RESPONSES TO SHORT-TERM REDUCTIONS IN LIGHT IN SOYBEAN LEAVES: EFFECTS OF LEAF POSITION AND DROUGHT STRESS[1]

Philip A. Fay[2] and Alan K. Knapp

Division of Biology, Ackert Hall, Kansas State University, Manhattan, Kansas 66506-4901, U.S.A.

This study examined how leaf position in the canopy affected photosynthetic and stomatal responses to short-term, minutes-long shade periods during a drought cycle in soybean (*Glycine max* [L.] Merr.). All soybean leaves had similar basic responses to short-term shade, including rapidly decreased photosynthetic rates (A_{CO_2}), slower decreases in stomatal conductance (g_s), and delayed stomatal reopening and photosynthetic recovery after leaves were reilluminated. Drought stress lowered overall A_{CO_2} and restricted photosynthetic and stomatal responses to short-term shade with the negative effects of drought being stronger in lower than in upper leaves. Some of the negative effects of drought persisted after drought was relieved, causing reduced overall water use efficiency, especially in lower leaves. These results indicate that leaf position effects on stomatal responses to short-term shade events become important during and after stress.

Introduction

Plant growth fundamentally depends on photosynthetic carbon gain, which, in turn, depends on resource availability. Sunlight and water are among the most variable essential plant resources. Cloud cover and within-canopy shading are two major causes of varying sunlight intensity to individual leaves (Pearcy et al. 1990; Knapp and Fay 1997). Cloud cover causes short-term, minutes-long shade periods, which reduce leaf photosynthesis (Knapp and Smith 1987, 1990a, 1990b, 1991; Fay and Knapp 1993; Knapp 1993) and often cause rapid stomatal closure that can delay photosynthetic recovery after saturating light levels return (Prinsley and Leegood 1986; Pearcy and Seemann 1990; Fay and Knapp 1995). Short-term shade most strongly affects leaves at the top of plant canopies where full sunlight is typical. In contrast, leaves growing within canopies experience low average light levels and high spatial/temporal variation as a result of leaf layering and movement. Photosynthetic performance of leaves within canopies depends more strongly on biochemical limitations (Pearcy and Seemann 1990; Pons and Pearcy 1992), and stomatal responses are often relatively slow (Kirschbaum and Pearcy 1988; Pearcy et al. 1994).

Although the onset of drought comes more slowly than the onset of light limitation, drought also causes large changes in leaf photosynthetic and stomatal function, inducing both stomatal and biochemical limitations on carbon gain and typically increasing rates of stomatal movement in response to changing light lev-

els (Davies and Kozlowski 1975; Knapp and Smith 1990a, 1990b; Barradas et al. 1994; Jones et al. 1995). These changes may develop over days or weeks (Bradford and Hsiao 1982), and their effects may persist after water availability is restored (Meidner and Mansfield 1968; Xu and Bland 1993).

This study examined how leaf position affected stomatal responses to short-term shade periods in soybean, *Glycine max* [L.] Merr cv. Flyer. Soybean was chosen for study because its photosynthetic and stomatal characteristics are well documented under steady-state (Beuerlein and Pendleton 1971; Secor et al. 1982; Allen et al. 1994) and extremely variable light conditions typical of within-canopy leaves (Pearcy et al. 1990; Pearcy and Seemann 1990; Sassenrath-Cole and Pearcy 1994). Our previous work (Fay and Knapp 1995) showed that soybean leaves growing under full sun field conditions were highly responsive to short-term periods of shade, but that under lower average light conditions typical of within-canopy leaves, stomatal responsiveness to short-term shade periods decreased. A short-term drought during this study allowed us to further examine how water limitation affected these responses to short-term shade, how drought effects might differ with leaf position in the canopy, and if drought effects persisted after the drought was relieved.

