Photosynthetic and stomatal responses to high temperature and light in two oaks at the western limit of their range

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Summary  Bur oak (Quercus macrocarpa Michx.) and chinquapin oak (Q. muehlenbergii Engl.) leaves were exposed to high temperatures at various photosynthetic photon flux densities under laboratory conditions to determine if species-specific responses to these factors were consistent with the distribution of these oaks in gallery forests in the tallgrass prairies of northeastern Kansas, USA. Measurements of the ratio of chlorophyll fluorescence decrease, Rsb, indicated that chinquapin oak maintained greater photosynthetic capacity than bur oak across all tested combinations of irradiance (100, 400, 700 and 1000 µmol m−2 s−1) and temperature (40, 42, 44, 46 and 48 °C). In both oak species, manipulation of leaf temperature to about 47 °C for 45 min in the field led to a 45% decrease in carbon assimilation up to one week after the heat treatment, and to sharp reductions in stomatal conductance. Photosynthetic recovery patterns indicated that bur oak took longer to recover from heat stress than chinquapin oak, suggesting that heat stress may be important in determining distribution patterns of these oak species. Based on a comparison of the results with data from other forest species, we conclude that the photosynthetic temperature tolerances of bur oak and chinquapin oaks facilitate their dominance at the western limit of the eastern deciduous forest.

Keywords: chlorophyll fluorescence, heat stress, Quercus macrocarpus, Quercus muehlenbergii.

Introduction


We have studied the interacting effects of light and temperature on two North American eastern deciduous forest oak species growing at the western limit of their range. Bur oak (Quercus macrocarpa Michx.) and chinquapin oak (Q. muehlenbergii Engl.) are canopy dominants in gallery forests lining streams dissecting tallgrass prairie (Abrams 1986). Water relations are a strong determinant of local tree distribution in these forests, with bur oak occupying more mesic, closed-canopy gallery forest locations, whereas chinquapin oak establishes in open, xeric upland sites (Abrams 1986, Abrams and Knapp 1986, Bragg et al. 1993). Leaf-level characteristics correlate fairly well with distributional patterns, with chinquapin oak having smaller leaves, lower photosynthetic rates and stomatal conductances, and higher photosynthetic temperature tolerance than bur oak (Hamerlynck and Knapp 1994a). Although the independent effects of light and high temperature on oak performance in tallgrass prairie gallery forests have been intensively studied (Knapp 1992, Hamerlynck and Knapp 1994a and 1994b), the interactive effects of these variables on photosynthesis of bur oak and chinquapin oak in this ecotonal system are unknown.

We manipulated light and temperature under laboratory conditions to assess species-specific responses to light and temperature, and we also manipulated leaf temperatures of attached entire leaves in the field under full-sun conditions to determine if photosynthetic recovery from heat stress correlated with the observed distribution of these species in tallgrass prairie gallery forests (Abrams 1986, Abrams and Knapp 1986, Bragg et al. 1993). Despite much research on the ecological implications of temperature optima in tree species (Chabot and Lewis 1976, Strain et al. 1976, Teskey et al. 1986, Jurik et al. 1988, Ranney and Peet 1994), few studies have been undertaken to assess the importance of photosynthetic recovery after heat stress (Methey and Trabaud 1993, Bassow et al. 1994).

Specifically, we tested four hypotheses. (1) Chinquapin oak has greater temperature tolerance across all irradiances than bur oak, facilitating its establishment in drier, more open...
gallery forest locations. There is evidence that chinquapin oak is more drought tolerant than bur oak (Abrams 1986, Abrams and Knapp 1986, Abrams 1990), and that drought tolerance can accompany thermal tolerance and a high light requirement (Berry and Bjorkman 1980, Seemann et al. 1984, Ivanov et al. 1992). (2) Low irradiance (about 100 µmol m\(^{-2}\) s\(^{-1}\)) and high temperature cause stress in bur oak and chinquapin oak. Elevated temperature depresses the photosynthetic light compensation point as a result of increased respiration rates relative to photosynthetic rates (Berry and Bjorkman 1980). (3) Chinquapin oak and bur oak have tolerances to combinations of light and temperature that correlate with seedling microenvironment conditions. Bur oak seedlings establish in lower light (about 400 µmol m\(^{-2}\) s\(^{-1}\)) microsites than chinquapin oak seedlings (700 µmol m\(^{-2}\) s\(^{-1}\)) (Bragg et al. 1993). We also postulated that, over the PPFD range 400–700 µmol m\(^{-2}\) s\(^{-1}\), the photosynthetic capacity of bur oak would be depressed more at higher temperature than that of chinquapin oak. (4) Photosynthetic recovery from heat stress is slower in bur oak than in chinquapin oak as a result of the larger leaves and heat-induced reductions of g, in bur oak.

