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Modification of paraheliotropic leaf movement in *Phaseolus vulgaris* by photon flux density

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Received 26 March 1990; received in revised form 6 September 1990; accepted for publication 2 October 1990

Abstract. The effects of modification of photon flux density (PFD, 400–700 nm) on paraheliotropic leaf movement were examined in *Phaseolus vulgaris* L. under controlled environmental conditions. The cosine of the angle of incidence to directional PFD ($\cos(i)$), a measure of leaf movement, was linearly and negatively related to PFD. That is, leaflets progressively oriented away from a direct light beam in response to increasing PFD. The minimum PFD causing paraheliotropic movement was approximately $25 \mu\text{mol m}^{-2} \text{s}^{-1}$. When PFD was varied, tissue temperature changed due to an altered energy balance. Since a change in pulvinus temperature can affect leaf movement, experiments were conducted to distinguish the effects of PFD signal and pulvinus temperature. Leaflets oriented to reduce incident PFD levels in response to increasing PFD (either white light or blue light) when pulvinus temperature was kept constant. From these results, we conclude that changes in PFD signals alone can control paraheliotropic leaf movements. *Phaseolus vulgaris* grown outdoors oriented their leaflets to face towards the sun in the morning and again in late afternoon, but avoided the sun's direct rays at midday. This diurnal pattern of paraheliotropic leaf movements can be explained on the basis of known paraheliotropic movements in response to PFD and air temperature.

Key-words: *Phaseolus vulgaris*; common bean; paraheliotropic leaf movement; photon flux density; air temperature; pulvinus temperature.

Introduction

Heliotropic leaf movements are active responses to the movement of the sun, and are of two types: diaheliotropism and paraheliotropism. In the former, leaf laminae remain perpendicular to a light source; whereas in the latter, leaf laminae orient obliquely to a direct light beam (Ehleringer & Forseth, 1980). It has been well documented that heliotropic leaf movements are induced by blue wavelengths but not others (Yin, 1938; Vogelmann & Björn, 1983; Sherriff & Ludlow, 1985; Koller, 1986). Heliotropic leaves orient in response to vectorial light (Koller, 1986), but maintain horizontal position under diffuse light (Sheriff & Ludlow, 1985). The locations of the photoreceptor responsible for these

heliotropic leaf movements differ among plant families. In the Malvaceae, the photoreceptors are located within the leaf lamina, whereas in the Fabaceae, they are located within the pulvinis (Koller, 1986). Sheriff & Ludlow (1985) observed that the diaheliotropic leaves of *Macroptilium atropurpureum* remained perpendicular to the light source at irradiances up to three times full sunlight. In a previous study, Fu & Ehleringer (1989) found that air temperature can affect paraheliotropic leaf movement through a change in pulvinus temperature.

Since increased photon flux density (PFD, 400–700 nm) results in both enhancing signal intensity incident on the photoreceptors as well as enhancing pulvinus temperature (via altered energy balance), it is possible that both factors may be separately contributing to the leaf reorientation response. The relative roles of these two factors in regulating paraheliotropic leaf movements have not been examined, but clearly are very important to understanding the mechanisms of environmental control over paraheliotropic movements.

Leaflets of *Phaseolus vulgaris* L. (common bean) undergo active paraheliotropic movements in the field and laboratory, under well-watered (Wien & Wallace, 1973; Berg & Hsiao, 1986; Fu & Ehleringer, 1989) and drought conditions (Dubetz, 1969). Illumination on the pulvinal region causes leaflet reorientation similar to illumination on the entire leaflet, but illumination on the leaflet blade alone is insufficient to induce the leaflet movement response (Wien & Wallace, 1973; Fu & Ehleringer, 1989). In this study, we investigated possible controls over paraheliotropic leaf movement by PFD in *P. vulgaris*. We also examined the extent to which the PFD effects in conjunction with air temperature changes explain diurnal patterns of paraheliotropic leaf movement under field conditions.

