Growth and Heterophylly in an Herbaceous Tropical Vine, *Syngonium* (Araceae).

A thesis presented

by

Thomas Shelby Ray Jr.

to

The Department of Biology

in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy
in the subject of
Biology
Harvard University
Cambridge, Massachusetts

July 1981

DEDICATION

This thesis is dedicated to the tropical rain forests, and to the poor people of the tropics, who are destroying the forests out of necessity and a lack of available alternatives.

ACKNOWLEDGEMENTS

I wish to thank Donald Strong for introducing me to the tropics and helping me to get started on vines. I thank Bob Cook for helping me to understand plants and for patience. I thank Barry Tomlinson for useful and accurate criticisms, and for helping me to get started on the anatomical work, which is not represented in this thesis. I thank Richard Lewontin for useful discussions and candid criticisms. I thank Kamal Bawa and Ken Sebens for their helpful discussions and reading of my early manuscripts. I thank Cathy Andrews for her love.

This work was supported by grants from the Atkins Fund and the Anderson Fund of Harvard University, and by a RIAS grant from the Organization for Tropical Studies. In addition, a substantial amount of the research was conducted while I supported myself by working part time as a station manager at Finca La Selva, an O.T.S. field station, and as a field assistant to E. O. Wilson.

CHAPTER ONE

INTRODUCTION

The subject of this thesis is the manner in which Syngonium triphyllum allocates its material resources among the various organs of which it is composed. I will concentrate on the relative investment in leaves and stems, how it affects growth, and its relationship to the ecological adaptations of the plant. Although I am primarily concerned with the ecological aspects of the problem, in its most general sense, it is an area of economic concern as it relates to the breeding of plants for increased yield. Breeding for an increased investment in one organ or another has been a major factor in increased crop yields (Evans, 1980), as exemplified by the cabbage species. Among the subspecies of Brassica oleracea are kale and cabbage which emphasize leaves, Brussels sprouts emphasizing axillary buds, broccoli and cauliflower the inflorescences, and kolhrabi the stem tissue. That the shifts in the manner in which the plant allocates its resources have been attained through breeding, points to the fact that in some plants the allocation of resources is under strict genetic control. This is an aspect in which the plants of this study differ from most plants. In the herbaceous vines of this study a single genotype will exhibit a variety of forms with widely differing relative investments in leaves and stems. This provides an ideal system for studying the effect of growth form on growth rate because genetic differences are controlled for, in that the various forms all occur in the same genotype.

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

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

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

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

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

> It has often been vaguely asserted that plants are distinguished from animals by not having the power of movement. It should rather be said that plants acquire and display this power only when it is of some advantage to them; but that this is of comparatively rare occurrence, as they are affixed to the ground, and food is brought to them by the wind and rain.

Although Darwin argued that plants possess the power of movement, he was not referring to the displacement of whole plants, but only of organs, as in the bending of leaves and tendrils, and of shoots in the process of nutation. As Bradshaw argues, the sessile nature of plants causes some of them them to respond to environmental changes by heterophyllic changes in form, rather that movements. In mobile plants, heterophylly is one of the most apparent response to the changes in microenvironmental conditions brought on by displacement in the forest. This is in part due to a fundamental difference in the kind of "movement" found in vines, from that found in animals. While the plant as a whole becomes displaced, over time, each part of the plant remains fixed in space for the duration of its existence, and so must be adapted to the immediate environmental conditions where it is found.

Many plants exhibit changes in form during their ontogeny. Most work on this topic has dealt with the anatomical or physiological aspects of developmental changes associated with changes in form. Some recent examples include: Allsopp, 1967; Franck, 1976; Greyson & Sawhney, 1972; Kaplan, 1970, 1973; Rogler & Wesley, 1975; Stein & Fosket, 1969; and Webster & Steeves, 1958. The general conclusion that can be drawn from this work is that the increase in size and frequently in complexity of successive primary leaves is correlated with the primary enlargement of the shoot axis, particularly of the apical meristem. A few studies have examined the environmental factors which affect changes in leaf form (Arber, 1919; Bostrack & Millington, 1962; Cook, 1969; Njoku, 1956). No general conclusion can be drawn from these studies, as the results are highly dependent on the organism used. The work of Cook & Johnson (1968) and Epling & Lewis (1952) dealt with the adaptive significance of heterophylly. Cook & Johnson (1968) conclude that strong heterophylly in the amphibious plant Ranunculus flammula is associated with "immature" (early successional) and "unpredictable" environments. The present investigation will be concerned with heterophylly in the tropical vine Syngonium triphyllum, which is associated with mobility that causes the plant to encounter successively, a predictable series of microhabitats in a fully mature tropical rain forest.

1. GROWTH HABIT

The overall growth habit is viewed as being composed of two major cycles, a small terrestrial cycle, the T cycle, in which the plant alternates between producing "leafy" and "stemmy" shoots (terms to be clarified later), and a large arboreal cycle, the A cycle, in which the plant ascends and descends trees. When a seed germinates, the plant first produces a rosette of leaves (T_l, terrestrial leafy, lower left of Figure 1). The form of subsequent growth then switches, and the plant produces a long slender stem with tiny leaves widely spaced on the stem (T_s, terrestrial stemmy). This stem is skototropic, and grows toward darkness in order to encounter trees, since tree trunks appear as silhouettes on the plant´s horizon (Strong & Ray, 1975). If a stem of type T_s does not encounter a tree after roughly two meters of extension, in its subsequent growth it will revert to the rosette form, T_l. The plant will thus establish a second photosynthetic base, from which a second stem of type T_s will be produced. The stem will alternate indefinitely between forms T_l and T_s until a tree is encountered. The stem will then begin to climb the tree. Leaves will continue to be widely spaced on the stem, but the stem diameter will gradually increase, as will the size of successive leaves, type A_a (arboreal ascending). As leaf size increases, so does its complexity. The leaves become palmately compound, with the largest leaves having five lobes. When the stem has reached its greatest diameter and the leaves their greatest size, the plant will flower and fruit. After that, flowering will be repeated after roughly every tenth leaf.

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

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

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

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

2. MATERIALS & METHODS

The study reported here was conducted at the Organization for Tropical Studies´ La Selva Field Station, located at the confluence of Rio Puerto Viejo and Rio Sarapiqui (10° 25´ N, 81° 1´ W) in Heredia Province, Costa Rica. The vegetation of La Selva, 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 is basically of two types: that gathered by destructive sampling, and that gathered by non-destructive sampling. In destructive sampling, plants were chosen representing all stages of the growth habit, from both primary forest and second growth. These individuals 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 diameter for internodes. The outlines of the lamina lobes were traced on notebook paper. These tracings were later xeroxed, cut out, and weighed in order to compute surface areas. All parts were then placed in envelopes and dried at 100° C until no further weight loss was noted (usually two days). The parts were then weighed on a Mettler balance. 227 segments were sampled in this manner, for the species Syngonium triphyllum. The data was used in the regression analysis presented in Tables 1 and 2. From the regression analysis, one derives formulas which can be used to estimate the dry weights and surface areas of the component parts of the plant, from measurements of linear dimensions alone.

The equations derived in the manner just described provide the basis for non-destructive sampling. In non-destructive sampling, the same linear measurements; internode length and diameter, petiole length, and lamina lobe lengths; were made on each part of an intact plant in its natural habitat. The linear measurements were then transformed by means of the equations in Table 1, to provide an estimate of the dry weight and leaf surface area distributions of living plants. 79 ramets (comprising 60 ramets at the initiation of the study) were sampled in this method, over periods of up to two and one half years. The sample ultimately included data on 4213 segments. This method was used to generate the data used in most of the analyses in this thesis.

CHAPTER TWO

ALLOMETRIES AND TRADE-OFFS

1. THE FORM OF THE SEGMENT

In this analysis, the fundamental unit is the segment defined as an internode and the leaf at its distal end (Figure 2). This unit has previously been called a phytomer or a module (White 1979). 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. In order to sort out this array of forms, 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.

1.1. The Component Parts

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

1.1.1. The lamina lobes

The leaves of S. triphyllum are either simple, palmately three lobed, or on rare occasions, five lobed. The second rank of lateral lobes never becomes well developed, thus I will not consider them in this analysis. When each rank of lobes is taken alone, the lobe length is closely correlated with both the lobe weight and the lobe surface area. The correlation coefficient for a log-log regression is r^2=.99 in all four cases (both central lobes and lateral lobes, correlating length with both weight 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 very little in shape over the range in size. If one examines a plot of length vs. weight 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 somewhat 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 weight and surface area are sufficiently close, that the form of a lamina lobe of a given rank, can be fully characterized by just one measurement: either length, or weight, or surface area.

1.1.2. The internode

The length of the internode is not correlated with its diameter (r^2=.08), thus two variables are needed to characterize the shape of the internode. The internode may be considered ideally as a cylinder, though this is far from the truth. The diameter 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

TABLE ONE Regression Equations

$Z=A+BX+CY^2$

N	A	B	C	r^2	Z	X	Y
150	.418	1.78	.732	.95	IW	ID	IL
159	-.107	2.01	0.0	.98	PW	PL	
144	-.127	2.07	0.0	.99	CLW	CLL	
146	-.409	1.93	0.0	.99	CLA	CLL	
91	-.464	2.37	0.0	.99	LLW	LLL	
107	-.654	2.07	0.0	.99	LLA	LLL	

IW=internode weight mg, ID=internode diameter mm, IL=internode length cm, PW=petiole weight mg, PL=petiole length cm, CLW=central lobe weight mg, CLL=central lobe length cm, CLA=central lobe area cm, LLW=lateral lobe weight mg, LLL=lateral lobe length cm, LLA=lateral lobe area cm, all variables log transformed before regression.

depression in the side of the stem just above each axillary bud, contributes additional irregularities to the shape (Figure 3). For the purposes of this analysis the diameter 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 diameter. Because this inherent error limits the degree to which the internode diameter can correlate with any other variable, special consideration should be given to any correlation with a reasonably high coefficient, such as $r^2=.90$. The length is measured from one node to the next, along a line parallel to the axis of the stem, to the nearest 1 mm. Two variables, length and diameter, can be used in regression to account for 95% of the variance in the weight of the internode (all variables are log transformed, see Table 1).

1.1.3. The petiole

The length of the petiole is closely correlated with its weight ($r^2=.98$), and its width, measured as internode diameter ($r^2=.91$, see Table 2). 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 weight. However the width (internode diameter) is a poor measure and should not be used, in preference to petiole length.

1.2. 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 weights: the inter-

TABLE TWO

Correlations Within The Segment

	N	ID	IL	IW	PW	LW	SW	SS
LS	36	.90	.36	.73	.87	.68	.81	.37
SS	128	.26	.65	.21	.43	.73	.13	
SW	128	.91	.08	.73	.85	.62		
LW	134	.75	.11	.17	.87			
PW	150	.95	.07	.47				
IW	150	.59	.49					
IL	210	.08						

ID=internode diameter, IL=internode length, IW=internode weight, PW=petiole weight, LW=lamina weight, SW=segment weight, SS=segment shape, LS=lamina shape, all variables are log transformed before regression (except SS & 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.

node weight (IW), the petiole weight (PW), the lamina weight (LW), and the sum of these three, the segment weight (SW). Since the form of the internode cannot be fully characterized by its weight alone, I have included its two linear dimensions in the table: internode length (IL), and internode diameter (ID). These six variables will be log transformed in all analyses, to equalize the variance over the range of the data. The last two variables describe shapes, and are expressed as proportions. The first is the segment shape (SS), which is the weight of the leaf (LFW, LFW=LW+PW) divided by the segment weight, and could be expressed explicitly as LFW/SW or (LW+PW)/(LW+PW+IW). Figure 2 shows examples of segments illustrating the two extremes of this variable. The leafy segment has a high value of SS, and the stemmy segment has a low value of SS. The last variable is lamina shape (LS), which is the central lobe weight (CW) divided by the lamina weight, (LW). Explicitly this is CW/LW, or CW/(CW+RLW+LLW), where RLW is the weight of the right lateral lobe, and LLW is the weight of the left lateral lobe. Thus, when LS=1, the lamina is simple, consisting of only one lobe. When LS=1/3, the lamina is three lobed, and the three lobes are of equal weights (assuming bilateral symmetry). In all analyses, these last two variables, SS & LS, will be transformed by the arcsin of the square root, 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 .9 or greater, and only these will be considered to be true allometies. Correlations with values of r^2 between .8 and .9 will be called moderately correlated, and those below .8 will be called poorly correlated.

1.2.1. The lamina lobes

The shape of the lamina as a whole is determined by the number of lobes it contains, and their relative sizes. Figure 4 shows the characteristic series of sizes and shapes assumed by the entire leaf, throughout the ontogeny of the plant. The growth habit description explains how initially simple leaves gradually become multi-lobed as they become larger on stems of increasing diameter, yet retain their mature lobed form as they decrease in size on 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.

The form of the lamina can be completely characterized by two variables, the weight 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 weight. These two variables have a poor correlation, r^2=.68, indicating that a lamina of any size can have almost any shape. Actually, very large laminas are always multilobed, 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.

1.2.2. The petiole & the lamina

The petiole weight and the lamina weight are moderately correlated, r^2=.87. None the less, there is still considerable variation in the size of leaves 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 leaves, and very small petioles almost always have small leaves. However, the correlation breaks down as one gets away from the extremes of the petiole size distribution.

1.2.3. The internode and the other parts

The weight of the internode is very poorly correlated with both the weight of the petiole r^2=.47, and the weight of the lamina r^2=.17. Likewise, the internode length, is not well correlated with any of the other variables. However, the internode diameter 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 diameter mentioned above. The highest correlation with internode diameter, ID, is petiole weight, PW, r^2=.95. This may well be due to the allomety between petiole length and width mentioned above. The next highest correlation is one of the most unexpected, and perhaps the most important. The internode diameter is strongly correlated with the weight of the entire segment, SW, r^2=.91.

At first one might think that this is simply a spurious correlation due to an expected correlation between ID and IW, and between IW and SW. However ID and IW have a correlation of $r^2=.59$, and IW and SW have a correlation of $r^2=.73$. The internode diameter is much more closely correlated with the segment weight than with the internode weight, 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: $r_{ID,SW.IW}=.89$, $r_{IW,SW.ID}=.63$, $r_{ID,IW.SW}=-.30$. I will return to a discussion of this allometry, as it has profound effects on the overall growth pattern of the plant.

The lamina shape, LS, is also highly correlated with the internode diameter, $r^2=.90$. LS is moderately correlated with PW ($r^2=.87$), but the partial correlations suggest that this is a spurious correlation, resulting from the high correlations between ID and PW, and ID and LS: $r_{ID,PW.LS}=.79$, $r_{ID,LS.PW}=-.49$, $r_{LS,PW.ID}=-.11$.

1.2.4. The segment shape

The segment shape, SS, is not well correlated with any other variable. Importantly, it is not correlated with segment weight, $r^2=.13$. Thus a segment of any size may have any shape.

1.3. Summary

There is essentially no allometry between the weights of the four component parts of the segment, the internode, the petiole, the central lobe, and the lateral lobes. There is a slight correlation between the petiole weight and the lamina weight, though this correlation holds only at the extremes of the size range, thus the sizes of the leaf and petiole cannot be considered to be allometrically related. The lack of allometry between the parts can be expressed by saying that a segment of any size can have any shape, or that for a segment of any given weight, that weight may be distributed in virtually any way 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 diameter with the segment weight, petiole weight, and lamina shape. Perhaps the most important of these is the allometry between internode diameter and segment weight. Consider the implications of this allometry. If one fixes the diameter of the internode, then the segment weight is also fixed, but the way in which the weight is distributed between the component parts is not. The weight may be largely in the leaf, or in the internode, due to the complete lack of correlation between segment weight, SW, and segment shape, SS, $r^2=.13$ If the weight is largely in the internode, the internode must be long, as the diameter 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 Figure 2 in which the two segments have been drawn with identical internode diameters, and thus segment weights, but with the segment shape at the two extremes of the range.

2. THE FORM OF THE WHOLE PLANT

The plant consists of a linear string of segments, with rare branching. The form of the plant is determined by the number of segments it contains, the way they are strung into branches, and the form (size and shape, as discussed in the previous section) of the individual segments. For the purposes of this chapter, I will not be concerned with branching patterns, and will focus on the pattern in which the forms of the individual segments are distributed along the stem, rather than the number of segments in the stem.

As an entry to this problem, consider the histograms of the two independent variables, segment weight (Figure 5) and segment shape (Figure 6), which taken together provide a fairly complete description of segment form. Each of these histograms contains 3250 points, representing all the segments comprising 76 individual plants, chosen so as to represent all of the growth forms equally. While the distribution of segment weights is roughly normal (or rather, log normal), the distribution of segment shapes is strongly bimodal. I will take advantage of the extreme bimodality of the segment shape distribution, by arbitrarily dividing it at the bottom of the trough, at SS=0.6 (at this value, 32% of the segment weight is in the leaf). I will call any segment greater than this value a leafy segment, and any segment less than this value a stemmy segment. In this manner I can compute that 73% of the segments in Figure 6 are leafy.

Due to its mobile nature, the plant is faced with two tasks, photosynthesis and vegetative dispersal, which are not necessarily accomplished efficiently by segments of the same shapes. In Figure 1 it can be seen that forms T_s and A_h are specialized for dispersal, while forms T_1 and A_a are specialized for photosynthesis. A photosynthetic form must have a large leaf area, while a dispersal form must have long internodes. That there is no single segment form which efficiently accomplishes both tasks, is in part a result of the trade-off between internode length and leaf size described in the previous section. It appears that this morphological trade-off has contributed to the evolution of an overall growth habit that involves a division of labor between adjacent groups of segments. This can be seen in Figures 7 thru 11 in which the values of SS have been plotted for each segment along the stem. Here one can see that groups of segments at one extreme of shape alternate with groups of segments at the other extreme of segment shape, and transitions between the two extremes are very rapid. The overall growth habit involves two different cycles between the extremes of form. One is the terrestrial cycle, T, which alternates between forms T_1 and T_s, the other is the arboreal cycle, including types A_a, A_d, and A_h. I will refer to the former as the T cycle, and the later as the A cycle. Figures 7, 8, & 9 show three plants in the T cycle, while Figures 10 & 11 show two plants in the A cycle. It can be seen that the T cycle alternates rapidly between the two extremes, though tending to stay somewhat more in the stemmy form, while the A cycle remains stable at one extreme or the other for many successive segments. In fact cycle A only switches from the leafy form to the stemmy form when it loses contact with a tree, and only switches from the stemmy form to the leafy form when it makes contact with a tree. In Figures 10 and 11, the letter "A" indicates a segment attached to a tree, the letter "D" indicates a segment hanging in the air, and the letter "H" indicates a segment on the ground (as in Figure 1).

The floor of the tropical rain forest has a scattering of small herbs, such as Syngonium and Philodendron rosettes, small palms, Dieffenbachias, etc. Elongating stems will often encounter these herbs and begin to climb them as if they were a tree. However, the stem will quickly outgrow them and return to the ground. This is illustrated in both Figures 10 and 11, in which shortly after reaching the ground, the stems, now type A_h, encounter small herbs. The stems quickly switch from the stemmy form to the leafy form. However, they outgrow their small host rapidly, and switch again to the stemmy form. In Figure 10, the plant branches just before reaching the ground (although the branching occurs before reaching the ground in the spatial sense, temporally the lateral branch is released after the primary branch encounters the ground). The second branch is illustrated on a displaced y-axis to avoid confusing overlap with the first branch. The second branch does not encounter a tree or herb to climb, and so remains stable in the stemmy form. In Figure 9 the stemmy form of cycle T encounters a tree and switches to the leafy form.

Figures 12 & 13 show the histograms of segment weight and segment shape respectively for cycle T only, and Figures 14 & 15 show the respective histograms of cycle A only. It can be seen that while cycle T consists of smaller segments than cycle A, the two cycles have the same bimodal peaks of segment shape. However, cycle T has proportionatley more segments in the left hump, 45%, compared to 18% in cycle A. This is evident in Figures 7, 8, & 9 as well, where it can be seen that in cycle T, groups of a few leafy segments are separated by larger groups of stemmy segments. In Figures 13 & 15 the relative sizes of the two humps are biased toward the right by the fact that the sample includes a number of individuals that consist only of the leafy form, without the stemmy form. Figures 16 & 17 are histograms of cycles T and A respectively, which include only plants exhibiting both extremes of form. These figures illustrate that in cycle T, the majority of the segments are of the stemmy form (55%), while in cycle A, the majority of the segments are of the leafy form (68%).

Figures 18 through 25 are histograms of the number of segments spent in each phase of the segment shape cycle. To illustrate what I mean by this, consider Figure 11. This stem starts out in the leafy phase of the cycle, where it remains for 65 segments before switching to the stemmy phase. It then remains in the stemmy phase for 34 segments before switching to the leafy phase for 8 segments, and then back to the stemmy phase for 5 segments. Thus this stem will contribute one entry into the histograms for each of the four values, 65, 34, 8, and 5. However, the values 65 and 5 do not represent complete half-cycles. That is, we do not know how many leafy segments preceeded the point where the data on this stem began, and we do not know for how many more segments the plant will remain in the stemmy form as it continues to elongate. Therefore I will consider the first and last phase on this plant to be incomplete, and the middle two phases to be complete.

Figures 18 and 19 are the cycle T distributions of the leafy and stemmy phases respectively, and only complete half-cycles are represented. It can be seen that the stemmy phase has a somewhat greater spread. Figures 20 and 21 represent the same distributions respectively, but both incomplete and complete half-cycles are included, for comparison.

Figures 22 and 23 are the cycle A distributions of leafy and stemmy phases respectively, only complete half-cycles are represented. It can be seen that cycle A involves much longer half-cycles than cycle T. In general, the phases of cycle A are so long, that due to senescence at the posterior end, stems rarely grow long enough to exhibit a complete half-cycle at one point in time. The longest phases of cycle A usually have to be recorded by measuring the plant repeatedly over a period of years as it grows at one end and dies at the other. The plants in this study were sampled repeatedly for periods of up to two and one half years. None-the-less, the longest complete phases of cycle A are poorly represented in the sample. In cycle A, unlike cycle T, lumping the incomplete phases with the complete phases gives a better impression of the length of the cycles. Although many of the phases thus represented are incomplete, they give us at least a minimum estimate of the length of the phases. Thus Figures 24 and 25 are the cycle A distributions of leafy and stemmy phases respectively, both complete and incomplete phases included. The high frequency of short phases in the A cycle results from stems of type A_h encountering small herbs on the forest floor, and momentarily changing forms, and fluctuations around the arbitrary transition point while changing phases.

Figures 18-25 indicate that both phases of the A cycle are much longer than both phases of the T cycle. Also, in the A cycle, the leafy phase appears to be longer than the stemmy phase, while in the T cycle, the stemmy phase is generally longer. These latter two conclusions are in agreement with Figures 16 and 17 which show the relative numbers of segments in the two phases of the two cycles.

CHAPTER THREE

DEVELOPMENTAL PATHWAYS AND ENVIRONMENTAL INFLUENCES

1. INTRODUCTION

The complex growth habit and diversity of forms illustrated in Figure 1, can be interpreted as a set of tactical responses to environmental parameters such as light and nutrient levels, resulting in an optimal overall growth strategy that maximizes the fitness of the plant. This growth habit may also be viewed as a collection of developmental pathways leading from the seedling to the mature plant. Both views have merit, and in this chapter I will examine the changes in form, and the manner in which environmental influences interact with developmental processes in producing the series of forms illustrated in Figure 1.

Because branching is rare in Syngonium, the plant can be viewed as a linear series of segments placed end on end. This makes it possible to examine changes in form of the plant in terms of the successive forms of individual segments along the stem. Therefore I will begin this analysis by describing a method to quantify the form of individual segments, then I will examine the way in which the form of successive segments change as the plant "moves" through its rain forest habitat.

2. QUANTIFYING THE FORM OF THE SEGMENT

In the second chapter of this thesis I examined the allometries within and between the individual organs which comprise the segment; the internode, the petiole, and the lobes of the leaf. Although it was not explicitly stated there, the analysis indicates that the form of a single segment can be fully specified by just two variables. The two variables can be called size and shape, where size is the weight of the segment, and shape is the manner in which the weight is proportioned among the component parts of the segment.

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

Three "Axioms" From Allometry:

$SW = f_1(ID)$	$PW = f_2(ID)$	$LS = f_3(ID)$
$r^2 = .91$	$r^2 = .95$	$r^2 = .90$

Let: Segment Weight = $SW = IW + PW + LW$

Segment Shape = $SS = LW / IW$

Consider: $IW + LW = SW - PW$

$$= f_1(ID) - f_2(ID)$$

$$= f_4(ID)$$

Combining The Equations:

$IW + LW = f_4(ID)$ and $SS = LW / IW$

We Find:

$IW = f_4(ID) / (1 + SS)$ and $LW = (SS \times f_4(ID)) / (1 + SS)$

$= f_5(ID, SS)$ $\qquad = f_6(ID, SS)$

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 $LW = f_6(ID, SS)$

Note: It was shown in the previous chapter that if one makes the approximately true assumption of bilateral symmetry, the size of all lobes of the lamina can be specified by the two variables LW and LS.

In the analysis described in this chapter, I have chosen to use a slightly different pair of variables to define the form of the segment. In place of ID, I will use segment weight, SW, which is allometrically related to ID, as an indicator of segment size. In place of segment shape as defined above, LW / IW, I will use leaf weight / segment weight, (LW + PW) / SW. This version of SS describes the leaf weight as a proportion of segment weight. The two variables SW and SS, as just defined are virtually orthogonal ($r^2=.13$), and adequately define the form of the segment in a way that can be intuitively grasped. In Figure 26 the two variables SW and SS are used to define the x and y axes of a "morphological space" that will be used throughout the remainder of this thesis for the graphical representation of the form of segments. A single point in this space simply represents the form of a single segment. The forms of segments characteristic of the four quadrants of the plane are sketched in. It is helpful to keep in mind that lamina shape is correlated with the x-axis. The two variables SW and SS do not exactly define the form of the segment, in the sense that the lengths of the two sides of a rectangle exactly define its form. However, the segment is not an abstract geometric object, and the two variables SW and SS account for enough of the variation in form to be adequate for this study.

3. DISTRIBUTION OF FORMS

Four of the classes of stems shown in Figure 1, classes T, A_a, A_d, and A_h can be objectively defined on the basis of where in the forest the segment is found, and without reference to the acutal form of the segment. If a segment is a part of a stem that is climbing a tree, it is type A_a. If it is a part of a stem that is hanging in the air and growing down toward the ground, it is type A_d. If it is a part of a stem that is on the ground, it is either type T or type A_h. If a terrestrial stem is connected to a large arboreal stem, via a hanging stem of type A_d, it is type A_h, otherwise it is type T.

The data set includes 3813 segments which have been characterized in the manner described above. There are 1285 of type T, 1978 of type A_a, 289 of type A_d, and 261 of type A_h. The distributions of the data for the four types in the axes described above, is shown in Figure 27.

