Environmental and Physiological Factors Influencing the Distribution of Oaks Near the Edge of Their Range

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Abstract. Several North American oaks reach the western limit of their distribution in gallery forests dissecting grassland ecosystems. Tree establishment and success in these systems may be limited by frequent drought, fire, grazing, and competitive interactions with grasses. On the Konza Prairie Research Natural Area, two oak species with distinct leaf morphologies and water relations, bur oak (*Quercus macrocarpa*) and chinquapin oak (*Q. muehlenbergii*), dominate different areas of gallery forests. At distributional extremes for other oak species, co-occurring oaks show similar differences in leaf morphology, water relations, and small-scale distribution. In this paper, we review the physiological responses of native Kansas oaks to parameters such as light level and temperature to clarify the ecophysiological mechanisms underlying tree distribution patterns near the edge of their range.

Key words: distribution, gallery forest, light, photosynthesis, *Quercus*, tallgrass prairie, temperature, water relations

Introduction

A wide range of environmental factors can limit species distribution. Examination of the physiological performance of plants at distributional extremes can clarify the mechanisms by which species maintain themselves in such locations, as well as identify common plant responses to selective variables in similar systems (Billings, 1973). Examination at distributional limits can also simplify study, since physiological performance can be matched to a few, easily identifiable factors (Hadley and Smith, 1983; Smith, 1985; DeLucia, 1987; DeLucia and Smith, 1987; Graves and Taylor, 1988; Day et al., 1989; Groom et al., 1991; Williams and Black, 1993). Thus, ecophysiological research has been dominated by work in systems that are considered extreme and dominated by abiotic forces, with clear species gradients. In this paper we explore the ecophysiological basis for tree distribution in the tallgrass prairie, where two eastern deciduous forest oaks near their western limit in distribution (Fowell, 1965). We argue that elucidating species-specific responses of these oaks to light and temperature, both of which interact with water relations, considered the primary determinant of oak distribution in this area (Abrams, 1986, 1990, and 1992), will clarify the physiological mechanisms determining the western limit of eastern North American oak distribution.

Light, temperature and water relations directly and complexly interact at the leaf level (Fig. 1). Leaf temperature is determined by the energy balance of the leaf, which is determined partially by the amount of direct beam solar radiation impinging on the leaf surface, as well as by ambient air temperature. Direct beam radiation contains the wavelengths of light that are of photosynthetic importance (photosynthetic photon flux density, PPFD; wavelength from 400 to 700 nm). Leaf temperature, in turn, strongly affects plant water status, since the amount of water vapor within the leaf that will pass through the stomata and into the atmosphere is highly sensitive to temperature (Campbell, 1977; Nobel, 1983; Jones, 1992). Leaf temperatures may be influenced by altering stomatal opening, which changes the degree of evaporative cooling, or by altering leaf angle and leaf shape, which alters interception of solar radiation and the convective exchange properties of the leaf (Campbell, 1977; Nobel, 1983; Heckathorn and DeLucia, 1991). However, direct beam irradiation and large infrared radiative inputs from surrounding vegetation and the ground can elevate leaf temperature well above air temperature (Nobel, 1983), which may increase water loss. Plants vary in their ability to function at very low tissue water potentials; nonetheless, water limitation almost always decreases plant growth and may alter competitive relationships (Kaiser et al., 1981; Kaiser and Heber, 1981; Kuppers, 1984; Epron and Dreyer, 1990 and 1992; Simoes and Baruch, 1991; Barton, 1993). It is apparent from their interactions that water relations should not be uncoupled from plant physiological responses to the primary variables (light and temperature) that determine water status. Therefore, species that separate along a moisture gradient could have unique responses to the environmental variables driving water status. Comparison of these physiological responses between species could lead to a more mechanistic understanding of species distribution.
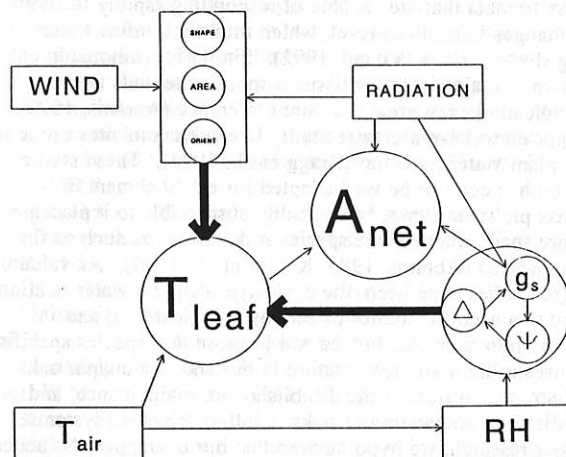

