VARIATION IN ENVIRONMENTAL GRADIENTS AND OZONE UPTAKE IN A DECIDUOUS FOREST CANOPY

1994

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ABSTRACT

From January to December 1994 meteorology and ozone (O_3) data were continuously collected at five elevations (0.5, 7.5, 12, 16, and 24 m above the ground) from the VMC research tower at the Proctor Maple Research Center (PMRC) in Underhill, VT. Examination of the O_3 data for 1994 revealed a similar pattern to that observed in 1992 and 1993. Ozone concentrations generally increase with height in the canopy, but the largest and only significant difference occurred between 0.5 m (just above the forest floor) and all other elevations with O_3 levels being lowest at 0.5 m. On average over the entire sampling season (mid May-mid November), O_3 concentrations were 23% lower at 0.5 than at 24 m, compared to 21% lower in 1993. This reduction in O_3 concentration just above the forest floor may result from inadequate mixing of air due to a boundary layer effect and lower air velocities at this level or the physical or chemical destruction of O_3. When number of hours of O_3 exposure at certain threshold concentrations during June, July, and August were tabulated for 1994, it was found that the number of hours of exposure at all concentrations were 20 to 100% lower in 1994 than in 1993. Examination of average seasonal diurnal patterns revealed that O_3 concentrations reach a daily low in early morning (around 7:00 AM) and maximums around midday to early afternoon. Stomatal conductance in sugar maple (*Acer saccharum* Marsh.) was found to generally increase with height in the canopy and decrease through the day. Leaf area index (LAI) was found not to vary in a linear pattern, but instead, was greatest near the top of the canopy (16 m) and at the bottom of the canopy (4 m) while intermediate strata had the lowest LAI values. Ozone uptake rates were estimated using the relationship: Ozone uptake = (stomatal conductance / 1.68) x ozone concentration x LAI. Rates of O_3 uptake by the forest canopy were found to be greatest near the top of the canopy and greater at noon than at 5 PM. Canopy structure and meteorological variables that influenced stomatal conductance appear to play key roles in controlling rates of O_3 uptake by the forest canopy.

INTRODUCTION

Collection of meteorological and ozone (O_3) data from five elevations on the VMC research tower located at the Proctor Maple Research Center (PMRC) in Underhill, VT continued throughout 1994. A continuous record of temperature, relative humidity, wind speed and direction, surface wetness, total solar irradiance, photosynthetically active radiation (PAR), ultraviolet-B (UV-B), and O_3 began in 1992 (1993 for UV-B) for both monitoring and research purposes.

These meteorological and O_3 data from different vertical heights throughout the canopy provide the basic information necessary to begin "scaling up" from the individual leaf to the whole-tree, stand/community, and even ecosystem levels. Micro-meteorological flux measurements often are not available and preclude effective scaling and model verification (Baldocchi and Harley, 1995). The spatial (horizontally and vertically through the canopy) and temporal distribution of pollutants such as O_3 would not be expected to be homogenous throughout the forest or even within any single stand. Current instrumentation and data collection on the forest research tower allowed us to begin looking at the vertical distribution of O_3 within a northern hardwood forest canopy.

Tropospheric O_3 is one of several pollutants of regional importance that is thought to be a stressor in forest canopies (Wang and Schaap, 1988; Smith, 1981). Trees act as an important filter for gases and aerosols because of their abundance and large surface areas for gaseous exchange. Although, the air in the interior of forest stands is generally less polluted than air over the surrounding open area due to this filtering action (GroB, 1993), few studies have measured pollutants at multiple locations in the canopy (Cavender and Allen, 1990; Lindberg and Lovett, 1985). The vertical distribution of pollutants in different forest communities is likely to vary widely.

The obvious pathway for gaseous pollutants such as O_3 to enter trees is through open stomata in the leaves. Uptake of O_3 or other gaseous pollutants through the stomata is regulated by stomatal conductance (Reich, 1987). Ozone in turn can impair stomatal function (Tjoelker, Volin, Oleksyn, and Reich, 1995; Reich, 1987) and affect the pattern of uptake into leaves and to leaf surfaces, ultimately influencing the distribution of O_3 concentrations in the canopy. Interactions with O_3 at the canopy-atmosphere interface have the potential to affect metabolism, reduce growth, and negatively impact the ability to respond to biotic and abiotic stresses (Tjoelker *et al.*, 1995; Chameides and Lodge, 1992; Chappelka and Chevone, 1992; Sasek and Richardson, 1989; Wang, Bormann, and Karnosky, 1986). Significant economic losses can result when a commercially important species such as sugar maple (*Acer saccharum* Marsh.) is affected. Tjoelker *et al.* (1995) found that when upper canopy branches of mature sugar maple were exposed to O_3 concentrations averaging 95 ppb for 6 hours per day throughout the growing season, that light-saturated rates of net photosynthesis were reduced by 56% while dark respiration was increased by 40%.

Objectives

The goal of this research is to improve our knowledge of variation in canopy-atmosphere interactions and begin scaling up from the individual leaf to the whole-tree and stand levels of forest structure. We are using a 22 m research tower, located in a mature hardwood stand, at the PMRC to collect basic meteorological and O_3 concentration data. At heights of 0.5, 7.5, 12, 16, and 24 m above the ground (from ground-level to above the canopy) we are:

1. monitoring ambient environmental conditions (meteorology and O_3) beneath, within, and above a northern hardwood forest canopy. Meteorological variables continuously measured and recorded as 15 minute means at all five heights include: temperature, relative humidity, wind speed and direction, and surface wetness. Variables continuously measured (recorded as 15 min means) above the canopy (22 m) include: total solar irradiance (400-1100 nm), PAR (400-700 nm), and UV-B (290-320 nm).

2. quantifying canopy structure and canopy-light relationships by measuring leaf area distribution (leaf area index, LAI) and PAR.

3. quantifying stomatal conductance of sugar maple leaves at different heights in the canopy in an effort to examine spatial and temporal variation in O_3 flux and begin scaling up to the stand level of forest structure.

