Stomatal and photosynthetic responses to shade in sorghum, soybean and eastern gamagrass

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We studied photosynthetic and stomatal responses of grain sorghum (*Sorghum bicolor* [L.] Moench cv. Pioneer 8500), soybean (*Glycine max* L. cv. Flyer) and eastern gamagrass (*Tripsacum dactyloides* L.) during experimental sun and shade periods simulating summer cloud cover. Leaf gas exchange measurements of field plants showed that short-term (5 min) shading of leaves to 300–400 μmol m^{-2} s^{-1} photosynthetic photon flux density reduced photosynthesis, leaf temperature, stomatal conductance, transpiration and water use efficiency and increased intercellular CO_2 partial pressure. In all species, photosynthetic recovery was delayed when leaves were reilluminated, apparently by stomatal closure. The strongest stomatal response was in soybean. Photosynthetic recovery was studied further with soybeans grown indoors (maximum photosynthetic photon flux density 1 200 μmol m^{-2} s^{-1}). Plants grown indoors had responses to shade similar to those of field plants, except for brief nonstomatal limitation immediately after reillumination. These responses indicated the importance of the light environment during leaf development on assimilation responses to variable light, and suggested different limitations on carbon assimilation in different parts of the soybean canopy. Photosynthetic oxygen evolution recovered immediately upon reillumination, indicating that the light reactions did not limit soybean photosynthetic recovery. While shade periods caused stomatal closure and reduced carbon gain and water loss in all species, the consequences for carbon gain/water loss were greatest in soybean. The occurrence of stomatal closure in all three species may arise from their shared phenologies and herbaceous growth forms.

Key words – A:C_i curves, eastern gamagrass, *Glycine max*, induction, light, oxygen evolution, photosynthesis, sorghum, *Sorghum bicolor*, soybean, stomatal conductance, *Tripsacum dactyloides*, water use efficiency.

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Introduction

A basic feature of gas exchange between leaves and the atmosphere is its sensitivity to fluctuations in resource availability. Sunlight may be the most rapidly and frequently varying plant resource. Variation occurs at several levels, from brief sunflecks under plant canopies (Pearcy 1988) to diurnal or seasonal variation caused by changes in daylength and solar angle (Allen et al. 1994). In many species, stomatal conductance varies with light availability to optimize CO_2 uptake and water loss to the prevailing environmental conditions (Jarvis and Morison 1981, Farquhar and Sharkey 1982).

An important source of variation in light availability in grasslands or agricultural fields is broken cumulus cloud cover. Clouds cause minutes-long periods of 20–40% full sunlight (Knapp and Smith 1987, 1990, 1991, Fay and Knapp 1993, Knapp 1993) which immediately limit carbon gain by reducing photosynthesis. Shade may also limit carbon gain after full sunlight returns as a result of stomatal closure (Knapp 1993), enzyme inactivation (Pearcy and Seemann 1990) or slow recovery of the light reactions (Prinsley and Leegood 1986). However, lost carbon gain may be partially offset by reduced water loss due to lower stomatal conductance and leaf temperature (Berry and Björkman 1980).

Photosynthetic and stomatal responses to shade are variable within and between species. Differences have been attributed to growth form, phenology, water availability, photosynthetic pathway, plant size, leaf biophysical attributes or water storage capacity (Knapp and Smith 1987, 1988, 1989, 1990, Knapp and Fahnestock 1990, Knapp 1992, 1993). In addition, since crop improvement efforts may have selected for photosynthetic and water use efficiency characteristics (Secor et al. 1982, Hay and Walker 1989, Kidambi et al. 1990), domestication may also affect leaf responses to shade.

Here we examine the photosynthetic and stomatal responses to shade in two crop species, sorghum (*Sorghum bicolor* [L.] Moench) and soybean (*Glycine max* L.) and the native species eastern gamagrass (*Tripsacum dactyloides* L.). Sorghum and soybean photosynthetic characteristics have received extensive study under steady-state conditions (Beuerlein and Pendleton 1971, Secor et al. 1982, Bunce 1983, Garrity et al. 1984, Krieg and Hutmacher 1986, Kidambi et al. 1990, Peng and Krieg 1992), but eastern gamagrass has received little attention (Coyne and Bradford 1985). In general, agricultural species are poorly understood compared to native species regarding responses to cloud-induced shade.

