Leaf-level responses to light and temperature in two co-occurring *Quercus* (Fagaceae) species: implications for tree distribution patterns

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Abstract

Leaf-level responses to light environment (sun vs. shade) and high temperature were compared in two gallery forest oaks, bur oak (*Quercus macrocarpa*) and chinquapin oak (*Quercus muehlenbergii*). Our goal was to determine if species-specific differences in response to light or temperature could explain the distribution of these oaks in tallgrass prairie gallery forests. On the Konza Prairie Research Natural Area in NE Kansas (USA), bur oak is more abundant than chinquapin oak along lower reaches of streams where the forests are most productive and canopy closure is greatest. We hypothesized that bur oak is better able to acclimate physiologically to reduced light availability than chinquapin oak. Leaf level acclimation to low light in both oaks occurred through reduced photosynthetic light compensation points (PLC) (bur oak, 60.77 ± 3.02 μmol photons m^{-2} s^{-1} in sun leaves vs. 29.25 ± 0.29 photons m^{-2} s^{-1} in shade leaves; chinquapin oak, 49.47 ± 2.82 photons m^{-2} s^{-1} in sun leaves vs. 26.48 ± 1.74 photons m^{-2} s^{-1} in shade leaves), resulting from nearly 50% reductions in dark respiration and specific leaf mass in both species. Apparent quantum requirement (Q_{req}; mol photons mol^{-1} O$_2$) did not differ between sun and shade leaves in either species, and only bur oak showed differences in sun and shade leaf shape. We also hypothesized that chinquapin oak, which is more abundant in exposed, upper stream reaches, has greater photosynthetic tolerance to the high temperatures characteristic of this region. The maximum temperature tolerances (T_{max}) of these oaks were compared by measuring increases in chlorophyll fluorescence. For most of the growing season, T_{max} in chinquapin oak was 2.0°C higher than in bur oak. Field measurements of leaf vs. air temperatures in seedlings and adult trees indicated that T_{max} was more likely to be exceeded in bur than in chinquapin oak, particularly in seedlings exposed to high solar radiation loads. We concluded that differences in thermal tolerance, in addition to previously documented differences in water relations are important determinants of distributional patterns of these oaks within gallery forests.

Keywords: Gallery forest; Light acclimation; Photosynthesis; *Quercus*; Tallgrass prairie; Temperature tolerance

1. Introduction

Quercus, one of the most widespread North American tree genera, often dominates savannas and gallery forests within grasslands (Weaver, 1954; Abrams, 1985, 1990: Aizen and Patterson, 1990). In these systems, two species of oaks usually co-occur (Aizen and Patterson, 1990), often

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with distinct leaf morphologies and photosynthetic characteristics (Callaway, 1992; Hollinger, 1992; Bragg et al., 1993). Such is the case in gallery forests on the Konza Prairie Research Natural Area (KPRNA) in the Flint Hills of northeastern Kansas, where bur oak (*Quercus macrocarpa* Michx.) and chinquapin oak (*Quercus muehlenbergii* Englm.) dominate gallery forests lining streams that dissect tallgrass prairie (Abrams, 1986, 1992). Tree establishment in this region requires coping with an environment of high light, high temperatures and an unpredictable water supply, in addition to competition from dominant grasses (Weaver, 1954; Knapp, 1985; Abrams, 1986, 1990; Bragg et al., 1993). Moreover, because few shade-tolerant, late successional hardwood tree species extend to this western limit of the North American deciduous forest (Abrams, 1990), shade-intolerant trees such as oaks must also cope with the low light environments of mature forests.

Bur oak and chinquapin oak are well-adapted to periodic drought and high light, facilitating establishment within grasslands (Abrams, 1990, 1992; Knapp, 1992; Bragg et al., 1993). Past research indicates that bur oak is most successful in more mesic sites with deep soils (Abrams, 1986), while chinquapin oak is more common at upland xeric locations, often in shallow, low phosphorus soils (Killingbeck, 1984, 1988; Abrams, 1986). These studies have focused on plant water relations for a mechanistic understanding of species distribution. For example, bur oak adjusts osmotically to drought (Abrams and Knapp, 1986; Abrams, 1990), its stomata rapidly respond to variable light, thereby conserving water (Knapp, 1992), and bur oak seedlings and saplings are frequently subjected to severe water stress, potentially limiting survivorship and establishment (Bragg et al., 1993). Chinquapin oak seasonally reduces osmotic potential (Abrams and Knapp, 1986), has lower stomatal conductances than bur oak, and may be considered even more drought tolerant (Abrams, 1990; Bragg et al., 1993).

