

WATERSHED-SCALE RESPONSES TO OZONE EVENTS  
IN A *PINUS STROBUS* L. PLANTATION

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**Abstract.** High O<sub>3</sub> levels during the 1984 growing season in the southern Appalachian Mountains caused extensive damage to a 28 yr old white pine plantation on a 13.4 ha watershed at the Coweeta Hydrologic Laboratory. Ozone stress effects included premature senescence and loss of foliage, stimulation of pine seedling germination, reduced basal area increment, and small but measurable increases in NO<sub>x</sub> and K<sup>+</sup> concentrations in stream water. There were no observable effects of O<sub>3</sub> damage on nutrient concentrations of stemwood and foliage but net nutrient accumulation was reduced due to lower stem production. Ozone injury did not predispose trees to root pathogens or bark beetle infestations.

### 1. Introduction

According to a critical review of the literature by McLaughlin (1988), laboratory and field research provides circumstantial evidence for the role of atmospheric pollution in reducing vigor or increasing mortality of forest tree species in Europe and the United States. Recent emphasis has been placed on gaseous pollutants such as NO<sub>x</sub> and a photochemical product, O<sub>3</sub>, as a possible cause of forest decline. Ozone is particularly significant because it occurs in phytotoxic concentrations over broad geographic regions.

Recent reviews have specifically examined the role of O<sub>3</sub> in the decline in North America (Chevone and Linzon, 1988); the impact of O<sub>3</sub> assimilate partitioning in plants (Cooley and Manning, 1987); and effects on vegetation (Krupa and Manning, 1988), forest health (Hakkarinen, 1987; Linzon, 1986), and growth and yield of trees (Fisher 1988). A common theme of these reviews is the difficulty in conclusively linking forest decline to a single stress factor such as O<sub>3</sub>. The effects of O<sub>3</sub> on physiological processes are reasonably well understood (Winer 1989; McLaughlin *et al.*, 1988), and a unifying theory for quantifying plant response to O<sub>3</sub> has been developed (Reich, 1987). However, studies in the greenhouse or open-top chamber studies on seedlings and saplings are difficult to extrapolate to mature trees and for ecosystems. Similarly, under natural conditions forest ecosystems are frequently subjected to multiple concurrent stresses, or trees may be exposed to cumulative impacts of a single or multiple stress. Both these situations preclude a conclusive interpretation of causal impacts on forests.

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In this paper we examine the effects of episodic O<sub>3</sub> events, which occurred during the growing season of 1984, on the health and function of a 28 yr old white pine (*Pinus strobus* L.) plantation. The analysis represents a unique opportunity to measure the responses of a natural mature forest ecosystem to a single pollutant.

## 2. Site Description

The study site is within the Coweeta Hydrologic Laboratory, a 2185 research area in the Nantahala Mountain Range of western North Carolina USA (Figure 1). The Laboratory is a site of long-term hydrology and ecology research with a focus on biogeochemical cycles of forest ecosystems. Annual precipitation varies from 180 cm at lower elevations (690 m) to 250 cm on the upper slopes (1550 m). Mean monthly temperatures range from 3.3°C in January to 21.6°C in July (Swift *et al.*, 1984). Coweeta is located in a rural, predominantly forested setting and farming is an important land use. Regional air mass movement is typically from the south and is strongly influenced by high and low pressure systems over the Gulf of Mexico. The nearest large city is Atlanta, Georgia which is 160 km to the southwest (Figure 1). Long-term records of wet and dry deposition chemistry measurements in the Coweeta basin show the influence of local land use disturbance such as plowing and burning (Swank and Henderson, 1976), the importance of sea-salt aerosols and anthropogenic emissions on deposition chemistry (Swank and Waide, 1984) and the effect of long-range transport of particulates on deposition chemistry in the basin (Swank, 1984).

The primary site of this study is Watershed 17 (WS 17), a 13.4 ha north-facing catchment with side slopes averaging 50%. Elevations range from 760 m at the weir to 1021 m on the ridge. The treatment history of the watershed includes cutting all hardwood vegetation in 1940 and allowing cutting of regrowth in most years until 1955. White pines were planted in 1956 and released from hardwood competition as required by cutting and applying herbicides. In 1985, stocking was 890 trees ha<sup>-1</sup> with a basal area of 46 m<sup>2</sup> ha<sup>-1</sup>. Stream gaging was initiated in 1936 and hydrologic and biogeochemical cycles of the ecosystem have been intensively studied for over 50 yr (Swank and Crossley, 1988).

A secondary site utilized in this study is Coweeta Watershed 1 (WS 1), a 16.1 ha south-facing catchment 1.5 km from WS 17 on the opposite side of the Coweeta Basin. The mixed hardwood forest on WS 1 was clear cut in 1956 and planted with white pine in 1957. Subsequently, the treatment history has been identical to WS 17 and in 1985 stocking was 1165 trees ha<sup>-1</sup> with a basal area of 47 m<sup>2</sup> ha<sup>-1</sup>. Hydrological and ecological processes have also been closely monitored for many years on WS 1.

