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PLANT PHYSIOLOGY

BY

DR. LUDWIG JOST

SUPPLEMENT

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DR. LUDWIG JOST

AUTHORIZED ENGLISH TRANSLATION BY

R. J. HARVEY GIBSON

SUPPLEMENT

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SUPPLEMENT

P. **1**, l. 36, *for* Changes of position . . . transformation of energy (P. **2**, l. 6), *read* Changes of position, or movements of the entire organism or of its parts, are not readily observable in all forms, still in every case they may be shown to exist by using appropriate means. We speak of these phenomena collectively as Movement.

2, ll. 13–15, *for* In the following . . . metabolism *read* In the following pages we have to treat of changes in form or the physiology of development, changes in space relationship or the physiology of movement, and metabolic changes or chemical physiology, and we shall begin with the last of these, metabolism.

ll. 42–4, *for* If a physicist were . . . bent over *read* If a physicist were to find that a wire, fixed at one end and bearing a metallic knob at the other, bent over, as gravitation acting on the knob would bend it, he might reasonably deduce that the wire did so

3, ll. 9–16, *for* Qualitative analysis . . . very limited *read* The results of qualitative analyses lead one to the conclusion that of the seventy or more elements that are present in the soil only a few are regular constituents of the plant body, namely, the following thirteen: H, O, Cl, S, N, P, Si, C, K, Na, Ca, Mg, Fe. The gain in scientific insight which such an analysis affords us is, however, all the more limited since in this enumeration, be it right or wrong, the elements present in small amount are entirely omitted. Were it asserted that all the elements were to be found if a careful search were made for them, it would be rash to contradict the assertion.

ll. 33–5, *for* We know . . . families *read* We may perhaps, in time, get to know of the existence of one or more compounds peculiar to each species; meanwhile we are already acquainted with many which are characteristic of certain genera or families.

ll. 49–54, *for* such as . . . student of Biology *read* more especially that of ČAPEK (*Biochemie*), and also those of EBERMAYER (*Phys. Chem.*), HAMMERSTEN (*Phys. Chem.*), and ABDERHALDEN (*Phys. Chem.*).

4, l. 12, *after* cholesterin *read* (phytosterin)

l. 13, *delete* but which have a more complex composition.

l. 23, *delete* Amido-compounds . . . acid-amides, *and for* The amido-acids *read* The amino-acids

ll. 25–6, *for* amido-succinic *read* amino-succinic ; *for* amido-caproic *read* amino-isobutyl-acetic acid ; *for* amido-propionic *read* amino-propionic

l. 27, *for* The acid-amides arise *read* Amides of amino-acids also frequently occur, which arise

l. 28, *for* amido-succinic-acid-amide *read* amino-succinamic acid

ll. 29, 36, 38, *for* etherial *read* essential

l. 38, *delete* 6. *and follow on* l. 37.

ll. 39–40, *delete* these bodies . . . determine ; *for* 1900 *read* 1906

l. 41, *for* 7. *read* 6., *and renumber succeeding paragraphs accordingly.*

ll. 49–50, *delete* the ' aromatic sugar '

5, l. 43, *for* amides *read* amino-acids

6, ll. 4–5, *for* while, on the other hand *read* and between these intercellular spaces filled with air. The volume relations existing between the cell-cavities and the intercellular spaces are very varied. In ordinary foliage leaves the intercellular spaces amount to about a quarter to one-fifth of the entire volume ; but that proportion is much exceeded in water plants. UNGER (1854) found that about two-thirds of the volume of the leaf of *Pistia* consisted of intercellular spaces, and only one-third of cell substance. The usual chemical analysis of a plant tells us nothing of these intercellular spaces, and yet these are of fundamental importance. All plants, however, are not so elaborately constructed;

7, ll. 44–7, *delete* We may further . . . swollen body

8, ll. 1–2, *for* (such as that . . . greatest value *read* was carried out by REINKE and RODEWALD (1881–3), and the service they thus rendered was especially valuable, inasmuch as they showed that such a sample by no means consisted of proteid only.

l. 15, *for* Amide bodies *read* Amino-acids

9, ll. 18–52, *for* This organization . . . homogeneous solution *read* In order to study this organization, protoplasm has been examined with the very newest and strongest objectives. These investigations, however, have led to no interpretation that has received universal acceptance. From the zoological-anatomical point of view several theories have been advanced based on the belief that protoplasm consisted of distinct fundamental units, granules, or fibrillae, or reticula formed by their union, or, finally, of small alveoli (BÜTSCHLI, 1892). From the botanical standpoint, on the contrary, it has been held that there is no constant and fixed structure in the protoplasm, but that, according to circumstances, it may be reticular, fibrillar, or alveolar (BERTHOLD, 1886 ; KLEMM, 1895 ; FISCHER, 1899 ; DEGEN, 1905). On the whole, botanists appear to lean more and more to the view held by BERTHOLD (1886), A. MEYER (1895), and A. FISCHER (1899), namely, that protoplasm is a fluid (water) in which a mixture of substances with large molecules, such as proteid, or even more complex bodies still, are in part dissolved, in part in a state of suspension. When microscopically examined, this fluid often appears quite homogeneous, but the ultra-microscope (GAIDUKOW, 1906) demonstrates distinct particles in it, as in colloidal solutions. Such colloidal solutions not infrequently exhibit the characters of ' pseudo-solutions ', differentiating themselves into a more fluid portion (i.e. water with solids in solution) and a more solid portion (i.e. solids containing dissolved water). Indeed, according to circumstances, the solids may assume the form of a honeycomb whose cavities contain fluid substances, or may take on the form of granules, fibrillae, or reticula. In protoplasm also, such a structure may be explained by pseudo-solution phenomena ; formation and redissolution of these structures may continue to take place during the life of the protoplasm (DEGEN, 1905). Similar structural appearances, again, may arise on the death of the protoplasm. As FISCHER (1899) has shown, the reagents employed in ' fixing ' act in a similar manner on the proteids of the protoplasm, and one is able to demonstrate very different structural features in the protoplasm according to the nature of the fixative employed.

Although, in spite of these investigations, the ultimate structure of the protoplasm has not as yet been unveiled, still no one can any longer believe that it is merely a homogeneous solution of the numerous substances found in it.

P. **11**, l. 44, *for* capable of swelling in *read* saturated with

13, ll. 3–11, *for* water enters . . . inflowing water *read* water continues to enter in spite of the counter-pressure exerted by the mercury. Finally, equilibrium is reached when the amount of the inflowing water is equivalent to that which the mercury can press out in the same unit of time. The pressure exerted on the inner surface of the porous pot is spoken of as osmotic pressure, and the height reached by the mercury gives a direct measure of it. The apparatus serves to compute the amount of osmotic pressure, and is hence termed an osmometer.

ll. 19–31, *for* and if it were . . . supporting clay cell *read* its volume is thereby increased. The cell-wall is thus elastically stretched, and, in its effort to contract, squeezes some of the water out of the vacuole. In this case, also, an equilibrium is reached in the long run, namely, when the amounts of water entering and passing out are equal. The osmotic pressure, which can be recognized in the case of the osmometer by the height of the column of mercury, is, in the case of the cell, demonstrated by the tension or extension of the cell-wall. If one of the long cells of *Nitella* be held between the finger and thumb, and pricked with a needle, it is possible to feel the contraction which results from the reduction of the pressure within. In the uninjured cell the protoplasm is pressed firmly against the cell-wall in consequence of this osmotic or turgor pressure ; without such a resistant layer it could not sustain the pressure any more than could the copper-ferrocyanide membrane without the porous pot.

