Response of stomatal conductance to drought in ponderosa pine: implications for carbon and ozone uptake

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Summary   To gain insight into the limitations imposed by a typical Mediterranean-climate summer drought on the uptake of carbon and ozone in the ponderosa pine (*Pinus ponderosa* Dougl. *ex* Laws.) ecosystem, we compared diurnal trends in leaf physiology of young trees in a watered and a control plot located in the Sierra Nevada Mountains, CA, USA (Blodgett Forest, 38°53′ N, 120°37′ W, 1315 m elevation). Predawn water potential of trees in the watered plot remained above −0.3 MPa throughout the growing season, whereas it dropped in the control plot from −0.24 to −0.52 MPa between late May and mid-August. Photosynthesis and stomatal conductance of trees in the watered plot were relatively insensitive to atmospheric vapor pressure deficit (VPD), whereas gas exchange of trees in the control plot varied with changes in soil water, VPD and temperature. Although the 1998 growing season was abnormally wet, we saw a pronounced drought effect at the control site. Over the 2 months following the onset of watering, carbon and ozone uptake were measured on three days at widely spaced intervals. Carbon uptake per unit leaf area by 1-year-old foliage of trees in the control plot was 39, 35 and 30% less, respectively, than in the watered plot, and estimated ozone deposition per unit leaf area (ozone concentration times stomatal conductance) was 36, 46 and 41% less.

Keywords: carbon flux, drought stress, ozone flux, photosynthesis, soil water.

Introduction

The Mediterranean climate of California and much of the Pacific Northwest imposes an annual and predictable drought stress on forests in the region. Despite a general understanding of the relationship between forest growth and summer drought in this ecosystem, new questions are emerging about forest health and forest physiological responses to climate in light of recent and predicted changes in atmospheric chemistry. Changes in precipitation and temperature patterns are anticipated throughout the region, and ozone concentrations are significantly above background values and may continue to rise. Adaptations to summer drought may cause these forests to respond to changes in climate and increased ambient ozone concentrations in ways that differ from the responses of forests elsewhere, and in ways that remain largely unexplored. Understanding the interactions among climate, and carbon and ozone uptake is an important part of understanding forest health in this region.

The growing season in the montane areas of California, Oregon and Washington is constrained by temperature to a period between April and October, and typically there is little precipitation between June and October. The trees in the region are physiologically most active early in the growing season (Bassman 1988, Patterson and Rundel 1993, Grulke 1998) when soil water content is high as a result of melting snow and spring rains. As the season progresses, gas exchange typically slows as soil water content decreases (Cleary 1970, Running 1976). Observed and predicted climate trends indicate that the Pacific Northwest may become wetter and warmer in the coming decades (IPCC 1996) and California may become drier and warmer (Field et al. 1999).

Tropospheric ozone concentrations have more than doubled in the northern mid-latitudes over the last 100 years (Stockwell et al. 1997) and concentrations have continued to increase in many remote forested regions over the last 20 years (Demerjian et al. 1992, Marenco et al. 1994, Stockwell et al. 1997). Average statewide ozone concentrations in California have declined over the last 17 years as a result of strict emission regulation, but they remain significantly higher than background values (CARB 1999) and ambient ozone concentrations routinely exceed state human health standards during the growing season in some montane forested areas (e.g., Sequoia National Park). Anticipated changes in climate and atmospheric chemistry have major implications for the forests of the western USA. If the climate becomes wetter, then increases in soil water should allow for enhanced stomatal conductance throughout the growing season, thus increasing overall carbon and ozone uptake. If, however, the climate becomes drier, carbon uptake should decline, but trees may be less prone to ozone injury.