## 3. Characterization of Ozone Events

In mid-July 1984, pronounced discoloration of white pine foliage was clearly visible from an overlook with a 400 m direct view into WS 1. Canopy discoloration was initially most obvious on the upper third of the watershed, but in the ensuing 2 wk about 75% of the 13 ha plantation showed foliar discoloration. The initial, general appearance from a distant view was of a stand severely infested with bark beetles.

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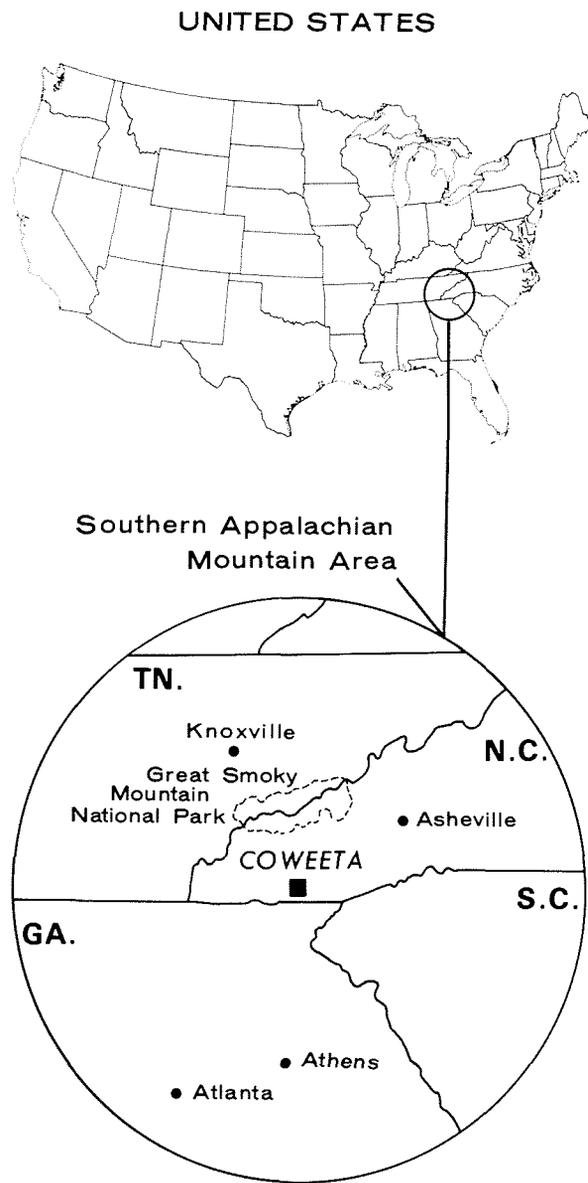


Figure 1. The Coweeta Hydrologic Laboratory is in the southern Appalachian Mountains of North Carolina. The Great Smoky Mountains National Park, another site of atmospheric pollution research is 65 km north of Coweeta.

Initial examination of fascicles revealed symptoms of foliar injury distinctive for O<sub>3</sub> damage. Chlorotic mottling was prevalent on needles of most affected fascicles and tipburn was also common. The preliminary diagnosis was confirmed by Dr. Charles Berry, a pioneer in research on SO<sub>2</sub> and O<sub>3</sub> damage to white pine (Berry, 1961). His visual examination of the stand in mid-August indicated that damage occurred from at least three separate O<sub>3</sub> episodes. In September it appeared that another damaging O<sub>3</sub> event occurred. Typically, foliar damage was most severe on dominant and codominant trees with the entire upper two-thirds of the crowns usually exhibiting visual symptoms. Other mature white pines in the nearby (within 1 km) valley showed no visible symptoms of damage. The white pine on WS 1 (1.5 km) also lacked significant visible damage. Ozone monitoring was not in place within the Coweeta Basin in 1984, but measurements were initiated in 1986. Ozone concentrations were monitored across an elevational gradient in the basin during the past 4 yr providing evidence for different diurnal patterns and levels of O<sub>3</sub> concentrations over relatively short distances. These patterns may partially explain the variable response of white pine in the Coweeta Basin to the 1984 events.

