

Paraheliotropic Leaf Movements in Common Bean under Different Soil Nutrient Levels

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ABSTRACT

The primary objective of this study was to investigate the possible physiological consequences of paraheliotropic leaf movements in response to soil nutrient levels in well-watered common bean (*Phaseolus vulgaris* L. cv. Cahone). In pot-grown plants, leaflets from low-fertilizer treatment (LF) plants oriented away from the sun's direct rays, receiving a significantly lower photosynthetic photon flux density (PPFD) than leaflets from high-fertilizer treatment (HF) plants. Leaf conductance and transpiration rate were significantly lower in LF treatment plants than in HF plants. Interactions among incident PPFD, transpiration rate, and leaf area resulted in equivalent leaf temperatures under different fertilizer levels. Leaf water potential was not significantly different between these treatments. Carbon isotope discrimination of HF plants was significantly lower than that of LF plants, indicating that intercellular CO₂ concentrations were lower and long-term water-use efficiency higher for HF plants. The variations in water-use efficiency most likely resulted from a lower ratio of photosynthesis to leaf conductance in LF plants than in HF plants. Similar tendencies were observed in field-grown plants. Photosynthetic light-saturation point was lower for LF plants than for HF plants. As a result of paraheliotropic leaf movements, incident PPFD on leaflets remained close to the photosynthetic light-saturation points in both treatments.

PARAHELIOTROPIC leaf movements, in which leaf laminae actively orient obliquely to the sun's direct rays, have been observed in common bean (Dubetz, 1969; Wien and Wallace, 1973; Berg and Hsiao, 1986; Fu and Ehleringer, 1989, 1991) and other legumes such as soybean [*Glycine max* (L.) Merr.] (Kawashima, 1969; Meyer and Walker, 1981; Wofford and Allen, 1982; Oosterhuis et al., 1985; Berg and Heuchelin, 1990), alfalfa (*Medicago sativa* L.) (Travis and Reed, 1983), and cowpea [*Vigna unguiculata* (L.) Walp.] (Shackel and Hall, 1979). These active leaf movements result in changes in incident radiation levels on a diurnal basis, thereby providing a mechanism for regulating or optimizing radiation-dependent physiological processes. Past studies have shown that paraheliotropic leaf movements could result in an enhancement of water-use efficiency (Ehleringer and Forseth, 1989), avoidance of photoinhibition during water stress (Ludlow and Björkman, 1984), and increase in leaf-level photosynthetic rate (Fu, 1990).

Soil nutrient levels may have an impact on leaf orientation, since nutritional status affects photosynthetic capacity and, therefore, the capacity of an individual leaf to utilize incident solar radiation. Forseth (1987) observed that leaves of low-fertilizer treatment plants were more vertical than those of high-fertilizer treatment plants in soybean at midday, consistent with

this expectation. However, little is known as to how changes in leaf movement under different nutritional levels interact with possible changes in gas-exchange capacity, tissues temperatures, or integrated processes such as long-term water-use efficiency (the ratio of photosynthetic C gain to transpirational water loss). This study was conducted to investigate paraheliotropic leaf movements and the effects of leaf movements on gas exchange activities in common bean under contrasting fertilizer treatments.

Carbon isotope discrimination (Δ) by leaves of C₃ plants is a measure of integrated values of the ratio between intercellular CO₂ concentration (c_i) and ambient CO₂ concentration (c_a) (Farquhar et al., 1982) and was used to estimate long-term water-use efficiency (Farquhar et al., 1989). Long-term water-use efficiency is negatively correlated with Δ in C₃ plants if v (leaf-to-air water vapor pressure difference divided by total atmospheric pressure) is similar among plants (Farquhar and Richards, 1984; Farquhar et al., 1989). In this study, long-term integrated estimates of c_i/c_a and water-use efficiency of LF and HF plants were determined with C isotope ratio analyses of leaf tissues.

