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Chapter 4

Ozone uptake by ponderosa pine in the Sierra Nevada: A measurement perspective

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Abstract

Measurements of ozone (O_3) deposition to sensitive forested ecosystems are needed to understand the processes controlling deposition, to quantify the physiologically relevant fraction of the total deposition, and to provide data sets for developing and testing deposition models. Ozone deposition to an ecosystem can occur through stomatal uptake, non-stomatal deposition, or through gas phase chemical reactions in the forest canopy. A variety of measurement approaches are needed to separate these terms. In this chapter we discuss approaches for measuring or estimating O_3 deposition at the leaf, soil, plant, ecosystem, and landscape scales. We then summarize major results from several years of measurements in a Sierra Nevada ponderosa pine plantation, showing that O_3 uptake was reduced by approximately 40% due to summer drought even in a relatively wet El Niño year, that significant interannual changes in O_3 uptake occur due to climatically driven changes in timing of phenology and moisture availability, that only 37% of total annual O_3 deposition occurs in summer, and that stomatal uptake accounts for less than half the ecosystem scale O_3 deposition in summer. We then put our Sierra Nevada O_3 deposition measurements in perspective by comparing our results with measured O_3 deposition velocity for sites outside the Sierra Nevada and by comparing ecosystem scale fluxes of O_3 to other trace gases. We conclude with a discussion of future needs for understanding O_3 deposition in the Sierra Nevada.

1. Introduction: The need for measurements of ozone uptake by ponderosa pine

The adverse effects of ozone (O_3) on ponderosa pine trees in the highly polluted mountains downwind of Los Angeles have been well documented over the past 50 years (Miller and McBride, 1988). However, high ambient O_3 concentrations are not necessarily coupled to high O_3 uptake by trees. To cause damage to trees, O_3 must enter leaves through stomatal pores (Reich, 1987; Darrall, 1989; Runeckles, 1992), which open and close under plant control.

The disparity between O_3 uptake and O_3 concentration in the pine forests of the Sierra Nevada has been shown experimentally. Using whole ecosystem measurements of O_3 uptake by the eddy covariance method, Bauer et al. (2000) found that periods of high O_3 deposition (measured as flux to the ecosystem) and periods of high O_3 concentration were decoupled from each other both seasonally and diurnally (Fig. 1). Maximum O_3 deposition coincided with maximum stomatal aperture and preceded the maximum O_3 concentration by about a month during the growing season. As a result, the period of maximum uptake occurred in early summer when the stomata were relatively unconstrained by drought stress but when O_3 levels were not at their seasonal maximum. During periods in late summer, low soil moisture and high atmospheric humidity deficits led to stomatal closure, and despite experiencing the highest ambient O_3 concentrations of the year, the O_3 uptake was lower. Similarly, the period of maximum hourly O_3 uptake occurred in the morning when stomatal conductance was highest, while maximum O_3 concentration occurred in the afternoon.

It is not surprising, therefore, that concentration-based indices of O_3 exposure do not correlate well with measured deposition. Panek et al. (2002) compared the most commonly used metrics of O_3 exposure—SUM0, SUM06, SUM08, and W126—to O_3 deposition measured over the same time period and found that of the metrics that are commonly used, SUM0 best corresponds to measured deposition, but only during periods when the stomata are unconstrained by drought (Fig. 2). Over the entire growing season, the time period when these metrics are usually employed, the estimate of O_3 exposure by SUM0 only explains about 60% of the variance in measured O_3 uptake (Panek et al., 2002). Over the course of the whole year, the discrepancy could be even larger (Kurpius et al., 2002). Thus, in the Sierra Nevada, assessment of O_3 exposure should be considered in terms of O_3 uptake and not in terms of exposure to ambient O_3 concentration.

Measuring O_3 uptake is a more difficult endeavor than measuring O_3 concentration. Because O_3 uptake measurements in the natural environment can be expensive and time-consuming, they are difficult to deploy over long time scales at a wide variety of locations. However, careful *in-situ* measurements at one or a few sites can provide the foundation for building and testing useful models of O_3 deposition.

Measurements at different spatial scales (leaf, whole plant, and whole ecosystem) can be used to elucidate the different processes controlling O_3 deposition, to quantify the physiologically relevant fraction of O_3 deposition, and to provide data sets to build and test physiologically based models. Long-term (year-round and multiyear) measurements of O_3 uptake can provide perspec-

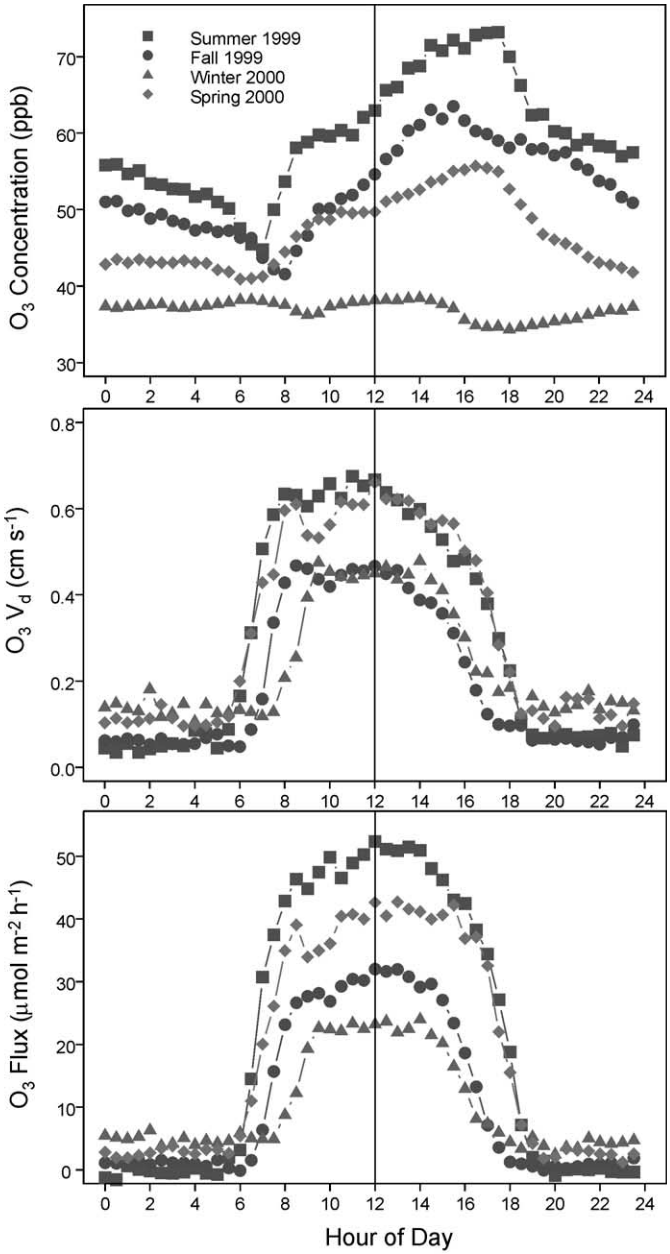


Figure 1. Seasonal patterns of diurnal O_3 concentration, deposition velocity (O_3 V_d) and flux.