At this point one could argue that the microenvironment in which the segment is located (on the ground, in the air, or on a tree) influences the form. While this is clearly true, given the differing distributions of the forms in the morphological space, it is a simplistic argument and leaves considerable variation unexplained. In order to understand the distributions of the forms, it is necessary to examine the distinctive pathways through the morphological space taken by stems of the four kinds.

4. CHANGES OF FORM

4.1. Representations

4.1.1. Anecdotes

Using the axes illustrated in Figure 26, an entire plant can be represented by a series of points, with points corresponding to adjacent segments connected by lines, Figures 28 and 29. Throughout this chapter I will refer to changes of form as occurring rapidly or slowly. It is important to understand that I am using a variable unit of time, the plastochron. The plastochron is the amount of time it takes the plant to produce a segment. In *S. triphyllum* this time varies from about eight days to nine months. Instead of thinking of a change of form as occurring per unit of time, perhaps it is best to think of it as occurring per segment along the stem. In Figures 28 and 29, long line segments indicate "rapid" changes, while short line segments indicate "slow" or "gradual" changes of form. The line segment indicates precisely how much the form changes from one segment to the next, as well as the direction of the change. Unless otherwise stated, references to rapid or slow changes of form will indicate changes per segment, not real time. Figures 28 and 29 illustrate the path through the morphological space taken by individual plants as they change form. These Figures are difficult to interpret because of the contortions that result from drift within a region, as the form changes gradually. Despite these contortions there are unmistakable and consistent trends. Visualization of these trends can be enhanced by using a moving average, as in Figures 30 and 31, representing the same individual plants as Figures 28 and 29 respectively, but using a five point moving average. However these figures remain anecdotal.

Figures 28 and 30 illustrate a plant of type T cycling between the two forms T_1 and T_s. The stem begins at the lower left where the letter "T" occurs, and cycles on a clockwise path. Figures 29 and 31 illustrate a plant which is initially climbing a tree. The stem starts at the upper left where the letter "A" occurs. The form then drifts toward larger and slightly leafier segments until the stem outgrows the tree, and begins to hang in the air, where the first letter "D" occurs. The form then rapidly shifts toward the stemmy shape and a somewhat smaller size, and stabilizes in the bottom center of the plane. The point at which the hanging stem reaches the ground is indicated by an "H". There is virtually no change in form as the stem grows across the ground. As often occurs, the type A_h stem of this plant encountered and began to climb a small herb. The point where this encounter occurs is indicated by an "A". The form then makes a swift change to a leafier shape. By the time the form has shifted to the leafy shape, the stem has already overgrown its small host plant. This point is marked by a "D". The form then swiftly shifts to the stemmy shape again, where it remains, even after returning to the ground again. The point where the stem reaches the ground is marked by an "H". In Figure 31, the changes of form lag behind the indicated points of gain or loss of contact with trees, because of the moving average. In Figure 29 however, it can be seen that the form responds suddenly and dramatically to gain or loss of contact with vertical objects.

4.1.2. General Trends

The data for all plants can be combined and summarized by representing individual transitions of form between successive segments as vectors. Adjacent pairs of segments are represented in Figures 28 and 29 as two points connected by a line. Given that the segments occur in an order, it is possible to assign a direction to each line segment, thus making them into vectors. The data base includes 3246 such vectors for *S. triphyllum*. These vectors can be combined by summation to observe trends in various regions of the morphological space.

In Figures 32 through 34, the morphological space has been broken into a 10 x 10 grid, and all vectors whose mid points fall within a given cell, have been summed together. The resultant vector sum is illustrated with its mid point at the center of the cell. Any sum based on less than four vectors has been excluded from the diagram. The arrow indicates the length and direction of the change in form to be expected from one segment to the next, on the average. Actual changes will generally be longer, and more erratic in terms of direction, but when averaged over several segments the net change per individual transition is precisely as indicated by the arrow. The arrow head on each vector sum represents information on sample size and variance. The acute angle between the two sides of the arrow head is the angular standard deviation of the vector sum, and the length of the arrow head is proportional to the log of the sample size (the number of vectors used in the sum). These three diagrams represent the developmental pathways of which the overall growth habit is composed.

4.2. The "A_a Pathway"

Figure 32 illustrates the changes of form characteristic of the A_a pathway. This diagram incorporates 1695 individual transitions. All stems of the A_a pathway originate as terrestrial stems of type T_s or A_h. The segments are initially small and stemmy at the time that they make contact with trees. They then undergo a rapid shift to the leafy shape, in response to contact with the tree, entering the lefthand region of the cloud of arrows. This transition is indicated by the long arrows at the lower left of Figure 32. At this point segments are small and leafy, and begin the gradual process of size increase that leads to sexual maturity.

When a stem enters the A_a pathway, after the initial transition of shape, it will be in the upper lefthand region of Figure 32. Thus immediately upon arriving at the tree, the stem will begin making small leaves. The stem of type A_h or T_s from which it originated is generally short lived, and will soon senesce away leaving the new arboreal stem without a photosynthetic subsidy. Thus the plant is initially in about the same situation as the type T_1 rosette both in terms of form, and in that it has limited leaf surface situated in a shady location. As the plant climbs and grows, the successive segments increase gradually in size. Therefore the form shifts gradually toward the upper right of the figure.

Taken as a whole, this diagram represents a developmental pathway leading from the elongate dispersal forms to the large leafy sexually mature form. When a stem reaches large segment sizes, flowering occurs, the stem terminates in the inflorescence, and is continued by a sylleptic branch. The first segment of this branch has an elongate internode of a smaller diameter than the preceeding internode, and a reduced leaf. Thus there is a shift in form from the right end of the data cloud, downward and to the left. In the next segment, the form will shift more toward the leafy shape, but of a size significantly smaller than the preceeding segments. The net result of this process is that the size of the segments decrease sharply after flowering. After this initial drop in size, the stem resumes the normal trend of gradually increasing segment weight until flowering occurs again. Thus the developmental pathway represented in this figure terminates in a clockwise cycle, not in a stable form.

4.3. The "A_{dh} Pathway"

Figure 33 illustrates the series of changes of form that occur when a stem leaves the developmental pathway illustrated in Figure 32. This generally occurs when a stem becomes detached from the tree that it is climbing, usually by overgrowing it. This may occur from any point in the A_a pathway, thus segments may initially be of any size characteristic of the A_a pathway. This diagram incorporates 453 individual transitions. Upon entering this pathway, there is initially a rapid shift toward stemmy segments, and a slightly smaller size. The shift in form is generally complete within a few plastochrons (i.e. ~5), after which the form remains virtually stable in a small region in the bottom center of the plane, with a tendency to drift gradually toward smaller segment sizes.

If a stem of type A_h is cut off from its origin in a stem of type A_a, and thus from its source of photosynthate, it will quickly shift to a much smaller segment size, and will thus leave the region of the plane characteristic of type A_h, and enter the region occupied by the T cycle. If it does not then encounter a tree within a short distance, it will shift into the leafy form T_1.

4.4. The "T Cycle"

The A_a and A_{dh} pathways taken together form the arboreal cycle. Because the trigger for switching between the two pathways appears to be gain or loss of contact with trees, it is possible to separate the data into the two pathways simply on the basis of whether the segments are attached to trees or not. Switching between the two pathways of which the terrestrial cycle is composed, T_1 (terrestrial leafy) and T_s (terrestrial stemmy), appears to be controlled by an internal mechanism, possibly photosynthate levels. Because of this there is no way to objectively separate the data into the two classes, thus the T_1 and T_s pathways are displayed together in Figure 34. Figure 34 illustrates the changes characteristic of the T cycle. This diagram incorporates 1025 individual transitions. Stems in the T cycle originate either as seedlings, or as cut stems of type A_h, as described below. Segments of the T cycle are restricted to the left 69% of the x-axis. In this figure the x-axis has been expanded so that the region of the morphological space occupied by the T cycle will fill the figure, in order to allow greater resolution of the complex processes occurring there. What is most apparent from the figure is that the form changes in a clockwise cycle, with rapid changes of shape and gradual changes of size.

I will describe how the changes depicted in Figure 34 might arise, based on the hypothesis that switching between the two pathways, T_1 and T_s occurs when the level of photosynthate available to the apex reaches critical levels. I will assume that the stem will switch from the leafy to the stemmy pathway when photosynthate rises above a certain threshold level, and that the stem switches from the stemmy to the leafy pathway when photosynthate drops below another, lower, threshold level. Consider the series of changes to be expected in a plant entering the cycle as a seedling. In Syngonium, seed reserves are used to produce a rosette of a few small leaves. Thus when the seed reserves have expired, the segment form will be in the upper left region of Figure 34.

At this point the plant will have a very limited light gathering capacity, with only a few relatively small leaves, generally on the shady forest floor, thus photosynthate levels will be low and the stem will produce small segments. However, leaves are long lived in Syngonium, generally lasting two years, thus as the plant grows, leaf surface will accumulate, and the level of available photosynthate will rise. The plant will gradually produce larger segments, thus the form will gradually shift from the upper left of Figure 34 to the upper right.

Eventually, if the plant does not suffer excessive herbivory, the photosynthate level will rise to the threshold that triggers the switch to the stemmy phase of the cycle. The form then shifts quickly from the upper right to the lower right of Figure 34. The segment size will now be smaller than before the shift to the stemmy phase, but it will initially be at the upper end of the size range characteristic of the stemmy phase, and photosynthate levels are initially high. At this point, new growth causes an increase in biomass without an increase in leaf surface area. The leaves produced on the stemmy segments are only 1 to 2 mm. long, and are short lived, lasting less than a month. Thus the amount of photosynthate utilized for respiration will increase, while the total amount of photosynthate generated by the plant will decrease due to ageing and senescence of a fixed leaf surface. This will result in a gradual decrease in the amount of photosynthate available to the apex for new growth. the size of the successive segments will decrease, such that the form shifts from the lower right to the lower left of Figure 34. When the level of photosynthate available to the apex drops to the threshold that triggers the switch from stemmy to leafy segments, the form will shift quickly from the lower left to the upper left of Figure 34. At this point the level of photosynthate available for new growth will be low, and the segments will be small, though somewhat larger than before the shift from the stemmy to the leafy phase of the cycle. The apex is now essentially in the same condition as when it started the cycle as a seedling, and the cycle just described will repeat indefinetly until the stem encounters a tree.

4.5. Mechanisms Governing Changes

The complete set of pathways illustrated in Figures 32 through 34 are condensed and schematically illustrated in Figure 35. I will suggest a set of simple mechanisms which could govern the changes in form, in order to understand how the processes illustrated in Figures 32 through 35 might arise. Because the mechanisms I am suggesting are entirely hypothetical at this point, I consider them to constitute a model of how the changes might occur rather than a description of how they do occur. I consider the factors effecting changes of form to be of two types. Those causing shifts between developmental pathways, and those affecting changes within developmental pathways.

4.5.1. Shifts between pathways

The factors that I believe to regulate the shifts between the four developmental pathways are summed up in Figure 36. Of the twelve possible transitions between the four states, only seven occur naturally, as indicated in the figure.

Switching between the two pathways of the terrestrial cycle, T_1 and

T_s, appears to be regulated by an endogenous factor. I hypothesize that the factor is the level of photosynthate available to the apex for new growth. As described above, I believe that there are two photosynthate threshold levels regulating the switching between T_1 and T_s. When the photosynthate level rises above the upper threshold, the plant switches from the T_1 pathway to the T_s pathway. When the photosynthate level drops below the lower threshold, the plant switches from the T_s pathway to the T_1 pathway.

Switching between the two pathways of the arboreal cycle, A_a and A_{dh}, appears to be regulated by gain or loss of contact with trees. It is not clear if the triggering factor is physical contact with a solid object, or the change in orientation that always accompanies gain or loss of contact with trees. When a stem in the A_{dh} pathway contacts a tree, it will switch to the A_a pathway. When a stem in the A_a pathway loses contact with the tree, it will usually switch to the A_{dh} pathway.

Switching from the T cycle to the A cycle occurs in only one way. When a stem encounters a tree, it enters the A_a pathway. Stems in the T_1 pathway are stationary rosettes, and are incapable of making contact with trees. In the T cycle, only the stemmy form, in the T_s pathway is capable of contacting trees. Switching from the T cycle to the A cycle occurs by a switch from the T_s pathway to the A_a pathway, and is triggered by making contact with trees.

Of the seven possible transitions between pathways, only one occurs without a change in segment shape. In the transition from the A_{dh} pathway to the T_s pathway, the segments remain stemmy, and the only change of form is a decrease in segment size. However this transition is marked by an important physiological change; stems of the A_{dh} pathway are orthotropic, while stems of the T_s pathway are skototropic. I hypothesize that the switch from A_{dh} to T_s occurs when the level of photosynthate available to the apex drops below some threshold level. This is one of two kinds of transitions from the A cycle to the T cycle.

The last remaining transition, also a transition from the A cycle to the T cycle, occurs from the A_a pathway to the T_s pathway. When a stem in the A_a pathway loses contact with a tree, it either enters the A_{dh} pathway or the T_s pathway. I hypothesize that the "choice" between the two is based on the level of photosynthate available to the apex at the time that contact with the tree is lost. If the photosynthate level is above the threshold involved in the transition from A_{dh} to T_s, loss of contact with a tree will cause a shift from A_a to A_{dh}. If the photosynthate level is below that threshold, loss of contact with a tree will cause a shift from A_a to T_s. The transition from A_a to T_s will generally occur shortly after a transition from T_s to A_a. That is to say, if a stem in the T_s pathway begins to climb a small herb that it "mistakes" for a tree, thus entering the A_a pathway, and then rapidly outgrows its support, it will return directly to the T_s pathway, rather than passing through the A_{dh} pathway.

4.5.2. Changes within pathways

Six of the seven transitions between pathways occur with a change of segment shape. In these cases the first change that occurs upon entering the new pathway is a change of shape, from leafy to stemmy or from stemmy to leafy segments. In fact all changes of shape occur as a result of a switch between pathways, and the change is usually complete within five or fewer plastochrons after entering a new pathway. Aside from these initial changes of shape, all changes of form that occur within pathways are changes in segment size. In general, in the two leafy pathways, T_l and A_a, there will be a gradual shift toward larger segments, and in the two stemmy pathways, T_s and A_{dh}, there will be a gradual shift toward smaller segments. I hypothesize that all changes in segment size (aside from those associated with changes in shape) occur in response to rising and falling photosynthate levels, regardless of the pathway involved. Rising photosynthate levels will cause increasing segment sizes, and falling photosynthate levels will cause decreasing segment sizes.

On stems of the two leafy pathways, T_l and A_a, photosynthate levels are likely to rise due to an accumulation of leaf surface. On stems of the two stemmy pathways, T_s and A_{dh}, photosynthate levels are likely to decline because the plant is no longer producing substantial leaves, while existing leaves are declining through senescence and herbivory. This could explain why in the leafy pathways there is a general trend toward larger segment sizes, and in the stemmy pathways there is a trend toward smaller segment sizes.

5. NATURE AND NURTURE

The overall growth habit is viewed as being composed of four distinct developmental pathways. Casual observation of the behavior of individual plants, as represented in Figures 7 through 11, or of the general trends within each pathway, as represened in Figures 32 through 35, might lead one to the conclusion that once the stem enters a given developmental pathway, there unfolds a genetically defined developmental process which proceeds along a given path, virtually regardless of environmental conditions as long as it is not triggered by specific stimuli to switch to another pathway.

I do not believe that this view accurately reflects the biological reality. If one accepts the hypotheses that I have presented concerning the factors regulating change of form, the concept of the unfolding of a genetically defined pathway becomes unnecessary. Given the hypotheses that I have presented, all that need be genetically defined in order to generate any of the pathways is: 1) The segment shape characteristic of the pathway. 2) The conditions necessary to remain in the pathway. 3) The relationship between photosynthate level and segment size (there is a positive correlation in all cases). 4) Conditions that trigger "special events" characteristic of the pathway (there is only one special event, flowering, which occurs only in the A_a pathway).

After the initial rapid change of shape characteristic of most transitions between pathways, the only change of form that occurs is a gradual increase or decrease of segment size, and it is this gradual shift in segment size that is the predominant trend in each pathway. Yet the shift in segment size is, I suggest, a response to rising or falling photosynthate levels, not the unfolding of a genetically defined developmental process. The level of photosynthate available to the apex for new growth must be a result of a combination of the light levels reaching the leaves, the respiratory needs of the plant, and the total leaf surface area of the plant, which will result from the relative rates of the production of new leaves, and senescence and herbivory of old leaves. In the case of long slender stems of types A_h and T_s, the availability of photosynthate to the apex may also be affected by the length of the stem separating the apex from the leaves, and the condition of the stem which may be degraded by damage from herbivores or falling debris.

I believe that it is possible for the pathways to operate in reverse, under exceptional environmental conditions. For example, if a stem in the A_a pathway has grown to a large segment size and then begins to experience a high rate of leaf herbivory, it should have a drop in total leaf surface area, causing a drop in available photosynthate, and leading to a decline in the size of successive segments. I am currently conducting experiments to determine if this is possible.

CHAPTER FOUR

FORM AND FUNCTION

1. INTRODUCTION

In his book The Movements And Habits Of Climbing Plants, Charles Darwin explains 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.

Darwin aptly observed that one of the key features of the viny habit is the efficient utilization of material resources made possible by dependence on other plants for support. The herbaceous vines of this study have built on this basic adaptation by evolving the capability for elaborate reorganization of material resources, resulting in dramatic changes of form. I would like to go on to address questions about why the plant changes form. What specialized functions do the various forms serve? In what way, if any, are the various forms adapted to the particular microhabitats in which they occur? What selective advantage, if any, is provided by specialization into various forms, as opposed to a single intermediate form of some type?

That I have prefaced the discussion of adaptation with three chapters containing an elaborate exploration of natural history, allometries, and developmental processes, is an indication that I basically agree with Gould and Lewontin´s 1979 critique of the adaptationist programme, when they state:

> ...organisms must be analysed as integrated wholes, with Bauplane so constrained by phyletic heritage, pathways of development and general architecture that the constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs.

I agree with them that such factors are of enormous importance, but I do not feel that they are necessarily more important or more interesting than selective forces. My own feeling is that any adaptive study should start, when possible, with an analysis of phyletic, developmental, and architectural factors. Once those factors have been thoroughly described and understood, one is in a much better position to address adaptive questions, because the constraints imposed on the organism by such factors will be understood, and one can then consider how selection might act on whatever variability is possible within those constraints. Furthermore, allometries and developmental pathways can be considered to be traits in themselves, on which selection may act, and so may to a limited extent display some of the characteristics of adaptations.

2. FUNCTIONS OF THE SPECIALIZATIONS

It goes without saying that the leafy forms are specialized for making leaves, and thus for carrying out the photosynthetic function, while the stemmy forms are specialized for making elongate stems, and thus serve the function of vegetative dispersal. However, it is not clear how segment size is related to these specializations. In order to look for clues as to the functional significance of the two extremes of size of each of the two segment shapes, I will examine the relationship between the form of the segment, and various growth parameters.

The technique used to do this is illustrated in Figures 37 through 45. For each segment of the plant, I compute the value of the growth parameter. The values are then sorted into size classes, and each size class is assigned a letter. The letters are then plotted on the axes used to describe the form of the segment. Where the positions of letters corresponding to different segments coincide, the mean value of the growth parameter is computed, and the letter corresponding to the mean value is plotted. From such a plot, a contour diagram can be drawn by hand, illustrating the general trends of the growth parameter as it varies with the form of the segment.

Figures 37 and 38 illustrate the distribution of leaf area per segment weight, measured as cm^2 / gram. This parameter is computed for each segment, by dividing the area of the leaf by the weight of the entire segment. The parameter is a measure of the efficiency of utilization of the plant's material resources for the production of leaf surface. Figures 39 and 40 illustrate the distribution of the rate of production of leaf area, measured as cm^2 / day. This parameter is computed for each segment by dividing the area of the leaf by the plastochron for that segment. Figures 41 and 42 illustrate the distribution of stem elongation per segment weight, measured as cm / gram. This parameter is computed for each segment by dividing the length of the internode by the weight of the segment. The parameter is a measure of the efficiency of utilization of the plant's material resources for elongation. Figures 43 and 44 illustrate the distribution of the rate of elongation of the stem, measured as mm / day. This parameter is computed for each segment by dividing the length of the internode by the plastochron for that segment.

Each of the four growth parameters finds its maximum value in a different one of the four extreme corners of the distribution of the data in the plane. Not surprisingly, the two parameters measuring leaf surface area find their maxima in the upper region of the plane corresponding to the leafy segments, and the two parameters measuring elongation find their maxima in the lower region of the plane corresponding to stemmy segments. What is more interesting is that the two parameters measuring the efficiency of utilization of material resources find their maxima at the left end of the plane corresponding to small segments, and the two parameters measuring time rates find their maxima at the right end of the plane corresponding to large segments.

The left hand region of the plane is occupied by the terrestrial cycle. In this cycle, the plant always has a small total leaf surface area, and in the primary forest where this study was conducted, always occurs on the shady forest floor where available light levels are relatively low. It is under such circumstances that photosynthate is most likely to be limiting. Thus one might expect that the terrestrial cycle would be under strong selective pressure to assume a form that makes efficient use of its photosynthetic resources. In the arboreal cycle, the plant will accumulate a much larger total leaf surface area, and will occur higher up in the forest where light levels are higher, thus photosynthate levels are not as likely to be limiting. Under such circumstances, selective pressure for efficient utilization of material resources will not be as intense, and the plant can more easily assume less efficient forms, which optimize other parameters. Larger plants naturally produce leaf surface area more rapidly, owing to their larger leaves. However, Figure 45 indicates that the intrinsic rate of increase of leaf surface area shows no strong correaltion with segment size, though there may be a weak trend toward higher values among smaller segments. The data displayed in Figure 45 shows the distribution of the intrinsic rate of increase of leaf surface, measured as cm^2 / day / cm^2. This is the rate of production of leaf surface, per unit of leaf surface. The parameter is computed for each stem on each plant (not each segment), by measuring the amount of new leaf surface added to the stem between two census dates, dividing by the time elapsed between censuses, and dividing by the geometric mean of the total leaf surface on the two dates. Thus while larger plants are able to produce leaf area more rapidly, this does not also involve a higher intrinsic rate of increase of leaf area. It is likely that once released from the constraints imposed by limited photosynthate found in the terrestrial cycle, the plant will delvelop larger segments in order to allow fruit production. Fruit production is only possible when segment sizes are large.

In summary, the examination of the correlation between growth parameters and segment form suggests that the terrestrial cycle is specialized for the efficient utilization of material resources, which are likely to be limiting in small plants on the shady forest floor. In the arboreal cycle, the plant gradually accumulates leaf surface, and so is gradually released from material resource limitations. It is thus better able to assume the large stature required for fruit production.

3. THE ROLE OF SPECIALIZATIONS

In the above discussion, I have considered the possible function of the various forms, and how those forms might be adaptive in the microenvironments in which they occur. I would now like to discuss how the specialization into various forms may provide an adaptive advantage over a single intermediate form. In order to do this, it is necessary to define a measure of fitness with which to compare a growth habit with specialized forms to a growth habit with a single intermediate form. The most commonly used definition of fitness, r, the intrinsic rate of increase, is not easily applicable to this situation, because of the difficulty of counting individuals in an organism that spreads and fragments as does Syngonium. Generally when it is not appropriate to count individuals, it is possible to sum weight instead. In this case it is not appropriate to sum weight, as the weight may be configured is such widely varying manners. A gram of stemmy segments can not easily be equated to a gram of leafy segments.

In clonal organisms, a highly satisfying measure of fitness involves the probability of extinction of the clone. The exact formulation used indicates the rate of change of the probability of extinction of the clone, and gives values for fitness which are numerically equivalent to r in some simple cases. In order to compute the probability of extinction of the clone one must take the product of the probability of death of each individual in the clone. To be able to use this measure of fitness, one must have an intimate knowledge of the demography of the organism. Unfortunately I lack such a knowledge of Syngonium. In fact my data includes only a few records of death. Most of the clones in my study appear to be undergoing true exponential growth. One clone doubled its number of individual ramets every six months, five times in a row. Syngonium does not appear to have a serious biological enemy. The almost complete lack of mortality may be a key to what is actually going on. Although only a few of the individuals in my census have suffered mortality, my study sites have not suffered a direct hit from a substantial tree fall. I have none the less, lost a few individuals to burial under falling debris such as large branches and large palm leaves. I suspect that burial under fallen debris may be the primary cause of death in Syngonium, as it is in seedlings and saplings of Pentaclethra, a common tree at La Selva (Hartshorn, personal communication). This cause of death is patchy in both space and time, and the fastest way for a clone to reduce the probability of extinction from this cause of mortality, is to spread out. This leads to a measure of fitness, the rate of spread of the clone, that is related to a very satisfying definition of fitness, the rate of change of the probability of extinction, and is at the same time practical. It is very easy to actually measure the rate of spread of the clone.

4. THE MYTHICAL BEAST

Now that a workable definition of fitness is at hand, I face the most difficult problem of all. How does one compare the fitness of a particular genotype to the fitness of its supposed ancestor when only the former is at hand for study. An experimental approach would be desirable, but it is not practical. However it is worthwhile to consider what one might do if the technology were available, Figure 46. This figure illustrates an experiment to test the hypothesis that in the terrestrial cycle alternation of forms gives the plant a higher fitness than remaining in one intermediate form. It would be desireable to create the ancestral genotype, and release both it and the extant genotype into the natural habitat in which they evolved, with replicates. One would then observe the spread of the clones for a period of hundreds or thousands of years, to determine not only which is more fit, but why.

With this in mind, it is possible to design a practical alternative experiment to examine the adaptive value of alternation of forms in the terrestrial cycle, Figure 47. The two genotypes can be simulated on the computer to see which spreads the fastest. Table 3 lists the components of the model.

TABLE 3

MODEL COMPONENTS:

Allometries
Growth Equation
Senescence Equations
Lower Limit On Plastochron
Behavioral Properties

The allometries are those discussed in chapter 2, relationships between leaf area and weight, internode lengths, diameters and weights, and trade offs between leaf weights and internode weights. The growth equation is derived from a regression of growth rate in milligrams per day and leaf surface area, for whole plants. The data used in this regression were taken by censusing individual plants in the primary forest repeatedly over a period of two and a half years, as describe in chapter 1. The measurements of the lengths of the organs of the plants allow me to estimate the leaf surface area and weight of the plants at each census date, and the growth rate can be computed by dividing the amount of new weight added by the time elapsed between censuses. The value of r^2 for the regression is .67, and the form of the equation is: $g = 1.108 - 2.573a + 1.386a^2 - .1717a^3$, where "g" is growth rate in log(mg/day) and "a" is log(leaf area).