Material and Methods

The study was conducted in a cultivated field at the Konza Prairie Research Natural Area near Manhattan, Kansas. Soybeans were grown using standard agronomic techniques in fine, mixed, mesic Typic Argiudoll soils. Photosynthetic and stomatal responses to short-term shade of upper and lower soybean leaves were studied during a natural drought cycle in July and August 1994. Upper leaves were considered to be those at the top of the 0.75-m canopy exposed to unobstructed light. Lower leaves were those 0.5 m or lower in the canopy, experiencing a light regime largely determined by the density and position of higher leaves. Thus, our leaf position effect also contains leaf age and shading history effects, but our goal was to document the position effect through the drought cycle and not to separate these under-

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[1] Abbreviations: A_{CO_2}, net photosynthetic carbon uptake, μmol m^{-2} s^{-2}; A_{O_2}, net photosynthetic O_2 evolution, μmol m^{-2} s^{-2}; C_i, intercelluar CO_2 concentration, μL L^{-1}; E, transpiration, mmol m^{-2} s^{-2}; g_s stomatal conductance to water vapor, mmol m^{-2} s^{-2}; PPFD, photosynthetic photon flux density, μmol m^{-2} s^{-2}; 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.

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

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Table 1 Leaf Temperature (t_{leaf}) and Vapor Pressure Deficit (VPD) Conditions Inside the Cuvette during Measurement of Soybean Leaf Responses to Short-Term Shade Periods

	Sun		Shade	
	t_{leaf}, °C	VPD, kPa	t_{leaf}, °C	VPD, kPa
Upper leaves:				
Day:				
202	32.64 ± 0.33	21.69 ± 0.66	29.86 ± 0.15	21.06 ± 0.41
232	32.43 ± 0.66	26.24 ± 1.32	29.27 ± 0.40	25.11 ± 0.93
239	35.20 ± 0.59	30.98 ± 1.86	33.08 ± 0.40	31.26 ± 1.67
Lower leaves:				
Day:				
202	32.69 ± 0.16	20.41 ± 0.41	29.52 ± 0.14	20.31 ± 0.32
232	36.99 ± 0.44	34.03 ± 1.04	32.50 ± 0.38	31.56 ± 0.79
239	37.56 ± 0.51	35.84 ± 1.66	34.85 ± 0.47	34.91 ± 1.30

Note.   Mean ± SE, by day and leaf position during full sun or shade.

lying mechanisms. The day-long average PPFD levels were 1390 μmol m^{-2} s^{-1} (CV = 26%) for upper leaves and 385 μmol m^{-2} s^{-1} (CV = 103%) for lower leaves. These light levels are comparable to previously published descriptions of soybean canopy light environments (Pearcy et al. 1990). Lower leaves showing signs of chlorosis were not selected for measurement. During the study, pods were filling and the canopy was closed.

Photosynthetic and stomatal responses to short-term shade periods were determined three times during a natural drought cycle: (1) predrought (July 21, day 202) when plants had received 44 mm of rainfall the previous 2 wk, (2) during drought (August 20, day 232) when plants had received only 0.1 mm rainfall the previous 2 wk, and (3) postdrought (August 27, day 239) after plants had received 38 mm of natural rainfall and at least 25 mm of supplemental irrigation (August 25, day 237).

Gas exchange measurements were made during a standard sequence of alternating full sunlight and shade cast with 70 × 70 cm neutral density screens (Fay and Knapp 1993). Measurements were made with a fast-response closed photosynthesis system (LiCor LI-6200, Lincoln, Nebr.) between 1000 and 1500 CDT, the time of maximum photosynthetic rates and RUBISCO activation (McDermitt and Zeiher 1985). Each measured leaf (13–20 cm^2 area) was first fixed to the cuvette and equilibrated to full sunlight for 15 min. The cuvette lid remained open during this equilibration. For lower leaves this required parting the canopy around the cuvette. Leaf gas exchange rates were measured at 1-min intervals for 8 to 10 min to verify equilibration to full sun and lack of thigmotropic responses to repeated measurements. The equilibration period was immediately followed by continued 1-min measurements through three 5-min shade periods (300–400 μmol m^{-2} s^{-1}) each separated by 8-min periods of full sun (PPFD >1700 μmol m^{-2} s^{-1}). Each gas exchange rate determination lasted less than 30 s and the cuvette was opened until the next 1-min measurement interval. This procedure was followed to avoid overheating the leaf and cuvette. Instrument operating parameters were set to minimize excursions in chamber RH. Average leaf temperatures and vapor pressure deficits (table 1) varied generally no more than 3°C and 2 kPa between sun and shade measurements. Some variation between measurement dates in vapor pressure deficits was unavoidable, a result of changes in ambient temperature and plant water status.