MATERIALS AND METHODS

For potted-plant observations, Cahone common bean was grown individually in 5-L pots outdoors at the University of Utah, Salt Lake City, UT, during the summer. The rooting medium (1:1:1 loam/vermiculite/perlite by volume) was watered twice daily to saturation, and fertilized once a week with 300 mL quarter-strength Hoagland solution (Hoagland and Arnon, 1938) per pot. On the 4th wk after sowing, 30 plants were divided randomly into two fertilizer treatments. In one of the treatments, plants continued to receive 300 mL quarter-strength Hoagland solution per pot weekly (HF), while in the second treatment plants received no further fertilization (LF). During the 7th wk after sowing, the following observations were made on two different days. Fully expanded leaflets were randomly selected from terminal and lateral positions on the top of canopies, where the leaf laminae and pulvinus were not shaded. Air and leaf temperatures were measured with 36 gauge copper-constantan thermocouples connected to a datalogger (Model CR21X, Campbell Scientific, Logan, UT). For measuring leaf temperature, thermocouples were placed on the lower surface of leaflets ($n = 14$) from both treatments. Maximum, incident and diffuse photosynthetic photon flux density (PPFD, 400–700 nm) were measured with a photon sensor (Model LI-185A, LI-COR Instruments, Lincoln, NE). For measuring incident PPFD on individual leaflets, the photon sensor was mounted on a Plexiglas plate (5 by 10 cm) and this plate was held parallel to the upper surfaces of leaflets. For measuring diffuse PPFD, the photon sensor was held in a shadow ≈ 10 cm from a shadow plate (a radius of 8 cm).

Abbreviations: c_a , ambient CO₂ concentration; c_i , intercellular CO₂ concentration; HF, high-fertilizer treatment; LF, low-fertilizer treatment; PPFD, photosynthetic photon flux density; v , leaf-to-air vapor pressure difference divided by total atmospheric pressure; Δ , carbon isotope discrimination.

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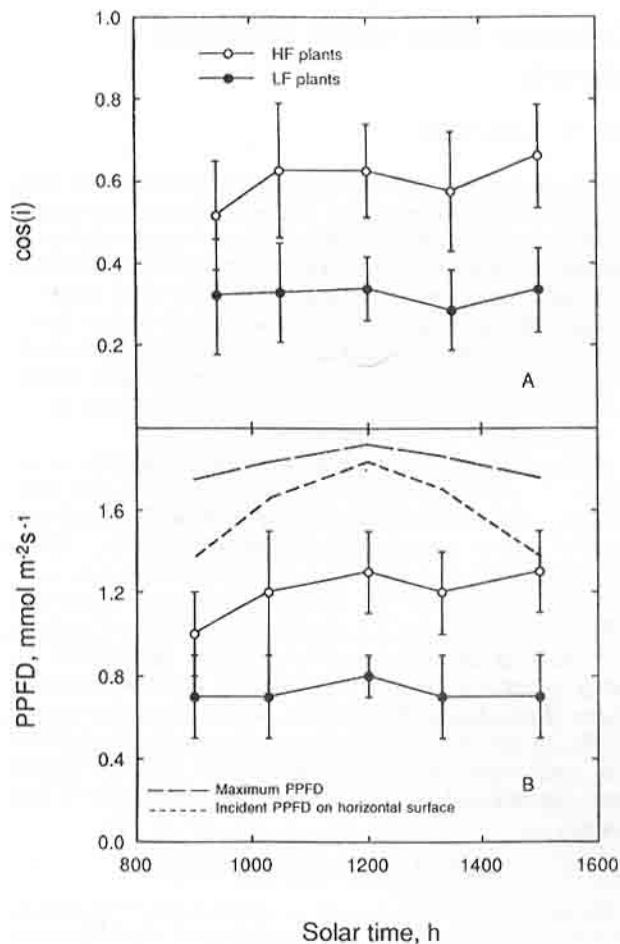


Fig. 1. (A) $\cos(i)$ of pot-grown common bean in a high-fertilizer treatment (HF) and a low-fertilizer treatment (LF) from mid-morning to mid-afternoon. (B) Maximum PPFD, incident PPFD on horizontal surface, and incident PPFD on leaflets of pot-grown HF and LF plants from mid-morning to mid-afternoon. Vertical bars represent standard deviations. Both $\cos(i)$ and incident PPFD were significantly different ($P < 0.001$) between HF and LF plants for the whole experiment period.

