DECIDUOUS CONIFERS: HIGH N DEPOSITION AND O_3 EXPOSURE EFFECTS ON GROWTH AND BIOMASS ALLOCATION IN PONDEROSA PINE.

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Abstract. Ponderosa pines (*Pinus ponderosa* Dougl. ex. Laws) 21 to 60 yr old were used to assess the relative importance of environmental stressors (O_3, drought) versus an enhancer (N deposition) on foliar retention, components of aboveground growth, and whole tree biomass allocation. Sites were chosen across a well-described gradient in ozone exposure (40 to 80 ppb per h, 24 h basis, 6 month growing season) and nitrogen deposition (5 to 40 kg ha^{-1} yr^{-1}) in the San Bernardino Mountains east of Los Angeles, California. A high level of chlorotic mottle indicated high O_3 injury at sites closest to the pollution source, despite potential for the mitigating effects of N deposition. At the least polluted site, foliar biomass was evenly distributed across three of the five needle-age classes retained. At the most polluted site, 95% of the foliar biomass was found in the current year's growth. High N deposition and O_3 exposure combined to shift biomass allocation in pine to that of a deciduous tree with one overwintering needle age class. Based on whole tree harvests, root biomass was lowest at sites with the highest pollution exposure, confirming previous chamber exposure and field studies. Aboveground growth responses in the high-pollution sites were opposite to those expected for O_3 injury. Needle and lateral branch elongation growth, and measures of wood production increased with increasing proximity to the pollution source. An enhancement of these growth attributes suggested that N deposition dominated the ponderosa pine response despite high O_3 exposure.

Keywords: ponderosa pine, ozone exposure, nitrogen deposition, drought stress, biomass allocation

1. Introduction

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) is the most sensitive western North American conifer to oxidant air pollution (Miller *et al*, 1983). The effects of ozone (O_3) exposure since the 1940's on bole growth of this species and others of the Sierran mixed conifer zone have been documented from dendrological studies (McBride *et al*, 1975; Peterson *et al*, 1991). Long-term changes in canopy health (Miller *et al*, 1989), and forest stand structure (McBride and Miller 1987; McBride *et al*, 1975) have been clearly correlated with exposure to oxidant pollution in the San Bernardino Mountains, east of Los Angeles, California.

Three sites were chosen across a gradient in pollution load in the San Bernardino Mountains (Miller *et al*, 1989). Tree attributes were also measured in an atmospherically clean site in northern California to provide an example of "typical" ponderosa pine. At these sites, O_3 exposure ranged from near global backround levels to some of the highest reported for forested lands in North America (Table I). At the sites nearest Los Angeles,

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high nitrogen (N) deposition accompanied high O_3 exposure, but decreased from west to east in the San Bernardino Mountains (Bytnerowicz and Fenn, 1996; Fenn *et al.*, 1996; Kiefer and Fenn, 1997; Fenn and Poth, 1999). Long term inputs of high N deposition on the western end of the pollution gradient are reflected in elevated soil N (Grulke *et al*, 1998) as well as isotopic composition of nitrate (NO_3^-) and ammonium (NH_4^+) in soil extracts (Fenn and Poth,1999). Drought stress, while an important variable, varied more between years than between sites within a year (Grulke *et al.*, 1998). Growing season length and cumulative degree days increased from the least to the most polluted site (Table I).

Low soil temperature (Gholz and Cropper, 1991), and nutrient (Haynes and Gower, 1995) and moisture availability (Hermann and Petersen, 1969) alter growth rates and resource allocation between above- and below-ground tissues in pine. These field responses as well as responses to experimentally modified variables in chamber exposure studies aid in interpreting the growth and biomass allocation patterns observed in this study. Qualitative comparisons were made across the three southern Californian sites, and between pairs of sites for direction and magnitude of tree response to dominant environmental gradients. For example, comparisons between Camp Paivika (CP) and Strawberry Peak (SP) provided insight on tree response with respect to a two fold change in O_3 exposure and N deposition under relatively mesic conditions (Table I). Comparisons between Lassen (LS), in northern California, and Camp Osceola (CO), on the eastern end of the San Bernardino Mountains, provided insight on tree response to the addition of moderate O_3 exposure in a droughty environment. Changes in tree attributes between mesic (1993, 1995) and xeric (1994) years elucidated the effects of drought (Grulke, 1999). Differences in tree response could also be attributed to genotypic differences between the four populations, but are unquantifiable at this time. The study reported here describes the relative importance of environmental stressors (O_3, drought) versus an enhancer (N deposition) on foliar retention, components of aboveground growth, and whole tree biomass allocation in a widespread, economically important tree species, ponderosa pine.

2. Methods

2.1. Site Locations and Tree Selection

Three sites were chosen along a pollution gradient within the Sierran mixed conifer zone (*sensu* Barbour 1988), in the San Bernardino Mountains east of Los Angeles, CA: Camp Paivika (CP) at the western-most end (34°14'05'N, 117°19'12'W, 1800 m), Strawberry Peak (SP) as an intermediate site (34°14'00'N, 117°08'12'W, 2240 m), and Camp Osceola (CO) at the eastern-most end (34°09'42'N, 116°51'00'W, 1820 m) (Table I). The fourth site was located in an atmospherically clean site near the southeastern corner of Lassen Volcanic National Park (LS) in the southern Cascade Mountains of California (40°20'11'N, 121°35'04'W, 1700 m), a northern extension of the forest type.