While the growth equation describes the growth at the distal end of the plant, a set of equations is needed to describe the senescence of the older segments at the proximal end of the plant. The data from which regression equations were derived is displayed in Figures 48 and 49. Figure 48 illustrates decay curves for leaves. The leaves were sampled periodically on plants in the primary forest, and at each census, it was estimated what percentage of the leaf surface area was missing, for each leaf. The data were plotted with various methods of dividing the leaves into classes, in order to determine what factors affect the leaf survivorship. From this analysis, it appeared that the size of the leaf is the most important factor, and that leaves fall primarily into two classes, large and small. Those leaves with an area of less than 1.5 cm^2 generally occur on stemmy segments, and are very short lived. It seems that they are merely produced as an artifact of producing a segment, and are discarded as soon as the segment is formed. Leaves greater than 10 cm^2 generally occur on leafy segments, and generally have a life span of about two years. Leaves between 1.5 and 10 cm^2 are very rare, and have a survivorship intermediate between that of large and small leaves. Petioles are held until the leaf is gone, and are then dropped.

Internodes fall into two survivorship classes, internodes of stemmy segments, and internodes of leafy segments. The internodes of stemmy segments have a lower survivorship. Internodes are considerably longer lived than leaves, and I feel that more data is needed before I will have an accurate assesment of the factors affecting their survivorship.

The next component of the model is a lower limit on the plastochron. This is necessary because there is a finite amount of time needed to produce a segment. From my measurement of over 800 plastochrons, I have chosen to use 9 days as the minimum. While this is not the lowest plastochron that I have recorded, it falls on the low side of the distribution, with only a few data having lower values.

The four components of the model just described will be held constant for both genotypes to be simulated. However, the fifth component, the behavioral properties, are those properties that will be varied in order to make the two genotypes different. I will refer to the two genotypes as cyclic, to describe the plant that alternates between making leafy segments and making stemmy segments, and acyclic to describe the plant that remains in a single intermediate form. Table 4 lists the behavioral properties of the two models.

In order to describe the behavior of the acyclic model, one need

TABLE 4

BEHAVIORAL PROPERTIES

Cyclic Model:	Acyclic Model:
Leafy Form:	1) Segment Weight *
	2) Segment Shape
1) Segment Weight *	
2) Segment Shape	
3) Number of Segments Per Cycle	
Stemmy Form:	
4) Segment Weight	
5) Segment Shape	
6) Number of Segments Per Cycle	

*fixed

only specify the size and shape of the segments produced. For the cyclic model, it is necessary to specify the size and shape of each of the two kinds of segments produced, as well as the number of segments of each type produced during each phase of the cycle. Thus the behavior of the acyclic plant can be described with two variables, and the behavior of the cyclic plant can be described with six variables. However, in order to make the two models comparable, and to restrict the size range of the segments to those sizes characteristic of the terrestrial cycle, I have set an upper limit on the segment size, and have chosen that segment size as the segment weight for the acyclic model, and for the leafy form of the cyclic plant. This leaves only one variable to be set for the acyclic plant, and five to be set for the cyclic plant.

The values of the remaining variables will be set so as to give the resulting growth habit the highest possible rate of elongation. In Figure 50, the growth rate for the acyclic plant is plotted against values of the single variable to be determined, segment shape. It can be seen that there is a very clear optimal value for segment shape, which falls at exactly 60% of the segment weight devoted to the leaf. Thus this is the value that will be used in the model for the acyclic form. A similar process is used for the five variables needed in the cyclic model. A set of initial values were chosen based on the behavior of a plant actually encountered in the field. Each of the five variables was then varied independently, to find its optimal value, and then all five variables were varied again, in the event that their optimal values had changed with resetting of the values of the other four variables.

The hexagons in Figure 51 identify the size and shape of each of the two optimal forms determined by the above process. The circle indicates the size and shape of the segments of the acyclic model. In Figure 52, the shapes of the two forms of the cyclic model are indicated, along with the form of the acyclic model, in order to show how the optimal values predicted by the model compare to the actual distribution of segment shapes found in nature. It can be seen that the two shapes for the cyclic model fall very close to the modal shapes found in nature. The size predicted for the stemmy segments is well within reason. The model indicates the optimal cycle makes 25 leafy segments followed by 30 stemmy segments, which means that 55% of the segments produced would be of the stemmy form. This prediction of the model compares favorably with the actual distribution of segments into the two forms of the terrestrial cycle. Figure 16 of chapter two illustrates the relative number of leafy and stemmy segments actually found in a natural population of plants in the T cycle. It was found that 55% of the segments are of the stemmy form, matching exactly the prediction of the model.

Figure 53 compares the rate of growth of the cyclic and acyclic growth habits, assuming that the two plants grow in a straight line and there is no branching. The upper two lines indicate the distance of the apex from the starting point as a function of time. The lower two lines indicate the length of the most distal fragment of each plant. The upper lines clearly indicate that the cyclic form can elongate faster than the acyclic form. However, the definition of fitness discussed above, was the rate at which the plant can cover area, not the rate at which the apex can move through the forest. Since the plants senesce away at the back end as they grow at the front end, they will only cover the territory they pass through if they establish permanent ramets along the way. Unless such establishment occurs, the plants will only cover an area equal to their length at any point in time. The lengths are indicate by the lower two lines.

The model predicts that the acyclic plant will senesce away at the back end at an even rate, due to the uniform nature of the segments. However, for the cyclic plant, the model predicts that fragmentation of the plant will be induced, because the stemmy segments have a lower survivorship, and so will senesce away before all of the leafy segments in the proximal rosette have senesced. When such fragmentation occurs, the proximal portion of the plant always releases an axillary branch in order to replace the active apical meristem that is now a part of the distal fragment. When an axillary branch is released in a rosette, it will initially produce leafy segments, and effectively renew the old rosette, before producing more stemmy segments. Thus the cyclic growth habit induces fragmentation of the stem, branching, and establishment of rosettes along the path that the plant takes through the forest, because of the nonuniform rate of senescence of stemmy and leafy segments. By the definition of fitness discussed above, the model predicts that the cyclic form is more fit than the acyclic form. Observations of plants in the field indicate that once formed, rosettes remain in place long after the connecting stemmy segments have senesced, thus confirming the predictions of the model. Because the acyclic plant is only mythical, one cannot be sure that the model accurately predicts its pattern of branching and establishment. Fortunately, the genus Monstera has a terrestrial phase comparable to the terrestrial cycle of Syngonium in which the form does not cycle, but rather remains in an intermediate form. Thus it should be possible in the future to study the behavior of this form to determine how the model might be adjusted to more accurately reflect reality.

The objective of carrying out such an analysis is presumably to be able to say that a certain trait evolved as a result of certain selective pressures. In this case it would be desirable to be able to say that the cyclic growth habit evolved from the acyclic growth habit as a result of selection for high rates of spread of clones. The analysis that I have presented does not allow me to make such a statement. I have not yet presented any evidence to suggest that the acyclic habit is the ancestral form, and the cyclic habit the derived form.

It does not make sense to explain why one form evolved from another unless it is known that such evolution did in fact take place. As mentioned above, the genus *Monstera*, also in the family Araceae, has the acyclic growth habit. Furthermore, the genus *Monstera* represents a relatively primitive state for the family, while the genus *Syngonium* represents a relatively derived state for the family, supporting the hypothesis that the cyclic state may have evolved from the acyclic state. However the family Araceae has not been fully characterized as to the details of the range of growth habits represented by the 110 genera and eight subfamilies into which the family has been classified. Until such a study has been conducted it will not be possible to make confident statements about the evolution of growth habits within the family.

CHAPTER FIVE

SUMMARY

The herbaceous tropical vine Syngonium triphyllum is generally unbranched. It grows at the anterior end and eventually senesces away at the posterior end. This growth habit causes the plant to become displaced great distances in the forest, and to encounter a variety of microhabitats. In order to always be adapted to the immediate environment, the new growth on the stem changes form when the stem moves from one microhabitat to another.

The plant is composed of a series of "segments" placed end on end. A segment consists of an internode and the leaf at its anterior end. An allometry exists between the diameter of the internode and the weight of the segment. Beyond this constraint, the weight of the segment may be partitioned in virtually any manner between the parts. This results in a trade-off between internode length and leaf size, such that a segment cannot simultaneously have a long internode and a large leaf.

The trade-off between leaf size and internode length brings into conflict the efficient achievement of two functions of the plant: vegetative dispersal which requires long internodes, and photosynthesis which requires large leaves. As a result, the plant has evolved a growth habit involving a division of labor between adjacent groups of segments. Series of photosynthetic (leafy) segments alternate with series of vegetative dispersal (stemmy) segments in a cyclic fashion.

The overall growth habit involves two such cycles. In one cycle,

cycle T, small terrestrial stems alternate rapidly between producing rosettes of leaves, and producing elongating stolons which orient skototropically toward trees. In this cycle, the plant sustains itself with a minimum of leaf production while growing toward trees as rapidly as possible, and the segments remain small (measured as weight or internode diameter). In the other cycle, cycle A, a plant on a tree will climb the tree and remain indefinetly in the leafy form, as it gradually thickens successive internodes, thereby producing successively larger segments. When the segments have reached the maximum size, the plant will begin to fruit, and will fruit repeatedly. Only upon losing contact with the tree (as by outgrowing it) will such a stem switch to the stemmy phase of the cycle. The stem will now elongate rapidly while producing greatly reduced leaves. These elongating stems grow down to and across the ground. They remain in the stemmy form until they encounter another tree to climb, but they do not orient toward trees. Thus in cycle T, the switching between stemmy and leafy forms is automatic and frequent, while in cycle A, switching between the forms occurs only with the gain or loss of contact with trees, and so is very infrequent.

A detailed analysis of the geometry indicates that the form of the segment can be fully characterized by just two independent variables. For this analysis, the two variables chosen to represent the form are segment weight, and leaf weight as percent of segment weight. These two variables can be described as size and shape respectively.

The two variables provide the basis for a set of axes to quantify the form of the segment. A single point in the plane defined by the axes represents the form of a single segment. The form of an entire plant can be represented by a series of points connected by lines, indicating the forms of successive segments along the stem.

If segments are classified as terrestrial, arboreal, or aerial, it can be shown that the three kinds of segments have very distinctive distributions in the plane. This suggests that the microenvironment in which a segment occurs, plays an important role in determining its form. However, this simplistic analysis leaves considerable variation unexplained.

A closer analysis indicates that the entire life cycle of the plant is composed of four distinctive developmental pathways. Within each of these pathways, the form of the segments usually goes through a characteristic series of changes. A set of hypotheses are proposed to explain the changes of form. It is hypothesized that the size of segments is regulated largely by the level of photosynthate available at the apex, with high levels causing large segments. The segment size corresponding to a particular level of photosynthate varies depending on the pathway. Changes of shape are triggered by two factors, either gain or loss of contact with tree, or threshold photosynthate levels, depending on the pathway involved.

The overall growth habit is viewed as a collection of developmental pathways. The pathways represent the tactical responses of the plant to environmental factors. Environmental influences cause switching between pathways, and affect the rate and direction of progress along a given pathway (particularly light levels).

An analysis of the relationship between the form of the plant and five growth parameters makes possible an exploration of the functional significance of the specializations of form. The analysis suggests that the terrestrial cycle is specialized for the efficient utilization of material resources, which are likely to be limiting in small plants on the shady forest floor. It is suggested that through the accumulation of leaf surface, the arboreal cycle is gradually released from material resource limitations, and is better able to assume the large stature required for fruit production.

In order to facilitate an exploration of the adaptive significance of the specialization of forms, a practical definiton of fitness is chosen: the rate of spread of the clone. This is viewed as being the most important factor in reducing the probability of extinction of the clone, given that the primary cause of mortality appears to be burial under falling debris.

In order to test experimentally the hypothesis that alternation of forms in the terrestrial cycle provides a selective advantage over remaining in an intermediate form, it would be desireable to create the later genotype, release the two genotypes into their natural habitat with replicates, and observe their relative growth rates over hundreds or thousands of years.

A feasible alternative to this approach is to simulate the cyclic and acyclic genotypes on the computer. A computer model comparing the two forms indicates that the cyclic form is able to elongate faster than the acyclic form. Furthermore, the model predicts that differential senescence rates of leafy and stemmy segments induces fragmentation, branching, and establishment of rosettes along the path taken by the cyclic form, whereas the acyclic form should simply senesce away at the back end as it advances. The result is that the cyclic habit not only moves faster than the acyclic habit, but is better able to cover area by establishment along the way.

Although the analysis suggests that the cyclic habit is more fit than the acyclic habit because it covers area faster, it does not make it possible to state that the cyclic habit evolved for this reason. In order to better understand the evolution of growth habit in Syngonium, it will be necessary to survey the range in growth habits throughout the family Araceae, in order to understand how it has changed with the evolution of the family.

BIBLIOGRAPHY

Allsopp, A. 1976. Heteroblastic development in vascular plants. Advances in Morphogenesis 6:127-71.

Arber, A. 1919. On heterophylly in water plants. Am. Naturalist 53:272-78.

Bostrack, J. M., and W. F. Millington. 1962. On the determination of leaf form in an aquatic heterophyllous species of Ranunculus. Bull. Torrey Botan. Club 89:1-20.

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. Advances Genet. 13:115-155.

Cook, C. D. K. 1969. On the determination of leaf form in Ranunculus aquatilis. New Phytol. 68:469-80.

Cook, S. A. and M. P. Johnson. 1968. Adaptation to heterogenous environments. I. Variation in heterophylly in Ranunculus flammula L. Evolution 22:496-516.

Darwin, C. 1865. On The Movements And Habits Of Climbing Plants. The Linnean Society of London.

Darwin, C. 1881. The Power of Movement in Plants. Da Capo Press, New York, 1966.

Epling, C. and H. Lewis. 1952. Increase of the adaptive range of the genus Delphinium. Evolution 6:253-67.

Evans, L. T. 1980. The natural history of crop yield. American Scientist 68:388-97.

Franck, D. H. 1976. Comparative morphological and early leaf histogenesis of adult and juvenile leaves of Darlingtonia Californica and their bearing on the concept of heterophylly. Bot. Gaz. 137(1):20-34.

Gould, S. J. and R. C. Lewontin. 1979. The spandrels of San Marcos and the Panglossian paradigm: a critique of the adaptationist programme. Proceedings of the Royal Society of London B 205:581-98.

Greyson, R. I. and V. K. Sawhney. 1972. Initiation and early growth of flower organs of Nigella and Lycopersicon: Insights form allometry. Bot. Gaz. 133(2):184-90.

Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi. 1971. Forest Environments in Tropical Life Zones: a Pilot Study. Pergamon Press, N.Y.

Kaplan, D. R. 1970. Comparative foliar histogenesis in Acorus calamus and its bearing in the phyllode theory of monocotyledonous leaves. Amer. J. Bot. 57:331-61.

Kaplan, D. R. 1973. Comparative developmental analysis of the heteroblastic leaf series of axillary shoots of Acorus calamus L. (Araceae). La Cellule 69:251-90.

Njoku, E. 1956. Studies in the morphogenesis of leaves. XI. The effect of light intensity on leaf shape in Ipomea caerulea. New Phytologist 55:91-110.

Rogler, C. E. and P. H. Wesley. 1975. Phase change in Hedera helix: Induction of the mature to juvenile phase change by gibberellin A3. Physiologia Plantarum 34:141-47.

Stein, O. L. and E. B. Fosket. 1969. Comparative developmental anatomy of shoots of juvenile and adult Hedera helix. Amer. J. Bot. 56(5):546-51.

Strong, D. R. and T. S. Ray. 1975. Host tree location behavior of a tropical vine (Monstera gigantea) by skototropism. Science 190:804-06.

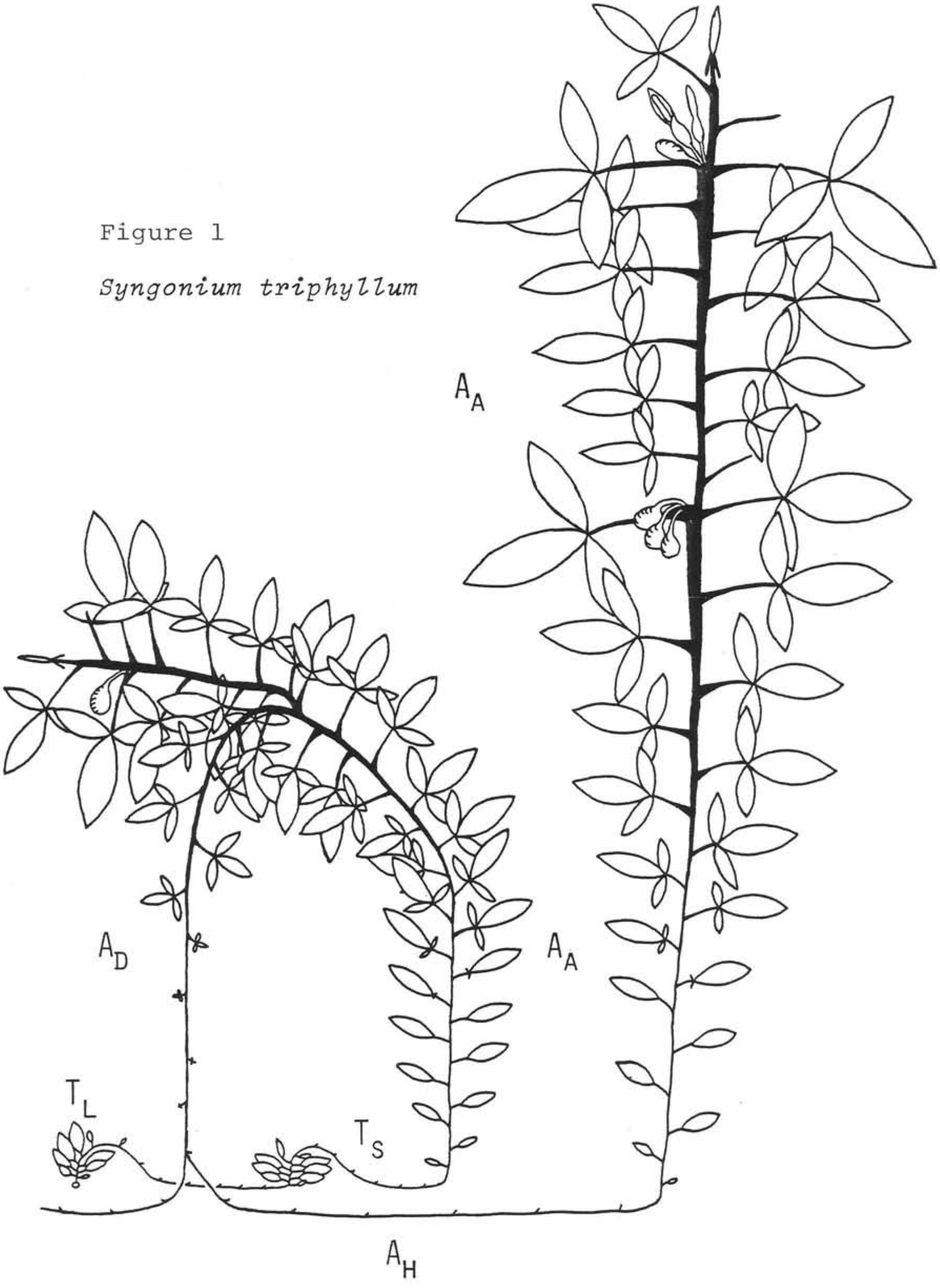
Tosi, J. A. 1969. Mapa ecologia de Costa Rica. Tropical Science Center, San Jose, Costa Rica.

Webster, B. D. and T. A. Steeves. 1958. Morphogenesis in Pteridium aquilinum. General morphology and growth habit. Phytomorphology 8 30-39.

White, J. 1979. The plant as a metapopulation. Ann. Rev. Ecol. Syst. 10:109-45.

Figure 1

Syngonium triphyllum



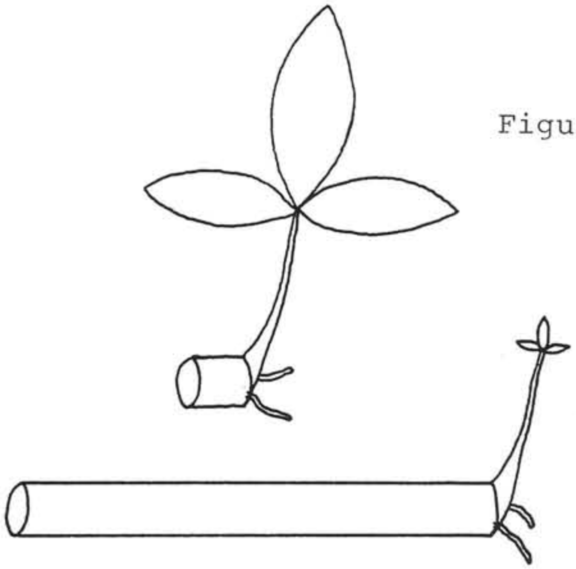


Figure 2

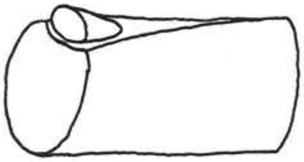


Figure 3

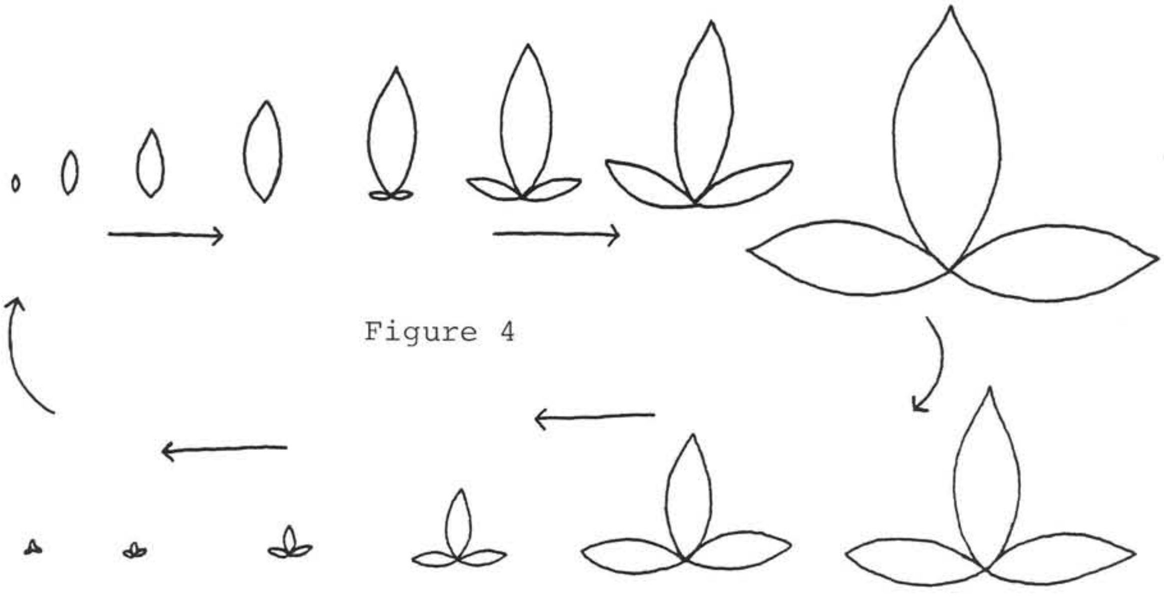


Figure 4

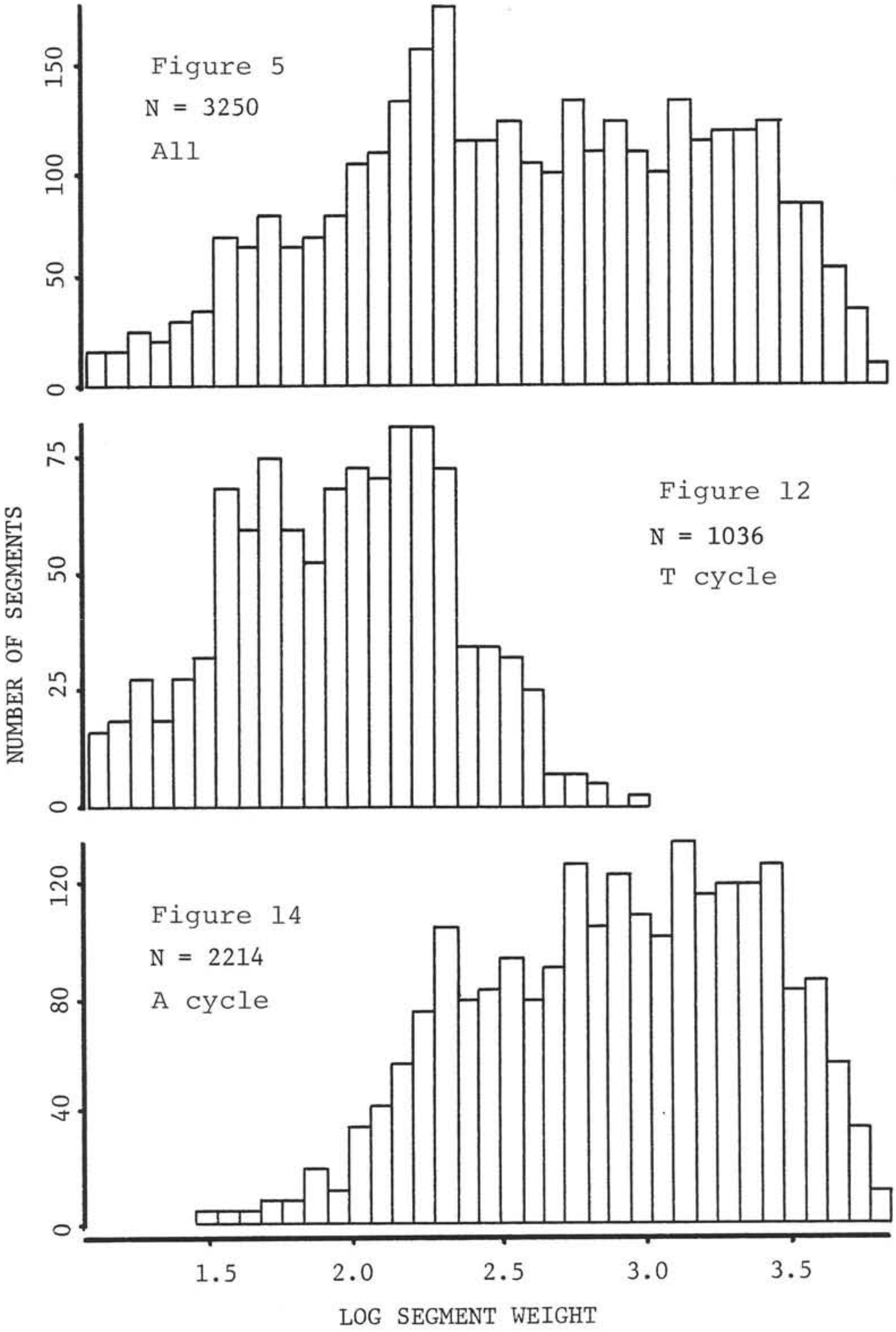


Figure 5
N = 3250
All
150
100
50
0
Figure 12
N = 1036
T cycle
75
50
25
0
NUMBER OF SEGMENTS
Figure 14
N = 2214
A cycle
120
80
40
0
1.5
2.0
2.5
3.0
3.5
LOG SEGMENT WEIGHT

