Int. J. Plant Sci. 157(3):303–308. 1996.

1058-5893/96/5703-0006$02.00

PHOTOSYNTHETIC AND STOMATAL RESPONSES TO VARIABLE LIGHT IN A COOL-SEASON AND A WARM-SEASON PRAIRIE FORB

PHILIP A. FAY[1] AND ALAN K. KNAPP

Division of Biology, Ackert Hall, Kansas State University, Manhattan, Kansas 66506-4901

Species differences in photosynthetic and stomatal responses to steady-state and variable light were examined in two co-occurring tallgrass prairie forbs, the cool-season legume *Baptisia bracteata* var. *glabrescens* and the warm-season composite *Helianthus annuus*. Previous studies indicated that these species might have similar responses to short-term, minutes-long shade because of their similar growth forms. However, photosynthetic carbon gain, oxygen evolution, transpiration, and leaf xylem pressure potential measurements showed that *Helianthus* was far more responsive than *Baptisia* to changes in light availability. *Helianthus* had higher photosynthetic capacity, photosynthetic temperature optimum, stomatal conductance, and transpiration rates, rapid stomatal closure during shade, and delayed photosynthetic recovery when light levels increased, traits common to species exposed to high temperatures or periodic drought stress. *Baptisia*, active under cooler, wetter conditions than *Helianthus*, had lower photosynthetic capacity, photosynthetic temperature optimum, stomatal conductance, and transpiration, and no stomatal response to shade, responses typifying species that experience little water stress. We suggest that environmental and physiological factors may combine to reinforce greatly different photosynthetic and stomatal responses to short-term shade in species with similar growth form, especially in habitats with long, seasonally varying growing conditions.

Introduction

Of the resources essential for plant growth, sunlight may be the most temporally variable. Sunlight intensity varies at scales of seconds (Pearcy 1988), minutes (Knapp and Smith 1989), days, and seasons (Allen et al. 1994). Cloud cover causes considerable variation in sunlight intensity, introducing short-term, minutes-long periods of moderate shade at 15%–20% of full sunlight. Plants repeatedly exposed to short-term shade experience reduced photosynthesis (Knapp and Smith 1987, 1990*a*, 1990*b*, 1991; Fay and Knapp 1993; Knapp 1993), and in some cases partial stomatal closure or loss of photosynthetic induction. These changes can temporarily suppress photosynthesis after saturating light levels return (Prinsley and Leegood 1986; Pearcy and Seemann 1990; Fay and Knapp 1995), further reducing overall carbon gain.

Numerous factors influence a species' propensity for stomatal closure during short-term shade, including growth form, photosynthetic capacity and transpiration rates, and environmental factors such as heat or drought (Knapp and Smith 1987, 1989, 1990*a*, 1990*b;* Jones et al. 1995). For example, in subalpine communities herbaceous species had higher photosynthetic and transpiration rates, lower leaf water potentials, and more rapid stomatal closure during shade compared to co-occurring woody species. These response patterns had different carbon gain and water-loss consequences for the two growth forms. Rapid stomatal closure in herbaceous species maximized overall water use efficiency during periods of variable sunlight, while weaker stomatal responses in woody species maximized overall carbon gain (Knapp and Smith 1989).

This study evaluates the photosynthetic and stomatal responses to steady-state light levels and short-term shade of two co-occurring tallgrass prairie C_3 forbs, the perennial *Baptisia bracteata* Muhl. ex. Ell. var. *glabrescens* (Larisey) Isely, plains wild indigo, and *Helianthus annuus* L., the common annual sunflower. Because they are herbaceous, they would be expected to have similar photosynthetic and stomatal responses to shade (Knapp and Smith 1989). However, they possess contrasting combinations of other traits, which instead could cause divergent stomatal and photosynthetic responses to short-term shade. *Baptisia* grows in the wetter, cooler part of the tallgrass prairie growing season. Flowering occurs from April through June (Great Plains Flora Association 1986), and plants are low-growing (20–40 cm tall) with small (1.5 × 5.0 cm) trifoliate leaves. *Baptisia* will likely have high leaf water potential, low transpiration rates, and low photosynthetic capacity, traits previously associated with constant stomatal conductance during periods of short-term shade (Knapp and Smith 1989). In contrast, *Helianthus* grows in the hotter, drier part of the growing season. Flowering lasts from July through September (Great Plains Flora Association 1986), plants are tall (1–2 m), have large (20 × 40 cm), simple leaves, high photosynthetic capacity (Ben et al. 1987), and are particularly sensitive to low leaf water potential (Sadras et al. 1993), traits correlated with rapid stomatal closure during short-term shade (Knapp and Smith 1989). These species' responses to periods of short-term shade were evaluated through measurements of field plant gas-exchange light-response curves, CO_2-saturated photosynthetic O_2 production capacity, and gas-exchange and leaf water-potential responses to standard sequences of experimental shading.

