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CYCLIC HETEROPHYLLY IN SYNGONIUM (ARACEAE)[1]

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ABSTRACT

Species in the genus *Syngonium* germinate on the ground and mature on the trunks of the trees. These vines consist of relatively unbranched shoots which grow through the forest for considerable distances both horizontally and vertically. In the three species of this study, the shape of the segment, measured as internode diam/length, falls into two distinct classes, leafy and elongate, and varies cyclicly along single shoots. Two cycles are recognized. One cycle occurs in small diam terrestrial shoots in which cycling seems to be controlled by endogenous factors, and occurs with a period of a few tens of segments. The other cycle occurs in shoots of larger diam which climb and descend from trees. In this cycle, alternation between the two forms is controlled by gain or loss of contact with trees, and shoots may remain within a phase of the cycle for hundreds of segments, as long as the substrate does not change.

SYNGONIUM (Araceae) is a monocotyledonous genus of herbaceous vines of neotropical lowland rain forests. Vines are unusual in that they have developed to a high degree, a faculty otherwise rare among plants, the ability to move. Seeds of *Syngonium* germinate on the ground, yet the plant becomes sexually reproductive high on the trunks of sometimes distant trees. An important aspect of the biology of *Syngonium* is that the germination site of the plant may be a great distance (relative to its size), both horizontally and vertically, from its site of maturation. This generally unbranched vine grows at its apical end while dying off at the basal end through senescence and herbivory; thus while each part of the plant remains fixed, in time the plant as a whole becomes displaced in the forest, causing the plant to encounter a wide variety of microhabitats.

The movements do not stop when the vine reaches its maturation site. Once established on a high tree trunk, a vine will not only flower and fruit and continue to climb, but will produce branches that return to the ground and grow to neighboring trees. Vegetative growth and dispersal in three dimensions is a major factor in the colonization of trees. The importance of movement in these plants has led to the evolution of two important behavioral responses: the ability to orient toward trees (Strong and Ray, 1975), and the ability of the plant to change the form of the leaves and stems when it grows from one microhabitat into another (Ray, 1981, 1983a, b). It is this latter response, heterophylly, which will be the focus of this paper.

Bradshaw (1965) makes an interesting observation on the relationship between movement and behavior:

> The infinity of different behavioral patterns which have evolved in animals relate to the degree animals are often able to move from one environment to another. Such behavioral plasticity has little equivalent in plants . . . . A plant is therefore . . . unable to move away from an environment which is unsuitable to it. Lacking behavioral plasticity, other types of plasticity are likely to be favored.

One of the "other types of plasticity" he refers to is heterophylly. Although Bradshaw's generalization that plants do not move is true, it cannot be said that no plants move, as was noted by Darwin (1881):

> 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.

Although Darwin argued that plants possess the power of movement, he was not referring to the displacement of whole plants, but only of organs, as in the bending of leaves and tendrils, and of shoots in the process of nutation. As Bradshaw argues, the sessile nature of plants causes some of them to respond to environmental changes by heterophyllic changes in

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form, rather than movements. In mobile plants, heterophylly is one of the most apparent responses to the changes in microenvironmental conditions brought on by displacement in the forest. This is in part due to a fundamental difference in the kind of "movement" found in vines, from that found in animals. While the plant as a whole becomes displaced over time, each part of the plant (except the apex) remains fixed in space for the duration of its existence, and so must be adapted to the immediate environmental conditions where it is found.

Many plants exhibit changes in form during their ontogeny. Most work on this topic has dealt with the anatomical or physiological aspects of developmental changes associated with changes in form. Some examples include: Webster and Steeves, 1958; Allsopp, 1967; Stein and Fosket, 1969; Kaplan, 1970, 1973; Greyson and Sawhney, 1972; Rogler and Wesley, 1975; Franck, 1976. One general conclusion that can be drawn from this work is that the increase in size and frequently in complexity of successive primary leaves is correlated with the primary enlargement of the shoot axis, particularly of the apical meristem. However, Bruck and Kaplan (1980) have shown that this is not always the case, and that in at least one species the reverse is true. Some studies have examined the environmental factors which affect changes in leaf form (Arber, 1919; Njoku, 1956; Bostrack and Millington, 1962; Cook, 1969). No general conclusion can be drawn from these studies, as the results are highly dependent on the organism used. The work of Epling and Lewis (1952), Cook and Johnson (1968), and Ray (1981, 1983a, b) dealt with the adaptive significance of heterophylly. Cook and Johnson (1968) conclude that strong heterophylly in the amphibious plant *Ranunculus flammula* is associated with "immature" (early successional) and "unpredictable" environments. The present investigation is concerned with heterophylly in tropical vines of the genus *Syngonium,* which is associated with mobility that causes the plant to encounter successively, a predictable series of microhabitats in a fully mature tropical rain forest.

MATERIALS AND METHODS—*Data collection*—The field study was conducted at the Organization for Tropical Studies' La Selva Field Station, located at the confluence of the Rio Puerto Viejo and the Rio Sarapiquí (10°25′N, 81°1′W) in Heredia Province, Costa Rica, and at privately owned Finca El Bejuco, located three km northwest of Finca La Selva. The vegetation is described in detail by Holdridge et al. (1971) in accordance with the Holdridge life zone system (Tosi, 1969).