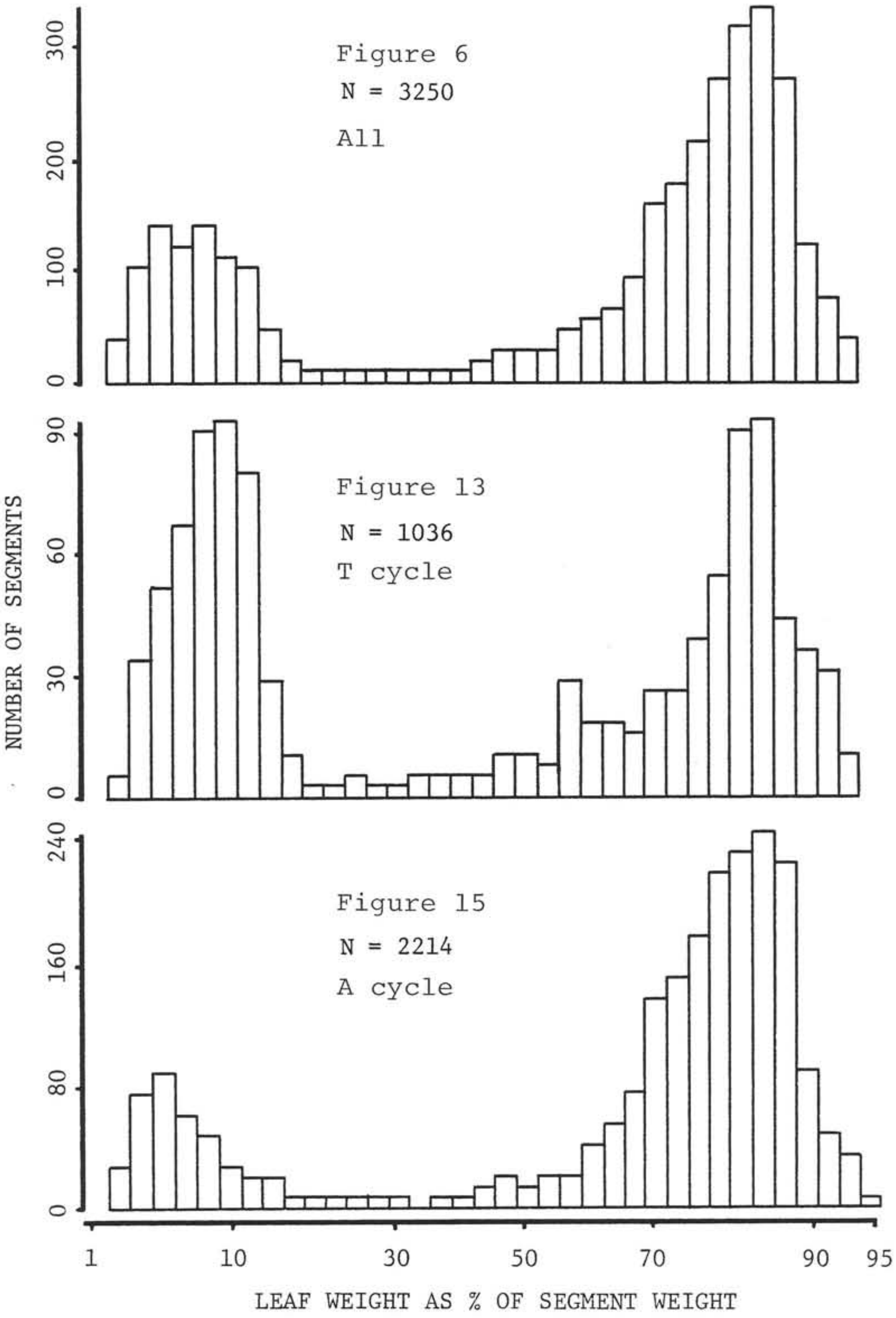


Figure 6
N = 3250
All

Figure 13
N = 1036
T cycle

Figure 15
N = 2214
A cycle

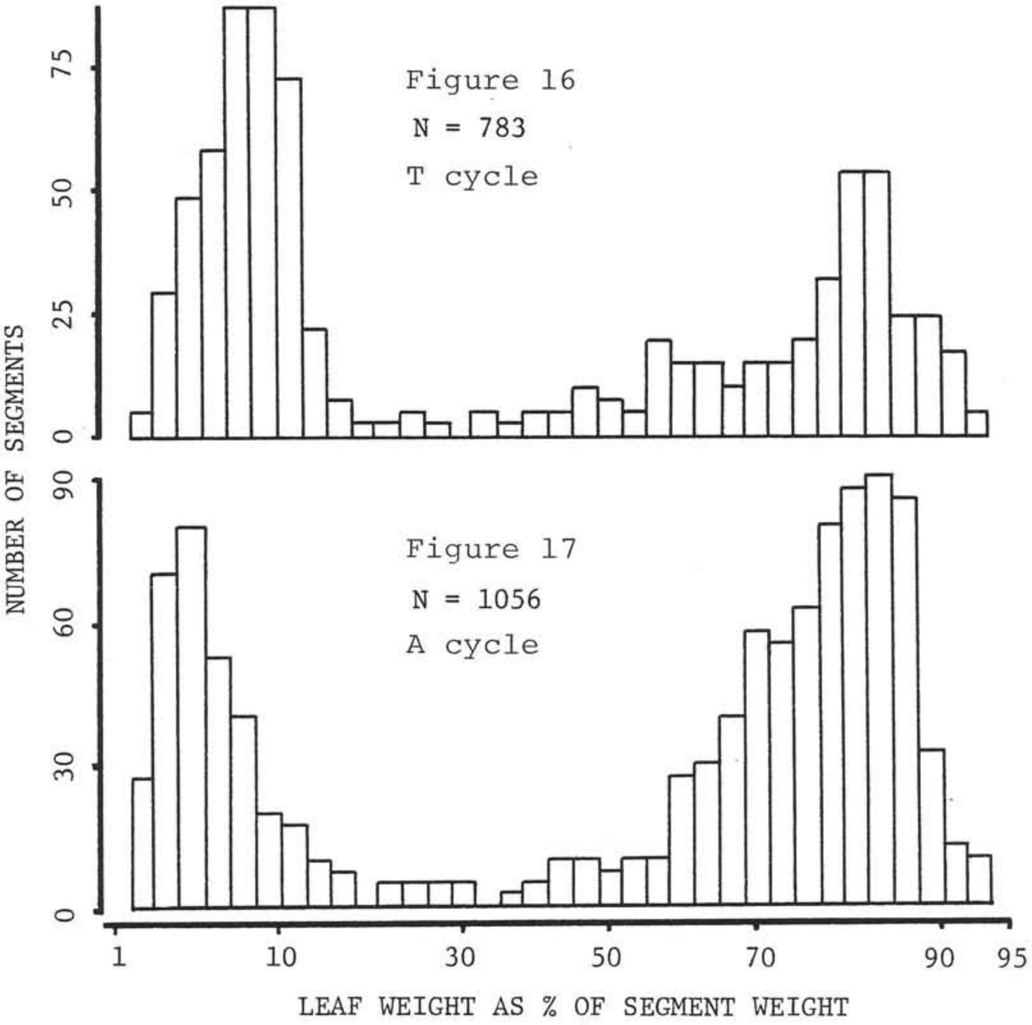


Figure 16

N = 783

T cycle

Figure 17

N = 1056

A cycle

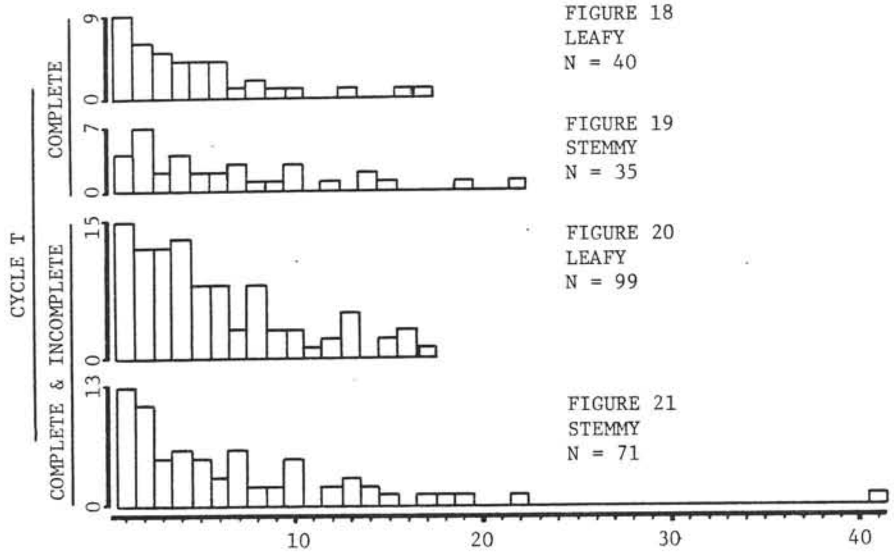


FIGURE 18
LEAFY
N = 40

FIGURE 19
STEMMY
N = 35

FIGURE 20
LEAFY
N = 99

FIGURE 21
STEMMY
N = 71

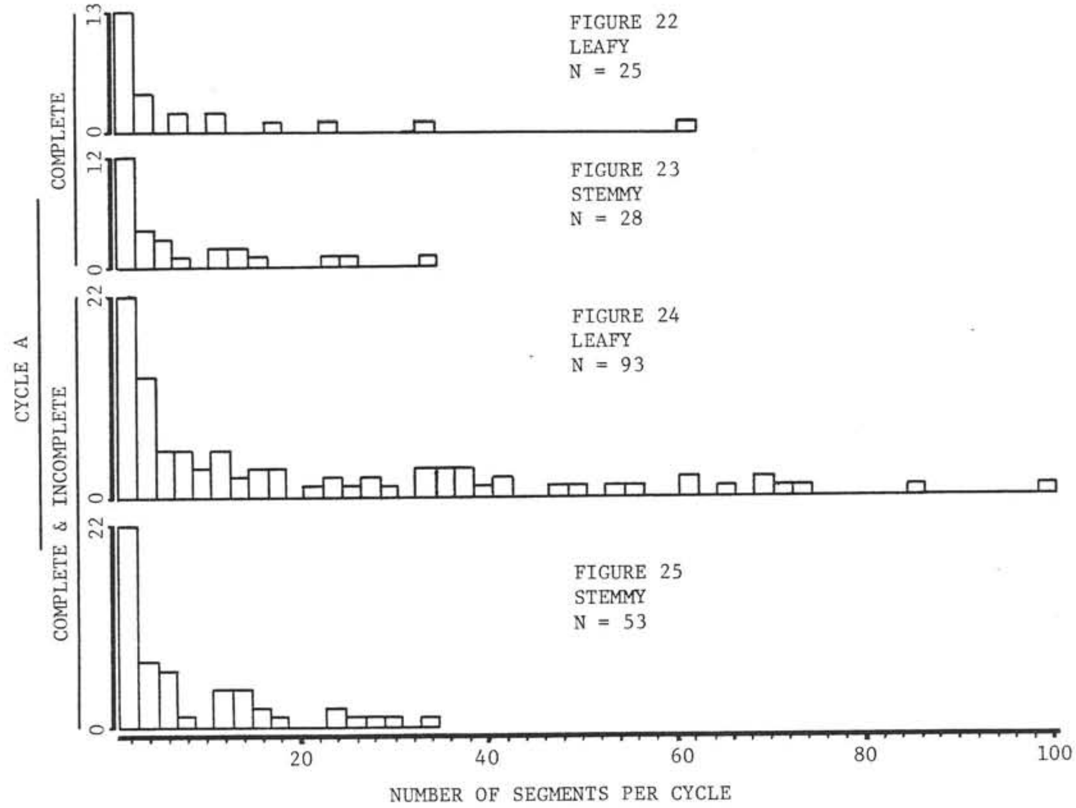


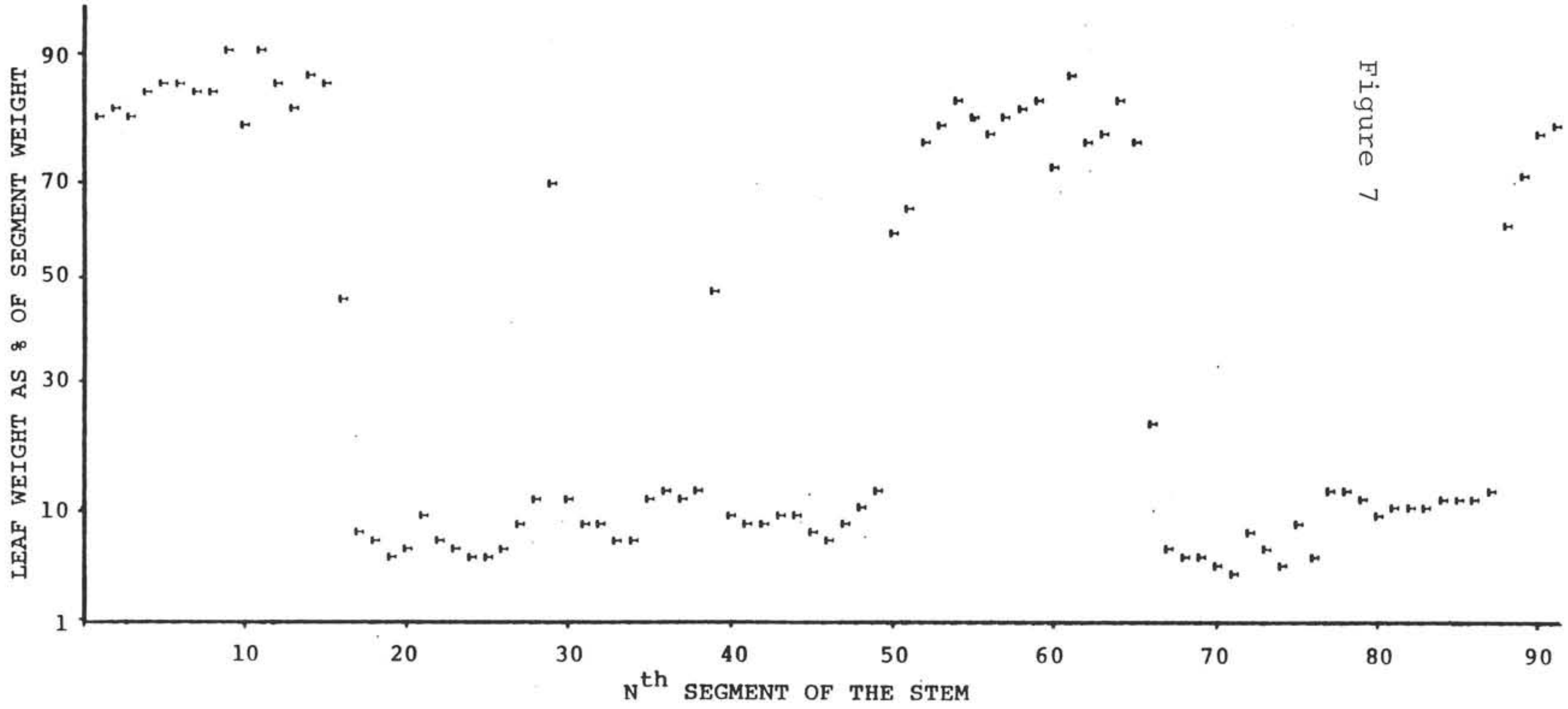
FIGURE 22
LEAFY
N = 25

FIGURE 23
STEMMY
N = 28

FIGURE 24
LEAFY
N = 93

FIGURE 25
STEMMY
N = 53

Figure 7


LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
70
50
30
10
1
10
20
30
40
50
60
70
80
90
N^th SEGMENT OF THE STEM

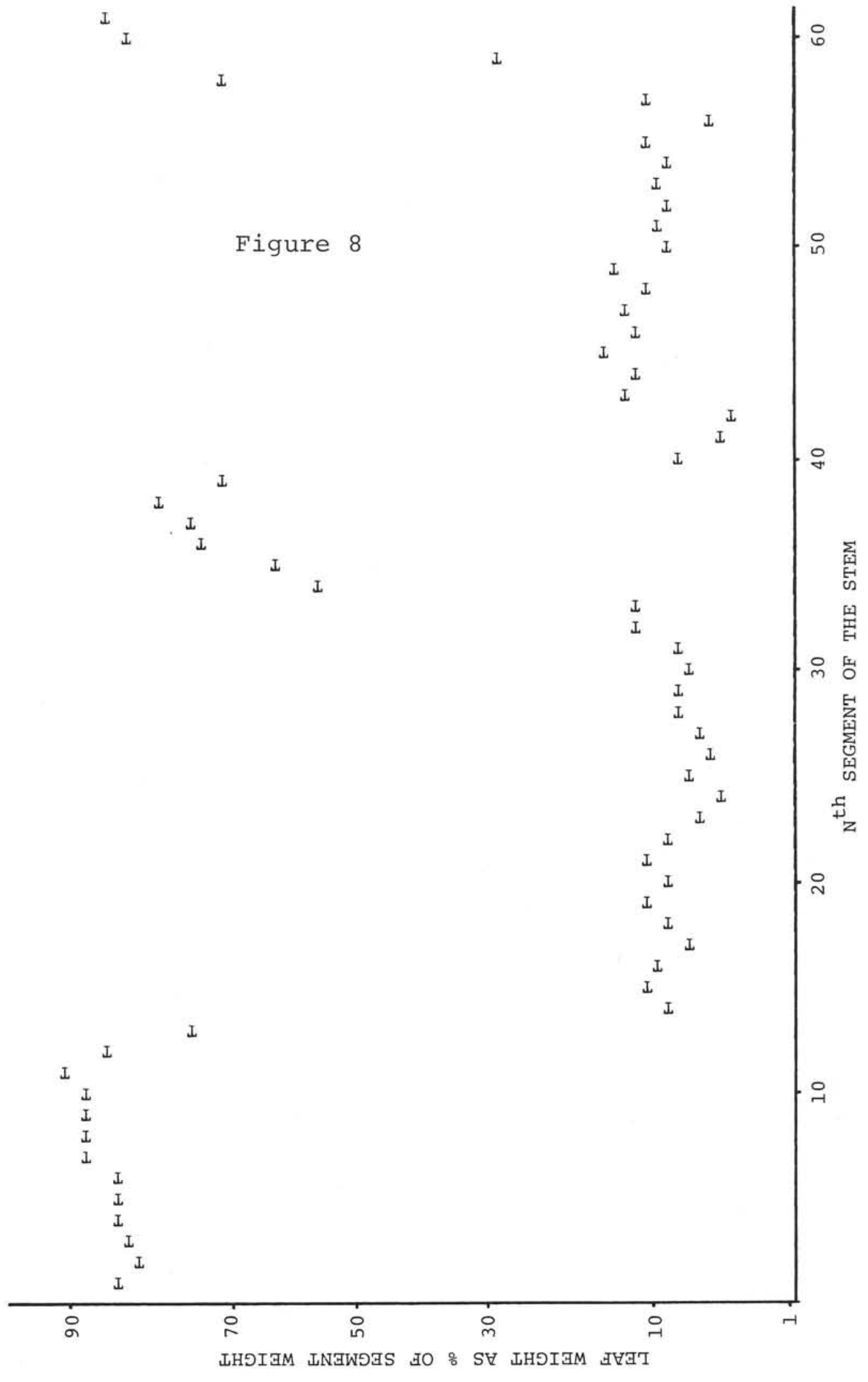

LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
70
50
30
10
1
N^th SEGMENT OF THE STEM
10
20
30
40
50
60

Figure 8

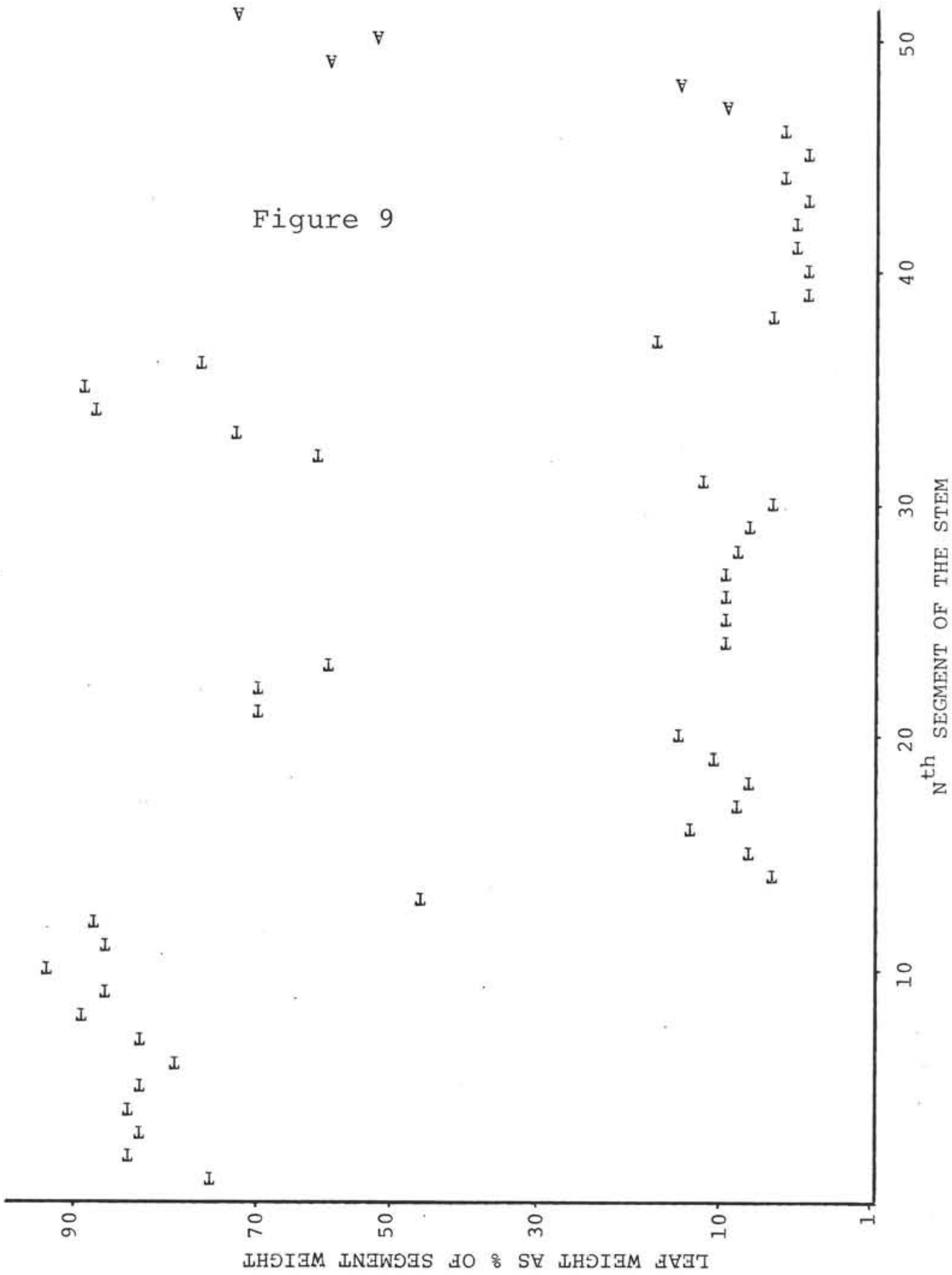
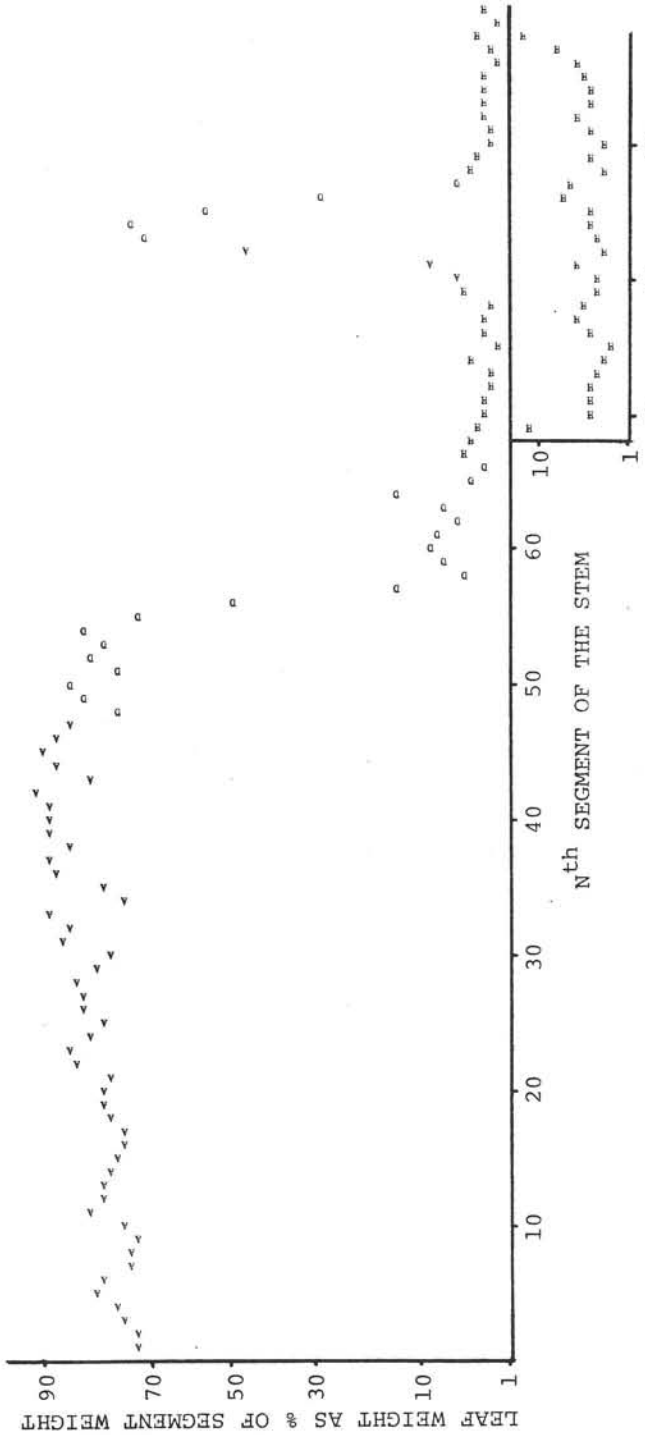

LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
70
50
30
10
1
N th SEGMENT OF THE STEM
10
20
30
40
50

Figure 9

Figure 10


LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
70
50
30
10
1
Nth SEGMENT OF THE STEM
10
20
30
40
50
60
70
80
90
10
1