A null-balance porometer (LI-COR Model LI-1600) was used to measure leaf conductance and transpiration rate. Leaf conductance and transpiration rate were measured only at 0930 and 1530 h solar time, since our preliminary experiments had shown that these times were the times of highest and lowest daylight leaf conductances, respectively. Incident PPFD, leaf conductance, transpiration rate, and leaf temperature were measured on 14 to 60 leaflets from both HF and LF plants during each sample period. Water potential of whole, unbagged, fully-expanded leaves (including one terminal and two lateral leaflets) on the top of canopies was measured ($n = 14$) with a pressure chamber (PMS Instruments, Corvallis, OR) for both treatments at 1500 h solar time. A leaf area meter (LI-COR Model LI-3100) was used to measure leaf area ($n = 18$) for plants in both treatments. Fully expanded terminal and lateral leaflets ($n = 5$) from the top of canopies in each treatment were collected for analyses of C isotope ratio and N content.

In a separate experiment, plants were grown in the Biology Experimental Garden at the University of Utah (Parleys soil, a fine-silty, mixed, mesic Calcic Argixeroll in a Calcic Argixeroll-Calcic Haploxeroll association) during the

summer. Plants were well watered daily by drip irrigation. Three weeks after sowing, all plants were fertilized with 4 g of a multipurpose fertilizer [16-16-8 (N-P-K)] per plant. The experimental design consisted of two fertilizer treatments applied to alternate rows of plants with eight rows and ≈ 100 plants for each treatment. The HF plants were fertilized again with 4 g of fertilizer per plant during the 4th wk, while LF plants did not receive any additional fertilizer after the 3rd wk. During the 7th wk after sowing, the following observations were made at 1400 h solar time. Leaflets measured in this experiment were fully expanded, and were randomly selected from terminal and lateral positions on the top of the canopies, where the leaf laminae and pulvinus were not shaded. Incident PPFD on upper-leaflet surfaces ($n = 46$) and leaf temperature ($n = 9$) from each treatment were measured with the same methods as in the pot experiment. Fully expanded terminal and lateral leaflets ($n = 3$) on the top of canopies were collected from each treatment for analyses of C isotope ratio and N content.

For analyses of C isotope composition, leaves were dried at 75 °C for 48 h, and ground to a fine powder in a Wiley mill. A 2 to 3 mg sample was combusted for 6 h at 850 °C in a sealed, evacuated Vycor tube (Corning Glass Works, Corning, NY) containing cupric oxide and silver foil, and then cooled to room temperature (Ehleringer and Osmond, 1989). The C isotope ratio of CO_2 produced by combustion was measured on an isotope ratio mass spectrometer (Finnigan MAT delta E, San Jose, CA). Leaf Δ values were calculated assuming a C isotope ratio of CO_2 in air of -8.0‰ (Mook et al., 1983; Farquhar et al., 1989).

Leaf N content of LF and HF plants was analyzed using the Kjeldahl digestion procedure. Leaf tissues were oven dried, ground to a fine powder in a Wiley mill, and analyzed with an autoanalyzer (Technicon, Tarrytown, NY).

Leaf position in relation to the incident light beam was quantified by $\cos(i)$ (the cosine of the angle between the incident light beam and the vector normal to the leaf lamina) calculated as

$$\cos(i) = \frac{P_c}{P_t} = \frac{P_i - P_d}{P_m - P_d}$$

where P_c is direct PPFD incident on the leaf lamina, P_t total direct PPFD on a perpendicular to the direct solar beam, P_i total incident PPFD (including direct and diffuse PPFD) on the leaf lamina; P_d diffuse PPFD; P_m maximum PPFD (including direct and diffuse PPFD) on a perpendicular to the direct solar beam.

