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Effects of Water Deficit on Biomass Accumulation and Water Use Efficiency in Soybean during Vegetative Growth Period

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Water deficit is the primary constraint of soybean [*Glycine max* (L.) Merr.] yield, and a physiological understanding of processes affected by water deficit is a key step in identifying and improving drought tolerance in soybean. The objectives of this research were to evaluate biomass and nitrogen accumulation patterns and water use efficiency (WUE) as possible mechanisms associated with the drought tolerance of Jackson. Biomass accumulation of Jackson was contrasted with the PI416937, which also has demonstrated tolerance to drought. For water-deficit trea- tment, total biomass accumulation was negligible for PI416937, but biomass accumulation continued at approximately 64% of the well-watered treatment of Jackson. Transpirational losses for Jackson and PI416937 were approximately the same for the water-deficit treatment, indicating that Jackson had superior WUE. Isotopic discrimination of ^{13}C relative to ^{12}C also indicated that Jackson had higher WUE. Results indicated that increased WUE for Jackson under water deficit showed it was tolerant to drought rather than had an avoidance mechanism.

Key words : soybean, water deficit, biomass, water use efficiency, carbon isotope discrimination.

Water deficit is the physiological limiting factor for soybean [*Glycine max* (L.) Merr.] production (Cooper *et al.*, 1991; Jin *et al.*, 1997). Sall and Sinclair (1991) identified the cultivar Jackson as water-deficit tolerant for N_2 fixation. Unlike other genotypes, N_2 fixation in Jackson during water deficits was unaffected until other physiological processes, such as transpiration, were also affected. Patterson and Hudak (1996) reported that PI416937 also had higher rates of N_2 fixation for a water-deficit treatment during the seed filling period compared to 'Forrest', and this resulted in higher yield under water deficits for PI416937 than Forrest.

The physiological basis for superior N_2 fixation during water deficits for Jackson or PI416937 is not quite clear. The higher rates of biomass accumulation during water deficit period for Jackson (Sall and Sinclair, 1991) or PI416937 (Patterson and Hudak, 1996) compared to other genotypes may be due to a higher water use efficiency (WUE; i. e., mg biomass produced per g water transpired), assuming that transpirational losses are similar among genotypes.

Instantaneous values of water use efficiency (WUE) based on leaf gas exchange properties depend on the gradient of CO_2 concentration from the atmosphere (C_a) to the inside of the leaf (C_i) divided by the water vapor pressure gradient from inside the leaf (e_i) to the atmosphere (e_a) (Farquhar and Richard, 1984; Ehleringer *et al.*, 1991; Ismail and Hall, 1993). This relationship may be described by the equation:

$$WUE = [C_a \cdot (1-C_i/C_a)] / [1.6 \cdot (e_i-e_a)] \qquad (1)$$

The constant in the denominator of equation (1) accounts for differences in gas diffusivities of water vapor and CO_2. Increases in WUE, therefore, may be gained by either decreasing the C_i to C_a ratio or decreasing the water vapor pressure gradient from leaves to the atmosphere.

In C3 plants, WUE is also related to the isotopic discrimination of ^{13}C relative to ^{12}C (Farquhar *et al.*, 1982). The magnitude of the discrimination (Δ, ‰) is due to differences in diffusivity of $^{13}CO_2$ and $^{12}CO_2$ (a, approximately 4.4‰), discrimination by RUBP carboxylase (b, 27‰), and the ratio of C_i to C_a (Farquhar *et al.*, 1982):

$$\Delta = a + (b - a) \cdot (C_i/C_a) \qquad (2)$$

Therefore, provides an integrated value of C_i/C_a over the life of the plant and is inversely related to WUE.

In this research the physiological basis for superior N_2 fixation of Jackson during water deficit was explored. It was hypothesized that the sustained biomass production of Jackson during water deficit period was due to a high WUE. This water-deficit tolerant genotype Jackson was compared to the soybean PI416937, which has delayed wilting, leaf osmotic adjustment, and higher leaf relative water content

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(RWC) under water-deficit condition than Forrest (Sloane *et al.*, 1990).