FIG. 1. Interactions of temperature, light, and water relations at the leaf level. Box (A) contains leaf physical characteristics that influence convective exchange properties. Box (B) illustrates leaf characteristics (g_s = stomatal conductance to water vapor, D = concentration gradient of water vapor between leaf and atmosphere, W = leaf water potential) that influence leaf evaporative exchange properties.

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Oaks in the Flint Hills of Kansas

In the Flint Hills of NE Kansas, bur oak (*Quercus macrocarpa*) and chinquapin oak (*Q. muehlenbergii*) dominate gallery forests lining stream courses that dissect the tallgrass prairie. In this region, mean annual rainfall is considered sufficient to allow for eventual forest coverage, but frequent drought and fire, as well as grazing, limit the expansion of tree species into the surrounding grasslands (Weaver, 1954; Axelrod, 1985; Abrams, 1985, 1990). Since European settlement and subsequent fire suppression, forest expansion has increased by nearly 40% (Abrams, 1988 and 1992; Knight et al., 1994). In addition to frequent drought and fire, woody species establishing in tallgrass prairie systems must often endure growing season conditions of extreme temperatures and high photosynthetic photon flux densities (PPFD) (Knapp, 1985), as well as competition for water from surrounding grasses (Bragg et al., 1993). Bur oak is generally more successful in lowland portions of gallery forest drainages, where overall productivity and canopy closure are greater, whereas chinquapin oak tends to establish in more often in open, upland locations (Abrams, 1986; Bragg et al., 1993), often associated with reduced phosphorus availability (Killingbeck, 1984, 1988). These differences in small-scale distribution along a putative moisture gradient are accompanied by distinct differences in leaf morphology, with bur oak having large, deeply lobed leaves, and chinquapin oak having smaller, shallowly scalloped leaf margins (Fowell, 1965). A similar pattern of distribution occurs in other oak species in the Ouichita Mountains of Oklahoma (Dooley and Collins, 1984).

Past research dealing with oak physiological ecology in this area has focussed on aspects of plant response coupled to water relations (Abrams, 1986; Abrams and Knapp, 1986; Knapp, 1992; Bragg et al., 1993). Bur oak is known to adjust tissue osmotic characteristics in response to drought (Abrams, 1990) and has stomata that are capable of responding rapidly to short-term changes in sunlight level, which might minimize water loss during shade periods (Knapp, 1992). Similarly, chinquapin oak is known to maintain lower tissue osmotic potentials than bur oak, indicating even greater drought tolerance (Abrams, 1990), and appears to have a greater ability to establish in sites prone to lower plant water potential (Bragg et al., 1993). These studies show both species to be well adapted for establishment in tallgrass prairie systems, but possibly susceptible to replacement by more shade tolerant tree species if disturbances such as fire are suppressed (Abrams, 1985; Knight et al., 1994). As valuable as these studies have been, the exclusive focus on water relations has led to a need for studies of ecophysiological light and temperature responses. Indeed, we propose that species specific responses to light and temperature in bur and chinquapin oaks could strongly influence the establishment, maintenance, and local distribution patterns of oaks in tallgrass prairie systems.

