American Journal of Botany 77(12): 1599–1609. 1990.

METAMORPHOSIS IN THE ARACEAE[1]

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In the Araceae, as in many other monocotyledons, the stem undergoes gradual thickening as successive internodes are produced. Along with this primary thickening of the stem, successive foliage leaves will be larger and often more complex. In many species, in addition to these and other gradual changes, there are abrupt changes, metamorphoses, that occur under certain conditions. Some metamorphoses are the result of endogenous cycling (e.g., *Syngonium, Rhektophyllum, Philodendron linnaei*), some are a response to changes in conditions in the environment, usually the gain or loss of contact with a substrate (e.g., *Syngonium, Monstera, Rhodospatha, Philodendron* section *Pteromischum*), and some occur when the plant reaches a certain level of maturity (e.g., *Monstera*). Some of these latter changes are associated with a transition from monopodial to sympodial growth (e.g., *Philodendron, Anthurium*). Metamorphosis enhances the developmental plasticity of the Araceae in two distinct ways: it allows for a more complex relationship between size and shape in the development to maturity, and it allows shoots to engage in dispersal activities and developmental holding patterns when conditions are not suitable for development to the adult form and reproduction.

Diversity of shoot developmental patterns in plants is very rich, while our understanding of it remains relatively poor. Goebel (1898) provided the terms homoblastic and heteroblastic to distinguish classes of shoot development; however, this dichotomy only begins to cope with the diversity. There is a need for quantitative methods to describe shoot development in order to add a greater precision to our understanding of the phenomenon. This paper provides such methods and applies them to the description of several species of climbing Araceae. The Araceae is a family in which unusually elaborate patterns of shoot development have evolved in association with the climbing habit.

In climbing Araceae, the apex is displaced through the forest, producing leaves and stems in a variety of microhabitats. However, individual organs of plants remain in a fixed location, and thus must be adapted to the conditions of their immediate local environment. In the normal development from the juvenile to the adult, the shoot grows from the forest floor to the upper level of the trunks of trees. The change in position during growth is accompanied by changes in environmental conditions (light, humidity, temperature, frequency of disturbance by falling debris, etc.) and associated selective pressures. The divergent selective pressures acting on the juvenile and adult stages of shoot development have resulted in the evolution of a great diversity of shoot developmental patterns leading to varying degrees of differences in the morphology of the juvenile and adult shoots.

In order to understand shoot development we must recognize that development in plants is hierarchically organized, occurring on several levels. The most familiar level of development is first-order development, in which primordial tissue develops in a highly deterministic and canalized fashion to produce mature organs. Through first-order development, in plants a leaf primordium develops into a leaf, and in animals a zygote develops into a mature organism. Second-order development, shoot development, involves a serial repetition of the first-order process, as successive segments are produced on a shoot. Third-order development, plant architecture, involves repetition of the second-order process, as successive shoots are produced in a branched plant to produce the overall architecture of the plant. Fourth-order development involves the reiteration of architectural models or the clonal reproduction of entire plants. The concept of levels of development has been discussed by Guerrant (1982) and Scott Wing (personal communication).

The study of allometry (Huxley, 1932; Gould, 1966; Alberch et al., 1979) has provided a useful paradigm for the quantitative analysis of

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[1] Received for publication 17 April 1989; revision accepted 2 August 1990.

The author thanks Carlos Campos and Leonel Campos for assistance, and Jim French, Richard Greyson, George Wilder, and anonymous reviewers for critical reviews of the manuscript. This study was supported in part by a grant from the University of Delaware Research Foundation, and in part by NSF grant BSR 8822576. Contribution No. 129 from the Ecology Program, School of Life and Health Sciences, University of Delaware.

first-order development. However, similar quantitative approaches are still lacking for the higher levels of development. This paper presents a methodology by which the allometric paradigm can be extended to the study of second-order development.

MATERIALS AND METHODS

This study was conducted in part at the Organization for Tropical Studies' La Selva Field Station, located at the confluence of Rio Puerto Viejo and Rió Sarapiquí (10°25′N, 81°1′W) in Heredia Province, Costa Rica, and in part at privately owned Finca El Bejuco located 3 km southwest of Finca La Selva, on the road to San José. The vegetation of the area, described in detail by Holdridge et al. (1971), is transitional between tropical wet and premontane wet forest life zones in the Holdridge System (Tosi, 1969).

In this study, data are presented on six species (vouchers follow species names): *Monstera skutchii* Croat & Grayum ined., Mike Grayum 5327 (MO); *Philodendron fragrantissimum* (Hook.) Kunth, Mike Grayum 5541 (MO); *P. grandipes* Krause, Mike Grayum 1758 (DUKE); *Syngonium macrophyllum* Engl., Barry Hammel 9835 (MO); *S. podophyllum* var. *peliocladum* (Schott) Croat, Barry Hammel 12787 (MO); and *S. triphyllum* Birdsey ex Croat, Tom Croat 35675 (MO). Individuals were chosen representing all stages of the growth habit of each species, except *M. skutchii* and *S. podophyllum,* for which only climbing shoots were sampled. The number of individuals and segments (sensu Ray, 1986, an internode and leaf) sampled for each species follow: *M. skutchii,* 37 individuals totaling 3,189 segments; *P. fragrantissimum,* 102 individuals totaling 4,623 segments; *P. grandipes,* 43 individuals totaling 1,280 segments; *S. macrophyllum,* 95 individuals totaling 4,399 segments; *S. podophyllum,* four individuals totaling 86 leaves; *S. triphyllum,* 139 individuals totaling 5,174 segments. These individuals were collected and dissected into internodes, petioles, and lamina lobes. The parts were individually cataloged, their node number recorded, and their linear dimensions measured; length and sometimes width for lamina lobes, length for petioles, and length and diameter for internodes. Because the base of the petiole spreads into a sheath that completely encircles the stem at the node, the diameter of the internode is considered to be the same as the width of the petiole and was used as such in the data analysis. In the Araceae, unlike in other monocotyledons, the petiole and sheath together are called the petiole (Madison, 1977; Ray, 1986).

