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Effect of Light Intensity and Temperature on Light-Avoiding Leaf Movements in Two *Phaseolus* Species

Research project in fullfilment of the Presidential Scholar
senior thesis requirements

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Introduction

The phenomenon of paraheliotropism has been long observed in plants. The idea that plants in a field would adjust the position of their leaves to become more parallel to the sun's rays is nothing new to those who had the curiosity to track such movements (Darwin 1881). In recent years much study has been directed at discovering why plants would make these movements and the mechanism that is used to achieve that movement.

Experimentation has yielded that the movement is driven by the pulvinus, a small "elbow" of tissue dividing the base of the leaf from the petiole. For legumes, the pulvinus was found to be the receptor that triggered the response as well as being the organ that actually effected the change. Only blue light was found to be the stimuli indicating that the pulvinus contains non-phytochrome blue light receptors. This separates the tropic movement from nastic movements which are triggered by both phytochrome red and blue light.

High temperatures, light intensities and water stress have all been hypothesized as having an influence upon the degree of response in plants exhibiting paraheliotropism. In the field where most tests are conducted, however, it is impossible to separate these three factors as one generally promotes the other. When laboratory tests that isolate one of the factors involved have been performed, individual relationships have shown themselves, but the interactions of two or more of the factors have not been investigated.

It was the purpose of this experiment to determine the

relationship between the factors of pulvinus temperature and light intensity in their role as factors that affect paraheliotropism. We also examined the differences in these relationships in two species adapted to different environments. The two species used were: *Phaseolus vulgaris* (common bean), a high yielding species which is grown in mesic climates, and *P. acutifolius* (tepary bean), an arid land bean which tolerates high temperatures and drought.

Literature Review

Leaf movement is a response of plants to environmental signals. The movements of various organs in response to light are widespread among plants (Darwin 1881). The term heliotropism was first used by A. B. Frank in 1868 to define all kinds of movement in response to light, and was later used only for the movement of plants towards light (Darwin 1881). Paraheliotropism was first used by Darwin (1881) : "the leaves of some plants when exposed to an intense and injurious amount of light direct themselves, by rising or sinking or twisting, so as to be less intensely illuminated." He viewed paraheliotropism as a mechanism to protect plants from heat injury by high light, and made detailed observations of paraheliotropism in *Phaseolus roxburgii, P. hernandesii, Cassia mimosoides, and Mimosa pudica*. In 1969, Dubetz observed paraheliotropic leaf movement of *P. vulgaris* in response to low water potential, showing that paraheliotropism can be induced by environmental factors other than light. Later paraheliotropism was also found to be affected by air temperature (Fu and Ehleringer 1989) and nitrogen availability (Kao and Forseth 1992).

In the nineteenth century, Pfeffer (1881) realized the pulvinus was the motor organ for most plant leaf movement. For most plants the site of light perception is the pulvinus (Wien and Wallace 1973, *P. vulgaris*; Vogelmann 1984, *Lupinus succulent*; Schwartz *et al.* 1987, *Melilotus*; Fu and Ehleringer 1989, *P. vulgaris*; Donahue and Berg 1990, *Glycine max*). Blue light is necessary for both diaheliotropism (light seeking movement) and

paraheliotropism; as red light does not stimulate leaf movements, a nonphytochrome blue light receptor is likely involved (Donahue and Berg 1990). The temperature effect on leaf movement acts directly on the pulvinus, and not on the lamina (Fu and Ehleringer 1989).

Effect of temperature. Field observations conducted with similar PFD, but different air temperatures showed that leaves of well-watered *Phaseolus* exhibited stronger paraheliotropism on hot days than on cool days (Fu and Ehleringer 1989). Laboratory research on well-watered *P. vulgaris* has also shown that when other environmental conditions were held constant, increased air temperature caused leaves to orientate more obliquely to a light source (Fu and Ehleringer 1989). Water potential was not measured in the above experiments; thus paraheliotropism in these experiments may also have been influenced by water potential. Leaf movements in response to air temperature may help leaf temperature to remain close to the thermal optimum for photosynthesis (Fu and Ehleringer 1989).

Effect of photon flux density. Field and laboratory observations of many species have shown the requirement of high levels of illumination for paraheliotropism (Darwin 1881; Forseth and Ehleringer 1982; Berg and Hsiao 1986; Fu and Ehleringer 1989). Research on the PFD effect was carried out on soybean (*Glycine max*) seedlings using the sun and artificial light sources (Berg and Heuchelin 1990). For both sun and artificial light, higher levels of PFD significantly increased paraheliotropism at a given plant

water potential.

Effect of water potential. The effect of plant water potential on paraheliotropism is a complex one, since paraheliotropism both responds to and affects water potential (Forseth and Ehleringer 1980; Berg and Hsiao 1986; Berg and Heuchelin 1990). For many plants, leaves change orientation during the day, as plant water potential declines (Dubetz 1969, *P. vulgaris*; Shackel and Hall 1979, *Vigna unguiculata*; Meyer and Walker 1981, *Glycine max*; Ludlow and Bjorkman 1984, *Macroptilium atropurpurem*; Oosterhuis *et al.* 1985, *Glycine max*). This movement reduces the leaf-to-sun incident angle, lowering light interception, especially during the middle of the day. This was also observed under a diffuse, but directional artificial light source in a growth chamber (Berg and Hsiao 1986; Berg and Heuchelin 1990). The immediate result of paraheliotropism in response to a decline in plant water potential is a reduction in light interception and absorption, reducing the leaf temperature below that of a horizontal leaf under the same circumstances (Meyer and Walker 1981). In addition, for some plants, paraheliotropism may turn the highly reflective adaxial surface to the light (Meyer and Walker 1981). The resulting reduction in leaf temperature is beneficial to the dry plant, since the lowered leaf temperature due to paraheliotropism acts together with stomatal closure to reduce water loss (Berg and Hsiao 1986; Berg and Heuchelin 1990; Ludlow and Bjorkman 1984). Leaves restrained from paraheliotropic movement had higher temperatures, lower water potentials (Berg and Hsiao 1986; Berg and Heuchelin 1990), and reduced photosynthetic

capacity due to high temperature (Gamon and Pearcy 1989). Paraheliotropism also protected water stressed leaves from damage by excess light (photoinhibition; Ludlow and Bjorkman 1984).