To determine how periods of shade affected carbon gain and water loss in these species, we measured their photosynthetic and stomatal responses to shade under typical field conditions. Regulation of photosynthetic recovery from shade was further examined in soybeans, which had the strongest stomatal responses in the field. Lab-grown plants were used for this part of the study.

Abbreviations – A_{CO_2}, photosynthetic C assimilation; A_{O_2}, photosynthetic O_2 evolution; C_a, ambient CO_2 partial pressure; C_i, intercellular CO_2 partial pressure; E, transpiration rate; g_s, stomatal conductance to H_2O vapor; T_l, leaf temperature; WUE, water use efficiency.

Materials and methods

Plant material and study site

Photosynthetic and stomatal responses to shade were measured in sorghum (*Sorghum bicolor* [L.] Moench cv. Pioneer 8500) and soybean (*Glycine max* L. cv. Flyer) grown in a lowland field using standard agronomic practices (C. Swallow, personal communication) at Konza Prairie Research Natural Area near Manhattan, KS. A natural stand of eastern gamagrass (*Tripsacum dactyloides* [L.] L.) was studied in a nearby annually burned lowland tallgrass prairie. For studies of soybean photosynthetic recovery from shade, Flyer soybeans were sown in 12-l pots in standard greenhouse potting mix (peat: Pertile:vermiculite, 1:1:1, v/v/v), fertilized with slow release pellets (Sierra 17-6-10 with micronutrients, Grace/ Sierra, Milpitas, CA, USA), and watered as required. Plants grew at ambient laboratory temperatures under

two 800 W multivapor high intensity discharge lamps ("Sunbrella", Environmental Growth Chambers, Chagrin Falls, OH, USA) which provided saturating photosynthetic photon flux density (PPFD) and a 14/10 h light/ dark photoperiod. After fruit development, plants were periodically depodded and pruned to maintain vegetative growth.

Photosynthetic and stomatal responses

To characterize photosynthetic responses to shade, leaf carbon uptake and water loss were measured with a portable, closed photosynthesis system (LI-6200, LiCor, Lincoln, NE, USA) while leaves received an illumination sequence of alternating full sun (PPFD > 1 700 μmol m^{-2} s^{-1}) and shade (300–400 μmol m^{-2} s^{-1}). The same procedure was used with all species. The illumination sequence was started by orienting a fully expanded leaf perpendicular to the sun for 15 min. Leaf gas exchange was then measured over a 50-min sequence, starting with another 10 min in full sun to insure equilibration and determine initial steady-state values of A_{CO_2} and g_s, followed by three periods of 5 min of shade each separated by 8 min of full sun. The 50-min sequence was repeated three (gamagrass) or four times (sorghum, soybean) on plants after seed head emergence. Shade was cast onto the entire plant by 70 × 70 cm neutral density screens. Throughout the illumination sequence photosynthetic C assimilation (A_{CO_2}), intercellular CO_2 partial pressure (C_i), transpiration rate (E), stomatal conductance to H_2O vapor (g_s), water use efficiency (WUE), and leaf temperature (T_l) were recorded at 1-min intervals on one (sorghum, soybean) to three (gamagrass) leaves with 10–30 cm^2 of leaf area fixed to a 1-l cuvette. The cuvette was opened between measurements to avoid overheating of the leaf and chamber. Instrument operating parameters were set to minimize changes in CO_2 and H_2O vapor concentrations in the cuvette during each measurement.

Values for A_{CO_2}, C_i, E, g_s and WUE were averaged at 1-min intervals across the replicate illumination sequences to yield a single average sun-shade-sun response. T_l was averaged over replicate preshade periods and shade periods, yielding one average for full sun and one for shade. Maximum rates of stomatal closure were calculated by regression analysis of the change in mean g_s from the onset of shade against the time elapsed since the onset of shade. These calculations used the linear part of the decrease in g_s. The maximal rate of stomatal opening was similarly calculated.

Natural variation in PPFD and T_l were measured on a randomly chosen sorghum leaf exposed to full sun at the top of the canopy and on a leaf within the canopy by using a quantum sensor (LiCor LI-190SB) mounted perpendicular to the ground beside each leaf and a copper-constantan thermocouple attached to the abaxial surface of each leaf. Sensor outputs were recorded at 1-min intervals with a data logger (LiCor LI-1000).