Material and methods[2]

Studies were conducted in 1993 at the Konza Prairie Research Natural Area, Manhattan, Kansas. *Baptisia* and *He-*

[1]Author for correspondence and reprints. E-mail fay@lter-konza.konza.ksu.edu; WWW http://climate.konza.ksu.edu.

Manuscript received October 1995; revised manuscript received December 1995.

[2]Abbreviations: A_{CO_2}, net photosynthetic carbon uptake (μmol m^{-2} s^{-1}); A_{O_2}, net photosynthetic O_2 evolution (μmol m^{-2} s^{-1}); C_i, intercellular CO_2 concentration (μL L^{-1}); E, transpiration (mmol m^{-2} s^{-1}); g_s, stomatal conductance to water vapor (mmol m^{-2} s^{-1}); PPFD, photosynthetic photon flux density (μmol m^{-2} s^{-1}); T_l, leaf temperature (°C); VPD, vapor pressure deficit (kPa); WUE, water use efficiency (A_{CO_2}/E); ψ_{leaf}, leaf xylem pressure potential (MPa).

lianthus were studied at comparable points in their life cycles; *Baptisia* during May in two populations on adjacent annually burned sites, and *Helianthus* during August in two populations growing on previously disturbed sites. Both species were flowering and beginning to develop fruits or achenes at these times. Abnormally high rainfall occurred through the 1993 growing season, and both species were well watered throughout the study. All measurements were made on recently expanded leaves.

Light-response curves were developed to assess the range of steady-state A_{CO_2} and g_s at various PPFD levels for *Helianthus* and *Baptisia.* Measurements were made with a fast-response closed gas-exchange system (LiCor LI-6200, Li-Cor, Lincoln, Nebr.) on one leaf (*Helianthus*) or two leaflets (*Baptisia*). Leaves were measured in situ with a 0.25-L (*Baptisia*) or 1-L (*Helianthus*) gas-exchange cuvette while irradiance was reduced from full sun (PPFD > 1700 μmol m^{-2} s^{-1}) to darkness by 70 × 70 cm neutral density screens. Gas-exchange rates were determined after 5 min at each light level. The cuvette was opened between measurements, and instrument operating parameters were set to minimize measurement time and avoid overheating the leaf and cuvette. Light-response curve sequences were repeated on a recently expanded leaf or pair of leaflets from four plants per species. A_{CO_2}, C_i, E, g_s, and WUE were expressed as means ± 1 SE by averaging the replicate measurements at each light level.

To determine field CO_2-saturated photosynthetic capacity, light-response curves were also measured with an O_2 electrode (Hansatech S1, Hansatech Ltd., Kings Lynn, Norfolk, U.K.) following the methods of Walker (1987). A temperature-controlled leaf chamber held an O_2 electrode and a 0.5 M sodium bicarbonate CO_2 source that provided saturating [CO_2] regardless of stomatal conductance (Walker 1987). LEDs (Hansatech LH36U) provided 660 ± 25 nm λ light at up to 1000 μmol m^{-2} s^{-1} PPFD, sufficient to support full sun A_{O_2}. System software (Hansatech "Leafdisc") calculated A_{O_2} rates at 30- or 60-s intervals based on the previous 20 s of measured O_2 evolution during preprogrammed illumination sequences.

For measurements, field leaves were collected randomly from the study populations, sealed in bags with damp paper towels to maintain turgor, and kept in the dark at ambient temperature, until measurement in the laboratory within 6 h of collection. An 8–10-cm^2 leaf disk was sealed in the chamber. After equilibration and calibration, illumination was increased each minute for 20 min from 0 to 1000 μmol m^{-2} s^{-1} PPFD. Light-response curves were measured in this way every 5°C from 15°C through 35°C (*Baptisia*) or 40°C (*Helianthus*) on four leaf disks per temperature for each species. Curves at 30°C were used for comparison with light-response curves from the field. Maximum A_{O_2} rates from each temperature were used to construct temperature-response curves. Means and standard errors were calculated from four replicate curves for each temperature and species.