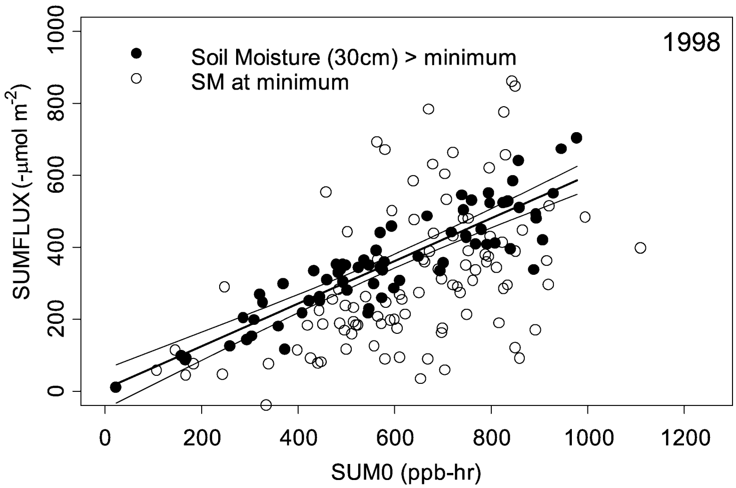


Figure 2. The relationship between the sum of O_3 flux into a young ponderosa pine canopy (SUMFLUX) and the O_3 concentration metric SUM0 for consecutive periods of differing soil moisture over the 1998 growing season. The regression line and the 95% confidence interval are shown (from Panek et al., 2002).

tive on seasonal and inter-annual changes in O_3 uptake and thus provide the only direct measure of the impacts of seasonal and interannual climate variability (such as seasonal drought stress or El-Niño) on physiological controls over O_3 uptake rates. Simultaneous measurements of ecosystem–atmosphere exchange of other associated gaseous species (e.g., H_2O, CO_2, biogenic hydrocarbons, nitrogenous pollutants) can be used to further elucidate the factors controlling O_3 deposition rates, and to provide perspective on O_3 deposition in terms of total gas exchange between forested ecosystems and the atmosphere.

In this chapter, we define the components of total O_3 uptake by forest ecosystems, and present current methods used for measuring, or inferring from measurements, the O_3 uptake at different scales of the ecosystem (leaf, soil, tree, whole ecosystem, and landscape). We then highlight O_3 uptake measurements made at a variety of scales over several years at the Blodgett Forest Research Station on the western slope of the Sierra Nevada approximately 75 km downwind of Sacramento. The site is a young, vigorously growing ponderosa pine plantation. There are both pragmatic and scientific reasons why this measurement site was chosen. The pragmatic reason is that ecosystem scale flux measurements are much simpler to interpret over a relatively uniform ecosystem with flat terrain, and the plantation satisfied those criteria. The scientific motivation is that O_3 and its precursors are transported downstream from urban sources around Sacramento leading to high concentrations of O_3

that are routinely observed in mid-level elevations of the Sierra Nevada. Although much emphasis has been placed on the impacts of O_3 on forests in central and southern California, forests of the Sierra Nevada in northern California are also impacted—albeit at lower rates (Miller and McBride, 1988; Miller et al., 1996). Moreover, as industry and population continue to expand in the Central Valley of California, and temperatures continue to rise as projected in climate change estimates for California forests, the northern Sierra Nevada will likely experience higher concentrations of O_3. These projected changes motivated us to measure the environmental and physiological controls on O_3 uptake and to understand their implications for future ecosystem functioning and carbon storage. Finally, we put O_3 deposition in context by comparison with exchange of other trace gases in forested ecosystems.

2. Defining uptake of O_3 by an ecosystem or landscape

Total uptake of O_3 by an ecosystem or landscape can be thought of as the net number of molecules of O_3 that cross a plane above the ecosystem in a given amount of time per unit area. The net movement of O_3 molecules into the ecosystem is a function of O_3 loss to several components of the system, including plants, other surfaces, and chemical reactions in the gas phase. Thus, total uptake (flux, FO_3) of O_3 by an ecosystem can be broken down into several terms:

$$\begin{aligned} FO_3 = {} & \text{Stomatal Uptake} + \text{Non-stomatal Deposition} \\ & + \text{Gas Phase Chemical Reactions.} \end{aligned} \tag{1}$$

Stomatal uptake refers to O_3 taken up by plants through their stomata, whose aperture is controlled by the physiological response of the plant to its environment. In general, the stomatal resistance is a function of environmental and physiological conditions, surface wetness and chemistry, and diffusivity of the pollutant (e.g., Turner et al., 1973; Jarvis and McNaughton, 1986). Panek et al. (Chapter 14, this volume) discuss in detail the plant stomatal response to environmental and physiological conditions and their relationship to O_3 deposition.

Ozone also deposits on non-stomatal surfaces of plants, such as stems, branches, boles and cuticles, and deposition to these surfaces occurs by chemical reaction or adsorption as a function of their surface properties and potentially as a function of environmental factors, such as moisture and temperature (Kerstiens and Lendzian, 1989; Rondon et al., 1993; Massman et al., 1995). Ozone deposits on other surfaces in the ecosystem as well, including soil and litter material, and this deposition also occurs by chemical reaction or adsorption as a function of their surface properties and environmental conditions (Turner et al., 1974; Leuning et al., 1979; Galbally and Roy, 1980; Zeller and Hehn, 1995; Massman, 1996).

Apparent O_3 deposition can occur by rapid reactions of O_3 with gases such as nitric oxide (NO) or volatile organic compounds (VOCs) that are emitted from plants, soil, or litter material. Generally, emissions of NO and VOCs occur as an exponential function of temperature and can also be enhanced by recent rainfall (e.g., Schade et al., 1999). The limited information on O_3 loss due to chemistry in natural environments indicates that a significant portion of total ecosystem O_3 flux can be lost through chemical reactions (Kramm et al., 1991, 1995; Mikkelsen et al., 2000; Kurpius et al., 2002).

Field measurement methods have been established for total ecosystem flux measurements, and for measurements of many different components within the ecosystem (described in detail in the next section). However, there are not established measurement approaches for each of the components of total O_3 uptake defined in Eq. (1). Instead, we have to rely on measurements of uptake by individual components of the ecosystem and the factors controlling them in order to infer the amount of O_3 uptake that occurs through each of these pathways. It is critical that we develop ways to differentiate each of these components because they each have different impacts on our environment. The primary concern of the forestry community with respect to O_3 is the physiological damage it causes to sensitive plant species. This physiological damage to plants is thought to occur mainly, if not exclusively, when O_3 is taken up through stomata. Some research has suggested that the leaf surface could be oxidized by O_3 (e.g., Coe et al., 1995) or that stress-induced emissions of ethylene or ethanol could be associated with O_3 deposition (e.g., Schade and Goldstein, 2002); thus, there could be additional biological effects associated with non-stomatal surface deposition or gas phase chemical loss through reactions with stress induced emissions, but these are likely to be minor compared to the damage associated with stomatal uptake. The regional atmospheric budget of O_3 is controlled by the balance between transport into and out of the region, photochemical production and loss, and deposition to the earth's surface. Thus, it is important to quantify total O_3 deposition because of its impact on local and regional O_3 concentrations. The amount of O_3 lost by gas phase chemical reactions with NO and reactive VOCs emitted by ecosystems is also important to quantify because of the potential impacts on regional photochemistry and radiation budgets. These reactions of O_3 with reactive VOCs can result in the production of hydroxyl radicals (the main oxidant in the troposphere) as well as production of secondary atmospheric aerosols, which affect both human health and the radiation balance over the ecosystems.

