powers 1981), particularly compared to the available information for more intensively managed and shorter rotation species like Douglas fir. A search of the National Agricultural Library database yields 1,086 references with ponderosa pine in the title or as a key word and 2,344 for Douglas fir. Further examination of the ponderosa pine citations reveals the paucity of nutritional data.

In this study we measured and compared foliar nutrients at four sites along the ozone gradient in the San Bernardino Mountains. We present data on foliar nutrient concentrations, and relate the concentrations to visible ozone symptoms (needle retention) in ponderosa/Jeffrey pine. Our objectives were to determine if foliar nutrient levels might be related to the severity of ozone stress incurred by mature trees, and to help define the range of nutrient concentrations seen in mature ponderosa/Jeffrey pine. In addition, we have examined the influence of air pollution on nutrient use by mature and container-grown ponderosa pine by comparing nutrient concentrations in needles and litter. The nutrient resorption efficiencies (the percent reduction in nutrient concentration upon senescence of leaves or needles) and resorption proficiencies (the concentration a nutrient is reduced to before needle abscission) determined for ponderosa pine are also reported.

Materials and Methods

Needle samples were collected from four plots located along a west to east ozone concentration gradient spanning 55 km in the San Bernardino Mountains. The plots were originally established in 1972-73 as part of a large interdisciplinary study of the effects of air pollution on the mixed conifer forest in the San Bernardino Mountains (Miller 1983). We sampled trees in the plots, in order of decreasing exposure, at Sky Forest (SF), Conference Center (CC), Camp Angelus (CA), and Heart Bar (HB). Ozone concentrations in the permanent plots were measured during July and August from 1974-78. The respective estimated 24-hour average ozone concentrations ($\mu\text{g}/\text{m}^3$) at the sites were 196 at SF and CC, 157 at CA, and 59 at HB (Miller and others 1989). Ozone concentrations have decreased slightly during the 1980s, but concentrations within the greater Los Angeles basin remain among the highest in the nation. Visible symptoms of ozone injury were still prominent at SF and CC, and to a lesser degree at CA.

We selected dominant and codominant trees for needle sampling. A minimum of 24 mature ponderosa pine trees with a dbh of at least 30 cm were sampled at each of the four sites, except at HB where Jeffrey pine was sampled. Trees with mistletoe, pest problems or obvious abnormalities were avoided. Current-year foliage was collected from exposed branches (one branch per tree) in the middle crown in late August of 1986. For each tree sampled we also recorded the number of annual whorls of needles and the presence of needle chlorotic mottle characteristic of ozone damage.

Sampled needles were dried and ground for chemical analysis. N and P were determined by standard colorimetric methods following Kjeldahl digestion. Calcium (Ca), magnesium (Mg), potassium (K), manganese (Mn), zinc (Zn), iron (Fe), and aluminum (Al) were analyzed by atomic absorption spectrometry after perchloric acid digestion of tissues. All analyses were done in the laboratories of the Institute of Soil Science and Forest Nutrition, Albert-Ludwigs University, in Freiburg, Germany.

In a separate study at Barton Flats in the San Bernardino Mountains, needles were collected in August of 1993 from mature ponderosa pines. This was done in late summer/early fall when new needles were fully expanded. More than 100 trees were sampled. Needles were divided into age classes, oven dried at 70 °C and ground to pass through a 40-mesh screen. Needles from each tree were analyzed for Ca, Mg, K, Mn, and Zn by atomic adsorption spectroscopy after perchloric - nitric acid digestion. Phosphorus (P) was determined from the same digest (Glaubig and Poth 1993). Coupled combustion - gas chromatographic analysis was used to measure total N and carbon (C). Older age classes of needles were only analyzed for total C and N.

Pine litter was collected during the fall from litter traps at Barton Flats. After collection, combined samples (all fall collection dates) were oven dried at 70 °C and ground to pass through a 40 mesh screen. Pine litter samples were also analyzed for C, N, P, Ca, Mg, K, Mn, and Zn. For mobile nutrients, nutrient efficiency (the percent reduction in nutrient concentration upon senescence of leaves or needles) was calculated.

