Heliotropic Leaf Movements in Common Beans Controlled by Air Temperature[1]

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ABSTRACT

Heliotropic leaf movements were examined in common beans (*Phaseolus vulgaris* cv Blue Lake Bush) under outdoor and laboratory conditions. Heliotropic leaf movements in well-watered plants were partly controlled by temperature, and appeared to be independent of atmospheric humidity and CO_2 concentration. When environmental conditions were held constant in the laboratory, increased air temperature caused bean leaves to orient more obliquely to a light source. Ambient CO_2, intercellular CO_2, and net photosynthesis were not correlated with the temperature-induced changes in heliotropic movements, nor did they significantly affect these movements directly. The effect of air temperature on leaf movements need not be mediated through a change in leaf water potential, transpiration, or leaf conductance. Air temperature modified laminar orientation in light through its effect on tissue temperature in the pulvinal region, not that of the lamina or petiole. However, under darkness the temperature effects on leaf movements were not expressed. Active heliotropic movements in response to air temperature allowed lamina temperature to remain close to the thermal optimum of photosynthesis. This temperature effect underlies a commonly observed pattern of leaf movements under well-watered conditions: a tendency for leaves to face the sun more obliquely on hot days than cool days.

Active and continuous leaf movements in response to the movement of the sun (heliotropic leaf movements) have been described for a large number of native plants and crops (3, 6, 7). Species with heliotropic movements orient their leaves perpendicularly, obliquely or parallel to the sun's direct rays, thus regulating the radiant energy incident by the leaf lamina. Heliotropic leaf movements are induced by blue light (15, 24, 26, 28). The site of light perception is located at the pulvinus in the Fabaceae (15, 22, 24, 25, 27), and in the leaf lamina in the Malvaceae (16, 23). Fisher and Wright (9) report that the heliotropic response was eliminated in the absence of ambient CO_2, suggesting an essential requirement of positive net photosynthesis for heliotropic leaf movements in *Lavatera cretica*. However, Koller (15) argued that it was unlikely that photosynthetic activity played any role in perception of vectorial excitation, since photosynthetically active red light was ineffective for vectorial excitation (23, 29). While many observations have shown that heliotropic leaf movements are controlled by vectorial light (15–17, 23, 27), little attention has been given to the possible dependence of heliotropic move-

ments on other environmental factors such as temperature and atmospheric humidity.

Heliotropic movements in which leaf laminae reorient away from the sun's direct rays have been reported to occur primarily in response to limited soil moisture availability (1, 2, 4, 10, 12, 18, 20). However, there are examples of both native and cultivated leguminous species that exhibit such heliotropic leaf movements even under conditions of adequate soil-water availability (2, 10, 11, 13, 14).

The purpose of this study was to examine the possible effects of air temperature and atmospheric humidity on leaf orientation in light in the absence of water stress. Common bean (*Phaseolus vulgaris*) was chosen for this study, since the species was already known to exhibit heliotropic leaf movements under a variety of conditions (2, 4, 27).

MATERIALS AND METHODS

Plant Material

Phaseolus vulgaris cv Blue Lake Bush were grown outdoors in 5-L pots with greenhouse soil (33% loam, 33% vermiculite, 33% perlite) during summer at the University of Utah, Salt Lake City, Utah. Plants were watered twice daily to ensure that water stress did not develop. Plants at an early fruiting stage were used for laboratory studies.

Measurements of Diurnal Parameters

For plants studied outdoors, the photon flux (400–700 nm) incident on a horizontal surface was measured with a quantum sensor (model LI-185A, LI-Cor Instruments, Lincoln, NE). Photon flux incident on leaf laminae was measured with photocells (NEC PH201A), which have a spectral sensitivity and cosine response similar to that of the quantum sensor, and which had also been calibrated directly against the quantum sensor. Air and leaf temperature were measured with 36-gauge copper-constantan thermocouples. Data were recorded on a datalogger (model 21, Campbell Scientific Inc., Logan, UT).