14, ll. 1–14, *for* In certain cells . . . takes place *read* We shall see later, however, that not all cells behave in the same manner as the beetroot cells used in DE VRIES's experiment. Even the beetroot behaves differently under certain conditions. As a matter of fact, many cells exhibit a perceptible exosmosis not only of sugar, but also of salts, proteid, asparagin, &c. (compare p. 9 of Suppl.).

15, ll. 36–48, *for* Thirty years ago . . . only to be expected *read* DE VRIES'S researches (1884) have shown

l. 49, *for* specific gravity *read* dissolved weight

l. 54, *for* gram-molecule to the litre *read* gram-molecular solution

16, ll. 17–18, *for* equivalent of 0·01 G.M. to the litre *read* equivalent of a 0·01 gram-molecular solution,

ll. 40–2, *for* their constituent ions . . . molecule does *read* their constituent ions. Thus potassium nitrate dissociates into the kation K^+ and the anion NO_3^-. Each free ion has the same osmotic value as the entire molecule.

ll. 49–55, *for* We have spoken . . . substances in solution *read* Previously one sought for the cause of osmotic pressure in the attraction existing between the soluble substance and its solvent ; nowadays, another explanation has come to be accepted. Following VAN 'T HOFF, one ascribes to substances in solution

17, l. 16, *for* cel *read* cell

l. 18, *for* sugar *read* cane sugar

l. 34, *delete* of *before* the pressure

ll. 42–3, *for* impacts . . . ions *read* impacts of the molecules and of the ions dissolved in water

l. 44, *after* theory *insert* which indeed is not the only one possible (comp. STEINBRINCK, 1904).

18, l. 14, *for* had best be avoided *read* cannot be discussed here (see Lecture XXXI).

l. 27, *for* atmospheres in *read* atmospheres even in

l. 28, *after* onion *read* and as much as forty atmospheres in the pulvini of grasses.

ll. 35–6, *for* manifestly . . . accumulated *read* merely an incidental effect of the nature of the stored

19, ll. 52–3, *for* alteration . . . a part *read* effect is due solely to a change in the acidity of the cell-sap.

21, ll. 12–30, *for* On this question . . . physical manner *read* NATHANSOHN'S osmotic researches (1902–4) have made us acquainted with a series of phenomena which are not to be interpreted in a purely physical manner. He found that many protoplasts are permeable to salts occurring in the environment, but that these do not go on entering until the concentration inside is the same as that outside ; he found, on the other hand, that osmotic equilibrium ensued when the concentration inside reached a certain definite fraction of the concentration outside. Should the concentration of the fluid outside increase, further entry takes place ; if it decreases the salt undergoes exosmosis until this definite relationship between the solutions inside and outside is re-established. Under these circumstances, it would be quite possible to induce permanent plasmolysis with a substance, although it continued to enter the cell. In this way we might explain the contradiction previously noted, namely, that all nutrients (salts, sugars) which necessarily reach the interior of the cell must induce plasmolysis. It is very desirable that these observations of NATHANSOHN'S should receive confirmation by further research.

It should be noted here that all the substances required by plants do not behave like salts and sugar. The essential gases, oxygen and carbon-dioxide more especially, may be shown to enter the protoplasm readily (J. K. GOEBEL, 1903). Protoplasm is also permeable to nitrogen and hydrogen, as numberless instances prove. Since, however, many lower organisms contain ' gas-vacuoles ', the surrounding protoplasm must be impermeable to the gases in them.

l. 52, *for* So far as purely physical . . . *to the end of the lecture, read* OVERTON (1895–1900) has made several attempts to refer the absorption of the materials by the plasma to the principle of 'selective solubility' ; viz. only those substances can enter the cell that are soluble in the plasmatic membrane. OVERTON'S researches indeed show that the substances that enter most rapidly are those, such as alcohol, ether, chloroform, chloralhydrate, &c. (for a complete list see OVERTON, 1899), that are characterized by their ready solubility in fatty oils. Since, however, there are several reasons for believing that the plasmatic membrane cannot consist of oil, OVERTON puts forward the hypothesis that it might be, in great part, composed of cholesterin. In fact, he has shown that solubility in cholesterin agrees much better with absorption by protoplasm than solubility in oil, and that this is especially true of aniline dyes. Hence, according to OVERTON (1899) the absorption of a fatty oil (Lecture XIII) and of xylol through a cholesterin layer would be just as intelligible as the absorption of water. In fact, cholesterin can absorb water, but NATHANSOHN (1904) has shown that its capacity for dissolving becomes completely altered by this absorption. For this and other reasons (comp. PFEFFER, *Phys.* I. 110, note) NATHANSOHN rejects the idea of a homogeneous external layer, and believes that the periphery of the plasma consists of a kind of mosaic of alternating cholesterin and living protoplasmic particles. The cholesterin would thus determine the permeability of the membrane for substances soluble in oil, while the protoplasmic particles would permit the passage

of water, salts, and also of atmospheric gases, oxygen, nitrogen, and carbon-dioxide, and would regulate the entry of these in the way above mentioned. This hypothesis is certainly in harmony with all the differences in permeability of protoplasm that have been observed. First with regard to specific differences. Bacteria and Cyanophyceae allow many substances to diosmose easily to which the protoplasm of other plants is impermeable ; *Penicillium* does not permit the entry of salts of copper, which are taken up readily by the majority of plants ; *Beggiatoa* absorbs sulphuretted hydrogen, which cannot enter certain other Algae living in its neighbourhood. Moreover, variations occur in the single individual, due to external or internal transformations. It is frequently the case in experiments that the characters of the plasmatic layer cannot be altogether natural ; precipitation membranes may arise, for example, by contact of the protoplasm with a salt solution or even with water, and under such circumstances we should be studying the characters of these membranes and not those of one naturally formed (BERTHOLD, 1886, p. 152 ; PFEFFER, *Phys.* I. 110, note). It is thus doubtful whether in DE VRIES's experiment referred to above (p. 7 of Suppl.), and which attempted to prove the impermeability of the protoplasm of beetroot to sugar, quite natural plasmatic layers were under consideration or layers which had been altered by water or deficiency in oxygen, or which had been freshly formed ; for it has been shown that under appropriate experimental conditions sugar can very readily undergo exosmosis from such store-houses of reserve (WÄCHTER, 1905).