We explored the interactions between drought and the uptake of carbon and ozone in a ponderosa pine (*Pinus ponderosa* Dougl. *ex* Laws.) plantation at 1315 m on the western slope of the Sierra Nevada Mountains, CA. Ponderosa pine is

an important species, both ecologically and economically, in the montane conifer forests of California, Washington and Oregon. It is highly sensitive to water availability (Barker 1973, Lopushinsky and Klock 1974)—showing rapid stomatal closure in response to drought, which limits water stress (Zhang et al. 1997) and carbon uptake (Cleary 1970). Drought and vapor pressure deficit (VDP) limitations reduced the use of intercepted light by 33%, according to model results for ponderosa pine forests on the eastern slopes of the Oregon Cascades (Law and Waring 1994). We have observed that canopy conductance decreases with progressive soil water stress over a typical growing season in the Sierra Nevada Mountains, CA (Goldstein et al. 2000).

Among western conifers, ponderosa pine is the most sensitive to ozone stress. Ozone enters foliage through open stomata and damages cell components (Darrall 1989, Reich 1987, Runeckles and Chevon 1992). However, when stomata are constricted because of drought stress, ozone flux (ozone concentration × stomatal conductance to ozone) into the foliage is limited and the effective ozone dose is reduced, regardless of ambient ozone concentrations. At our site in the Sierra Nevada Mountains, CA, eddy covariance measurements demonstrated a progressive decrease in ozone uptake over the summer season while ozone concentrations remained high (Figure 1, modified from Bauer et al. 2000). Thus increased rainfall seems likely to enhance the vulnerability of ponderosa pine to ozone damage; although the magnitude of this effect will depend, in part, on the response of stomatal conductance to increased soil water content.

In this study, we compared the physiological activity of ponderosa pine trees growing under natural drought stress conditions with trees growing under well-watered conditions. We analyzed relationships between stomatal conductance and environmental moisture variables to determine the environmental controllers of conductance. We measured photosynthesis and followed changes in photosynthetic response curves. We also estimated ozone deposition to trees in both treatments, to determine the degree to which drought stress protects trees adapted to a Mediterranean climate from ozone uptake.

Methods

Site description

Blodgett Forest Research Station is a 1200-hectare mixed coniferous forest located in the middle elevation (1300–1500 m) of the central Sierra Nevada near Georgetown, California (38°53′42.9″ N, 120°37′57.9″ W). Typical wind patterns at the site include up-slope flow during the day and down-slope flow at night. The control plot was located in a ponderosa pine plantation adjacent to Blodgett Forest, on land owned by Sierra Pacific Industries. The plantation is relatively flat, and contains a homogeneous mixture of 6- to 8-year-old ponderosa pine with other trees and shrubs scattered throughout the ecosystem making up less than 30% of the biomass. Total leaf area index of shrubs and trees at the beginning of the season
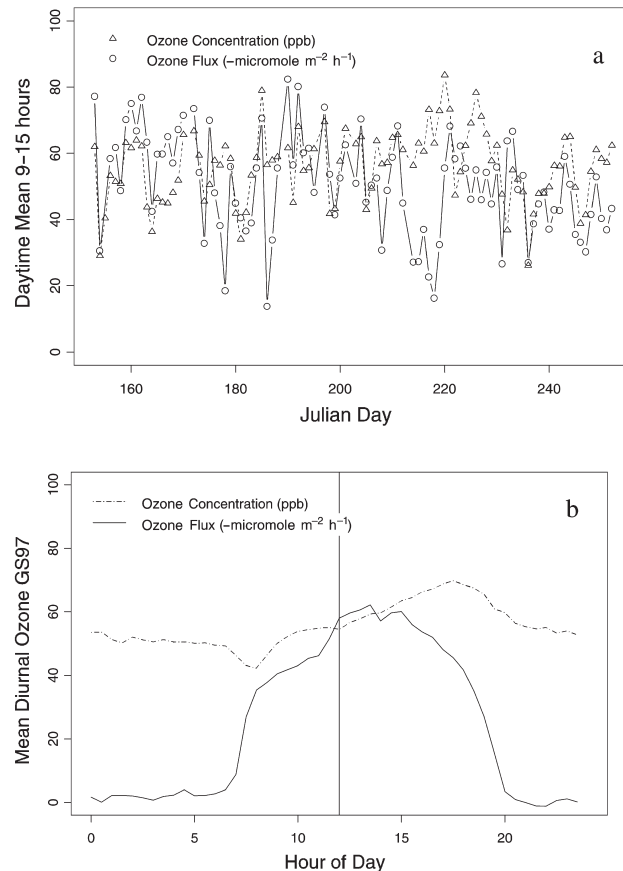