In contrast to water relations studies, species-specific responses to other potentially important environmental factors such as light or high temperatures are lacking. Plant responses to light and temperature have provided mechanistic explanations for the dynamics of establishment, distribution, and phenology in a wide variety of plant species (Boardman, 1977; Berry and Bjorkmann, 1980; Monson and Williams, 1982; Monson et al., 1983; Groom et al., 1991; Callaway, 1992; Williams and Black, 1993). Species-specific responses to light and high temperature are central to alternate, but not exclusive, hypotheses explaining the distributional patterns of these oaks at the western edge of their range. As noted above, these trees establish in high light environments, but persist in closed-canopy forests. Bur oak may be better able than chinquapin oak to acclimate to low light levels, allowing bur oak to dominate more productive, mesic forest locations. Moreover, at xeric, upland sites, tree establishment may be constrained by high temperatures and low water availability (Knapp, 1985). Leaf biophysical characteristics, such as large leaf size (often over 75 cm^2 in sun leaves) in bur oak, coupled with low water availability for latent energy exchange, may cause leaf temperatures to exceed the thermal tolerance in bur oak, allowing chinquapin oak to dominate upland sites. The purpose of this study was to evaluate these alternative hypotheses by comparing physiological and morphological responses of bur oak and chinquapin oak to light and high temperature. We predicted (1) that bur oak would have greater photosynthetic and morphological plasticity in response to sun vs. shade light environments than chinquapin oak, but (2) that chinquapin oak photosystems would be less sensitive to high temperatures than in bur oak.

2. Materials and methods

2.1. Study area

Research was conducted on the Konza Prairie Natural Research Area (KPNRA), a 3487 ha tallgrass prairie in the Flint Hills of NE Kansas. Extensive gallery forests occur along most of the streams within KPNRA, with much of the overs-

tory dominated by bur oak (*Quercus macrocarpa* Michx.) and chinquapin oak (*Quercus muehlenbergii* Englm.) (Abrams, 1986). This study focused on trees growing in the King's Creek and Shane Creek watersheds of KPRNA. Field work in 1992 examined physiological and morphological responses to light in the two oak species, while 1993 research examined physiological responses and field measurements of leaf temperature.

2.2. Sun and shade leaf comparisons

Photosynthetic measurements

Sixteen sun and 16 shade leaves from each species were sampled in June and July, 1992. Sun leaves were collected from the outermost south facing branches, shade leaves from the innermost canopy. Field measurements of light levels indicated that shade leaves for both oaks were exposed to similar midday light levels (less than $200 \mu \text{mol m}^{-2} \text{s}^{-1}$). All samples were collected from 09:00 to 10:00 h (CDT), stored in plastic bags with wet filter paper to maintain turgor, and transported to the laboratory for determination of photosynthetic capacity with an O_2 electrode system (Hansatech Ltd., England). Leaf discs (10 cm^2) were placed into saturating CO_2 provided by 0.5 M NaHCO$_3$, then pre-illuminated for 2 min with 1000 μmol m^{-2} s^{-1} of light (660 nm) from a high intensity light emitting diode (LED) light source (Model LH36U, Hansatech Ltd., King's Lynn, UK). The temperature was maintained at 25°C by continuously circulating water from a water bath (Isotemp Model 9000, Fischer Scientific, Pittsburgh, PA) through the electrode housing. After pre-illumination, maximum photosynthetic capacity (A_{max}) was estimated at 2000 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) for 2 min using a Bjorkmann lamp (Model LS2, Hansatech Ltd.). Light response curves were generated using LEDs (660 nm) controlled by the LEAFDISC software control package (Hansatech Ltd.). PPFD was initially 1000 μmol m^{-2} s^{-1} and was decreased in steps varying from 200 to 10 μmol m^{-2} s^{-1} every 30 s to darkness. Apparent quantum requirement (Q_{req}; mol photons mol^{-1} O$_2$),

photosynthetic light compensation point (PLC), and dark respiration (R_d in μmol O$_2$ consumed m^{-2} s^{-1}) were derived from a least squares regression fit to ten points in the linear portion of the curve (LEAFDISC, Hansatech Ltd.).

