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Foraging behaviour in tropical herbaceous climbers (Araceae)

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Summary

1. Climbing aroids grow through the forest, and demonstrate changes in their shoot developmental patterns associated with the changes in microhabitat resulting from displacement of the apex. Through allometric development or metamorphosis, shoots are able to shift growth forms: by altering their mobility, meristems of climbing species may disperse from their site of germination on the ground to their site of maturation on tree trunks, and then become sessile. Some species have the ability to become mobile again should environmental conditions change.

2. Shoot developmental patterns in Araceae lie along a continuum from sessile to mobile, within which four broad classes of growth form can be recognized, based on the shape of the internodes: acaulescent, in which internodes are ten or more times as wide as long; caulescent, in which internodes are about as wide as long; climbing or creeping, in which internodes are about ten times as long as wide; and flagellar, in which internodes are thirty or more times as long as wide.

3. The relationship between shoot development and foraging behaviour is two-fold. The set of shoot developmental pathways allowed by the genetic system of a species determines its overall foraging pattern. Environmentally mediated switching between pathways or alterations of rates or directions of progress within pathways allow adjustments to the foraging pattern.

4. Foraging behaviour is illustrated for five species of climbing Araceae: *Anthurium subsignatum*, *Monstera skutchii*, *Philodendron fragrantissimum*, *Philodendron scandens* and *Syngonium triphyllum*. For comparison, data are presented on one terrestrial species, *Dieffenbachia seguine*. Data are based on measures of lengths and diameters of successive internodes along shoots. Shoot development is represented graphically by plotting the trajectories traced by successive shoot segments through an internode size–shape space.

Key-words: allometry, growth form, metamorphosis, vegetative dispersal, vines

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Introduction

In *The Movement And Habits Of Climbing Plants*, Charles Darwin (1875) offered an explanation of the adaptive significance of the viny habit:

> 'Plants become climbers, in order, it may be presumed, to reach the light, and to expose a large surface of leaves to its action and to that of the free air. This is effected by climbers with wonderfully little expenditure of organized matter, in comparison with trees, which have to support a load of heavy branches by a massive trunk. Hence, no doubt, it arises that there are in all quarters of the world so many climbing plants belonging to so many different orders.'

The material economy of climbers is achieved by having long slender internodes which are incapable of self support. Therefore, these plants must climb upon others. The climbing habit of the Araceae, a family of herbaceous monocotyledons, is expressed in elongated and relatively unbranched stems. This results in a plant whose one apical shoot meristem is displaced relatively rapidly through the forest, and whose trailing stem eventually senesces behind it. Thus the plant grows like a leafy snake moving through the forest. The consequence of this growth habit is a kind of mobility, which is, however, unlike the mobility of animals: the only organ which is actually displaced is the terminal meristem. All leaves and internodes remain fixed in the locations in which they were formed, and therefore must be able to survive under the circumstances of their immediate local environment. Yet the moving meristem will encounter a variety of micro-habitats as it grows through the forest, crossing the forest floor, climbing trees and other plants, and descending from the trees to the forest floor again.

Where there is movement in an organism, there is need for some type of behaviour to cope with the consequences of movement, to ensure that movements will be orientated rather than random, and to react to the objects and changing circumstances encountered as a result of movement. Bradshaw (1965) commented on this relationship between movement and behaviour:

> '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.'

Bradshaw argued that the sessile nature of plants causes them to respond to environmental changes by ontogenetic changes in form (e.g. heterophylly) rather than movement. Some plants are capable of moving, however, and a large part of the behavioural plasticity that may be observed in mobile plants involves heterophylly. Plasticity allows mobile plants to respond to the changes in local environment brought about by movement. Behavioural adaptations for movement in plants may be physiological, such as the skototropism which allows aroid climbers to orientate themselves towards trees (Strong & Ray 1975), or they may be developmental, resulting in heterophilic or heteroblastic changes in form in response to changing circumstances (Ray 1981, 1983a,b, 1986, 1987a, 1990b).

Foraging behaviour in perennial herbs has been defined by Slade & Hutchings (1987a) as the process whereby an organism searches or ramifies within its habitat to acquire essential resources. It is generally considered that in plants the primary characteristics determining the patterns of foraging are internode length, the probability of branching at nodes and branching angle (Bell 1974, 1979; Harper & Bell 1979; Bell & Tomlinson 1980; Slade & Hutchings 1987a,b,c; Hutchings & Slade 1988). This paper explores foraging behaviour amongst predominantly climbing members of a family of plants in which branching plays a minimal role, and yet within which developmental plasticity of unbranched shoots provides an analogue to the phalanx–guerrilla continuum described by Clegg (1978). The diversity of growth habits in the Araceae has been reviewed by Simmonds (1950), Madison (1978), Knecht (1983) and Croat (1988). Five species of climbing aroids and one terrestrial aroid are described to illustrate two aspects of the relationship between shoot development and foraging behaviour: (i) the suite of shoot developmental pathways allowed by the genetic system of a species determines the overall foraging pattern (growth habit), and (ii) switching between pathways or alterations of rates or directions of progress within pathways, which are in part mediated by the environment, enable localized adjustments to be made within the overall foraging pattern.

Materials and methods

STUDY SITE AND SPECIES

The study was conducted in part at La Selva Field Station (Organization for Tropical Studies) located at the confluence of Río Puerto Viejo and Río Sarapiquí (10°25′N, 81°1′W) in Heredia Province, Costa Rica, and in part at Finca El Bejuco (privately owned), located 3 km south-west of Finca La Selva. The vegetation of the area, described in detail by Holdridge *et al.* (1971), is characterized as the transition between Tropical Wet and Premontane Wet Forest life zones in the Holdridge System (Tosi 1969).

Six species were selected for study (Fig. 1). All are herbaceous members of the Araceae, and were studied in the primary rain forest, their principal habitat (except *Philodendron scandens*, see below). One species, *Dieffenbachia* cf. *seguine* (L.) Schott, is a caulescent terrestrial herb, not a climber, and is included in the study for comparison. The five climbing species are: *Anthurium subsignatum* Schott, a low climber; *Monstera skutchii* Croat and Grayum ined. (voucher: Mike Grayum 5327 **MO**), a medium-high climber; *S. triphyllum* Birdsey ex Croat, a medium-high climber; *Philodendron fragrantissimum* (Hook.) Kunth, a medium-high climber; and *P. scandens* C. Koch and Sello, a high climber. Vouchers for these species (except *M. skutchii*) have been listed in Ray (1987b,c).

The architecture of the six species conforms to the model of Chamberlain (Hallé, Oldeman & Tomlinson 1978). The shoots generally only branch when the apex terminates in an inflorescence, and a sympodial renewal shoot develops, resulting in a physiognomically unbranched shoot. The pattern and frequency of sympodial renewal varies widely between the six species. At one extreme (in *S. triphyllum*) sympodial renewal occurs irregularly and only rarely (i.e. once per several hundred leaves), and at the other (in *P. scandens*) sympodial renewal occurs after exactly every second leaf, even in the most juvenile shoots (Ray 1987c, 1988).

The physiognomically unbranched shoots are modular: each shoot consists of a linear series of 'segments' (*sensu* Ray (1986)), each segment being an internode, leaf, bud and adventitious roots (Fig. 2). Where sympodial renewal occurs after every second leaf (as in *P. scandens* and adult *P. fragrantissimum*), the segments are sympodial, and each segment consists of an internode, bud, and two leaves: a prophyll (reduced to a cataphyll) and a foliage leaf (Ray 1986, 1987b). Where sympodial renewal

Fig. 1. Morphology and habitat of six species of Araceae in the primary rain forest of north-eastern Costa Rica. (a) *Dieffenbachia seguine*, (b) *Anthurium subsignatum*, (c) *Philodendron scandens*, (d) *Philodendron fragrantissimum*, the small juvenile leaves of the monopodial shoots are visible on the trunk below the large adult leaves of the sympodial shoots, (e) adult form of *Monstera skutchii*, (f) juvenile form of *M. skutchii*, (g) climbing form of *Syngonium triphyllum*, (h) terrestrial flagellar form of *S. triphyllum*, (i) free-living terrestrial individual of *S. triphyllum*, transforming from the leafy to the flagellar form.

