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GROWTH CORRELATIONS WITHIN THE SEGMENT IN THE ARACEAE[1]

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ABSTRACT

The segment is defined as an internode and the associated petiole and lamina. In many climbing members of the family Araceae, there is great variation in the relative sizes and shapes of the three component parts of the segment. In *Syngonium standleyanum* Bunting, it was found that the form of the internode may be characterized by its length and diam, the petiole by its length, and the lamina by its wt and its shape (the ratio of central lobe wt to lamina wt). The sizes and shapes of the various components of the segment were found not to be allometrically related, with three exceptions: the internode diam is allometrically related to the segment wt, petiole wt, and lamina shape. In the four species of Araceae studied, the strong correlation between the diam of the internode and the wt of the entire segment results in a trade-off between making a large leaf or a long internode. For an internode of a given diam, the total dry wt of the segment is fixed, but may be proportioned in virtually any manner between the leaf and internode, from 95% of the wt in a large leaf, to 98% of the wt in a long internode. The complete form of the segment may be defined by just two variables. A suitable pair of variables is internode diam, and the ratio of internode diam to internode length.

CLIMBING AROIDS exhibit many heterophyllic and heteroblastic changes within their complex growth habit. Climbing stems exhibit heteroblasty with successive internodes of greater diam, and successive leaves of larger size and greater complexity of shape (Fig. 1). In addition, many species of climbing aroids exhibit the ability to produce elongate stems which allow them to return to the ground after reaching the top of the tree, and to grow across the ground to colonize another tree[2] (Ray, 1981, 1983a, b). When these stems are produced we see another series of heteroblastic changes in the sizes and shapes of successive organs. In descending stems, successive internodes become longer and narrower, and leaves become smaller, although leaves retain complex shapes into much smaller sizes than those in which they were first seen (Fig. 1).

In order to study the changes in form of the successive organs produced along the stems of aroids, it has proven useful to treat the stem as being composed of a series of units. These units which I call segments, consist of an internode and its attached leaf (Fig. 2), and have been termed phytons, phytomers, and articles in previous literature. White (1979) has reviewed the history and use of this concept of the modular construction of plants. White concludes that the concept has not been widely accepted as being useful, although it has more often been found useful when applied to monocotyledons.

I chose to use the segment concept for the convenience it provided in organizing data on the sizes and shapes of the successive organs produced on aroid stems. However when I carried out an analysis of correlations between the sizes and shapes of the component organs of the segment, the internode, petiole, and lamina, I found a surprising correlation which I report here. The correlation, between the internode diam and the segment wt, places interesting constraints on the overall form of the segment, and suggests that at least in the four species studied, *Syngonium macrophyllum* Engler, *S. standleyanum, S. stenophyllum* Birdsey ex Croat & Grayum, and *P. schottianum,* the concept of the segment may have some developmental basis.

Although some additional variations exist, there are two basic types of segments produced in the Araceae. These are segments produced by monopodial growth, and segments produced by sympodial growth (Fig. 2). In monopodial growth, a series of segments is produced by the activity of a single shoot apex. In mono-

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[2] This ability is virtually restricted to those climbing taxa with monopodial or polyphyllous sympodial growth, e.g., *Syngonium, Rhodospatha, Monstera, Philodendron* section *Pteromischum* and *Anthurium* section *Polyphyllium.* Two exceptions to this generalization are *P. schottianum* Wendl., and *P. brunneocaule* Croat & Grayum, which are monophyllous sympodial when mature but produce elongate stems. I am preparing a manuscript documenting this pattern.