Photosynthetic recovery in soybean

Regulation of photosynthetic recovery after exposure to periods of shade was examined in soybeans by using gas exchange measurements of A_{CO_2}, g_s, C_i to confirm the basic responses seen in the field, A_{CO_2}:C_i curves to test for nonstomatal limitations on recovery, and measurements of A_{O_2} responses to shade to evaluate possible limitations in the light reactions.

A_{CO_2}, g_s and C_i were determined on fully expanded soybean leaves by using a slightly modified illumination sequence. Leaves were positioned on a 250-ml cuvette and equilibrated for at least 10 min to saturating PPFD ($> 1\,000$ μmol m^{-2} s^{-1}). Then measurements were recorded at 1-min intervals through 8 min of saturating PPFD, 5 min of shade (300–400 μmol m^{-2} s^{-1}), then 8 more min of saturating PPFD. The protocol was repeated on 9 leaves. Shade was provided by the same neutral density screens used in the field. As in the field, precautions were taken to minimize deviations of the cuvette environment from ambient.

Separate A_{CO_2}:C_i curves were developed for the two light levels. These curves were then used to predict the fully induced A_{CO_2} expected for a given C_i. We followed the method of McDermitt et al. (1989), modified so that leaves could be equilibrated at high C_a (1 700 μl l^{-1}) to ensure saturating C_i. High C_a was produced by mixing 3 000 μl l^{-1} and 0 μl l^{-1} CO_2 certified gases. The mixture was humidified and then circulated through the 250-ml cuvette with the system in open mode. A leaf was then closed in the cuvette and equilibrated for at least 10 min. Ambient vapor pressure deficit was maintained by diverting part of the humidified gas flow through magnesium perchlorate desiccant. Measurement started when the system was switched to closed mode. A_{CO_2} and C_i were recorded as leaf photosynthesis depleted the CO_2 in the system. Vapor pressure deficit was maintained within 3% of ambient during the 20- to 30-min measurement sequence by continual adjustment of gas flow through the desiccant. The measurement sequence for a leaf was stopped when A_{CO_2} was less than 1 μmol m^{-2} s^{-1}. Twelve leaves were measured at 1 000 μmol m^{-2} s^{-1}, 5 at 300 μmol m^{-2} s^{-1}. Exponential equations and 95% prediction intervals were fit to the data using the curve fit feature of a computer graphics program (Slidewrite, Advanced Graphics Software, Inc., Carlsbad, CA, USA).

Photosynthetic O_2 evolution responses to shade were measured with a Clark-type O_2 electrode (S1, Hansatech Ltd, Kings Lynn, Norfolk, UK) housed in an air-tight water-jacketed chamber (Hansatech LD2/2) connected to a constant-temperature circulating water bath. The electrode was operated with 50% saturated KCl electrolyte. A felt pad saturated with 0.5 M sodium bicarbonate provided saturating CO_2 concentrations for the leaf regardless of stomatal aperture (Walker 1987). All measurements were made at 30°C on 10-cm^2 leaf discs. The electrode operating software (Hansatech Leafdisc) calculated the photosynthetic rates and controlled the LED bank (Hansatech LH36U) which provided up to 1 000 μmol m^{-2} s^{-1} PPFD with a peak λ of 660 nm and range of 50 nm.