Laboratory Studies

Leaf movements were observed on intact leaves placed in a ventilated chamber, in which air and leaf temperature, atmospheric humidity, wind speed, ambient CO_2 and photon flux could be controlled. Leaves enclosed within the FEP Teflon-walled chamber were freely able to reorient. Two light sources were used: a 1500 W metal halide lamp, which

provided a uniform irradiance over the entire leaf, and a 75 W microscope illuminator (Clay-Adams Inc., New York, NY), which provided a narrow beam that could be focused onto different portions of a single leaflet. In order to determine whether the leaf movements were a tropic versus a nastic response, an initial experiment was conducted in which the light originated from overhead (90°) or from an angle of 45°. In both cases, the leaf angle changes were dependent on angle of the incident beam, and therefore we conclude that the leaf movements were tropic responses. In order to simplify experiments, both light sources were fixed directly above the chamber. Photon flux was measured with a quantum sensor (model LI-185A). Supplemental near-infrared radiation, used as a heat source, was provided by a microscope illuminator filtered through a long-pass filter that removed wavelengths below 800 nm (filter LL-800, CORION, Holliston, MA). Air temperature and relative humidity inside the chamber were measured with a thermistor and thin-film capacitance chip (Vaisala Instruments, Helsinki, Finland). Leaf lamina, pulvinus and petiole temperatures were measured with 36-gauge copper-constantan thermocouples inserted into the tissue and recorded with a datalogger (model 21X, Campbell Scientific Inc., Logan, UT). The chamber was an open-ventilated system. Air to the chamber was mixed to defined CO_2 concentration with a mass flow controller (model 5850, Emerson Electric Co., Hatfield, PA) and/or a flowmeter (model 604, Matheson, East Rutherford, NJ). Changes in both incoming CO_2 concentrations (measured with an infrared gas analyzer [model Mark II, Analytical Development, Hoddington, England]) and atmospheric humidity levels (by changing the incoming dew point temperature) were used to control chamber atmospheric conditions.

Leaf water potentials were measured with a pressure chamber (PMS Instruments, Corvallis, OR).

Photosynthetic measurements of individual, intact leaflets were measured with an open gas exchange system (5).

Measurements of Leaf Movements

To detect leaf movements, cos(i), the cosine of the angle between the incident light beam and the vector normal to the leaf lamina, was measured with a protractor and/or an inclinometer (10). To facilitate data collection, only the central leaflet was measured, although all three leaflets exhibited heliotropic leaf movements. Cos(i) is a measure of the fraction of the direct beam incident on the leaf lamina, and will vary between 0 (when the lamina is parallel to the incident light beam) and 1 (when the lamina is perpendicular to the beam). Common beans exhibit not only heliotropic movements but also nyctinastic movements at night (21). To remove any potential interference by nyctinastic movements, all experiments were conducted during daylight hours.

RESULTS

Outdoor Observations

Under well-watered but otherwise natural environmental conditions, there were active heliotropic leaf movements by common beans (Fig. 1). Leaf laminae tended to face the sun
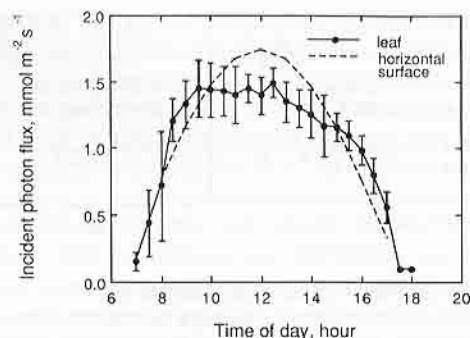
Figure 1. Diurnal courses of solar radiation incident on a horizontal surface and on leaves of *P. vulgaris* on September 1, 1986. Vertical bars are standard errors for leaf measurements.

in the morning, receiving a greater photon flux than was incident on a horizontal surface. By midday, leaves oriented away from the sun's direct rays so that the incident photon flux was less than that on a horizontal surface. However, leaf laminae again began to face the sun by late afternoon.

In the sun, heliotropic leaf movements in well-watered bean plants were highly correlated with air temperature. Cos(i) values were measured on bean plants at noon on 17 different days with similar photon flux level but different air temperatures. Leaf laminae oriented away from the direct solar rays when air temperatures were increasing ($r = 0.44$, $n = 136$, P < 0.0001). Since the gradient in water vapor pressure between leaf and atmosphere divided by total atmospheric pressure (Δw) was also influenced by temperature, it was not possible to clearly separate the influences of temperature and atmospheric humidity on leaf movements with these data.