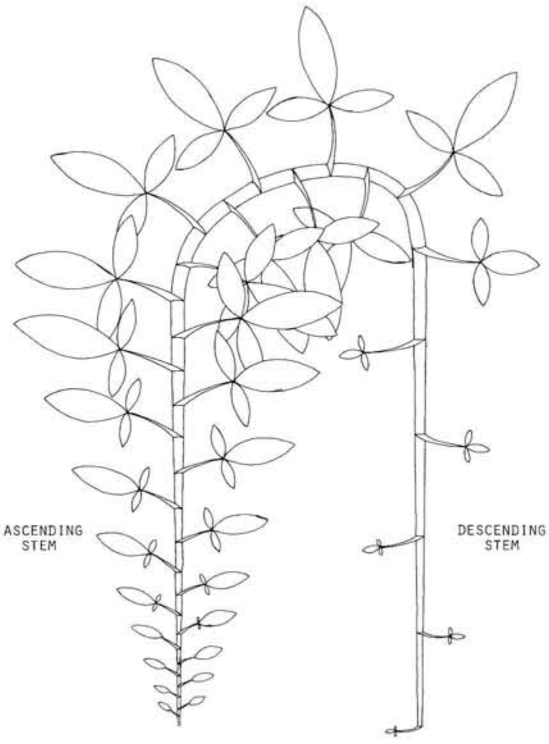

Fig. 1. The series of segment forms found on stems of *S. standleyanum.* On the left we see a climbing stem developing from the seedling to the mature adult. On the right we see a descending stem returning to the ground to colonize other trees.

podial segments the base of the petiole spreads into a sheath which completely encircles the stem at the node. In the Araceae, unlike in other monocotyledons, the petiole and sheath together are called the petiole (Madison, 1977).

In sympodial growth, the shoot apex terminates after the foliage leaf by differentiating into an inflorescence bud which often aborts. The shoot is then continued by a sylleptic axillary bud. The sympodial segment includes a cataphyll, a foliage leaf, and an inflorescence bud (in *Anthurium* there are two cataphylls for each foliage leaf). In sympodial segments the petiole base does not encircle the stem, but rather the often aborted terminal inflorescence, therefore the sheath is not as well developed. Petiole sheaths are more apparent in sympodial segments when the inflorescence develops, because the petiole base (sheath) encircles the peduncle. Because the formation of elongate stems is virtually restricted to taxa with predominantly monopodial segments, only monopodial segments will be considered in this analysis.

I am interested in studying the form of segments, and how it changes during the growth of the plant. In order to facilitate this, I wish to develop a system for quantifying the form of the segment, which specifies as much as possible about the form, with the fewest variables. It is not my objective to quantify fine details of form such as leaf venation patterns. I would be satisfied to define each individual organ of the segment in terms of its linear dimensions, weight, surface area, and the outline of the shape (as applicable).

MATERIALS AND METHODS—The study reported here was conducted in part at the Organization for Tropical Studies' La Selva Field Station, located at the confluence of Rio Puerto Viejo and Río Sarapiquí (10°25′N, 81°1′W) in Heredia Province, Costa Rica, and in part at privately owned Finca El Bejuco located three km northwest of Finca La Selva, on the road to San Jose. 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).

The data presented here were gathered by sampling plants representing all stages of the growth habit of the four species. Growth in *Syngonium* is polyphyllous sympodial, producing predominantly monopodial segments. In *P. schottianum* growth is initially monopodial, but switches to monophyllous sympodial shortly before maturity is reached, thereafter producing only sympodial segments as long as the stem continues to climb. In *P. schottianum,* only segments from the monopodial phase of growth are considered in this analysis. The individual plants were collected, and dissected into their component parts: internodes, petioles, and lamina lobes. The parts were individually cataloged, and their linear dimensions measured: length for lamina lobes and petioles, and length and diam for internodes. Leaf outlines were also traced for use in a separate study. All parts were then placed in envelopes and dried until no further wt loss was noted. The dried parts were weighed on a Mettler balance. In all measurements of the petiole, the sheath was not measured separately, but is simply treated as a part of the petiole.

The internode may be considered ideally as a cylinder, though this is far from the truth. The diam is not uniform along the length of the internode, but tends to taper slightly toward one end. The cross-section is somewhat elliptical, not round. Furthermore, the depression in the side of the stem just above each axillary bud contributes additional irregularities to the