Figure 1. Data from the eddy flux tower site demonstrating that peak ozone flux is decoupled from peak ozone concentration, both seasonally (a) and diurnally (b) (redrawn from Bauer et al. 2000).

before bud break was 5.3 and increased over the experimental period to 9.0 after full elongation of the current-year foliage (Goldstein et al. 2000).

Ozone concentration (Model 1008, Dasibi Environmental Corp., Glendale, CA), air temperature and relative humidity (HMP 45C-L Temperature and RH probe, RM Young Co., Traverse City, MI), net and photosynthetically active radiation PAR (LI190SZ Quantum Sensor, Li-Cor Inc., Lincoln, NE) were measured 6 m above the canopy. Soil water was measured at 10-, 30- and 50-cm soil depths by time domain reflectometry (Campbell Scientific Inc., Logan, UT). All measurements were made from May 1 to October 31 and stored as half-hourly means.

The size and growth characteristics of all ponderosa pine trees in a 10×50 m transect were measured in the control plot, including height, diameter at 1.3 m above ground (DBH), whorl number and heights along the trunk, number of branches per whorl, branch length and aspect, foliar age-class retention, internode, candle and foliar length. Six trees were selected to represent the mean of these characteristics.

The watering treatment was applied to trees growing on a level area within 1 km of the control site. The trees were of similar size and age to those in the control plot, interspersed by

larger trees of several species, including *P. ponderosa*, *Calocedrus decurrens* (Torr.) Florin, *Pseudotsuga menziesii* (Mirb.) Franco and *Abies concolor* (Gord.) Lindl *ex* Hildebr. Eight trees were selected for comparability with trees in the control plot. Six of the eight trees were sampled. The trees were irrigated twice weekly, beginning July 19, with approximately 2300 dm³ of water, divided evenly among the trees. At the beginning of the treatment, soil water content at 30-cm depth in the control plot was 20.5%. Environmental conditions in the watered plot were assumed to be similar to those in the control plot.

Both sites occur on the Cohasset soil series, comprising relatively uniform soils of an andesitic nature, predominantly loam or clay-loam (taxonomic description: fine-loamy, mixed, mesic, ultic haploxeralf). Cohasset soils are inherently porous, primarily because of the high proportion of fine particles (silt or clay) that have a large and reactive surface area. The soil's ability to adsorb and retain water and minerals is relatively high and accounts for its high productivity status (L. Paz, University of California, Berkeley, unpublished data).

Hydrologic status

The hydrological status of the trees at both sites was monitored throughout the season. Water potential was measured before dawn on one east-facing twig from each tree with a pressure chamber (PMS Instruments, Corvallis, OR).

Physiological variables

Net photosynthesis, stomatal conductance and transpiration were measured with an LI-6400 photosynthesis system (Li-Cor, Inc.). Measurements made under identical conditions of light, temperature and vapor pressure deficit (VPD) showed no statistically significant differences in photosynthetic rates between the upper, middle and lower crown, or between north-versus south-facing branches. Variability between trees was such that five trees were sufficient to detect a 10% difference in photosynthesis or stomatal conductance ($\alpha = 0.1$, $\beta = 0.1$, 2-tailed). Therefore the following sampling scheme was employed. One north- and one south-facing branch were selected from the middle canopy layer of each tree to characterize the range of prevailing light conditions. Two fascicles of three needles each in the 1997 age-class (1-year-old) were marked and measured throughout the growing season. The 1998 (current-year emerging) foliage was included in the sampling scheme when it was long enough to fit inside the chamber without damage. All calculations are 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 and total leaf surface area determined as: $(2\pi R + 2 \times R_1 + 2 \times R_2 + 2 \times R_3) \times$ length. The six trees were measured in the same order on each sampling occasion over a measurement period of 1.5 to 2 h.