Materials and Methods

Two bean species, *Phaseolus vulgaris* (common bean) and *P. acutifolius* (tepary bean), were placed for 4-5 days in a 26 C germination chamber and then were transferred to a temperature controlled greenhouse. The plants were kept in a well-watered condition. They were used when they had developed their first trifoliolate leaves.

A 2 mil fine wire thermocouple was attached to the underside of the pulvinus of the terminal leaflet of the trifoliolate leaves. This was done in the greenhouse to limit exposure to low light levels before the beginning of the experiment. A micro-voltmeter (Bailey Instruments, Saddlebrook, NJ) was used to determine the temperature of the pulvinus. The experiment used a 1000 watt phosphor-coated metal halide lamp (Sylvania, Fall River, MA) as a radiation source. A quantum sensor (LiCor Incorporated, Lincoln, NE) was used to measure the amount of photosynthetically active radiation (μmol m^{-2} s^{-1}) before the experiment began. The trifoliolate leaves were inserted into a clear acrylic cuvette as shown in Fig. 1. An infra-red heat mirror was also used to cover top of the cuvette to shield the inside of the cuvette from the infra-red radiation produced by the lamp. By changing the distance of the cuvette from the lamp, the PAR levels were controlled. The rest of the plant was not subject to the conditions inside of the cuvette. A dampened cloth was used to cover the plant to moderate the light intensities, temperatures and humidity that the rest of the plant experienced. The temperature in the cuvette was controlled by a fan drawing air across a heat exchanger cooled by

a water bath (VWR Scientific, Niles, IL). Manipulation of the water bath temperature allowed control over the temperature of the air flowing into the cuvette.

When the leaves were initially placed in the cuvette, a zero time measurement was made. The pulvinus temperature was recorded as well as the leaf angle with respect to horizontal (Fig. 2). The leaf angle was measured with an inclinometer. As the temperature of the pulvinus was manipulated The leaf angle was measured every five minutes until its movement had stabilized. Then the temperature was again changed. At the end of the experiment, the water potential of the leaf was measured in a pressure chamber (Soilmoisture Equipment, Santa Barbara, CA).

Trials were made at four light intensities (PFD): 500, 750, 1000, and 1500 μmol m^{-2} s^{-1}. At each light intensity the pulvinus temperature was manipulated to 21, 24, 27 and 30 C. A single plant was used per light intensity level.
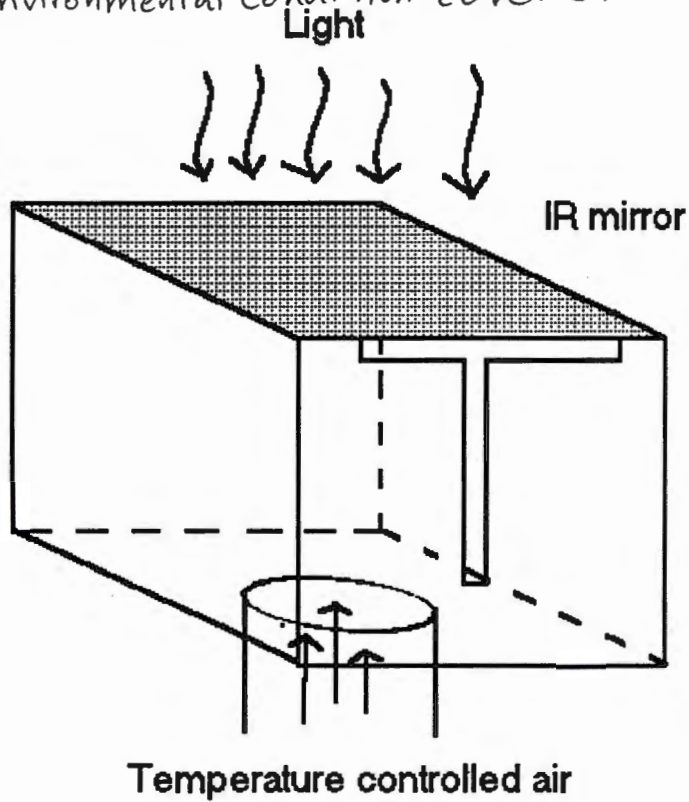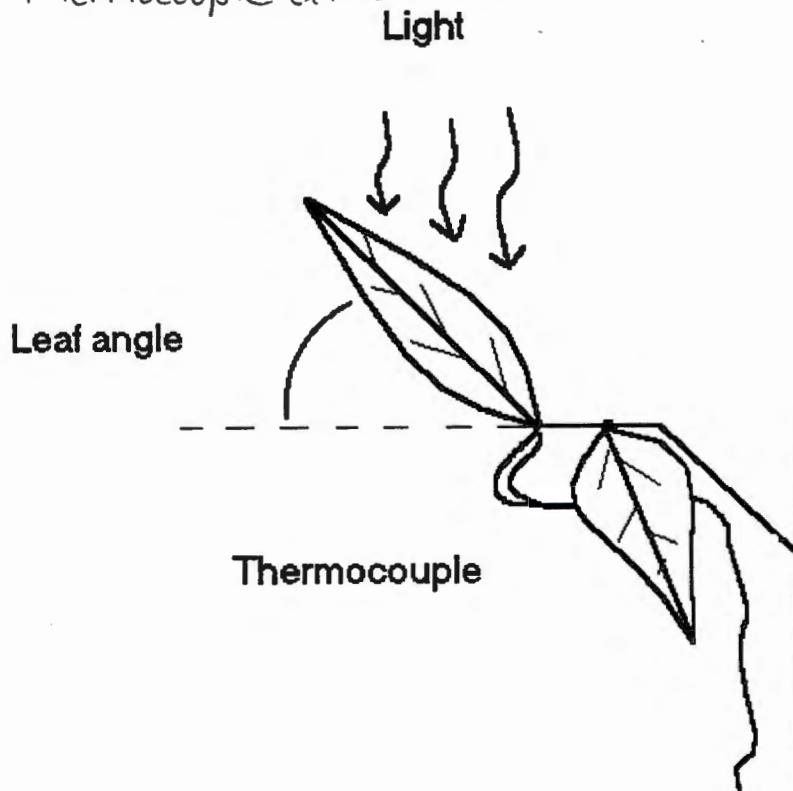
Fig. 1. Environmental Condition cuvette.