At each of the four sites, a regionally typical stand was chosen, a plot was established (1992) in a natural, multi-aged stand, and the 12 most uniformly average trees in a 21 to 60 yr tree age class were selected (Grulke *et al.*, 1998; Grulke, 1998). Data from trees in two tree age classes (21 to 40 and 41 to 60 yr old) were combined when there was no significant difference in net photosynthetic rates or respiration (Grulke, 1998; 1999), leaf N, foliar retention, or needle and branch growth rates at the $p \leq 0.05$ level (t-test). "Average" trees within the stand were selected on the basis of bole diameter, total height, percent chlorotic mottle of 1 yr old foliage (Miller *et al.*, 1996), number of needle age classes, and distance to the nearest intra- and interspecific tree as a measure of inferred competition. Individual trees were widely spaced and generally had no canopy influence from another intensively chosen tree on site. Thus, individual whole trees were used as within-site replication.

TABLE I
Summary of environmental gradients across the four study sites.

	LS	CO	SP	CP
Ozone exposure, ppb per h				
all hourly values	38 [42][b]	62 [64]	69 [76]	79 [80]
hourly values >40 ppb[a]	2 [8]	28 [33]	38	56 [57]
N deposition, kg ha^{-1}[c]	n.d.	6-9	n.d.	20-40
Soil N, %[d]				
A_1	0.01	0.08	0.11	0.20
B_1	0.01	0.04	0.07	0.09
Pre-dawn xylem potential, MPa[a]	-1.0 [-1.1]	-1.1 [-1.7]	-0.9 [-1.6]	-1.0 [-1.5]
Annual precipitation, cm[e] (1980-1992)	161.1	89.7	95.8	98.0
Cumulative degree days, °C[f]	580 [680]	1310 [1230]	1980 [1820]	2650 [2840]
Length of growing season, days[f]	88 [105]	133 [78]	113 [105]	181 [170]

[a] Summarized from Grulke (1999) and Grulke *et al.* (1998).
[b] When two numbers are listed, the first number represents mesic years (1993, 1995) and the second represents the xeric year [1994].
[c] Values for N deposition are broad due to variations in canopy structure (summarized from Fenn and Kieffer 1999).
[d] Summarized from Grulke *et al.* (1998).
[e] Annual precipitation was averaged over the hydrologic years 1980 through 1997 (San Bernardino County Water Resources).
[f] Temperature data has been summarized from this study.

2.2. Microenvironmental Monitoring

Microenvironmental monitoring stations were installed at each of the sites and were operational from January 1, 1993 to October 15, 1995. Thermocouples at 1.5 m in the air were monitored in 5 min intervals, and data were averaged and stored at 1 h intervals. Cumulative degree days were calculated from daily mean temperatures from January 1. Growing season length is defined here from air temperature as the first day in the year followed by 5 consecutive days ≥15°C to the last day of the year preceeded by at least 5 consecutive days ≥ 15°C. Methodology and values for other supporting microenvironmental data have been published elsewhere (Grulke et al., 1998; Grulke 1999).

2.3. O_3 Injury, Foliar Retention, and Growth Measures

Estimates of foliar chlorotic mottle (Miller *et al.*, 1996), number of live needle age classes, proportion of foliage retained within a needle age class (length of foliage/branchlet length within a whorl), and needle and primary lateral branch growth were measured as in Grulke and Lee (1997) and Grulke *et al.* (1998). Measures were taken monthly on five branches in the lower one third of the canopy on each of 12 trees in 1993 and 1994 and six trees in 1995, but are reported here at the time of maximum response to environmental stressors or enhancers generally occurring in mid September. Branchlet diameter was measured at the base of current year growth only in September, 1995 with digital calipers to the nearest 0.01 mm. For the above measurements, values from the five branches were averaged to yield a single value for each tree at each site. Tree height (measured with a meter tape or clinometer to the nearest 0.5 m) and bole diameter (measured at 1.4 m to the nearest 0.1 cm) were taken in 1992 at the time of plot establishment.

2.4. Biomass Measures

Whole tree biomass harvests were made on three trees (average for the total stand population of 21 to 60 yr old trees) at each site in early September, 1993. All coarse and fine roots were excavated to the best of our ability to bedrock, generally encountered at 1.5-2 m. Fine roots were at an annual minimum at the time of sampling (Grulke *et al*, 1998). In the field, foliage was stripped from branches by needle age class, and packaged in paper sacks by canopy thirds based on the length of the live crown. Foliage was placed in ovens at 105°C within 10 h of collection for 2 d, then weighed on a top loading balance to the nearest 0.1 g. Branches were also bundled and processed by upper, middle, and lower third of the canopy. In the laboratory, a subset of 40 branchlets per canopy third were measured for total length and diameter at the base of the current year growth. The trunk was cut into five parts for easier transport. Roots were separated into coarse (≥ 1 cm in dia.), medium (> 2 mm, < 1 cm in dia.), and fine (≤ 2 mm dia.) size classes, dried, and weighed. Branches, bole, and roots were dried in a large lumber drying oven at 105°C and weighed on a high capacity top loading scale (30 kg capacity) at 2 d intervals until no additional weight loss was observed.

