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Plant responses to elevational gradients of O_3 exposures in Virginia

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ABSTRACT In Shenandoah National Park, O_3 monitoring data were characterized and attempts were made to relate O_3 concentration levels to visible foliar injury observed for five plant species surveyed. Foliar injury for three species increased with elevation. The 24-h monthly mean O_3 concentrations tended to increase with elevation; however, the number of elevated hourly occurrences did not. Although the frequency of high hourly O_3 concentrations did not consistently increase with elevation, O_3 exposures in the park may have been high enough to provoke an effect that may have been enhanced by vegetation sensitivities that differed as a function of altitude.

Ozone (O_3) is a gaseous air pollutant that occurs at ground level in almost all areas of the United States and can be phytotoxic where primary pollutants are emitted and meteorological and topographic conditions result in advection of polluted air (1). O_3 injury to vegetation was first reported about 40 years ago (2–5) and is now found throughout much of North America. Experiments with O_3 show visible O_3 injury symptoms including necrosis, chlorosis, and stipple (6, 7). In addition, studies demonstrate that ambient O_3 can cause reductions in the growth and productivity of crops and forest species (8–11). Because O_3 exposures may be high in some rural forested areas, O_3 may play a role in modifying the condition of high-elevation forests (12).

The influence of meteorology and topography should be considered when evaluating the geographic extent and severity of O_3 impact. The diurnal pattern of O_3 buildup during daylight hours and subsequent decay at night are often observed at sites where other local air pollutants are present (13). However, monitoring data at some high-elevation sites, such as the southern Appalachian Mountains in North Carolina (14) and parts of New York State (15), show that O_3 can persist at night. In addition, O_3 may increase in concentration with elevation (13, 16).

In this study, we characterized O_3 and sulfur dioxide (SO_2) concentrations at sites in Virginia that differ in elevation. The objectives were to (*i*) relate O_3 exposure patterns to elevation, (*ii*) determine whether vegetation grown at high-elevation sites was more affected by O_3 exposures than vegetation grown at lower sites, and (*iii*) explore the potential for nighttime O_3 to cause visible foliar injury. A unique feature of this study is its regional scope; the study area encompassed ≈24,000 km^2 (80 km × 300 km).

Air Pollution Exposure Patterns

O_3 concentrations were monitored at three stations in western Virginia from May through December 1982 and a fourth monitoring station was added in July. All stations were located in rural, forested areas (Fig. 1) at different elevations far from strong sources of air pollution. The sites were located near Blacksburg, VA (600 m elevation), Rocky Knob, VA (900 m), and Salt Pond Mountain, VA (950 m) and in SNP (1067 m). O_3 monitors were operated continuously. Except for the Rocky Knob (76%) and Blacksburg (78%) sites, the analyzers operated at least 80% of the study period.

Unlike the other three sites, a distinct change in diurnal values was observed at the lower-elevation, Blacksburg site. The monthly mean O_3 concentrations in the morning (0600 h) were always lower than those measured in the late afternoon (1500 h) (Fig. 2). The monthly mean O_3 concentrations measured at each site, calculated from 24 hourly mean values recorded for each day, showed a tendency for an increase with elevation for the May–December 1982 monitoring period (Fig. 3 *Upper*).

SO_2 exposures can potentially affect plants and, therefore, the data were reviewed. SO_2 hourly mean monitoring data collected at the same sites showed few occurrences ≥0.05 ppm, with the maximum hourly mean SO_2 concentration observed in October (0.065 ppm). Because of the infrequent elevated SO_2 hourly concentrations, the cooccurrence of elevated levels of O_3 and SO_2 houly mean concentrations was minimal and, therefore, in this study, O_3 was considered the major pollutant of concern.

The Big Meadows O_3 site in SNP was the only monitoring site located within the vegetation survey areas. In 1982, this site experienced 292 hourly mean O_3 concentrations ≥0.08 ppm from May through October (i.e., 8% of the hourly concentrations monitored were ≥0.08 ppm) and 39 hourly concentrations ≥0.10 ppm. In 1983, O_3 was monitored at three sites that differed in elevation in the SNP. The sites were located at Sawmill Run (457 m), Dickey Ridge (640 m), and Big Meadows (1067 m). Over the sampling period, all of the sites experienced better than an 80% data capture rate.