Materials and methods

Plant material

Phaseolus vulgaris cv. Blue Lake Bush (a snap bean) were grown outdoors in 7 dm^3 PVC containers with greenhouse soil (33% loam, 33% vermiculite, and 33% perlite) during the summer months at the University of Utah, Salt Lake City, Utah, U.S.A. Plants were watered to field capacity twice daily and fertilized biweekly with quarter-strength Hoagland solution. All plants used in this study were flowering.

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Measurements of leaf movement

To detect leaflet movement, leaf angle was measured with a protractor and/or inclinometer (Fu & Ehleringer, 1989). The $\cos(i)$, the cosine of the angle between the incident light beam and the vector normal to the leaflet lamina, is a measure of the fraction of the direct light beam incident on the leaf and varies between 0 and 1. The more directly the leaflet faces the light source, the higher the $\cos(i)$ value and the greater the PFD incident on the leaflet.

Laboratory experiments

In experiments to measure the minimum PFD (400–700 nm) necessary to induce leaflet movements, a 75-W tungsten microscope illuminator (Clay-Adams Inc., New York, U.S.A.), which provided more precise control at lower PFD values, was used to provide a spot illumination incident upon the pulvinus of central leaflet. A cut-off filter (model 203, Lee Filters, Andover, U.K.) was used to reduce the near infrared red wavelengths emitted by this lamp. Air temperature adjacent to leaves in these experiments, measured with a thermistor (Vaisala Instruments, Helsinki, Finland), was kept constant at $21.0 \pm 0.3^\circ\text{C}$. The entire plant with the light source was surrounded by a black cloth to eliminate other light sources.

For laboratory experiments, intact leaflets were placed in a ventilated chamber, in which environmental conditions such as air temperature, atmospheric humidity, wind speed and PFD could be controlled (Fu & Ehleringer, 1989). The leaflets could orient freely in the chamber. A 1500-W, phosphor-coated, metal halide lamp (hereafter referred to as 'white light'), directly above the chamber, provided a uniform irradiance over the entire leaf. PFD (400–700 nm) was measured with a quantum sensor (model Li-185A, Li-Cor Instruments, Lincoln, NE, U.S.A.). Air temperature and relative humidity within the chamber were measured with a thermistor and thin-film capacitance chip (Vaisala Instruments, Helsinki, Finland). Pulvinus temperature was measured with 36-gauge, copper-constantan thermocouples inserted into the tissue and recorded with a data logger (model CR21X, Campbell Scientific Inc., Logan, UT, U.S.A.).

For laboratory-based studies of the paraheliotropic leaf orientation in response to blue light, a slide projector (model E-2, Kodak) coupled to a high-intensity grating monochromator (Bausch & Lomb Inc., Rochester, NY, U.S.A.) was used to produce blue light (400–450 nm). A cut-off filter was used to eliminate all wavelengths below 350 nm. PFD of blue light was measured with a quantum sensor (model Li-185, Li-Cor Instruments, Lincoln, NE, U.S.A.). Air temperature adjacent to leaves in these experiments, measured with a thermistor (Vaisala Instruments, Helsinki, Finland), was kept constant at $21.2 \pm 0.3^\circ\text{C}$. For these experiments, entire plants with the light source were surrounded by a black cloth to eliminate other light sources.