3. Results

3.1. Visible O_3 Injury Symptoms

Chlorotic mottle increased with increasing O_3 exposure (Table II), a result well known for this pollution gradient (Miller *et al.*, 1989). The data are presented here to place the 21- to 60-yr-tree age class within the context of data already published for mature trees. Chlorotic mottle was low and did not statistically differ at the two least polluted sites, Lassen (LS) and Camp Osceola (CO) in any of the three years of study. The two western-most and polluted sites in the San Bernardino Mountains, Strawberry Peak (SP) and Camp Paivika (CP), had significantly higher chlorotic mottle in 1993 (1992 and 1993 had higher than average precipitation; San Bernardino County Water Resources Division) relative to the less polluted sites. However, in the xeric year [1994] and in the following year (1995), the greater chlorotic mottle differed significantly only at CP.

3.2. Foliar Retention

The measure of foliar retention has three components: the number of live needle age classes (whorls) retained, the proportion of foliage retained within a whorl, and the relative biomass allocation to the multiple needle age classes. Across the pollution gradient, as chlorotic mottle increased, the number of whorls decreased (Table II). The least polluted site, LS, consistently had the greatest number of whorls, which was greatest in the mesic years. The least polluted site in southern California, CO, had a similar number of whorls retained in 1993 and 1994 as at LS, but in 1995 (the growing season following the drought) had one fewer whorl than the cleanest site. Trees at the western end of the San Bernardino Mountains consistently had fewer whorls, and CP had significantly fewer whorls than all other sites in both 1994 and 1995.

The proportion of foliage retained within a whorl increased slightly with increasing pollution: 0.60 (LS), 0.65 (CO), 0.70 (SP), and 0.75 (CP), but none of these differences were statistically significant in a mesic year (1993). The abrupt (interannual) loss of within-whorl needle retention, and the number of whorls retained is clearly illustrated (Figure 1). At the cleanest site (LS), drought in 1994 increased needle senescence two fold only in the oldest whorl (7 yr old). The needle age at which half the foliage was lost decreased with increasing pollution load (CO: half of 4-5 yr old needles; SP: half of 3 yr old needles; CP: half of 2 and 3 yr old needles).

With increasing pollution exposure, more of the canopy foliar mass (whole tree) was distributed over fewer needle age classes (Figure 2). At the least polluted site, LS, 92% of the needle mass was evenly distributed over 4 needle age classes. At CO, 80% of the needle mass at CO was evenly distributed over 2 needle age classes, with 3 yr old needles comprising most of the remaining needle mass. Approximately two thirds of the needle mass of trees at SP were current year needles, and one third of the mass was 1 yr old. At CP, the most polluted site, 95% of the needle mass was current year foliage, resulting in trees with only one overwintering needle age class. Although more needle age classes were retained at the latter two sites, their mass did not contribute significantly to that of the canopy. Within site error was high because only three trees were harvested per site.

3.3. ABOVEGROUND GROWTH

The effect of environmental influences on growth was assessed from elongation growth (needle and lateral branches) and measures of wood production (branch and bole diameter growth). Multiple year measurements of growth were conducted in the lower third of the canopy and extensive measures of growth were made within tree canopies in a mesic year (1993, second of two years of above-average precipitation; San Bernardino County Water Resources Division). Differences among sites were tested with an analysis of variance and differences between paired sites were tested with a t-test. Statistical significance was reported at $p \leq 0.05$.

Needle length in the lower third of the canopy was greatest at the two western-most sites in the San Bernardino Mountains, SP and CP, in all three years (Table II). Despite differences in heat sum and degree days (Table I), needle length did not differ significantly between the two sites. In 1993, needle length did not differ significantly across the southern Californian sites, but the northern site had shorter needles probably due to both heat sum and a short growing season (Table I). In 1994 and 1995, needle length at LS and CO did not differ significantly. In those years, SP and CP differed significantly from LS and CO.

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Lateral primary branch length of current year growth measured in the lower third of the canopy showed similar trends to that of needle length. Branchlet length was significantly lower at LS and CO relative to SP and CP in all three years of study. During the drought year, branchlet length was low and did not significantly differ across the southern Californian sites. Needle and branchlet length was lowest (but not significantly) for the most xeric site (CO) in the year following the drought suggesting a possible residual effect. Lower branchlet length at CP in 1995 may reflect the combined effect of O_3 exposure and the residual effect of drought stress in the previous year. Branchlet length measured from whole tree harvests was the lowest in the lower third of the canopy at all sites. Tree height was greatest at CP relative to all other sites (Table II). Trees at CO, the most xeric southern Californian site, were significantly shorter relative to all other sites. Trees at LS and SP had similar height.

Table II.

Summary of foliar injury[a], number of needle age classes, and growth across the four sites.

