

Ozone uptake, water loss and carbon exchange dynamics in annually drought-stressed *Pinus ponderosa* forests: measured trends and parameters for uptake modeling

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Summary This paper describes 3 years of physiological measurements on ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) growing along an ozone concentration gradient in the Sierra Nevada, California, including variables necessary to parameterize, validate and modify photosynthesis and stomatal conductance algorithms used to estimate ozone uptake. At all sites, gas exchange was under tight stomatal control during the growing season. Stomatal conductance was strongly correlated with leaf water potential ($R^2 = 0.82$), which decreased over the growing season with decreasing soil water content ($R^2 = 0.60$). Ozone uptake, carbon uptake, and transpirational water loss closely followed the dynamics of stomatal conductance. Peak ozone and CO₂ uptake occurred in early summer and declined progressively thereafter. As a result, periods of maximum ozone uptake did not correspond to periods of peak ozone concentration, underscoring the inappropriateness of using current metrics based on concentration (e.g., SUM0, W126 and AOT40) for assessing ozone exposure risk to plants in this climate region. Both $J_{\max}$ (maximum CO₂-saturated photosynthetic rate, limited by electron transport) and $V_{\max}$ (maximum rate of Rubisco-limited carboxylation) increased toward the middle of the growing season, then decreased in September. Intrinsic water-use efficiency rose with increasing drought stress, as expected. The ratio of $J_{\max}$ to $V_{\max}$ was similar to literature values of 2.0. Nighttime respiration followed a Q_{10} of 2.0, but was significantly higher at the high-ozone site. Respiration rates decreased by the end of the summer as a result of decreased metabolic activity and carbon stores.

Keywords: gas exchange, photosynthesis, physiology, pollution, ponderosa pine, stomatal conductance, water potential.

Introduction

Annually drought-stressed forest ecosystems in Mediterranean climates, such as those along the west coast of the USA and in southern Europe, are subject to a different climate than the mesic forests of the northeastern, southeastern and mid-western USA and of northern Europe, where much of our understanding of forest response to environmental variability has

been developed. Mediterranean-climate ecosystems receive most of their precipitation in the winter and spring, but very little between June and October. This has a profound influence on biosphere–atmosphere interactions during the growing season. Central to the differences in ecosystem responses to differing climates, and important to all biosphere–atmosphere interactions, is the role of stomata. Stomata open and close in response to changes in their environment—light, humidity, water stress, and temperature—thus restricting water loss, maximizing carbon uptake, and directly and indirectly affecting pollutant uptake.

Several stomatal conductance algorithms are used in forest physiological models (see review by Panek et al. 2003), and models describing stomatal conductance have been developed and applied with success in mesic ecosystems with 3–4-month growing seasons (e.g., see review by Wesely and Hicks 2000). Although drought is known to have a profound effect on stomatal conductance, few models describe stomatal conductance in annually drought-stressed ecosystems like those of California, eastern Oregon and Washington, and southern Europe. Water- and light-use efficiencies, carboxylation capacities and respiration rates are known to vary in drought-adapted plants and affect stomatal conductance (and thus ozone and carbon uptake). Different climates and eco-regions may require different modeling approaches (Musselman and Massman 1999, Emberson et al. 2000b, Massman et al. 2000). Reworking existing models to include these physiological traits is necessary if accurate estimates of both plant pollutant exposure and biosphere response to changes in climate are to be obtained.

Tropospheric ozone is a phytotoxic air pollutant responsible for crop and forest damage worldwide. Historically, ozone exposure has been evaluated on the basis of ambient atmospheric concentrations; however, ozone must enter foliage through stomatal pores to cause damage. Therefore, stomatal conductance is a critical component of estimates of the effects of ozone exposure. To quantify and model ozone uptake, controls on stomatal conductance must be understood. The need to move beyond concentration-based measures of ozone exposure to measures based on stomatal uptake is only now being

incorporated into debates on ozone regulation, and only in Europe under the UN-ECE Convention on Long-range Transboundary Air Pollutants (UN-ECE 2002). Landscape-scale ozone pollution models in Europe now contain stomatal conductance algorithms (Tuovinen and Laurila 1993, 1996, Emberson et al. 2000a, 2000b, 2001, Tuovinen 2000, Tuovinen et al. 2001a, 2001b).

There is a need, therefore, to revisit the physiological controls on drought-adapted species in relation to both recent advances in modeling of stomatal conductance and consequences for ozone and carbon uptake. This scrutiny is especially important for species growing in ozone-polluted regions subject to seasonal drought stress (such as California) and for drought-adapted species subject to changes in water availability induced by climate change. Modeling is complicated by differences in species' responses to variable environmental conditions. A variety of modeling approaches to estimating stomatal conductance is available, but not all models perform equally well in all environments and with all species. This necessitates field studies to collect environmental and physiological data to parameterize existing conductance models, test and validate approaches to modeling conductance, modify existing models and perhaps develop new approaches, and to do so for several years over a range of conditions in a drought-stressed ecosystem. The collection of field measurements, in combination with model development and testing, was the purpose of this study.

This paper describes 3 years of physiological measurements on ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) along an ozone concentration gradient in the Sierra Nevada, CA, including measurements of environmental and physiological parameters needed to drive current algorithms in plant physiological models used to estimate photosynthesis, transpiration, stomatal conductance, and other gas exchange parameters. Ponderosa pine is an ecologically and economically important forest species in the western USA that has adapted to the seasonal summer drought in California and the Pacific Northwest, and is very sensitive to ozone. Ozone injury in ponderosa pine has been identified and measured in California for more than four decades (Miller et al. 1963, 1996, Arbaugh et al. 1998). Because air pollution has been observed to play a role in modifying physiological relationships (Broadmeadow 1999, Medlyn et al. 1999), measurements were made at sites with varying pollutant exposure.

The data set covers a suite of environmental and physiological measurements. Continuous environmental measures included temperature, relative humidity, vapor pressure deficit (VPD), photosynthetically active radiation (PAR), soil water content and temperature, precipitation and ozone concentration. Physiological measures included predawn and afternoon water potential; $J_{\max}$ (maximum CO_2 -saturated photosynthetic rate, limited by electron transport) and V_{cmax} (maximum rate of Rubisco-limited carboxylation); diurnal trends in photosynthesis, stomatal conductance and transpiration; and dark respiration, quantum efficiency and light compensation point. The data set spans three 5-month growing seasons and one winter, and is replicated on each of the two most recent foliage age

classes at four sites widely dispersed along the Sierra Nevada. Ponderosa pine retains two to five age classes of foliage, but most commonly around three. This extensive data set is well suited to parameterizing, testing and validating physiological models, a project that is described in a companion paper (Misson et al. 2004).

Methods

The region

The Sierra Nevada is typified by a Mediterranean climate, with little precipitation between June and October. Soil water content and atmospheric humidity decline over the summer months, causing a predictable seasonal summer drought. Sierra forests receive ozone in plumes that originate in the urban centers of the San Francisco Bay Area, Bakersfield, Fresno, Sacramento and Los Angeles (Cahill et al. 1996) as well as the transportation corridors within the central valley. Gross-scale air mass trajectories move eastward off the ocean and into the Central Valley, then southeastward within the valley (Figure 1). The transverse Tehachapi range at the base of the Central Valley deflects air masses up-slope and into the Sierra Nevada at Sequoia/Kings Canyon National Park. In 1999, the National Park Service ranked Sequoia National Park the most ozone-polluted national park in the country (National Park Service 1999a, 1999b). In 1991, a network of 11 ozone sta-

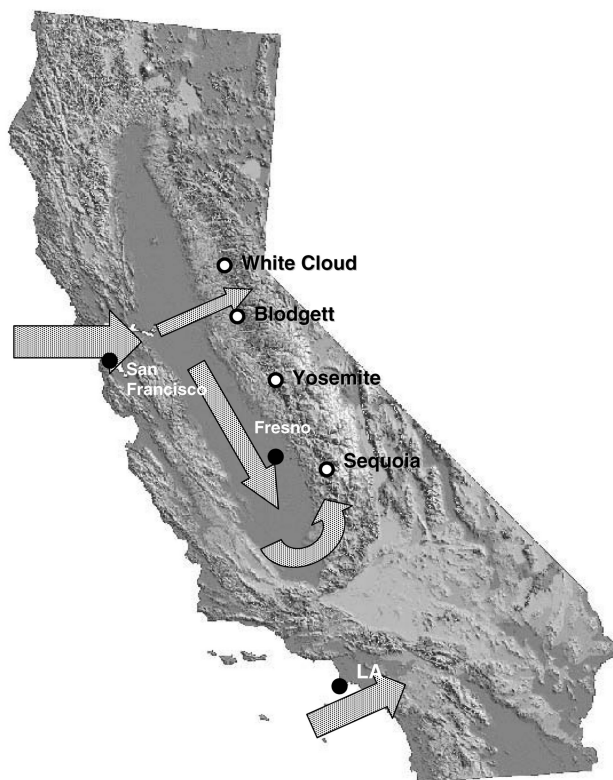


Figure 1. Location of study sites in the Sierra Nevada, CA, USA in relation to major air mass trajectories carrying ozone and ozone precursors (digital relief map from USGS 2003).

tions was installed at remote forested sites along the Sierra Nevada as a part of the Forest Ozone REsponse STudy (Project FOREST, Carroll and Dixon 1995, Cahill et al. 1996). Ozone concentrations generally increased from north to south along the Sierra. Distinct diurnal profiles, characteristic of daytime upslope winds, were evident at some, but not all, of the sites, indicating that patterns of ozone deposition cannot be generalized across all forest sites (Carroll and Dixon 1995).