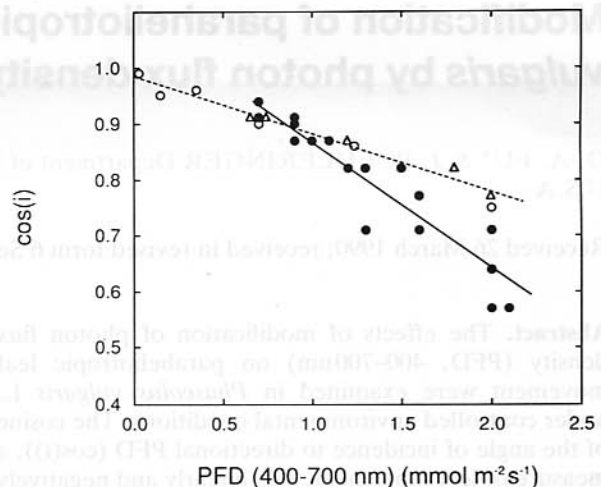


Figure 1. The dependence of $\cos(i)$ on PFD (400–700 nm) in *P. vulgaris*. The filled circles (●) represent $\cos(i)$ in response to PFD when air temperature was kept at $27.0 \pm 0.3^\circ\text{C}$, leaf-to-air water vapor gradients at $2.9 \pm 0.1 \text{ Pa mPa}^{-1}$, and wind speed constant. The solid line is the regression. The pulvinus temperature increased in these measurements as PFD increased because of increased energy loads on the pulvinal region. The dashed line represents the relationship between PFD and $\cos(i)$ with pulvinus temperature kept constant at $27.0 \pm 0.3^\circ\text{C}$ by adjusting either air temperature (○) or wind speed (△).

To facilitate data collection, only the central leaflet was measured in all laboratory experiments, although all three leaflets exhibited reorientation movements. All laboratory experiments were conducted during daylight hours to eliminate any potential interference by nyctinastic movements.

Outdoor observations

The diurnal movement of leaves on plants grown outdoors were recorded between 0900 and 1500 h solar time under clear skies, when physical structures did not obscure the sun's direct beam. PFD (400–700 nm) of sunlight was measured with a quantum sensor (model Li-185A) and air temperature with 36-gauge, copper-constantan thermocouples. Both measurements were continuously recorded on a data logger (model CR21X). Leaf reorientation was measured on all three leaflets.

Data analysis

Statistical analyses were conducted using Statworks™ on a Macintosh microcomputer.

Results

Effect of PFD (400–700 nm) on paraheliotropic leaflet movement

Attached leaflets of bean plants were placed inside a ventilated chamber, and pulvinus were illuminated under a white light source (microscope illuminator). Leaflets did not exhibit any visible orientation response

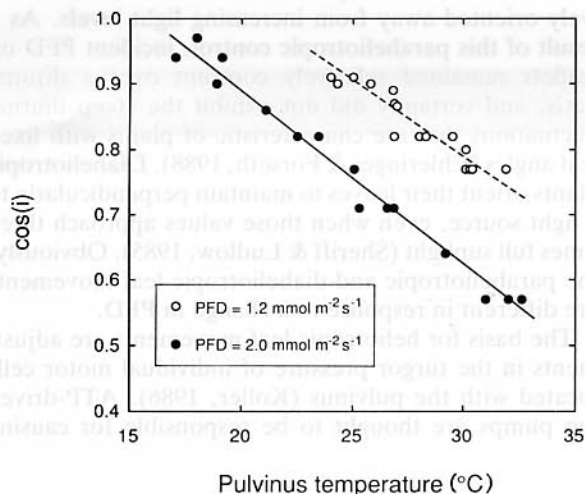


Figure 2. The dependence of cos(i) on pulvinus temperature in *P. vulgaris* under contrasting PFD levels. The solid and dashed lines represent PFD values of 1.2 and 2.0 mmol m⁻² s⁻¹, respectively.

until PFD incident on the pulvinus was above 25 ± 5 μmol m⁻² s⁻¹, at which leaflets oriented about 5°.

In a follow up experiment, a brighter white light source (metal halide lamp) was used to illuminate whole leaves. Cos(i) was then measured as PFD changed. Leaflets actively oriented away from the light beam in response to increasing PFD when other environment conditions were kept constant (Fig. 1). The cos(i) response was linearly related with PFD up to 2.0 mmol m⁻² s⁻¹ (approximately full sunlight). The observed dependence of cos(i) on PFD (400–700nm) was

$$\cos(i)_{\text{PFD}} = 1.10 - 0.23 \cdot \text{PFD}$$

at an air temperature of 27°C. The correlation coefficient for the regression was 0.88.