Characteristic:	LS	CO	SP	CP	F	p
Chlorotic mottle						
1993	1±0a	8±2a	19±5b	24±5b	7.53	<0.001
1994	2±1a	1±1a	12±2a	35±7b	18.33	<0.001
1995	2±0a	2±0a	8±1a	28±5b	24.97	<0.001
Number of needle age classes						
1993	5.6±0.2a	5.6±0.4a	3.2±0.2b	2.6±0.2b	33.81	<0.001
1994	5.2±0.2a	4.7±0.2a	3.3±0.2b	2.2±0.2c	39.20	<0.001
1995	5.9±0.3a	4.6±0.1b	4.0±0.2b	2.8±0.2c	31.56	<0.001
Elongation growth:						
Needle length, mm (lower third of the canopy)						
1993	104±4a	130±7bc	151±5bd	142±8b	11.83	<0.001
1994	116±7a	113±7ac	148±7bd	152±4bd	11.19	<0.001
1995	105±10a	95±10a	130±5b	150±6b	9.52	<0.001
Lateral primary branchlet length, mm (lower third of the canopy)						
1993	35±3a	48±5a	57±5b	64±12b	3.26	0.030
1994	22±3a	35±6ac	41±6bc	41±5bc	3.05	0.038
1995	24±4a	20±3ac	61±8bd	40±10ac	7.47	0.002
Branchlet length, mm (whole canopy measurements in 1993)						
Upper 1/3	131±19a	60±19a	132±41a	103±41a	1.14	0.389
Middle 1/3	69±15a	32±5a	60±23a	46±16a	1.08	0.410
Lower 1/3	22±3a	20±3a	31±6a	31±11a	0.70	0.577
Tree height, m (1992)	5.1±0.3a	2.7±0.2b	5.0±0.3a	7.4±0.5c	27.34	<0.001
Enlargement growth:						
Branchlet diameter, mm (lower third of the canopy)						
(1995)	nd	5.9±0.3a	7.3±0.3b	7.2±0.3b	7.81	0.002
Branchlet diameter, mm (whole canopy measurements in 1993)						
Upper 1/3	7.1±1.9a	7.1±1.2a	7.7±1.3a	9.1±0.3a	0.45	0.724
Middle 1/3	4.7±0.7a	5.7±0.7a	5.1±0.5a	5.6±0.2a	0.63	0.614
Lower 1/3	3.6±0.3a	5.0±0.4b	4.1±0.0b	4.7±0.2b	5.50	0.029
Bole diameter, cm (1992)	3.4±0.2a	2.2±0.2b	3.9±0.2a	5.5±0.3c	16.77	<0.001

[a] Differing letters indicate significant differences at the $p \leq 0.05$ level.