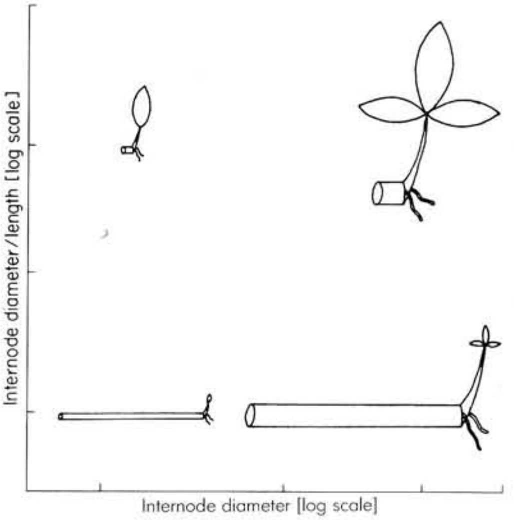

Fig. 2. Axes used to quantify the form of segments in Araceae. A single point in the plane represents the form of a single segment. Segment forms characteristic of the four quadrants are illustrated for *Syngonium triphyllum*.

occurs after every third leaf (as in *A. subsignatum*) each sympodial unit consists of two segments, one monopodial and one sympodial, which together bear two cataphylls and a foliage leaf. The measurements presented for sympodial shoots of *A. subsignatum* are actually measures of lengths and diameters of sympodial units, not internodes.

In the six species studied, all stem growth is above ground. In terrestrial species, and in the stolons and terrestrial juvenile stems of climbers, the shoots are initially erect, but eventually become prostrate when they collapse under their own weight. Thus all growth is initially above ground. Prostrate stems soon become shallowly buried under leaf litter and debris. Buried stems generally sprout adventitious feeder roots. Climbing stems sprout morphologically distinct clinging roots from each segment, as well as more widely spaced feeder roots which grow downwards and ramify in the soil.

DATA COLLECTION

Morphological data

Data were gathered over an 11-year period (1977–88) from live plants, either measured *in situ* in the primary rain forest, or removed from the primary rain forest and immediately measured in the laboratory before the plants could dehydrate. *P. scandens*, which is capable of climbing to the top of the canopy, is sun-tolerant and has become common on fence posts and trees in pastures. Material of this species (which is highly allergenic to humans) was collected from pastures.

Only measurements of internode lengths and diameters are reported here, although other measurements were made (i.e. internode weights; petiole and foliage leaf lengths, weights and areas). Individuals were collected and dissected into internodes, petioles, and lamina lobes. The parts were individually catalogued, their node number recorded, and their dimensions measured. For each segment, it was noted whether the segment was monopodial or sympodial. In addition, each segment was classified into one of four groups based in part on the micro-habitat in which it was located: arboreal (climbing a tree trunk), descending (a free-hanging shoot, descending toward the ground from a tree which the shoot had earlier climbed), free-living terrestrial (a terrestrial shoot with no posterior connection to an arboreal shoot), and parasitic terrestrial (a terrestrial shoot which is connected posteriorly, through a descending shoot, to an arboreal shoot, and which may therefore receive a photosynthetic subsidy from the usually larger arboreal shoot).

Individuals were chosen representing all stages of the growth habit of each species, except *M. skutchii*, for which only climbing shoots were sampled (due to the rarity of other forms). The number of individuals and segments sampled for each species follow: *Anthurium subsignatum*, 75 individuals totaling 3465 segments; *Dieffenbachia* cf. *seguine*, 38 individuals totaling 925 segments; *M. skutchii*, 37 individuals totaling 3189 segments; *P. fragrantissimum*, 102 individuals totaling 4623 segments; *P. scandens*, 27 individuals totaling 1094 segments; *S. triphyllum*, 139 individuals totaling 5174 segments. Further details of the micro-habitats and monopodial–sympodial categories are given in the Figure legends.

An assisted natural experiment

A specimen of *Syngonium triphyllum* was climbing a slender palm when the palm tree fell over by natural causes. The fall did no damage to the *Syngonium* shoot or roots, which are quite flexible. The fallen palm trunk was raised above the ground on Y-shaped stakes, and the top of the palm trunk was cut off at the level of the apex of the *Syngonium* shoot. This forced the *Syngonium* shoot to leave the palm shoot and transform itself into its flagellar form (Fig. 1h). As soon as the transformation to the flagellar form was complete, the flagellar shoot was trained onto a nearby tree, causing it to switch back to the climbing form. The prostate climbing shoot on the raised palm trunk quickly began to sprout lateral shoots. All lateral shoots were cut off as soon as the enlargement of the buds was apparent.

The purpose of these manipulations was to provide an apex at the base of a tree in the juvenile form, with an unusually high level of available photosynthate, comparable perhaps to what a large adult plant would have. The mature shoot on the prostate palm trunk had 32 large multi-lobed leaves, and the plant was denied any photosynthetic sink other than the one climbing apex.

DATA ANALYSIS

Size–shape space and developmental trajectories

Most of the data analyses in this paper are graphical representations of developmental trajectories through a size–shape phase space. Developmental trajectories often constitute allometries, which represent 'the differences in proportions correlated with changes in absolute magnitude of the total organism or of the specific parts under consideration' (Gould 1966). Development can be visualized as a scattergram representing the allometry of development, or as the trajectory through the morphological space taken by the growing organism. The graphical methods used here define a size–shape space in a manner consistent with the methods recommended by Alberch *et al.* (1979) for the analysis of developmental trajectories.

In order to represent developmental trajectories in two dimensions, a single size variable (internode diameter) and a single shape variable (internode diameter/length quotient) were used. The two axes are a 'size–shape space' (Fig. 2), within which the developmental trajectory will show a slope of zero if there is no change in shape associated with increase in size. The trajectory will have a non-zero slope only if there is a change in shape during growth.

Representation of segments

As a result of the internal correlations within the segment, it is possible to make a very simple characterization of the form of the entire segment as follows: size = log internode diameter; shape = log (internode diameter/length quotient) (Fig. 2). Ray (1986) has shown that this provides an approximate description of the form of all components of the segment, and closely characterizes the form in terms of segment mass, and the proportion of the segment mass placed in the leaf.

A point in this size–shape space represents the form of a single segment. The mass of the entire segment, the size of the petiole, and the complexity of the lamina are all positively correlated with the internode diameter (Ray 1986). At a given diameter, longer internodes are associated with smaller leaves; thus, the ratio of internode diameter to length indicates not only the shape of the internode, but also the proportioning of material between the leaf and internode, thereby influencing the size of the leaf associated with the internode (Ray 1986).

Segments are represented differently for *Anthurium subsignatum*. For sympodial shoots, the lengths and diameters of the sympodial units (two internodes) are plotted. This is done because each sympodial unit bears only one foliage leaf. For monopodial shoots of this species, internode lengths and diameters are plotted.

Representation of individual shoots

The forms of successive segments on a shoot can be represented by a series of points. When points representing successive segments are connected, a jagged line results which traces out the developmental trajectory of an individual shoot through the size–shape space. Use of a moving average can smooth out the contortions in the line making the trend of development clearer.

Representation of populations of shoots

Two techniques for representing patterns of development of populations of shoots are the 'spaghetti diagram' and the vector field. The spaghetti technique simply uses the method of representing a single shoot described above, but plots many shoots together on a single graph. The result may be a tangle of trajectories. Such tangles can often be resolved through the vector-field technique described below.

The change in form from one segment to the next is represented as a vector in the size-shape space by plotting the $x-y$ coordinates for each of two successive segments, and then drawing an arrow from the point representing the first segment to the point representing the second. To bring together the data for many individual plants, the size–shape plane is broken into a grid. The vectors representing all transitions of form between adjacent segments for all plants are placed on the grid. All vectors with midpoints falling within a particular cell of the grid are summed together, and only the normalized resultant vector is plotted in that cell.

The length and direction of the resultant vector represent the average change in form from one segment to the next in that region of the size–shape space. The angle between the two sides of the arrowhead is made equivalent to the angular standard deviation of the vector sum, and the length of the sides of the arrow head is made proportional to the log of the sample size of the vector sum. The midpoint of the resultant vector is placed at the centroid of the x and y coordinates of the midpoints of the vectors used in the summation. A resultant vector is plotted in a cell only if a specified minimum number of vectors were in the sum; in this study four to six vectors were used, depending on the concentration of the data in the size–shape space. The result is a vector field that represents the average shoot developmental pathway for a population of plants. The mathematical procedure for generating the vector field is summarized in the Appendix.