In speaking of a newly-formed plasmatic layer arising in the place of the old one we must not omit to emphasize the fact that such new formations have been shown to occur in certain regions of the protoplasm. It occurs, for instance, in *Vaucheria*, on the surface of every particle of protoplasm which exudes from a wound, and which rounds itself off into a sphere ; it may be observed to take place, also, on every cut surface in a Myxomycete plasmodium, as also in the interior of a plasmodium after the introduction of soluble foreign bodies (e.g. asparagin ; PFEFFER, 1890). In conclusion, we may note, further, that exosmosis and endosmosis depend not only on the characters of the protoplasm but also on those of the cell-wall, for it, too, may often render the cell impermeable to certain substances, e.g. when it becomes suberised (comp. KRÖMER, 1903). Now since suberisation may take place in a few hours after wounding (APPEL, 1906), it might be possible to explain in this way the absence of exosmosis of sugar in DE VRIES's beetroot experiment.

On the whole, therefore, it must be specially noted that recent research has tended to explain the contradiction that previously existed between the results of plasmolysis and experiences with reference to the nutritive necessities of the plant. One saw that the plants absorbed from the soil a number of substances which, on the evidence of plasmolysis, could not pass through the protoplasm. We now know that almost all bodies can pass through the protoplasm, but that it regulates the material exchange by altering its characters. This knowledge certainly forces upon us the conviction that the material exchange is a complicated vital phenomenon and not, as used to be thought, a simple physical process.

P. **26**, ll. 19–21, *for* and also . . . considerable *read* but chiefly, and widely, with the number and size of the spaces left between the soil particles : the water capacity is, however, always very considerable.

28, l. 20, *for* (1748) *read* (1731–3)

ll. 24, 26, *for* 1882, p. 19 *read* Lectures, p. 13.

ll. 39–44, *for* Root-hairs are . . . which have the effect *read* As BÜSGEN (1905) has shown, different types of absorptive roots occur in trees. One type (e.g. Ash) has long but sparingly-branched absorptive roots, showing no

variation in thickness, whether they be primary or secondary roots; they permeate large masses of soil, but do not lay these completely under contribution, because the absorptive apices are relatively few in number. In another type (e.g. Beech) the roots are much more richly branched, and hence a far greater number of absorptive ends are present in the same area. Further, in this case the lateral roots are always thinner than the primary roots; they permeate smaller masses of soil, but make greater use of them.

In some roots the ordinary epidermal cells act as water absorbers, but in the majority of cases the absorbent cells are tubular outgrowths of the outer layer of cells, the so-called root-hairs. These are often of considerable length, and have the effect

l. 49, *after* period *read* as indeed does the root epidermis also as a rule.

l. 50, *after* with difficulty, *read* inasmuch as the contiguous hypodermal cells, for the most part, become suberised, sooner or later.

l. 56, *for* 1865 *read* Lectures, p. 257

29, ll. 38–43, *for* 'If we assume . . . trickling away *read* 'Naturally water particles are held the more firmly by the soil the nearer they are to the surfaces of the particles of which the soil is composed.

30, l. 3, *heading of middle column should read*, Original amount of water in g. retained by 100 g. of dry soil.

ll. 52–4, *delete* In reality . . . of the cell-wall.

31, l. 5, *delete* thus

32, l. 21, *after* root *read* (compare, however, the observations of URSPRUNG, 1906, p. 518).

ll. 23–4, *for* we are thus compelled . . . of water *read* we are thus compelled to believe that the vital activity of protoplasm plays a very important part in the absorption of water as well as in that of substances dissolved in it (Lecture II).

ll. 47–54, *delete* This cuticle . . . is entirely absent.

33, ll. 2–4, *for* The cuticle . . . SCHWARZ, 1883) *read* The epidermis of the root, on the other hand, has no cuticle, and its outer walls are thus easily permeable to water (KRÖMER, 1903).

l. 8, *for* (HALES, 1748, p. 78) *read* (HALES, 1731–3, chap. I).

ll. 19–21, *delete* In this instance . . . by transpiration.

l. 31, *for* ignored. In tropical regions *read* ignored (BURGERSTEIN, 1904) This is true even of plants like *Dipsacus*, whose fused leaf margins form receptacles often filled with water (ROSTOCK, 1904). In desert plants, on the other hand (VOLKENS, 1887; SPALDING, 1906), the absorption of dew by aerial parts may be of some significance, and in tropical regions,

ll. 54–5, *delete* These hairs . . . Flora, 94, 464).

34, ll. 14–16, *for* The whole plant . . . grey colour *read* The whole plant is, however, covered with hairs such as occur on the leaf bases of other forms, and it is by these that it absorbs all the water it requires. (As to the mechanics of the water absorption, see MEZ, 1904; STEINBRINCK, 1906; and Lecture XXXII.)

Bibliography, *for* HALES. 1748, &c. *read* HALES. 1731–3. Vegetable Staticks. London.

P. **36**, l. 6, *for* e.g. BURGENSTEIN, 1887–1901 *read* (see BURGERSTEIN, 1904),

l. 13, *for* uniform, and *read* and at the same time

ll. 16–17, *for* it may be . . . loss of water *read* the decrease in weight from hour to hour may be considered to be a direct measure of the loss of water.

ll. 33–4, *for* e.g. VESQUE . . . KOHL (1886), *read* (see BURGERSTEIN, 1904, p. 13)

l. 51, *after* the cell-sap. *read* which then becomes more concentrated. *for* But the cell-sap . . . retarding transpiration (P. **37**, l. 6) *read* Now one should imagine that, owing to the osmotic energy of the cell-sap and the imbibition energy of the membrane as well as of the plasma, the exposed surface of a plant would, at least under similar conditions, give off less water vapour than a water surface of the same extent. In practice, however, it has been found that evaporation from expressed sap takes place at least as rapidly as from pure water (WISSER, 1904). Since, however, the surface of a plant actually gives off usually far less water than a free water surface, there must exist arrangements in the plant by means of which transpiration is retarded. One of these, more especially, is the cuticle.

37, ll. 7–8, *for* between varieties of cuticle *read* in behaviour of the external wall of the epidermal cells

l. 10, *for* gelatinous *read* non-suberised

38, l. 4, *for* Pneumachodes . . . 1896) *read* (comp. HABERLANDT, *Phys. Anat.*), *and insert*: As in the experiment above quoted, so also in nature, a movement of gases can be detected taking place through the stomata when a difference exists between the atmospheric pressure and the pressure in the intercellular spaces. Such a difference may arise, e.g., by mechanical compression of these spaces when the plant parts are bent through the agency of wind or animals, or by chemical alteration of the intercellular gases in CO_2-assimilation (Lecture IX) and in respiration (Lecture XVI). In addition to such movements of gas in bulk, gaseous diffusion also always plays an important part; it is due to unequal concentration of the gases in two different regions, and is quite analogous to diffusion of dissolved bodies in a fluid medium.

l. 27, *after* non-existent *read* (see Lecture X). Thus may be explained the fact that under certain conditions transpiration from a leaf may almost equal the evaporation from an equal surface of water (LIVINGSTON, 1906).

l. 38, *after tulipifera read* or (in winter) of *Cyclamen*,

ll. 47–50, *for* Even assuming that . . . alterations in these *read* The amount of transpiration taking place from any plant organ depends not only on the structure of the cuticle and on the number and size of the stomata, but also, and more especially, on its superficial extent and on its internal anatomy (intercellular spaces). Even when all these structural factors are taken into consideration still we are unable to estimate the total amount of transpiration from an organ, since it is dependent in very large measure on external conditions.

