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Paraheliotropism in two *Phaseolus* species: combined effects of photon flux density and pulvinus temperature, and consequences for leaf gas exchange

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Abstract

Phaseolus species exhibit paraheliotropic (light-avoiding) leaf movements in response to environmental stimuli. We investigated the response of two ecologically contrasting species, *Phaseolus vulgaris* (mesic) and *Phaseolus acutifolius* (xeric), to various combinations of photosynthetic photon flux density (PFD) and pulvinus temperature to compare the control and consequences, in terms of photosynthetic gas exchange, of paraheliotropism under identical conditions. Leaflet angles were measured in a cuvette that exposed the leaf to controlled PFD and pulvinus temperature. A gas exchange system was used to determine carbon assimilation, stomatal conductance and water use efficiency (WUE) in response to environmental factors and leaf movements. The effect of tilting leaves was compared with an equivalent reduction of PFD for horizontal leaves. Both species showed significant (but different) responses to PFD and temperature, with increased light avoidance at high levels of both factors. *P. acutifolius* exhibited greater light avoidance under equivalent conditions. The gas exchange consequences of changing leaf angles were similar but not identical to those of an equivalent modification of radiation level. The photosynthetic cost of the leaf movements was negligible, but there was a substantial increase in WUE, especially for *P. acutifolius*. Thus, the benefits of paraheliotropism are achieved at virtually no cost to the plant.

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Keywords: *P. vulgaris*; *P. acutifolius*; Common bean; Tepary bean; Leaf movements

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1. Introduction

The leaves of some plants change orientation throughout the day, increasing or decreasing light interception in response to environmental conditions. These reversible alterations in leaf orientation are due to differential volume changes in tissue of the pulvinus, located at the base of each

leaf or leaflet (Darwin, 1881; Pfeffer, 1881). Motor cells on one side of the pulvinus swell osmotically while those on the opposite side shrink, effecting a curvature of the pulvinus through turgor-based volume changes (Mayer et al., 1985). Paraheliotropic leaf movements are those that reduce light interception by tipping the leaf blade closer to parallel to the incoming radiation.

Environmental stresses, specifically drought, high temperature and high photon flux density (PFD), increase paraheliotropic leaf movements (Darwin, 1881; Dubetz, 1969; Shackel and Hall, 1979; Forseth and Ehleringer, 1980; Oosterhuis et al., 1985; Berg and Heuchelin, 1990). Drought is often accompanied by elevated temperatures and high PFD, so that under natural conditions it is difficult to separate the effects of water potential, temperature and PFD. Under controlled conditions, however, these factors have been shown to increase paraheliotropic movements independently. High PFD or high temperatures may increase light avoidance even in well-watered plants (Fu and Ehleringer, 1989). Many studies have focused on leaf or air temperature (e.g. Sato, 1990; Yu and Berg, 1994), not on the temperature of the pulvinus that carries out the movement, but it is clear that the pulvinus responds directly to temperature (Fu and Ehleringer, 1989) and PFD (Donahue and Berg, 1990).

Paraheliotropism may ameliorate and postpone environmental stress for plants under arid conditions, and can be expected to vary among environments and among related species (Wofford and Allen, 1982; Prichard and Forseth, 1988). Light avoidance by leaves reduces leaf temperature (Forseth and Teramura, 1986; Gamon and Pearcy, 1989), which decreases transpirational water loss (Forseth and Ehleringer, 1982), and keeps leaf temperatures nearer photosynthetic optima (Fu and Ehleringer, 1989). Such movements can also reduce the potential for photoinhibition or photo-damage (Hirata et al., 1983; Ludlow and Björkman, 1984; Gamon and Pearcy, 1989). Paraheliotropism acts in addition to other mechanisms that may protect photosystems, such as chloroplast movements (Gorton et al., 1999). While several benefits may arise from paraheliotropism, there is a potential cost in terms of a loss

of photosynthesis if leaves experience a substantial reduction in PFD. Some of the 'lost' photosynthetically active radiation (PAR) may be intercepted by leaves lower in the canopy (Mooney and Ehleringer, 1978), but this does not apply to seedlings, maximally exposed to the physical environment due to lack of self-shading. However, a potential loss of carbon assimilation associated with lower PFD may still be offset by favorable effects from reduced temperature and transpiration. The overall change in water use efficiency (WUE) can be modeled (Forseth and Ehleringer, 1983) but needs verification for different species and conditions. In addition, leaf optical properties, determined in part by leaf internal structure (Vogelmann et al., 1996) may vary with the angle of incidence of the light. This could affect the relationship between light interception and photosynthetic gas exchange characteristics, making the consequences of tilting of leaves not equivalent to a corresponding reduction in PFD.

