# THE RELATION OF LEAF AND STEM.

## A NOTE IN STRUCTURAL BOTANY.

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THIS paper is intended only as a preliminary note of results attending an inquiry which the author hopes some day to complete in detail. As, however, the facts so far ascertained are of interest, and up to the present the further investigations fully support them, it has been thought well to offer a brief statement on the subject.

The method adopted was one of direct measurement and calculation, the explanation of ascertained facts being sought afterwards. Here, however, explanations and theoretical deductions will be set first, and practical confirmation supplied at the last.

Leaf and stem are alike integral parts of the plant; of these the leaf is the less permanent institution. Flowering stems may or may not carry leaves in addition to the flowers, and hence may in some cases be entirely dependent on the other parts of the plant. An ordinary stem with its foliage depends on the roots for the great part of the water and the whole of the mineral substances required for its nutrition; but the roots and stem alike are indebted to the leaf for their supply of carbon and carbohydrates. The leaf itself, from the time when it first breaks bud, develops chlorophyll and becomes self-supporting so far as carbon is concerned. Green stems may to some extent be self-supporting also.

In the majority of plants, however, the leaves are the great assimilating agents which collect carbon from the air, and manufacture the crude sap, supplied to them by the roots through the intermediary of the stem, into true nutrient sap. The Fungi and other plants devoid of chlorophyll are not now under consideration.

Since stem, trunk, and root are alike indebted to the leaves for their nutriment, it is evident that the leaves must manufacture more nutrient sap than is required for their own purposes.

The first call upon a leaf is to supply material for its own growth and maintenance, the second to supply material for the stem on which it grows. Since considerable subaerial portions of almost every plant are without leaves, it is obvious that the stem immediately adjoining a leaf must hand on a portion of the nourishment it receives to the branch and trunk below it to maintain and increase their growth, and the trunk again of necessity has to yield up to the roots sufficient for their requirements. A flowering stem devoid of foliage leaves also derives its nourishment from the leaves on other stems.

It is reasonable to suppose that during its period of growth each leaf retains for its own use a considerable percentage of the nutrient materials it manufactures; after attaining its full growth it retains little or none. The stem. even during the growth of the leaf, is itself growing, as is necessary firstly to provide a support sufficiently strong for the constantly increasing leaf-area, secondly to carry the leaf as it increases in area further away from the adjacent leaves, and thus avoid overlap and overcrowding. This growth of stem is maintained in strict unison with the requirements of the leaf by the fact that the leaf itself. as the provider of nourishment, regulates by its size the amount of nutrient material provided to the stem, and the growth of the stem is proportionate to this amount. So far we are dealing with a terminal leaf and the section of stem lying between it and the next. By the growth of the terminal leaf and its stem interleaf a further burden is put on the remaining stem, which must be strengthened to endure it; this is provided by the surplus from the first interleaf, which only absorbs a percentage for its own growth. The trunk bearing the stem again requires to be strengthened to bear the increased weight of the stem as a whole, and the nourishment for this is derived from the stem, which takes toll only on the nourishment sent on to it by the first interleaf. The root system has to be expanded to meet the growing wants of the plant, and the material for this expansion is supplied by the trunk, which retains only as much as it needs of the nourishment sent on to it by the stem, and so the surplus nourishment from the leaf is finally utilised, or, if not immediately required, may be stored for use. 2 G

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So far, we have spoken of strength only, but a further element has to be considered—the provision for passage of water and substances in solution to and fro between the roots and leaves. All other things being equal, this carrying capacity of a stem depends on its cross-sectional area, which in cylindrical stems varies as the square of the diameter. The more leaves, therefore, the greater should be the diameter of the stem. Subject to further qualification, the square of the diameter of the stem at any point should always have a constant ratio in each plant to the sum of the areas of the leaves beyond that point.

In a plant of simple growth the leaves occur at intervals along the stem, which intervals bear a definite ratio to the width or length of the leaves. The stem between the points of attachment of any two leaves is for present purposes called an interleaf.

Examine the stem of a hazel or other convenient plant, and it will be found that each interleaf is of uniform diameter throughout its length. The stem does not taper in the form of an elongated cone, but is made up of a series of cylinders of diameters constantly increasing towards the trunk; each increase in diameter takes place at the point of attachment of a leaf or shoot. This is precisely equivalent to the case of a water-main with a series of small supplies led into it at intervals; where each supply joined the main an increase in its diameter would be necessary to enable it to convey the enhanced quantity. It is not in strict accord with the requirements of strength. which demand a longitudinal geometrical taper throughout the stem, and not sudden accessions at intervals. strength of the stem at any point is proportionate to the fourth power of its diameter, and should bear a constant ratio to the sum of the moments of all the leaves up to the end of the stem about that point, plus some allowance for the weight of and wind pressure on the stem itself. It is obvious that, should the stem either prove insufficient to carry the fluids required, or unable to support itself and the leaves, the plant cannot continue to live unless in the latter case it is either of a trailing or climbing habit.