Photosynthetic rates on leaves from potted plants of both fertilizer treatments were measured in response to changes in PPFD with an open gas-exchange system (Ehleringer, 1983). Intact leaflets were inserted into a cuvette, in which leaf temperature was 30 °C, CO_2 concentration was 355 $\mu\text{L L}^{-1}$, and v was 30 kPa MPa^{-1} . The PPFD incident on leaflets was increased gradually to 2.0 $\text{mmol m}^{-2}\text{s}^{-1}$ during a period of 25 min, and photosynthetic rate was measured after a constant rate had been attained. Subsequently, PPFD was decreased in steps and photosynthetic rate measured after a constant rate was achieved.

Comparisons between treatments were analyzed using a Student's t -test.

RESULTS

Pot Studies

The $\cos(i)$ values of both treatments were much lower than 1.0 (Fig. 1A), indicating that leaflets were oriented obliquely to the sun's direct rays. $\cos(i)$ was significantly greater ($P < 0.001$) for HF plants than for LF plants during the whole measurement period,

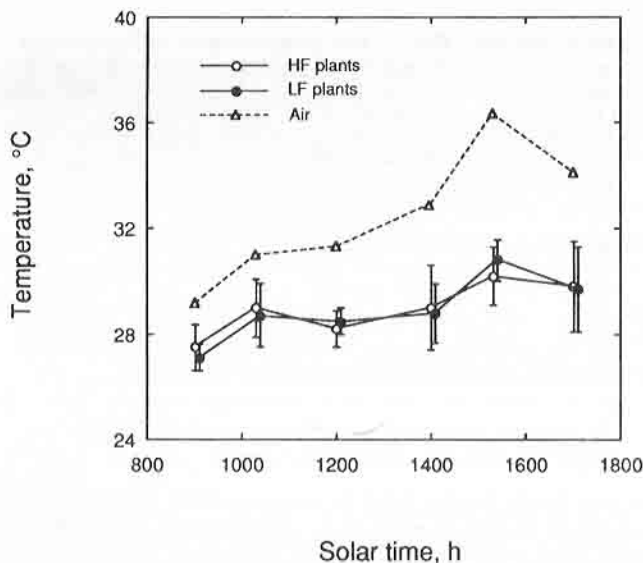


Fig. 2. Air and leaf temperatures of pot-grown common bean in a high-fertilizer treatment (HF) and a low-fertilizer treatment (LF). Vertical bars represent standard deviations. Air temperature was significantly different ($P < 0.001$) from leaf temperatures of HF and LF plants for the whole experiment period. Leaf temperature was not significantly different ($P > 0.05$) between HF and LF plants for the whole experiment period.

but the shape of the $\cos(i)$ curve in HF plants was generally similar to that in LF plants (Fig. 1A). Leaf laminae of LF plants were oriented more obliquely to the sun's direct rays than those of HF plants. The shape of the incident PPFD curves in HF and LF plants was different from that of incident PPFD on a horizontal surface (Fig. 1B), but were generally similar to those of typical paraheliotropic leaves (Ehleringer and Forseth, 1989; Fu and Ehleringer, 1989). Leaflets of HF plants received significantly greater ($P < 0.001$) total incident PPFD than those of LF plants during the whole measurement period (Fig. 1B). Despite orientation differences, leaf temperatures were not significantly different between HF and LF plants; however, both sets were significantly lower than air temperature ($P < 0.001$), especially when air temperature was high (Fig. 2). During the course of the measurements, air temperature changed about 8 °C, while leaf temperatures in both treatments changed <4 °C. The leaf conductance and transpiration rate of HF plants were significantly higher ($P < 0.01$) than those of LF plants in the morning and afternoon (Table 1). However, the