3. Measurement scales and methods

There are several scales at which O_3 uptake can be measured in the field, each with its own advantages and limitations, each with a set of questions for which it is most appropriate. No single technique can be used to answer the range of important questions regarding O_3 deposition. Choice of the approach or combination of approaches depends on the scientific questions being addressed, the biophysical characteristics of the study site, and the facilities and funding available to the investigator. In the following sections, we outline some of the most commonly used approaches for measuring or estimating O_3 uptake at different scales, including direct measurements by enclosure and micrometeorological approaches, as well as indirect estimates using measurements of conductance, sap flow, or remotely sensed properties. We devote most of our attention to discussing how a combination of these approaches can be used to understand O_3 deposition to ecosystems, the largest scale at which deposition measurements have been routinely made, and to identify and separate the different components of O_3 deposition. Our discussion of these approaches draws heavily on material we have previously published (Bauer et al., 2000; Panek and Goldstein, 2001; Panek et al., 2002; Kurpius et al., 2002), and we direct interested readers to those papers and other literature cited here for more detailed information.

3.1. Leaf

Measurements of O_3 uptake at the scale of individual leaves or branches can be accomplished by using enclosure-based methods. Leaf-level measurements are made with leaf enclosure systems that are designed to impact the environment of the leaf as little as possible. Some enclosures include the capacity to control the temperature, light, moisture, and carbon dioxide concentration surrounding the leaf, thereby allowing the investigator to mimic current environmental conditions or to alter them in order to investigate plant responses. Interpretation of measurements of O_3 loss in a controlled leaf chamber are complicated by the fact that O_3 deposition occurs both through the stomata and on the surfaces of the leaf and gas phase chemical loss could also occur, yet only the deposition through stomata is thought to cause biological damage. In order to determine the rate of O_3 uptake through stomata at the leaf level, enclosures can be used to estimate stomatal conductance to water vapor by using Fick's Law. Conductance to O_3 can then be estimated based on the ratio of the diffusivities of water and O_3—1.51 according to Massman (1998). Conductance to O_3 can then be multiplied by ambient O_3 concentration to estimate leaf-level O_3 uptake (e.g., Panek and Goldstein, 2001). Leaf-level O_3 uptake estimates based on conductance measurements are indirect, but they provide the best available assessment of the amount of O_3 actually taken up by the leaf, which is the relevant parameter in terms of potential physiological effects on the plant.

Chamber-based measurements are also attractive because they are relatively inexpensive and portable, allowing for measurements to be made over broad spatial scales and potentially including areas with large gradients in O_3 concentration, elevation, or resources such as water that might impact leaf-level uptake rates. A major difficulty with leaf-level enclosure measurements is one of scaling. Leaf-level processes do not necessarily scale linearly to the canopy level, thus extrapolating them requires additional information about the ecosystem (see Panek et al., Chapter 14, this volume). A second difficulty with leaf-level enclosure measurements is that they are labor intensive. Unless automated, they fail to capture all of the temporal variation in O_3 uptake due to changing environmental conditions.

Regardless of the scale at which O_3 deposition is measured, leaf-level physiological measurements provide the most direct information for interpreting changes in physiological function. Strong relationships between stomatal conductance and photosynthesis at the leaf level demonstrate the need to understand controls on both (Reynolds et al., 1992; Harley and Baldocchi, 1995), especially in drought stressed ecosystems (Panek et al., Chapter 14, this volume). Biochemical changes in photosynthetic capacity in response to drought have feedbacks to conductance and can be elucidated best by measurements at the leaf level.

3.2. Soil

There is limited information on O_3 deposition to soils. Most estimates of O_3 fluxes to soil have relied on inferred resistances based on near-surface O_3 measurements (e.g., Turner et al., 1973; Leuning et al., 1979; Massman, 1993) or eddy covariance measurements above bare soil (e.g., Gusten et al., 1996). Measurements of O_3 uptake at the soil surface can also be accomplished by using enclosure-based methods. Enclosures can be simple passive devices of known volume that cover the soil surface while measuring the change in concentration of O_3 with time in order to determine a flux. Alternatively, enclosures can be flow-through devices where the flux is calculated based on the rate of flow, chamber volume, and difference in concentration between the incoming and outgoing airflows. Disadvantages of chamber measurements include: (a) potential impacts on the environment where fluxes are being measured by changing variables such as temperature, moisture, pressure, and turbulence; (b) chambers cannot be used to observe natural changes in uptake conditions; and (c) chambers measure fluxes over a very specific and small location, typically over a very limited duration.

3.3. Tree

Estimates of O_3 uptake at the whole tree level could be accomplished by using whole-tree chamber measurements. However, these measurements would necessarily combine O_3 uptake through stomata with O_3 uptake on non-stomatal surfaces and gas phase chemical loss by reactions with biogenically emitted compounds. An alternative approach to estimate only stomatal O_3 uptake is to estimate tree conductance by using sap flow measurements then scale to O_3 conductance and multiply by the measured O_3 concentration (Kurpius et al., 2002). Stand-level stomatal O_3 flux to the trees can then be estimated by scaling the measurements based on sapwood density of the stand. Scaling to the stand requires that measurements be done on a range of trees that are representative. Unfortunately, scaling to the stand can be complicated by individual differences in tree allometry, which could even be related to O_3 damage itself. For monospecific, even-aged, even-sized stands, this scaling is relatively straightforward, but it is a major limitation for multi-specific, multi-aged, multi-sized stands that are more typical in the Sierra Nevada. Although the sap flow method is indirect, it does provide an estimate of O_3 actually taken up by the tree, which is the relevant measure in terms of potential physiological effects on the plant. Limitations to the sap flow method include hydraulic resistance limitations to flow, which set an upper arbitrary limit to estimates of transpiration and therefore conductance.

3.4. Ecosystem

Although the use of enclosures has advantages in that they are portable and inexpensive and the use of sap flow measurements can be used to infer the conductance of a whole tree continuously over long time periods, micrometeorological approaches using towers or aircraft to measure O_3 flux at the ecosystem or regional scale have other important advantages. With micrometeorological approaches, it is possible to measure fluxes without disturbing the soil or plant surface. Moreover, micrometeorological approaches inherently average over a surface area that increases with height of the measurements over the surface, which represents integrated fluxes from a larger proportion of the ecosystem including all of its components rather than from small plots within it. Micrometeorological approaches also allow the examination of fluxes over continuous timescales from minutes to years, providing the opportunity to observe changes in fluxes due to changing environmental, physiological, and phenological conditions.