For this study I measured internode length, internode diam, petiole length, and the length of each lobe of the leaf for each segment along the shoot of a number of individuals of each of three species of *Syngonium.* Segment is defined as an internode and the leaf at the distal end, Ray (1986). The term segment as used here is synonymous with the terms "phytomer" and "stem unit" (White, 1979; Critchfield, 1985). The numbers of segments measured were: for *S. macrophyllum* Engl., 3,181 segments of 91 individuals; for *S. triphyllum* Birdsey ex Croat, 4,052 segments of 85 individuals; for *S. birdseyanum* Croat & Grayum ined., 2,505 segments of 66 individuals. An attempt was made to include individuals representing, the full range of forms for each species. In a subset of the segments for each species, the component parts of the segment—internode, petiole, and lamina lobes—were dried and weighed, and the leaf surface areas were measured.

Data analysis—The data including dry wts and surface areas were used in regression analyses reported in Ray (1986), which confirm that for each of these three species, the form of the segments can be fully characterized by two variables. For many segments along any shoot, particularly the elongate segments, the leaves and petioles are missing, and only the internodes remain. In this paper I wish to show how segment form changes along long stretches of shoot, thus it is necessary to be able to quantify the form even in segments where only the internode remains. I will quantify the form of the segment using log of internode diam, ID, and the log of the ratio of internode diam to internode length (internode shape, IS). These measures tell us the size and shape of the internode. Additionally, one may accurately estimate both the size and shape of the leaf from measures of internode length and diam alone (Ray, 1986). In short, the complete form of the entire segment can be completely specified by these two measures alone.

When examining the data in Fig. 2–13, it is important to keep in mind that although I present only ID and IS, leaf form may be interpreted from them as follows: ID is an index of the wt of the segment and the shape of the leaf, and IS is an index of the proportioning of the wt between the leaf and internode. A larger value of ID indicates a larger segment and a more divided leaf. A larger value of IS indicates a greater proportion of the segment wt in the leaf, and thus a larger leaf and a shorter inter-

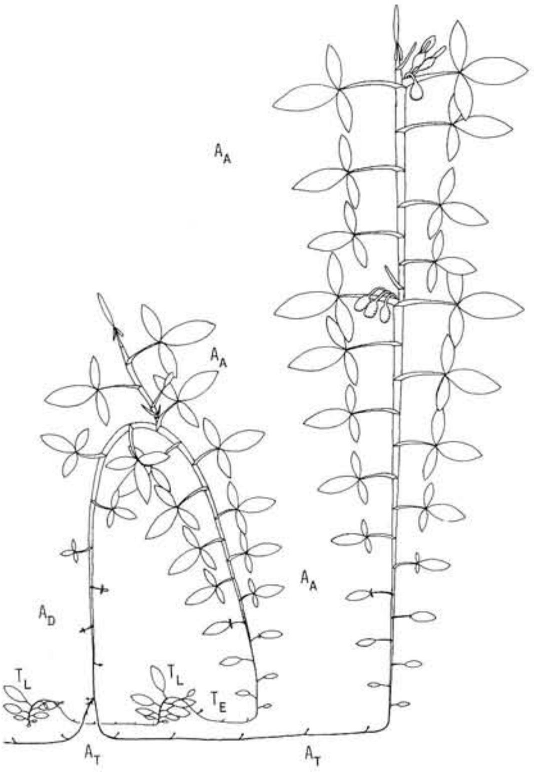


Fig. 1. The growth habit of *Syngonium* as typified by *S. triphyllum.*

node. Both ID and IS interact to determine the size of the leaf, but the shape is related only to ID.

I will take advantage of the extreme bimodality of the internode shape distribution (Fig. 5–7), by arbitrarily dividing it at the bottom of the trough, at $IS = -1.2$ (at this value, the internode is about 16 times as long as wide) in *S. triphyllum* and *S. macrophyllum,* and at $IS = -1.4$ (internode 25 times as long as wide) in *S. birdseyanum.* I will call any segment greater than this value a leafy segment, and any segment less than this value an elongate segment.

Figures 14–25 are histograms of the number of segments in each phase of the cycle. To illustrate what I mean by this, consider Fig. 8 representing the terrestrial cycle of *S. triphyllum.* The division point between the leafy phase and the elongate phase is indicated by the dashed line. This shoot starts out in the leafy phase of the cycle, where it remains for 12 segments before switching to the elongate phase. It then remains in the elongate phase for 23 segments before switching to the leafy phase for 4 segments, then back to the elongate phase for 19 segments, then back to the leafy phase for a final 5 segments. Thus this shoot will contribute one entry into the histograms for each of the five values, 12, 23, 4, 19, and 5. The values 12, 4, and 5 enter into the histogram for the leafy phase (Fig. 14), and the values 23 and 19 enter into the histogram for the elongate phase (Fig. 15). These histograms represent the distribution of the lengths of the phases.

The first and last phases from Fig. 8 (with lengths of 12 and 5 segments respectively) are not complete phases. That is, we do not know how many leafy segments preceded the point where the data on this shoot began, and we do not know for how many more segments the plant will remain in the leafy form as it continues to grow. In general, the phases of the arboreal cycle are so long, that due to senescence at the posterior end, many shoots do not exhibit a complete phase at one point in time. The longest phases of the arboreal cycle usually have to be recorded by measuring the plant repeatedly over a period of yrs as it grows at one end and senesces at the other. The plants in this study were sampled repeatedly for periods of up to four and one half yrs. Nonetheless, the longest complete phases of the arboreal cycle are poorly represented in the sample. Although many of the phases represented are incomplete, they give us at least a minimum estimate of the length of the phases.