Switching between developmental pathways, i.e. metamorphosis, generally involves abrupt changes in size and shape, and generates long vectors. Where the data include more than one pathway, with metamorphosis between them, recognition of individual pathways can be enhanced by vector filtering which suppresses the long vectors associated with metamorphosis. When this is done, the individual pathways are more clearly distinguishable, as the intervening metamorphic connections are eliminated (Ray 1990b).

Shoot simulations

The method of using the allometric characteristics of a shoot to draw a simulation of the shoot was introduced by Ray (1990a,b); however, it is applied somewhat differently here. The emphasis here is on the changing forms of successive internodes, not of leaves. Therefore, in the simulations of this study all leaves are drawn schematically with exactly the same form, differing only in size. In addition, these simulations incorporate the correlations between the sizes of the separate components of the segment (leaves and internodes) reported by Ray (1986). The algorithm used first calculates the leaf size in direct proportion to the internode diameter. The leaf size is subsequently adjusted in direct proportion to the segment shape.

Results

Dieffenbachia seguine (Fig. 1a) is a caulescent terrestrial species (chosen to contrast its habit with that of the climbing species). Shoot development shows increase in size without change in shape (Fig. 3). Stems grow erect, supporting a tuft of leaves above the ground. However, the shoots generally do not exceed 1 m in height before they fall over under their own weight. This results in substantial lateral displacement of the apex, and is the source of mobility in this species. After the stem falls over, the apex rights itself, and resumes upward growth. Internode diameters range from *c.* 2 to 40 mm, while the shape remains roughly constant with internodes being about as long as wide (Fig. 3).

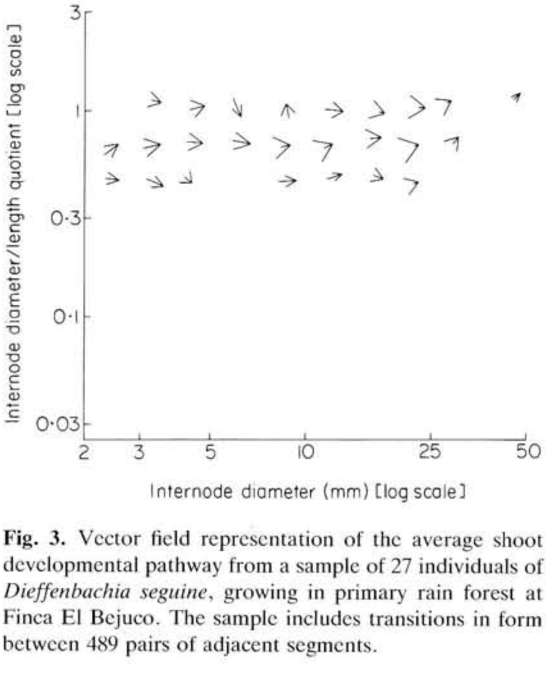

Fig. 3. Vector field representation of the average shoot developmental pathway from a sample of 27 individuals of *Dieffenbachia seguine*, growing in primary rain forest at Finca El Bejuco. The sample includes transitions in form between 489 pairs of adjacent segments.

Anthurium subsignatum (Fig. 1b), a low climber, develops by both monopodial and triphyllous sympodial growth (two cataphylls and a foliage leaf per sympodial unit; Ray 1987c, 1988; Ray & Renner 1990). Monopodial stems starting out at small diameters assume a wide range of internode shapes (Fig. 4). However, as internode diameters increase to *c.* 8 mm, internode shapes converge to a narrower range with lengths of *c.* 10 times the width, allowing the shoot to climb rapidly. At this diameter *A. subsignatum* switches to triphyllous sympodial growth, and changes abruptly to a more sessile form with short, wide internodes. Through the switch from monopodial to sympodial growth, internode length actually decreases as the internode diameter increases, ending in internodes that are about three times as wide as long at the maximum diameter of *c.* 25 mm (Fig. 4). Monopodial development has been illustrated with a spaghetti diagram in Fig. 4 because the wide variance of the pathways combined with the relatively low density of data do not produce a coherent vector diagram. Sympodial shoot development in the same figure is represented by a vector field.

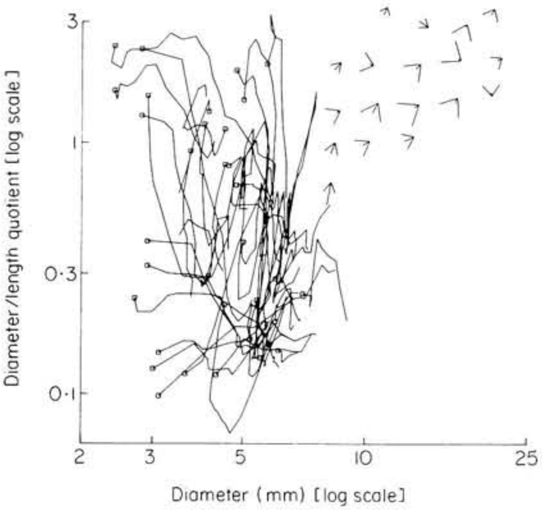

Fig. 4. Spaghetti representation of monopodial shoot development, and vector field representation of sympodial shoot development from a sample of *Anthurium subsignatum* shoots growing in primary rainforest at Finca El Bejuco. Only shoots with more than six segments were used in the spaghetti diagram, a total of 34 shoots incorporating 559 segments. A five-point moving average was used to smooth the lines. Circles indicate the beginning of each line. Note that many lines begin along the left periphery, but most lines converge upon the lower right of the scramble. The vector field is based on a summation of 578 vectors. For sympodial shoots, the lengths and diameters of the sympodial units (two internodes) are plotted; for monopodial shoots, individual internode lengths and diameters are plotted.

When a climbing shoot of *A. subsignatum* reaches the top of the tree, the stem remains negatively geotropic, and continues to grow upwards. When the stem outgrows its support to the point that it can no longer support itself, it falls over, the apex rights itself, and the stem begins to climb again. In this way, the stems of *A. subsignatum* form loops in the tops of small trees. *A. subsignatum* shows no shoot developmental response to gaining or losing contact with trees. Even terrestrial individuals not in contact with trees attempt to grow vertically, sending out long horizontal adventitious roots to support themselves by clinging to surrounding vegetation. *A. subsignatum* is a relatively low climber. It metamorphoses into the sessile form at a height of <2 m, and climbs very slowly thereafter (Fig. 5a).

Philodendron scandens (Fig. 1c), a high climber, exhibits a single shoot developmental pathway that keeps the plant in an always-mobile growth form, with internodes 10–25 times as long as wide (Fig. 5e; Fig. 6). As a result, shoots of this species rapidly climb and overgrow even the tallest trees. The shoots, unable to switch to a more sessile form, continue to elongate extensively after overgrowing the tree, and unlike *A. subsignatum* are not capable of righting themselves. These stems become pendant and will hang all the way to the ground. Whilst the pendant stems are restricted virtually to the same developmental pathway as the ascending stems (Fig. 6a), successive segments are smaller in diameter rather than larger, resulting in a pathway that is roughly the reverse of that traversed by the climbing form (Fig. 6b).

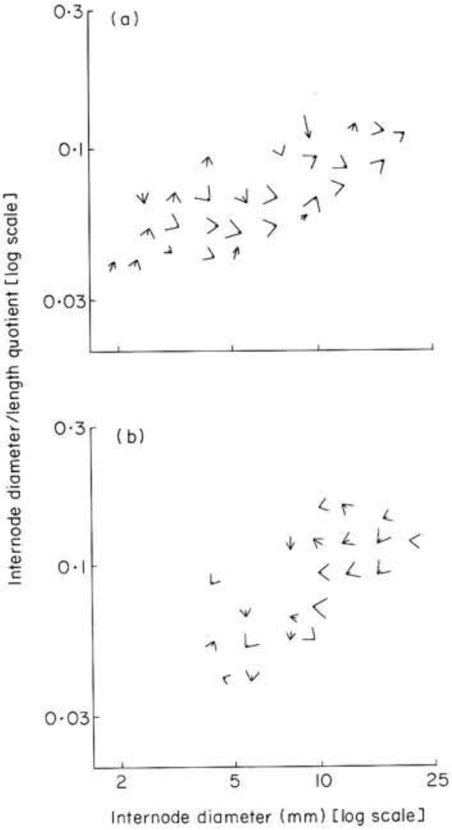

Fig. 6. Vector-field representation of shoot development in (a) arboreal climbing shoots (based on 511 vectors) and (b) aerial descending shoots (based on 352 vectors) of *Philodendron scandens* growing in cow pastures and fence rows in Chilamate, Costa Rica.