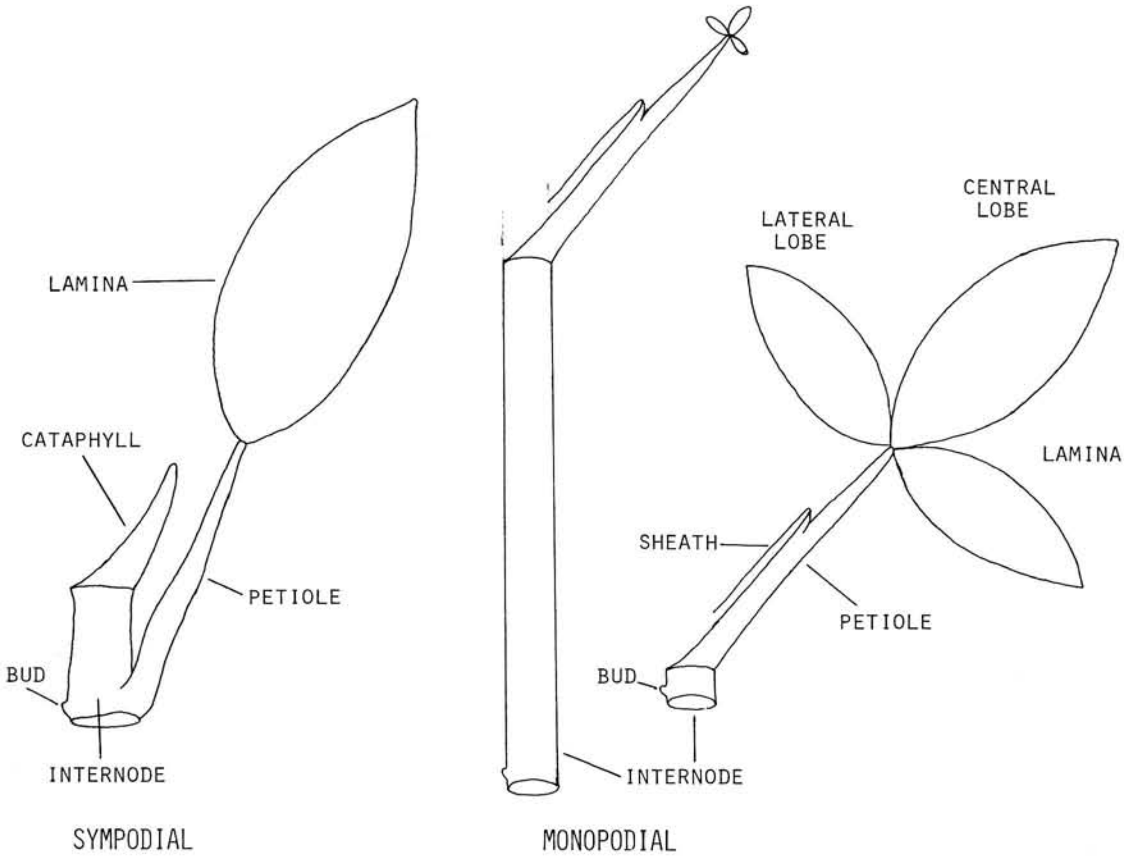

Fig. 2. The two kinds of segments, monopodial and sympodial, are illustrated. Because monopodial segments show great variation in proportioning of the parts, two extremes of form of monopodial segments with a common internode diameter are illustrated. The wt may be proportioned largely in the leaf producing a short internode and large leaf, or largely in the internode producing a long internode and small leaf.

shape. The length of the internode is measured from one node to the next, along a line parallel to the axis of the stem, to the nearest 1 mm. The diam of the internode was taken as the greatest girth of the stem, measured in the middle of the internode with calipers accurate to 0.1 mm. It should be noted that there is considerable error inherent in this measure of internode diam. Because this inherent error limits the degree to which the internode diam can correlate with any other variable, special consideration should be given to any correlation with a reasonably high coefficient, such as $r^2 = 0.90$.

The data obtained in the manner described above were subjected to regression analysis to test for correlations between the dimensions of the component parts of the segment. All size measures were log-transformed before analysis in order to equalize the variance over the range of the data. Two additional measures were included in the analysis, segment shape, defined as the proportion of the wt of the segment contained in the leaf (petiole and lamina), and lamina shape, defined as the proportion of the lamina wt contained in the central lobe. As is standard practice with proportions, these measures were transformed as the arcsin of the square root before analysis in order to equalize the variance over the range of the data.

Allometric relationships between two dimensions of a single organ generally have very high correlations, as can be seen in Table 1. When comparing the dimensions between two different organs, whose sizes are allometrically related, one also finds very high correlations, though not as high as correlations within a single organ. In this examination of relationships between the different organs of the segment, I will arbitrarily define good correlations as those with values of r^2 of 0.9 or greater, and only these will be considered to be true allometries. Correlations with values of r^2 between 0.8 and 0.9 will be called moderately corre-

