Variation in Leaf Movements among Common Bean Cultivars

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ABSTRACT

Common beans (*Phaseolus·vulgaris* L.) orient their leaves in response to directionality of the sun's direct beam. This study was initiated to test for genetic variability in leaflet orientation, especially variability related to geographic origin. We also determined genetic variability in diurnal, seasonal, and environmental influences on leaflet orientation. The studies included 75 Mesoamerican and Andean common bean lines and two tepary bean (*Phaseolus acutifolius* Gray) lines at two sites. *Cos i* (cosine of the angle of incidence to direct sunlight) varied in the order tepary bean > Andean common bean > Mesoamerican common bean. Within sites, variability in seasonal and year-to-year patterns of leaf movement was significant, but there were large differences in rankings of lines across sites. Imposed drought decreased *cos i*, but values of *cos i* in drought and irrigated treatments remained correlated. Movements of the two lateral leaflets were highly correlated with each other for most of the day, but within many common bean lines were not related to the movements of the terminal leaflet. Thus, at the canopy level the overall impact of the pronounced movements of the terminal leaflet were diminished by movements of the lateral leaflets. The results show substantial genetic variability in both short-term and long-term leaflet movements in beans, some of which is related to geographic origin.

C OMMON BEANS are capable of orienting their leaf angle and leaf azimuth in response to changes in the position of the sun's direct beam (1, 23), with the effect of reducing the incident solar radiation load on individual leaflets. These changes in leaf orientation are associated with a blue light receptor, which induces changes in turgor among pulvinar cells (11, 21, 25). The rapid, reversible orientation of leaf laminae (termed heliotropism) has been shown to be an important physiological mechanism in enhancing water- and nitrogen-use efficiency (5, 13, 15) and/or reducing high light and high temperature damage to the photosynthetic apparatus (10, 12, 15, 16, 18). Thus, heliotropism might be a valuable selective trait for breeding programs directed at improving the adaptation of common bean to drought and/or low moisture environments. At the canopy level, the adjustment of leaflet angles of alfalfa canopies has been shown to result in greater light penetration into lower portions of the canopy resulting in an overall increase in canopy photosynthesis (22). As a result, it has also been suggested that heliotropic movements may be beneficial to both increased water-use efficiency under drought and to increased crop productivity under well watered conditions.

Heliotropic leaf movements in common bean are affected by water availability, air temperature, and photon flux density (1, 4, 8, 9). Varietal-level differences in the degree of leaflet orientation (23) have been shown for a limited number of cultivars and Sato (20) reported varietal differences in leaf movements in response to light intensity and air temperature for two cultivars. While these results clearly indicate that variation in leaf movements exists among bean cultivars, the extent of this variation, particularly under field conditions is not known. Additionally, all three pulvini of a bean trifoliate leaf can respond to the incident direct solar beam (23). The significance of possible leaflet differences has not been examined, although Sato (20) first suggested that there could be functional differences in the movements among these leaflets.

In this study, we examined leaflet orientation among many common bean cultivars and a limited number of tepary bean cultivars. The objectives of this study were to determine (i) variations among cultivars in the degree of leaflet orientation, (ii) if the variation was related to the original domestication center of that cultivar, (iii) the spatial and temporal repeatability of leaf orientation measurements, and (iv) if the diurnal pattern of leaflet orientation differed among cultivars.