The environmental factors temperature and PFD directly affect both leaf angles and photosynthetic gas exchange, and leaf movements further affect gas exchange in turn, so determining the consequences of changes in these factors for paraheliotropic plants presents a significant challenge. Species selected for cultivation in contrasting environments, but grown and studied under identical conditions, allow us to compare ways in which leaf angles are influenced by environmental factors, and how these factors affect photosynthetic gas exchange through leaf movements. In the present study, two species of *Phaseolus* were compared. *Phaseolus vulgaris*, common bean, is a highly productive species widely grown as a commercial crop in mesic habitats. In contrast, *Phaseolus acutifolius*, tepary bean, is grown on a limited basis in xeric, often hot, habitats (Federici et al., 1990). These two species have distinct gas exchange characteristics (Castonguay and Markhart, 1992). This study tested two hypotheses: (1) the pulvini of *P. vulgaris* and *P. acutifolius* respond differently to various combinations of pulvinus temperature and PFD, and (2) resulting differences in leaf orientation lead to corresponding contrasts in photosynthetic gas exchange.

2. Materials and methods

2.1. Plants and growth conditions

P. acutifolius var. *latifolius* G. Freeman and *P. vulgaris* L. cv. Redcloud were grown in a mixture of soil:perlite:peat moss:sand (2:2:2:1) in 15 cm pots. Seeds were germinated at 26 °C and grown in the greenhouse under natural light in Cedar Falls, Iowa, USA, during the summer. Typical midday temperatures were near 30 °C and maximum PFD values were near 1400 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Plants were fertilized every other week with 0.35% (v/v) Peters Plant Food (20-20-20 N-P-K plus micronutrients; Scotts, Marysville, OH, USA). Insecticides were applied as needed. Trials were conducted on the first trifoliolate leaf of each plant, within 3 days of full expansion (approximately stage V3), about 21 days after sowing.

2.2. Measurement of leaflet angle

An entire trifoliolate leaf was inserted into a clear acrylic cuvette 30–60 min prior to the beginning of a trial, maintaining the original angle of the petiole and the leaflets. The rest of the plant was at approximately 25 °C, and was covered loosely with a light-colored, damp cloth for trials at high PFD. An infrared mirror (Optical Coatings Limited, Inc., Santa Barbara, CA, USA) formed the top of the cuvette, reducing the heat load from the 1000 W phosphor coated metal halide lamp (Sylvania, Fall River, MA, USA) positioned directly above. PFD for a horizontal surface inside the cuvette was measured using a quantum sensor (400–700 nm) and light meter (LI-COR, Lincoln, NE, USA). PFD inside the cuvette was adjusted by changing the distance between the lamp and the cuvette.

The temperature of the pulvinus was continuously monitored with a thermocouple meter (Bailey Instruments, Saddlebrook, NJ, USA) using a 2 mil (0.05 mm) type T thermocouple attached to the abaxial side of the secondary pulvinus of the terminal trifoliolate leaflet. The pulvinus temperature was controlled by altering the temperature of the air flowing through the cuvette. The temperature of the cuvette air supply was controlled by a

heat exchanger through which the air passed as it entered the cuvette from below. The angle of the terminal trifoliolate leaflet with respect to horizontal was determined with an inclinometer (Angle Finder, Dasco, Rockford, IL, USA). Angles above horizontal were represented as positive values; those below horizontal were assigned negative values. The cosine of the angle was multiplied by the PFD incident on a horizontal surface to yield the PFD incident on the surface of the leaf. The terminal leaflets studied tipped upward or downward; they did not display axial rotation.

Each plant was exposed to a single PFD level of 500, 750, 1000 or 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. At each intensity tested, the pulvinus temperature was first adjusted to 30 °C and the leaflet angle recorded at 5 min intervals. When the angle remained constant for three to four measurements (10–15 min), the pulvinus temperature was reduced to 27 °C and angles recorded at 5 min intervals until the leaflet stabilized again. Following the same procedure, the stabilized leaflet angles were recorded at 24, then 21 °C. Each series of measurements of leaf angles at four temperatures was made for a single plant at one light intensity. At each light intensity, four to seven individuals of each species were tested. Immediately following the trial, the trifoliolate leaf was excised and leaf water potential determined with a Scholander-type pressure chamber (Soil Moisture Equipment, Santa Barbara, CA, USA).

