LIGHT PERCEPTION FOR SUN-TRACKING IS ON THE
LAMINA IN CROTALARIA PALLIDA (FABACEAE)

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Trifoliolate leaves of Crotalaria pallida Aiton (Fabaceae) exhibit sun-tracking behavior in simulated days and in response to a fixed, oblique light. The site of light perception for sun-tracking is on the lamina, necessitating transport of a signal from the lamina to the site of response (the pulvinule at the base of the leaflet). Evidence for the site of light perception on the lamina includes the following: (1) leaflet movement in response to oblique light is not affected by shading the pulvinule or by illuminating the pulvinule with vertical light; (2) leaflet movement is stopped by shading the lamina while illuminating the pulvinule with oblique light. The proximal end of the leaflet is the most sensitive region for light perception. Light reaching the midveins is not necessary for leaflet reorientation. Presentation times of as little as 10 min followed by darkness resulted in partial leaflet movement in young leaves. This indicates that the signal was not inductive in nature. Estimates of the rate of signal transport range from 3 to 12 cm/h, within the range of phloem transport.

Key words: Crotalaria pallida; diahliotropism; Fabaceae; sun-tracking.

The leaves of many plants maintain their lamina normal to the sun throughout the day. This sun-tracking movement, also called diahliotropism, occurs in at least 16 families (Ehleringer and Forseth, 1980) and is common in the Fabaceae. Many members of the Fabaceae also exhibit paraheliotropic leaf movement, lamina orientation parallel to the sun ray’s, in response to midday stresses such as high light irradiances, high temperature, or water stress (Koller, 1990). Diahliotropic leaf movements maximize light interception and hence photosynthesis (Ehleringer and Forseth, 1980). The occurrence of both diahliotropic and paraheliotropic leaf movements allows leaves to avoid situations of high water loss, yet maximize photosynthesis during the morning and evening (Koller, 1990). At night, these same leaves exhibit nyctinastic leaf folding.

Lamina reorientation is controlled by differential volume changes in the motor cells of the pulvinus located at the base of the lamina. In compounds leaves, reorientation can occur by action of pulvinules at the base of the leaflets and possibly by action of the pulvinus at the base of the rachis (Koller, 1990). Differential expansion and contraction of cells are driven by the transport of osmotically active solutes followed by water movement. For the species reported, light in the blue range is active in sun-tracking (Yin 1938; Vogelmann and Bjorn, 1983; Sheriff and Ludlow, 1985; Donahue and Berg, 1990; Koller 1990).

The mechanism of sun-tracking has been examined in only a few species. The site of light perception for sun-tracking reportedly varies with plant species. In the Fabaceae, a site in the pulvinule is reported for Glycine max L. (Donahue and Berg, 1990), Phaseolus vulgaris L. (Sato and Gotoh, 1983), and Macroptilium atropurpureum (Sheriff and Ludlow, 1985), although for the latter species, illumination of the proximal 1–2 mm of the lamina is necessary for complete reorientation. For Lupinus palaeustinus Boiss. (Koller and Shak, 1990) the site of perception is reported to be on the lamina. For Lupinus succulentus Doug. the site is reported to be on the adaxial surface of the pulvinule toward the base of the leaflet (Vogelmann, 1984). The site of light perception for sun-tracking is on the lamina for two species of the Malvaceae, Lavatera cretica L. (Schwartz and Koller, 1978) and Malva neglecta (Yin, 1938).

Recent, detailed studies with common bean (Phaseolus vulgaris L.) indicate that their leaf movements are not true sun-tracking movements. Instead the movements are reversible, phototropic responses of the pulvinules (Koller and Ritter, 1994; Ritter and Koller, 1994). Koller and Ritter (1994) report that in the trifoliolate leaves of bean, the direction of laminar reorientation to oblique light is the same whether light is directed toward or away from the tip of an individual leaflet. Motor cells of the pulvinules receiving the light contract and the opposing cells expand. Further, the leaves do not follow the light in a simulated day as do the leaves of Lavatera cretica (Ritter and Koller, 1994). These results lead the authors to describe the leaf movements of bean and possibly other trifoliolate legumes as quasiphototropic.

