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Ozone deposition to a ponderosa pine plantation in the Sierra Nevada Mountains (CA): A comparison of two different climatic years

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Abstract. Ponderosa pine is one of the most sensitive species to ozone and a dominant species in the Sierra Nevada Mountains. To assess the factors controlling ozone deposition to the forest and to study the forest response, we established a research site in a ponderosa pine plantation ~75 km northeast of Sacramento. Ozone concentration and ozone flux, along with relevant environmental variables, were measured from June to September in 1997 and from May to November in 1998. Summer of 1997 had very low soil moisture and an early budbreak, while summer of 1998 had very high soil moisture and later budbreak. Soil moisture and vapor pressure deficit exerted a strong control on ozone deposition in the dry year (1997), but the relationship was less clear in the wet year (1998). During the dry year ozone concentration and flux became decoupled owing to stomatal closure, but this did not occur explicitly in 1998. Phenology also proved to be important in controlling ozone deposition. Early in summer 1997 cumulative ozone flux was 50% higher than that of 1998: the difference can be attributed to the late budbreak in 1998. Further, the highest ozone deposition velocity in both years occurred 3-4 weeks after budbreak. Total cumulative ozone flux during the summer was 6% lower in 1998 due mainly to later budbreak even though drought stress reduced ozone flux late in summer 1997. Our results show that interannual climate variability impacts temporal patterns, physiological controls, and magnitude of ozone deposition to sensitive Mediterranean-type ecosystems.

1. Introduction

Tropospheric ozone is a secondary pollutant that is produced by photochemical oxidation of nitrogen oxides (NO_x) and hydrocarbons (VOCs) [*Haagen-Smit*, 1952]. Ozone or its precursors are transported downstream from urban sources and the high concentration of ozone observed in remote regions of the Sierra Nevada has been attributed to atmospheric transport from sources in the Central Valley of California [*Cahill et al.*, 1996]. At concentrations often measured in the Sierra Nevada, ozone deposition is known to be toxic to plants, and in fact, the mixed conifer forest of the Sierra Nevada is the most prominent example of an ecosystem in North America with evidence of widespread injury and growth reductions associated with ozone [*Miller and McBride*, 1988; *Peterson et al.*, 1991]. Of the tree species found in the Sierra Nevada Mountains, ponderosa pine (*Pinus ponderosa*) is known to be among the most sensitive to ozone damage. Previous studies have shown that ozone has negative effects on productivity that are correlated with decreasing stomatal conductance and photosynthesis, premature leaf abscission, and decreases in leaf size, all of which decrease total carbon accumulation [*Arbaugh et al.*, 1998; *Bytnerowicz*, 1996; *Coleman et al.*, 1995; *Pell et al.*, 1994; *Peterson et al.*, 1991; *Sasek and Richardson*, 1989; *Taylor et al.*, 1982; *Temple et al.*, 1993; *Unsworth and Ormrod*, 1982]. While much emphasis has been placed on the impacts of ozone on forests in southern California, forests of the Sierra Nevada Mountains in northern California are also impacted but at lower rates [*Cahill et al.*, 1996; *Miller and McBride*, 1988; *Miller et al.*, 1996]. Moreover, as industry and population continue to grow in the Central Valley of California, forests in the northern Sierra Nevada Mountains will likely experience higher ozone concentrations.

Ozone does not affect plants externally; only the amount that diffuses into the leaf will have an impact on plant processes. Most previous studies relate ozone damage to ozone concentration; however, ozone injury depends on the amount of ozone uptake by vegetation (i.e., ozone flux or ozone deposition), not just the amount in the surrounding atmosphere [*Musselman and Massman*, 1999; *Van Ooy and Carroll*, 1995] (J. A. Panek and A. H. Goldstein, A controlled field experiment on the relation between drought stress and stomatal conductance: Implications for carbon storage and ozone deposition, submitted to *Tree Physiology*, 1999, hereinafter referred to as Panek and Goldstein, submitted manuscript, 1999). It is therefore extremely important to distinguish between ambient concentration and flux when examining exposure of plants to ozone.

The major pathway of ozone deposition to foliage is through the stomata. In a dry, transpiring ecosystem, stomatal resistance has been shown to be the most dynamic and influential resistance to transfer of ozone to an ecosystem [*Baldocchi et al.*, 1987; *Galbally and Roy*, 1980; *Heath*, 1975; *Turner et al.*, 1974]. Accordingly, factors that affect stomatal openings such as temperature, humidity, and water and light

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availability could strongly influence overall ozone deposition to plants. This means that there should be a direct link between climate and the amount of ozone taken up by plants. For example, high temperatures and low humidities decrease plant stomata aperture and so would be expected to reduce ozone uptake and thus reduce ozone damage [*Van Ooy and Carroll*, 1995]. Likewise, drought conditions which result in low soil moisture have been shown to reduce plant responses to ozone because of lowered stomatal conductance [*Temple et al.*, 1993]. It is well established that light (specifically, photosynthetically active radiation), air temperature, soil moisture, and vapor pressure deficit influence canopy conductance, but how this is linked to ozone deposition is not well understood.

In order to quantify whole ecosystem ozone deposition and the factors that control it, we established a field site in a Sierra Nevada ponderosa pine plantation and continuously measured ozone concentration, ozone flux, and relevant environmental variables during late spring to early fall in 1997 and 1998. In this paper we investigate the factors that controlled ozone deposition and how they differed in a dry year (1997) and a wet year (1998).

2. Site Description, Measurement, and Data

2.1. Site Description

A field site was established in May 1997 in a ponderosa pine plantation in the Sierra Nevada Mountains; this site is part of the Ameriflux network. The ponderosa pine plantation is owned by Sierra Pacific Industries, located adjacent to Blodgett Forest Research Station, a research forest of the University of California at Berkeley near Georgetown, California (38°53'42.9"N, 120°37'57.9"W) at 1300 m elevation (Figure 1). A 10 m tower was erected on the site in order to make measurements above the canopy. The forest upwind of the tower, comprising the sampled footprint, is a homogeneous canopy of trees dominated by ponderosa pine (*Pinus ponderosa*); at the time the tower was erected the trees were 5-6 years old and 3-4 m high. The canopy also includes individuals of Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*) and black oak (*Quercus kelloggii*). The major understory shrubs are manzanita (*Arctostaphylos* spp.) and *Ceonothus* spp. In 1997 ~55% of the ground area was covered by shrubs, 30% was covered by conifer trees, 2% was covered by deciduous

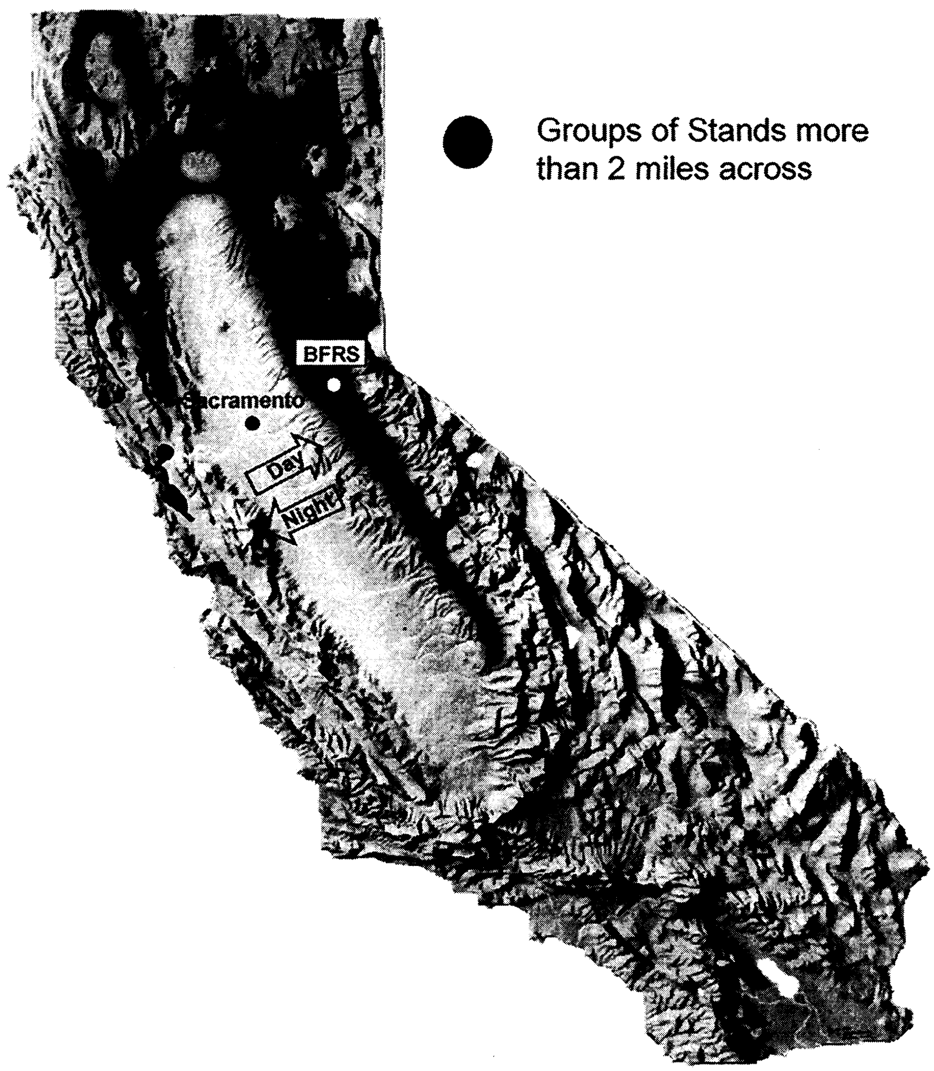

Figure 1. Map of California showing Blodgett Forest Research Station, airmass trajectories around Sacramento, and distribution of ponderosa pine trees.

trees, 7% was covered by forbs, 3% was covered by grass and 3% was covered by stumps. The leaf area index (LAI) for this site was estimated to be 6.4 in 1997 and 9.0 in 1998. A ponderosa pine plantation that is 7-8 years older is located 200 m to the southwest of the measurement site upwind of the tower during the day. Two independent model estimates of the tower footprint both indicate that roughly 90% of the footprint was within the young plantation (200 m of the tower) during the daytime [*Baker et al.*, 1999; *Hsieh et al.*, 1997].