Vouchers for the three species are: *S. birdseyanum* Mike Grayum 2786 (Duke), *S. triphyllum* Tom Croat 44233 (MO), and *S. macrophyllum* Barry Hammel 9835 (MO).

RESULTS—*Natural history*—The overall growth habit of *Syngonium* is viewed as being composed of two major cycles, a small terrestrial cycle, the T cycle, in which the plant alternates between producing "leafy" and "elongate" shoots, and a large arboreal cycle, the A cycle, in which the plant ascends and descends from trees, again alternating between producing leafy and elongate shoots. When a seed germinates, the plant is initially in the T cycle, and first produces a rosette of leaves (T_L, terrestrial leafy, lower left of Fig. 1). The form of subsequent growth then switches, and the plant produces a long slender stem with tiny leaves widely spaced on the stem (T_E, terrestrial elongate). This shoot is skototropic (grows toward darkness) in order to encounter trees, since tree trunks appear as silhouettes on the plant's horizon (Strong and Ray, 1975). If a shoot of type T_E does not encounter a tree after roughly two m of extension, in its subsequent growth it will revert to the rosette form, T_L. The plant will thus establish a second photosynthetic base, from which a second shoot of type T_E will be

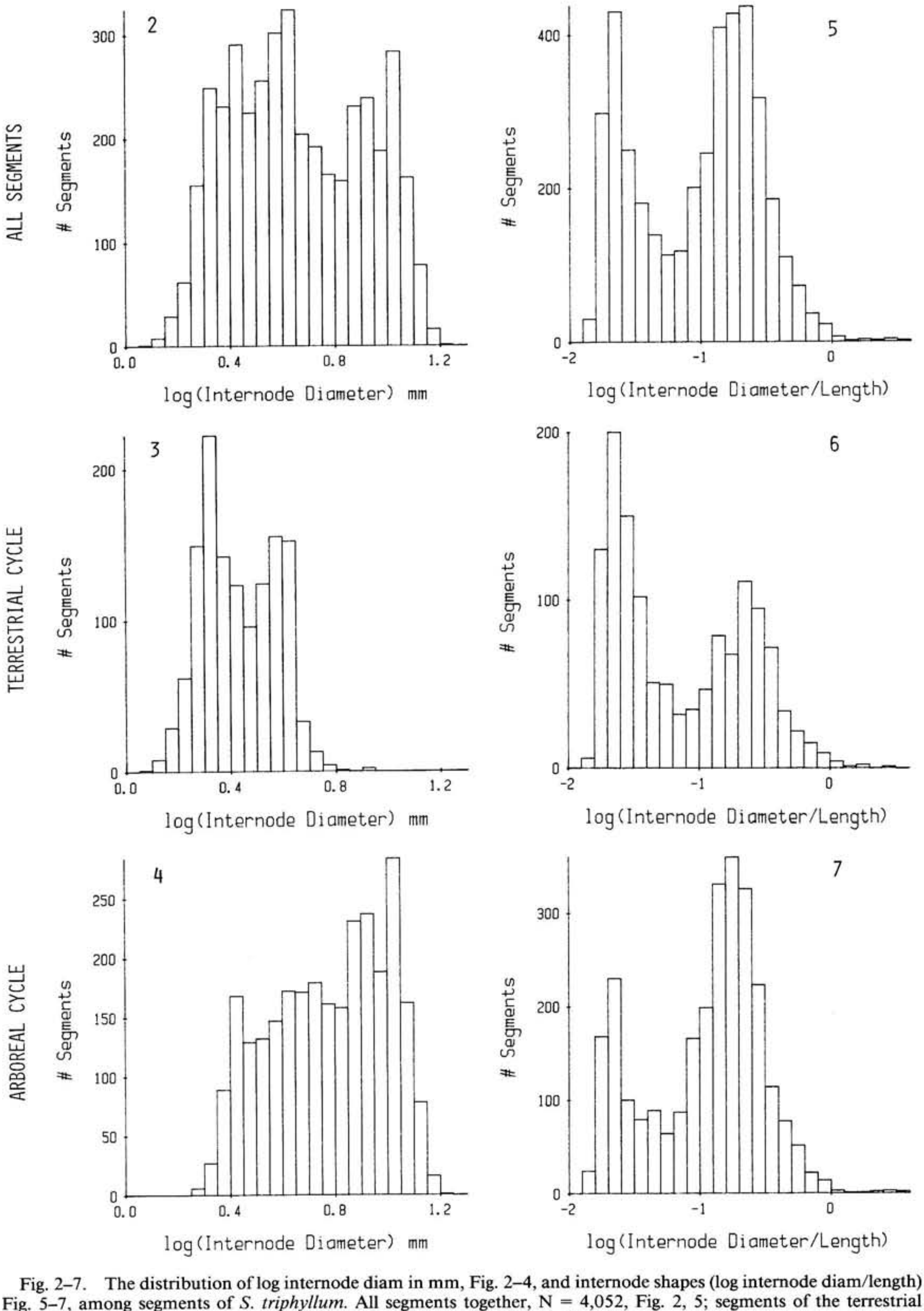
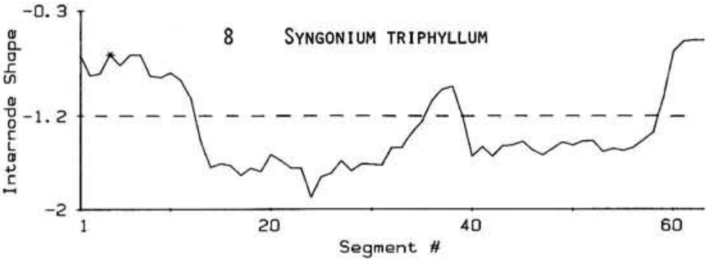