Results and Discussion

Foliar concentrations of K and Mg were highest at the high pollution sites SF and CC (*fig. 1*). Foliar N was significantly higher at SF than at any other site (*fig. 2*). Nutrients did not appear to be severely limiting for mature ponderosa pine, as was reported in a previous study (Huettl and others 1990, Powers 1991).

Critical levels of N and P in ponderosa pine foliage (Powers 1981) are reportedly 9 and 0.8 g/kg. Below these levels the N and P supply becomes deficient for adequate growth. Foliar concentrations of K, Mg, and Ca in this study appear to be within the range of values for ponderosa pine reported in the literature (Clayton and Kennedy 1980). Levels of Fe and Al were highest in the two high-pollution sites (SF and CC), and Mn levels were very high at CC compared to the other sites (*fig. 3*). Zn was highest at HB, but showed no pattern of variation across the ozone gradient. Micronutrient levels are within the normal ranges reported for ponderosa pine (Powers 1981).

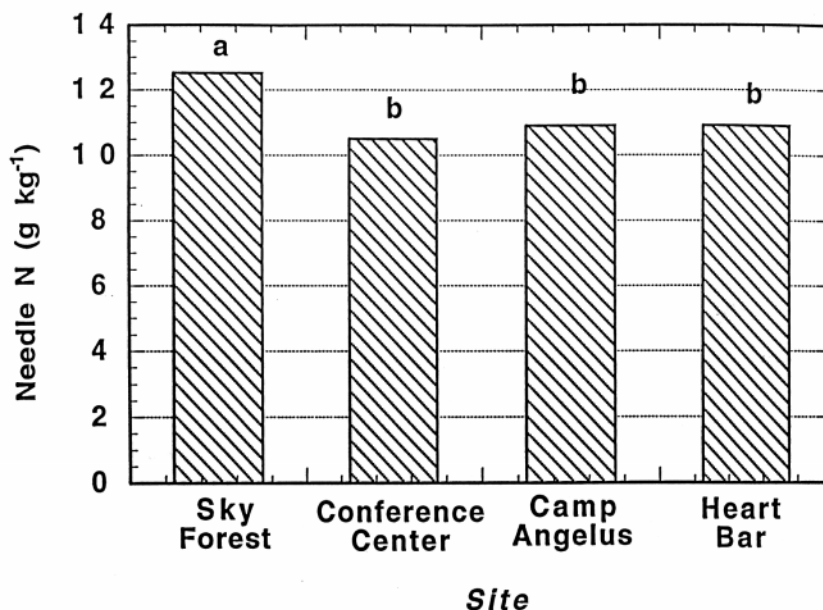


Figure 1 — Macronutrient concentrations for current-year foliage of mature ponderosa pine trees in the San Bernardino Mountains. Letters associated with bars indicate significant differences in foliar concentrations between the plots according to Tukey's multiple comparison test ($p=0.05$).

Figure 2 — Nitrogen concentrations for current-year foliage of mature ponderosa pine trees in the San Bernardino Mountains. Letters associated with bars indicate significant differences in foliar concentrations between the plots according to Tukey's multiple comparison test ($p=0.05$).

