

LAW OF MODIFICATIONS¹

BY

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While appreciating the honour done to me, I am conscious of my unworthiness. During the hour before me, I propose to discuss certain biological phenomena which are regarded as adaptive. The plant organism in which we are all interested exhibits these adaptive structures so commonly that they have attracted the attention of botanists since almost the beginning of botany itself. It is not possible for anybody, very much less for me, to enumerate and explain all such structural modifications. My purpose will be served if I can put certain principles underlying these adaptations and thereby succeed in directing your attention to the further and more intense study of these structures.

For every organism, there is a set of conditions which we consider as normal. Under such conditions the organism develops in a specific manner. Thus, for example, for the existing seed-plants, mesophytic conditions are regarded as normal. Under these conditions we expect the plant to develop in a particular manner from germination to seed-production and death. If the conditions change, or, which is the same thing, if the plants grow in a set of conditions very different from the normal, we find structural modifications, microscopic and macroscopic, many of which are regarded as adaptive, that is to say, produced in response to the surroundings.

There is, however, a large number of modifications which cannot be explained in this way. Thus, while discussing the forms of leaves, Goebel² says, "We find that many forms appear through variation and cannot at any rate be regarded as direct adaptations to environment." Another example is the development of anthocyanin pigment. No common adaptive significance can be attributed to all cases of anthocyanin development. Thus, Miss Wheldale³ says, "For the time being we may safely say that it has not been satisfactorily determined in any one case whether its development is either an advantage or a disadvantage to the plant."

¹ Presidential Address at the Annual Meeting of the I. B. S., at Nagpur, 1931.

² Goebel, K.—*Organography of Plants*, Vol. II, p. 345. (English translation.)

³ Wheldale—*The Anthocyanin Pigments of Plants* (1916), p. 141.

From these and other such instances it is clear that all observed modifications in organisms growing in abnormal surroundings cannot be explained as constituting an advantage by themselves, although physiological significance of many such characters has been attempted and found. Regarding the origin of these adaptations various explanations have been given. The teleological explanations are so well known that one need not pause to discuss them. This much can be said that teleology does not easily satisfy us. On the other hand, Lamarck, Darwin and others have all fixed their attention on the apparently adaptive structures and have offered explanations which have been accepted, discussed and doubted in turn. While most people are paying attention to characters which are clearly adaptive, very few have turned towards those characters which have no clear adaptive significance, such as the presence or absence of a few hairs on the leaves or the presence or absence of a little pigment. Among such characters may be counted those abnormalities we call monstrosities. If any explanation should be given of variations, it must include the monstrosities.

To my mind, it seems to be a mistake to search for explanations in the modifications which we can easily observe. It would perhaps be more profitable to find out the internal adjustment of which the external form is the outcome. Such an explanation has been attempted by Klebs¹. He says, "The manifestation of each form, which is inherent as a potentiality in the specific structure, is ultimately to be referred to external conditions. An insight into this connection is, however, rendered exceedingly difficult, often quite impossible, because the environment never directly calls into action the potentialities. Its influence is exerted on what we may call the inner world of the organism, the importance of which increases with the degree of differentiation. The production of form in every plant depends upon processes in the interior of the cells, and the nature of these determines which among the possible characters is to be brought to light."

Although we are far from knowing all the internal factors which, in response to the external conditions, bring about the observable modifications in the organism, the solution of the problem seems to lie in that direction. The path is certainly difficult but, if any solution is to be found, a search along this path must be made. When the solution is found, it must be such

¹ Klebs, G.—Darwin and Modern Science (1910), p. 223 *et seq.*

that it can satisfactorily explain not only what we call adaptations but also what we call monstrosities and those structures whose adaptive values are obscure at present.

The internal conditions are various. The concentration of the sap, the amount of sugar present, the osmotic pressure, the permeability, the acid or alkaline reaction of the sap, and physical forces may, each or all of them, play a part in bringing about the responses which result in the observed modifications. In order to guide our search, we ought to have a working principle, and I venture to suggest one. I hope to adduce some evidence in support of this principle before I conclude, but I should like to state at the outset what, to my mind, appears as the underlying principle of all modifications.