The site is characterized by a Mediterranean climate, with the majority of precipitation falling between September and May and very little rain in the summer. Since 1961, annual precipitation has averaged 64 cm. Summer temperatures typically range from 14° to 27°C, and winter temperatures typically range from 0° to 9°C (data from Blodgett Forest Archives). Trees generally break bud in mid-May to early June and set bud late June to early August. The predominant daytime airmass trajectory at the site comes upslope from the Sacramento Valley (Figure 1). The site receives nighttime air downslope from the Sierra Nevada Mountains to the east. The soil is in the Cohasset series and was formed in material weathered from andesitic lahar.

Infrastructure for the canopy-scale flux measurements included the measurement tower (Upright Inc.), a temperature controlled instrument building (9 m^2), and an electrical generation system powered by a diesel generator. The measurement tower was placed toward the eastern side of the plantation to maximize the ponderosa pine plantation fetch during the day. The generator was located 500 feet to the northwest of the tower, as far outside of the major airflow paths as possible. Hydrocarbon measurements at the site indicated that exhaust from the generator affected our measurements less than 5% of the time and contamination occurred only at night [*Lamanna and Goldstein*, 1999].

2.2. Measurements

From June to September 1997 and from May to November 1998, ozone concentration and ozone flux were continuously measured. Environmental parameters such as wind direction and speed, air temperature and moisture, net and photosynthetically active radiation (R_{net} and PAR, respectively), soil temperature and moisture, atmospheric pressure, and pine needle temperature were also monitored. Additional continuous measurements at the site included CO_2 and H_2O concentration and flux [*Goldstein et al.*, 2000] and concentrations and fluxes of a wide variety of volatile organic compounds [*Lamanna and Goldstein*, 1999; *Schade et al.*, 1999].

Measurements were made 9 m above the ground from a horizontal beam that projected 2 m into the daytime wind direction (220°). The data acquisition system was separated in two main parts: (1) a fast response system which stored data at high frequency (up to 10 Hz) and (2) a slow-response system which stored averaged data over 30 min. The fast-response system was used to measure wind speed in three directions, virtual temperature, wind direction, and eddy covariance fluxes of trace gases (O_3, CO_2, and H_2O), sensible heat, and momentum in the vertical direction. The fast-response system consisted of a three-axis sonic anemometer (ATI Electronics Inc.) that measured at 10 Hz, a LI-COR CO_2/H_2O analyzer (LI-COR Inc., model 6262) that measured at 5 Hz and 3 Hz in 1997 and at 10 Hz in 1998, and a closed-path fast response chemiluminescent O_3 analyzer that measured at 10 Hz. The fast ozone sensor was built by Jim Womack (National Oceanic and Atmospheric Administration – Atmospheric Turbulence and Diffusion Division) based on a design by Hans Gusten [*Gusten and Heinrich*, 1996]. The sensor is based on the chemiluminescent reaction of ozone with a Coumarin-impregnated target. The slow-response system provided stable references with which to calibrate the fast-response instruments as well as information on the environmental parameters. The slow-response system consisted of a UV photometric O_3 analyzer (Dasibi 1008-RS), a LI-COR CO_2/H_2O analyzer (LI-COR Inc., model 6262), a propeller wind monitor (R.M. Young Co.), net radiation thermopiles (R.E.B.S. Inc.), incoming photosynthetically active radiation (Li-Cor), relative humidity capacitive sensors (Vaisala, Inc.), air temperature thermistors (Fenwal Electronics, model UUT51J1), soil temperature thermistors (Campbell Scientific Inc.) buried at 5, 10, and 15 cm, soil heat flux plates (Campbell Scientific Inc.), soil moisture probes (Campbell Scientific Inc., model CS615 Water Content Reflectometer) at 10 and 20 cm depth in 1997 and at 10, 30, and 50 cm depth in 1998, and fine-wire thermocouples (Omega Inc., type T) measuring needle temperature.

Ambient air for the fast-ozone instrument was sampled 10 cm downwind of the sonic anemometer at 6-7 L min^{-1} through a 2 μm filter (Zefluor, Gelman Sci.). In 1997 the fast-ozone instrument was placed on the tower, and air was sampled through 4 m of 0.635cm Teflon tubing to the instrument. In 1998 the fast-ozone instrument was placed in the temperature-controlled shed with 13 m of tubing between the sample inlet and the instrument. Adjustments were made to account for the time lags associated with travel through the sampling tube. Ambient air for the slow-ozone instrument was sampled at the same height as for the fast-ozone instrument at 2.5 L min^{-1} through a 2 μm filter (Zefluor, Gelman Sci.) and 13 m of 0.635 cm Teflon tubing for both years.

2.3. Data Analysis and Calculations

All fast-response data was logged continuously and saved in 30 min increments on a computer in the instrument building at the site. Data from the slow-response system were stored on a Campbell Scientific datalogger.

Fluxes of ozone between the forest canopy and the atmosphere were determined 9 m above the ground (~5 m above the canopy) by eddy covariance (e.g., [*Gusten et al.*, 1996; *Leuning and Judd*, 1996; *Moncrieff et al.*, 1996]). The eddy covariance technique measures the flux of a scalar (energy, mass) at a point centered on instruments placed at some height above the surface. Ozone flux was calculated as

$$F_{O3} = \overline{w'O_3'}, \tag{1}$$

where F_{O3} is ozone flux, w the vertical wind velocity, and O_3 the concentration of ozone at the measurement height. The prime indicates instantaneous deviation from the mean, and the overbar indicates the time average of 30 min. Positive flux represents mass and energy transfer from the surface into the atmosphere while negative flux represents mass and energy transfer from the atmosphere into the surface; ozone flux is typically negative. Fluxes were calculated from each sonic data set using RAMF (Routinen zur Auswertung

Meteorologicscher Forschungsflüge, Routines for the Processing of Meteorological Research Flights) software routines which were developed at the Flinders Institute for Atmospheric and Marine Sciences, Flinders University of South Australia [*Chambers et al.*, 1997].

Ozone deposition velocity (O_3 V_d), the rate which ozone is deposited to the ecosystem is ozone flux normalized for concentration:

$$O_3\ V_d = -F_{O3}/[O_3]\ . \qquad (2)$$

Ozone flux indicates the total amount of ozone going into the ecosystem and is strongly influenced by changes in ozone concentration. Removing the effect of ozone concentration allows us to examine how factors other than ozone concentration , such as PAR, air temperature, vapor pressure deficit, and soil moisture, influence deposition rates.

Vapor pressure deficit was calculated as the difference between saturated and measured vapor pressure at ambient air temperature above the plantation. A rearranged Penman-Monteith equation was used to calculate canopy resistance (r_c) [*Monteith and Unsworth*, 1990; *Shuttleworth et al.*, 1984]. Canopy resistance to ozone was calculated from canopy resistance to water vapor based on the diffusivities of the gases,

$$r_{c,O3} \;=\; ((MW\,O_3)^{1/2} / (MW\,H_2O)^{1/2})\, r_{c,H2O}\,, \qquad (3)$$

and canopy conductance was calculated as the inverse of canopy resistance.

Trees at the field site were monitored throughout the season for their hydologic status. Water potential was measured before dawn on one east facing twig from each of six trees using a pressure bomb (PMS Instruments, Corvallis, Oregon) (Panek and Goldstein, submitted manuscript, 1999).

2.4. Error Analysis

Corrections and adjustments were made to account for potential systematic errors in the eddy covariance fluxes. Adjustments were made for the time lag between sampling and instrument response and to align the vertical velocity measurement to normal to mean streamlines. The time lag between the sampling and instrument response was determined by maximizing the covariance between the vertical wind and ozone concentration. In 1997 the time lag was 2.0 s and in 1998 the time lag was 5.0 s; these values were extremely consistent throughout the measurement period. Errors may occur in the calculation of covariances because of inappropriate orientation of the vertical wind sensor. These potential errors due to misalignment of wind sensors with respect to the local mean streamline were eliminated by a three-dimensional coordinate rotation of the mean wind vectors [*Gusten et al.*, 1996]. The rotation angle needed to align the vertical velocity measurement to normal to mean streamlines was typically 0.6°.

Systematic errors associated with the eddy covariance fluxes include damping of the high-frequency fluctuations by the closed path fast-ozone analyzer and travel through the sampling tube, sensor separation between the vertical wind measurement and ozone sample inlet, and the inability of the sonic anemometer to resolve fine-scale eddies in light winds. Errors due to sensor separation arise when the vertical wind measurement and gas inlet are not located at the same point in space. Damping of fluctuations in gas concentration occurs when air is passed through a tube to a closed path analyzer because of radial variation in streamwise air velocity and because of radial diffusion; the tube acts as a low-pass filter [*Leuning and Judd*, 1996]. Errors due to sensor separation and damping of high-frequency eddies were corrected using spectral analysis techniques as outlined by *Kaimal and Finnegan* [1994] and *Rissmann and Tetzlaff* [1994]. Using cospectral analysis (a means to characterize contributions to the covariance between two quantities as a function of frequency), it is possible to derive a scaling factor to correct a covariance estimate. Assuming that the observations of w are reliable, a comparison of the "observed" normalized cospectra with a theoretically "correct" cospectra should indicate the effect of errors such as sensor separation and damping of high-frequency eddies. Since modern temperature sensors are typically fast and reliable, the normalized temperature cospectra is commonly used as a surrogate for the "correct" cospectra. Under ideal conditions the shapes of the power spectra for $w'T'$ (sensible heat flux) and $w'O_3'$ should be similar [*Rissmann and Tetzlaff*, 1994]. Sensible heat flux can be considered the "ideal" flux; by comparing the power spectra of the sensible heat flux to those of the ozone flux (the "less ideal" flux), errors due to sensor separation and damping of high-frequency eddies were assessed. Spectral analysis revealed an underestimation of ozone flux of roughly 16%. Correction factors for each half hour were calculated and applied to the fluxes during the times when the sensible heat flux data were reliable. Additionally, spectral analysis indicated that fluxes were dominated by eddies with frequencies between 0.1 and 0.01 Hz.