Ozone concentrations during the summer of 1984 were generally high throughout the region. Lacking O<sub>3</sub> data for our specific location in 1984, we selected nearby rural O<sub>3</sub> monitoring stations whose records were available for the period of interest. Look Rock, a monitoring station for Great Smoky Mountains National Park (GSMNP) (Figure 1), is on Chilho Mountain in east Tennessee at an elevation of 792 m and about 65 km from Coweeta. The diurnal patterns of O<sub>3</sub> concentrations at Look Rock (Reisinger and Valente, 1985) are similar to patterns at the top of Coweeta WS 17 and another high-elevation monitoring site (data collected in 1984) in the GSMNP (Figure 2). In spring and summer, the diurnal cycle is characterized by a small amplitude with minimum concentrations at midmorning, followed by a broad, flat maximum in the afternoon which is maintained throughout the night. Average hourly concentrations at Coweeta are about 15% lower than average values at this GSMNP station. During the growing season in 1984, O<sub>3</sub> concentrations at Look Rock frequently averaged over 80 ppb for periods of over consecutive hours with maximum hourly concentrations of 90 ppb (Table 1). Taken together, diurnal patterns and concentrations of O<sub>3</sub> in 1984 indicate that white pine on WS 17 were exposed to relatively high levels of O<sub>3</sub> for extended periods. Moreover, stomatal conductance to diffusion was probably optimal because precipitation was abundant throughout the growing season and trees were not subject to water stress. Other evidence, although indirect, for O<sub>3</sub> damage to the pine is also available. Clones propagated from trees visibly damaged on WS 17 in 1984 have been used in dose-response experiments and also outplanted in bioindicator plots collocated with O<sub>3</sub> monitoring stations at Coweeta. Exposure of the clones to O<sub>3</sub> concentrations of 80 ppb for 8 hr or longer has caused foliar damage symptomatic of O<sub>3</sub>.

Our characterization of the visible and physical evidence for foliar damage in 1984 does not provide unequivocal proof that other oxidizing pollutants or factors of air pollution did not contribute to the observed damage. However, rainfall acidity during the growing season at Coweeta over the past 17 yr is typically in a pH range of 3.7 to 5.3; during 100% of all precipitation events were above pH 4.2. Furthermore, over the past 17 yr, measurements of SO<sub>2</sub> and HNO<sub>3</sub> acid vapor at Coweeta have shown conc

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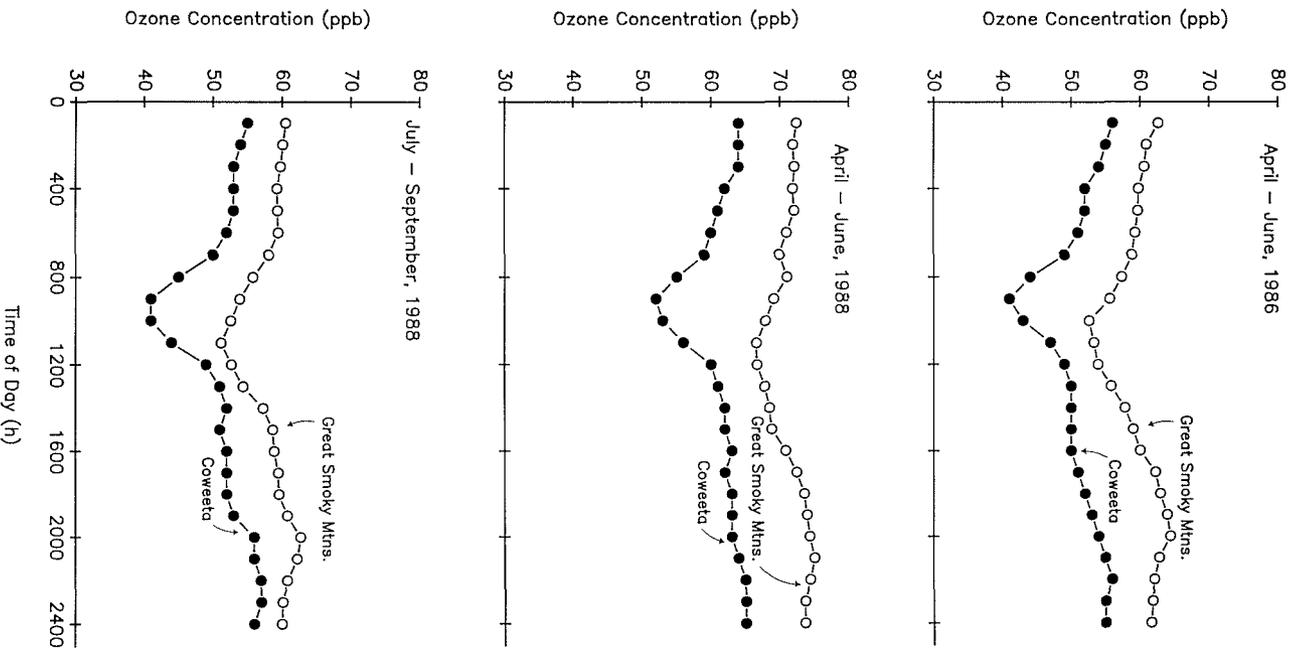


Figure 2. Diurnal O<sub>3</sub> concentrations at two high-elevation sites, Coweeta (1010 m) and GSMNP (Cove Mountain 1262 m), in the southern Appalachian Mountains for the second and third quarters of 1988 and the second quarter of 1986.

Table I

Ambient O<sub>3</sub> concentrations at Look Rock, TN,\* near the GSMNP during selected periods in 1984.

