Plant responses to elevational gradients of O₃ exposures in Virginia

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Communicated by Ellis B. Cowling, October 17, 1988

ABSTRACT In Shenandoah National Park, O₃ monitoring data were characterized and attempts were made to relate O₃ 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 O₃ concentrations tended to increase with elevation; however, the number of elevated hourly occurrences did not. Although the frequency of high hourly O₃ concentrations did not consistently increase with elevation, O₃ 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 (O₃) is a gaseous air pollutant that occurs at ground level in almost all areas of the United States and can be phytotoxic where primary polluters are emitted and meteorological and topographic conditions result in advection of polluted air (1). O₃ injury to vegetation was first reported about 40 years ago (2–5) and is now found throughout much of North America. Experiments with O₃ show visible O₃ injury symptoms including necrosis, chlorosis, and stipples (6, 7). In addition, studies demonstrate that ambient O₃ can cause reductions in the growth and productivity of crops and forest species (8–11). Because O₃ exposures may be high in some rural forested areas, O₃ 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 geophysical extent and severity of O₃ impact. The diurnal pattern of O₃ 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 O₃ can persist at night. In addition, O₃ may increase in concentration with elevation (13, 16).

In this study, we characterized O₃ and sulfur dioxide (SO₂) concentrations at sites in Virginia that differ in elevation. The objectives were to (i) relate O₃ exposure patterns to elevation, (ii) determine whether vegetation grown at high-elevation sites was more affected by O₃ exposures than vegetation grown at lower sites, and (iii) explore the potential for nighttime O₃ to cause visible foliar injury. A unique feature of this study is its regional scope; the study area encompassed ∼24,000 km² (80 km × 300 km).

Air Pollution Exposure Patterns

O₃ 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). O₃ 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 O₃ concentrations in the morning (0600 h) were always lower than those measured in the late afternoon (1500 h) (Fig. 2). The monthly mean O₃ 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).

SO₂ exposures can potentially affect plants and, therefore, the data were reviewed. SO₂ hourly mean monitoring data collected at the same sites showed few occurrences ≥0.05 ppm, with the maximum hourly mean SO₂ concentration observed in October (0.065 ppm). Because of the infrequent elevated SO₂ hourly concentrations, the cooccurrence of elevated levels of O₃ and SO₂ hourly mean concentrations was minimal and, therefore, in this study, O₃ was considered the major pollutant of concern.

The Big Meadows O₃ site in SNP was the only monitoring site located within the vegetation survey areas. In 1982, this site experienced 292 hourly mean O₃ concentrations ≥0.08 ppm from May through October (i.e., 8% of hourly concentrations monitored were ≥0.08 ppm) and 39 hourly concentrations ≥0.10 ppm. In 1983, O₃ 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.

O₃ 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 O₃ concentration than the other two sites at lower elevation. Although the high-elevation site also had the highest 24-h monthly O₃ 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

Abbreviation: SNP, Shenandoah National Park.
Meadows resulted in high 24-h averages. The higher 24-h average O₃ 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 O₃ Injury

A survey was made in 1982 to determine the geographic extent of visible foliar O₃ injury in SNP and to investigate the possible relationship between injury and elevational trends in O₃ exposures. The survey involved inspecting 7–10 individual plants of 5 native plant species at 24 sites in SNP (Fig. 1). The survey for visible O₃ 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 O₃ 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 O₃ 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 O₃ Exposures on Plants

To assess the potential for nighttime O₃ to injure foliage, turnip plants [Brassica rapa (L.) cv. "Shogun"] were raised in open top chambers and exposed to combinations of daytime and nighttime O₃ exposure. These plants were chosen because previous studies showed they were sensitive to O₃. 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 O₃ 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 O₃ 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 O₃ injury and harvested for growth analysis. A portable gas-exchange system (Li-COR model 1600) was used to...
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 O₃ 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 O₃. 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 O₃ only at night induced injury.

Analysis of plant growth showed important O₃ effects only in the first trial (Table 1); severe water stress may have stunted plants in the second trial, and O₃ 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 O₃ 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 O₃. O₃ also caused decreases in root/shoot ratios. Such shifts in root/shoot ratios from O₃ treatments may be detrimental to plants with small root systems and enhanced root 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 O₃ 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 O₃ 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 O₃ (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 O₃ 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, O₃ occurs at high concentrations in the late evening or early morning hours (15). In 1982, at Big Meadows, 56% of the hourly mean concentrations ≥0.10 ppm were between the late evening hours (1900–2359 h) and early morning hours (0000–0959 h).
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