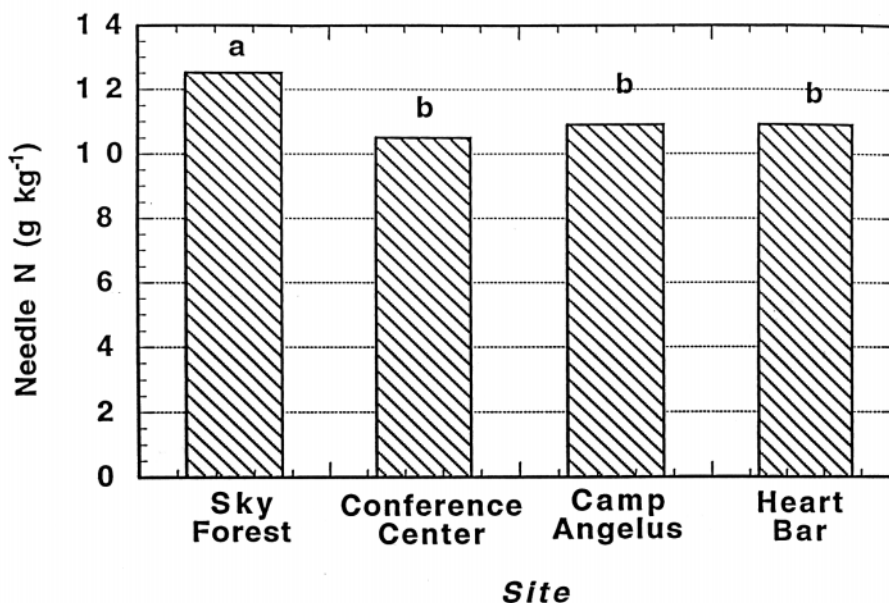
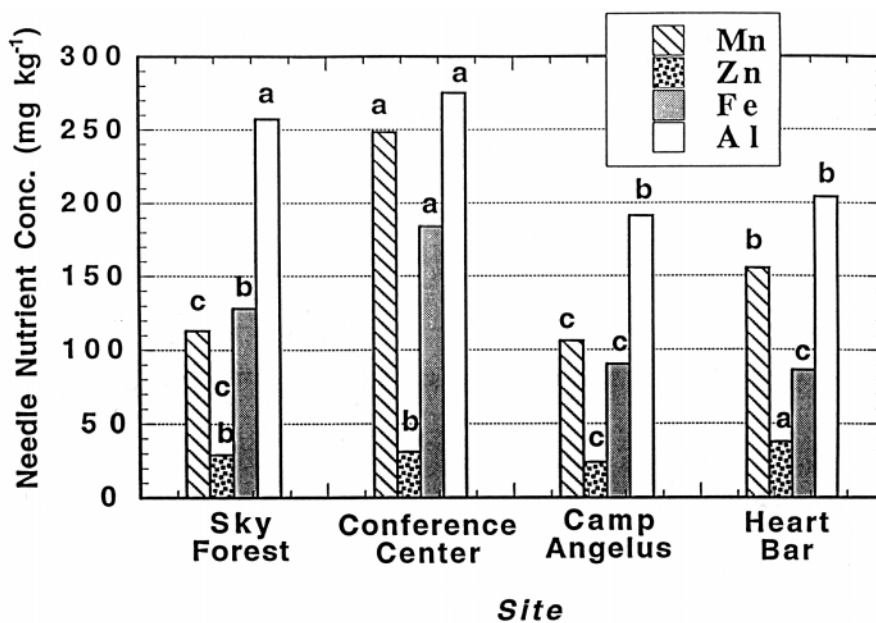


Figure 3 — Micronutrient concentrations for current-year foliage of mature ponderosa pine trees in the San Bernardino Mountains. Letters associated with bars indicate significant differences in foliar concentrations between the plots according to Tukey's multiple comparison test ($p=0.05$).



Ozone stress is the main inciting factor leading to premature needle abscission of ponderosa pine in the high-pollution sites in the San Bernardino Mountains. Other factors, such as drought stress, could also reduce needle retention. However, the high-pollution sites receive higher levels of precipitation (Miller and others 1989), yet needle retention is much greater in the drier, less-polluted sites. Thus, the number of annual whorls of needles retained, especially when accompanied with symptoms of chlorotic mottle, is considered a reliable measure of the level of ozone stress affecting ponderosa pine. In some cases there are statistically significant differences in nutrient concentrations between trees retaining 2 or 3 years of foliage at the two high pollution sites. Trees with only two annual whorls (the current-year and the previous year) at SF have higher needle concentrations of P, K, Zn, and Fe than trees with three annual whorls (fig. 4, 5, and 6); presumably the higher concentrations in the current-year whorls are the result of ozone-induced senescence and nutrient retranslocation.

