

saplings of the aforementioned tree species. Dominant trees were approximately 70 years old.

Porometer Sampling

One-sided, unit-area stomatal conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$) measurements were obtained with a LI-COR steady state porometer (model LI-1600) at five heights on a 22 m walk-up tower (Upright Inc.) located approximately 200 meters from the PMRC laboratory facility. The porometer also measured photosynthetic photon flux density (PPFD; $\mu\text{mol m}^{-2} \text{s}^{-1}$), leaf and cuvette temperature, and relative humidity at each leaf. The instrument was calibrated for flow rate and relative humidity prior to the field season. Silica gel desiccant was changed daily, thermocouples and aperture pads were changed weekly, a dry down procedure was performed after every sample day to check the efficacy of the RH sensor.

Two adult and three juvenile *Acer saccharum* trees were sampled to determine the vertical and diurnal variation in stomatal conductance. The adult trees were accessible from the tower and the three juvenile trees were located 4 m south of the tower. Foliage could be reached at five heights (1-3.9 m [near saplings]; 4-6.9 m [lowest branches]; 7-9.9 m [middle canopy]; 10-12.9 m [upper canopy]; and 13-16 m [top of canopy]). Each height consisted of a 3 m thick stratum within the canopy (Figure 6). All leaves on the mature trees were within 1 meter from the tower. Five to six leaves were sampled at each height during each time interval. Measurements were made within 10- 20 s after clamping the cuvette onto the leaf. Time intervals began at 8:00, 10:00, 12:00, 14:00, 16:00, and

18:00 (EST). Approximately 40 minutes were required to complete sampling at all 5 heights during a given interval. Randomly selected leaves were tagged with colored thread each day to ensure that leaves were not re-sampled. An attempt was made to sample leaves in a wide range of light environments and nodal positions. Stomatal conductance data were collected on 11 days in July and August 1998 (12, 14, 15, 18, 19, 21, 22 July and, 13, 14, 17, 19 August). All measurements were made in the field under moderate ambient air temperatures (between 20 °C and 30 °C).

Ozone Measurement

Ozone concentrations (ppb) were monitored throughout the growing season from early May until early November 1998 at five heights on the tower on 1 m extensions located at 0.5 m [forest floor], 7.5 m [lower canopy], 12 m [upper canopy], 17 m [top of canopy], and 24 m [above canopy]. Measurements were made every 3 minutes during the May-November period. Air samples were drawn through Teflon tubing to a TECO-49 ultraviolet photometric O₃ analyzer (Thermo Environmental Corporation, Franklin, MA, USA) located in a field laboratory at the bottom of the tower. Data were logged directly to a computer using an analog to digital converter (ADC-1, Remote Measurement Systems, Seattle, WA).

Modeling Ozone Uptake

Foliar ozone uptake was calculated as the product of stomatal conductance at each height and time interval and the mean hourly ozone concentration at the appropriate

height. Conductance to water vapor was adjusted to conductance to ozone by dividing g_s by 1.68, the diffusivity coefficient of ozone, which accounts for the differences in molecular weight between water and ozone (Wang *et al.* 1995). Ozone concentration in the substomatal cavity was assumed to be zero (Laisk *et al.* 1989). Ozone uptake was calculated both as an average rate per unit leaf area ($g_{\text{ozone}i}$: $\mu\text{mol m}^{-2} \text{h}^{-1}$) at each height and over the whole canopy (g_{ozone} : $\text{mmol ha}^{-1} \text{h}^{-1}$), and cumulative uptake of canopy layers was calculated by multiplying the average uptake at each height by the leaf area index (LAI) of that height ($g_{\text{ozone}i}(\text{LAI}_i)$: $\text{mmol ha}^{-1} \text{h}^{-1}$) using the equation: $g_{\text{ozone}} = \sum [g_{\text{ozone}i}(\text{LAI}_i)]$, where i signifies a specified canopy layer (Frederickson *et al.* 1995). For the purposes of calculating whole canopy ozone uptake and cumulative ozone uptake at each layer; the LAI of contiguous layers was identified (1-3.9 m, 4-6.9 m, 7-9.9 m, 10-12.9 m, 13-16 m).

Leaf Area Index (LAI)

LAI (projected leaf area per unit of ground area) was estimated indirectly for the whole canopy and at each height using a Ceptometer (Decagon Devices, Inc., Pullman, WA, USA) to measure photosynthetically-active radiation (PAR) on 4 clear, cloudless days when the canopy was in full leaf in July and August between 11:00 and 12:00 (EST). On all 4 days canopy-wide radiation transmittance to the forest floor was measured at 15 locations at the bottom of the canopy, and also at each of 4 heights within the canopy. These values were compared to 1996 data from an ambient station at Ranch Brook (on Mt. Mansfield, 400 m elevation) which measured PAR in full sun (Tallent-

Halsell 1994). Canopy transmittance could then be calculated as the ratio of PAR beneath the canopy and in the open. The data from Ranch Brook were corrected for the time zone, solar declination, and zenith of the sun specific to each measurement day and time. LAI of contiguous layers (1-3.9 m, 4-6.9 m, 7-9.9 m, 10-12.9 m, 13-16 m) of the canopy was identified to calculate uptake of ozone of each layer (Figure 6).

Meteorological Data

Meteorological data were collected from five heights on the tower by instruments mounted on short extensions at 0.5 m, 7.5 m, 12 m, 17 m, and 24 m (Figure 6). Relative humidity was measured with a Campbell Scientific sensor (model 207), temperature was measured with a Campbell Scientific probe (model 107), wind speed and direction were measured with a R.M. Young anemometer (model 05305). All data were collected by a Campbell Scientific (model 21X) data logger located in a trailer at the bottom of the tower. Fifteen-minute means were obtained for each environmental factor for June, July, and August. Solar irradiance was measured above the canopy at 24 m by a LI-COR pyranometer sensor (model LI-200SA). Hourly averages were obtained.

Soil Water Content

Gravimetric soil moisture was determined from samples obtained from a 10 × 10 m area located 5 m south of the tower. One sample was taken on each of the 11 complete days of conductance sampling from the top 20 cm with a soil auger. Wet samples were weighed to an accuracy of ±0.01 g, oven dried at 115° C for 4 days, and then re-weighed.

Data Analysis

Data were analyzed using the general linear models procedure and regression techniques of Statistical Analysis Systems (SAS, Inc., 1996, Cary, North Carolina, USA). To test for differences across heights and time for stomatal conductance, ozone concentration, ozone uptake, and meteorological data, a 3-way repeated measures ANOVA was used. It was assumed that compound symmetry was not a problem since the covariance for each observation would not have been constant due to efforts made to avoid re-sampling of leaves. The Student-Neuman-Kuels test was used to assess pairwise differences when main or interactive effects were significant. When interaction between height and time was observed the error term for height \times time \times date was used. When data did not meet the assumption of normality they were ranked and a non-parametric test was used to test for differences, and normality plots were examined for all variables. The level of significance is $p \leq 0.05$ for all reported statistical differences.

Results and Discussion

Stomatal Conductance (g_s)

Conductance decreased with increasing depth in the canopy for all time intervals (Figure 1). For all days, significant differences between canopy strata were found indicating that conductance is not homogenous across heights. Repeated measures analysis of variance indicated that interaction exists between the main effects of height and time, suggesting that patterns of conductance were dependent on time ($p=0.0001$, Table 1a).

Table 1. Sums of Squares and probabilities associated with g_s , O_3 , and uptake (per unit leaf area and cumulative) across heights and times (N=315).