The status of the photosynthetic system—carboxylation efficiency and maximum rates of electron transport—was determined from the response curves of net photosynthesis versus leaf internal CO_2 concentration. The Farquhar photosynthesis model was fit according to the equations and parameters given in De Pury and Farquhar (1997) and Medlyn et al. (1999). Values of V_{max} (maximum rate of carboxylation), J_{max} (CO_2-saturated photosynthetic rate) and R_d (daytime respiration in the absence of photorespiration) were determined using a program developed by D. Ellsworth (Brookhaven National Lab/Duke FACE Experiment, Duke University, Durham, NC). 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. These response curves were generated at the beginning and end of the season for trees at the control and watered sites. Instantaneous water-use efficiency (WUE) was calculated by dividing photosynthesis by transpiration.

Results

Growth characteristics

Over the course of the growing season, trees in the control plot increased in DBH by 1.4 ± 0.7 cm and in height by 0.7 ± 0.2 m. Snow fell during a 1-week period at the end of May and temperatures remained low into the beginning of June. The low temperatures prevented terminal shoot elongation in ponderosa pine and development lagged by a month relative to the previous, more typical, year. Vigorous new height growth began in early June. Terminal shoot extension was complete by mid-July. Branch shoot extension was completed by the end of June, during which time needles were about 2 cm long. Subsequent elongation resulted in a final, mean needle length of 11.8 ± 2.6 cm by the end of the growing season.

Hydrologic status

Soil water content Soil water content in the control plot was about 30% by soil volume at 30-cm depth through May and June, which was three times higher than during the same period in the previous, more typical, year. Soil water content in the control plot began to drop at the beginning of July (Figure 2) and reached a low of 16.5% (at 30-cm depth) by the beginning of August, after which it remained stable.

Water potential Water potential measurements demonstrated that although trees in the control plot never experienced severe drought stress, there was a treatment effect (Figure 3). Predawn water potentials dropped below -0.5 MPa by the end of the season in trees in the control plot, 0.2 MPa lower than in the watered plot. Trees in the control plot had a significantly lower predawn water potentials than watered trees within 10 days after the irrigation treatment began. However, in contrast to the previous year, trees in the control plot did not experience severe drought stress (Figure 3). Predawn water potentials at the beginning of the 1997 growing season were the same as at the end of the 1998 season. In 1997, water potentials dropped to -1.0 MPa by the end of the growing season.
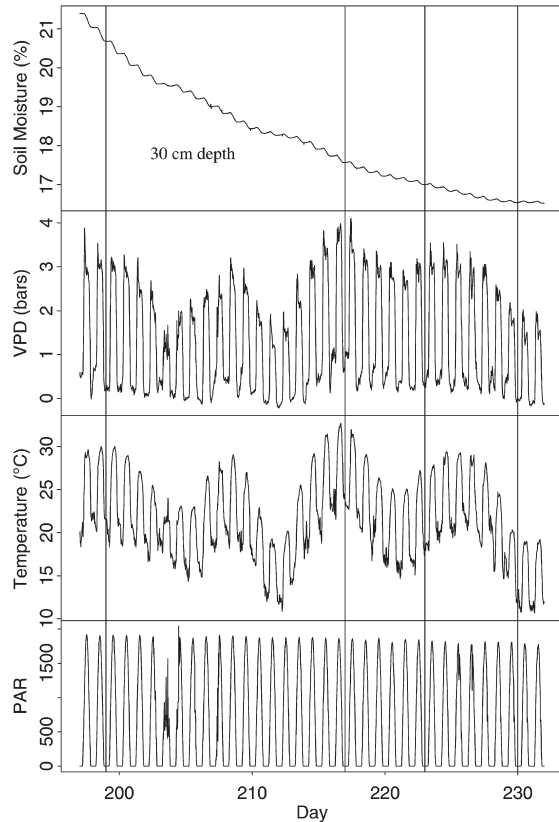
Figure 2. Trends in environmental variables from July 17 to August 18, 1998. Vertical lines indicate sampling dates.

sure deficit and temperature, the data presented are means of all measurements made for both north- and south-facing branches on six trees per measurement period.