Materials and methods

Study area

Measurements were made from July 7 to September 9, 1994 on trees growing in the Konza Prairie Research Natural Area (KPRNA, 39° N 96°32’ W), a 3487-ha tallgrass prairie preserve in the Flint Hills of northeastern Kansas, USA. Warm-season C\(_4\) grasses are the dominant vegetation on KPRNA, though extensive gallery forests line streambeds dissecting the prairie (Abrams 1986, Knight et al. 1994). The climate is warm continental, with hot, humid summers, and cold, dry winters (Borchert 1950). Growing season temperatures range from 17 to 43 °C. Tallgrass prairie is characterized by frequent and unpredictable drought (Borchert 1950, Fahnstock and Knapp 1994), and growing season conditions of high, though variable, photosynthetic photon flux densities (PPFD, ranging from 100 to 2100 µmol m\(^{-2}\) s\(^{-1}\)), Knapp 1985, Knapp 1993, Fay and Knapp 1993). Compared to mean values over the last 10 years, rainfall during the 1994 growing season was average, and temperatures were slightly lower than average in July but typical for August and September.

Fluorescence and oxygen evolution measurements

Bur oak and chinquapin oak leaves were collected between July 7 and August 8, 1994, at representative locations in gallery forests on KPRNA. Leaves were harvested from 0930 to 1030 h CST, sealed in plastic bags containing moistened paper to maintain turgor, and transported to the laboratory for analysis of concurrent photosynthetic oxygen evolution and chlorophyll fluorescence. Five leaves of each species were exposed for 45 min to 20 treatment combinations of temperature (40, 42, 44, 46, and 48 °C) and PPFD (100, 400, 700, and 1000 µmol m\(^{-2}\) s\(^{-1}\)), for a total sample size of 200. Oxygen evolution was measured with a Clark type oxygen electrode (Hansatech Instruments, Ltd., Kings Lynne, UK) in saturating (5%) CO\(_2\) conditions provided by a bicarbonate buffer. The experimental leaf temperatures were maintained during the measurements by attaching the electrode housing to a water bath (Isotemp Model 9000, Fisher Scientific, Pittsburgh, PA). Differences in water bath and leaf chamber temperatures were accounted for by correlating water bath temperatures with leaf temperatures measured with a fine wire type copper-constantan thermocouple. Chlorophyll fluorescence was measured with a FDP/2 fluorescence probe and TR1 transient recorder (Hansatech Instruments). The ratio of fluorescence decrease, \(R_{\text{ad}} ([F_p - F_t]/F_p\), where \(F_p\) = peak fluorescence yield, \(F_t\) = steady-state trace fluorescence after illumination), provides an index of photosynthetic capacity (Lichtenthaler 1988, Lichtenthaler and Rinderle 1988), where \(R_{\text{ad}} > 3.0\) indicates unimpaired photosynthetic function, \(R_{\text{ad}} \leq 1.0\) indicates irreversible photosynthetic damage, and intermediate values indicate reversible photosynthetic stress (Lichtenthaler 1988). Use of \(R_{\text{ad}}\) as an indicator of photosynthetic capacity eliminates the need for accurate estimation of baseline fluorescence, \(F_p\), which is often difficult at PPFDs > 100 µmol m\(^{-2}\) s\(^{-1}\) (Lavorel and Etienne 1977). Before each chlorophyll fluorescence measurement, leaf samples were dark acclimated for 5 min at the measurement temperature, and then exposed for 15 min to red light (\(\lambda = 660\) nm, half-power bandwidth \(\pm 30\) nm) from an LED light source (LH36U, Hansatech Instruments).