It is already known that paraheliotropic leaf movement can be affected by pulvinus temperature (Fu & Ehleringer, 1989). Since changes in PFD also affect tissue temperature, an additional experiment was conducted to eliminate the effects of a change in pulvinus temperature. The pulvinus temperature was held constant by adjusting either air temperature or wind speed as PFD was changed. Under these conditions, we observed that changes in PFD still resulted in leaflet reorientation even though pulvinus temperature remained constant (Fig. 1). These observations suggested that PFD as a signal can control paraheliotropic movement, and it is not necessary that this effect is manifested through changes in pulvinus temperature. The sensitivity of leaflet cos(i) to PFD was decreased when pulvinus temperature was held constant, as compared to conditions in which pulvinus temperature also occurred as a result of changes in radiant heat.

The cos(i) response to leaflets to changes in pulvinus temperature was next measured under 60% and 100% full sun conditions (1.2 and 2.0 mmol m⁻² s⁻¹, respectively). Leaflets with equivalent pulvinus

temperatures oriented more obliquely to a light source at higher PFD level (Fig. 2). At both light levels, cos(i) was linearly and negatively related with pulvinus temperature, and the relationships under both PFD levels paralleled each other (Fig. 2). These results suggested that there was little interaction between the effects of the PFD signal and pulvinus temperature within the range of pulvinus temperatures measured in the experiment. Thus, it is reasonable to conclude that the effects of these parameters were additive.

Effect of blue light (400–450 nm) on leaflet movement

Since only blue light can induce heliotropic leaf movements (Koller, 1986), we examined the sensitivity of leaf movements to a change in blue light. When leaflet pulvini were illuminated by a monochromator, increased PFD of blue light caused cos(i) to decrease linearly when other environmental conditions were held constant (Fig. 3). The paraheliotropic response was extremely sensitive to a change in the intensity of blue light, when compared with the response to white light. Pulvinus temperature remained constant during these experiments, since changes in energy input associated with changes in blue light intensities were insufficient to affect tissue temperature. These observations also indicated that PFD can affect paraheliotropic leaf movement without affecting in pulvinus temperature.

Effect of air temperature on leaf movement

As a complementary experiment, the dependence of leaflet cos(i) on temperature was measured under controlled conditions within the ventilated chamber. To more closely mimic field conditions, air temperature and not pulvinus temperature was used as the independent variable. The cos(i) response to a change in air temperature (T) was

$$\cos(i)_{\text{temp}} = 1.85 - 0.045 \cdot T$$

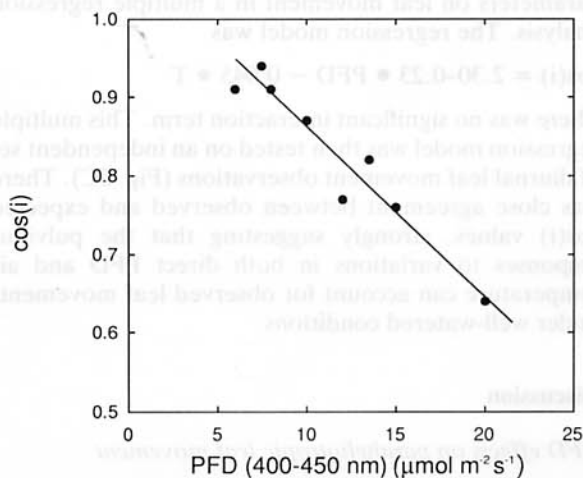


Figure 3. The dependence of cos(i) on PFD of blue light (400–450 nm) in *P. vulgaris*. Air temperature during these measurements was 21.2 ± 0.3°C and pulvinus temperature 21.0 ± 0.3°C.