MATERIALS AND METHODS

Seeds of 75 common bean lines originating from Mesoamerican and Andean-American domestication centers and two tepary bean cultivars from Mexico were planted at the Experimental Field Station of the Colorado State University near Cortez, CO, in June 1991. Each cultivar had 20 replicate plants in each of three blocks. From the Mesoamerican domestication center, the common bean lines included A 54, A 59, BAT 1298, Beryl, Bill Z, Cahone, CO 635, CO 1760, CO 22625, CZ 25317, CZ 35241, CZ 35277, CZ 59188, CZ 81-13183, EMP 105, G 5201, Harold, ISB 459, KO 334, LEF-2-RB, NW 63, NW 410, Othello, Roza, Rufus, RS 101, SAN XTBAL, Starlight, UI 114, UNS 117, UI 126, UI 686, V 8025, Viva, and WYO 167. From the Andean-American domestication center, the common bean lines included ABA 11, AFR 180, AFR 244, AFR 245, AFR 246, AFR 285, AFR 286, AFR 309, AND 366, AND 367, AND 673, AND 675, AND 676, Calima, DRK 10, G 4523, KID 22, KID 23, LRK 1, LRK 6, LRK 7, PVA 1111, PVA 1454, PVA 3048, Sacramento, SUG 18, SUG 25, SUG 28, SUG 31, SUG 32, Taylor, Victor, WAF 130, ZAA 2, ZAA 14, ZAA 63, ZAA 64, ZAA 88, ZAA 102, ZAA 105, and ZAA 108. The tepary bean lines originated from Mexico and included Bufftep and Sonora. In June 1992, 50 cultivars were planted, including 18 that had also been planted in 1991. Light interception by leaflets were measured 7 wk after germination in each of the 2 yr.

Twenty-four common bean cultivars were planted in June 1991 at the University of Utah at Salt Lake City (SLC), including 14 cultivars in common with those planted at Cortez. All of these plants were well watered until the first trifoliate had developed. Plants were then separated into two different watering regimes, with half of the plants receiving water to field capacity every other day (wet treatment) and the other half receiving no further irrigation except natural rainfall (dry treatment). Light interception on leaflets was measured on 3-wk-old (vegetative stage) and 8-wk-old (reproductive stage) beans.

Since bean leaves have been shown to increase light interception in the morning and again in the late afternoon, while reducing interception at midday period (1), we evaluated heliotropic leaflet movements by measuring the light interception at 0700 and 1300 h (MST). All the measurements were completed within an hour during each sample period. Only the most recently, fully expanded leaflets were used for these measurements.

Cosine of incidence (cos i) is commonly used to quantify the tracking activity of a leaf or leaflet (7). A cos i value of 1.0 represents a leaflet that is oriented perpendicular to the direct solar beam, receiving full direct sunlight, while a cos i value of 0 represents a leaflet that is oriented parallel to the direct solar beam, receiving no direct sunlight. To measure cos i values, the total photon flux (400-700 nm) intercepted by a leaflet was measured by holding a photon sensor (LI-COR, Inc., Lincoln, NE) mounted on a clear plastic paddle parallel to the leaflet. Maximum, reflected, and diffuse photon fluxes were then measured by orienting the photon sensor perpendicular to the sun, then to the soil, and finally toward the sky but shaded from direct beam, respectively. Total photon flux on a horizontal surface was measured by holding the sensor horizontal at plant height. The cos i values were then calculated as the ratio of the difference between total and diffuse photon flux on a leaflet over the difference between photon flux on a solar perpendicular and the diffuse value.

A sample of 40 to 50 leaflets per cultivar was randomly selected for the cos i measurements in 1991, from which the average cos i value was then calculated. In 1992, cos i values of terminal and lateral leaflets on a trifoliate leaf were distinguished to evaluate the potential differences in light interception. Diurnal courses of cos i values of terminal and lateral leaflets on 11 common bean cultivars at Cortez were measured in August 1992. A one-way analysis of variance was conducted to test for difference in the patterns of diurnal leaflet movements among cultivars and also between leaflets.

RESULTS

Variation among Cultivars

Among 77 bean cultivars, the average cos i values of leaflets measured between early morning and midday periods varied significantly. The average cos i values of leaflets early in the morning ranged from a low of 0.47 ± 0.02 (mean ± S.E.) (cv. UI 126) to a high of 0.74 ± 0.02 (cv. Sonora) and at midday from 0.22 ± 0.02 (cv. CO 22625) to 0.60 ± 0.02 (cv. ZAA 14). The range of midday leaflet cos i values among cultivars (0.38) was larger than that in early morning (0.27). When cultivars were categorized by species and origin, the differences were statistically significant (Table 1). The two tepary bean cultivars in the study had the highest average cos i values (the highest light interception), Andean-American common beans had intermediate values, and Mesoamerican common beans had the lowest average cos i values, both in early morning and midday periods.