2.3. Photosynthetic gas exchange

Gas exchange was measured on the youngest fully expanded terminal trifoliolate leaflet with a PACSYS 9900 steady-state photosynthetic gas exchange system (DDG, San Diego, CA, USA), using an external infrared gas analyzer (LI-COR 6252, LI-COR). Leaflet area (one surface) was measured by weighing tracings of the leaflet and was used as the basis for reporting gas exchange data. Illumination was supplied with the metal halide lamp and measured as described above. For each trial, PFD was measured inside the cuvette, parallel to the leaf surface. Two methods were used to alter the PFD at the leaf surface: metal screens 20 cm above the horizontal cuvette; and

altering the angle of the cuvette with respect to horizontal, so that the leaflet was at an acute angle to the rays from the light source, duplicating paraheliotropic leaf orientation. The top of the cuvette was cylindrical, so that the centrally-placed leaflet received light entering the cuvette normal to the cuvette surface. The angle of the cuvette (and therefore, the leaf surface) was measured with an inclinometer as described above. Screens were used to obtain the following series (in order) of approximate PFDs: 100, 200, 260, 460, 730, 950 and 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, the last achieved with no screen. Following the measurement at 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, the cuvette angle was adjusted and the measurements continued. The angles used were 34, 51, 65 and 76° from horizontal, which correspond to 1100, 740, 510 and 320 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, incident on the leaf surface. Each leaflet was measured at the eleven PFD levels (with screens, then tilted) in the order given. Leaflets were allowed to reach photosynthetic equilibrium at each light level before gas exchange measurements were recorded. While measuring leaflet gas exchange, the rest of the seedling was shielded from the light source with a thin dampened white cloth. Leaves from five to six plants of *P. vulgaris* and four to five of *P. acutifolius* were each measured at three leaf temperatures, 24, 27 and 30 °C. Following gas exchange measurements, leaflet water potential was determined using a pressure chamber as described above. For each measurement, A (carbon assimilation), g_s (stomatal conductance), T_1 (leaf temperature), E (transpiration) and PFD were measured. WUE was calculated as A/E , and expressed as ($\mu\text{mol CO}_2$ per mmol H_2O).

2.4. Statistical analysis

Statistical analyses for leaflet angles and gas exchange characteristics were conducted using a SAS (Cary, NC, USA) Proc Mixed program. For responses to temperature and PFD for the two species, a repeated measures ANOVA design was used. For differences between points on individual curves, SIGMASTAT (Jandel Scientific; SPSS, Chicago, IL, USA) was used. A curve fitting program (TABLE CURVE, Jandel Scientific; SPSS) was used

to obtain A at 1025 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (light saturation), and to compare gas exchange characteristics between tilted and horizontal leaves at equivalent light levels. Comparisons between equivalent shaded and tilted leaves were made at 460, 730 and 1025 $\mu\text{mol m}^{-2} \text{s}^{-1}$ using values from the fitted curves.

3. Results

3.1. Effects of PFD and temperature on leaflet angle

The angle of terminal trifoliolate leaflets above horizontal was affected by pulvinus temperature (Fig. 1, $P < 0.0001$) and PFD (Fig. 2, $P < 0.0001$) for both *P. vulgaris* and *P. acutifolius*. In general, at each PFD, leaf angles increased as the temperature of the pulvinus increased (Fig. 1). For *P. vulgaris*, the change in leaf angle between the lowest and highest temperatures tested was statistically significant at $P < 0.05$ at each PFD (Fig. 1A). For *P. acutifolius*, the increase in leaf angle between 21 and 30 °C was statistically significant at all PFD values except 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1B).

Leaf angle increased as PFD increased from 500 to 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in both species for every temperature tested (Fig. 2, data replotted from Fig. 1). The increase in leaf angle was statistically significant at each temperature in *P. vulgaris* (Fig. 2A), but for *P. acutifolius* the increase in leaf angle associated with the increase in PFD to 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was only statistically significant at 30 °C (Fig. 2B). Leaf angles at 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were not significantly different from those at 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for either species at any pulvinus temperature tested (Fig. 2). Plants used in this study were well watered. Values of leaf water potential (ψ_L) for trifoliolate leaves ranged from -0.42 to -0.80 MPa, with a mean of -0.56 MPa ± 0.02 (S.E.M.). In this range, the water status of the leaves in this experiment exerted no statistically significant effect upon leaf angle for plants under similar conditions.