Fig. 2–7. The distribution of log internode diam in mm, Fig. 2–4, and internode shapes (log internode diam/length) Fig. 5–7, among segments of *S. triphyllum.* All segments together, N = 4,052, Fig. 2, 5; segments of the terrestrial cycle, N = 1,316, Fig. 3, 6; segments of the arboreal cycle, N = 2,738, Fig. 4, 7.

TERRESTRIAL CYCLE



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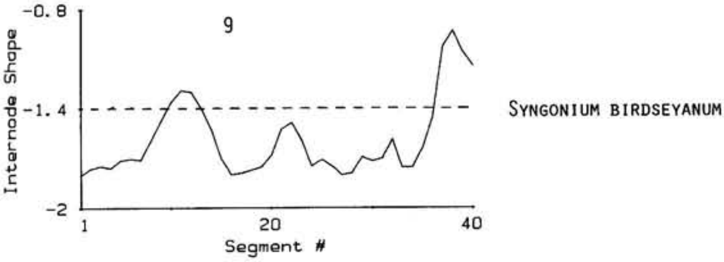

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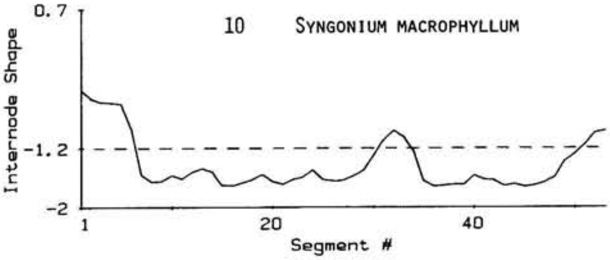

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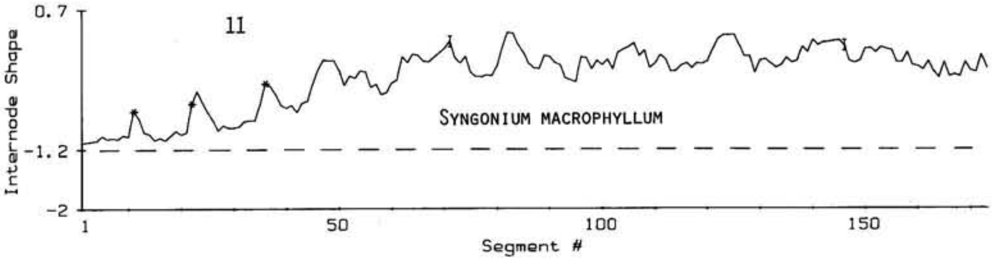
ARBOREAL CYCLE



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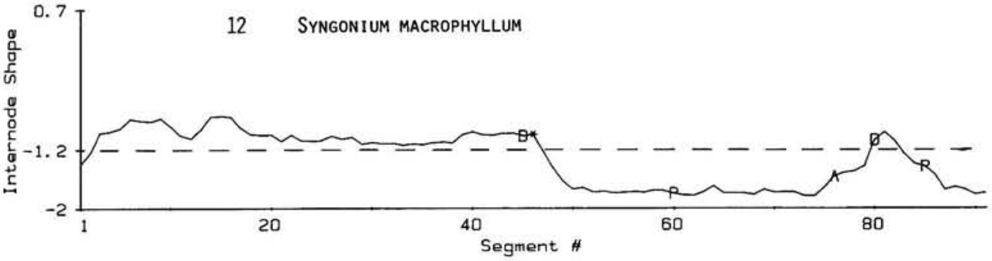

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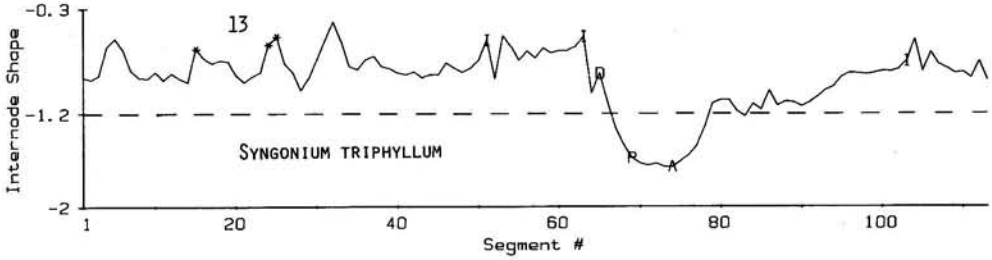

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produced. The shoot will alternate indefinitely between forms T_L and T_E until a tree is encountered.