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Injury score</th>
<th>Root</th>
<th>Shoot</th>
<th>Whole plant</th>
<th>Root/shoot</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trial 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open</td>
<td>1.9</td>
<td>4.8874\textsuperscript{ab}</td>
<td>9.4450\textsuperscript{b}</td>
<td>14.5981\textsuperscript{bc}</td>
<td>0.6115\textsuperscript{ab}</td>
</tr>
<tr>
<td>FF</td>
<td>0.1</td>
<td>5.1836\textsuperscript{a}</td>
<td>6.6093\textsuperscript{a}</td>
<td>11.7929\textsuperscript{ac}</td>
<td>0.9079\textsuperscript{a}</td>
</tr>
<tr>
<td>FN</td>
<td>0.9</td>
<td>3.7742\textsuperscript{b}</td>
<td>11.4875\textsuperscript{b}</td>
<td>15.6300\textsuperscript{b}</td>
<td>0.3583\textsuperscript{b}</td>
</tr>
<tr>
<td>NF</td>
<td>0.6</td>
<td>3.9371\textsuperscript{ab}</td>
<td>11.8564\textsuperscript{b}</td>
<td>17.4021\textsuperscript{b}</td>
<td>0.2936\textsuperscript{b}</td>
</tr>
<tr>
<td>NN</td>
<td>3.7</td>
<td>4.2014\textsuperscript{ab}</td>
<td>9.0607\textsuperscript{a}</td>
<td>10.4993\textsuperscript{a}</td>
<td>0.8164\textsuperscript{a}</td>
</tr>
<tr>
<td>Trial 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open</td>
<td>1.3</td>
<td>0.5967\textsuperscript{ab}</td>
<td>4.0996\textsuperscript{b}</td>
<td>4.6963\textsuperscript{b}</td>
<td>0.1504\textsuperscript{a}</td>
</tr>
<tr>
<td>FF</td>
<td>0.0</td>
<td>6.354\textsuperscript{b}</td>
<td>7.1343\textsuperscript{a}</td>
<td>7.7696\textsuperscript{a}</td>
<td>0.1046\textsuperscript{b}</td>
</tr>
<tr>
<td>FN</td>
<td>1.2</td>
<td>0.5204\textsuperscript{a}</td>
<td>4.4389\textsuperscript{b}</td>
<td>4.9593\textsuperscript{b}</td>
<td>0.1064\textsuperscript{b}</td>
</tr>
<tr>
<td>NF</td>
<td>0.4</td>
<td>0.8452\textsuperscript{b}</td>
<td>6.0233\textsuperscript{ab}</td>
<td>6.6868\textsuperscript{ab}</td>
<td>0.1444\textsuperscript{ac}</td>
</tr>
<tr>
<td>NN</td>
<td>1.7</td>
<td>0.6654\textsuperscript{ab}</td>
<td>5.5286\textsuperscript{ab}</td>
<td>6.193\textsuperscript{ab}</td>
<td>0.1196\textsuperscript{abc}</td>
</tr>
<tr>
<td>Trial 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open</td>
<td>0.2</td>
<td>4.7068\textsuperscript{a}</td>
<td>13.7671\textsuperscript{a}</td>
<td>18.7306\textsuperscript{a}</td>
<td>0.3456\textsuperscript{a}</td>
</tr>
<tr>
<td>FF</td>
<td>0.2</td>
<td>4.2842\textsuperscript{a}</td>
<td>13.1785\textsuperscript{a}</td>
<td>17.0668\textsuperscript{a}</td>
<td>0.3226\textsuperscript{a}</td>
</tr>
<tr>
<td>FN</td>
<td>0.6</td>
<td>4.7781\textsuperscript{a}</td>
<td>12.6315\textsuperscript{a}</td>
<td>17.4173\textsuperscript{a}</td>
<td>0.3723\textsuperscript{a}</td>
</tr>
<tr>
<td>NF</td>
<td>0.4</td>
<td>5.1868\textsuperscript{a}</td>
<td>14.7574\textsuperscript{a}</td>
<td>19.9442\textsuperscript{a}</td>
<td>0.3442\textsuperscript{a}</td>
</tr>
<tr>
<td>NN</td>
<td>0.7</td>
<td>3.7432\textsuperscript{a}</td>
<td>12.0917\textsuperscript{a}</td>
<td>15.8432\textsuperscript{a}</td>
<td>0.3068\textsuperscript{a}</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Chamber</th>
<th>Treatment* (day/night)</th>
<th>Conductance, † cm s⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>OP1</td>
<td>+/+</td>
<td>NA 0.11 ± 0.01</td>
</tr>
<tr>
<td>CH1</td>
<td>-/−</td>
<td>0.75 ± 0.03</td>
</tr>
<tr>
<td>CH2</td>
<td>−/+</td>
<td>0.73 ± 0.04</td>
</tr>
<tr>
<td>CH3</td>
<td>+/−</td>
<td>0.71 ± 0.04</td>
</tr>
<tr>
<td>CH4</td>
<td>+/+</td>
<td>0.73 ± 0.02</td>
</tr>
</tbody>
</table>

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 O₃ 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 O₃ sensitivity of some plants but not others.

Elevation and microclimatic factors may influence O₃ concentrations within different portions of a survey plot, resulting in high and low O₃ exposures within a single sample plot. For example, the availability of air drainage channels and the extent of overstory foliage may affect O₃ 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 O₃ injury. Since many of the high hourly mean O₃ concentrations at the high-elevation sites occurred in the late evening and early morning hours, species differences in susceptibility to nighttime O₃ exposures may be an important factor. Whether sensitivity to O₃ 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 O₃ and would not absorb more O₃ at high-elevation sites than at low-elevation sites.

Increased foliar O₃ injury to some species with increased elevation implies that plants growing at high elevations may receive greater O₃ doses than plants growing at lower elevations or that the sensitivity of plants to O₃ may change with elevation. Based on our analysis, ambient O₃ 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, O₃, and other pollutants, such as acidic fog, SO₂, NO₂, etc. play in affecting forest growth at differing altitudes.

We acknowledge the National Park Service for supporting part of this effort with funds to J. Skelly and B. Chevone (Virginia Polytechnic Institute and State University); K. Hinkelmann (Virginia Polytechnic Institute and State University) and P. Muir and B. McCune (Oregon State University) for helpful discussions concerning statistical approaches; the National Park Service for providing air quality data; and The Center for Data Systems and Analysis at Montana State University for characterizing the air quality data.