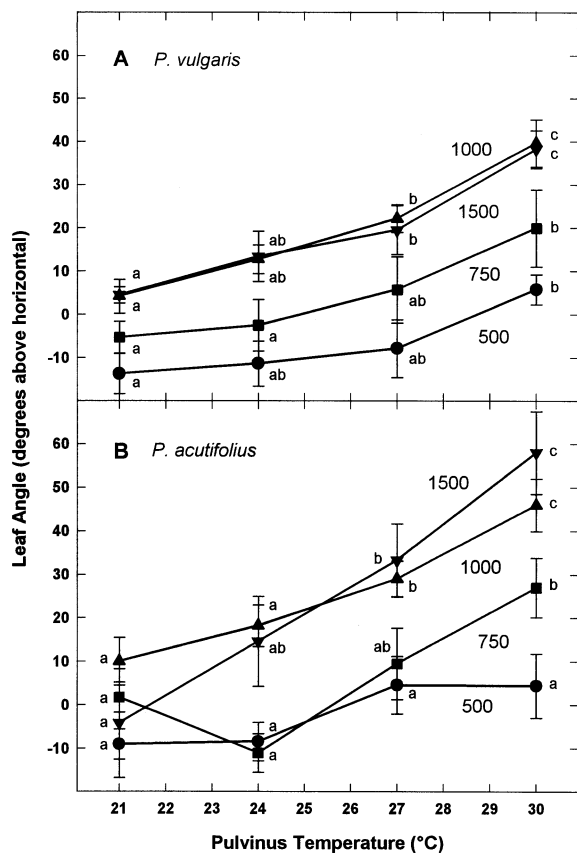


Fig. 1. Effect of pulvinus temperature on leaf angle at four PFDs for *P. vulgaris* and *P. acutifolius*. Circles, squares, triangles and inverted triangles represent data from 500, 750, 1000 and 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Each symbol represents the mean of four to seven samples; error bars indicate S.E.M. Similar letters within a PFD level denote no significant difference between leaf angles at $P < 0.05$ (a posteriori Bonferroni design ANOVA).

3.2. Combined effect of PFD and temperature upon leaf angle

While responses to pulvinus temperature and PFD were observed for both species, *P. acutifolius* responded more strongly to increases in these factors (difference between species $P < 0.04$). Thus the maximum leaf angle attained by *P. acutifolius* at the highest PFD and temperature was greater than that of *P. vulgaris* (Figs. 1 and 2). Neither *P. vulgaris* nor *P. acutifolius* exhibited a significant interaction between temperature and PFD effects.

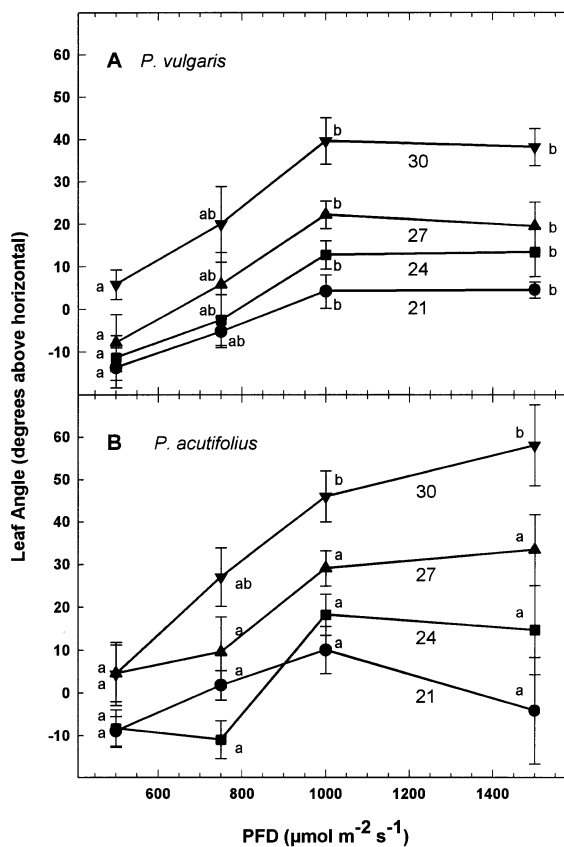


Fig. 2. Effect of PFD on leaf angle at four pulvinus temperatures for *P. vulgaris* and *P. acutifolius*. Data have been replotted from Fig. 1 to illustrate the effect of PFD. Circles, squares, triangles and inverted triangles represent data from 21, 24, 27 and 30 °C, respectively. Number of samples, error bars and letters within a temperature level are as in Fig. 1.