TABLE 1. S. standleyanum *regression equations,* $Z = A + BX + CY^2$. *IW = internode wt mg, ID = internode diam mm, IL = internode length cm, PW = petiole wt mg, PL = petiole length cm, CLW = central lobe wt mg, CLL = central lobe length cm, CLA = central lobe area cm², LLW = lateral lobe wt mg, LLL = lateral lobe length cm, LLA = lateral lobe area cm², all variables log-transformed before regression*

N	A	B	C	r^2	Z	X	Y
150	0.418	1.78	0.732	0.95	IW	ID	IL
159	−0.107	2.01	0.0	0.98	PW	PL	
144	−0.127	2.07	0.0	0.99	CLW	CLL	
146	−0.409	1.93	0.0	0.99	CLA	CLL	
91	−0.464	2.37	0.0	0.99	LLW	LLL	
107	−0.654	2.07	0.0	0.99	LLA	LLL	

lated, and those below 0.8 will be called poorly correlated.

Vouchers have been made for all four species: *S. macrophyllum* Ray 7, 8, 9, 10, *S. stenophyllum* Ray 17, 18, 19, *S. standleyanum* Hammel 13206, *P. schottianum* Hammel 13308. The Ray vouchers have been deposited in the Gray Herbarium of Harvard Univ. The Hammel vouchers have been deposited in the Duke Univ. Herbarium.

RESULTS—Both the size and shape of the segment vary widely. The lamina can be large or small, and simple or compound; internodes can be short and thick or long and slender, and petioles can be long or short. Figure 1 shows the characteristic series of sizes and shapes assumed by the entire segment, throughout the ontogeny of the plant. Initially simple leaves gradually become multi-lobed as they become larger on climbing stems of increasing diameter, yet retain their mature lobed form as they decrease in size on descending stems of increasing internode length, and decreasing diameter. Thus we can see that the developmental pathway taken by a stem of decreasing leaf size, is not simply a reverse of the path taken by a stem with increasing leaf size. Furthermore, multi-lobed leaves may be either large or small. In order to sort out this array of forms I will begin by presenting the results of the analysis of the *S. standleyanum* data. I choose to make the analysis with this species because the leaf form is variable yet relatively simple, making quantification easier than in the other three species. I will first discuss the range in size and shape of the component parts of the segment, which obey strict allometries. I will then discuss the correlations between the parts, which although few, result in some interesting properties.

The component parts—The segment is composed of three distinct components: the internode, the petiole, and the lamina which can be subdivided into the central lobe and the lateral lobes.

The lamina lobes—The leaves of *S. standleyanum* are either simple, or tripartite. When each rank of lobes is taken alone, the lobe length is closely correlated with both the lobe wt and the lobe surface area. The correlation coefficient for a log-log regression is $r^2 = 0.99$ in all four cases (both central lobes and lateral lobes, correlating length with both wt and area); see Table 1. For both central and lateral lobes, the slope of the line relating length to area is very close to 2.0 (Table 1), indicating that the lobes change little in shape over the range in size.

If one examines a plot of length vs. wt in which both central and lateral lobes are displayed, it is clear from visual inspection that the two ranks of lobes fall on distinct lines. However the separation is slight, and is complete only in the lower half of the size range, where lateral lobes fall below central lobes. The same is true of a plot of length vs. area showing both lobes. This indicates that although the lobes have very nearly the same shape at the larger sizes, the central lobe is wider than the outer lobe at the small end of the size range. In summary, the relationship between the length of a lobe and its wt and surface area are sufficiently close that the form of a lamina lobe of a given rank can be adequately characterized by just one measurement: either length, or wt, or surface area.

The internode—The length of the internode is not correlated with its diam ($r^2 = 0.08$, Table 2); thus at least two variables are needed to characterize the shape of the internode. Two variables, length and diam, can be used in regression to account for 95% of the variance in the wt of the internode (Table 1). For my purposes, I will consider these two variables to adequately characterize the internode.