Upon encountering a tree, the shoot will enter the A cycle and begin to climb the tree. Leaves will continue to be widely spaced on the stem, but the stem diam will gradually increase, as will the size of successive leaves, type A_A (arboreal ascending). As leaf size increases, so does its complexity. The leaves become palmately compound, with the largest leaves having three to seven lobes, depending on the species. When the stem has reached its greatest diam and the leaves their greatest size, the plant will flower and fruit. Flowering is terminal, but the shoot will be continued by a sylleptic axillary branch, growth is polyphyllous sympodial[2]. Flowering will be repeated occasionally, the frequency depending on the species, the vigor of the plant, and seasonal factors.

When a climbing shoot reaches the top of a tree, usually a small tree (as small trees are more common in the forest), the shoot will continue to grow, until it becomes detached from the tree and hangs down in the air. The subsequent growth will then involve a decrease in stem diam, with reduced leaves spaced widely on long internodes, type A_D (arboreal descending). Upon reaching the ground these shoots will extend for distances of ten or twenty m while producing tiny widely spaced leaves, type A_T (arboreal terrestrial). These stems are thicker, with the leaves more widely spaced than shoots of type T_E, and they do not appear to be skototropic, but rather grow in straight lines. Eventually the shoot will reach a tree and begin to climb, returning again to type A_A. If a shoot of type A_T is cut off from its arboreal origin before contacting a tree, it will revert to the T cycle.

As illustrated in Fig. 1, branching usually occurs in only two situations: 1) When the shoot begins to hang down, a branch will emerge below the point of detachment from the tree. This branch will remain in the tree top producing large leaves until it also overgrows the tree, while the hanging branch grows to another tree. 2) When a hanging shoot reaches the ground, branching often occurs. Branching also occurs when the shoot flowers, as the inflorescence is terminal, and the shoot is continued by a sylleptic branch, however this is regenerative branching rather than proliferative branching.

Due to senescence occurring at the posterior end of the shoot, no plant will ever represent all the stages shown in Fig. 1 at one instant. It is uncommon for a shoot to contain as many as one hundred internodes. Based on observations of the growth rates of the various stages, I estimate that it might take ten or more yrs for a plant to pass through the complete series of forms illustrated in Fig. 1.

All species of *Syngonium* show this basic life history. The most significant differences between the species are in the maximum stem thickness and leaf size attained, and in the propensity to fruit. In this paper I deal with three species. The largest of the three, *S. macrophyllum,* produces the most fruit at each fruiting, and fruits the most often. The smallest of the three, *S. birdseyanum,* apparently never, or at least very rarely fruits. The intermediate sized species is *S. triphyllum* which fruits occasionally when mature.

The plant consists of a linear string of segments, with rare branching. The form of the plant is determined by the number of segments it contains, the way they are strung into branches, and the form (size and shape as discussed in Ray, 1986) of the individual segments. In this paper I will focus on the pattern by which the forms of the individual segments are distributed along the shoot.

The data—in this paper are represented in three ways: histograms of ID and IS for *S. triphyllum* (Fig. 2–7); plots of how IS cycles along shoots of individual plants of all three species (Fig. 8–13); and histograms of the lengths of the phases of the cycles of all three species (Fig. 14–25).

The distribution of ID in Fig. 2 is roughly normal (or rather, log normal), though there is a slight bimodality. Figures 3 and 4 indicate

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[2] A sylleptic branch is one in which the bud producing the branch develops without rest. The term "polyphyllous sympodial" indicates that a variable number of leaves are produced before the shoot terminates in another inflorescence. See also footnote 3.

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Fig. 8–13. Segment shapes (log internode diam/length) plotted for each successive segment along the stem for six individuals. Asterisks indicate that the stem was continued by an axillary branch due to damage to the apex. The letter "I" indicates that an inflorescence was formed at this segment, Fig. 11, 13. In Fig. 12, 13, the letter "D" indicates that the stem, initially climbing, overgrew its vertical support. The letter "P" indicates that the now descending stem made contact with the ground. The letter "A" indicates that the stem, now growing across the ground, made contact with a new vertical support.