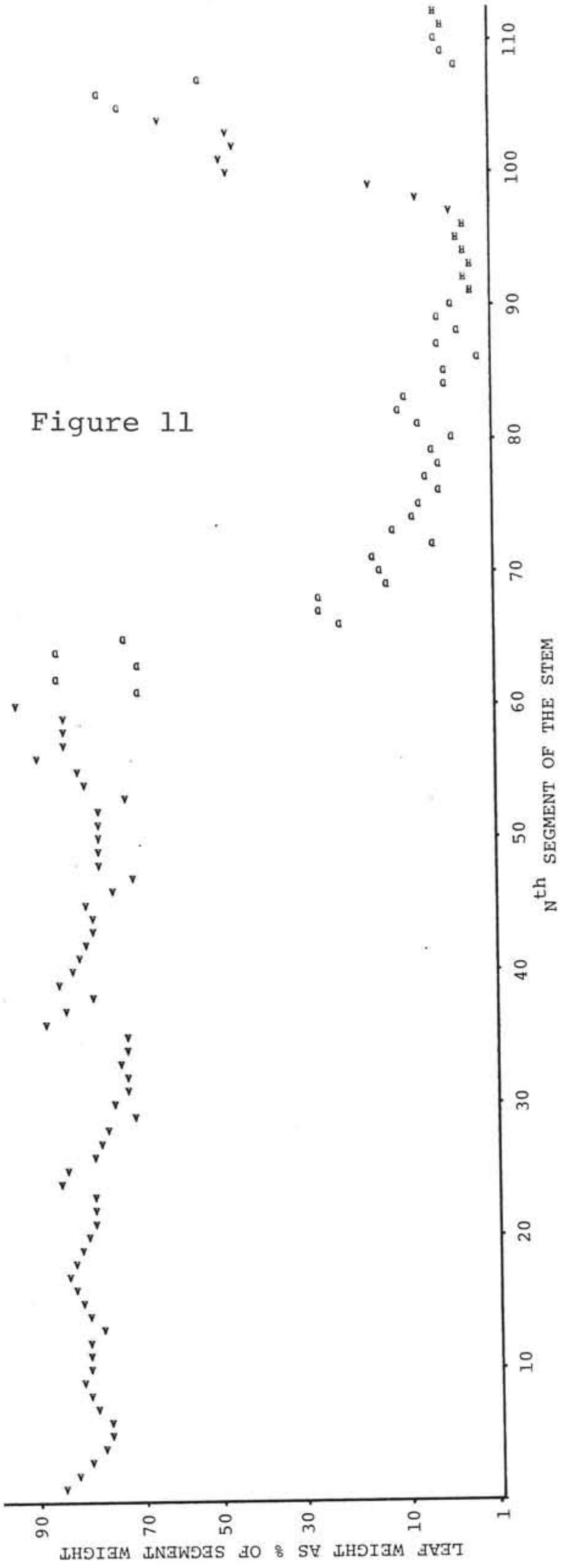

LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
70
50
30
10
1
N^{th} SEGMENT OF THE STEM
10
20
30
40
50
60
70
80
90
100
110

Figure 11

Figure 26

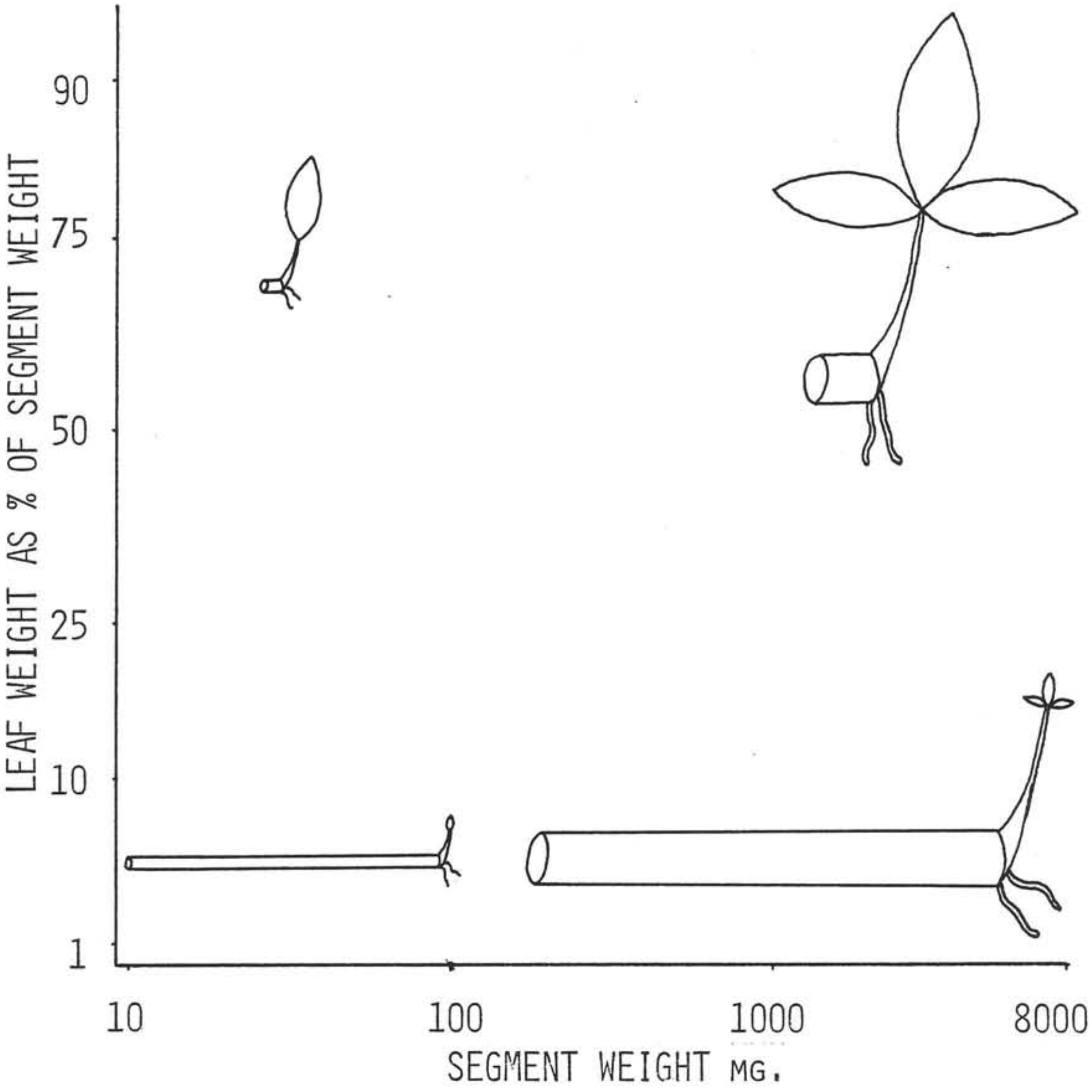

LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 27

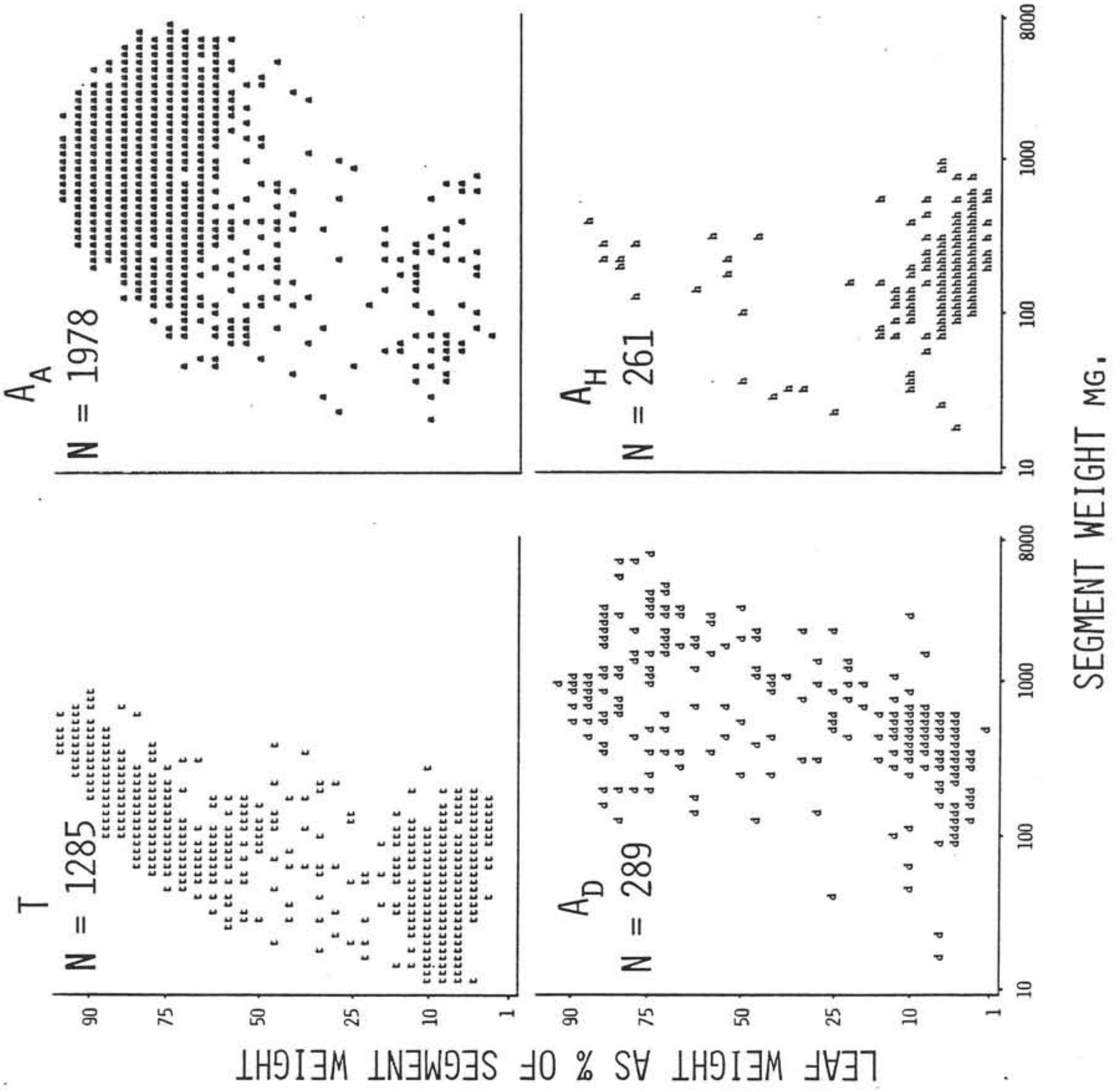

T
N = 1285
A_A
N = 1978
A_D
N = 289
A_H
N = 261
LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
SEGMENT WEIGHT MG.
10
100
1000
8000

Figure 28

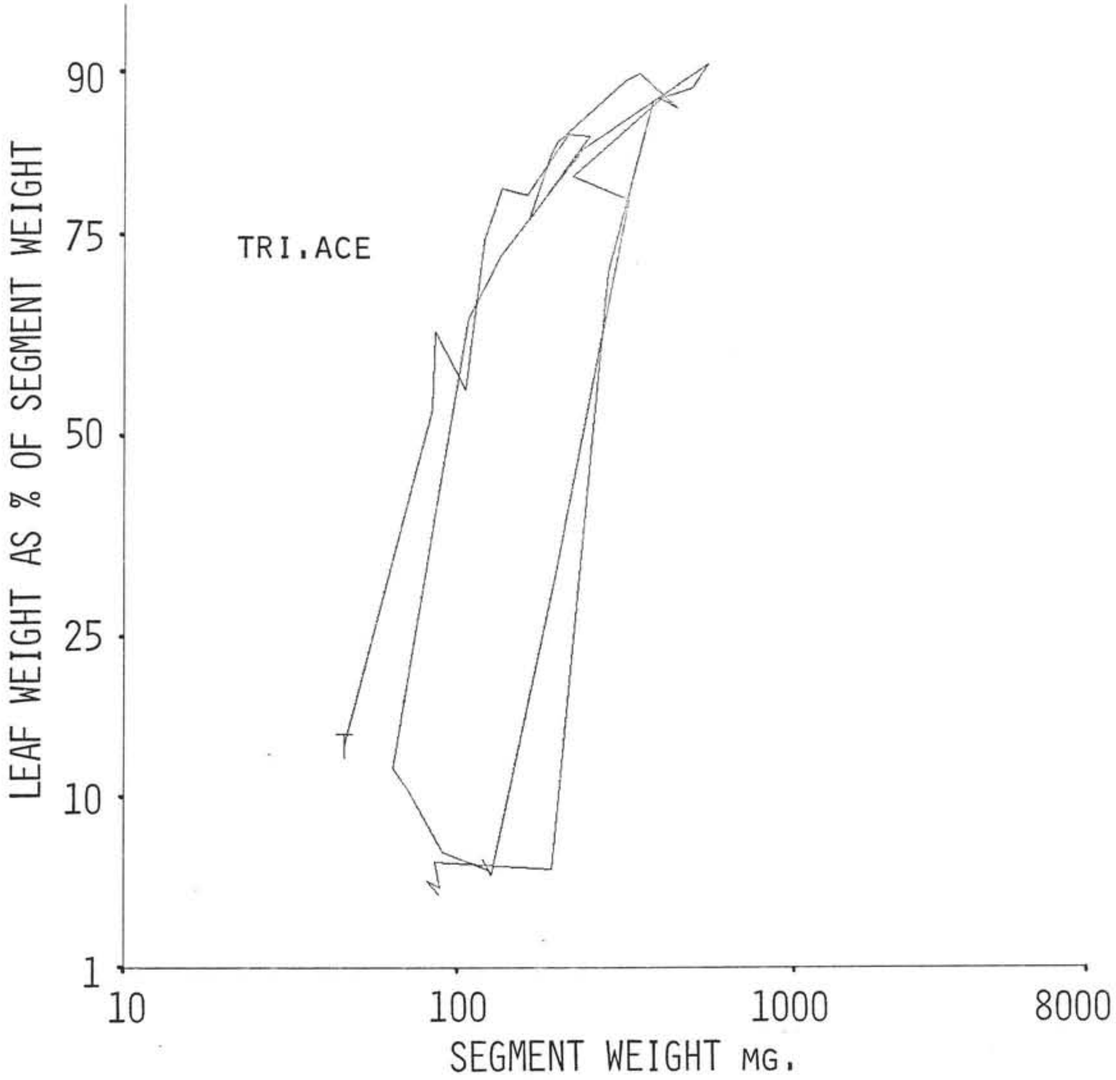

90
75
50
25
10
1
LEAF WEIGHT AS % OF SEGMENT WEIGHT
TRI.ACE
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 29

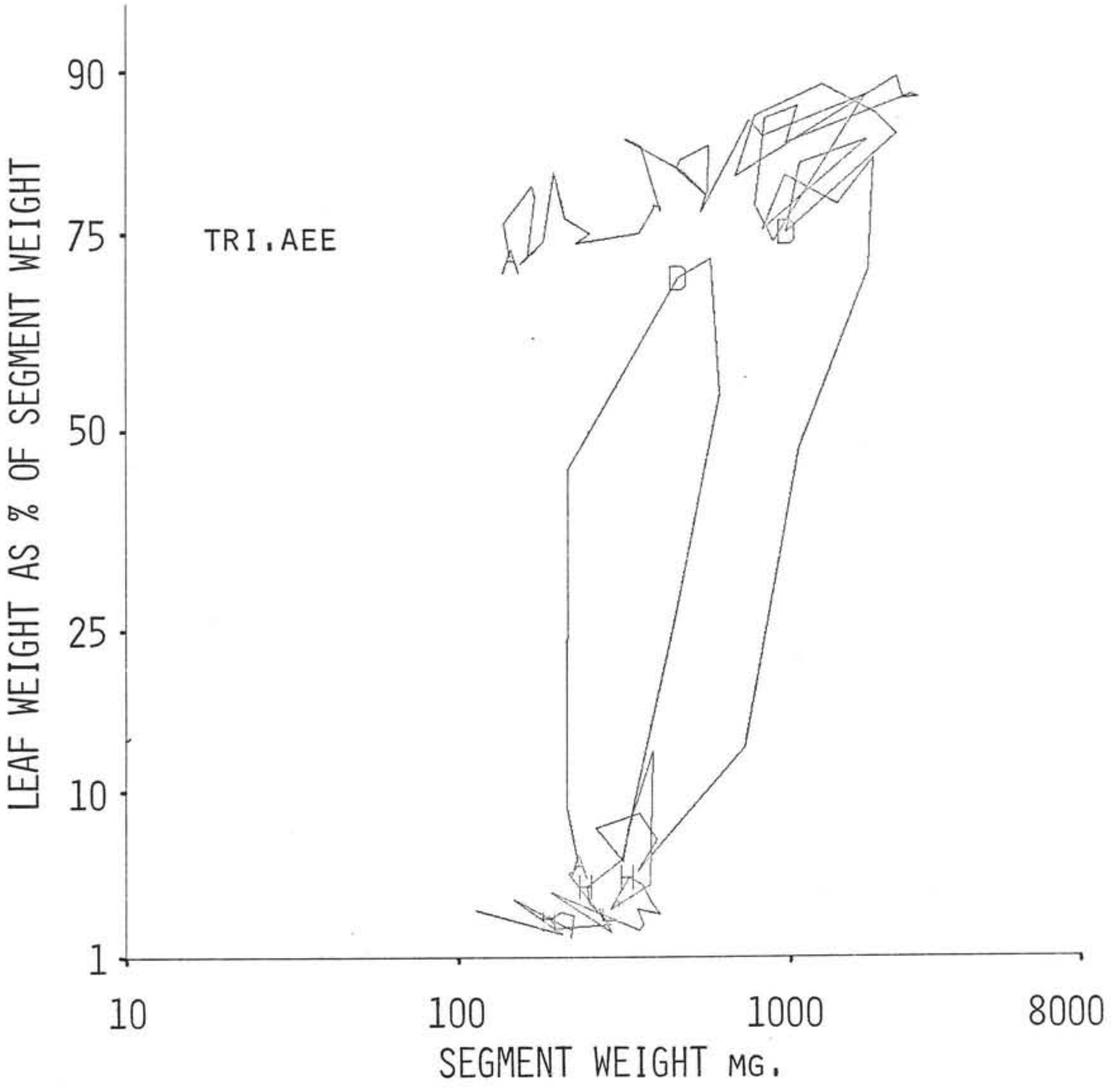

90
75
50
25
10
1
TRI.AEE
A
D
D
H
H
10
100
1000
8000
LEAF WEIGHT AS % OF SEGMENT WEIGHT
SEGMENT WEIGHT MG.

Figure 30

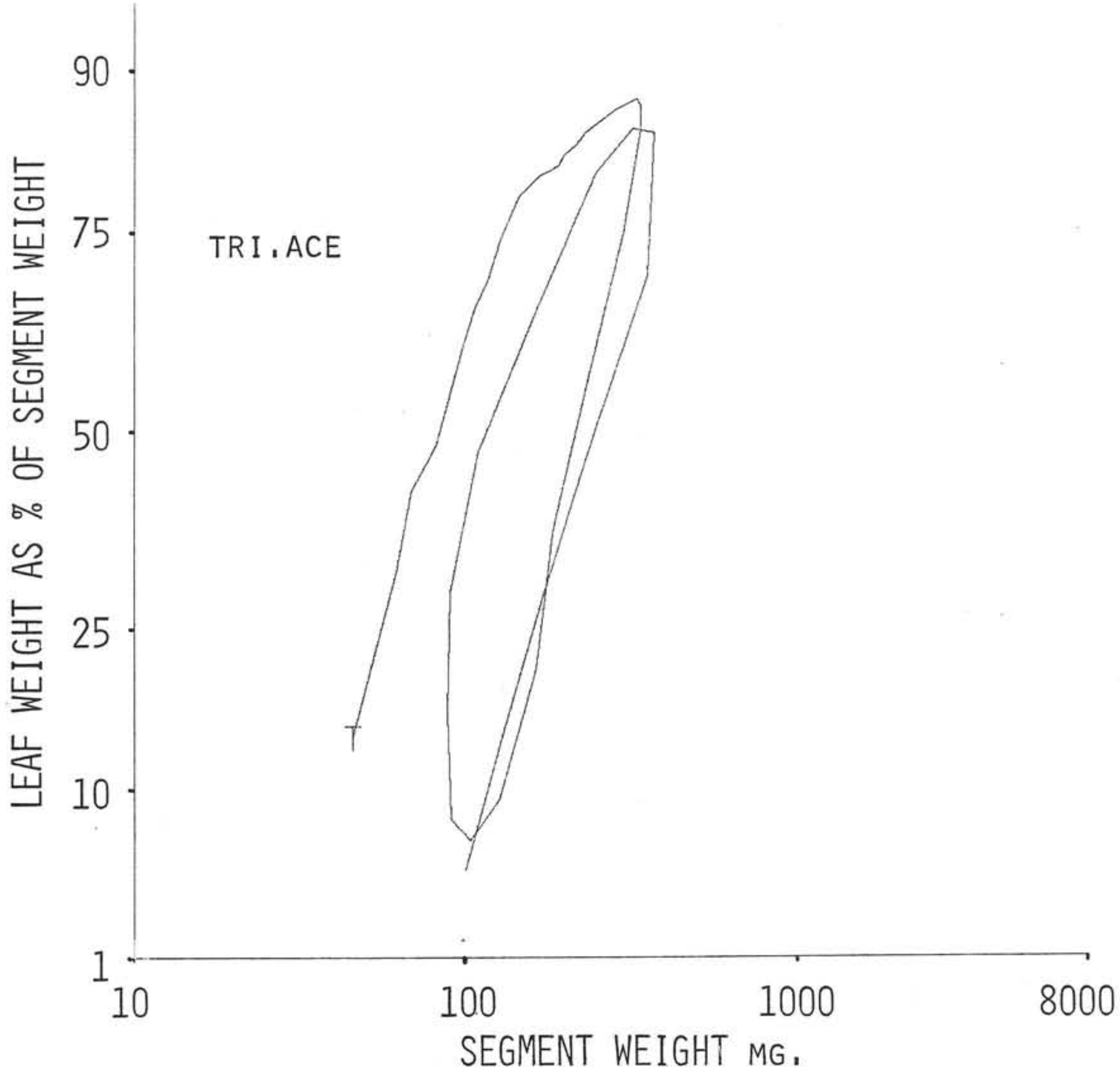
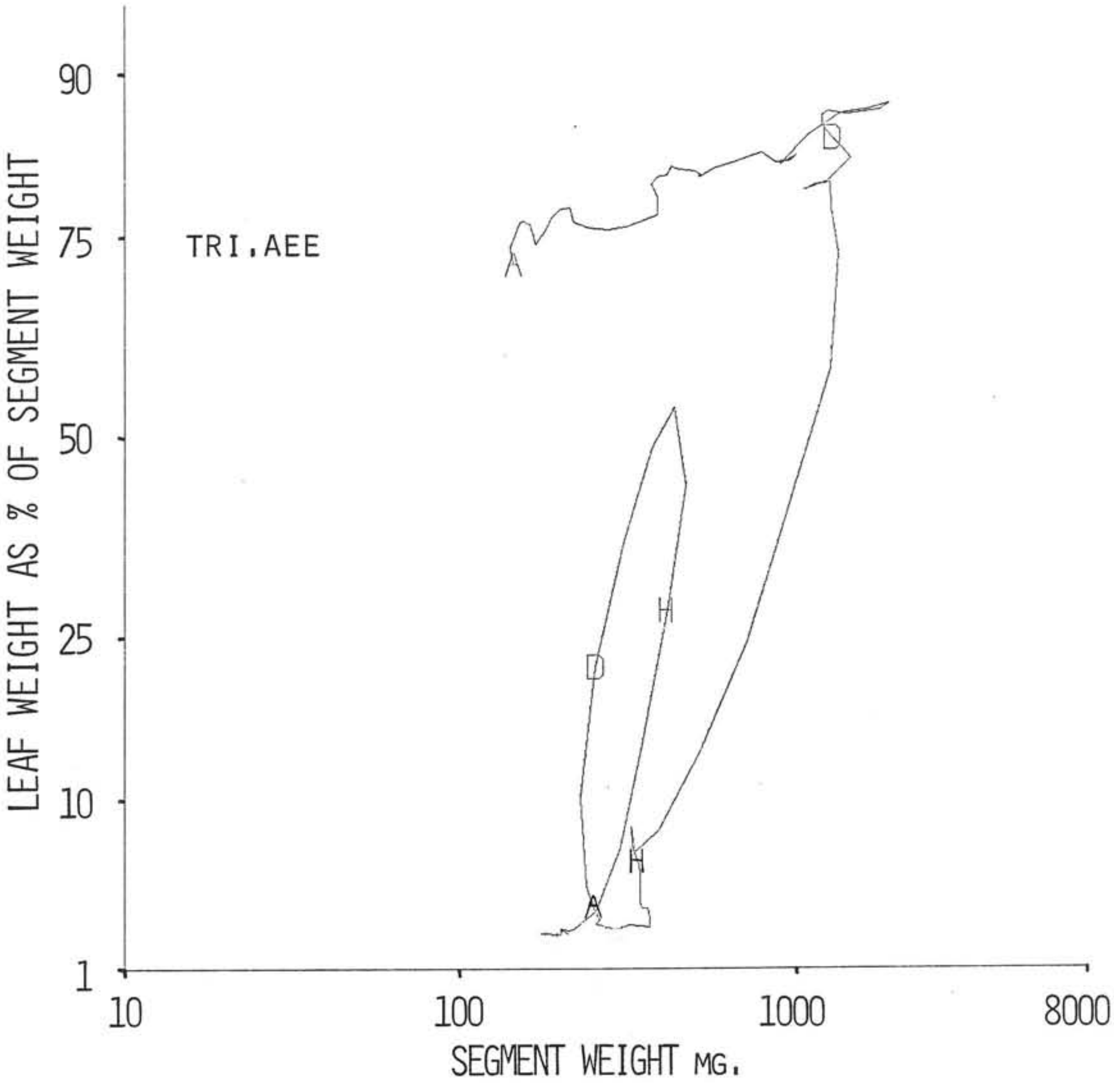

LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
TRI.ACE
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 31



LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
TRI.AEE
A
D
H
A
D
H
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 32

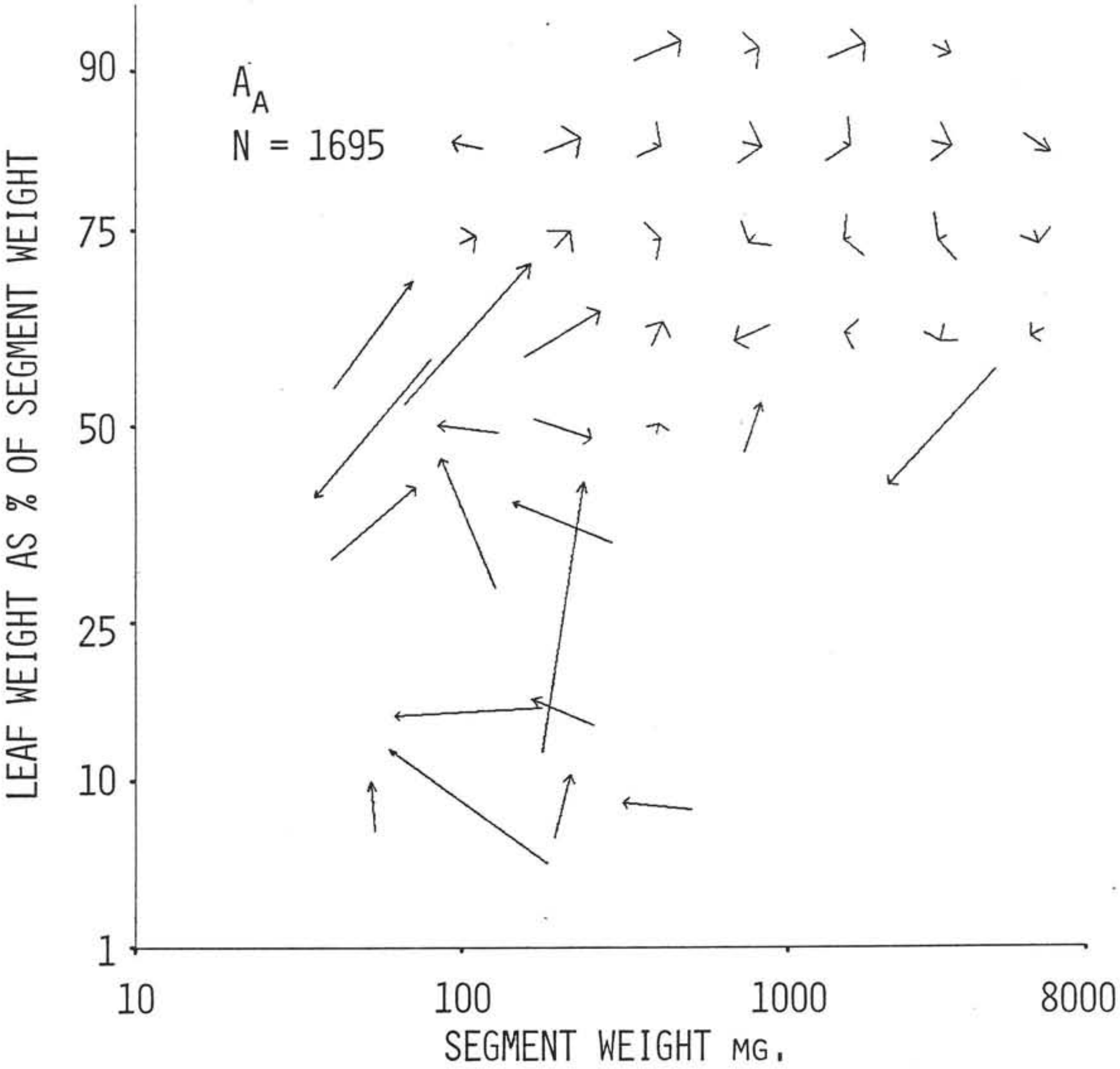

A_A
N = 1695
90
75
50
25
10
1
10
100
1000
8000
LEAF WEIGHT AS % OF SEGMENT WEIGHT
SEGMENT WEIGHT MG.