The petiole—The length of the petiole is closely correlated with its wt ($r^2 = 0.98$, Table 1), and its width, measured as internode diam, $r^2 = 0.91$, Table 2 (the petiole base [sheath]

TABLE 2. *Correlations within the segment for* S. standleyanum. *ID = internode diam, IL = internode length, IW = internode wt, PW = petiole wt, LW = lamina wt, SW = segment wt, SS = segment shape, LS = lamina shape, all variables log-transformed before regression (except SS and LS, which are transformed by arcsin of square root). All table entries are values of r squared. Values of N refer to all entries in that row*

	N	ID	IL	IW	PW	LW	SW	SS
LS	36	0.90	0.36	0.73	0.87	0.68	0.81	0.37
SS	128	0.26	0.65	0.21	0.43	0.73	0.13	
SW	128	0.91	0.08	0.73	0.85	0.62		
LW	134	0.75	0.11	0.17	0.87			
PW	150	0.95	0.07	0.47				
IW	150	0.59	0.49					
IL	210	0.08						

wraps around the internode, so the internode diam is also a measure of the width of the petiole). Thus like the lobes of the lamina, the form of the petiole can be adequately characterized by just one variable, either the length, or width, or wt. However the width (internode diam) is a poor measure and should not be used in preference to petiole length or wt.

Correlations between the parts—Table 2 contains the values of r^2 for the twenty-eight pairs of eight variables. These eight variables include four wt: the internode wt (IW), the petiole wt (PW), the lamina wt (LW), and the sum of these three, the segment wt (SW). The two linear dimensions of the internode are included: internode length (IL), and internode diam (ID). Two additional variables describe shapes, and are expressed as proportions, segment shape (SS; SS = [LW + PW]/SW), and lamina shape (LS; LS = CLW/LW where CLW is the wt of the central lobe). When LS = 1, the lamina is simple, consisting of only one lobe. When LS = ⅓, the lamina is three-lobed, and the three lobes are of equal wt (assuming bilateral symmetry).

The lamina lobes—The shape of the lamina as a whole is determined by the number of lobes it contains, and their relative sizes. The form of the lamina can be adequately characterized by two variables, the wt of the entire lamina, LW, and the shape of the lamina, LS, making the approximately true assumption of bilateral symmetry, such that the two outer lobes have the same wt. These two variables have a poor correlation, $r^2 = 0.68$, indicating that a lamina of any size can have almost any shape. Actually, very large laminas are always three-lobed, though small to medium sized laminas may be any shape. Thus there is no allometry between the size of the central lobe and the size of the lateral lobes.

The petiole and the lamina—The petiole wt and the lamina wt are moderately correlated, $r^2 = 0.87$. Nonetheless, there is still considerable variation in the size of laminas attached to a petiole of a given size, particularly in the middle of the range of petiole size. The strength of the correlation derives in part from the fact that very large petioles almost always have large laminas, and very small petioles almost always have small laminas. However, the correlation breaks down as one gets away from the extremes of the petiole size distribution.

The segment shape—The segment shape, SS, is not well correlated with any other variable. Importantly, it is not correlated with segment wt, $r^2 = 0.13$. Thus a segment of any size may have almost any shape.

The internode and the other parts—The wt of the internode is very poorly correlated with both the wt of the petiole, $r^2 = 0.47$, and the wt of the lamina, $r^2 = 0.17$. Likewise, the internode length, is not well correlated with any of the other variables. However, the internode diam shows unexpectedly high correlations with several of the other variables. These correlations are all the more surprising in light of the intrinsic error in the measurement of internode diam mentioned above. The highest correlation with internode diam, ID, is petiole wt, PW, $r^2 = 0.95$. This may well be due to the allometry between petiole length and width mentioned above.

The lamina shape, LS, is also highly correlated with the internode diam, $r^2 = 0.90$. LS is moderately correlated with PW ($r^2 = 0.87$), but the partial correlations suggest that this is a spurious correlation, resulting from the high correlations between ID and PW, and ID and LS: $r_{\mathrm{ID,PW.LS}} = 0.79$, $r_{\mathrm{ID,LS.PW}} = -0.49$, $r_{\mathrm{LS,PW.ID}} = -0.11$.

The next high correlation is one of the most unexpected, and perhaps the most important. The internode diam is strongly correlated with the wt of the entire segment, SW, $r^2 = 0.91$. At first one might think that this is simply a spurious correlation due to an expected cor-

TABLE 3. *Values of the correlation coefficient, r squared, for correlations between the dimensions of the component parts of the segment in three species of the Araceae. ID = internode diam, IL = internode length, IW = internode wt, PW = petiole wt, LW = lamina wt, SS = segment shape, SW = segment wt*