The trifoliolate leaves of soybean may have a response to oblique light similar to that of the common bean. Donahue, Berg, and Vogelmann (1990) report that an increase in the relative light on one side of the pulvinule results in bending toward that side. Thus, a reevaluation of the nature of lamina reorientation in soybean and bean, both of which perceive light for leaf movements on the pulvinules, indicates that the movement may be fundamentally different from the sun-tracking leaf movements of species that perceive light on the lamina.

This study examines the site of light perception for lamina reorientation in a plant that shows true diahliotropic leaf movements and has trifoliolate leaves. The plant used is Crotalaria pallida Aiton., one of many sun-tracking legumes. C. pallida is a woody shrub native to South Africa (Allen and Allen, 1981). It has trifoliolate leaves with the leaflets connected to the petiole by 3–4 mm long pulvinules (Fig. 1). Populations growing in Central Florida appear to show diahliotropic, paraheli-
ototropic, and nyctinastic leaf movements in the field. This study examines the nature of diapheliotropic movements and the site of light perception for diapheliotropism in C. pallida.

MATERIALS AND METHODS

Plant material—Crotalaria pallida Aiton was collected from the Rollins College campus. Mature, dry seeds had a germination rate of 3%. However, seeds that were removed from the pods while still green and enlarged germinated very well and were used as the seed source. Immature seeds were germinated in vermiculite, and seedlings were transplanted to 12-cm pots in a mixture of two parts sand to three parts Pro-mixBX (Premier, Red Hill, PA). Plants were grown in a growth chamber at 25°C and 300 μmol·m⁻²·s⁻¹ provided by fluorescent and incandescent lighting from above with a 12-h photoperiod and a 12-h dark period. Plants were watered once per week with half-strength Hoagland’s solution plus micronutrients (Hoagland and Arnon, 1950) modified to contain FeEDTA at a final concentration of 400 mg/L.

Plants used for the day simulation experiments were grown outside in 12-cm pots at a maximum light intensity of 1500 μmol·m⁻²·s⁻¹ and a temperature variation of 22°C–35°C.

Measurement of leaflet movement—Leaflet movement occurred in three dimensions: (1) elevation above or below the horizon; (2) rotation around the axis of the midvein; and (3) movement in the horizontal plane (azimuth). Plants in the growth chamber had a leaflet orientation parallel to the horizon. Plants were transferred to a table with a single source of oblique light at a fixed angle, 45° above the horizon. The plant was placed so that the midveins of the lateral leaflets were in line with the lamp. In this arrangement, the lateral leaflet farthest from the light was oriented such that its proximal end was toward the lamp and the leaflet elevated above the horizon. The lateral leaflet closest to the light was oriented with its distal end nearest the lamp and it moved downward or below the horizon. The final result was that both leaflets were perpendicular to the vectorial light. Measurements of leaflet angle were reported as degrees above (positive) or below (negative) the horizon. Movement of the terminal leaflet was usually only rotational, but occasionally movement occurred that changed the azimuth. Measurements of terminal leaflet movement were only used when rotational movement occurred.

Leaflet angles were measured from negatives of time-lapse photographs viewed in a dissecting microscope with an ocular protractor. The horizon was determined by aligning the protractor with grid marks photographed behind the plant.

The lamp used for most experiments was an incandescent 200-W bulb with a silver reflector. Fluence rate was varied by changing the distance and by using 40-W and 100-W bulbs for lower fluence rates. Microscope illuminators (Bausch and Lomb, Rochester, NY) were used to illuminate the pulvinus alone and to illuminate only specified parts of the lamina. All light was passed through an infrared reflector (Thermashield, Edmund Scientific Company, Barrington, NJ) to reduce the heat. Light fluence rate in the photosynthetically active radiation range was measured with a LI-COR Quantum Meter (LI-COR, Lincoln, NE).

Simulation of light throughout a day—Plants growing outside in natural light demonstrated light avoidance, that is, paraheliotropic leaflet movements, within 1.5 h of sunrise. Therefore, sun-tracking fidelity was measured in a laboratory-simulated day. Light throughout the day was simulated in the laboratory by moving the 200-W bulb, with the silver reflector and infrared reflector, through a 110° arc over 12 h beginning at 30° above the horizon. The light source was moved 10° every hour. The plant was photographed at the end of each hour, before the next movement of the lamp. Light fluence rate normal to the lamina at all positions was 150 μmol·m⁻²·s⁻¹.