Several kinds of graphical representations of the data are used in this paper. One kind is scattergrams of the shape of the component organs of the segments, plotted against the size of the segments. These scattergrams represent allometric relationships between the dimensions of organs during development. The measure of segment size used in this study is always internode diameter, while the measure of organ shape used varies depending on the organ and the species. The internode shape is measured as the internode diameter divided by the internode length. The petiole shape is measured as the petiole length divided by the petiole width, with petiole width measured as internode diameter. Each of these graphical representations defines a size-shape space in a manner consistent with the methods recommended by Alberch et al. (1979) for the analysis of developmental trajectories.

Representation of leaves—Often one of the most obvious changes occurring in second-order development is a change in the form of successive leaves. These changes may be complex and subtle, and often cannot be characterized in detail by simple ratios. It is desirable to be able to describe leaf form ontogeny as accurately as possible.

One technique that is particularly appropriate for this purpose is "eigenshape" analysis (Lohmann, 1983; Lohmann and Schweitzer, 1990; Ray, 1990). In this technique, the tangent angle to the outline of the leaf is measured at a number of equal length steps (e.g., 100) around the outline, and a principal components analysis is conducted on the angle measures. From the analysis one derives a series of eigenshapes that represent the principal components of variation of the tangent angles, and the loadings of each sample leaf on the eigenshapes. A size-shape space for leaf outlines can be constructed using the leaf length, perimeter length, or leaf area as a measure of size, and the loadings on the eigenshape functions as measures of shape.

In this paper, eigenshape analysis is used only for the shoot simulations illustrated in Fig. 1. The data used in the analysis are based on a sample of 86 leaves of *Syngonium podophyllum* var. *peliocladum.* The leaf outlines were digitized using the automatic outline tracing routine of the BioSonics OPRS image acquisition system, made available by Norman MacLeod of the University of Michigan.

Ray (1990) applied eigenshape analysis to leaf shape, using the method as developed by

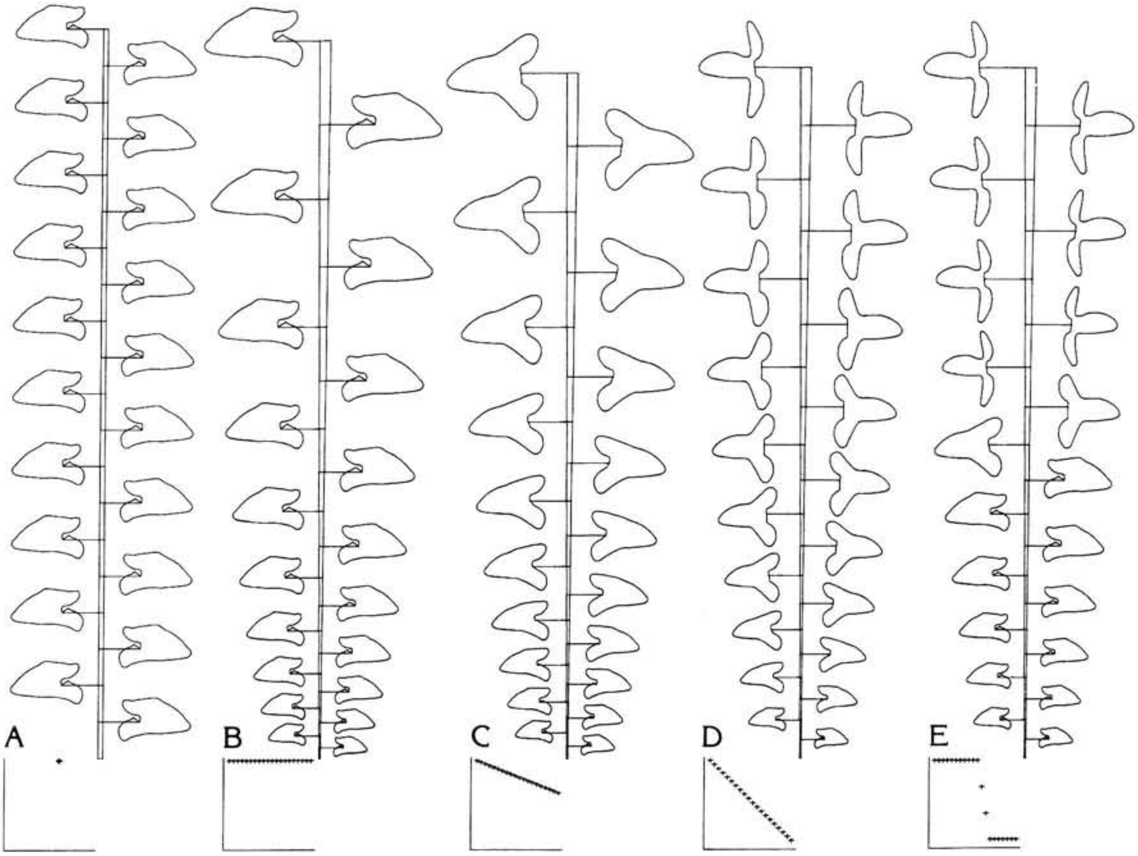

Fig. 1. Simulations of isomorphic (A), allomorphic (B–D), and metamorphic (E) shoot development. The axes beneath each figure plot the values of size and shape for each segment on the shoot. The x axis is the length of the leaf perimeter, and the y axis is the loading on the first eigenvector (eigenshape). The scales of the axes are the same for each shoot, to facilitate comparison.

