Seasonal trends in photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature

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Summary Understanding seasonal changes in photosynthetic parameters and stomatal conductance is crucial for modeling long-term carbon uptake and energy fluxes of ecosystems. Gas exchange measurements of CO\(_2\) and light response curves on blue oak leaves (*Quercus douglasii* H. & A.) were conducted weekly throughout the growing season to study the seasonality of photosynthetic capacity (\(V_{\text{cmax}}\)) and Ball-Berry slope (\(m\)) under prolonged summer drought and high temperature. A leaf photosynthetic model was used to determine \(V_{\text{cmax}}\).

There was a pronounced seasonal pattern in \(V_{\text{cmax}}\). The maximum value of \(V_{\text{cmax}}\), 127 µmol m\(^{-2}\) s\(^{-1}\), was reached shortly after leaf expansion in early summer, when air temperature was moderate and soil water availability was high. Thereafter, \(V_{\text{cmax}}\) declined as the soil water profile became depleted and the trees experienced extreme air temperatures, exceeding 40 °C. The decline in \(V_{\text{cmax}}\) was gradual in midsummer, however, despite extremely low predawn leaf water potentials (\(\Psi_{pd}\), ~−4.0 MPa). Overall, temporal changes in \(V_{\text{cmax}}\) were well correlated with changes in leaf nitrogen content. During spring leaf development, high rates of leaf dark respiration (\(R_{d}\), 5–6 µmol m\(^{-2}\) s\(^{-1}\)) were observed. Once a leaf reached maturity, \(R_{d}\) remained low, around 0.5 µmol m\(^{-2}\) s\(^{-1}\). In contrast to the strong seasonality of \(V_{\text{cmax}}, m\) and marginal water cost per unit carbon gain (\(\partial E/\partial A\)) were relatively constant over the season, even when leaf \(\Psi_{pd}\) dropped to ~−6.8 MPa. The constancy of \(\partial E/\partial A\) suggests that stomata behaved optimally under severe water-stress conditions. We discuss the implications of our findings in the context of modeling carbon and water vapor exchange between ecosystems and the atmosphere.

Keywords: Ball-Berry slope, dark respiration, marginal water cost per unit carbon gain, maximum carboxylation rate, maximum electron transport capacity.

Introduction

The process-based biochemical model of Farquhar et al. (1980) has emerged as the dominant paradigm for computing photosynthesis at the leaf (Collatz et al. 1991, Harley and Tenhunen 1991, Baldocchi 1994, Leuning et al. 1995), canopy (Baldocchi and Harley 1995, de Pury and Farquhar 1997), landscape (Kimball et al. 2000, Williams et al. 2001) and continental (Sellers et al. 1996a, 1996b, Bonan 1998, Foley et al. 1998) scales in modeling studies in biogeochemistry, ecology, climate and ecosystem physiology. The model of Farquhar et al. (1980) quantifies leaf CO\(_2\) assimilation rate (\(A\)) by considering how it is limited by either its ribulose 1,5-bisphosphate (RuBP) saturation rate at low intercellular CO\(_2\) concentration (\(C_i\)) or its RuBP regeneration rate at high \(C_i\). This mechanistic model has a wide appeal for three reasons. First, the model can quantify how leaf photosynthesis responds to changes in light, temperature, CO\(_2\), O\(_2\) and leaf nitrogen. Second, the model is easy to parameterize with cuvette-based gas exchange measurements (Harley and Baldocchi 1995, Dang et al. 1998, Wilson et al. 2000a, Medlyn et al. 2001). And third, the model is applicable at multiple scales because the spatial and temporal variations of its parameters are constrained by one another (Wullschleger 1993) and because its model parameters scale with functional variables, such as leaf nitrogen (Schulze et al. 1994, Ellsworth and Reich 1996).

Application of the Farquhar model to contemporary biogeo-science problems requires the simultaneous assessment of \(C_i\) and stomatal conductance (\(g\)) (Leuning 1990, Collatz et al. 1991, Harley and Tenhunen 1991). In principle, \(C_i\) is determined based on an electrical conductance analogy between photosynthesis and \(g\). Stomatal conductance is evaluated by an empirical function that is proportional to the product of photosynthesis and atmospheric relative humidity (RH) and is inversely related to CO\(_2\) concentration at the leaf surface (\(C_i\)) (Ball et al. 1987, Leuning 1990, Collatz et al. 1991).

At present, we have a good understanding of how photosynthesis model parameters, maximum carboxylation velocity (\(V_{\text{cmax}}\)), maximum rate of electron transport (\(J_{\text{max}}\)) and dark respiration (\(R_d\)) vary with genus and species, plant functional type and leaf nitrogen content (Wullschleger 1993). Little is known, however, about how \(V_{\text{cmax}}, J_{\text{max}}, R_d\) and stomatal conductance model parameters of tree species vary over the

In most canopy modeling studies, photosynthetic capacity is specified according to literature values, or a few short-term measurements at the field site, or is deduced from its relationship to leaf nitrogen content (e.g., Baldocchi and Harley 1995, Aber et al. 1996, Williams et al. 2001). The relationship between $V_{\text{cmax}}$ and leaf nitrogen is not universal, however; it varies with species (Wilson et al. 2000a) and canopy position (Meir et al. 2002) as a result of partial acclimation to light, among other factors.

A majority of short-term studies determine stomatal conductance with Ball-Berry slope values ($m$) around 9 (±20%) for well-watered C3 species. As soil water deficits develop, experimental evidence suggests decreasing $m$, especially for Mediterranean Quercus (oak) spp. (Tenhunen et al. 1990, Harley and Tenhunen 1991, Sala and Tenhunen 1996). Nevertheless, one school of thought holds $m$ constant but varies $V_{\text{cmax}}$ with air temperature and soil water stress (Sellers et al. 1996b, Colello et al. 1998).