The inability of the sonic anemometer to resolve fine-scale eddies in light winds (such as at night) produces two effects: (1) selectively systematic errors in sensible heat flux and (2) the inability to correct the ozone flux data using spectral analysis techniques that assume $w'T'$ is the "correct" cospectrum. During the daytime, turbulence was typically strong enough to produce reliable measurements; however, nighttime flux measurements were less reliable. Therefore the daytime ozone fluxes were corrected using spectral techniques, but the correction based on spectral analysis was not applied to the nighttime data. We do not consider this to be a significant problem for our analysis as the main focus of this work is on daytime hours, the time when plants are active, ozone concentration is highest, and turbulence is strongest.

The stated precision of the Dasibi ozone instrument in 1 ppbv and yearly factory calibrations has confirmed its accuracy to within 1%. Our energy budget (R_{net} = sensible heat flux + latent heat flux + soil heat flux) was closed to within 12% on average indicating that daytime errors associated with the eddy flux system are unlikely to exceed this. Errors associated with nighttime fluxes are likely to be greater than this due to the inability of the sonic anemometer to resolve fine-scale eddies in light winds.

3. Results

3.1. Climate

Daytime mean (800 – 1800 LT) measurements of PAR, soil moisture, air temperature, and vapor pressure deficit for

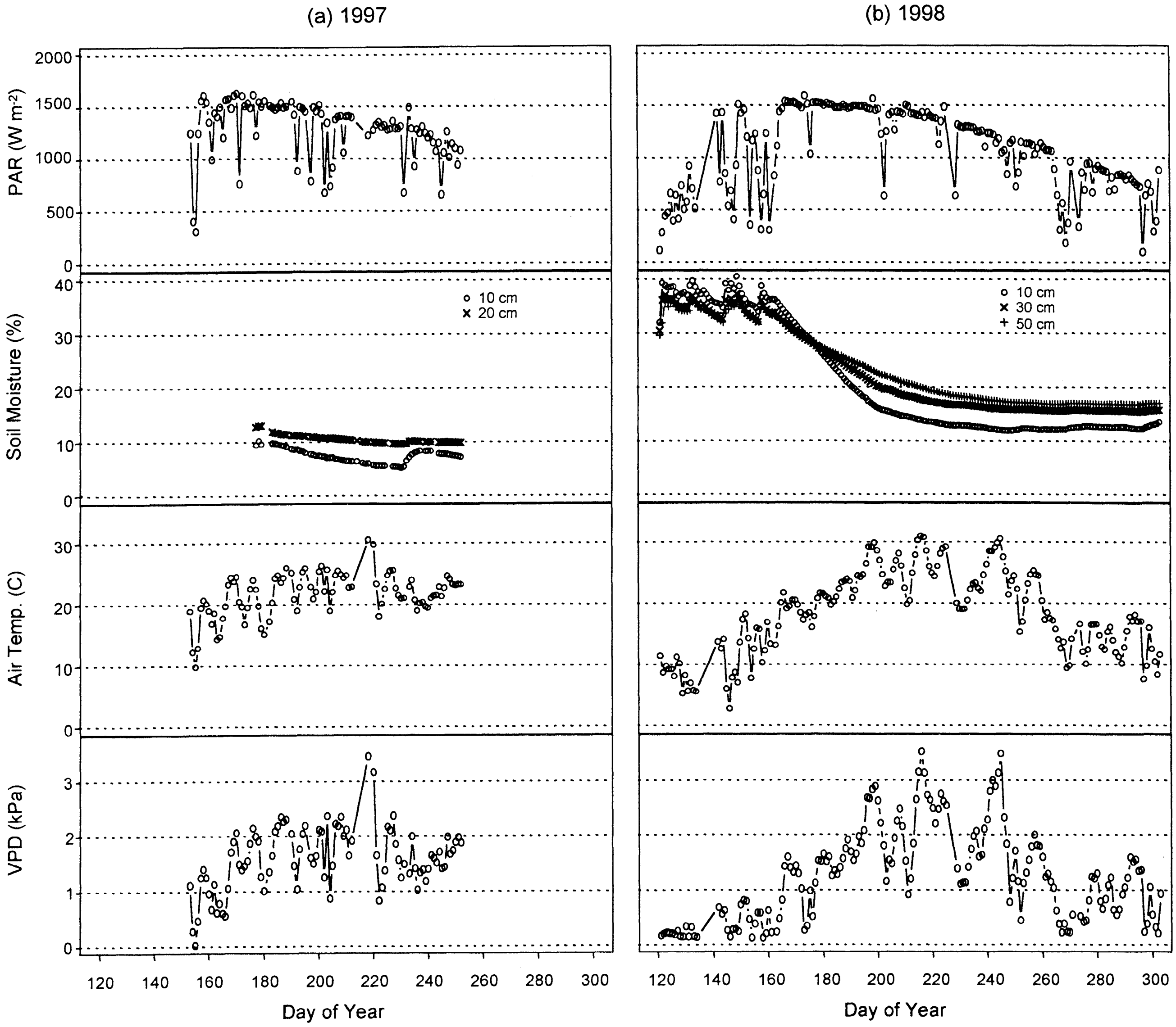

Figure 2. 1997 daytime mean PAR, soil moisture at 10 and 20 cm, air temperature, and vapor pressure deficit and 1998 daytime mean PAR, soil moisture at 10, 30, and 50 cm, air temperature, and vapor pressure deficit.

1997 and 1998 are shown in Figure 2. Owing to the Mediterranean climate, this area typically remains sunny and hot with little rainfall for most of the summer. The climatic variables show that this was true for the entire measurement period in 1997 and after June 15 (day 166) in 1998.

In general, spring 1997 was warm and dry while spring 1998 was cool and wet (Table 1). Warmer temperatures in spring 1997 resulted in an earlier budbreak in 1997 compared to 1998. Further, owing to the differences in spring rainfall in 1997 and 1998, summer soil moisture in 1997 was relatively low and summer soil moisture in 1998 was relatively high. On day 177, soil moisture at 10 cm was 9.5 and 30% in 1997 and 1998, respectively (Figure 2). In both 1997 and 1998, soil moisture decreased through the summer. The summer minimum at 10 cm was 5% in 1997 and 12% in 1998.

The pre dawn water potential of the pine trees provides information on the water status of the trees. Water potential in ponderosa pine ranges from −0.2 MPa under optimal conditions to −0.7 MPA, when drought-induced stomatal closure occurs [*Bassman*, 1988]. In late spring 1997 the pre dawn water potential was already below −0.4 MPa (Panek and Goldstein, submitted manuscript, 1999) (Table 2). The pre dawn water potential continued to decrease during the summer indicating drier soil conditions and less water available to the plants. Pre dawn water potential reached −1.0 MPa by the end of the summer in 1997 indicating extant drought stress. In contrast, pre dawn water potential in 1998 remained above or close to −0.3 MPa until day 200 indicating

Table 1. Spring Rainfall, Last Day of Freezing Temperature, Budbreak, and Soil Moisture at 10 cm for 1997 and 1998

	1997	1998
Rainfall: Feb. 1 to June 1, cm	18	117
Rainfall % of normal: Feb. 1 to June 1, cm	-27%	+176%
Last day of temperature < 0°C (day of year)	121	146
Budbreak (day of year)	145-150	180-185
Soil moisture: day 177, %	9.3	33.0
Soil moisture: lowest point, %	5.2	11.8

Table 2. 1997 and 1998 Predawn Water Potential (MPa) of the Ponderosa Pine Trees

	Predawn Water Potential, MPa	
Day	1997	1998
151	-0.43	
155		-0.24
158	-0.49	
168	-0.63	
177		-0.26
182	-0.60	
188		-0.31
196		-0.28
203	-0.71	
210		-0.45
217		-0.53
223		-0.53
241	-1.0	

little or no water stress. By day 210 in 1998 the pre dawn water potential had decreased to –0.4 MPa and by day 220 the pre dawn water potential was around –0.5 MPa. This indicates that the trees were mildly drought-stressed by day 220. While the ecosystem did become dry in the summer of 1998, the ecosystem started out with more soil moisture in 1998 than in 1997 and so the drought stress was delayed until later in the summer and was relatively mild.

Air temperature and vapor pressure deficit varied together in both years during the measurement period (Figure 2). In 1997, air temperature and vapor pressure deficit were highest in the middle of the summer (days 170-225) with one extreme heat event in 1997 that occurred around day 219. In 1998 daytime mean air temperature and vapor pressure deficit remained fairly low until day 180 but then steadily increased to the maximum that occurred on day 216. Summer 1998 had a more prolonged period of hot and dry air conditions with four extreme heat events.