Lohmann (1983) and Lohmann and Schweitzer (1990). However, Ray (1990) pointed out that their construction of the ϕ^* outline function involves an unnecessary "removal of a circle" step, and that their normalization was performed in an unconventional manner (across angle measures within each specimen) that reduces the efficiency by which the principal components represent the variation in the data. For these two reasons, the eigenshape analysis has been implemented differently here than in Ray (1990).

The ϕ^* function represents the angle of the n^{th} step on the outline as the difference between the angle of the step on the outline and the angle of the corresponding step on a circle. In my analysis, the ϕ^* function is replaced by the ϕ function (Zahn and Roskies, 1972) which simply records the angular direction in the plane at each step (with the angle of the first step set to zero). In addition, normalization in my analysis is made for each of the 100 angles across the 86 specimens, rather than for each of the 86 specimens across the 100 angles.

While eigenshape analysis is a more detailed method of characterization of leaf shape, it requires the digitization of a large number of coordinates along the leaf outline. Because I have only recently gained access to the technology for doing this efficiently, examples have also been presented here where leaf shapes are characterized by simple ratios. These methods have been applied to species whose leaf forms are fairly simple.

For *Monstera skutchii,* leaf shape was measured as the length of the lamina divided by the width of the lamina. The width of the lamina was measured as the widest line perpendicular to the midrib. For *Philodendron fragrantissimum,* this same measure of shape could not be used because of asymmetries in the cordate leaf. On one side of the leaf, the widest point is just above the point of attachment of the petiole, but on the other side, the widest point is on the lobe, below the point of attachment of the petiole. Therefore, in this species, the measure of leaf shape used was length divided by the half-width of the blade. The half-width of the blade is measured from the midrib to the widest point on the leaf margin, in a line perpendicular to the midrib, on the side of the leaf with the widest part forwardmost.

Index of metamorphosis—The distinction between allomorphosis and metamorphosis is that allomorphosis involves a single allomorphic pathway, while metamorphosis involves switching between allomorphic pathways (see Fig. 1, Results). Metamorphosis itself is usually characterized by an abrupt shift in form. To highlight this shift, an index of the rate of change in shape from one segment to the next has been added to some of the scattergrams. This index is plotted on the same horizontal axis as the scattergrams, to allow a direct comparison.

The index of rate of change of shape is computed in the following fashion. For each pair of points (x_{1i}, y_{1i}) and (x_{2i}, y_{2i}) in the scattergram that represent adjacent segments on the same shoot, the mean value of x is computed, $x_{mi} = (x_{1i} + x_{2i})/2$ and the change in y, $\Delta y_i = y_{2i} - y_{1i}$ (these calculations are made with the log transformed data). These values are then used to compute a moving average of the rate of change in y over the range of values of x.

The moving average is computed by setting up a "window" of x values, from some lower x value to an x value about 20% above the lower value (a constant distance of 0.08 on the log transformed axis). The width of this window is adjusted consistent with the sample size of the data cloud. Sparser clouds with less data require a larger x window in order for enough points to be included in the window. For all values of x_{mi} that fall within the x window, we compute a mean value of x, $x_m = \Sigma x_{mi}/n$ and a mean value of y, $\Delta y = \Sigma \Delta y_i/n$ where n is the number of values of x_{mi} falling in the window. The x window is then moved up the x axis a distance of 1/100th of the length of the x axis, and new values of x_m and Δy are computed. These successive values are plotted as points connected by a line on the graph with the scattergram, using the same horizontal axis, but a separate vertical axis represented on the right.

It has been found that the index of change in shape, Δy, is highly erratic unless at least 15 points were used in its computation. When samples of 20 or more points are used in each window, the value of Δy is stable, but reflects changes in the rate of change in form. This allows us to see pulses in the rate of change in form associated with metamorphosis.

Vector filtering—The vector field technique provides a clear representation of allomorphic pathways. In the vector field technique, the change in form from one segment to the next on the shoot is represented by a vector connecting the two points in the size-shape space that represent those two segments. The region of the size-shape space where the data occur is divided into a grid, and all vectors that fall within one cell of a grid are summed together. Only the resultant vector is plotted for each cell.

In species with two or more allomorphic pathways, the metamorphoses between the pathways can introduce confusing complexities into the vector field diagrams. These complexities can be sorted out by taking advantage of the fact that when the shoot is undergoing metamorphosis between two pathways, the vectors from the metamorphosing portion of the shoot are mostly relatively long. By filtering out the long vectors, it is possible to resolve the individual allomorphic pathways separately, as has been done in Fig. 11 for *S. triphyllum.* In order to select a maximum length for filtering, a histogram of the y component of the vectors (Δy) is plotted. The spread of the histogram provides guidance in choosing a threshold; only the tails of the distribution are removed. In Fig. 11, vectors were removed whose y component exceeded a value of 0.15.

Shoot simulations—Once the allomorphic pathways of a population have been characterized by the techniques described here, it becomes possible to run the analysis in reverse and use the computer to draw plants with a specified set of developmental characteristics. Generally, trajectories through any size-shape space can be characterized as allometries. The parameters of the allometries can be coded into a program, and the form of a segment can be reconstructed from the values of the size-shape parameters. By stepping these parameters through the successive sizes and shapes of an allometry governing the allomorphic pathway, the forms of successive segments can be generated and drawn together as a shoot (Fig. 1).

The simplest way of doing the simulation is to have a separate allometry describing the relationship between size and shape for each of the three organs of the segment, the internode, petiole, and lamina. The endpoints of each of the allometries can be entered into the program, and the program can interpolate evenly spaced steps between the endpoints for each organ, according to the number of segments specified to occur in passing through the complete trajectory. However, more complex models may incorporate correlations between the dimensions of the three organs as described in Ray (1986), or may involve switching between allomorphic pathways, metamorphosis.

