Slow-motion world of plant 'behavior' visible in rain forest

Tropical vines change their forms—and their strategies—sometimes even reaching out for the darkness

Sheer diversity and a degree of adaptation unimagined at temperate latitudes help produce the stunning effect a tropical rain forest—the jungle we fantasize—has on the first-time observer. Panama, for example, is smaller than South Carolina, yet contains more species of trees (and birds and many other groups) than all of North America north of Mexico.

The high diversity is qualitative as well as quantitative. Adaptations occur in the tropics that simply do not occur in temperate zones. These adaptations, sometimes unexpected, sometimes bizarre, inevitably provoke the curiosity of the researcher. During several years of work in the rain forests of Costa Rica, my own curiosity was aroused by the adaptations of vines—adaptations so unusual as to alter my thinking about plants.

In the tropics vines are ubiquitous, and have rarely been better described than by Henry Walter Bates in 1863: "The tree trunks were only seen partially here and there, nearly the whole frontage from ground to summit being covered with a diversified drapery of creeping plants, all of the most vivid shades of green; scarcely a flower to be seen, except in some places a solitary scarlet passion-flower, set in the green mantle like a star."

Since 1974 my colleagues and I have tried to unravel the life histories of these specialized plants and their relations to the rain forest around them. Starting with fragile seedlings in the litter of the forest floor, we have followed them into the canopy 80 to 100 feet overhead. Returning several times to Costa Rica, we have become accustomed to trusting our lives to a rope, joining the birds and epiphytic orchids in the treetops to see how vines succeed in the most competitive environment on Earth.

It is my contention that, to better exploit their fellow plants, vines have evolved an elaborate behavioral repertoire. Few biologists consider plants to exhibit any behavior at all, and with good reason. The notion of behavior is closely linked to movement, something rare in plants. However, it cannot be said that plants are incapable of movement. As Charles Darwin pointed out in *On the Movements and Habits of Climbing Plants*: "It has often been vaguely asserted that plants are distinguished from animals by not having the power of movement. It should rather be said that plants acquire and display this power only when it is of some advantage to them; but that this is of comparatively rare occurrence, as they are affixed to the ground, and food is brought to them by the wind and rain."

A vine starts its life as a seed, which may be dispersed by a bird or bat, but which germinates on the ground. It matures and fruits, completing its life cycle, in the top of a tree where light levels are high. The tree is often far from the site...
spent most of its life wandering through the forest in search of a suitable site for flowering.

Aroid vines (those in the family of Araceae) are characteristically unbranch- ed; the stems are linear in shape. They grow at one end while gradually dying off at the other as a result of senescence. In an accelerated time frame they would appear somewhat like green leafy snakes moving through the forest. But there is something very different about the movement of the plant "snake." While the body of the plant becomes displaced over time, no part of the plant actually moves (there is reason to believe, however, that some nutrients are removed from senescent leaves and transported through the stem to be used in the formation of new leaves at the growing end).

Mobility in any organism creates the need for orientation. Vines need an efficient way of getting from their site of germination to the sunlight high in the trees. This can be thought of as a two-step process. First the vine must encounter the tree, and only then may it climb up into the light. The former process is the more interesting, as the latter can be effected by simply clinging to a tree and growing up the trunk.

To understand the problem of finding a tree, imagine yourself to be a seedling on the shady forest floor. Looking around, you see the light-green canopy above, and silhouetted against this are the long dark tree trunks. The key word here is dark. An efficient way of getting to the nearest tree is to grow toward darkness, a response called skototropism that is very unusual for organisms that depend directly on solar energy. Skototropism in plants is well developed only in vines, and it expresses itself only when the vine is "searching" for a tree. Once the tree is found, the plant switches back and starts growing toward light.

Skototropism can produce a spectacular visual effect on the forest floor. Monstera gigantea fruit contain thousands of seeds, and when the fruit ripens, the seeds are scattered on the ground beneath the parent plant. The seeds germinate immediately, forming slender green leafless sprouts which can grow up to a meter in length as they search for a tree. The seedlings may occur in great densities around a tree bearing a mature plant, and will all grow toward the tree, appearing like short green spokes of a wheel against the brown leaf litter, with the tree like an axle joining the wheel at the hub.

Skototropism has a very short etymology, beginning in 1974 when Donald R. Strong jr. and I discovered the phenomenon in Costa Rica. A tropism is an organism's characteristic of growing in the direction of something it needs, such as light or water. But this tropism was so different from any other that we felt the need to give it a new name. We finally settled on skotos, the Greek word for "darkness, gloom" and formed the word skototropism—growth toward darkness.

The phenomenon is not simply negative phototropism, growth away from light. This can be shown by a simple experiment in which vine seedlings are placed in the center of a circular arena (above). The arena consists of a wall of white cardboard. At one place on the wall a black felt strip is attached. At an angle of 90 degrees from this black strip, the wall is cut away and replaced by a translucent panel; a light is placed behind it.