3.3. Photosynthetic gas exchange

The value of A for *P. acutifolius* was approximately twice that of *P. vulgaris* at all temperatures and PFDs tested (Fig. 3, $P < 0.0001$ between species). Assimilation was higher for *P. acutifolius* at 24 and 27 °C than at 30 °C; for *P. vulgaris* the corresponding differences in A were small. The two species differed significantly in their responses to temperature ($P = 0.0001$) and PFD ($P < 0.0001$). Assimilation reached saturation in both species at PFD levels well below those of full sun (Fig. 3). Saturation of A occurred at lower PFD levels in *P. vulgaris*, around 500–700 $\mu\text{mol m}^{-2} \text{s}^{-1}$

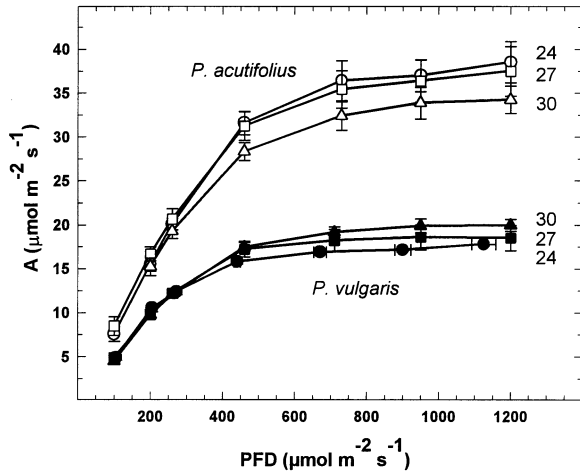


Fig. 3. Effect of PFD and leaf temperature on A of terminal trifoliolate leaflets for *P. vulgaris* and *P. acutifolius*. Filled symbols represent data from *P. vulgaris* and open symbols represent data from *P. acutifolius*. Circles, squares and triangles represent 24, 27 and 30 °C, respectively. Each symbol represents the mean of five to six samples (*P. vulgaris*) or four to five samples (*P. acutifolius*). Error bars represent S.E.M.

s^{-1} , than in *P. acutifolius*, where A did not reach saturation until 800–1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. All measurements were taken on well-watered plants, as described above.

Stomatal conductance (g_s) was higher in *P. acutifolius* than in *P. vulgaris* under the same

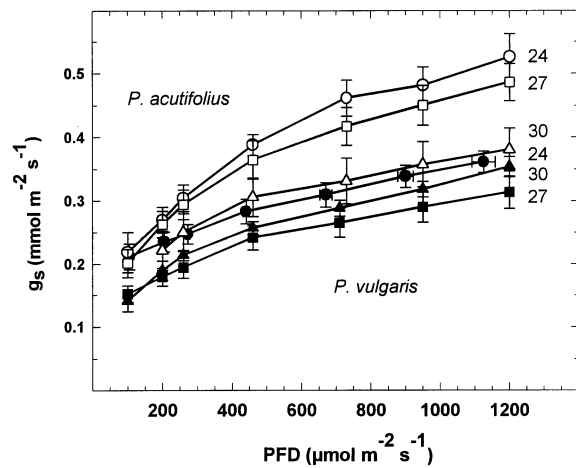


Fig. 4. Effect of PFD and leaf temperature on g_s of terminal trifoliolate leaflets for *P. vulgaris* and *P. acutifolius*. Symbols, number of samples and error bars are as in Fig. 3.

conditions (Fig. 4, $P < 0.0001$ between species). For both species, g_s increased with increasing PFD throughout the range tested. Conductance typically decreased as leaf temperature increased, especially in *P. acutifolius*. The two species differed significantly in their responses of g_s to temperature ($P < 0.0001$) and PFD ($P = 0.001$).

WUE was significantly higher in *P. acutifolius* than in *P. vulgaris* under equivalent conditions ($P < 0.0001$). WUE increased as PFD increased in both species until approximately 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$, where it reached a maximum (Fig. 5). At higher PFD levels a decline in WUE was observed. The effect of PFD was significant for each species ($P < 0.0001$). The most obvious effect on WUE of changes in environmental factors was the increase