4. testing the hypothesis that within-canopy O_3 concentration and O_3 uptake are a function of meteorology and canopy structure.

METHODS

Throughout 1994 meteorological variables including ambient temperature, relative humidity, wind speed and direction, and leaf surface wetness were continuously collected at five elevations alone a vertical gradient on the VMC research tower. Elevations sampled include: 0.5 m (just above the soil surface), 7.5 m (below the main canopy), 12 m (within the canopy), 16 m (top of the canopy), and 24 m (ambient). Ozone concentrations in parts per billion (ppb) at each of these five elevations were also recorded from 11 May to 9 November. Concentrations of O_3 were tabulated by hour-of-the-day (11 May-31 August) to look at the average seasonal diurnal pattern in concentration at all five heights. Total solar irradiance, PAR, and UV-B (starting on 25 July 1993) data were collected only at the 22 m level. All data were stored as 15 min averages by a Campbell Scientific 21X datalogger or directly to a computer. For further details about instrumentation, please see the 1992 VMC Annual Report.

Stomatal conductance measurements were made on several dates during mid July and August 1994, at 5 heights [4, 9, 11, 13, and 16 m (top of the canopy)], on two sugar maple trees accessible from the 22 m research tower at PMRC. Due to weather and equipment related interruptions in measurements, complete data sets for spatial and temporal analysis were obtained for only two days. A LI-COR 1600 steady state porometer was used to make one-sided stomatal conductance measurements (mmol H_2O $m^{-2} s^{-1}$). The instrument was calibrated for flow rate and relative humidity prior to each set of measurements. Measurements were stratified by leaf-age classes and position (sun or shade leaves) over the vertical distribution of the canopy over time.

Estimates of expected O_3 uptake into plant leaves through stomata were based on physiological models similar to those elucidated by Farquhar, Dubbe, and Raschke (1978) and Cowan (1977). Gas exchange rates were estimated using diffusion gradients based on negligible leaf-internal O_3 concentration (Wang, Hinckley, Cumming, and Braate, 1995; Laisk, Kull, and Moldau, 1989). The following relationship was used to estimate expected O_3 uptake.

Ozone uptake = (stomatal conductance / 1.68) x ozone concentration x LAI

The expected rates for O_3 uptake were estimated using stomatal conductance and O_3 concentration data from the top of the canopy (16 m) and total LAI. Expected rates were then compared to observed O_3 uptake calculated as the sum of uptake for the five individual canopy heights.

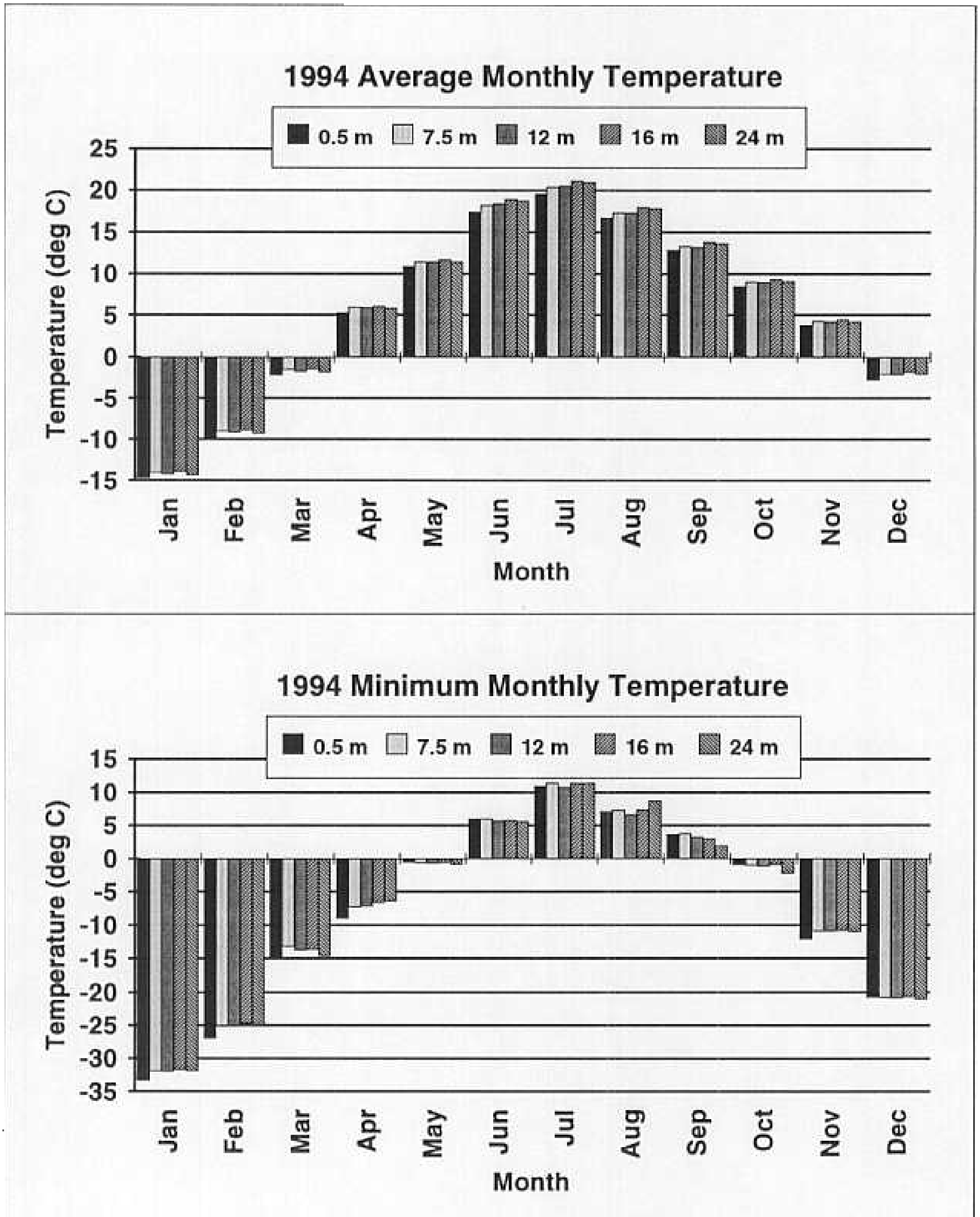
In August 1994 LAI was estimated from PAR attenuation data collected from the forest canopy research tower using a Sunfleck Ceptometer (Decagon Devices, Pullman, WA). Measurements were made at 4, 9,11, 13, and 16 m above the forest floor at the same heights that stomatal conductance data were collected. In addition to enhancing the long-term record of LAI at the forest tower, these data were used to estimate O_3 uptake by the forest canopy.