Photosynthetic and stomatal responses to short-term shade periods were determined with field gas-exchange measurements during a standard sequence of alternating periods of full sunlight and shade cast with neutral density screens. Leaves were equilibrated in an open cuvette to full sunlight for 15 min. Then, leaf gas-exchange rates were measured at 1-min intervals for 8–10 min to verify equilibration, followed by measurements through three 5-min shade periods (300–400 μmol m^{-2} s^{-1}) each separated by 8-min periods of full sun. The entire procedure was repeated on one leaf (*Helianthus*) or one pair of leaflets (*Baptisia*) from each of four plants per species. A_{CO_2}, C_i, E, g_s, and WUE values were expressed as means ± 1 SE by averaging the replicate sun-shade sequences at 1-min intervals to yield a single sun-shade-sun response.

Because leaf water status may influence stomatal responses to light, the effects of short-term shade on ψ_{leaf} were measured with a pressure chamber (PMS-1000, PMS Instruments, Corvallis, Oreg.) on *Helianthus* and *Baptisia* plants subjected to alternating 10-min sun and 10-min shade periods. Leaves were sampled at ca. 2-min intervals and immediately measured. The sun/shade/sun cycle was repeated five times on randomly selected leaves from 15 plants available within the experimentally shaded area. Data were presented as means ± SE calculated by averaging measurements at 2-min intervals.

Exposure to short-term shade periods significantly delayed *Helianthus* photosynthetic recovery after reillumination, so further measurements of A_{O_2} responses to PPFD increases were made to determine whether this delay was detectable under non-CO_2-limited conditions. A_{O_2} was recorded while leaf disks were equilibrated for 10 min at 0, 150, or 300 μmol m^{-2} s^{-1} PPFD, followed by a step increase to 1000 μmol m^{-2} s^{-1}. Means and SEs were calculated from four replicates of each illumination sequence.

Results

Light-response curves indicated that *Helianthus* leaves had higher steady-state A_{CO_2}, C_i, g_s, and E, and lower WUE than *Baptisia* at most light levels (fig. 1). *Helianthus* A_{CO_2} and g_s increased markedly with increasing PPFD, but *Baptisia* g_s and E were essentially constant above 800 μmol m^{-2} s^{-1}.

A_{O_2} light-response curves (fig. 2) followed similar trajectories as A_{CO_2} light-response curves. Both species achieved slightly higher maximum A_{O_2} rates compared to their maximum A_{CO_2} rates. Temperature-response curves for A_{O_2} (fig. 3) indicated a lower photosynthetic temperature optimum for *Baptisia* than for *Helianthus.*

Gas exchange in *Helianthus* was far more responsive to short-term shade than in *Baptisia* (fig. 4). In *Helianthus,* shade immediately decreased A_{CO_2} and WUE, stimulated a transient photorespiratory burst of CO_2, and increased C_i. As shade continued, A_{CO_2}, WUE, and C_i approached new steady-state shade levels. Shade greatly reduced g_s and E, although more gradually than for A_{CO_2}. Shade caused the same qualitative changes in *Baptisia* A_{CO_2}, C_i, and WUE as in *Helianthus,* but of smaller magnitude. *Baptisia*'s g_s and E were unaffected.

Reillumination of *Helianthus* leaves reversed changes caused by shade. Full recovery of g_s to preshade levels required more than 8 min. There was a similar delay in photosynthetic recovery. For *Baptisia,* photosynthetic recovery after increased PPFD was immediate.

Helianthus also had lower, more shade-responsive ψ_{leaf} than *Baptisia* (fig. 5). Periods of shade increased *Helianthus* ψ_{leaf}, but only minimized fluctuations in *Baptisia.* Both species returned immediately to preshade states when PPFD was increased to full sun levels.

Helianthus A_{O_2} recovery was not delayed in CO_2-saturated leaves (fig. 6) during illumination increases