O_3 levels in 1983 at the Big Meadows site were similar to those monitored in 1982, with monthly means of 24-h concentrations ranging from 0.03 ppm to 0.06 ppm (Fig. 3 *Lower*). During 1983, with few exceptions, the high-elevation site, Big Meadows, had a higher monthly O_3 concentration than the other two sites at lower elevation. Although the high-elevation site also had the highest 24-h monthly O_3 concentrations, the low-elevation site (Sawmill Run) had the greatest number of exceedances at or above 0.10 ppm. We carefully evaluated the data capture rates for each of the sites and found that this same pattern was observed in 1984 and 1985, independent of data capture. Unlike the higher-elevation sites, a distinct change in diurnal values was observed at Sawmill Run.

The high-elevation site at Big Meadows had a smaller number of concentrations at or below the minimum detectable level than did the low-elevation site at Sawmill Run. The smaller number of hourly average concentrations that occurred at or below the minimum detectable level at Big

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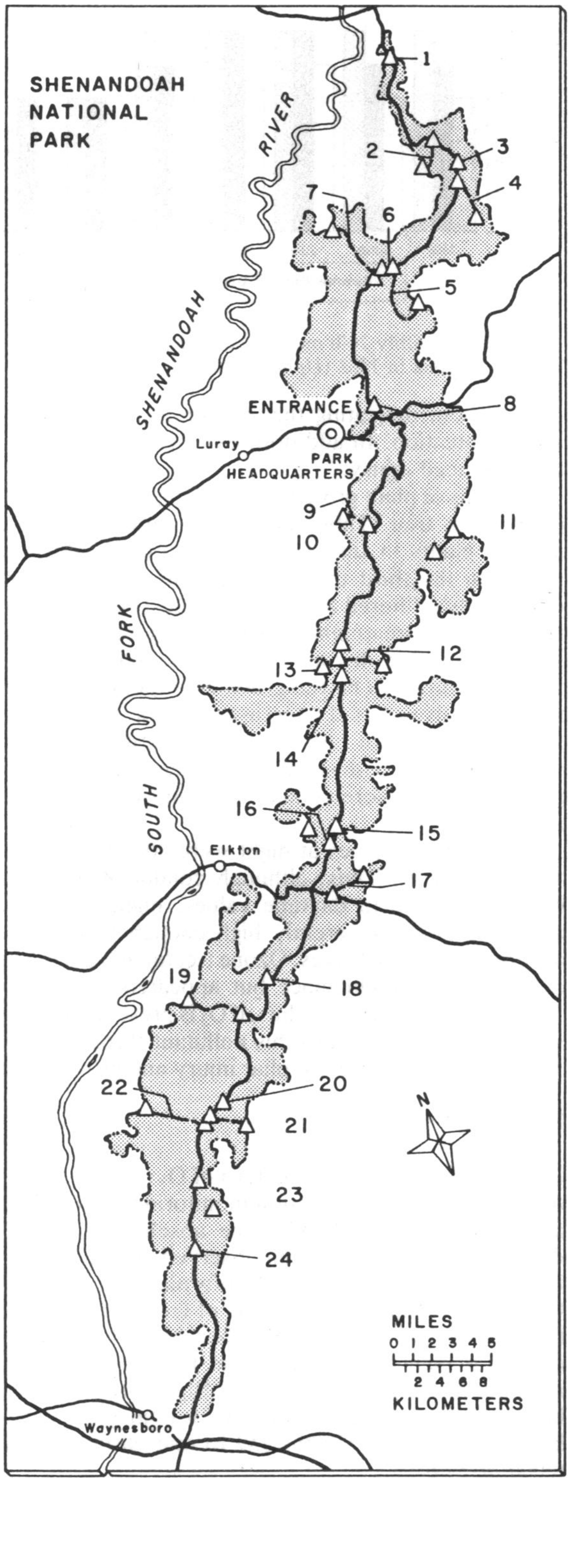
Abbreviation: SNP, Shenandoah National Park.