Variable	Type III SS	F-Value	Pr > F
a. Stomatal Conductance (g_s)			
Height	299579	298.34	0.0001
Time	236508	121.50	0.0001
Height x Time	32987	10.5	0.0001
b. Ozone Concentration (O_3)			
Height	62356.3	58.65	0.0002
Time	16417.82	6.7	0.0001
Height x Time	79591.7	19.81	0.0001
c. Uptake per unit leaf area			
Height	303.2	35.54	0.0001
Time	172.2	30.99	0.0001
Height x Time	44.22	9.02	0.0001
d. Cumulative Uptake			
Height	4296.5	32.8	0.0001
Time	473.56	29.64	0.0001
Height x Time	655.58	655.6	0.0001

Table 2. Relationships between stomatal conductance (g_s) ($\text{mmol m}^{-2} \text{s}^{-1}$), ozone (O_3) (ppb), and ozone uptake (per unit leaf area [$\mu\text{mol m}^{-2} \text{h}^{-1}$]) and meteorological variables in a sugar maple canopy.

Independent Variable	(a) g_s	(b) Ozone	(c) Ozone Uptake
PPFD (Photosynthetic Photon Flux Density)	$r^2=0.482, p=0.0001$	$r^2=0.0033, p=0.001$	$r^2=0.384, p=0.0001$
Air Temperature	not significant	$r^2=0.412, p=0.0001$	$r^2=0.416, p=0.0001$
Wind Speed	$r^2=0.1, p=0.0001$	$r^2=0.101, p=0.0001$	$r^2=0.087, p=0.0001$

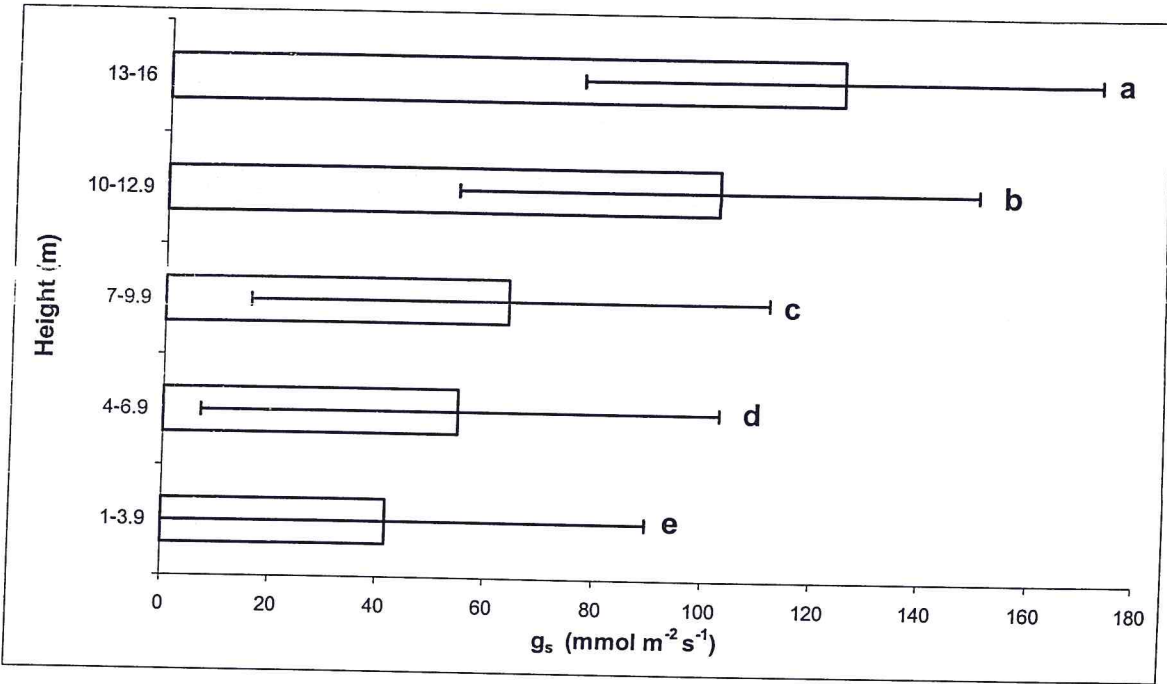


Figure 1. Average g_s (mmol m⁻² s⁻¹) for 11 days at 5 heights in a sugar maple canopy (N≈65 for each height), July-August 1998. Error bars represent one standard deviation, distinct letters identify significant differences in g_s between canopy layers.

Stomatal conductance was significantly higher in the upper canopy throughout the day. Differences in conductance between layers were at least in part due to differences between saplings and adults. The three trees sampled in the lowest canopy layer (1-3.9 m) were saplings. The mean g_s of the saplings was significantly lower than that of the 2 mature sugar maple trees sampled ($p=0.0003$). The g_s of the saplings was on average 55% lower when compared to the leaves in the other 4 strata. However, the average sapling g_s was only 25% lower than the mature trees when compared to leaves in strata exposed to similar light conditions (4-6.9 m). Samuelson (1994) found that g_s was 50% lower in understory red maple and black cherry saplings. Laurence *et al.* (1996) also found lower g_s in sugar maple saplings. Saplings have lower numbers of chloroplasts per cell, and hence show lower rates of photosynthesis and conductance (Larcher 1995).

Differences in stomatal conductance between heights were largely due to differences in light availability as found by Iacobelli and McCaughey (1993) in a birch and aspen canopy. Forty-eight percent of the variation in conductance was explained by photosynthetic photon flux density (PPFD) ($r^2=0.482$, $p=0.0001$, $N=315$, Table 2a). PPFD decreased with increasing depth in the canopy and showed a diurnal pattern with maxima during the 12:00-13:00 interval and minima after dark (Figure 2b). Stomata were assumed to close at night (Larcher 1995). The diurnal pattern of PPFD was more pronounced in the upper canopy, and interaction between height and time was found, suggesting that height differences were time dependent. The pattern of decreasing stomatal conductance with decreasing radiation has been observed in other canopy level studies. Iacobelli and McCaughey (1993) found lower g_s in the lower canopy of a birch

and aspen canopy because less sunlight penetrated to that level. Roberts *et al.* (1990) found decreasing conductance with decreasing height and radiation in an Amazonian rain forest, and Köstner *et al.* (1992) observed the same pattern in a *Nothofagus* canopy.

A clear diurnal pattern of g_s was also observed (Figure 2a). Conductance increased until reaching maxima of around $200 \text{ mmol m}^{-2} \text{ s}^{-1}$ during the 12:00-13:00 interval (EST), and then decreased steadily until reaching zero conductance between 18:00-19:00. The daily pattern of g_s was clearly associated with the daily course of PPFD.

Higher levels of sunlight indirectly regulate stomatal opening by driving photosynthesis, which depletes internal concentrations of CO_2 , thus causing stomata to open. Sunlight also directly stimulates stomata to open (Larcher 1995). On average, the upper canopy (10-16 m) was exposed to 94% higher PPFD than the lower canopy layers (1-9.9 m). Leverenz *et al.* (1982) found that the upper whorl of a sitka spruce canopy absorbed 80% of the total radiation.

Profiles of solar radiation in a canopy cause structural variation as well. Leaf phenology was not addressed in this study, but it is well documented that sugar maple is remarkable for its high degree of plasticity between sun and shade leaves (Larcher 1995). Ellsworth and Reich (1993) and Reich *et al.* (1990) found that leaves in the upper canopy of a sugar maple stand had higher leaf mass per area (LMA) because they developed in high light and as a result were thicker, had greater mesophyll density, and longer palisades cells. They attributed vertical differences in leaf gas exchange to variation in LMA. Sun leaves show faster rates of gas exchange due to their greater photosynthetic capacity. These structural differences account for vertical variation in stomatal

conductance. Harley *et al.* (1996) also found higher conductance in upper canopy leaves with higher specific leaf area and nitrogen content.