Before the watering treatment began, stomatal conductances did not differ significantly between trees in the two plots (Figure 4a). Over the course of the experiment, stomatal conductance of trees in the watered plot rose to, and remained at, a maximum of 0.15 mol m^{-2} s^{-1}. In the control plot, stomatal conductance of the trees dropped over the same time period in response to environmental moisture variables (Figures 4b–4d).

The diurnal pattern of net photosynthesis before the watering treatment began reflects the difference in skyline between the plots (Figure 5a). Trees forming the horizon around the watered site were taller than those at the control site, making sunrise later and sunset earlier. When the sun was above the trees, however, the pretreatment values for net photosynthesis at the two sites were not significantly different. Over the course of the experiment, net photosynthesis of trees in the watered plot rose to a maximum of 8 μmol m^{-2} s^{-1} and remained there. In the control plot, net photosynthesis of the trees decreased over the course of the experiment in response to changes in environmental variables (Figures 5b–5d).

Current-year (1998) foliage   The 1998 foliage continued to elongate throughout the course of the study. During the treat-

Patterns in gas exchange

At the beginning of the 1998 growing season, initial gas exchange measurements were made at three heights within the canopy, on 1997 and 1996 age-classes of foliage, and on north- and south-facing foliage. Because no significant differences ($\alpha = 0.05$) were found among the foliage age classes when measured under the same conditions of light, vapor pres-
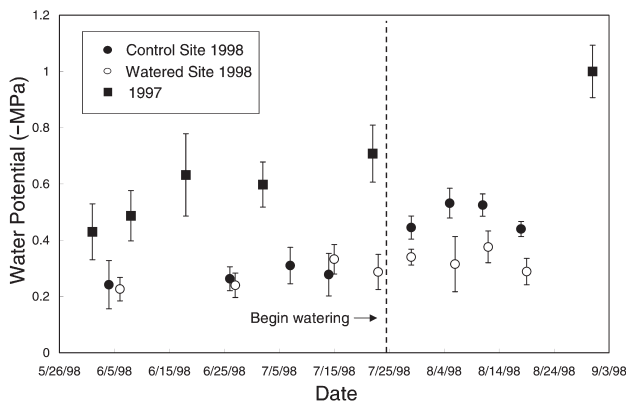

Figure 3. Predawn water potentials of ponderosa pine in the control and watered plots over the course of the experiment. Error bars are ± 1 SD.
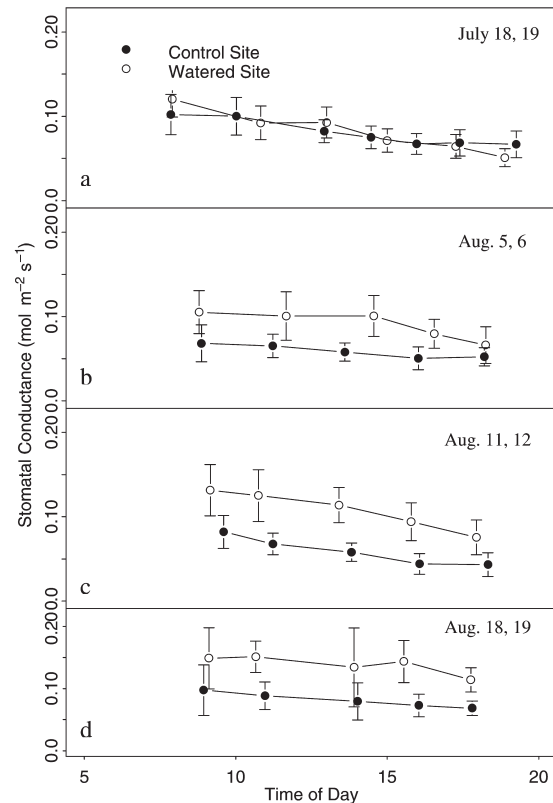

Figure 4. Comparison of diurnal trends in stomatal conductance of ponderosa pine in the control and watered plots over the course of the experiment. Error bars are ± 1 SD.

ment period, current-year foliage had a higher photosynthetic rate and stomatal conductance than 1-year-old foliage at both sites.