The cos i values of leaflets varied between 0700 and 1700 h (Table 2). In general, leaflets had a higher cos i value in the morning and again in the late afternoon, with a lower cos i value during the midday period. In effect, leaves of different cultivars exhibited a continuum between near diaheliotropism (cos i = 1) (in the early morning and late afternoon) and complete paraheliotropism (cos i = 0) (during midday periods). Within a cultivar, the diurnal changes in cos i values of terminal leaflets were more pronounced than those of lateral leaflets, especially

Table 1. Mean ± S.E. of cosine of incidence (cos i, measured at 0700 h or 1300 h, MST) of leaflets of tepary bean (n = 2) and common bean lines, originated from Andean-American (n = 41) and Mesoamerican (n = 34) domestication centers, planted in June of 1991 at Cortez, Colorado.

Group	Cos i at 0700 h	Cos i at 1300 h
Mesoamerican	0.59 ± 0.01a†	0.37 ± 0.01a
Andean	0.61 ± 0.01a	0.41 ± 0.01b
Tepary	0.71	0.51

† Within each column, values followed by different letters are significantly different at P = 0.05 (t-test).

Table 2. Diurnal courses of *cos i* of a horizontal surface, the average of *cos i* of three leaflets and *cos i* of terminal leaflets of two Andean bean cultivars (G 4523 and Sacramento) and nine Meso-American bean cultivars planted in June of 1992 at Cortez, CO.

| Cultivar | Average *cos i* of three leaflets | | | | | | *Cos i* of terminal leaflets | | | | | |
| | Time (h) | | | | | | Time (h) | | | | | |
	0700	0900	1100	1300	1500	1700	0700	0900	1100	1300	1500	1700
Horizontal	0.31	0.67	0.85	0.93	0.74	0.43	0.31	0.67	0.85	0.93	0.74	0.43
G 4523	0.59a†	0.53b	0.63a	0.47c	0.47c	0.53b	0.56a	0.46b	0.64c	0.57a	0.63c	0.65c
Sacramento	0.59ac	0.68b	0.63ab	0.64ab	0.58c	0.65b	0.62a	0.70b	0.62a	0.71b	0.70b	0.77c
A 54	0.47a	0.28b	0.51ac	0.53ac	0.57cd	0.61d	0.47ac	0.33b	0.52c	0.53c	0.45a	0.63d
Beryl	0.56a	0.27b	0.43cd	0.28b	0.42c	0.48d	0.68a	0.15b	0.27c	0.18b	0.46d	0.64a
Bill Z	0.44ab	0.48a	0.45ab	0.44ab	0.41b	0.51c	0.48a	0.41b	0.28c	0.47a	0.40b	0.53d
Cabone	0.55a	0.64b	0.50a	0.45c	0.52a	0.66b	0.60a	0.51b	0.31c	0.33c	0.45d	0.59a
CZ 35241	0.57a	0.45b	0.58a	0.53a	0.56a	0.66c	0.70a	0.19b	0.24b	0.33c	0.44d	0.63e
CZ 35277	0.52a	0.56a	0.50ab	0.52ac	0.49b	0.57c	0.37a	0.47b	0.39ac	0.44bc	0.44bc	0.63d
KO 334	0.43a	0.23b	0.38a	0.39a	0.42a	0.57c	0.49a	0.24bc	0.20b	0.27c	0.46d	0.57e
Othello	0.47a	0.19b	0.37c	0.38c	0.33c	0.50a	0.38a	0.11b	0.26c	0.14b	0.23c	0.44d
UI 114	0.44a	0.42a	0.44a	0.46a	0.45a	0.58b	0.38a	0.24b	0.31c	0.32c	0.41a	0.51d

† Values followed by different letters within rows of the same *cos i* (average *cos i* or *cos i*) measurement are significantly different ($P < 0.05$) tested by Tukey procedures.

during the midday period (1100–1300 h). This result would certainly suggest that terminal leaflets have greater rotational capacities than adjacent lateral leaflets.