Another influential factor governing stomatal opening is water availability (Larcher 1995). Iacobelli and McCaughey (1993) attributed day to day differences in g_s to changes in soil water content. During the summer of 1998 it rained 580 mm, which is approximately half of the yearly average in this region of Vermont, and also the most summer precipitation on record since 1897. It is likely that due to the abundance of rainfall, no water deficit was experienced by the vegetation at the study site. No trends in soil water content were identified, and no relationship between g_s and soil water content was observed.

Beadle *et al.* (1985) observed afternoon decreases in g_s in response to increased vapor pressure gradient. In this study there was no evidence of afternoon stomatal closure, most likely reflecting the abundant water supply.

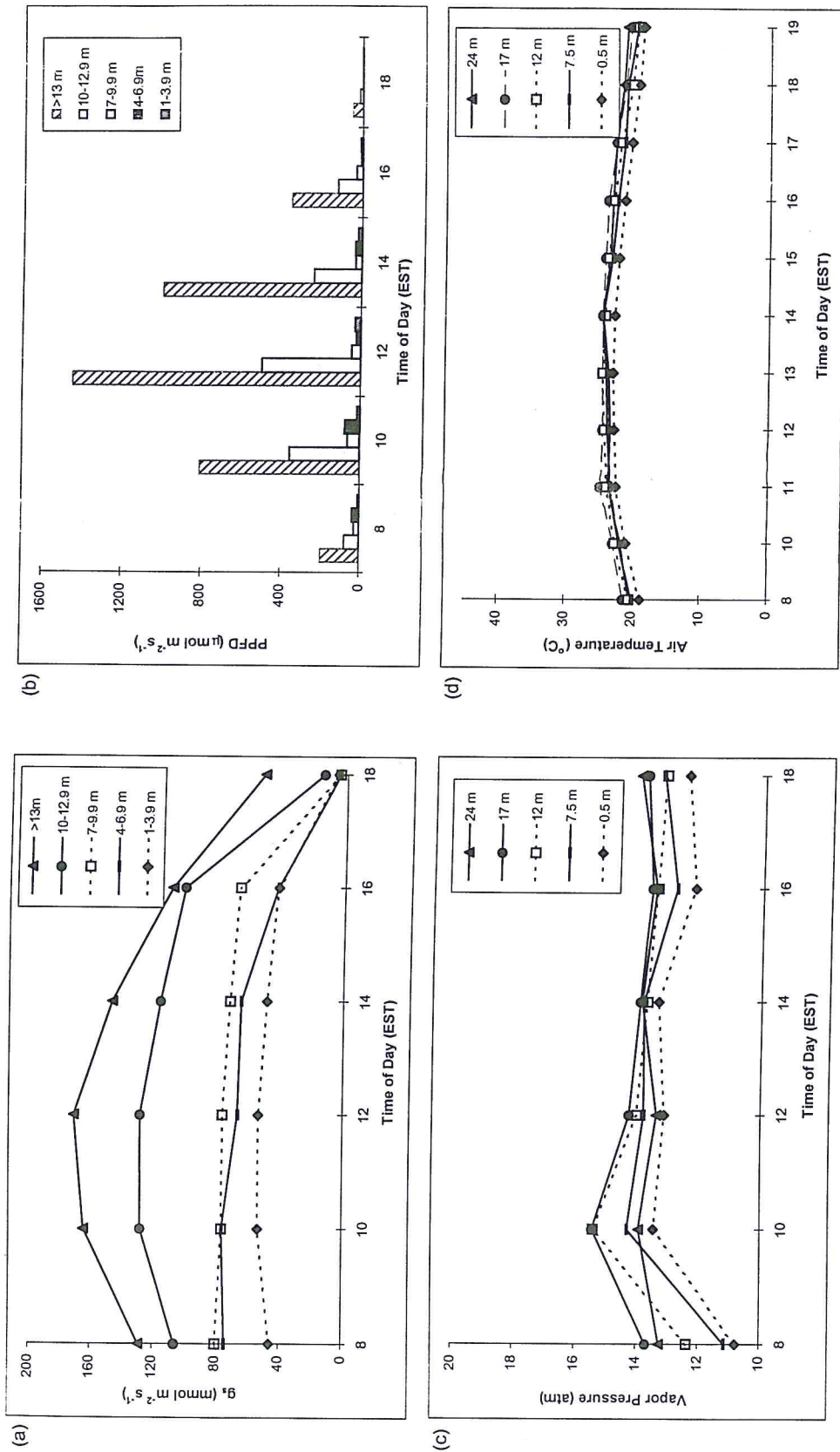


Figure 2. Average diurnal patterns for 11 days at 5 heights in a sugar maple canopy of (a) g_s ($\text{mmol m}^{-2} \text{s}^{-1}$), (b) PPFD ($\text{mmol m}^{-2} \text{s}^{-1}$), (c) partial pressure of water vapor (atm), and (d) air temperature ($^{\circ}\text{C}$).

Conductance to water vapor is affected by external factors that alter the water vapor pressure gradient between the leaf interior and the surrounding air. The steepness of the gradient rises with increasing dryness (decline in vapor pressure) and increasing temperature (Taiz and Zeiger 1998). The greatest partial pressure of water vapor (atm) was observed in the canopy between 12-17 m (Figure 2c). This does not suggest that a steep vapor pressure gradient was driving conductance in the upper canopy.

Patterns of Ozone

Ozone concentrations decreased with increasing depth in the canopy (Figure 3). Ozone concentrations were highest within and above the forest canopy and lowest at the forest floor, with an average difference of 22%. Differences in ozone between the canopy and forest floor were greatest at night, with an average difference of 29%. Skelly *et al.* 1996 found the same pattern with an average difference in ozone of 13% between the canopy and forest floor in a red oak and black cherry forest. Many other researchers have found similar spatial patterns (Frederickson *et al.* 1995; Güsten 1998). Ozone profiles in a canopy are caused by the combination of the physical process of dry deposition and chemical reactions with advected air masses containing nitrogen compounds and hydrocarbons. At the forest floor ozone oxidizes NO, which is emitted by soil microorganisms (Fontan *et al.* 1992; Frederickson *et al.* 1995). In the presence of greater sunlight in the upper canopy ozone is produced by the photolysis of NO₂ (formed from the oxidation of NO) (Baumbach and Baumann 1989; Hargreaves *et al.* 1992). Hydrocarbons that are emitted by trees, can also contribute to the higher ozone concentrations in the upper canopy (Johansson and Janson 1993).