MATERIALS AND METHODS

Cultural details

Two genotypes of soybean, Jackson and PI416937, were evaluated for the response of their biomass and nitrogen accumulation, leaf area development, and water use efficiency to water deficits. These genotypes represented putative tolerance to water deficit. Seeds of Jackson and PI416937 were sown in November 18, 1995 in 15 cm diameter pots, with a volume of approximately 1.9 L, in a greenhouse at Fayetteville, Arkansas (latitude 36° 5'N). The potting mixture was a N-free peat, perlite, and vermiculite media obtained from Sun Gro Horticulture Inc., 1830 Knob Hill, Garland, TX75403. The potting mixture was inoculated with *Bradyrhizobium japonicum* (USDA 110) at the time of sowing. Natural illumination was supplemented with 1000 W metal halide lamps for a day length of 15 h.

Pots were weighed at 0900 h each day, and well-watered (control) plants were maintained at 70% of their pot capacity weight (FTSW=0.58) by rewatering daily until initiation of water-deficit treatments. At the V6 growth stage (Fehr and Caviness, 1977), half the plants were allowed to dry until the pot weight was 36% of the pot capacity weight (FTSW= 0.11). One day after all pots were at the target weight, half of the plants were harvested (Harvest 1). Pots for the remaining plants were sealed inside plastic bags to minimize evaporative losses. Plants were maintained at the target weight for an additional 14 days and harvested (Harvested 2), and transpiration was calculated gravimetrically per plant on a daily basis.

Measurements of biomass and shoot-N content

On each harvesting date, plants were separated into leaves, stems, roots, and nodules. Plant tissue was dried at 65°C for a minimum of 48 h and weighed. Leaves, stems, and petioles were bulked and ground to pass a 0.425-mm sieve. Total N in the ground shoot was determined on a 100 mg subsample by the Dumas method (Bergersen, 1980) with a Leco FP-228 determinator (Leco Corp., St. Joseph, MI) at the Soil Testing/Plant Analysis Laboratory, University of Arkansas. Relative water content (RWC) and specific leaf weight (SLW) were determined at each harvest.

Carbon isotope discrimination (Δ)

Carbon isotope composition ($\delta^{13}C$), the $^{13}C/^{12}C$ ratio relative to the PeeDee Belemnite standard, was determined on each sample with mass spectroscopy by Isotope Services, Inc. (Los Alamos, NM). The carbon isotopic composition values were converted to carbon isotope discrimination (Δ) as described by Hubick *et al.* (1986) assuming a $^{13}C/^{12}C$ ratio for air of -8.00‰ relative to the PeeDee standard. Discrimination can be defined in terms of δ notation as;

$$\Delta = (\delta_a + \delta_p) / (1 + \delta_p) \qquad (3)$$

where subscripts a and p refer to atmospheric CO_2 (source) and plant material (product), respectively.

Nitrogenase activity

Nitrogenase activity was determined on intact, excised roots in a closed system by the acetylene reduction assay. Ethylene concentration in the gas samples was quantified with a Vista 6000 gas chromatography (Varian, Walnut Creek, CA) equipped with a flame ionization detector and a 2 m poropak N column.

Photosynthesis

One and four days after plants had reached their target pot weights, photosynthesis was measured at midday on the center leaflet of the uppermost fully expanded trifoliate leaf. Measurements were made with a LI-COR 6200 (LI-COR, Inc., Lincoln, NE) photosynthesis system with pots positioned under a 1000 W metal halide lamp, providing a minimum PAR flux density at the leaf surface of 900 $\mu mol\ m^{-2}\ s^{-1}$.

Experimental design and statistical analysis

This experiment was a split-plot arrangement of treatments in a randomized complete block design with four replications. Times of harvest were the main plots and subplots were a factorial arrangement of genotypes and water-deficit treatments. Data were analyzed by harvest, and significant differences were based on the least significant difference ($P \leq 0.05$). Genotypic responses to water deficits between harvests were evaluated by linear regression (Purcell and King, 1996).

RESULTS

Biomass accumulation

Shoot, root and total dry weights of water-deficit PI416937 at 15-day after treatment initiation (harvest 2) was similar to that of 1-day after treatment initiation (harvest 1) (Table 1). In contrast, dry weight for Jackson tended to increase between harvest 1 and harvest 2. Shoot nitrogen content followed a trend similar to shoot biomass accumulation between harvest 1 and harvest 2 (Table 1). Water deficit decreased shoot dry weight and shoot nitrogen content of both genotypes at harvest 2 (Table 1). Nodule dry weight was decreased in water-deficit plants of both genotypes (Table 1). Nodule dry weight of water-deficit plants at harvest 2 ranged from 70.6% to 73.3% of well-watered plants (Table 1).