Meadows resulted in high 24-h averages. The higher 24-h average O_3 concentration was associated more with a lack of hourly mean concentrations at or near the minimum detectable level than with a large number of elevated concentrations.

Regional Assessment of Visible Foliar O_3 Injury

A survey was made in 1982 to determine the geographic extent of visible foliar O_3 injury in SNP and to investigate the possible relationship between injury and elevational trends in O_3 exposures. The survey involved inspecting 7–10 individual plants of 5 native plant species at 24 sites in SNP (Fig. 1 *Left*). The survey for visible O_3 injury was made from September 9 to September 18, 1982. A mean injury value for each non-tree species was calculated by counting injured and uninjured leaves on plants and the percentage of injured surface on each leaf. Visible injury for trees was calculated from 10 leaves collected with a pole pruner. The 24 survey sites were located throughout SNP. The surveyed species included tulip poplar (*Liriodendron tulipifera*), wild grape (*Vitis* sp.), black locust (*Robinia pseudoacacia*), virgin's bower (*Clematis virginiana*), and milkweed (*Asclepias* sp.). These species are commonly found throughout SNP and have recognizable O_3 injury symptoms.

Although the extent of injury varied from site to site, no trends were apparent along either SNP's north–south axis or its east–west axis. Injury data for each species at each site were plotted against elevation, which showed that visible O_3 injury increased with elevation for three of the five surveyed species (*C. virginiana*, *R. pseudoacacia*, and *V.* sp.) (Fig. 4). Correlations between elevation and injury for these species are significant ($P < 0.1\%$) and regression slopes differ from 0 ($P < 0.1\%$).



Effects of Nighttime O_3 Exposures on Plants

To assess the potential for nighttime O_3 to injure foliage, turnip plants [*Brassica rapa (L.)* cv. "Shogun"] were raised in open top chambers and exposed to combinations of daytime and nighttime O_3 exposure. These plants were chosen because previous studies showed they were sensitive to O_3. Three turnip crops were raised at the Salt Pond site during the summer of 1984. Each of the crops was grown for about 45 days beginning in either June, July, or September. There were replicates of five treatments: open plots with ambient O_3 during the day and night, as well as chambers with continuously filtered ambient air, continuously unfiltered ambient air, filtered air during the day and unfiltered air at night, and unfiltered air during the day and filtered air at night. Switching between filtered and unfiltered air was achieved by equipping some chambers with both filtered and unfiltered blowers controlled with a time clock. "Nighttime" was defined as a 10-h period from 2100 through 0700. Hourly mean ambient O_3 levels in the chambers ranged from 0.05 to 0.10 ppm and were reduced to 0.025 ppm or less during filtration.

Fourteen 4-liter pots were evenly spaced in each chamber and sunk in holes so that their tops were at ground level. Seeds were planted and, after 45 days, plants were scored for visible O_3 injury and harvested for growth analysis. A portable gas-exchange system (Li-COR model 1600) was used to

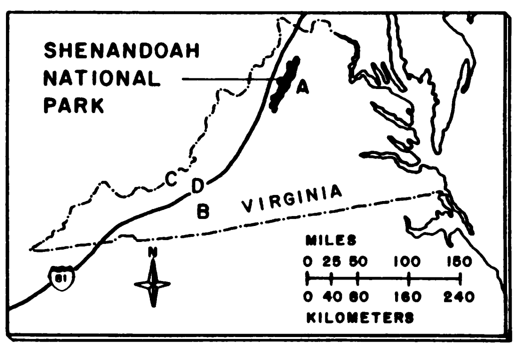


FIG. 1. (*Above*) Map of Virginia showing the boundaries of Shenandoah National Park (SNP) (shaded area) and the 1982 O_3 monitoring stations (A = Big Meadows, SNP; B = Rocky Knob; C = Salt Pond; and D = Blacksburg). (*Left*) Detailed map of SNP showing the numbered plots (1–24) where vegetation was surveyed for visible foliar O_3 injury and locations of 1983 O_3 monitoring stations.