Oak savanna ecosystems growing in the Mediterranean climate of California are an ideal system for studying how photosynthesis and stomatal conductance model parameters respond to environmental change and perturbations. Oak savannas exist in regions that experience prolonged summer periods without rain (Major 1988), after the soil profile has been filled by winter and spring rainfall. As the soils dry over the season, the trees experience a wide diurnal range of temperature (e.g., 30 °C), periods with extremely high temperatures (e.g., $>70$ kPa). We note that the prolonged summer drought experienced in California is more severe than that faced by Mediterranean and Australian savanna ecosystems. One of the lowest reported values of predawn leaf water potential in the Mediterranean savanna is $-3.0$ MPa (Joffre et al. 1999) and in the Australian savanna, $-2.5$ MPa (Eamus et al. 2001). In contrast, oaks growing in the coastal range of California have been reported to experience predawn water potentials as low as $-3.5$ MPa (Griffin 1973, Callaway et al. 1991), and we found values as low as $-6.8$ MPa.

The purpose of our study was to quantify photosynthetic capacity ($V_{\text{cmax}}$, $J_{\text{max}}$ and $R_{\text{d}}$) and $m$ of blue oak (Quercus douglasii H. & A.) leaves and to examine the seasonal variation in those parameters. The specific questions addressed were (1) how are photosynthetic capacity and $m$ affected by leaf age, summer drought and high temperature; (2) are seasonal variations in photosynthesis model parameters related to changes in leaf nitrogen content; and (3) do stomata operate optimally under prolonged drought and high temperature.

### Materials and methods

#### Site description

The study was conducted during the 2001 growing season in an oak–grass savanna in the foothills of the Sierra Nevada in California, USA (38°26′ N, 120°58′ W and 177 m a.s.l.). The dominant tree species of the savanna is blue oak with a mean canopy height of 7.1 m and a maximum leaf area index of only about 0.6 as measured with a plant canopy analyzer (LAI-2000, Li-Cor, Lincoln, NE). The site comprised about 194 stems ha$^{-1}$, with a mean diameter at breast height (DBH) of 0.199 m and a basal area of 18 m$^2$ ha$^{-1}$ (Kiang 2002). Mean area of individual leaves was 6.1 ± 1.7 cm$^2$ ($n = 113$).

Climate at the site is Mediterranean with clear days, high temperatures and virtually no rainfall during the summer. In contrast, the winter is relatively cold and wet. Mean annual temperature was 16.2 °C in 2001 and precipitation was 558 mm. These values are close to climatic means, determined over 30 years at nearby weather stations (mean air temperature is 16.3 °C and mean precipitation is 543.7 mm).

The soil of the oak–grass savanna is an Auburn, very rocky silt loam (Lithic haploxerepts). The soil contains 48% sand, 42% silt and 10% clay. Bulk density of the surface layer (0–30 cm) is around 1.5 ± 0.1 g cm$^{-3}$. The soil profile is about 0.75 m deep and overlies fractured rock. Conventional wisdom indicates that the roots of blue oak are unable to penetrate the rock layer and tap groundwater (Griffin 1973).

#### Environmental conditions

Air temperature and relative humidity were measured with a shielded and aspirated sensor (HMP-35 A, Vaisala, Helsinki, Finland) at our meteorological field station. Soil volumetric water content was measured with a frequency domain reflectometer probe (ML2x, Delta-T Devices, Burwell, Cambridge, U.K.) at depths of 5, 20 and 50 cm. Meteorological variables were logged at 5-s intervals with digital data loggers (CR10X or CR23X, Campbell Scientific, Logan, UT) and were averaged over 0.5-h periods.

#### Predawn leaf water potential

Predawn leaf water potential ($\Psi_{\text{pd}}$) was monitored every 2 weeks with a pressure chamber (Model 3000, Soil Moisture Equipment, Santa Barbara, CA). Measurements were usually started 2 h before sunrise and completed by dawn. Measurements were made on 10 trees and two leaves per tree. The water potential of a leaf was measured immediately after it had been excised with a razor blade from the crown at a height of 4 to 5 m. It typically took less than 3 min from leaf excision to completion of the measurement.

#### Gas exchange measurements

All gas exchange measurements were made with a portable steady-state photosynthetic system (Li-Cor Li-6400). The system was calibrated at the beginning and end of the season against secondary calibration gases that were referenced to standards prepared by NOAA’s Climate Monitoring and Diag-
nastics Laboratory. The span for water vapor was calibrated with a Li-Cor dew point generator (Li-610). Zeros for both CO2 and water vapor were calibrated with 99.99% nitrogen gas, obtained by passing the nitrogen through soda lime and magnesium perchlorate. Calibration results showed that the zero shifts and span for both CO2 and water vapor were negligible during the study.

The experiment started on April 18, 2001, shortly after leaves unfolded. Two sets of photosynthesis (A) measurements were conducted: the responses of leaf photosynthesis to CO2 concentration (A/C) and photosynthetically active radiation (A/Q). Before making measurements, leaves were acclimated in the chamber for more than 30 min at ambient temperature, ambient CO2 concentration (360 µmol CO2 mol–1) and a Q of 1600 µmol m–2 s–1, a value at which photosynthesis is at least 95% saturated. For production of A/C curves, the CO2 concentration in the leaf chamber was raised to 1000 µmol mol–1 while exposed to constant and saturating sunlight. Leaves were allowed to equilibrate for 8 min before logging data. The CO2 concentration was then lowered and the procedure repeated. The CO2 concentrations used to generate the A/C curves were 1000, 700, 500, 360, 200, 150, 100 and 50 µmol mol–1. For production of A/Qp curves, Qp was increased to 2000 µmol m–2 s–1 while the CO2 concentration was kept constant at 360 µmol mol–1. Then Qp was sequentially lowered to 1400, 1000, 600, 400, 200, 100 and 50 µmol m–2 s–1. During gas exchange measurements, the vapor pressure deficit (VPD) was typically 1.0 to 3.5 kPa, depending on leaf temperature and transpiration rate. A full A/Ci or A/Qp response curve usually took about 2 h to complete. All leaf gas exchange measurements were conducted between mid-morning and early afternoon. During this time, leaf temperatures were held between 25 and 33 °C.

