INTERPRETATION OF PLANT STRUCTURE*

BY PROF. D. THODAY

UNIVERSITY COLLEGE, BANGOR

STRUCTURE AND FUNCTION

UNDER the influence of Darwin's concept of 'survival of the fittest', a tendency to assume all structural features to be adaptive was strengthened. It is, of course, essential that the structure of plant organs should enable them to carry out their functions adequately; but perfect adaptation of tissues to their functions would be difficult to define.

The study of xerophytes provides an instructive example.

Before the physiological adaptation of plants to their environments can be properly assessed, we need far more exact knowledge regarding the quantitative relations of their different functions to the environmental factors, and regarding the balancing of those functions.

The question to be answered is not how an organ is adapted to its function, but rather *how its form and structure affect its functioning*.

Quantitative investigation of the effects of minute structural features is often beset with great difficulty. We have not even yet reached finality in the solution of problems presented by stomatal diffusion, as affected by wind and other external conditions and by the size and proximity of the stomatal pores, although much intensive work has advanced our knowledge considerably; nor do we know just how much effect to attribute to the sinking or raising of stomata, or other special devices.

While the exact laws of the diffusion of gases through stomata are difficult to establish, it might be thought that the *distribution* of stomata at least would lend itself readily to adaptational interpretation. Actually, the facts point very largely in the reverse direction. Salisbury's statistical studies in particular have shown that, on the whole, plants in more exposed places have a higher stomatal frequency, and that for a given species the proportion of stomata to epidermal cells is more constant over a range of moisture conditions than stomatal frequency, variations in which are to be interpreted largely as the consequence of different degrees of expansion subsequent to the initiation of the stomata.

This turns the attention away from adaptation to the process of development. Salisbury's results indicate that stomatal frequency is determined by factors at work in two phases of leaf development. The first is the formative phase in which the posi-

tion and number of stomata are determined in relation to the epidermal cells, mainly by internal influences depending on the hereditary make-up of the plant. The second is the expansion phase, in which the degree of separation of the stomata, already initiated, is determined.

Goebel has shown how problems of development may be attacked inductively in his "Gesetzmässigkeiten im Blattaufbau". The general result of his studies of leaf development was to bring out the repetitive nature of the patterns that are laid down, the units of a pattern showing, at the time of initiation, remarkable constancy of scale. Thus at the growing edge of a fern frond bifurcation of the veins keeps their spacing within certain limits, just as the size of cells in meristems tends to remain more or less constant owing to division when an upper limit is reached. The uniformity of size of the meshes in a net-veined leaf is a similar phenomenon which has been studied by Schuster. Stomata and also root-hair initial-cells show an approximation to uniformity of spacing at their initiation, however much the fact may afterwards be obscured by expansion of cells between the initials, or inhibition of their further development. Küster has emphasized the correlational aspect of such regularities, as depending upon mutual relations between the different tissues or structural elements that make up the pattern.

Another example of a quantitative approach to problems of adaptation is afforded by attempts to correlate the dimensions of parts served and tissues serving them. It is obvious that as the foliage of a tree increases in extent the amount of conducting tissue in the stem increases too; and that from the small twig through branches to the main trunk the amount increases parallel with the increasing number of leaves to be supplied. Jaccard directed attention to the quantitative aspect of this relation; and his pupil Rübel examined it in greater detail for the herbaceous plant, *Helianthus annuus*. Salisbury had already correlated the vascular structure of petioles with the dimensions of the leaf blades, with special reference to the xylem and transpiration.

The correlations displayed were not exact and showed considerable variations. Yet they are remarkable enough, and specially worthy of note when we begin to inquire how such correlations come about. An interaction between one part and another is implied. This aspect has been investigated both experimentally and by anatomical analysis.

* From the presidential address to Section K (Botany) of the British Association, delivered at Dundee on September 1.

Jost's classical experiments on *Phaseolus* seedlings (1893) showed that severance of leaf-trace bundles in the middle of an internode interrupted their development below the point of severance, but not above it, although neither part could function normally.

In herbaceous plants, cambial activity at any given level often exhibits local variations which are related to active development of different leaves above. In the sunflower this is conspicuously shown.

That the developing organs actually influence the growth of the stem below them, to considerable distances, is a natural inference.