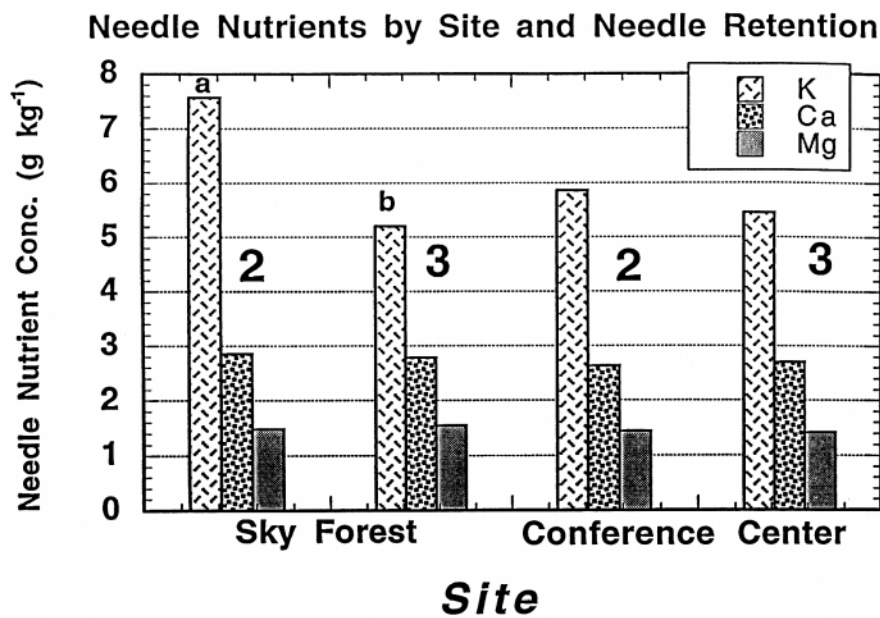


Figure 4 — Macronutrient (K, Ca, and Mg) concentrations for current-year foliage of mature ponderosa pine trees in the San Bernardino Mountains retaining two or three years of foliage. Letters associated with bars indicate significant differences in foliar concentrations between trees at the same plot according to Tukey's multiple comparison test ($p=0.05$).

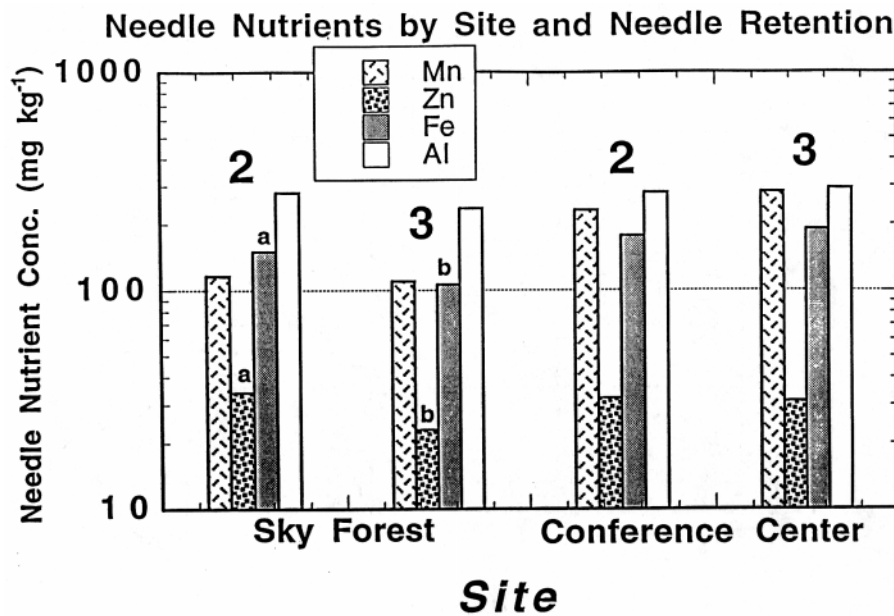
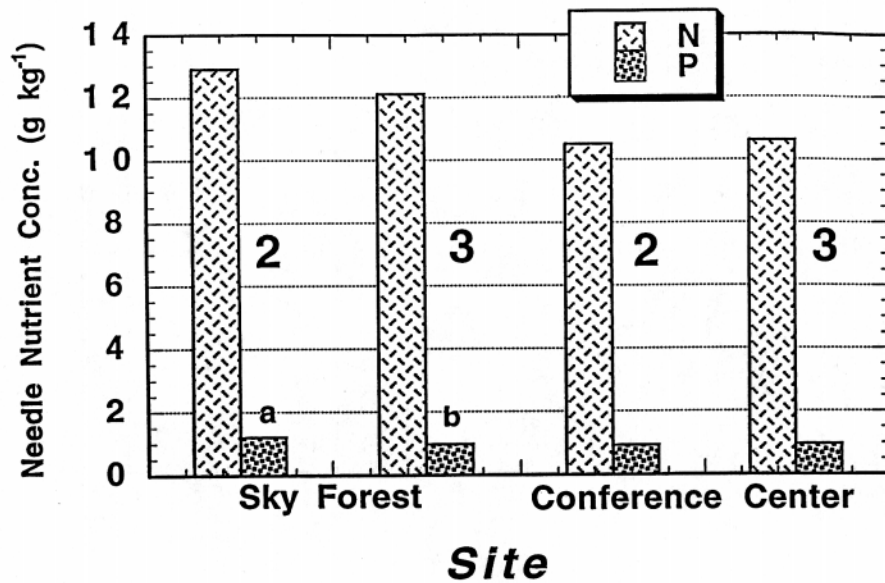