leaf water potentials in HF and LF plants were not significantly different in the afternoon (Table 1). The Δ value of HF plants was significantly lower ($P < 0.01$) than that of LF plants (Table 1), indicating that leaflets from HF plants had lower c_i/c_a ratio than that of leaflet from LF plants. Integrated c_i was therefore lower in leaflets of HF plants than in leaflets of LF plants since c_a in both treatments was the same. Values of v were similar in both treatments, because of similar air temperature, relative humidity, and leaf temperatures. Thus, it was impossible to compare long-term water-use efficiency levels in the different treatments by comparing Δ values. Accordingly, long-term water-use efficiency was higher in HF plants than in LF plants.

Leaf N content (expressed on both area and mass bases) and leaf area were significantly greater ($P < 0.01$) for HF plants than for LF plants (Table 2).

Field Studies

Total incident PPFD on leaflets at 1400 h was higher for HF plants than for LF plants, but leaf temperatures were not different (Table 3). Leaf N content on a mass basis was higher, and Δ value was lower for HF plants than for LF plants (Table 3). The Δ values indicated that HF plants had lower c_i and higher long-term water-use efficiency than those of LF plants. The patterns of these parameters for field-grown plants were similar to those for pot-grown plants.

Gas Exchange Measurements

Maximum photosynthetic capacity of HF plants was approximately three times that of LF plants (Fig. 3). Photosynthetic rate of HF plants was not saturated until 1.3 $\text{mmol m}^{-2} \text{s}^{-1}$ PPFD, while LF plants were light saturated by 0.8 $\text{mmol m}^{-2} \text{s}^{-1}$ (Fig. 3).

DISCUSSION

Results from both pot and field experiments showed that, as a result of paraheliotropic leaf movements, leaflets of common bean under low fertilizer regimes received less incident PPFD. These observations agree with the results of Forseth (1987), who show that leaflets of soybean were more vertical for LF plants than for HF plants at midday. Leaves of common bean responded to nutrient stress in a manner analogous to paraheliotropic responses to water-deficit stress (Dubetz, 199; Oosterhuis et al., 1985; Berg and Hsiao, 1986), high PPFD (Berg and Heuchelin, 1990; Fu and

Table 1. Leaf conductance, transpiration rate, leaf water potential, and C isotope discrimination (Δ) of common bean in a high-fertilizer treatment (HF) and a low-fertilizer treatment (LF). Fully expanded terminal and lateral leaflets on the top of canopies were measured on 7-wk-old plants grown in pots outdoors.

Treatment	Leaf conductance		Transpiration rate		Leaf water potential 1500 h	Δ
	0930 h	1530 h	0930 h	1530 h		
	$\text{mmol m}^{-2} \text{s}^{-1}$				MPa	‰
HF plants	508 (47)†	394 (25)	14.2 (0.6)	23.1 (2.2)	-0.85 (0.05)	19.63 (0.10)
LF plants	388 (23)	308 (53)	10.7 (0.8)	18.1 (3.0)	-0.90 (0.11)	22.67 (0.14)
Significance	**	**	**	**	NS	**

** Significantly different at $P < 0.01$; NS, not significantly different at $P > 0.05$.

† Numbers in parentheses are \pm standard deviations.

Table 2. Leaf N contents and leaf size of common bean in a high-fertilizer treatment (HF) and a low-fertilizer treatment (LF). Fully expanded terminal and lateral leaflets on the top of canopies were measured on 7-wk-old plants grown in pots outdoors.

Treatment	Leaf N content		Leaf area
	mg g ⁻¹	mg cm ⁻²	cm ²
HF plants	46.2 (0.3)†	0.244 (0.008)	15.5 (2.4)
LF plants	23.1 (1.4)	0.115 (0.005)	10.8 (0.9)
Significance	**	**	**

** Significantly different at $P < 0.01$.

† Numbers in parentheses are \pm standard deviations.