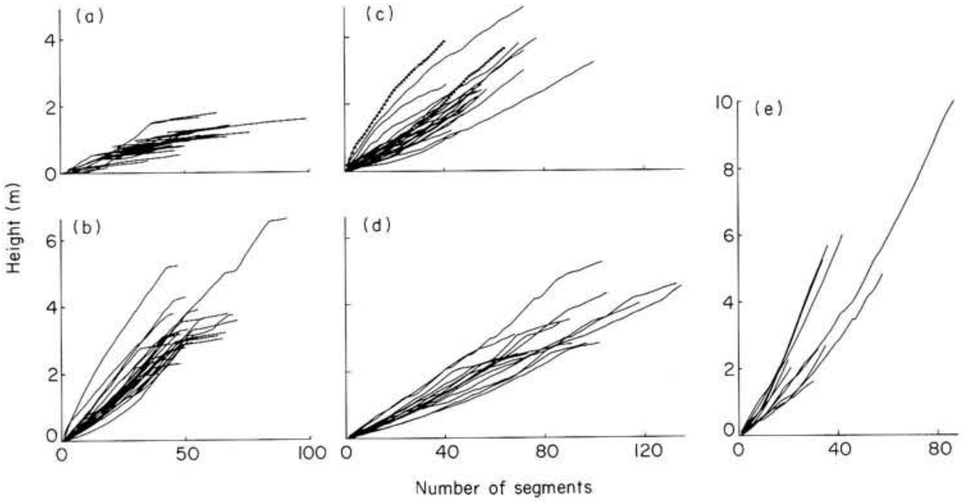

Fig. 5. Height (m) of climbing shoots, as a function of the number of segments produced by the climbing shoot for five species (a) *Anthurium subsignatum*, (b) *Philodendron fragrantissimum*, (c) *Syngonium triphyllum*, (d) *Monstera skutchii*, growing in primary rain forest at Fincas El Bejuco and La Selva, and (e) *Philodendron scandens*, growing in cow pastures and fence rows in Chilamate. Two shoots of *S. triphyllum* are highlighted: these represent the states of the shoots before (lower) and after (higher) a manipulation to increase the photosynthate available to the apex. All species are plotted on the same scales to facilitate the comparison of the slopes of lines. Note that these data do not directly reveal the rate of climbing, because the time interval between segments varies widely, generally increasing as the stem thickens; stems generally thicken as they climb.

Philodendron fragrantissimum (Fig. 1d), a medium-high climber, has monopodial growth in stems of *c.* 10 mm in diameter, and diphyllous sympodial growth in larger-diameter stems (Ray 1987c, 1988; Ray & Renner 1990). In climbing shoots (Fig. 7a), internodes maintain the same proportions (*c.* 13 times as long as wide) throughout monopodial growth, with internode diameters ranging from *c.* 2·5 mm to 10 mm. At the switch from monopodial to sympodial growth, there is a sharp change to a more sessile form with shorter segments, ending with sexually mature segments of about the same size and shape as in *A. subsignatum*. The abrupt change from mobile to sessile forms (Fig. 5b) indicates that *P. fragrantissimum* generally reaches a higher position than *A. subsignatum* before becoming sessile.

When *P. fragrantissimum* overgrows a supporting tree, it responds to the loss of contact with the tree by switching to another developmental pathway, which results in flagellar forms (Blanc 1980; Ray 1987b; illustrated for *S. triphyllum* in Fig. 1h) with slender elongate internodes and reduced leaves (Fig. 7b). These flagellar shoots descend to the ground and grow across the ground until they make contact with another tree. The switch to flagellar growth occurs regardless of whether the stem is monopodial or sympodial at the time of loss of contact with the tree. Flagellar shoots rapidly decrease in diameter and switch from sympodial to monopodial growth at the same internode diameter, *c.* 10 mm, as the switch from monopodial to sympodial in climbing shoots.

Flagellar shoots rapidly reach a stable shape, in which internodes are *c.* 35 times as long as wide, and range in diameter from *c.* 10 mm to 3 mm. This form allows the plant great mobility for the colonization of neighbouring trees. Flagellar shoots will re-ascend if they contact a tree, although they grow in a straight line along the ground and do not orientate themselves towards trees.

Monstera skutchii (Fig. 1e,f) is a medium-high climber. In this species, metamorphosis occurs at a critical internode diameter, again *c.* 10 mm, but the metamorphosis occurs while growth remains monopodial (Fig. 8). Climbing shoots <10 mm in diameter produce round leaves which are appressed to the trunk of the tree (Fig. 1f). The leaves are supported by short petioles whose sheaths encircle the shoot. Internodes range in diameter from *c.* 1 mm to 10 mm, and remain about eight times as long as wide. At a diameter of *c.* 10 mm, metamorphosis occurs to a more sessile developmental pattern which produces relatively elongate leaves which are held away from the shoot and the tree trunk on long petioles (Fig. 1e). The internodes may increase in diameter to >20 mm, and are *c.* twice as long as wide. Like *P. fragrantissimum*, *M. skutchii* reaches a medium height before switching

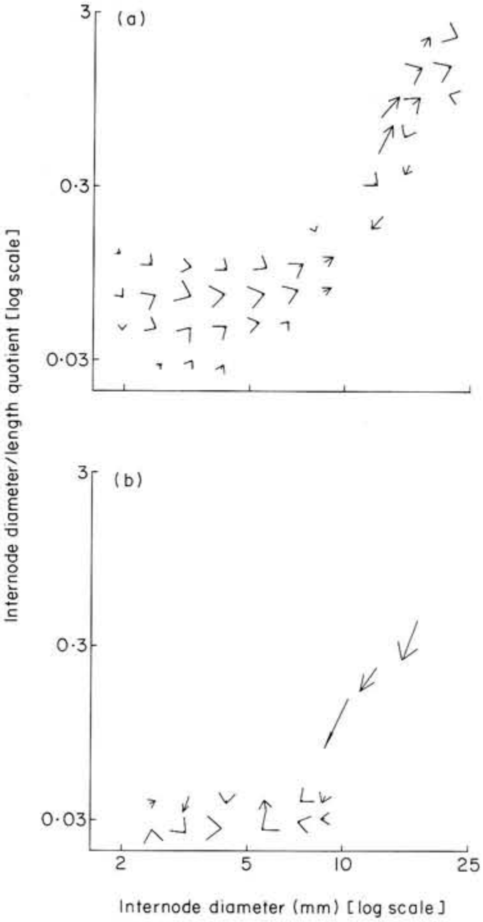

Fig. 7. Vector-field representation of (a) arboreal climbing shoots and (b) flagellar shoot development of *Philodendron fragrantissimum* growing in primary rain forest at Finca El Bejuco. In (a) the seven columns of arrows on the left are from monopodial shoots and the three columns of arrows on the right are from sympodial shoots; the monopodial field is based on 2647 vectors, the sympodial field on 331 vectors. In (b) the lower two rows of arrows are from monopodial shoots and the upper three arrows are from sympodial shoots; the monopodial field is based on 437 vectors, the sympodial field on 55 vectors.

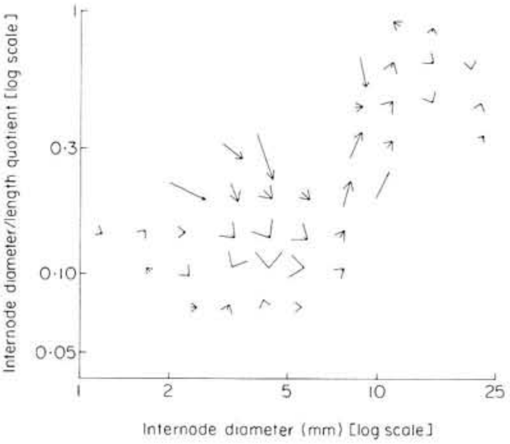

Fig. 8. Vector-field representation of arboreal climbing shoot development of *Monstera skutchii* growing in primary rain forest at Finca El Bejuco, based on 2868 vectors.

to the sessile form. The two species differ in that the most sessile form of *M. skutchii* is relatively more mobile than that of *P. fragrantissimum* (Fig. 5d).

In addition to the two climbing forms, the shoot will switch to a flagellar form if a climbing shoot overgrows a tree. Seedlings develop by yet another pathway, producing stolons with internodes of *c.* 1–1·5 mm in diameter and 2–5 cm in length. These seedling shoots bear only cataphylls, and remain in the stoloniferous form of growth until they encounter a tree to climb. Orientation towards trees is facilitated by skototropism (Strong & Ray 1975).