Shading had an immediate impact on the leaf movements of bean plants. When the direct solar beam was blocked, leaf laminae assumed a horizontal position over a 30 min period, and from that point on there were no further leaf movements while leaves remained shaded. If only the pulvinus base of leaf lamina was shaded, and the lamina and petiole remained sunlit, the lamina exhibited a pattern not significantly different as if the entire leaf was shaded (Student's $t = -0.85$, $n = 20$, P $= 0.40$). When only the pulvinus was illuminated and the other parts of leaf were shaded, cos(i) was not significantly different from that of an entire leaf under illumination (Student's $t = 0.49$, $n = 20$, P $= 0.63$). These results indicated that the light was required for the leaf movements and that the site of light perception was the pulvinus.

Heliotropic Movement Independent of Atmospheric Humidity

Bean leaves from well-watered plants were examined for the possible dependence of heliotropic leaf movements on changes in atmospheric humidity. Leaves within the chamber were illuminated with a metal halide lamp. Water content of the air, expressed as either RH or Δw (leaf-to-air water vapor pressure gradient divided by total atmospheric pressure), in the chamber was changed, but other environmental conditions remained constant. The cos(i) of leaves did not significantly respond to a change in RH or Δw (Fig. 2). These results indicated that heliotropic leaf movements, at least under well-
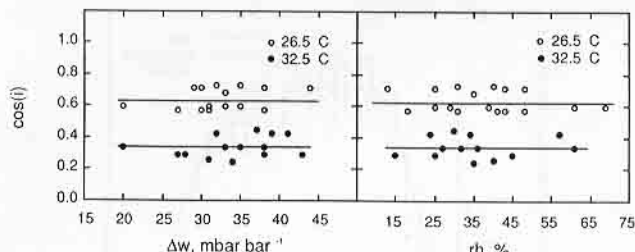
Figure 2. Cos(i) independence of atmospheric humidity (Δw and RH) for *P. vulgaris* under laboratory conditions at two temperature levels (26.5 and 32.5°C). Photon flux was 2.0 mmol m^{-2} s^{-1}, and ambient CO_2 concentration was 355 μL L^{-1}. Cos(i) *versus* Δw: $r = 0.39$, $n = 15$, $P = 0.12$ (at 26.5°C); and $r = 0.26$, $n = 14$, $P = 0.38$ (at 32.5°C). Cos(i) *versus* RH: $r = 0.19$, $n = 15$, $P = 0.46$ (at 26.5°C); and $r = 0.03$, $n = 14$, $P = 0.91$ (at 32.5°C).
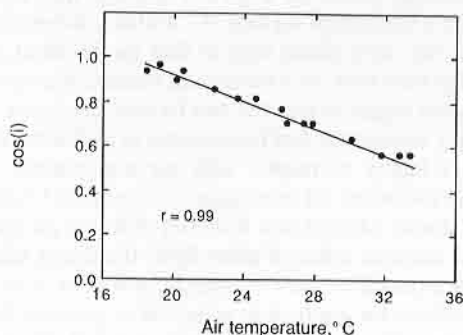
Figure 3. Correlation between cos(i) and air temperature for *P. vulgaris* under laboratory conditions when leaves were allowed to freely transpire. Photon flux was 2.0 mmol m^{-2} s^{-1}, Δw was 30 mbar bar^{-1}, and ambient CO_2 concentration was 355 μL L^{-1}.

watered conditions, were independent of atmospheric humidity under the range of conditions used in the experiment.

## Dependence of Heliotropic Movements on Air Temperature

Bean leaves from well-watered plants within the chamber were again illuminated with a metal halide lamp. Increased air temperature caused bean leaves to orient more obliquely to a light source, decreasing the incident photon flux, when other environmental parameters were held constant (Fig. 3). However, in darkness or under very low diffuse photon flux (less than 50 μmol m^{-2} s^{-1}) the change in cos(i) before and after a change in air temperature was negligible (change in cos(i) was 0.00 ± 0.01, $n = 5$). Thus, a minimum photon flux was required for the effects of air temperature on leaf movements to be expressed.