I can conceive of three different directions the seedlings might grow. The plants might, in effect, take account of the light coming from all directions. Because the side of the arena containing the black panel would be darker, seedlings would be attracted in that direction; but they would also seek to avoid the bright light source itself, and so would grow off at an angle toward the dark side of the arena. Alternatively, the seedlings could grow directly away from the light source, or directly toward the dark panel.

Therese Gurski, a junior at Lourdes High School in Chicago, has completed the experiment as a science fair project, under my direction. Her results show unambiguously that the Monstera gigantea seedlings headed straight for the dark panel, almost as if they had a mechanism for focusing the light, and could "see" where they were going. To find a tree in the forest, the seedlings must grow toward discrete sources of darkness.

The philosopher class

I have only been able to find one reference to the kind of movement that I have observed, in a passage by Ambrose Bierce, a dialogue on whether machines—and plants—can think. The protagonist asks: "'And what, pray, does it [a machine] think with—in the absence of a brain?'

'The reply coming with less than his customary delay, took his favorite form of counter-interrogation: "'With what does a plant think—in the absence of a brain?'

'Ah, plants also belong to the philosopher class! I should be pleased to know some of their conclusions; you may omit the premises.'

'Perhaps,' he replied, apparently unaffected by . . . irony, 'you may be able to infer their convictions from their acts. I will spare you the familiar examples of the sensitive mimosa, the several insectivorous flowers and those whose stamens bend down and shake their pollen upon the entering bee in order that he may fertilize their distant mates. But observe this. In an open spot in my garden I planted a climbing vine. When it was barely above the surface I set a stake into the soil a yard away. The vine at once made for it, but as it was about to reach it after several days I removed it a few feet. The vine at once altered its course, making an acute angle, and again made for the stake. This manoeuvre was repeated several times, but finally, as if discouraged, the vine abandoned the pursuit and ignoring further attempts to
divert it traveled to a small tree, further away, which it climbed.'
"And all this?"
"Can you miss the significance of it? It shows the consciousness of plants. It proves that they think."

The movement of the leafy "snake" creates an interesting problem. The plant grows across great distances, encountering widely varying microenvironments, from the cool dark of the forest floor where debris falling from the treetops creates a high risk of mortality, to those treetops where the fresh air and bright tropical sunlight provide a benign atmosphere. The plant must be adapted to all of the conditions that it encounters. At the same time, every part of the plant remains fixed and thus must be highly fit in whatever surroundings it finds itself. A vine might adjust to this life history by evolving a form that is universally adapted, having a high fitness in the various microenvironments. Or it might evolve flexibility, so that it may express a different form in each habitat. Thus each part of the vine would assume the form which is best designed for the microenvironment in which it must live. The latter approach is what we actually see in tropical vines.
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With climbing ropes in place, author pulls himself up toward the canopy.

To really understand how this works we must look closely at how vines are constructed. Aroid vines are composed of segments placed end to end. The segments consist of a piece of stem with a leaf and a pair of rootlets attached at the forward end. The segments are produced one at a time, at the growing end of the vine. The precise size and shape of each segment can vary widely in response to the type of environment in which it is being formed.

As a rule, vines make thicker segments in better environments. The ground is clearly the worst environment in the rain forest for a plant, because of the low light levels and falling debris. In *Monstera gigantea* the terrestrial segments are the smallest. The lower part of tree trunks is a habitat of intermediate quality. A vine on a tree has escaped most of the danger from falling debris, but on the lower part of the trunk the leaves are still shaded by the many layers of vegetation above. Here the *Monstera* assumes medium stature. If the vine reaches the higher part of the tree trunk, it has found the best conditions. In the presence of full sunlight and fresh air, and with the support of a sturdy tree trunk, *Monstera gigantea* will undergo a transition in form that reflects its name. The stem grows and the leaves expand to a length of two meters, com-
Monitora gi, gantea seedlings, left, head for the tree trunk in background. Climbing the tree, center, they develop small leaves. At the top of the tree, vine produces frondlike leaves and fruit (right).

pletely changing their shape and coming to resemble enormous fronds (above). This behavior is understandable in that a plant that is capable of moving from a poor to a good environment would not be likely to invest its precious resources in constructing a full-sized plant body in the worst of environments.

Variation in shape can be understood even better by looking at the genus Syngonium. The shape of the leaf is more uniform, but the significance of changes in the relative size of leaf and stem is more obvious. Two segments of exactly the same weight may look totally different: one with a long stem and small leaves, the other with a short stem and very large leaves.

The first form, the long stem, is one adapted almost entirely for "movement." A segment with 95 percent of its material in a long stem and only a vestige of a leaf is barely able to photosynthesize, but the plant has moved forward a distance equal to the length of the stem. A segment which has placed 95 percent of its material in a large leaf, with an extremely short stem separating it from the previous leaf, has created a large apparatus for gathering light, while the plant has moved forward only slightly.