A_{CO_2}, Ci, E, and g_s were expressed as means ± 1 SE by averaging the replicate sun-shade-sun sequences (three sequences per leaf, two to four leaves per date/leaf position combination), yielding a single sun-shade-sun response curve. Small samples sizes were acceptable because soybean leaf responses were highly repeatable in this and previous studies (Fay and Knapp 1995). Cumulative carbon gain and water loss during the sun-shade-sun cycle were estimated by summing mean A_{CO_2} and E during the response curve. Mean rates of stomatal closure during each shading were determined from linear regression of g_s versus time in each shade period, based on the linear part of the decrease in g_s. The rate of stomatal opening after onset of full sun was similarly calculated.

Soybean leaf photosynthetic capacity was determined during (day 237) and after (day 238) drought by measuring light response curves with an oxygen electrode (Hansatech S1, Hansatech Ltd., Kings Lynn, Norfolk, U.K.) following methods of Walker (1987). The measurement apparatus consisted of a temperature-controlled chamber that held an oxygen electrode and a 10-cm^2 leaf disk in the gas phase above a 0.5-M sodium bicarbonate CO_2 source. The sodium bicarbonate saturated soybean leaves with 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, which proved adequate to light-saturate soybean leaves under these conditions. System software (Hansatech "Leafdisc") calculated A_{O_2} rates at 30- or 60-s intervals based on the previous 20 s of measured oxygen evolution during preprogrammed illumination sequences.

For measurements, field leaves were collected, immediately sealed in plastic bags with damp paper towels to maintain turgor, and kept in the dark at ambient temperature until measurement in the lab. A 10-cm^2 leaf disk was sealed in the chamber. After equilibration and calibration, illumination was increased each min for 20 min from 0 to 1000 μmol m^{-2} s^{-1} PPFD. Light response curves were measured at 30°C on four leaves per canopy position per measurement day. Photosynthetic capacity was determined from average A_{O_2} at 1000 μmol m^{-2} s^{-1} and quantum requirements from the initial slopes of the light response curves.

ψ_{leaf} was assessed whenever A_{CO_2} or A_{O_2} measurements were made. Leaves growing in full sun at the top of the canopy (n = 5–12) were collected at midday (1200 and 1400 hours), sealed in plastic bags as before, and immediately
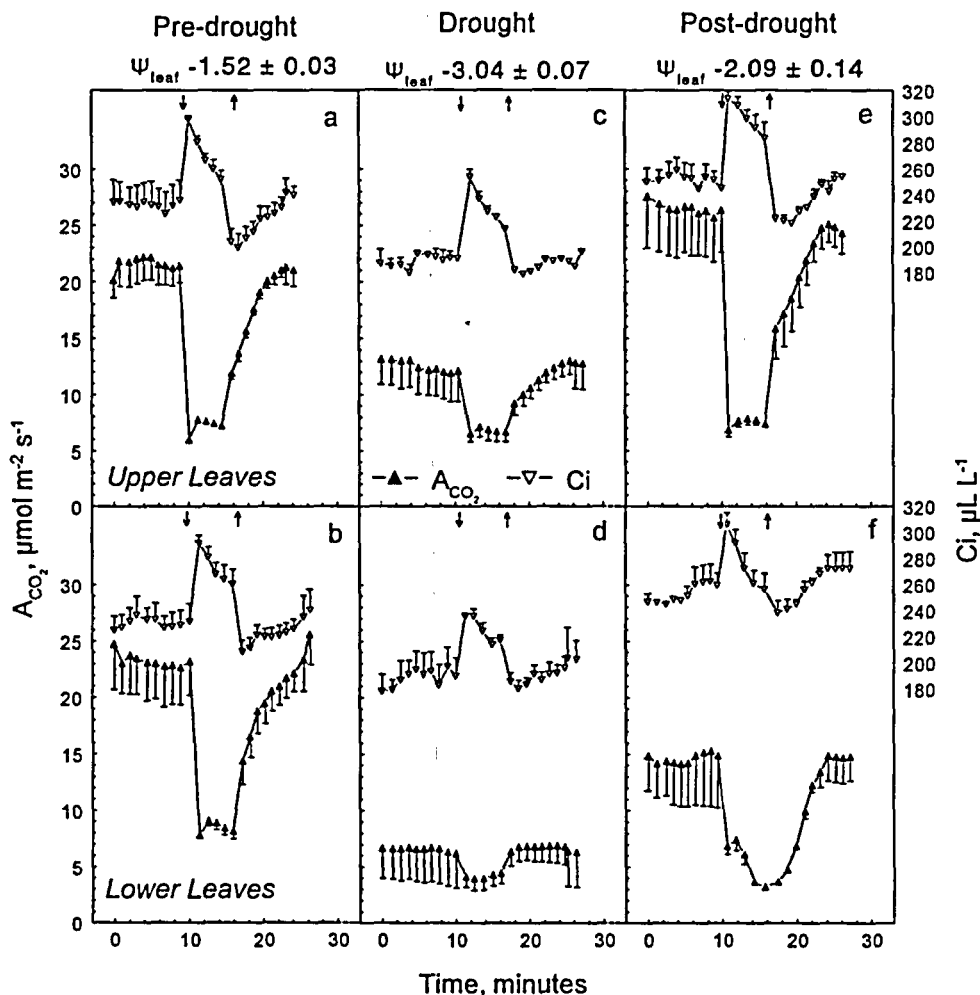
Fig. 1 A_{CO_2} and Ci responses (mean ± SE) to short-term shade for upper and lower soybean leaves during a natural drought cycle. Arrows indicate the beginning and end of shade periods. Missing error bars fell within the symbols.