39, ll. 14–35, *for* Dry soil hinders . . . guard cells of the stomata *read* Dry soil retards transpiration very markedly. It has been supposed that this was due to concentration of the cell-sap, or that the retardation of transpiration was to be explained by the abundance of salts in the soil. As a matter of fact, however, increased concentration of the cell-sap in the plant affects transpiration only very slightly, and it has also been shown that frequently quite dilute solutions have a marked influence on transpiration; dilute acids retard, dilute alkalis accelerate it. Hence the effect of soluble substances and of the amount of water in the soil obviously cannot be purely physical, but, on the other hand, complex, inasmuch as changes in the plant are first of all induced, and these indirectly affect transpiration. Changes in the plant, however, when at all rapid, are due to the activity of the stomata.

ll. 47–9, *for* Other plants . . . shows a stoma *read* Variations in the structure and mechanics of stomata are treated of in detail by HABERLANDT (*Phys. Anat.*). Fig. 8 shows a stoma

40, l. 33, *for* by pressure in the cells *read* by the pressure of the cells
l. 49, *for* such as is effected by plasmolysis *read* as in plasmolysis,

41, ll. 15–22, *for* because many . . . closing of the stoma *read* because when wilting begins the stomata often lose water most rapidly, and in consequence close.
l. 32, *after majus read* and *Cyclamen*

42, l. 33, *for* moreover, *read* in this way

43, l. 6, *after* conditions *read* and that the progress of evaporation from a free water surface and from the plant (LIVINGSTON, 1906) is affected very differently by external factors.
ll. 44–6, *delete* The influence . . . 119).

44, ll. 10–13, *for* ASKENASY (1876) . . . they confirm *read* As a matter of fact, ASKENASY (1876) was able to observe very high temperatures in succulent plants.
l. 23, *for* oily *read* succulent
l. 24, *for* is of special interest *read* which URSPRUNG (1903) has confirmed in all essentials, gains in interest
l. 28, *after* vital conditions *read* This opportunity may be taken of noting that F. DARWIN (1904) has invented an apparatus capable of automatically registering the temperature of plant organs, which at the same time permits of inferences being drawn as to the degree to which the stomata have opened.

44, Bibliography, *for* HALES. 1748, &c. *read* HALES. 1731–3. Vegetable Staticks. London.
for LEITGEB. 1896 *read* LEITGEB. 1886.
for NOLL. 1902, &c. *read* NOLL. 1903. A Text-book of Botany. Eng. ed. London, p. 188.
for SCHIMPER. 1898, &c. *read* SCHIMPER. Plant Geography. Eng. ed. Oxford. 1903.

P. **46**, l. 22—P. **47**, l. 2, *for* If a large number . . . confirmed this conclusion. *read* One might imagine that this was the general way in which movements of water took place in the plant, but experiments demonstrate that this view is quite erroneous.

47, ll. 14–16, *for* Such experiments as these . . . in larger plants *read* If in experiments of this sort evaporation could be entirely prevented from cells which were not directly in contact with the water, these cells must certainly in the long run become saturated with water by means of osmotic suction. Since, however, this water movement has to overcome very considerable opposition, it goes on too slowly, and on that account suffices only for small, few-celled organisms living in damp situations and transpiring moderately. In larger plants,
l. 18, *for* but that *read* and hence

48, ll. 2–4, *for* by a simple . . . the same result *read* by the following simple experiment.
l. 18, *after* performed *read* The ringing experiment is a very old one (comp. MOEBIUS, 1907), but it is as conclusive to-day as ever it was (URSPRUNG, 1906).

49, ll. 29–30, *for* ends of the vessels . . . has been submerged *read* ends of the vessels directly, or is forced into them by atmospheric pressure.

50, l. 34, *for* (1748) *read* (1731–3)
l. 49, *for* per cent. (*bis*) *read* per mille

51, l. 7, *for* p. 240 *read* p. 258

52, l. 24, *for* 1390 *read* 1038

l. 28, *for* and these . . . pressures *read* possibly the greatest pressure

ll. 50–2, *for* root which . . . to pass *read* root also which excrete water with like energy; but since other cells, exposed to this pressure, also permit water to filter through them,

l. 53, *for* plus *read* versus

53, l. 3, *for* that bleeding- *read* that the bleeding-

ll. 5–10, *for* and so on . . . conditions of bleeding *read* and that such regions are not in uninterrupted communication with each other. Why intercommunication between two closely-related regions, e. g. in the xylem of a tree, is not unrestricted we shall discover when we consider the external conditions of bleeding (p. 54).

54, ll. 16–19, *for* a much greater effect . . . Malays); *read* a much greater stimulus is necessary, for the Malays, during the four or five weeks previous to flowering, inflict repeated blows on the base of the bole with a wooden hammer, and

l. 40, *delete* whilst what may be termed . . . permeability of the protoplasm (P. **56**, l. 20).

56, ll. 26–9, *for* In the uninjured plant . . . infliction of the wound *read* In the uninjured plant, however, water is pressed into the vascular strand. It is true we are often able to demonstrate this only after the infliction of the wound;

l. 32, *for* made. *read* made; in fact, conclusive proof of this is available.

l. 51—P. **57**, l. 6, *for* In *Colocasia* . . . pure water *read* A complete picture of the process as occurring in *Colocasia* has been furnished us by MOLISCH (1903). In an immature leaf as many as 163 small drops were expressed per minute, and with such force that they were shot out to some distance; in older leaves larger drops fell on the ground at the rate of 190 per minute. An individual leaf may give off in a single night even 100 g. of water. In the expressed fluid only traces of organic materials and ash were demonstrable.