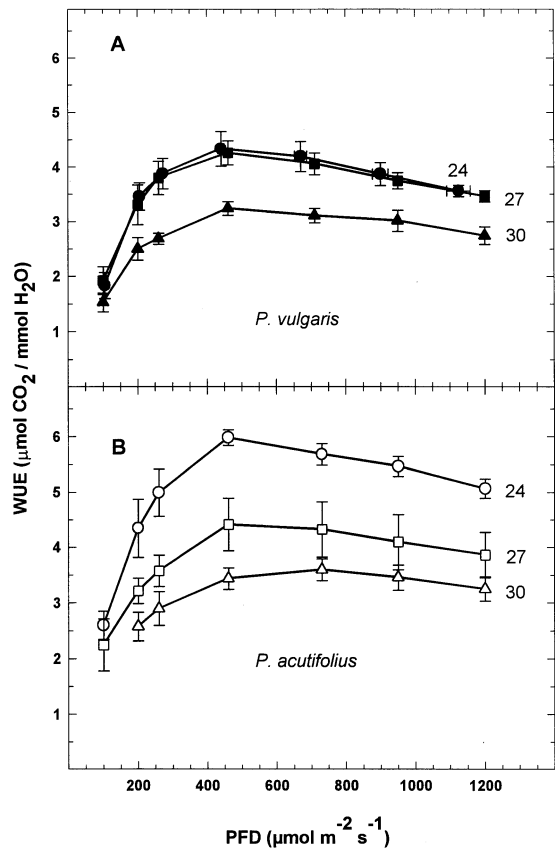


Fig. 5. Effect of PFD and leaf temperature on WUE of terminal trifoliolate leaflets for *P. vulgaris* and *P. acutifolius*. Symbols, number of samples and error bars are as in Fig. 3.

in WUE at lower temperatures, especially evident in *P. acutifolius*. There was a significant difference between species in the response of WUE to temperature ($P < 0.0001$).

3.4. Effect of leaf orientation on the relationship between PFD and *A*

No statistically significant difference in *A* was found between horizontal leaves and equivalently tilted leaves when all data were analyzed together or when separated by species and temperature (Fig. 6). Similarly, no significant differences in g_s or WUE were found between horizontal and tilted leaves for either species. However, when values of *A* at $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ were interpolated from measurements of adjacent values (Fig. 6), tilted leaves of *P. acutifolius* had assimilation rates averaging 4–12% lower than equivalently shaded leaves. Differences for *P. vulgaris* were small, 1.5–2.5%.

4. Discussion

4.1. Separate effects of temperature and PFD on leaf angle

The two species, *P. vulgaris* and *P. acutifolius*, exhibited the same general pattern of response to increases in pulvinus temperature, an increase in angle (Fig. 1). Increased paraheliotropism with increased temperature has been widely reported for a variety of species (e.g. Ludlow and Björkman, 1984; Fu and Ehleringer, 1989; Kao and Forseth, 1992; Yu and Berg, 1994). Investigations in the field (Berg and Hsiao, 1986) and in the laboratory (Berg and Heuchelin, 1990) have shown that these natural changes in leaf orientation reduce leaf temperature typically by a few °C, but in some cases differences of up to 5–6 °C have been demonstrated (Forseth and Teramura, 1986). Thus the leaf does not experience the full effect of increases in environmental temperature, a situation that may have considerable consequences.

Pulvini of both species exhibited increasing leaf angles as PFD increased, up to an apparent saturation of response at $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$

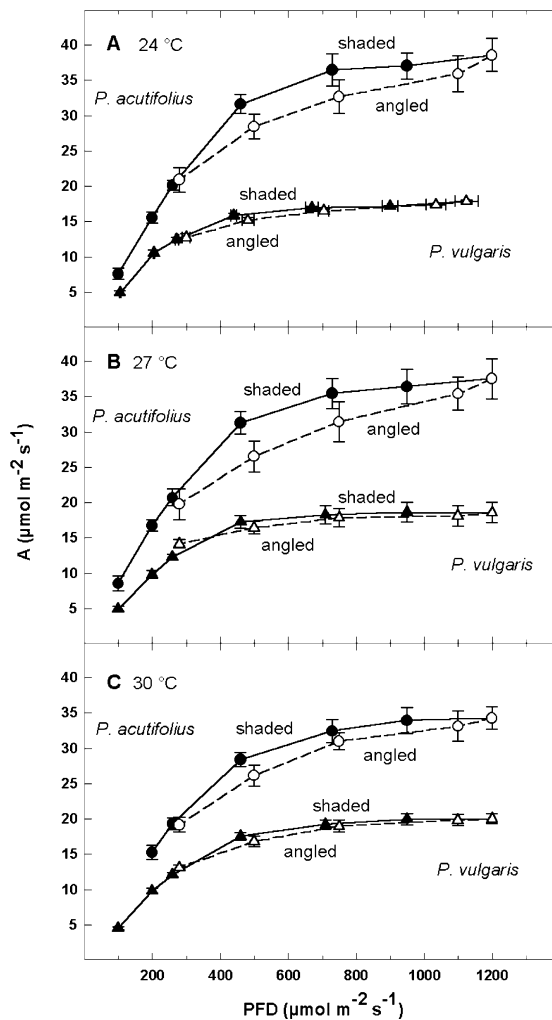


Fig. 6. Effect of leaf orientation on *A* of terminal trifoliolate leaflets for *P. vulgaris* and *P. acutifolius*. *A* was measured in horizontal leaflets (filled symbols) at different PFDs (shaded), and at different leaf angles (open symbols) corresponding to PFDs of 1100, 740, 510 and $320 \mu\text{mol m}^{-2} \text{s}^{-1}$. Measurements were taken at 24, 27 and 30 °C. Triangles represent data from *P. vulgaris* and circles represent data from *P. acutifolius*. Number of samples and error bars are as in Fig. 3.