The strength of the stem does not, however, vary directly as the fourth power of the diameter throughout its length. At and near the growing point the woody fibre is not fully developed, and hence there is no fair comparison between the younger and the older portions.

The final "how" is rarely ascertainable in Nature's



Diagram of Leaf and Stem.

mechanism; thus it is extremely difficult to suggest how it is that the leaves of a given species of tree or plant never exceed a certain size, but, granted that there is such limit, it should be possible to ascertain the manner in which the relation between leaf and stem is maintained.

Let Figure I represent a hazel twig bearing six leaves and a terminal bud not yet opened into leaf.

The area of the youngest leaf may be represented by A, that of the next by  $A_1$ , the next  $A_2$ , and so on; the seventh leaf-connection is shown, but not the leaf. The areas of these leaves will form an ascending series thus:—

$$A < A_1, A_1 < A_2, A_2 < A_3, A_3 < A_4, A_4 < A_5, A_5 \cdots A_n = A_{n+1},$$

that is, both  $A_n$  and  $A_{n+1}$  are the areas of fully-grown leaves, while all the other leaves are still growing. A great many circumstances may contribute to irregularity of foliage, but under constant and favourable conditions the area of a leaf will bear a direct relation to the time which has elapsed since it broke bud. From actual measurement this rule appears to be as follows: Let T be the time which has elapsed since the leaf having area A broke bud, and  $T_n$  the corresponding time for leaf having area A, then  $\frac{T}{T_n} = \left(\frac{A}{A_n}\right)^2$ . This rule only holds good as between leaves which have not completed their growth up to the first leaf which has attained full growth. It is, of course, completely useless where varying conditions have prevailed during growth; still it is absolute, all other things being equal.

Take the following instance, in which the leaves broke bud at almost equal intervals of time, and accordingly  $\frac{T}{T_3} = \frac{1}{4}, \quad \frac{T}{T_2} = \frac{1}{3}, \quad \frac{T}{T_1} = \frac{1}{2}$ ; the areas of the leaves were A = 3.51 square ins.,  $A_1 = 4.77, \quad A_2 = 6.10, \quad A_3 = 7.42$ , and  $\left(\frac{A}{A_3}\right)^2 = \frac{12.3201}{55.0564} = \frac{1}{4.4}; \quad \left(\frac{A}{A_2}\right)^2 = \frac{12.3201}{37.210} = \frac{1}{3.02};$  $\left(\frac{A}{A_1}\right)^2 = \frac{12.3201}{22.7529} = \frac{1}{1.86}.$ 

This is not a specially selected instance, but, on the other hand, is one taken haphazard from several hazel twigs observed. Mathematically translated this relation involves the following facts. Each leaf commences to manufacture nutriment from the time it breaks bud; the powers of a leaf to feed itself and the plant are directly proportioned to its

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area; throughout its active growth each leaf and every leaf on the same twig retains to itself a definite proportion of the nutriment it provides.

The interleaf lengths of stem have been marked on the figure as B,  $B_1$ ,  $B_2$ , etc.; these in continued uniform circumstances of growth are directly proportioned to the area of the leaves, but in actual fact the relation is rarely exact.

If it be assumed that each interleaf of the twig absorbs a definite percentage of the nutriment supplied to it, a formula could be devised for the diameter of the stem at each interleaf, which should be fairly accurate for an ideal growth. The variation in length of the interleaves is neglected in this formula, and hence a slight error is introduced, as also by the use of diameters instead of squares of diameters on one side of the equation this formula is largely empirical in its present form.

Let D be the diameter of interleaf between leaf A and leaf  $A_1$ ,  $D_1$ , between  $A_1$  and  $A_2$  and so on, then—

$$\frac{\mathbf{D}}{\mathbf{D}_{1}} = \frac{\mathbf{A}}{\mathbf{A}_{1} + \frac{\mathbf{A}^{2}}{\mathbf{A}_{1} \times 2}} \text{ and } \frac{\mathbf{D}_{1}}{\mathbf{D}_{2}} = \frac{\mathbf{A}_{1} + \frac{\mathbf{A}^{2}}{\mathbf{A}_{1} \times 2}}{\mathbf{A}_{2} + \frac{\mathbf{A}_{1}^{2}}{\mathbf{A}_{2} \times 2} + \frac{\mathbf{A}^{4}}{\mathbf{A}_{2}^{2} \times 2}}$$

Figure 2 shows graphically the application of this formula to a selected instance. The calculated diameter of the stem for the various interleaves is shown in full line, the actual measurements are given in a dotted line. The points at which the ordinates represent the successive interleaves are shown by circles on the full line. If theory and fact agreed absolutely these two lines should coincide; their divergence measures the error, in this case extremely slight.