Site selection

Three sites were selected from the 11 Project FOREST sites, to represent high, moderate and low ozone exposure, along the ozone concentration gradient: Sequoia/King's Canyon National Park, White Cloud, and Yosemite National Park, respectively (Figure 1, Table 1). A fourth site was established in a young ponderosa pine plantation adjacent to an AmeriFlux eddy covariance site at Blodgett Forest Research Station (Goldstein et al. 2000). Trees at the fourth site were 7 years old at the beginning of the study and the stand was subjected to typical management practices including understory shrub removal in spring 1999 and a pre-commercial thin in spring 2000. At each site, one plot with a southern exposure, an open canopy, and trees with branches near the ground was selected. Site characteristics are presented in Table 1.

Soil characteristics

The four sites span two soil types. Sequoia and Yosemite soils are derived from granitic parent material, whereas Blodgett and White Cloud soils are andesitic in origin. Sequoia soils are up to 150 cm in depth and are classified as sandy, mixed, mesic pachic Xerumbrepts (Huntington and Akeson 1987). Yosemite soils are up to 1 m in depth, comprise loamy sand and gravelly loamy sand, and are classified as coarse-loamy, isotic, mesic humic Dystroxerept (R. Taskey, California Polytechnic State University, San Luis Obispo, CA, personal communication). Both Blodgett and White Cloud soils occur on the Cohasset soil series, comprising a reddish-brown andesitic soil. Blodgett soils are up to 130 cm deep, are relatively uniform, and are classified as fine-loamy, mixed, mesic ultic Haploxeralf (L. Paz, EIP Associates, San Francisco, CA, unpublished data). White Cloud soils are up to 240 cm deep and comprise cobbly clay loam underlain by a substratum of weathered andesitic conglomerate (Brittan 1975).

Physiological measurements

Within each mature ponderosa pine plot (Sequoia, Yosemite and White Cloud), six trees were selected for physiological measurements; each tree had south-facing branches close to the ground, was greater than 40 years old, and had a history of ozone injury assessment within Project FOREST. Mean diameters (DBH) of trees at Sequoia, Yosemite and White cloud were 23.4 ± 6.1 (SD), 40.8 ± 9.9 and 22.9 ± 5.0 cm, respectively. At Blodgett Forest, six saplings were randomly selected from within the fetch of the eddy covariance tower. Two fascicles of 1-year and 2-year age classes on the terminal whorls of south-facing branches were tagged on all trees in May and measured throughout the growing season. Separate foliage from the same whorl was used for diurnal measurements and response curves (i.e., net photosynthesis versus leaf internal CO_2 concentration (A/C_i) and net photosynthesis versus photosynthetically active radiation (A/PAR)).

Each site was visited monthly from May (before bud break, beginning Julian Day (JD) 121) to September (end JD 273) over two growing seasons (1999–2000), and bimonthly from November 2000 to October 2001. Diurnal trends in gas exchange, including net photosynthesis, stomatal conductance and transpiration, were followed monthly as trees responded to a typical soil drying cycle over the growing season. Midday gas exchange maxima were recorded over one winter as soils resaturated. The A/C_i response curves were measured every month and through the winter of 2000–2001. The A/PAR response curves and nighttime respiration were measured at high soil water content in June, and were repeated at low soil water content in August.

Gas exchange was measured on the two most recent age classes of needles on one south-facing branch from each tree throughout the growing season because this aspect represents the maximum light availability and minimum humidity that needles experience. To measure diurnal trends in gas exchange, two fascicles of three needles each were randomly chosen from the terminal whorl and enclosed in a 2×6 cm chamber in natural light; the chamber environment was modified to match ambient humidity and temperature. Measurements were made with an LI-6400 (Li-Cor, Lincoln, NE) after the stability of the reading reached a coefficient of variation of less than 0.6%. Response curves were measured in a 3×2 cm

Table 1. Site locations and characteristics.

Site	Location	Slope	Elevation (m)	No. days exceeding state standard in 2001
Sequoia/King's Canyon National Park	36°33'55" N, 118°46'36" W	30%	1920	21 ^{1,2}
Yosemite National Park	37°42'43" N, 119°42'19" W	10%	1220	3 ^{1,2}
Blodgett Forest Research Station	38°53'43" N, 120°37'58" W	2%	1315	19 ^{1,3}
White Cloud	39°19'00" N, 120°50'45" W	10%	1326	10 ^{1,4}

¹ California 1-h standard is 0.09 ppm. Data from California Air Resources Board (CARB) Air Quality Data Statistics (<http://www.arb.ca.gov/adam/welcome.html>).

² Data courtesy of the National Park Service.

³ Data courtesy of A. Goldstein, University of California, Berkeley.

⁴ Data courtesy of CARB.

chamber with a red/blue light source, and the chamber environment was modified to maintain relative humidity near maximum (around 50%) and leaf temperature at 25 °C. The A/C_i curves were analyzed after the method of D.S. Ellsworth (University of Michigan, Ann Arbor, MI). That is, the Farquhar photosynthesis model was fitted according to equations and parameters given in de Pury and Farquhar (1997) and Medlyn et al. (1999) to determine V_{cmax} , J_{max} and R_d (daytime respiration in the absence of photorespiration). Instantaneous water-use efficiency was calculated as the ratio of net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) to transpiration ($\text{mmol m}^{-2} \text{s}^{-1}$), normalized for VPD (kPa). Nighttime respiration measurements were made between 2100 and 0400 h in a temperature-controlled 2×6 cm chamber. Measurements were made at 5 °C intervals, after stabilizing for 5 min at the given temperature. The Q_{10} was calculated as the ratio of respiration rate at $T + 10$ °C to the rate at T . All-sided leaf area was used in gas exchange calculations because stomata occur over the entire surface area of ponderosa pine needles. Leaf area was calculated as described by Panek and Goldstein (2001). Predawn and midday leaf water potentials were made on each tree on the day of gas exchange measurements with a pressure chamber (PMS Instruments, Corvallis, OR).

Phenological measurements

Extension of needles and terminal candle was measured monthly at each site. Measured needles were on the same two fascicles on which physiological measurements were made.

Environmental measurements

A suite of meteorological instruments was installed at the Sequoia, Yosemite and White Cloud sites. Measurements, made at 10 s intervals and averaged over each hour, included air temperature (°C; CS500, Campbell Scientific Instruments (CSI), Logan, UT), relative humidity (%; CSI CS500), VPD (kPa), PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$; Li-Cor LI-190SZ), rainfall (mm h^{-1} ; CSI TE525), volumetric soil water (proportion; CSI CS615) and soil temperature (°C; CSI 107 Temperature Probe). Soil temperature and soil water content measurements were made at depths of 10 and 50 cm. Meteorological data and ozone data from the Blodgett Forest site were provided by A. Goldstein (University of California, Berkeley). Ozone was measured at Yosemite and Sequoia by the National Park Service (data managed by Air Resource Specialists, Denver, CO) and at White Cloud by the California Air Resources Board (CARB).