In the example of Fig. 1, the allometry was based on the data derived from the eigenshape analysis of *Syngonium podophyllum.* Two leaves (d2 and d20 from Ray, 1990) were chosen as the endpoints of the allometry. Each leaf is characterized by a size (perimeter length) and a shape (the loadings on the first five eigenshapes). Each figure represents a different pattern of stepping through the size-shape space between the two points represented by the two leaves. The successive values of leaf perimeter and the loading on the first principal component are illustrated on the size-shape axes below each shoot.

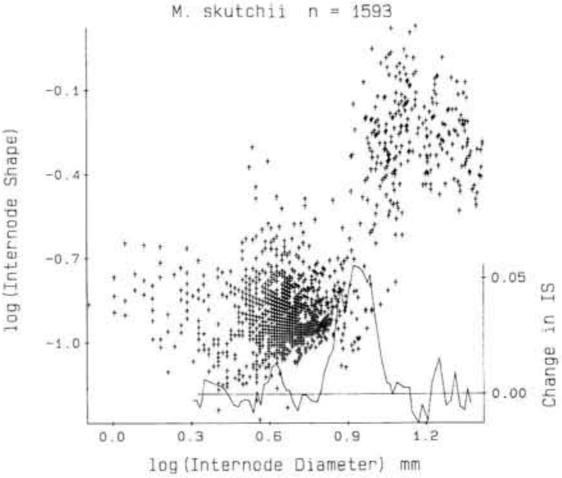

Fig. 2. Relationship between internode shape and internode diameter in *Monstera skutchii.* Internode shape is measured as internode diameter divided by internode length. The scattergram corresponds to the axes on the left, and the tracing corresponds to the axes on the right. The axes on the right measure the change in internode shape, Δy, see Materials and Methods.

RESULTS

In order to describe the results I must present a new terminology for classes of shoot development, which are illustrated in Fig. 1. Case A illustrates shoot development in which there is no change in either size or shape. Case B represents change in size, but no change in shape. Case C represents change in size, with slight change in shape. Case D represents change in size with great change in shape. Case E represents change in size with no change in shape, except at a certain size, at which there is an abrupt change in shape.

The term isomorphosis will be used to refer to shoot development that occurs with no change in either size or shape, case A. The term allomorphosis will be used to refer to shoot development in which changes in form occur gradually, within the context of a single linear trajectory, cases B through D. The term metamorphosis will be used to refer to shoot development involving switches between simple linear trajectories, usually indicated by abrupt changes in morphology, case E. The term allomorphic pathway will be used to refer to the trajectory through size-shape space traced by a shoot growing allomorphically. By definition, the graph of an allomorphic pathway is roughly linear and unbroken, as illustrated in cases B through D. Metamorphosis involves a switch between at least two allomorphic pathways.

M. skutchii undergoes a striking metamorphosis from a round appressed leaf to an elongate leaf held away from the stem. Although different in shape, both leaf forms of *M. skutchii* are entire, making the quantification of the leaf shape relatively simple. It has been observed that in *M. skutchii* metamorphosis occurs when the climbing stem reaches a specific internode diameter of just under 1 cm. This seems to be the most reliable indicator for this particular metamorphosis, and stem diameter will be used as the independent variable in the quantitative analysis of this and most of the species that follow. Each of the three component parts of the segment, the internode, the petiole, and the lamina, undergoes an abrupt change in form at the occurrence of metamorphosis in *M. skutchii.* These changes can be seen in Figs. 2–4, in which the shape of each organ is plotted as the ratio of length to width or width to length, against the internode diameter. In each case, it can be seen that there is a break in the allometry between organ shape and internode diameter at a diameter of just below 1 cm. Organs on stems of less than 1 cm in diameter have a significantly different shape than those on stems of greater than 1 cm in diameter.

What often distinguishes metamorphosis between allomorphic pathways from development within an allomorphic pathway is the relative rate of change. This contrast is highlighted in Figs. 2–4 by the line indicating the rate of change in shape from one segment to the next, Δy (see methods section). For each of the three organs, it can be seen that Δy fluctuates around zero (no change), until the 1-cm threshold is approached. Δy then begins to rise, reaching a peak at an internode diameter of about 9 mm, and then declines again to zero.

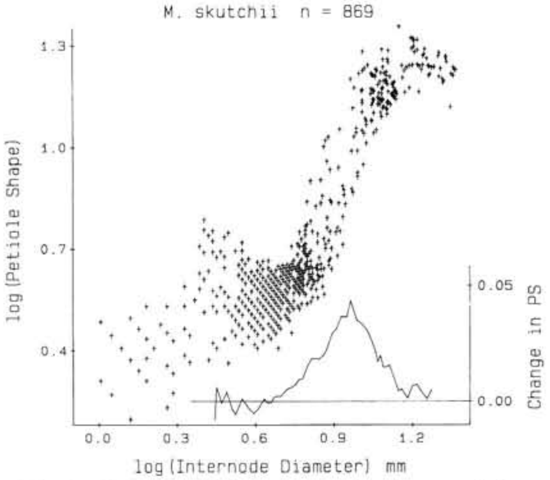

Fig. 3. Relationship between petiole shape and internode diameter in *Monstera skutchii.* Petiole shape is measured as petiole length divided by petiole width.