To represent further facts in the case the formula should take into account the actual interleaf lengths and the expenditure of nutriment on the growing leaves themselves.

Thus, let  $\frac{A}{p}$  represent the amount of the total nourishment from leaf-area A which goes to the leaf-growth for leaf A,  $\frac{A_1}{p}$  for leaf  $A_2$ , etc., then—

$$\frac{\mathbf{A} - \frac{\mathbf{A}}{p}}{\left(\mathbf{A} - \frac{\mathbf{A}}{p}\right) + \left(\mathbf{A}_{1} - \frac{\mathbf{A}_{1}}{p}\right)} = \frac{\mathbf{B} \times \mathbf{D}^{2}}{\mathbf{B} \times \mathbf{D}^{2} + \mathbf{B}_{1} \times \mathbf{D}_{1}^{2}} \text{ and}$$

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FROM LEAVES CALCULATED OF TERS DIAME MEASURED

DATUM LINE

Comparison of Calculated and Actual Diameters of Stem. (Hazel.)

Formula 
$$\frac{D}{D_1} = \frac{A}{A_1 + \frac{A^2}{A_1 \times 2}}$$

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------VOLUME DATUM LINE

Comparison of Curves of Progressive Leaf-areas and Progressive Volume of Stem. (Hazel.)

$$\frac{\mathbf{A} - \frac{\mathbf{A}}{\mathbf{p}}}{\left(\mathbf{A} - \frac{\mathbf{A}}{\mathbf{p}}\right) + \left(\mathbf{A}_1 - \frac{\mathbf{A}_1}{\mathbf{p}}\right) + \left(\mathbf{A}_2 - \frac{\mathbf{A}_2}{\mathbf{p}}\right)} = \frac{\mathbf{B} \times \mathbf{D}^2}{\mathbf{B} \times \mathbf{D}^2 + \mathbf{B}_1 \times \mathbf{D}_1^2 + \mathbf{B}_2 \times \mathbf{D}_2^2}$$

until we reach the point at which the leaves are full grown, at which each leaf will be  $A_n$  without any deduction. Which being translated means that the cubic content of any stem is proportionate to the leaf-area it bears after making allowance for the retention of nutritious matter by the growing leaves themselves. This formula is constructed on true principles and is in no way empirical.

Figure 3 gives two instances of this applied to actual twigs. The corrected leaf-area is shown by a dotted line. and the actual volume of the stem by a full line; each leafattachment is represented by a circle on the full line. The scale for the ordinates is in each case so selected that the total corrected leaf-area shall fall on the same point as the total cube content of the stem; under these circumstances the two lines should coincide throughout their length if the relation suggested above is accurate. Again it will be seen that the theory is borne out. Such a complex relation could never occur by mere accidental coincidence. The final correction remains to be applied, and that is a term in the ratio which shall allow for irregularities and abnormal growths: to do this it is necessary to watch the growing twig and note the exact time at which each leaf breaks bud, and also its increase in area at definite intervals. When this is done it is found that the cubic content of the stem is directly proportioned to area of the leaves it carries, the time it has carried each leaf, and the rate of growth of the several leaves. This involves considerable labour to collect and observe examples, but up to the present the author has reason to believe each case observed gives approximately exact results. Time has not served to prepare diagrams or properly complete this final investigation.

The connection between the dimensions of stem and area of leaves is therefore one of direct nutrition, and the plant ensures sufficient strength and capacity for water-carriage in the stem by the simple expedient of arranging a direct control over the stem by the leaves it has to carry; the more the leaves and the greater their area, the greater the supply of nutriment to the stem and the fuller its development. Growth in length of the stem is checked at the same time as growth in area of adjacent leaves, but the circumferential cambium continues to provide for growth in diameter. This again is the direct result of nutrition, of the assumption of a woody texture by the inner portion of the stem, and the removal in a forward direction of the growing point. The same woody texture and the vascular system serve to limit the amount of nourishment the stem can absorb by hurrying the fluids past to more distant regions in the plant. We can observe the method adopted by the plant in proportioning its parts, but we are still at a loss to solve such simple questions as the mechanical and chemical agencies which define the shape and limiting size of individual leaves or which regulate so exactly the proportion of length of stem, interleaf, and area of leaf.