Change of acetylene reduction activity (ARA) between harvest 1 and harvest 2 was similar for water-deficit and well-watered treatments of Jackson (Table 2). However, in

Table 1. Dry weight for each part of plant and shoot nitrogen content for water-deficit (WD) and well-watered (WW) treatments of Jackson and PI416937 at harvest 1 and harvest 2.

Harvest	Genotype	Treat	Dry weight				Shoot-N content
			Shoot	Root	Nodule	Total	
			---g plant^{-1}---		mg plant^{-1}	mg plant^{-1}	mg plant^{-1}
1	Jackson	WD	2.49	0.82	170.85	3.48	81.6
		WW	2.96	0.89	192.85	4.04	91.8
	PI416937	WD	3.49	1.13	206.05	4.83	126.5
		WW	3.27	0.91	181.93	4.36	122.8
	LSD (0.05)[†]		0.61	0.48	50.05	1.04	21.4
2	Jackson	WD	3.23	1.38	152.23	4.76	95.0
		WW	4.34	1.61	215.50	6.16	132.8
	PI416937	WD	3.17	1.29	182.98	4.65	95.5
		WW	5.36	1.54	249.78	7.15	182.3
	LSD (0.05)		1.38	0.60	58.77	1.97	40.7
Dif.[‡]	Jackson	WD	0.74	0.56	-18.62	1.28	13.4
		WW	1.38	0.72	22.65	2.12	41.0
	PI416937	WD	-0.32	0.16	-23.07	-0.18	-31.0
		WW	2.09	0.63	67.85	2.79	59.5

[†] LSD is for comparison of means within a harvest day.
[‡] subtract harvest 1 from harvest 2.

Table 2. Acetylene reduction activity, nodule activity, leaf area, relative water content (RWC) and specific leaf weight (SLW) for water-deficit (WD) and well-watered (WW) treatments of Jackson (J) and PI416937 (PI) at harvest 1 and harvest 2.

Harv.	Geno-type	Treat	Acetylene reduction	Nodule activity	Leaf area	RWC	SLW
			μmol plant^{-1} h^{-1}	μmol^{-1}	cm^2 plant^{-1}	%	mg cm^{-2}
1	J	WD	23.22	0.14	390	91.3	2.36
		WW	37.23	0.20	483	92.3	2.43
	PI	WD	24.24	0.12	719	90.5	2.09
		WW	31.23	0.18	701	93.8	2.02
	LSD (0.05)[†]		9.98	0.04	162	3.1	0.31
2	J	WD	10.50	0.03	633	90.1	2.85
		WW	24.61	0.12	1013	93.3	2.51
	PI	WD	10.95	0.04	596	89.8	3.01
		WW	23.52	0.09	1327	91.9	2.31
	LSD (0.05)		12.15	0.03	307	ns	0.50
Dif.[‡]	J	WD	-12.72	-0.11	243	-1.2	0.49
		WW	-12.62	-0.08	530	1.0	0.08
	PI	WD	-13.29	-0.08	-123	-0.7	0.92
		WW	-7.71	-0.09	626	-1.9	0.29

[†] LSD is for comparison of means within a harvest day.
[‡] subtract harvest 1 from harvest 2.

Table 3. Regression analysis and the relative increase of shoot biomass, total biomass, and shoot nitrogen between harvests for water-deficit (WD) and well- watered (WW) treatments.

Dependent variable	Genotype	Trt	R^2	Slope ± SE	Intercept ± SE	Relative† increase ± SE
				g plant^{-1} d^{-1}	g plant^{-1}	%
Shoot biomass	Jackson	WD	0.71**‡	0.06 ± 0.01	2.4 ± 0.2	30 ± 3
		WW	0.65*	0.11 ± 0.03	2.9 ± 0.3	47 ± 11
	PI416937	WD	0.00^{ns}	0.00 ± 0.02	3.5 ± 0.2	-1 ± 6
		WW	0.63*	0.16 ± 0.05	3.1 ± 0.5	64 ± 20
Total biomass	Jackson	WD	0.70**	0.10 ± 0.03	3.38 ± 0.26	37 ± 4
		WW	0.57*	0.16 ± 0.06	3.88 ± 0.58	53 ± 15
	PI416937	WD	0.07^{ns}	0.02 ± 0.03	4.81 ± 0.28	5 ± 7
		WW	0.63*	0.21 ± 0.07	4.15 ± 0.67	64 ± 20
				mg plant^{-1} d^{-1}	mg plant^{-1}	%
Shoot N	Jackson	WD	0.40^{ns}	1.04 ± 0.52	80 ± 5	16 ± 4
		WW	0.65*	3.19 ± 0.95	88 ± 9	45 ± 10
	PI416937	WD	0.44^{ns}	-1.76 ± 0.88	128 ± 8	-18 ± 6
		WW	0.57*	4.58 ± 1.63	118 ± 16	45 ± 17