In our research, we hypothesized that bur oak should be better able to photosynthetically adjust apparent quantum requirement (Q_r; mol O_2 per mol light) in low light, as many tree species do (McMillen and McClendon, 1983; Kozlowski et al., 1991), because distribution patterns indicate that bur oak establishes in areas of higher productivity with greater canopy closure (Abrams, 1986; Bragg et al., 1993). Because all North American tree species use the C_3 photosynthetic pathway, how efficiently a species captures and utilizes light is more important ecologically than differences in photosynthetic pathway (Bjorkman, 1981; Kozlowski et al., 1991). By adjusting Q_r to be more efficient at low PPFD and reaching photosynthetic light saturation at lower light levels, some species can maximize integrated canopy carbon gain (Bjorkman, 1981; McMillen and McClendon, 1983; Kozlowski et al., 1991). We found no differences within or between bur and chinquapin oak in Q_r. We did find that bur oak had greater plasticity in leaf morphology in response to light environment (via changing specific leaf mass, leaf area, and leaf shape) than chinquapin oak, as well as higher overall photosynthetic capacity (Hamerlynck and Knapp, 1994). These morphological responses might maximize whole canopy photosynthesis by keeping inner canopy light levels above the photosynthetic light compensation point (Horn, 1971; McClendon and McMillen, 1982; Kozlowski et al., 1991) or optimize convective heat exchange efficiencies of leaves exposed to full sun (Campbell, 1977). We also expected chinquapin oak, which establishes in drier, more exposed locations, to have a higher maximum photosynthetic temperature tolerance (T_{max}; T_2 in Schreiber and Berry, 1977; Smillie and Nott, 1979) than bur oak. We found that chinquapin oak consistently had higher T_{max} (46° - 50° C) than bur oak (43° - 48° C) throughout the growing season, even in locations where both trees grew together (Hamerlynck and Knapp, 1994). This suggests that physiological temperature tolerance in these oaks is controlled more by genetic than environmental factors (Pearcy et al., 1977; Seemann et al., 1984; Williams et al., 1986). Similar measurements of plant high temperature tolerance have helped explain patterns in phenology and species coexistence in other systems (Monson and Williams, 1982; Monson et al., 1983; Williams et al., 1986). Under field conditions, bur oak tended to have leaf temperatures closer to air temperature, while chinquapin oak, especially smaller individuals, often had leaf temperatures elevated 6° to 10° C above ambient air temperatures (Hamerlynck and Knapp, 1994). These findings indicate that temperature and light do seem to be important direct factors, independent of water relations, in the distribution of oaks in tallgrass prairie gallery forests (Hamerlynck and Knapp, 1994) and might have implications in the distribution of other oak species.

In North America, oak diversity is highest in the southeastern portion of the continent, with the edges of oak distribution represented by only one or two species (Aizen and Patterson, 1990). Recent research in oak ecophysiology has examined differences in nitrogen allocation and whole canopy photosynthesis (Hollinger, 1992; Reich et al., 1991); shade tolerance responses and succession (McClendon and McMillen, 1982; Callaway, 1992); photosynthetic performance and limitations in response to drought (Bahari et al., 1985; Abrams et al., 1990 and 1994; Epron and Dreyer, 1990 and 1993; Ni and Pallardy, 1992; Kubiske and Abrams, 1993; Pallardy and Rhoads, 1993); and the relationship between light environment and photosynthetic and anatomical characteristics in relation to species distribution (Kloeppel et al., 1993; Walters et al., 1993; Ashton and Berlyn, 1994). In all these studies, each oak species differed in leaf morphology, with one oak having large, deeply lobed leaves, and the other having small, shallowly lobed leaves. Therefore, examining leaf traits in other oak systems at other edges of oak distribution, and noting if the suite of traits noted here in the gallery forests of Kansas - leaf morphology correlated to differences in photosynthetic performance, temperature tolerance, and leaf temperatures - may further elucidate the physiological mechanisms controlling the distribution of oaks at the edge of their range.

Acknowledgements

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