Date	Time period (hr)	Mean O <sub>3</sub> concentrations (ppb)	Maximum hourly O <sub>3</sub> concentration (ppb)
May 12	1000-2400	80	93
May 19	1000-2400	81	93
May 20	0100-2400	87	93
June 4	1000-2400	89	98
June 5	0100-2400	73	93
June 7	1000-2400	83	98
June 24	1000-2400	76	88
June 27	1000-2400	78	93
July 9	1000-2400	73	91
August 18-19	1000-0700	84	93
September 17-18	1300-0800	83	98
September 20-21	1500-0900	78	83
September 21-22	1500-0900	86	119
September 23	0100-0900	78	78
October 6-7	1300-0900	85	108

\* In 1984 the monitoring station was operated by the Air Pollution Control Division of the State of Tennessee.

trations to be low with maximum concentrations of 7.8 and 8.0  $\mu\text{g m}^{-3}$  respectively. Likewise, analyses have shown very low concentrations of trace metals in precipitation at Coweeta (Lindberg and Turner, 1988). Thus, it is highly unlikely that a pollutant other than O<sub>3</sub> was the primary cause of damage to the pine on WS 17.

#### 4. Results and Discussion

##### 4.1 Growth responses

The most conspicuous impact of O<sub>3</sub> damage to white pine on WS 17 was premature senescence and loss of foliage, particularly past year (> 1 y old foliage). Damaged needles were abundant on the forest floor in August although litterfall traps were not installed until September 15, 1984. On WS 17 and WS 1, the effects of O<sub>3</sub> on needle loss were still obvious. Over a 5 mo period (September to February), foliage litterfall on WS 17 was 299 g m<sup>-2</sup> (SE = 27) compared to 190 g m<sup>-2</sup> (SE = 18) on WS 1.

subsequent years, foliage litterfall for the two populations was the same. Leaf area on WS 17 was so markedly reduced that light intensities at the forest floor were sufficiently increased to stimulate widespread pine seedling germination, a process not previously observed in the stand.

The effect of O<sub>3</sub> damage on tree growth was examined by measuring radial growth of trees sampled in both WS 17 and WS 1. Twelve dominant and codominant trees were sampled on each watershed. Sample trees on WS 17 were from the upper third of the catchment where visible foliar damage was most prevalent. Two cores were taken on opposite sides of sample trees at DBH and parallel to the slope. Extracted cores were stored in drinking straws, transported to the laboratory, mounted in a jig, shaved to provide a clean, flat surface for measurement. Annual growth widths were measured to 0.01 mm under a microscope (375x) using an incremental measuring instrument coupled to a microcomputer. Measurements from the two cores were averaged and annual growth expressed as basal area increment (BAI in cm<sup>2</sup>).

During the period of 1979 to 1983, BAI of trees in both plantations varied widely from year-to-year and growth rates of sample trees were higher on WS 17 compared to WS 1 (Figure 3). These differences were probably due to site quality from which sample trees were selected. However, growth patterns over this period were similar for the two populations. In 1984, BAI of trees on WS 17 decreased dramatically whereas BAI of trees on WS 1 was unchanged. In fact, growth rates of trees from the O<sub>3</sub> damaged plantation dropped below those of trees on WS 1. In the following year, growth on WS 17 continued to decline, there was also a similar decline on WS 1 which may be partly associated with below average precipitation during several months of the growing season. Statistical analysis of growth response on WS 17 was performed by comparing BAI in 1984 to the average BAI of the preceding 5 yr (1979 to 1983). Data were analyzed by analysis of variance, with plantation included as a block factor in the analysis. Sample tree blocking was necessary because there was a positive relationship between BAI and initial tree size (block effects were highly significant [ $p < 0.0001$  in the analysis]). The 18% reduction in BAI in 1984 was significantly different ( $p < 0.05$ ) from the previous 5 yr period (Table II).

Analysis of tree growth within the O<sub>3</sub> impacted population and between O<sub>3</sub> symptomatic and O<sub>3</sub> asymptomatic populations provides strong evidence for a significant growth reduction of larger trees due to O<sub>3</sub> damage. A more intensive study is in progress to assess impacts across the entire range of tree sizes. For example, it is plausible that intermediate canopy trees, which showed much less visible O<sub>3</sub> damage, could have positive growth responses to increased light availability resulting from the reduction in leaf area of larger competing trees.

Dose-response O<sub>3</sub> experiments were conducted on three clones selected from dominant trees visually damaged in 1984 on WS 17. In 1985, stem material was selected from the upper crown (about 25 m) of parent trees and 30 ramets were grafted from each clone. Ramets were maintained under an open, lattice covered structure at Coweeta, and by 1988 clonal material was typically 0.7 to 1.0 m tall. In July 1988, nine ramets of each clone were exposed to concentrations of 0, 100, and 200 ppb of O<sub>3</sub> over a 24-hour period in stirred chambers operated by the U.S. Agricultural Research Experiment Station, Raleigh, North Carolina. Plants were exposed to