On the basis of the environmental and phenological conditions, the measurement period of each year was divided into four time periods (Table 3). In 1997 these time periods were defined largely by soil moisture, air temperature, and vapor pressure deficit. The first time period in 1997 (days 153-175) was a period of highest soil moisture, highest PAR, low air temperature, and low vapor pressure deficit. In time period 2 (days 176-216), soil moisture and PAR had decreased, and air temperature and vapor pressure deficit had increased. Time period 3 (days 217-221) was a short period with extremely high air temperature and vapor pressure deficit; PAR was slightly lower and soil moisture was very low. Time period 4 (days 222-253) was the last time period and had lowest PAR; soil moisture, air temperature and vapor pressure deficit were moderately low. In 1998, phenology was considered in defining the time periods in addition to soil moisture, air temperature, and vapor pressure deficit. The first time period (days 120-197) covers the time until shortly after budbreak. The time period just after budbreak (198-213) had high air temperatures and vapor pressure deficit but also high soil moisture and high PAR. By the third time period (days 214-226), soil moisture had decreased substantially but was still higher than the highest point measured in 1997. During time period 3 air temperature and vapor pressure deficit were high, and PAR had decreased. The fourth time period (days 239-303) had the lowest soil moisture and had moderate to low vapor pressure deficit and air temperatures and low PAR. It is also important that during the fourth time period the oldest needles began to senesce and photosynthetic and stomatal activity decreased to winter levels (Panek and Goldstein, submitted manuscript, 1999).

3.2. Seasonal Ozone Concentration and Flux

During the summer, daytime mean ozone concentration typically ranged from 40 to 80 ppb (Figure 3). The highest ozone concentration measured during the 1997 measurement period occurred during the major heat event (days 217 to 220); half-hour values were often greater than 100 ppb and went above 120 ppb on days 219 and 220. In 1998, ozone concentrations were low before day 160 and after day 260 and relatively high in between days 160 and 260. Ozone concentration exceeded 100 ppb only a few times during the measurement period in 1998 and did not get as high as in 1997.

In both years, flux of ozone to the ecosystem was highest ~3-4 weeks after budbreak with daytime mean ozone flux of 70-80 μmol m^{-2} hr^{-1} (Figure 3). Following the peak in both years, ozone flux gradually decreased, corresponding to increasing water stress. In 1997 the lowest ozone fluxes of the measurement period occurred during the major heat event: this was coincident to the time of highest ozone concentration (days 217-220). In 1998, ozone flux was low prior to budbreak and in midfall as the trees began shutting down.

Table 3. Time Periods and Corresponding Environmental and Phenological Conditions Used for Analysis

Time Period	Symbol	Environmental Conditions
1997		
153-175	filled square	highest soil moisture of 1997; highest PAR[a] of 1997; low air temperature and VPD[b]
176-216	filled circle	moderate soil moisture; moderate PAR; high air temperature and VPD
217-221	filled triangle	very low soil moisture; moderate PAR; very high air temperature and VPD
222-253	filled diamond	lowest PAR of 1997; moderate soil moisture; moderate temperature and VPD
1998		
120-197	filled square	pre budbreak
198-213	filled circle	very high soil moisture; high PAR; high air temperature and VPD
214-226	filled triangle	high soil moisture; lowest PAR; high air temperature and VPD
239-303	filled diamond	moderate soil moisture; lowest PAR; low air temperature and VPD; senescence and reduced activity

[a] PAR = photosynthetically active radiation
[b] VPD = vapor pressure deficit

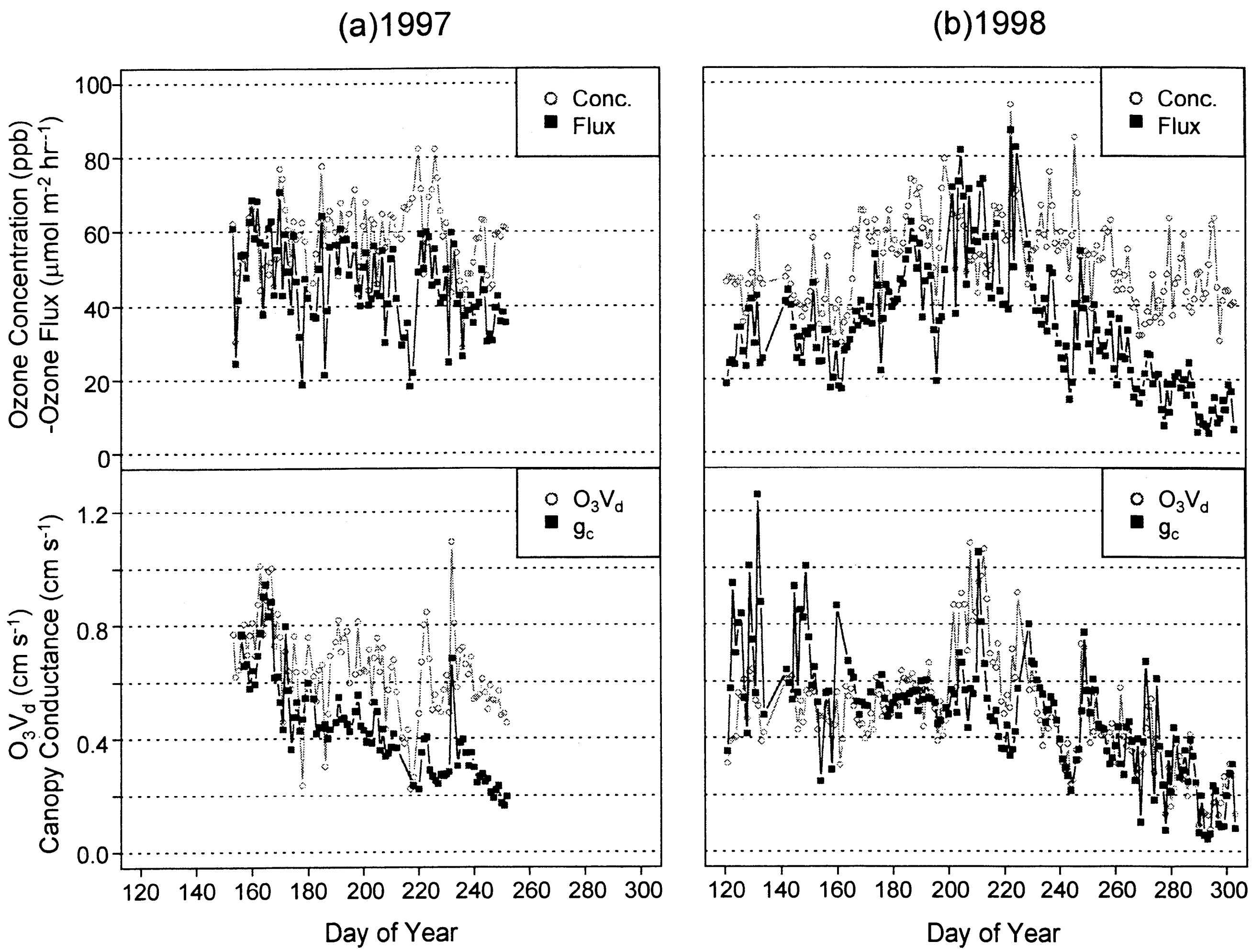

Figure 3. (a) 1997 daytime mean ozone concentration and ozone flux versus day of year, and daytime mean ozone deposition velocity and canopy conductance versus day of year. (b) 1998 daytime mean ozone concentration and ozone flux versus day of year, and daytime mean ozone deposition velocity and canopy conductance versus day of year.

During the summer 1998, ozone flux did not show any decreases as dramatic as in 1997.

Ozone concentration and ozone flux were found to significantly vary together ($p \ll 0.01$ for both years). The data were examined based on the time periods outlined in Table 3. Ozone concentration and ozone flux were found to be coupled 75% or more of the time in all but two time periods. The first of the time periods with coupling less than 75% occurred during time period 3 of 1997 (the heat event). During this period the coupling between ozone concentration and flux dropped to 25%. Ozone flux remained very low during this time period despite the high ozone concentration. Decoupling to this extent did not occur at any time during the summer of 1998 even though air temperatures and vapor pressure deficits were as extreme and continued for longer periods of time. The second time period with coupling of ozone concentration and ozone flux less than 75% occurred in 1998 with senescence and a seasonal decline in activity (time period 4): the coupling between ozone concentration and ozone flux was 65% during this period.

In 1998, while daytime mean ozone concentration and daytime mean ozone flux were coupled during each measurement period, the exact relationship between them varied greatly over the whole field season. For example, given a daytime mean ozone concentration of 65-66 ppb, daytime mean ozone flux was found to vary from 41 µmol m^{-2} hr^{-1} and 82 µmol m^{-2} hr^{-1} (Table 4).

3.3. Seasonal Ozone Deposition Velocity

Daytime mean ozone deposition velocity followed the same general trend as ozone flux in both years (Figure 3) with the highest ozone deposition velocity occurring 3-4 weeks after budbreak. Since the timing of budbreak is strongly influenced by timing of the last freezing temperature, climate plays an important role in the timing of peak ozone deposition velocity. According to the 1998 data the peak in ozone deposition occurred around day 205 even though daytime mean PAR had peaked over 40 days prior, soil moisture at 10

Table 4. Ozone Concentration and Flux for Days 170, 205, 234, and 296 in 1998

Day of Year	O_3 Concentration, ppb	O_3 Flux, µmol m^{-2} hr^{-1}
170	65	41
205	65	82
234	65	34
296	65	15

and 50 cm had decreased to 15 and 25%, respectively, air temperature was high (daytime mean air temperature of 25 30°C) and vapor pressure deficit was moderately higl (daytime mean vapor pressure deficit of 1.5-2.0 kPa).

There is a direct relationship between canopy conductanc and ozone deposition velocity (r^2=0.68 in 1997 and r^2=0.63 1998 after day 180). Canopy conductance was significant. higher than ozone deposition velocity in 1998 at the beginning of the measurement period (Figure 3). This occurred because the soil was wet and soil evaporation was an important component of canopy conductance. After the soil surface dried, agreement between ozone deposition velocity and canopy conductance improved. During days 217-220 in 1997 (the heat event) canopy conductance dropped substantially. Low canopy conductance results in low gas exchange as was observed in the ozone flux (Figure 3). Canopy conductance did not get this low in the summer of 1998.