Ozone uptake calculation

Ozone uptake ($\text{FO}_{3\text{stom}}$; $\mu\text{mol O}_3 \text{m}^{-2} \text{h}^{-1}$) was calculated from ozone concentration ($[\text{O}_3]$; ppb or $\text{nmol O}_3 \text{mol}^{-1} \text{air}$), stomatal conductance to water vapor (g_w ; $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), with appropriate unit conversions, and a value of 1.51 for the relative diffusivity of ozone to water in air (Massman 1998):

$$\text{FO}_{3\text{stom}} = ([\text{O}_3]g_w)/1.51$$

This method of estimating ozone uptake depends on the assumption that stomata are exposed to ambient ozone concen-

trations. Three attributes of the ponderosa pine forest support the validity of this assumption: (1) the open, widely spaced nature of the mature ponderosa pine forest leads to good mixing of the atmosphere within the forest; (2) whorls are arranged on the outer surface of the tree crown and therefore the crown lacks significant depth; and (3) the leaf boundary layer of coniferous needles is small. The assumption was explicitly tested by comparing the relative importance of aerodynamic conductance (g_a ; m s^{-1}), leaf boundary layer conductance (g_b ; m s^{-1}), cuticular conductance (g_{ct} ; m s^{-1}) and stomatal conductance (g_s ; m s^{-1}) to overall ozone flux based on data from 396 measurements spanning four sites and 3 years. The algorithms used were from Zeller and Nikolov (2000) and Nikolov et al. (1995). Total leaf ozone flux ($\text{FO}_{3\text{leaf}}$) is calculated as a resistance network, with g_a^{-1} and g_b^{-1} in series and with canopy stomatal and cuticular conductances in parallel ($\text{FO}_{3\text{leaf}} = \Delta\text{O}_3/(g_a^{-1} + g_b^{-1} + (g_s + g_{ct})^{-1})$), where ΔO_3 is the difference between $[\text{O}_3]$ above the canopy and at the active surface, assuming $[\text{O}_3] = 0$ at the surface. Calculated aerodynamic conductance was 10 to 100 times greater than measured g_s at moderate to high g_s and up to 600 times greater at low g_s . Boundary layer conductance was 10 to 40 times greater than g_s at moderate to high g_s and up to 400 times greater at low g_s . This demonstrates that stomatal conductance is small relative to the conductance pathway that brings ozone to the leaf, and there is little resistance to ozone entering the leaf. At the leaf surface, cuticular and stomatal conductances are in parallel, and g_{ct} was less than 0.5% of g_s , demonstrating that the major pathway for ozone into the leaf is by way of stomata. Thus, it is appropriate to assume that ozone uptake can be calculated as the product of ozone concentration and stomatal conductance to ozone in this canopy type.

Results

Environmental variables

Air temperature, precipitation, and relative humidity Only slight variations in temperature occurred from year to year, and were consistent among sites. Fall 2000 cooled faster than other years, and May 2001 was warmer than other years (Figure 2). Winter–spring 2000 had higher precipitation than the other years at all of the sites (Figure 2). Sequoia had significantly higher precipitation than the other sites in all years, whereas Yosemite and White Cloud received the least precipitation. Relative humidity (RH) was lower in spring and fall in 2001 than in 2000, and Yosemite and White Cloud had drier summers than the other sites in all years (Figure 2). Response to the pre-commercial thin is seen in the high RH values at Blodgett Forest in spring 2000.

Soil water and temperature Soils at all sites dried progressively from mid-May, after rains stopped (Figure 3), through September. Soil water resaturation occurred quickly after the first winter precipitation and soils remained saturated throughout the winter. Sequoia and Yosemite showed consistently lower soil water contents during the growing season than

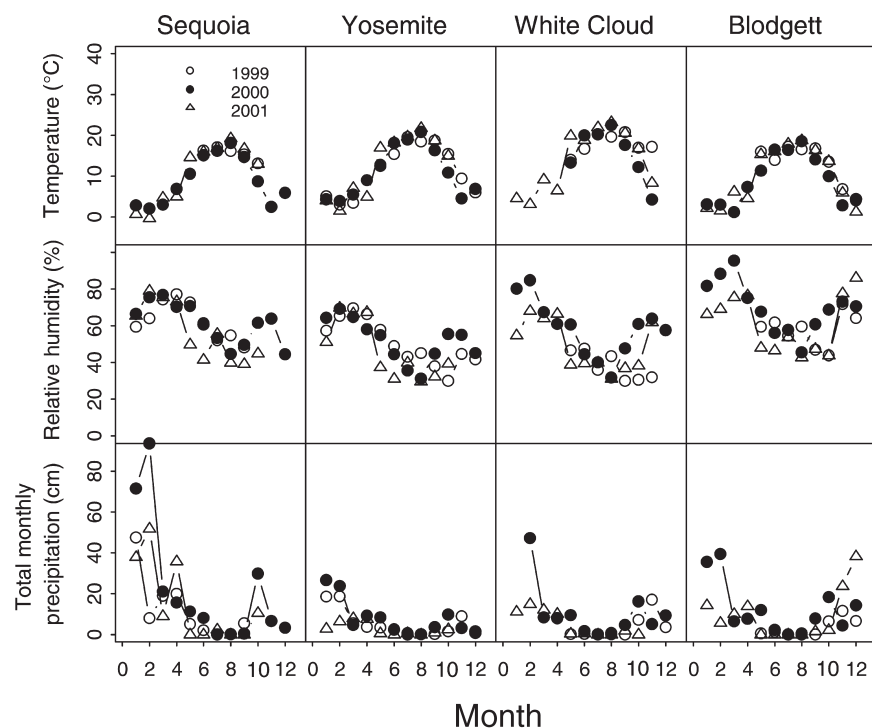


Figure 2. Mean monthly temperature, mean monthly relative humidity, and total monthly precipitation trends at each study site for 1999–2001.

White Cloud and Blodgett Forest. Soil temperatures remained between 2 and 10 °C during the winter, despite fluctuations in air temperature between –5 and 15 °C (data not shown). This cycle of summer soil drying and moderate winter soil temperatures is unique to Mediterranean climates.

Leaf water potential

Predawn leaf water potential suggested leaf water stress in response to decreasing soil water content over the summer (Figure 3). Leaf water potential was more negative in trees at Sequoia and Yosemite than in trees at the other sites, consistent with the lower soil water contents at Sequoia and Yosemite. Based on leaf water potential data, soil water content at 50-cm

depth appeared to be a good indicator of soil water availability (Figure 4a).

Growth and phenology

Timing of bud break was similar at all sites in all years, occurring in late May to early June (Figure 5). Leaf elongation continued through mid-August, whereas candle growth terminated slightly earlier. Final needle length was similar in trees at all sites except Sequoia, where new needles were significantly shorter than at the other sites at the end of all three growing seasons ($P < 0.0001$). Candle length was significantly greater in trees at the Blodgett site than at the other sites, as expected for young, actively growing ponderosa pine (Figure 5).

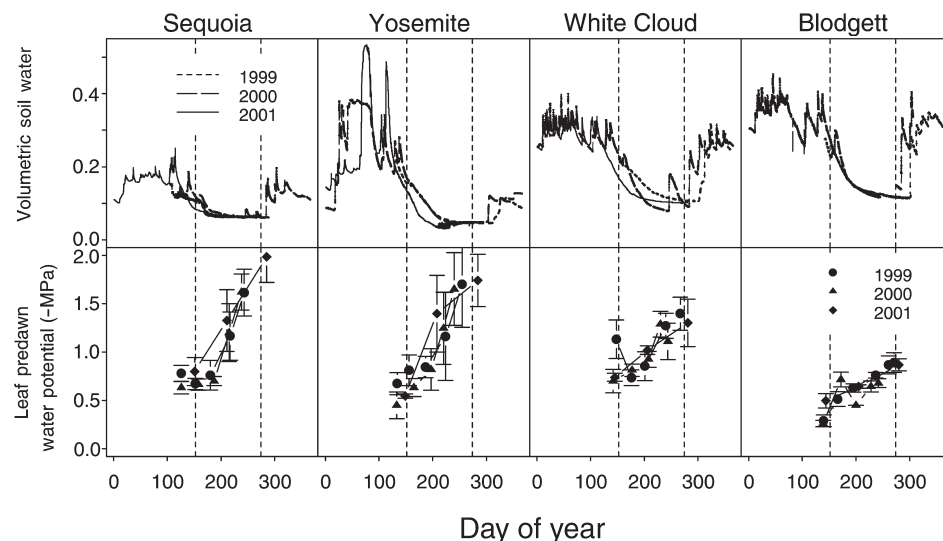


Figure 3. Soil water content measured continuously from 1999 to 2001 and predawn leaf water potential measured monthly at each site during three growing seasons. Vertical dashed lines indicate June 1 and October 1.