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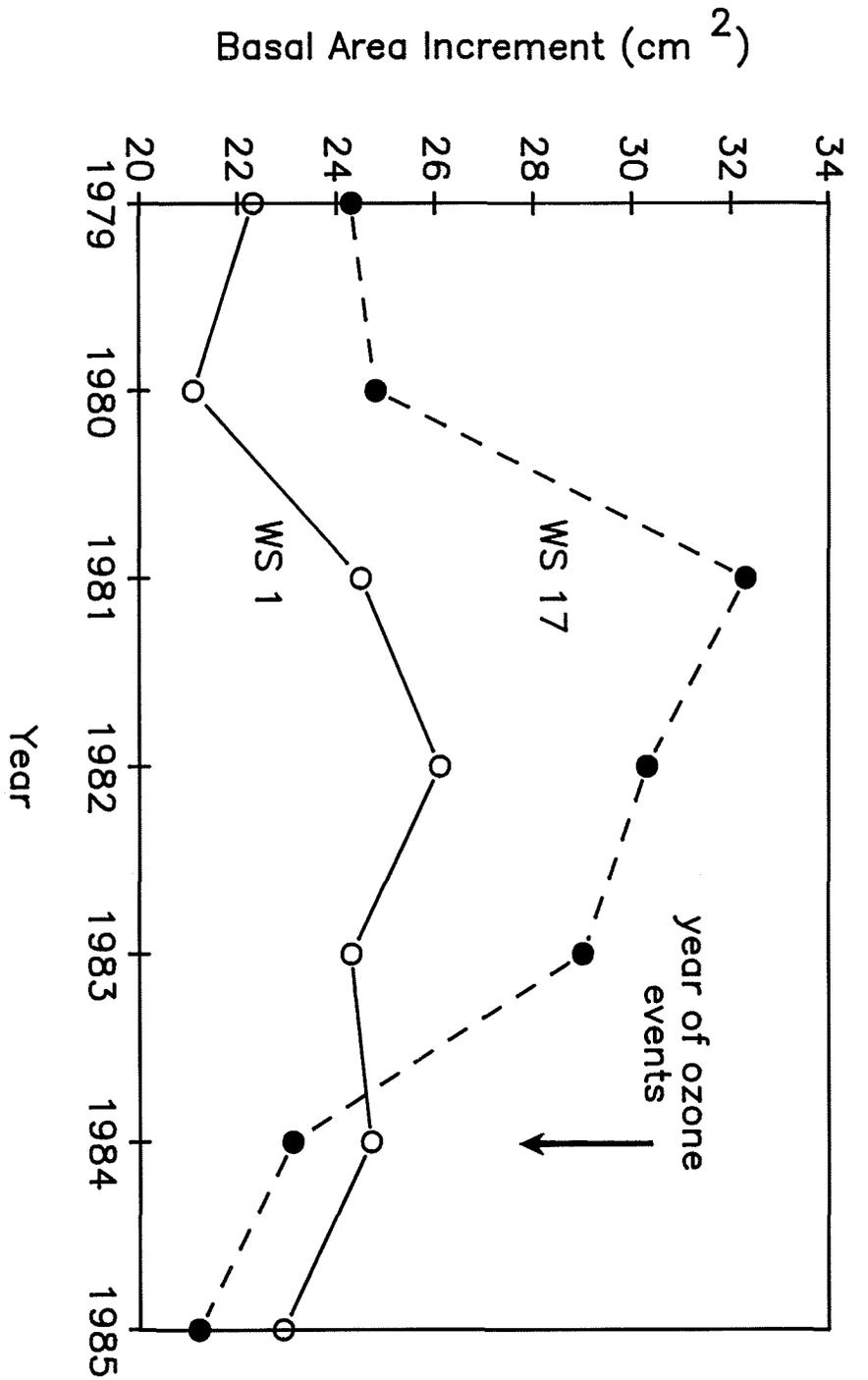


Figure 3. Annual BAI for dominant and codominant 28 yr old white pine on Coweeta WS 17 (O<sub>3</sub> symptomatic in 1984) and WS 1 (O<sub>3</sub> asymptomatic from

Table II

Comparison of BAI ( $\text{cm}^2$ ) of white pine on Coweeta WS 17 in 1984 to year average BAI from 1979 to 1983. Values are significantly different (ANOVA) at the  $p < 0.05$  level ( $n = 12$ )

	BAI ( $\text{cm}^2$ )	F-value	P > F
1979-1983 $\bar{X}$	28.14	7.13	0.0218
1984	23.05		

different treatments for 5 hr day<sup>-1</sup> on four consecutive days in week. Between exposures, ramets were watered and maintained in clean filtered air.

Findings most relevant to this paper are the impacts of O<sub>3</sub> exposure on net photosynthetic rate (P<sub>net</sub>). Photosynthetic rates were measured using a LCA2 Portable Photosynthesis System) on current-year foliage and year foliage (> 1 yr) immediately after exposures at the end of week 1 and 2. Three ramets of each clone were used for each exposure and rates were averaged across all clones ( $n = 9$ ). After the first week exposure, P<sub>net</sub> was significantly lower for the 100 ppb and 200 ppb exposures compared to the zero O<sub>3</sub> exposures (Table III).