Environmental control of gas exchange Among the environmental variables studied, soil water and VPD were best correlated with stomatal conductance in the control plot, explaining 69% of the variability in stomatal conductance over the experimental period (Table 1). Net photosynthesis was highly correlated with stomatal conductance, as well as with temperature and soil water. These variables explained 81% of the variation in net photosynthesis (Table 1). Although PAR obviously plays an important role in stomatal conductance, PAR was eliminated from the analysis because midday values at constant PAR were used.

Photosynthetic response curves Before the site treatment, maximum rates of carboxylation (V_{max}) and electron transport (J_{max}) and respiration rates (R_d) did not differ significantly between trees at the control and watered site (Table 2) (one-sided t-test at $P = 0.05$). There was no significant effect of aspect of foliage origin on these values. From earlier ongoing monthly monitoring of biochemical limitations to photosynthesis at the site, we have observed general increases in V_{cmax} and J_{max} with increasing soil drought over the course of the growing season (data not shown). We had interpreted these increases to repre-

Table 1. Ability of environmental factors to explain variability in gas exchange. Results of forward/backward stepwise linear regression. The full model and the variables that contributed P values greater than 0.15 are presented.

Variable	$P > F$	Cumulative model R^2
Full Model: Conductance = Soil water + VPD + Temperature		
Soil water (30 cm)	0.0006	0.40
VPD	0.0001	0.69
Full Model: Photosynthesis = Conductance + Temperature + Soil water + VPD		
Conductance	0.0001	0.54
Temperature	0.0001	0.63
Soil water (30 cm)	0.0006	0.81

sent a biochemical shift to higher efficiency in response to progressive drought. However, contrary to expectation, we found that watering increased V_{max} and J_{max} significantly in trees in the watered plot relative to the control site (t-test at $P = 0.05$), indicating an increase in the inherent ability of the photosynthetic system to assimilate carbon independently of stomatal conductance (Table 2). However, neither V_{cmax} nor J_{max} at either site increased to the degree that we have observed in a normal drought year. So, although the atypically wet El Niño conditions precluded the expected increase in V_{cmax} and J_{max} in trees in the control plot, we believe another mechanism underlies the increase in these values in response to watering. Such a mechanism could involve mobilization, and increased uptake, of nitrogen by trees in the watered plot. The value of R_d was significantly more negative in trees in the watered plot than in the control plot, reflecting a greater respiration cost. Temperature did not account for the increases in V_{cmax} and J_{max} in response to watering. Although there was a 9 °C temperature difference between the first and second measurement period, temperatures were similar between sites at each measurement period. Furthermore, when values were adjusted for temperature (see method in Law et al. 2001), the differences remained significant.

Before the site treatment, neither quantum efficiency nor maximum light-saturated photosynthesis of the trees differed significantly between the sites (Table 3). Furthermore, they did not change significantly over the course of the experiment at either site. Thus, soil water had little effect on the ability of the photosynthetic system to capture and use light energy independently of its effects on stomatal conductance.