Wavelength effects on leaflet movement—Light was provided by a 30-W quartz-halogen Fiber-Lite illuminator with a fiber optic light guide and focusing lens (Dolan-Jener Industries, Woburn, MA). Individual color filters were fixed to the end of the lens. Glass filters (Edmund Scientific, Barrington, NJ) used were: filter No. 52531 that provided wavelengths below 460 nm and filter No. 52528 that provided wavelengths greater than 600 nm. Fluence rate over the photosynthetically active range was measured with a LI-COR Quantum Meter.

Site of light perception—Leaflet orientation to a fixed light at 45° was measured while light was blocked from specific areas. Light was blocked from the pulvinule by coating all sides of it with India ink or loosely wrapping it with aluminum foil. The aluminum foil blocked light to a level below detection by the light meter (0.01 μmol·m⁻²·s⁻¹). Midveins were shaded with black construction paper held on the lamina with vaseline. Transmittance through the black construction paper was 0.06%. The lamina was shaded by positioning black construction paper above the lamina as close as possible without touching it. To prevent light from reaching the lamina at the junction of the paper and the lamina, the proximal 1 cm of the lamina was painted with India ink.

Leaflet reorientation to a fixed, oblique light was measured after parts of the lamina were removed from the distal end of the leaflets. Both of the lateral leaflets on any one leaf were cut at the same time to prevent the mass of the remaining lamina from affecting the position of the lateral leaflet that was cut. The cut ends were coated with vaseline to prevent desiccation.

In one set of experiments the pulvinules received light from the vertical direction, and areas on the lamina received oblique light at 45°.
Figs. 2–3. Leaflet movement during a simulated day. A single lamp was moved 10°/h. The solid line shows the angles expected if the leaflets were normal to the light. 2. Measurements of lateral and terminal leaflets whose distal end was closest to the light at 0700 and of laterals with midveins perpendicular to the arc of the light movement. 3. Measurements of lateral and terminal leaflets whose proximal end was closest to the light at 0700. Vertical bars represent SD of the means of eight leaflets.

Microscope illuminators provided light in both orientations. To prevent vertically orientated light from reaching the lamina, the proximal 5 mm of the lamina was covered with India ink, and a piece of black construction paper was held vertically between the pulvinule and the lamina. The fluence rate at the leaflet level from each illuminator was 70 μmol·m⁻²·s⁻¹. The areas illuminated obliquely were between 0.8 and 1 cm² in either the distal or proximal region.

Presentation time—Young plants with five or six leaves were given 5, 10, 20 min, or continuous light at a 45° angle. After the appropriate time, the plants were transferred to darkness. Dim (<1 μmol·m⁻²·s⁻¹), diffuse light from another room was used for photography at 1-h intervals. Other plants were exposed to oblique light for 10 min followed by continuous, vertical room lighting.

RESULTS

Simulation of light throughout the day—Sun-tracking fidelity was demonstrated in daylight simulation experiments (Figs. 2, 3). The plants used in the experiments were raised outside and maintained for 2 d before measurements in the laboratory under simulated day conditions by moving the lamp 10° every hour. Throughout the simulated day all of the leaflets were within 15° of the angle expected if the laminae were maintained at a 90° angle to the incident light.

Lateral and terminal leaflets with their distal ends facing the lamp in the morning were declined at an angle below the horizon. These leaflets appeared to be 10° ahead of the lamp changes until 1500 at which time the leaflets were elevated above the horizon (Fig. 2). In contrast, leaflets positioned with their proximal end toward the light in the morning were elevated above the horizon in the morning. These leaflets lagged behind the expected angle between 1000 and 1400 (Fig. 3). Rotation of lateral leaflets was measured as negative, below the horizon, in the morning and as positive in the afternoon. The rotating laterals also appeared to be ahead of the expected angle until 1100. From 1100 to 1400, the rotating laterals appeared to be stalled in the horizontal position (Fig. 2).

Kinetics of leaflet movement to light at a fixed angle—Sun-tracking was also demonstrated by the movement of the leaflets in response to light at a fixed angle of 45°. The first movement of the leaflets occurred 40—45 min after the beginning of oblique light (Fig. 4; Table 1). The final angle was reached within 4—4.5 h and was within 0°–10° of that expected if the laminae were perpendicular to incident light. All of the leaflets of a leaf were orientated in the same plane at the end of leaflet movement.
Table 1. Summary of the response of lateral leaflets to oblique light at 45° either without or with the pulvinule covered with ink. N = 8.