Table III

Mean net photosynthesis (SE) in  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for white pine clones exposed to controlled O<sub>3</sub> concentrations. Statistical tests (ANOVA,  $p < 0.05$ ) were made between treatments within week and age class. Treatments followed by the same letter do not differ (LS-Means;  $p < 0.05$ ).

Treatment*	1 wk		2 wk	
	Current	Past	Current	Past
0	4.16(0.33) <sup>a</sup>	3.35(0.23) <sup>a</sup>	3.67(0.60) <sup>a</sup>	3.06(0.25)
100 ppb	1.53(0.35) <sup>b</sup>	1.83(0.24) <sup>b</sup>	1.92(0.64) <sup>ab</sup>	1.76(0.27)
200 ppb	1.39(0.31) <sup>b</sup>	1.91(0.23) <sup>b</sup>	1.73(0.56) <sup>b</sup>	2.21(0.27)

\* O<sub>3</sub> treatments: 5 hr day<sup>-1</sup>, 4 days week<sup>-1</sup>

There were no significant differences in P<sub>net</sub> rates between 100 and 200 ppb exposures and rates were similar between current-year and year foliage. Compared to P<sub>net</sub> rates at zero O<sub>3</sub> levels, rates were reduced an average of 55% for the two O<sub>3</sub> exposures. Similar reductions

in Pnet were observed after the second week of exposures (Table III). Although the minimum O<sub>3</sub> level (100 ppb) is slightly higher than episodic ambient levels estimated for 1984, these chamber experiments indicate that reduced rates of Pnet are potentially a significant cause of the growth reductions associated with the O<sub>3</sub> episodes.

#### 4.2 Nutrient responses

The effects of O<sub>3</sub> stress on ecosystem nutrient dynamics were examined by analyzing nutrient concentrations of vegetation and stream water. In the latter case, 16 yr of continuous stream chemistry data provided a good baseline for detecting changes in biogeochemical cycles. For vegetation the opportunity to detect impacts was more limited.

Increment cores used in growth analysis were analyzed for nutrients by routine procedures established at Coweeta (Reynolds and Deal, 1987). Concentrations of the major cations and P in stemwood increment of 1984 were essentially identical to the average stemwood nutrient concentrations of the preceding 5 yr (Table IV). Foliar nutrients were not sampled in 1984, but potential impacts of O<sub>3</sub> stress were examined from nutrient analysis of needlefall collected in 1985, which primarily represented current-year foliage exposed to the O<sub>3</sub> episodes in 1984. Nutrient concentrations were compared to foliar values for needlefall in 1987 because 1986 was a record drought, and hence atypical of nutrient recycling processes. There were no consistent differences in nutrient concentrations of needlefall between years (Table IV), but the lack of sampling prior to senescence in 1984 limits our evaluation of O<sub>3</sub> impact on foliar nutrients. Thus, the main observable effect of O<sub>3</sub> stress on aboveground plant nutrient was reduced net plant accumulation of major cations and P since stemwood concentrations remained unchanged but wood increment was significantly reduced.

Table IV

Summary of nutrient concentrations in stemwood and needlefall for white pine on Coweeta WS 17 prior to, during, and/or after O<sub>3</sub> damage in 1984.

Vegetation component	Year(s)	Nutrient concentrations (% d.w.)				
		K	Ca	Mg	P	N
Stemwood	1979 to 1983	0.027	0.043	0.010	0.005	0.06
	1984	0.027	0.043	0.008	0.005	NA
Foliage (needlefall)	1987	0.179	0.526	0.106	0.025	0.41
	1985	0.119	0.619	0.102	0.029	0.45

\* Insufficient sample tissue available for chemical analyses.

Stream water chemistry has been sampled weekly on WS 17 and other Coweeta watersheds since 1971 (Swank and Waide, 1988). Prior analysis has shown that changes in concentrations of nitrate-N (NO<sub>3</sub><sup>-</sup>-N) are

sensitive indicator of forest ecosystem disturbances at Coweeta such as clearcutting, insect infestations, and species conversions (Swank, 1988). Monthly  $\text{NO}_3^-$ -N concentrations for the stream draining WS 17 during 1984 and 1985 are similar in both pattern and level to the long-term average monthly concentrations (Figure 4). However, throughout 1985  $\text{NO}_3^-$ -N levels were substantially above average values. Seasonal concentration patterns were similar with lowest levels in the winter months and highest levels in late summer. Throughout the 1985 growing season, monthly  $\text{NO}_3^-$ -N concentrations frequently exceeded long-term concentrations by more than 70%. Over 1985, the average monthly concentration increased from a baseline value of 0.15 to 0.27  $\text{mg L}^{-1}$ . These changes are highly significant since the standard error of estimates for monthly long-term concentrations are typically less than 10% of the mean.