Constancy of *cos i* Value Measurements

To examine the constancy of *cos i* values over time, we compared *cos i* value of the same cultivars in two different years (1991 vs. 1992), between locations within the same growing season (Salt Lake City, UT, and Cortez, CO), during both vegetative and reproductive developmental stages within a site, and under adjacent wet- and dry-treatments within a site.

The inter-annual correlation between 1991 and 1992 in midday *cos i* values of leaflets of different common bean cultivars planted at Cortez was significant ($r = 0.54$, $P < 0.05$), although the correlation of early morning observations was not significant (Table 3). Neither the early morning nor the midday comparisons of the across-site comparisons were statistically different. Together these results indicate that leaf movement patterns between years are repeatable, but perhaps site specific. Differences in climate may result in differential *cos i* responses among cultivars.

In contrast, the early morning and midday *cos i* comparisons of the irrigated and droughted plants were significantly correlated. Plants grown under irrigated conditions had a significantly higher midday average *cos i* value (0.47 ± 0.02) than plants grown under droughted

Table 3. Correlation coefficient (*r*) for the relationship of cosine of incidence of common bean leaves measured between years (1991 and 1992 at Cortez, CO), across sites (1991 in both Cortez, CO, and Salt Lake City, UT), between treatments (1991, Salt Lake City, wet vs. dry soil-water treatment), and at different developmental stages (1991, Salt Lake City, vegetative vs. reproductive stage).

Source	*Cos i* at 0700 h	*Cos i* at 1300 h
years	0.08	0.54*
sites	0.12	0.25
soil moisture	0.69*	0.67*
developmental stage	0.19	0.53*

* Indicates significance at $P = 0.05$.

conditions (0.31 ± 0.02) ($P < 0.05$, paired *t*-test), consistent with the results of earlier studies.

The leaflet *cos i* values of cultivars sampled during vegetative and reproductive growth stages within a single season were positively correlated. There was a small shift in *cos i* values with the average midday *cos i* value of cultivars during the vegetative stage (0.51 ± 0.02) higher than that during the reproductive stage (0.47 ± 0.02).

Variation among Leaflets

We suspected that the low repeatability of *cos i* value measurements in Table 3 might be due to the differential movement capacities of terminal versus lateral leaflets. Therefore, we compared *cos i* values of terminal and lateral leaflets movement of 18 cultivars in early morning and again at midday. In the early morning observations, the *cos i* values of each of the three leaflets were significantly different from each other (Table 4). During the midday period, *cos i* values of the two lateral leaflets tended to be more similar to each other and differences in *cos i* values between terminal and lateral leaflets persisted. We did not observe a significant relationship between *cos i* of terminal and lateral leaflets during the course of a day. Lateral leaflet orientations for a given leaf were not significantly correlated with each other in the earliest and last observations of the day when the sun is at a lower elevation. However, the *cos i* of two lateral leaflets was significantly correlated through the day (Fig. 1), indicating that similar leaf movement constraints were operating on lateral leaflets. Although there was no significant relationship in the *cos i* values between two lateral leaflets at 0700 h ($r = 0.31$, $n = 11$, $P > 0.05$) and 1700 h ($r = 0.43$, $n = 11$, $P > 0.05$), a significant, positive linear relationship was calculated at 0900 h ($r = 0.85$, $n = 11$, $P < 0.05$), 1100 h ($r = 0.77$, $n = 11$, $P < 0.05$), 1300 h ($r = 0.83$, $n = 11$, $P < 0.05$) and 1500 h ($r = 0.83$, $n = 11$, $P < 0.05$) when solar elevations were higher.

Lateral and terminal leaflets often exhibited different diurnal movement patterns. Since the *cos i* value of the

Table 4. Cosine of incidence of terminal and lateral leaflets measured at 0700 h (MST) and 1300 h (MST).