Strong support for the reality of such influences has been forthcoming from one of the most spectacular advances in knowledge in recent years—the discovery of chemical agents controlling growth, which was an outcome of investigations on the curvature of shoots in response to light. The growth-promoting substances, called auxins, are highly active. One fifty-millionth of a milligram produces a measurable effect on the oat coleoptile. They are produced especially by actively growing parts of shoots—sprouting buds, shoot-tips and young expanding leaves. They not only influence growth in length, but also produce other effects which are of greater interest in the present connexion.

It has been shown experimentally by Snow and confirmed by others that auxin stimulates cambial activity. Söding has actually detected auxin in the cambium of trees in spring and summer. He states that it appears there a little in advance of the resumption of cambial activity in the spring. Since it is produced by developing buds and young leaves and travels downwards, the downward spread of cambial activity from the base of the awakening buds in spring is thus accounted for in terms of an effect of auxin which is experimentally demonstrable. The basipetal conduction combined with tangential localization exhibited in this instance gives strong support to the interpretation, already suggested, of the localized cambial activity in the intact sunflower stem, as indicating a causal influence proceeding downwards from the actively growing leaves.

Evidence has also been adduced of stimulating agents of a chemical nature liberated from wounded tissues.

The demonstration that such hormones exist and are effective in influencing plant development is of far-reaching significance. It is a challenge to students of plant structure to view their data dynamically. The statement that one part of a plant influences another is no longer to be understood merely as a convenient way of expressing a correlation, in a figurative sense, but is a legitimate hypothesis in a causal sense.

THE PHYLETIC OUTLOOK

The evolution theory gave a new meaning to natural relationships, as revealed by the systematist, and a new aim to the systematist himself. Previously a natural system was conceived as a system of classification depending on the balance of similarities, estimated from a consideration of all the characters of the species, as compared with an artificial system depending on particular characters selected for their convenience. The ancestry of species now became, in theory, the main basis for a natural classification.

It was soon realized that, as similarities in some features are often accompanied by dissimilarities in others, similarity might not always signify relationship. Fossils themselves, moreover, provided clear evidence that similar organs or structures have been evolved independently along different lines, by different phyla, so that the possession of seeds, for example, is not evidence of common ancestry for all seed-bearing plants.

Modern genetics reveals, as the most prolific cause of variation, irregularities in the process of nuclear division and the behaviour of the chromosomes, and changes in the substance or structure of the chromosomes, which appear to be entirely erratic and haphazard.

If, however, we turn from the minor variations which differentiate species and horticultural varieties and survey the major events that have marked the evolution of plants, it is difficult to regard these as haphazard. Besides seeds, already mentioned, a number of features are found with even wider distribution, common to groups which cannot be traced to a common origin. Such are the alternation of sexual and asexual generations; archegonia; the formation of spores in tetrads, following a reduction division; air-space systems and stomata; vascular tissues; then fertilization, evolved also in the animal kingdom, and the cell as the unit of construction; the nucleus with its chromosomes and their highly organized behaviour in division. The enumeration need not come to an end on the plane of cellular, structural organization, for chemical parallels are quite as remarkable. Consider, for example, the similar enzymes and enzyme complexes responsible for carbohydrate metabolism in yeast, in the higher plant and in animal muscle; the hæmins found in plant and animal cells alike, and the related substances, chlorophyll in the green plant and hæmoglobin in animal blood, with uniquely important functions. Finally, there are the proteins and other important basal constituents of living matter.

The idea was suggested by F. F. Blackman in 1921, in reference to Nef's work on the inter-

changeability of carbohydrates, that the biologically important carbohydrates are just those which are chemically most likely to arise—most readily formed, most stable, etc. May we not extend this idea to explain the universality of particular chemical compounds or radicals—like the amino-acids, limited in number, found in protoplasm?

The conditions for an epoch-making event like the arrival of chlorophyll were provided by the previous course of chemical evolution, in common characters of living matter, and by particular variants of them under particular conditions, which may have occurred but rarely in combination, but are scarcely to be envisaged as unique.

If it is legitimate to regard chemical events in this way, as occurring with a frequency concordant with their inherent probability, may we not carry this idea on to the higher plane of cellular organization and structure? To do so is to direct attention to the nature of that stability and developmental harmony which are so conspicuous a feature of living organisms; for persistence and occurrence become more and more determined and limited by the pre-existing system through which evolution works. Natural selection of harmonious changes may have been more important than elimination of functionally unfit mature organisms. It is developmental harmony which is important, of which functional efficiency of adult organs is but a part.

We are thus once again led to the consideration of development. If we can obtain light on the laws of harmonious development, we may be in a better position to understand the nature of those major changes which the great pageant of evolution unfolds.

