Table 3. Changes in Direction Resulting From Ants Moving in Opposite Directions.

| Trail | #Encounters | #Direction Changes | ERI |
|---|---|---|---|
| A* | 132 | 50 | 721 |
| B† | 135 | 14 | 282 |
| Control | 136 | 3 | 1521 |

*trail had greatly reduced activity level (shutting down)
†trail from which we removed leaves

delity among media on different foraging trails. Although ants from the highly active trail remained faithful (with one exception), ants from the less active trail were found to migrate to the more active trail. While watching the lower activity trail, we observed a sharp decline in the number of ants traveling in each direction, and almost no leaf transport, indicating that the trail was closing down. The trail was shut down by 2100. The abandonment of this trail, and the movement of its ants to the other trail, indicate that there may be communication between the ants regarding trail status.

By examining a control trail, a closing trail (A), and a manipulated trail (B), we tried to determine if the presence of a leaf was an indication that a trail was open. We found that ants on the control trail turned around significantly less per encounter than ants on either trail A or B. Because the number of direction changes was higher for the closing trail (A) than for the manipulated trail (B), it appears that the presence of a leaf is not the only factor in communicating that a trail is closing.

The encounter rate index (ERI) was significantly higher on the control trail than on trail A, indicating that there were more antennae contact events per ant-passing event. No difference in ERI was found between the control and trail B. We have postulated that when a trail is closing down, it would be more effective to have many encounters to dissuade workers from entering the trail, but this was not supported by our data. It appears that ants have more encounters on active trails.

Although we cannot conclude from this experiment that the ants are informing each other that the trail is closing, it is apparent that some communication is occurring, either through physical contact or chemical signals. Our results indicate that the presence or absence of a leaf carried by an ant has some effect on turnaround rate, but it does not account for every reversal.

## Literature Cited

Stevens, G.S. *Atta cephalotes*. In D.H. Janzen, ed. 1983. *Costa Rican Natural History*. Univ. Chicago Press: Chicago, IL. pg. 689-90.



# A Comparison of Marantaceae (*Calathea* spp.) Leaf Movement in Sun and Shade Environments

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*Abstract*. We studied a mechanism of temperature regulation in Marantaceous plants by examining changes in orientation of leaves in areas of shade and sun. We established leaf orientation by measuring several angles in three dimensions, and thus traced changes in orientation in relation to the position of the sun. The plants in sunlight folded their leaves around the central axis in response to this exposure, displaying reflective undersurfaces. In contrast, leaves in the shade did not fold about the central axis. Additionally, the leaves in the sun were tilted to receive only 53% of the incoming solar radiation, while those in the shade were positioned to receive 74%. Thus, plants in sunlight change leaf orientation in a way that reduces the likelihood of physiological heat stress. (CNO)

## Introduction (CNO)

Although light is frequently a limiting resource to plant growth, photosynthesis of many species is saturated at intensities below full sunlight (Larcher 1983). Plants may even suffer physiological heat stress at high leaf temperatures (Barbour, et al. 1986). To avoid heat stress, Marantaceae can fold and rotate their leaves and raise the entire blade vertically, thus lowering the heat load. They angle their reflective undersurface towards the sun and turn the upper surface away from the light. However, the response of Marantaceae leaves to incident solar radiation has not been quantified. We hypothesized the Marantaceae would change the orientation of their leaves differentially in areas of shade and sun, so that sunlit leaves would reduce the area exposed to solar radiation, while the shaded leaves would tend to maximize their exposure to sunlight.

## Methods (ALG)

We selected 10 leaves from 10 different Marantaceae, five in a predominantly shady environment, and five in a predominantly sunny environment. All of the plants were located within 150m of the Sirena Park Station in Corcovado National Park, Costa Rica. Every two hours, from 0700 to 1700 hours on 27 January 1992, we measured the orientation of the leaves and the position of the sun as follows:

I. For the sun:
  a)compass heading ($Z_s$)
  b)angle from horizontal measured with a clinometer ($\delta$).
II. For the leaf:
  a)angle between the vertical and the midrib ($\theta$)
  b)angle between the perpendicular to the midrib in the leaf plane and the vertical ($\phi$)
  c)compass heading along the midrib toward the center of the plant ($Z_l$)

d) angle between the central (vertical) axis of the plant and the midrib, taken along the bottom of the leaf ($\beta$)

e) angle between the two leaf laminae ($\gamma$)

For angles taken with respect to the vertical, down was defined as 0°. We grouped plants into sun and shade habitats by their sun exposure at the time of sampling. Thus, a leaf on the east edge of a sunny field at 0700 would be classified as a shade leaf, and a plant in a forest gap at 1200 would be classified as a sun leaf. We excluded measurements where the leaf was not clearly in the sun or shade. In our analysis, we calculated the incident solar radiation as a percentage of possible incident solar radiation by the following equation [the Guerrerio-Peart-Webb (GPW) index]:

$$\% \text{ incident solar radiation} = \sin\Omega, \text{ where}$$

$$\Omega=\cos^{-1}[\{[(\cos^2\theta+\cos^2\delta- 2\cos\theta\cos\delta\cos\alpha)^2 + (\sin\delta-\sin\theta)^2 ]^{1/2} -2\}\div-2], \text{ and}$$

$a$=the difference between $Z_s$ and $Z_l$.

$\theta$ and $\delta$ are defined above. $\Omega$ takes into account the difference between $\theta$ and $\delta$ and between $Z_s$ and $Z_l$ only. It does not take into account twisting ($\phi$) or the folding of the laminae ($\gamma$) (see Appendix A for the derivation of the GPW index).