Light

IR mirror

Temperature controlled air

Fig. 2. Detail of leaf angle measurement and thermocouple attachment

Light

Leaf angle

Thermocouple

Results

Temperature Effects

In general, leaf angles showed increases corresponding to increases in temperature in *P. vulgaris* (Fig. 3, Table 1). At 500 μmol m^{-2} s^{-1} leaf angles were not significantly affected by increases in temperature at the lower temperatures. At 30 C the leaf angles were significantly different from those seen at 21 C. The leaf angles at 500 μmol m^{-2} s^{-1} do not appreciably move away from horizontal (Fig. 3). For 750 μmol m^{-2} s^{-1} leaf angles were not significantly affected by increases in temperature until 30 C was reached. Here a difference was seen between 30 C and both 21 and 24 C. For 1000 μmol m^{-2} s^{-1} increases in leaf angles showed a correspondence to temperature at the highest temperatures. No significant difference was found between 21 and 24 C or between 24 and 27 C Leaf angles at 27 C showed an increase over those at 21 C and leaf angles at 30 C were statistically different than all of the lower temperature. At 1500 μmol m^{-2} s^{-1} increases in leaf angles showed a correspondence to temperature at the highest temperatures. No significant difference was found between 21 and 24 C or between 24 and 27 C Leaf angles at 27 C showed an increase over those at 21 C and leaf angles at 30 C were statistically different than all of the lower temperatures. When the two lowest PFDs were pooled leaf angles showed no increase due to temperature until 30 C, where the leaf angles were statistically greater than all of the other cells. When the two highest PFDs were pooled increases in leaf angles showed a correspondence to temperature at the highest temperatures. No

significant difference was found between 21 and 24 C or between 24 and 27 C Leaf angles at 27 C showed an increase over those at 21 C and leaf angles at 30 C were statistically different than all of the lower temperature. Overall, as you increase in light intensity the effect of temperature on leaf angles becomes more significant beginning with the highest temperatures and moving to the lower temperatures (Fig. 3).

In general leaf angles showed a correspondence to increasing temperatures in *P. acutifolius* (Fig. 3, Table 2). However, at 500 μmol m^{-2} s^{-1}, there was no significant increase in leaf angles due to increased pulvinus temperatures. At 750 μmol m^{-2} s^{-1} an increase in leaf angle corresponding to an increase in temperature was seen only at 30 C where the leaf angles were significantly different from the two lowest temperatures (Table 2). At 1000 μmol m^{-2} s^{-1} a great increase in leaf angles was seen in response to the higher temperatures. Leaf angles at 27 C were significantly different from those at 21 C. Leaf angles at 30 C were greater than all of the lower temperatures (Table 2). A much more marked increase in leaf angles due to increased temperatures was seen at 1500 μmol m^{-2} s^{-1} where the two highest temperatures were significantly higher than any of the temperatures below them. No difference was seen in the two lowest temperatures (Table 2). When the two lowest light intensities were pooled, 21 and 24 C were no different and neither were 27 and 30 C. 30 C was greater than 21 and 24 C. Leaf angles did no significantly increase with a temperature increase from 21 to 24 C, yet 27 C was greater than 24 C and not

significantly different from leaf angles at 21 C (Table 2). When the highest light intensities were pooled, significant increases in leaf angle occurred with every increase in pulvinus temperature (Table 2).

Light Effects

As light intensities increased from 500 μmol m^{-2} s^{-1} to 1000 μmol m^{-2} s^{-1}, the leaf angles of *P. vulgaris* increased (Fig. 4). There was no increase in leaf angle as light intensity increased from 1000 μmol m^{-2} s^{-1} to 1500 μmol m^{-2} s^{-1}: a saturation had occurred. The leaf angles at the lowest light intensity were all near horizontal (Fig. 4). For every temperature and temperature combination 500 and 750 μmol m^{-2} s^{-1} were not significantly different. No increase in leaf angle was seen with an increase in light intensity between 750, 1000, and 1500 μmol m^{-2} s^{-1} for any of the temperatures or temperature combinations (Table 3).

As light intensities increased from 500 to 1000 μmol m^{-2} s^{-1}, the leaf angles of *P. acutifolius* increased (Fig. 4). There was no increase in leaf angle as light intensity increased from 1000 to 1500 μmol m^{-2} s^{-1}: a saturation had occurred. The leaf angles at the lowest light intensity were all near or at horizontal (Fig. 4). At 21, 24, and 27 C leaf angles did not significantly increase with increases in light intensity (Fig. 4). At 30 C leaf angles are not significantly increased by an increase in light intensity from 500 to 750 μmol m^{-2} s^{-1}. No significant difference was seen between leaf angles at the three highest light intensities at 30 C. The two lowest temperatures combined showed no effect of light intensity on leaf angle. The two

highest temperatures combined showed a pattern similar to that at 30 C (Table 4).