<table>
<thead>
<tr>
<th>Pulvinule covered</th>
<th>Time of first response (min)</th>
<th>Maximum rate (deg/h)</th>
<th>Final angle</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>18</td>
<td>40.4</td>
</tr>
<tr>
<td></td>
<td>SD = 16.8</td>
<td>SD = 4.6</td>
<td>SD = 5.57</td>
</tr>
<tr>
<td>Pulvinule uncovered</td>
<td>46</td>
<td>14</td>
<td>35.6</td>
</tr>
<tr>
<td></td>
<td>SD = 12.0</td>
<td>SD = 1.9</td>
<td>SD = 5.46</td>
</tr>
</tbody>
</table>

Spectral and intensity requirements for leaflet movement—Leaf movement was considered to be diapheliotropic when both of the lateral leaflets responded such that the leaflet closest to the lamp declined below the horizon (negative angle) and the leaflet farthest from the lamp elevated above the horizon (positive angle). This is important when considering the effect of wavelength and fluence rate on diapheliotropic leaf movement. Diapheliotropic movement in response to vectorial light occurred only with white or blue light (Table 2). Wavelengths in the red region presented at a 45° angle resulted in declination of all leaflets identical to the movement seen in dim, diffuse light (1 μmol·m⁻²·s⁻¹) (Table 2).

Diapheliotropic leaflet movement occurred between fluence rates of 2–250 μmol·m⁻²·s⁻¹ (Fig. 5). Above this range with the incandescent lamp, the leaflets showed a paraheliotropic movement in which the leaflets all elevated above the horizon (data not shown). At fluence rates <2 μmol·m⁻²·s⁻¹, both leaflets declined below the horizon. At fluence rates between 2 and 25 μmol·m⁻²·s⁻¹, the reorientation of leaflets was not complete, that is, the leaflets farthest from the lamp did not elevate the full 40°–45° above the horizon (Fig. 5). Their leaflet pairs closest to the lamp, however, did decline below the horizon to the same degree as leaflets at higher fluence rates. This declination may have resulted from an additive effect of a weak diapheliotropic signal and a signal to the pulvinules of low light, both of which result in a declination of the leaflets.

The rate of leaflet movement in response to vectorial light increased with light intensity up to 75 μmol·m⁻²·s⁻¹ after which it remained at ≈ 20°/h (Fig. 5). The final angle reached after 4.5 h of vectorial light showed less variance with intensity, remaining constant at ≈ 40° at fluence rates above 25 μmol·m⁻²·s⁻¹.

Table 2. Effect of wavelength on reorientation of lateral leaflets to vectorial light at 45°. N = 8.

<table>
<thead>
<tr>
<th>Wavelength (nm)</th>
<th>Fluence rate (μmol·m⁻²·s⁻¹)</th>
<th>Leaflet final angle (degrees from horizon)</th>
</tr>
</thead>
<tbody>
<tr>
<td>White</td>
<td>900</td>
<td>−41</td>
</tr>
<tr>
<td>Blue (400–460)</td>
<td>45</td>
<td>−37</td>
</tr>
<tr>
<td>Red (600+)</td>
<td>400</td>
<td>−29</td>
</tr>
<tr>
<td>Diffuse, white</td>
<td>1</td>
<td>−27</td>
</tr>
</tbody>
</table>

* Mean of both lateral leaflets, N = 22.

Responsive area of the lamina—Removing 75% of the lamina from the distal end did not stop leaflet movement (Table 3). Leaflet movement was stopped by removal of 90% of the lamina. In Lavatera cretica, light movement. The proximal 1 cm of one lateral leaflet was painted with India ink and the rest of the lamina was shaded. The other leaflet of the pair was illuminated along with the pulvinule of the lamina-covered lateral. Final leaflet angle of the lamina-covered leaflets was 4.5° from the horizon (SD = 6.1, N = 12) compared to 21° (SD = 7.7, N = 12) for the paired lateral leaflets receiving light on both the pulvinule and proximal half of the lamina.