The extent to which elevated  $\text{NO}_3^-$ -N concentrations can be related to  $\text{O}_3$  damage on WS 17 was examined in several ways. First, it was surprising to see a lag between cause and effect; i.e. no change in stream chemistry in 1984 when  $\text{O}_3$  damage occurred but a stream chemistry response in 1985. Previous research at Coweeta has shown similar delays following disturbances such as clearcutting. The lag between changes in biogeochemical cycles on the landscape, and their measurable effects at the weir, integrates the responses of biological and hydrological processes and physical factors such as soil depth (Swank, 1988). Since the stream draining WS 1 was assumed to be a "control" (no  $\text{O}_3$  damage on WS 17). Although baseline concentrations of  $\text{NO}_3^-$ -N on WS 1 are lower than WS 17, both show the same mean monthly concentration maxima and minima (Figure 4). In 1984 concentrations on WS 1 were slightly below the average long-term monthly concentrations while values in 1985 were slightly above the average (i.e. 0.04 vs 0.06  $\text{mg L}^{-1}$  in the growing season). In both years, monthly differences were not significant because they encompass the standard error of the monthly long-term means. It appears that a small but significant release of  $\text{NO}_3^-$ -N was associated with the  $\text{O}_3$  damage on WS 17.

Response patterns for other stream nutrients, examined in the same manner, were similar to that for  $\text{NO}_3^-$ -N. For example, concentrations of  $\text{K}^+$ , a biologically important and mobile nutrient, were elevated in 1985 on WS 17, while there was little or no change on WS 1 (Figure 4). Changes in  $\text{Ca}^{2+}$  concentrations on WS 17 were smaller and only occurred several months while  $\text{Mg}^{2+}$ ,  $\text{NH}_4^+$ -N and  $\text{PO}_4^{3-}$  concentrations did not differ from long-term averages.

Taken collectively, these data indicate that the nutrient cycle for some ions was altered by  $\text{O}_3$  damage to white pine on WS 17. Changes in several key processes could be postulated to explain elevated nutrient levels in stream water such as: (1) accelerated mineralization and nitrification in response to increased forest floor temperature as a result of the leaf area reduction, and (2) reduced plant nutrient accumulation. However, altered nutrient cycles due to  $\text{O}_3$  damage are probably short-lived and the small elevated concentrations of stream nutrients measured in this study are of little consequence to stream water quality.

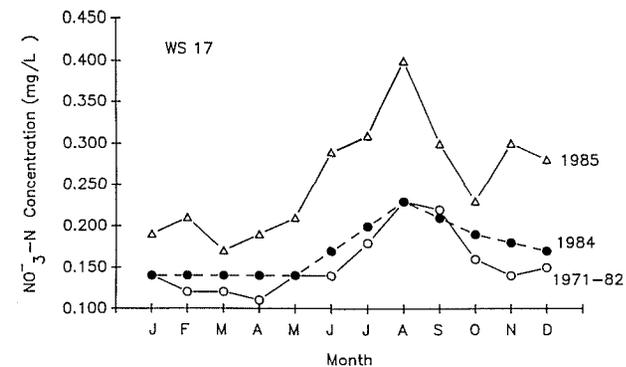
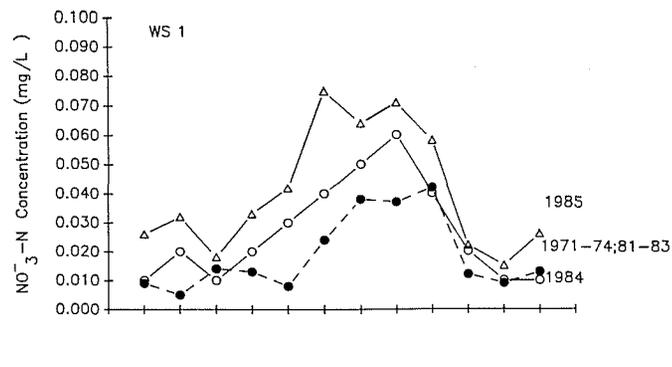


Figure 4. Mean monthly concentrations of  $\text{NO}_3^-$ -N in streams draining white pine-covered watersheds at Coweeta for baseline years compared to monthly concentrations during 1984 and 1985. White pine on WS 17 was  $\text{O}_3$  symptomatic in 1984 while pine on WS 1 was asymptomatic.