†Relative increase : the difference between harvests divided by average at harvest 1, multiplied by 100.

^{ns}, *, and ** indicate nonsignificance and significance at the 0.05 and 0.01 levels, respectively, for the regression equation as determined by an *F*-test.

PI416937, great reduction of ARA was observed in water-deficit treatment as compared to well-watered treatment (Table 2). ARA of water-deficit plants relative to well-watered plants ranged from 62 to 78% at harvest 1, and from 43 to 47% at harvest 2 (Table 2). At harvest 1, acetylene reduction on a plant basis was decreased in water-deficit treatment for Jackson and PI416937 in comparison to well-watered treatment, due to decreased nodule activity for drought stress treatment rather than decreased nodule mass (Table 1 and 2). In contrast, at harvest 2, the decreased acetylene reduction in drought stressed plants was due to a decrease of both nodule mass and nodule activity (Table 1 and 2).

Change of relative water content (RWC) to water deficit between harvests was similar for Jackson and PI416937, and the reduction due to water deficit was small (Table 2). RWC of water-deficit plants was greater than 96% of well-watered plants at both harvests (Table 2). Despite of the small changes in RWC, there were large genotypic differences in plant growth responses to water deficit. Leaf area between harvests for the water-deficit treatment increased 243 cm^{2}plant^{-1} (62%) for Jackson and decreased 123 cm^{2}plant^{-1} (-12%) for PI416937 (Table 2). For PI416937, the decrease in leaf area was associated with both decreased leaf production and increased leaf senescence. Associated with decreased leaf area was an increase in specific leaf weight (SLW) of the water-deficit treatment between harvests of 0.49 mg/cm^2 (21%) for Jackson and 0.92 mg/cm^2 (44%) for PI416937 (Table 2). It was evident that plasma membrane of leaf cells became thicker and more compressed at the water-deficit condition, as it covers a smaller area than before.

Regression of shoot nitrogen versus days for the water-deficit treatment was nonsignificant for both genotypes (Table 3). The relative increase in shoot nitrogen between harvests, however, was significantly greater for the water-deficit treatment of Jackson (16%) than the water-deficit treatment of PI416937 (-18%).

The total biomass accumulation rate for the water-deficit treatment was approximately five times greater for Jackson than for PI416937 (Table 3). The greater biomass accumulation for the water-deficit treatment of Jackson compared to PI416937 may be associated with similar transpirational losses for well-watered plants of Jackson and PI416937.

Water use efficiency (WUE) and nitrogen use efficiency (NUE)

There was no significant differences between genotypes in the minimum fraction of transpirable soil water (FTSW) values on any given day (Fig. 1). These data indicate that, for the water-deficit treatment, the amount of water available for transpiration, growth, and dry matter production was similar for both genotypes. Therefore, as an estimate of WUE between harvests, biomass was regressed against cumulative water transpired between harvests (i.e., water loss at harvest 1 was 0 cumulative water loss) (Table 4).

The greater biomass accumulation per gram of water tran-

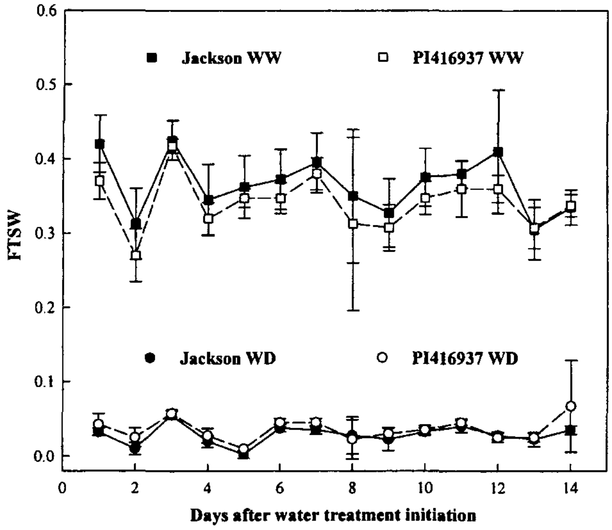

Fig. 1. Changes in fraction of transpirable soil water (FTSW) during water treatment period of Jackson and PI416937.

