

Host Tree Location Behavior of a Tropical Vine (*Monstera gigantea*) by Skototropism

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Abstract. Seedlings of the arboreal, ground-germinating, tropical vine *Monstera gigantea* (Engler) are shown to grow directly toward potential host trees; they do not find hosts by haphazard growth or random searching. Our experiments show that these vines are attracted to the darkest sector of the horizon. In nature trees provide these dark sectors. We term this response skototropism (growth toward darkness). Skototropism is probably produced by a modification of the molecular and cellular mechanisms that produce negative phototropism. We introduce the new term to emphasize the adaptive nature of the response; whereas the term "negative phototropism" can imply either growth away from light or growth toward darkness, only growth toward darkness can lead the vine directly to a host. This is because, in nature, hosts will not be aligned 180° from the lightest sector of the horizon relative to the vine.

Arboreal vines are a mainly tropical phenomenon; species diversity of this group is much higher at low latitudes (1) where perennially warm and moist conditions allow the high surface-to-volume ratio of their elongate form. This form allows vines the unique advantage of lateral movement across the canopy, to occupy diverse areas not available to trees anchored

at a single site. The capacity for lateral canopy movement, however, costs vines their self-supportive ability and presents arboreal species with the problem of finding a host tree to climb. Many biologists have been concerned with the mechanism of vine host location. Darwin interpreted his experiments with the vine *Bignonia capreolata* to show that hosts are found by

Fig. 1. Seedlings of *Monstera gigantea* converging upon a will-be host tree, at Finca La Selva, Costa Rica. Notice erect shoot tips; which serve to constantly apprise of host location relative to the minor diversions of forest floor debris.



“apheliotropism” (growth away from light) (2). Other mechanisms have been hypothesized through the years: negative geotropism (3), random searching (2, 4), and positive phototropism (5). In this report we give the first description of actual host location in a natural vine population and demonstrate the location mechanism to be skototropism (growth toward darkness); seedlings of *Monstera gigantea* locate trees by growing toward the darkness of a tree silhouette.

Monstera gigantea (Araceae) is a vine of Caribbean lowland forests. It germinates terrestrially, immediately after dispersal from inflorescences set partway up trunks of canopy trees. Seedlings have single slender prostrate stems with tiny bract-like leaves at nodes. There are three distinct ontogenetic morphologies during the vine's progress from ground to mature height: a seedling stage of horizontal terrestrial growth, a “saucer-leafed” stage maintained during host tree ascent, and an adult stage. In the adult morphology the species flowers repeatedly in direct sunlight and continues to climb. We observed seed set to be simultaneous, with the entire contents of an inflorescence falling to the ground en masse within several meters. This means that seedlings tend to climb the parent tree, or very nearby ones.

Host finding behavior of *Monstera gigantea* seedlings can be conspicuous in nature. Thousands of bright green seedlings are seen in contrast against the brown leaf litter, creeping inward from all sides of the tree. The seedlings appear as short spokes of a wheel with the tree as the hub (Fig. 1). In this behavior the tip of the elongating stem simply stands up, bends, and grows toward the tree, independently of compass direction between the two. The mean angle of growth relative to the host tree is calculated as \bar{a}

$$\bar{a} = \arctan \frac{\sum_{i=1}^n \sin a_i}{\sum_{i=1}^n \cos a_i}$$

where n is the number of seedlings and a_i is the angle of growth of individual seedlings (I). When $\bar{a} = 0$, average growth among seedlings is directly toward the tree. The standard deviation in growth angle among seedlings relative to the host tree is s (I)

$$\left[s = \frac{180}{\pi} \left\{ -2 \ln \left[\frac{\sum_{i=1}^n \sin a_i}{n} \right]^2 + \left(\frac{\sum_{i=1}^n \cos a_i}{n} \right)^2 \right\}^{1/2} \right]^{1/2}$$