For measurement, a leaf disk was inserted and the electrode calibrated with the leaf in the dark. After the electrode restabilized, illumination was gradually increased from 0 to 1 000 μmol m^{-2} s^{-1} over 10 min. This ensured full and consistent induction of the leaf. PPFD was then decreased to either 300, 200 or 100 μmol m^{-2} s^{-1} for 5 min, followed by 1 000 μmol m^{-2} s^{-1} for 5 more min. Throughout this 20-min sequence, A_{O_2} was calculated at 30-s intervals based on the previous 20-s of O_2 evolution. Each illumination sequence was replicated 4 times. The CO_2 pad was rinsed with distilled H_2O and resaturated with bicarbonate solution for each new leaf disk. All rates were corrected for the O_2 electrode temperature response, because the water bath did not entirely eliminate electrode responses to temperature fluctuations during large changes in PPFD. Correction factors were determined empirically by running the PPFD sequences with a damp filter paper disk in place of the leaf disk, while the apparent photosynthetic rate was recorded. This was replicated 3–4 times per light regime.
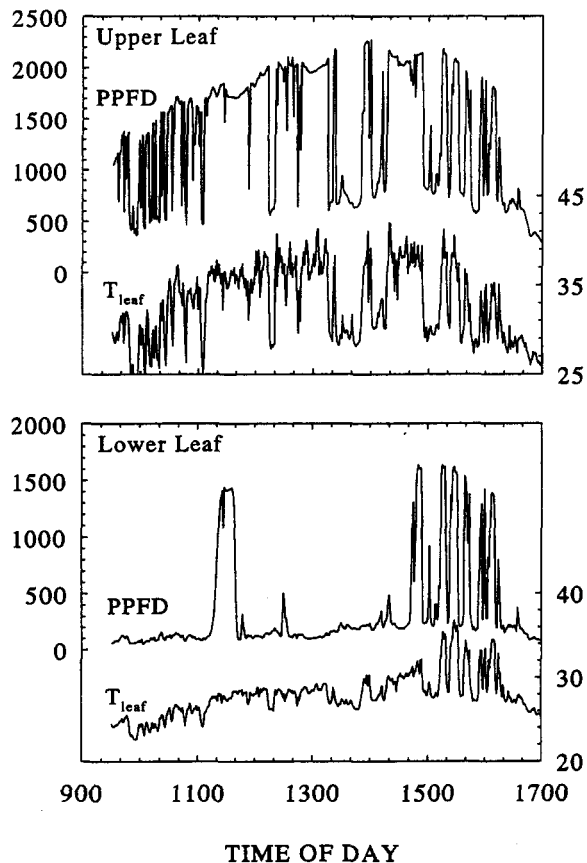

Fig. 1. Representative variation in PPFD (μmol m^{-2} s^{-1}, left axis) and T_l (°C, right axis) on an upper and lower leaf in a sorghum canopy during a partly cloudy day (5 August, 1992).
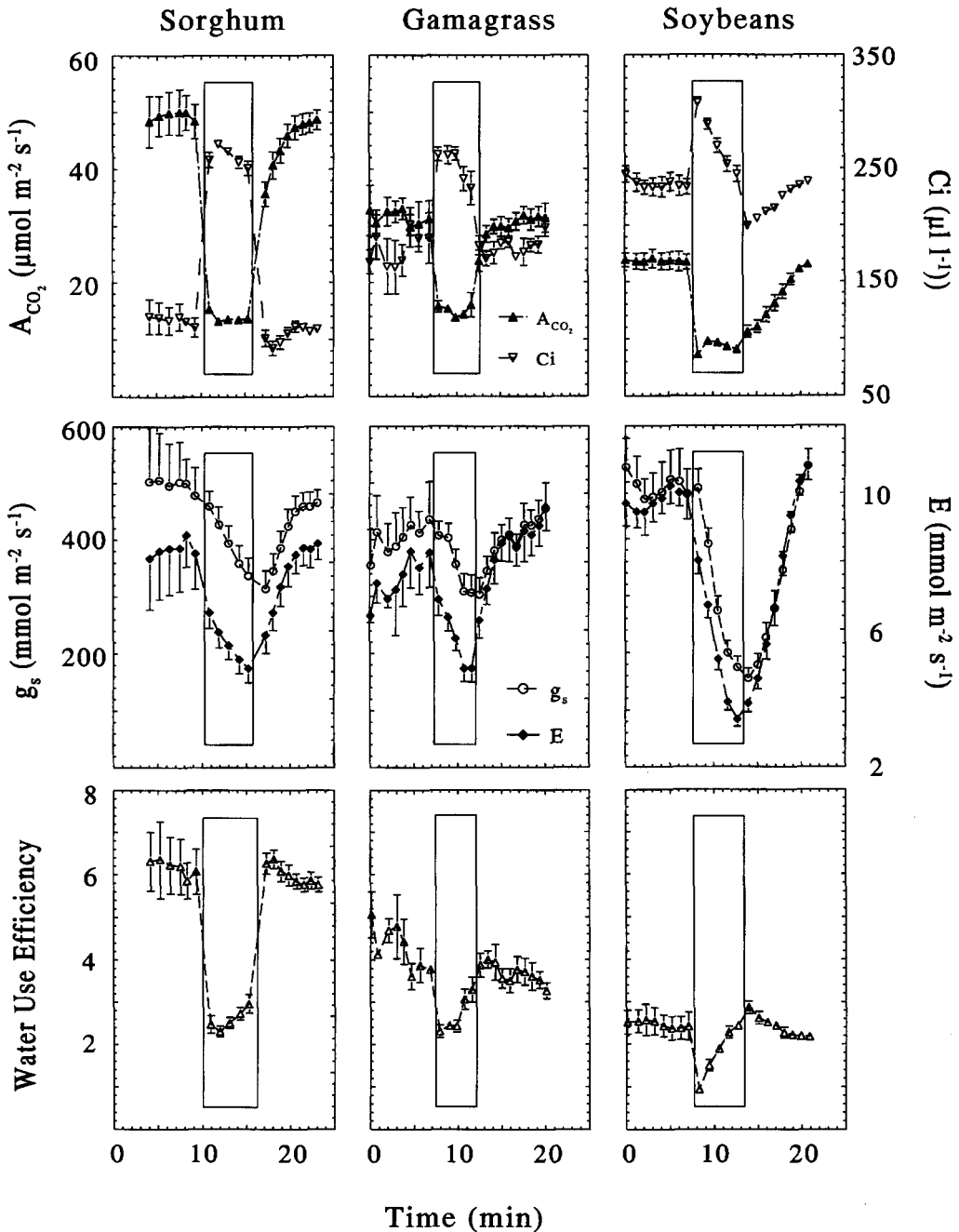
Fig. 2. Mean ± SE A_{CO_2}, C_i, g_s, E and WUE dynamics of sorghum, eastern gamagrass and soybean during alternating periods of sun (PPFD > 1 700 μmol m⁻² s⁻¹) and shade (300–400 μmol m⁻² s⁻¹). Boxes enclose means during shade. Vapor pressure deficits averaged 2.00 to 2.50 kPa. Error bars are missing where the SE fell within the symbols.