Origin	Cultivar	0700 h (MST)			1300 h (MST)		
		Terminal	Lateral 1	Lateral 2	Terminal	Lateral 1	Lateral 2
Andean	ABA 11	0.57a†	0.73b	0.57a	0.48a	0.75b	0.81b
Andean	G 4523	0.56a	0.61b	0.59b	0.57a	0.42b	0.43b
Andean	Sacramento	0.62a	0.66b	0.50c	0.71a	0.60b	0.61b
Andean	WAF 130	0.43a	0.65b	0.50c	0.47a	0.57b	0.57b
Meso	CZ 35241	0.70a	0.55b	0.44c	0.33a	0.61b	0.66c
Meso	Beryl	0.68a	0.70a	0.28b	0.18a	0.27b	0.39c
Meso	Cahone	0.60a	0.75b	0.31c	0.33a	0.45b	0.56c
Meso	BAT 1298	0.60a	0.69b	0.40c	0.43a	0.36b	0.42a
Meso	SAN × TBA	0.58a	0.64b	0.44c	0.23a	0.43b	0.43b
Meso	CO 97373	0.53a	0.73b	0.41c	0.36a	0.45b	0.48b
Meso	A 59	0.51a	0.73b	0.34c	0.36a	0.20b	0.39a
Meso	KO 334	0.49a	0.58b	0.22c	0.27a	0.42b	0.46c
Meso	Bill Z	0.48a	0.68b	0.16c	0.47a	0.43b	0.40c
Meso	A 54	0.47a	0.61b	0.34c	0.53ab	0.50a	0.55b
Meso	UI 126	0.40a	0.81b	0.33c	0.21a	0.31b	0.44c
Meso	Othello	0.38a	0.72b	0.30c	0.14a	0.40b	0.33c
Meso	UI 114	0.38a	0.68b	0.25c	0.32a	0.50b	0.52b
Meso	CZ 35277	0.37a	0.74a	0.45c	0.44a	0.59b	0.53c
%							
a		100	11	6	100	6	11
b		0	9	6	6	94	44
c		0	0	88	0	0	44

† For each cultivar at 0700 h or at 1300 h of measurements, values followed by different letters are significantly different ($P < 0.05$) tested by Tukey LSD procedures.

two opposite lateral leaflets of a leaf were significantly correlated, the average *cos i* value of the two lateral leaflets was compared to the *cos i* value of the respective terminal leaflet. Over the course of the day, lateral leaflets often changed their orientation less than terminal leaflets; as a consequence, variation in the *cos i* value of terminal leaflets tended to be larger throughout the day. Three distinct leaflet movement patterns existed among terminal leaflets of the different cultivars (Fig. 2). In some cultivars, such as Sacramento, both terminal and lateral leaflets moved in such a way that *cos i* values remained high and did not change significantly through the day. Plotted for comparison on each figure is the expected *cos i* for a fixed horizontal leaflet surface. The CZ 35241 line characterized a second pattern that appeared among cultivars; this was one in which terminal leaflets oriented towards the sun early in the morning and again late in the day (resulting in a high *cos i* value), but oriented away from the sun at midday (resulting in a low *cos i* value). In this pattern, lateral leaflets moved in such a way as to keep a relatively high and constant *cos i* value through the day. The Othello cultivar characterized the
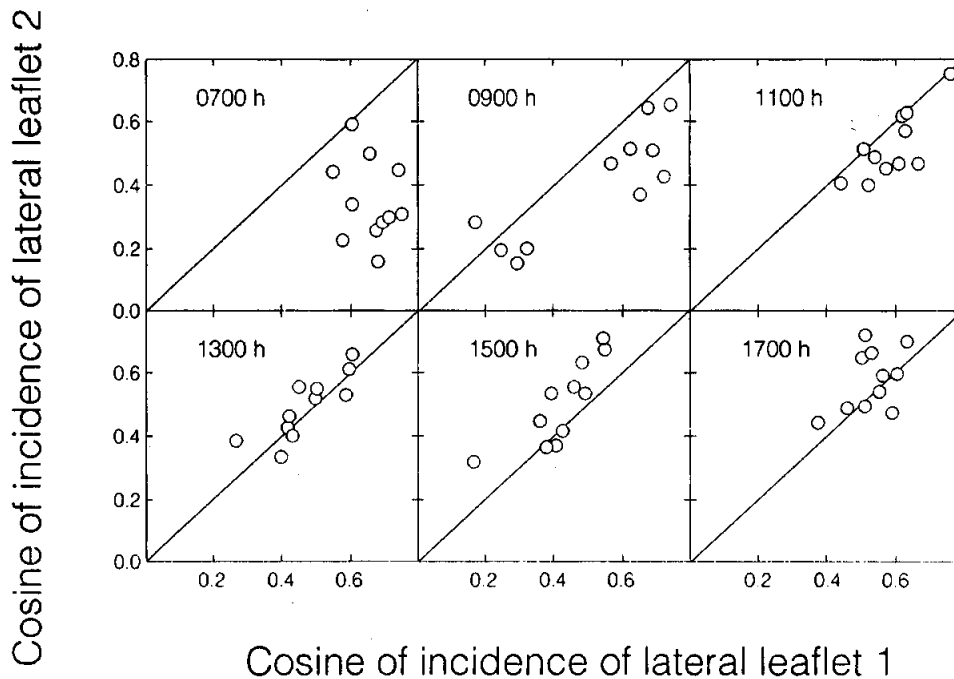