(Fig. 2). A similar pattern was seen by Berg and Heuchelin (1990), with little difference between angles at 1400 and $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$. In contrast, Fu and Ehleringer (1991) showed continued increases in light avoidance as PFD increased to levels near those of full sun. This discrepancy may be due to a number of factors,

such as plant growth conditions or cultivars, which can vary widely in their responses (Wofford and Allen, 1982; Kao et al., 1994). Some studies (Berg and Heuchelin, 1990) have not fully distinguished between the direct effect of increased PFD and the radiation-induced rise in tissue temperature associated with increased PFD, but the independent effects of PFD and pulvinus temperature were demonstrated for well watered plants of *P. vulgaris* by Fu and Ehleringer (1991). It is also possible that the leaf angle would have peaked between 1000 and 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, then dropped, but this pattern has not been reported elsewhere. The limitation in leaf movement beyond 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ could be due to saturation of the photoreceptor, or of some element of the signal transduction pathway, but probably not of the basic proton pumping mechanism, because at higher temperatures the ‘saturated’ leaf angle is increased further.

4.2. Interaction of temperature and PFD

Maximum values of leaf angle for *P. acutifolius* were nearly 50% greater than those of *P. vulgaris* under the same conditions (Figs. 1 and 2). This more pronounced light avoidance by the xeric species should be beneficial to the plant as a whole in the more stressful environment in which it grows. Overall, for both species, the relationship between the temperature effect and the response to PFD was additive: there was no interaction between the two factors. The degree of light avoidance was particularly pronounced for *P. acutifolius* at the higher temperatures (Fig. 7). On this figure, the vertical distance between the symbols and the dashed line ($x = y$) indicates the degree of light avoidance for the conditions given. The combination of the two responses may be particularly helpful to seedlings, which experience not only direct and indirect radiation from above, but reflection and radiation from the soil surface, all tending to increase leaf temperature. At the same time, the seedlings depend on a limited rooting volume to resupply lost water. Thus considerable benefit accrues to the plant from these paraheliotropic responses, but this can be

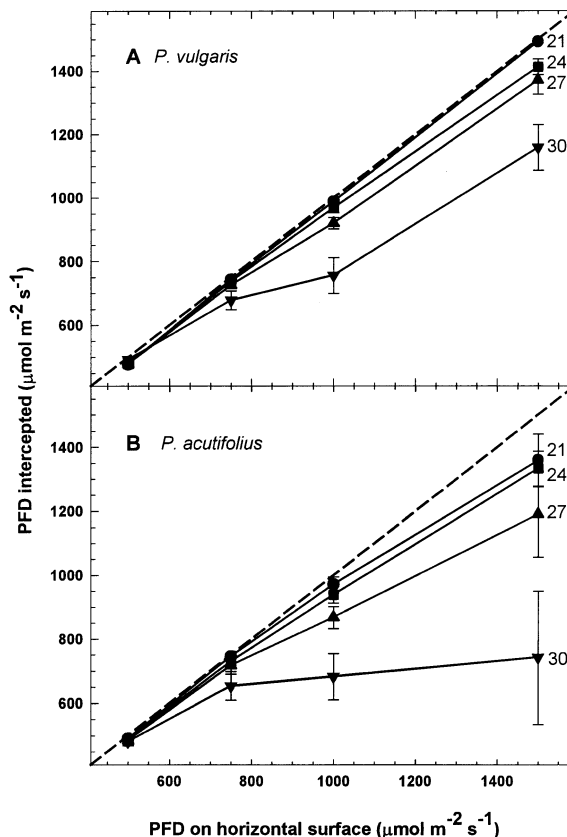


Fig. 7. Effect of overhead PFD on PFD intercepted by a paraheliotropic leaf at four pulvinus temperatures for *P. vulgaris* and *P. acutifolius*. Vertical deviation from the dotted line ($\text{PFD}_{\text{horizontal surface}} = \text{PFD}_{\text{leaf surface}}$) represents decreased light interception by the leaf. Symbols, number of samples and error bars are as in Fig. 2.

evaluated only in light of the corresponding potential costs to the plant.