Canopy conductance is believed to be strongly controlled y the climatic factors of PAR, soil moisture, VPD, and air emperature; therefore these factors should exert control over ɔzone deposition velocity. There was a negative linear correlation between ozone deposition velocity and vapor pressure deficit in 1997. The intercept of this relationship was controlled by soil moisture (Figure 4). In 1998, there was no clear relationship between ozone deposition velocity and vapor pressure deficit (Figure 4). The relationship in 1997 indicates that VPD is controlling stomatal aperture which is in turn dominating the uptake of ozone. The lack of relationship in 1998 could be due to two factors. Dew and other forms of moisture might have been acting as a sink for ozone, so that ozone deposition velocity was only weakly tied with stomatal aperture and confounded the expected relationship with VPD. More likely it has to do with the abundant understory of *Ceonothus* and manzanita. Both are highly drought-tolerant shrubs which can remain physiologically active to water

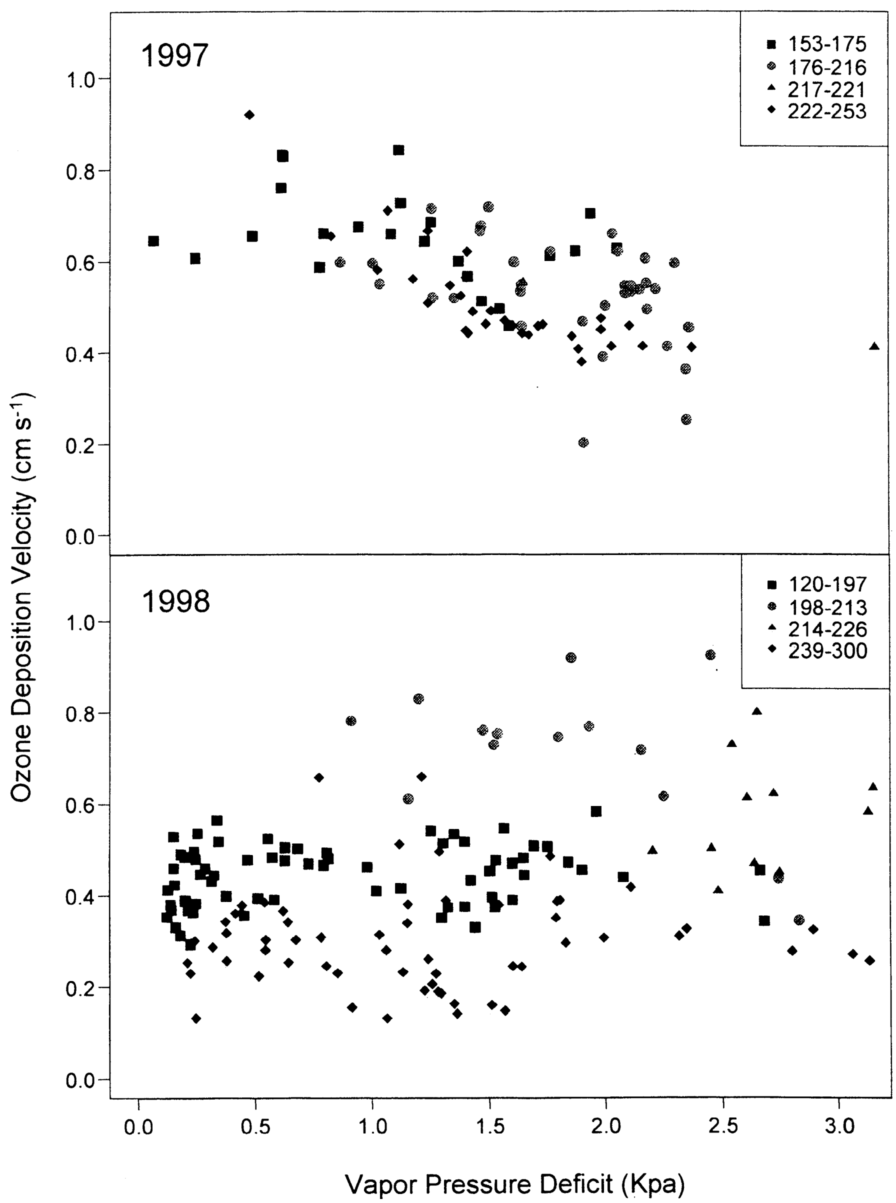

Figure 4. Daytime mean ozone deposition velocity versus vapor pressure deficit for 1997 and 1998.

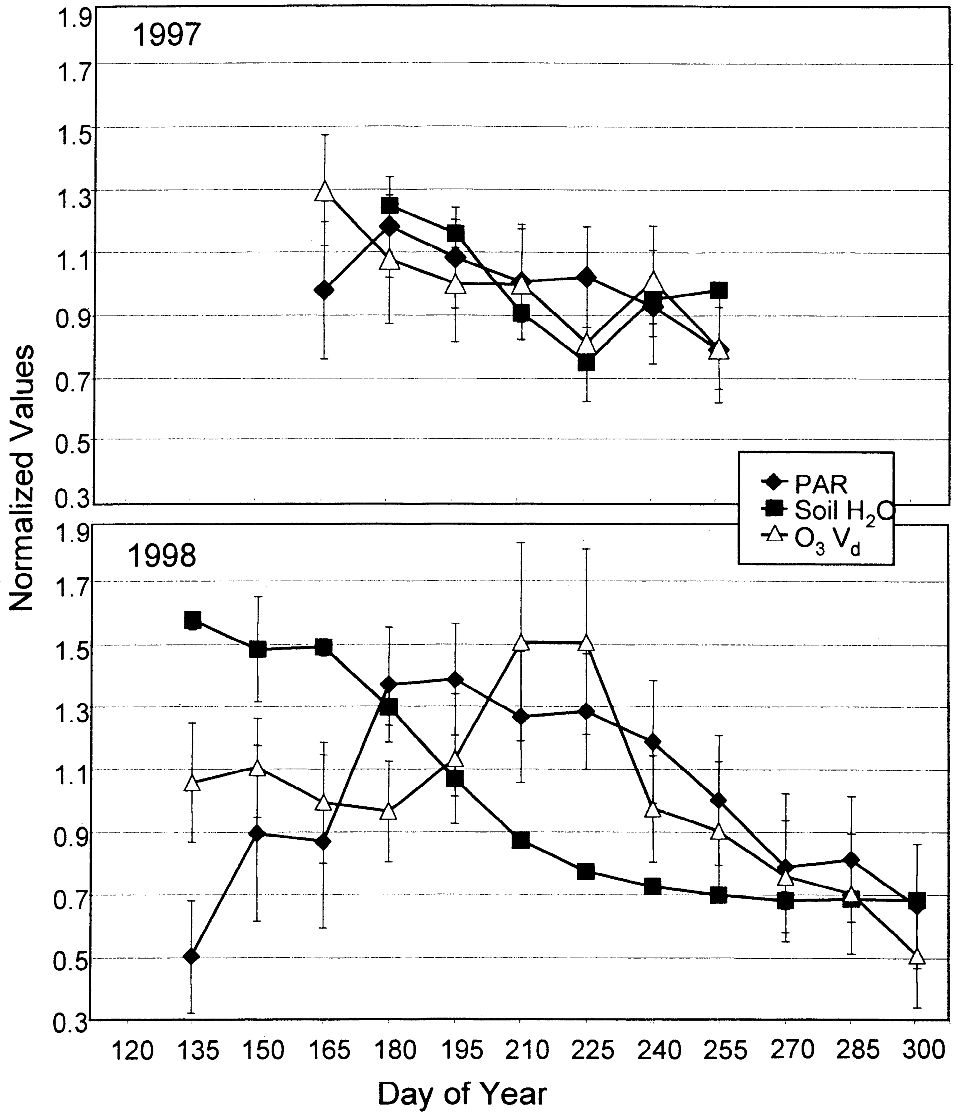

Figure 5. 15-day averages of normalized PAR, soil moisture, and ozone deposition velocity for 1997 and 1998.

potentials of around –8 MPa [*Dunne and Parker*, 1999]. They were probably not drought stressed in 1998, and therefore stomatal aperture did not respond to VPD. Since vapor pressure deficit and air temperature are directly related, air temperature showed a similar relationship as vapor pressure deficit to ozone deposition velocity.

PAR and soil moisture change on a timescale of weeks instead of days so 15-day averages of PAR and soil moisture at 10 cm were compared to ozone deposition velocity (Figure 5). In 1997, ozone deposition velocity decreased after day 183 with PAR; however, the relationship between ozone deposition velocity and soil moisture was more striking (Figure 5). The 15-day averages for 1998 show ozone deposition velocity was independent of soil moisture until after day 225 when soil moisture had dropped to 13%. Even then, ozone deposition velocity appeared to be more strongly related to PAR (Figure 5).

3.4. Diurnal Ozone Concentration and Flux

The diurnal patterns of ozone concentration and flux in 1997 and 1998 were similar (Figure 6). Ozone concentration and ozone flux were similarly lowest at night. While both ozone concentration and flux were highest during the day, their diurnal patterns were dissimilar. After sunrise ozone concentration increased until the maximum was reached at around 1800 LT and then diminished to the nighttime level. In contrast to ozone concentration, ozone flux increased rapidly just after sunrise and then reached its maximum shortly after noon. By 1800 LT, when ozone concentration was at its maximum, ozone flux was at half of its daytime maximum and went to essentially zero shortly after. Therefore ozone concentration and flux were decoupled during the day.