Field gas exchange measurements

From August 10 to September 9, 1994, 10 leaves each of bur oak and chinquapin oak were exposed to a potentially stressful high temperature (about 47 °C) in the field by enclosing entire leaves in plastic bags for 45 min. This temperature exceeded or equaled published thermal tolerances, and was similar to maximum field leaf temperatures for these trees (Hamerlynck and Knapp 1994a, Agati et al. 1995). During enclosure, PPFD was reduced from about 1900 to about 1500 µmol m\(^{-2}\) s\(^{-1}\), but was still above light saturation (Knapp 1992, Hamerlynck and Knapp 1994a, 1994b). Leaf temperatures were monitored by attaching a thermocouple to the abaxial surface before enclosure. Carbon dioxide was supplied by breathing into the bags through a dessicant column about every 5 min. Humidity in the bags rapidly approached saturation as a result of evapotranspiration from the leaves, making the bag environment similar to the electrode housing under laboratory conditions. We monitored both short-term (1, 10, 20, 40, and 60 min) and long-term (24 h and 7 day) recovery of photosynthetic gas exchange capability under ambient conditions. Control values were obtained from gas exchange measurements of 10 unbagged leaves on the same branches as the heat-treated leaves made immediately before the heat treatment was imposed and concurrently with the 60 min, 24 h and 7 day recovery. Air temperature at the time of the heat treatment and after 24 h was 30–33 °C with PPFD greater than 1800 µmol m\(^{-2}\) s\(^{-1}\). Seven days later, air temperature was 25–27 °C and PPFD was unchanged. All gas exchange measurements were made with an LI-6200 portable photosynthesis system (LI-Cor, Inc., Lincoln, NE). Net photosynthesis (\(A_{\text{n}}\)) stomatal conductance to water vapor (g), and internal CO\(_2\) concentrations (C) were
estimated from the equations of von Caemmerer and Farquhar (1981). System parameters were used to calculate leaf transpiration in the cuvette, which was used to estimate instantaneous water use efficiency (WUE, \( \mu \text{mol CO}_2 \mu \text{mol}^{-1} \text{H}_2\text{O} \)). Leaf temperature \( (T_{\text{leaf}}) \) was measured by a fine wire thermocouple pressed to the underside of the leaf throughout measurement.

**Statistical analysis**

Three-way analysis of variance (Statistix v4.1, Analytical Software, St. Paul, MN) was used to detect differences in \( R_{\text{fd}} \) and \( O_2 \) evolution, using species, temperature, and irradiance as main effects. Additionally, two-tailed \( t \)-tests were used to determine if mean \( R_{\text{fd}} \) departed significantly from critical values of 3.0 and 1.0 (Zar 1974). Field gas exchange measurements were repeated measures, and a split-plot analysis of variance was used, with species as the whole-plot factor and recovery time as the sub-plot factor. A level of 0.05 was considered significant, with means separation by LSD.

**Results**

*Fluorescence and oxygen evolution*

Pooled across all temperature and light treatment combinations, chinquapin oak maintained higher \( R_{\text{fd}} \) (2.07 ± 0.175 [SE]) than bur oak (1.74 ± 0.155) \( (F = 12.41, \text{df} = 1,160, P < 0.05) \) (Figure 1). In bur oak, \( R_{\text{fd}} \) was reduced below the critical values of 3.0 and 1.0 more often than in chinquapin oak. Over the PPFD range 400–1000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) and the temperature range 40–44 °C, bur oak had no \( R_{\text{fd}} \) values significantly above 3.0, but two values (temperature/light treatments 40/1000 and 44/700) were significantly below 3.0. Whereas chinquapin oak had \( R_{\text{fd}} \) values greater than 3.0 for four of the light/temperature combinations (treatments 40/400, 42/700, 42/1000 and 44/700) and \( R_{\text{fd}} \) values of 3.0 in the other treatments. At 46 °C, \( R_{\text{fd}} \) of bur oak was generally below 1.0 at all irradiances except 700 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), whereas chinquapin oak maintained \( R_{\text{fd}} \) above or equal to 1.0, except at 100 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). At 48 °C, all \( R_{\text{fd}} \) values of both species were below 1.0 indicating permanent damage. In both species, \( R_{\text{fd}} \) at 100 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) PPFD remained at the damage threshold of 1.0 at leaf temperatures up to 44 °C, and then declined below 1.0 at leaf temperatures above 46 °C. Overall, there were no significant effects of species on the \( R_{\text{fd}} \) responses to light and temperature, but the temperature × light interaction was significant \( (F = 13.25, \text{df} = 12,160, P < 0.05) \), indicating that the \( R_{\text{fd}} \) response to temperature was dependent on irradiance.