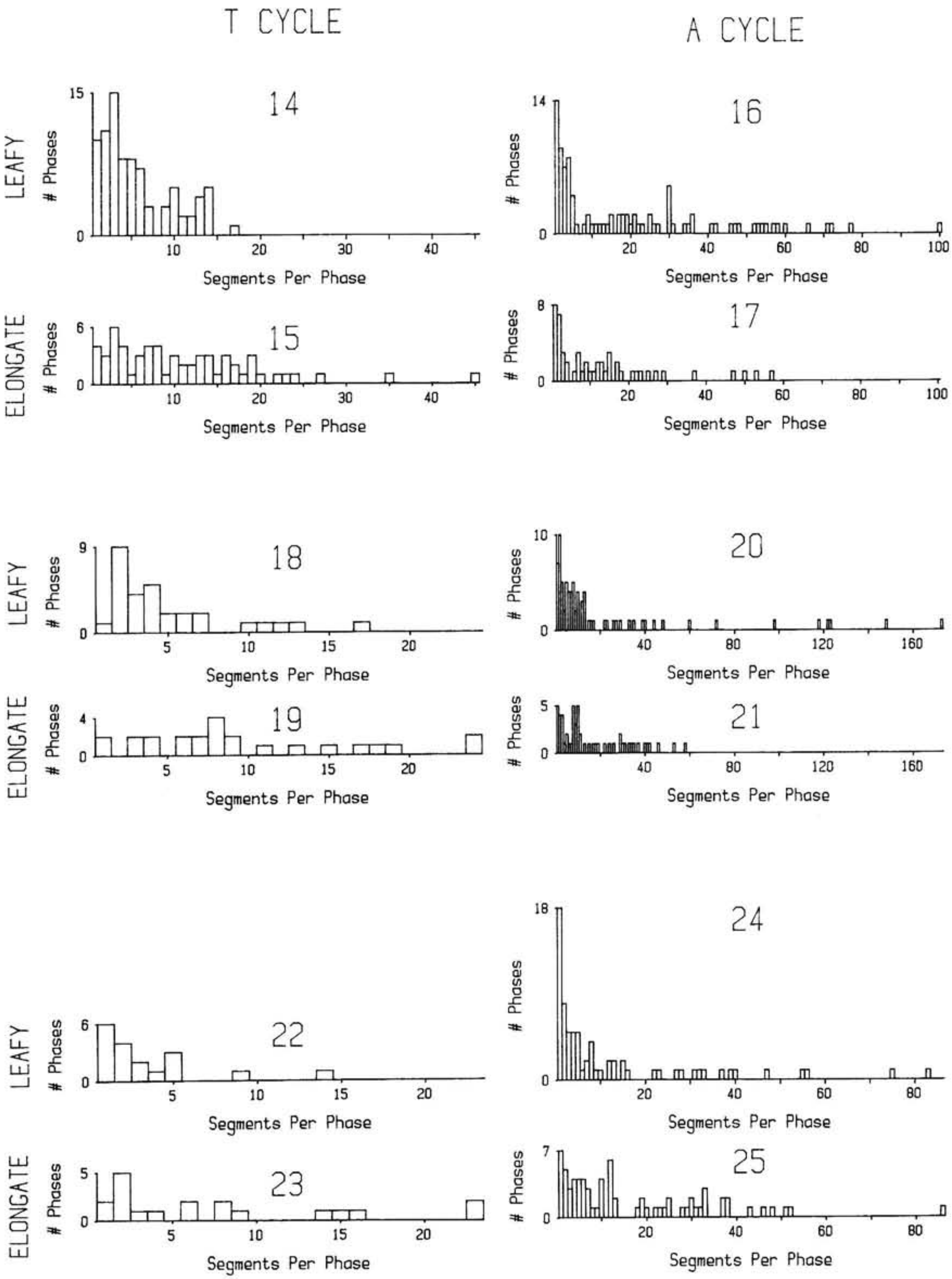

Fig. 14–25. Frequency distributions of the number of segments in each phase of the cycle. All figures lump together both complete and incomplete cycles.

the origin of this bimodality: segments in the arboreal cycle (Fig. 4) generally have a larger diam than segments in the terrestrial cycle (Fig. 3). Figure 5 shows that the distribution of IS is strongly bimodal. Figures 6–7 indicate that the bimodality in this case does not derive from a difference between the two cycles, but that each cycle is strongly bimodal in the same way. The data for *S. macrophyllum* and *S. birdseyanum* show a similar pattern.

Figures 8–13 show the changes in IS along long stretches of shoot in six individuals of the three species. Figures 8–10 are the terrestrial cycle, corresponding to forms T_L and T_E of Fig. 1. Figures 11–13 are the arboreal cycle, coresponding to forms A_A, A_D, and A_T of Fig. 1. It can be seen that alternation between the leafy and elongate phases occurs with greater frequency in the terrestrial cycle than in the arboreal cycle. Figure 11 shows that a shoot may remain in one phase of the arboreal cycle for a very large number of segments. Also, Fig. 11 indicates that there may be rhythmic fluctuations of form within the leafy phase of the arboreal cycle.

Figures 14–25 support the suggestion of Fig. 8–13, that the phases of the arboreal cycle tend to be longer (have more segments) than the phases of the terrestrial cycle. Also, Fig. 14–25 suggest that in the terrestrial cycle the elongate phase tends to be longer than the leafy phase. On the other hand, in the arboreal cycle, the leafy phase tends to be longer than the elongate phase. These latter two conclusions are in agreement with Fig. 6–7 which show the relative numbers of segments in the two phases of the two cycles.

The median lengths of the phases of the cycles are as follows: for *S. triphyllum,* T cycle leafy 4, elongate 10, A cycle leafy 11, elongate 9; for *S. macrophyllum,* T cycle leafy 4, elongate 8, A cycle leafy 4, elongate 5; for *S. birdseyanum,* T cycle leafy 3, elongate 6, A cycle leafy 5, elongate 12. This supports the observation that in the T cycle, the elongate phase includes more segments per cycle. The length of the phases of the A cycle are highly variable and are determined by what the apex of the shoot comes into contact with as it moves through the forest.

DISCUSSION—Due to its mobile nature, the plant is faced with two tasks, photosynthesis and vegetative dispersal, which are not necessarily accomplished efficiently by segments of the same forms. In Fig. 1 it can be seen that forms T_E and A_T are specialized for dispersal, while forms T_L and A_A are specialized for photosynthesis. A photosynthetic form must have a large leaf area, while a dispersal form must have long internodes. That there is no single segment form which efficiently accomplishes both tasks is in part a result of the trade-off between internode length and leaf size described in Ray (1986).