Leaf nitrogen content

After gas exchange measurements were made, leaves were collected for analysis of area, mass per area (LMA) and nitrogen content. Leaf area was determined with an optical area meter (Li-Cor Li-3100). Leaves were oven dried at 70 °C for at least 48 h to assess dry mass. Leaf samples were ground and collected for analysis of area, mass per area (LMA) and nitrogen content. Leaf nitrogen content was measured with a PDZ Europa, Sandbach, U.K.)

Calculation of Vcmax, Jmax and Rd

The parameters Vcmax, Jmax, and Rd were estimated from A/Ci curves by nonlinear regression. It is generally assumed that A is limited solely by the maximum rate of carboxylation at low Ci (Farquhar et al. 1980a). Therefore, Vcmax and Rd were estimated from the lower region of A/Ci curves, where Ci was less than 150 µmol mol–1:

\[
A = \left(1 - \frac{0.5\alpha}{\tau C_i} \right) \frac{V_{\text{cmax}} C_i}{C_i + K_i (1 + O/K_o)} - R_d
\]

(1)

where O and C_i are the partial pressures of oxygen and CO2 in the intercellular air space, τ is the Rubisco specific factor (defined as V_{\text{cmax}} K_o / V_{\text{cmax}} K_i). K_i and K_o are the Michaelis-Menten constants for CO2 and O2, respectively, and R_d represents CO2 evolution from mitochondria in the light, rather than that from photorespiratory carbon oxidation (Farquhar et al. 1980a).

At higher C_i exposures, A is limited by the regeneration of RuBP via electron transport. Hence, J_{\text{max}} can be estimated from the A/Ci curve when C_i exceeds 250 µmol mol–1:

\[
A = \left(1 - \frac{0.5\alpha}{\tau C_i} \right) \frac{J C_i}{C_i + O/\tau} - R_d
\]

(2)

where J is the potential rate of electron transport and is dependent on photon flux and J_{\text{max}}:

\[
J = \frac{\alpha I}{\sqrt{1 + (\alpha I/J_{\text{max}})^2}}
\]

(3)

where I is the absorbed photon flux density and α (0.24) is the efficiency of light conversion. We normalized V_{\text{cmax}}, J_{\text{max}} and R_d to 25°C according to Equations 8 and 9 of Harley et al. (1992), and the temperature coefficients were from Bernacchi et al. (2001). A complete list of model parameters and their units is given in Table 1.

Stomatal conductance was evaluated by the Ball-Berry empirical stomatal conductance model (Ball et al. 1987):

\[
g = g_0 + m \frac{ARH}{C_a}
\]

(4)

where RH is the relative humidity at the leaf surface, C_a is the CO2 concentration at the leaf surface, and g_0 and m are the intercept and slope obtained from least squares regression. To determine these parameters, we used only the data when CO2 concentration was higher than ambient. This procedure avoided the poor behavior of the Ball-Berry model at sub-ambient atmospheric CO2 concentrations when photorespiration rates increase disproportionately (Leuning 1995).

A long time step (8 min) was used to generate A/C_i and A/Q_p curves because stomata respond more slowly to changes in environmental conditions than photosynthesis (Pearcy 1990). Shorter time steps are problematic because they cause unstable estimates of m. This problem became evident during preliminary tests, when we found that m and the coefficient of determination of the regression (r^2) were sensitive to the time step. For example, when a 3-min time step was used we found that m = 1.6 and r^2 = 0.13. Increasing the time step to 8 min produced m = 8.75, in line with literature values (Collatz et al. 1991), and r^2 = 0.91.

Calculation of ∂E/∂A

Marginal water cost per unit carbon gain (∂E/∂A) was computed from ∂E/∂g and ∂A/∂g as described by Farquhar et al. (1980b). The partial derivative ∂E/∂g was computed according to an Ohm’s Law model for vapor transfer:
where $b = \frac{1}{\varepsilon r_h}$ and $\Delta w$ is the difference in the mole fraction of water vapor inside and outside the leaf. The variable $\varepsilon$ represents the rate of increase of latent heat content in saturated air with respect to an increase in sensible heat content. It is a function of leaf temperature, and was computed with a regression equation obtained by Thomas et al. (1999a). The boundary layer resistance for heat, $r_h$, was computed from

$$\frac{1}{r_h} = \frac{1}{112 r_b} + \frac{8 \sigma T^3}{C_p}$$

where $r_b$ is the boundary layer resistance for heat transfer, $C_p$ is the heat capacity of air at constant pressure, and $\sigma$ is Stefan’s constant. The second term on the right-hand side of Equation 6 represents the resistance to heat transfer by long-wave radiation, assuming unit emissivity and considering transfer from both sides of the leaf in parallel (Cowan 1977).

The term $\partial A/\partial g$ was obtained from the empirical relationship:

$$A = \frac{K_1 g}{K_2 + K_3 g}$$

where $A$ is the net CO$_2$ assimilation rate. The constants $K_1$, $K_2$ and $K_3$ were fitted by nonlinear least squares regression. The partial derivative $\partial A/\partial g$ can be expressed:

$$\frac{\partial A}{\partial g} = \frac{K_1}{K_2 + K_3 g} - \frac{K_1 K_3 g}{K_2 + K_3 g}$$

The method used to assess $\partial E/\partial A$ was a simplified version of a larger set of equations (Thomas et al. 1999a). Application of the simplified version requires that leaf boundary layer resistance be small and leaf temperature be near the optimum for photosynthesis (Field et al. 1982), which were valid assumptions in this study.

