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species in the subfamily Swietenioideae) are planted in the open and at close spacing. The borer attacks the tender terminal shoot and kills it, causing excessive branching and poor form from a commercial point of view. The many studies on, and attempts to control, this borer are described in Grijpma (1973) and Whitmore (1976).

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Syngonium triphyllum (Mano de Tigre)

T. Ray

The life history patterns described here refer to *Syngonium triphyllum* in particular but may be considered to apply in general to all climbing aroids, which in the New World are principally in the four genera *Anthurium*, *Monstera*, *Syngonium*, and *Philodendron*. Earlier I discussed these growth patterns with respect to the genus *Monstera*.

S. triphyllum moves both horizontally and vertically in order to reproduce sexually. The seeds germinate on the forest floor, but the plant matures high on the trunks of trees. From its site of germination the plant grows across the ground to a tree, then grows up the tree before flowering. Most of the plants that are climbed by *S. triphyllum* are too small to support the vine to maturity, but it has the flexibility to return to the ground to seek another tree. These growth patterns may be considered a foraging strategy for light and support structures (trees).

A plant of *S. triphyllum* can be considered to be composed of a series of "segments" placed end to end. Each segment consists of an internode with a leaf, an axillary bud, and a pair of rootlets at the distal end. Branching occurs only rarely. The vine grows at the distal end while dying off through senescence and herbivory at the proximal end (new roots are produced at the nodes as the stem elongates). Thus, although no part of the plant (other than the apex) actually moves, the plant as a whole becomes displaced over time.

Figure 7.113 shows the important components of the life history. When a seed germinates on the ground, it first produces a series of about ten small leaves. Each new leaf is larger (about 3–15 cm long), and they are packed close together on a stem about 2.5 mm in diameter (type T_l, terrestrial leafy, fig. 7.113). Subsequent segments are then produced in a quite different form, consisting of long, slender internodes, each about 8 cm long and 2 mm in diameter, with leaves only 5 mm long (type T_s, terrestrial stemmy, fig. 7.113). These stems are skototropic (grow toward darkness) as a means of encountering tree trunks rapidly (Strong and Ray 1975). If the stem does not encounter a tree after producing about thirty of these slender segments, it will revert to its original leafy form. It will remain in the leafy form for

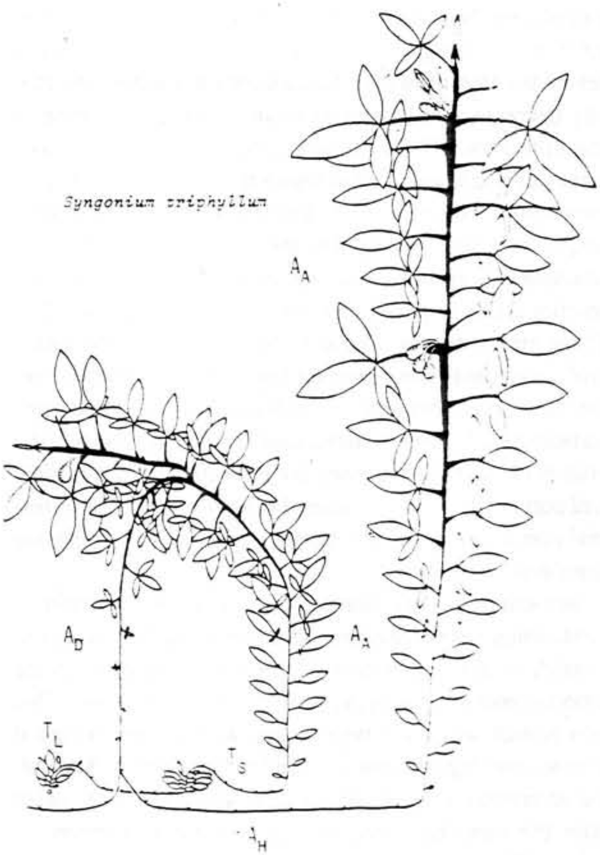

FIGURE 7.113. *Syngonium triphyllum* (drawing, T. Ray).

roughly another ten to fifteen segments, after which it will switch back to the leafless form. The stem will continue to alternate indefinitely between these two forms until the leafless form encounters a tree.