Further evidence that light perception for sun-tracking resides on the lamina comes from experiments in which the pulvinules were exposed to vertical illumination while part of the lamina was exposed to oblique light at the same fluence rate. When a proximal area of the lamina was exposed to oblique light, normal leaflet movement occurred despite the vertical illumination to the pulvinule (Fig. 6). However, when a distal region of the leaflet was exposed to oblique light while the pulvinule was exposed to vertical light, no leaflet movement occurred (Fig. 6).

Fig. 5. Dependence of the final angle (°) and the rate of leaflet movement (°/h) on fluence rate. Leaflets closest to the light showed a declination below the horizon and hence both a negative final angle and rate of leaflet movement. Leaflets farthest from the light showed positive responses. Data points are the means of 10—12 leaflets and the error bars larger than the symbols represent SD.
perception for sun-tracking is associated with the major, palmately arranged veins (Schwartz and Koller, 1978). Covering the midvein of C. pallida either with a water-based paint or a strip of construction paper did not stop normal leaflet movement to oblique light (Table 3).

**Presentation time and dose response**—Mature plants with leaflets between 6 and 9 cm in length exhibited nyctinastic leaf folding when transferred to the dark or to dim, diffuse light (Table 2). Leaves of younger plants (those with only 5–6 leaves of length 3–5 cm) remained horizontal upon transfer to darkness or dim, diffuse light. The leaflets of younger plants showed the same response to continuous oblique illumination as did leaflets of mature plants. Therefore, younger plants were used to measure presentation times and the dose response for sun-tracking. No leaflet movement occurred in response to 5 min of oblique illumination (Fig. 7). However, as little as 10 or 20 min of oblique light followed by dim, diffuse light resulted in partial leaflet reorientation (Figs. 7, 8). Both the rate of leaflet movement and the final angle of leaflet reorientation were dependent on total fluence (Fig. 7). There was a linear relationship between leaflet final angle and the log of fluence for varying fluence rates at 10- and 20-min presentation times. Oblique light for 10 or 20 min followed by normal room lighting, resulted in no leaflet movement (data not shown).

**DISCUSSION**

The trifoliolate leaves of C. pallida exhibit true diaphototropic movements. Diaphototropic leaf movements in C. pallida were demonstrated by simultaneous elevation and declination of opposite lateral leaflets in response to oblique light at a fixed angle (Fig. 4). The rate of leaflet movement to a fixed light at 45° was 14°±20°/h, and the accuracy of the final leaflet angle was within 5°±10°. A similar rate (15°/h) and degree of accuracy (15°) are reported for Lupinus succulentus (Vogelmann and Bjorn, 1983). Leaves of Mactropilium atropurpureum moved at a rate of 12°±30°/h and with an accuracy of 15° (Sheriff

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**TABLE 3. Effect of several treatments on leaflet reorientation to 4.5 h of oblique light at 45°.**

<table>
<thead>
<tr>
<th>% of distal end of leaflet removed</th>
<th>Treatment</th>
<th>Final angle</th>
<th>SD</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>75</td>
<td>Pulvinule covered</td>
<td>34</td>
<td>9.8</td>
<td>12</td>
</tr>
<tr>
<td>90</td>
<td>Pulvinule covered</td>
<td>9</td>
<td>5.1</td>
<td>8</td>
</tr>
<tr>
<td>Intact</td>
<td>Midvein shaded</td>
<td>38</td>
<td>3.2</td>
<td>10</td>
</tr>
</tbody>
</table>

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Fig. 6. Reorientation of leaflets to oblique light while the pulvinule received vertical light. The distal ends of the leaflets always faced the oblique light. Three representative recordings of individual leaflets from ten experiments are shown.

Fig. 7. Time course of leaflet movement of young plants to a fixed, oblique light at presentation times of 5, 10, and 20 min. Plants were exposed to oblique light for the specified times, then transferred to dim, diffuse light. Each curve is representative of eight trials.

Fig. 8. Fluence response of the final angle of leaflet movement. Treatments included presentation times of 10 min (○) at fluence rates ranging from 18 to 150 μmol·m⁻²·s⁻¹ and 20 min (●) at fluence rates ranging from 75 to 300 μmol·m⁻²·s⁻¹. Data points are means of the absolute values of 15–20 leaflets and the error bars represent SD. The correlation coefficient of linear regression is r.
and Ludlow, 1985). Diaheliotropic leaf movements of *C. pallida* were further demonstrated by the tracking of leaflets to an angle within \( \pm 15^\circ \) of normal to incident light during a simulated day (Figs. 2, 3). Other sun-tracking plants show a similar degree of variance of sun-tracking fidelity. Leaves of *Lavatera cretica* remained within \( 11^\circ \pm 14^\circ \) of the light in a simulated day (Koller and Levitan, 1989).