**Results**

**Weather and soil water content**

To assess seasonal variation in leaf photosynthesis and stomatal conductance model parameters, we need detailed information on the seasonality of key environmental drivers. Seasonal variations in daily maximum air temperature ($T_{air\_max}$), daily minimum air temperature ($T_{air\_min}$), daytime mean VPD, volumetric soil water content ($\theta_v$) and precipitation are presented in Figure 1. Daytime mean VPD was averaged for the period from sunrise to sunset. After leaves unfolded (~ Day 100), maximum air temperatures increased markedly with time, ranging from moderate (~ 10 °C) in the spring to extreme (> 40 °C) by early summer (Figure 1a). The high air temperatures in early summer approached values that inhibit many photosynthetic processes (Björkman 1981). Minimum temperatures in the summer were between 10 and 20 °C, so that leaves experienced a 20 to 30 °C range in temperature over the course of a day.

Leaves experienced much day to day variation in VPD. Mean daytime vapor pressure deficit swung between 1 and 5 kPa within a few days when air masses changed (Figure 1b). The general pattern, though, was a progressive increase in VPD corresponding with the seasonal rise in air temperature. However, there were frequent episodes when leaves experienced a VPD as high as 7.5 kPa in the afternoon (hourly data not shown).

Total precipitation in 2001 was 558 mm, which was close to
the normal. About 98% of the precipitation fell in the wet season (October–April). The last rainfall (24.1 mm) was on April 21 (Day 111, Figure 1c).

There was enough winter precipitation to recharge the soil water profile. Volumetric soil water content, averaged from 5-, 20- and 50-cm depths, was near field capacity if not higher in the wet season. Within a month after the last winter rainfall, \( \theta_v \) declined to a steady-state low of about 0.11 cm \(^3\) cm\(^{-3}\) (Figure 1d). A shallow soil profile, relatively light soil texture and high evaporative demand contributed to the rapid depletion of soil water.

**Leaf ecophysiological parameters**

Seasonal variations in \( \Psi_{pd} \), LMA, leaf nitrogen content per unit area (\( N_a \)), \( g \), maximum net photosynthetic rate (\( A_{max} \)) and \( C_i/C_a \) ratio are presented in Figure 2. We defined \( A_{max} \) as the rate of photosynthesis at ambient \( \text{CO}_2 \) concentration (360 \( \mu \text{mol mol}^{-1}\)) and saturating \( Q_p \) (1600 \( \mu \text{mol m}^{-2} \text{s}^{-1}\)). During the early growing season, \( \Psi_{pd} \) was around –0.3 MPa, indicating high soil water availability (Figure 2a). As the growing season progressed and the trees extracted water from the soil profile, \( \Psi_{pd} \) diminished continually. By midsummer, \( \Psi_{pd} \) was typically below –3.0 MPa and by the end of the summer it had fallen to –6.8 MPa. We note that \( \Psi_{pd} \) continued declining in the summer even after the integrated soil water content had reached an asymptote near 0.11 cm \(^3\) cm\(^{-3}\).

Both LMA and \( N_a \) increased rapidly during early leaf development (before Day 112). Thereafter LMA continued to increase gradually for the rest of the season, whereas \( N_a \) decreased (Figures 2b and 2c).

Seasonal changes in \( g \) and \( A_{max} \) showed a similar pattern during the growing season (Figures 2d and 2f). They increased rapidly in spring until the leaf reached maturity and then gradually declined until leaf senescence in September. The peak values of \( g \) and \( A_{max} \) lasted only about 2–3 weeks, a relatively short period compared with many other plant species (Wilson et al. 2000a). The pronounced decline in \( A_{max} \) and \( g \) was presumably a result of the negative impacts of water deficits and extreme temperatures (Björkman 1981, Cornic 1994). We note that maximum \( A_{max} \) occurred 2 to 3 weeks after maximum LMA was reached, suggesting that physiological activity of the leaf continued after structural development had stopped. High rates of \( R_d \) (see following section) also support this conclusion.

The \( C_i/C_a \) ratio (Figure 2f) declined over the season from 0.7 to 0.5. Low \( C_i/C_a \) values were an artifact of drought-induced stomatal closure and the subsequent readjustment between the supply and demand for carbon dioxide.

**Variations in \( V_{cmax} \), \( J_{max} \) and \( R_d \)**

Strong seasonal variations in the photosynthesis model parameters (\( V_{cmax} \), \( J_{max} \) and \( R_d \)) are shown in Figure 3. During leaf development, \( V_{cmax} \) and \( J_{max} \) increased rapidly with time and reached maximum values of 127 and 345 \( \mu \text{mol m}^{-2} \text{s}^{-1}\), respectively, around Day 137 (Figures 3a and 3b). As observed for \( A_{max} \), the period of maximum photosynthetic capacity lasted less than 3 weeks. Thereafter, there was a rapid decline in \( V_{cmax} \) and \( J_{max} \), as the leaves experienced water deficits and extreme air temperatures. From mid- to late summer, \( V_{cmax} \) decreased slowly with time, whereas \( \Psi_{pd} \) continued to decrease markedly (Figure 2a). Toward the end of the growing season, there was another rapid decline in \( V_{cmax} \) caused by leaf senescence as \( \Psi_{pd} \) approached the extreme low of –6.8 MPa.