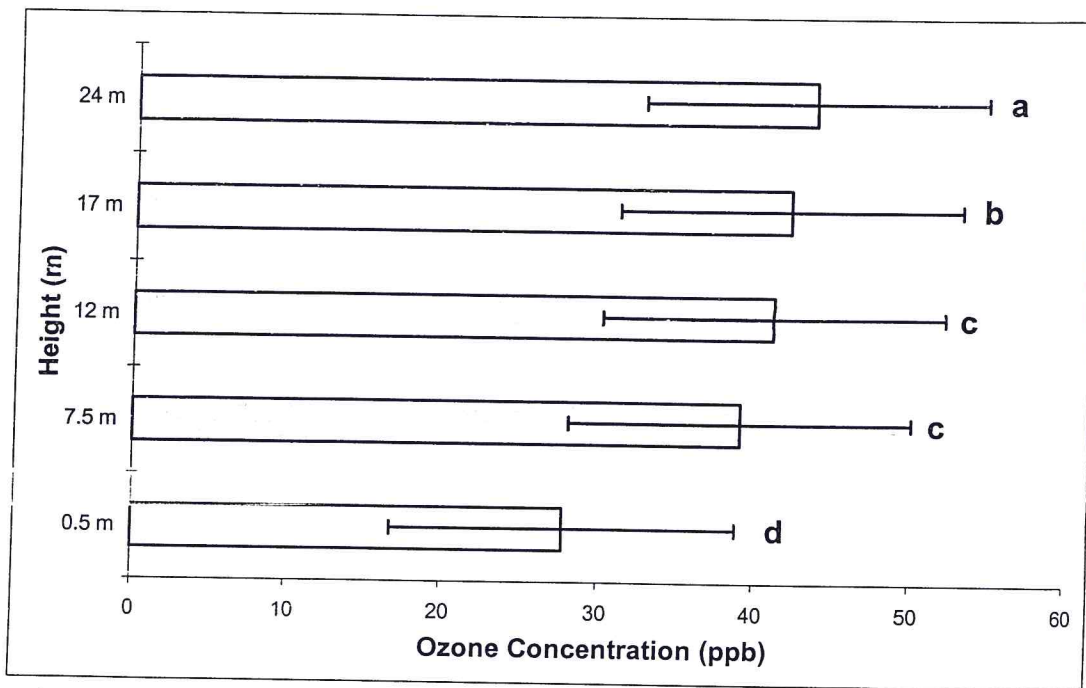


Figure 3. Average ozone concentration (ppb) at 5 heights in a sugar maple canopy for June-August 1998. Error bars represent one standard deviation, letters identify significant differences in O_3 among heights over the 11 days of study.

Analysis of variance results showed interaction between height and time, suggesting that vertical variation of ozone concentration in the canopy was time dependent ($p=0.0001$, Table 1b). This was reflected in the diurnal pattern of ozone concentration which exhibited minima in the early morning between 7:00 and 8:00, followed by a rapid increase, until reaching maxima between 12:00 and 13:00 (Figure 4). A similar pattern was observed in many studies (Baumbach and Baumann 1989; Enders *et al.* 1989; Fuentes *et al.* 1992; Taylor and Hanson 1992; Coe *et al.* 1995; Frederickson *et al.* 1995; Pilegaard *et al.* 1995; Skelly *et al.* 1996). Rapid increases in the morning have been attributed to photochemical production of ozone by the photolysis of NO_2 (Fontan *et al.* 1992).

Ozone showed a seasonal decreasing trend. This may be a result of decreased temperatures and light intensity. Ozone concentrations are highest during summer months due to lower wind speeds, higher light intensity, and greater NO emissions (Coe *et al.* 1995; Baumbach and Baumann 1989). July showed the highest average ozone due to a three day period of enhanced ozone concentrations (July 14, 15, 16). The average daily ozone concentrations for 1998 were similar to previous years (1994, 1995, 1996), although the number of hours in which the ozone concentration exceeded specified thresholds was lower in 1998. This may be due to the unusually high level of precipitation, reducing the overall amount of photochemically produced ozone during that summer.

Ozone concentrations exceeded 40 ppb for 900 hours, 60 ppb for 120 hours, and 80 ppb for 24 hours between June and August 1998. Compared to previous years, 1998 was characterized by shorter high ozone events, but similar daily averages and seasonal trends.

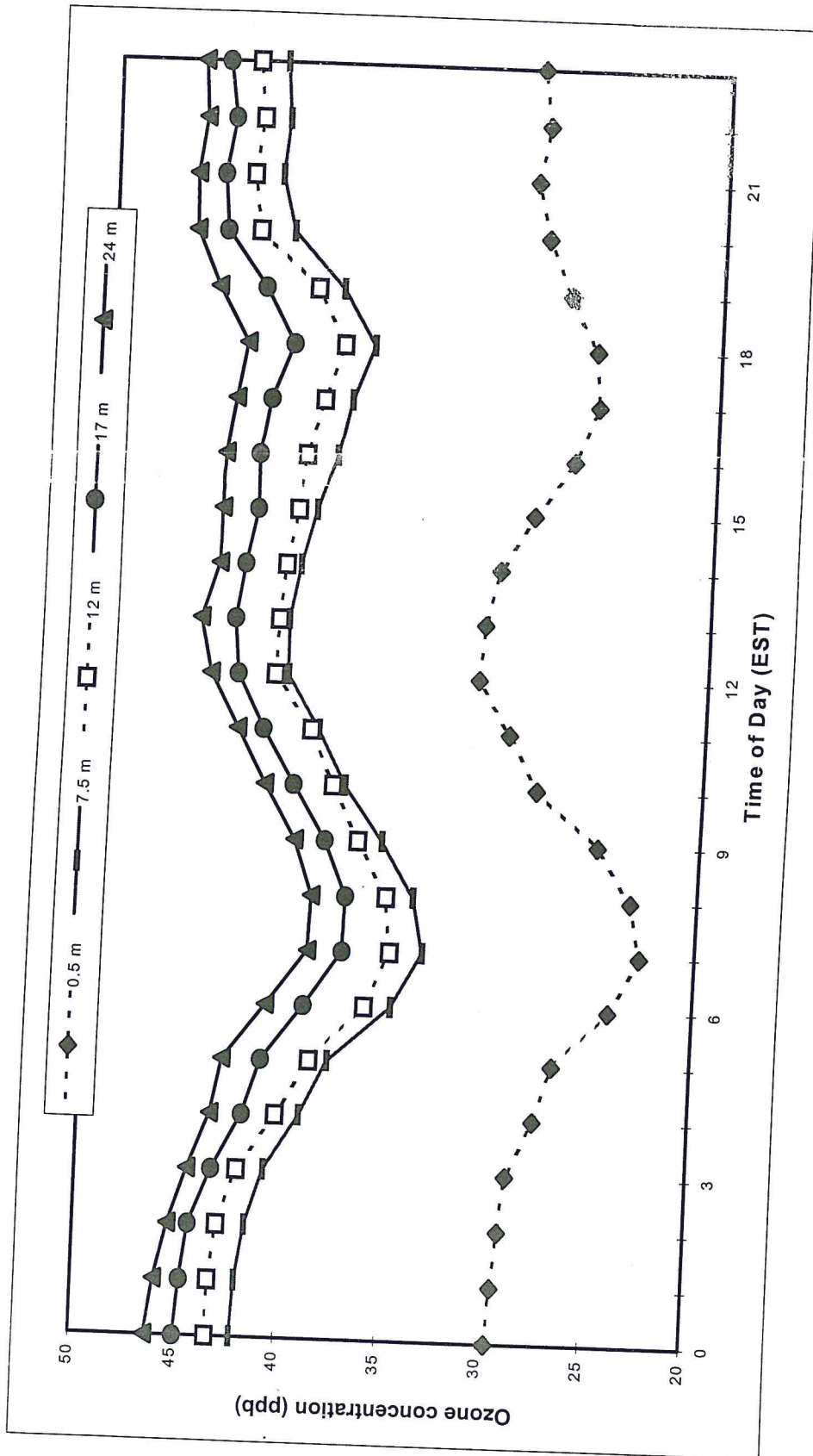


Figure 4. Diurnal pattern of average ozone concentration at 5 heights in a sugar maple canopy, June-July 1998.

Uptake of Ozone

Average uptake per unit leaf area ($\mu\text{mol m}^{-2} \text{h}^{-1}$), cumulative uptake per canopy layer ($\text{mmol ha}^{-1} \text{h}^{-1}$), and total canopy uptake ($\text{mmol ha}^{-1} \text{h}^{-1}$) were calculated. For all days the average uptake per unit leaf area was $7.8 \mu\text{mol m}^{-2} \text{h}^{-1}$, and all values ranged between $0.17 \mu\text{mol m}^{-2} \text{h}^{-1}$ and $34 \mu\text{mol m}^{-2} \text{h}^{-1}$. Uptake per unit leaf area decreased with depth in the canopy (Figure 5a). Vertical differences in uptake per unit leaf area ($\mu\text{mol m}^{-2} \text{h}^{-1}$) were found to be more a function of differences in g_s than ozone profiles. Samuelson and Kelly (1996) who studied ozone uptake in a black cherry, red maple and northern red oak canopy and Frederickson *et al.* (1995) who studied black cherry also found vertical variation in uptake to be a function of vertical differences in g_s , although values for uptake were on average greater in these studies.