Flux gradient measurements have been used in the past to estimate O_3 fluxes, but the current state-of-the-art micrometeorological technique for measuring ecosystem scale O_3 fluxes is eddy covariance. This method quantifies vertical fluxes of scalars between the earth's surface and the atmosphere from the covariance between vertical wind velocity (w') and scalar (c') turbulent fluctuations averaged over 30-minute periods (e.g., Baldocchi et al., 1988). The vertical wind speed is measured using a sonic anemometer, and the scalar (O_3 concentration) must be measured by an instrument with a response time approaching 10 Hz. Generally these O_3 instruments are based on chemiluminescence measurements with ethene or coumarin dye where a photon is released as a result of the reaction and is detected with a photon multiplier tube (e.g., Munger et al., 1996; Bauer et al., 2000). The fast response time is required so that concentration changes can be observed faster than the changes in vertical wind speed carrying the bulk of fluxes into and out of the forest. Turbulent fluctuations are determined from the difference between instantaneous and mean scalar quantities.

One significant systematic error associated with the eddy covariance method is the inability of the sonic anemometer to resolve fine-scale eddies in light winds (Goulden et al., 1996; Moncrieff et al., 1996). The inability of the sonic anemometer to resolve the vertical wind occurs mainly at night as the fluctuations become dominated by small, high-frequency eddies; thus, in general the nighttime fluxes measured by this method are significantly less reliable than the daytime fluxes.

Eddy covariance is most useful for flux measurements over horizontally homogeneous surfaces with long fetch and flat terrain. However, O_3 deposition and damage in the Sierra Nevada occurs in landscapes that are anything but homogeneous. Variations in topography create the largest problem for applying eddy covariance methods broadly in Sierra Nevada forests. In order to accurately apply the eddy covariance method it is currently necessary to find a site with relatively uniform properties of ecosystem structure and little or no slope.

3.5. Landscape

There is currently no good way to measure O_3 deposition at landscape scales over mountainous terrain such as the Sierra Nevada. Eddy covariance measurements of O_3 flux can be made from an airplane, but these measurements are only possible for discrete short time periods, and they are difficult to interpret when made over non-uniform mountainous terrain. Models of stomatal O_3 deposition that account for physiological activity of the plants in response to the local environment (phenology, radiation, temperature, moisture) currently provide the best approach to estimating biologically relevant O_3 deposition at the landscape scale. This approach has recently been adopted for modeling stomatal O_3 fluxes across Europe, showing at the landscape scale that flux based approaches to estimating biologically relevant O_3 deposition suggest a different spatial distribution for potential damage than simple exposure-based indices (Emberson et al., 2000). Emberson et al. (2000) stress the need to validate the model with field measurements, but it is important to recognize that field validations are only currently possible at the leaf, tree, or ecosystem scales.

4. Summary of measurements in the Sierra Nevada

In this section, we highlight O_3 uptake measurements made at a variety of scales over several years at the Blodgett Forest Research Station.

4.1. Site description—Blodgett Forest

The measurement site is near Blodgett Forest Research Station (38°53′42.9″N, 120°37′57.9″W, 1315 m elevation) on the western slope of the Sierra Nevada. The site is characterized by a Mediterranean climate with mean yearly precipitation of 163 cm falling mainly between September and May and very little rain in summer. It consists of a typical clear-cut commercially managed plot, planted with *Pinus ponderosa* in 1990. Large amounts of woody litter and stumps can still be found throughout the plantation. Among the pines there are also a few individuals of Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), black oak (*Quercus kellogii*), sugar pine (*Pinus lambertiana*), and incense cedar (*Calocedrus decurrens*). The understory was dominated by manzanita (*Arctostaphylos* spp.) and whitethorn (*Ceanothus cordulatus*), which, however, was almost completely cut throughout the plantation during routine shrub removal in spring 1999.

A walk-up tower was erected in 1997, when the trees were 6–7 years old and 3–4 meters tall. The trees have grown by approximately 0.7 m per year on average. Meteorological data and trace gas mixing ratios and fluxes (CO_2, H_2O, O_3, and hydrocarbons) were measured approximately 5–6 m above the average tree height (Lamanna and Goldstein, 1999; Bauer et al., 2000; Goldstein et al., 2000). The tower fetch area extends approximately 200 m to the SW during daytime. The nighttime fetch is less well defined but generally lies in the opposite, NE direction (see Goldstein et al., 2000, for a more detailed description).

Ozone concentration and ecosystem scale O_3 flux, along with relevant environmental variables, were measured continuously during spring through fall of 1997 and 1998, and continuously since spring 1999. Ozone concentration was measured by using an ultraviolet (UV) photometric O_3 analyzer (Dasibi 1008-RS, Glendale, CA). Ozone flux was determined as the half-hour average of the covariance between the instantaneous deviation from the mean vertical wind and instantaneous deviation from the mean O_3 at 12 m above the ground.

High frequency (10 Hz) wind data were obtained by using a three-axis sonic anemometer (ATI Electronics Inc., Boulder, CO). High frequency (10 Hz) O_3 data were obtained by using a fast response chemiluminescent O_3 analyzer built by Jim Womack (National Oceanic and Atmospheric Administration—Atmospheric Turbulence and Diffusion Division) based on a design by Gusten et al. (1996). The fast response O_3 data was calibrated to the UV photometric O_3 analyzer, which provided a stable reference. The environmental measured variables included photosynthetically active radiation (PAR) (Li-Cor Inc., Lincoln, NE), air temperature and humidity (Vaisala Inc., Woburn, MA), and soil moisture (Campbell Scientific Inc., Logan, UT). Vapor pressure deficit was determined as the difference between saturated and measured vapor pressure at ambient air temperature above the plantation. Ozone deposition velocity (O_3 V_d), the rate that O_3 is deposited to the ecosystem, was calculated as negative O_3 flux normalized for concentration. In an actively transpiring ecosystem, stomatal conductance is the most dynamic and influential component of O_3 V_d. For a complete list of measurements and additional descriptions of the field site and instrumentation see Bauer et al. (2000), Goldstein et al. (2000), and Schade and Goldstein (2001).

Sap flow measurements were made from June 1, 2000, to May 31, 2001, to determine ecosystem transpiration and to then estimate stomatal conductance to O_3. Eight sensor sets were deployed: two sensor sets—one on the east side and one on the west side—in each of four trees. The sampled trees were chosen to represent the size distribution of the stand. The heat-ratio method (Burgess et al., 2001) was utilized, with each sensor set consisting of two thermistor probes and one heater probe inserted radially into the sapwood at 1.3–1.4 m above the ground. The thermistor probes were placed 6 mm above and 6 mm below the heater probe. Each thermistor measured temperature at two distances along the probe—5 mm and 15 mm from the inner end of the probe—to assess flow differences between inner sapwood versus outer sapwood. A 15–20 cm wide collar of reflective insulation was placed around the tree covering the sensors to prevent direct solar radiation from impacting the measurements. For a full description of errors and reliability associated with the heat-ratio method see Burgess et al. (2001). Stand transpiration (E_t, mm h^{-1} or mm day^{-1}) was estimated from $E_t = JS$, where J is the sap flux density (mm^3 mm^{-2} h^{-1}) and S is the cross-sectional sapwood area per ground area (m^2 m^{-2}). Based on comparison with above-canopy flux measurements, there was half-hour time lag between when sap began moving through the trunk and when it was transpired, due to the hydraulic capacitance of the trees (for further details see Kurpius et al., 2002).