Light Avoidance

P. acutifolius exhibited a greater degree of light avoidance than did *P. vulgaris* (Fig. 5). The light avoidance was markedly increased in the highest temperatures (Fig. 5).

Interaction of Light and Temperature

The interaction of temperature and light to produce a leaf angle for given conditions was not statistically significant in *P. vulgaris* as a whole (Table 5). The interaction of temperature and light to produce a leaf angle for given conditions was statistically significant in *P. acutifolius* as a whole (Table 5). For the same conditions, *P. acutifolius* generally attained higher leaf angles than those seen in *P. vulgaris* (Fig. 6, Fig. 7).

Effect of Water Potential

Water potentials of the individuals measured ranged from $\Psi= -4.2$ bars to $\Psi= -8.0$ bars. In general the water potential of the plant did not affect the leaf angles in *P. vulgaris* (Table 5). In general the water potential of the plant did not affect the leaf angles in *P. acutifolius* (Table 5). This excludes the 500 μmol m^{-2} s^{-1} light intensity, for which there were no dry individuals.

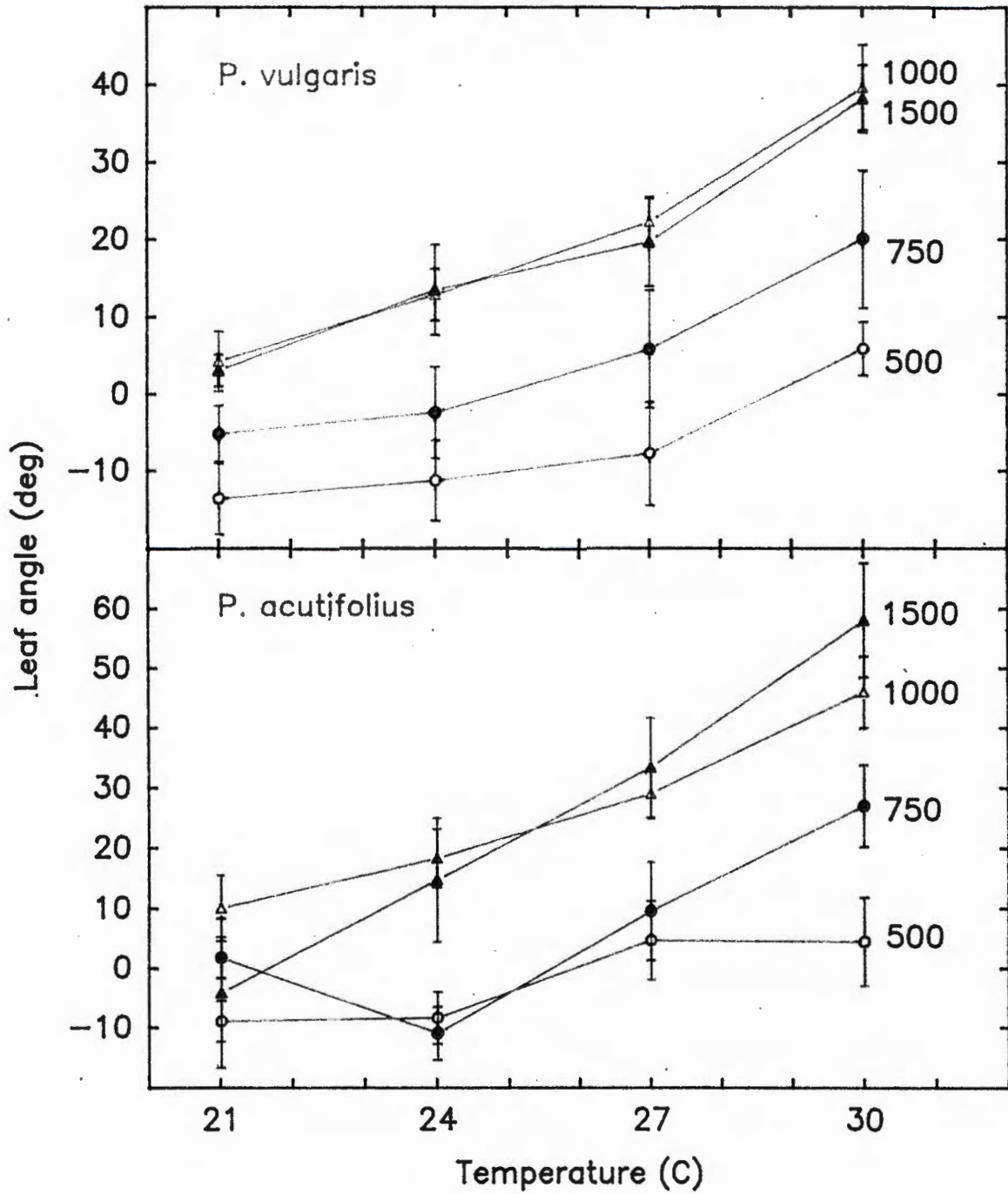Figure 3. Effect of temperature on leaf angles of P. vulgar and P. acutifolius