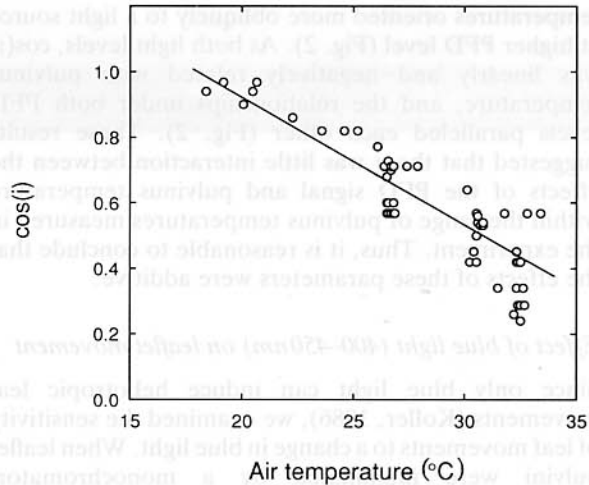


Figure 4. The dependence of $\cos(i)$ on air temperature in *P. vulgaris*. PFD (400–700 nm) during these measurements was $2.0 \text{ mmol m}^{-2} \text{ s}^{-1}$.

when PFD was held constant at $2.0 \text{ mmol m}^{-2} \text{ s}^{-1}$ (Fig. 4). The correlation coefficient for the regression was 0.81.

A diurnal pattern of paraheliotropic leaf reorientation

Outdoors observations were conducted under clear skies and moderate air temperatures. Diurnal curves of PFD (400–700 nm) of sunlight and air temperature are shown in Fig. 5A and B. The $\cos(i)$ values of all leaflets were at a maximum early in the morning, decreased at midday hours (Fig. 5C). That is, leaflets tended to face the sun in the morning and to avoid the direct rays of the sun at midday hours.

Since both PFD and air temperature (the effect on paraheliotropism is through pulvinus temperature) affect leaflet movement, we examined the effects of both parameters on leaf movement in a multiple regression analysis. The regression model was

$$\cos(i) = 2.30 - 0.23 \bullet \text{PFD} - 0.045 \bullet T$$

There was no significant interaction term. This multiple regression model was then tested on an independent set of diurnal leaf movement observations (Fig. 5C). There was close agreement between observed and expected $\cos(i)$ values, strongly suggesting that the pulvinus responses to variations in both direct PFD and air temperature can account for observed leaf movements under well-watered conditions.

Discussion

PFD effects on paraheliotropic leaf movement

Our observations clearly show that $\cos(i)$ was linearly and negatively related to PFD when all other environmental conditions were constant, i.e. leaflets progress-

ively oriented away from increasing light levels. As a result of this paraheliotropic control, incident PFD on leaflets remained relatively constant over a diurnal basis, and certainly did not exhibit the steep diurnal fluctuations that are characteristic of plants with fixed leaf angles (Ehleringer & Forseth, 1988). Diaheliotropic plants orient their leaves to maintain perpendicularly to a light source, even when those values approach three times full sunlight (Sheriff & Ludlow, 1985). Obviously, the paraheliotropic and diaheliotropic leaf movements are different in response to a change in PFD.

The basis for heliotropic leaf movements are adjustments in the turgor pressure of individual motor cells located with the pulvinus (Koller, 1986). ATP-driven ion pumps are thought to be responsible for causing