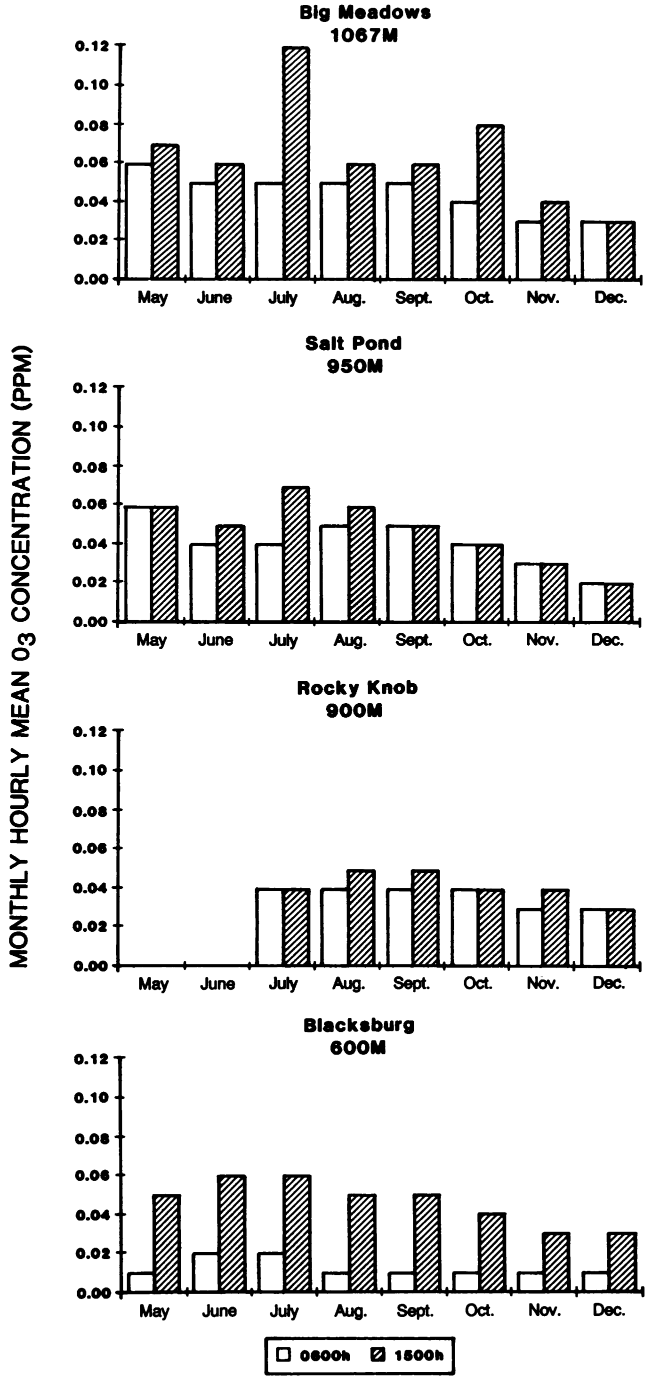


FIG. 2. Monthly hourly mean O_3 concentrations at 0600 h and 1500 h at four sites in rural Virginia.