returned to the lab for measurement in a pressure chamber (PMS-1000, PMS Instruments, Corvallis, Oreg.).

Results

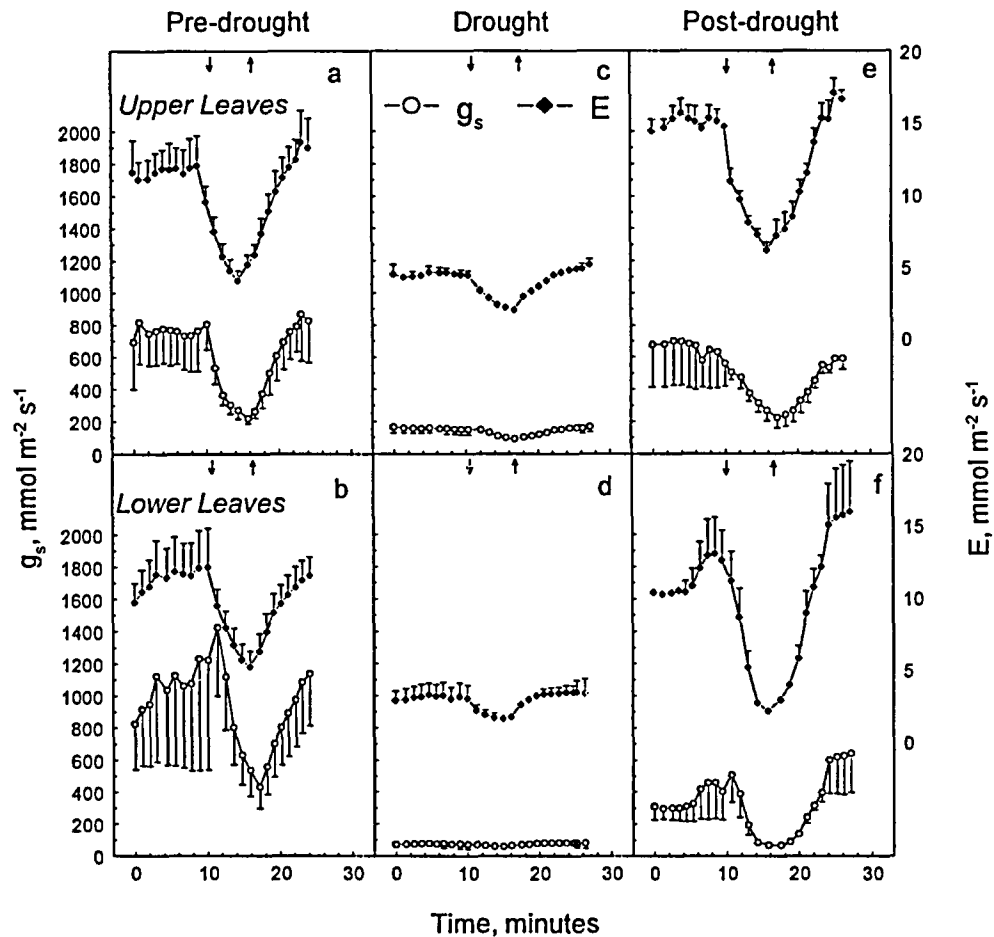### Basic Leaf Responses to Short-term Shade Periods