Because high leaf temperatures are usually accompanied by high radiation loads, we analyzed the responses of \( R_{\text{fd}} \) to the most common high temperature × high light combinations (40–48 °C × 700 and 1000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) PPFD) that occur in the field. At high irradiances, \( R_{\text{fd}} \) of chinquapin oak was above or equal to 3.0 until 44 °C, did not significantly decrease below 3.0 until 46 °C, and was below 1.0 at 48 °C (Figure 2). In contrast, \( R_{\text{fd}} \) of bur oak was significantly below 3.0 at 44 °C, and was significantly below 1.0 at 46 °C.

Despite the differences in \( R_{\text{fd}} \) responses between the species, there were no significant differences between species in pho-
tosynthetic oxygen evolution in response to combinations of PPFD and high temperature (Figure 3). There was a significant temperature × light interaction on $A_{\text{net}}$ ($F = 10.55$, df = 12,160, $P < 0.05$), most likely because the curves converged at 48 °C. Leaves exposed to elevated temperature and low PPFD (100 µmol m$^{-2}$ s$^{-1}$) were not significantly above photosynthetic compensation point ($A_{\text{net}} = \text{respiration}$) at 40 °C, and declined to rates well below photosynthetic compensation point at temperatures between 42 and 48 °C. At higher PPFDs (400–1000 µmol m$^{-2}$ s$^{-1}$), $A_{\text{net}}$ declined as the temperature increased from 40 °C to the photosynthetic compensation point at about 44 °C. Only in chinquapin oak leaves at a PPFD of 1000 µmol m$^{-2}$ s$^{-1}$ was $A_{\text{net}}$ significantly above (1.9 ± 0.58 µmol m$^{-2}$ s$^{-1}$) the photosynthetic compensation point at 44 °C. At 46 and 48 °C, light effects on $A_{\text{net}}$ were indistinguishable statistically.

Field gas exchange

In the field, bur oak had 15 and 46% significantly higher $A_{\text{net}}$ and $g_s$, respectively, than chinquapin oak (Table 1), and slightly higher $C_i$ (6%, $P < 0.05$). The $T_{\text{leaf}}$ of bur oak was about 1.5 °C lower than that of chinquapin oak. Both oak species showed broad responses in $A_{\text{net}}$ and $g_s$ to leaf temperatures ranging from 26 to 40 °C (data not shown).

In both species, increasing leaf temperature to 46.7 ± 0.46 °C, about 18 °C above ambient air temperature, at a PPFD of about 1500 µmol m$^{-2}$ s$^{-1}$, led to significant reductions in short-term $A_{\text{net}}$ (Figure 4). The ANOVA showed no significant species main effect on $A_{\text{net}}$ in the leaves sampled, or any significant time × species interaction. Within 1 min of raising leaf temperature to about 47 °C, $A_{\text{net}}$ declined by about 70% from pre-exposure values in both oaks and then increased to new reduced maxima of 11.6 ± 1.40 and 9.3 ± 1.00 µmol m$^{-2}$ s$^{-1}$ in bur oak and chinquapin oak, respectively, after 10 min. Stomatal conductance ($g_s$) declined 74% from pre-exposure values in bur oak compared with a 50% reduction in chinquapin oak, which led to a significant species × time interaction

Table 1. Gas exchange characteristics of field-grown bur oak (Quercus macrocarpa) and chinquapin oak (Q. muehlenbergii) at the Konza Prairie Research Natural Area. Species differences at $P < 0.05$ are indicated by different letters (one-way ANOVA). Each number is the mean of 30 measurements, with ± 1 SE of the mean.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Bur oak</th>
<th>Chinquapin oak</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_{\text{net}}$ (µmol m$^{-2}$ s$^{-1}$)</td>
<td>17.76 (0.549)a</td>
<td>15.48 (0.519)b</td>
</tr>
<tr>
<td>$g_s$ (mmol m$^{-2}$ s$^{-1}$)</td>
<td>422.4 (20.85)a</td>
<td>289.5 (11.07)b</td>
</tr>
<tr>
<td>$C_i$ (µl l$^{-1}$)</td>
<td>247.0 (3.35)a</td>
<td>233.5 (1.76)b</td>
</tr>
<tr>
<td>WUE (µmol mmol$^{-1}$)</td>
<td>1.43 (0.067)a</td>
<td>1.53 (0.081)a</td>
</tr>
<tr>
<td>$T_{\text{leaf}}$ (°C)</td>
<td>34.6 (0.48)a</td>
<td>36.1 (0.44)b</td>
</tr>
</tbody>
</table>