Vertical differences in cumulative uptake ($\text{mmol ha}^{-1} \text{h}^{-1}$) were a result of differences in LAI between canopy layers. The layer with the highest leaf area (10-12.9 m) had the highest cumulative uptake of ozone with an average of $420 \text{ mmol ha}^{-1} \text{h}^{-1}$ (54% of total), although the top of the canopy (>13 m) had the greatest conductance, and hence the greatest uptake per unit leaf area (Figure 5b). The lowest average cumulative uptake ($0.122 \text{ mmol ha}^{-1} \text{h}^{-1}$) occurred in the lower canopy (4-6.9 m), where LAI was 0.02 (Figure 6). The highest average cumulative uptake of ozone occurred on July 14, during the 3-day period when the highest ozone concentrations were recorded. The greatest conductance values were measured on July 14 as well.

Samuelson and Kelly (1996) found that ozone uptake per unit leaf area was at least double for red oak and red maple canopy trees and six times greater for black cherry canopy trees than for understory saplings of each. Frederickson *et al.* (1995) also found greater uptake of ozone in black cherry trees at the upper crown level.

Interaction between the main effects of time and height was found when testing for differences across height and time in both uptake per unit leaf area and cumulative uptake of ozone, indicating that height differences were not constant across time ($p=0.0001$, Table 1c). A clear diurnal pattern of both was identified (Figure 7a and 7b). Maxima were reached between 12:00-13:00 and minima presumably occurred after stomata were shut, which was usually after 18:00-19:00 in this study. The average cumulative uptake at each of five strata were summed to estimate the total canopy ozone uptake. The mean ozone uptake of the whole canopy was $727 \text{ mmol h}^{-1} \text{ ha}^{-1}$, with values ranging from $160 \text{ mmol h}^{-1} \text{ ha}^{-1}$ to $993 \text{ mmol h}^{-1} \text{ ha}^{-1}$ depending on time of day.

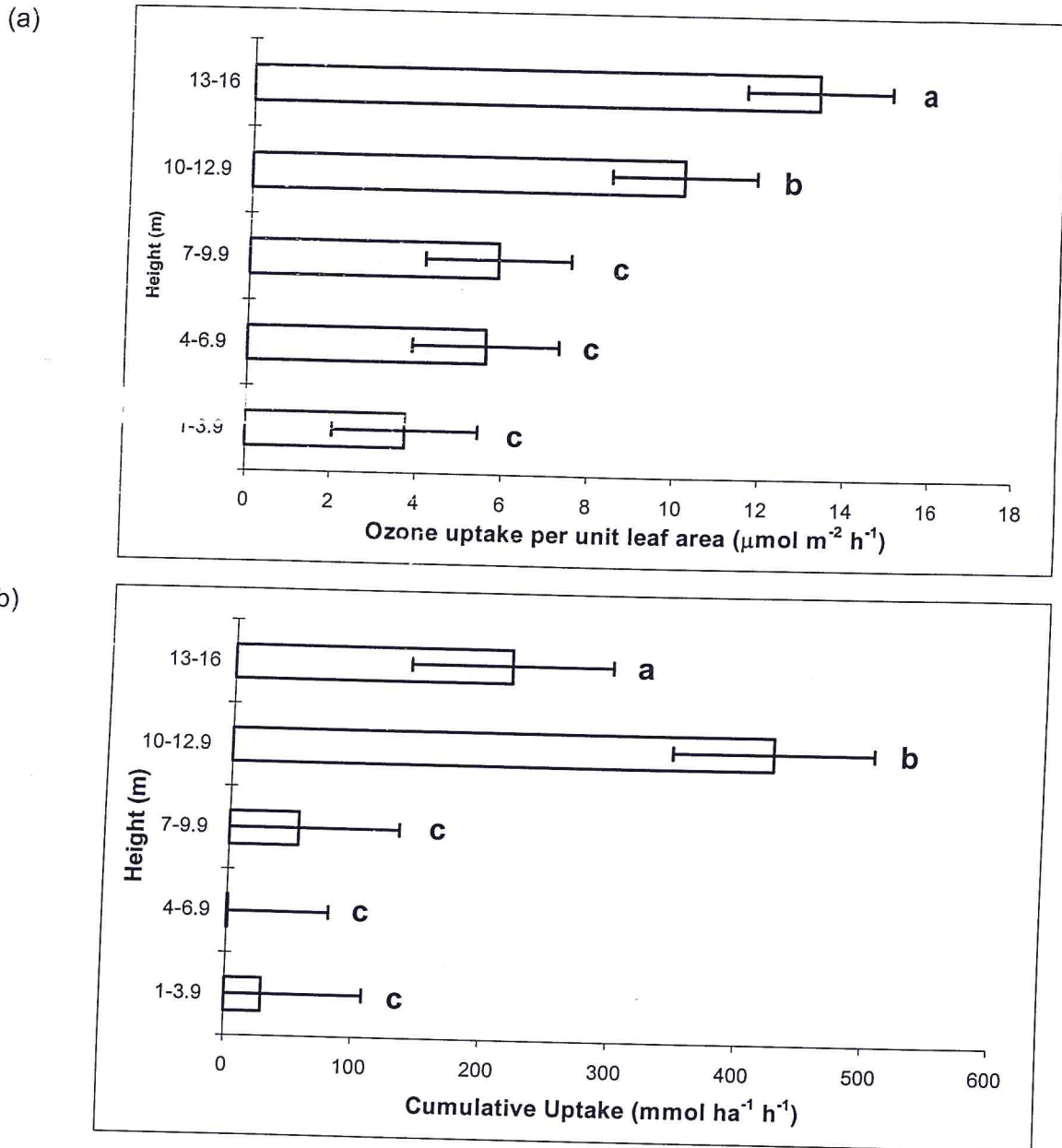


Figure 5. (a) Average uptake per unit leaf area ($\mu\text{mol m}^{-2} \text{h}^{-1}$) and (b) cumulative uptake ($\text{mmol ha}^{-1} \text{h}^{-1}$) of 11 days at 5 heights in a sugar maple canopy, July-August 1998 ($N \sim 65$ at each height). Error bars represent one standard deviation, distinct letters identify significant differences in uptake between heights.