Results

Natural sunlight variation

Extensive variability in PPFD and T_l occurred on partly cloudy days. In an 8-h period, a sorghum leaf at the top of the canopy (Fig. 1) experienced 19 shade periods below 700 μmol m⁻² s⁻¹ PPFD. These changes in PPFD caused up to 12°C changes in T_l, which can strongly influence A_{CO_2} and E. In contrast, lower leaves in the canopy spent at least half the day at <300 μmol m⁻² s⁻¹ PPFD, but received several short periods of nearly full sun (≥ 1 500 μmol m⁻² s⁻¹ PPFD). T_l was lower in general than in the upper canopy leaf and was less affected by periodic high PPFD.

	Leaf temperature (°C)		Stomatal movement (mmol m^{-2} s^{-1} min^{-1})	
	Sun	Shade	Closure	Opening
Sorghum	31.94 ± 0.15[a]	29.65 ± 0.22[b]	26.1 ± 2.9[a]	35.8 ± 4.3[b]
Gamagrass	34.77 ± 0.10[a]	32.75 ± 0.13[b]	25.7 ± 6.5[a]	21.0 ± 8.1[a]
Soybean	32.95 ± 0.17[a]	30.20 ± 0.25[b]	64.1 ± 10.3[a]	62.2 ± 5.5[a]

Responses to shade

There was a suite of coordinated leaf physiological responses to shade in all three species. In sorghum, full sun preshade A_{CO_2} averaged ca 50 µmol m^{-2} s^{-1} (Fig. 2). Shade caused an immediate large reduction in A_{CO_2}, a large increase in C_i, gradual stomatal closure and reduced E and WUE. Much of the reduction in E occurred in the first minute of shade, due to lower T_l (Tab. 1). However continued stomatal closure appeared to cause the continued decrease in E, and led to a slight recovery in WUE by the end of the shade period.

Reillumination immediately increased sorghum A_{CO_2} to about 75% of full-sun rates, decreased C_i and initiated reopening of stomata. These parameters then gradually recovered to full-sun values. Stomatal recovery was faster than stomatal closure (Tab. 1). E immediately increased after reillumination because of higher T_l (Tab. 1), then increased in parallel with g_s back to full-sun levels. WUE immediately recovered.