Figure 3. Effect of leaf temperature on net photosynthetic oxygen evolution ($A_{\text{net}}$) of bur oak and chinquapin oak exposed to 1000 (circle), 700 (upright triangle), 400 (square) or 100 (inverted triangle) µmol m$^{-2}$ s$^{-1}$ PPFD. Horizontal line indicates photosynthetic compensation point ($A_{\text{net}} = \text{respiration}$). Each point is the mean of five measurements, bars indicate ± 1 SE of the mean.

Figure 4. Short-term recovery kinetics of net photosynthesis ($A_{\text{net}}$) and stomatal conductance ($g_s$) in bur oak and chinquapin oak leaves exposed to about 47 °C for 45 min in the field. Each bar is the mean of 10 measurements, error bars indicate ± 1 SE of the mean, letters indicate significant differences at $P < 0.05$ (two-way ANOVA).
(F = 4.7, df = 5, 90, P < 0.05). In bur oak and chinquapin oak, gs reached constant post-exposure values after a 20 and 10 min recovery that were 41 and 22% below pre-exposure values, respectively.

Twenty-four h after heat treatment (Figure 5), A\textsubscript{net} in bur oak leaves was significantly lower (52%) than in chinquapin oak leaves, and 79% lower than in control bur oak leaves, whereas A\textsubscript{net} in chinquapin oak was the same after 24 h as after 1 h, i.e., about 52% of the control value. Stomatal conductance was 84 and 46% of control values in bur oak and chinquapin oak, respectively, after 24 h of recovery. One week following heat stress, both oaks had A\textsubscript{net} of about 9.1 ± 1.35 µmol m\textsuperscript{-2} s\textsuperscript{-1} compared with rates in control bur oak and chinquapin leaves of 17.1 ± 1.07 and 15.0 ± 0.67 µmol m\textsuperscript{-2} s\textsuperscript{-1}, respectively. After one week of recovery, both A\textsubscript{net} and gs in bur oak had decreased by 84% compared with control values, whereas A\textsubscript{net} in chinquapin oak remained unchanged during the first 24 h after heat treatment at about 50% of the control value.

Discussion

Fluorescence analyses showed that chinquapin oak may be slightly more thermotolerant than bur oak (Figures 1 and 2), which is consistent with earlier observations (Hamerlynck and Knapp 1994a). Because changes in R\textsubscript{id} result from decreased F\textsubscript{p} and increased F\textsubscript{i}, which, in turn, reflect changes in photochemical (q\textsubscript{p}) and non-photochemical (q\textsubscript{np}) fluorescence quenching (Lichtenthaler 1988, Epron and Dreyer 1990, Methy and Trabaud 1993), and increasing temperature decreases q\textsubscript{p} and increases q\textsubscript{np} (Georgiva and Yordanov 1994), the reductions in R\textsubscript{id} could be due to PSII instability, limited electron transfer to Q (Armond et al. 1978, Berry and Bjorkman 1980, Naus et al. 1992), changes in thylakoid membranes (McCain et al. 1989, Harding et al. 1990, Kuropatwa et al. 1992), or photoinhibition (Havaux 1993, 1994). The ability of chinquapin oak to maintain R\textsubscript{id} at slightly higher values than bur oak suggests that this species may allocate resources to stabilize photosystem II (Berry and Bjorkman 1980, Kuropatwa et al. 1992, Naus et al. 1992), protect against...

Thermal tolerance has been linked to photosynthetic responses to drought (Ivanonv et al. 1992) and light (Berry and Bjorkman 1980, Midmore and Prange 1992, see Armond et al. 1978, Al-Khatib and Paulsen 1989, and Mishra and Singhal 1992). In three Mediterranean oak species with differing drought tolerances, $R_{db}$, $q_p$, and $q_{dp}$ did not respond directly to severe water stress (Epron and Dreyer 1990, Epron et al. 1992, Epron and Dreyer 1993). In our study, the differences in $R_{db}$ suggest that photosynthetic responses to high temperature and light may be linked to drought tolerance. Reductions in $R_{db}$ of bur oak and chinquapin oak in response to high temperature were similar to other oaks (Methy and Trabaud 1993), but less than in maple and walnut (McCain et al. 1989, Agati et al. 1995). In our study, it is unlikely that differences in thermal tolerance were due to growth conditions, which strongly influence temperature responses (Seemann et al. 1984, Williams et al. 1986, Jones 1992), because leaf samples were taken from locations where the oak species co-occurred.