Syngonium triphyllum (Fig. 1g–i) is a medium-high climber with a very complex pattern of shoot development involving four distinct pathways (Fig. 9). When in contact with a tree (Fig. 9a, Fig. 1g), it exhibits a developmental pathway with internode diameters increasing from *c.* 2 mm to 15 mm. As the internode diameter increases, there is a gradual shift from elongate mobile segments (*c.* 40 times as long as wide) to shorter more sessile segments (half as wide as long). This results in a strongly allometric shoot developmental pathway.

Like *P. fragrantissimum* and *A. subsignatum*, *S. triphyllum* is a medium-high climber. However, it differs from those two in that it does not metamorphose to a more sessile form as it climbs (Fig. 5c).

When a climbing stem looses contact with a tree (Fig. 9b), the shoot switches to a flagellar pathway analogous to those of *P. fragrantissimum* and *M. skutchii*. This pathway involves a highly mobile growth form, with internodes *c.* 40 times as long as wide, and successive internodes decrease in diameter to a lower limit of *c.* 1·7 mm. This form is maintained after reaching the ground (Fig. 1h).

When a juvenile shoot is on the ground and does not receive photosynthate through a stem connected to leaves in a tree (Fig. 1i; Fig. 9c,d), the shoot cycles through two pathways that are widely separated in shape, and remain at the lower end of the size range. The vector field generated by the data for the two pathways plotted together, along

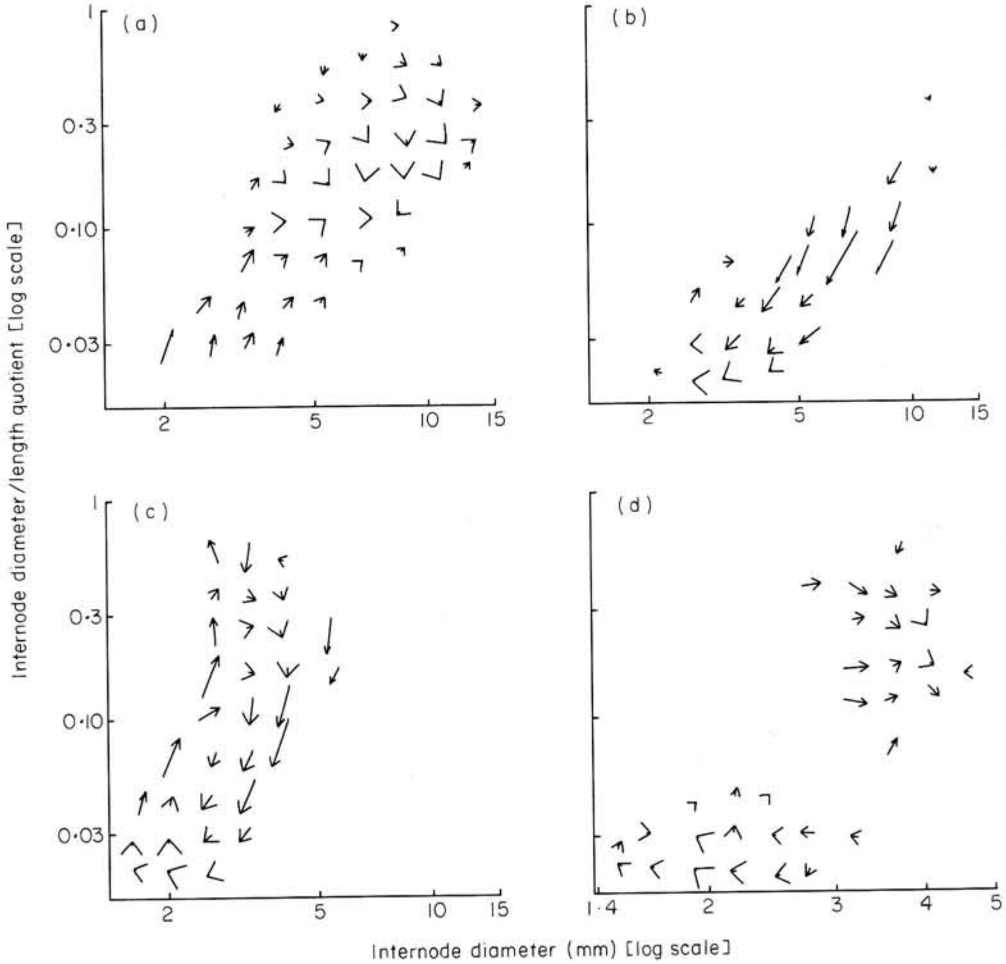

Fig. 9. Vector-field representation of four classes of shoots of *Syngonium triphyllum* growing in primary rain forest at Finca El Bejuco and Finca La Selva: (a) arboreal ascending ($n = 1811$); (b) aerial descending, and terrestrial connected to arboreal shoot ($n = 612$); (c) terrestrial free living ($n = 1150$); (d) the terrestrial free-living cycle consists of two distinct pathways which can be visualized with vector filtering, vectors whose y components are greater than 0·15 (log scale) are excluded. The x-axis has been cropped in (d) to provide greater resolution.

with the metamorphosing of shoots between the two pathways are illustrated in Fig. 9c. The terrestrial cycle is illustrated at higher resolution in Fig. 9d (the x-axis has been cropped), and vector filtering has been used to separate the two distinct pathways of the terrestrial cycle. The leafy sessile phase of the terrestrial cycle ranges from *c.* 3 mm to 5 mm in diameter, and tends toward slightly more-elongate segments as it enlarges. The small-diameter segments are about twice as long as wide, and the larger segments about eight times as long as wide. The flagellar mobile phase of the cycle ranges from *c.* 3 mm to 1·5 mm in diameter, and maintains a roughly constant shape of *c.* 40 times as long as wide, as it decreases in diameter. Shoots in the flagellar phase are skototropic (Strong & Ray 1975), and orientate themselves toward nearby trees.

Development of individual shoots of *S. triphyllum* are responsive to the changes in microhabitat that result from growth movements (Fig. 10). A shoot began its growth climbing a tree, in the upper left region of the plane (Fig. 10). After forty-six segments of gradual size increase, the shoot reached the top of the tree and overgrew it (indicated by the letter a). As a result of losing contact with the tree, the shoot switched into a second developmental pathway exhibiting a more elongate (mobile) form. Within fourteen segments, the shoot reached the ground (indicated by the letter b), and began growing across the ground. After 13 segments of slightly decreasing size, the shoot encountered a small herbaceous plant and began to climb it (indicated by the letter c). Contact with a vertical support triggered a switch back to the original leafy developmental pathway. However, after three more segments, as the shoot was midway through its second metamorphosis, the shoot overgrew the small plant it was climbing (indicated by the letter d). This triggered a third metamorphosis back to the mobile form characteristic of shoots not climbing trees. Within five more segments the shoot returned to the ground (indicated by the letter e) and remained in the elongate form with gradually decreasing segment sizes for another twelve segments as it grew across the ground.

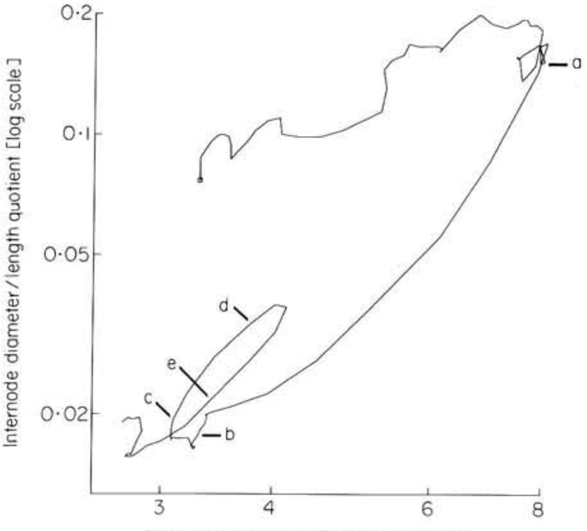

Fig. 10. The shoot developmental trajectory of an individual of *Syngonium triphyllum* growing in primary rain forest at Finca La Selva. The stem illustrated is initially climbing a tree, then returns to the ground, begins to climb a small herb, overgrows the herb and returns to the ground again. These growth movements cause the stem to undergo metamorphosis three times. The letters indicate the points of gain (c) or loss (a,d) of contact with trees and gain of contact with the ground (b,e). The start of the shoot, upper left, is marked with a small circle. A five-point moving average is used to smooth the curve.