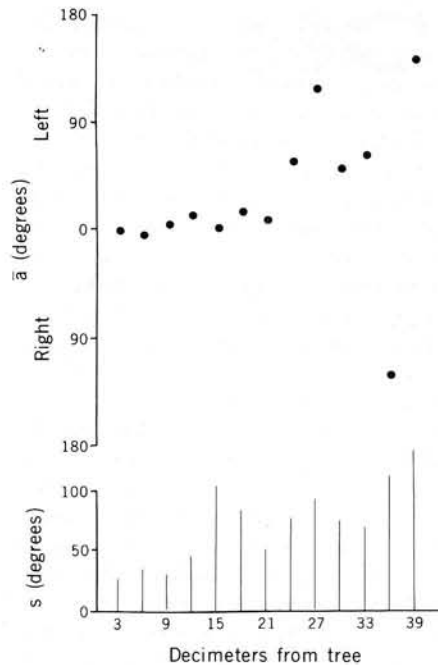


Fig. 2. Average angle of growth (\bar{a}) and standard deviation of growth angle (s) among vine seedlings found along a 4-m transect out from the base of a potential host tree. When the average direction of growth is directly toward the tree $\bar{a} = 0$, and when all seedlings are growing in the same direction $s = 0$. The formulas are given in the text. Note that the vine population's accuracy (\bar{a}) and precision (s) of host location decreases with increasing distance from the tree. These patterns obtain in all directions from potential host trees, indicating that the seedlings are attracted directly to the trees.

In Fig. 2 we show how the accuracy and precision of seedling growth angle decreases with distance from the tree; the mean growth angle wanders from 0° , and the variance among seedlings in growth angle increases with increasing distance from the potential host tree. The same relationship was observed to hold on all sides of the tree (see Fig. 1). Seedlings fall naturally around 19 trees and in several experimental situations produced convergence from all quarters.

That the seedlings converge from all directions indicates that they are finding the tree by skototropism, by growth toward the darkest sector of the horizon independently of the angle between this dark sector and the lightest sector of the horizon. We introduce this new term to emphasize the adaptive nature of the response. On the forest floor potential host trees are dark sectors on a haphazardly chiaroscuro horizon, and direction toward a potential host is almost never 180° from the lightest sector, relative to the seedling. Hence, this response is not growth away from the light, but an adaptation that serves to lead the vine directly to a host tree. There is no reason to suspect that skototropism is not un-

derlain by cellular and molecular mechanisms similar to those causing the classical negative phototropism of laboratory plant physiology (6, 7).

There is no apparent trend for individual *Monstera* seedlings more distant from a potential host tree to have grown more tortuously than close seedlings. Seedling stems at all distances from potential host trees are contorted. This contortion results from growth around and over fallen leaves and other forest floor objects.

The relative darkness as well as distance of objects also influences the propensity to attract these vine seedlings. We set pairs of seedlings parallel to both sides of shade cloth panels at 5-cm intervals from 1 to 100 cm away from the panels. We used five different panels with one to five thicknesses of cloth. A single thickness passes 60 percent of the light. The panels were placed on the forest floor, and faced east-west. Seedlings responded differently only to the first two panels, to 40 percent as opposed to 64 percent shade. Responses to the four panels of shade of 64, 78, 81, and 89 percent were identical. At these panels all of the closer seedlings turned 90° and grew toward the panel within 6 days; the most distant seedlings had turned toward the panels within 30 days. Closer seedlings at the panel of 40 percent shade began to turn only after 12 days, and only about half of those within 30 cm had turned by the end of the 34-day experiment; there was no response at greater than 30 cm. Over 90 percent of seedlings at the higher shades were growing toward the panels at the end of the experiment, whereas only 7 of 14 surviving on the east side and 9 of 14 surviving on the west side of the 40 percent darkness panel were doing so at termination. These experiments were done beneath dense canopy, where the seedlings occur naturally. Hence, the seedlings are discriminating 40 percent light intensity differences at the very low intensity (10 to 100 lux) of the forest floor.