Measurements for which the geometrical assumptions of $\Omega$ were not applicable, such as $\alpha$ greater than 180°, were not included in the incident radiation analysis.

## Results (ALG)

After classifying the data, we obtained 38 observations of shaded leaves and 15 observations of sun-exposed leaves. Shade leaves all had an interlaminar angle of 180°, while for sun leaves the mean angle was 132±18°. This difference in interlaminar angle between sun and shade leaves was significant by a Mann-Whitney U-test ($U=570$, $p<0.001$). For the incident solar radiation analysis, 21 of the shade measurements were excluded for reasons described above. The remaining shade leaves were positioned to receive 74±29% of the incident solar radiation, while the 15 sun leaves were positioned to receive only 53±28% of the incident solar radiation ($U=184$, $p<0.025$; Table 1).

## Discussion (ALG)

We observed the most motion in the leaves exposed to direct sunlight. These leaves oriented themselves almost edge-on to the sun with a slight tendency toward more exposure of the white reflective underside and shading of the top surface. They accomplished this by bending and twisting their petioles in the 10-20cm below the leaf base, and by folding their laminae inward.

One plant, originally in the shade, demonstrated the great range of motion possible when it was exposed to sun. At 0939 the leaf was fully shaded with its surface oriented toward the sun at 46° above the horizontal. When we returned two hours later the leaf was in full sunlight and had turned 150°, flipping completely over, so that its surfaces were now perpendicular to the sun's rays. An additional two hours later the plant was back in full shade and had returned to its original position. This represents a minimum angular speed of 1.2° per minute.

The plants exposed to direct sunlight kept their laminae turned toward each other, presumably to minimize area exposed to the sun. Additionally, the leaves in direct sun rotated to present a small area to the sun. Because of complications in the calculations, we were able to incorporate the effects of only four of the 7 measured parameters in our calculations. However, based on our observations, we believe the trends described above would be even stronger if the twisting and folding were taken into account. Further analysis of this phenomenon should include the twisting and folding parameters in the calculations.

## Literature Cited


Barbour, M. G., T. Burk and W. Pitts. 1986. *Terrestrial Plant Ecology*, 2d edition.


Table 1. Angle between sun and leaf surface ($\Omega$) and fraction of possible solar radiation incident on the leaf ($\sin\Omega$).

| Sun Leaves | | | | | Shade Leaves | | | | |
|---|---|---|---|---|---|---|---|---|---|
| environment | leaf # | time | $\Omega$ | $\sin\Omega$ | environment | leaf # | time | $\Omega$ | $\sin\Omega$ |
| sun | 1 | 0909 | 28.5 | 0.477 | shade | 1 | 0731 | 144 | 0.587 |
| sun | 1 | 1107 | 12.4 | 0.215 | shade | 1 | 1352 | 95 | 0.996 |
| sun | 2 | 0914 | 24.7 | 0.418 | shade | 1 | 1533 | 76 | 0.970 |
| sun | 2 | 1116 | 5.7 | 0.099 | shade | 1 | 1729 | 94 | 0.997 |
| sun | 2 | 1332 | 18.1 | 0.311 | shade | 2 | 0942 | 169 | 0.190 |
| sun | 2 | 1513 | 54.5 | 0.814 | shade | 2 | 1143 | 66 | 0.914 |
| sun | 3 | 0919 | 12.6 | 0.218 | shade | 2 | 1355 | 42 | 0.669 |
| sun | 3 | 1118 | 13.4 | 0.232 | shade | 2 | 1535 | 24 | 0.406 |
| sun | 4 | 1125 | 137.1 | 0.680 | shade | 2 | 1732 | 25.5 | 0.431 |
| sun | 4 | 1340 | 57.1 | 0.840 | shade | 3 | 0947 | 168 | 0.207 |
| sun | 4 | 1523 | 35.0 | 0.573 | shade | 3 | 1145 | 114.5 | 0.909 |
| sun | 5 | 1132 | 59.0 | 0.857 | shade | 3 | 1737 | 114.8 | 0.907 |
| sun | 5 | 1345 | 59.0 | 0.857 | shade | 4 | 0954 | 56.0 | 0.829 |
| sun | 5 | 1527 | 66.0 | 0.914 | shade | 4 | 1154 | 88.7 | 0.998 |
| shade | 1 | 1140 | 25.8 | 0.435 | shade | 5 | 0959 | 86.8 | 0.998 |
| | | | | | shade | 5 | 1158 | 103.4 | 0.973 |
| | | | | | sun | 4 | 0720 | 144.3 | 0.583 |
| mean % of possible solar radiation = 0.53 ± 0.28 | | | | | mean % of possible solar radiation = 0.74 ± 0.29 | | | | |

## Appendix A

Derivation of Gurrerio-Peart-Webb Index (GPW Index). Symbols are explained in the methods section of the text.

$P = \cos^2\theta+\cos^2\delta-2\cos\theta\cos\delta\cos\alpha$ (by law of cosines)

$Q = \sin\delta-\sin\theta$

$R = (P^2+Q^2)^{1/2}$

$R = 1+1-2\cos\Omega$ (by law of cosines)

$\Omega= \cos^{-1}\{[(P^2+Q^2)^{1/2} -2]\div-2\}$

$\Omega= \cos^{-1}[\{[(\cos^2\theta+\cos^2\delta-2\cos\theta\cos\delta\cos\alpha)^2+(\sin\delta-\sin\theta)^2]^{1/2}-2\}\div-2\}]$