SEEDLING STRUCTURE

As an example of the application of causal principles to old problems, I propose to consider the structure of seedlings.

The broad survey achieved by British workers revealed large differences within closely related groups, which made it more difficult to interpret resemblances as of phylogenetic significance. A high degree of correlation was observed, on one hand, between slender smallness of seedlings and diarch root structure, with two xylem poles extending right up the hypocotyl; and, on other hand, between large diameter and tetrarch or polyarch structure, with stem-like pattern in the hypocotyl. Both Compton and T. G. Hill and de Fraine emphasized seed size as an important factor influencing seedling structure.

Another factor of a similar kind was the influence of the plumule, the traces from which, when precociously developed, shared with the cotyledon traces in the early structure of the hypocotyl. In

certain cases, particularly among the Amentiferae, the traces from the plumular leaves were found to be triads like those from the cotyledons (Davey, 1916), and these with their central xylem strand extend above the cotyledonary node into the epicotylar stem itself. Phylogenists were inclined to interpret this as a more extensive persistence of primitive structure in a relatively primitive group. But the occurrence of a root-like solid core of xylem in the epicotyl of the Viciae, an advanced group among the Leguminosae, scarcely harmonizes with phyletic ideas, as Compton pointed out, and makes phylogenetic interpretations appear less certain.

Bugnon tried to approach the facts objectively, without phyletic aim or preconceptions, from the developmental point of view. As has been recognized since the work of Sanio, the differentiation of the leaf-trace bundles progresses basipetally from the node. Bugnon observed that in *Mercurialis annua*, as in many other plants, they normally fork into two, so avoiding incoming bundles immediately below, before uniting with other bundles lower down. The cotyledon traces likewise fork, though they do this sooner and in relation to the vascular system of the root.

Turning to the radicle, Bugnon notes that the root structure is quite typical. All other roots, however, arise from organs already differentiated. They form their own characteristic pattern of vascular arrangement, and this is linked by commissural elements to the appropriate tissues already present in the parent organ. In the case of the radicle, an exactly similar root apparatus has to be linked up, not with tissues fully differentiated, but with tissues still in a meristematic condition. The connecting tissues are therefore similar to ordinary conducting strands, not special commissural elements.

Bugnon did not, so far as I am aware, attempt to extend the same principles of interpretation to the wider range of facts which have been brought to light, and it appears worth while to see how far this can be done.

In the first place, from a causal point of view, certain principles may be regarded as established. The first is the power of self-determination inherent in growing organs and especially in apical growing points—each developing a characteristic pattern of external form and internal structure. The second is the influence of apical developing organs on the structure of other parts still capable of growth—this applying particularly in the basipetal direction and therefore mainly to the influence of the shoot apex and young leaves on the parts below them.

With regard to the root, a spectacular demonstration of its power of self-determination has been

provided by Philip R. White who, following on the pioneer work of Robbins and Maneval, succeeded in 1934 in proving that root-tips cut from the plant can be grown continuously for years in a nutrient solution containing the essential salts, sugar, and a small concentration of an extract of yeast.

In the large adventitious roots of many Monocotyledons, it is particularly evident that no relation exists between the pattern laid down in the root primordium and that already present in the stem to which it has to be connected. The repetitive nature of the pattern and its inherent stability also become more obvious. The alternation of exarch xylem strands with phloem strands, in a ribbon with definite radial polarity, expresses a harmonious balance of influences and developmental processes. The fundamental uniformity of the root pattern throughout the great majority of vascular plants is further evidence of this inherent stability.

To turn to the shoot: it will probably be admitted that the shoot apex is a self-determining and dominant centre of development. It controls the polarity of the shoot, and round it the repetitive pattern of leaf primordia unfolds. The apical bud as a whole controls also primary development and secondary growth in the stem below. There is much in the system of relations exhibited which is reminiscent of the part played by organizers in the development of animal embryos.

In the determination of primary structure in the stem the leaf primordia play a predominant part. The number of vascular strands in the leaf base depends partly on hereditary factors, but partly on size. This is particularly clear in Monocotyledons, where the bundles arise in succession, separated by parenchyma, as the new leaf primordium extends round the apex.