Upon encountering a tree, the stem begins to climb. Successive segments have gradually thicker stems and larger leaves. The internodes remain roughly 7 cm in length, until at about 20 cm the lamina develops lateral lobes. The central lobe may reach a length of 28 cm, and the lateral lobes grow to about 20 cm (type A_a, arboreal ascending, fig. 7.113). Occasionally a second rank of lateral lobes may occur, resulting in a palmately five-lobed leaf, but these outermost lobes rarely reach 10 cm in length.

When the stem reaches a diameter of roughly 14 mm, the plant is capable of flowering. Inflorescences are produced terminally, and the axis of the stem is continued by an axillary branch. The successive segments again increase in diameter until, after about ten segments, the stem again reaches a size capable of fruiting and the cycle is repeated. At each flowering, one to four spadices are produced. Each infructescence contains 50–150 fruits. Pollen is transferred by *Cyclocephala* sp. (Scarabaeidae), and fruits are dispersed by the collared aracari, *Pteroglossus torquatus*.

When a climbing stem reaches the top of a tree, usually a small tree, the stem ultimately becomes detached from the tree and hangs down in the air (this often happens before the stem flowers). Successive internodes then rapidly decrease in diameter to about 3 mm and increase in length to about 18 cm. At the same time, the successive leaves decrease in size but retain their mature form until they virtually disappear into the petiole (type A_d, arboreal descending, fig. 7.113). The stem retains this form after reaching the ground, where it elongates rapidly until it reaches a tree (type A_h, arboreal horizontal, fig. 7.113). These stems do not appear to be skototropic but rather grow horizontally in a straight line. Upon reaching a tree, the stem goes through the process of stem thickening (establishment growth) described earlier for type A_a. If a branch of type A_h becomes disconnected from the arboreal part of the stem, as when the stem breaks, the terrestrial portion of the stem assumes a form indistinguishable from type T.

Branching occurs regularly in only two situations. First, when a stem reaches the top of a tree and begins to dangle, an axillary branch is generally released from the arboreal part of the stem, near the top of the tree. This new branch will be of type A_a and will remain so until it also reaches the top and is forced to hang down. Second, the terrestrial type A_h has a tendency to branch, often after the stem has been cut, as commonly happens in nature. The new branch is of type A_h.

As the plant moves through the forest, the successive segments change size and shape in a consistent pattern as described above. All changes in form are completely reversible. Under the right conditions, stem of any form can change, through the appropriate intermediate stages, to a stem of any other form. Before examining the ecological significance of these changes in form, it is useful to consider in detail the precise geometry of the changes. Exactly what aspects of the form are changing, and what are the constraints on those changes?

None of the three component parts—internode, petiole, and leaf—is strongly correlated in its size (measured as dry weight), but an important and unifying correlation can be found. The dry weight of the entire segment is tightly correlated with the diameter of the internode. With this relationship between diameter and total weight, there are strong geometric constraints on the way the form of the segment may vary. The plant may produce a long (heavy) internode with a small leaf, or a large (heavy) leaf with a short internode, but it may not produce a long internode with a large leaf. There is a direct trade-off between leaf size and internode length. The ratio of the leaf weight to the internode weight often changes significantly from one segment to the next. It is by adjusting the weight of the segments, and the distribution of the weight among the parts of the segments, that *S. triphyllum* is able to tune its growth form to meet the varying conditions it encounters as it moves between microhabitats in the forest.

This trade-off between producing a large leaf and a long internode creates a morphological conflict between satisfying the plant's need for mobility and its need for photosynthesis. This conflict is particularly apparent in the case of type T, a small terrestrial plant that must provide all of its own photosynthate while moving to a tree. It is apparently for this reason that there arises a "division of labor" among adjacent groups of segments. Segments of forms T_l and A_a are specialized for photosynthesis, while segments of forms T_s and A_h are specialized for mobility.

The growth of type T is probably limited by photosynthate, since it has a small leaf surface area and lives on the shady forest floor. I have shown that the two forms, T_l and T_s are optimizing their use of photosynthate, in the sense that within the range of morphologies available to *S. triphyllum*, type T_l is the form in which leaf surface area per unit dry weight (cm^2/g) is maximized, and type T_s is the form in which segment length per unit of dry weight (cm/g) is maximized.

Type A_d can be considered transitional between forms A_a and A_h. Types A_a and A_h do not exhibit morphologies that optimize the use of photosynthate. However, I have shown that type A_a maximizes the time rate of production of leaf surface (cm^2/day) and type A_h maximizes the time rate of elongation of the stem (cm/day). Thus while the small forms, T_s and T_l, maximize elongation and leaf production with respect to utilization of dry matter, the large forms, A_a and A_h, maximize those parameters with respect to time.