Tree canopy conductance from the sap velocity measurements was calculated based on Monteith and Unsworth (1990) with the modification of neglecting aerodynamic conductance; this method has been successfully used on open conifer stands such as loblolly pine (*Pinus taeda*) (Phillips and Oren, 1998) and Douglas fir (*P. menziesii*) (Tan and Black, 1976).

A note on scaling: the two biggest issues in scaling sap flow measurements are in non-uniform sapwood and non-uniform stand properties. Sap flux density can vary spatially within the conducting wood (see Lassoie et al., 1977; Miller et al., 1980; Hatton and Vertessy, 1989, 1990; Dye et al., 1991; Olbrich, 1991). Sapwood xylem of plantation trees that are evenly spaced are known to be fairly regular (Kostner et al., 1998). The distribution of sensors within and around the sample trees showed very little variation in sap flow based on depth or aspect. Errors from within stand variability can be reduced by stratifying trees within the stand by size class (Hatton et al., 1995; Kostner et al., 1998). Since we were working in a very uniform plantation of even-aged and evenly distributed trees, these scaling issues should be minimized.

Leaf-level net photosynthesis, conductance, and transpiration were measured with a LiCor 6400 photosynthesis system (LiCor Inc., Lincoln, NE). Preliminary measurements indicated that there was little variability from tree to tree within the plantation and in gas exchange with height or aspect; thus, our assumptions of homogeneity were correct. We were able to use six trees to capture a 10% difference in gas exchange. Two fascicles of three needles each in the age-classes were marked and measured throughout the duration of the growing season. Because ponderosa pines have stomata on all leaf surfaces, gas exchange calculations were made on a total leaf area basis. Leaf area was calculated by assuming each fascicle was a cylinder divided into three needles. The radius (R) of each needle was measured separately by using a micrometer and total leaf surface area by using the following equation: $[2\pi R + 2R_1 + 2R_2 + 2R_3] \times$ length.

The status of the photosynthesis system—carboxylation efficiency and maximum rates of electron transport—were determined from the response curves of net photosynthesis vs. leaf internal CO_2 concentration. Quantum efficiency was determined by regression analysis of the light limited portion of the light curve. Light-saturated photosynthetic rates were determined from the light-saturated portion of the curve. Instantaneous water-use efficiency (WUE) was calculated by dividing photosynthesis by transpiration.

4.2. Results

4.2.1. Impacts of drought stress on ozone uptake at the leaf level

A watering experiment at the Blodgett site showed a pronounced drought effect on O_3 uptake at the leaf level (Panek and Goldstein, 2001). Even in a wet El Niño year, stomatal conductance to O_3 was lower at the control site, leading to a 41% reduction in estimated stomatal O_3 uptake (O_3 concentration times

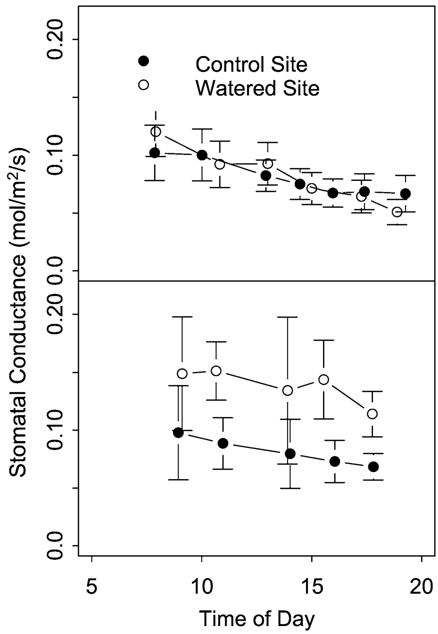


Figure 3. The diurnal trend in leaf-level stomatal conductance compared between the control and watered young ponderosa pine site at the beginning (top) and end (bottom) of the watering experiment. Stomatal conductance is per unit total leaf area. Error bars are ±1 SD (redrawn from Panek and Goldstein, 2001).

stomatal conductance), compared to the watered site, by the end of the season (Fig. 3). Watering increased V_{max} (maximum rate of carboxylation) and J_{max} (CO_2-saturated photosynthetic rate) significantly at the watered site relative to the control site (using a one-sided T-test, significance level 0.05), indicating an increase in the inherent ability of the photosynthetic system to assimilate carbon independent of stomatal conductance. Because this year was wet, neither V_{cmax} nor J_{max} increased to the degree we have observed in a normal drought year. Respiration rates were significantly more negative at the watered site, reflecting a greater respiration cost. Neither quantum efficiency nor maximum light-saturated photosynthesis was significantly different between the sites pretreatment (see Panek and Goldstein, 2001, for details). They did not change significantly over the course of the experiment at either site. Thus, it is evident that soil moisture had no significant effect on the ability of the photosynthetic system to capture and use light energy independent of its effects on stomatal conductance during this relatively wet year.

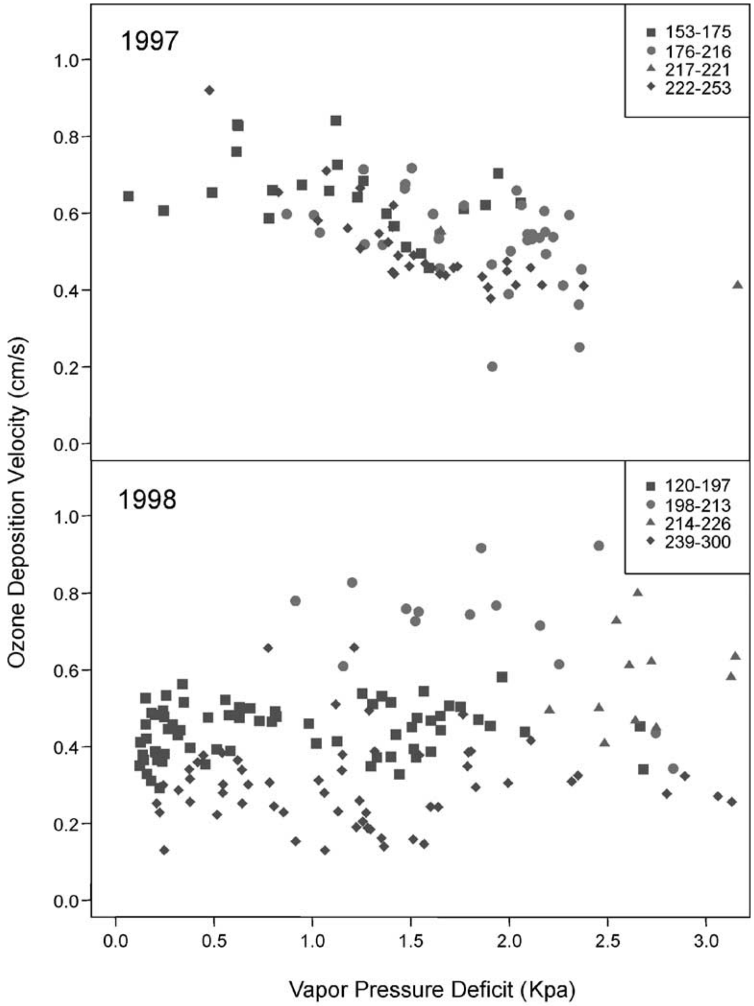
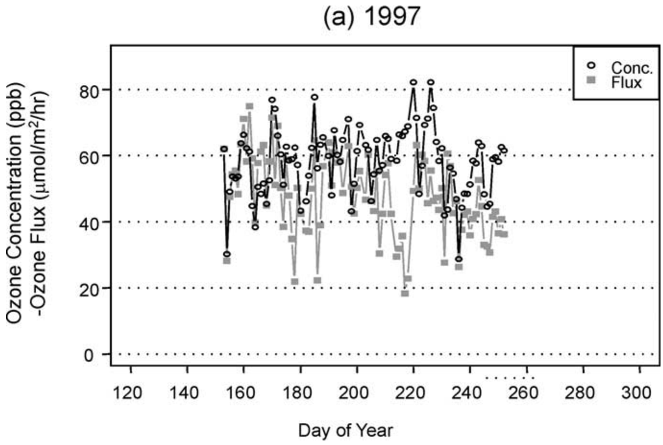


