# The behavior of north- and south-facing leaves of *Calathea* spp. in response to the daily cycle of sun exposure

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*Abstract: Calathea* spp. can reduce physiological heat stress by changing the position of their leaves to minimize sun exposure. Similarly, they can maximize exposure to light under low-light conditions when heat stress is not a factor. Leaves are positioned radially around the plants, and some leaves receive more direct sunlight than others when the sun is in the south (i.e. in the northern winter). We measured leaf position and orientation on 11 *Calathea* plants to examine how biomechanical constraints influence the capacity of the plant to intercept light while minimizing heat stress in its leaves. Results suggest that the neutral orientation of south-facing leaves facilitates efficient light capture at low light intensity. As sun exposure increased through the day, both north- and south-facing leaves changed their orientation by altering leaf pitch, thus reducing the angle of incidence of the sun to the leaf and consequent heat gain. Acute folding of south-facing leaves appears to compensate for their lesser ability to alter pitch angle and thus avoid hear gain. The extraordinary ability of *Calathea* spp. to alter leaf position enables it to optimize photosynthesis and minimize heat stress even though leaves have different biomechanical constraints.

*Key Words: light incidence,* Marantaceae, *phototropism, pulvinus*

## Introduction

Varying levels of light intensity throughout the day create a complex optimization problem for plants. At low levels of exposure, as in the morning, plants are probably light limited and need to maximize their exposure to light. Plants typically become light saturated at less than full sunlight. In the middle of the day, in direct sunlight, overheating can reduce photosynthetic rate, and eventually respiration can exceed photosynthesis. Sun exposure can also increase the risk of desiccation where water is limiting (Begon et al. 1990). Therefore, it is advantageous to minimize sun exposure when light intensity and temperature are high, conditions commonly experienced by tropical plants growing in the open.

*Calathea* spp. (Marantaceae) are giant herbs, typically with many large basal leaves whose petioles and blades are each > 1 m in length. They have a special mechanism to regulate sun exposure: by changing the turgor pressure in the pulvinus (a slightly thickened portion of the petiole), these plants can adjust the orientation of their photosynthetic surface. They can rotate and shift the angle of their leaves in response to the movement of the sun. They can also fold their leaves around the midvein.

Leaves within a *Calathea* spp. plant vary in their mechanical constraints and the micro-environments that they experience. They differ in their radial orientation around the central axis of the plant and the basal angle that the petiole makes with the ground. Apart from their pulvinar flexibility (which we assume to be equal for all leaves), their range of movement is likely to be limited by neighboring leaves. We will call the position when the pulvinus is not twisted or bent relative to the petiole the "neutral position" of a leaf. Because the neutral position varies among leaves, so does the angle at which leaves encounter incident light (Fig. 1). Thus, some leaves receive more direct sunlight and experience more heat stress in a neutral position than do others. At the latitude of Corcovado National Park, Costa Rica, the sun traverses the southern sky for most of the year. It reaches only about 70° above the horizon in early February, based on our field observations. Therefore, south- facing leaves (growing on the north side of the plant) encounter





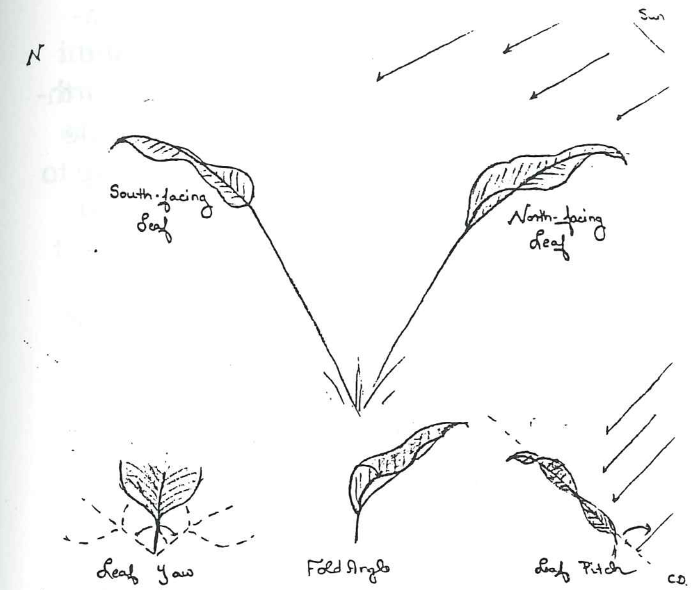


FIG. 1. The angle at which leaves encounter incident light varies among individual leaves. We measured the angle of the midrib from the horizontal (pitch), the interlaminar (fold) angle, and the angle of the pulvinus to the plane of the arched petiole (yaw).

more direct sunlight and are at greater risk of heat stress than north-facing leaves (growing on the south side of the plant; Fig. 1).

We examined how these positional constraints influence the movement of leaves. Constraints on leaf movement can influence the ability of the plant to optimize exposure (maintaining high photosynthetic rates, while avoiding heat stress). We hypothesized that (1) both north- and south-facing leaves would orient to maximize exposure at times of low light intensity, (2) north- and south-facing leaves would alter their orientation over the course of the day to minimize heat stress, and (3) south-facing leaves would be constrained in their ability to minimize heat stress by altering pitch (Fig. 1) and, thus, would make greater use of their ability to fold.