57, l. 28, for *Vicia sepium* read *Vicia Faba*

last line, *for* deliminated *read* delimited

58, l. 19, *for* MOLISCH *read* MOLL

59, ll. 1–2, *for* absorbing hygroscopic water *read* absorbing water hygroscopically

ll. 12–17, *for* There is practically . . . our present subject *read* Any attempt to arrive at an explanation of the unilateral exudation of water from plant cells (comp. PFEFFER, 1892) forces us to the belief that the phenomenon is without doubt an osmotic one. It is evident, however, that we cannot or may not attribute all the various instances to the same causes, for the product of secretion varies from pure water to a quite concentrated sugar solution. Glancing first at those cells which produce sap which is extremely poor in materials, we may assume that they possess protoplasm which is completely impermeable to the substances dissolved in the vacuole, and the question then arises, How can water be unilaterally expressed from such a turgescent cell? In an ordinary cell the incoming stream of water due to osmosis is, on all sides, just as great as the outgoing stream induced by the counter-pressure of the cell-wall (p. 13); should more water come out at some particular place than enters there, then more must enter at some other place than comes out. In order to explain this variation in behaviour of different sides of the cell it

was previously assumed that the plasmatic membrane possessed different qualities, for it was customary to hold that the height of osmotic pressure was dependent on the character of the plasmatic membrane. Should one half of a cell be composed of a membrane which gives a lower osmotic pressure than the other half, then water must of necessity at once flow out on that side. This assumption has, however, been shown to be erroneous ; the height of osmotic pressure, as PFEFFER (1890, p. 303) has shown and as is obvious from the kinetic theory of osmotic pressure, depends only on the number of dissolved molecules and ions and not on the character of the plasma ; any precipitation membrane, whatever its chemical and physical characters may be, more especially whether it be thin or thick, gives the same pressure so long as it is impermeable. The following conception which we owe to PFEFFER (1877) is, on the other hand, physically correct. If the cell-sap at different points in the cell has different concentrations, then at the region of higher concentration the inflow must exceed the outflow until an equality is reached between the two sides ; hence there results a unilateral exudation of water, and this is effected with a pressure corresponding to the difference in the concentration on the two sides of the cell. Such a difference in concentration could not occur in a physical experiment, for an equilibrium must necessarily arise on account of diffusion ; should a similar equalization be effected and maintained in the cell, one must clearly realize that an expenditure of energy is necessary for that purpose—an expenditure which the living cell can certainly furnish at any time, but which is impossible in a physical apparatus such as PFEFFER'S osmotic cell. This explanation is also in accord with the fact that unilateral expression of water is at once inhibited if we, by withdrawal of oxygen or by subjecting the cells to the influence of chloroform, reduce them to the condition of non-living purely physical pieces of apparatus.

GODLEWSKI (1854) has arrived at an entirely different conception of the cause of unilateral exudation of water. He postulates continuous variations in the height of osmotic pressure, resulting from the fact that osmotically active material is used up and once more reconstructed. At each reduction in the osmotic pressure exudation of water is brought about by contraction of the elastically distended cell-wall, and if such contractions succeed each other at longer or shorter intervals the cells at once exhibit pulsations. Although there is much to be said for this idea it nevertheless appears to us not in all respects satisfactory ; first, because it does not explain why in these pulsations the water should be excreted on one side only, and, secondly, because when the osmotically active material again increases the water previously expressed must be again reabsorbed. A third interpretation is one especially applicable to such cells as give off sap rich in dissolved substances, such as nectar and the sacchariferous bleeding-sap of many plants. If we assume that the sugar arises locally out of or on the cell-membranes, it must withdraw water osmotically from the cell. Since WILSON (1881) succeeded apparently in stopping the secretion by thoroughly washing off this extracellular sugar in the case of many nectaries and also in *Pilobolus*, this explanation is often accepted as correct in cases like those referred to, in spite of individual arguments to the contrary. Since LEPESCHKIN (1906) has, however, shown conclusively (as it appears to us) that in *Pilobolus* no such osmotic suction takes place, it will be necessary to re-investigate the phenomenon in the case of nectaries. Individual cases of bleeding-pressure might also be referred to osmotic suction, due to materials which are produced from the membranes of the cells or of the vessels. WIELER has estimated that the osmotic pressure of the bleeding-sap of the birch can reach two and a half atmospheres, so that one might very well imagine that the bleeding-pressure actually observed in this tree should be regarded as osmotic. Indeed one might claim this to be

even more probable in the case of the more sacchariferous sap of *Acer*, *Agave*, and Palmaceae. It is quite out of the question, however, to regard bleeding-pressure in general as osmotic pressure in this sense, for we find no relation existing between the height of the pressure of the sap and its concentration ; in the vine more especially a feeble concentration of the sap occurs along with high pressure. WIELER has instituted experiments specially with the view of settling this point ; he permitted osmotically active solutions to be absorbed by the vessels of the root-stump, but failed to induce bleeding thereby.

Further, one has difficulty in assuming that such large amounts of sugar as are obtained from palms and *Agave* can arise from the cell-walls ; they must be produced from their interiors. They must therefore pass through the plasma, and that layer cannot therefore be as impermeable as we have hitherto regarded it. As soon, however, as we assume a unilateral permeability of the plasma the conditions of unilateral expression of water are again fulfilled, because in that way certainly a permanent difference in the concentration of the sap on different sides of the cell is established. If also the qualitative difference of the plasmatic membranes in different regions of the cell consists in its impermeability on the one hand and partial permeability on the other, a unilateral exudation of fluid may then certainly result. One should note, however, that it is never pure water but always cell-sap that filters out, though that sap may certainly be very dilute.

At present we are not in a position to advance decisive reasons for the acceptance of one or the other of the explanations offered of the unilateral exudation of fluid from the cell. Still, after weighing probabilities, one would rather incline to the view that the condition essential to bleeding lies in a difference of concentration of sap on opposite sides of the cell, induced and maintained often (possibly in the case of dilute sap) by an expenditure of energy on the part of the cell, but also often (in the case of concentrated sap) by the unilateral permeability of the protoplasm.

l. 25, *delete* a secretion

l. 46, *for* the significance to be attached to *read* its significance in this case to lie in

60, l. 2, *for* save *read* besides

l. 5, *for* e. g. *read* even

Bibliography, *for* HALES. 1748, &c. *read* HALES. 1731–3. Vegetable Staticks. London.

61, ll. 16–23, *for* Indeed the older physiologists . . . (1891, p. 938), *read* This fact is shown more clearly by an experiment performed by STRASBURGER on the copper beech (1891, p. 938).

l. 34, *for* A glance at *read* But the estimate is certainly not an exact one, for a glance at

l. 35, *for* shows clearly that *read* shows more clearly than an experiment that

62, ll. 19–20, *for* and it will . . . that this plant *read* and thus only can we explain how, as was shown in the last lecture, this plant

ll. 24–8, *for* If a sharp line . . . be given *read* If a sharp line of demarcation existed between the heart and sap wood, and if we could assume on the one hand that the whole of the sap wood was of equal value for conductive purposes, and that the whole of the heart wood was valueless, still only approximate estimates of the area of the wood actually concerned in the transport of water could be arrived at.

63, ll. 9–12, *for* in the plant, since . . . raised in the plant *read* in the plant. In all the numerous explanations hitherto offered no attempt has been made

to show that the amount of water raised in the unit of time is enough to compensate for that lost in transpiration ; all that has been done has been to prove that water can be raised to the required height by the assumed forces.

l. 39, *for* 139 *read* 103·8 ; *for* two *read* one and a half

l. 41, *for* 20 m. *read* 15 m.

l. 42—P. **64**, l. 16, *for* Let us take . . . supplied to the leaves *read* In other cases, and frequently even in high trees (e.g. Coniferae, *Morus*, *Fraxinus*, *Acer pseudoplatanus* ; compare WIELER, 1893), a bleeding-pressure of only 12, 21, 313 mm. has been found ; further, it must be specially noted that the maximum pressure occurs only in spring, before the leaves come out. Later on, when transpiration is active, the pressure within the tree is generally less than that of atmospheric air, i.e. there is a so-called negative pressure (see pp. 53 and 71).