Fig. 1. The diurnal changes in the relationship of cosine of incidence of 2 lateral leaflets of 11 bean cultivars planted in the field near Cortez, Colorado in June of 1992. Each point represents the average cosine of incidence of ten leaflets. Solid lines represent one-to-one relationship.
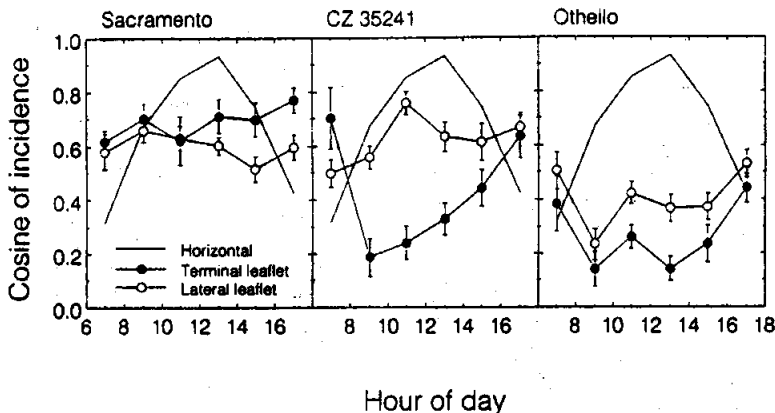
Fig. 2. Comparison of diurnal changes in cosine of incidence on a horizontal surface, of terminal leaflets ($n = 10$) and lateral leaflets ($n = 20$) of 3 bean cultivars planted in the field near Cortez, Colorado in June of 1992. Bars are 1 standard error.

third leaflet movement pattern: One in which both lateral and terminal leaflets moved in such a way as to reduce leaflet orientation to the sun at midday (low *cos i* value), but exhibited a non-responsive orientation in the early morning and again in the late afternoon (indistinguishable from that of a horizontal surface).

DISCUSSION

The greater change in *cos i* value of terminal leaflets when compared with changes in the average *cos i* value of three leaflets (Table 2, Fig. 2) suggested that terminal leaflets had a greater reduction in the light interception than lateral leaflets. The large difference between *cos i* values of terminal leaflets and the average *cos i* value of all three leaflets during the midday period indicated that terminal leaflets displayed a stronger paraheliotropic behavior than lateral leaflets. The possible canopy-level impact of any temperature reduction or water-use efficiency savings associated with paraheliotropic terminal leaflet movements appears diminished by the reduced response by the lateral leaflets.