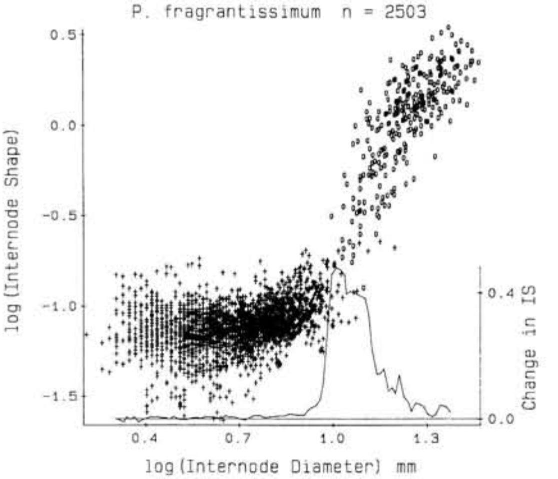

Fig. 5. Relationship between internode shape and internode diameter in *Philodendron fragrantissimum.* Internode shape is measured as internode diameter divided by internode length. Segments from monopodial growth (+); segments from sympodial growth (O).

Above a diameter of about 1.1 cm, Δy again fluctuates around zero. In other words, the shape of each of the three organs remains stable until the internode diameter range of about 0.7–1.1 cm, within which abrupt changes in form occur. Above this threshold size range the shapes of the three organs stabilize again, but in shapes different from those they assumed before metamorphosis. It should be kept in mind that while there may be little change in the shape of successive organs outside the episode of metamorphosis, they are constantly increasing in size, both in and out of the metamorphic episode.

In *Philodendron fragrantissimum,* when a climbing stem reaches a diameter of about 1 cm, there is a switch from monopodial growth to diphyllous sympodial growth (Ray, 1987c, 1988) in which each meristem produces two leaves before terminating in an inflorescence. In Figs. 5–7, organs from monopodial growth are represented by the symbol +, while organs from sympodial growth are represented by the symbol O. This transition entails a change in the developmental program; however, unlike in the case of *M. skutchii,* not all of the organs of the segment are affected equally.

The shape of the lamina undergoes gradual allometric change throughout the thickening of

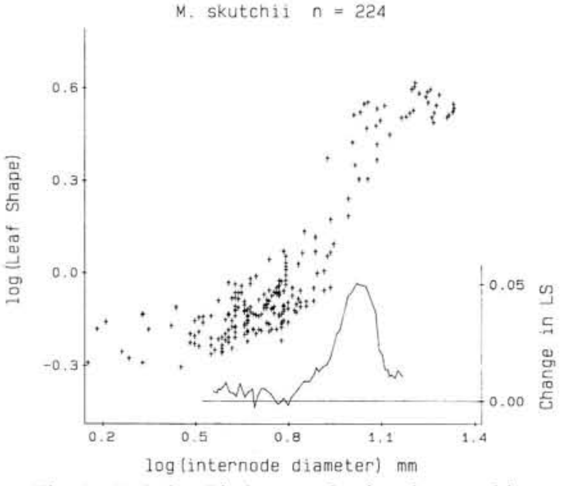

Fig. 4. Relationship between lamina shape and internode diameter in *Monstera skutchii.* Lamina shape is measured as lamina length divided by lamina width.

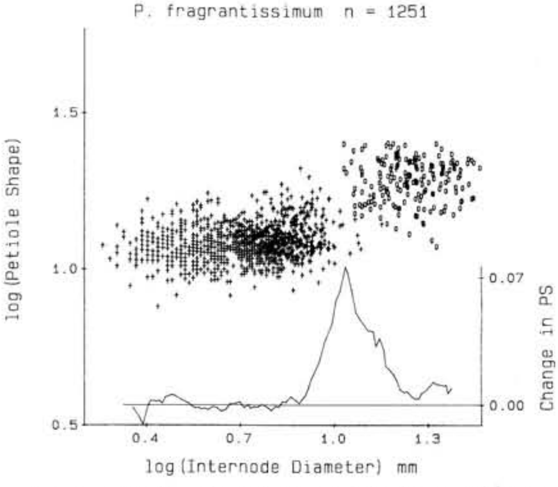

Fig. 6. Relationship between petiole shape and internode diameter in *Philodendron fragrantissimum.* Petiole shape is measured as petiole length divided by petiole width. Segments from monopodial growth (+); segments from sympodial growth (O).

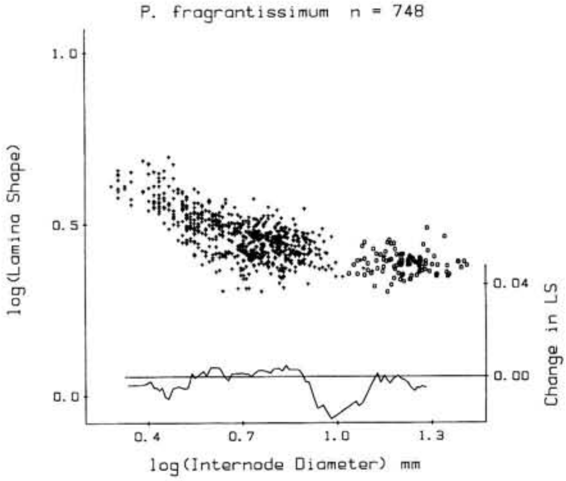

Fig. 7. Relationship between lamina shape and internode diameter in *Philodendron fragrantissimum*. Lamina shape is measured as lamina length divided by lamina half-width (see Materials and Methods). Segments from monopodial growth (+); segments from sympodial growth (O).