I have come to believe that "*If an organism, an organ or even a cell is subjected to a stress, physical or chemical, the organism, the organ or the cell changes in such a way that the effect of the imposed stress is nullified.*"

This will be referred to in what follows as the *Law of Modifications*. It will be seen that this is analogous to the well-known rule of le Chatelier which "states, in effect, that if a chemical system which is in equilibrium be subjected to a constraint, a change will take place in the system which is in opposition to the constraint"¹.

In the case of the chemical system, the constraint may be the alteration of any one of the conditions on which the equilibrium depends, e.g., the temperature, pressure or concentration. When, however, we come to the organism considered as a system in dynamic equilibrium, the conditions are much more numerous than in the chemical system inasmuch as the various constituent parts of the organism have their equilibria dependent on different sets of conditions. These conditions may be internal or external, may be physical or chemical. The external may influence the internal and the physical the chemical. Thus Klebs² discussing the influence of environment on plants says, "A way, however, is opened for investigation; experience teaches us that this inner world is not a constant factor: on the contrary, it appears to be very variable. The dependence of *variable internal* on *variable external* conditions gives us the key with which research may open the door."

¹ Fenton, I. H. J.—Outline of Chemistry, 1921, p. 159.

² Klebs, G.—Darwin and Modern Science, p. 228.

Among the external conditions, which, of course, may vary in intensity for various plants and various organs of the same plant, may be mentioned the quality and quantity of light, amount of moisture, either in liquid or gaseous condition, the pressure, the amount of oxygen, the concentration of various salts held in solution in the water surrounding the absorbing organs of the plants, and temperature. Similarly among the internal conditions may be included the osmotic pressure, acidity or alkalinity of the sap and the presence of certain colloids, apart from temperature and pressure. These internal conditions may be influenced by the external conditions in conformity with the law of modifications we have stated at the outset of this discourse.

One has neither the time nor equipment to quote the very numerous illustrations that one would like to in support of the statements. It would serve my purpose to give a few instances to make my point clear. These illustrations I shall draw either from the work of others or from personal observations.

Light.—If a plant is grown in absence of light, certain modifications are produced which counteract the effects of want of light. Thus, for example, Priestley and Ewing found that “etiolated stems are prone to develop a functional endodermis, in species where such a layer is lacking in the stem grown under normal conditions”.¹ The explanation they offer seems to support our Law of Modifications. They say that this endodermal layer checks the outward passage of sap, and hence leads to an accumulation of nutrient material, which determines meristematic activity in the tissues immediately within the endodermis, and thus leads to excessive root production. The absence of light means absence of photosynthesis and thus probably progressive fall in osmotic strength. Accumulation of nutrient material by the formation of a functional endodermis and production of new roots would lead to greater absorptive power of the plant leading to accumulation of salts and thus the progressive fall of osmotic strength will be checked. It would be of interest to compare the proportion of ash to dry matter in etiolated plants with that in normal plants.

It is needless to mention the case of creepers and climbers in this connection. The changes in habit of these plants most probably have originated in response to a change in the intensity of light. The effect of this modification has certainly undone the stress imposed by lack of sufficient light.

¹ Arber, A.—*Monocotyledons*, 1925, p. 11.

The case of chromatic adaptation of the red algae, and certain blue green algae (i.e. *Oscillaria Sancta*) under experimental conditions, as found by Gaidukov¹ also fit in with our law.

I would close this section with reference to a case which seems to me a case of adaptation to light, and that is the flower of *Quisqualis indica*, Linn. The flowers are white during the night when they bloom, but they begin turning pink at dawn. What is the nature of the stress which light imposes on the flower and how this is undone by the development of pigment is under investigation. Stahl's² view that the development of anthocyanin raises the temperature clearly does not fit this case. As we have noted above, one explanation may not fit all cases. The same phenomenon may be the result of the response of the organism to a variety of stresses imposed on the system. It must be left to research to find out the particular cause in a particular case or group of cases.

Moisture.—Water plants are the best examples that can be given as illustrations. The teleological explanations do not satisfy us any longer. Physico-chemical explanations have been attempted in many cases, and in each case one finds that the organism responds in a way that reduces the stress imposed. In most of the water plants, however, the modifications one sees are not direct result of water, but they are indirectly brought about by water which restricts other factors such as light and oxygen supply, and increases the pressure on deep water organisms. One modification which seems to be the direct outcome of water is the general absence of cuticle and presence of mucilage on water plants. What the actual process is is not clear, but it is evident that the presence of mucilage ensures a fairly constant layer (chemically speaking) just outside the epidermis.