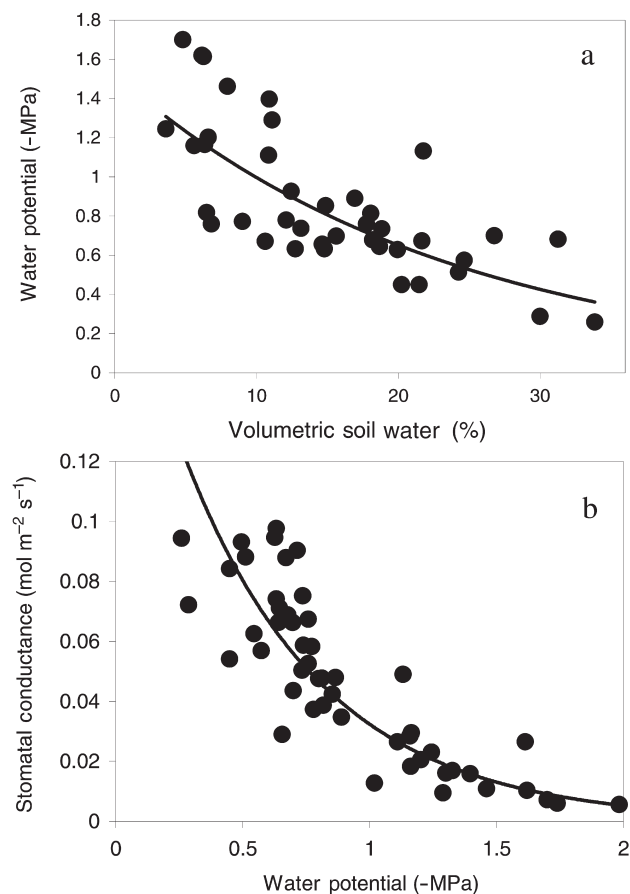


Figure 4. (a) Water potential was a moderately close function of soil water content at 50 cm depth, $y = 1.5e^{-0.0425x}$, $R^2 = 0.60$. (b) Stomatal conductance was a close function of water potential, $y = 0.2e^{-1.8177x}$, $R^2 = 0.82$.

Gas exchange

Stomatal conductance Stomatal conductance decreased with increasing water stress over the summer. Water potential alone explained 82% of the day-to-day variation in midday stomatal conductance at all sites (Figure 4b). A shift in peak stomatal conductance from midday to early morning accompanied the decrease in maximum stomatal conductance as drought increased in severity over the summer (Figure 6). This shift was not entirely explained by VPD, which showed little correlation with stomatal conductance ($R^2 = 0.08$), even at low soil water contents ($< 16\%$, $R^2 = 0.24$), or with residuals from the stomatal conductance–water potential relationship ($R^2 = 0.04$). Stomatal conductance was moderately well related to photosynthesis when data from all 3 years were combined ($R^2 = 0.63$, $P < 0.0001$). However, when the data were divided by month, increasing tightness of the linear relationship was observed through the growing season (Figure 7) ($r^2 = 0.58$ in May, $r^2 = 0.70$ in September). This was a result of divergence in the relationship at the early and late portions of the day earlier in the season at maximum leaf water potential. Early in the season, stomatal conductance increased quickly in the early morning without a related increase in PAR. Stomatal opening independ-

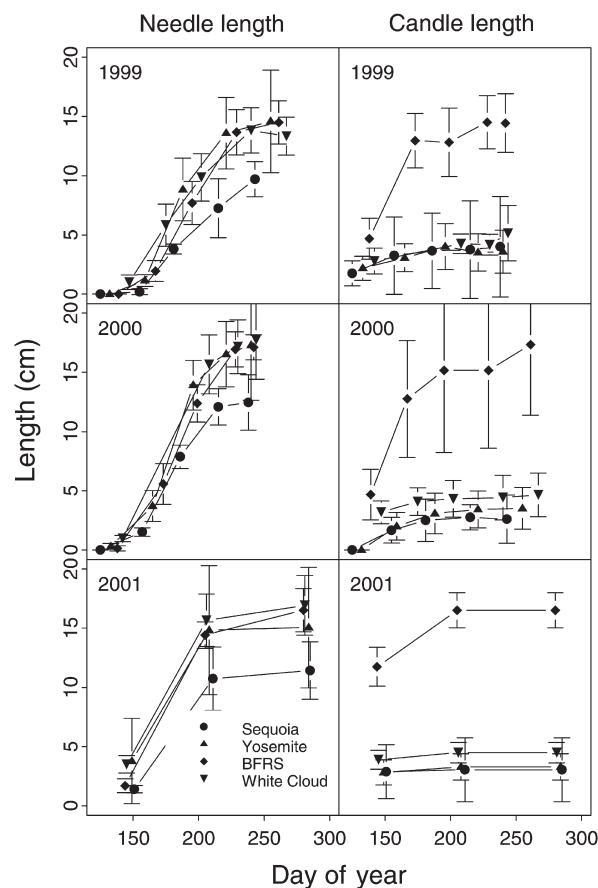


Figure 5. Phenological changes over three growing seasons at all study sites (BFRS = Blodgett Forest Research Station). Error bars are ± 1 SD. Needles at Sequoia were significantly shorter than needles at other sites in all 3 years.

ent of light has been reported previously and has been attributed to endogenous cycles (Tobiasson 1982, Kaiser and Kappen 1997), abscisic acid dynamics (Jackson et al. 1995) and humidity response (Meidner 1986). Also, stomata stayed open at the end of the day even at low irradiances. If only measurements from 1200 to 1400 h were considered over the 3 years, the relationship between net photosynthesis and stomatal conductance was strong (Figure 7).

I compared stomatal conductance of 1-year-old, 2-year-old and current-year foliage. The current-year foliage was too fragile to put in the cuvette until August; therefore, comparisons were made only from August onward. Comparisons were made each growing season from 1999 through 2001 for every tree during the diurnal measurements. Foliage was subject to current environmental conditions. In general, there was no significant difference between current-year and 1-year-old foliage; however, there was a significant difference between 1-year-old and 2-year-old foliage (data not shown). This was probably caused by differences in irradiance, because ambient PAR was consistently lower in the older foliage. Soil water was not limiting during winter, and stomatal conductance was highly dependent on air and soil temperatures, and on PAR. Under warm, sunny conditions in March and November 2000,

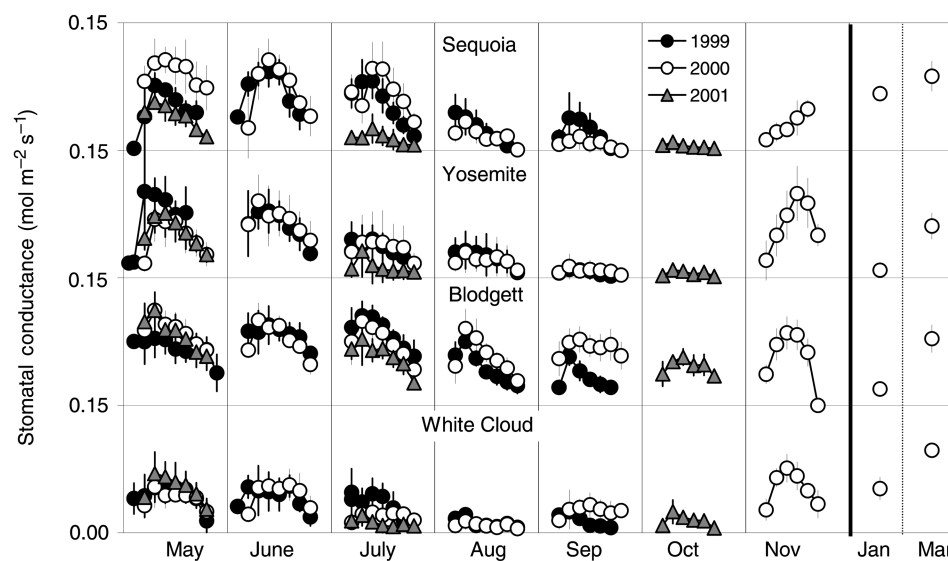


Figure 6. Diurnal patterns of stomatal conductance at each study site for 3 years. Individual panels represent one day of diurnal measurements taken every 2 h from 0600 to 1800 h PST each month at each site during the growing season. Values are means of six trees. Measurements were also made in the winter of 2000–2001. Error bars are ± 1 SE.

stomatal conductance reached peak values comparable with spring values (Figure 6).

The pattern of progressively decreasing stomatal conduc-

tance from May to September varied little among sites. In general, trees at Sequoia and Blodgett had higher stomatal conductances than trees at Yosemite and White Cloud. Throughout the summer, trees at Sequoia showed the largest decrease in stomatal conductance, whereas trees at Blodgett showed the smallest decrease (Figure 6).