Paraheliotropic leaf movements in common bean have been shown to be affected by water availability (1, 4), with low soil-water availability resulting in steeper midday leaf angles (a reduced *cos i* value). The increase in paraheliotropism decreases incident radiation levels on a leaf surface and thus reduces transpirational water loss through a reduction in leaf temperature. Consistent with this, our results also showed that common bean lines grown under a dry treatment had a higher midday leaf angle, thus a lower *cos i* value compared to those grown under a wet treatment. The differential response of midday leaf orientation by cultivars from different geographic origins is consistent with their physiological response to drought stress. Mesoamerican common beans, which have been shown to be more susceptible to drought stress (2, 17), tended to have the highest midday leaflet angles (the lowest *cos i* values), while the more drought-resistant tepary beans tended to have the lowest midday leaflet angles (the highest *cos i* value), and Andean common beans tended to have intermediate *cos i* values (Table 1).

The consistent rankings of midday *cos i* values across

years, between vegetative and reproductive developmental stages, and under different soil-water treatments suggest that midday *cos i* values may be a stable feature that could be used in adapting crops to different climatic regimes. However, there was a significant genotype by environment interaction, resulting in non-significant correlations in leaf movements between Salt Lake City and Cortez. The basis for this lack of consistency between sites is unclear at this time, although possible air temperature and humidity differences between the sites may have contributed to a genotype by environment interaction. Air temperature and light level are known to affect paraheliotropic leaf movements (8, 9, 14) and a differential leaf-orientation response to these factors has been shown for common bean cultivars (20).

Differences in leaf movements between terminal and lateral leaflets have been reported among soybean cultivars by Wofford and Allen (24). These authors suggested that two leaflet movements were complementary, rather than in opposition to each other. Our results with common bean were not as conclusive. Three distinct leaflet-movement differences exist among cultivars, which result in a differential response to conditions where the sun is either low or high in the sky. The two most clearly interpretable responses are ones in which the leaflet movements result in either constant, high solar radiation loads during the day (e.g., cv. Sacramento in Fig. 2) or constant, low solar radiation loads during the day (e.g., cv. Othello in Fig. 2). The third and confusing pattern (e.g., cv. CZ 35241 in Fig. 2) involved movements of the terminal leaflets so as to reduce incident solar radiation loads, while the two lateral leaflets moved so as to maintain high incident solar radiation levels.

These first two leaflet movement responses are consistent with the notion of adaptation to short-growing seasons involving leaf movement patterns that are strongly diaheliotropic (5, 6) and adaptation to low midday humidity conditions involving strong paraheliotropic behavior (6). Strong paraheliotropic behavior at midday is potentially easier to evolve since it entails only the development of steep leaflet angles at midday when leaflet azimuthal orientation is effectively unimportant. In contrast, strong diaheliotropic behavior involves coordinated movements

of both leaf angle (vertical orientation) and leaf azimuth (compass direction).

The high genotype by environment interaction in values of common beans grown at different locations may limit the utility of this character in improving crop adaptation. Comstock and Ehleringer (3) have shown that the stomatal sensitivity to humidity (and therefore transpiration rates) differs among common bean lines. It is likely that if leaflet movements are responsive to temperature (8) that leaf temperature differences among cultivars may have contributed to the inconsistency of leaflet movement patterns. This may also explain why midday leaflet movement differences were consistent in midday observations (when temperatures are more likely to be equivalent) than in the early morning observations (when temperatures are likely to vary the greatest).

In previous studies of species with compound leaves, there was a consistent, coordinated leaf movement pattern among leaflets in both ecological (7, 19) and agricultural species (24). The inconsistency of the responses among lateral and terminal leaflets in some common bean lines makes it challenging to scale leaflet-level responses to the canopy level and to evaluate the potential adaptive value of this feature to crop production or water-use efficiency. This situation is further compounded by the inconsistency in leaflet movement patterns across sites, making it difficult to evaluate the impact of this character on plant performance under well watered conditions.

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