			Syngonium macrophyllum			
$N = 129$	ID	IL	IW	PW	LW	SS
SW	.89	.18	.82	.79	.38	.01
SS	.11	.56	.12	.25	.63	
LW	.58	.09	.07	.78		
PW	.91	.00	.40			
IW	.57	.53				
IL	.03					
			Syngonium stenophyllum			
$N = 65$	ID	IL	IW	PW	LW	SS
SW	.95	.07	.90	.93	.60	.40
SS	.49	.22	.13	.62	.77	
LW	.62	.14	.29	.82		
PW	.95	.00	.71			
IW	.79	.26				
IL	.07					
			Philodendron schottianum			
$N = 49$	ID	IL	IW	PW	LW	SS
SW	.94	.52	.93	.92	.57	.04
SS	.07	.52	.18	.00	.13	
LW	.53	.08	.37	.78		
PW	.88	.30	.77			
IW	.91	.73				
IL	.53					

relation between ID and IW, and between IW and SW. However ID and IW have a correlation of $r^2 = 0.59$, and IW and SW have a correlation of $r^2 = 0.73$. The internode diam is much more closely correlated with the segment wt than with the internode wt, and ID and SW are much more closely correlated than are IW and SW. The partial correlations suggest that the correlation between ID and SW cannot be explained as resulting from a spurious correlation: $r_{\mathrm{ID,SW.IW}} = 0.89$, $r_{\mathrm{IW,SW.ID}} = 0.63$, $r_{\mathrm{ID,IW.SW}} = -0.30$.

Because of the importance of the correlation between ID and SW, I conducted an analysis of correlations in the three additional species mentioned above. The results of the regression analysis are contained in Table 3. There is a consistently high correlation between the internode diam and the segment wt.

Since the segment wt is the sum of the wt of the internode, petiole, and lamina, one must consider the possibility that the high correlation between the internode diam (a measure of petiole width) and the segment wt is a spurious correlation resulting from the petiole wt being a component of the segment wt. However, the petiole wt is only a small component, with average values ranging from 10% to 18% of the segment wt (Table 4).

TABLE 4. *Petiole wt as proportion of segment wt*

Species	Minimum	Maximum	Mean	S.D.	Sample
S. macrophyllum	0.02	0.59	0.18	0.12	134
S. standleyanum	0.03	0.22	0.10	0.06	74
S. stenophyllum	0.03	0.26	0.14	0.07	57
P. schottianum	0.03	0.18	0.11	0.04	47

The correlation between internode diam and segment wt is only surprising because of the great variation in the proportioning of wt among the component parts of the segment. If the parts were always proportioned roughly the same within a species, we would expect the correlation because of general allometries among parts which increase in size together as segments get larger. However, the wt within a segment may be proportioned in radically different ways in different segments from the same individual or species. Table 5 shows the range of segment shape, SS, for the four species. Mean values are not reported because this variable generally has a bimodal distribution. Instead the two modal values are reported. Even modal values vary as widely as from 6% to 83% within a species.

Figure 3 shows segment shape plotted against internode diam in order to illustrate how the full range of segment shapes are found over the full range of segment sizes. The points occurring in the upper half of the plane have been represented by the letter 'X', to indicate that these are the segments with the large leaves, and the points in the lower half of the plane have been represented with the letter 'O', to indicate that these are the segments with most of the wt in the stem. In Fig. 4, segment wt is plotted against internode diam, using the same data set as Fig. 3. The leafy segments are again represented by 'X' and the elongate segments are again represented by 'O'. We can see that for any given internode diam, segments all have about the same wt, regardless of whether they are leafy or elongate segments.

TABLE 5. *Leaf wt (lamina and petiole) as proportion of segment wt*

Species	Minimum	Maximum	Lower mode	Upper mode	Sample
S. macrophyllum	0.02	0.95	0.02	0.75	130
S. standleyanum	0.03	0.89	0.06	0.83	74
S. stenophyllum	0.03	0.87	0.06	0.66	65
P. schottianum	0.03	0.87	0.09	0.56	49