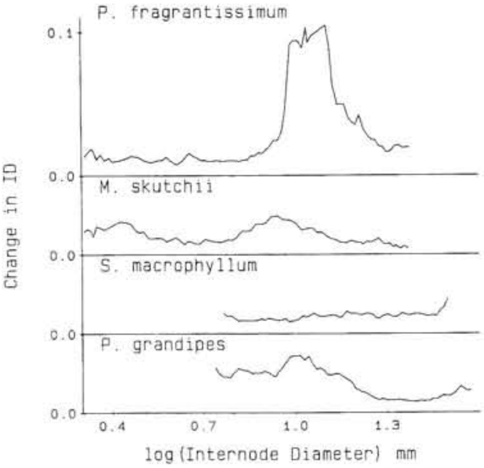

Fig. 8. Rate of increase of internode diameter as a function of internode diameter for four species: *Philodendron fragrantissimum, Monstera skutchii, Syngonium macrophyllum,* and *Philodendron grandipes.* Change in internode diameter is computed like Δy, see Materials and Methods.

the stem but does not show abrupt change or a break in the allometry at the time of metamorphosis (Fig. 7). The petiole is altered in that there is a tremendous reduction in the development of the sheath in diphyllous sympodial growth. Otherwise, the shape of the petiole shifts only slightly in metamorphosis (Fig. 6). The internode, however, is strongly affected by the metamorphosis, and this can be seen in Fig. 5. At the time of metamorphosis there is a large and abrupt break in the allometry, from a more to a less elongate internode shape.

Figures 5–7 include plots of Δy which show the rates of change of the three shape indices plotted against the internode diameter. While the index Δy shows only a slight pulse for lamina shape, it shows a pulse in the rate of change of internode shape that is an order of magnitude greater than that shown by the petiole. It is also an order of magnitude greater than the pulse in Δy shown by any of the organs of any of the other species of this study. The extraordinary magnitude of the rate of change in internode shape in *P. fragrantissimum* appears to be related to another unusual feature of the metamorphosis in this species. In all of the other species analyzed, at the time of metamorphosis there may be a pulse in the rate of change in the shape of one or more organs, but the rate of increase in internode diameter remains fairly constant. In *P. fragrantissimum,* however, the rate of change in internode diameter also pulses dramatically at the time of metamorphosis (Fig. 8).

The abrupt increase in internode diameter creates an artifact in that it amplifies the magnitude of the index Δy. This artifact can be removed by dividing each value of Δy_i by the corresponding change in internode diameter for that pair of segments. In other words, we can examine the slope of the trajectory through size-shape space rather than the rate of change in shape. When this is done, the pulse in the rate of change of internode shape in *P. fragrantissimum* comes into line with the magnitude seen in other organs showing metamorphosis in other species. By this same index, neither the petiole shape nor the leaf shape show visible pulses in the rate of change in *P. fragrantissimum.*

In each of the examples just given, the transition in question occurs at a critical internode diameter, making it possible to demonstrate the occurrence of the transition using the parameter Δy. The examples of metamorphosis that follow do not occur at a critical internode diameter; therefore, they cannot be characterized with Δy.

In addition to the metamorphosis associated with the transition from monopodial to sympodial growth in *P. fragrantissimum,* there are additional allomorphic pathways between which metamorphoses are triggered by gain or loss of contact with trees. Figure 9 illustrates the two allomorphic pathways for monopodial shoots. A vector field is plotted for monopodial shoots climbing trees. The scattergram in the same figure represents the forms of segments on monopodial flagellar shoots hanging in the air or on the ground (but attached to a shoot on a tree). A scattergram is used for the flagellar

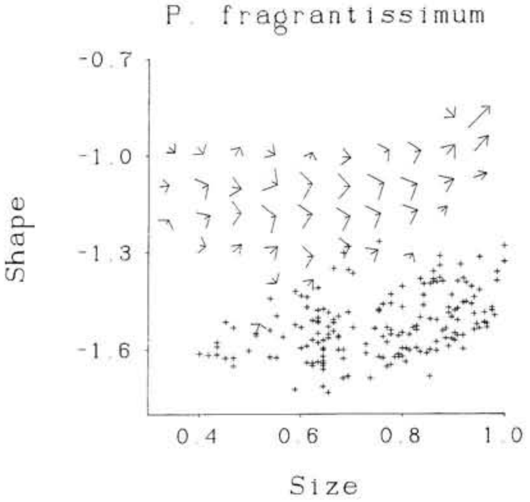

Fig. 9. Relationship between internode shape and internode diameter in monopodial shoots of *Philodendron fragrantissimum* for the arboreal ascending pathway represented by the vector field ($N = 2{,}096$), and the flagellar pathway represented by the scattergram ($N = 181$). Size is log of internode diameter, in mm; shape is the log of the ratio of internode diameter to length.

shoots because the sample of these segments is smaller ($N = 181$) than that for segments on climbing shoots ($N = 2{,}226$). Vector fields can only be generated from fairly large data sets. The data group into two clusters, based on whether the internodes are on a tree (vector field), or in the air or on the ground (scattergram). The two clusters represent two allomorphic pathways between which metamorphosis occurs in response to gain or loss of contact with vertical supports.

Metamorphosis also occurs between two allomorphic pathways, leafy and elongate, in the terrestrial cycle of *Syngonium* (Ray, 1981, 1983, 1987a). Figures 10 and 11 illustrate these two allomorphic pathways for *S. triphyllum*. However, it is even more difficult to characterize this metamorphosis because it is triggered by some endogenous factor. It is, therefore, not possible to divide segments into the two allomorphic pathways involved, either on the basis of internode diameter or the type of substrate to which they are attached.

Visualization of the two allomorphic pathways is aided by plotting a scattergram of size and shape for all segments in the terrestrial cycle as has been done for *S. triphyllum* in Fig. 10, which shows a greater density of data in two clusters. These two clusters represent the two allomorphic pathways between which metamorphosis occurs. The scatter of points between the two clusters represents the metamorphosing segments. Resolution of the two allomorphic pathways can be enhanced by the vector filtering technique, in which the long vectors associated with abrupt changes in form are filtered out, as shown in Fig. 11 (see Materials and Methods section).