All that we have done is to carry the inquiry one step further and get a rational expression for certain relations and a knowledge of the principles governing them. The detailed mechanism still evades us. It may be of interest to note that in a growing hazel leaf about 40 per cent. of the nutritive matter is absorbed by the leaf itself, and 60 per cent. handed on to the stem for the general purposes of the plant.

Sir John Lubbock has drawn attention to the fact that, *cæteris paribus*, the size of the leaf has relation to the thickness of the stem; this as between plants of varying species, and gives the following table:<sup>1</sup>—

				ameter o in inche	f f s. lea	Approximate area of six upper leaves in inches.		
Hornbeam				.06		14		
Beech .				.09		18		
Elm .				.11		34		
Hazel				.13		55		
Sycamore				·13		60		
Lime .				.14		60		
Mountain Ash				.16		60		
Chestnut.			0.5	.15		72		
Elder .				.18		93		
Ash .				.18		100		
Walnut .				.25		220		
Ailanthus				•3		240		
Horse Chestna	at .			•3		300		

This table exhibits no ratio which shall be constant between diameter of stem and area of leaf. Thus it <sup>1</sup> Flowers, Fruits, and Leaves, p. 100.

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happens that the area of leaf in square inches is to the diameter of the stem in inches as  $\frac{1}{1000}$  in the case of the horse chestnut; from this the ratio rises until in the hornbeam it becomes  $\frac{1}{233}$ . Bearing in mind the results we have already obtained, we see that the comparison should have been between relative leaf-areas and cube-capacities of stem, but it is impossible to supply even the lengths of the stems measured for this table. If, however, we assume that all the stems were equal in length, we could square the diameters and thus get a correct comparison. Knowing that the lengths vary greatly, we yet come much nearer accuracy by this method, and it is surprising that so many different species should admit comparison at all. The following table will prove interesting.

		Diameter of stem in inches,		Approximate area of six upper	
Hornbeam			:0036	Tea	14
Beech			.0081		18
Elm .			.0121		34
Hazel			.0169		55
Sycamore			·0169		60
Lime .			·0196		60
Mountain Ash			.0256		60
Chestnut			$\cdot 0225$		72
Elder .			.0324		93
Ash .			.0324		100
Walnut			.0625		220
Ailanthus			.09		240
Horse Chestnu	ıt		.09		300

Now, comparing the ratios, we have: horse chestnut  $\frac{1}{33338}$  and hornbeam  $\frac{1}{35358}$ . The intermediate plants on the table also fall in line.

Figure 4 gives the comparison of these two tables graphically. Such scales have been adopted for the ordinates as will cause all the curves to coincide on the ordinate for the horse chestnut; if the ratio were constant the curves would then coincide throughout. The line of diameters of stems hopelessly fails in this, but the line of areas of stems, or, in other words, the line of the squares of the diameters faithfully follows the line of leaf-areas. Such discrepancies as still exist are largely due to the absence of correction for length. The author intends, by careful measurement, to reconstruct this table free of the residual error. The question of compound leaves differs somewhat from that of leaf and stem. It may suffice for the time to state that in the compound leaf of the ash the diameters of the central stalk between the attachments of the leaflets are such that their squares bear an approximately constant ratio to the sum of the areas of the leaflets beyond them. The diameter under the first leaflet is somewhat larger than this rule would give, and the diameter at or near the attachment to the stem somewhat smaller. In a variety of leaves of widely different appearance this feature was constant.

When, however, an abnormal leaf, which is equally pinnate, is taken, that is in which there is no terminal leaflet, the ratio between leaflet-area and diameter squared is very close indeed. The explanation of this is probably simple, but awaits a few confirmatory measurements of other compound leaves. Figures 5 and 5a show graphically the average results from three unequally pinnate ash leaves and the average from two equally pinnate.

The whole question can be carried into great detail, involving even the diameters of the vascular bundles in the leaves themselves, but it then becomes fit reading for specialists only, and the author is content if he has succeeded in directing attention to the broad principles which govern the relation of leaf to stem. So far as he is aware the facts are new to botany. Every care has been taken with the necessary measurements, and the formulæ have been allowed to construct themselves on a calculating machine, theories being subsequently adapted to the figures.

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## FIGS. V. AND V.A.

## RELATION OF LEAF AND STEM.