3.5. Diurnal Ozone Deposition Velocity

An analysis of ozone deposition velocity was done for four time periods representing different climate regimes (Figure 7). A phenomenon observed during all periods was a morning "gasp": low-ozone deposition velocity values at night followed by a rapid increase shortly after sunrise and a spike in the early morning. Overnight plants recharge their water supply so when they first open their stomata in the morning, they have the highest water potential they will have for the day. Also, air temperature and vapor pressure deficit are typically low in the morning. The combination of the low air temperature and vapor pressure deficit coupled with the high water potential when the plants first opened their stomata likely resulted in the high ozone deposition velocity in the early morning.

The diurnal pattern of ozone deposition velocity was examined for each of the time periods outlined in Table 3 (Figure 7). The first time period in 1997 (days 153-175) was a period of highest soil moisture, highest PAR, low air temperature, and low vapor pressure deficit. This period had the highest midday maximum value of 1.0 cm s^{-1} that occurred shortly after noon. In time period 2 (days 176-216), soil moisture and PAR had decreased, and air temperature and vapor pressure deficit had increased. The maximum value during this period was only 0.8 cm s^{-1} and the diurnal pattern was slightly shortened due to shorter day length (PAR). Time period 3 (days 217-221) was a short period with extremely high air temperature and vapor pressure deficit, and very low soil moisture. Midday maximum ozone deposition velocity reached only 0.5 cm s^{-1} and then went to zero earlier than any other time period. High air temperature and vapor pressure deficit on top of the low soil moisture caused severely restricted ozone uptake. This was especially important as this was the period of highest ozone concentration. Time period 4 (days 222-253) was the last time period and had lowest PAR; soil moisture, air temperature, and vapor pressure deficit returned to low values similar to those in time period 2. The diurnal pattern during this time looked very similar to that of time period 2 in both shape and magnitude; the biggest difference being the shorter diurnal cycle due to day length.

The first time period of 1998 (days 120-197) was wet and cool; however, ozone deposition velocity remained low (hourly maximum of 0.6 cm s^{-1}) until after budbreak (Figure 7). The time period just after budbreak (198-213) had high air temperatures and vapor pressure deficit but also high soil moisture. This was the period of highest ozone deposition velocity (hourly maximum of 1.1 cm s^{-1}). By the third time period (days 214-226), soil moisture had decreased substantially but was moderately high. This period had air conditions as hot and dry as the short period in 1997 that had drastically reduced ozone deposition velocity. Despite the hot and dry air conditions, ozone deposition velocity during this period was fairly high with hourly maximum values of 0.8 cm s^{-1}. Therefore, with moderate soil moisture levels in 1998, high air temperature and vapor pressure deficit did not markedly reduce ozone deposition velocity. The fourth period (days 239-303) had the lowest soil moisture and had moderate to low temperatures. Ozone deposition velocity was low during this period as a result of both low soil moisture, decreased photosynthetic activity, and senescence of older needles.

3.6. Cumulative Ozone Flux

Daytime cumulative ozone flux for 1997 and 1998 starting on day 155 is shown in Figure 8. In 1997 the rate of ozone uptake remained fairly steady for the entire measurement period. In contrast, the rate of ozone uptake in 1998 was low at first, became high in the middle of the summer, and then became low again in early fall. Early in the summer there were marked differences between 1997 and 1998 in the amount of cumulative ozone flux: by day 175, cumulative ozone flux of 1997 was 50% higher than that of 1998. This difference was likely the result of delayed budbreak in 1998. After budbreak ozone flux in 1998 increased substantially and cumulative flux increased at a rate higher than at any time in 1997. In 1998 there was 30% more biomass which likely

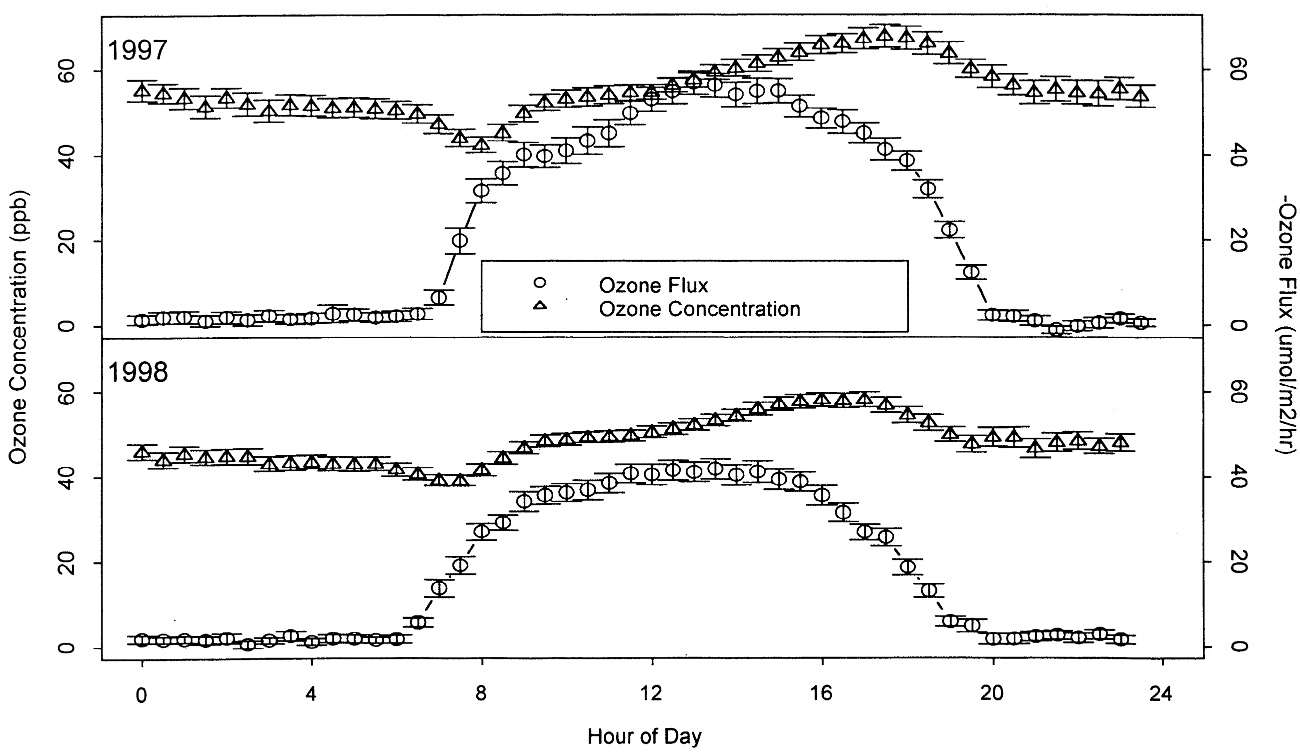

Figure 6. Mean hourly values of ozone concentration and ozone flux into the ecosystem for 1997 (days 151 to 252) and 1998 (days 121 to 303).

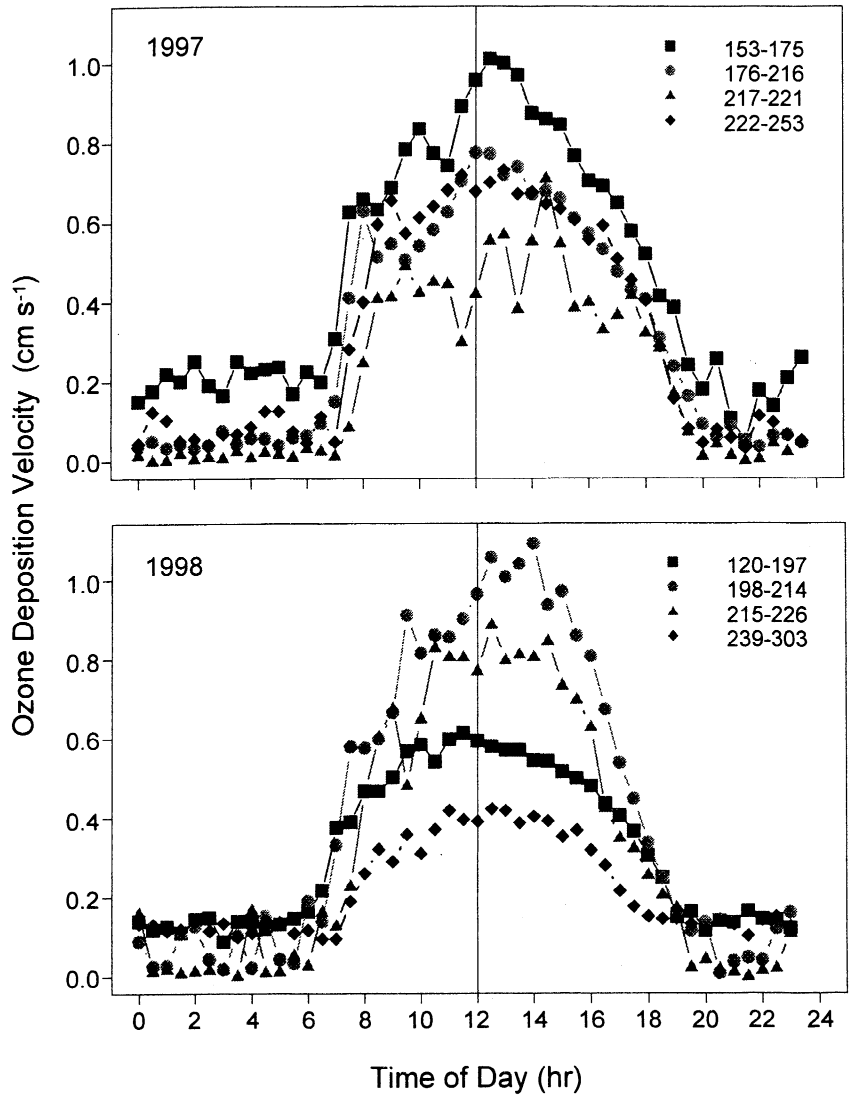

Figure 7. Mean hourly values of ozone deposition velocity, broken down into 4 time periods for 1997 and 1998.

enhanced the rate at which this ecosystem was able to take up ozone. The difference in cumulative ozone flux between 1997 and 1998 shrunk to 4% by day 220: this was just after the heat event in 1997 and the peak rate of ozone flux in 1998. By day 250 the total amount of ozone taken up by the ecosystem in the wet year versus the dry year differed by only 6%. After day 250 in 1998 the system began taking up ozone at a reduced rate as the trees and shrubs began shutting down in the fall.