It appears that this morphological trade-off has contributed to the evolution of an overall growth habit that involves a division of labor between adjacent groups of segments. This can be seen in Fig. 8–13 in which the values of IS have been plotted for each segment along the shoot. Here one can see that groups of segments at one extreme of segment shape alternate with groups of segments at the other extreme of shape, and transitions between the two extremes are very rapid. The bimodal distributions of IS shown in Fig. 5–7 also indicate that segments fall predominantly at the two extremes of form with relatively few intermediates.

The arboreal cycle—remains stable at one extreme or the other for many successive segments as shown in Fig. 11–13. Within the arboreal cycle, switching between the leafy and elongate forms appears to be controlled by gain or loss of contact with trees, or possibly by the changes of orientation associated with gaining or losing contact with trees.

Figure 11 shows that in the A cycle the segment form may remain in one phase of the cycle for a very large number of segments as long as there is no change in the substrate. The IS is plotted for each segment along a shoot of *S. macrophyllum* 173 segments long. The shoot in this figure is climbing a tree, thus the shoot is in the arboreal cycle, and all segments are classed as type A_A. Although there are fluctuations in the segment shape, all of the segments on this shoot are above the dotted line indicating the arbitrary dividing point between leafy and elongate segments. The fluctuations in this figure seem to occur in a regular cycle with a period of roughly 12 segments. The plastochron for these plants is roughly one month, thus it looks as though these cycles may reflect a seasonal phenomenon. I hope to explore this possibility further and will report on the results when they are available.

Figure 12 shows a shoot in the A cycle switching between the leafy and elongate phases in response to gain or loss of contact with a vertical support. The floor of the tropical rain forest has a scattering of small herbs, such as *Syngonium* and *Philodendron* rosettes, small palms, *Dieffenbachias,* etc. Elongating shoots will often encounter these herbs and begin to climb them as if they were a tree. However, the shoot will quickly outgrow them and return to the ground. Figure 12 shows an individual of *S. macrophyllum* whose shoot climbs a tree, then after 44 segments in the leafy form, overgrows the tree. The shoot quickly switches to the elongate form and returns to the ground, growing for an additional 31 segments before encountering a small herb. It begins to climb the herb, switching to the leafy form, but quickly overgrows the herb, then returns to the ground switching again to the elongate form.

Figure 13 shows similar changes in a shoot of *S. triphyllum* that was manipulated experimentally. A mature flowering individual in the arboreal cycle was climbing a small diam palm stem. The palm stem was cut at the base, and at the top (even with the apex of the *Syngonium* shoot), and laid horizontally supported above the ground. These manipulations were made without damaging the shoot or roots of the *Syngonium*. The *Syngonium* shoot responded by switching immediately to the elongate form. As soon as this transition seemed to be complete, the shoot was trained onto a nearby tree. The shoot then responded by switching again to the leafy form, where it remained as it continued to climb the tree. It soon reached maturity and flowered again. These examples illustrate that in the arboreal cycle, the shoots of *Syngonium* are very sensitive to objects that they contact as they move through the forest, and that they respond to those objects by changing the form of the segments produced.

The high frequency of short phases in the A cycle results from shoots of type A_T encountering small herbs on the forest floor and momentarily changing forms; data in which measurements stop just after a change in form or start just before a change in form; and fluctuations around the arbitrary transition point while changing phases (e.g., Fig. 13, just after returning to the leafy phase).

The terrestrial cycle—alternates between leafy and elongate forms, but the cycling seems to be endogenously controlled. I have not observed any factor in the environment that might be a cue for changing forms. Figures 8–10 illustrate the cycling pattern for the three species of *Syngonium*. It can be seen that the T cycle alternates frequently between the two extremes of IS, though tending to stay somewhat more in the elongate form. Figure 8 illustrates what I believe is a typical pattern. A rosette is formed, consisting of as many as a dozen leafy segments. The form then switches to elongate segments, and the shoot may continue in this form for tens of segments. If a tree is not found by this skototropic shoot, it will produce another rosette, consisting of only a few leafy segments, before producing another long stretch of elongate segments.

In summary—the growth habit of *Syngonium* consists of two developmental cycles. In the arboreal cycle switching between the leafy and elongate phases of the cycle is controlled by gain or loss of contact with a vertical support. Therefore a shoot will remain indefinitely in one phase of the cycle unless there is a change in the substrate. The phases of the arboreal cycle tend to be long. In the terrestrial cycle, there is no obvious environmental factor controlling the switching between the two phases of the cycle. It appears that switching is regulated by some endogenous mechanism. A plausible regulatory mechanism could be rising and falling photosynthate levels, with an upper threshold causing the switch from the leafy to the elongate phase, and a lower threshold causing the switch from the elongate to the leafy phase. Fluctuations on a finer scale within phases (as seen in Fig. 11) may represent cycles occurring on another level.

Comparison with other species—Cyclic heterophylly of the type found in the arboreal cycle, controlled by gain or loss of contact with trees, is widespread among climbing members of the Araceae. It appears to be universal among climbing species with monopodial or polyphyllous sympodial growth. I have observed this cycling among 25 such species, and among two additional species of Araceae with monophyllous sympodial[3] growth. This kind of cycling has been described for *Monstera* (Madison, 1977; Ray, 1983a).