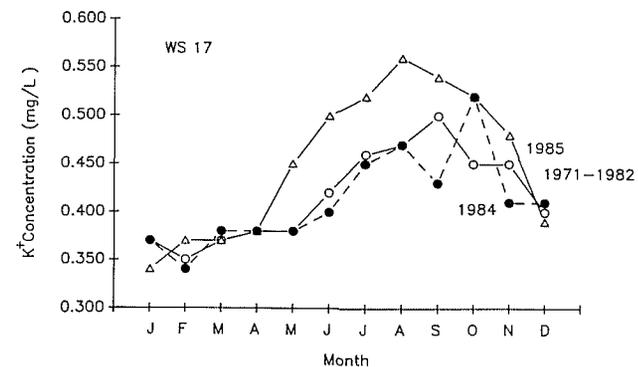
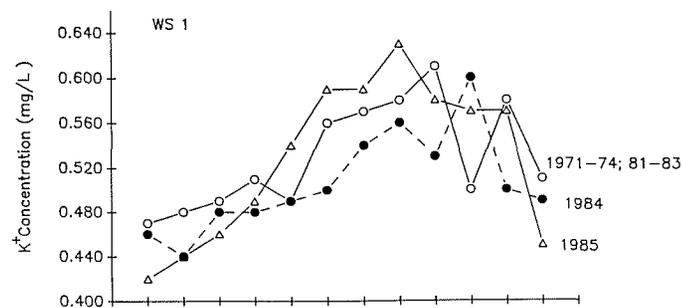


Figure 5. Mean monthly concentrations of  $\text{K}^+$  in streams draining white pine-covered watersheds at Coweeta for baseline years compared to monthly concentrations during 1984 and 1985. White pine on WS 17 was  $\text{O}_3$  symptomatic in 1984 while pine on WS 1 was asymptomatic.

### 4.3 Disease and insect responses

Several studies have indicated that oxidant air pollution may predispose pines to biotic stresses such as insects and root diseases (James et al. 1980; Lackner and Alexander, 1983; Miller, 1983). Two studies initiated on WS 17 in 1985 to assess increased susceptibility of tree root pathogens and to bark beetle attacks.

A root disease survey was conducted in the white pine plantation WS 1 ( $O_3$  asymptomatic) and WS 17 ( $O_3$  symptomatic) in late fall 1985. Soil-root samples were taken from 10 plots systematically distributed throughout each watershed and roots were clinically examined for disease symptoms (Leininger et al., 1990). No root pathogens were found on segments taken from WS 17 and less than 1% of all root segments sampled on WS 1 contained the only true root pathogen recovered, *Heterobasium annosum* (Fr.) Bref. Thus, it is unlikely that root disease and  $O_3$  interacted pathogenically on WS 17.

Predisposition of  $O_3$ -damaged white pine to bark beetle attacks was studied on WS 17 (Berisford, 1987). A technique for inducing bark beetle attacks by simulated lightning strikes was applied to eight codominant white pines with evidence of severe  $O_3$  damage and eight trees of similar size with no apparent damage. The response of *Ips* spp. beetles to treated trees and adjacent untreated trees within 15 m of treated trees was monitored for 9 weeks. Treated trees were immediately attacked by *Ips* spp. beetles including *I. gradicollis* (Eichnoff), *I. pini* (Say), and relatively small numbers of *I. avulsus* (Eichnoff). Statistical analysis showed no significant differences in timing of initial attacks, attack density, attack sequence, or species of *Ips* relative to  $O_3$  damage. Furthermore, there were no attacks on adjacent trees which were stressed by the simulated lightning treatment. Findings indicate that the stress at the level which occurred on WS 17 was insufficient to predispose trees to *Ips* beetle attacks. Subsequent observations of the plantation during the severe drought period of 1986 to 1988 showed epidemic populations of southern pine beetle (*Dendroctonus frontalis* Zimmerman) caused widespread mortality of pitch pine (*Pinus rigida* Mill.) revealed no attacks of this beetle in the white pine population.

## 5. Conclusions

Ozone damage to white pine on WS 17 was clearly visible in the growing season of 1984. Reductions in BAI of dominant and codominant trees were attributed to the combined effects of reduced photosynthesis and senescence and loss of foliage due to  $O_3$  stress. However, there were no obvious carryover effects of  $O_3$  on growth in 1985. Growth response of all tree sizes in the population are under study but impacts are currently unknown. There were no observable effects on nutrient concentrations of stemwood or needlefall, but net nutrient accumulation was reduced due to reductions in wood increment. Evidence for altered ecosystem biogeochemical cycles induced by  $O_3$  damage was found in small elevated  $NO_3^-$ -N and  $K^+$  concentrations in stream water. However, the magnitude of nutrient releases were of little consequence to water quality. Ozone stress did not predispose trees to root pathogens or bark beetle attack.

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The O<sub>3</sub> events and related white pine damage in 1984 represented ac conditions. Ozone injury was followed in 1986 through 1988 with the m severe drought observed in the region in this century. During 19 precipitation substantially exceeded average values. We have documen large growth reductions and changes in stream chemistry associated w drought conditions; although this ecosystem was severely stressed consecutive years by O<sub>3</sub> and drought, stemwood increment and str nutrient have returned to prestress levels during 1989. It appears t impacts of episodic O<sub>3</sub> stress in a relatively vigorous forest ecosyst as represented by the white pine forest on WS 17, are short-lived, that processes of growth and biogeochemical cycles are highly resili to stress. The same observation may or may not apply when O<sub>3</sub> exposure chronic and there are few visible damage symptoms.

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