Figure 4. Daytime mean O_3 deposition velocity versus vapor pressure deficit for 1997 and 1998.

4.2.2. Inter-annual differences in ozone uptake at the canopy scale

Ozone concentration and O_3 flux, along with relevant environmental variables, were measured from June to September 1997 and from May to November 1998 (see Bauer et al., 2000, for more details). Summer 1997 had very low soil moisture and an early budbreak, while summer 1998 had very high soil moisture and later budbreak. Soil moisture and vapor pressure deficit exerted



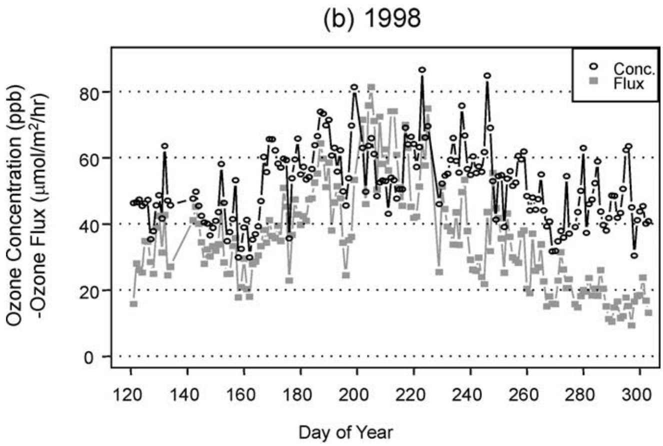


Figure 5. 1997 (a) and 1998 (b) daytime mean O_3 concentration and O_3 flux versus day of year.

strong limitations on O_3 deposition in the dry year (1997), but the relationship was less clear in the wet year (1998) (Fig. 4). During the dry year, O_3 concentration and flux became decoupled due to stomatal closure, but this did not occur explicitly in 1998 (Fig. 5). Phenology also proved to be important in controlling O_3 deposition. Early in summer 1997 cumulative O_3 flux was 50% higher than that of 1998: the difference can be attributed to lower temperatures causing late budbreak in 1998. The ponderosa pine trees at this site typically hold three to four age classes of needles; thus, late budbreak in 1998 caused a significant difference in leaf area index compared to the same period in 1997.

Further, the highest O_3 deposition velocity in both years occurred 3–4 weeks after budbreak. Therefore, phenology and its drivers such as air temperature are important. Total cumulative O_3 flux during the summer was 6% lower in 1998, mainly due to later budbreak even though drought stress reduced O_3 flux late in summer 1997. Our results show that interannual climate variability impacts temporal patterns, physiological controls, and magnitude of O_3 deposition to sensitive Mediterranean-type ecosystems.

4.2.3. Seasonal patterns of ozone uptake at the canopy scale

Ozone concentration and ecosystem scale fluxes have been measured year-round at Blodgett Forest (Kurpius et al., 2002). The ecosystem was most active with respect to photosynthesis and respiration during the summer, but maintained a low level of physiological activity during the fall, winter, and spring. Cumulative O_3 flux for the year starting June 1999 through May 2000 was 114 mmol m^{-2} with the contribution for each season being 37% for summer, 20% for fall, 16% for winter, and 27% for spring (Fig. 6). Nearly two-thirds of annual O_3 deposition occurred during non-summer months. Both O_3 concentration and O_3 V_d (O_3 V_d is O_3 flux normalized for O_3 concentration) were important in driving patterns in O_3 flux but O_3 flux was more closely related to O_3 V_d. Further, the relationships between O_3 V_d (and therefore O_3 flux) and the climatic variables were not static over the year, changing mainly with water status and phenology. Understanding how climate and phenology interact to change the efficiency of O_3 uptake by an ecosystem is therefore a key step in improving models of O_3 deposition. The transitions between the rainy and dry seasons were not only important in driving patterns in O_3 V_d through

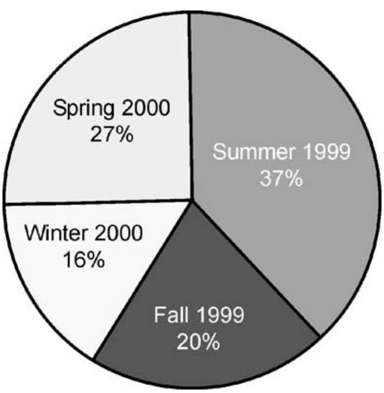


Figure 6. Cumulative daytime O_3 flux for each season of the year, expressed as a percentage of total annual O_3 deposition.

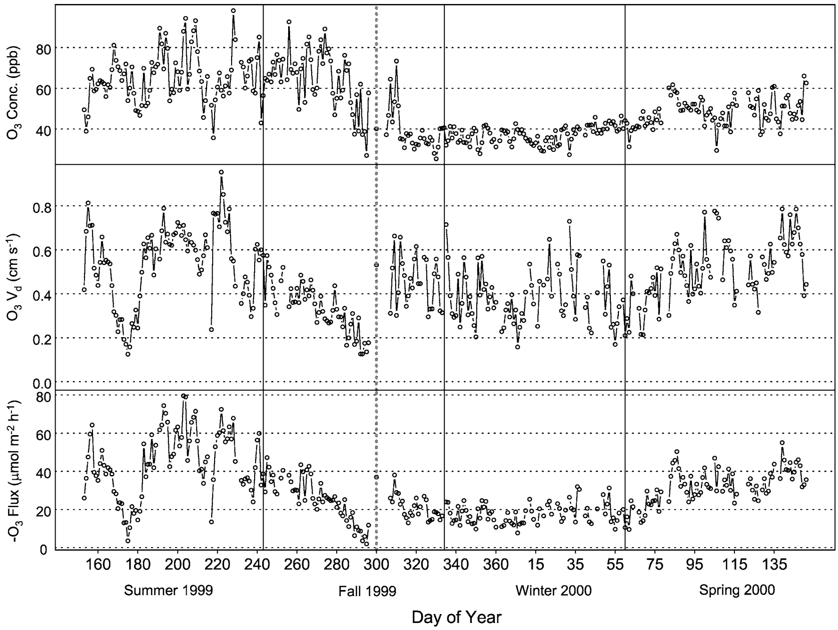


Figure 7. Daytime mean O_3 concentration, flux, and deposition velocity (hours 800–1800). Dotted vertical line represents the onset of the rainy season.

climate and phenology but also greatly affected O_3 concentration (Fig. 7). Climate change could have a large impact on the timing of these transitions, thus altering ambient O_3 concentration and deposition patterns.