Previous work (9) indicated an effect of ambient CO_2 on heliotropic movements, suggesting a possible dependence of heliotropic leaf movements on current photosynthetic activity. Since a change in temperature may cause a change in photosynthetic activity, bean leaves were examined for the possible dependence of heliotropic movements on a change in photosynthetic activity in conjunction with a change in air temperature. Leaves from well-watered plants were placed within the chamber and illuminated with a metal halide lamp.

Under exposure to two extreme CO_2 concentrations in the chamber (355 μL L^{-1} and less than 3 μL L^{-1}), there were no detectable differences in the sensitivity of leaf movements to changes in air temperature (Fig. 4). When chamber CO_2 concentration was less than 3 μL L^{-1}, intercellular CO_2 concentrations were likely close to the compensation point, and there was virtually no net photosynthetic CO_2 uptake. From these results we conclude that ambient CO_2, intercellular CO_2 and net photosynthesis were not correlated with the temperature-induced changes in heliotropic movements, and that they did not directly affect these movements.

Berg and Hsiao (2) reported that leaf water potential was correlated with heliotropic leaf movements in beans. Therefore, the temperature-induced changes in leaf orientation were evaluated in the absence of leaf water potential change to examine the possibility that the effect of air temperature on heliotropic movements was through its effect on leaf water potential. In these experiments, water was withheld from bean plants for several days until predawn leaf water potentials had declined to approximately -6 bars. The plants were kept in darkness for 14 h before the observations. Since our earlier observation had indicated that the pulvinus was the site of light perception for leaf movements, only the pulvinus was illuminated. The leaf water potential of the observed leaflet was measured immediately following an observation, and the leaf water potential before the observation was measured on another leaflet from the same plant. The leaf water potentials were not significantly different before and after observations (Student's $t = -0.39$, $n = 6$, $P = 0.71$). There were no detectable changes in leaf conductance or transpiration during these observation periods. Despite constancy in these leaf water relation parameters, cos(i) of leaves from plants under contrasting leaf water potentials was still dependent on air temperature (Fig. 5). Thus, these effects of air temperature on leaf movements need not be mediated through changes in leaf water potential, transpiration or leaf conductance. Since the leaf laminae remained in darkness during the measurements, these data provided additional support for our earlier suggestion that net photosynthesis was not necessary for leaf heliotropic movements.

We had hypothesized that air temperature affected heliotropic leaf movements through its effect on tissue tempera-
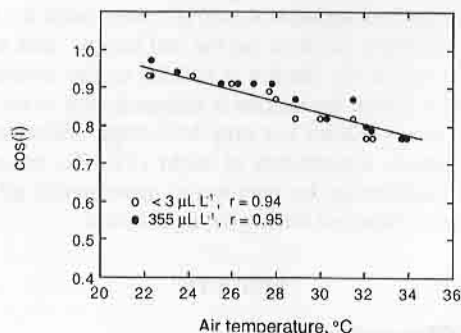
Figure 4. Correlation between cos(i) and air temperature for *P. vulgaris* under laboratory conditions at different ambient CO_2 concentrations (355 and less than 3 μL L^{-1}). Photon flux was 1.2 mmol m^{-2} s^{-1}.
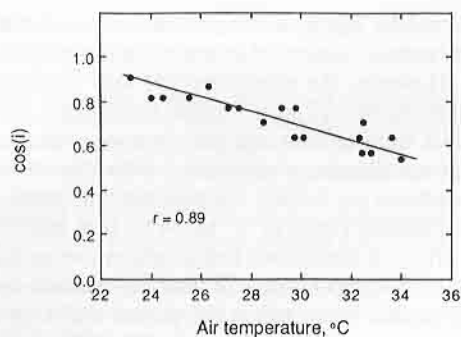
Figure 5. Correlation between cos(i) and air temperature for *P. vulgaris* under laboratory conditions when only pulvinus was illuminated with microscope illuminator. The transpiration rate and leaf conductance were not detectable, leaf water potential was constant, and photon flux was 1.6 mmol m^{-2} s^{-1}.