RESULTS AND DISCUSSION

Meteorology. Meteorological data were collected from January to December 1994 at all five elevations on the research tower. The data are summarized in monthly files as 15 minute, hourly, and daily averages and are available to VMC cooperators or other researchers in Microsoft Excel, Lotus 123, or ASCII formats. Figure 1 shows examples of some of the data summarized on a monthly basis to look at overall annual trends.

Ozone. Examination of O_3 concentrations during 1994 at all five elevations on the research tower revealed a similar spacial (vertically up through the canopy) pattern to 1992 and 1993. Ozone concentrations generally increased with height in the canopy and concentrations near the forest floor (0.5 m) were significantly lower than those at any other height during much of the sampling season (mid-May to mid-November; Fig. 2). Concentrations of O_3 at the upper four heights (7.5, 12, 16, and 24 m) were not significantly different. In 1993 O_3 concentrations at 24 m (top of the tower) were significantly higher than those at 12, 7.5 and 0.5 m, but were only significantly higher than those at 0.5 m in 1994. The largest difference among heights in O_3 concentration was recorded in early July and occurred between the extremes in height (0.5 vs 24 m) and exceeded 26 ppb, compared to a 30 ppb maximum difference in 1993. When averaged

Figure 1. Average and minimum monthly temperature and average and maximum monthly wind speed at five elevations (0.5, 7.5, 12, 16, 24 m above the ground) along a vertical gradient and maximum monthly photosynthetically active radiation (PAR; 22 m only) on the VMC Research Tower at the Proctor Maple Research Center in Underhill, VT.



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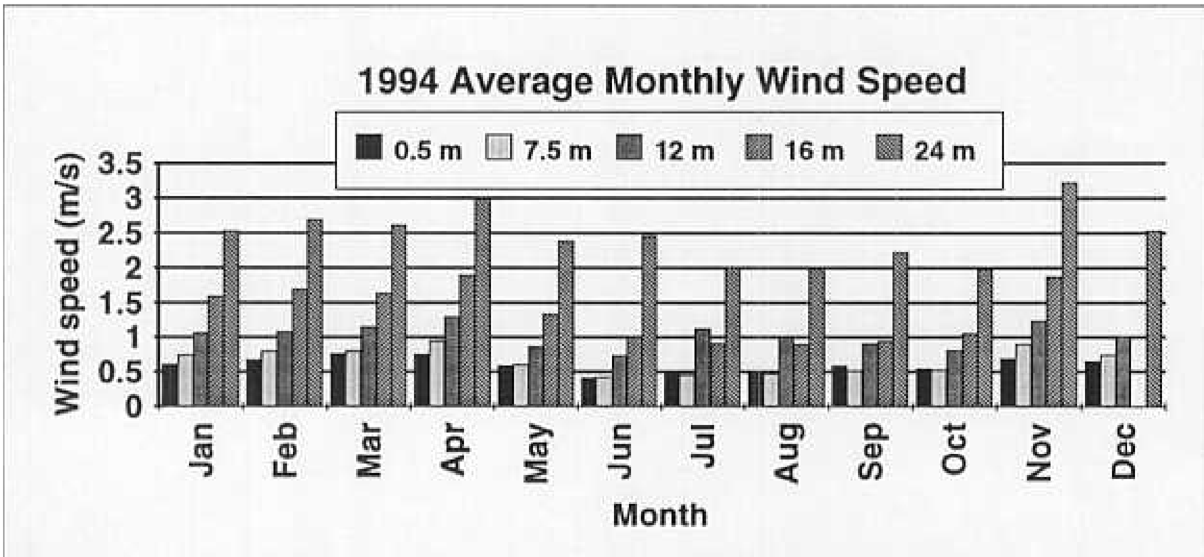
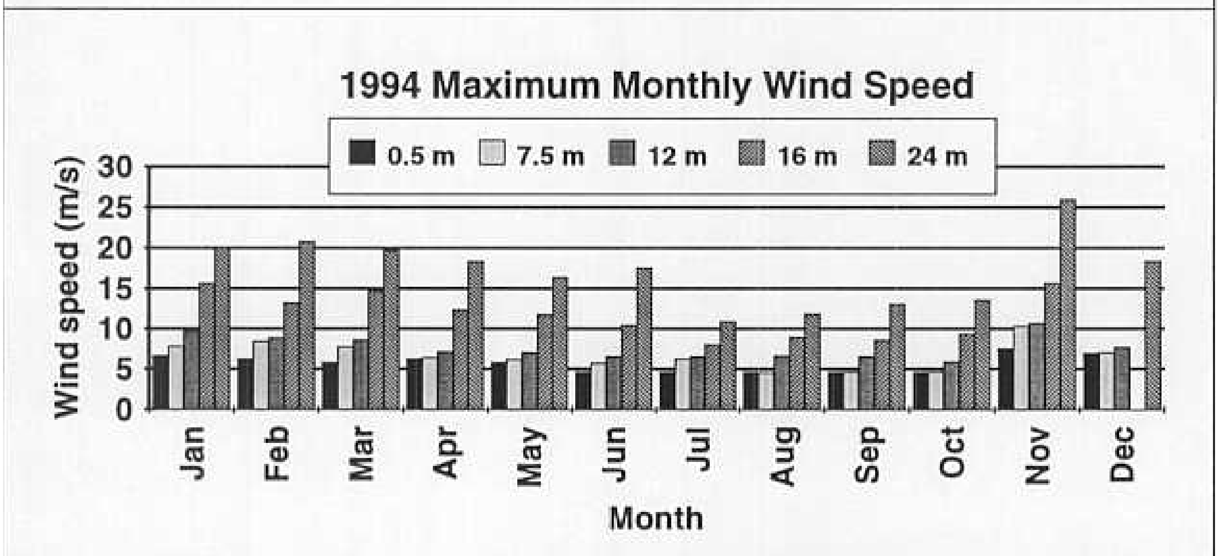