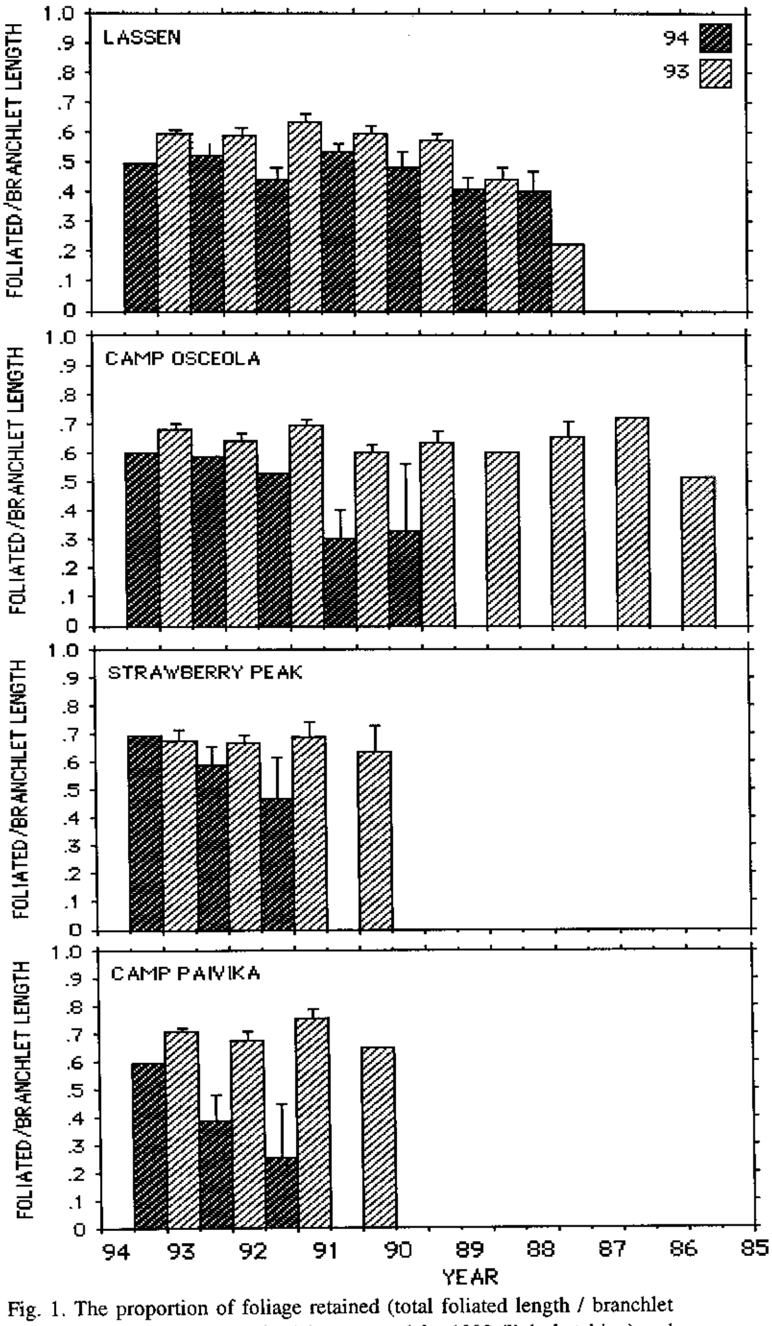

Fig. 1. The proportion of foliage retained (total foliated length / branchlet length, within a needle age class) is presented for 1993 (light hatching) and 1994 (dark hatching). The bars represent the average value for 12 trees, ± 1 S.E.

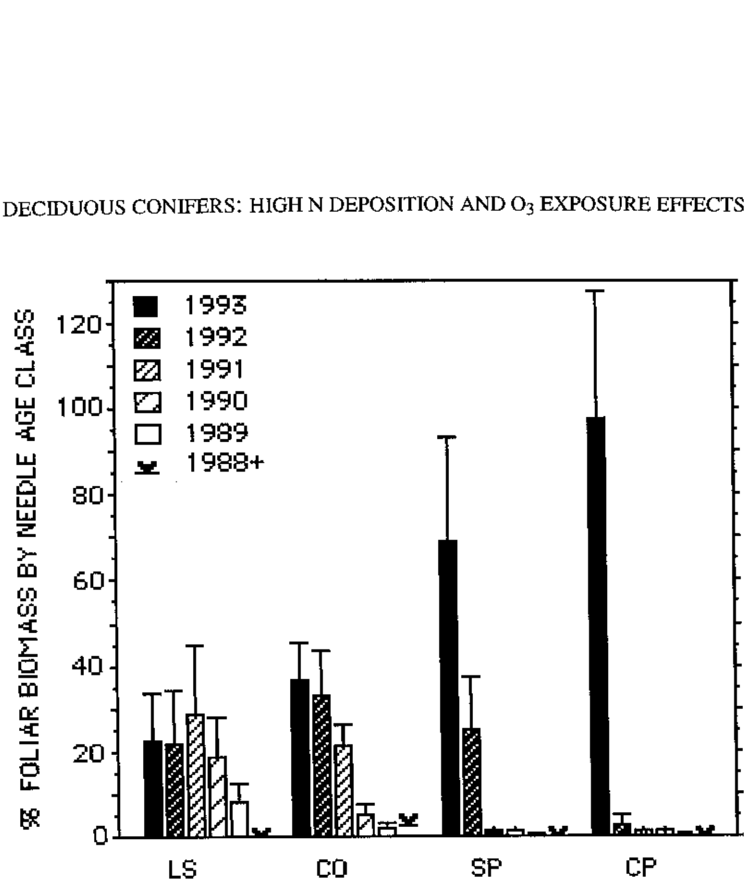

Fig. 2. Proportion of needle biomass relative to the whole canopy for each needle age class. Bars represent the average of three trees per site, ± 1 S.E.

Branchlet diameter measured in the lower third of the canopy in 1995 was significantly lower at CO relative to the other southern Californian sites (Table II). Similar to needle elongation growth, branchlet diameter measured from whole tree harvests in 1993 was lowest in the lower third of the canopy. Based on whole canopy measurements, there were significant differences in branchlet diameter between LS and the southern Californian sites. Mid-canopy branchlet diameter did not differ significantly across all sites. In the upper third of the canopy, branchlet diameter increased from LS and CO, to SP, to CP, but differences were not statistically significant due to high within-site variability. Bole diameter for 21 to 60 yr old trees was significantly greater at CP than SP and LS, and was significantly lower at CO relative to all other sites.

3.4. Whole Tree Allocation of Biomass

Total tree biomass varied seven fold across the four sites (Table III). Although the three trees harvested were average relative to the stand population of 21 to 60 yr old trees, at least one tree of the three trees at each site was ± 1 S.D. of the mean of the sample. Whole tree biomass was greatest at CP, similar at both LS and SP, and lowest at CO. Total canopy foliar mass varied ten fold across the four sites. The trees at the most polluted site had significantly greater foliar mass than at SP, and both CP and SP had significantly greater foliar mass than the two least polluted sites, LS and CO. Foliar mass in the upper and middle third of the canopy was significantly greater at CP relative to the other sites. Trends in branchlet mass within the canopy were similar to that of foliar mass, but differences between sites were not statistically significant.

Table III
Components of canopy biomass[a] for whole trees harvested in 1993.