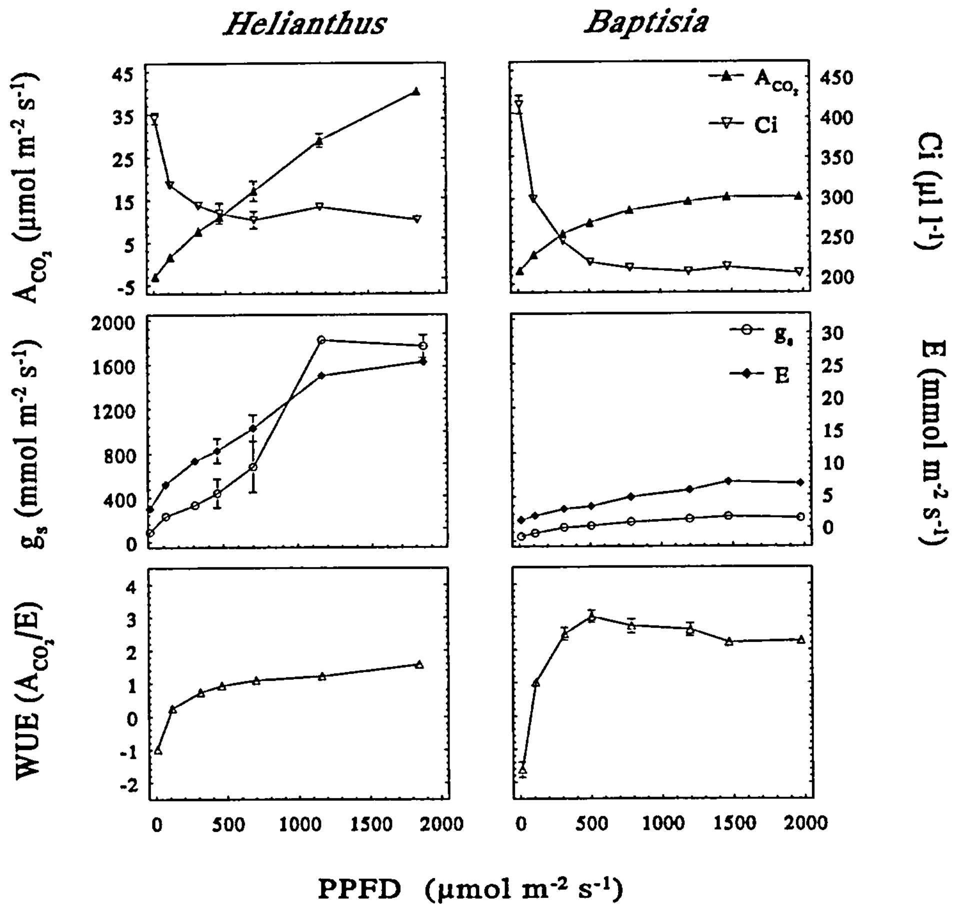

Fig. 1 Leaf gas-exchange steady-state light-response curves for *Helianthus annuus* and *Baptisia bracteata* var. *glabrescens*. Means ± standard error (SE). Missing SEs fell within the symbols.

from 300 to 1000 µmol m^{-2} s^{-1} PPFD. However, delayed Ao_2 recovery occurred during illumination increases from 150 to 1000 µmol m^{-2} s^{-1}, and delays were most pronounced during increases from 0 to 1000 µmol m^{-2} s^{-1}.

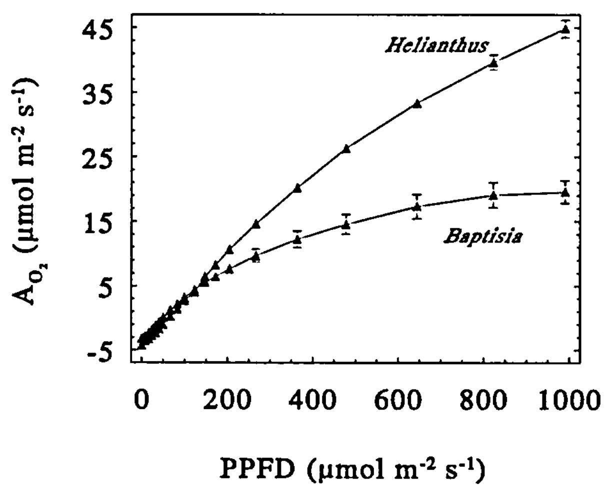

Fig. 2 Photosynthetic O_2 evolution (means ± SE) steady-state light-response curves at 30°C for *Helianthus annuus* and *Baptisia bracteata* var. *glabrescens*. Missing error bars fell within the symbols.

Discussion

Baptisia bracteata var. *glabrescens* and *Helianthus annuus* had markedly different photosynthetic and stomatal responses to short-term shade. In *Baptisia*, shade periods caused little change in ψ_{leaf} and no change in g_s, allowing immediate photosynthetic recovery after shading. When *Helianthus* was shaded, its stomata closed and ψ_{leaf} increased, reducing water loss and water stress, but at the cost of delayed photosynthetic recovery when light levels increased. These strong differences occurred even though abundant rainfall kept both species well watered throughout the study, which should minimize stomatal closure during short-term shade periods (Knapp and Smith 1990*a*). These species also share a herbaceous growth form and so might be expected to have similarly responsive stomata (Knapp and Smith 1989).