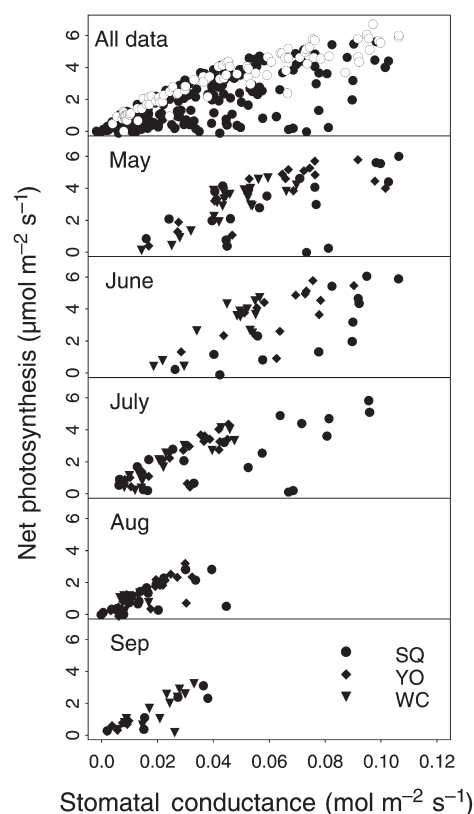


Figure 7. Relationship between stomatal conductance and net photosynthesis for 3 years at the mature sites. Each value represents the mean of six trees. Measurements were taken every 2 h over one day of each month at every site. Open circles in the top panel are midday measurements showing that the tight relationship between stomatal conductance and photosynthesis was limited to midday values ($A_{\text{net}} = 53.3g_s + 0.82$, $r^2 = 0.87$, $P < 0.001$).

Ozone uptake versus ambient ozone concentration The progressive decrease in stomatal conductance during the summer led to a marked decrease in ozone uptake despite little change or an increase in ozone concentrations over the growing season. Figure 8 shows the trend for Yosemite in 1999, but the trend was similar at all mature sites in all years. The annual fluctuation in ozone uptake in comparison with annual ozone concentrations is shown in Figure 9. On a daily timescale, the progressive left skewing of the trend in diurnal stomatal conductance caused a similar skewing of ozone uptake, despite higher afternoon ozone concentrations (Figure 10). Thus, highest ozone uptake occurred early in the growing season and progressively earlier in the day as soil water content decreased over the season (Figure 11), leading to a decoupling between periods of high ozone uptake and high ozone concentration (Figures 8–10).

Like stomatal conductance, ozone uptake was highest in trees at the Sequoia and Blodgett sites and lowest in trees at the Yosemite and White Cloud sites. The decline in ozone uptake over the season was least pronounced in trees at the Blodgett site. Ozone uptake in the winter was highly dependent on temperature and light, because of light and temperature effects on stomatal conductance. Ozone uptake was higher in the winter than in late summer. Lower ozone concentration in general kept winter uptake values slightly below the spring maxima (Figures 9 and 11).

Transpiration The decrease in stomatal conductance during the summer caused transpiration to decrease, despite an increase in VPD that would be expected to drive higher transpiration rates (Figure 12). One-year-old foliage had significantly

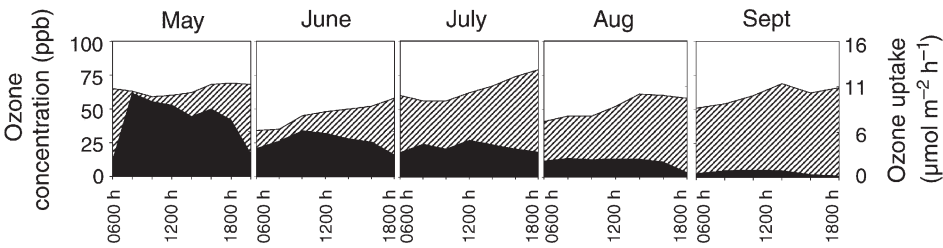


Figure 8. Ozone concentration (hatched areas) plotted with ozone uptake (solid areas) for the Yosemite site in 1999, showing increasing decoupling of concentration and uptake over the season. This decoupling pattern was similar at all mature sites in all years.

Ozone uptake was calculated as stomatal conductance to ozone $\times$ ozone concentration. Individual panels present 1 day of diurnal measurements taken every 2 h from 0600 to 1800 h PST in each month during the growing season.

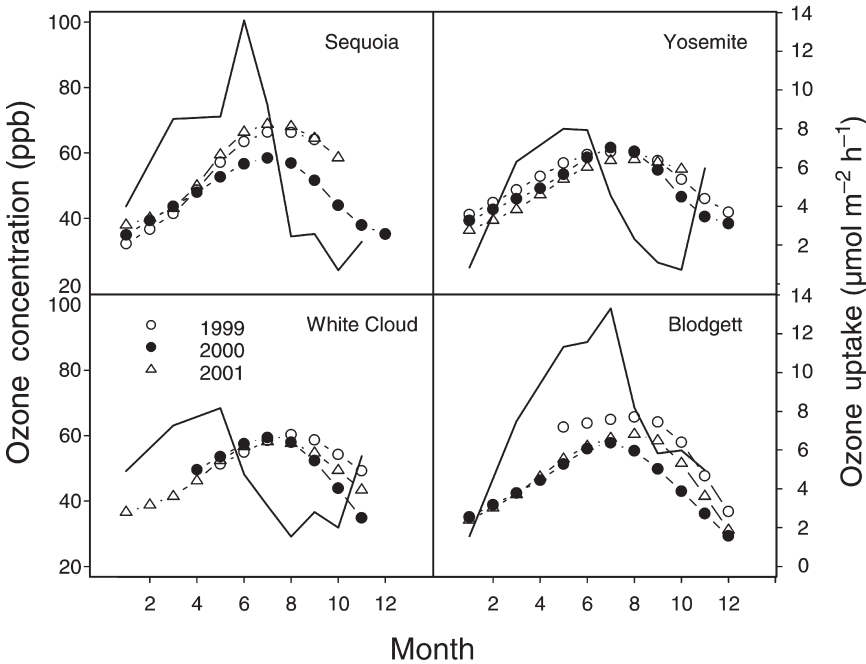


Figure 9. Annual patterns in ozone concentration for 3 years at all study sites. Symbols indicate monthly means of ozone concentration from 0600 to 2000 h. Line indicates mean midday ozone uptake averaged over 3 years.

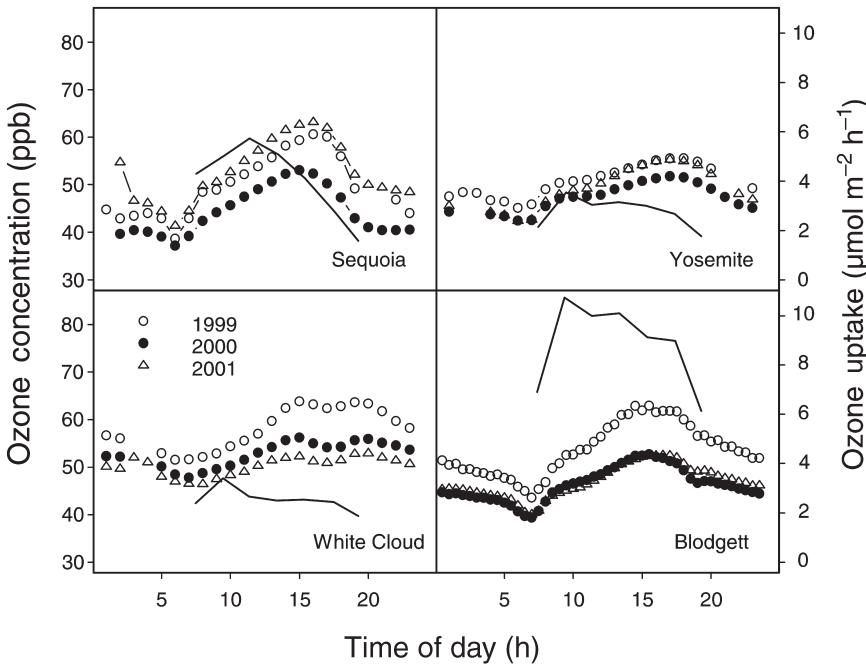


Figure 10. Diurnal pattern in ozone concentration for 3 years at all study sites. Symbols indicate mean hourly concentration averages compiled by hour over the entire year. Line indicates mean ozone uptake averaged from July through September for 3 years.