4.2.4. Separating ozone uptake into stomatal and non-stomatal pathways

Major advances in quantifying O_3 deposition to ecosystems have been made by using above-canopy techniques—such as eddy covariance—that allow for the direct measure of O_3 flux into natural systems. However, from above-canopy flux measurements alone, it is impossible to differentiate between deposition through stomatal openings of trees versus non-stomatal surfaces or within-canopy chemical loss. Therefore, there is a need to partition O_3 fluxes into plant stomatal and non-stomatal components. Sap flow measurements provide an indirect but reliable measure of O_3 uptake by trees. Sap flow measurements were used to determine O_3 uptake by ponderosa pine trees in the Sierra Nevada year-round starting in June 2000 at Blodgett Forest. Concurrently, total ecosystem O_3 flux was measured by using eddy covariance (Kurpius et al., 2002). Mean total O_3 flux to the ecosystem was 46.6 μmol m^{-2} h^{-1} (±15.1) in summer 2000, 27.6 µmol m^{-2} h^{-1} (±14.2) in fall 2000, 8.2 µmol m^{-2} h^{-1} (±5.1) in winter 2001, and 21.1 µmol m^{-2} h^{-1} (±11.6) in spring 2001. Mean O_3 flux through the stomata was 14.6 µmol m^{-2} h^{-1}(±4.1) during summer 2000, 12.9 µmol m^{-2} h^{-1} (±5.8) during fall 2000, 5.6 µmol m^{-2} h^{-1} (±2.8) during winter 2001, and 12.7 µmol m^{-2} h^{-1} (±3.7) during spring 2001. The percentage of total annual O_3 deposition that occurred through the stomata was 31% in summer, 47% in fall, 69% but highly variable in winter, and 60% in spring. The difference between total O_3 flux to the ecosystem and stomatal O_3 flux to the trees varied exponentially with air temperature but did not scale as well with other environmental variables such as light, suggesting that much of the non-stomatal deposition was actually due to chemical loss either on surfaces or within the forest canopy. The influence of biogenic volatile organic compound and/or nitric oxide emissions in controlling the non-stomatal O_3 deposition requires further study.

4.2.5. Comparison to ozone deposition velocity measured at other sites

Ozone deposition velocity measured over land surfaces generally ranges from 0.1 to 1.0 cm s^{-1} during the day and 0 to 0.3 cm s^{-1} during the night (Table 1). The highest deposition velocities have been measured over deciduous forests and cotton fields during the summer, while the lowest deposition velocities have been observed over the Sahara Desert. Coniferous forests generally have deposition velocities in the middle to high end of this range. Deposition velocities to grasses are highly variable, depending mostly on water and phenology. Ozone deposition velocity is generally higher over landscapes with well-watered, photosynthetically-active vegetation, and are lower in non-growing months due to climatic and phenological limitations. For example, in Portugal (Pio and Feliciano, 1996) winter deposition was found to be higher than summer due to the seasonality of biological productivity at that site. Overall, nighttime O_3 deposition velocities were found to be low.

Measurements of O_3 deposition velocity to the ponderosa pine plantation at Blodgett Forest (Table 2) include seasonal variations that have not been observed for most sites (Kurpius et al., 2002). Ozone deposition velocity reached maximum daytime values of 0.8–0.9 cm s^{-1} in early summer, about 3 weeks after budbreak. This is a young, vigorously growing plantation and has higher O_3 deposition velocities in early summer than are generally reported for coniferous stands. With the onset of drought stress in late summer, the daytime O_3 deposition declined to 0.5–0.6 cm s^{-1} and further decreased to 0.2 cm s^{-1} in the fall prior to the onset of the rainy season. The first rains resulted in an increase in daytime deposition velocity to 0.5 cm s^{-1}. Ozone deposition velocity was 0.4 cm s^{-1} in winter, slightly higher than reported for other forested sites because the conifer trees at Blodgett remain photosynthetically active during

Table 1. Ozone deposition velocities reported for a variety of land types and times of year,

Surface	Location	Season	O_3 V_d ($cm\,s^{-1}$)		Source
			Day	Night	
Cotton field	Central Valley, California	summer	0.8	0.1	Pederson et al. (1995)
Grape vineyard	Central Valley, California	summer	0.5	0.2	Pederson et al. (1995), Padro et al. (1994)
Dry grass	Central Valley, California	summer	0.1	0	Pederson et al. (1995)
Short-grass steppe	Eastern Colorado	summer	0.7	0.3	Massman (1993)
Norway spruce stand	Western Jutland, Denmark	summer	0.7	0.35	Pilegaard et al. (1995)
Desert	Sahara Desert	spring	0.1	0.04	Gusten et al. (1996)
Deciduous forest	Canadian Forces Base Borden	summer	1.0	0.25	Padro et al. (1991)
Deciduous forest	Canadian Forces Base Borden	winter	0.3	0	Padro et al. (1992)
Deciduous forest	Harvard Forest, Central Massachusetts	summer	0.8	0.15	Munger et al. (1996)
Deciduous forest	Harvard Forest, Central Massachusetts	winter	0.35	0.15	Munger et al. (1996)
Grass	West coast Portugal	early summer	0.3	0.05	Pio and Feliciano (1996)
Grass	West coast Portugal	late summer	0.2	0.05	Pio and Feliciano (1996)
Grass	West coast Portugal	winter	0.3	0.1	Pio and Feliciano (1996)
Mediterranean psuedosteppe	Italy	spring/summer	0.2		Cieslik and Labatut (1997)
Norway spruce stand	Simlaangsdalen, Sweden	summer	0.35–0.5	0	Rondon et al. (1993)
Scots pine stand	Jadraas, Sweden	summer	0.5–0.7	0.2	Rondon et al. (1993)
Norway spruce stand	Western Jutland, Denmark	summer	0.7	0.3	Mikkelsen et al. (2000)

Table 2. Ozone deposition velocities found for the ponderosa pine plantation at Blodgett Forest Research Station (values derived from 1997–2000 data).

Time of year	O_3 V_d (cm s^{-1})	
	Day	Night
Early summer	0.8–0.9	0.05
Late summer	0.5–0.6	0.05
Fall (pre-rain)	0.2	0.05
Fall (post-rain)	0.5	0.05
Winter	0.4	0.15
Early spring	0.5	0.1
Late spring	0.8	0.1

warm days in the winter months. Ozone deposition velocity steadily increased from early spring (0.5 cm s^{-1}) to late spring (0.8 cm s^{-1}). Most of the focus in O_3 deposition studies has been on summer months, with only a few winter measurements, and there is a paucity of information in the peer reviewed literature on spring and fall O_3 deposition velocities. This data is especially useful because the transitions from periods of high to low O_3 deposition velocity can provide insight into the mechanisms controlling O_3 deposition.