Like other sun-tracking plants, leaflet reorientation in *C. pallida* appears to be a blue-light response (Table 2). Both *Macroptilium atropurpureum* (Sheriff and Ludlow, 1985) and *Lupinus succulentus* (Vogelmann and Bjorn, 1983) respond to blue but not red or yellow. *Malva neglecta* (Yin, 1938) and *Lavatera cretica* (Koller, 1990) show leaf movement to vectorial light of blue wavelengths. Leaflet reorientation to vectorial light in *Glycine max* (Donahue and Berg, 1990) and *Phaseolus vulgaris* (Ritter and Koller, 1994), which may not be a true diheliotropic response, also responded to blue light. However, in *Phaseolus vulgaris*, leaf reorientation also responded to red light, suggesting the involvement of a second, red-absorbing photoreceptor (Ritter and Koller, 1994).

The site of light perception for sun-tracking in *C. pallida* was clearly shown to be on the lamina and not within the pulvinule. Leaflet movement was not stopped by coating the pulvinule with India ink (Fig. 4; Table 1), even when 75% of the lamina was removed (Table 3). However, no leaflet movement in response to oblique light occurred when the lamina was shaded and only the pulvinule was exposed to oblique light. Further, leaflet reorientation was triggered by oblique light striking the proximal end of the lamina despite the simultaneous, vertical illumination of the pulvinule (Fig. 5). The latter results were similar to those for *Lupinus palaestinus* in which leaflets moved in response to oblique light to the lamina while the pulvinule was receiving oblique light from a different angle (Koller and Shak, 1990).

The orientation of the lamina to directional light and the site of light perception for lamina movement in the trifoliolate leaves of *C. pallida* differ substantially from those of the trifoliolate leaves of *Phaseolus vulgaris* and *Glycine max*. Unlike *C. pallida*, the site of light perception for lamina orientation in *P. vulgaris* (Sato and Gottoh, 1983; Koller and Ritter, 1994) and *G. max* (Donahue and Berg, 1990) is within the pulvinules. Lamina orientation in the latter plants is controlled by contraction of cells of the pulvinule that are exposed to direct light at a higher fluence rate than cells on the opposing side (Donahue, Berg, and Vogelmann, 1990; Koller and Ritter, 1994). If lamina orientation is controlled by response of the pulvinules to light gradients in the manner described above, then in certain situations not all of the leaflets would be expected to orient normal to incident light. For example, oblique light in the direction parallel to the midveins of the two opposite lateral leaflets would expose the adaxial side of the pulvinules of both leaflets and should result in contraction of those cells and cause elevation above the horizon. In reality, the situation is more complex because as the angle of the sun changes during the day, the angle of light incidence on the pulvinule alters the light interception of the pulvinule. This can be measured with a fiber optic microprobe as an altered light gradient across the pulvinule (Donahue, Berg, and Vogelmann, 1990). Experimental data with *P. vulgaris* in a simulated day (Ritter and Koller, 1994) show that the lateral leaflet with its distal end oriented toward the morning light did not move because the pulvinule was shaded, while the opposite lateral leaflet elevated above the horizon during the first 1–2 h after sunrise. In contrast, all leaflets of trifoliolate leaves of *C. pallida* responded in unison such that the laminae were in one plane normal to the light (Figs. 2–4).

Leaf movements of *P. vulgaris* have been referred to as quasiphototropic because they do not show true diheliotropic leaf movements (Ritter and Koller, 1994). More specifically, the leaflets do not distinguish light from a distal to proximal direction from light oriented from the proximal to the distal end (Koller and Ritter, 1994). It is possible that leaflets of *G. max* are also not really diheliotropic because the pulvinular cells respond in a similar way as those of *P. vulgaris*; cells exposed to light contract and the opposing cells expand. A pulvinular site for light perception for leaf reorientation in legumes was based on the pulvinular light reception in these two species.