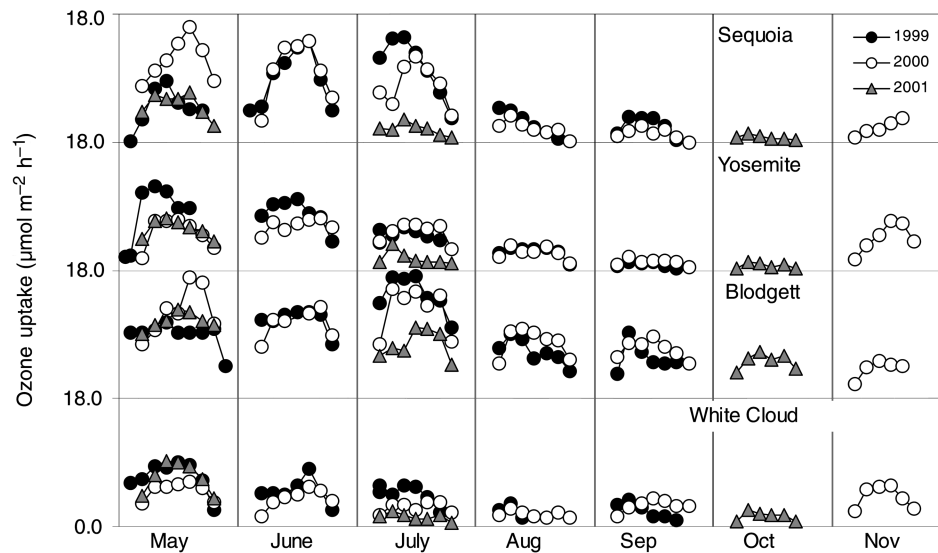


Figure 11. Diurnal pattern of ozone uptake at each of the sites for 3 years. Individual panels show 1 day of diurnal measurements taken every 2 h from 0600 to 1800 h PST each month during the growing season at each site. Values are means of six trees.

higher transpiration rates over the growing season than 2-year-old foliage (data not shown). Transpiration rates of current-year and 1-year-old foliage were not significantly different. Winter transpiration rates were dependent on environmental variables, such that when stomatal conductance values approached peak summer values on warm, sunny mid-winter days, transpiration also rose but remained below peak summer values because of lower evaporative demand. Transpiration rates were highest at Blodgett, followed by Sequoia, Yosemite and White Cloud. Transpiration rates of trees at Blodgett did not show the seasonal drop seen in trees at the other sites.

Dynamics of CO_2 exchange

Net photosynthesis The drop in stomatal conductance was matched by a decrease in net photosynthetic rates over the growing season and a left-skewing of the diurnal trend toward morning (Figure 13). Early in the summer, net photosynthesis responded to irradiance; however, later in the season when the

soil was dry, photosynthesis peaked in the morning and declined throughout the day despite high PAR. Photosynthetic rates were significantly different between 1-year-old and 2-year-old age classes (paired t -test, $\alpha = 0.05$, $P < 0.0001$), but did not differ between 1-year-old and current-year needles.

Analysis of A/PAR curves showed similar quantum efficiencies and maximum net photosynthetic values in trees at all mature sites (Table 2). Quantum efficiencies, maximum net photosynthesis values, and compensation point were all significantly lower in 2-year-old foliage than in 1-year-old foliage (paired t -test, $\alpha = 0.05$, $P < 0.02$, 0.0001 and 0.007, respectively). Because the A/PAR curves were measured at $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ for all foliage, this intrinsic difference between age classes may help explain the age-class differences in net photosynthesis observed during diurnal measurements under ambient conditions.

Quantum efficiency, maximum photosynthesis and compensation point were all higher in young plantation trees at

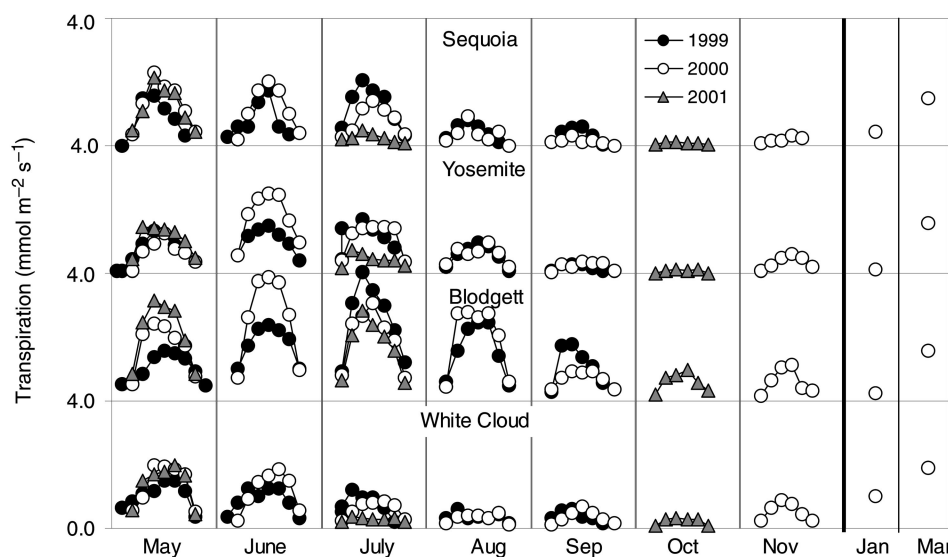


Figure 12. Diurnal pattern of transpiration at four study sites over 3 years. Individual panels show 1 day of diurnal measurements taken every 2 h from 0600 to 1800 h PST each month during the growing season at each site. Values are means of six trees. Measurements were also made in the winter of 2000–2001.

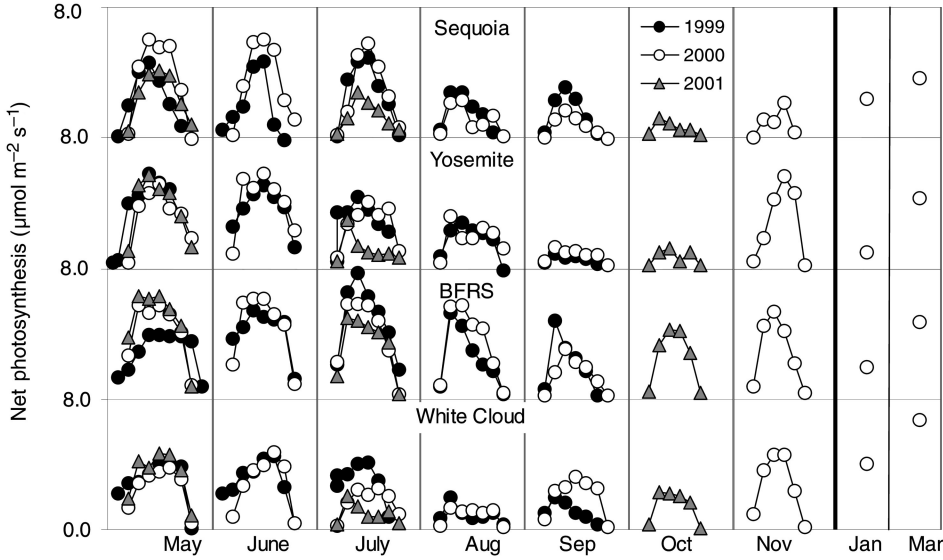


Figure 13. Diurnal pattern of net photosynthesis at four study sites over 3 years. Individual panels show 1 day of diurnal measurements taken every 2 h from 0600 to 1800 h PST each month during the growing season at each site. Values are means of six trees. Measurements were also made in the winter of 2000–2001.

Blodgett than in trees at the mature sites. This difference was consistent across all age classes and in both 1999 and 2000, although not significant at $\alpha = 0.05$ because of moderately high within-site variation.

WUE, V_{cmax} , and J_{max} In some species, limitations to carbon uptake imposed by drought stress can be overcome by increases in water-use efficiency (WUE) or increases in carboxylation efficiency. Intrinsic WUE, as measured by the quotient of midday net photosynthesis over transpiration normalized for VPD, increased over the growing season with increasing drought stress (Figure 14). The ranking of intrinsic WUE by site matched the ranking of drought stress as indicated by predawn water potential: White Cloud > Yosemite > Sequoia $\geq$ Blodgett. Both V_{cmax} and J_{max} (Table 3) increased toward midsummer, then decreased. The relationship between V_{cmax} and J_{max} was close and linear (Table 4, Figure 15a), and did not differ significantly between sites. The slope of the $V_{\text{cmax}}/J_{\text{max}}$ relationship was around 2 (Table 4, Figure 15a), consistent with values for other species (Wullschlegel 1993, Medlyn et al. 1999). At no site was there a significant relationship between V_{cmax} or J_{max} and any site variables such as soil water content, temperature, or water potential (regression analysis, data not shown).