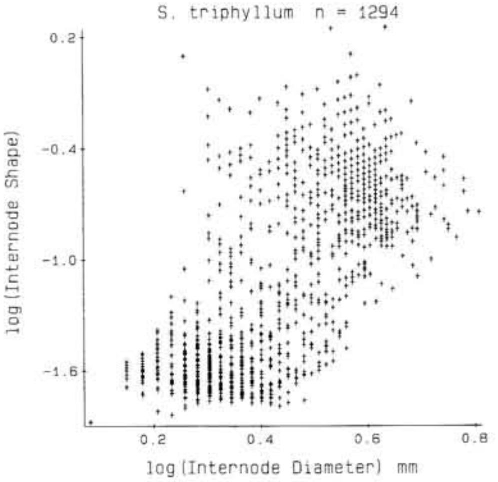

Fig. 10. Relationship between internode shape and internode diameter in the terrestrial cycle of *Syngonium triphyllum*. Internode shape is measured as internode diameter divided by internode length.

DISCUSSION

Terminology—Goebel appears to have been the first to introduce terms (heteroblasty and homoblasty) distinguishing between the degree of changes in the forms of successive leaves along shoots (Goebel, 1898, p. 143).

> "... *the adaptation of the juvenile form to external relationships is different from that*

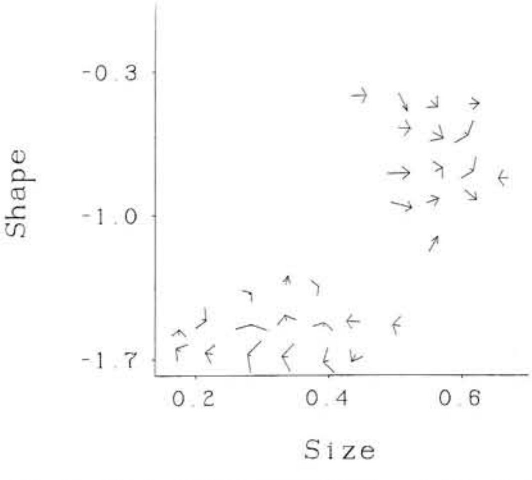

Fig. 11. Vector field diagram of the terrestrial cycle of *Syngonium triphyllum*, with vector filtering. Vectors whose y component exceeds 0.15 have been filtered out.

of the adult form, a fact which appears in a very striking way in the 'larval form' of many animals. The differences between the two sections of the developmental history show themselves in very different degrees; there are cases where they are very slight and the two sections may quite gradually pass one into the other. I have designated this latter condition the *homoblastic* development, and that in which the differences are great the *heteroblastic.*"

From Goebel's definitions of the terms, it seems that homoblastic might be applied to cases A through C of Fig. 1, and heteroblastic might be applied to cases D and E. Goebel did not distinguish between size and shape when discussing changes in form; therefore, it is not clear if he intended the term homoblastic to apply to case B where successive leaves change in size but not in shape, or if he would apply the term to case A where a shoot grows without change in either size or shape. However, the examples cited indicate that he would apply the term heteroblasty to cases D and E.

The two terms introduced by Goebel are not adequate to describe the diversity of shoot developmental patterns observed in the Araceae, in part because they do not consider the fundamental distinction between development involving a single allomorphic pathway and development involving metamorphosis between multiple allomorphic pathways. Furthermore, over the years the distinction made by Goebel has been lost. The term homoblastic has fallen into disuse, and the term heteroblastic has come to refer to both kinds of change (Greyson, Walden, and Smith, 1982). The terminology of Goebel cannot be used to make the distinction between metamorphosis and allomorphosis without changing their meaning.

The data—The data presented here show that second-order developmental trajectories in the Araceae fall within constraints that have the characteristics of allometries, similar to those that are well known to constrain first-order development. However, in some of the data there is a sharp break in the allometric relationship, as metamorphosis causes a switch from one allometry to another.

Data illustrating four examples of metamorphosis have been presented here. 1) In the example of Figs. 2–4, *M. skutchii* undergoes a metamorphosis affecting all three component organs of the segment when a climbing shoot reaches a diameter of about 1 cm. The metamorphosis seems to be endogenously triggered, is associated with a particular internode diameter in climbing shoots, and does not involve a switch between monopodial and sympodial growth.

This kind of metamorphosis is quite rare. I have observed its occurrence only in the genus *Monstera,* where it is even further restricted to the section *Marcgraviopsis.* Madison (1977) made use of the presence or absence of certain types of metamorphoses in defining sections of the genus *Monstera.* However, Blanc (1978) has described what appears to be the same phenomena in unnamed species of *Rhaphidophora* and *Scindapsus,* genera closely related to *Monstera* in the subtribe Monsterinae. Blanc (1978) also reports an undetermined species of *Philodendron* from Guyana that shows a metamorphosis in leaf form in shoots sympodial both before and after the change in leaf form.

2) In the example of Figs. 5–7, *P. fragrantissimum* undergoes a metamorphosis when a climbing shoot reaches a diameter of about 1 cm and switches from monopodial to sympodial growth. In this instance, the forms of the lamina and petiole are little affected by the metamorphosis (except for a sharp reduction in the development of the sheath of the petiole), while the internode is strongly affected. This example illustrates that individual organs may undergo metamorphosis independently of the other organs of the segment.

A switch from monopodial to homeophyllous sympodial growth is common among species in the genera *Anthurium* (excluding section *Polyphyllium*), *Callopsis, Cyrtosperma, Lagenandra, Lasia, Orontium, Philodendron* (excluding section *Pteromischum*), *Pinellia, Pistia, Podolasia, Spathicarpa, Symplocarpus,* and *Urospatha.* These taxa are all homeophyllous sympodial when mature, and many (but not all) of the species are monopodial when immature. Therefore, in many species, at some point in their development, there is a switch from monopodial to homeophyllous sympodial growth.