Dark respiration was high during leaf development (Figure 3c) and then gradually declined as leaves matured. Once leaves were fully mature, as indicated by maximum \( V_{cmax} \), \( R_d \) remained relatively stable around 0.5 \( \mu \text{mol m}^{-2} \text{s}^{-1}\).

**Relationship between \( V_{cmax} \) and leaf \( N \)**

To determine whether the temporal variation in \( V_{cmax} \) was mediated through changes in leaf nitrogen content, pooled data were analyzed by simple linear regression. There was a strong
correlation between mass-based $V_{cmax\_m}$ (µmol g$^{-1}$ s$^{-1}$) and leaf nitrogen concentration $N_m$ (g g$^{-1}$) ($r^2 = 0.71$, intercept $-0.86$, slope 72.18, $n = 51$, $P < 0.0001$) (Table 2). On the other hand, correlation on an area basis ($V_{cmax\_a}$ versus $N_a$) was weak ($r^2 = 0.31$, intercept $-56.42$, slope 47.38, $P < 0.0001$), even though the relationship was significant. The poor correlation was most likely caused by a corresponding temporal change in LMA. Previous studies have shown that LMA is negatively correlated with leaf A (Reich and Walters 1994, Reich et al. 1997, 1999, Peterson et al. 1999). To control the effect of LMA on...
Vcmax, we used a multiple linear regression of the form
\[
V_{cmax} = b_0 + b_1 N + b_2 \text{LMA}
\]
We found that the slopes \((b_1)\) for mass- and area-based multiple regressions were the same (Table 2). This result is consistent with the work of Peterson et al. (1999), who showed that \(b_1\) was independent of the unit of expression when the effect of LMA was included in the regression. Furthermore, multiple regression improved \(r^2\) from 0.31 to 0.70.

**Impact of \(\Psi_{pd}\) on \(g\)**
To quantify the impact of soil water deficits on the physiological functioning of leaves, we plotted \(g\) against \(\Psi_{pd}\) (Figure 4). Stomatal conductance decreased with decreasing \(\Psi_{pd}\) in a non-linear fashion. These data differ from those reported by others (Hsiao 1973, Biscoe et al. 1976), which showed a threshold value of \(\Psi_{pd}\) at which stomatal closure is observed.

**Ball-Berry slope and \(\partial \delta E/\partial A\)**
We assessed the Ball-Berry stomatal conductance model using \(A/C_i\) and \(A/Q_p\) measurements from the whole season. Specifically, we plotted \(g\) against \(\text{ARH}/C_a\) (Figure 5). The correlation between \(g\) and \(\text{ARH}/C_a\) was linear and significant \((r^2 = 0.88, P < 0.0001)\). The value of \(m\) was 8.88, typical for oak (Harley and Baldocchi 1995), and the intercept was 0.006 \(\text{mol m}^{-2} \text{s}^{-1}\).

The strong correlation between \(g\) and \(\text{ARH}/C_a\) during the growing season suggests that leaf age and severe water stress did not alter \(m\) for blue oak. The constancy of \(m\) has significant implication for the application of coupled photosynthesis–stomatal conductance models, which are often used as sub-models in larger-scale modeling studies, for example, SiB2 (Sellers et al. 1996b) and LSM (Bonan 1998).

The finding that severe water stress and extremely high air temperature did not alter \(m\) led us to ask: do stomata operate optimally under such unfavorable conditions? To answer this question, we examined \(\partial \delta E/\partial A\) with the results presented in Figure 6a. We found that \(\partial \delta E/\partial A\) was fairly constant for the whole season, except for the data sets from April 18 and 27 (Days 108 and 117, respectively). We also observed that \(\partial \delta E/\partial A\) was invariant across the range of \(\Psi_{pd}\) values (Figure 6b). These data suggest that stomatal behavior of blue oak is consistent with the optimal water use theory of Cowan and Farquhar (1977) under severe drought conditions. The low values of \(\partial \delta E/\partial A\) for the first two data sets are most likely due to the low VPD that was experienced by the leaf in the early season because the method that we used to compute \(\partial \delta E/\partial A\) is sensitive to VPD (Thomas et al. 1999b).

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**Table 2. Simple and multiple linear regression coefficients for maximum carboxylation velocity \((V_{cmax})\) versus leaf N content \((N)\) and leaf mass per area \((\text{LMA})\) on mass and area bases \((n=51)\). Units: \(V_{cmax_a} = \mu\text{mol m}^{-2} \text{s}^{-1}; V_{cmax_m} = \mu\text{mol g}^{-1} \text{s}^{-1}; N_a = \text{g m}^{-2}; N_m = \text{g g}^{-1}; \text{and LMA} = \text{g m}^{-2}.\)**

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**Figure 4.** Relationship between predawn water potential \((\Psi_{pd})\) and stomatal conductance \((g)\). Values of \(g\) represent the mean and standard deviation of 3–6 measurements. Values were obtained from gas exchange measurements conducted after leaves fully matured.

**Figure 5.** Relationship between measured stomatal conductance \((g)\) and the product of net photosynthesis \((A; \mu\text{mol mol}^{-1})\) and relative humidity \((\text{RH})\) divided by external \(\text{CO}_2\) concentration \((C_a; \mu\text{mol mol}^{-1})\). Only data when \(C_a > 360 \mu\text{mol mol}^{-1}\) were used. The linear regression equation is \(g = 8.88 \text{ARH}/C_a + 0.006\) \((r^2 = 0.88, P < 0.0001)\).
Discussion