In a good environment, Syngonium segments naturally specialize for "feeding"—and for immobility. They put most of their substance into large leaves not only to take advantage of abundant sunlight, but to reduce forward motion to a minimum so they will not carry themselves out of the good environment.

Segments in a poor environment have a more interesting problem. They must move, but they also have to "feed" themselves. So several contiguous segments will take on the leafy form to gather what sunlight there is. The next group assumes the long-stemmed form, to make the maximum forward progress. The pattern cycles back and forth until the vine encounters a tree.

This division of labor is repeated when a vine climbs a small tree, only to find it is shaded by taller trees. When the top of the tree is reached, the plant has not yet found the high light levels that it needs to fruit. Generally the vine branches at this point. One stem will remain in the tree while the other returns to the ground in search of another tree. The stem in the tree continues to make relatively large leafy segments, while the stem that has returned to the ground makes long slender leafless segments. The stem in the tree is carrying on the photosynthesis needed to support the stem searching for another tree. If the searching stem is broken off from the stem in the tree, it will produce its own leaves, and behave like the free living terrestrial form described earlier.

This example illustrates how a moderately large arboreal vine can be transformed to a smaller terrestrial form similar to the one it took much earlier in its life. The development of vines is not unidirectional. The vine is not genetically programmed to produce a progression of forms leading it directly from the seedling to the mature fruiting plant.
A poisonous snake, caught in a loop, unexpectedly joined author in treetops.

Rather, the series of configurations expressed is entirely dependent on the sequence of environments that the vine encounters as it moves through the rain forest. No two individuals will show precisely the same series of shapes.

"Genetic individuals" are capable of being broken up into many independent "physiological individuals," each of which will have a different history. Thus the fate of a seedling can be quite complex. Even after reaching a large mature fruiting form, an individual may become transformed into a small terrestrial plant resembling a seedling. This may happen when the plant grows off the top of the tree and returns to the ground as described before. It may also happen if the vine is blown out of the treetops by a storm or falls with a broken tree branch. After being moved to the forest floor, subsequently produced segments will take on the configuration appropriate for that environment. The vine retains complete flexibility of form throughout its life.

In short, vines move through their rain forest habitat with a high degree of orientation, "searching" for trees to climb and then "seeking" light. As they encounter different environments, they assume different shapes. The changes in form directly affect the amount of photosynthesis that takes place. Thus the plant remains finely tuned to its environment and maintains a high fitness throughout its journeys.

Is it appropriate to speak of "plant behavior?" This interesting semantic question impinges on how we see the world as animals. There is a division of opinion on the matter, and the line is not drawn neatly between botanists and zoologists, but rather along philosophical grounds. There are those who feel that behavior requires the existence of a nervous system, an adaptation that is unique to the animal kingdom

On the other side there are those who believe that plants have been misunderstood by us animals—that we lack sensitivity to the ways of plants. For example, awareness, in humans at least, takes place on a much faster time scale than the behavior described in this article. In an accelerated time frame one could not help but notice a vine's highly oriented growth movements, and the changes in form in response to environmental qualities. One would surely be compelled to categorize such actions as behavior.

Ultimately, the semantic question can be settled by agreement on a carefully thought-out definition of the term. Yet the argument will persist until we broaden our ways of thinking in an effort to understand the nature of plants. Perhaps then we may even admit them to the "philosopher class."

No longer an arboreal species, biologists use safety devices in case they fall.
**Additional reading**

**USGS (p. 40)**

*Exploration and Empire, The Explorer and the Scientist in the Winning of the American West* by William H. Goetzmann, Knopf, 1966


*A Guide to Obtaining Information from the USGS 1978* by P. E. Clarke, H. E. Hodgson and G. W. North, USGS circular 777

**Rodeos (p. 56)**

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*Rodeo* by Douglas Kent Hall, Ballantine Books, 1976

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**Kathakali (p. 68)**

*Dance Dialects of India* by Ragini Devi, Vikas (Bombay, London), 1972

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**Pheromones (p. 78)**

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**Scarlet Letter (p. 86)**


**Black Confederates (p. 94)**

*Southern Negroes, 1861-1865* by Bell Irwin Wiley, Yale University, 1988

*A Diary from Dixie* by Mary Boykin Chesnut, D. Appleton, 1905

*The Negro in the Civil War* by Benjamin Quarles, Russell & Russell, 1955

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**Cities (p. 102)**


*Inner City Historic Preservation* by Arthur P. Ziegler Jr., The Allegheny Press (Pittsburgh), 1971


**Vines (p. 121)**

*The Power of Movement in Plants* by Charles Darwin, D. Appleton, 1888

"Evolutionary Significance of Phenotypic Plasticity in Plants" by A. D. Bradshaw, *Advances in Genetics*, (Vol. 13), 1965