Figure 5 — Micronutrient concentrations for current-year foliage of mature ponderosa pine trees in the San Bernardino Mountains retaining two or three years of foliage. Letters associated with bars indicate significant differences in foliar concentrations between trees at the same plot according to Tukey's multiple comparison test ($p=0.05$).

In a previous study at Strawberry Peak, a site 4 km west of SF, current-year foliage of ponderosa pine trees retaining only one annual whorl contained significantly higher levels of P than foliage of trees retaining two annual whorls (Fenn 1991). Phosphorus and potassium are highly mobile and are readily remobilized in plants. Zinc is considered to be intermediate in terms of plant mobility (Epstein 1972, Salisbury and Ross 1985). Zinc remobilization is closely related to leaf senescence (Marschner 1986). Iron generally shows low to intermediate plant mobility (Epstein 1972, Salisbury and Ross 1985). The retranslocation of micronutrients is markedly increased during foliar senescence (Marschner 1986).

We did not detect significantly higher nutrient concentrations in current-year foliage of trees with either two or three annual whorls at CC. Although estimated ozone concentrations at SF and CC were reported to be equivalent based on limited data (Fenn 1991), the severity of ozone damage to ponderosa pine was greater at SF than at CC (Miller and others 1989). This difference may explain why higher

Figure 6 — Nitrogen and phosphorus concentrations for current-year foliage of mature ponderosa pine trees in the San Bernardino Mountains retaining two or three years of foliage. Letters associated with bars indicate significant differences in foliar concentrations between trees at the same plot according to Tukey's multiple comparison test ($p=0.05$).



levels of nutrients were not found in foliage of trees with fewer annual whorls at CC, contrary to the results at SF in this study, and in an earlier study at Strawberry Peak in the San Bernardino Mountains (Fenn 1991). More severe ozone damage at SF may be a result of greater water availability, resulting in greater stomatal uptake of ozone. Available soil water in the top 90 cm (19 and 13 percent) and annual precipitation from 1973 to 1977 (109 and 90 cm) were higher at SF than at CC (Miller and others 1989). Ambient temperature is not expected to vary greatly between CC and SF based on their proximity and similar elevations (1,705 m at SF and 1,610 m at CC; Miller and others 1989).