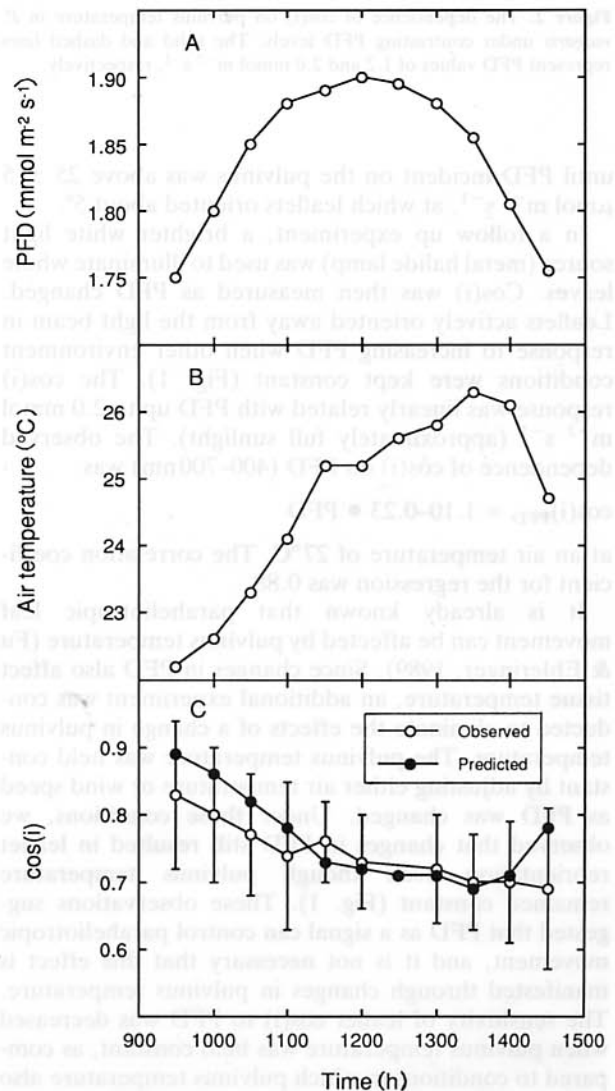


Figure 5. (A) The diurnal pattern of PFD of sunlight in Salt Lake City. (B) The diurnal pattern of air temperature outdoors in Salt Lake City. (C) The observed and predicted diurnal courses of $\cos(i)$ for leaves of *P. vulgaris* outdoors in Salt Lake City. Vertical bars represent \pm one standard deviation.

changes in turgor; inhibitors are known to block ion transport and thus inhibit leaf movements (Wainwright, 1977). Our study suggests that the PFD effect can be mediated through PFD signal perception. Since a change of PFD (400–450nm) incident on pulvinus can cause a change in $\cos(i)$ when pulvinus temperature was constant, the perceptions of PFD signal appears to be located at least in the pulvinus region of bean plants. The photons of the wavelength range that can induce heliotropic response (such as blue light (Koller, 1986)) may provide PFD signals to modify paraheliotropic leaf movements. On the other hand, the photons of the wavelengths that can not induce paraheliotropic response (e.g. yellow and red wavelengths) may affect paraheliotropic leaf movement by changing pulvinus temperature. It has been observed that a change in pulvinus temperature can not affect leaf movement under darkness (Fu & Ehleringer, 1989). Therefore, photons of yellow or red wavelengths can not modify paraheliotropic leaf movement without minimum critical PFD of blue light.

Diurnal paraheliotropic leaf movement

Under field conditions, leaf laminae orient less obliquely to the sun's direct rays in the early morning than at midday period. It has been shown that humidity cannot affect paraheliotropic leaf movement (Fu & Ehleringer, 1989), but vectorial light (Koller, 1986), PFD and air temperature (Fu & Ehleringer, 1989) can. We combined the effects of PFD from vectorial light and air temperature on leaf movement to expect the $\cos(i)$ in the daytime. Since the expected $\cos(i)$ agreed well with the observed $\cos(i)$ in the diurnal curve, this diurnal pattern of paraheliotropic leaf reorientation appears to be mainly controlled by PFD from the sun that moves across the sky, and by air temperature. The limitation of the physical structure of the pulvinus may also be a factor related with the diurnal pattern, especially when the angle between sun's direct rays and horizontal

surface is small. Since the model to predict $\cos(i)$ was based on the experiments in which a light source was fixed above the plants, the model did not account for variations in solar altitude. The variation of paraheliotropic response to light from different altitude may be the reason why predicted $\cos(i)$ values in the early morning and late afternoon were less close to observed $\cos(i)$ values than those during midday period.

Acknowledgments

This research has been supported by grants from U.S. Department of Agriculture-Competitive Research Grants Office.

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