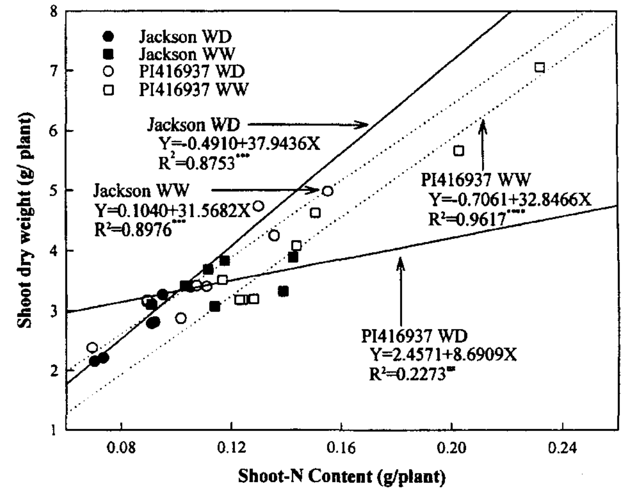

Fig. 2. Relationships betweens shoot dry weight and shoot nitrogen content for 14 days after water treatment initiation of Jackson and PI416937.

spired for the water-deficit treatment of Jackson compared to PI416937 indicated a greater WUE of Jackson. Shoot WUE, total WUE, and shoot nitrogen WUE (mg N g^{-1} water) were similar for Jackson under water-deficit and well-watered treatments. Shoot WUE, total WUE, and shoot nitrogen WUE were also similar for Jackson and PI416937 in the well-watered treatment. In contrast, there was no significant accumulation of shoot biomass, total biomass, and shoot nitrogen per gram of water transpired for PI416937 in the water-deficit treatment. The negative slope of shoot biomass and shoot nitrogen versus transpired water for the water-deficit treatment of PI416937 may be due to senesced leaves that were not collected and included in the analysis.

As an estimate of nitrogen use efficiency (NUE) between harvests, shoot biomass was regressed against shoot nitrogen content. NUE was the highest for water-deficit Jackson at 37.9 g/g (Fig. 2). Well-watered Jackson and PI416937 were similar at 31.6 and 32.9 g/g, respectively. The Lowest NUE was for water-deficit PI416937 at 8.7 g/g, due to a decrease of both shoot biomass and shoot nitrogen content (Table 1).

Carbon isotope discrimination (Δ)

As an integrated measure of WUE during the treatment period, Δ was compared between genotypes and water treat-

Table 4. Regression analysis of shoot biomass, total biomass, and shoot nitrogen against cumulative water transpired during treatment period.

Dependent variable	Genotype	Treat	R^2	Slope ± SE	Intercept ± SE
				$water^{-1}$ $plant^{-1}$	$plant^{-1}$
Shoot biomass	Jackson	WD	$0.71^{**\dagger}$	0.90 ± 0.23	2.5 ± 0.1
		WW	0.76^{**}	0.70 ± 0.16	2.9 ± 0.2
	PI416937	WD	0.01^{ns}	-0.06 ± 0.34	3.5 ± 0.2
		WW	0.70^{**}	0.90 ± 0.24	3.2 ± 0.4
Total biomass	Jackson	WD	0.71^{**}	1.59 ± 0.41	3.5 ± 0.2
		WW	0.68^{**}	1.10 ± 0.31	4.0 ± 0.5
	PI416937	WD	0.08^{ns}	0.33 ± 0.50	4.8 ± 0.3
		WW	0.70^{**}	1.20 ± 0.32	4.3 ± 0.6
Shoot N	Jackson	DR	0.41^{ns}	0.02 ± 0.01	0.08 ± 0.00
		WW	0.73^{**}	0.02 ± 0.01	0.09 ± 0.01
	PI416937	DR	0.44^{ns}	-0.03 ± 0.01	0.13 ± 0.01
		WW	0.64^{*}	0.03 ± 0.01	0.12 ± 0.01

$^{\dagger ns}$, *, and **indicate nonsignificance and significance at the 0.05 and 0.01 levels, respectively, for the regression equation as determined by an F-test.