Ehleringer, 1991), high temperature (Fu and Ehleringer, 1989), and low N (Kao and Forseth, 1991). That is, the leaf-level response to such stresses is a sun-avoiding reorientation, reducing incident solar radiation and thermal loading.

The paraheliotropic response to soil nutrient variations may adjust microenvironmental and foliar conditions. Low incident PPFD, low transpiration rate and small leaf size for LF plants resulted in leaf temperatures similar to those of HF plants having a larger leaf size and experiencing both higher incident PPFD levels and transpiration rates. Our pot and field studies showed that the leaf temperatures of both treatments were much lower than air temperature, and were near the thermal optimum for photosynthesis for common bean grown under similar environmental conditions (Fu and Ehleringer, 1989). Leaflets from the different fertilizer treatments oriented differently to the direct sun's rays. In both cases, the result was that incident PPFD levels remained close to the photosynthetic saturation point. Fu (1990) suggested that photosynthetic rates of paraheliotropic leaves receiving PPFD levels near the photosynthetic light-saturation points may exceed those of leaves having higher incident PPFD levels, since the additional incident PPFD serves only to increase leaf temperature and v_p , and may result in decreases in leaf conductance. The canopy-level paraheliotropic response would allow for greater light penetration into the canopy, potentially resulting in greater photosynthetic rates by lower canopy-level leaves (Travis and Reed, 1983; Fu, 1990).

Both pot and field studies indicated the same tendency of paraheliotropic response to soil mineral nutrition. However, the average values of incident PPFD in the HF treatment at 1400 h were ≈ 1.2 mmol m⁻² s⁻¹ in pot-grown plants, and ≈ 1.4 in field-grown plants; the average values of incident PPFD in the LF treatment at 1400 h were ≈ 0.7 in pot-grown plants, and ≈ 1.2 in field-grown plants. Since types and amount of fertilizers, and other environmental conditions were not the same in pot and field studies, the difference between incident PPFD in pot-grown plants and field-grown plants probably resulted from the variations in soil water availability (Dubetz, 1969; Oosterhuis et al., 1985; Berg and Hsiao, 1986), air temperature (Fu and Ehleringer, 1989), or soil mineral nutrition.

The available data evaluating Δ and mineral nutrition are limited. In a recent study, Hubick (1990) showed that Δ was not significantly affected by nitrogen treatments in peanut (*Arachis hypogaea* L.), while both our pot and field studies showed that HF

Table 3. Incident PPFD, leaf temperature, carbon isotope discrimination (Δ), and leaf N content of common bean in a high-fertilizer treatment (HF) and a low-fertilizer treatment (LF). Fully expanded terminal and lateral leaflets on the top of canopies were measured on 7-wk-old plants grown in a field. Incident PPFD and leaf temperature were measured at 1400 h solar time.

Treatment	Incident PPFD	Leaf	Δ	Leaf N content
		temperature		
	mmol m ⁻² s ⁻¹	°C	‰	mg g ⁻¹
HF plants	1.38 (0.24)†	28.3 (0.4)	19.60 (0.17)	44.1 (0.1)
LF plants	1.18 (0.26)	28.5 (0.2)	20.24 (0.20)	39.2 (2.5)

† Numbers in parentheses are \pm standard deviations.

plants (with higher leaf N content) had significantly lower Δ values (i.e., lower integrated c_i and higher long-term water-use efficiency) than those of LF plants (with less leaf N content). Our results of estimated integrated c_i are in agreement with an observation by Kao and Forseth (1991) that c_i , measured with a gas-exchange system, in soybean plants was higher in low-N treatment than in high-N treatment. In an analysis of some chaparral species, Field et al. (1983) observed tradeoffs between water-use efficiency and N-use efficiency (photosynthesis per unit N) that were consistent with our observations. Increasing c_i for a given leaf N level (for instance by increasing leaf conductance) will result in an increased N-use efficiency, but a lower water-use efficiency. Von Caemmerer and Farquhar (1981) and Fu (1990) showed that photosynthetic rate was positively associated with c_i for a given leaf N level in common bean, leading one to conclude that increased photosynthetic rate by increasing c_i was associated with a decreased water-use efficiency (as a trade-off). Changing leaf N levels will complicate this pattern, e.g., our results indicated that