At the other extremity, in xerophytes, the lack of water induces a number of modifications most of which have been explained teleologically, but there are some which cannot be so explained. The general explanation can only be found if we search for the stresses imposed by the habitat and the way the system reacts under such stress. Insufficiency of water or excessive loss of water or both would be creating internal constraints which lead to responses in opposition to these. Thus, for example, on the restricted water content of the plant depends the formation of pentosans³ to which the succulence of xerophytes is due.

¹ Gaidukov, N.—Quoted in Stiles' *Photosynthesis*, 1925, pp. 175-76.

² Wheldale, M.—*The Anthocyanin Pigments of plants* (1916), p. 135.

³ Spoehr, H. A.—*Carbohydrate Economy of Cacti*, (1910), p. 77.

The production of pentosans is a move which counteracts further desiccation. Similarly, the development of cutin on the epidermis which is brought about by the changed sap concentration due to the dry atmosphere checks further loss of water and thus reduces the stress.

Similar stresses probably lead to the lignification of tissues in certain types of xerophytes. This perhaps has led to the confinement of the growing regions in the nodes of the bamboo and other grasses to inside the clasping leaf-base. The exterior of the leaf-base exposed to the habitat develops more strengthening elements and thus clasps the node more tightly than ever. The enclosed portion of the node remains soft and meristematic.

In cases where no obvious biological explanation is forthcoming, as, for example, in the case of hairs on xerophytes, one has to study the details of the process of hair production, and it is likely that an explanation will be forthcoming.

Oxygen.—Again, we go to the water plants for illustrations as to how a change in the concentration of oxygen in the environment leads to modifications. The development of aerenchyma is a modification which may be attributed to insufficiency of oxygen. The submerged plant-organs are subjected to a habitat which has less oxygen than the atmosphere, and, therefore, "Water plants have considerably less oxygen at their disposal in each unit volume of the surrounding medium than is the case with land plants"¹. Under such restricted supply of oxygen, the cells divide and grow in a way leading to the formation of lacunae. The result is that oxygen produced during photosynthesis accumulates in these air spaces and the stress imposed is undone to some extent. Another instructive example is the aerenchyma which serves as a float to some water plants. Such floats are found in *Jussiaea* roots, and *Neptunia* stems, and the petioles of *Eichhornia* and *Trapa*, and on the peduncle of *Utricularia stellaris*. In all these cases restriction of oxygen supply seems to be the cause and the development takes place near the surface. Thus, in the case of *Jussiaea*, Arber remarks, "The present writer would prefer to say that the presence of a minimum of oxygen is possibly a necessary condition for the process of suberisation, which is inhibited when the oxygen content of the cell-sap falls below a certain point"². The same reason probably holds in the case of *Neptunia* and *Utricularia stellaris*. The case is slightly different with *Eichhornia*. In this weed, which is monocotyledonous, the

¹ Arber, A.—Water Plants (1920), p. 255.

² *Ibid.*, p. 189.

growing region of the petiole is at the base, while the most expanded portion of it is a little way above the surface of water. The initiation of the lacunae takes place just under water as in the cases just cited but expansion takes place above water. It is just possible that humidity of the surrounding air affects the expansion. The leaves and scapes of *Scirpus articulatus* develop extensive aerenchyma even in the aerial parts. Here also the meristematic region is the base which is under water. In dicotyledonous plants like *Enhydra fluitans*, the cambium is the meristem, and this is perhaps the reason why the submerged portions have lacunae while the aerial shoots have not.

This is only one type of modification to undo the constraint imposed by lack of oxygen. But where other factors limit the size, lack of oxygen induces other types of development. Thus in *Myriophyllum*, the leaf-segments are hair-like and rounded so that all parts have access to oxygen dissolved in water. The segments do not possess any lacunae. Podostemads which grow in running water are modified by the current into thalloid forms while they are at the same time subject to some restriction as regards oxygen. The result is that they produce other types of modifications. Thus *Podostemon subulatus* simulates an alga *Bostrychia moritziana* which also grows in rapids¹. *Oenone multibranchiata*, another Podostemad, produces "gill-tufts" in similar surroundings².

Pressure.—That pressure modifies form is well known in the case of deep-sea organisms. Even in organisms which live in shallow water, the extra pressure due to the column of water over them seems to produce modification. The modification of form met with in the leaves of water plants seems to me to be a case in point. The submerged dicotyledons and pteridophytes have generally dissected laminae, while the monocots have ribbon-like leaves. These two groups differ in the development in their leaves.