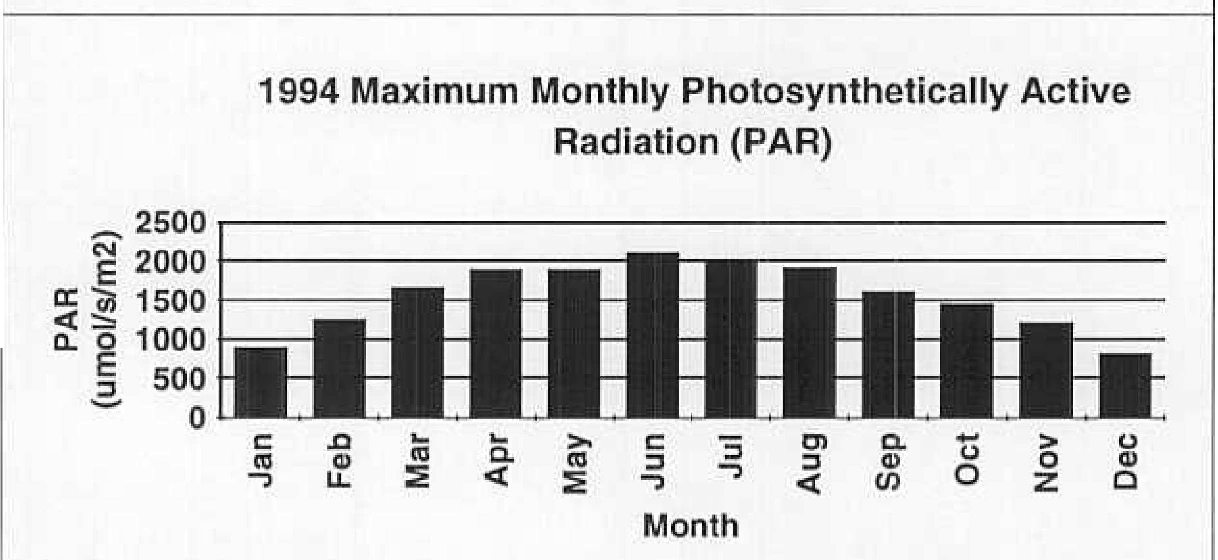
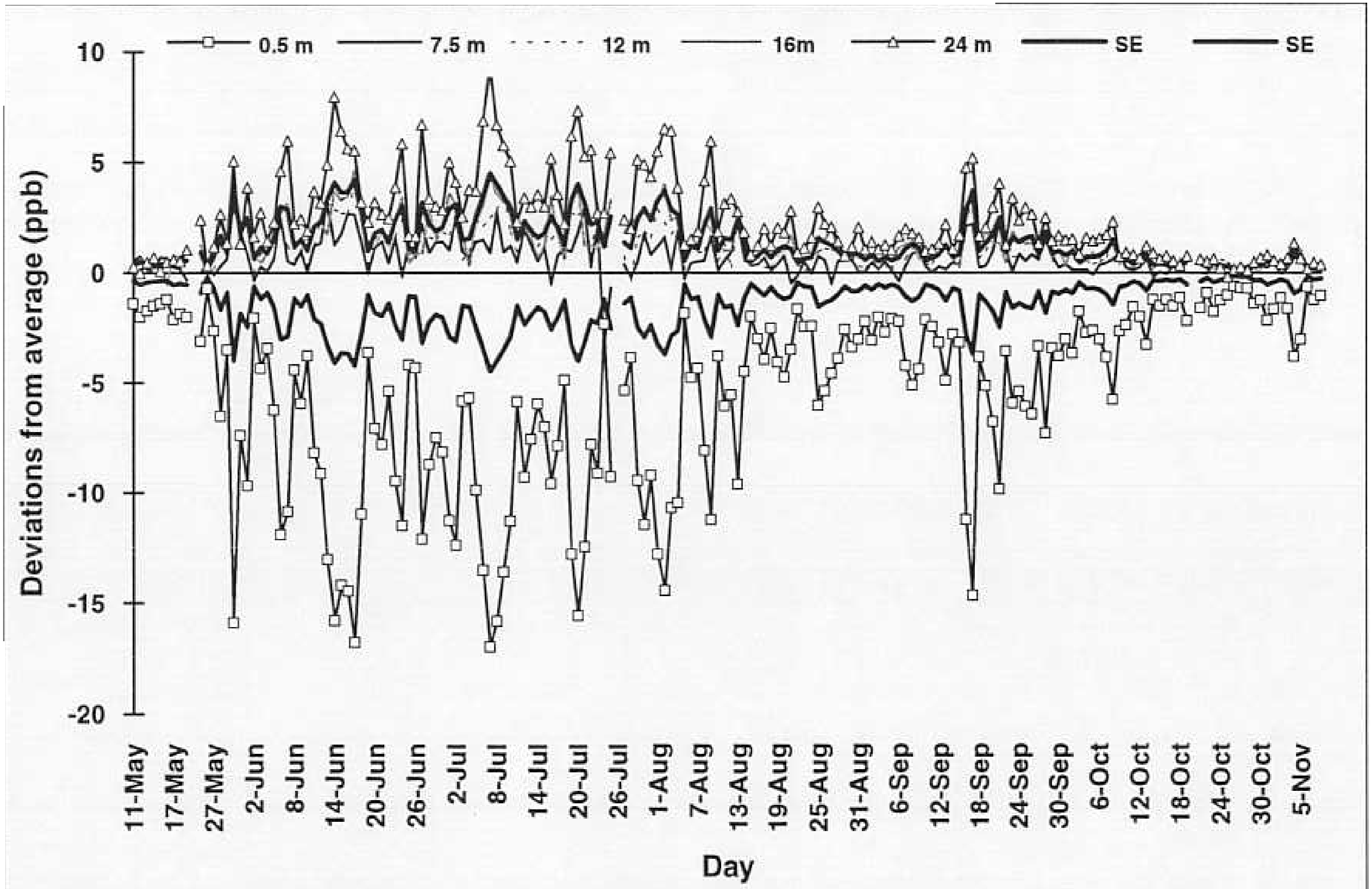


Figure 2. Variation in 7-hour-average (9 AM-4 PM) ozone concentration with height for 1994, measured at five elevations (0.5, 7.5, 12, 16, 24 m above the ground) along a vertical gradient on the VMC Research Tower at the Proctor Maple Research Center in Underhill, VT and expressed as deviations from average ozone concentration for all five heights.