Water-use efficiency

Midday instantaneous water-use efficiency (WUE) rose slightly in trees in the watered plot by the last day of the experiment, but almost doubled in trees in the control plot as a result of a steep and progressive decrease in transpiration. In trees in the watered plot, transpiration and carbon uptake increased together. Despite the large change in WUE in trees in the control plot, differences in WUE between sites were not significant at the end of the experiment.
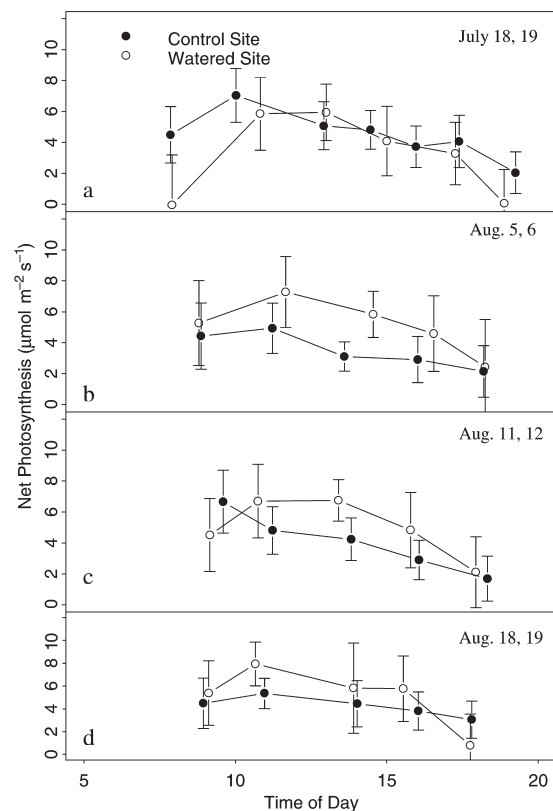

Figure 5. Comparison of diurnal trends in photosynthesis of ponderosa pine in the control and watered plots over the course of the experiment. Error bars are ± 1 SD.

Table 2. Biochemical limitations to photosynthesis derived from A/C_i curves. Results of response curve fitting for control versus watered plots on the initial (i) day versus the final (f) day of the experiment. Values are means ± 1 SD.

Contrast	T_l[1]	V_{cmax}	J_{max}	R_d
Control$_i$ versus Watered$_i$				
$\quad$C$_i$	22	29.1 ± 7.0	65.1 ± 18.0	−0.66 ± 0.65
$\quad$W$_i$	20	32.3 ± 4.3	60.5 ± 15.0	−0.60 ± 0.36
$\quad P(T \le t)$		ns	ns	ns
Control$_i$ versus Control$_f$				
$\quad$i	22	29.1 ± 7.0	65.1 ± 18.0	−0.66 ± 0.65
$\quad$f	31	30.0 ± 4.0	53.6 ± 11.2	−0.01 ± 0.70
$\quad P(T \le t)$		ns	ns	ns
Control$_f$ versus Watered$_f$				
$\quad$C$_f$	31	30.0 ± 4.0	53.6 ± 11.2	−0.01 ± 0.70
$\quad$W$_f$	29	38.1 ± 8.2	73.5 ± 19.1	−0.96 ± 0.9
$\quad P(T \le t)$		0.03	0.03	0.04

[1] Abbreviations: T_l = Leaf temperature at time of measurement (°C); V_{cmax} = maximum rate of carboxylation (μmol CO_2 m^{-2} s^{-1}); J_{max} = maximum rate of electron transport (μmol electrons m^{-2} s^{-1}); R_d = Farquhar-defined respiration rate (μmol CO_2 m^{-2} s^{-1}), see text; and ns = not significant at $P = 0.05$, based on a t-test.

Discussion

Water is an important factor controlling the physiology of the ponderosa pine ecosystem. Although soil drought, along with atmospheric humidity, is known to impose limitations on stomatal conductance through effects on predawn xylem water potential (Running 1976, Running and Coughlan 1988), the interaction between drought-induced limitations on physiological processes and uptake of pollutants such as ozone remains largely unexplored. In a comparison of two ponderosa pine ecosystems—one undergoing a natural soil drought and the other not—we found that increasing soil drought caused decreases in xylem water potential. This response, combined with increased VPD, reduced stomatal conductance that, in turn, limited carbon and ozone uptake. Limitations to stomatal conductance were relieved by watering.