In monopodial growth, the shoot is produced by the continued activity of a single apical meristem. In sympodial growth in the Araceae, the meristem is consumed in the production of a terminal inflorescence (which sometimes aborts), and continued growth of the shoot is effected by a sylleptic lateral meristem. In homeophyllous sympodial growth, each renewal shoot produces a fixed number of leaves; one, two, three, or four. In anisophyllous sympodial growth, renewal shoots produce a variable and generally larger number of leaves (Ray, 1987c, 1988; Ray and Renner, 1990).

While all homeophyllous species undergo a change in the mode of third-order development (shoot organization) at the switch from monopodial to homeophyllous sympodial growth, it is usually not accompanied by significant changes in the shapes of organs (apart from the reduction in the sheaths of the sympodial leaves, sensu Ray, 1986, and the appearance of prophylls). Gross morphological changes are most pronounced among climbing species where the switch is usually associated with a shift from a mobile to a sessile form, but are often lacking in terrestrial and epiphytic species where the form remains always sessile. The only genera in which I am certain that there are both climbing species and a switch from monopodial to homeophyllous sympodial growth are *Anthurium* and *Philodendron,* the two largest genera in the family.

3) In addition to the cases in which metamorphosis seems to be associated with a threshold internode diameter, there are other examples in which metamorphosis seems to be regulated by an endogenous factor, but in which the endogenous factor is not readily identifiable. This kind of metamorphosis occurs in the terrestrial forms of the genus *Syngonium.* Ray (1987a) has described how internode shape cycles between an elongate form and a short form in three species of *Syngonium.* In these species, groups of several adjacent leafy segments alternate with groups of tens of adjacent elongate segments with reduced leaves. Figures 10 and 11 illustrate this phenomenon for *S. triphyllum.* This pattern of metamorphosis seems to be quite rare outside of the genus *Syngonium.* Blanc (1980) describes a similar phenomenon in two species, *Philodendron linnaei* Kunth, and *Rhektophyllum mirabile* N. E. Brown, and Ray (1987a) observed something similar in *Anthurium interruptum* Sodiro.

4) All the examples of metamorphosis discussed thus far appear to have been regulated by some endogenous factor. Sometimes the factor is associated with internode diameter; in other cases it is an unknown factor, possibly photosynthate levels. In addition to metamorphoses stimulated by endogenous factors, there are others that occur in response to stimuli in the environment, most notably, gain or loss of contact with trees or other vertical supports. This pattern of metamorphosis was illustrated for *P. fragrantissimum* (Fig. 9).

For many species in many genera (*Anthurium, Syngonium, Philodendron, Rhodospatha, Monstera*) gain of contact with a vertical support causes the plant to enter an allomorphic pathway leading to short internodes bearing well-developed leaves and an increase in the diameter of successive internodes until the maximum size characteristic of the species is reached. For these species, loss of contact with a vertical support will cause a metamorphosis to an allomorphic pathway that produces elongated internodes bearing reduced leaves with a decrease in the diameter of successive internodes (Ray, 1987a). These elongate shoots have been referred to as flagellar shoots (Blanc, 1980; Ray, 1987b). The ability to produce flagellar shoots appears to be almost universal among climbing aroids with monopodial, anisophyllous, or intermittent homeophyllous growth, and almost universally lacking among species with homeophyllous growth. I am aware of only three homeophyllous species capable of producing flagellar shoots: *Philodendron fragrantissimum, P. brunneocaule,* and *P. linnaei.*

Evolutionary perspective — As a shoot climbs a tree, it will generally (though not always) be moving into regions of gradually higher light levels and temperatures, lower humidity, and less disturbance by falling debris. Differing configurations of laminas, petioles, and internodes may be suitable for differing environmental conditions. Selection can act to mold an allomorphic pathway that provides a succession of forms during shoot development that adaptively match the succession of environmental conditions encountered by the population of developing shoots on the average.

The introduction of metamorphoses that allow switching between two or more allomorphic pathways with distinct allometries provides a means of reducing the constraints of allometry. By connecting two or more allometries that may differ in slope or intercept or both, metamorphosis makes it possible for the relationships between size and shape to follow paths during development that are more complex than the simple linear path of a single allometry.

The genetic makeup of an individual will determine the number of allomorphic pathways available to it and the characteristics of those pathways. However, environmental influences can affect the rate or even the direction of movement through a pathway. Hypothetically, if higher light levels are encountered, successive internodes may thicken more rapidly causing more rapid allomorphic change, or a size at which metamorphosis occurs may be reached more rapidly. Additionally, in taxa in which some metamorphoses are triggered by factors in the environment, environmental influences may determine which of several possible pathways is occupied at a given moment.

In addition to allowing shoots to follow more complex paths during development from the juvenile to the adult, metamorphosis in the Araceae allows another developmental complexity, of a kind not found in animals. When metamorphosis occurs in insects and amphibians, it is part of a unidirectional developmental process leading from the zygote to the mature adult. While metamorphosis occurs in this context in the Araceae, it may also introduce developmental processes that do not lead to the adult form. In the Araceae, multiple and repeated metamorphoses may link two to five allomorphic pathways into complex developmental patterns, some components of which are not a part of the process of development to the adult form, and may even lead to more juvenile forms. Examples of this may be seen in the terrestrial cycle of *Syngonium* (Figs. 10–11) and in the climbing and descending shoots of *P. fragrantissimum* (Fig. 9).

The introduction of metamorphosis enhances the developmental plasticity of the Araceae in two distinct ways. It allows for a more complicated relationship between size and shape in the development to the adult form. It also allows for switching to developmental processes that do not lead to the adult form or that lead to more juvenile forms, thereby allowing shoots to engage in dispersal activities or developmental holding patterns when conditions are not suitable for development to the adult form and reproduction.

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