To estimate stomatal limitations not assessed by O$_2$ evolution, field photosynthetic gas exchange was measured in July 1992, with a LiCOR LI-6200 portable photosynthesis system (LiCOR Instruments, Lincoln, NE). Fifteen to 20 cm^2 of leaf area was held perpendicular to full incident sunlight in a 1 l cuvette. Sixteen photosynthetic measurements based on reductions of 10–15 μl l^{-1} CO$_2$ were made. Maximum field capacity (A_{field} in μmol CO$_2$ uptake m^{-2} s^{-1}), stomatal conductance to water vapor (g_s in mmol m^{-2} s^{-1}), and internal CO$_2$ concentrations (C_i in μl l^{-1}) were determined.

Morphological measurements

An optical leaf area meter (CIS Model CI-202, CID Instruments, Moscow, ID) was used to estimate silhouette leaf area and a shape factor (*SF*) from 20 sun and shade leaves. The shape factor is a decimal value indicating the degree of departure from unity, as described by a circle with the same perimeter and area as the leaf sample (CID Instruments, Moscow, ID). Ten square centimeters of leaf tissue were then removed, dried at 80°C for 48 h, and weighed to estimate specific leaf mass (SLM in mg cm^{-2}).

2.3. Temperature measurement and response

Physiological measurements

The seasonal course of high temperature tolerance for *Q. macrocarpa* and *Q. muehlenbergii* was quantified using a chlorophyll fluorescence temperature response technique adapted from Schrieber and Berry (1977) and Smillie (1979). Near mid-June, July, August and September, 1993, six leaf samples from different trees of each species were collected from the Shane Creek and King's Creek drainages in locations where both species occurred. Three small (less than 1 m tall and 2 cm diameter at breast height (dbh)) and three large (over 10 cm dbh) individuals were sampled. All leaves were gathered from 08:00 to
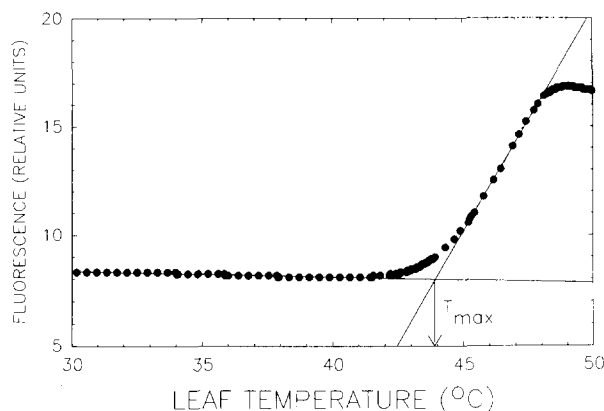
Fig. 1. A typical response of steady state chlorophyll fluorescence yield (F_t) to increasing temperature in bur oak (*Quercus macrocarpa*). T_{max} (T_2 in Schrieber and Berry, 1977; Smillie, 1979) is defined as shown on the figure.

10:00 h CDT, placed into plastic bags containing moistened filter paper to maintain turgor, and transported immediately to the laboratory for fluorescence analysis. Ten square centimeters of leaf tissue were placed into an O_2 electrode housing (Model LD2, Hansatech Ltd.) attached to a temperature-controlled water bath (Isotemp Model 9000, Fischer Scientific) at an initial temperature of 30°C. Fluorescence was measured with a Hansatech FDP/2 fluorescence probe using a Hansatech TR1 transient recorder in continuous monitor mode under PC control provided by the LEAFDISC software program. Steady state chlorophyll fluorescence (F_t, in Lavorel and Etienne, 1977) was established by illuminating the leaf sample for 10 min with 550 μmol m^{-2} s^{-1} red light (660 nm) from a LED light source (LH36U, Hansatech Ltd.). Leaf temperature (T_{leaf}) was measured continuously with a fine wire type-T thermocouple woven through the mid-section of the leaf, with data recorded on a LI-1000 data logger (LiCOR Instruments). Once F_t and leaf temperature had stabilized, T_{leaf} was increased at a rate of 1.5°C min^{-1}

to approximately 60°C. The upper temperature tolerance of the photosynthetic apparatus (T_{max}; T_2 in Schrieber and Berry, 1977) was determined as the point at which F_t quenching relaxed, causing an inflection in the fluorescence trace (Fig. 1). The value T_2 has been found to correspond with irreversible decreases in photosynthetic quantum yield (Schrieber and Berry, 1977; Pearcy et al., 1977; Monson and Williams, 1982; Seemann et al., 1984).