Note: SE=standard error. The area inside the SE lines represents 2 SE's (+1 and -1 SE).

over the entire season, O_3 concentrations measured near the forest floor (0.5 m) were 23% lower than those recorded at the top of the tower, compared to 21% lower in 1993. When averaged over the entire season, O_3 concentrations were 10% lower in 1994 than 1993 and this reduction was consistent over all five sampling heights. As reported in 1993, O_3 concentrations have been previously shown to increase with elevation, but this phenomenon has usually been observed along elevational gradients on mountains where monitoring stations are separated by several hundred or even thousands of meters in elevation (Lefohn, 1992). We have speculated that lower concentrations of O_3 near the forest floor may be due either to a boundary layer effect caused by inadequate mixing of air near the soil surface during the growing season, the chemical destruction of O_3 in the presence of olefinic hydocarbons such as propylene and isoprene (Chameides & Lodge, 1992) or NO_x produced by soil micro-organisms, or the physical destruction of O_3 caused by O_3 coming in direct contact with leaf surfaces, bark, or soil.

In 1994 we also looked at the diurnal pattern of O_3 concentrations averaged over the season at all five heights (Fig. 3). Data from 11 May to 31 August 1994 were averaged by hour-of-the-day to arrive at an hour-by-hour seasonal summary of O_3 concentrations. These data were plotted and examined graphically to look at average diurnal patterns of O_3 concentrations at various height in the canopy. The trend of O_3 concentration generally increasing with height in the canopy was apparent. The diurnal pattern of O_3 concentrations was similar at all five elevations in the canopy with the most obvious difference being the lower magnitude of concentrations just above the forest floor (0.5 m). On average, O_3 concentrations near the forest floor were 9-12 ppb lower than at any other height in the canopy. Concentrations of O_3 at all heights reached a daily low at about 7:00 AM and then increase to peak concentrations between 1:00-3:00 PM with time to peak concentration also generally increasing with increasing height. That is, O_3 concentrations near the forest floor (0.5 m) reached peak daily concentrations at about 1:00 PM while concentrations at 24 m reach their maximum between 2:00-3:00 PM. Concentrations at all heights then decrease until about 4:00 PM when slight increases in concentrations at all levels were noted. By 9:00 PM, O_3 concentrations again begin to slowly decease during the night until they again reach their daily minimum at around 7:00 AM.

Total number of hours during June, July, and August that hourly average O_3 concentrations exceeded different thresholds were again examined in 1994 (Fig. 4). We found that the number of hours of exposure at concentrations between 60 to >100 ppb was down by 20 to 100% when compared to 1993. For example, at 60 ppb, a concentration which may cause injury to certain sensitive plants, we found that the forest floor was exposed for only 37 hours in 1994, compared to 77 hours in 1993. At the top of the forest canopy (24 m) the number of hours of exposure to concentration of 60 ppb or greater was down 20% from 1993. Only one hour of O_3 exposure at a concentration of 100 ppb or greater (at 7.5 m) was observed in 1994. This compares to at least 17 hours of exposure at this relatively high concentration at all levels of the canopy, except near the forest floor, in 1993.

Figure 3. Diurnal pattern of seasonal average ozone concentrations for the period of 11 May through 31 August, 1994 at five elevations (0.5, 7.5, 12, 16, and 24 m above the ground) along a vertical gradient on the VMC Research Tower at the Proctor Maple Research Center in Underhill, VT.