Table 5. Analysis of variance for the effects of carbon isotope discrimination (Δ).

Source	DF	MS
Model	13	2.94**[†]
Replication	3	0.42*
Harvest time (A)	1	0.07
Error a	3	
Genotype (B)	1	3.83**
Water treatment (C)	1	22.69**
B×C	1	0.01
A×B	1	0.66*
A×C	1	7.05**
A×B×C	1	0.31
Error b	17	

[†]ns, *, and **indicated nonsignificance and significance at the 5% and 1% levels, respectively.

Table 6. Carbon isotope discrimination (Δ) for water-deficit and well-watered treatments of Jackson and PI416937 at harvest 1 and harvest 2.

Treatment	Harvest 1[†]		Harvest 2	
	Jackson	PI416937	Jackson	PI416937
	‰			
Water-deficit	20.5±0.52[§]	21.5±0.23	20.1±0.31	20.1±0.85
Well-watered	21.4±0.41	22.3±0.13	22.6±0.80	23.1±0.50
LSD (0.05)[‡]	0.5		0.5	

[†] Harvest 1 : 1 day after treatment initiation, Harvest 2 : 15 days after treatment initiation.

[‡] LSD is for comparison of means within a harvest day.

[§] Values are the mean se (n=4).

ments. Analysis of variance of Δ data indicated a significant main effects of genotype and water treatment, and a highly significant harvest by water treatment interaction (Table 5). The main effect of genotype was a lower Δ for Jackson compared to PI416937, which indicates a higher WUE for Jackson. At the day 1 harvest, Δ was lower for the water-deficit treatment of both genotypes compared to the well-watered treatment, and Δ was lower for Jackson than PI416937 within water-deficit and well-watered treatments. At harvest 2, Δ was significantly less for the well-watered treatment of Jackson compared to PI416937, and for the water-deficit treatment, Δ was lower than the well-watered treatment for both genotypes (Table 6).

Because transpiration was not measured prior to imposition of water treatments, it was not possible to compare directly the relationship between WUE from germination to harvest and Δ. As a relative indicator of the relationship between WUE and Δ, the total biomass of plants at harvest 2 was divided by the water transpired between harvests and plotted against Δ (Fig. 3). Therefore, the ordinate is a measure of WUE that is overestimated by the amount of water transpired prior to harvest 1. This analysis assumes that WUE, prior to imposition of the water treatments, was approximately the same for all plants. Fig. 3 clearly indicates that WUE was increased by the water-deficit treatment, and that WUE was negatively associated with Δ.

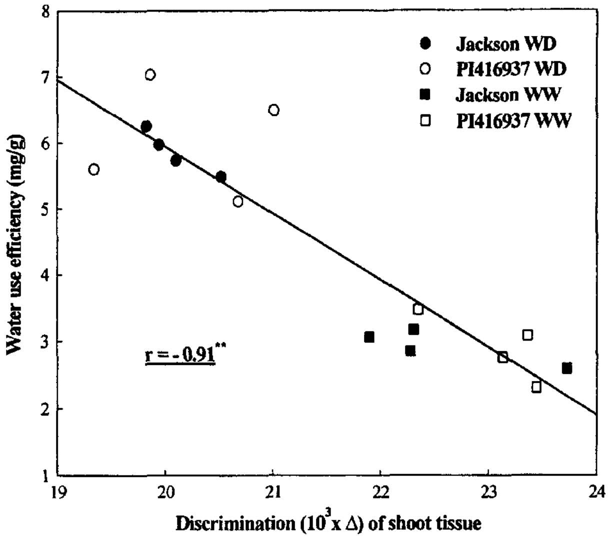

Fig. 3. Correlation between carbon isotope discrimination (Δ) of shoot tissue and water use efficiency.

These data indicate that water deficit increased WUE in both genotypes and that WUE was greater for Jackson than PI416937 in the well-watered treatment. Although the net production of biomass between harvests was negligible for the water-deficit treatment of PI416937 due to leaf abscission, new biomass produced apparently differed in Δ.