In a previous study in the San Bernardino Mountains, N and P retranslocation in ponderosa pine occurred just before or during needle senescence and death (Fenn 1991). In the present study we sampled foliage in August, during the summer growing season. A considerable amount of nutrient retranslocation probably occurred later in fall. However, where the ozone stress is sufficient to result in premature needle loss, nutrient retranslocation may occur earlier in the season. The timing of nutrient retranslocation may also differ for the various mobile elements. Had we collected foliage later in fall, concentrations of other mobile elements may have also increased in current-year foliage, especially in trees severely damaged by ozone. N and Mg were not higher in new foliage of trees with only two annual whorls. Because of the mobility of N and Mg in plants (Salisbury and Ross 1985), they would also be expected to retranslocate to younger foliage before abscission of older needles. Retranslocation of N at the high-pollution sites may be reduced because of a fertilizer effect of high N deposition (Fenn and Bytnerowicz 1993). Reduced retranslocation of N from senescing foliage in response to fertilization has been observed in several tree species (Flanagan and Van Cleve 1983).

Increased nutrient uptake by ozone-impacted trees could also account for the increase in nutrient concentrations in trees retaining only two annual whorls. This seems unlikely, however, given that ozone has been shown to reduce root growth and root carbohydrate content in ponderosa pine (Andersen and others 1991). The greatly reduced foliar biomass of ozone-stressed ponderosa pine is likely to result in reduced total photosynthetic rates in the long term; although younger foliage has been shown to compensate, at least in the short term, for the loss of older foliage in ozone-stressed ponderosa pine seedlings (Beyers and others 1992). Assuming that total photosynthate production is reduced in mature ozone-stressed ponderosa pine trees, it is doubtful that increased nutrient uptake occurs in ozone-stressed trees.

Which nutrients have been conserved, presumably by retranslocation, could be influenced by the supply of nutrients in the soil. P, K, Zn, and Fe were all found in higher concentrations in current-year foliage of trees at SF that retained only two annual whorls of needles. No data are available for soil concentrations of Zn or Fe in the four plots. P levels in soil are similar in the high- and moderate-ozone sites in the San Bernardino Mountains, but are significantly lower in the eastern low-ozone sites (Fenn 1991). In the original studies in the 18 permanent plots established along the ozone gradient, the soils at SF, CC and HB contained 0.49, 0.57, and 0.52 milliequivalents of K per 100 g soil (Arkley and others 1977). Soil at HB contains only 0.88 milliequivalents of Mg per 100 g, which is also reflected in the lower Mg concentrations in foliage at HB. It is unlikely that the apparently slight differences in soil P and K concentrations that occur at SF and CC account for why at SF, but not at CC, new foliage of trees with two annual whorls had higher nutrient levels than trees with three annual whorls. Apparently ozone stress (as indicated by needle retention), and not soil deficiency, is the primary factor that causes enhanced nutrient retranslocation in the more severely ozone-impacted trees at SF.

It may be a general phenomenon in perennial plant species sensitive to ozone that ozone exposure results in enhanced nutrient retranslocation to younger foliage, especially under nutrient-limiting conditions. The concentration of N and S in current-year foliage of loblolly pine (*Pinus taeda* L.) was higher in seedlings exposed to ozone than in plants exposed to sub-ambient ozone levels (Tjoelker and Luxmoore 1991). Phosphorus concentrations in foliage also increased ($p=0.10$) in seedlings exposed to ozone; and K tended to increase, but differences were not significant (Tjoelker and Luxmoore 1991). Leaves from cottonwood (*Populus deltoides* J. Bartram ex Marsh.) saplings exposed to ozone abscised prematurely and had higher concentrations of N than control plants (Findlay and Jones 1990).

Higher nutrient concentrations in current-year foliage of ponderosa pine with prematurely-abscised needles is indicative of how ponderosa pine trees respond to ozone stress. Before total senescence and abscission of older foliage, mobile nutrients are retranslocated to younger foliage, which then assume a larger physiological role. After two seasons of ozone exposure, ponderosa pine seedlings compensated for loss of older foliage by increasing net assimilation rates and N concentration of current-year foliage (Hom and Reichers 1991). Nutrient retranslocation to current-year foliage, and enhanced productivity of new foliage appear to be key adaptive mechanisms in ponderosa pine for overcoming the ozone-induced loss of productivity from older foliage.