Low PPFD (100 µmol m$^{-2}$ s$^{-1}$) and high temperature resulted in stress to both oaks (Figures 1 and 3). Under conditions of low irradiance and high temperature, photosynthetic carbon assimilation is reduced by rapid increases in respiration (Berry and Bjorkman 1980, Midmore and Prange 1992). Decreased $R_{db}$ at an irradiance of 100 µmol m$^{-2}$ s$^{-1}$ was caused by reduced $F_p$, possibly because of reduced electron transfer to $Q$ from PSII (Lichtenthaler 1988). Although it may seem unlikely that many leaves would experience leaf temperatures exceeding 40 °C at a PPFD of 100 µmol m$^{-2}$ s$^{-1}$, inner canopy shade leaves can experience transient periods of both high irradiance and leaf temperature (Pearcy 1990). We have preliminary evidence (Hamerlynck, unpublished data) that shade leaves of both oak species have equal, or greater, heat tolerances than sun leaves. It is possible, therefore, that shade leaf photosynthesis, which contributes significantly to daily and seasonal carbon gain (Kozlowski et al. 1991), could be limited by interactions between temperature and light.

Bragg et al. (1993) suggested that bur oak seedlings establish in lower PPFD microenvironments than chinquapin oak because they are less drought tolerant. At PPFDs between 400 and 700 µmol m$^{-2}$ s$^{-1}$ and temperatures from 40 to 44 °C, bur oak $R_{db}$ was equal to or below the critical value of 3.0, whereas chinquapin oak had $R_{db}$ values significantly above 3.0 at 400 µmol m$^{-2}$ s$^{-1}$, and equal to 3.0 at 700 µmol m$^{-2}$ s$^{-1}$. These findings support our hypothesis that chinquapin oak is more thermostolerant than bur oak to the light and temperature combinations likely to prevail in the field. Our observations also provide evidence that bur oak and chinquapin oak seedling establishment is influenced primarily by differences in temperature tolerance and irradiance, as has been suggested for other tree species (Pearcy 1990, Küppers and Schneider 1993, Poorter and Oberbauer 1993).

We have no explanation for the lack of a species effect on the responses of $O_2$ evolution to high temperature and light. It is possible that the $O_2$ evolution response was slower than the fluorescence response (Epron and Dreyer 1990), and that the sampling times were not sufficiently frequent to resolve specific differences. We note that the laboratory measurements were made on evenly heated, isolated tissue and so may differ from whole-leaf responses in the field (Jones 1992). Field measurements with attached leaves at 40 ± 1 °C (data not shown) often showed $A_{net}$ to be well above the 10.0–12.0 µmol m$^{-2}$ s$^{-1}$ range measured at similar temperatures and irradiances in the laboratory. In addition, measurement in saturating CO$_2$ in the O$_2$ electrode housing may shift the photosynthetic temperature optimum to higher values and narrow the response, resulting in greater proportional decreases at temperature extremes compared to measurement at atmospheric CO$_2$ concentrations (Mooney et al. 1978, Berry and Bjorkman 1980).

Heat treatment in the field reduced $A_{net}$ in both oaks, indicating that damage occurred (Figure 4). In both oaks, stomata closed substantially in response to elevated temperature (Figure 4). Stomatal closure at high temperatures is well documented, (cf. Roessler and Monson 1985, Samuelson and Teskey 1991, Bassow et al. 1994, Ranney and Peet 1994), though exceptions occur (Al-Khatib and Paulsen 1989, Dufrene and Saugier 1993). Roessler and Monson (1985) concluded that stomata closed because of increased VPD, whereas $A_{net}$ reductions were temperature dependent. Our results indicate stomatal closure in these oaks was more closely coupled to increased temperature than to increased VPD, because $g_s$ was reduced in a saturated vapor pressure environment. The concurrent decreases in $g_s$ and $A_{net}$ (Figures 4 and 6) indicate that, in these oaks, $g_s$ may rapidly adjust to short-term changes in photosynthetic capacity, as occurs over longer periods (Wong et al. 1979, Chandler and Dale 1993, Hamerlynck and Knapp 1994). Reduced $g_s$ may also indicate damage to the stomatal apparatus. In wheat exposed to similar irradiance and temperatures, $g_s$ increased and $A_{net}$ declined, indicating that high temperature and light mainly affected mesophyll function (Al-Khatib and Paulsen 1989).