Respiration Respiration rates had a Q_{10} close to an expected value of 2.0 for all the sites (Table 5). Respiration rates in June

and August were not significantly different, indicating that Q_{10} was unaffected by drought stress. The slope of the relationship between temperature and respiration rate remained constant throughout the growing season (Figure 16); however, the intercept increased in August compared with June, leading to significantly lower respiration rates at 25 °C (R_{25}) in August than in June, while maintaining Q_{10} near 2.0 (Table 5). The Q_{10} values in trees at the Sequoia site were significantly higher than in trees at the other sites (paired t -test and $\alpha = 0.05$), consistent with ozone pollution stress increasing respiration rates through

Table 2. Ponderosa pine light response measurements across the Sierra Nevada in June 2000. Means $\pm$ 1 SD are shown for 1-year-old foliage.

Site	Quantum efficiency	Maximum net photosynthesis	Compensation point
Sequoia	0.021 $\pm$ 0.003	6.4 $\pm$ 0.6	35.3 $\pm$ 13.0
Yosemite	0.021 $\pm$ 0.005	6.4 $\pm$ 1.2	41.0 $\pm$ 19.5
Blodgett	0.022 $\pm$ 0.003	7.0 $\pm$ 0.8	47.2 $\pm$ 12.0
White Cloud	0.019 $\pm$ 0.003	6.5 $\pm$ 0.7	28.4 $\pm$ 15.5

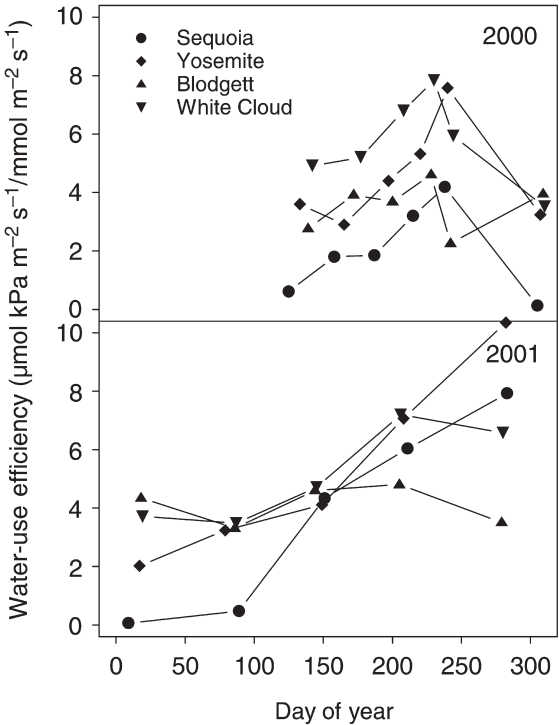


Figure 14. Water-use efficiency, normalized for ambient vapor pressure deficit, at all study sites in 2000 and 2001.

Table 3. Mean $\pm$ 1 SD for maximum rate of Rubisco-limited carboxylation (V_{cmax}) and maximum CO_2 -saturated photosynthetic rate, limited by electron transport (J_{max}) by month for years 1999 and 2000.

Site	Month	V_{cmax} 1999	V_{cmax} 2000	J_{max} 1999	J_{max} 2000
Sequoia	5	33.7 $\pm$ 8.1	37.7 $\pm$ 13.7	77.3 $\pm$ 22.1	67.7 $\pm$ 16.5
	6	33.5 $\pm$ 5.1	33.8 $\pm$ 3.6	72.6 $\pm$ 13.2	80.3 $\pm$ 8.3
	7	63.0 $\pm$ 20.7	38.1 $\pm$ 2.9	129.2 $\pm$ 41.9	82.0 $\pm$ 4.4
	8	28.8 $\pm$ 3.6	34.1 $\pm$ 3.5	59.7 $\pm$ 1.2	75.3 $\pm$ 6.5
Yosemite	5	34.1 $\pm$ 7.1	29.1 $\pm$ 4.7	64.7 $\pm$ 16.9	49.4 $\pm$ 4.4
	6	40.9 $\pm$ 9.0	41.4 $\pm$ 11.0	81.1 $\pm$ 15.5	94.4 $\pm$ 27.0
	7	48.2 $\pm$ 14.7	42.6 $\pm$ 6.8	87.4 $\pm$ 29.1	87.1 $\pm$ 10.6
	8	36.3 $\pm$ 2.6	37.1 $\pm$ 1.8	61.1 $\pm$ 2.9	78.7 $\pm$ 4.0
Blodgett	5	29.6 $\pm$ 4.5	30.6 $\pm$ 5.4	62.5 $\pm$ 13.5	51.9 $\pm$ 12.3
	6	42.6 $\pm$ 12.2	42.7 $\pm$ 5.7	96.0 $\pm$ 29.0	93.2 $\pm$ 15.9
	7	45.3 $\pm$ 8.9	50.3 $\pm$ 6.2	90.8 $\pm$ 29.3	110.9 $\pm$ 13.8
	8	38.4 $\pm$ 7.0	36.4 $\pm$ 3.8	91.6 $\pm$ 14.2	72.4 $\pm$ 7.7
White Cloud	5	35.2 $\pm$ 4.1	45.9 $\pm$ 6.4	78.9 $\pm$ 12.0	96.4 $\pm$ 13.9
	6	59.0 $\pm$ 10.1	42.2 $\pm$ 3.6	122.0 $\pm$ 14.1	92.2 $\pm$ 11.1
	7	37.7 $\pm$ 8.4	38.7 $\pm$ 10.5	68.2 $\pm$ 17.3	85.9 $\pm$ 17.6
	8	NA	42.0 $\pm$ 18.1	NA	69.5 $\pm$ 23.7

increased maintenance and repair costs. Daytime respiration rates in the absence of photorespiration (R_d obtained from A/C_i curves) were highly correlated with V_{cmax} (Figure 15b; $R^2 = 0.87$ and 0.62 in 1999 and 2000, respectively, $P < 0.0001$).

Discussion

Stomatal conductance and ozone

At all sites studied in the Sierra Nevada, stomatal conductance was highest from late May through early July, then decreased progressively until October in response to drying soils. Furthermore, peak stomatal conductance became progressively more skewed toward morning. Ambient ozone concentrations, however, exhibited a progressive increase over the season and a diurnal peak in the early afternoon. These patterns created a decoupling between periods of peak ozone uptake (early growing season and early morning) and periods of peak ozone

concentrations (late growing season and afternoon). Thus, ozone concentration is not the most important factor in determining ozone uptake in the Sierra Nevada. Current standards for assessing ozone exposure risk to vegetation in the USA and Europe are based on ozone concentration (e.g., SUM0, SUM06, W126 and AOT40). However, this study demonstrates that these indices do not adequately describe the risk of ozone uptake in the annually drought-stressed forests of the Sierra Nevada because ambient ozone concentration is not

Table 4. Relationship between maximum rate of Rubisco-limited carboxylation (V_{cmax}) and maximum CO_2 -saturated photosynthetic rate, limited by electron transport (J_{max}). Model: $J_{\text{max}} = \beta_0 + \beta_1 V_{\text{cmax}}$.

Measurement year	Age	β_0	β_1	R^2	P
1999	Current year	-2.8	1.9	0.75	< 0.01
	One year old	2.8	2.0	0.87	< 0.0001
	Two years old	-1.6	2.1	0.81	< 0.0001
2000	Current year	5.0	2.0	0.82	< 0.0001
	One year old	3.2	2.0	0.71	< 0.0001
	Two years old	5.9	2.0	0.64	< 0.0001
2001	One year old	26.5	1.5	0.64	< 0.0001
1999/2000	One year old	3.8	2.0	0.83	< 0.0001
	One year old	-	2.1	0.98	< 0.0001

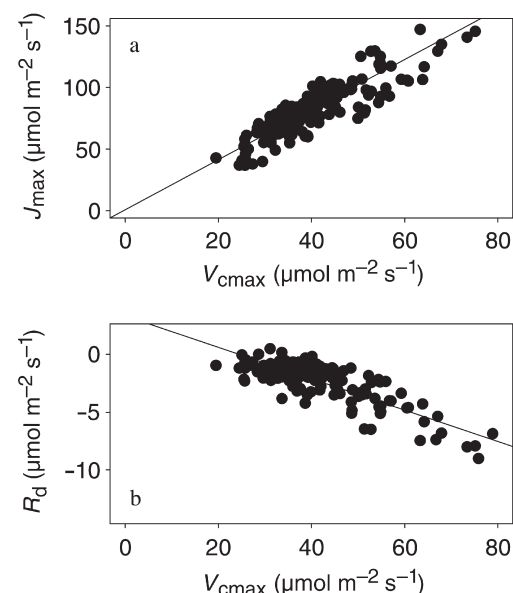


Figure 15. Linear relationships between maximum rate of Rubisco-limited carboxylation (V_{cmax}) and (a) maximum CO_2 -saturated photosynthetic rate, limited by electron transport (J_{max}) and (b) daytime respiration in the absence of photorespiration (R_d). Details of the relationships are presented in Table 3.