Eastern gamagrass responded to shade in the same ways as sorghum, except that changes during shade were smaller (Fig. 2). Full-sun A_{CO_2}, g_s and WUE were lower and C_i was higher than in sorghum, but values were similar during shade. Also, gamagrass stomata opened and closed at the same rate (Tab. 1), and stomatal closure during shade brought gamagrass WUE nearly back to full-sun levels.

Soybean responses to shade differed from sorghum and gamagrass responses in several ways (Fig. 2). There was an initial postshade photorespiratory burst (Vines et al. 1983) followed by a continued decrease in A_{CO_2} and rapid stomatal closure (Tab. 1). C_i rapidly increased almost to C_a immediately after shading, but then decreased almost to full-sun levels. Stomatal closure and lower T_l caused a large reduction in E and recovery of full-sun WUE by the end of the shade period.

Unlike sorghum and gamagrass, soybean A_{CO_2}, g_s and C_i required the full 8 min to recover from shade. A_{CO_2} and C_i recovered at a constant rate, C_i after a large initial decrease. Stomata reopened as rapidly as they had closed (Tab. 1), E and g_s returned to full-sun levels, and WUE immediately recovered. The parallel increases in A_{CO_2}, g_s and C_i suggest that stomatal closure limited photosynthetic recovery during reillumination.

Photosynthetic recovery in soybean

The photosynthetic and stomatal responses of lab-grown soybeans to shading resembled field plant responses in most respects (Fig. 3) and again suggested that stomatal closure limited photosynthetic recovery during reil-
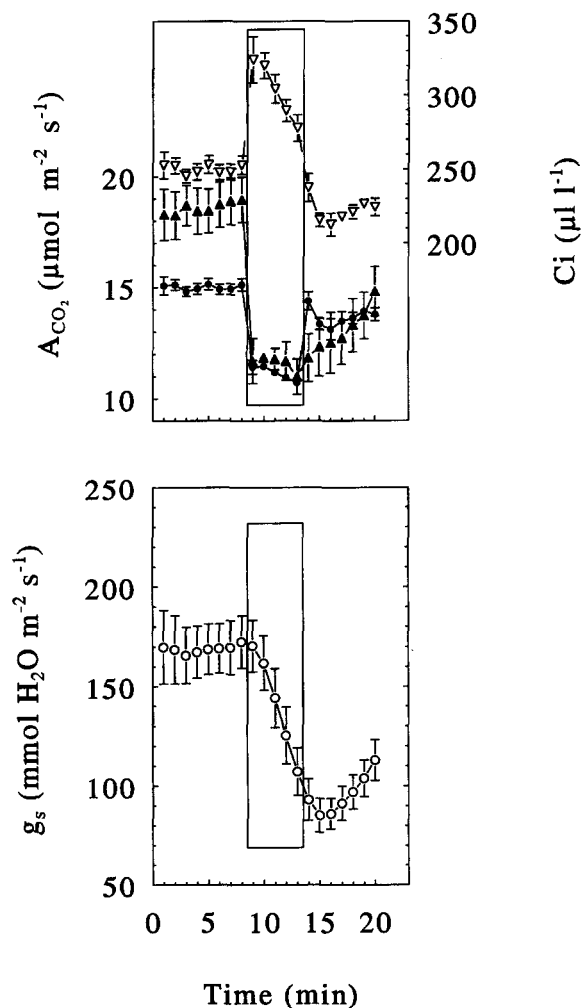