64, ll. 52–4, *for* It is obvious . . . of air entirely. *read* HULETT (1903) replaced the gypsum by a porous porcelain plate in which a precipitate of copper-ferrocyanide had been laid down. In this way the permeability of the plate to air was greatly decreased, and accordingly, with a barometric pressure of 74·4 cm., HULETT obtained a mercury column in the tube 111·1 cm. in height.

65, ll. 5–6, *for* it would . . . produced by *read* one would produce obviously a vacuum when the mercury reached a height corresponding to the

l. 23, *after* (1900) *read* and HULETT (1903)

66, ll. 1–4, *for* If in place . . . conditions obtaining *read* It is of interest, in respect of the conditions obtaining in the plant, to note that STEINBRINCK (1906) with the aid of his high-tension siphon has proved that a considerable cohesion can also be shown to exist in a rapidly flowing liquid. Further, a certain percentage of dissolved air does not at once destroy the cohesion (DIXON and JOLY, 1894), but doubtless that percentage must not be excessive, for it was noticed quite generally that a rupture of the stretched water column is the more readily prevented the more the air is extracted from it. If now, in place of the porcelain plate used in HULETT's experiment, we employ a clay cell, in whose wall a precipitation membrane has been laid down, the apparatus would present a great likeness to the conditions obtaining

ll. 20–37, *for* At the same moment . . . cells of the root. *read* The osmotic pressure in leaf parenchyma is, however, very high. EWART (1905) often found it to be equivalent to a 6 per cent., 8 per cent., or even 10 per cent. solution of KNO_3. In the last case a force = 46·7 atmospheres or 482 m. of water would have to be overcome before plasmolysis could take place. Again, since EWART has shown (1905, p. 78) that leaves on the lofty branches of a tree have a distinctly higher osmotic pressure than those inserted lower down, it is of the utmost importance that detailed researches should be made as to the amount of this pressure. Certainly one must not measure the suctional power of the water column pendent to the cell by its length only ; we must take into account as well the friction against the walls of the vessels and the opposition to its passage presented by the living root-cells.

67, ll. 2–16, *for* The following table . . . 10–66 cm. *read* Typical tracheids (*Pinus*) have a diameter of 0·03 mm. and a length of as much as 4 mm. Those of *Nelumbium* (0·6 mm. broad and 120 mm. long) remind one of vessels, which latter may often be narrower than tracheids, but, at the same time, may be 2–3 m. in length. We may readily convince ourselves of the great length of tracheae by blowing through a dry stem of *Cobaea*, whose lower end has been submerged.

68, ll. 2–7, *for* In the spiral . . . the three types *read* The thin regions are spoken of as ' pits ' ; these pits are, in annular and spiral tracheae and tracheids,

of similar form to the thickened regions, and alternate regularly with them, but in reticulate types they are round or elliptical.

l. 24, *for* deliminated *read* delimited

69, l. 1, *for* are on an average about 1 mm. long, 0·02 mm. broad *read* may be 4 mm. long, 0·03 mm. broad,

l. 7, *for* a millimetre apart *read* four millimetres

l. 9, *for* fifty *read* one hundred and thirty-three

ll. 12–13, *for* let us turn . . . which may *read* STRASBURGER'S experiments (1891) with the fresh wood of the silver fir may be readily understood ; they may

ll. 25–45, *for* Similar results . . . uniform thickness ? *read* These experiments do not indeed suffice to give us a numerical basis for estimating the resistance offered by a thickened cell-wall and a bordered pit to the passage of water, still they demonstrate how much the transit of water is facilitated by the pits. Under these circumstances the question we have to ask ourselves is, why is the whole wall not uniformly thin ?

70, ll. 8, 9, *for* We need not . . . thickening *read* In spiral vessels also, which frequently go on increasing greatly in length, the opening out of the spiral band is a special adaptation, without which a vigorous extension would not be possible.

71, l. 35—P. **72**, l. 22, The alternating . . . accepted as proved *read* The alternating air-bubbles and water columns (the so-called JAMIN'S chain) show considerable differences in size ; SCHWENDENER found the average length of the air-bubble to be 0·3 mm. and of the water column 0·2 mm., and EWART (1905, p. 76) records similar results. In such a system, movement of water must obviously take place quite otherwise than in tubes filled with water from end to end.

One very important question, which doubtless can be solved experimentally, is whether only those vessels which are full of water act as water-conducting elements, or whether those which contain chains of air-bubbles and water columns can carry out this function also. According to STRASBURGER'S observations the amount of air in the vessels in the periphery of the stem is less than that in the centre, and the youngest annual ring contains no air at all. Could it be proved that this state of affairs was at all general (according to EWART, 1905, the young vessels contain air, but his observations undoubtedly require confirmation) it would be a strong argument in support of the cohesion theory, and one could hold the view that the ascent of sap was rendered possible by the cohesion of water particles ; but such a view can certainly not be substantiated.

72, l. 34, *for* cavities of the vessels *read* cavities in a cell-wall

ll. 34–5, *for* in a microscopic sense *read* too small for the microscope

l. 42—P. **74**, l. 47, *for* Taking into account . . . superincumbent water columns *read* Taking into account the sum total of our knowledge of the subject, we must at least reckon with the possibility of the ascent of sap being either exclusively or in part carried out by vessels containing JAMIN'S chains. The extensive literature on the subject, into which we cannot enter, discusses, sometimes critically (SCHWENDENER, 1983 ; STEINBRINCK, 1894), sometimes in a more fanciful way, the problem how water can reach a height of 150 m. in such a conduit purely by the suctional force of transpiration, some assuming that the air-bubbles remain stationary, some that they move along with the water columns. No final decision has been arrived at on the question ; it has not been decided whether transpiration alone is capable of producing this effect or whether other forces must be regarded as co-operating agents. In one

of the most recent publications on the subject, which brings into the forefront not theoretical considerations but practical observations (EWART, 1905), such an effect of transpiration is regarded as quite impossible. EWART's view is shortly as follows :—suctional force must be sufficient not only to raise a water column to the top of the highest tree, but must also be able to overcome the resistance which the water meets with in its ascent, a resistance which EWART has measured. He calculated the amount of water which must pass through the stem in a unit of time in order to replace that lost in transpiration, and afterwards estimated the pressure required to move this amount at the necessary rate. He found that a water column would be needed which would be 5–7 times as great as the height of the plant. Hence in the case of a tree 150 m. high a pressure of 1,000 m. of water, i. e. 100 atmospheres, would be necessary. If this pressure were induced by the osmotic suction of parenchymatous cells they would require to possess a cell-sap isosmotic with a 28 per cent. solution of KNO_3 ; EWART holds that that is impossible.