Field leaf temperatures

To determine whether leaf temperatures in the field (T_{leaf}) may be near T_{max}, T_{leaf} were measured in late August 1993 in conditions favoring elevation of T_{leaf} above air temperature (i.e. wind less than 2 m s^{-1} and PPFD more than 1800 μmol m^{-2} s^{-1}). T_{leaf} was measured with an infrared thermometer (IRT; C-600M Linear Laboratories, Los Altos, CA) from 13:30 to 16:30 h CDT on leaves in full sunlight. The IRT was held at a 45° angle 1.5 cm above the exposed leaf surface, taking care not to shade the leaf surface during measurement. T_{leaf} and time of measurement were recorded for large trees (bur oak, $n=68$; chinquapin oak, $n=65$) and saplings ($n=108$ for each species). Most large-tree measurements were made on leaves 1.5–2.0 m above the ground surface, while leaves from saplings were sampled from near the top of the grass canopy (0.5–1.0 m in height). Air temperature (T_{air}) during the sampling period was measured continuously with a shielded type-T fine wire thermocouple suspended about 1.5 m above the ground surface.

2.4. Statistical analysis

We used individual two-way ANOVA to compare differences within (shade leaf vs. sun leaf and saplings vs. large trees) and between species for all physiological and morphological data at the 0.05 level of significance. Post-hoc testing for interaction effects was also performed (STATISTIX 4.0, Analytical Software, St. Paul, MN).
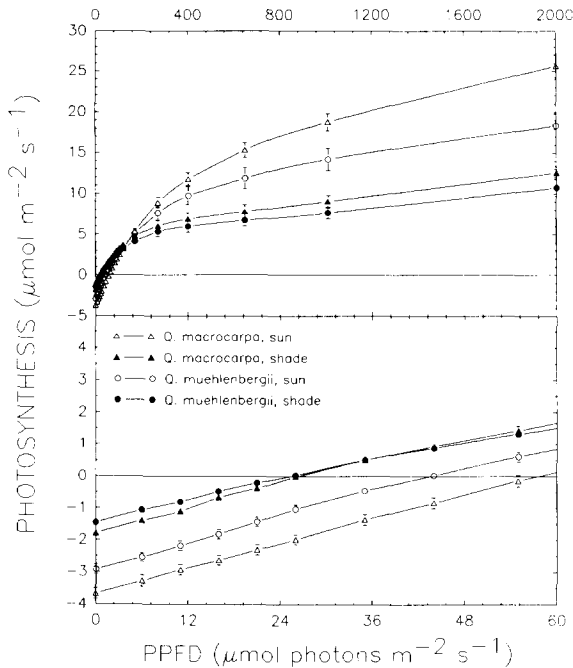
Fig. 2. Entire (top) and linear portions (bottom) of photosynthetic light saturation responses of bur oak (*Quercus macrocarpa*; triangles) and chinquapin oak (*Q. muehlenbergii*; circles) sun (open symbols) and shade leaves (closed symbols) from Shane Creek drainage, KPRNA (the vertical bar represents one standard error, $n = 16$).

3. Results

3.1. Sun and shade leaf comparisons

Photosynthetic measurements

Maximum photosynthetic capacity (A_{max}) for bur oak sun leaves was 41% higher than chinquapin, but A_{max} values in shade leaves were not different (Fig. 2 and Table 1). There were no differences between sun and shade leaf apparent quantum requirement (Q_{req}) in either species (Fig. 2 and Table 1) but bur oak shade leaves had significantly lower Q_{req} (18.7%) than chinquapin shade leaves. Photosynthetic light compensation point (PLC) for shade leaves of both species were significantly lower (51.9% for bur oak, 46.5% for chinquapin oak) than in sun leaves (Table 1). Lower PLC were apparently a result of lower shade leaf dark respiration rates (R_d), not decreases in Q_{req}. Bur oak sun leaves had significantly higher R_d than chinquapin sun leaves, and shade leaves for both species showed about a 2-fold decrease in R_d compared with sun leaves (Table 1).

Photosynthetic field data (Fig. 3) indicated that bur oak did not have higher photosynthetic rates (17.8 ± 0.80 μmol m^{-2} s^{-1}) than chinquapin oak (16.9 ± 0.50 μmol m^{-2} s^{-1}) under field conditions. Stomatal conductances in bur oak were higher (454.7 ± 26.2 mmol m^{-2} s^{-1}) than in chinquapin oak (348.2 ± 15.0 mmol m^{-2} s^{-1}), and were accompanied by higher C_i (240.58 ± 5.65 μl l^{-1} for bur oak vs. 222.25 ± 5.24 μl l^{-1} for chinquapin).