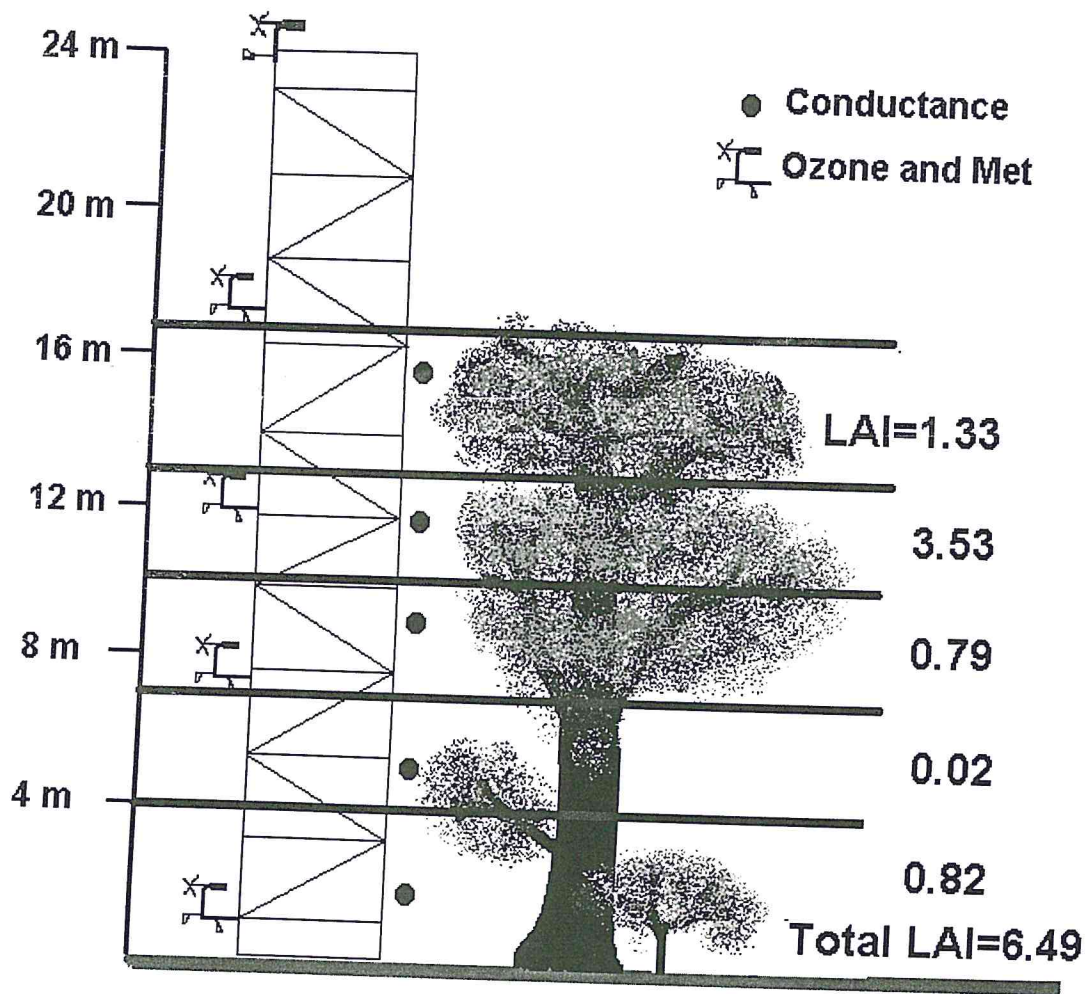


Figure 6. Schematic diagram of tower and corresponding heights where stomatal conductance, ozone, and meteorological data were measured, and LAI was calculated.

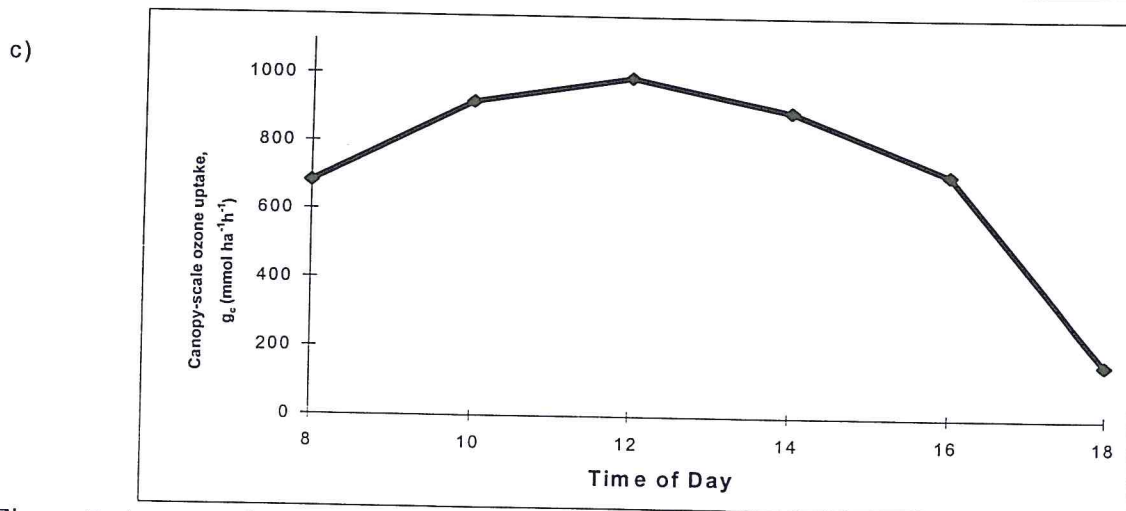
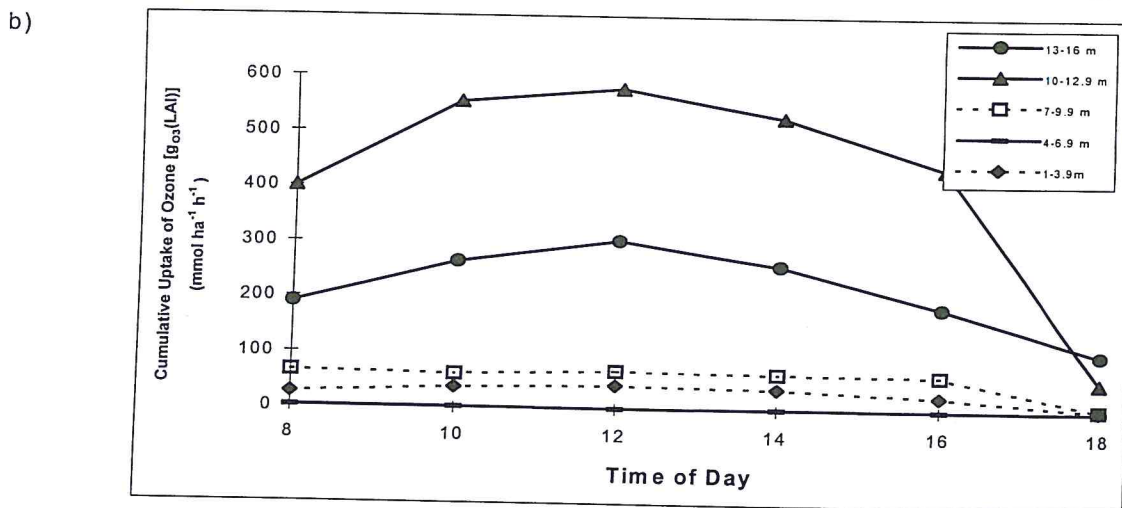
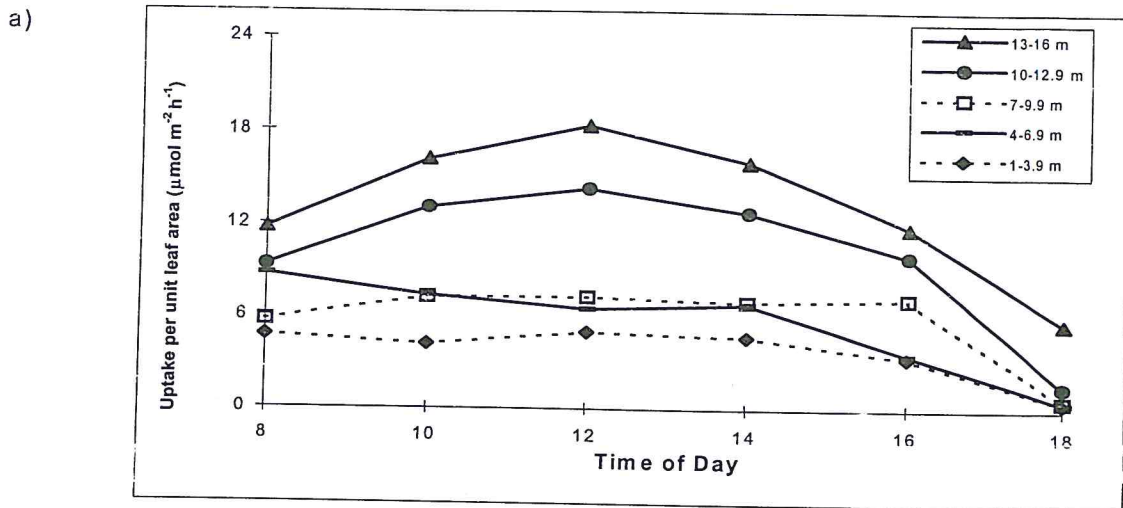


Figure 7. Average diurnal pattern of (a) uptake per unit leaf area ($\mu\text{mol m}^{-2} \text{h}^{-1}$), (b) cumulative uptake ($\text{mmol ha}^{-1} \text{h}^{-1}$), and (c) canopy uptake ($\text{mmol ha}^{-1} \text{h}^{-1}$) for 11 days at 5 heights, July-August 1998.