Baptisia and *Helianthus* had stomatal responses to shade much like other species with similar leaf-level physiological characteristics. For example, *Baptisia* responded like other species (Knapp and Smith 1989) with low Aco_2, g_s, *E*, water stress, high respiratory carbon demands from nonphotosynthetic tissues (Zajicek et al. 1986), wilt-resistant leaves, and constant g_s and ψ_{leaf} during shade followed by rapid photosynthetic

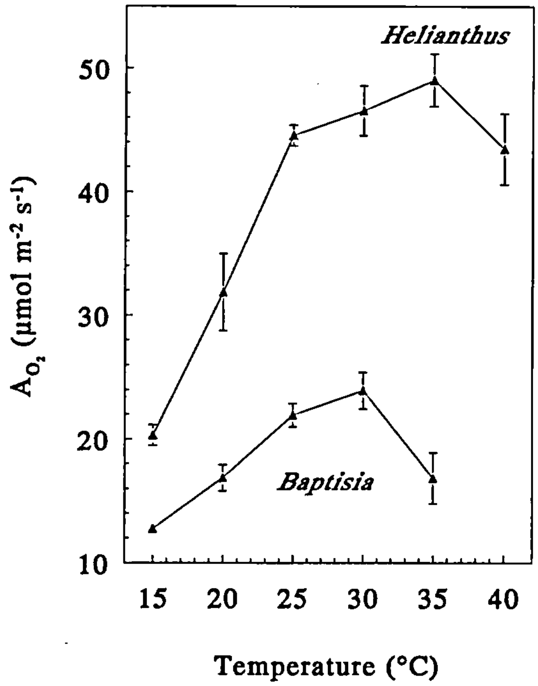

Fig. 3 Photosynthetic O_2 evolution (means ± SE) steady-state temperature-response curves for *Helianthus annuus* and *Baptisia bracteata* var. *glabrescens*. Missing SEs fell within the symbols.

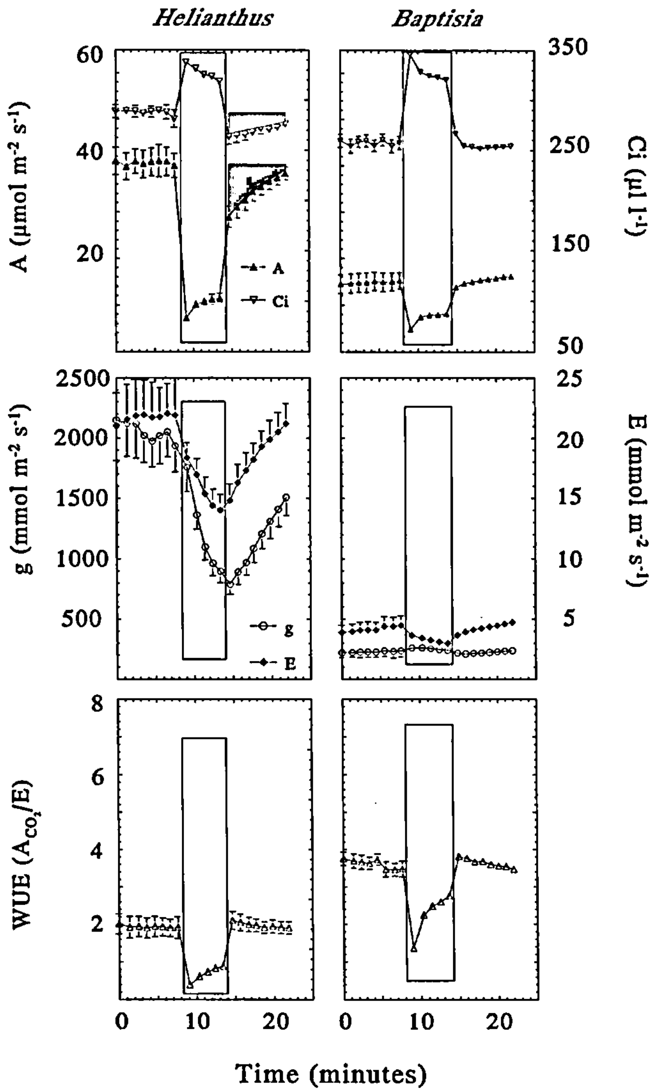

Fig. 4 Leaf gas-exchange responses (means ± SE) to 5-min periods of 300–400 µmol m^{-2} s^{-1} PPFD shade (boxed area) in *Helianthus annuus* and *Baptisia bracteata* var. *glabrescens*. Shaded areas in *Helianthus* curves indicate period of delayed photosynthetic recovery and the trajectory if photosynthetic recovery had tracked light levels. Missing SEs fell within the symbols. For *Helianthus*, full sun T_l = 29.3 ± 0.2, VPD = 18.7 ± 0.5; for *Baptisia*, T_l = 24.7 ± 0.3, VPD = 16.5 ± 0.3.

recovery. The fact that other species with these traits were woody species suggests that in some cases patterns in stomatal and photosynthetic responses to short-term shade may depend less on growth form than on the combination of physiological characteristics they possess.