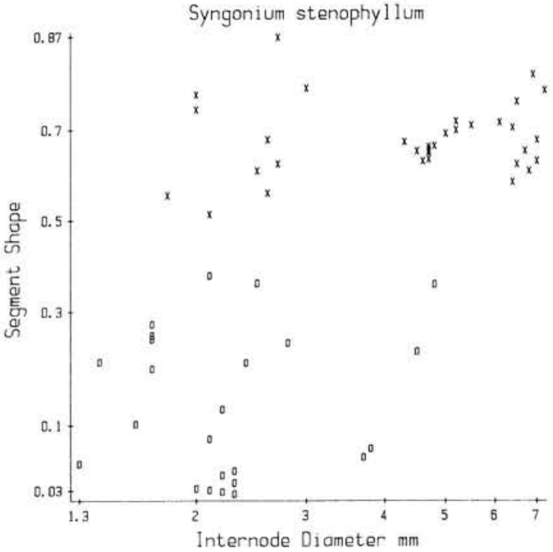

Fig. 3. Segment shape plotted against internode diam for *S. stenophyllum*. Segment shape is measured as the leaf wt (lamina and petiole) as a proportion of the segment wt. This variable is transformed as the arcsin of the square root. Internode diam is measured in mm, and log-transformed. Segments falling in the upper half of the plane are plotted with the letter 'X' to indicate that the leaf is proportionately large, and segments falling in the lower half of the plane are plotted with the letter 'O' to indicate that the wt is proportioned largely in the stem.

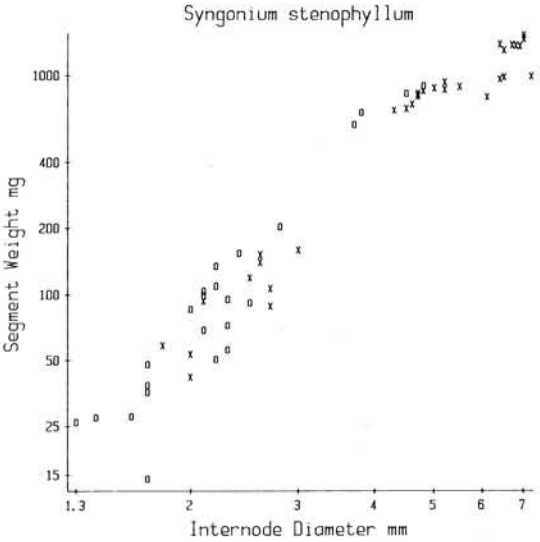

Fig. 4. Segment wt plotted against internode diam for *S. stenophyllum*. Segment wt is measured in mg, internode diam in mm, and both variables are log-transformed. This figure is based on the same data as Fig. 3, segments represented by the letter 'X' are leafy segments, and segments represented by the letter 'O' are elongate segments, as in Fig. 3.

DISCUSSION—There is essentially no allometry between the wt of the component parts of the segment: the internode, the petiole, the central lobe, and the lateral lobes. The lack of allometry between the parts can be expressed by saying that a segment of any size can have many shapes, or that for a segment of any given wt, that wt may be distributed in many ways among the parts. In the midst of this seeming lack of correlation, there are three very important allometries that severely restrict the way in which the form of the segment can vary. These are the allometries of the internode diam with the segment wt, petiole wt, and lamina shape. Perhaps the most important of these is the allometry between internode diam and segment wt.

Consider the implications of this allometry. If one fixes the diam of the internode, then the segment wt is also fixed, but the way in which the wt is distributed between the component parts is not. The wt may be largely in the leaf, or in the internode, due to the complete lack of correlation between segment wt, SW, and segment shape, SS, $r^2 = 0.13$. If the wt is largely in the internode, the internode must be long, as the diam is already fixed. One may have a long internode and a small leaf, or a short internode and a large leaf, but it is not possible simultaneously to have a large leaf and a long internode. Thus there is a trade-off between leaf size and internode length. This trade-off is illustrated in Fig. 2 in which the two monopodial segments have been drawn with identical internode diam, and thus segment wt, but with the segment shape at the two extremes of the range.

Although it has not been explicitly stated, this analysis indicates that the form of a single segment can be adequately specified by just two variables. The two variables can be called size and shape, where size is the wt of the segment, and shape is the relative sizes of the component parts of the segment.

From the above analysis, we know that the form of each organ of the segment can be adequately characterized by just one variable, wt, except for the internode. The internode must be defined by two variables (i.e., length, diam, and/or wt). This analysis also indicates that there are three fundamental allometries governing the size relationships between the components of the segment. The internode diam (ID) is allometrically related to the segment wt (SW), the petiole wt (PW), and the lamina shape (LS). These three allometries are the "axioms" which can be used to demonstrate that the geometry of the segment can be defined by just two variables, ID and SS.