We used data obtained during the three post-treatment measurement periods to determine: (1) how much a typical Mediterranean drought limits carbon uptake in ponderosa pine; and (2) how much the drought protects these forests from ozone uptake and subsequent damage. We calculated the percent differences in net photosynthesis between trees in the control plot and the watered plot. We calculated ozone fluxes by multiplying ozone concentration by stomatal conductance to ozone. Then we calculated percent differences between ozone flux in the control plot and the watered plot (Table 4).

Leaf-level carbon uptake in this ponderosa pine system was about 35% below that occurring in the absence of summer drought. Ozone uptake was reduced by about 40% by summer drought. We note that these values represent only three snapshots during a growing season that was influenced by El Niño climate patterns, and therefore do not represent the entire growing season. Although most years are typically drier than the 1998 year, these data illustrate several important points. There exists the capacity for young, vigorously growing ponderosa pine forests to increase their carbon uptake if summer rainfall (and consequently soil water content) increases, at

Table 3. Biochemical limitations to light capture, derived from light curves. Values are means ± 1 SD. Abbreviations: i = initial day of the experiment; f = final day of the experiment; ns = not significant.

Contrast	P_{max}[1]	Quantum efficiency	Compensation point
Control$_i$ versus Control$_f$			
$\quad$i	6.2 ± 1.7	0.017 ± 0.003	34.0 ± 11.0
$\quad$f	6.7 ± 1.2	0.021 ± 0.005	36.3 ± 6.8
$\quad P(T \le t)$	ns	ns	ns
Control$_f$ versus Watered$_f$			
$\quad$C	6.7 ± 1.2	0.021 ± 0.005	36.3 ± 6.8
$\quad$W	7.9 ± 1.6	0.024 ± 0.003	41.1 ± 8.6
$\quad P(T \le t)$	ns	ns	ns

[1] Abbreviation and units: P_{max} = maximum net photosynthetic rate (μmol CO_2 m^{-2} s^{-1}); quantum efficiency (mol CO_2 mol photon^{-1}); and compensation point (μmol photon m^{-2} s^{-1}).

Table 4. Effects of drought on carbon and ozone uptake in the ponderosa pine forest at three sampling times post-treatment.

% Uptake at watered site over control site	Sample date		
	Aug 6, 1998	Aug 12, 1998	Aug 19, 1998
Carbon	+ 39	+ 35	+ 30
Ozone	+ 36	+ 46	+ 41

least in the short term. Most of this increase would be brought about by increased stomatal conductance over the day and over the season. Photosynthetic capacity (V_{cmax}, J_{max}) increased in trees in the watered plot during the wet summer of 1998. However, based on our unpublished observations that V_{cmax} and J_{max} increased with increasing soil drought over the course of the growing season in other years, we conclude that increases in these factors with summer drought in more normal drought years might also be expected. Increased WUE efficiency in the control plot did not make up for the losses in carbon uptake caused by reduced stomatal conductance.

Increased soil water availability and consequent increases in stomatal conductance could lead to increased ozone uptake by ponderosa pine, because ponderosa pine forests are currently protected from periods of high ozone concentration in the late summer by low stomatal conductance. Although ozone flux into the foliage increases with increased stomatal conductance, this does not necessarily mean that ozone damage increases. Tissue responses to ozone damage include protective and repair processes, and changes in carbon allocation that may confound the direct relationship between dose and symptoms. There may also be an interaction between carbon and ozone uptake. For example, increased uptake of carbon may help trees cope with damage from increased ozone uptake. Over the long term, there may be adaptations to increased soil water availability that influence both carbon and ozone uptake rates.

An implication of this study is that, even if ozone concentrations do not increase in the next few decades, changes in climate that result in increased soil water availability may make the ponderosa pine forests growing in the Mediterranean climate of California and the Pacific Northwest vulnerable to ozone damage at ozone concentrations from which they were previously protected. The key to determining the degree to which these ponderosa pine forests are vulnerable to the interaction between pollution and climate lies in understanding the physiological link between climate and stomatal conductance.

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