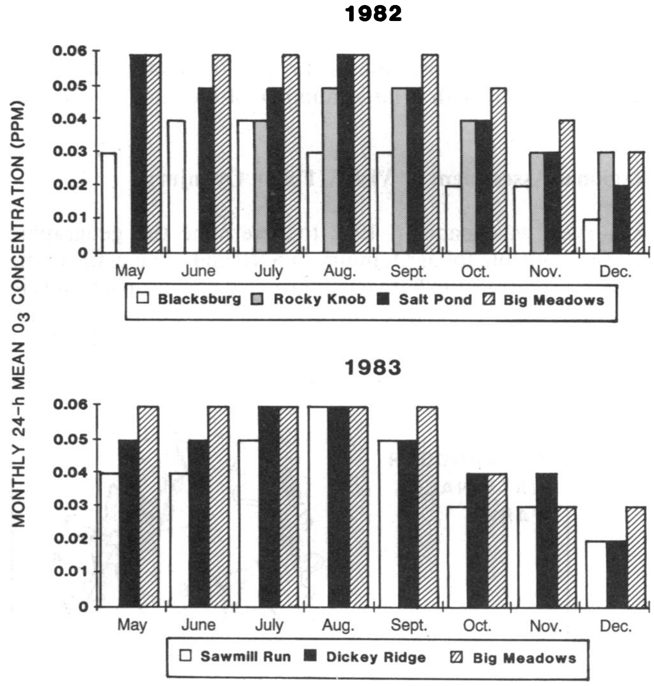


FIG. 3. Monthly 24-h mean O_3 concentrations measured at sites in rural Virginia in 1982 (*Upper*) and 1983 (*Lower*).

measure stomatal conductance of fully expanded leaves of 30-day-old plants during the last trial. Measurements were made during both the day and the night.

Turnips in either open plots or continuously unfiltered chambers had the greatest foliar injury during all three trials (Table 1). However, injury was greatest during the June to mid-July trial and decreased with each subsequent crop. Decreased injury may have reflected reduced O_3 concentrations that occurred during successive experiments. Plants raised in continuously filtered air had little or no injury. Plants receiving filtration during part of each 24-h period were protected to some extent, showing less injury than those continuously exposed to ambient O_3. Plants raised with nighttime filtration were less injured than plants raised with no filtration, indicating that filtration in the dark provided some protection. In addition, exposing plants to O_3 only at night induced injury.

Analysis of plant growth showed important O_3 effects only in the first trial (Table 1); severe water stress may have stunted plants in the second trial, and O_3 stress was not severe in the third trial. In the first trial, plants raised in continuously filtered air had the largest root (hypocotyl and root). All O_3 treatments, including those restricting exposures only to the day or to the night, reduced root growth, which is known to be the growth component most sensitive to O_3. O_3 also caused decreases in root/shoot ratios. Such shifts in root/shoot ratios from O_3 treatments may be detrimental as plants with small root systems and enhanced shoot growth become more vulnerable to subsequent stresses such as drought.

Conductance values at night were 20–30% of the daytime value (Table 2). Thus, although conductance at night was reduced relative to daytime values, nighttime values were appreciable and apparently high enough to allow some O_3 absorption into the leaves. Ozone treatments did not appear to alter daytime conductance but appeared to cause reduced values at night (Table 2). Thus, if O_3 is present during the night, some species can absorb this pollutant through the stomata, which may result in both foliar injury and growth reductions.

Discussion

In our analysis, a diurnal pattern of O_3 (17, 18) was observed only at the two low-elevation monitoring sites at Blacksburg and Sawmill Run in SNP. The absence or dampening of diurnal O_3 patterns has been observed at high-elevation sites in New York (15, 19, 20), California, (12, 21), and North Carolina (14), and in some parts of Germany (20). At Whiteface Mountain and several other high-elevation sites, O_3 occurs at high concentrations in the late evening or early morning hours (13). In 1982, at Big Meadows, 56% of the hourly mean concentrations $\geq$0.10 ppm were between the late evening hours (1900–2359 h) and early morning hours (0000–0959 h).