Fig. 3. Mean ± SE A_{CO_2}, C_i and g_s dynamics of soybeans grown indoors during alternating periods of sun (PPFD > 1 000 µmol m^{-2} s^{-1}) and shade. ●, Photosynthetic rates predicted from the A_{CO_2}:C_i curves in Fig. 4. Other symbols as in Fig. 2. Boxes enclose means during shade.
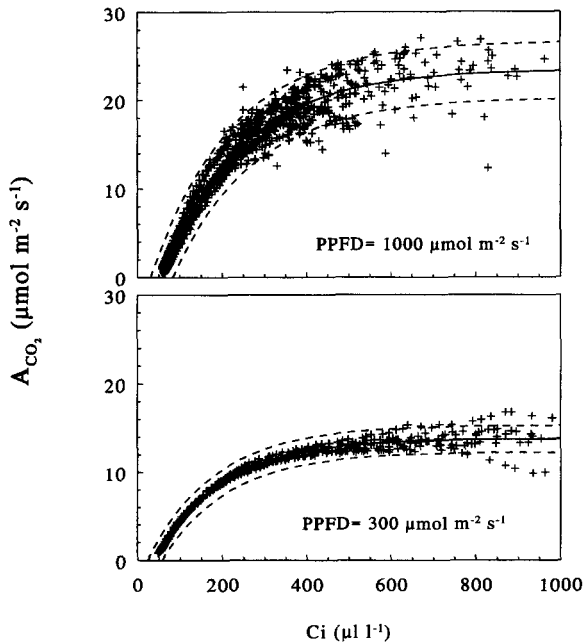
Fig. 4. A_{CO_2}:C_i curves from laboratory-grown soybeans at irradiances of 1000 and 300 μmol m^{-2} s^{-1}. Solid lines are exponential regressions fit to the data, dashed lines are 95% prediction intervals. At 1000 μmol m^{-2} s^{-1}, A_{CO_2} = 23.48–31.45$e^{(-Ci/190.67)}$. At 300 μmol m^{-2} s^{-1}, A_{CO_2} = 13.79–17.85$e^{(-Ci/156.82)}$. For both light levels r^2 >95%.

and improved WUE while carbon gain was low, but also contributed to delayed photosynthetic recovery.

Similar photosynthetic and stomatal responses in sorghum and eastern gamagrass may reflect their close taxonomic relationship, shared photosynthetic pathway, overlapping phenologies and herbaceous growth form. Sorghum and gamagrass responded much like closely related C_4 grasses (Smith 1977) *Andropogon gerardii* and *Sorghastrum nutans* (Knapp 1993, P. A. Fay and A. K. Knapp, unpublished data). All are warm-season species, growing under high temperatures and evaporative demands. Under these conditions, the water conservation benefits of stomatal closure during shade may outweigh the accompanying photosynthetic costs (Knapp and Smith 1990). Herbaceous growth forms often have stomata that are responsive to shading (Knapp and Smith 1989, 1990). These patterns suggest that sorghum, gamagrass and other C_4 grasses have many shared traits
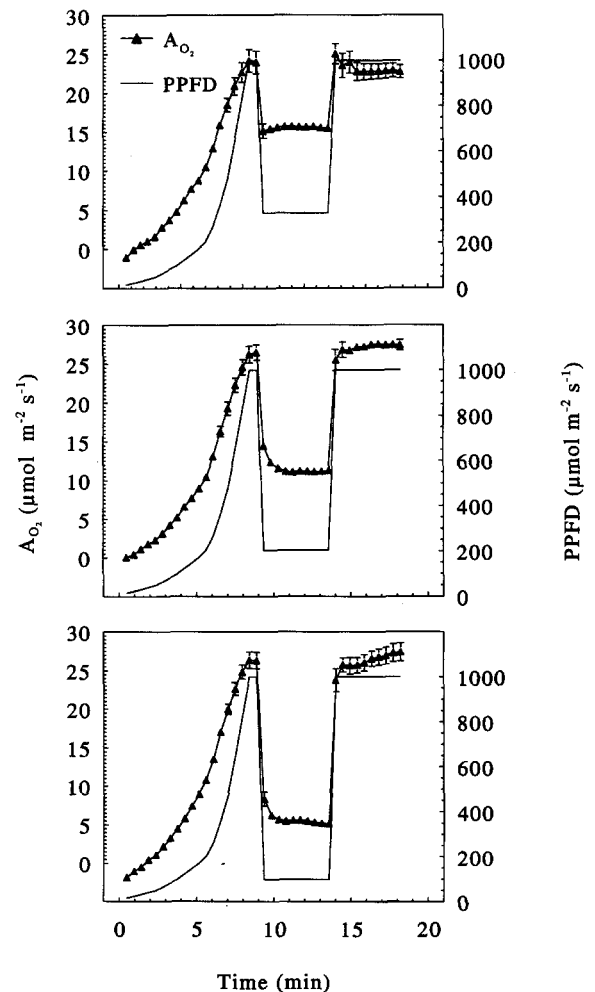
lumination. However, there were two notable differences. First, recovery was slower than that in field plants and not complete within the 8-min reillumination phase. Second, C_i decreased gradually during the first minutes of reillumination, rather than immediately as in field plants. This suggests nonstomatal limitation of photosynthetic recovery after reillumination.