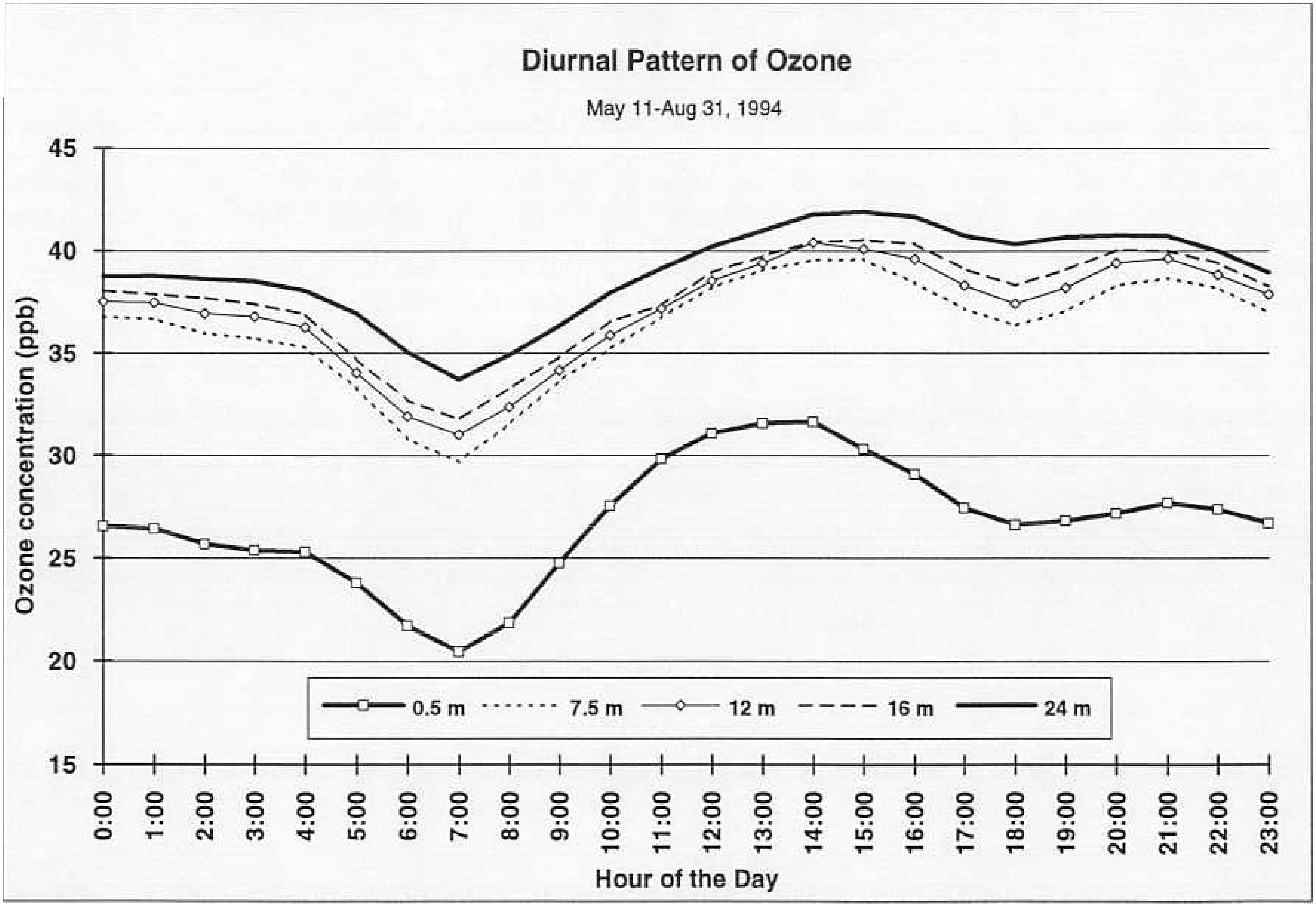
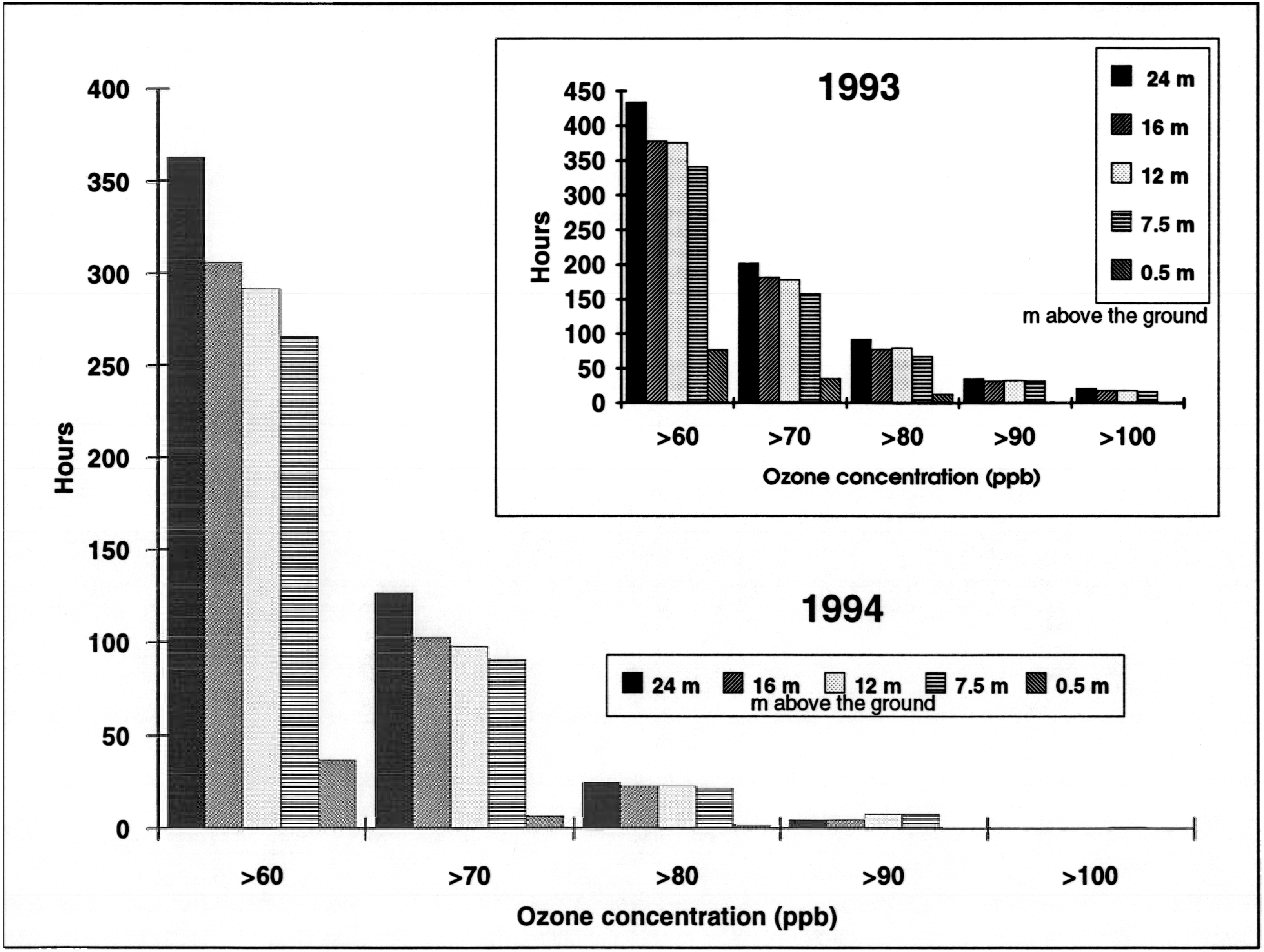


Figure 4. Number of hours during June, July, and August 1993 and 1994 that hourly ozone concentrations exceeded certain thresholds at five elevations (0.5, 7.5, 12, 16, and 24 m above the ground) along a vertical gradient on the VMC Research Tower at the Proctor Maple Research Center in Underhill, VT.