Morphological measurements

Specific leaf mass (SLM) values for sun leaves were significantly higher in bur (12.01 ± 0.31 mg cm^{-2}) than in chinquapin oak (10.88 ± 0.22 mg cm^{-2}; Fig. 4), while shade leaf SLM did not differ (7.07 ± 0.2 mg cm^{-2} and 6.74 ± 0.27 mg cm^{-2}, respectively) between species. Average leaf area was greater in bur oak leaves (Fig. 4) regardless of leaf type (70.3 ± 5.44 cm^2 and 147.4 ± 8.49 cm^2 for bur oak sun and shade leaves, respectively; 38.5 ± 3.25 cm^2 and 80.3 ± 3.87 cm^2 for corresponding chinquapin leaves). Thus, shade leaves of both species were approximately twice the size of sun leaves. Bur oak significantly altered leaf shape (shape factor; *SF*) between sun (0.346 ± 0.027) and shade (0.429 ± 0.020) leaves (Fig. 4). The 20% reduction in *SF* of bur oak sun leaves was due to deeper lobing, not increases in lobe number. In contrast, *SF* values in chinquapin sun leaves (0.503 ± 0.021) and shade leaves (0.562 ± 0.031) were not significantly different.

3.2. High temperature responses and leaf temperatures

Fluorescence responses

Seasonally, the upper photosynthetic temperature tolerance (T_{max}) increased for both oak species (Fig. 5). Bur oak T_{max} increased from 43.3 ± 0.72°C in June to 47.9 ± 0.35°C in August. From June to August, chinquapin oak had significantly higher T_{max} than bur oak increasing

Table 1
Inter- and intraspecific sun/shade leaf photosynthetic comparisons of *Quercus macrocarpa* and *Q. muehlenbergii* leaves (SE in parentheses, $n = 16$)

Variable	Sun leaf	Shade leaf	Leaf diff.	Interaction
A_{max} (μmol m^{-2} s^{-1})				
Bur oak	25.66 (1.403)	12.56 (0.777)	*	*
Chinquapin oak	18.24 (1.389)	10.72 (0.995)	*	
Species diff.	*	NS		
Q_{req} (mol photon mol^{-1} O$_2$)				
Bur oak	17.76 (0.565)	19.09 (1.141)	NS	NS
Chinquapin oak	20.34 (1.481)	23.48 (1.574)	NS	
Species diff.	NS	*		
PLC (μmol photon m^{-2} s^{-1})				
Bur oak	60.77 (3.020)	29.25 (2.289)	*	NS
Chinquapin oak	49.47 (2.824)	26.48 (1.744)	*	
Species diff.	*	NS		
R_d (μmol O$_2$ m^{-2} s^{-1})				
Bur oak	3.43 (0.168)	1.62 (0.190)	*	NS
Chinquapin oak	2.52 (0.145)	1.22 (0.123)	*	
Species diff.	*	NS		

The asterisk indicates significant differences at $P = 0.05$.
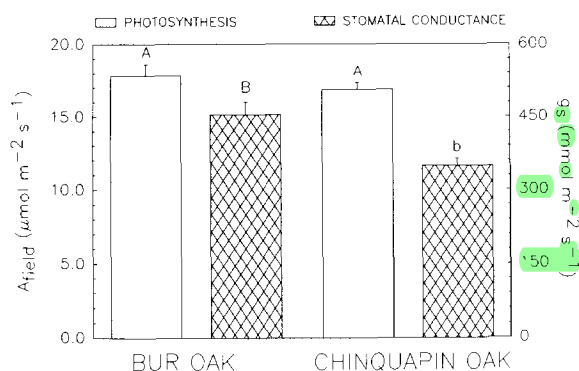

Fig. 3. Mean rates of field photosynthesis (A_{field}; open bars) and stomatal conductance to water vapor (g_s; cross-hatched bars) for bur oak (*Q. macrocarpa*) and chinquapin oak (*Q. muehlenbergii*) sun leaves from Shane Creek drainage, KPRNA, from 20–30 July 1992. Cases of letters differ at significance of 0.05 (the vertical bar represents one standard error, $n = 16$).

from 46.0 ± 0.55°C in June to 50.0 ± 0.87°C in August. This corresponded to about a 2.0°C higher temperature tolerance in chinquapin oak than bur oak. Only in September, when chinquapin T_{max} decreased slightly, was T_{max} identical between species.