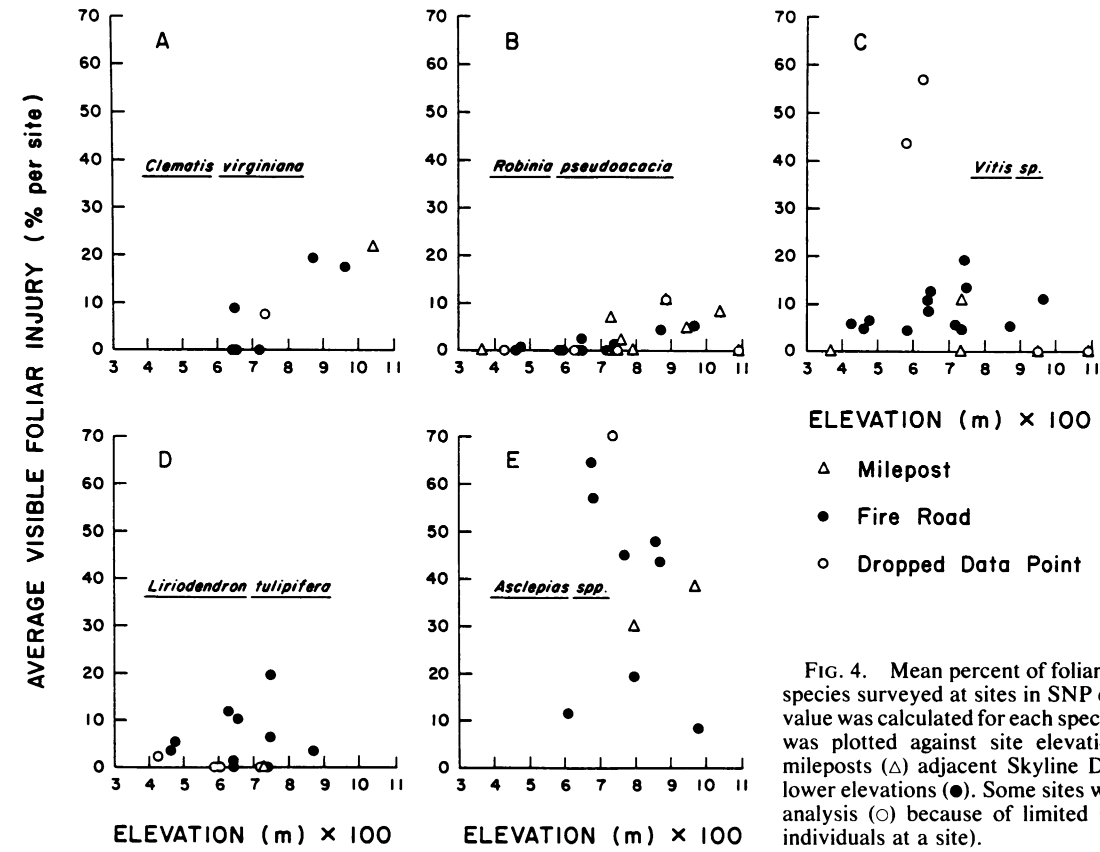


FIG. 4. Mean percent of foliar O_3 injury observed for five species surveyed at sites in SNP during 1982. A single injury value was calculated for each species at each site and the value was plotted against site elevation. Sites were located at mileposts (△) adjacent Skyline Drive or along fire roads at lower elevations (●). Some sites were omitted from statistical analysis (○) because of limited sample size (two or fewer individuals at a site).

In our study, we used the 24-h monthly mean and the number of hourly O_3 concentrations greater than or equal to several concentration thresholds to characterize O_3 exposures. We found that the 24-h monthly mean O_3 concentration values measured in 1982 and 1983 in the southern Appalachians tended to increase with elevation; however, the number of elevated O_3 occurrences observed in 1983 did not necessarily increase with altitude. Thus, we found no simple relationship between elevation and the frequency of high O_3 exposures.

For *C. virginiana*, *R. pseudoacacia*, and *V.* sp., foliar injury increased with elevation. However, many reasons may

Table 1. Visible foliar injury score and growth analysis of turnips raised in three trials during the summer of 1984