Comparison of \( V_{\text{cmax}} \) in blue oak with data for the Quercus genus and other tree species
The maximum value of \( V_{\text{cmax}} \) (127.3 µmol m\(^{-2}\) s\(^{-1}\); May 17 (Day 137)) was 30% higher than most published values for the same genus. Dreyer et al. (2001), for example, reported \( V_{\text{cmax}} \) of 87.7 and 90.5 µmol m\(^{-2}\) s\(^{-1}\) in Quercus petraea Matt. Liebl. and Quercus robur L., respectively, for nursery-grown plants in shade. Wilson et al. (2000a) and Harley and Baldocchi (1995) studied fully sunlit white oak (Quercus alba L.) and chestnut oak (Quercus prinus L.) trees near Oak Ridge, Tennessee and reported a maximum \( V_{\text{cmax}} \) of 78 µmol m\(^{-2}\) s\(^{-1}\). Turnbull et al. (2002) reported values of \( V_{\text{cmax}} \) that ranged between 44 and 57 µmol m\(^{-2}\) s\(^{-1}\) for Quercus rubra L. and Q. prinus at a field site in New York State. We note that the maximum \( V_{\text{cmax}} \) for blue oak is outside the range (11–119 µmol m\(^{-2}\) s\(^{-1}\), mean 47 µmol m\(^{-2}\) s\(^{-1}\)) of a variety of broad-leaved deciduous tree species (Wullschleger 1993).

Significance of high \( V_{\text{cmax}} \) values
It is well known that tree species adapt to prolonged drought and high irradiances and temperatures by developing small thick leaves (Nobel 1977, Groom and Lamont 1997). A recent compilation of data for 558 broad-leaved and 39 needle-leaved tree species at 182 geographic locations confirmed a positive correlation between solar radiation and LMA and a negative correlation between mean precipitation in the driest 3 months and LMA (Niinemets 2001). Therefore, we conclude that high LMA (> 160 g m\(^{-2}\)) and area-based nitrogen concentrations increase with high irradiances and prolonged summer drought on leaf morphology. We also conclude that small thick leaves rich in nitrogen have high photosynthetic capacity. This conclusion is based on the observation that maximum leaf photosynthesis rates correlate positively with leaf nitrogen (Field 1983).

The reason why \( V_{\text{cmax}} \) is higher in blue oak than in other tree species can be deduced from leaf nitrogen concentrations. Our survey of the literature indicates that published values of area-based leaf nitrogen in oak leaves rarely exceed 3.0 g m\(^{-2}\) (Reich et al. 1991, Reich et al. 1998, Meir et al. 2002, Turnbull et al. 2002). Because nitrogen concentrations of blue oak leaves exceed those of other oak species, they must have the structure and capacity (e.g., ample Rubisco) to achieve high \( V_{\text{cmax}} \) values (see Table 2).

Seasonality of \( V_{\text{cmax}} \) and its association with severe soil water deficits and high temperature
Dynamic seasonal changes in environment and phenology resulted in a strong seasonality of photosynthetic parameters. The seasonal pattern of \( V_{\text{cmax}} \) was divided into five phases: (1) leaf development; (2) spring maximum; (3) early summer fast decline; (4) gradual summer decline; and (5) leaf senescence.

During the leaf development phase, \( V_{\text{cmax}} \) increased steadily as the leaf matured; however, \( V_{\text{cmax}} \) did not reach the spring maximum until about 2 weeks after LMA had reached steady state. This suggests that leaf development had not ended when LMA reached steady state. The high \( R_{\text{p}} \) after leaf expansion (Figure 3c) also indicates that the leaf had not reached maturity. Similar results have been reported for evergreen broad-leaved tree species in Japan (Miyazawa et al. 1998). Thus, it may not always be true that maximum photosynthetic rate on a leaf area basis occurs around the end of leaf expansion.

The fast decline phase of \( V_{\text{cmax}} \) started around Day 144 (Figure 3a), coinciding with the onset of summer drought, as indicated by soil water content (Figure 1d) and predawn leaf water potential (Figure 2a). Many mechanisms underlying drought-induced reduction in photosynthetic capacity have been identified, including increased mesophyll resistance (Pearcy 1983); reduced Rubisco activity (Medrano et al. 1997, Parry et al. 2002); and reduced electron transport capacity (Epron and Dreyer 1992, Sanchez-Rodriguez et al. 1997). Unfortunately, however, the dominant mechanism responsible for the fast decline in \( V_{\text{cmax}} \) cannot be determined without other physiological measurements. Future measurements of chlorophyll fluorescence ( Valentini et al. 1995) and analysis of stomatal versus nonstomatal limitations (Wilson et al. 2000b) will help.

Besides drought, high temperature probably contributed to the fast early summer decline in \( V_{\text{cmax}} \). As illustrated in Figure 1a, leaves experienced many days when \( \text{T}_{\text{air, max}} \) exceeded 40 °C. With partial stomatal closure and low transpiration rates, leaves probably experienced temperatures greater than air temperature. Physiological studies show that high temperatures decrease photosynthesis by reducing PSI activity (Björkman and Powles 1984, Weiss and Berry 1988, Epron and Dreyer 1992). Damage to PSII as a result of high tempera-
ture can be more severe when plants are drought stressed (Hamerlynck et al. 2000), as occurred in this study. Because of the temporal correspondence between leaf nitrogen concentration and \( V_{\text{cmax}} \), we conclude that these environmental stresses affected structural and biochemical properties of the leaf as quantified by leaf nitrogen, and produced the decline in \( V_{\text{cmax}} \).

The rate of decline in \( V_{\text{cmax}} \) decreased during the middle of the summer when water-loss due to tree transpiration was reduced by stomatal closure. Trees may have been able to tap groundwater, for fine roots can penetrate through the crevices of bedrock. The mild air temperature and low VPD experienced during the period may also have contributed to the reduced rate of decline in \( V_{\text{cmax}} \).