Now, in seedlings the conditions are unique. At two ends of a short meristematic axis are two self-determining centres of different kinds in close proximity, two opposite poles, a shoot pole and a root pole, each of which is capable of impressing its own inherent pattern on the meristematic tissues to which it gives rise. Under these conditions we cannot assume that the spheres of influence of each will be sharply defined, or that they will necessarily be fixed. If the influence of the poles depends on hormones emanating from them, the boundary might well change with changes in relative vigour of the two organizing centres, and differ also from one species to another.

It appears reasonable, therefore, as a working hypothesis to interpret the structure of seedlings in the following way:

(1) The cotyledons and, if the plumule is precocious, the plumular primordia, influence the number

of procambial strands in the hypocotyl and its diameter growth at an early formative stage. The form of the cotyledons plays a part. Nutritive and other factors afterwards affect the expansion of the hypocotyl and the degree of separation of the bundles by parenchyma.

(2) Differentiation within the strands of procambium is controlled initially by the root apex in the majority of cases, but to a variable distance upwards. The triad represents the smallest unit of the root pattern, existing as a detached arc, whether in the hypocotyl or a dorsiventral cotyledon.

(3) In the upper part of the seedling, sometimes only in the blade of the cotyledon, sometimes also in the petiole, or even lower, the shoot itself holds sway, and in place of a triad is found a single bundle. The intervening region is one of compromise and accommodation between the two patterns.

(4) With increasing activity of the shoot, further development is stimulated, from above downward, in the formation of centrifugal xylem on the inside of the phloem strands. These appear to be the main channels of the basipetal influence. In Dicotyledons the centrifugal xylem is commonly if not generally the result of cambial activity, which ultimately extends down into the root itself.

One factor in the determination of the relative preponderance of root and shoot is very probably the production of auxin by cotyledons and plumule.

We have seen how a substance of known composition, auxin, acts as an agent in the co-ordination of different parts of a plant, but this does not mean that we can explain the activities that are co-ordinated. Great as have been the advances in biochemistry, we are not yet furnished with the means of expressing in physico-chemical terms the delicacy and subtlety of the adjustments exhibited even in plants.

Take, for example, the adhesive disk and haustorium of a mistletoe seedling. This remarkable organ is the result of a series of co-ordinated responses in the growth of the little green meristematic knob from which it arises. Contact pressure leads to one-sided growth, by which it brings itself face downward on to the surface, to which it adheres with the aid of a special viscous material. There follows further growth of its now dome-shaped outer shell, the edge of which moves slowly outwards as the area of attachment widens. Under the dome, cells of the lower surface grow out as papillae, which adhere closely to the epidermis or cork of the host twig. By the outward and upward movement of the growing shell and a contraction of tissue within it, the papillae are lifted sideways and the adhering outer protective layer is torn up. Then new papillae fasten themselves to the next cork layer and the tearing process is repeated. In this way several such layers may be picked up until

a breach is made in the periderm, giving access to the living tissues within. Through this slit the wedge-shaped haustorium grows.

It is strikingly obvious in a specialized organ such as this, where growth is closely and uniquely adjusted in response to a particular environment and in relation to a peculiar, special mode of life, that structure and behaviour are interdependent. There is, however, no logical justification for neglecting to interpret the development of ordinary plant organs on similar lines. The main difference is that the cells respond chiefly to internal influences,

though the organ as a whole exhibits tropic curvatures in response to appropriate external stimuli.

It is not possible to pursue this line of thought further; but reference should be made to the work that has already been done by Schüepf, Priestley, Adriance Foster, Helm, Grégoire, Snow, the veteran Schoute, and many others towards the elucidation in detail of the course of differentiation in the shoot of Dicotyledons and Monocotyledons, from which are gradually emerging a better understanding of the principles of their developmental organization.

NUCLEAR REACTIONS IN STELLAR EVOLUTION

BY PROF. G. GAMOW,

GEORGE WASHINGTON UNIVERSITY, WASHINGTON, D.C.

(1). THE question of the sources of energy of stars, and the closely connected question of stellar evolution, have presented for a long time the most important unsolved problem of theoretical astrophysics. The first step towards the understanding of the physical processes leading to the tremendous energy liberation which is responsible for the observed radiation of stars was made about ten years ago. It was shown¹, on the basis of the quantum theory of nuclear transformations, that, at the very high temperatures existing in the interior of stars, the ordinary thermal collisions between the particles possess sufficient energy to produce artificial nuclear transformations. It was also shown that the energy liberation in such *thermo-nuclear reactions* is sufficiently high to explain the radiation of stars only in the case of collisions between the protons and the nuclei of light elements (up to about atomic number 10). It took, however, ten more years before our knowledge concerning nuclear reactions developed to such an extent that it became possible to choose particular nuclear reactions as responsible for the energy-production in different cases and to give on this basis a clear and consistent picture of stellar evolution. The exact formula for the energy production of a thermo-nuclear reaction (per gram per second) can be written in the form²:

$$\epsilon = \frac{4}{3^{1/2}} \rho X_1 X_2 \frac{\hbar \Gamma r_0^2 Q}{m_1 m_2 m e^2 Z_1 Z_2} \exp. \left(\frac{2v_0 m e^2 Z_1 Z_2}{\hbar^2} \right)^{1/2} \tau^2 e^{-\tau} \quad (1)$$

Here ρ is the density of the gas, X_1 and X_2 the concentrations (by weight) of the two reacting

types of nuclei, m_1 and m_2 their masses ($m = m_1 m_2 / (m_1 + m_2)$), $Z_1 e$ and $Z_2 e$ their electric charges, r_0 the combined radius, Q the energy production per reaction, and $\Gamma/\hbar$ the probability of reaction after the penetration through the potential barrier. The dependence upon temperature is given through τ , which is defined by:

$$\tau = 3 \left(\frac{\pi^2 m e^4 Z_1^2 Z_2^2}{2 \hbar^2 k T} \right)^{1/2}, \quad . \quad . \quad . \quad (2)$$

T being the absolute temperature of the gas and k the Boltzmann constant.

This formula was used³ in choosing the nuclear reaction responsible for the energy liberation of the sun. The complete list of all possible reactions between the protons and different light nuclei is given in the accompanying table, together with the values of Q and Γ :

Reaction	Q (mMU)	Γ (ev.)	ϵ ($\frac{\text{erg.}}{\text{gm. sec.}}$)
$^1\text{H} + ^1\text{H} \rightarrow ^2\text{H} + e^+$	1.53	Ref. 4	2.2
$^1\text{H} + ^1\text{H} \rightarrow ^2\text{He} + \nu$	5.9	1	$1 \times 10^{+17}$
$^1\text{H} + ^3\text{H} \rightarrow ^4\text{He} + \nu$	21.3	10	$3 \times 10^{+16}$
$^1\text{H} + ^3\text{H} \rightarrow ^4\text{He} + ^1\text{H} + e^+$	4.1	5×10^4	$1 \times 10^{+16}$
$^1\text{H} + ^3\text{H} \rightarrow ^4\text{He} + ^1\text{H} + e^+$	18.6	4×10^4	$5 \times 10^{+15}$
$^1\text{H} + ^3\text{H} \rightarrow ^4\text{He} + ^1\text{H} + e^+$	2.4	10^4	$3 \times 10^{+15}$
$^1\text{H} + ^3\text{H} \rightarrow ^4\text{He} + \nu$	9.2	10	$3 \times 10^{+14}$
$^1\text{H} + ^3\text{H} \rightarrow ^4\text{He} + \nu$	9.4	10^4	$3 \times 10^{+11}$
$^1\text{H} + ^12\text{C} \rightarrow ^13\text{C} + \nu$	0.4	0.02	1.1
$^1\text{H} + ^12\text{C} \rightarrow ^13\text{C} + \nu$	2.0	0.6	180
$^1\text{H} + ^12\text{C} \rightarrow ^13\text{C} + \nu$	8.2	30	$3.6 \times 10^{+4}$
$^1\text{H} + ^12\text{C} \rightarrow ^13\text{C} + \nu$	7.8	5	30
$^1\text{H} + ^12\text{C} \rightarrow ^13\text{C} + \nu$	5.2	10^3	$4.5 \times 10^{+4}$
$^1\text{H} + ^12\text{C} \rightarrow ^13\text{C} + \nu$	0.5	0.02	$7 \times 10^{+4}$
$^1\text{H} + ^12\text{C} \rightarrow ^13\text{C} + \nu$	8.8	10^3	55
$^1\text{H} + ^12\text{C} \rightarrow ^13\text{C} + \nu$	10.7	10	$7 \times 10^{+4}$
$^1\text{H} + ^12\text{C} \rightarrow ^13\text{C} + \nu$	8.0	10	$8 \times 10^{+9}$
$^1\text{H} + ^12\text{C} \rightarrow ^13\text{C} + \nu$	7.0	10	$3 \times 10^{+11}$

The last column gives the calculated energy liberation of different reactions for the conditions