In this relation it must be noted that the osmotic value of the leaf parenchyma of lofty trees must be empirically determined by itself ; as high a pressure as that mentioned is improbable but still possible, since in other cells it may reach as high, if not higher values, when the concentration of the external medium is sufficiently great (Lecture XXXIII). EWART has doubtless over-estimated the opposition offered by the wood to the longitudinal carriage of water (compare DIXON, 1906) not only because he took as a basis very high transpiratory values where, in nature, the water reserves would come into play, but also because he possibly did not always take care to keep the cut surface of his experimental twigs free from agents which clog the vessels.

Every hypothesis as to the significance of the mechanics of water conduction appears to be founded on an extraordinarily limited groundwork of observation, and to rest on one-sided experimental determinations.

74, l. 53, *for* If the water *read* If most of the water

75, l. 8—P. **76**, l. 19, *for* A complete discussion . . . Abt. 243) *read* A detailed account of these views and of the criticisms to which they have given rise (ZIMMERMANN, 1885 ; SCHWENDENER, 1886) need not be presented here ; the fact that water can move as easily upwards as downwards (p. 61) at least does not speak in their favour.

In what follows we will disregard these special hypotheses and confine ourselves to the question whether the living cells are in any way concerned in the ascent of sap. Attempts have been made to solve the problem by killing longer or shorter stretches of woody stems and seeing whether they still retained their powers of conduction. We have to thank STRASBURGER (1891, 1893) for the most thorough experiments in this direction, experiments which led him to the conclusion that the living cells were quite ineffective. His experiments, however, were not proof against the vigorous criticisms of PFEFFER (1892) and URSPRUNG (1904, 1906). URSPRUNG has conducted a large number of experiments of a similar nature, and arrived at quite different results. He found that, generally speaking, no matter what agent he employed for killing the cells, the conductive capacity for water was injured the more rapidly, the longer the pieces were that were killed. He convinced himself that the deficient conductive capacity was not due to stoppage of the vessels nor to increased evaporation from the dead regions, nor yet to alterations in the JAMIN'S chains. We readily admit that the conclusions he has arrived at from more recent experiments (1906) appear to be much better founded than those he deduced from his previous ones (1904) ; whether, however, his line of argument is above criticism we must leave the future to decide.

l. 41, *add* (After the MS. of this lecture had been completed there appeared a paper by URSPRUNG (1907) dealing in a very critical manner with the various possible methods of ascent of water.)

77, l. 50, *after* matter *read* by LAVOISIER

78, l. 22—P. **79**, l. 23, *delete* The nature of the salts . . . constituent of plant ash.

79, ll. 24–49, *for* The total amount . . . by italics *read* The total amount of ash depends, in the first instance, on the specific peculiarities of the plant, for different species grown on similar soils give different percentages of ash. WOLFF'S *Ash Analysis* (p. 137) shows us that, of several common weeds grown in the same soil, the ash of *Rumex Acetosella* amounts to 8·14 per cent., of *Geranium dissectum* to 9·98 per cent., of *Sedum Telephium* to 11·96 per cent., and of *Myosotis arvensis* to 17·85 per cent. The existence of specific differences between plants in amount of ash may also be deduced from the tables given in Lecture I (pp. 3, 5). These tables give averages of, often, very numerous analyses, for, as may be readily imagined, the amount of ash varies extremely in individual plants according to circumstances. Thus in a substratum in which there is much mineral matter, either soluble or actually in solution, the amount of ash rises, but vigorous transpiration, more especially, increases the absorption of water and thus also increases the quantity of mineral matter in the plant. According to EBERMAYER (1884) the leaves of actively transpiring trees, such as the ash or willow, contain 7–10 per cent. of ash, while those of the feebly-transpiring pine contain only about 1·5 per cent. It is readily comprehensible that the leaves are the organs richest in ash, since the greatest evaporation takes place there, and since it is in them that the minerals accumulate, carried there by the transpiration current. Stems are always for this reason poorer in ash, as the following table shows :—

Percentage of minerals in dry weight (CZAPEK, *Biochemie*, II. 781)

	Lupinus luteus	*Nicotiana Tabacum*	*Brassica Rapa*	*Achyranthus aspera*
Leaves	6·06	11·87	20·84	24·33
Stems	3·86	7·73	9·18	8·67

In certain leaves the amount of ash is even greater, e.g. 30 per cent. in *Beta vulgaris* and 50 per cent. in *Mesembryanthemum crystallinum*. Since, as we shall presently find, the ash is not superfluous, much less injurious, but on the contrary is a quite essential constituent of the plant, transpiration must be an exceedingly important process, and must not be regarded in the light of a necessary evil (comp. p. 43).

The individual elements which occur regularly in appreciable quantity in the ash of all plants are only nine in number, i. e. Cl, S, P, Si, and the metals K, Na, Ca, Mg, Fe. The following table (WOLFF, 1880) shows the composition of the ash of certain plants ; the special abundance of an element is emphasized by italics :—

80, *after the table read*

In addition to these nine elements which have been determined quantitatively, aluminium and manganese are also as a rule demonstrable, and it is further possible to determine here and there the presence of traces of a large number of other elements whose names we need not mention.

Confining ourselves to substances which have been quantitatively determined, we may next ask more exactly whether any relations exist between the amount of these bodies present in the soil and the amount present in the plant. Such relations can actually be demonstrated. MALAGUTI and DUROCHER'S (1858) analyses show, for example, that the calcium carbonate in plants

grown in chalk soils amounts roughly to 45 per cent. of the pure ash, while the same species contain only 30 per cent. when grown in a sandy soil. The ash contains correspondingly more chlorine when the plant is grown on a seashore, where sodium chloride is abundant, than when grown inland :—

Percentage of chlorine in pure ash (CZAPEK, *Biochemie*, II. 810).

	On the seashore.	20–25 km. distant from the shore.
Beta vulgaris (root)	15·29	12·30
,, ,, (leaf)	21·39	16·61
Potatoes (tubers)	12·62	7·96

It would be quite erroneous, however, to assume that in general the amount of a certain substance in the plant depends on that present in the environment. It is well known, for instance, that iodine is present in seawater only in minute traces, but it occurs in many of the tangles in relatively large proportions. Inversely, a substance abundant in the environment may occur in the plant in relatively much smaller amount. This fact is illustrated by WOLFF'S (1871, p. 132) analysis of the ash of *Lemna trisulca* as compared with that of the water in which the plant grew :—

Minerals present in 100 parts of pure ash.