Treatment	Injury score	Dry weight, g: Root	Shoot	Whole plant	Root/shoot
Trial 1					
Open	1.9	4.8874[ab]	9.4450[b]	14.5981[bc]	0.6115[ab]
FF	0.1	5.1836[a]	6.6093[a]	11.7929[ac]	0.9079[a]
FN	0.9	3.7742[b]	11.4875[b]	15.6300[b]	0.3583[b]
NF	0.6	3.9371[ab]	11.8564[b]	17.4021[b]	0.2936[b]
NN	3.7	4.2014[ab]	9.0607[ab]	10.4993[a]	0.8164[a]
Trial 2					
Open	1.3	0.5967[ab]	4.0996[b]	4.6963[b]	0.1504[a]
FF	0	0.6354[ab]	7.1343[a]	7.7696[a]	0.1046[b]
FN	1.2	0.5204[a]	4.4389[b]	4.9593[b]	0.1064[bc]
NF	0.4	0.8452[b]	6.0233[ab]	6.8685[ab]	0.1444[ac]
NN	1.7	0.6654[ab]	5.5286[ab]	6.1939[ab]	0.1196[abc]
Trial 3					
Open	0.2	4.7068[a]	13.7671[a]	18.7306[a]	0.3456[a]
FF	0.2	4.2842[a]	13.1785[a]	17.6068[a]	0.3226[a]
FN	0.6	4.7781[a]	12.6315[a]	17.4173[a]	0.3723[a]
NF	0.4	5.1868[a]	14.7574[a]	19.9442[a]	0.3442[a]
NN	0.7	3.7432[a]	12.0917[a]	15.8432[a]	0.3068[a]

Exposures to ambient O_3 were in open top chambers where plants were in open plots (open), air filtered day and night (FF), air filtered during the day only (FN), air filtered during the night only (NF), and air never filtered (NN). Analysis of variance of weights shows significant treatment effects ($P < 0.05$) and treatment means are separated by Scheffe's tests. Means within a column followed by an identical superscript letter are not significantly different ($P < 0.05$). Injury scores were analyzed with the Krusco–Wallace test and showed significant ($P < 0.05$) treatment effects.

Table 2. Stomatal conductance for turnips raised in open top chambers at the Salt Pond site on October 14, 1984

Chamber	Treatment* (day/night)	Conductance,† $cm \cdot s^{-1}$	
		Day	Night
OP1	+/+	NA	0.11 ± 0.01
CH1	−/−	0.75 ± 0.03	0.20 ± 0.02
CH2	−/+	0.73 ± 0.04	0.15 ± 0.01
CH3	+/−	0.71 ± 0.04	0.19 ± 0.02
CH4	+/+	0.73 ± 0.02	0.12 ± 0.02

OP, open plot; CH, open top chamber; NA, no analysis.
*Treatments expressed as either unfiltered (+) or filtered (−) air during the day or night.
†Conductance calculated as the mean values for three leaves on five plants or 15 measurements per chamber.

account for the fact that *A.* sp. and *L. tulipifera* showed no relationship between elevation and injury. Differences in O_3 injury trends with elevation observed for the five study species may be related to other environmental factors. For example, temperature and humidity, which change with elevation, may influence the O_3 sensitivity of some plants but not others.

Elevation and microclimatic factors may influence O_3 concentrations within different portions of a survey plot, resulting in high and low O_3 exposures within a single sample plot. For example, the availability of air drainage channels and the extent of overstory foliage may affect O_3 concentrations near ground level where understory plants grow. These factors may account for imperfect correlation between visible foliar injury and elevation. Also, *L. tulipifera* and *A.* sp. may not have shown any trend in foliar injury with elevation because they were distributed over a narrower elevation range than the other three species.

Stomatal factors may also influence elevational gradients of O_3 injury. Since many of the high hourly mean O_3 concentrations at the high-elevation sites occurred in the late evening and early morning hours, species differences in susceptibility to nighttime O_3 exposures may be an important factor. Whether sensitivity to O_3 in the dark is a general phenomenon for plants remains to be determined. For example, plants that close stomata at night may not absorb nighttime O_3 and would not absorb more O_3 at high-elevation sites than at low-elevation sites.

Increased foliar O_3 injury to some species with increased elevation implies that plants growing at high elevations may receive greater O_3 doses than plants growing at lower elevations or that the sensitivity of plants to O_3 may change with elevation. Based on our analysis, ambient O_3 should be carefully studied as a factor in assessing the environmental effects of air pollution on high-elevation forests (22–24). Any analysis of forest response to air pollutants in mountainous regions should evaluate the role that naturally occurring stresses, O_3, and other pollutants, such as acidic fog, SO_2, NO_2, etc. play in affecting forest growth at differing altitudes.

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