4.3. Effect of PFD and temperature on gas exchange

Assimilation was approximately twice as high for *P. acutifolius* as for *P. vulgaris* (Fig. 3), as has been reported previously (Castonguay and Markhart, 1992). As expected, *A* rose as PFD increased, with a lower saturation PFD for *P. vulgaris* than for *P. acutifolius*, the difference corresponding to the habitats usual for these species. In these trials involving leaf gas exchange, leaf temperature was controlled. The temperatures

tested allowed examination of the effect of lowering the temperature within the range expected for paraheliotropic, as opposed to horizontal, leaves with radiation directly overhead. Assimilation varied little with temperature (Fig. 3). Although *P. acutifolius* has been characterized as generally more tolerant of high temperatures than *P. vulgaris* (Lin and Markhart, 1996), this was not seen in the limited range tested here (Fig. 3). Given the reduction in light interception associated with paraheliotropism at specific PFD levels, there was little photosynthetic cost associated with the leaf movements, even in the short term.

Conductance rose significantly as PFD increased for both species, and was somewhat higher for *P. acutifolius* than for *P. vulgaris*, in agreement with the work of Castonguay and Markhart (1991). Although g_s , expressed on a leaf area basis, is higher for *P. acutifolius*, the small leaf size of this xeric species limits water loss from the plant as a whole. *P. acutifolius* differed from *P. vulgaris* in that for the xeric species, g_s was reduced at higher temperatures, again limiting water losses under the hot, dry conditions in which this plant usually grows.

WUE was also greater for *P. acutifolius* than for *P. vulgaris*, and was improved significantly by the level of temperature reduction commonly seen in the field for paraheliotropic leaves. For both species, reducing leaf temperature from 30 to 27 °C yielded an improvement in WUE of about a third. For *P. acutifolius*, an additional, larger improvement in WUE was seen between 27 and 24 °C. This offers a clear benefit for plants that may experience water deficits on a daily or longer basis. In addition, the shift of intercepted PFD to lower levels in paraheliotropic leaves (Fig. 7) means that the actual PFD experienced by the leaf lies closer to the peak values of WUE (Fig. 5), which occur near the lowest levels of PFD where A is saturated (Fig. 4). Again, the benefits of temperature-reducing paraheliotropism are more significant for the species from the xeric habitat.

4.4. Tilted versus shaded leaves

For both species, the effects on gas exchange of changing leaf orientation appear to be largely due

to a simple reduction in light interception associated with the cosine of the angle of incidence (Fig. 6). This has been assumed (but not demonstrated) in other investigations (e.g. Forseth and Ehleringer, 1983). There was some difference between the tilted and equivalently shaded leaves near $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, but this was quite small compared with treatment effects, and was probably due to the fact that the leaflets were not absolutely planar. Tissue optical properties that altered the quantity or distribution of light capture at low leaf angles could have led to an alternative, more complicated relationship (Vogelmann et al., 1996), but did not do so.

4.5. Benefits and costs of paraheliotropism for plants in the field

Many of the most significant consequences of changes in leaf angle are experienced not by the motor organ directly responding to the conditions, but by the leaf blade. The same factors that control the orientation of the leaf by acting on the pulvinus also affect the leaf directly and indirectly. The direct effect of paraheliotropism as shown in this investigation is a reduction in the PFD experienced by the leaf (Fig. 7), which other studies have demonstrated to lower leaf temperature and improve water status (Berg and Hsiao, 1986; Berg and Heuchelin, 1990; Saitoh et al., 1994). *P. acutifolius* is substantially more effective at reducing PFD levels, especially under conditions where the PFD on a horizontal leaf is beyond the maximum useful for photosynthesis. The process of reducing radiation absorbed by the leaf may benefit the plant in three ways. The first is through a reduction in leaf temperature, which can prevent thermal damage. The second is that limiting PFD may reduce photodamage. The third, demonstrated in this study, acts through shifting WUE to more favorable values, so that the plant as a whole may postpone the onset of growth-limiting (or survival-limiting) water deficits without an unfavorable effect on carbon balance. The factors that directly control the pulvinar response, and, therefore, leaf angle, are the same factors that affect the leaf itself. Except in extreme cases where the leaf actually shades the pulvinus, the direct,

immediate interaction is in one direction; the pulvinus influences the leaf, but not the reverse. Thus, paraheliotropic leaf movements offer plants a reversible, fast-acting stress avoidance mechanism at little cost to the plant. It has now been shown that the response to high PFD and temperature is more pronounced in the species more subject to these stresses in nature. Thus, both hypotheses are accepted. The two species respond differently to PFD and temperature, and the resultant differences in leaf angle lead to corresponding contrasts in photosynthetic gas exchange.

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