Field leaf temperatures

A frequency distribution of field leaf temperatures (T_{leaf}) measured indicates that sapling T_{leaf} was elevated more often and to a greater extent above air temperature (T_{air}) than leaves on large trees (Fig. 6). Leaves from chinquapin oak saplings were usually 3–7°C (average 4.47 ± 0.27°C) above T_{air}, while leaves from bur oak saplings were elevated less above T_{air} (3.33 ± 0.19°C). Leaves from large bur oak trees remained similar to T_{air} (-1 to 2°C; average 1.40 ± 0.26°C), while T_{leaf} from large chinquapin oaks were often 2–4°C (mean value 3.64 ± 0.29°C) warmer than T_{air}. Only T_{leaf} in saplings elevated above T_{air} by more than 8°C. Average T_{leaf} were 35.1 ± 0.22°C and 37.8 ± 0.20°C for leaves from large and sapling bur oaks, respectively, and 37.1 ± 0.32°C and 38.4 ± 0.26°C for leaves from large and sapling chinquapin oaks.

4. Discussion

4.1. Leaf photosynthesis and morphology

The light response curves and values for Q_{req} in this study (Fig. 2 and Table 1) closely match
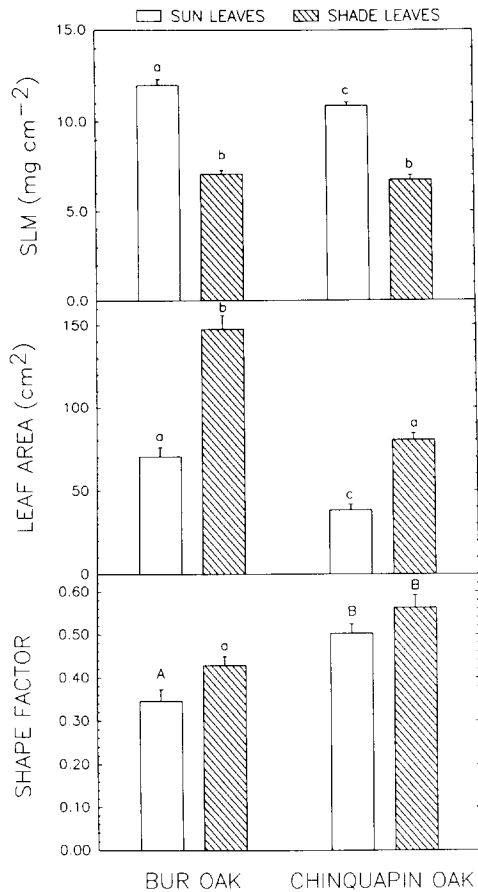
Fig. 4. Mean specific leaf mass (SLM, top), leaf area (middle) and shape factors (bottom) for sun (open bars) and shade (diagonally hatched bars) leaves of bur oak (*Q. macrocarpa*) and chinquapin oak (*Q. muehlenbergii*) from Shane Creek drainage, KPRNA (the vertical bar represents one standard error, $n=20$). Letters differ significantly at $P=0.05$. Shape factor can only be compared within species (see text for details).

Fig. 5. The 1993 seasonal course of upper physiological temperature tolerances (T_{max}) of bur and chinquapin oak leaves from the King's Creek and Shane Creek drainages of the KPRNA. See Fig. 1 caption for explanation of T_{max} measurement. Letters differ at $P=0.05$ probability level ($n=6$; bars indicate standard error of the mean).

those found in other oaks (Hollinger, 1992; Knapp, 1992), and other tree species (Kozlowski et al., 1991; Groom et al., 1991; Stickan and Zhang, 1992). The lack of shade leaf Q_{req} adjustment, especially in bur oak (Fig. 2 and Table 1) was unexpected, but has been reported in other species (Boardman, 1977; Kozlowski et al., 1991). Clearly, bur and chinquapin oaks are photosynthetically adapted to high light environments. The only difference between sun leaf and shade leaf photosynthesis was a reduction in shade leaf PLC (Fig. 2 and Table 1), perhaps a
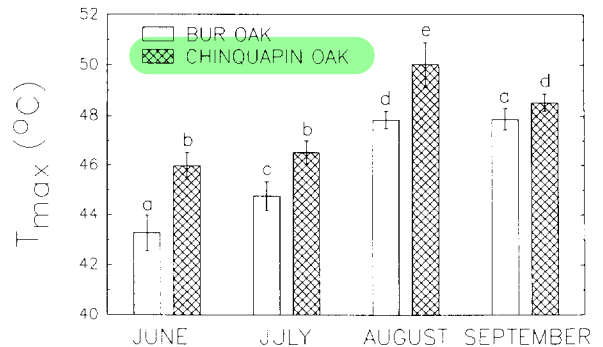
result from a reduction in R_d due to smaller SLM and leaf area (Fig. 4). Such responses in PLC, R_d and SLM have been reported in other tree species (McMillen and McClendon, 1983; Kozlowski et al., 1991; Stickan and Zhang, 1992).