4.2.6. Comparison between O_3 deposition and exchange of other trace gases

Ozone uptake accounts for only a small fraction of the total exchange of mass between ecosystems and the atmosphere. Fig. 8 provides some perspective on the amount of O_3 exchange observed compared to other trace gases. Water dominates the biosphere-atmosphere flux. For every molecule of O_3 deposited, approximately 4×10^5 molecules of water are released. Carbon dioxide is the next most actively exchanged trace gas, with a net molecular ecosystem exchange (photosynthesis minus respiration) approximately 750 times that of O_3. A variety of other trace gases are exchanged, including many volatile organic compounds (e.g., Schade and Goldstein, 2001). One of the dominant volatile organic compounds emitted by the ponderosa pine ecosystem is methylbutenol, a five carbon unsaturated alcohol that has important impacts on regional photochemistry including O_3 production. Methylbutenol is emitted at roughly half the molecular rate at which O_3 is deposited. Monoterpenes are another class of volatile organic compounds emitted by the ecosystem. These compounds have ten carbons and can react quickly with O_3 (lifetimes of minutes to hours). Beta-pinene is one of five monoterpenes which has been measured as an emission from the ponderosa pine plantation (Schade et al., 1999), and it is emitted at roughly 4% of the molecular rate at which O_3 is deposited. The total emissions of measured monoterpenes is closer to 10–15% of the rate of O_3 deposition,

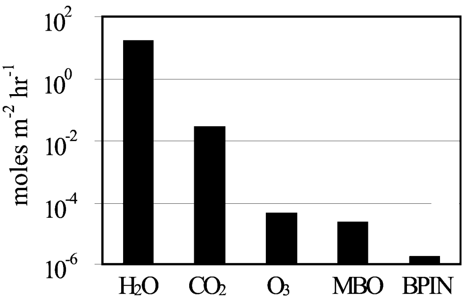


Figure 8. Absolute value of daytime median ecosystem scale fluxes for a subset of trace gases measured above the ponderosa pine plantation at Blodgett Forest between July 6 and September 8, 1999, 9:00–16:00 PST, plotted on a log scale. Ozone (O_3) and carbon dioxide (CO_2) fluxes are due to uptake by the ecosystem, while water (H_2O), methylbutenol (MBO), and beta-pinene (BPIN) fluxes are due to emissions from the ecosystem. Ozone fluxes are roughly six orders of magnitude smaller than water, three orders of magnitude smaller than carbon dioxide, similar magnitude to methylbutenol, and one order of magnitude larger than beta-pinene.

but there are probably other highly reactive monoterpenes and sesquiterpenes (larger more reactive compounds) emitted that react with O_3 before they can be measured as a flux above the forest canopy.

The amount of O_3 deposited is only indirectly related to exchange of most other trace gases. However, the processes controlling exchange are highly coupled; thus, measuring fluxes of several gases simultaneously can provide more insight into controls over O_3 deposition than measuring O_3 flux alone. For example, the plants emit water through transpiration as a function of stomatal conductance and vapor pressure deficit, and stomatal conductance also controls the biologically relevant deposition velocity of O_3. Thus, measuring water fluxes and water availability (soil moisture, vapor pressure deficit, leaf water potential, etc.) provides information on controls over stomatal deposition of O_3. Ozone deposition may also cause stress responses in the plant, resulting in the production and emission of trace gases. Schade and Goldstein (2002) recently reported a strong correlation between O_3 deposition and ethanol emission in ponderosa pines, suggesting that ethanol emissions may indicate O_3-induced plant stress.

The interaction between O_3 and other gases exchanged with ecosystems can also impact regional atmospheric composition. For example, oxidation by O_3 is the major loss process for several biogenically emitted mono and sesquiterpenes. These reactions result in the production of secondary aerosols that scatter light and can potentially change local radiation levels, thus altering stomatal conductance and rates of carbon uptake (e.g., Fuentes et al., 2001). The photochemistry of O_3 production is also tightly coupled to atmospheric composition and biosphere–atmosphere exchange of O_3, volatile organic compounds, and oxides of nitrogen (e.g., Dreyfus et al., 2002). Understanding the processes controlling regional O_3 concentration and deposition therefore depends on understanding the processes controlling exchange of a variety of trace gases between ecosystems and the atmosphere.

5. Conclusions and future needs

Ozone uptake can be measured at several different scales ranging from the leaf level to the whole ecosystem, and the measurements at each scale are useful for different purposes. Direct measurements of O_3 uptake through stomata are not common. More typically, O_3 deposition through stomata is estimated from measurements of conductance at the leaf level, or by estimates of conductance at the whole tree level based on sap flow measurements. These measurements of stomatal conductance are critical for understanding the biologically relevant deposition of O_3 to plants. Ozone deposition at the whole canopy scale can be achieved by flux gradient approaches or more commonly by eddy covariance measurements. These measurements cannot differentiate between deposition to stomata versus non-stomatal surfaces versus gas phase chemical reactions within the forest canopy. However, the total O_3 deposition is important to quantify because it impacts the regional O_3 concentrations.

Our measurements in the Sierra Nevada clearly show that O_3 deposition is limited by stomatal conductance as a function of phenology and water availability. Thus, O_3 exposure indices do not adequately represent O_3 uptake during times of peak O_3 concentrations when drought stress limits conductance, as occurs through most of the summer in the Sierra Nevada. When ponderosa pine trees were kept well watered throughout the growing season, their potential for O_3 deposition increased on average by 41% percent late in the growing season, even in a wet El Niño year.

Measurements of total O_3 deposition at the canopy scale over several years revealed significant interannual difference in deposition due to climatically driven changes in timing of phenology and interannual differences in moisture availability. Year-round measurements also revealed that total O_3 deposition in summer was only responsible for 37% of the total annual deposition, with the other 63% occurring in fall, winter, and spring, times that are not traditionally thought of as significant for O_3 damage to ecosystems. Typically, O_3 exposure metrics use accumulations for about half the year from mid-April to mid-October. Investigation of the impact caused by O_3 deposition during the rest of the year would therefore be a prudent next step.

Measurements at a combination of scales can reveal significantly more information about O_3 deposition to ecosystems than measurements at a single scale, and provide significant new insight into processes controlling total deposition. Simultaneous measurements of O_3 deposition at the canopy scale and estimates from water flux measurements at the whole tree scale revealed that in summer less than half of the total ecosystem O_3 deposition was due to uptake through stomata and suggested that the remainder was due to deposition to other surfaces and gas phase reaction with biogenically emitted reactive trace gases.

Expected changes in human population, land use patterns, and climate in California motivate the need for understanding impacts of these changes on air quality and O_3 deposition to the forests of the Sierra Nevada. A combination of measurements at the leaf, whole tree, and ecosystem scales can and should continue being used to understand the mechanisms controlling O_3 deposition to sensitive ecosystems and the response of those ecosystems. Future work should also focus on estimating O_3 deposition over larger areas. Estimating deposition of O_3 over larger scales will necessarily rely on understanding both the distribution of O_3 concentrations and the temporal and spatial variability of stomatal conductance for O_3 sensitive trees. Measurements, as described in this chapter, can provide the basic understanding of processes controlling biologically relevant O_3 uptake, but biophysical models informed by these measurements currently provide the most promise for estimating uptake at larger scales and over the more complex terrain that exists in most of the Sierra Nevada.

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