Canopy characteristic:	LS	CO	SP	CP	F	p
Branchlet mass per branchlet, g						
Upper one third	2.3±0.4a	2.2±0.8a	2.4±1.0a	3.4±1.6 a	0.31	0.815
Middle one third	0.8±0.3a	0.6±0.2a	0.9±0.2a	0.8±0.3a	0.27	0.844
Lower one third	0.2±0.0a	0.3±0.1a	0.3±0.1a	0.4±0.1a	1.07	0.414
Foliar mass, g						
Upper one third	199±90a	88±27a	287±45a	1475±500b	1138	0.004
Middle one third	432±233a	127±46a	501±222a	1628±227b	10.99	0.003
Lower one third	221±112a	116±22b	608±261a	1356±683a	2.31	0.153
Total foliage, kg	0.9±0.4a	0.3±0.1a	1.4±0.5b	4.0±1.2c	5.44	0.025
Total tree mass, kg	31.2±19.2a	6.6±1.6a	35.3±4.8a	47.1±17.1a	1.685	0.247

[a] Differing letters indicate significant differences at the $p \leq 0.05$ level.

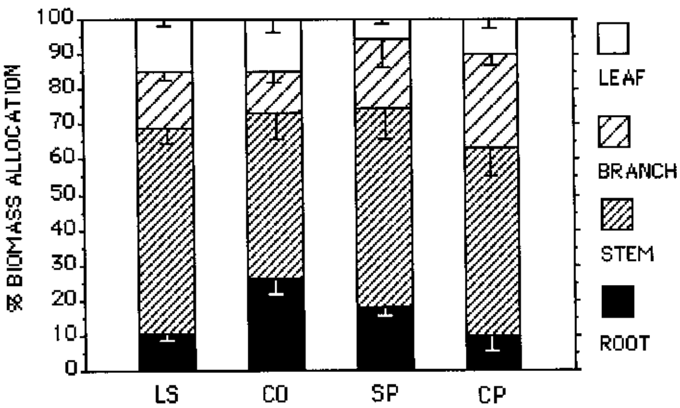

Fig. 3. Percent dry weight of root, leaf, branch, and bole biomass averaged for three whole trees harvested per site. Error bars are as described for Fig. 2.

Biomass allocation to leaf, branch, bole, and roots was also variable between individuals within a site (Figure 3). The proportion of biomass allocated to fine root biomass was a minor component (0.3 and 2%) at this mid-September harvest, and did not appear to be a major source of error. The proportion of biomass allocated to the bole was greatest at CP, followed by SP and LS. The xeric site in southern California, CO, had the lowest proportion of branch biomass of all the sites. Although CP had the greatest foliar biomass of all the sites (Table III), the proportion of foliage was among the lowest of the four sites. Root biomass was greatest at CO, and least at CP and LS. Foliar mass was greatest at CO and LS, and least at SP and CP (Figure 3).

4. Discussion

4.1. Foliar Injury and Retention

Chlorotic mottle of pine foliage is a definitive characteristic of exposure to oxidants (Miller *et al.*, 1963; 1996), and is supported by long term studies of canopy health on mature trees (Miller *et al.*, 1989). In this study, high oxidant exposure resulted in significant foliar injury along the western end of the pollution gradient, which was not mitigated by high N deposition. In a drought year, chlorotic mottle declined at three of the four sites, but was greatest at the most polluted site. After mid July in this year, gas exchange was low and no further decline in photosynthetic capacity was observed with increasing O_3 exposure (Grulke, 1998). Stomatal functioning was severely impaired (incomplete closure) at the most polluted site (Grulke, 1999), and trees at this site may have experienced much greater O_3 uptake over the growing season relative to the other sites.

The number of live needle age classes (whorls) is a well-established attribute inversely associated with high O_3 exposure in pine (Miller *et al.*, 1996). High O_3 exposure reduced foliar retention in chamber studies with ponderosa pine and when combined with drought stress, reduced foliar mass (Beyers *et al.*, 1992). However, N fertilization has also been found to promote senescence of the oldest needle age classes in pine (Oren and Schulze, 1989; Gower *et al.*, 1993; Reich *et al.*, 1995). If N is readily available, it may be more C cost-effective to drop older foliage that has lower photosynthetic capacity and accompanying respiratory losses. Older needles appear to function primarily as a repository for nutrient-containing compounds (Chapin *et al.*, 1990), but if absent can limit new branchlet growth through a lowered branch C balance (Jonasson, 1989).

O_3 exposure, N deposition, and drought stress all lower some aspect of needle retention in pine. In this study, three components of needle retention were analyzed: the number of whorls retained, the proportion of needles retained within a whorl, and the proportion of foliar biomass in each needle age class. Across the pollution gradient, as chlorotic mottle increased, the number of whorls decreased. Whorl number also decreased in a xeric year relative to mesic years. Needle retention within a whorl did not vary across the pollution gradient in a mesic year, but was significantly reduced by drought stress. In the xeric year, needle loss within a whorl was exacerbated with increasing O_3 exposure and N deposition. Also with increasing O_3 exposure and N deposition, the proportion of the foliar mass was concentrated in increasingly fewer needle age classes. Despite the presence of multiple needle age classes at the most polluted site, their contribution to total canopy foliar mass was minor. At the most polluted site, 95% of the needle mass was current year foliage, resulting in trees with only one overwintering needle age class.