The two highlighted shoots of *S. triphyllum* (Fig. 5c) illustrate the result of the assisted natural experiment. The lower of the two shoots is the trajectory of the original climbing shoot which had 32 large multi-lobbed leaves when its support fell over. This shoot had flowered twice and reached a diameter of 15·8 mm. It first flowered after producing 58 segments on the tree. After it overgrew its fallen and cut support, it switched to the flagellar form, with internode diameters decreasing to as narrow as 4·2 mm and internode lengths increasing to as long as 20·8 cm. When it was trained manually onto a nearby tree, it climbed very rapidly, producing the higher of the two shoots highlighted (Fig. 5c). This was the most rapid climbing rate of all the shoots in the data set, indicating one effect of the manipulation. In addition, this shoot reached a diameter of 11·6 mm and flowered after producing only 30 segments on the tree, a record for rapidity of flowering in this species.

Discussion

In the Araceae, shoot developmental patterns and foraging behaviour are intimately intertwined. The array of shoot developmental pathways, presumably reflecting the genotype of a species, determines the growth habit of the species (i.e. terrestrial, low climber, high climber, etc.). But changing micro-environmental conditions, resulting in part from growth movements, influence switching between those pathways, and affect the rate or direction of progress within a single developmental pathway.

The size and shape of the internodes and the pattern by which they change along the shoot determine the shoot's position along a continuum from sessile to mobile, and in a gross way contribute to the determination of the growth form associated with that shoot. Most individual shoots show little change in shape as successive segments increase or decrease in size. Such isometric shoots can be placed into one of four broad structural and functional categories: acaulescent sessile, caulescent sessile, climbers or creepers, and flagellar shoots. These represent four distinct growth forms. The forms of the shoots and the pathways through size–shape space associated with each of the four categories are illustrated in Fig. 11.

Species with acaulescent shoot development (e.g. *Arisaema*, *Symplocarpus*) have internodes which are 10 or more times as wide as long (Fig. 11a) a growth habit associated with completely sessile tuberous or cormous species (not found among the species of this study). Species with this type of shoot development may be terrestrial or epiphytic, depending in large part on the behaviour of their roots. In terrestrial species with this growth habit, leaves occur at ground level, or are held above the ground by petioles; the stem itself does not rise above the ground.

Species with caulescent terrestrial shoot development (e.g. *Aglaonema*, *Dieffenbachia*) have approximately equal internode lengths and widths (Fig. 11b). In these species the stem grows up from the ground, holding the leaves above the ground. These stems are capable of standing upright and supporting the crown of leaves on their own. However, after they have grown to a certain height, they will fall over under their own weight, the apex will right itself, and the stem will begin to grow upwards again. These shoots are slightly mobile, as falling over causes some lateral displacement of the shoot tips.

Species with climbing or creeping shoot development (e.g. *Monstera*, *Philodendron*) have internodes *c*. 10 times as long as wide (Fig. 11c). Shoots in this internode–shape range do not have the strength to support upward growth, and must creep along the ground, or climb on other plants in order to grow upwards. This shape allows for a considerable mobility so that the shoot can climb a tree or grow across the ground, while at the same time allowing for deployment of enough leaf surface to sustain the shoot.

Species with an exclusively flagellar shoot development (Fig. 11d) would be unable to deploy enough leaf surface to provide adequate photosynthate. Thus flagellar shoots always occur in combination with other shoot developmental pathways (e.g. *Monstera*, *Philodendron*, *Syngonium*). Flagellar shoots have internodes that are 30 or more times as long as wide, and produce leaves reduced to cataphylls, resulting in a highly mobile shoot which deploys virtually no leaf surface. These shoots allow climbing species to return to the ground and colonize other trees. Flagellar shoots may be viewed as elongating umbilical cords for the dispersal of apical meristems.

In contrast to the foregoing isometric shoots, the change in the size of successive segments in some shoots is accompanied by substantial changes in the shapes of successive leaves or internodes. Such an allometric shoot development and its associated

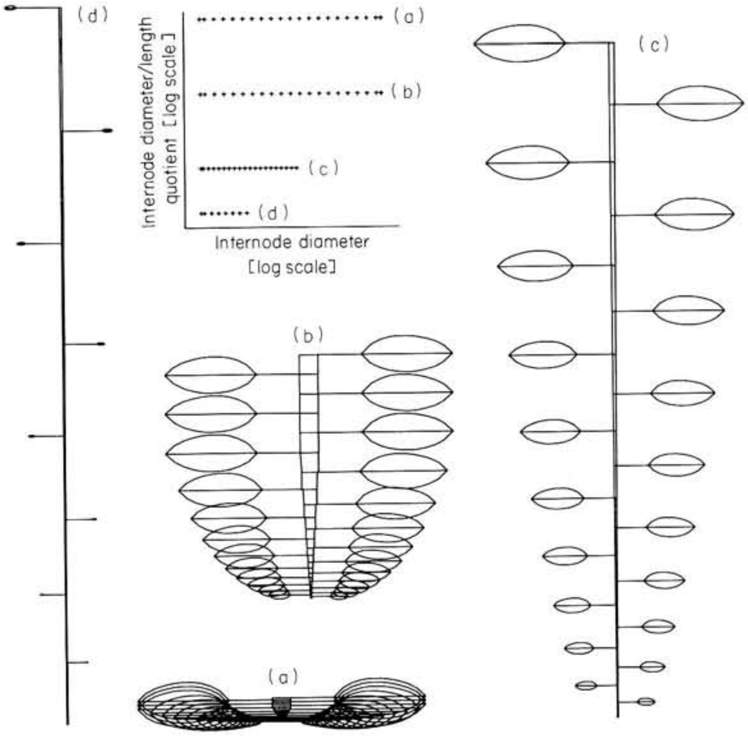

Fig. 11. Isometric shoot development models in Araceae. Each of the four shoots traverses a path through the size–shape phase space that is horizontal, but they differ in their *y*-axis intercept values: (a) intercept = 1; (b) intercept = 0; (c) intercept = −1; (d) intercept = −1·6.

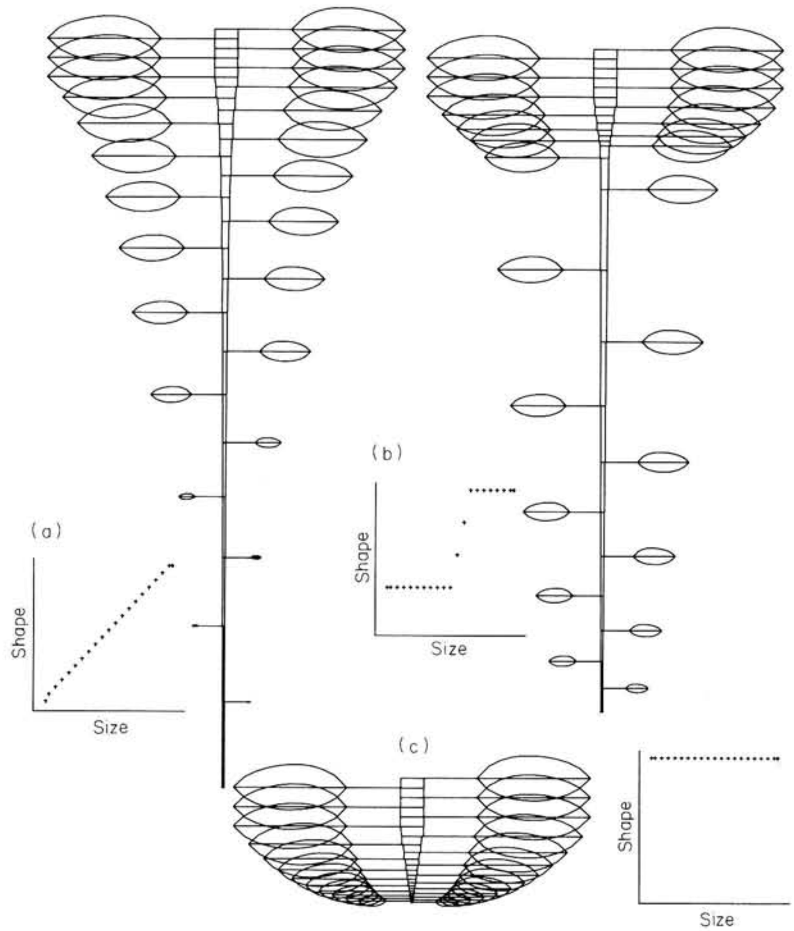

Fig. 12. Allometric and metamorphic shoot development models in Araceae compared with isometric model of the same adult form. (a) Allometric development with shape (log internode diameter/length) ranging from −1·55 to 0·4; (b) metamorphosis between two isometric pathways, the first with an intercept of −1 and a second with an intercept of 0·4; (c) isometric development with an intercept of 0·4. All three shoots have the same range of size, and all three end up with the same adult segment size and shape (note that the last five segments are identical on all three shoots, the shoots only vary in how they reach the final form). The axes used here are the same as in Fig. 11.

growth habit (e.g. *Syngonium*) is illustrated in Fig. 12a. This pathway shows a gradual transition in shape as the stem thickens, from an initially highly mobile flagellar shoot to a moderately elongate form which allows the stem to both climb and deploy leaf surface, to a sedentary form which is reached at maturity. This makes it possible for shoots on trees to climb rapidly while juvenile, and become sessile when mature, utilizing only a single developmental pathway.