An important function of type A_a is seed production. A comparison of several species indicates that those species that have thicker stems at maturity fruit more often and produce more seeds at each fruiting. Thus stem thickening is an important prerequisite for sexual reproduction. The ecological significance of type A_a can not be fully understood until the processes of stem thickening and seed production are studied in more detail. The genus *Syngonium* is very uniform in its growth habit. All species show the stages indicated in figure 7.113. The species vary primarily in maximum size attained (measured as stem diameter or leaf size), and this is correlated with the frequency of fruiting and number of fruits produced. The species with the largest size at maturity produce seven to eleven fruits at a node, and they produce fruits at every second or third node once maturity is reached. *S. triphyllum* is a medium-sized species that usually produces one fruit at a node (though it may produce as many as four), and it fruits only occasionally, fruits generally being separated by at least ten nodes. The smallest species apparently never, or at least rarely, fruit. In these species new individuals are established by spreading and fragmentation of existing individuals.

At La Selva, one such "asexual" species is *S. stenophyllum*. There is no evidence of seed production in the La Selva population of *S. stenophyllum*—that is, one cannot find infructescences or seeds. Furthermore, it occurs only in the primary forest and is completely lacking in the cacao groves where the seed-producing species of *Syngonium* attain abnormally high densities. Transplants do well in the cacao groves, suggesting that the species is absent because it lacks the seed dispersal necessary for colonization. On rare occasions one can find 4 mm long aborted vestigial inflorescences in this species. In 1977 I planted several individuals of *S. stenophyllum* in a palm grove where light levels are much higher than in the primary forest. Three years later one of these individuals was collected in flower, but it is not known if it would have produced viable fruit. It appears that under exceptional conditions the small species produce fully developed flowers and may produce fruit.

The genus *Syngonium* was revised in 1955 (Birdsey 1955), but many more species have turned up since then. There appear to be about ten species in Costa Rica. The genus has recently been revised again by Tom Croat (1982).

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Tabebuia ochracea ssp. ***neochrysantha*** (Guayacán, Corteza, Cortes, Corteza Amarilla)

A. H. Gentry

This is one of three closely related species of yellow-flowered *Tabebuia* that occur in Costa Rica. The three species replace each other in different life zones—*T. ochracea* is in dry forest, *T. guayacan* in moist forest, and *T. chrysantha* (in Costa Rica) in wet forest. All three are "big bang" mass flowerers in which all individuals of the species bloom on the same day and the flowers (fig. 7.114) last only about 4 days. They bloom in the dry season while deciduous (usually 4 days after one of the infrequent dry season showers) and are an unbelievable mass of color for their few days of flowering. Sometimes there are two or three flowering bursts in a single dry season. *T. ochracea* and its allies are pollinated by a variety of bees, especially euglossines and anthophorids, and are robbed by hummingbirds and xylocopids. The seeds have membranaceous wings and are wind dispersed.

Tabebuia ochracea ranges from El Salvador to Brazil; the subspecies *neochrysantha* ranges from El Salvador to northwestern Venezuela. It has leaves (fig. 7.115) densely stellate pubescent beneath (appearing tannish) and has golden woolly calyxes and fruits with long hairs. *T. chrysantha* (Mexico to Peru and Venezuela) has stellate hairs scattered over the leaves and short reddish stellate hairs on calyxes and fruits. *T. guayacan* (Mexico to Venezuela) has stellate hairs only in the leaf axils, thick stellate calyx trichomes, and a rough, spiny fruit that has very few or no stellate hairs.

T. ochracea is one of the commonest species in upland Guanacaste dry forests (frequency of 100% for 100 m^2 quadrats and densities of thirty-four individuals over 1 in dbh/1,000 m^2 at La Pacifica) and its seedlings can literally cover the ground in the dry season (e.g., at La Pacifica in 1972 there were an average of forty-eight seedlings/m^2 shortly after seed release).

The woods of these species are among the hardest and heaviest in the Neotropics. Specific gravities up to 1.5 mean that the wood "sinks like a rock." The wood is also exceptionally durable—for example, nearly all the dead trees still standing in Gatún Lake from the forests inundated by the construction of the Panama Canal are *Tabebuia guayacan*. The dark brown heartwood of these species contrasts strikingly with the white sapwood and is much prized for furniture and household untensils. In coastal Ecuador, where this esteem has led to serious depletion of the *Tabebuia* populations, fake "guayacan"