## Methods

We selected 11 *Calathea* spp. plants in a clearing off the Sendero Naranjos, approximately 150 m from the Sirena Biological Station in Corcovado National Park, Costa Rica. Based on flower and leaf characteristics, we believe that only one species of *Calathea* was represented in our samples. Using a compass to determine the bearing from the central axis of the plant, we selected the most north-facing and the most south-facing leaf on each plant. To test the assumption that north- and south-facing leaves were the same size, we measured the total leaf length from base to tip of 11 north and 11 south-facing leaves.

On 5 February 2003, we measured the orientation of the 22 individual leaves every two hours between 07:00 and 17:00. Using a clinometer and compass, we measured the angle of the midrib from the horizontal (pitch), the interlaminar angle (fold), and the angle of the pulvinus to the plane of the arched petiole (yaw; Fig. 1). We also noted whether the leaf was in the sun or shade. At each measurement time, we recorded the bearing to and azimuth of the sun, using a sundial fashioned from two 1 m measuring sticks.

We tested whether north- and south-facing leaves have the same range of motion by comparing their range in pitch, fold, and yaw. We calculated the angle of incidence of sunlight for each leaf at each measurement time. Data are presented as means ± SE.

## Results

Leaf pitch at the beginning of the day was significantly greater for south- facing leaves (56.7° ± 4.96) than for north-facing (14.0° ± 3.08) (Fig. 2; $t = 7.31$, $df = 20$, $P < 0.001$). South-facing leaves were 20.7 ± 13.8 cm longer than north-facing leaves, but this difference was not significant (paired-t = -1.50, $df = 10$, $P = 0.16$). There was no significant difference in shading between north- and south-facing leaves ($X^2 = 1.16$, $df = 1, 132$, $P = 0.56$). Self-shading (by leaves on the same plant) was evidently not a factor in sun exposure.

Over the course of the day, south-

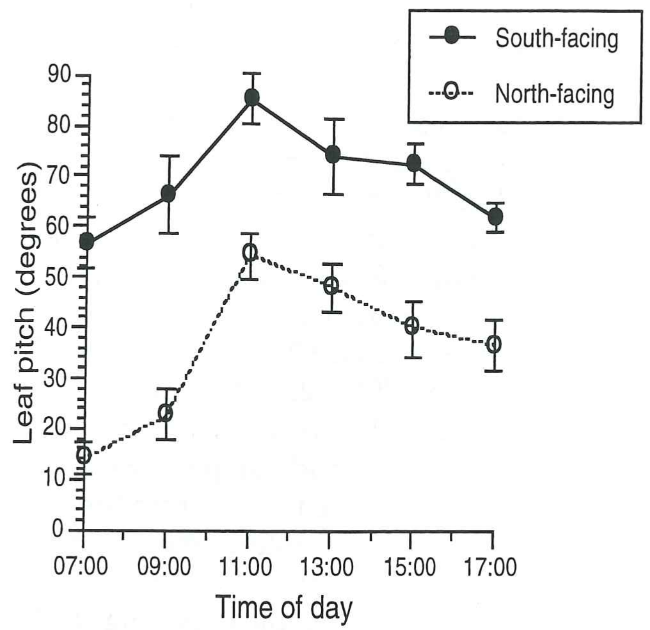


FIG. 2. Change in mean pitch of north- and south-facing leaves of *Calathea* spp. over the course of the day (n = 11). Pitch is expressed as the angle of the midrib from the horizontal.

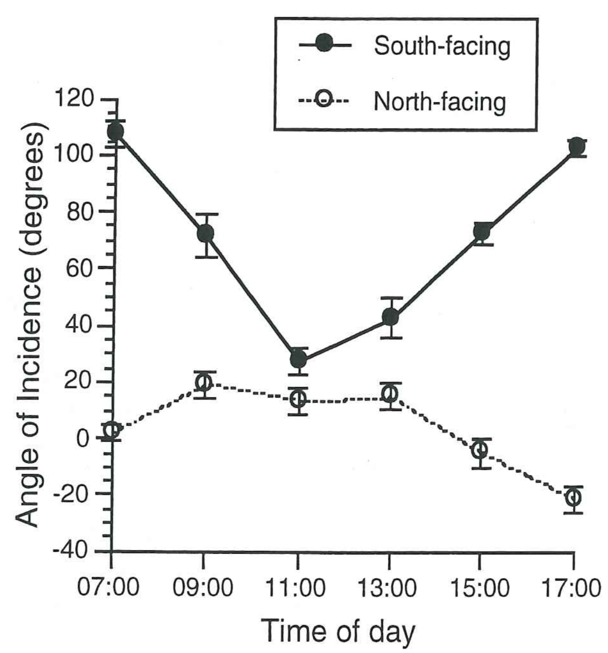


FIG. 3. Change in observed angle of incidence of sunlight on north and south-facing leaves of *Calathea* spp. over a one-day period at Sirena Biological Station, Corcovado National Park, Costa Rica (n = 11).

and north-facing leaves exhibited comparable range of leaf pitch angles (39.9° and 42.0° respectively; Fig. 2). South- and north-facing leaves both changed the magnitude of their interlaminar angles by folding up to 74 degrees but south-facing leaves folded more, achieving more acute angles (Fig. 4; $t = -1.52$, $df = 20$, $P = 0.14$). We observed no difference in the lateral range of motion of the pulvinus (yaw) between north- and south-facing leaves, and mean yaw angle was small (4.7° and 4.8°, respectively; $t = -0.07$, $df = 10$, $P = 0.94$).