Photosynthetic rates predicted from the A_{CO_2}:C_i curves (Fig. 4) also suggested a brief initial period of nonstomatal limitation of A_{CO_2} after reillumination, replaced by stomatal limitation as high PPFD continued. During shade, predicted and actual A_{CO_2} were equal (Fig. 3). At reillumination, actual A_{CO_2} remained low while predicted A_{CO_2} increased, marking the period of nonstomatal limitation. After 3–4 min of high PPFD, actual and predicted A_{CO_2} converged and increased, suggesting the transition to stomatal limitation of A_{CO_2}.

Photosynthetic O_2 evolution responses to shade (Fig. 5) indicated that the light reactions did not contribute to limitation of photosynthetic recovery. A_{O_2} returned to steady-state rates within 1 min of reillumination from all shade PPFDs.

Discussion

Periods of shade reduced carbon gain in all three species, through light limitation and delayed photosynthetic recovery when full sun returned. Stomata closed during shade in all three species, which reduced transpiration

Fig. 5. Mean ± SE A_{O_2} recovery in laboratory-grown soybeans after periods of 300, 200 or 100 μmol m^{-2} s^{-1} PPFD. Illumination regime shown by line without symbols. Error bars not shown fell within the symbols.

leading to a shared pattern of stomatal closure at the expense of delayed photosynthetic recovery.

In addition, the similarities between sorghum and native C_4 grasses suggest that shade responses have not changed with domestication. Sorghum had higher full-sun A_{CO_2}, g_s, and WUE than gamagrass, but similar rates of stomatal movement. Selection for more rapid stomatal responses could enhance sorghum WUE (Kidambi et al. 1990, Peng and Krieg 1992) during periods of intermittent shade.

Soybean was the most responsive to shade of the species examined in the present study. Stomata of soybean moved much more rapidly than those of sorghum and gamagrass. This rapid movement caused large reductions in water loss and re-established WUE rapidly during shade at the cost of a long lag in photosynthetic recovery. Soybean is like sorghum and gamagrass in its phenology and growth during high temperatures and evaporative demands. The exceptional stomatal responsiveness of soybean to shade may be a consequence of its comparatively low WUE.

Under field conditions we saw no evidence for nonstomatal limitation of photosynthetic recovery. Ribulose bisphosphate carboxylase light-saturates around 400 μmol m^{-2} s^{-1} (Sassenrath-Cole and Pearcy 1994), so at the shade PPFDs used in our study enzyme inactivation should have been minimal. Shade PPFD caused brief nonstomatal limitation of photosynthetic recovery in soybeans grown indoors with lower maximum PPFD. However the stomata in these plants remained responsive to shade and still provided the primary limitation on photosynthetic recovery. Previous studies have shown that growth at low light levels raised soybean induction requirements and lowered maximum A_{CO_2} (Pearcy and Seemann 1990, Sassenrath-Cole and Pearcy 1994). These results indicate that the light environment of a leaf during development affects its photosynthetic responses to variable light in addition to its steady-state characteristics (Bunce 1983) and may indicate different limitations on carbon assimilation in different parts of the soybean canopy.

Despite the lag in soybean A_{CO_2} recovery, no lag was observed in soybean A_{O_2} recovery. Changing light levels may affect O_2 evolution dynamics differently than CO_2 dynamics (Kirschbaum and Pearcy 1988, Krall and Pearcy 1993). O_2 is produced by photosynthetic electron transport, which can potentially respond to light without delay regardless of leaf induction state. CO_2 uptake occurs at the Calvin cycle, where rate-limiting steps in photosynthesis occur. However, an induction period for A_{O_2} may appear when light intensities change at lower levels (Prinsley and Leegood 1986) suggesting that the light reactions might contribute to slow photosynthetic recovery after shading for leaves within soybean canopies.

In conclusion, shade periods a few minutes in length reduced carbon gain and water loss in all species. The consequences of shade for carbon gain and water loss were greatest in soybean. Because carbon gain has a fundamental relationship to crop yield (Zelitch 1982) and plant growth in native systems (Osmond et al. 1987), the costs of delayed photosynthetic recovery in terms of yield or fitness need to be quantified. This will improve steady-state crop physiological models (e.g. Rosenthal et al. 1989, Collatz et al. 1992) and improve our understanding of resource limitation in native systems.

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