4.2. Growth and Biomass Allocation

Needle, branch, and bole growth was greatest at the most polluted site (CP), and declined with decreasing pollution exposure across the southern Californian gradient. Needle, branch, and stem mass were greatest at the most polluted sites (CP, SP). Of the environmental factors differing between the sites, this response might be expected in response to differences in ecosystem energy inputs (cumulative degree days, season length) or N deposition. Season length was similar between three of the four sites: the northern Californian site, and the eastern and intermediate sites in southern California (averaging LS: 97 d, CO: 105 d, and SP: 109 d, versus CP: 170 d). Despite the differences in cumulative degree days, some attributes of tree growth at the cleanest site in northern California were most comparable to the xeric site in southern California (needle length in a xeric year and the following year; branch length in the lower third of the canopy in any year), and others (needle length after 2 yr of above-average precipitation; tree height; bole diameter) were more similar to the intermediate pollution exposure site (SP). If cumulative degree days were dominating the growth response, a three fold difference between LS and SP would be expected to have a significant effect on these attributes. Despite high O_3 exposure, N deposition dominated the growth response at the most polluted sites (CP, SP).

As a single stressor, oxidant exposure in chamber studies generally reduces growth and biomass in pine (as reviewed in Reich, 1987; Darrall, 1989; Bytnerowicz and Grulke, 1992; Matyssek *et al.*, 1994). Nitrogen fertilization increases foliage, branch, and bole mass in pines (*Pinus ponderosa*: Powers, 1983; Gholz *et al.*, 1991; Raison *et al.*, 1992; Gower *et al.*, 1993; Tingey *et al.*, 1996; *Pinus radiata*: Fife and Nambiar 1997). In studies of other conifers, needle length and specific leaf weight increased in response to fertilization (Chandler and Dale, 1990; Raison *et al.*, 1992). Although foliar retention is generally reduced with N fertilization, some of the greater canopy biomass observed in long term studies could be accounted for by the retention of branches in the lower canopy (Powers, pers. comm.). The trees at the most polluted site had significantly greater foliar mass than at SP, and both CP and SP had significantly greater foliar mass than the two least polluted sites, LS and CO. Although CP had the greatest foliar biomass of all the sites, as a proportion, foliage was among the lowest of the four sites at CP. The least polluted sites had the highest proportion of whole tree biomass in foliage. The most polluted sites had the highest proportion of biomass allocated to the bole. Drought stress increased the proportion of whole tree biomass allocated to root biomass (CO compared to SP and CP). The low proportion of root biomass at the most polluted site supported measures of standing live root biomass in another study across the same gradient (Grulke *et al.*, 1998).

Trees at the xeric site in southern California (CO), had the lowest whole tree biomass, height, and bole diameter, a function of drought and moderate O_3 exposure.

This site also had the lowest proportion of whole tree biomass allocated to branches. Needle and branchlet length was lowest for the most xeric site (CO) in the year following the drought suggesting a possible residual effect. The significant drought stress experienced in 1994 did not have as large an effect on needle and branch elongation growth as was expected. These data were taken in the lower third of the canopy, which may be the least responsive tissue to environmental influences external to the canopy due to shading and within-tree competition for resources. Branchlet length and diameter, and branchlet and foliar mass were greater in the upper two thirds of the canopy, but differences were significantly greater only for foliar mass at the most polluted site. Thus future studies of tree growth response to oxidant injury, N deposition, and drought stress should be conducted in the mid or upper canopy.

5. Conclusions

High O_3 exposure and its effects on chlorotic mottle of foliage at sites closest to the Los Angeles, California air basin are significant. This is a definitive response to oxidant pollution, and high N deposition did not eliminate the foliar O_3 injury. O_3 exposure, N deposition, and drought stress all lower the number of live needle age classes, and at sites where they may all be present, this tree attribute cannot be used to distinguish their singular effects. Retention of needles within a whorl was lowered by drought stress, and was further exacerbated when drought stress was combined with O_3 exposure. The significant increase in needle and branchlet elongation growth, and the increase in branchlet and bole enlargement growth are responses that result from long-term N deposition, and provide strong evidence that N deposition overrides O_3 exposure effects at the most polluted site. The effects of N deposition on elongation growth are overridden by drought stress. Based on whole tree harvests, root biomass was lowest at sites with the highest pollution exposure, confirming previous chamber exposure and field studies. Whole tree measures indicate that at the least polluted site, foliar biomass was evenly distributed across three of the five needle-age classes retained. At the most polluted site, 95% of the foliar biomass was found in the current year's growth. High N deposition and high O_3 exposure combine to shift biomass allocation in pine to that of a deciduous tree.

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References

Barbour, M. G.: 1988, Pgs. 131-164, In: *North American Terrestrial Vegetation*, eds, Barbour, M. G., Billings, W. D. Cambridge University Press, NY.

Beyers, J. L., Riechers, G. H. and Temple, P. J.: 1992, *New Phyt.* **122**, 81-90.

Bytnerowicz, A. and Fenn, M. E.: 1996, *Env. Poll.* 92, 127-146.