South-facing leaves received more direct sunlight (i.e. had a significantly higher angle of light incidence) than north-facing leaves (Fig. 3). This was especially true at times of low light exposure. Thus, time of day and orientation of leaves were both significant predictors of change in the angle of light incidence for north- and south-facing leaves ($F = 35.3$, $df = 5$, $P < 0.001$). South facing leaves folded significantly more than north-facing leaves (Fig. 4; $t = -3.26$, $df = 10$, $P = 0.009$), and

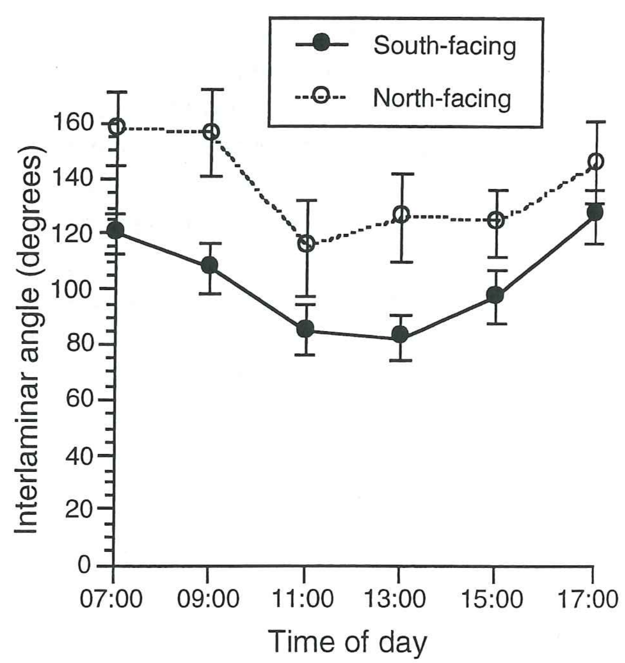


FIG. 4. Mean interlaminar angle of north-facing and south-facing leaves of *Calathea* spp. throughout the day. Smaller angles reflect more folding and less exposed surface area.





interlaminar angle was smallest during the mid-day period (Fig. 4). Small interlaminar angles imply more folding.

## Discussion

During the early morning and evening, when light is limited, south-facing leaves were oriented almost perpendicular to the sun. In contrast, north-facing leaves were aligned parallel to incident sunlight in the morning and exposed their reflective underside to the sun in the late afternoon, apparently making inefficient use of the available light. This suggests that the neutral orientation of south-facing leaves facilitates maximizing light exposure and efficient photosynthesis at low light availability. North-facing leaves probably experience less heat stress and thus they may be capable of photosynthesizing efficiently over the hot part of the day. The energy required for north facing leaves to tilt leaves towards the sun at early and late hours may be prohibitive. The necessary angle at the pulvinus would result in a large moment of force about the base of the petiole. The mechanical work required to raise and lower the leaf to a position with such extreme pitch could be a severe energy cost.

As sun exposure and intensity increased over the course of the day, both north- and south-facing leaves altered their orientation by changing leaf pitch to decrease the angle of incidence of the sun to the leaf, and thus reduce heat stress. North-facing leaves were able to reduce heat gain easily as their neutral orientation favored a shallow angle of light incidence. They rarely experienced incident light at an angle greater than 20 degrees and often exposed their reflective underside to the sun.

South-facing leaves also changed their leaf pitch substantially to minimize incident radiation, though not as effectively as north-facing leaves. At midday, they encountered light at an incident angle of 30 - 40 degrees relative to the leaf surface. It is possible that south-facing leaves are not capable of bending all the way over to align themselves with the sun's rays, since the pulvinus has limited flexibility around the pitch angle of neutral orientation. We did not observe obstruction to leaf movement by other leaves, but this could have been an additional factor limiting leaf movement. Although south-facing leaves may be limited in their ability to achieve optimum angles of incidence, they compensate for higher levels of incident light at midday by folding their leaves more, and longer, than north-facing leaves. Thus folding, in concert with change in leaf pitch, may provide significant regulation of light exposure and heat gain.

The extraordinary flexibility and control displayed by leaves of *Calathea* spp. allows north- and south-facing leaves to deal with environmental conditions differently within their different mechanical constraints. This plasticity of form appears effective in reducing stress and may increase the competitive ability of the species in natural gaps and clearings in tropical wet forests.

## Literature Cited


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