Figure 33

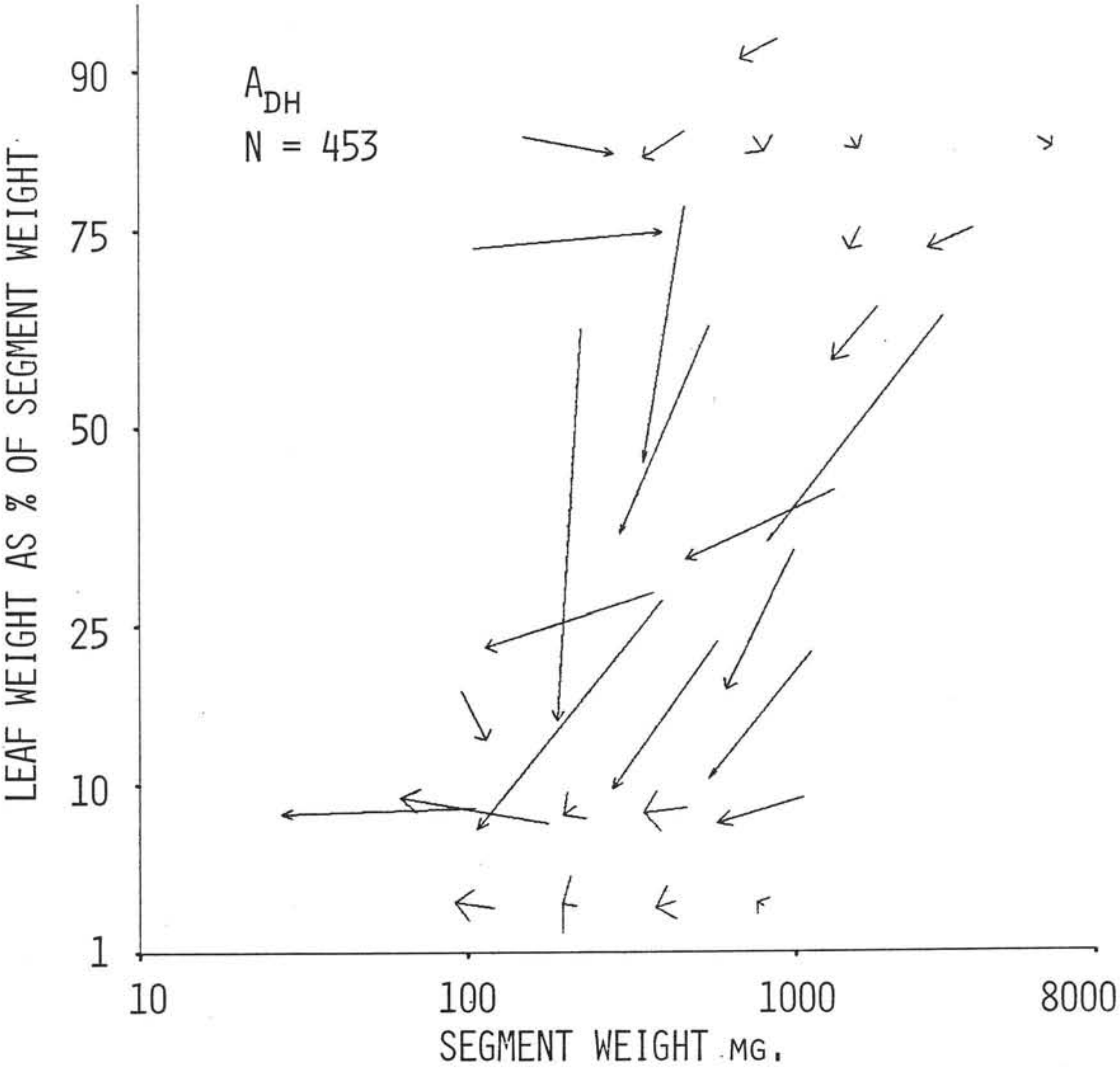

A_{DH}
N = 453
LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 34

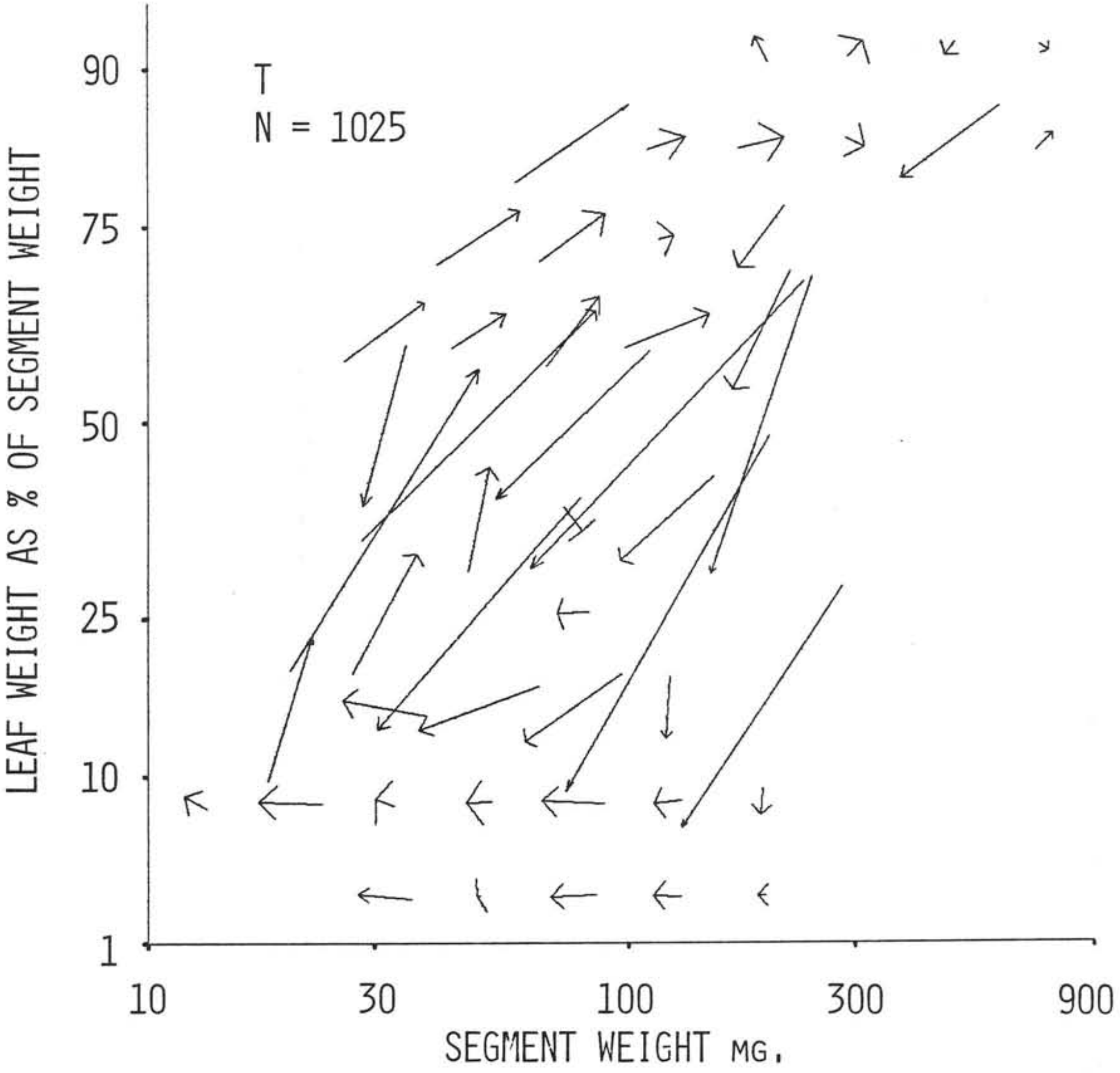

T
N = 1025
LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
30
100
300
900
SEGMENT WEIGHT MG.

Figure 35

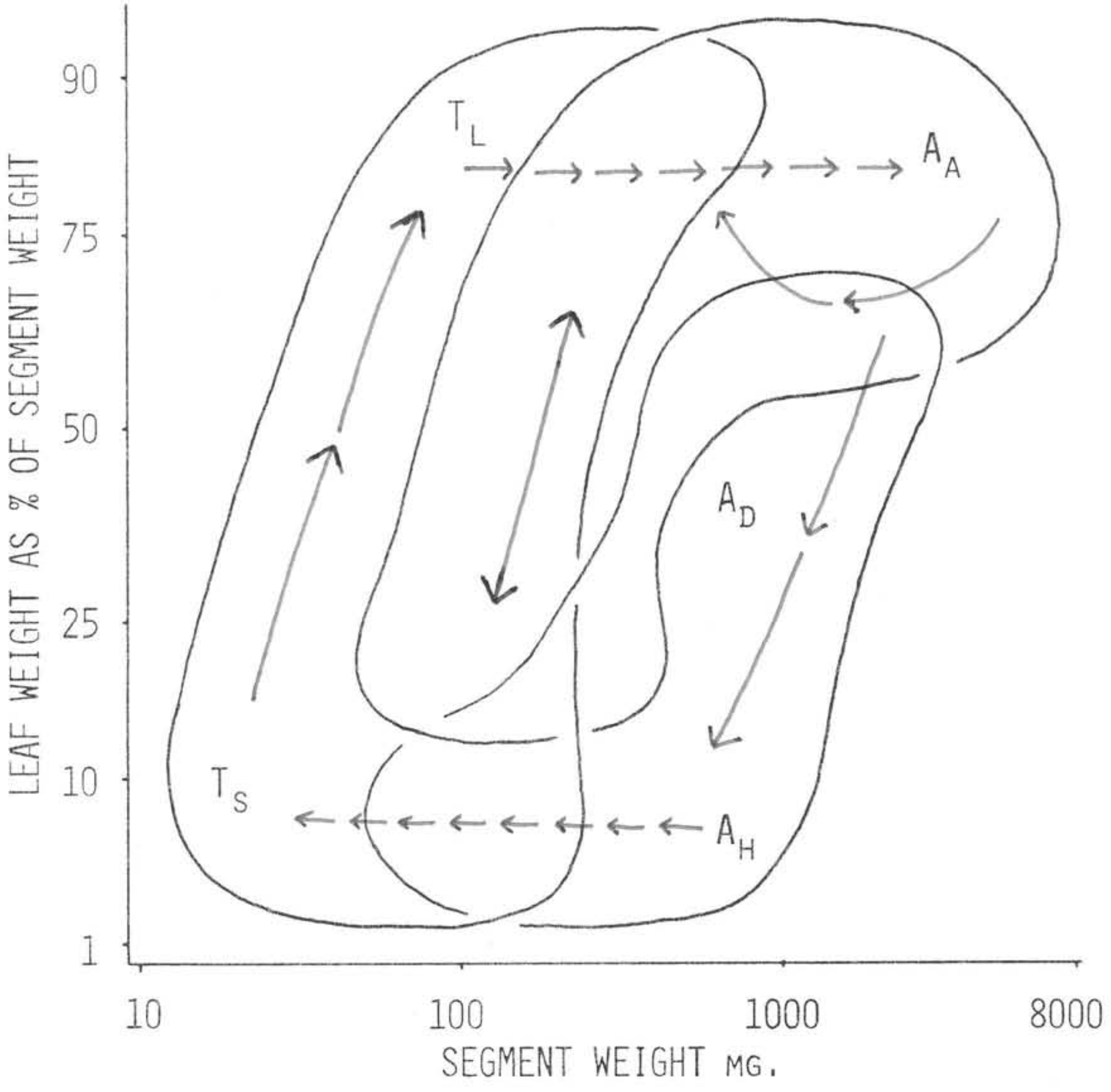
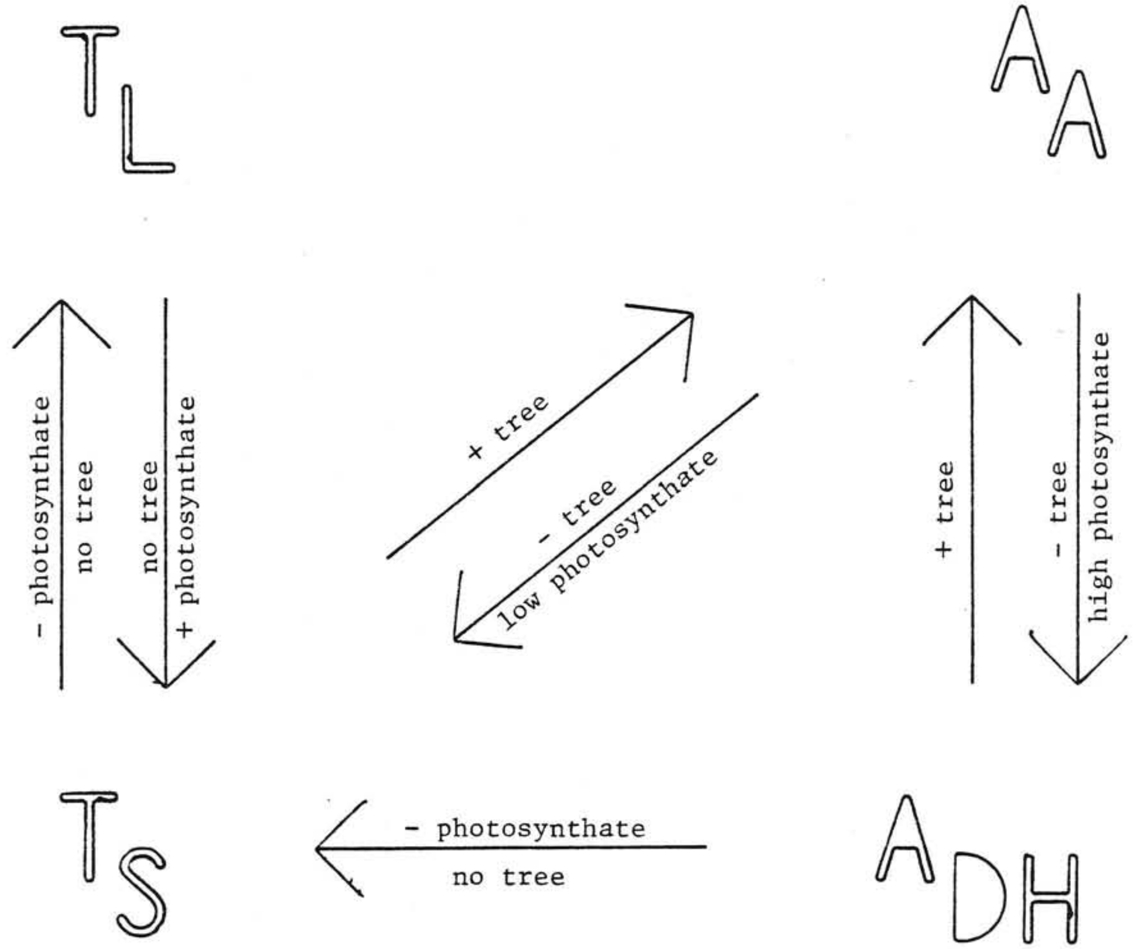

LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
100
1000
8000
SEGMENT WEIGHT MG.
T_L
A_A
A_D
T_S
A_H

Figure 36



T_L
A_A
- photosynthate
no tree
no tree
+ photosynthate
+ tree
- tree
low photosynthate
+ tree
- tree
high photosynthate
T_S
- photosynthate
no tree
A_{DH}

Figure 37

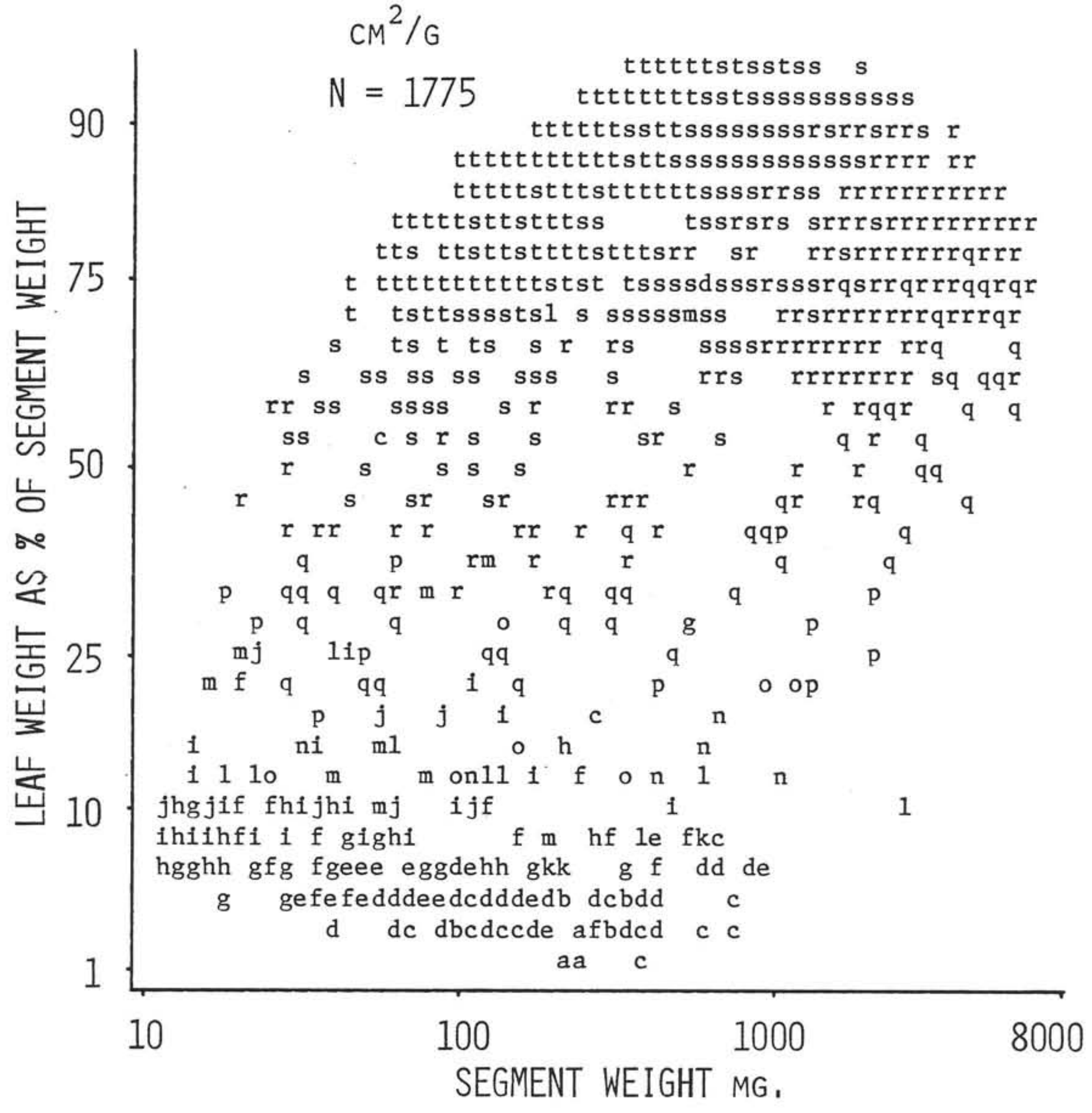

CM^2/G
N = 1775
LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 38

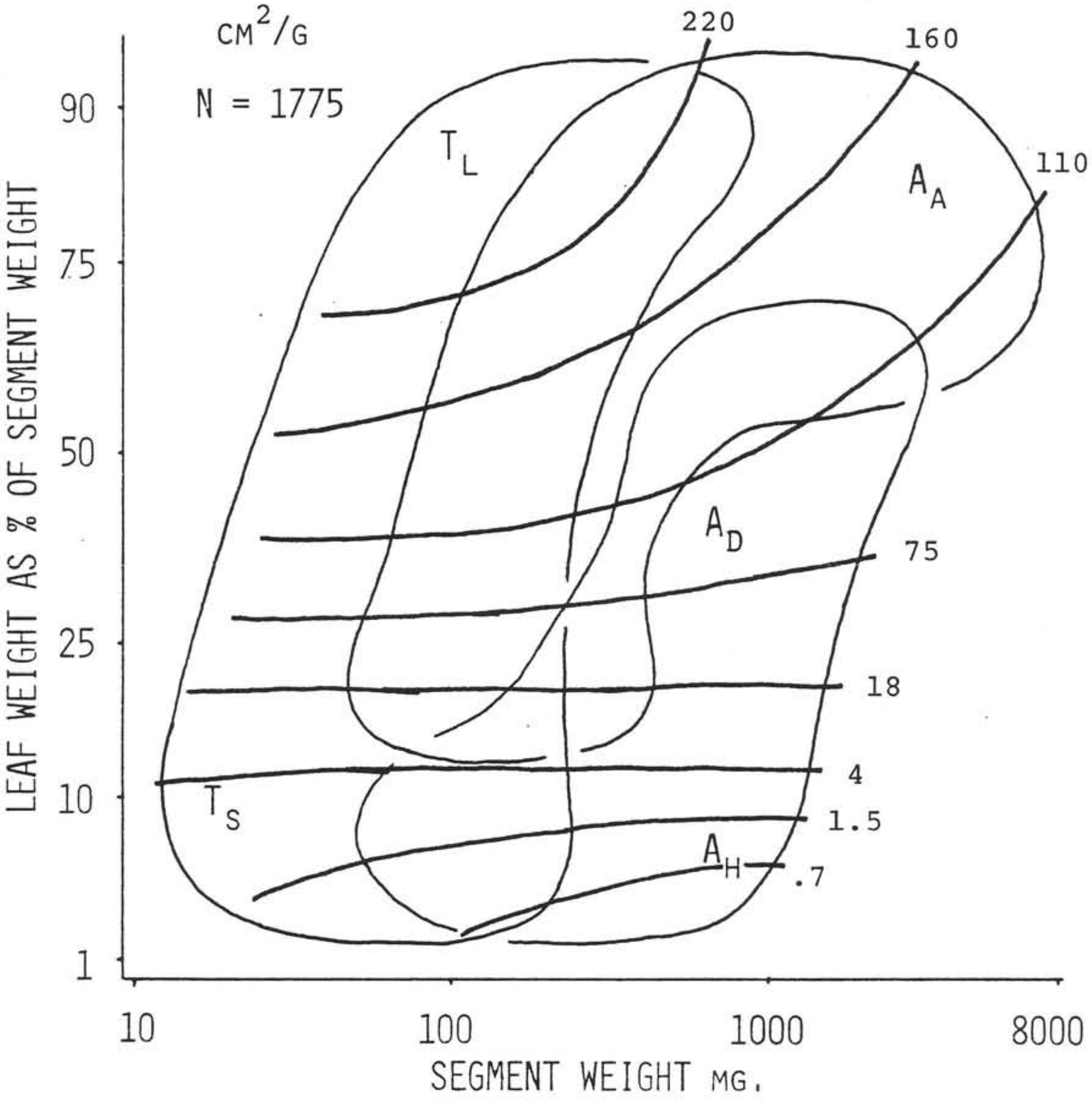

CM^2/G
N = 1775
220
160
110
75
18
4
1.5
.7
T$_L$
T$_S$
A$_A$
A$_D$
A$_H$
LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 39