Considering these findings from a canopy scale perspective it is important to consider the potential ozone injury that could result. Fifty-nine percent of the total canopy conductance and uptake of ozone occurred between 10-12.9 meters, and 86% occurred above 10 meters. Reich *et al.* (1990) calculated that 86% of the carbon gain occurred in the upper and middle canopy layers in an sugar maple and red oak forest, and that 66% of the carbon gain in an oak and *Machia* forest occurred in the top third of the canopy. Leverenz *et al.* (1992) found that 40 -50% of carbon gain occurred in the top quarter of a sitka spruce canopy.

Since many researchers have found that ozone caused decreases in stomatal conductance (Rebbeck *et al.* 1993; Samuelson 1994; Pearson 1995; Samuelson *et al.* 1996; Pääkonen *et al.* 1996, Momen *et al.* 1997; Zuethen *et al.* 1997), the combined effect of higher ozone concentration and stomatal conductance rates in the upper canopy may result in an overall decline in carbon gain in forests. As concentrations of ambient ozone and its precursors continue to increase, as they are predicted to do (Ollinger *et al.* 1997), this problem may become more severe in the future. Reich *et al.* (1990) used a model to show that daily canopy carbon gain can be reduced by 57% at a high ozone dose in a sugar maple canopy. Tjoelker *et al.* (1995) showed that ozone exposure eventually lead to a loss of stomatal regulation in sugar maple. If this is the case sugar maple trees could initially show a decline in carbon gain followed by the uptake of large doses of ozone thus making them increasingly susceptible to physiological and biological dysfunction.

This study demonstrates that stratified sampling is necessary to accurately calculate canopy scale uptake of ozone. This study describes the interaction of various factors which influence ozone uptake and potential response to ozone in a sugar maple canopy. Large spatial and diurnal variation in g_s and ozone reported by this study indicate the importance of canopy position and time of day in the evaluation of forest tree uptake. Scaling up from measurements of g_s and ozone at one height and time underestimated estimates of ozone uptake by 50% on average.

Leaves in the lower canopy and saplings were observed to receive a lower dose of ozone in this study. Nevertheless, it is important to consider the possible effects of ozone uptake in the lower strata. Tjoelker *et al.* (1995) found that sugar maple shade leaves were more sensitive to ozone exposure. This may be because sun leaves produce more antioxidants, which are a defense against ozone damage (Matyssek *et al.* 1995).

In the summer of 1998, after August 25 approximately 25% of leaves in the study canopy were browsed to the point that sampling was not possible. Most of the insect damage appeared to be caused by the maple leaf cutter (*Paraclemensia acerifoliella*), the maple trumpet skeletonizer (*Epinotia aceriella*), and the maple spindle gall maker (*Vasates aceriscrumena*) (Johnson and Lyon 1988). It is likely that this damage to the foliage resulted in reductions of carbon gain.

In this study ozone injury was not assessed, however, a reduction in sugar maple vigor has been reported throughout the Northeastern United States and Southeastern Canada in the past 20 years (Payette *et al.* 1996). This decline is generally associated with early leaf abscission, abnormal coloration, dieback, reduced productivity, and death. Frequently

this weakens trees, predisposing them to attack by fungi or insects. For example, Fortin *et al.* (1997) found that forest tent caterpillar larvae preferred sugar maple foliage treated with 3x-ambient ozone. Many studies have assessed the damage to vegetation caused by the combination of acid rain and ozone (Eamus and Murray 1991; Laurence *et al.* 1996, Momen 1997). These studies have suggested that forest decline is likely to be the result of an interplay of pollutants.

Much of the variation in cumulative ozone uptake was positively correlated with solar radiation and temperature (38% and 41%, respectively). With this in mind, uptake of ozone may be exacerbated by global warming as temperature increase and growing seasons lengthen (Ollinger 1997).

Conclusions

It is clear from other studies that ozone exposure can result in severe reductions in net carbon gain. It was found in this study that 86% of the total canopy ozone uptake occurs in the upper canopy where the greatest proportion of stomatal conductance and photosynthesis is observed. This may result in severe reductions in stomatal conductance and photosynthesis, thereby reducing the overall carbon gain in forest canopies.

This research also demonstrates that understanding the patterns of ozone uptake in forest canopies requires stratified sampling. Large spatial and temporal variation in g_s and ozone reported by this study indicate the importance of canopy position and time of day in the evaluation of forest tree uptake and response to ozone. Gradients of light, temperature, and humidity were found in this forest canopy, and complex relationships between plants and these environmental variables control stomata and gas exchange. Scaling up from measurements of g_s and ozone at one height and time underestimated estimates of ozone uptake by 50%.

It is important to characterize the specific environmental factors that influence ozone uptake in a particular system since interspecific differences in g_s will confound regional estimates. Canopies of individual species must be investigated to accurately estimate ozone uptake in forests. It is of interest to scientists and resource managers to quantitatively predict the amount of ozone that will be taken up by particular vegetation types the filtering effect of forest is well understood.