The attractiveness of a tree trunk is also a function of its diameter; trees with large diameters will orient seedlings at greater distance than those with small trunks. The seedlings whose growth angles are represented in Fig. 2 were orienting toward a tree 75 cm in diameter. Although the orientation decreases gradually with distance, a distinct drop-off of orientation appears between 1.9 and 2.1 m. At this distance the silhouette comprised roughly 22° to 20° of the horizon. Our experiments with the attractive power of experimentally placed vertical boards of various widths (1 to 30 cm) confirms that the silhouette must comprise more than a few degrees of the horizon in order to attract seedlings. The nar-

rowest boards attracted from only a few centimeters, whereas the widest ones attracted seedlings at distances up to 70 cm. Seedling mortality resulting from burial under falling debris, leaves, and branches is very high, and the growth of seedlings is very slow (less than 10 cm/month); therefore only those seedlings within a few decimeters are able to reach the host before being buried under dead leaves.

As skototropism might be dangerous for a photosynthesizing plant, we set up a dark cul-de-sac to see how far vine seedlings would grow into the dark. We placed a box with three sides and a top on the ground next to several seedlings. The open side of the box, 1 m wide and 15 cm high, was perpendicular to the growth direction of the vines. After 2 months the vines had grown into the box and in a sinusoidal pattern parallel to the open end. They were caught, oscillating just inside the mouth of the box. The vines apparently switch to positive phototropism when the light grows very dim, but switch again to skototropism when the light grows brighter. This switching could be homologous to the first positive and first negative phototropic responses found in taxa used in laboratory plant physiology. However, *Monstera gigantea* shows no second positive phototropic response. At all but minimal light levels these vines are skototropic, hence this response is distinct from those described by classical laboratory plant physiology (6, 7).

Skototropism ceases when the horizontally growing seedling meets a tall, vertical surface. In our experiments, seedling growth changes to positively phototropic within 1 month of meeting the tree. During this period leaf morphology changes into

that of the second, saucer-leaved stage. The positively phototropic response of the second stage is demonstrated by the growth of seedlings that encounter the tree deep in a crotch between a pair of buttresses; growth in this case is upward but also distinctly outward into areas more exposed to sunlight. The first saucer leaves are small, about 1 cm in diameter, and are light green. During ascent the leaves darken; the highest saucer leaves can be 25 cm in diameter and are often dark green and covered with epiphyllae. The transformation from the saucer-leaf to adult stage occurs when the vine emerges into direct sunlight. We infer this from observations of the transition positions on the host trunk from saucer-leaved to adult *Monstera gigantea*. When the species ascends a trunk in unshaded sunlight it assumes adult morphology at only a few meters above the ground. Also, we have not found the adult morphology beneath understory canopy.

Skototropism is the only means yet proposed that will lead a vine directly to a host. Random searching (2, 4), negative geotropism (3), positive phototropism (5), or growth away from the light (2, 8) can only lead the seedling into an area where there may be a host, or into a light area where the vine can photosynthesize until it finds a host by random movement. Because of its obvious adaptive value skototropism may be a general mechanism for host location in ground-germinating arboreal vines (9). We can find only one previous author, though, with data that can be interpreted to indicate a whole-plant skototropic response. In this case an unidentified vine species is described as pursuing a stake that was moved daily to a different

position relative to the sun's diurnal course. However the author offers this, not as evidence of skototropism, but as "proof" of the "consciousness of plants," "that they think," and that "plants belong to the philosopher class" (10).

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References and Notes

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9. Since this report was submitted we have gathered similar evidence that another Costa Rican vine species [*Syngonium*, new species (Birdsey, nomen in edit)] is skototropic. This second species, however, has a different life history and morphology strategy. It will be described in subsequent publications (T. S. Ray, Jr., in preparation).
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11. We thank C. Harris, M. E. Thornton, R. Dressler, R. Fox, P. Homann, M. Birdsey, and C. Vezat-Ropical for help with various portions of this work. The data were gathered at the La Selva field unit of the Organization for Tropical Studies, Sarapiquí, Costa Rica, during June through November 1974. Support was from NSF grant GB 42575 to D.R.S.

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