Helianthus had physiological traits similar to those of other herbaceous species with rapid stomatal responses (Knapp and Smith 1989). These traits included high A_{CO_2}, g_s, and E, water stress, large wilt-prone leaves, and decreased g_s and increased ψ_{leaf} during shade followed by delayed photosynthetic recovery. Although *Helianthus* responded to shade as expected, stomatal closure during shade is not restricted to herbaceous growth forms. Stomatal closure in the oak *Quercus macrocarpus* during short-term shade (Knapp 1992; Hamerlynck and Knapp 1994) occurred at rates comparable to some herbaceous species (Fay and Knapp 1993).

In addition to having the stomatal and photosynthetic responses to shade expected from their physiological characteristics, *Baptisia* and *Helianthus* had shade responses that might be expected for their typical growing conditions. For example, *Baptisia* grows during the cooler, wetter, first half of the tallgrass prairie growing season. These would be ideal conditions for a species to maximize carbon gain through constant g_s during shade, because low evaporative demand and leaf energy loads coupled with consistently high ψ_{leaf} could limit the benefits of water conservation through stomatal closure by causing delayed photosynthetic recovery after shade.

In contrast, *Helianthus* grows during the hot, dry half of the growing season, and encounters high evaporative demand and leaf energy loads, and low ψ_{leaf}. These conditions are detrimental to *Helianthus* growth in numerous ways, reducing leaf expansion (Sadras et al. 1993), hydraulic conductance (Koide 1985), photosynthetic capacity (Ben et al. 1987; Johnson et al. 1987; Martin and Ruiz-Torres 1992), and plant size (Hara 1986). These would be ideal circumstances to minimize water loss through stomatal closure during shade. The benefits of reduced transpiration and increased ψ_{leaf} may offset the carbon-gain cost of delayed photosynthetic recovery by min-

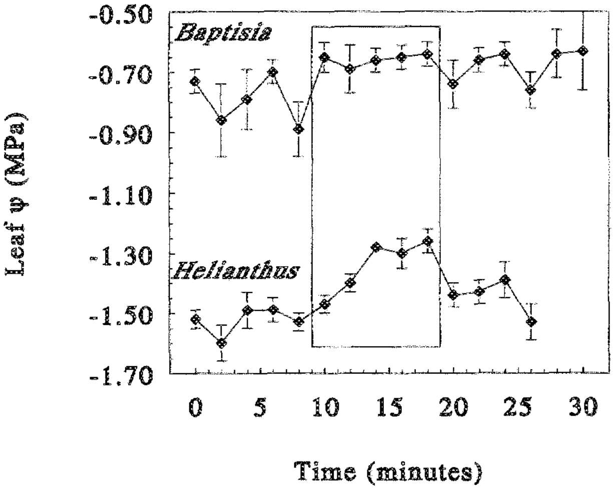

Fig. 5 Midday leaf water-potential response (means ± SE) to 10 min shade (boxed area) in *Helianthus annuus* and *Baptisia bracteata* var. *glabrescens*. Missing error bars fell within the symbols.

imizing the negative effects of water deficit on plant growth and physiology.

A defining difference between *Baptisia* and *Helianthus* was their rate of photosynthetic recovery from shade. Photosynthetic recovery rates depend primarily on the extent of previous stomatal closure and on biochemical induction loss during the shade period (Lange et al. 1987; Kirschbaum and Pearcy 1988). Neither factor limited *Baptisia*'s photosynthetic recovery, since g_s remained constant and A_{CO_2} increased immediately upon reillumination.