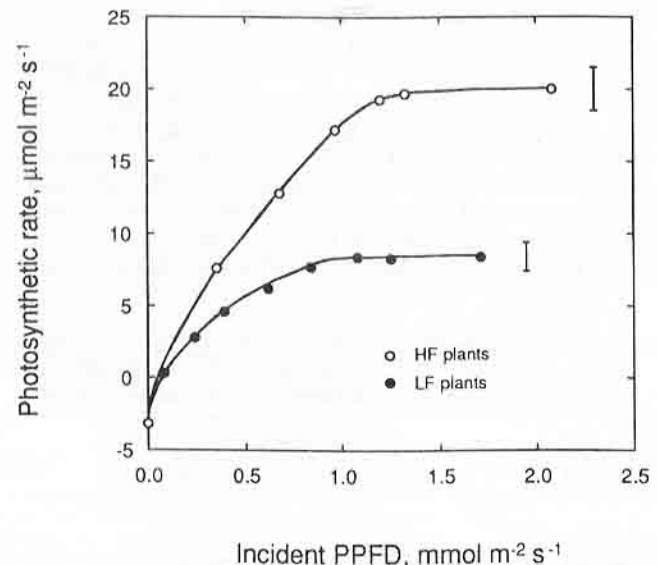


Fig. 3. Dependence of photosynthetic rate of pot-grown common bean in a high-fertilizer treatment (HF) and a low-fertilizer treatment (LF) on incident PPFD. Vertical bars represent standard deviations.

LF plants had higher c_i values and lower water-use efficiencies (higher Δ values) than HF plants. These results suggest that a marginal increase in photosynthetic rates of LF leaflets resulted from the higher c_i values. However, even though c_i was higher in LF plants than in HF plants, photosynthetic rate was still much higher for HF plants. Leaf N content of HF plants was about double that of LF plants, and photosynthesis is often positively associated with N content (Field and Mooney, 1986; Evans, 1989). The lower water-use efficiency for LF plant most likely resulted from a lower ratio of photosynthesis to leaf conductance in LF plants than in HF plants. It seems that the stress response to low nutrient levels in our study is consistent with general response patterns for a large number of environmental stresses (Chapin, 1991).

Kao and Forseth (1991) showed that leaves of soybean from a low N treatment oriented more obliquely to a light beam than those from a high N treatment. We suggest that paraheliotropic response to fertilizer levels may be linked with N deficits. However, the mechanism of this phenomenon is not known.