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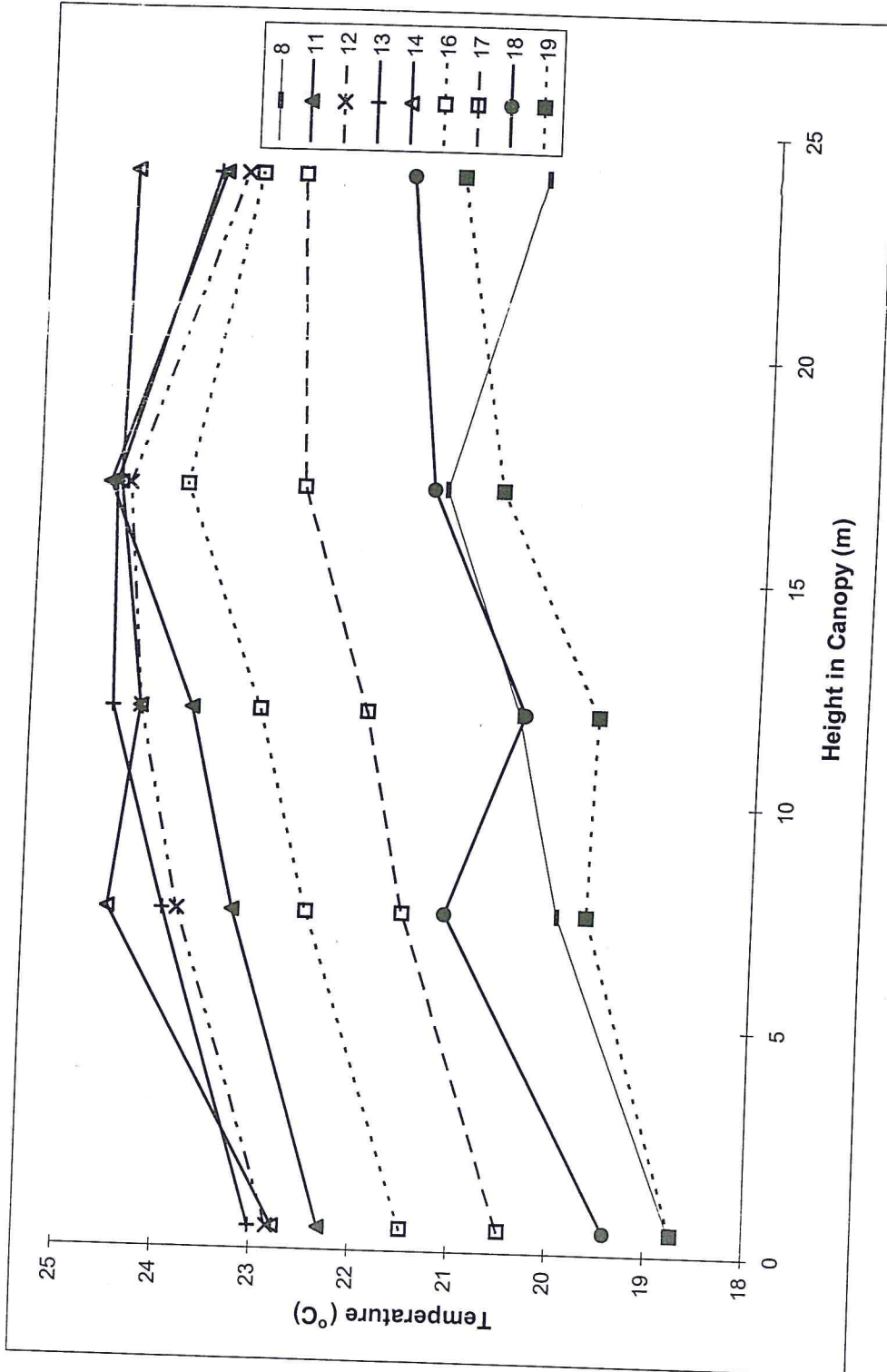
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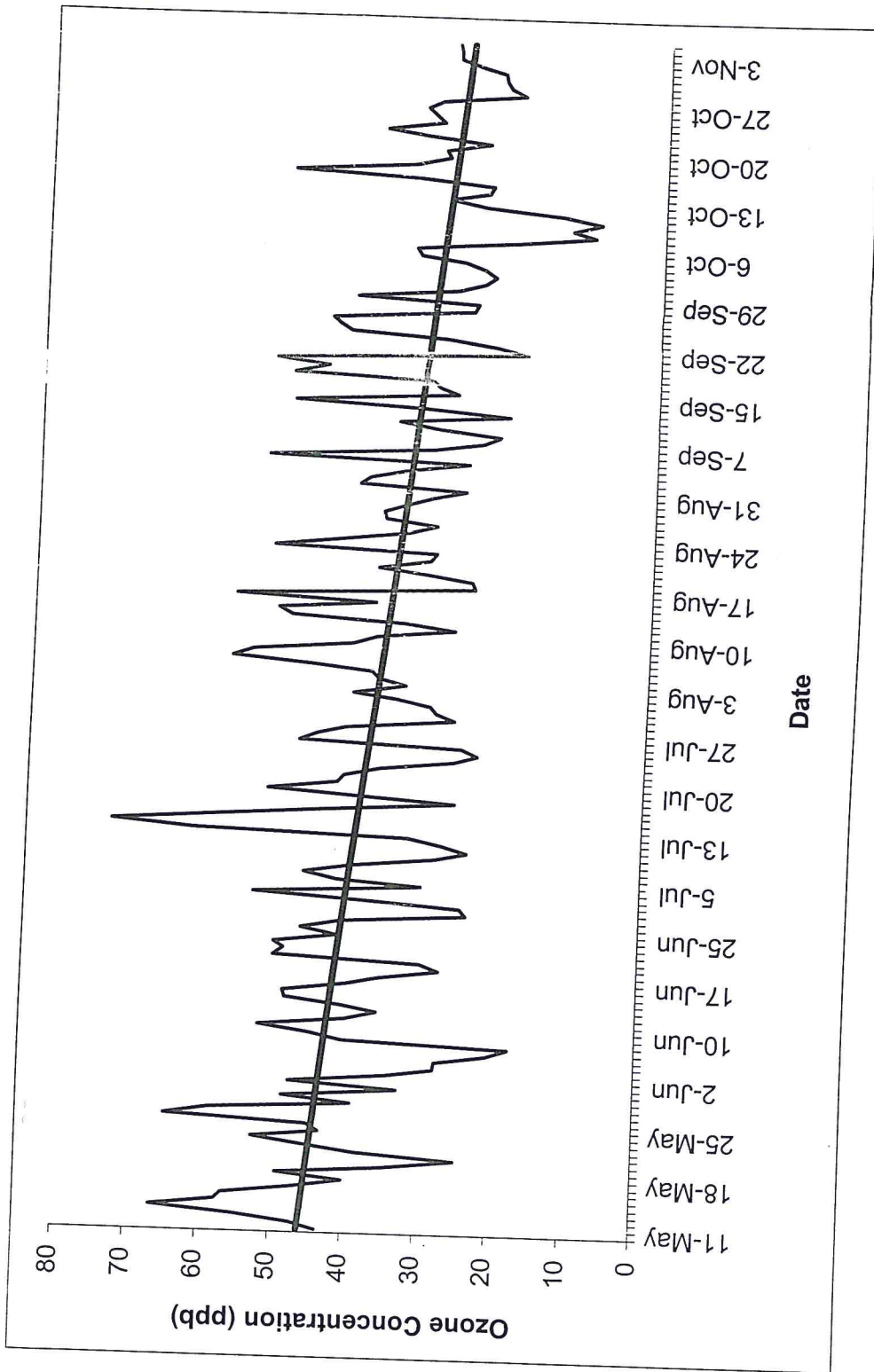
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Appendix A: Temperature profiles at five heights in a sugar maple canopy in Underhill, Vermont, July-August 1998. (Each line represents a time of day EST)



Appendix A. Average profiles of temperature (°C) at 5 heights in a sugar maple canopy (11 days), July-August 1998. Each line represents a time interval during the day (EST).

Appendix B: Seasonal trend of ozone in a sugar maple canopy in Underhill, Vermont, May-November 1998.



Appendix B. Average daily ozone concentration in a sugar maple canopy, Underhill Vermont. Line represents seasonal trend, May-November 1998.

Appendix C: Average Values for Stomatal Conductance, Uptake (per unit leaf area and cumulative), LAI, and Ozone at five heights in a sugar maple canopy, July-August 1998.

Appendix C. Average values of (a) stomatal conductance, (b) ozone uptake per unit leaf area, (c) cumulative uptake, (d) leaf area index of each strata and entire canopy, (e) total ozone uptake of canopy, and (f) ozone concentration at five heights in a sugar maple canopy, July-August, 1998, (N=11 days, 65 replicates per height).

	1-3.9 m	4-6.9 m	7-9.9 m	10-12.9 m	13-16 m	Total
(a) Stomatal Conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)	41.64	54.94	63.96	102.38	124.96	-
(b) Uptake per unit leaf area ($\mu\text{mol m}^{-2} \text{h}^{-1}$)	3.75	5.6	5.8	10.1	13.2	-
(c) Cumulative uptake per canopy layer ($\text{mmol ha}^{-1} \text{h}^{-1}$)	29.0	1.2	4.8	424.5	217.5	-
(d) Total canopy uptake ($\text{mmol ha}^{-1} \text{h}^{-1}$)	-	-	-	-	-	727
(e) LAI (leaf area index)	0.82	0.02	0.79	3.53	1.33	6.49
(f) Ozone (ppb)	27.9	34.2	39.1	40.3	43.5	