Bytnerowicz, A. and Grulke, N. E.: 1992, Pages 183-233, In *The Response of Western Forests to Air Pollution*, eds. Olson, R., Binkley, D., Bohm, M. Springer-Verlag, NY, USA.

Chandler, J. W. and Dale, J.E.: 1990, *Tree Phys.* **6**, 41-56.

Chapin F. S., III, Schulze, E.-D. and Mooney, H. A.: 1990, *Ann. Rev. Ecol. Syst.* **21**, 423-47.

Darrall, N. M.: 1989, *Plant, Cell, Env.* **12**, 1-30.

Fenn, M. E. and Kiefer, J.W.: 1999, *Env. Poll., (in press).*

Fenn, M. E. and Poth, M. A.: 1999, *Ecol. Stud.* **134**, 288-316.

Fenn, M. E., Poth, M. A. and Johnson, D. W.: 1996, *For. Ecol. Manage.* **82**, 211-230.

Fife, D. N. and Nambiar, E. K. S.: 1997, *For. Ecol. Manage.* **93**, 137-152.

Gholz, H. L. and Cropper, W. P.: 1991, *Can. J. For. Res.* **21**, 1742-1747.

Gholz, H. L., Vogel, S. A., Cropper, W. P., Jr., McKelvey, K., Owel, K. C., Teskey, R. O. and Curran, P. J.: 1991, *Ecol. Monogr.* **61**, 33-51.

Gower, S. T., Haynes B. E., Fassnacht, K. S., Running, S. W. and Hunt, E. R., Jr.: 1993, *Can. J. For. Res.* **23**, 1704-1711.

Grulke, N. E.: 1998, *Air Waste Manag. Assoc., 91st Annual Meeting Proc.*, TA-37.05.

Grulke, N. E.: 1999, *Ecol. Stud.* **134**, 126-163.

Grulke, N. E., Andersen, C.P., Fenn, M.E. and Miller, P.R.: 1998, *Envir. Poll.* **103**, 63-73.

Grulke, N. E. and Lee, E.H.: 1997, *Can. J. For. Res.* **17**, 1658-1668.

Haynes, B. E. and Gower, S.T.: 1995, *Tree Phys.*: **15**, 317-325.

Hermann, R. K. and Petersen, R.G.: 1969, *For. Sci.* **15**, 226-237.

Jonasson, S.: 1989, *Oikos* **56**, 121-131.

Kiefer, J. W. and Fenn, M.E.: 1997, *For. Ecol. Manage.* **94**, 47-59.

Matyssek, R., Reich, P., Oren, R. and Winner, W.: 1994: In *Ecophysiology of Coniferous Forests*, eds. Smith, W. K., Hinckley, T. M. Academic Press, San Diego, CA, USA.

McBride, J. R. and Miller, P. R.: 1987, Pages 217-228, In *Effects of Atmospheric Pollutants on Forests, Wetlands, and Agricultural Ecosystems* , eds. Hutchinson, T.C., K.M. Meema, K.M. Springer-Verlag, NY, USA.

McBride, J. R., Semion, V.P. and Miller, P.R.: 1975, *Calif. Agric.* **8**, 9.

Miller, P. R., Longbotham, G.J, and Longbotham, C.R.: 1983, *Plant Disease* **67**, 1113-1115.

Miller, P. R., McBride, J.R., Schilling, S.L. and Gomez, A.P.: 1989, Pages 309-323, In: *Effects of Air Pollution on Western Forests*, eds Olson, R.K., Lefohn, A.S., Transactions, Air Waste Manage. Assoc. Symposium, Anaheim, CA.

Miller, P. R., Parmeter, J. R., Taylor, O. C. and Cardiff, E. A.: 1963, *Phytopath.* **53**, 1073-1076.

Miller, P. R., Stolte, K. W., Duriscoe, E. and Pronos, J. (tech coor): 1996, *Monitoring ozone air pollution effects on western pine forests.* USDA Forest Service, Pacific Southwest Region, GTR-155, Albany, CA, USA.

Oren, R. and Schulze, E.-D.: 1989, *Ecol. Stud.* **77**, 425-443.

Peterson, D. L., Arbaugh, M. J. and Robinson, L.J.: 1991, *The Holocene* **1**, 50-61.

Powers, R. F.: 1983, Pages 388-397, In: *IUFRO Symposium on Forest Site and Continuous Productivity*, eds Ballard, R., Gessel, S.P. USDA FS Gen. Tech. Rep. PNW-163.

Raison, R. J., Myers, B. J. and Benson, M. L.: 1992, *Forest. Ecol. Manage.* **52**, 139-158.

Reich, P. B.: 1987, *Tree Phys.* **3**, 63-91.

Reich, P. B., Koike, T., Gower, S. T. and Schoettle, A. W.: 1995, Pgs. 225-254, In: *Ecophysiology of Coniferous Forests*, Smith, W.K., Hinckley, T.M., Academic Press, San Diego, CA.

San Bernardino County Water Resources Division, http://www.co.san-bernardino.ca.us/pwg/waterresources.

Tingey, D. T., Johnson, M. G., Phillips, D. L., Johnson, D. W. and Ball, J. T.: 1996, *Tree Phys.* **16**, 905-914.