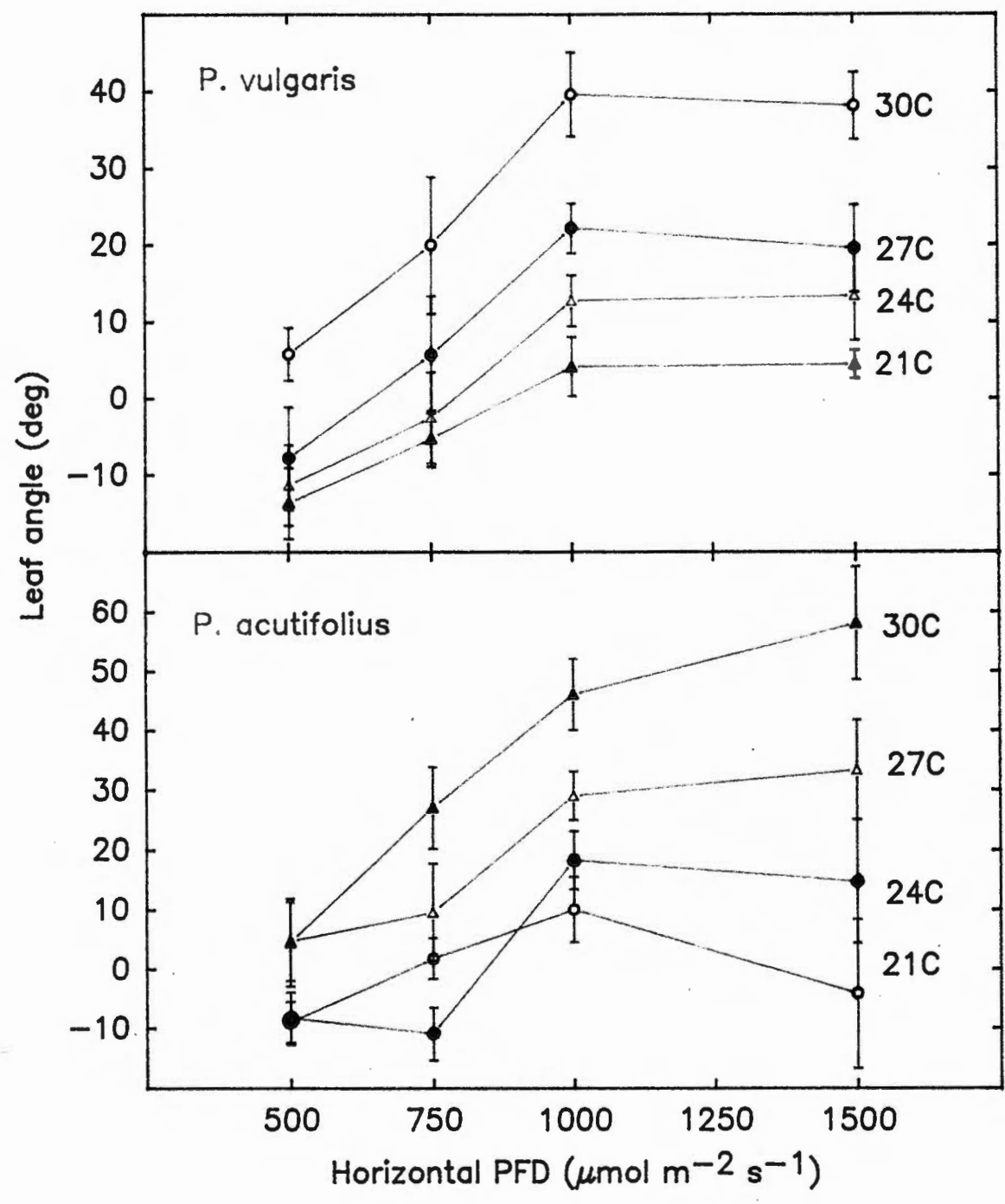Figure 7. Effect of light intensity (PFD) on leaf angles of P. vulgaris and P. acutifolius

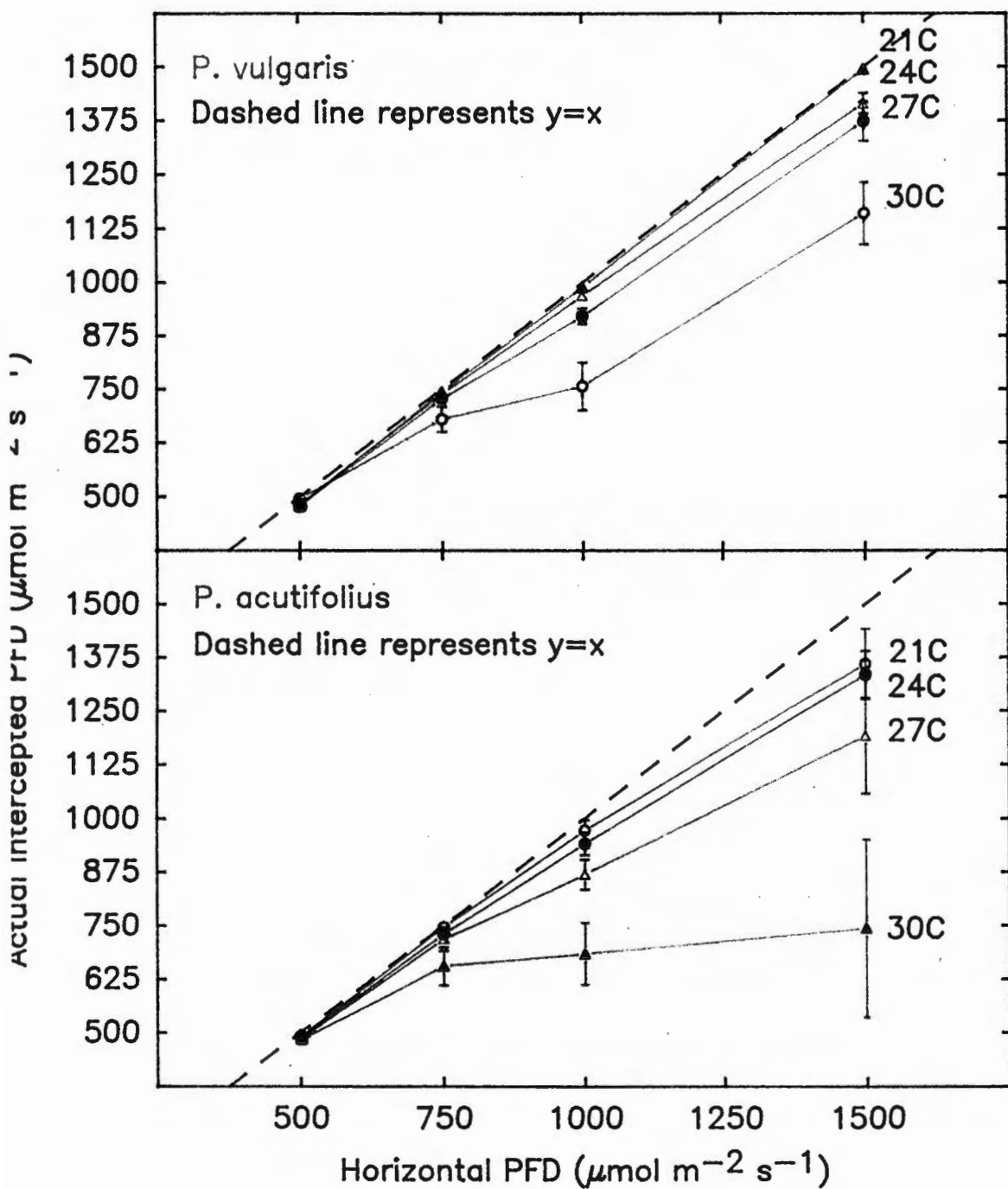Figure 5. Light avoidance demonstrated by P. vulgaris and P. acutifolius.