4. Discussion

Data for summers in 1997 and 1998 indicate that this remote area of the Sierra Nevada Mountains receives significant amounts of ozone during the day. The current national standard for ozone is 80 ppb over 8 hours. During the summer, ozone levels at our site often neared or exceeded this limit.

While the presence of ambient ozone (i.e., ozone concentration) produces the potential for ozone damage to plants, only the amount taken up (i.e., ozone flux) actually damages the plant. Ozone flux to an actively transpiring ecosystem is determined by both ozone concentration and canopy conductance. The significance of this dual control on ozone flux lies in how coupled or decoupled the patterns of ozone concentration and stomatal conductance are. On an hourly timescale, high ozone concentration might not be associated with high fluxes to plants if their stomates are not fully open: this was observed on an hourly timescale at our site in the afternoon during the summer in both 1997 and 1998. Alternatively, high ozone flux can occur even if ambient ozone concentration is low if canopy conductance is high: this was also observed on an hourly timescale at our site in the early morning during the summer in both 1997 and 1998. On a daily timescale, ozone concentration and ozone flux were coupled for all but the hottest and driest days. The coupling of ozone concentration and flux makes the ponderosa pine trees susceptible to high ozone doses during periods of high ozone concentration. While closure of stomates to prevent water loss affords the trees some level of protection from ozone, water stress can also have detrimental effects on tree vigor and growth.

Even though ozone concentration and flux varied in the same direction on a daily timescale during most of the measurement period, they were not related in a set quantitative way. The changing relationship between ozone concentration and ozone flux adds additional complexity in determining ozone dose to plants from ozone concentration data so that even when ozone concentration and flux were coupled, no quantitative assessment could be made of dose to plants without additional information on plant physiological activity. Often, exposure of plants to ozone is determined by ambient ozone concentration. Both the decoupling of ozone concentration and flux and varying relationship between ozone concentration and flux demonstrate that daily ambient concentration does not provide an adequate measure of ozone dose to plants.

The role of climate had significant effects on the rates of ozone deposition as mediated through stomatal conductance. Examples include the morning gasp, the severely reduced ozone uptake during the 1997 heat event, and the high ozone deposition roughly 3 weeks after budbreak. The exact relationship between ozone flux and the climatic variables is not easy to tease apart because the climatic variables are not independent of each other. For example, vapor pressure deficit was closely related to ozone deposition velocity in the year with low soil moisture but not in the year with higher soil moisture.

Even with the interdependence of the climatic variables, some general conclusions can be drawn. Phenology affected ozone uptake through timing of budbreak in the spring and senescence and reduced activity in the fall. Minimum temperature during the spring was important in determining the timing of the highest ozone deposition during the summer because it determined when budbreak occurred. In both years, ozone deposition rates peaked roughly 3 weeks after budbreak. The increase in biomass is likely part of the explanation for the increase in ozone uptake shortly after budbreak, but it is also possible that new foliage is a more effective sink for ozone than older foliage. It has been observed that new red spruce needles are more effective at removing ozone than older red spruce needles [*Rebbeck et al.*, 1993]. It is not known why new needles are more effective at ozone uptake, but it has been postulated that new needles have more oxidizeable sites and that over time the oxidizeable sites become "used up" [*Wieser and Havranek*, 1996]. It is also noteworthy that budbreak not only affected the timing of peak ozone deposition velocity but also the cumulative ozone flux. In 1998 the delayed budbreak resulted in a shortened period of active gas exchange and thus a lower cumulative ozone flux than that of 1997. In addition to allowing us to capture the ozone deposition signal before and after budbreak, the 1998 data set was long enough to allow us to observe the reduced fall activity and senescence. Ozone deposition rates became very low as this occurred.

The water status of a plant is influenced by both water in the air (vapor pressure deficit) and water in the soil (soil moisture). Owing to the low precipitation and high vapor pressure deficits, ecosystems in the Sierra Nevada Mountains typically become water limited in the middle to late summer. With this increasing drought stress, pines close their stomates earlier in the day to prevent water loss which limits uptake of ozone. Therefore drought stress can result in decreased ozone uptake by pine. Ozone deposition was observed to decrease as soil moisture decreased in both years although this effect was much more pronounced in 1997. Ozone deposition was also observed to decrease with increasing vapor pressure deficit; however, this relationship was much stronger in 1997 than in 1998. Therefore, during the year when the trees were severely drought-stressed (1997), ozone deposition velocity was much more sensitive to vapor pressure deficit. This suggests that there is a threshold of soil moisture: when soil moisture stays above this threshold (1998) the water status of the plants does not play an important role in ozone deposition, but when soil moisture drops below this threshold the water status of the plants plays an important role in controlling ozone deposition. The relationship between vapor pressure deficit and ozone deposition is especially important because

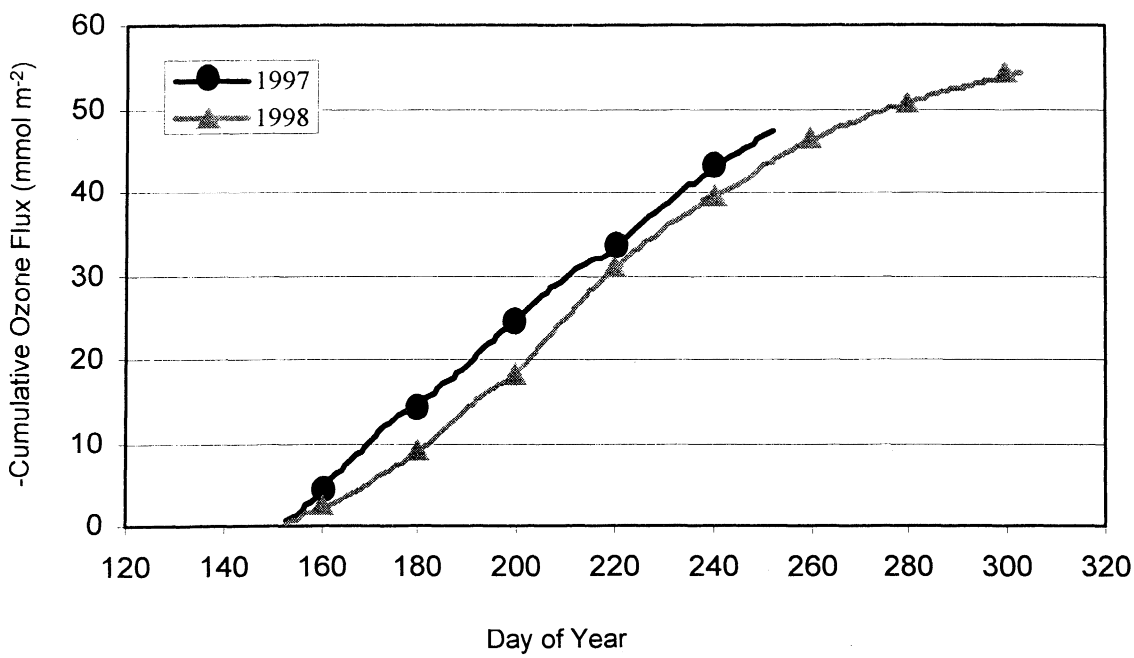

Figure 8. Cumulative ozone flux in 1997 and 1998.

times of high vapor pressure deficit tend to correspond to times of high ozone concentration. This occurs because vapor pressure deficit and ozone concentration are related through air temperature: an increase in air temperature causes an increase in both vapor pressure deficit and ozone concentration. Therefore the response of plants to vapor pressure deficit affords plants some protection from high doses of ozone when soil moisture is low. The results from this study suggest that soil moisture plays an important role in this relationship.

It is clear that climate plays an important role in ozone deposition to ponderosa pine ecosystems in the Northern Sierra Nevada Mountains. Despite the drastically different climates in 1997 and 1998, cumulative ozone flux for 1997 and 1998 differed by only 6%. It is possible this indicates that cumulative seasonal ozone flux is independent of annual climate variations; however, the data more strongly suggest that the two extreme years simply had different limiting factors. In 1997 the water status of the plants appears to have acted as the major control on ozone deposition. In 1998 water availability was high, and so the water status of the plants did not exert strong control on ozone deposition. However, spring and early summer of 1998 were not only anomalously wet but also anomalously cold resulting in delayed budbreak. Since the new foliage are likely more effective at taking up ozone and late budbreak results in a shorter period of active gas exchange, delayed budbreak translates into lower cumulative ozone uptake. On the basis of the results of this study, we can hypothesize that very dry and cold years should be water-limited and have a delayed budbreak and therefore should have the lowest ozone uptake. Conversely, wet and warm years should not be water limited and should have an early budbreak: these years would be expected to have the highest ozone uptake.

The focus of this discussion has been on the ponderosa pine trees because they are a dominant tree species in the Sierra Nevada Mountains, they are economically important, and they are among the most sensitive tree species to ozone. However, it is important to note that the shrubs at the study site (and throughout the Sierra Nevada Mountains) are an important component of the ecosystem. The presence of shrubs would not decrease the total amount of ozone being taken up by the ponderosa pine trees, but it likely elevates the total amount of ozone being deposited to this ecosystem. Removal of shrubs is a common management practice on commercial tree stands: the effect of this practice on ozone deposition is an active area of research at this site.