Relationships between intercellular and ambient CO_2 concentrations

In comparison with the well-watered treatment, stomatal conductance on days 1 and 4 after water treatment initiation were decreased for the water-deficit treatment for both genotypes, and photosynthesis for the water-deficit treatment was decreased on day 4 but not on day 1 for both genotypes. A comparison of the ambient CO_2 (C_a) concentration versus the internal leaf CO_2 (C_i) over a wide range of C_a values indicated a consistently lower C_i/C_a for the water deficit compared to the well-watered treatment, regardless of genotype (Fig. 4). A smaller C_i/C_a indicates an increased gradient in the CO_2 concentration from the inside to the outside of the leaf, which should result in increased WUE.

DISCUSSION

Tolerance to water deficits for Jackson (Sall and Sinclair, 1991; Serraj and Sinclair, 1996) was confirmed in compari-

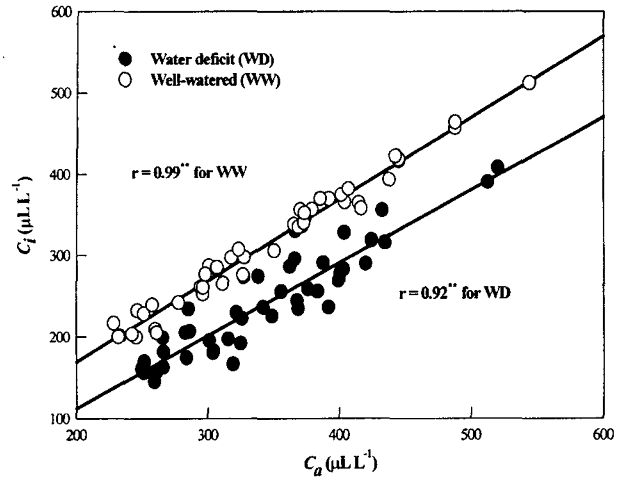

Fig. 4. Correlations between intercellular (C_i) and ambient (C_a) CO_2 concentrations measured in different water treatment plots.

sons with PI416937. There was no indication that PI416937 had a higher RWC for the water-deficit treatment compared to Jackson (Table 2), agreed with other reports in PI416937 from greenhouse experiments (Goldman *et al.*, 1989). Compared to Jackson during vegetative growth period, PI416937 was more sensitive to water deficit for biomass accumulation rates (Table 3). Importantly, differences between Jackson and PI416937 were observed under conditions that ensured similar amounts of soil water (Fig. 1). Therefore, PI416937 may avoid drought by superior rooting patterns (Hudak and Patterson, 1995) and it may have the ability of roots to grow and extract water from high Al soils and subsoils (Goldman *et al.*, 1989).

In response to water deficit, Jackson and PI416937 had similar transpirational losses, but Jackson accumulated considerably more biomass, resulting in a higher WUE. Carbon isotope discrimination (Δ) on harvest 1 also indicated a higher WUE for the water-deficit treatment of Jackson compared to PI416937 (Table 6). According to Levitt's (1980) hierarchy of comparative stress responses, dehydration avoidance is characterized by preventing a stress from occurring, and dehydration tolerance is characterized by the ability to continue physiological activity during a stress. The significance of higher WUE for the water-deficit treatment for Jackson was that it indicates tolerance to drought rather than an avoidance mechanism. Increased soil water extraction of PI416937 might be important in field environments in postponing water deficit, but this trait might be of less importance in environments where the rooting volume was restricted, such as in a pot. These results were in agreement with the conclusion of Patterson and Hudak (1996) that PI416937 avoided droughts. Mian *et al.* (1996) also reported that WUE of PI416937 was considerably lower than Young, and that PI416937 avoided rather than tolerated droughts.

The relationship between Δ and WUE observed in the greenhouse often is not found in field environments (Turner, 1993), and the significance of values must be interpreted with caution. Jackson, however, also had greater rates of biomass and nitrogen accumulation under water deficit relative to several other genotypes in field experiments (Sall and Sinclair, 1991; Serraj *et al.*, 1997) at similar levels of soil moisture. This provides evidence that increased WUE for Jackson may also be important in field drought situation.

The superior tolerance of N_2 fixation to water deficit found in Jackson represents an important genetic resource. Serraj and Sinclair (1996) found that tolerance of N_2 fixation under water deficit condition was present in one parent of Jackson (Volstate) but not in the other (Palmetto), indicating that this might be a heritable trait. Combining drought tolerance of N_2 fixation with avoidance mechanisms may be an important means of improving non-irrigated soybean production.

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