Transient high temperature stress had more severe effects on the photosynthetic recovery of bur oak than of chinquapin oak (Figure 4 and 5). Under normal field conditions, bur oak had higher $A_{net}$, $g_s$, and $C_i$ than chinquapin oak. Bur oak also had lower $T_{leaf}$, but similar WUE to chinquapin oak (Table 1.) and other C$_3$ tallgrass prairie plants (Turner et al. 1995). Differences in $g_s$ are consistent with the observed distribution of these oaks in tallgrass prairie gallery forests (Abrams 1986). Large leaves and high $g_s$ in bur oak could maximize $A_{net}$ under favorable conditions, as indicated by higher $C_i$ (Table 1), but might restrict this oak to mesic gallery forest locations. After heat treatment, $g_s$ and $A_{net}$ in bur oak were similar to chinquapin oak (Figures 4 and 5). Reduced $g_s$ after heat stress, combined with large leaves, appeared detrimental to bur oak’s photosynthetic recovery. Reduced $g_s$ limits evaporative cooling, whereas slower convective heat loss by large leaves may raise $T_{leaf}$ above the thermal tolerance limit during recovery (Campbell 1977, Jones 1992, Hamerlynck and Knapp 1994). A comparison of gas exchange responses 24 h and 7 days after recovery (Figure 5) provides evidence to support this idea.
Twenty-four h after heat stress, $T_{\text{leaf}}$ was 36–39 °C in both oaks, but only in bur oak were the values of $A_{\text{net}}$ and $g_s$ less than after 1 h of recovery. After 7 days of recovery, $A_{\text{net}}$ of bur oak had increased but was still less than the control value. Thus, large leaves and greater proportional reductions in $g_s$ after heat stress (Figure 7) could limit bur oak to moist forest sites, whereas small leaves and smaller proportional reductions in $g_s$ after heat stress, as well as low $g_s$ under favorable conditions, could allow chinquapin oak to establish and maintain populations in exposed dry locations. We conclude that reductions in $g_s$ after heat stress may not affect $T_{\text{leaf}}$ as much in chinquapin oak as in bur oak, thus allowing for more rapid photosynthetic readjustment in chinquapin oak.

In the field, $A_{\text{net}}$ was not depressed below the compensation point after exposure for 45 min at light × temperature combinations that reduced $R_{\text{d}}$ below the damage threshold after only 5 min (Figure 1), which indicates that $R_{\text{d}}$ and other fluorescence signals may overestimate the impact of high temperature on intact leaves under field conditions (Schreiber and Berry 1977, Lichtenhalter 1988, Agati et al. 1995). However, the estimated thermal tolerances of these oaks (Figure 1) were similar to desert shrubs (Mooney et al. 1978, Seemann et al. 1984, Midgley and Moll 1993), xeric Mediterranean oaks (Methy and Trabaud 1993), shortgrass prairie species (Monson and Williams 1982, Roessler and Monson 1985), and tropical species (Smillie and Nott 1979, Dufrene and Saugier 1993), although higher than those reported for many North American oak species found further east (Chabot and Lewis 1976, Tinge et al. 1979, Jurik et al. 1988, Loreto and Sharkey 1990), as well as many deciduous broadleaf and conifer species (Teskey et al. 1986, Jurik et al. 1988, Bassman and Zwier 1991, Foster 1992, Ranney and Peet 1994, Vann et al. 1994). The ability to recover over 50% of photosynthetic capacity after extreme heat stress may be crucial for the success of these oaks in tallgrass prairie gallery forests. Even after prolonged exposure to 47 °C, photosynthesis of bur oak and chinquapin oak was equal to or higher than $A_{\text{net}}$ at optimum temperatures (22 to 30 °C) for other oak and hardwood species (Chabot and Lewis 1976, Jurik et al. 1988, Foster 1992). We conclude that the thermal tolerance characteristics of bur oak and chinquapin oak contribute to the persistence of these species in deciduous forest extending west into the hot, arid grasslands of the central plains of North America.

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References