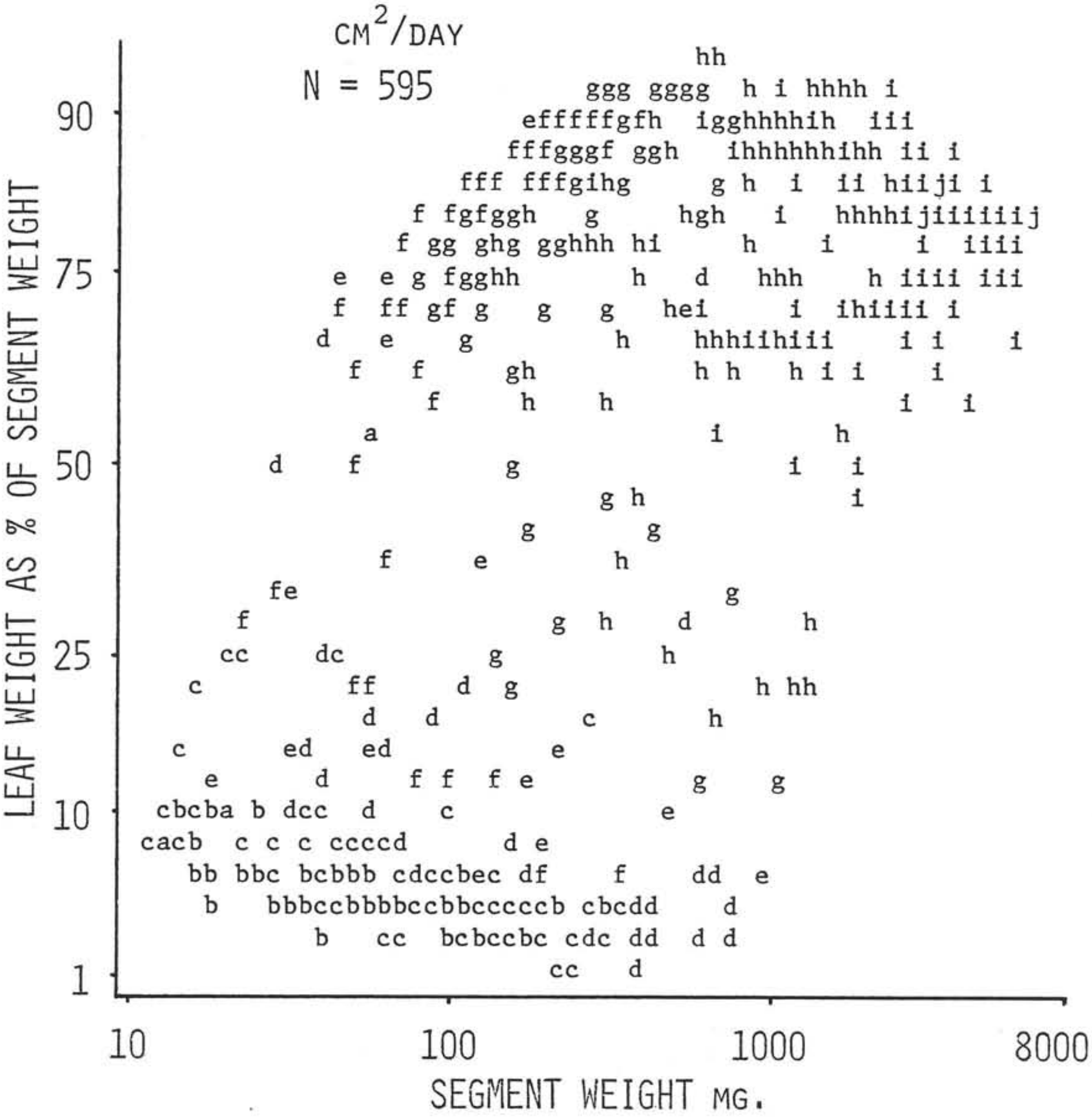

CM^2/DAY
N = 595
LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 40

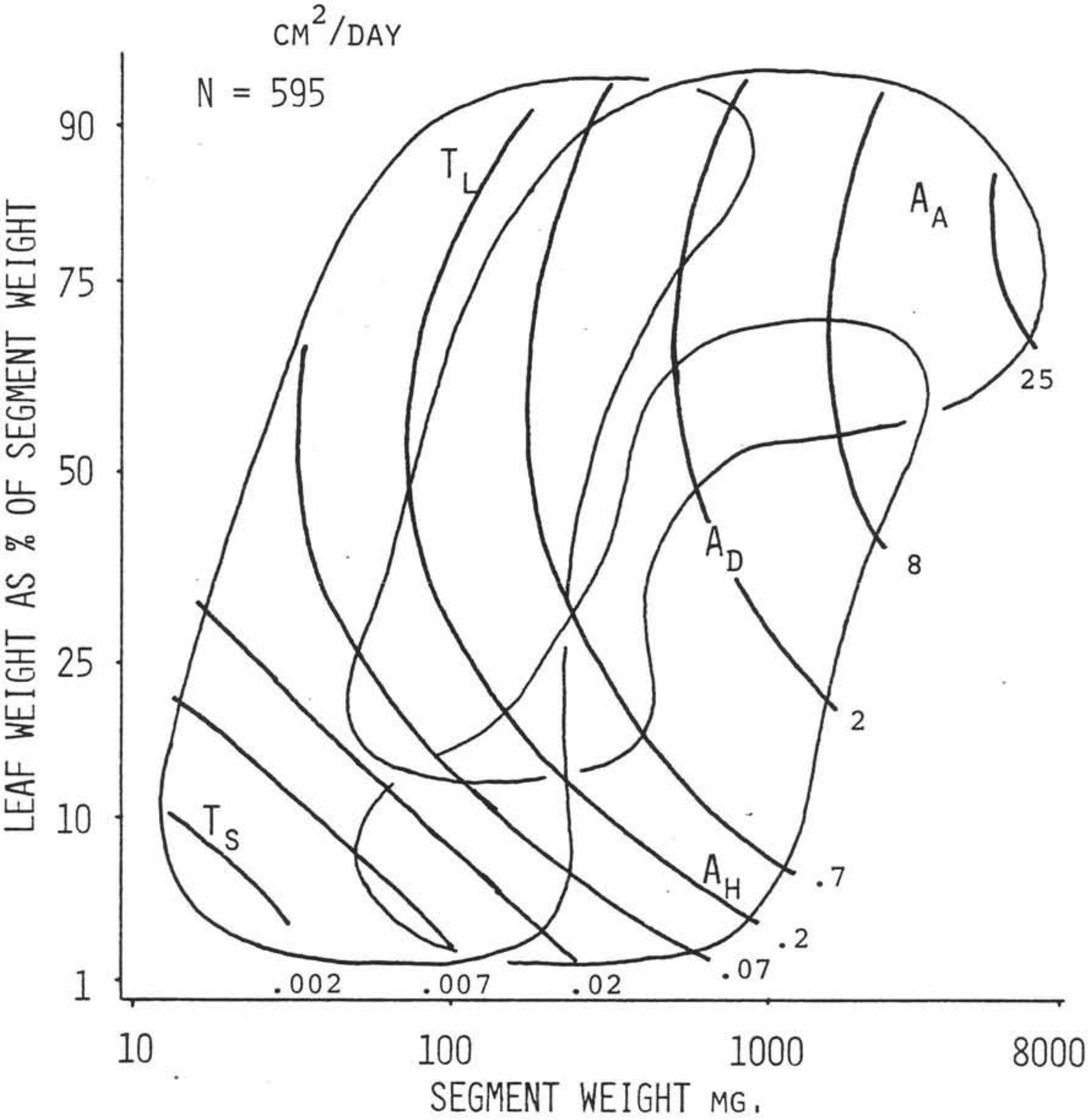

CM^2/DAY
N = 595
T_L
A_A
A_D
A_H
T_S
25
8
2
.7
.2
.07
.002
.007
.02
90
75
50
25
10
1
LEAF WEIGHT AS % OF SEGMENT WEIGHT
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 41

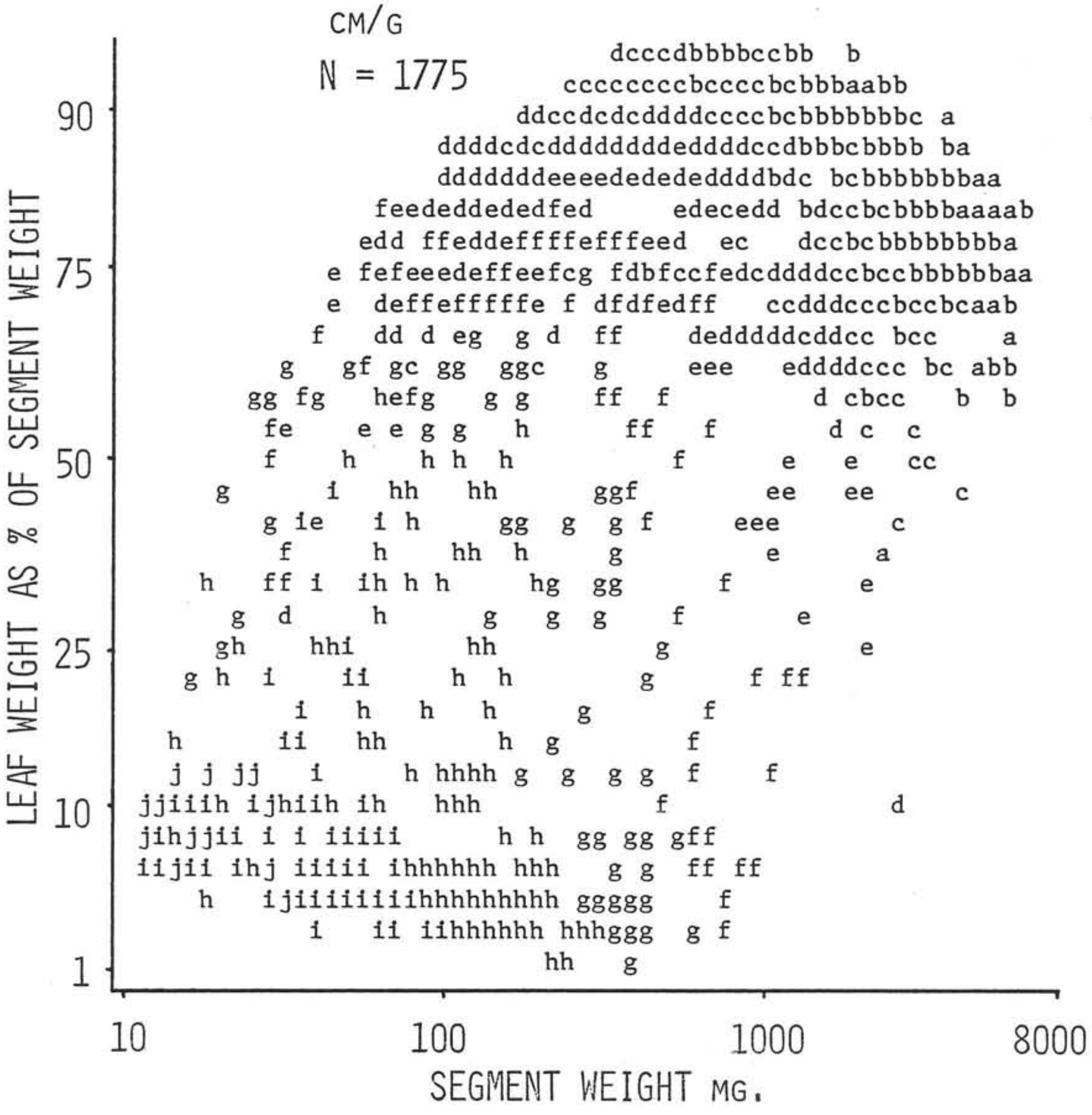

CM/G
N = 1775
LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 42

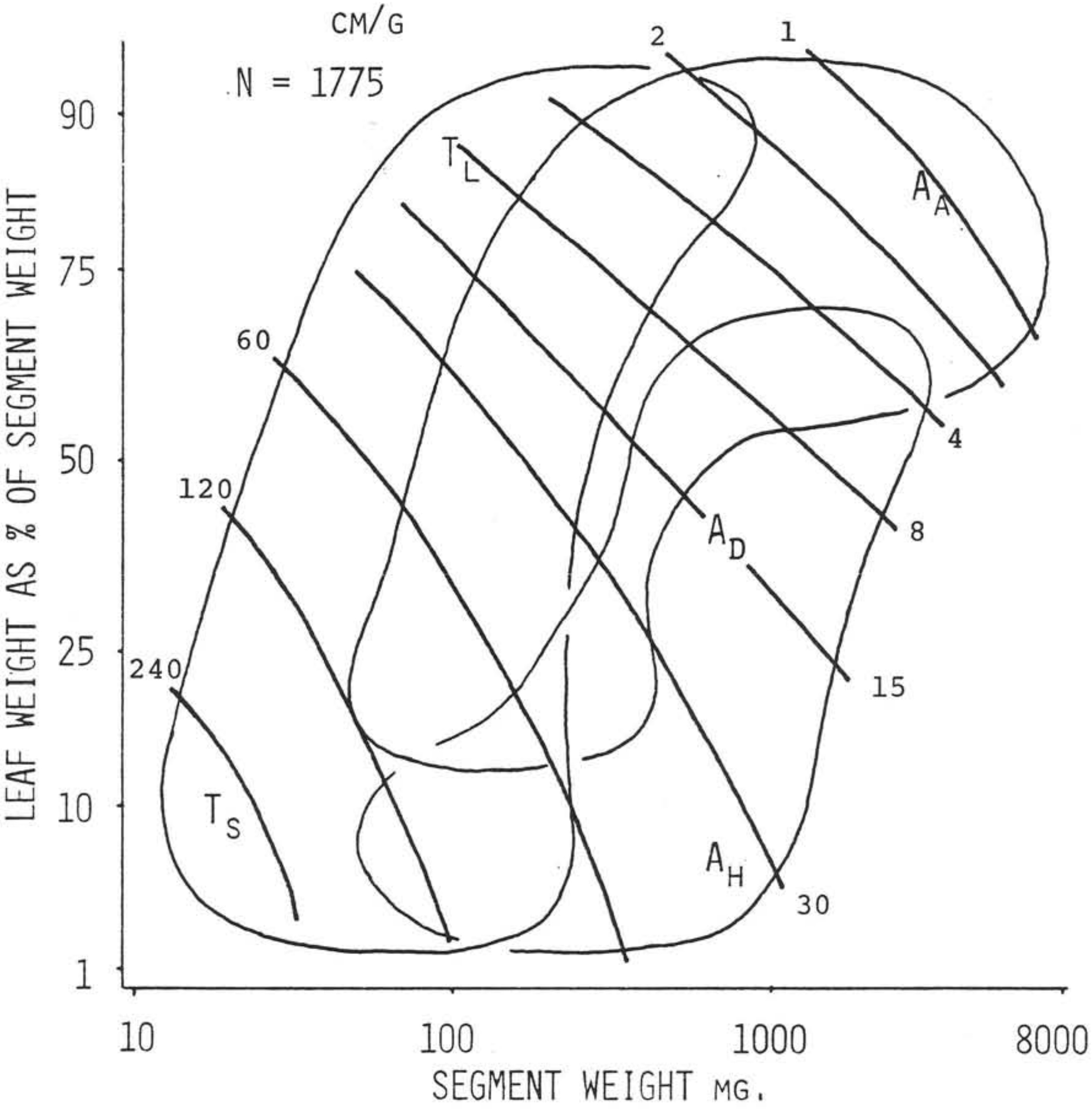

CM/G
N = 1775
LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
100
1000
8000
SEGMENT WEIGHT MG.
2
1
T_L
A_A
60
120
240
4
8
15
30
A_D
A_H
T_S

Figure 43

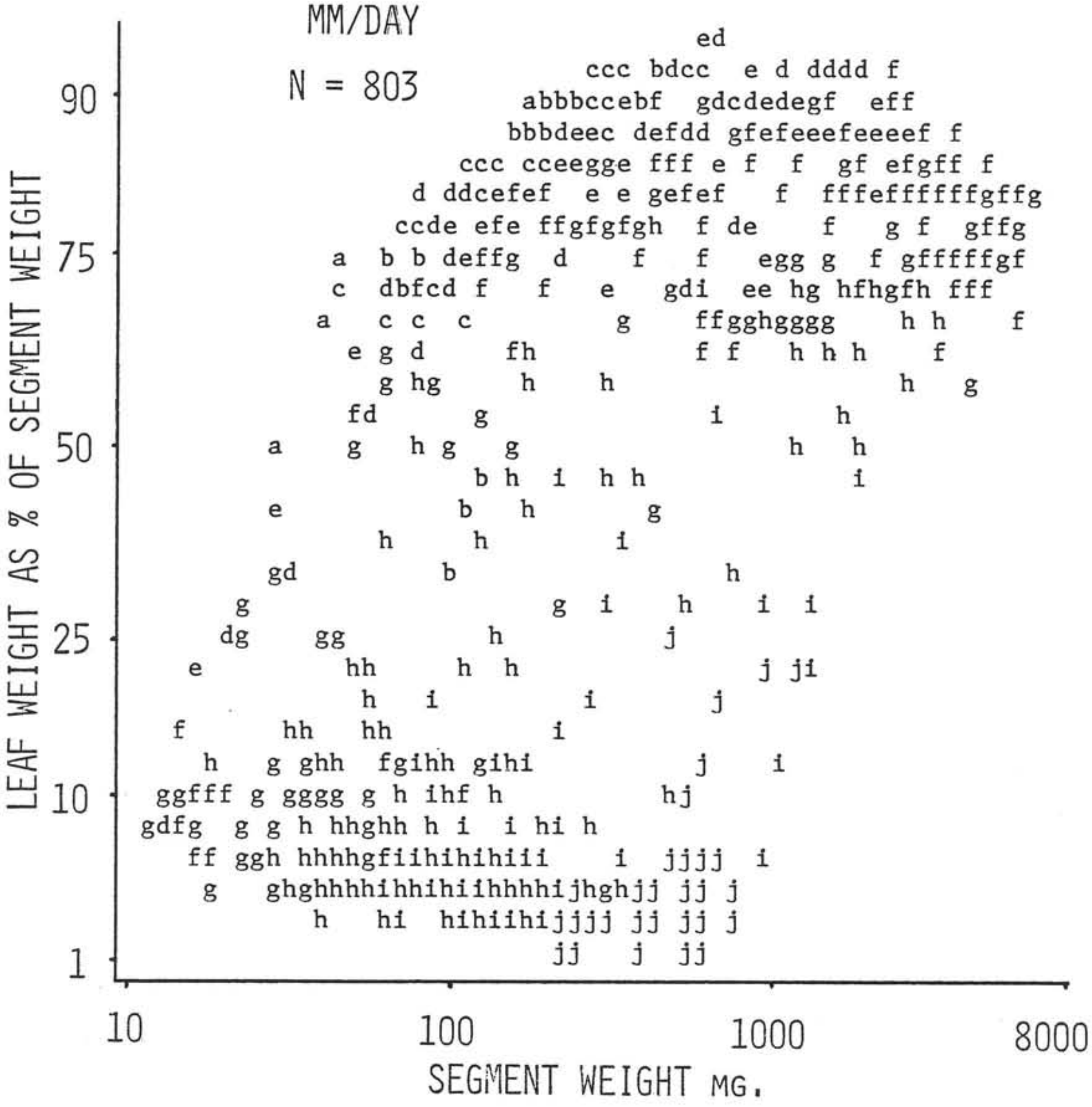

MM/DAY
N = 803
LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 44

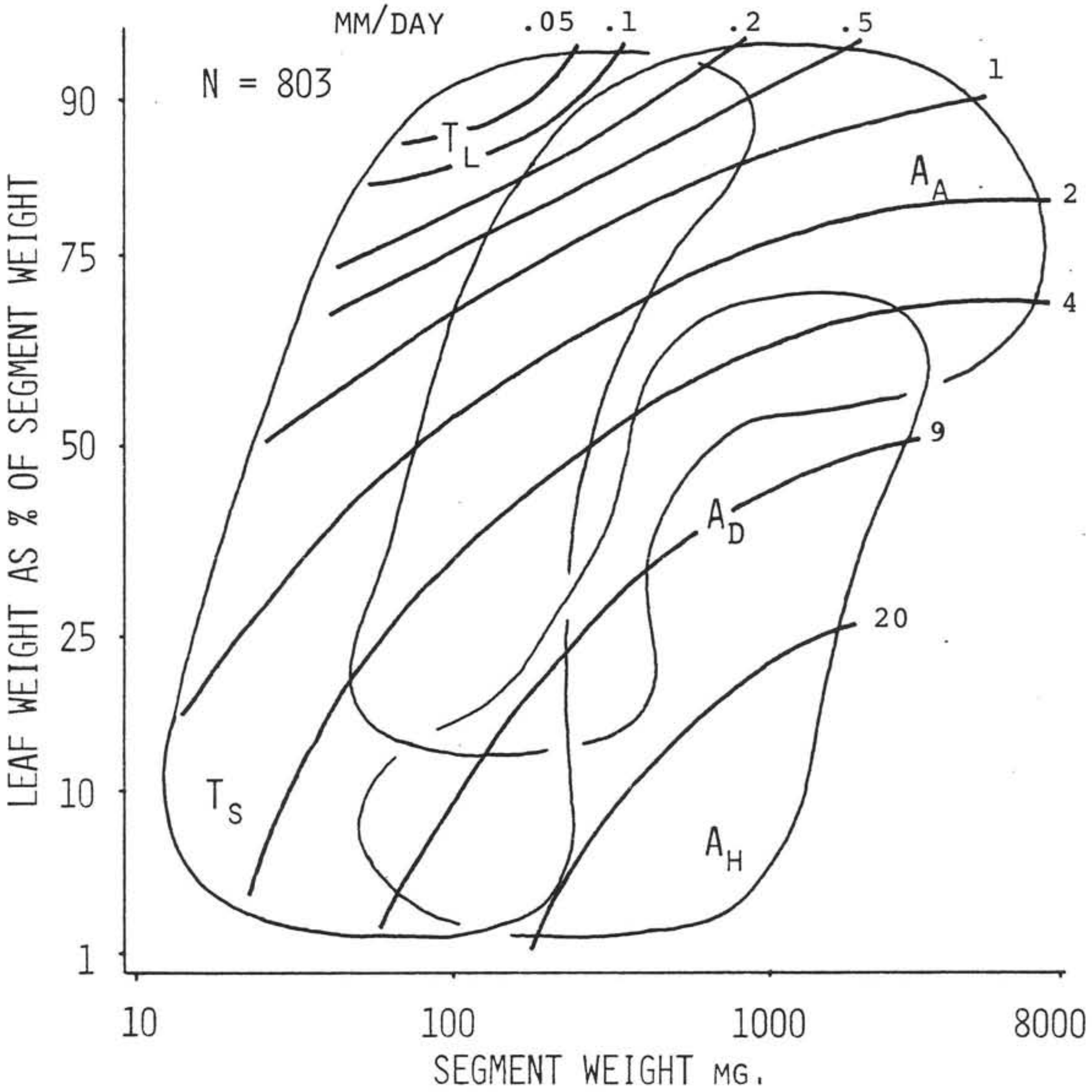

MM/DAY
.05
.1
.2
.5
1
2
4
9
20
N = 803
T_L
A_A
A_D
A_H
T_S
LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 45

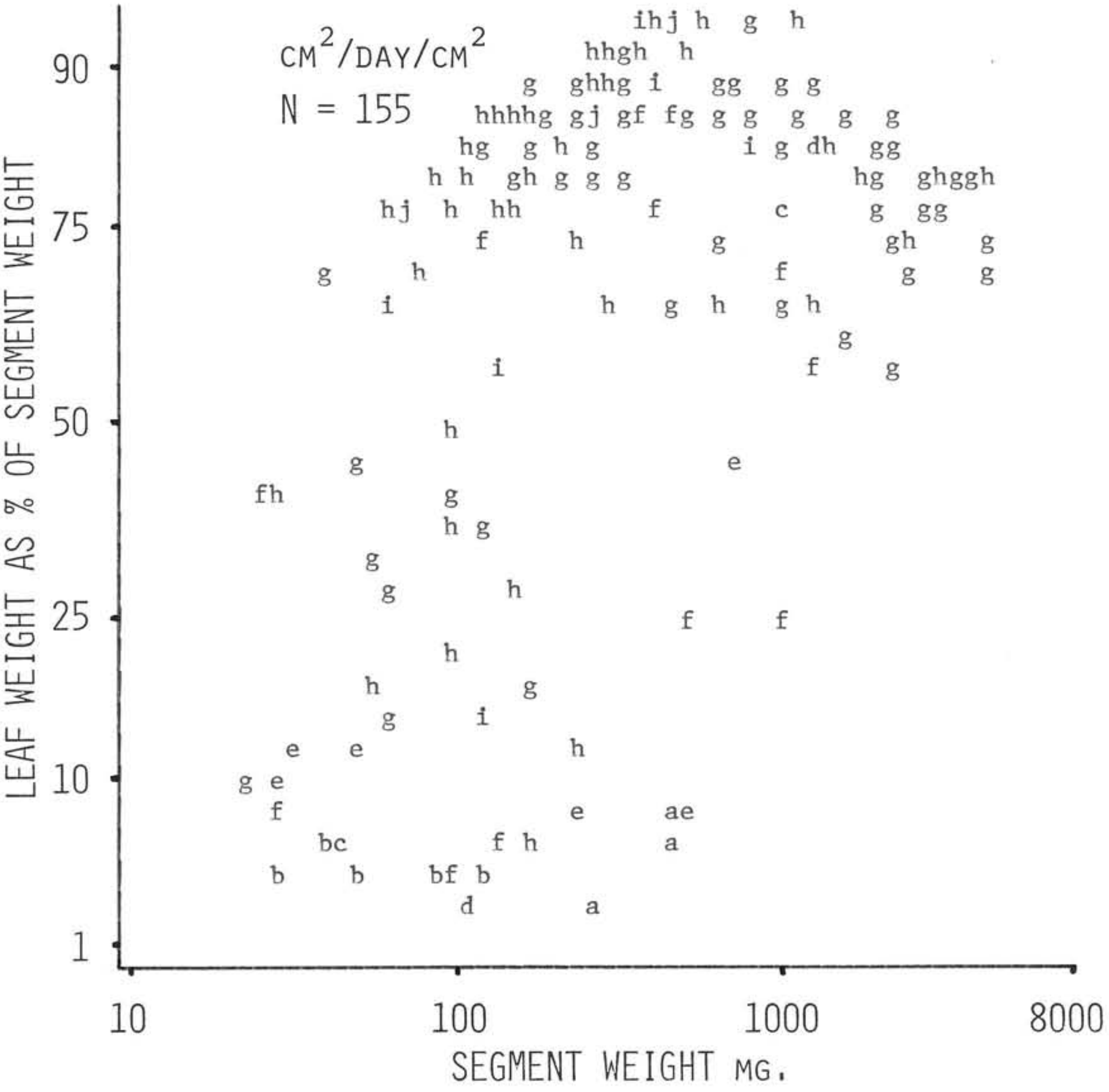

$CM^2/DAY/CM^2$
N = 155
LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
10
100
1000
8000
SEGMENT WEIGHT MG.