5. Conclusions

This region of the Sierra Nevada Mountains experienced moderately high levels of ozone in both summer of 1997 and summer of 1998. The effect of these chronic, moderately high levels of ozone on ponderosa pine trees is likely to be manifested in biochemical alterations (i.e., antioxidant levels) rather than observable needle damage. While the total ozone deposition during the summer in 1997 and 1998 were similar, it is clear that the patterns of and controls on ozone deposition in each year were dissimilar. Thus interannual climate variability had a strong influence on the physiological function of this Mediterranean-type ecosystem, resulting in strong interannual differences in the temporal pattern of ozone deposition. Ozone concentration and ozone flux were found to be decoupled over the course of the day and under dry climatic conditions. The implications of this are that the pines are not necessarily receiving high doses of ozone when the ozone concentration is high. Unfortunately, this also means that daily ambient ozone concentration is not a reliable metric to assess the potential for ozone damage to pines in the Sierra Nevada Mountains. Both climatic factors and phenology were found to play a major role in controlling ozone deposition. This general conclusion has been supported by previous modeling efforts; however, specific phenomena related to this drought-stressed ecosystem such as the "morning gasp" have yet to be produced or investigated using models. Further, the effect of vapor pressure deficit on ozone deposition was found to depend on soil moisture: this, also, deserves additional attention in a modeling framework.

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References

Arbaugh, M.J., P.R. Miller, J.J. Carroll, B. Takemoto, and T. Proctor, Relationships of ozone exposure to pine injury in the Sierra Nevada and San Bernadino Mountains of California, USA, *Environ. Poll.*, *101*, 291-301, 1998.

Baker, B., A. Guenther, J. Greenberg, A. Goldstein, and R. Fall, Canopy fluxes of 2-methyl-3-buten-2-ol over a ponderosa pine forest by relaxed eddy accumulation: Field data and model comparison, *J. of Geophys. Res.*, *104*, 26,107-26,114, 1999.

Baldocchi, D.D., B.B. Hicks, and P. Camara, A canopy stomatal resistance model for gaseous deposition to vegetated surfaces, *Atmosph. Environ*, *2* (1), 91-101, 1987.

Bassman, J.H., Photosynthesis and water relations of ponderosa pine, in *Ponderosa Pine: The Species and its Management*, edited by D.M. Baumgartner and J.E. Lotans, pp. 45-71, Washington State University, Pullman, Wash., 1988.

Bytnerowicz, A., Physiological aspects of air pollution stress in forests, *Phyton (Horn)*, *36*, 15-22, 1996.

Cahill, T.A., J.J. Carroll, D. Campbell, and T. Gil, Air quality, In *Sierra Nevada Ecosystem Project*, Wildland Resour. Cen., Davis, Calif., 1996.

Chambers, S.D., J.M. Hacker, and A.G. Williams, *RAMF Version 8.1 User's Manual*, 2nd Ed., Flinders University of South Australia, Adelaide, Australia, 1997.

Coleman, M.D., J.G. Isebrands, R.E. Dickson, and D.F. Karnosky, Photosynthetic productivity of aspen clones varying in sensitivity to tropospheric ozone, *Tree Physiol.*, *15*(9), 585-592, 1995.

Dunne, J.A., and V.T. Parker, Species-mediated soil moisture availability and patchy establishment of Psuedotsuga menziessi in chapparal, *Oecologia*, *119*(1), 36-45, 1999.

Galbally, I.E., and C.R. Roy, Destruction of ozone at the earth's surface, *Q. J. R. Meteor. Soc.*, *106*, 599-620, 1980.

Goldstein, A.H., N.E. Hultman, J.M. Fracheboud, M.R. Bauer, J.A. Panek, M. Xu, Y. Qi, A.B. Guenther, and B. Baugh, Effects of climate variability on the carbon dioxide, water, and sensible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA), *Agric. For. Meteorol.*, *101*, 113-129, 2000.

Gusten, H., and G. Heinrich, On-line measurements of ozone surface fluxes, 1, Methodology and instrumentation, *Atmos. Environ.*, *30*(6), 897-909, 1996.

Gusten, H., G. Heinrich, E. Monnich, D. Sprung, J. Weppner, A.B. Ramadan, M. Eldin, D.M. Ahmed, and G.K.Y. Hassans, On-line measurements of ozone surface fluxes, 2, Surface-level ozone fluxes onto the Sahara Desert, *Atmosph. Environ.*, *30*(6), 911-918, 1996.

Haagen-Smit, A.J., Chemistry and physiology of Los Angeles Smog, *Ind. Eng. Chem.*, *44*, 1342-1346, 1952.

Heath, R.L., Ozone, in *Responses of Plants to Air Pollution*, edited by J.B. Mudd, and T.T. Koslowski, Academic, San Diego, Calif., 1975.

Hsieh, C.I., G.G. Katul, J. Schieldge, J.T. Sigmon, and K.R. Knoerr, The Lagrangian stochastic model for fetch and latent heat flux estimation above uniform and nonuniform terrain, *Water Resour. Res.*, *33*, 427-438, 1997.

Kaimal, J.C., and J.J. Finnegan, *Atmospheric Boundary Layer Flows - Their Structure and Measurement*, 289 pp., Oxford Univ. Press, New York, 1994.

Lamanna, M., and A.H. Goldstein, In-situ measurements of C2-C10 VOCs above a Sierra Nevada pondersa pine plantation, *J. of Geophys. Res.*, *104*, 21,247-21,262, 1999.

Leuning, R., and M.J. Judd, The relative merits of open- and closed-path analysers for measurement of eddy fluxes, *Global Change Biol.*, *2*, 241-253, 1996.

Miller, P.R., and J.R. McBride, Trends of ozone damage to conifer forests in the western United States, particularly southern California, in *Air Pollution and Forest Decline: Proceedings of the 14th International Meeting for Specialists in Air Pollution Effects on Forest Ecosystems*, edited by J.B. Bucher, and I. Bucher-Wallin, pp. 56-64, International Union of Forest Research Organizations, Interlaken Switzerland, 1988.

Miller, P.R., M.A. Poth, A. Bytnerowicz, M.E. Fenn, P.J. Temple, J.C. Chow, J.G. Watson, C. Frazier, M. Green, and D.W. Johnson, Ecosystem alterations in soil nutrient cycling: An integrated measure of cumulative effects of acidic deposition on a mixed conifer forest in southern California, Calif. EPA Air Resour. Board, Sacramento, 1996.

Moncrieff, J.B., Y. Malhi, and R. Leuning, The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water, *Global Change Biol.*, *2*, 231-240, 1996.

Monteith, J.L., and M.H. Unsworth, *Principles of Environmental Physics*, 291 pp., Edward Arnold, London, 1990.

Musselman, R.C., and W.J. Massman, Ozone flux to vegetation and its relationship to plant response and ambient air quality standards, *Atmos. Environ.*, *33*, 65-73, 1999.

Pell, E.J., N.A. Eckardt, and R.E. Glick, Biochemical and molecular basis for impairment of photosynthetic potential, *Photosynthesis Res.*, *39*, 453-462, 1994.

Peterson, D.L., M.J. Arbaugh, and L.J. Robinson, Regional growth changes in ozone-stressed ponderosa pin (*Pinus ponderosa*) in the Sierra Nevada, California, USA, *Holocene*, *1*, 50-61, 1991.

Rebbeck, J., K.F. Jensen, and M.S. Greenwood, Ozone effects on grafted mature and juvenile red spruce: photosynthesis, stomatal conductance, and chlorophyll concentration, *Can. J. For. Res.*, *23*, 450-456, 1993.

Rissmann, J., and G. Tetzlaff, Application of a spectral correction method for measurements of covariances with fast-response sensors in the atmospheric boundary layer up to a height of 130 m and testing of the corrections, *Boundary Layer Meteorol.*, *70*, 293-305, 1994.

Sasek, T.W., and C.J. Richardson, Effects of chronic doses of ozone on loblolly pine - photosynthetic characteristics in the 3rd growing season, *For. Sci.*, *35*, 745-755, 1989.

Schade, G.W., A.H. Goldstein, and M.S. Lamanna, Are monoterpene emissions influenced by humidity?, *Geophys. Res. Lett.*, *26*, 2187-2190, 1999.

Shuttleworth, W.J., et al., Eddy correlation measurements of energy partition for Amazonian forest, *Q. J. R. Meteorol. Soc.*, *110*, 1143-1162, 1984.

Taylor, G.E., Jr., D.T. Tingey, and H.C. Ratsch, Ozone flux in Glycine max (L.) Merr.: sites of regulation and relationship to leaf injury, *Oecologia*, *53*, 179-186, 1982.

Temple, P.J., G.H. Riechers, P.R. Miller, and R.W. Lennox, Growth responses of ponderosa pine to long-term exposure to ozone wet and dry acidic deposition and drought, *Can. J. For. Res.*, *23*, 59-66, 1993.

Turner, N.C., P.E. Waggoner, and S. Rich, Removal of ozone from the atmosphere by soil and vegetation, *Nature*, *250*, 486-489, 1974.

Unsworth, M.H., and D.P. Ormrod, *Effects of Gaseous Air Pollution in Agriculture and Horticulture*, Butterworths, London, 1982.

Van Ooy, D.J., and J.J. Carroll, The spatial variation of ozone climatology on the western slope of the Sierra Nevada, *Atmosph. Environ.*, *29*, 1319-1330, 1995.

Wieser, G., and W.M. Havranek, Evaluation of ozone impact on mature spruce and larch in the field, *Plant Physiol.*, *148*, 189-194, 1996.

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