Table 1. *P. vulgaris* temperature effects (Bonferroni design ANOVA). Similar letters denote no significant difference between cells in a row at the 5% confidence level.

		Temperature		
PFD	**21**	**24**	**27**	**30**
500	A	AB	AB	B
750	A	A	AB	B
1000	A	AB	B	C
1500	A	AB	B	C
Low	A	A	A	B
High	A	AB	B	C

Table 2. *P. acutifolius* temperature effects (Repeated measures design ANOVA) Similar letters denote no significant difference between cells in a row at the 5% confidence level.

		Temperature		
PFD	**21**	**24**	**27**	**30**
500	A	A	A	A
750	A	A	AB	B
1000	A	AB	B	C
1500	A	A	B	C
Low	AB	A	BC	C
High	A	B	C	D

Table 3. *P. vulgaris* PFD effects (Repeated measures design ANOVA) Similar letters denote no significant difference between the cells in a row at the 5% confidence level.

Temperature	PFD			
	500	750	1000	1500
21	A	AB	B	B
24	A	AB	B	B
27	A	AB	B	B
30	A	AB	B	B
Low	A	AB	B	B
High	A	AB	B	B

Table 4. *P. acutifolius* PFD effects (Repeated measures design ANOVA) Similar letters denote no significant difference between the cells in a row at the 5% confidence level.

Temperature	PFD			
	500	750	1000	1500
21	A	A	A	A
24	A	A	A	A
27	A	A	A	A
30	A	AB	B	B
Low	A	A	A	A
High	A	AB	AB	B

Table 5.   *P. vulgaris* and *P. acutifolius* light intensity and temperature interactions and water potential effect statistics (repeated measure design ANOVA).

Temperature and PFD Interaction

P. vulgaris	$p = 0.6508$
P. acutifolius	$p = 0.0001$

Water Potential Effect

P. vulgaris	$p = 0.1057$
P. acutifolius	$p = 0.7098$

PVMEANS.XLC

Legend:
- 30-40
- 20-30
- 10-20
- 0-10
- -10-0
- -20--10

Figure: 7. Response surface graph of light intensity (PPD), temperature, and leaf angle in P. acctifolius.