The results of this study with *C. pallida* clearly demonstrate that the photoreceptors for sun-tracking are within the lamina. This places in question the conclusion that the site of light perception for sun-tracking in all legumes is on the pulvinules. Leaflets of *Lupinus* perceive light for sun-tracking movements either on the proximal end of the lamina within 1 mm of the pulvinule as reported for *L. palaestinus* (Koller and Shak, 1990) or on the adaxial side of the pulvinule near the lamina for *L. succulentus* (Vogelmann, 1984). The cause of the discrepancy between these two reports as to the placement of the photoreceptors relative to the site of response is not known. For leaflet orientation of *Macroptilium atropurpureum* (Sheriff and Ludlow, 1985) the site of light perception is reported to be within the secondary pulvini, but the full response requires the proximal 1–2 mm of the lamina. The results reported here emphasize the need to examine further the site of light perception in other sun-tracking species.

The placement of light perception for sun-tracking on the lamina in *C. pallida* necessitates transfer of a signal from the lamina to the pulvinules, which are responsible for lamina reorientation. Such a signal must also be present in other species that perceive light for sun-tracking on the lamina, namely *Lavatera cretica* (Schwartz and Koller, 1978), *Malva neglecta* (Yin, 1938), *Lupinus palaeustinus* (Koller and Shak, 1990). In *Lavatera* the site of light perception is along the veins. The site on the lamina for light perception in *C. pallida* was not the midvein (Table 3). Covering the midvein of *Lupinus succulentus* also did not stop movement (Vogelmann, 1984). The most responsive part of the lamina of *C. pallida* appeared to be the proximal end of the lamina as seen in two sets of experiments. When the pulvinule was exposed to vertical light, the leaflets moved in response to oblique light only if the light was directed to the proximal half of the lamina, but not if the light was directed to the distal half (Fig. 5). The part of the lamina directly connected to the pulvinule was not necessary for light perception because in the experiments with vertical light to the pul-
vinule, 5 mm of the lamina directly connected to the pulvinule were shaded with India ink. In addition, leaflet movement in response to oblique light occurred even when only 25% of the proximal part of the lamina remained attached to the pulvinule (Table 3). For a lamina length of 8.5 cm, 25% remaining was 2 cm. Therefore the signal from the lamina to the pulvinule must be moving at least 2 cm.

Complete leaflet reorientation perpendicular to incident light required continuous illumination. Presentation times of 10 and 20 min followed by dim, diffuse light resulted in movement, but only to within 20–25° of what was expected (Figs. 7, 8). These results imply that the signal transmitted from the lamina to the pulvinule is not inductive in nature. Instead, the 10- and 20-min exposures to oblique light may have stimulated the production of a signal that moved to the pulvinule and initiated solute and water movements. However, for orientation to be complete, the stimulus was needed for a longer duration.

Two possible mechanisms for a transported signal are a chemical moving in the phloem or light channeled from the lamina to the pulvinule. Light piping could be occurring in the vascular tissue as it does in other plant tissues (Mandoli and Briggs, 1982). However, it is unlikely to account for communication between the lamina and the pulvinule in C. pallida for two reasons. First, light being channeled from the lamina to the pulvinule would surely be swamped by light reaching the pulvinule directly from the vertical direction. In the experiment shown in Fig. 6, the lamina did respond to oblique light while the pulvinule received vertical light. Secondly, it seems unlikely that light channeling was responsible for pulvinule response because a presentation time substantially shorter (only 10 min) than the time of detection of movement (40 min) resulted in at least partial response (Fig. 7; Table 1). However, it is always possible that a sufficient amount of light was channeled into the pulvinule in a directional fashion in 10 min and the response time was needed for ion redistribution.

A more likely hypothesis for the signal is a chemical transported in the phloem. A minimum distance of 2 cm for travel of the signal from the lamina to the pulvinule and a minimum time of 10 min from the shortest presentation time, or a maximum time of 40 min for first detection of a response (Table 1), place the rate of signal movement between 3 and 12 cm/h. This rate is within the range or slightly less than reported phloem translocation velocities of 10–100 cm/h for herbaceous plants (Crafts and Crisp, 1971). A chemical known to be involved in regulating cell volume changes in pulvinules is 4-O-β-D-glucopyranosyl-6'-sulfate)gallic acid (Kallas, Meier-Augenstein, and Schildknecht, 1990). A variation of this class of chemicals could be a likely candidate for a chemical signal in pulvinule control of sun-tracking.

LITERATURE CITED


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