In these oaks, adjustment in leaf morphology seemed to be the primary response to changes in light, and bur oak altered SLM, leaf area and leaf shape more than chinquapin oak (Fig. 4). These data are consistent with our hypothesis that bur oak is better able to acclimate to reductions in light during canopy closure. The marked increase in lobing depth in bur oak sun leaves (Fig. 4) could maintain inner canopy light levels above shade leaf photosynthetic saturation (Fig. 2; Horn, 1971). Similar canopy responses have been modeled on a resource basis with other oak species (Hollinger, 1992). Chinquapin oak altered leaf morphology only slightly (Fig. 4). The major adjustment in chinquapin to low light was to increase leaf area. Since chinquapin leaves tended to be much smaller than bur oak, it is possible this small leaf area limits alterations to leaf perimeter shape.

Small leaf size in chinquapin oak will increase convective cooling by increasing boundary layer conductance (Campbell, 1977) and in combination with low stomatal conductance (Fig. 3) could enhance survival of chinquapin oak in high temperature, dry habitats. In Konza Prairie gal-
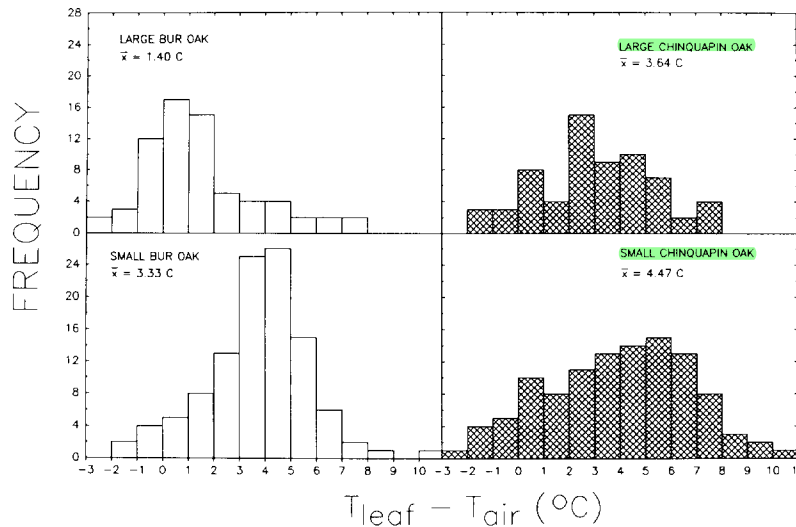
Fig. 6. Frequency distributions of leaf temperature (T_{leaf}) deviations from air temperature (T_{air}) from bur oak and chinquapin oaks of two different size classes. T_{air} was measured at 1.5 m height. T_{leaf} measurements were made 1.0–1.5 m above the ground (large trees) and 0.3–1.0 m above the ground (saplings); $n = 68$ for large bur oak, $n = 65$ for large chinquapin oak, $n = 108$ for saplings of both species.

lery forests, at the extreme limits of upland forest distribution, chinquapin oak is the only oak (and often the only tree) species present (M.D. Abrams, personal observation, 1992). Moreover, in forests where only two to three oak species coexist, habitat preference is almost invariably accompanied by distinct differences in leaf morphology (Abrams, 1986; Gibson et al., 1990; Reich et al., 1990; Callaway, 1992; Hollinger, 1992; Ni and Pallardy, 1992). In most instances, small, shallowly lobed oak species have lower stomatal conductances and photosynthetic capacities, and greater drought tolerance, than oaks with large, deeply lobed leaves (Epron and Dreyer, 1990; Callaway, 1992; Hollinger, 1992; Acherar and Rambal, 1992; Ni and Pallardy, 1992; Bragg et al., 1993). Overall, these data support the mechanistic explanation of tree distribution based on water availability.

4.2. Temperature responses and tree distribution

Differences in photosynthetic temperature tolerance and field leaf temperatures between these two oaks are consistent with the hypothesis that chinquapin oak dominates more xeric, upland locations (Abrams, 1986), in part because bur oak is more likely to be negatively impacted by high temperatures in these sites. Previous research using T_2 values to estimate T_{max} has focused on identifying differences in thermal tolerance among phenologically or geographically distinct species (Smillie and Nott, 1979; Monson and Williams, 1982; Williams et al., 1986), or the effects of growth temperature (Pearcy et al., 1977; Seemann et al., 1984). In this study, a consistent difference in T_{max} was measured in two closely related species growing under similar field conditions. The differences in T_{max} between chinquapin and bur oak were probably not due to different growth temperatures, which are known to affect fluorescence kinetics (Pearcy et al., 1977; Seemann et al., 1984). All samples were taken from locations where both species occurred in similar microclimates. Also, leaf samples from saplings, which often have higher T_{leaf} compared with leaves from larger trees (Fig. 6), did not differ in T_{max} within species (data not shown).