Three "axioms" from allometry:

$SW = f_1(ID)$	$PW = f_2(ID)$	$LS = f_3(ID)$
$r^2 = 0.91$	$r^2 = 0.95$	$r^2 = 0.90$

Let:

$$\text{Segment Wt} = SW = IW + PW + LW$$
$$\text{Segment Shape} = SS = LW/IW$$

(SS is defined differently here than in the Tables.) Consider:

$$\begin{aligned} IW + LW &= SW - PW \\ &= f_1(ID) - f_2(ID) \\ &= f_4(ID) \end{aligned}$$

Combining the equations

$$IW + LW = f_4(ID)$$

and

$$SS = LW/IW$$

we find:

$$\begin{aligned} IW &= f_4(ID)/(1 + SS) \\ &= f_5(ID, SS) \end{aligned}$$

and

$$\begin{aligned} LW &= (SS \times f_4(ID))/(1 + SS) \\ &= f_6(ID, SS) \end{aligned}$$

We can now specify the form of all the component parts of the segment, in terms of just two variables, ID and SS:

Petiole (one variable needed):
 $PW = f_2(ID)$
Internode (two variables needed):
 ID and $IW = f_5(ID, SS)$
Lamina (two variables needed):
 $LS = f_3(ID)$ and $LW = f_6(ID, SS)$

The above analysis establishes that only two variables are needed to adequately define the form of the entire segment, specifying the dimensions of all the component parts. The two variables used in the analysis are ID and SS. However, the form of the segment may also be defined by other pairs of orthogonal variables, some of which may be more easily determined. In practice, it takes many measurements to compute the value of SS. It is desirable to find another variable orthogonal to ID, which can be reliably determined in the field for all segments, with a minimal number of nondestructive measurements. I have found that the ratio of internode diam to internode length ($ID/IL = IS$) is just such a variable. IS is orthogonal to ID ($r^2 = 0.12$), and coincidentally, is moderately correlated to SS ($r^2 = 0.84$). Also, both ID and IS can be measured quickly and easily in the field without disturbing the plant.

The two variables ID and IS can be used to define the x and y axes of a "morphological space" that can be used for the quantification and graphical representation of the form of segments. A single point in this space simply represents the form of a single segment. I have shown that this method can be used to quantify segment form in *S. standleyanum*. I would like to be able to use this same method with other species. It was shown above that two of the three "axioms," $SW = f(ID)$ and $PW = f(ID)$, hold for three additional aroid species. It is not as easy to test the third "axiom," $LS = f(ID)$, with other species because their leaf shapes vary in more complex ways. However, it is a well known generality that leaf complexity increases with stem diam. This relationship is one of "Corner's rules" (Corner, 1949; Hallé, Oldeman and Tomlinson, 1978). My observations of lamina shape in other aroids, though not quantitative in nature, suggest that in all species, lamina shape is correlated with internode diam and not with lamina size, as was found in the quantitative analysis of *S. standleyanum*. These observations are described and illustrated for *Monstera tenuis* in Ray, 1983a. The analysis presented here, and my observations of other aroid species suggest that Corner's rule that leaf complexity increases with stem diam, holds even among species with variable internode length.

I am led to suggest a modification of Corner's rules that "the stouter the main stem, the bigger the leaves and the more complicated their form." Such rules are adequate for species without significant variation in internode elongation. However, when there is significant variation in internode elongation among stems of the same diam, my data suggest that the rule should be stated as "the stouter the main stem, the bigger the segment, and the mass must be partitioned between the leaf and internode, thus the leaf will be small if the internode is long, and the leaf large if the internode is short. The leaf complexity increases with the width of the stem regardless of the size of the leaf." This reformulation of Corner's rules would appear to make them more general, encompassing plants which produce elongate internodes. It remains to be seen if these modified rules hold for species other than the four examined here.

My observations support the idea that monopodial segments are developmentally integrated units, at least in the four species considered. Perhaps the internode diam is an index of the size of the apical meristem. The size of the apical meristem may then determine the amount of tissue used in producing each segment, regardless of how the developing tissue is partitioned among the component organs of the segment.

ADDENDUM

I have been informed by Mike Grayum and Tom Croat that *S. stenophyllum* is now called *S. birdseyanum* Croat and Grayum ined., and that *P. schottianum* is now called *P. fragrantissimum* (Hook.) Kunth. The vouchers remain the same as indicated above. Additional vouchers are *S. birdseyanum* Mike Grayum 2786 (Duke), *P. fragrantissimum* Mike Grayum 5541 (MO).

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