DEVELOPMENTAL PATTERNS

The genetic–developmental system of a species may make available only a single shoot developmental pathway. However, such developmental systems are relatively limiting, because changes in mobility are possible only if the shoots are allometric. Most species of Araceae, with a single shoot developmental pathway, are terrestrial, while most climbers exhibit metamorphosis between multiple shoot developmental pathways. Genetic systems that provide the species with multiple developmental pathways allow complex growth patterns which facilitate the ability to change mobility. Such complexity supports a great diversity of subtly different climbing growth habits in the Araceae.

Metamorphic shoots

Many species accomplish a change in mobility by means of a metamorphosis between pathways specialized for different functions (Ray 1990b). In its most rudimentary form, this can involve switching between two isometric pathways (Fig. 12b). This combination of two pathways is typical of the climbing phases of many species (e.g. *Monstera* or *Philodendron*). The climbing species (Fig. 12a,b) both achieve precisely the same form as adults. For comparison, Fig. 12c represents an isomorphic terrestrial species with the same mature segment form.

Climbers

In climbers, the seeds germinate on the ground, but the plant matures on the trunks of trees. Climbing species must at some time assume a mobile form in order to move from the site of germination to the site of maturation. However, it is not necessarily appropriate to be always mobile. Upon arrival at a favourable location on the trunk of a tree, it is advantageous to switch to a sessile form. The sessile form will have short internodes and will be able to remain in the favourable location for a long time, producing many leaves in that location. Thus climbing species generally have more-complex shoot developmental patterns, involving shifts between mobile and sessile forms.

The climbing patterns (Fig. 5) of the five species discussed in this paper may be divided into three groups on the basis of the height to which they grow: *A. subsignatum* the low climber; *S. triphylum*, *P. fragrantissimum* and *M. skutchii* the medium-high climbers; and *P. scandens* the high climber (*P. scandens* may reach greater height, Fig. 1d, but it was not possible to obtain data from the highest shoots). The three species may be divided into two groups on the basis of the presence or absence of an abrupt shift from a mobile to a sessile growth form: *S. triphyllum* and *P. scandens* maintain a fairly constant high slope, while the remaining three species abruptly shift to an almost flat line (become relatively sessile) after reaching some height.

Vegetative dispersal

It is advantageous to be able to become mobile again, even after the sessile form has been reached, if environmental conditions deteriorate. For many species of Araceae, the ability to produce flagellar shoots provides this capacity. Flagellar shoots are produced by climbing shoots if they reach the top of a tree, or fall from a tree, or if the tree falls over. In some climbers, the juvenile terrestrial phases also use flagellar shoots for dispersal. In every case, the flagellar shoots are linked by metamorphosis to other more sessile developmental pathways (Figs 1h,i and 10). 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 (Ray 1987c). Only three homeophyllous species seem to be capable of producing flagellar shoots: *Philodendron fragrantissimum*, *P. brunneocaule* and *P. linnaei* (Ray 1987b,c, 1988).

DEVELOPMENTAL ADJUSTMENT

The species described here illustrate several classes of developmental adjustments within their overall developmental patterns: switching between flagellar and leafy shoots in response to gain or loss of contact with trees; switching between flagellar and leafy shoots in response to an unknown endogenous factor (perhaps photosynthate levels); a change in the direction of development within a single pathway in response to gain or loss of contact with trees; a change in the rate of progress along a pathway in response to an apparent change in photosynthate levels.

Switching pathways

Behavioural responses to the changes in microhabitat brought about by movement in *Syngonium* are expressed as changes in developmental trajectories (Fig. 10). The shoot undergoes metamorphosis (switching between developmental pathways) three times, thereby tracing out a very complex path. In this individual, metamorphosis is triggered by gain or loss of contact with a tree (or other vertical support). This type of developmental adjustment, switching between shoot developmental pathways in response to gain of contact with trees, is widespread in the Araceae. Among the six species of this study, it is found in *P. fragrantissimum* (Fig. 7). *M. skutchii* (Fig. 8) and *S. triphyllum* (Figs 9 and 10).

The free-living terrestrial cycle of *Syngonium* (Fig. 9c,d) involves a switching between two distinct pathways which is not controlled by any obvious external factor. A probable endogenous factor regulating the switching is the availability of photosynthate to the apex. Hypothetically, when the photosynthate level is high, the shoot switches to the flagellar form, and when photosynthate is low the shoot switches to the leafy form. On this hypothesis, the terrestrial plant monitors its internal state and switches between two developmental states according to its need to produce photosynthetic surface, or its ability to produce mobile flagellar shoots, which are, it is supposed, largely photosynthate sinks.

Reversal of pathways

P. scandens (Fig. 6) illustrates a different type of developmental response to the loss of contact with trees. The shoot developmental pathway traversed by aerial descending shoots does not differ greatly in slope and intercept from that traversed by arboreal ascending shoots. However, the aerial shoots traverse the pathway in a direction opposite that exhibited by arboreal shoots.

Change in shoot developmental rates

The two highlighted shoots of *Syngonium* (Fig. 5c) support the notion that enhanced photosynthate availability to the apex can accelerate the rate of progress along the pathway of arboreal shoots. The result of this manipulation is that the climbing shoot reached its maximum diameter and flowered, in a shorter time and at a lower level on the trunk than is normal. Presumably elevated light or mineral levels could produce qualitatively similar results, while decreased levels could produce opposite effects.

Related work

Clegg (1978) described a foraging–behavioural continuum between guerrilla and phalanx growth forms. Clones with guerrilla growth forms are predominantly linear, with little branching and long internodes, resulting in widely spaced ramets; in phalanx growth there is rich branching and ramets are closely packed. In this study, a sessility–mobility continuum is found within shoots of relatively unbranched plants. At the sessile extreme, internodes are wide and short, while leaves are large; at the mobile extreme, internodes are long and slender, while leaves are reduced to cataphylls.

This paper has emphasized internode diameter and shape, and the pattern by which these factors vary along individual shoots during shoot development. Shoot developmental patterns in the Araceae have been elaborated by evolution to an unusual degree, but diverse forms of shoot development occur in other taxa. Noble, Bell & Harper (1979) illustrated (their Fig. 2) changes in the forms of successive internodes along shoots of a rhizomatous sand sedge, *Carex arenaria*. Within single axes, internodes shorten where 'shoots' arise from 'rhizomes'. In addition, they note that there are two types of aerial shoots, 'long' and 'dwarf', which arise from rhizomes with long and short internodes, respectively. Slade & Hutchings (1987a,b,c) and Hutchings & Slade (1988) showed that internode lengths vary along stolons in a manner which shows an apparently adaptive response to nutrient and lighting conditions in *Glechoma hederacea*, a clonal perennial herb. Peñalosa (1975, 1983) described the behaviour of shoots in *Ipomoea phillomega*, a tropical rain-forest liana. He found that there were two distinct classes of shoots, 'stolons' and 'twiners', and several additional sub-classes. The various classes of shoots vary in their internode lengths and leaf sizes. He found that, in general, internodes are longer and leaves smaller under more shaded conditions.

The emphasis in this paper has been on the influence of developmental patterns within single shoots on foraging behaviour. This influence is well illustrated by the Araceae where shoot developmental patterns are the principal mediators of foraging behaviour. This suggests taking a closer look at the phenomenon in more-richly branched plants, in which shoot development is integrated with other mechanisms (primarily branching) in determining foraging behaviour.