A reduction in leaf nitrogen concentration was not the only factor that limited photosynthetic capacity. We found that nitrogen-use efficiency (NUE; defined as mol CO\(_2\) assimilated per g leaf nitrogen) also decreased over the study period (Figure 7). This is consistent with other reports on NUE in drought-afflicted deciduous tree species (Reich et al. 1989, Abrams and Mostoller 1995), but is not a universal finding. Wilson et al. (2000a) reported that drought-related reduction in \( V_{\text{cmax}} \) did not correlate with changes in leaf nitrogen content. They explained their result in terms of a seasonally dependent change in the fractional allocation of leaf nitrogen to Rubisco.

High NUE early in the growing season came at the cost of maintaining high water-use efficiency (WUE; CO\(_2\) assimilated per mol of H\(_2\)O transpired), as illustrated in Figure 7. As water availability decreased later in the season, WUE improved while NUE decreased. Reich et al. (1989) demonstrated a similar negative correlation for \( U. \) americana L. under long-term water stress. This type of relationship also exists for several desert evergreen species (Field 1983, Lajtha and Whitford 1989). The inverse relationship between NUE and WUE suggests that blue oak trees maximize WUE or NUE depending on which resource is most limited (Reich et al. 1989).

**Constancy of \( m \) and \( \partial E/\partial A \)**

The Ball-Berry stomatal model (Equation 4) developed by Ball et al. (1987) has become popular because it couples stomatal conductance with important physiological and environmental variables, i.e., photosynthetic rate, relative humidity and CO\(_2\) concentration. Furthermore, many short-term experimental data have shown that the model accounts for most of the variation in stomatal response between different species exposed to different temperature, light, humidity (Collatz et al. 1991, 1992) and CO\(_2\) regimes (Medlyn et al. 2001). Detailed studies on how water stress and leaf age affect \( m \) are lacking, however.

Harley and Tenhunen (1991) showed that \( m \) decreased as leaves aged. Because of insufficient data, they did not estimate \( m \) by linear regression of ARH/C\(_{a}\) and \( g \). Instead, they interpreted \( m \) values so that an appropriate \( C_i \) value of 200 to 240 µmol mol\(^{-1}\) was produced. This method of obtaining \( m \) values is prone to errors, because \( C_i \) can change, especially under stress conditions (Sage 1994).

The effect of decreasing soil water content on \( m \) is in dispute. Several European teams working with Mediterranean trees (e.g., Harley and Tenhunen 1991, Sala and Tenhunen 1996) assert that \( m \) decreases as the soil dries. On the other hand, scientists from the Carnegie Institute of Washington, where the Ball-Berry model was developed, assert that \( m \) remains constant and \( V_{\text{cmax}} \) decreases as the soil dries (Sellers et al. 1996b, Colello et al. 1998).

We found that the linear relationship between \( g \) and ARH/C\(_{a}\) was unaffected by water stress or leaf age, indicating that \( m \) was constant (Figure 5). This observation suggests that the response of stomata to water stress parallels that of photosynthesis, reinforcing the link between stomatal conductance and photosynthetic capacity observed under normal, nonstress conditions (Wong et al. 1979).

We also found that neither water stress nor leaf age significantly affected \( \partial E/\partial A \), which is consistent with the optimization theory of stomatal behavior (Cowan 1977, Cowan and Farquhar 1977) and with numerous studies. Most studies, however, have focused on changes in leaf-to-air vapor pressure difference (Farquhar et al. 1980b, Hall and Schulze 1980, Field et al. 1982). Few studies have focused on other environmental factors like leaf temperature (Thomas et al. 1999b), radiation or soil water content (Hall and Schulze 1980, Grieb et al. 1988, Thomas et al. 1999b). Thomas et al. (1999b), working with potted plants, observed a decline in \( \partial E/\partial A \) as pre-dawn water potential dropped, suggesting an increase in the efficiency of stomatal behavior. So far, there are no field data showing how \( \partial E/\partial A \) responds to changes in leaf age or soil water content.

The simplified method that we used to calculate \( \partial E/\partial A \) was based on several assumptions (Field et al. 1982). The more rigorous method to evaluate \( \partial E/\partial A \) proposed by Cowan and Farquhar (1977) requires data on maximum, minimum and optimum leaf temperature for photosynthesis over the growing season—data that were unavailable to us.

Many studies have shown that optimal temperatures for photosynthesis and stomatal conductance vary with seasonal and inter-annual temperature changes (Mooney et al. 1978, ...
Dang et al. 1998, Medlyn et al. 2002a, Ogle and Reynolds 2002). The constancy of $\partial E/\partial A$ indicates that stomata behave optimally, i.e., they maximize the ratio of carbon gain to water loss over the season.

**Implications for biophysical models**

Biochemically based photosynthesis models (Farquhar et al. 1980a) are now widely used (Harley and Tenhunen 1991, Baldocchi and Harley 1995, de Pury and Farquhar 1997). The main objective of these modeling exercises is to understand how photosynthesis responds to environmental perturbations, including elevated atmospheric CO$_2$ concentration, high temperature and drought. The key parameters in the leaf-level photosynthesis model are $V_{\text{max}}$, $J_{\text{max}}$ and $R_d$. Several studies have investigated the temperature response of these parameters (Dreyer et al. 2001, Medlyn et al. 2002a) in order to quantify the relationship between them and leaf nitrogen content for different tree species (Harley et al. 1992, Niinemets and Tenhunen 1997, Le Roux et al. 1999, Meir et al. 2002). Only a few studies have focused on seasonal variations in $V_{\text{max}}$, $J_{\text{max}}$, and $R_d$, and their relationship with leaf nitrogen content (Wilson et al. 2000a, Medlyn et al. 2002a, Nogués and Alegre 2002). We found that more than 70% of the observed seasonal variations in $V_{\text{max}}$ could be explained by changes in leaf nitrogen content (Table 2). This indicates that it is possible to predict leaf photosynthetic parameters based on leaf nitrogen content, which is relatively easy to obtain.