Tallgrass prairies are frequently subject to intense heat and drought (Weaver, 1954). For example, maximum daily air temperatures have
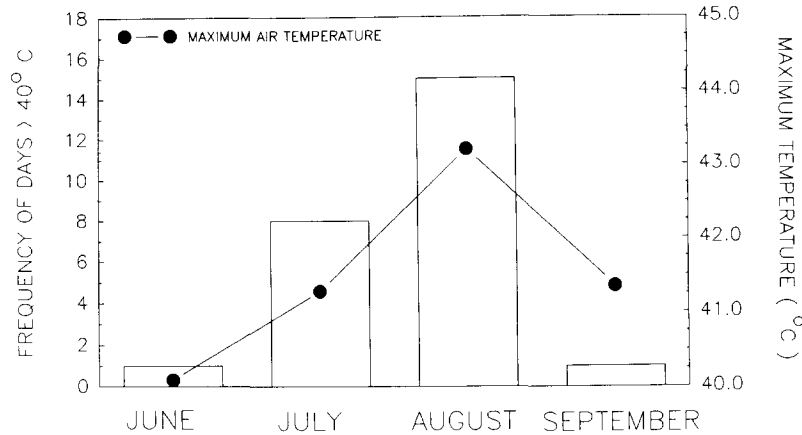
Fig. 7. Frequency distribution of days with maximum air temperatures greater than 40°C ($n=25$) over a 10 year period (1982–1992) from the KPRNA Long Term Ecological Research Weather Station. Maximum air temperatures during this period are superimposed.

exceeded 40°C 25 times during a recent 10 year period (1982–1992) on KPRNA (Fig. 7). Measurements of T_{leaf} in 1993 indicate that both species may be subject to temperatures that could exceed their respective T_{max}, especially in smaller individuals (Figs. 6 and 7). The 1993 summer was one of the wettest on record, hence T_{leaf} may be elevated above T_{air} even more in a dry year when latent heat loss via transpiration (especially important for bur oak) is reduced. Thus, during drought periods, high T_{leaf} coupled with low water availability could strongly impact the establishment and growth of these trees. In particular, bur oak could be negatively affected owing to its lower T_{max} (Fig. 5), larger leaves and higher transpiration rates relative to chinquapin oak.

A large number of recent studies have stressed the role of water relations and mechanisms of physiological drought tolerance in the distribution and establishment of oaks (Bahari et al., 1985; Gordon et al., 1989; Abrams, 1990; Epron and Dreyer, 1990; Abrams and Menges, 1992; Acherar and Rambal, 1992; Kubiske and Abrams, 1992; Epron et al., 1992; Bragg et al., 1993; Kuhns et al., 1993; Rambal, 1993). However, temperature and water relations are always tightly coupled, and in this midwestern grassland, selection for increased thermal tolerance may allow establishment in areas subject to combined water and thermal stress. Hence the characteristics identified as crucial for success of chinquapin oak in xeric sites; small leaves, low stomatal conductance with reduced photosynthetic capacity (Figs. 2, 3 and 4), and drought tolerant tissue (Abrams and Knapp, 1986; Abrams, 1990) are necessarily coupled with the ability to tolerate high temperatures. On a physiological level, it is possible that the higher T_{max} in chinquapin oak may result from increased allocation to PSII stability (Berry and Bjorkmann, 1980; Naus et al., 1992). Indeed, in other oak species with similar leaf morphology, PSII efficiency has been found to be unimpaired at low water potentials (Epron and Dreyer, 1990, 1992; Ni and Pallardy, 1992; Epron and Dreyer, 1993). Possibly, photosynthetic drought hardiness and the high T_{max} noted here are related.

5. Conclusions

In summary, we found that of the two variables studied, light and high temperature, species-specific differences in high temperature tolerance, coupled with drought tolerance and resistance mechanisms, best explain the observed establishment and distribution patterns of these oaks in gallery forests at the western edge of their range. In contrast, differences in photosynthetic adjustment open and closed canopy

light environments did not appear to influence distributional patterns.

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