All soybean leaves showed several basic responses to short-term shade periods, regardless of drought stress or position in the canopy (figs. 1, 2). Shade caused an immediate sharp decrease in A_{CO_2} and sharp increase in Ci (fig. 1), followed by smaller changes as leaves equilibrated to the new PPFD. The E and g_s values (fig. 2) also decreased during shade, but less abruptly than A_{CO_2}. Reillumination reversed these changes. However, A_{CO_2} usually increased more gradually than it had decreased, perhaps because Ci did not recover rapidly. As a result, A_{CO_2} returned to preshade rates generally in parallel with stomatal reopening.

Drought

Scarce rainfall between days 202 and 232 lowered ψ_{leaf} and all full-sun gas exchange parameters (figs. 1–

2). Full sun A_{CO_2}, Ci, g_s, and E values decreased 50% (figs. 1a–d, 2a–d) as plants became drought stressed. As a result, photosynthetic and stomatal responses to short-term shade were strongly restricted compared to predrought responses. For example, shade caused much smaller decreases in A_{CO_2} and E and minimized change in g_s (table 1). On reillumination, all gas exchange parameters recovered to preshade levels within 5–6 min of full sun illumination versus 8–9 min seen in plants prior to drought stress. The net effect of drought stress was to reduce cumulative carbon gain by 53% and cumulative water loss by 65% (table 2) compared to predrought, thus increasing overall WUE.

Rainfall after day 237 increased soybean ψ_{leaf} and full-sun gas exchange parameters (figs. 1c–f, 2c–f), in most cases to predrought rates. This allowed the return of strong photosynthetic and stomatal responses to short-term shade. However, some residual effects of drought remained. Compared to predrought, rates of change in g_s (table 1) were slower in most cases, cumulative carbon gain was 15% less, and cumulative

Fig. 2 g_s and E responses (mean ± SE) to short-term shade for upper and lower soybean leaves during a natural drought cycle. Arrows indicate the beginning and end of shade periods. Missing error bars fell within the symbols.

water loss was 11% greater (table 2), resulting in the lowest overall WUE.

Leaf Position

Leaf position had more subtle effects than drought stress on soybean photosynthetic and stomatal responses to short-term shade. Predrought upper and lower soybean leaves (figs. 1a–b, 2a–b) had nearly indistinguishable responses to shade, except that rates of change in g_s were faster in lower than in upper leaves (table 2). However, upper and lower leaves had

equal cumulative carbon gain and water loss over the course of the sun-shade-sun sequence (table 3).

During drought, lower leaves were more severely impacted than upper leaves (figs. 1c–d, 2c–d). Although upper and lower leaves had equal Ci, lower-leaf A_{CO_2} was 50% of upper-leaf A_{CO_2} throughout the sun-shade-sun cycle. Also, g_s and rates of change in g_s (table 2) were reduced in lower versus upper leaves, and E was slightly reduced. Overall cumulative carbon gain, water loss, and WUE (table 3) were reduced in lower leaves.

Table 2 Rates of Stomatal Opening and Closing during Experimental Sun-Shade-Sun Cycles (mmol m^{-2} s^{-2} min^{-1}, ± SE) for Upper and Lower Soybean Leaves

	Predrought		Drought		Postdrought	
	Closing	Opening	Closing	Opening	Closing	Opening
Upper	56.24 ± 16.09	55.72 ± 33.98	12.52 ± 2.59	9.37 ± 0.77	41.16 ± 7.88	59.02 ± 11.29
Lower	78.01 ± 44.53	78.18 ± 29.42	3.89 ± 0.94	4.89 ± 1.20	48.83 ± 16.70	123.48 ± 26.98*

Note. Predrought (day 202) while drought stressed (day 239) and postdrought (day 239).
* Significant (at 0.05) difference between closing and opening by two-sample t-test.