Another important consideration of plant nutrient relations and ozone exposure is the influence of plant nutrient status on sensitivity to ozone. The co-occurrence of chronic N deposition in many areas with elevated ozone concentrations further emphasizes the importance of investigating the interactions and relationships between atmospheric deposition, soil-plant nutrient relations, site fertility, and plant sensitivity to ozone. For instance, Tjoelker and Luxmoore (1991) found that growth of current-year foliage of loblolly pine was more sensitive to elevated ozone concentrations when seedlings were grown in soil with higher levels of N.

The upper limit for needle N content can be defined by growing trees in defined nutrient-rich conditions. Results from such a study with seedlings (Bytnerowicz and others 1990) yielded needle N concentrations of 12.8 g/kg. The lowest needle N concentrations that can support growth are those in ponderosa pine stands that have developed on extremely poor soils. Isolated stands growing on nutrient depleted soils formed on hydrothermally altered parent materials in the Sierra Nevada of California had needle N concentrations of 8.1 g/kg (Schlesinger and others 1989). Mature needles on the trees at the Barton Flats sites had N concentrations ranging from 6.25 to 9.92 g/kg depending on the needle age. This comparison seems to demonstrate little difference between the Barton Flats site and remote sites in California, Nevada and Arizona (Klemmedson and others 1990, Schlesinger and others 1989, Powers 1981). However, N deposition at Barton Flats was above historic background levels.

With initial N deposition we would expect greater N availability to trees (Aber and others 1989, Schulze and others 1989, van Dijk and Roelofs 1988). This difference would parallel the situation at more fertile sites or sites that are fertilized. As a result trees could conserve energy by translocating less N before needles are abscised. At sites with poor soil fertility 60 percent of needle N is typically translocated before needles are abscised (Schlesinger and others 1989). Fertile volcanic soils with associated greater N availability result in less N translocation and reabsorption (48 percent) before needle abscission (Klemmedson and others 1990). At Barton Flats only 45 percent of N is reabsorbed before needle abscission. This is the lowest resorption efficiency reported in the literature for ponderosa pine. Resorption efficiency (the percent reduction in nutrient concentration upon senescence of leaves or needles) has recently been contrasted by Killingbeck (1996) with resorption proficiency (the nutrient concentration achieved in senesced leaves or needles). Plants that can reduce N concentrations in senesced leaves below 7 g/kg are highly proficient. Ponderosa and Jeffrey pines at Barton Flats could reduce the concentration of N in senesced needles to 4.4 g/kg and so were highly proficient in N resorption.

P and K resorption efficiencies at Barton Flats by ponderosa pine were 60 percent and 70 percent effective, respectively. This level of P reabsorption matches that found for ponderosa pine growing on very infertile soils (Schlesinger and others 1989). The P resorption proficiency for these two sites differ considerably: 0.59 g/kg at Barton Flats compared to 0.42 g/kg at the infertile soil sites in the Great Basin (Schlesinger and others 1989). Killingbeck (1996) has defined complete resorption proficiency in evergreen species as reducing the P concentration below 0.4 g/kg and incomplete resorption as a P final concentration greater than 0.5 g/kg. Clearly, P resorption proficiency at Barton Flats is incomplete.

The poor correlation of needle nutrient content with indicators of air pollution damage may be the result of the plants' ability to compensate physiologically for some air pollution damage and the variability of response between genotypes (Wellburn 1994). The principal air pollutant causing visible injury and thought to be responsible for growth changes is ozone (Peterson and others 1991, Temple and Miller 1994). The influence of ozone on nutrition is certainly indirect and chronic, whereas the response of a needle may be integrated over the much shorter time span (the lifetime of the needle). Consequently the possibility of developing a simple diagnostic needle nutrient analysis to assess air pollution influences seems remote.

Ozone exposure can lead to physiological disruptions that cause changes in the nutrient concentrations of current-year ponderosa pine needles. At SF, the site receiving the greatest ozone exposure, concentrations of P, K, Zn, and Fe in current-year foliage were highest in ponderosa pine trees with the most severe ozone injury, presumably due to retranslocation from older, ozone-damaged needles to younger foliage. Further studies are needed to elucidate mechanisms whereby ozone-stressed trees respond to, and in some cases possibly compensate for, acute and chronic ozone exposures and the interaction of these responses with associated N deposition.

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