Legend:
- 50-60
- 40-50
- 30-40
- 20-30
- 10-20
- 0-10
- -10-0
- -20--10
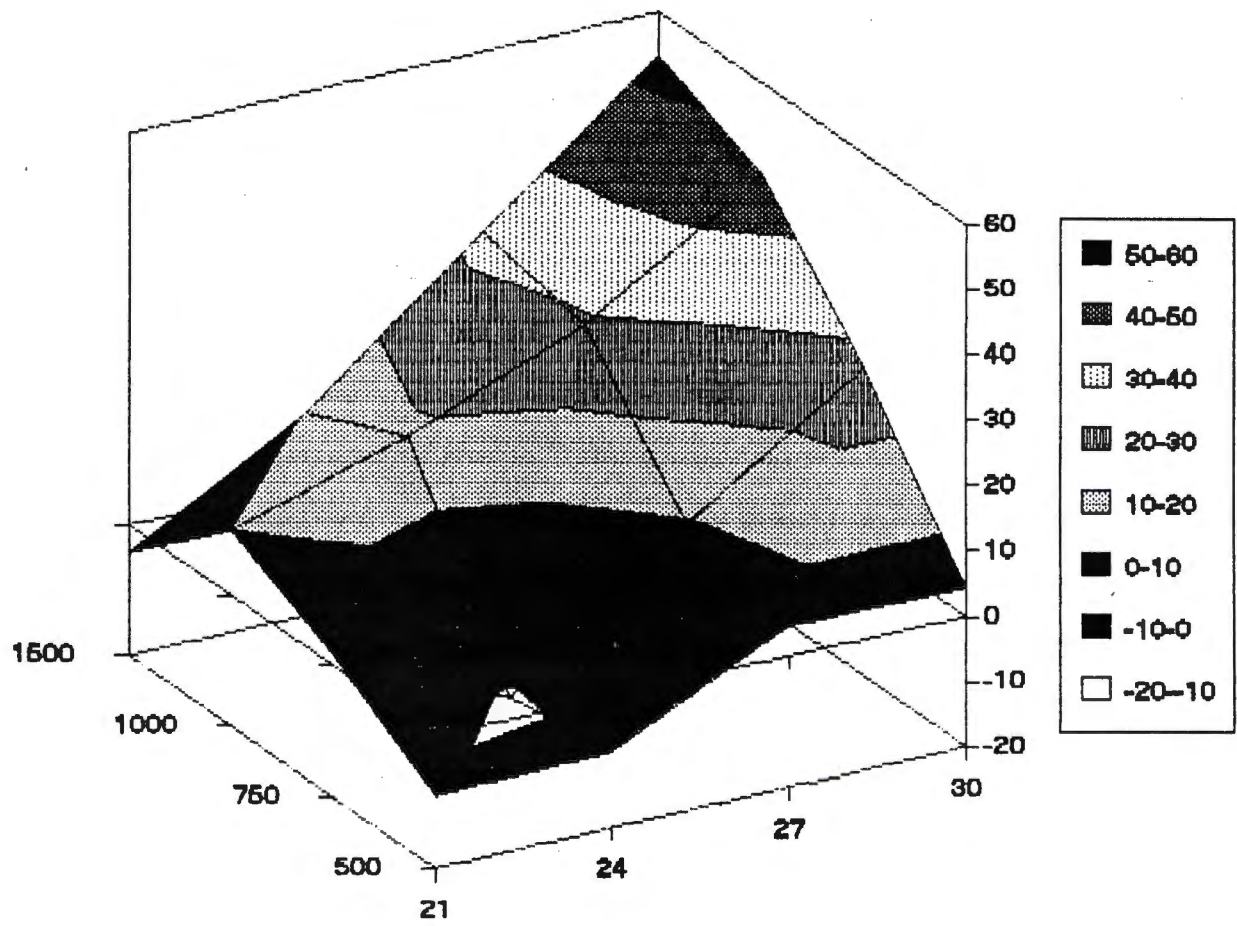
Discussion

Temperature Effects

Both species showed an increase in leaf angle corresponding to an increase in pulvinus temperature. This is similar to what was seen in whole plants and excised pulvini (Fei, poster 1993). Other studies of different light-avoiding species have noted the close relationship between increased leaf temperatures and increased light avoidance, but have failed to measure the organ that is driving the movement (Jurik *et al.* 1990, Gamon and Pearcy 1989). This has significance when considered with studies by Whitson *et al.* (pers. comm. 1993) which establish that the pulvinus receives little or no water or photosynthetic products from the leaf or surrounding tissue.

A paraheliotropic response to temperature would be useful to plants that have to commonly deal with temperature conditions much above optimum. The response has many implications dealing with photodamage risks, transpiration losses, carbon loss through increased respiration. It has been established that paraheliotropic leaf movements serve to keep leaves cooler than they otherwise would have been (Berg and Hsiao 1986). Ludlow and Bjorkman (1984) noted the leaf temperature reduction that took place as a result of paraheliotropism. The plant is able to maintain leaf temperatures lower than would otherwise be found. The temperature increase serves as a critical early response to potentially harmful light conditions as the plant tissue is heated by the increasing PFD. Since conditions in the field during the average growing season could reasonably be expected to

exceed 30 C, it is unknown whether or not the plants eventually saturate in their response to high temperatures on the hottest of days. In our study they did not. On cool, bright days this facet of the mechanism may also serve to keep the plants in a position where they may still be productive, whereas a system reliant on light alone may have caused a great amount of light avoidance, reducing the plants carbon fixing capabilities where no damage was imminent.

Studies by Fu and Ehleringer (1989) on whole plants in the field and in the laboratory have determined that temperature alone can affect paraheliotropism. But the water potential of these plants was not measured and may have contributed to this movement. The plants in our study all maintained a favorable water status, and only a particular leaf was subjected to the conditions of the experiment. Eliminating the factor of plant water stress, it also minimizes the likelihood of some manner of stress signal reaching the pulvinus from the rest of the plant.

The *P. acutifolius* showed a much more striking response to temperature at the high temperature levels than did the *P. vulgaris* (Fig. 3). This would seem to follow from its adaption to the hot, desert climes to which it is native.

PFD Effects

Both of the species exhibited strong increases in leaf angle in response to increasing light intensities. This effect occurred even at the lowest light intensity, around one-quarter of full sunlight (Fig. 4). In light of the findings of Puffett (pers. comm., 1993) this would not be unusual, for the

photosynthetic capacity of the plants was found to be saturated at low PFDs (approximately one-third of full sunlight). When the photosynthetic maximum has been reached, the leaves tilting acts as a protective measure to reduce the chances of damage to the photosystems. Also, in a high leaf index canopy, the leaf tilting would possibly increase the photosynthetic efficiency of the entire plant by allowing light to penetrate to lower canopy levels which would otherwise be below saturation in photosynthetic capacity.

The effect saturates at half of full sunlight. Sato and Gotoh (1983) also noted saturation of the light effect at 40 klux in their study, but without noting the effects of temperature and water potential. In nature these plants would be exposed to PFDs up to 2000 μmol m^{-2} s^{-1}, so it is reasonable to assume that the light effect is routinely saturated at its maximum value. A limit of leaf angle movement influenced by light intensity suggests that a physiological limit of the cellular mechanisms, involving either in signal perception or signal translation.