Table 3 Cumulative Photosynthetic Carbon Gain (A_{CO_2}, μmol m^{-2} s^{-2}), Transpirational Water Loss (E, mmol m^{-2} s^{-2}), and Water Use Efficiency (A_{CO_2}/E) for Upper and Lower Soybean Leaves Predrought (day 202) While Drought Stressed (day 237) and Postdrought (day 239)
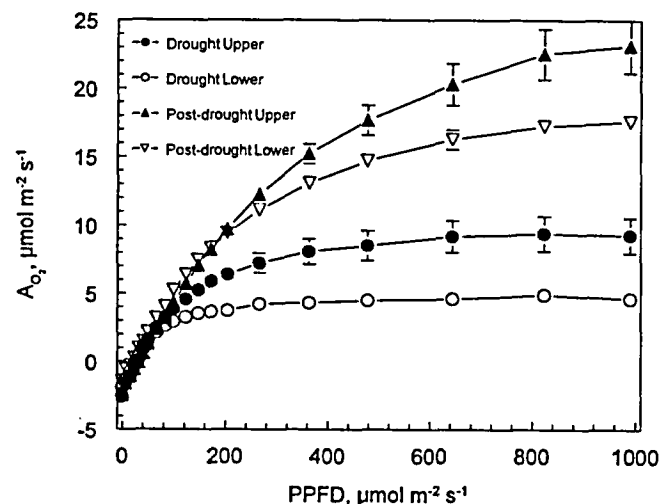
	Predrought			Drought			Postdrought		
	A_{CO_2}	E	WUE	A_{CO_2}	E	WUE	A_{CO_2}	E	WUE
Upper	411.99	234.41	1.75	262.87	95.23	2.76	465.41	291.68	1.59
Lower	452.72	237.37	1.91	147.16	69.01	2.13	268.42	233.60	1.15

Note. Cumulative values are simple sums of the gas-exchange rates measured during the sun-shade-sun photosynthesis and transpiration curves in fig 1 and 2.

Residual negative effects of drought after rainfall were much stronger in lower than in upper leaves (figs. 1e–f, 2e–f). Despite equal Ci in upper and lower leaves, lower-leaf A_{CO_2} failed to recover to predrought rates. Rates of stomatal opening were higher than rates of closing for lower leaves (table 2), but since g_s was still comparatively low, stomatal closure caused a large decrease in A_{CO_2} during shade that was not observed in upper leaves. Photosynthetic recovery was delayed in lower versus upper leaves. Upper leaves regained 50% of full sun A_{CO_2} in the first minute of reillumination compared to a slight A_{CO_2} increase in lower leaves. Combined, these changes caused lower leaves to have the lowest overall WUE of the study.

Photosynthetic capacity

The effects of leaf position and drought stress on CO_2-saturated A_{O_2} (fig. 3) corroborated field photosynthetic CO_2-uptake rates. A_{O_2} was low during drought and increased after rainfall. Regardless of drought stress, upper leaves had higher CO_2- and PPFD-saturated A_{O_2}, but leaf position had less effect than drought. Quantum requirements were unaffected by leaf position or drought stress (table 4).

Discussion

Leaf-level gas exchange in soybean responded to short-term shade periods like other fast-growing herbaceous species (Fay and Knapp 1996). The onset of shade caused immediate large reductions in A_{CO_2}, followed by stomatal closure and reduced E. The return of full sun reversed these changes, with the important difference that in most cases, photosynthetic recovery was delayed so that A_{CO_2} returned to full-sun values generally in parallel with stomatal reopening. Soybean's rapid stomatal closure compared to other species and delayed photosynthetic recovery helps maintain WUE during short-term shade by minimizing E while carbon gain is low (Knapp and Smith 1989; Fay and Knapp 1995, 1996).