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REFERENCES

- Berg, V.S., and S. Heuchelin. 1990. Leaf orientation of soybean seedlings: I. Effect of water potential and photosynthetic photon flux density on paraheliotropism. *Crop Sci.* 30:631-638.
- Berg, V.S., and T.C. Hsiao. 1986. Solar tracking: Light avoidance induced by water stress in leaves of kidney bean seedlings in the field. *Crop Sci.* 26:980-986.
- Chapin, F.S., III. 1991. Integrated responses of plants to stress: a centralized system of physiological responses. *BioScience* 41:29-36.
- Dubetz, S. 1969. An unusual phototropism induced by drought in *Phaseolus vulgaris*. *Can. J. Bot.* 47:1640-1641.
- Ehleringer, J.R. 1983. Ecophysiology of *Amaranthus palmeri*, a Sonoran Desert summer annual. *Oecologia* 57:107-112.
- Ehleringer, J.R., and I.N. Forseth. 1989. Diurnal leaf movements and productivity in canopies, p. 129-142. In G. Russell et al. (ed.) *Plant canopies: their growth, form and function*. Cambridge Univ. Press, Cambridge.
- Ehleringer, J.R., and C.B. Osmond. 1989. Stable isotopes, p. 281-300. In R.W. Pearcy et al. (ed.) *Plant physiological ecology field methods and instrumentation*. Chapman & Hall Ltd, London.
- Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* 78:9-19.
- Farquhar, G.D., J.R. Ehleringer, and K.T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Mol. Biol.* 40:503-537.
- Farquhar, G.D., M.H. O'Leary, and J.A. Berry. 1982. On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. *Aust. J. Plant Physiol.* 9:121-137.
- Farquhar, G.D., and R.A. Richards. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Aust. J. Plant Physiol.* 11:539-552.
- Field, C.B., J. Merino, and H.A. Mooney. 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. *Oecologia* 60:384-389.
- Field, C.B., and H.A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants, p. 25-55. In T.J. Givnish (ed.) *On the economy of form and function*. Cambridge Univ. Press, Cambridge.
- Forseth, I.N. 1987. Responses of photosynthesis and leaf angle to water and nutrient stress in soybean, p. 205-206. In J. Biggens (ed.) *Progress in photosynthesis research*. Vol. 4. Martinus Nijhoff Publishers, Dordrecht, the Netherlands.
- Fu, Q.A. 1990. Paraheliotropic leaf movements in *Phaseolus vulgaris* L. Ph.D. diss. Univ. of Utah, Salt Lake City (Diss. Abstr. Int. 9100078).
- Fu, Q.A., and J.R. Ehleringer. 1989. Heliotropic leaf movements in common beans controlled by air temperature. *Plant Physiol.* 91:1162-1167.
- Fu, Q.A., and J.R. Ehleringer. 1991. Modification of paraheliotropic leaf movements in *Phaseolus vulgaris* by photon flux density. *Plant Cell Environ.* 14:339-343.
- Hubick, K.T. 1990. Effects of nitrogen source and water limitation on growth, transpiration efficiency and carbon-isotope discrimination in peanut cultivars. *Aust. J. Plant Physiol.* 17:413-430.
- Kao, W.Y., and I.N. Forseth. 1991. The effects of nitrogen, light and water availability on tropic leaf movements in soybean (*Glycine max*). *Plant Cell Environ.* 14:287-293.
- Kawashima, R. 1969. Studies on the leaf orientation-adjusting movement in soybean plants: I. The leaf orientation-adjusting movement and light intensity on leaf surface. *Proc. Jpn. Crop Sci. Soc.* 38:718-729.
- Ludlow, M.M., and O. Björkman. 1984. Paraheliotropic leaf movement in Siratro as a protective mechanism against drought-induced damage to primary photosynthetic reactions: Damage by excessive light and heat. *Planta* 161:505-518.
- Meyer, W.S., and S. Walker. 1981. Leaflet orientation in water-stressed soybeans. *Agron. J.* 73:1071-1074.
- Mook, W.G., M. Koopmans, A.F. Carter, and C.D. Keeling. 1983. Seasonal, latitudinal, and secular variations in the abundance of isotopic ratios of atmospheric carbon dioxide: I. Results from land stations. *J. Geophys. Res.* 88:10915-10933.
- Oosterhuis, D.M., S. Walker, and J. Eastham. 1985. Soybean leaflet movements as an indicator of crop water stress. *Crop Sci.* 25:1101-1106.
- Shackel, K.A., and A.E. Hall. 1979. Reversible leaflet movements in relation to drought adaptation of cowpeas, *Vigna unguiculata* (L.) Walp. *Aust. J. Plant Physiol.* 6:265-276.
- Travis, R.L., and R. Reed. 1983. The solar tracking pattern in a closed alfalfa canopy. *Crop Sci.* 23:664-668.
- von Caemmerer, S., and G.D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153:376-387.
- Wien, H.C., and D.H. Wallace. 1973. Light-induced leaflet orientation in *Phaseolus vulgaris* L. *Crop Sci.* 13:721-724.
- Wofford, T.J., and F.L. Allen. 1982. Variation in leaflet orientation among soybean cultivars. *Crop Sci.* 22:999-1004.