Cyclic heterophylly of the type found in the terrestrial cycle, controlled by some endogenous factor, is comparatively rare. I have observed this with certainty only in the genus *Syngonium*, where it seems to be universal (Ray 1981, 1983b). However Blanc (1980) describes what appears to be this kind of cycling in two species of Araceae, *Philodendron linnaei* Kunth, and *Rhektophyllum mirabile* N. E. Brown. In *R. mirabile*, the growth habit seems to be pre-

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[3] In monopodial growth, flowering occurs on axillary short shoots and does not interrupt the formation of the main shoot by a single apex. In monophyllous sympodial growth, after the shoot terminates in an inflorescence (which often aborts at the primordial stage), each continuation shoot will produce only a single foliage leaf before terminating in another inflorescence, and being replaced by another continuation shoot with one foliage leaf. These terms will be discussed in greater detail in the next two papers of this series.

cisely analogous to what I have described in *Syngonium,* with an arboreal and a terrestrial cycle, the latter with an endogenously controlled cycle. *Philodendron linnaei* has a quite different growth habit. Its seeds germinate on trees, and so the species is truly epiphytic. A single growing shoot produces alternately, groups of leafy and groups of elongate segments, as the shoot climbs the tree. When the species reaches maturity, subsequent growth remains in the leafy form. During the period of alternation between forms, cycling would appear to be controlled by some endogenous mechanism. I have observed something similar to this in *Anthurium interruptum* Sodiro, a creeping epiphyte in which a few elongate internodes alternate with a few leafy internodes, however my observations on this species are very limited.

Some other examples of cyclic heterophylly occurring on single shoots have been reported in other taxa. Several authors describe cyclic heterophylly in amphibious plants in which switching between aquatic and aerial growth forms occurs on a seasonal basis and is at least in some cases controlled by photoperiod (Burns, 1904; England and Tolbert, 1964). Critchfield, 1970b described growth in Boston Ivy *Parthenocissus tricuspidata* (S. & Z.) Planch., in which every third node bears a flower or bud, while the intervening two nodes bear tendrils. This is a developmental cycle of sorts, but is much more rigidly controlled. It seems as if construction of the shoot is based on units of three segments. This would seem to be analogous to the growth found in *Anthurium,* where there is a rigid cycle of three leaves: a prophyll with no axillary bud, followed by a mesophyll with an axillary bud, followed by a foliage leaf subtending a terminal inflorescence. The cycle is then repeated beginning with a new prophyll. *Philodendron* shows a similar pattern but with two leaves: a prophyll with an axillary bud and a foliage leaf subtending a terminal inflorescence. In *Anthurium* and *Philodendron,* the units being repeated are successive branches on a linear sympodium. The tropical African woody liane *Triphyophyllum peltatum* (Hutch. & Dalziel) Airy Shaw, in the juvenile phase, produces a series of lanceolate leaves alternating with a few glandular filiform carnivorous leaves. The glandular leaves are produced just before the rainy season, and so alternate in a seasonally cyclic fashion with the lanceolate leaves (Menninger, 1965; Green, Green and Heslop-Harrison, 1979).

In many species of woody plants there are preformed leaves and neoformed leaves. In preformation, the leaves are initiated the year before they expand, and overwinter in the bud. In neoformation leaf primordia mature immediately after they are initiated, without any intervening period of rest. There is often a difference in form between preformed and neoformed leaves, thus a species which bears both types may be heterophyllous as a result. Since one type of leaf will follow the other on the same shoot each year, this results in a seasonally cyclic heterophylly (Titman and Wetmore, 1955; Critchfield, 1960, 1970a, b, 1971; Clausen and Kozlowski, 1965; Kozlowski and Clausen, 1966; Wilson, 1966; Steingraeber, 1982).

In the examples just cited, there is cyclic variation of leaf form on single shoots, however, the authors generally do not emphasize variation in internode length. If we look however, at examples in which different kinds of shoots are formed on the same plant, we find many examples of marked variation in internode length between shoots. It is interesting to compare the dimorphic shape of segments in single shoots of *Syngonium* to the dimorphism between shoots commonly found in trees. It has been widely reported that certain species of trees and some woody vines bear "long shoots" and "short shoots" (Titman and Wetmore, 1955; Critchfield, 1960, 1970a, b, 1971; Clausen and Kozlowski, 1965; Kozlowski and Clausen, 1966; Wilson, 1966; Dickinson and Phipps, 1984).

There is a division of labor between leafy and elongate shoots in relatively unbranched *Syngonium,* with leafy shoots providing the photosynthetic surface and generally bearing the inflorescences, and elongate shoots providing mobility. Similarly, there is a division of labor between long and short shoots of richly branched woody plants. Short shoots bear most of the photosynthetic surface, and generally bear the flowers. Long shoots are responsible for building the branch system and thereby for establishing the overall structure of the tree. The division of labor between groups of leafy segments and groups of elongate segments seems to be functionally analogous to the division of labor between short shoots and long shoots. We seem to see similar solutions to similar problems faced by plants with radically different growth habits: sessile branched systems and mobile unbranched systems.

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