Table 5. Measured Q_{10} and dark respiration rates at 25 °C (R_{25} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) for all sites, including well-watered (June) and drought-stressed (August) conditions, and 2-year-old, 1-year-old and current-year needle age classes.

Site	One-year-old				Two-year-old				Current-year	
	June		August		June		August		August	
	Q_{10}	R_{25}	Q_{10}	R_{25}	Q_{10}	R_{25}	Q_{10}	R_{25}	Q_{10}	R_{25}
Sequoia	2.0	−0.43	2.1	−0.32	2.3	−0.43	2.6	−0.37	2.1	−0.32
Yosemite	1.8	−0.37	1.5	−0.23	1.9	−0.38	1.9	−0.27	1.3	−0.30
Blodgett	2.1	−0.33	1.9	−0.29	1.5	−0.33	2.3	−0.22	1.7	−0.26
White Cloud	1.8	−0.38	1.8	−0.30	1.8	−0.28	1.4	−0.41	1.5	−0.39

correlated with ozone uptake. Furthermore, current indices define the relevant period of ozone exposure as limited to the summer months; however, this study shows significant gas exchange in ponderosa pine throughout the winter, which may exceed that of late summer, the degree of activity depending on temperature and light. Stomatal conductance can be high in the winter, and although ozone concentrations tend to be low, cumulative ozone uptake in the winter may be up to 20% of annual uptake (Kurpius 2001). The 40-year history of assessing ozone injury in ponderosa pine in California in relation to ozone concentration, in which dose:response was defined as (ozone concentration):(plant response), will have to be redefined as (ozone uptake):(plant response) and reexamined. A final implication of these annual patterns, especially for modeling, is the inadequacy of averaging long-term (e.g., seasonal) stomatal conductance values to estimate ozone uptake. Instead, there is a need to describe independently the significant dynamics of stomatal conductance and ozone concentration over the seasonal and annual cycle before combining them to estimate uptake rates.

Net photosynthesis

Net photosynthesis in ponderosa pine at the mature sites appeared to be limited by stomatal conductance. Stomatal conductance and net photosynthesis are generally tightly correlated in mesic environments. In this study, however, there was scatter in the relationship, indicating independent behavior of the two processes in the early morning and early evening, which was limited to well-watered conditions. Trees at these Sierra Nevada sites demonstrated an ability to increase carboxylation capacity through July but not beyond, indicating some capacity to counter limitations imposed on gas exchange by drought stress, but not for the entire drought period. There was no evidence that the $V_{\text{cmax}}:J_{\text{max}}$ relationship in trees at Sequoia, the most ozone-polluted site, had a slope different from that in trees at the other sites, as observed in *Quercus* spp. (Broadmeadow 1999). For modeling, therefore, J_{max} can be consistently predicted if V_{cmax} is known.

Instantaneous water-use efficiency (A/E), normalized for VPD, increased as soil drought increased throughout the sum-

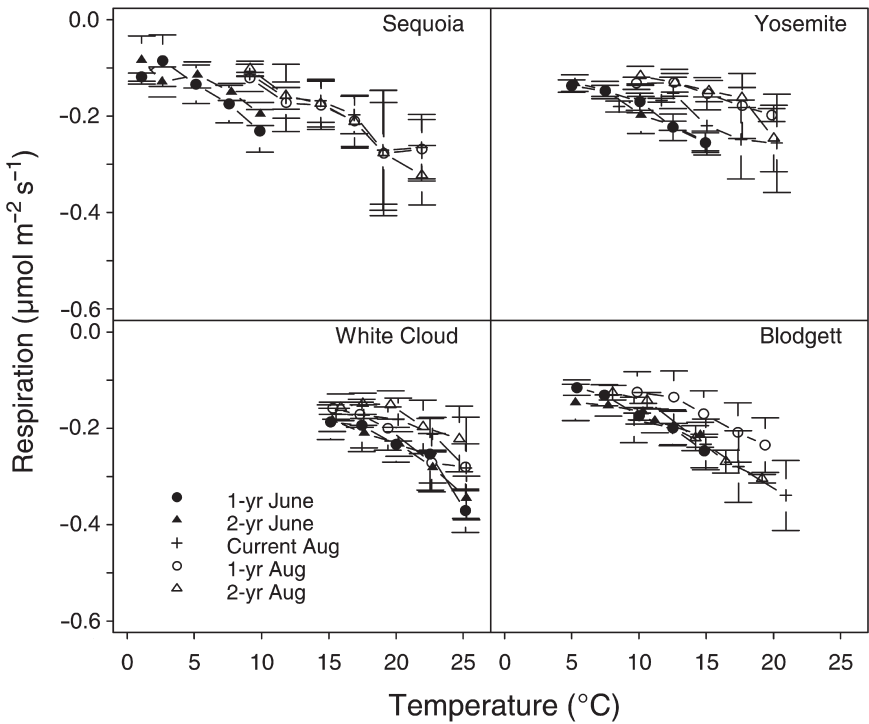


Figure 16. Respiration response to temperature at all study sites in 1999. Means $\pm$ 1 SD are shown. Measurements were made in June (high soil water content) and August (low soil water content) on different age classes of foliage.

mer. The ranking of WUE by site, White Cloud > Yosemite > Sequoia $\geq$ Blodgett, matched the ranking of predawn water potential, indicating a response to drought intensity. Parameter V_{cmax} did not rank by site in the same order, suggesting that some of the compensation is stomatal and seen as an adjustment in WUE, and some is biochemical and seen in V_{cmax} . The lower WUE values in the winter demonstrated that this response is plastic and varies with environmental conditions.

Respiration

Leaf respiration rates were affected by drought and possibly by ozone pollution. Although Q_{10} across sites was close to the expected value of 2.0, trees at the most ozone-polluted site, Sequoia, had significantly higher Q_{10} values than trees at the other sites. Respiration rates have been observed to increase in plants exposed to ozone (Amthor 1988, Amthor and Cumming 1988, Grulke et al. 1989) because of increased maintenance and repair of injured tissue. In this case, the slope of the response to temperature, not the intercept, was modified by pollution stress. Drought stress changed the intercept of the relationship between temperature and respiration, but not the slope, resulting in significantly lower late-season respiration rates compared with early-season rates. This response mirrored a drop in photosynthate assimilation, and thus reflects decreases in plant physiological activity and carbon reserves with increasing drought stress.

Modeling approaches

Because stomatal conductance controls gas exchange in ponderosa pine in the Sierra Nevada, modeling stomatal conductance correctly is critical to estimates of gas exchange in the Sierra Nevada. Many climate models and gaseous deposition models have incorporated a stomatal component (see review by Wesely and Hicks 2000). There are many different approaches to modeling conductance (see review by Panek et al. 2003). The data set described in this paper is well suited to testing and modifying existing stomatal conductance algorithms, including the two that are most widely used—the Jarvis approach (Jarvis 1976) and the Ball-Berry approach (Wong et al. 1979, Ball et al. 1987, Leuning 1990, Collatz et al. 1991). Comparisons between these approaches, and the consideration of others, are needed to identify the strengths and weaknesses of each model for use in drought-stressed ecosystems. A companion paper by Misson et al. (2004) identifies and explores that need by using the data set described in this paper to compare the Jarvis and Ball-Berry approaches to modeling stomatal conductance, and also considers another modeling approach based on hydraulic conductance links to stomatal conductance (Williams et al. 1996, 2001).

Conclusions

In Sierra Nevada ponderosa pine, the exchange of gases between the atmosphere and the biosphere was strongly influenced by seasonal summer drought. Stomatal conductance was significantly influenced by soil water content through leaf water potential during the growing season, which decreased

ozone uptake, carbon uptake, and transpirational water loss over the growing season. Independently, drought influenced V_{cmax} , J_{max} , WUE and dark respiration, and thus the dynamics of carbon exchange. As a result, in ponderosa pine in the Sierra Nevada, periods of maximum carbon and ozone uptake occurred at the beginning of the growing season and during the winter, whereas the trees were nearly dormant during August–September. Ozone uptake by ponderosa pine did not correspond to periods of peak ozone concentration, which has historically been used as a metric for ozone exposure. Thus the relationships that have been reported between ozone exposure and tree response will need to be reconsidered.

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