Table I. *Change in Cos(i) in Response to Increased Tissue Temperatures of the Pulvinus, Middle Lamina Over Veinal Regions, Noncentral Lamina over Nonveinal Regions, and Petiole Portions of Leaf*

For all observations, the pulvinus was illuminated with 1.2 mmol m^{-2} s^{-1} photon flux (400–700 nm) and the temperatures of various parts was raised 4.5°C with infrared radiation as a heat source. Data are means ± one standard deviation.

Portion of Leaf Receiving Additional Heating	Change in Cos(i)
Pulvinus	0.12 ± 0.04***
Central portions of lamina	0.00 ± 0.01ns
Noncentral portions of lamina	0.00 ± 0.01ns
Petiole	0.00 ± 0.01ns

*** $p < 0.001$, NS = nonsignificant from zero.

ture at a site(s) within leaves. To detect these location(s), experiments were conducted in which only the pulvinus base of leaf lamina was illuminated with visible light. A second microscope illuminator, coupled with a near-infrared filter to provide a radiant heat source, was then used to raise the tissue temperature of various parts of leaf (lamina, petiole or pulvinus). This near-infrared heat source increased tissue temperatures by changing tissue energy balance, but did not change air temperature within the chamber. In control experiments, when the pulvinus region of leaf lamina was illuminated with only near-infrared radiance (in the absence of visible light), there was no impact on leaf movements (change in cos(i) = 0.00 ± 0.01, $n = 8$). At a constant air temperature, leaf lamina reorientation in the light in response to supplemental near infrared heating occurred only when pulvinus temperature was increased (Table I). Leaf lamina did not reorient when tissue temperatures of either the petiole (2 cm away from pulvinus) or lamina (central, lateral or veinal positions at least 2 cm away from pulvinus) were increased by infrared heating. Thus, we conclude that temperature modifies leaf orientation of beans in the light by affecting tissue temperature in the pulvinal region, not that in the lamina or the petiole.

## Dependence of Lamina Temperature on Heliotropic Movements

A major consequence of heliotropic leaf movements in response to changes in air temperature was to affect the

incident photon flux on the leaf lamina, so that leaf lamina temperature changed. The observed leaf lamina temperature within the cuvette approached air temperature when air temperature was approximately 29°C (Fig. 6). At air temperatures below 29°C, leaf lamina temperatures exceeded air temperatures. At air temperatures above 29°C, leaf lamina temperatures were below air temperatures. Since leaf laminae oriented more perpendicularly to the light source received a higher photon flux when air temperature was lower, leaf lamina temperature rose above air temperature. At higher air temperatures, leaf lamina reorientation to an angle more oblique to the light source resulted in reduced energy absorption so that leaf lamina temperature was lower than air temperature. It appeared that heliotropic leaf movements moderated leaf lamina temperatures such that they remained near 29°C in the experimental conditions.

The impact of these temperatures on photosynthesis was determined by measuring the dependence of net photosynthesis on leaf lamina temperatures using an open gas exchange system. Under saturating photon fluxes and typical atmospheric conditions, the photosynthetic temperature optimum was between 29 and 32°C (Fig. 7). However, the dependence of photosynthesis on temperature was relatively flat, and as a result photosynthetic rates decreased less than 10% over the broader temperature range of 27 to 34°C. In combination
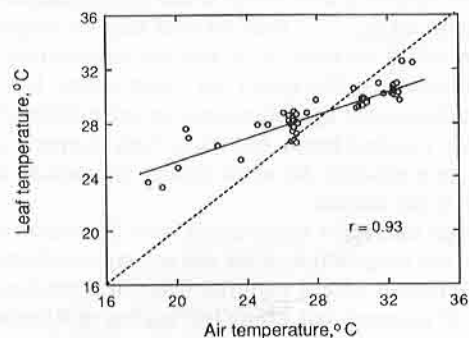
Figure 6. Correlation between leaf lamina temperature and air temperature for *P. vulgaris* under laboratory conditions when photon flux was 2.0 mmol m^{-2} s^{-1}. The *dashed line* represents the 1:1 curve.
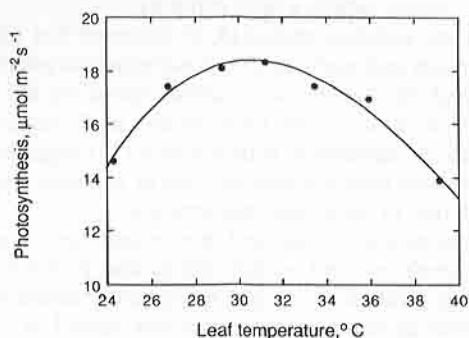
Figure 7. Regression between net photosynthesis and the leaf lamina temperature for *P. vulgaris* under open gas exchange system, when photon intensity was 2.0 mmol m^{-2} s^{-1}, and Δw was 30 mbar bar^{-1}. Absolute photosynthetic rates among plants varied ± 10%, but there was no significant variation in the shapes of the response curves.