Stomatal conductance and leaf area index. On several dates in mid-July and August stomatal conductance measurements were made at five heights (4, 9, 11, 13, and 16 m) on leaves of sugar maple trees accessible from the forest research tower at PMRC. Stomatal conductance generally increased with height in the forest canopy and decreased through the day, with exceptions believed to be related to changing environmental gradients (Table 1). As a result on some occasions, on some sampling dates, the highest values were actually measured at the second highest level (13 m) rather than at the top of the canopy. Stomatal conductance is influenced by environmental factors such as available moisture, leaf temperature, relative humidity, and to a lesser degree, wind speed. Examination of meteorology data for 27 July and 11 August showed that relative humidity averaged 9% lower at the top of the canopy (16 m) than at the next lowest height (13 m). Leaf temperature presumably, was higher in direct sunlight (high radiation and slightly warmer air temperature) near the top of the canopy than lower down at the 13 m level. Low humidity and high leaf temperature both have a negative influence on stomatal conductance. Excessive temperatures may trigger a temporary partial closure of stomata during the middle of the day termed "midday closure" (Noggle and Fritz, 1983). This phenomenon helps prevent excessive water loss through the stomata and reduces the heat load on the leaf. These factors may help explain the reduction in conductance near the top of the canopy when compared to the next lowest height.

Table 1. Stomatal conductance and ozone measured in late July and early August 1994 and estimated LAI following full leaf-out in 1994 from five heights (4, 9, 11, 13, and 16 m) in a mature sugar maple stand at the Proctor Maple Research Center in Underhill, VT.

Height	Stomatal conductance		Ozone	LAI
	7/27/94 12 PM	8/11/94 5 PM		
(m)	(umol m^{-2} s^{-1})	(umol m^{-2} s^{-1})	(uliters)	
16	102	77	0.0344	.6
13	13	123	0.0333	0.5
11	78	93	0.0328	0.3
9	80	79	0.031	0.7
4	56	36	0.0302	1.2

Leaf area index (LAI) did not exhibit the same linear relationship as did stomatal conductance and ozone concentration. Instead, LAI was greatest near the top of the canopy (16 m) with an average value of 1.6, followed values of 1.2 and 0.7 at 4 and 9 m, respectively (Table 1). The intermediate heights of 11 and 13 m had the lowest LAI values. The thickness of the various canopy strata were not equal, so differences in LAI may be due either to differences in stratum thickness, foliage density, or leaf size.

Ozone uptake. In sugar maple, expected uptake of O_3 tended to be highest near the top of the canopy (14-16 m) and lowest at mid-canopy (11 m; Fig. 5). Because the upper canopy stratum did have greater leaf area (LAI) while actually having somewhat lower stomatal conductance on some sampling dates, when compared to the 13 m level, it appears that greater leaf area more than compensated for lower stomatal conductance and accounted for the higher O_3 uptake. When corrected for leaf area, lower canopy heights had similar rates of O_3 uptake to the upper canopy. Because neither stomatal conductance nor ambient O_3 concentrations were exceptionally low at mid-canopy on sampling days, lower leaf area (LAI=0.3) appears to explain the lower rates of uptake. This would indicate that canopy structure is an important factor in determining within-canopy O_3 concentrations. Ozone uptake was generally found to be similar to or lower at 5 PM than at noon (Fig. 5). This supports the theory that gas exchange generally reaches a maximum near midday and slows near the end of the day (Beadle et al., 1985; Iacobelli and McCaughey, 1993). The greatest differences between O_3 uptake at noon and at 5 PM were found in the highest (16 m) and lowest (4 m) canopy strata. Differences between midday and afternoon uptake rates were much smaller at the three intermediate heights. When averaged across all heights, expected values for O_3 uptake were found to be 13% higher than observed (Fig. 6). Differences in the way that expected and observed O_3 uptake rates were calculated may help explain this pattern. Expected O_3 uptake was estimated using stomatal conductance and ozone concentration data from the top of the canopy and total canopy LAI. Observed O_3 uptake rates were calculated as the sum of rates at individual canopy heights. Because conductance and O_3 concentrations were generally lower at lower heights in the canopy, expected uptake of O_3 was overestimated when based on upper canopy parameters.

CONCLUSIONS

In 1994 we began the process of scaling up from individual leaf measurements to the whole-canopy level. At the same time, we were able to begin testing the hypothesis that within-canopy O_3 concentration is a function of meteorology and canopy structure. The issue of scaling has become increasingly important with emphasis on an ecosystem approach to research and management and growing concerns about the impacts of global warming. Several recent studies have used rather complex gas-exchange models as tools for predicting flux and movement gases such as CO_2 and N and water vapor at the canopy level (Baldocchi and Harley, 1995; Leuning, Kelliher, DePury, and Schulze, 1995). The relationship (model) tested here, although relatively simple compared to others, did predict O_3 uptake quite well and differences between expected and observed uptake rates can be explained by within-canopy variation in leaf area and stomatal conductance and diurnal patterns in stomatal conductance. This would indicate that canopy structure and stomatal conductance are important determining factors in O_3 uptake. Stomatal conductance data

Figure 5. Estimated ozone uptake rates by a mature sugar maple canopy at 12 noon and 5 PM, in mid summer 1994, at five heights (4, 9, 11, 13, 16 m) along a vertical gradient on the VMC Research Tower at the Proctor Maple Research Center in Underhill, VT.