In the monocotyledons, the growing region is generally basal and is protected by the bases of older leaves while in dicotyledons the lamina develops later than the petiole, although the primodium may be laid down early. Thus in the monocotyledons the growing region of the leaf is not subjected to so great a pressure as the blade in the dicotyledons. The pressure of water prevents the meristem from producing a laminate leaf and the segments become acicular and thereby nullify the stress, as the pressure is uniform

¹ Arber, A.—Water Plants (1920), p. 114.

² Ibid., p. 118.

on all sides. Even in the case of monocotyledons which possess a lamina, this fails to develop under water. Same explanation applies to such pteridophytes as *Salvinia*.

Another interesting effect of pressure is observed in *Eichhornia*. This water-weed produces leaves with swollen petioles, and the leaves from the beginning possess a large amount of air-spaces. When a seedling with sufficient amount of lacunae is submerged, the upward thrust exerted by the water puts the plant under stress. The result is that a transverse meristem is formed and the seedling breaks off from the root-stock and floats up, thus nullifying the stress exerted by pressure.

Concentration of salts outside.—The halophytes are *par excellence* illustrations of our law under this head. Increase in the osmotic strength of the solution outside puts the organism under stress decreasing the entry of water. The organism changes the osmotic strength of the cells to counteract the stress. Thus, Rybin, and Ursprung, Blum, all found¹ that prolonged immersion in solutions of increased concentration increases the osmotic strength of the cells of the absorbing zone of the roots. We have indications of similar change in the case of parasites like *Cuscuta*. If the twig of the host on which *Cuscuta* is growing is supplied with solutions of sugar under pressure, it is found that increased absorption of sap takes place and copious starch formation occurs in the tissues of the parasite.

Another interesting type of modification is the gall formation. Whether caused by insect or fungus, the damaged tissue must have an amount of toxin whatever that may be. This toxin puts a local stress and the cells divide and form a large number of cells. The effect being an innocuous dilution of the toxin resulting in the removal of the strain.

As regards temperature inducing changes in plants, illustrations are difficult, as we do not know enough about chemical reactions going on in plant cells. Some cases are clear. Thus the development of anthocyanin pigments in plants are known to increase the temperature of the tissue of many plants and this development takes place when the temperature of the habitat falls. This is found in autumn leaves and Wheldale ascribes this to the accumulation of carbohydrates due to slow diffusion from the leaves. But such cases as the roots of some water plants such as *Eichhornia* are difficult to explain. These organs develop a blue pigment on the approach of cold weather. It is

¹ Maximov, N. A. — The Plant in Relation to Water (1929), p. 94.

to be seen whether carbohydrates accumulate in these organs more in the cold weather than in summer. Equally difficult is the case of *Quisqualis indica* already referred to.

These illustrations, which could be multiplied, are obvious, but there are numerous cases where modifications occur, which have no apparent adaptational significance. In this class are to be included the monstrosities. These monstrosities, one believes, are the results of organic response to transient stresses imposed by the external or internal conditions. Those of us who are interested in these abnormalities should pay a little more attention to unravelling the conditions under which these occur than to mere recording them. Then only we shall be in a position to state what causal stress brings about the particular modification under examination. Our knowledge will be on a sure footing if we could reproduce the modification by experiment. The conditions may be so subtle, especially, if we take into consideration the cosmic rays as has been suggested lately, that we may not at all reproduce the conditions in the laboratory. We have also to take into account the time of exposure to any set of conditions before the result can be produced. Moreover, the developmental stage at which the organism is exposed to the modifying conditions is also important. If everything is favourable, then it seems possible to reproduce the modifications at will. The goal is still far and arduous, but that need not deter us from attempting an approach.

It should not be inferred from what has been said that the whole of life is physical and chemical. We are only understanding the details while the main thing is mysterious as ever.

Now, I must bring my remarks to a close and thank you all for the patient hearing you have given me. I have run the risk of saying nothing that was perhaps not known to you in order to emphasise the fact that morphological study could still be profitable if pursued from a physiological standpoint. The barrier that is often raised between different branches, which are really different aspects, is harmful. Form and function are so intimately related that the study of one cannot be complete without the study of the other.