The regulation of photosynthetic recovery in *Helianthus* requires further study. Stomatal limitation was at least partly responsible, since during recovery C_i fell below preshade values, and A_{CO_2} and C_i increased in parallel with g_s after reillumination. The occurrence of biochemical induction loss is less certain. Preliminary indications are that no biochemical induction loss occurred in the light reactions, the site of photosynthetic oxygen production, since no delay occurred in CO_2-saturated A_{O_2} recovery from 300 μmol m^{-2} s^{-1} PPFD. However, this does not entirely rule out induction loss in the Calvin cycle, the site of CO_2 uptake and several rate-limiting steps in photosynthesis (Sassenrath-Cole and Pearcy 1994), since asynchronies between A_{O_2} and A_{CO_2} have been reported (Kirschbaum and Pearcy 1988; Krall and Pearcy 1993). Lower shade PPFDs may result in induction loss in the light reactions (Prinsley and Leegood 1986), since A_{O_2} recovery was delayed after PPFD increases from 0 and 150 μmol m^{-2} s^{-1}.

In conclusion, environmental and physiological factors may combine to reinforce different photosynthetic and stomatal responses to short-term shade in species with similar growth form, especially in habitats with long, seasonally varying growing conditions. *Baptisia*'s divergence from the growth form generalization (Knapp and Smith 1989), combined with several other exceptions among both herbaceous and woody species (Woods and Turner 1971; Knapp and Smith 1988, 1990*a;* Knapp 1992; Fay and Knapp 1993; E. P. Hamerlynck and A. K. Knapp, unpublished), indicates that growth form may not be a generally applicable explanation for species differences in stomatal responses to variable light.

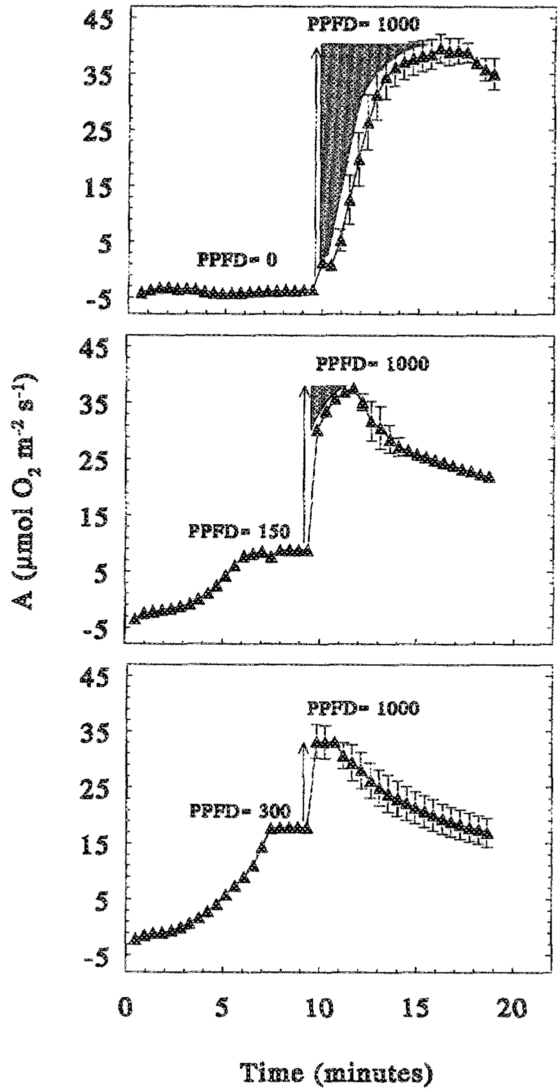

Fig. 6 Photosynthetic O_2 evolution (means ± SE) responses to PPFD increases from 0, 150, or 300 to 1000 μmol m^{-2} s^{-1} in *Helianthus annuus*. Shade areas indicate periods of slow photosynthetic responses to increased light, and trajectory if photosynthetic recovery had tracked PPFD. Missing SEs fell within the symbols.

Acknowledgments

We thank Erik Hamerlynck for assistance with the O_2 electrode, and Clarence Turner for discussion. Research funded by the USDA (NRICGP 90-02435) and the Konza Prairie LTER program (NSF BSR-9011662). Konza Prairie Research Natural Area is a preserve of the Nature Conservancy, and managed for ecological research by the Division of Biology, Kansas State University.

Literature cited

Allen LH, RR Valle, JW Mishoe, JW Jones 1994 Soybean leaf gas-exchange responses to carbon dioxide and water stress. Agron J 86:625–636.

Ben G-Y, CB Osmond, TD Sharkey 1987 Comparisons of photosynthetic responses of *Xanthium strumarium* and *Helianthus annuus* to chronic and acute water stress in sun and shade. Plant Physiol 84:476–482.

Fay PA, AK Knapp 1993 Photosynthetic and stomatal responses of *Avena sativa* (Poaceae) to a variable light environment. Am J Bot 80:1369–1373.