Interaction of Light and Temperature

In *P. vulgaris* the temperature and PFD effects did not significantly interact. However, although the effects are independent, some linkage exists for a certain level of blue light is necessary for paraheliotropism to take place (Donahue and Berg 1990). In *P. acutifolius* the effects statistically showed some interaction. Berg and Heuchelin (1989) previously demonstrated the independence of the effects of temperature and PFD in soybean seedlings. This suggests that these effects may

have independently evolved as affecters of paraheliotropism. The more aggressive paraheliotropic response of *P. acutifolius* may be a result of its interacting mechanism and a clue to evolutionary and adaptational differences.

The more aggressive paraheliotropic response of the *P. acutifolius* to light intensity and temperature is also noteworthy in another respect. The large differences seen here in leaf angles was due only to changes in light intensity and temperature. In the field the *P. acutifolius* would have other advantages in a hot, bright, and dry environment over *P. vulgaris* due to some whole plant characteristics. These include the morphological adaptations such as high root/stem ratios or characteristics such as the mesophyll drying tolerances noted by Castonguay and Markhart (1991).

Water Potential

The role of water potential in paraheliotropism is a complex one. Light-avoiding leaf movements of plants serve to increase plant water potential, but plant water potential in turn causes paraheliotropism. We kept all of the plants in this study in a well-watered condition and the plant itself was not subjected to the conditions of the experiment. Eliminating the complications of water potential effects gives a clearer picture of the pulvinus temperature and light intensity effects and clears the way for some insight into the workings of these mechanisms.

Conclusion

There are several general findings which can be concluded from the experiments. First, pulvinus temperature does have an effect on paraheliotropism in both species. This effect was greater at the higher temperatures and was very small at the lowest light levels. Second, light intensity (PFD) does affect paraheliotropism and that there are saturation levels of this effect which are similar for both species. At low light intensities almost no paraheliotropism was seen. Also, these paraheliotropic responses took place under generally well-water conditions. Finally, there are differences between the responses of the two species. *P. acutifolius* proved itself to be a more aggressive light avoider under all conditions than *P. vulgaris*, especially those of high temperatures and light intensities. These relationships will help us understand how plants adapt to more rigorous conditions of growth and develop defenses that reduce stress. Answers to such questions of differing adaptations to harsh environmental conditions are of great importance to the world today when we consider that more and more of our food supply is going to be grown on sub-optimal lands by people who cannot afford to support high input crops. The effort must be made to adopt the traits of plants well-adapted to the harsh conditions into breeding programs for high yield varieties.

Literature Cited

Berg V.S.; Heuchelin, S. Leaf orientation of soybean (*Glycine max*) seedings. I. Effect of water potential and photosynthetic photon flux density on paraheliotropism. Crop Sci. 30:631-638; 1990.

Berg V.S.; Hsiao, T. Solar tracking: Light avoidance induced by water stress in leaves of kidney bean seedlings in the field. Crop Sci. 26:980-986; 1986.

Castonguay Y.; Markhart III, A.H. Saturated rates of photosynthesis in water-stressed leaves of common bean and tepary bean. Crop Sci. 31:1605-1611; 1991.

Darwin, C. The power of movement in plants. New York: Appleton; 1881.

Donehue R.; Berg V.S. Leaf orientation in soybean (*Glycine max*) seedings. II. Receptor sites and light stimuli. Crop Sci. 30:638-643; 1990.

Dubetz, S. An unusual photonastism induced by drought in *Phaseolus vulgaris*. Can. J. Bot. 47:1640-1641; 1969.

Forseth, I.N.; Ehleringer, J.R. Solar tracking response to drought in desert annual. Oecologia 44:159-163; 1980.

Forseth, I.N.; Ehleringer, J.R. Ecophysiology of two solar tracking desert winter annuals. II. Leaf movements, water relations and microclimate. Oecologia 54:41-49; 1982.

Fu, Q.A.; Ehleringer, J.R. Heliotropic leaf movements in common beans controlled by air temperature. Plant Physiol. 9:1162-1167; 1989.

Gamon, J.; Pearcy, R. Leaf movement, stress avoidance and photosynthesis in *Vitis californica*. Oecologia 79:475-481; 1989.

Kao, W.Y.; Forseth, I.N. The effects of nitrogen, light and water availability on tropic leaf movements in soybean (*Glycine max*). Plant, Cell and Environment 14:287-293; 1991.

Ludlow, M.; Bjorkman, O. paraheliotropic leaf movement in Siratro as a protective mechanism against drought-induced damage to primary photosynthetic reactions: Damage by excess light and heat. Planta 161:505-518; 1984.

Meyer, W.E.; Walker, S. Leaflet orientation in water-stressed soybeans. Agron. J. 73:1071-1074; 1981.

Oosterhuis, D.; Walker S.; Eastham J. Soybean leaflet movements as an indicator of crop water stress. Crop Sci. 25:1101-1106; 1985.

Pfeffer, W. The Physiology of plants, Vol 3. Translated into English and Edited by Ewart, A.J. The Claredon Press, Oxford; 1881.

Sato, H.; Gotoh, K. Studies on leaf orientation movements in kidney beans (*Phaseolus vulgaris* L.). Japan J. Crop Sci. 52:515-520; 1983.

Schwartz, A.; Gilboa, S.; Koller, D. Photonastic control of leaflet orientation in *Melilotus indicus* (Fabacea). Plant Physiol. 84:318-323; 1987.

Shackel, K.; Hall, a. Reversible leaflet movements in relation to drought adaptation of cowpeas, *Vigna unguiclata* (L.) Walp. Aust. J. Plant Physiol. 6:265-276; 1979.

Vogelmann, T.C. Site of light perception and motor cells in a sun-tracking lupine (*Lupinus succulentus*). Plant Physiol. 62:335-340; 1984.

Wein, H.C.; Wallace, D.H. Light induced orientation in *P. vulgaris* L. Crop Sci. 13:721-724; 1973.