In many previous modeling exercises, $R_d$ was assumed to scale linearly with $V_{\text{max}}$ and LMA (Field 1983, Collatz et al. 1991, 1992, Niinemets and Tenhunen 1997, Reich et al. 1998, Wohlfahrt et al. 1998). We did not observe a linear relationship between $R_d$ and $V_{\text{max}}$ or $R_d$ and LMA. The rate of leaf dark respiration was high during leaf development (Figure 3c), but once the leaf matured, $R_d$ was relatively low. Similar results include those of Wilson et al. (2000a), who found that $V_{\text{max}}$ was fairly insensitive to $R_d$ and Miyazawa et al. (1998), who observed high $R_d$ before full leaf maturation in six evergreen tree species. Thus, the method of interpolating $R_d$ from $V_{\text{max}}$ and LMA needs to be reconsidered.

Another important parameter in the coupled photosynthesis–Ball-Berry stomatal conductance model is $m$. Although the Ball-Berry model is empirical, it is easy to parameterize compared with other more sophisticated models (e.g., Jarvis 1976). We found that neither leaf age nor water stress significantly affected $m$ (Figure 5). Other studies have shown that, for many species, $m$ does not change in response to elevated CO$_2$ concentration (Harley et al. 1992, Medlyn et al. 2001). Thus a single value of $m$ may be applicable under most conditions expected in the near future, including elevated atmospheric CO$_2$ concentration, severe drought and high temperature. With a constant value of $m$, Baldocchi and Meyers (1998) were able to predict CO$_2$ and water vapor fluxes that agreed with eddy covariance measurements for wheat, soybean, boreal conifer and temperate deciduous forest.

The parameter $V_{\text{max}}$ was highly correlated with $A_{\text{max}}$ (Figure 8). This relationship could be used to obtain $V_{\text{max}}$ in cases where it is too time-consuming to produce A/C curves. Temporal variations in $J_{\text{max}}$ also correlated well with changes in $V_{\text{max}}$ after a curvilinear fashion. The ratio $J_{\text{max}}/V_{\text{max}}$ varied from around 2.5 in spring when $V_{\text{max}}$ was at a maximum to around 1.0 in the senescence phase, suggesting that seasonal changes in N allocation to electron transport and Rubisco do not occur in parallel. Our values of $J_{\text{max}}/V_{\text{max}}$ were lower than those reported by Wilson et al. (2000a), who also showed that the slope was seasonally dependent, ranging from 2.11 to 3.33 in oak, maple and sugar maple species. In a study of broadleaf and coniferous species, Medlyn et al. (2002b) reported that $J_{\text{max}}/V_{\text{max}}$ varied considerably among species with a mean of 1.67. Thus, $J_{\text{max}}/V_{\text{max}}$ may be species-specific and seasonally dependent—a thing to keep in mind when scaling $V_{\text{max}}$ to $J_{\text{max}}$.

The importance of accurate estimation of $V_{\text{max}}$ to the performance of canopy photosynthetic models is known (Aber et al. 1996, Dang et al. 1998, Wilson et al. 2001). The seasonality of photosynthetic parameters should be taken into account when modeling long-term CO$_2$ and water vapor exchanges between terrestrial ecosystems and the atmosphere. In fact, Wilson et al. (2001) found that doing so led to improved agreement between model predictions and measured canopy CO$_2$ flux data. They found that the use of early season maximum $V_{\text{max}}$ values for the entire growing season overestimated carbon uptake by as much as 300 g C m$^{-2}$ year$^{-1}$—half the rate measured by the eddy covariance method. And with mean values of $V_{\text{max}}$, they were unable to simulate the seasonality of carbon uptake by the forest.

To model carbon exchange between terrestrial ecosystems and the atmosphere, information is needed on the seasonality of photosynthetic parameters and on how those parameters change in the course of a day as the leaf experiences variations in temperature and VPD. Several research groups have begun studying the temperature dependence of photosynthetic parameters (Bernacchi et al. 2001, Dreyer et al. 2001, Medlyn et al. 2002b). One study shows that temperature dependence may be seasonal and species-specific (Medlyn et al. 2002b), implying that studies of blue oak are needed to investigate the sea-
sonal temperature dependence of $V_{\text{cmax}}$ and $J_{\text{max}}$, especially under drought conditions.

Estimates of $V_{\text{cmax}}$ from A/C, could be inaccurate if mesophyll resistance changed or if patchy stomatal closure occurred, which it sometimes does under water stress conditions (Epron and Dreyer 1993, Mott 1995). Wilson et al. (2000) reviewed several of the effects that changed mesophyll resistance and patchy stomatal closure might have on estimates of $V_{\text{cmax}}$. They concluded: “including a drought-dependent $V_{\text{cmax}}$ parameterization may not be physiologically correct, but will accurately estimate fluxes.”

In conclusion, large seasonal variations in soil water content, air temperature and VPD resulted in strong seasonality in photosynthetic capacity, including $V_{\text{cmax}}$, $J_{\text{max}}$ and $R_{s}$, and in strong stomatal control of transpiration in blue oak trees in the foothills of the Sierra Nevada of California. Water stress and high temperature had significant affects on the seasonality of these physiological parameters. Most of the seasonal variation in $V_{\text{cmax}}$ could be explained by changes in leaf nitrogen content when the effect of LMA on $V_{\text{cmax}}$ was controlled. The Ball-Berry slope remained fairly constant during the growing season, indicating that photosynthetic capacity and stomatal conductance responded in parallel to seasonal changes in soil water content and temperature. Therefore, the Ball-Berry relationship can be applied under water stress conditions without modification. Stomatal behavior was optimal at different leaf ages and under different degrees of water stress.

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