——— 1995 Stomatal and photosynthetic responses to shade in sorghum, soybean and eastern gamagrass. Physiol Plant 94:613–620.

Great Plains Flora Association 1986 Flora of the Great Plains. University Press of Kansas, Lawrence.

Hamerlynck EP, AK Knapp 1994 Stomatal responses to variable sunlight in bur oak (*Quercus macrocarpa* Michx.) leaves with different photosynthetic capacities. Int J Plant Sci 155:583–587.

Hara T 1986 Growth of individuals in plant populations. Ann Bot 57:55–68.

Johnson RC, DW Mornhinweg, DM Ferris, JJ Heitholt 1987 Leaf photosynthesis and conductance of selected *Triticum* species at different water potentials. Plant Physiol 83:1014–1017.

Jones HG, DO Hall, JE Corlett, A Massacci 1995 Drought enhances stomatal closure in response to shading in sorghum (*Sorghum bicolor*) and in millet (*Pennisetum americanum*). Aust J Plant Physiol 22:1–6.

Kirschbaum MUF, RW Pearcy 1988 Gas exchange analysis of the relative importance of stomatal and biochemical factors in the induction of *Alocasia macrorrhiza*. Plant Physiol 86:782–785.

Knapp AK 1992 Leaf gas exchange in *Quercus macrocarpa* (Fagaceae): rapid stomatal responses to variability in sunlight in a tree growth form. Am J Bot 79:599–604.

——— 1993 Gas exchange dynamics in C_3 and C_4 grasses: consequences of differences in stomatal conductance. Ecology 74:113–123.

Knapp AK, WK Smith 1987 Stomatal and photosynthetic responses during sun/shade transitions in subalpine plants: influence on water use efficiency. Oecologia 74:62–67.

——— 1988 Effect of water stress on stomatal and photosynthetic responses in subalpine plants to cloud patterns Am J Bot 75:851–858.

——— 1989 Influence of growth form on ecophysiological responses to variable sunlight in subalpine plants. Ecology 70:1069–1082.

——— 1990*a* Contrasting stomatal responses to variable sunlight in two subalpine herbs. Am J Bot 77:226–231.

——— 1990*b* Stomatal and photosynthetic responses to variable sunlight. Physiol Plant 78:160–165.

——— 1991 Gas exchange responses to variable sunlight in two Sonoran desert herbs: comparison with subalpine species. Bot Gaz 152:269–274.

Koide R 1985 The effect of VA mycorrhizal infection and phosphorus status on sunflower hydraulic and stomatal properties J Exp Bot 36:1087–1098.

Krall JP, RW Pearcy 1993 Concurrent measurements of oxygen and carbon dioxide exchange during lightflecks in maize *Zea mays* L. Plant Physiol 103:823–828.

Lange OL, W Beyschlag, JD Tenhunen 1987 Control of leaf carbon assimilation—input of chemical energy into ecosystems. Pages 149–163 *in* ED Schulze, H Zwölfer, eds. Potentials and limitations of ecosystem analysis. Ecological Studies, vol 61. Springer, Berlin.

Martin B, NA Ruiz-Torres 1992 Effects of water-deficit stress on photosynthesis, its components and component limitations, and on water use efficiency in wheat (*Triticum aestivum* L.). Plant Physiol 100:733–739.

Pearcy RW 1988 Photosynthetic utilisation of lightflecks by understory plants. Aust J Plant Physiol 15:223–238.

Pearcy RW, JR Seemann 1990 Photosynthetic induction state of leaves in a soybean canopy in relation to light regulation of ribulose-1,5-bisphosphate carboxylase and stomatal conductance. Plant Physiol 94:628–633.

Prinsley RT, RC Leegood 1986 Factors affecting photosynthetic induction in spinach. Biochim Biophys Acta 849:244–253.

Sadras VO, FJ Villalobos, E Fereres 1993 Leaf expansion in field-grown sunflower in response to soil and leaf water status. Agron J 85:564–570.

Sassenrath-Cole GF, RW Pearcy 1994 Regulation of photosynthetic induction state by the magnitude and duration of low light exposure. Plant Physiol 105:1115–1123.

Walker D 1987 The use of the oxygen electrode and fluorescence probes in simple measurements of photosynthesis. Oxygraphics, Sheffield. 203 pp.

Woods DB, NC Turner 1971 Stomatal response to changing light by four tree species of varying shade tolerance. New Phytol 70:77–84.

Zajicek JM, BA Daniels-Hetrick, CE Owensby 1986 The influence of soil depth on mycorrhizal colonization of forbs in the tallgrass prairie. Mycologia 78:316–320