Drought

After two weeks of essentially no rain, soybean responses to short-term shade changed in several respects. Full-sun A_{CO_2} and E were much lower; short-term shade caused smaller reductions in A_{CO_2} and E but, unexpectedly, virtually no stomatal closure. Most studies have found increased stomatal responsiveness to short-term shade at lower ψ_{leaf} (Davies and Kozlowski 1975; Barradas et al. 1994; Jones et al. 1995). Constant g_s during short-term shade cycles would be expected in woody species, species with low overall A_{CO_2}, or in plants experiencing little water stress (Knapp and Smith 1989; Fay and Knapp 1996).

Jones et al. (1995) suggested that stomata should be most responsive to shading during early phases of drought stress prior to complete stomatal closure. In this study, drought stress-induced stomatal closure appeared to have progressed to where stomata were unable to close further in response to shade. The precedence of the drought response over the short-term shade response exemplifies how reductions in one

Fig. 3 CO_2-saturated A_{O_2} light response curves (mean ± SE) for upper and lower soybean leaves during drought (day 237) and during postdrought after rainfall (day 238). Missing error bars fell within the symbols.

Table 4 Quantum Yields (μmol O_2 per μmol photons) of Upper and Lower Soybean Leaves While Drought Stressed (day 237) and during Recovery after Rainfall (day 238)

	Drought	Postdrought
Upper	0.078 ± 0.008	0.071 ± 0.003
Lower	0.071 ± 0.007	0.068 ± 0.007

Note. Leaf position, water status, and their interaction all $P > 0.45$ by two-way ANOVA.

plant resource can change plant responses to variation in another resource (Osmond 1983).

When relieved from drought stress, soybean leaves partially regained their predrought photosynthetic and stomatal responses to short-term shade. However, post-drought short-term shade responses were less effective than predrought responses at maximizing WUE. For example, compared to predrought, E was higher, overall WUE was lower, and stomatal response rates were slower after drought. Such persistent effects of drought indicate weakened stomatal control of E and possibly greater delays in photosynthetic recovery after short-term shade. Increased ABA concentrations that result from drought can cause stomatal closure (Davies et al. 1990), but ABA impacts on stomatal responses to variable light are unknown.

Leaf Position

Upper leaves fared better than lower leaves during the drought cycle. For example, cumulative carbon gain of upper leaves (table 3) was depressed during drought but fully recovered after water availability was restored. In contrast, carbon gain in lower leaves was more severely depressed by drought than in upper leaves, and lower leaves only partially recovered post-drought. A combination of factors is likely responsible for the more severe effects of drought on lower leaf carbon gain during short-term shade. First, lower leaves may be older than upper leaves, and leaf aging typically lowers photosynthetic capacity and stomatal conductance (Field 1987). Second, lower leaves occupy a more shaded light environment than when they initially developed. Shading also lowers photosynthetic capacity and stomatal conductance (Boardman 1977) and may exacerbate the aging process (Field 1987). The combined effects of age and increased shading appear to have degraded the photosynthetic and stomatal responses of lower leaves to the short-term shade light regimes they experienced earlier in their development.

Upper and lower soybean leaves experienced dif-ferent limitations on carbon gain during short-term shade cycles. For example, lower leaves appeared to have greater nonstomatal limitation of A_{CO_2} than did upper leaves during drought, because lower leaves had lower full-sun A_{CO_2} than did upper leaves at the same full-sun Ci (Lauer and Boyer 1992). Greater nonstomatal limitation of A_{CO_2} in lower leaves appeared to remain postdrought. The Ci value returned to pre-drought levels in both upper and lower leaves, but lower leaf A_{CO_2} remained at half of upper leaf rates. These patterns are supported by the lower CO_2-saturated A_{O_2} rates in lower leaves compared to upper leaves, by previous studies of soybean photosynthetic recovery from short-term shade (Fay and Knapp 1995), and by studies of soybean induction kinetics (Pearcy and Seemann 1990; Sassenrath-Cole and Pearcy 1994).

Conclusion

Drought stress had two major effects on soybean leaf photosynthetic and stomatal responses to short-term shade. First, typical responses to short-term shade were suppressed by drought but recovered within a few days of rewatering. Second, lower canopy leaves were less effective at responding to short-term shade after drought. Soybeans frequently encounter periods of drought and variable sunlight regimes. As a result, leaf-level photosynthetic and stomatal responses to drought and shade individually and in combination may have important consequences for whole-plant carbon gain, growth, and reproductive success (Givnish 1988).

Acknowledgments

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