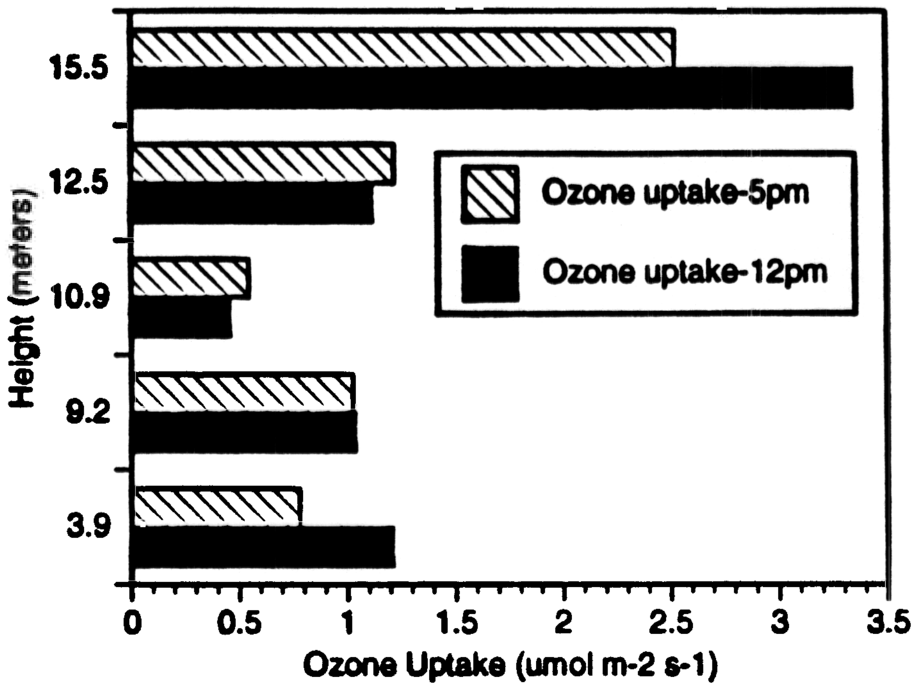
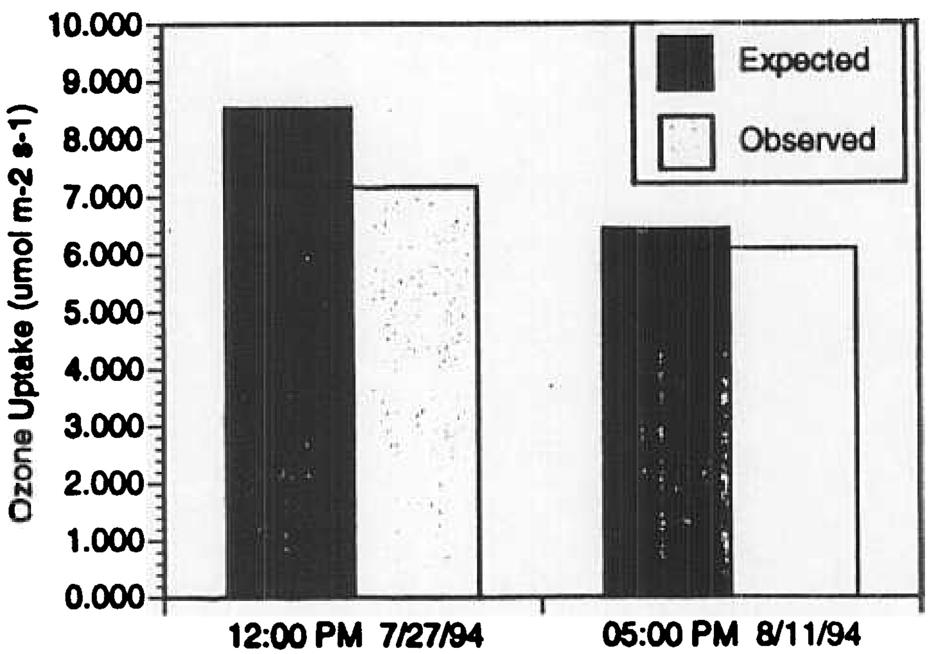


Figure 6. The average (averaged across height) difference between expected and observed ozone uptake at 12 noon and 5 PM, during mid summer 1994, in a mature sugar maple canopy at the Proctor Maple Research Center in Underhill, VT. Expected values were estimated using stomatal conductance and ozone concentration from the top of the canopy and total LAI. Observed values were calculated as the sum of ozone uptake at five canopy heights.



tends to show that meteorological variables such as relative humidity, air temperature, radiation, and leaf temperature influence stomatal conductance and affect O_3 uptake rates.

Although this was a relatively small experiment with limited data, several important points about O_3 uptake rates did emerge. Ozone is taken up at higher rates near the top of the canopy than at other heights. This portion of the canopy also had the greatest leaf area and relatively high, although not always the highest, rates of stomatal conductance. Despite relatively high leaf area at the lowest canopy level (4 m; LAI=1.2), stomatal conductance was lowest compared to all other heights and O_3 uptake rates were similar to mid-canopy heights (9 and 11 m) with the lowest leaf area and slightly higher rates of stomatal conductance. Ozone uptake was usually greater near midday and decreased toward the end of the day. This latter finding generally corresponds to the diurnal patterns for stomatal conductance and ozone availability. The smaller difference between expected and observed rates of O_3 uptake at 5 PM than at noon tends to indicate that biological and environmental gradients in the canopy are probably less in the afternoon than at midday.

On a seasonal basis, O_3 concentrations in 1994 were 10% lower than in 1993 and this reduction was consistent across all five sampling heights. This reduction was also reflected in hours of O_3 exposure at different concentrations during June, July, and August. Maximum hours of exposure at 100 and 90 ppb or greater were 1 and 8 hours, respectively in 1994 compared to 21 and 32 hours in 1993. Tjoelker *et al.* (1995) found that when upper canopy branches of mature sugar maple were exposed to O_3 concentrations averaging 95 ppb for 6 hours per day throughout the growing season, a significant reduction in light-saturated rates of net photosynthesis and increase in dark respiration occurred. While concentration of O_3 at PMRC rarely approach or exceed this experimental concentration and length of exposure (dose) are much lower than those imposed in this experiment, it is not known what if any effects, long-term exposure to lower O_3 concentrations (50-60 ppb) may have on sugar maple growth and health.

FUTURE PLANS

As in the past, this data will continue to be available upon request to VMC cooperators and other researchers. Collection of meteorology and O_3 data at the VMC research tower will continue through December 1995.

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