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References

Alberch, P., Gould, S.J., Oster, G.F. & Wake, D.B. (1979) Size and shape in ontogeny and phylogeny. *Paleobiology*, **5**, 296–317.

Batschelet, E. (1965) *Statistical Methods for the Analysis of Problems in Animal Orientation and Certain Biological Rhythms*. American Institute of Biological Sciences, Washington, DC.

Bell, A.D. (1974) Rhizome organization in relation to vegetative spread in *Medeola virginiana*. *Journal of the Arnold Arboretum*, **55**, 458–468.

Bell, A.D. (1979) The hexagonal branching pattern of *Alpinia speciosa* L. (Zingiberaceae). *Annals of Botany*, **43**, 209–223.

Bell, A.D. & Tomlinson, P.B. (1980) Adaptive architecture in rhizomatous plants. *Botanical Journal of the Linnean Society*, **80**, 125–160.

Blanc, P. (1980) Observations sur les flagelles des Araceae. *Adansonia*, series 2, **20**(3), 325–338.

Bradshaw, A.D. (1965) Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics*, **13**, 115–155.

Clegg, L. (1978) *The morphology of clonal growth and its relevance to the population dynamics of perennial plants*. PhD thesis, University of Wales.

Croat, T.B. (1988) Ecology and life forms of Araceae. *Aroideana*, **11**, 4–55.

Darwin, C. (1875) *The Movements and Habits of Climbing Plants*. John Murray, London.

Gould, S.J. (1966) Allometry and size in ontogeny and phylogeny. *Biological Review*, **41**, 587–640.

Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B. (1978) *Tropical Trees and Forests, an Architectural Analysis*. Springer, Berlin.

Harper, J.L. & Bell, A.D. (1979) The population dynamics of growth form in organisms with modular construction. *Population Dynamics* (eds R.M. Anderson, B.D. Turner & L.R. Taylor), pp. 29–52. Blackwell Scientific Publications, Oxford.

Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. & Tosi, J.A. (1971) *Forest Environments in Tropical Life Zones: a Pilot Study*. Pergamon Press, New York.

Hutchings, M.J. & Slade, A.J. (1988) Morphological plasticity, foraging and integration in clonal perennial herbs. *Plant Population Ecology* (ed. A.J. Davy, M.J. Hutchings & A.R. Watkinson), pp. 83–109. Blackwell Scientific Publications, Oxford.

Knecht, M. (1983) *Aracées de la Côte d'Ivoire*. Phanerogamarum Monographiae Tomus XVII. J. Cramer, Hirschberg.

Madison, M. (1978) The genera of Araceae in the northern Andes. *Aroideana*, **1**(2), 31–53.

Noble, J.C., Bell, A.D. & Harper, J.L. (1979) The population biology of plants with clonal growth. I. The morphology and structural demography of *Carex arenaria*. *Journal of Ecology*, **67**, 983–1008.

Peñalosa, J. (1975) *Shoot dynamics of tropical lianas*. PhD thesis, Harvard University.

Peñalosa, J. (1983) Shoot dynamics and adaptive morphology of *Ipomoea phillomega* (Vell.) House (Convolvulaceae), a tropical rainforest liana. *Annals of Botany*, **52**, 737–754.

Ray, T.S. (1981) *Growth and heterophylly in an herbaceous tropical vine*, Syngonium *(Araceae)*. PhD thesis, Harvard University.

Ray, T.S. (1983a) *Monstera tenuis*. *Costa Rican Natural History* (ed. D.H. Janzen), pp. 278–280. University of Chicago Press, Chicago.

Ray, T.S. (1983b) *Syngonium triphyllum*. *Costa Rican Natural History* (ed. D.H. Janzen), pp. 333–335. University of Chicago Press, Chicago.

Ray, T.S. (1986) Growth correlations within the segment in the Araceae. *American Journal of Botany*, **73**, 993–1001.

Ray, T.S. (1987a) Cyclic heterophylly in *Syngonium* (Araceae). *American Journal of Botany*, **74**, 16–26.

Ray, T.S. (1987b) Leaf types in the Araceae. *American Journal of Botany*, **74**, 1359–1372.

Ray, T.S. (1987c) Diversity of shoot organization in the Araceae. *American Journal of Botany*, **74**, 1373–1387.

Ray, T.S. (1988) Survey of shoot organization in the Araceae. *American Journal of Botany*, **75**, 56–84.

Ray, T.S. (1990a) Application of "eigenshape" analysis to second order leaf shape ontogeny in *Syngonium podophyllum* (Araceae). *Proceedings of the Michigan Morphometrics Workshop* (eds F.J. Rohlf & F. Bookstein), pp. 201–213. University of Michigan Museum of Zoology, Ann Arbor, MI.

Ray, T.S. (1990b) Metamorphosis in the Araceae. *American Journal of Botany*, **77**, 1599–1609.

Ray, T.S. & Renner, S. (1990) Comparative studies on the morphology of the Araceae. A. Engler, 1877. Translation with an introduction, updated nomenclature, and a glossary. *Englera*, **12**, 1–152.

Simmonds, N.W. (1950) Notes on the biology of the Araceae of Trinidad. *Journal of Ecology*, **38**, 277–291.

Slade, A.J. & Hutchings, M.J. (1987a) The effects of nutrient availability on foraging in the clonal herb *Glechoma hederacea*. *Journal of Ecology*, **75**, 95–112.

Slade, A.J. & Hutchings, M.J. (1987b) The effects of light intensity on foraging in the clonal herb *Glechoma hederacea*. *Journal of Ecology*, **75**, 639–650.

Slade, A.J. & Hutchings, M.J. (1987c) Clonal integration and plasticity in foraging behaviour in *Glechoma hederacea*. *Journal of Ecology*, **75**, 1023–1036.

Strong, D.R. & Ray, T.S. (1975) Host tree location behavior of a tropical vine (*Monstera gigantea*) by skototropism. *Science*, **190**, 804–806.

Tosi, J.A. (1969) *Mapa ecologia de Costa Rica*. Tropical Science Center, San José, Costa Rica.

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Appendix

For each adjacent pair of segments whose forms have been quantified in terms of size = x and shape = y, there is a single vector $\mathbf{v}_i$, whose endpoints are the (x, y) coordinates of the points representing the forms of the two segments: the distal (anterior) segment (x_{1i}, y_{1i}) and the proximal (posterior) segment (x_{2i}, y_{2i}). Each of the n vectors whose midpoints mx_i and my_i (see below) fall within a given cell of the grid are used in the sum to compute the resultant vector. The vectors will be treated not in terms of the coordinates of their endpoints, but in terms of the x and y coordinates of their midpoints (mx_i, my_i), their x and y components Δx_i and Δy_i, and their angular direction θ_i:

$mx_i = (x_{1i} + x_{2i})/2$ the midpoint of each vector on the x axis
$my_i = (y_{1i} + y_{2i})/2$ the midpoint of each vector on the y axis
$\Delta x_i = (x_{1i} - x_{2i})$ the length of each vector on the x axis
$\Delta y_i = (y_{1i} - y_{2i})$ the length of each vector on the y axis
$\theta_i = \arctan(\Delta y_i / \Delta x_i)$ the angular direction of each vector, in radians

For each cell of the grid, seven sums must be computed, from which the resultant vector can be constructed:

$n =$ the number of vectors in the cell
$\Delta x = \Sigma_{i=1}^{n} \Delta x_i$
$\Delta y = \Sigma_{i=1}^{n} \Delta y_i$
$ux = \Sigma_{i=1}^{n} \cos(\theta_i)$ sum of the x components of unit vectors in the directions θ_i
$uy = \Sigma_{i=1}^{n} \sin(\theta_i)$ sum of the y components of unit vectors in the directions θ_i
$mx = \Sigma_{i=1}^{n} mx_i$
$my = \Sigma_{i=1}^{n} my_i$

From these sums we may compute the x and y components of the normalized resultant vector, $\Delta x/n$ and $\Delta y/n$, respectively, and the coordinates of the midpoint of the resultant vector: $(mx/n, my/n)$. The equation $uv = (ux^2 + uy^2)^{1/2}/n$ gives the length, uv, of a normalized resultant vector derived by the summation of unit vectors in the directions θ_i. The value uv, can be used to compute s, the angular standard deviation (in radians) of the vector sum (Batschelet 1965): $S = [2(1 - uv)]^{1/2}$.