with our observations of heliotropic movements in response of air temperature, it appeared these leaf movements resulted in lamina temperatures remaining close to optimal photosynthetic temperatures.

DISCUSSION

Active leaf movements in response to the diurnal movement of the sun across the sky are termed heliotropic movements (6, 7). These movements are of two types: diaheliotropic and paraheliotropic. In leaves with diaheliotropic movements, cos(i) remains constant at 1.0 throughout the day because leaf folding or cupping can not occur. However, leaves with paraheliotropic movements are capable of adjusting cos(i) to a range of values between 0 and 1. It is a misconception to consider that heliotropic movements are only those in which leaves are oriented parallel to the sun's rays (*i.e.* a cos(i) of 0).

Previous studies have clearly established that heliotropic leaf movements are controlled by vectorial light (15–17, 23, 27). Our results demonstrate that air temperature can play a dominant role in determining the extent of paraheliotropic adjustment to those heliotropic movements in common bean. While paraheliotropic leaf movements have been thought to occur under water stress conditions, our observations show that they can also occur in well-watered plants, and that leaves from well-watered plants orient much more obliquely to the sun at noon on hot days than on cool days. A simple mechanism in which vectorial light and air temperature control leaf movements could explain our observations. It is reasonable that directional light stimulates an orientation of leaflets toward the incident beam, but that a high temperature stimulates a reorientation so as to reduce the actual intensity incident on the lamina.

Although the leaflet movements were dependent on temperature, this temperature effect was not expressed until leaves were illuminated with a vectorial light. In a previous study, Nilsen (19) reported that winter leaf curling of *Rhododendron* species was highly correlated with changes in temperature under darkness. The temperature-controlled heliotropic leaf movements of beans in our study are distinguishable from thermotropic leaf movements in *Rhododendron* in that bean leaf movements require a light stimulus.

While two previous studies (8, 9) indicated that photosynthetic activity and ambient CO_2 concentrations affected heliotropic leaf movements in *Lavatera cretica*, we did not observe any dependence on these factors in *P. vulgaris*. Our results are in agreement with Koller's (15) suggestion that photosynthesis does not play any role in perception of vectorial excitation in heliotropic movements.

Whereas paraheliotropic leaf movements can change photon flux levels incident on leaf lamina and therefore change lamina temperature, these leaf movements themselves were not affected by lamina temperature but instead by temperatures in the pulvinal region. Since leaf lamina and pulvinus differ in water vapor conductance and in size and shape, energy transfer characteristics should vary between these two tissues at a given air temperature and level of radiant energy intercepted by them. Under our experimental conditions, which simulated outdoor environments, heliotropic movements affected by pulvinus temperature caused lamina temperature to remain close to the optimal photosynthetic temperatures. However, the correlation between lamina and air temperatures shown in Figure 6 might be shifted if the energy transfer rates from lamina and pulvinus were changed as in outdoor versus laboratory conditions. Since the dependence of photosynthesis on lamina temperature was relatively flat in the temperature range of 27 to 34°C, it is expected that under a variety of conditions heliotropic movements would result in lamina temperature still near the thermal optimum of photosynthesis, when plants are grown under conditions similar to those in our experiments (25–35°C daytime air temperature).

Previous studies have reported that paraheliotropic leaf movements were correlated with changes in soil and leaf water potentials (2, 6, 7, 20). Our observations clearly show that air temperature can influence the extent of paraheliotropic leaf movements even in the absence of changes in soil and plant water status. We hypothesize that the control of paraheliotropic leaf movements by air temperature occurs not only under well-watered conditions but also under water stress.

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