Figure 46

Figure 47

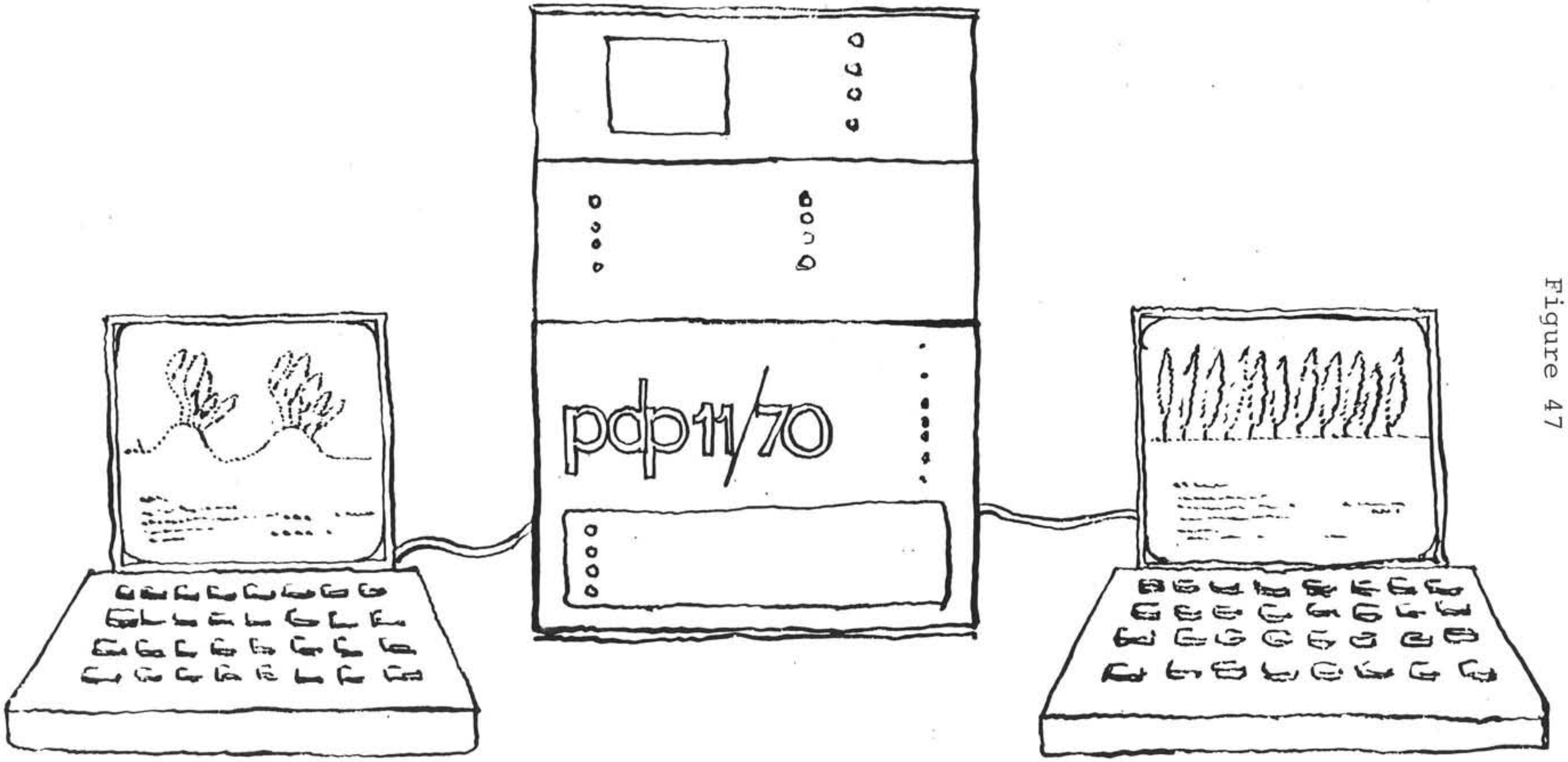


Figure 48

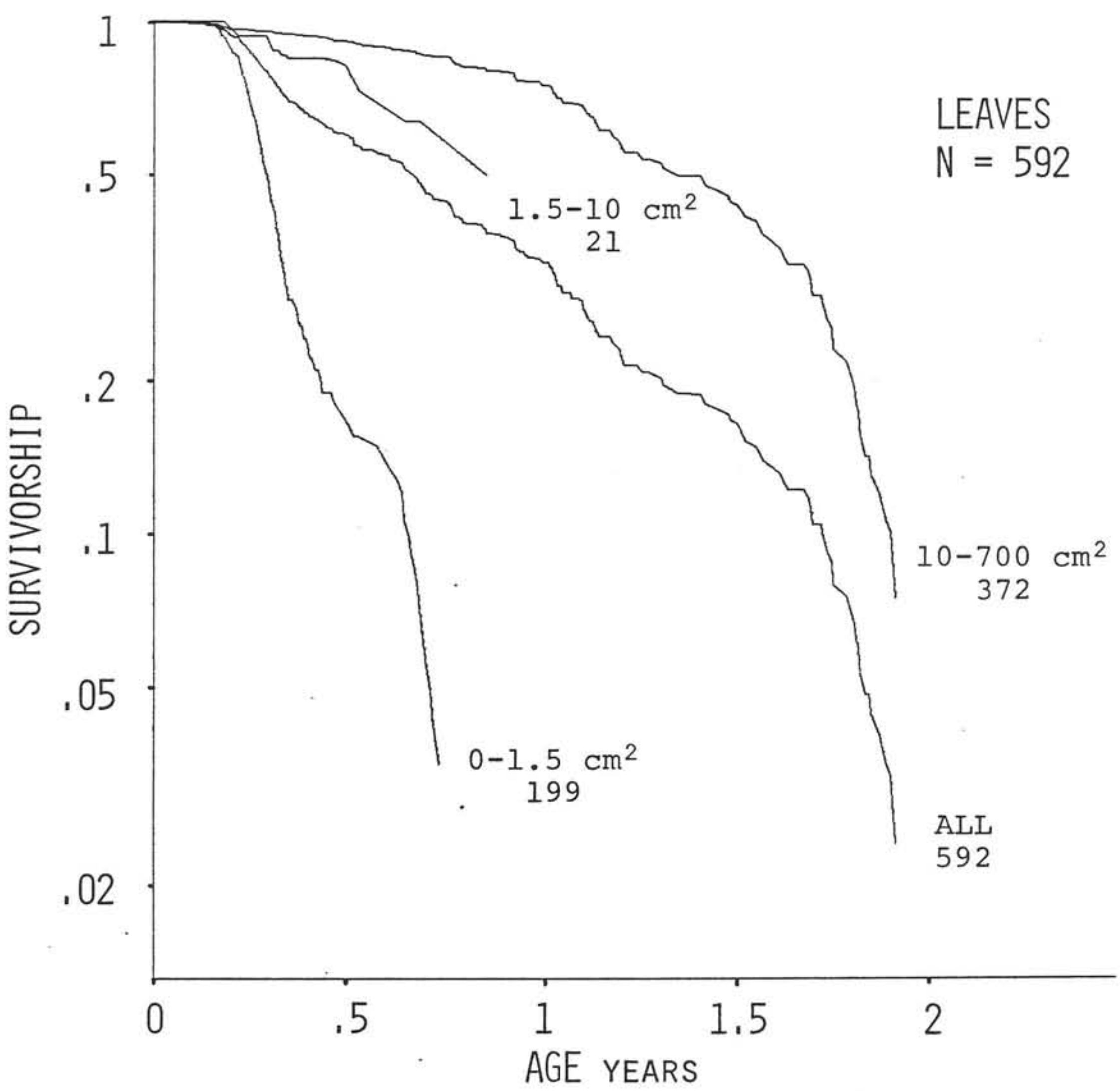

1
.5
.2
.1
.05
.02
SURVIVORSHIP
0
.5
1
1.5
2
AGE YEARS
LEAVES
N = 592
1.5-10 cm²
21
10-700 cm²
372
0-1.5 cm²
199
ALL
592

Figure 49

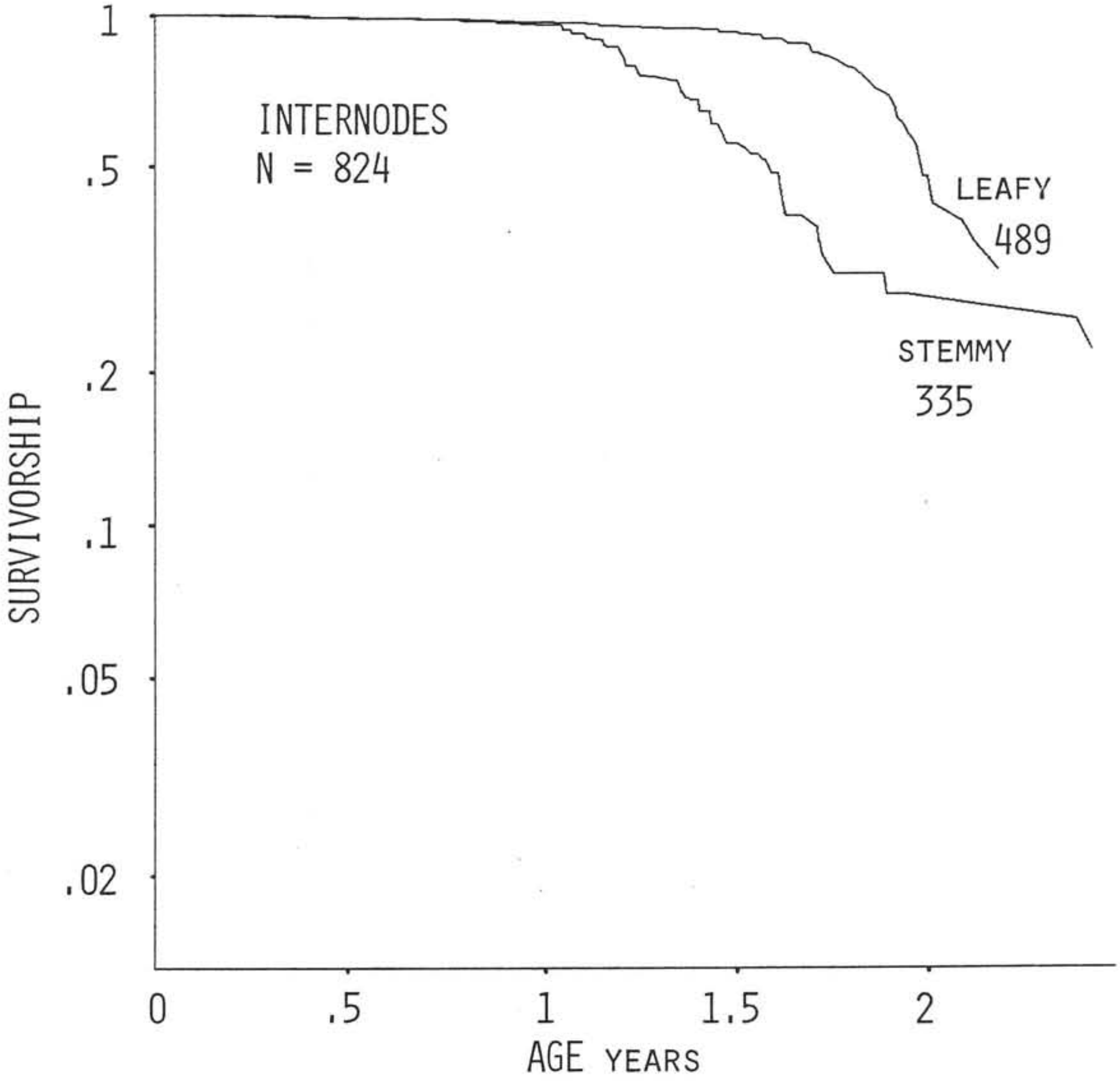

1
.5
.2
.1
.05
.02
SURVIVORSHIP
INTERNODES
N = 824
LEAFY
489
STEMMY
335
0
.5
1
1.5
2
AGE YEARS

Figure 50

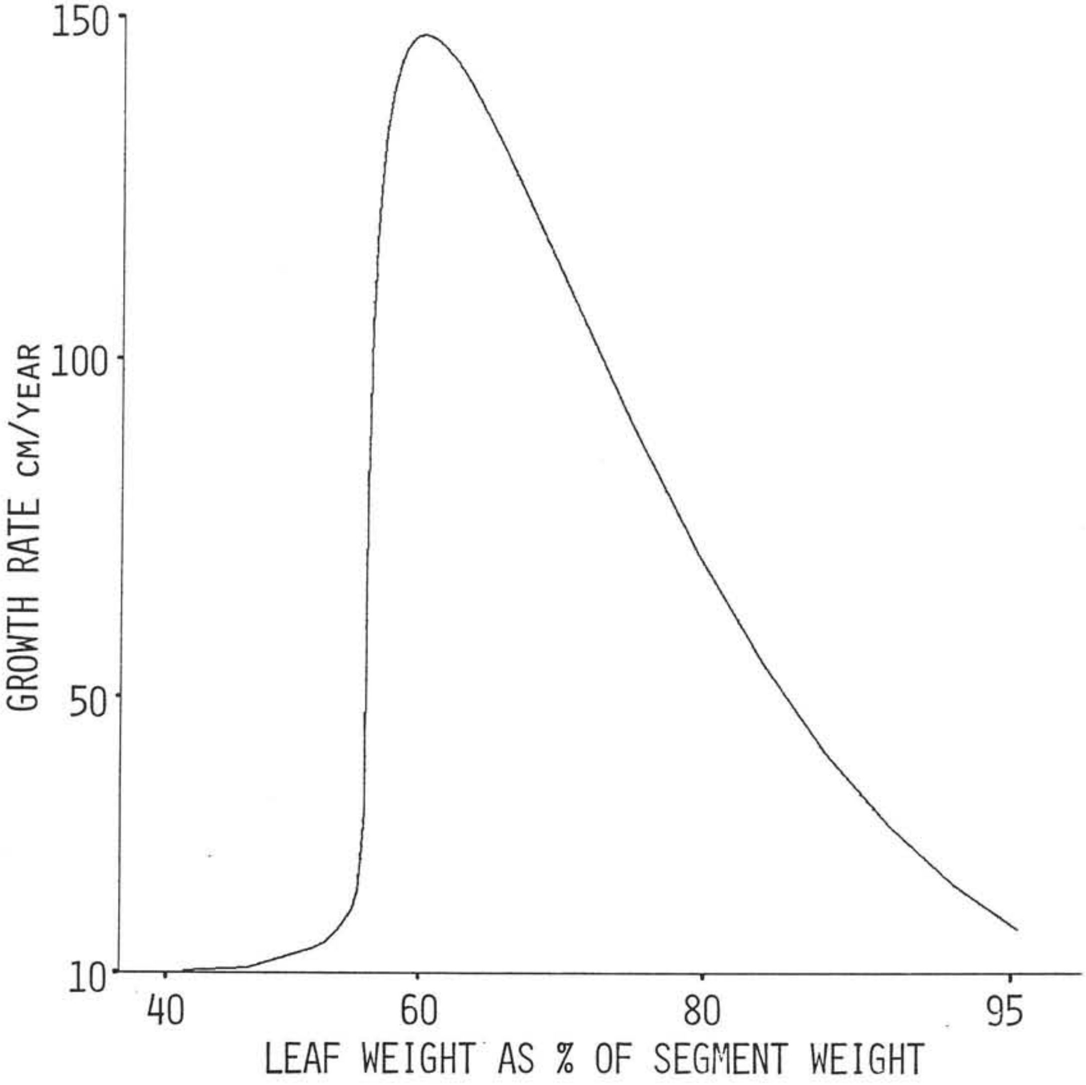

150
100
50
10
GROWTH RATE CM/YEAR
40
60
80
95
LEAF WEIGHT AS % OF SEGMENT WEIGHT

Figure 51

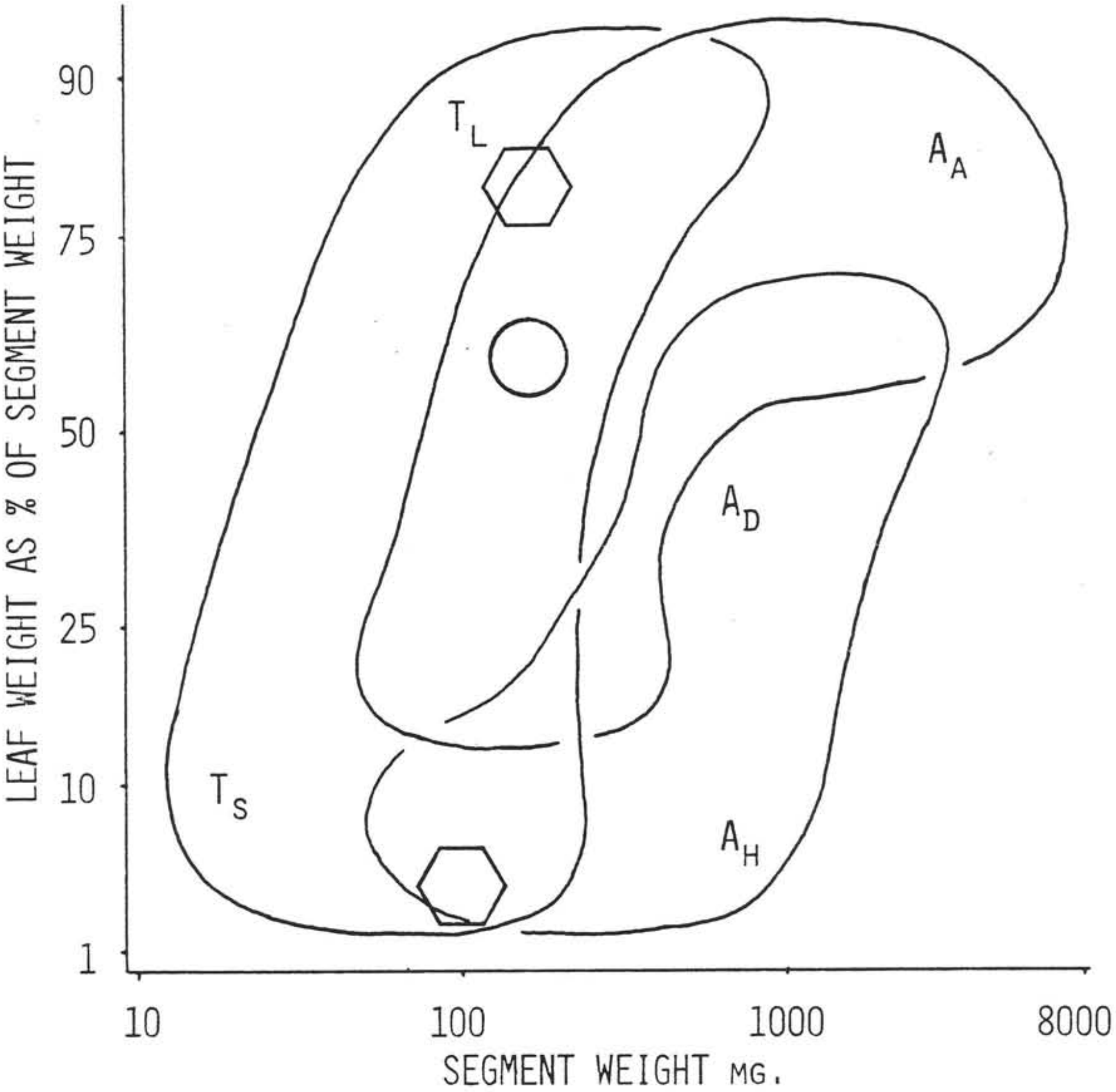

LEAF WEIGHT AS % OF SEGMENT WEIGHT
90
75
50
25
10
1
SEGMENT WEIGHT MG.
10
100
1000
8000
T_L
T_S
A_A
A_D
A_H

Figure 52

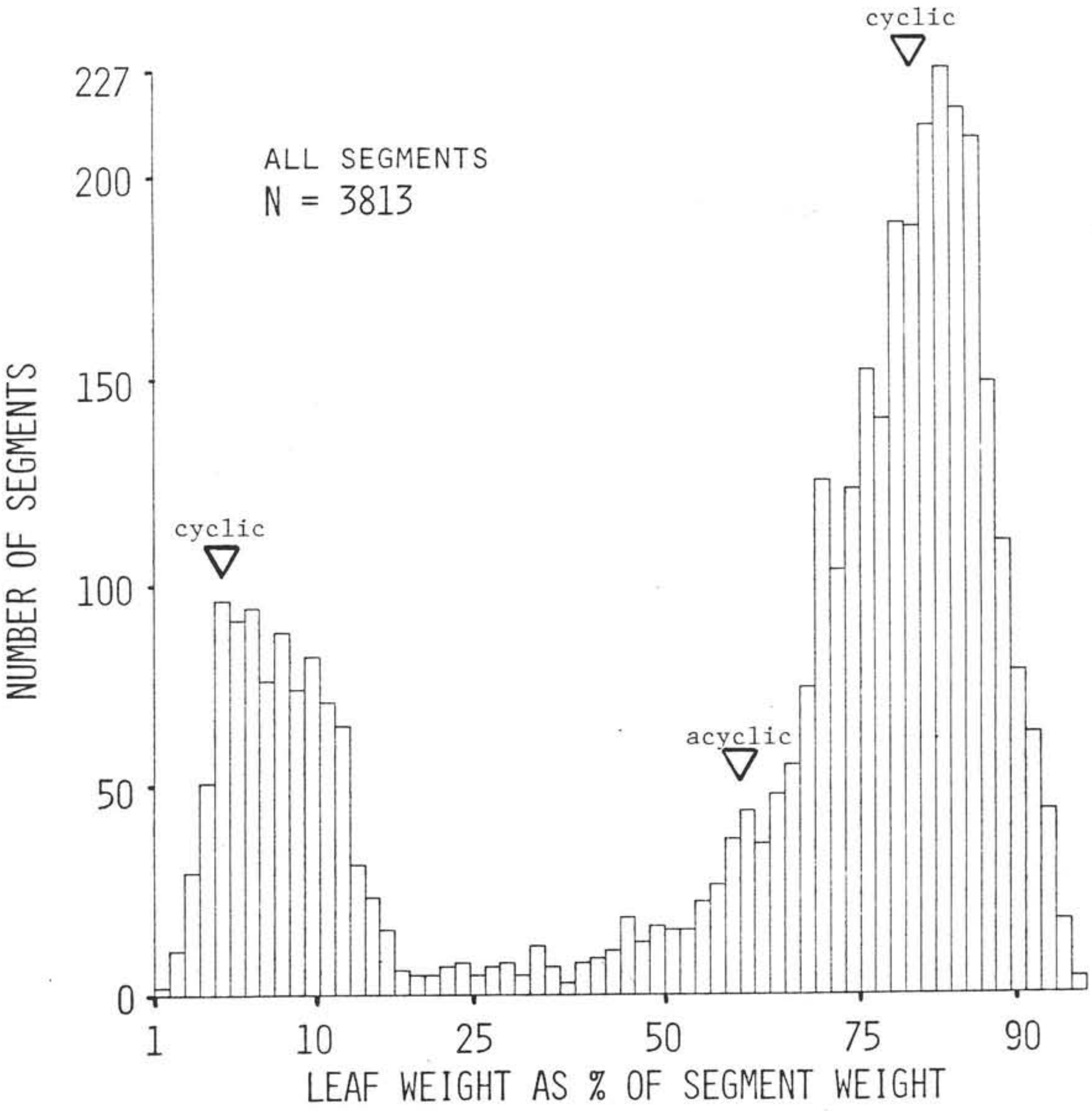
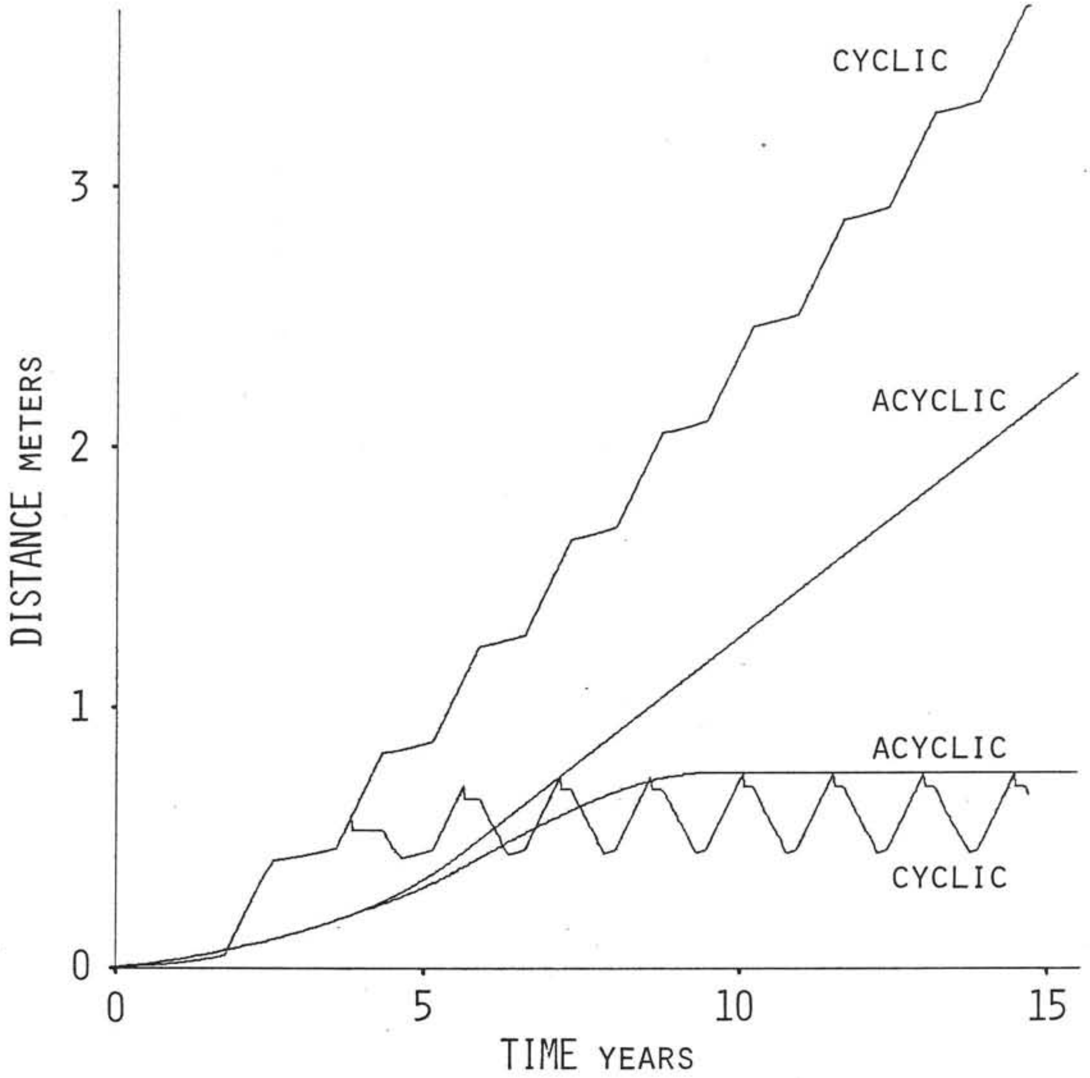

cyclic
227
ALL SEGMENTS
N = 3813
200
150
NUMBER OF SEGMENTS
cyclic
100
acyclic
50
0
1
10
25
50
75
90
LEAF WEIGHT AS % OF SEGMENT WEIGHT

Figure 53


CYCLIC
ACYCLIC
ACYCLIC
CYCLIC
DISTANCE METERS
0
1
2
3
TIME YEARS
0
5
10
15