	K_2O	Na_2O	CaO	MgO	Fe_2O_3	P_2O_5	So_3	SiO_2	Cl
Water	5·15	7·60	45·56	16·00	0·94	3·42	10·79	4·23	7·99
Lemna	18·29	4·06	21·86	6·60	9·57	11·35	7·91	16·05	5·55

Why K, Fe, P, and Si should be absorbed in relatively much greater quantity than the proportion in which they are present in the water is quite unknown. The absorbed substances may be deposited partly in the cell-wall, but certainly they are also in part taken up by the protoplasm. We have already clearly established the fact that protoplasm exhibits great variability in its power of permitting the passage of dissolved substances, that the absorption in one case goes on simply in obedience to physical laws, until similar concentrations are reached in the solutions inside and outside the cell, while in other cases the absorption ceases long before this equilibrium is attained (Lecture II). We concluded from this that absorption of a substance continues to take place, more especially if the entering solution becomes permanently altered within the cell, as in the case of certain aniline dyes. We must assume that the minerals are also often accumulated in the cell because they become built up into other combinations, very probably organic in their nature.

l. 5 *after table, for* this view LIEBIG (1840) supported very *read* this view was held by C. SPRENGEL (1839), and LIEBIG (1840) supported it very

81, ll. 20–34, *for* The following substances . . . of the seed *read* As an instance of the results of water culture we will select out of the older literature on the subject the experiments of BIRNER and LUCANUS (1866). These authors used a nutritive solution which contained per litre of water about 0·5 g. $MgSo_4$, 1·5 g. KNO_3, 1 g. H_2KPO_4 and 1 g. $Fe_2(PO_4)_2$ and obtained an increase in the dry weight of oats equivalent to 138 times the weight of the seed.

l. 48—P. **82**, l. 3, *for* Numberless experiments . . . primary import *read* Numberless experiments have been carried out more recently with such nutritive solutions ; those invented by KNOP, and by SACHS more especially, have been often employed. Their composition is as follows :—

KNOP (1868, p. 606 ; 1884).

0·25 g. Magnesium sulphate
1·00 g. Calcium nitrate
0·25 g. Acid potassium phosphate
0·12 g. Potassium chloride
Trace of Ferric chloride

SACHS (1882, p. 284).

1·0 g. Potassium nitrate
0·5 g. Sodium chloride
0·5 g. Calcium sulphate
0·5 g. Magnesium sulphate
0·5 g. Finely ground Calcium phosphate
Trace of Ferric chloride

Since salts, as we now know, dissociate, at least partially, when in solution in water, it is obviously a matter of indifference whether the base in the nitrate be K or Ca, or that in the sulphate be Ca or Mg. In all probability salts which do not dissociate are of no importance so far as absorption by the plant is concerned, and hence the vital point only is that the kations K^+, Ca^{++}, Mg^{++}, Fe^{++} or F^{+++} and the anions SO_4^- and $H_2PO_4^-$ (as well as NO_3^-) should be present.

The reaction of the nutritive solution is, however, of great importance. In alkaline fluids most plants die or at least suffer serious injury; aquatic plants are exceptional in this respect (MOLISCH, 1895–6; BENECKE, 1898), for these forms thrive better in weak alkaline than in weak acid solutions. In the case of all other plants a feebly acid reaction must be maintained in the culture fluid. Under certain circumstances the reaction of the solution may become alkaline by the more vigorous absorption of certain ions, and in such cases it is advisable from time to time to add to the solution a few drops of phosphoric acid, and so maintain a feeble acid reaction. More recently CRONE (1904) has shown that neutral nutritive solutions are, under certain circumstances, more favourable than acid ones; he also discovered that soluble compounds of iron and of phosphoric acid are far less serviceable than those which are sparingly soluble. The solution he used, and with which he obtained satisfactory results, was composed of 1 g. KNO_3 0·5 g. $MgSO_4$, 0·5 g. $CaSO_4$, 0·25 g. $Ca_3(PO_4)_2$, 0·25 g. $Fe_3(PO_4)_2$ in 1,000 g. of water.

It will be a valuable piece of work to invent a really scientific nutritive solution, keeping in mind the poisonous effects of certain ions (of which we shall speak later on) and their counteraction by other ions.

In addition to the composition of the nutrient fluid and the reaction dependent on it, its concentration and its amount are of primary import.

82, l. 4, *for* per cent. (*bis*) *read* per mille

l. 14, *after* success *read* (NOBBE, 1864–68)

ll. 39–43, *for* The culture methods . . . improvement *read* Special care must be taken to maintain purity in the salts used in cultures for lower plants such as Algae and Fungi, because these organisms require extremely small quantities of nutrient salts in accordance with their small size. Numerous erroneous conclusions have been arrived at by neglecting the solubility of glass vessels (compare BENECKE, 1896 and 1907). Apart from this, many complications often occur in these plants as compared with higher types, owing to the fact that Fungi, for instance, have quite special requirements, inasmuch as, in addition to minerals, they also demand organic nutrients (Lecture XIV).

l. 48, *for* to the majority *read* occur in the majority.

ll. 53–4, *for* It has been shown . . . Algae require *read* On the other hand, it has been shown by BENECKE (1894–1907) and MOLISCH (1895–6) that many Fungi, Algae, and Bacteria require

83, ll. 8–10, *delete* and on taking . . . by the plant.

l. 14, *after* globulins *read* and other compounds afterwards to be mentioned.

ll. 19–20, *for* nor . . . form *read* Fungi, however, grow well in the less oxidized sulphur acids. Sulphur and phosphorus cannot, however, be used in the elemental condition.

ll. 21–53, *delete* Further, sulphuric acid . . . without this element.

84, l. 1, *after* unsuitable *read* to higher plants

ll. 7–34, *for* The case appears . . . may produce it. *read* In considering the function of potassium in the higher plant it might be thought that it would be easy to obtain definite knowledge on the subject by studying the

effect of a normal water-culture solution containing no potassium. As a matter of fact, however, the results of such studies, e.g. those of SCHIMPER (1890) and of WILFARTH and WIMMER (1903), are so divergent that it is impossible to draw any certain conclusions from them. In other cases also, e.g. in relation to phosphorus and calcium, the effects of water-cultures which do not contain these elements are ambiguous. Of one reason for that we shall speak later; at present we must content ourselves with assuming that potassium is a constituent of protoplasm and hence is an essential nutrient. Most proteid bodies, as a matter of fact, contain ash, and it is quite possible that these bodies, at least in part, are directly concerned in the building up of the proteid molecule.

The lower plants behave quite otherwise in their demand for metals of the alkalis. Replacement of K by Na, Li, and NH_4 is generally ineffectual, and it is only in the case of the Cyanophyceae perhaps (BENECKE, 1898, p. 96) that Na may replace K. On the other hand, according to BENECKE (1907), certain Bacteria can live perfectly well without K, when presented with Ru or Cs salts in proper concentrations. Many Mould Fungi behave in the same way, for in their case Ru or Cs suffices for the formation at least of vegetative organs. Since, however, reproductive organs are not formed under these conditions, it would appear that K is as essential to them as it is to higher plants.

ll. 37–8, *delete* Water-cultures . . . potassium.

ll. 43–4, *for* Magnesium . . . chlorophyll *read* Magnesium also appears to be plentifully present in chlorophyll.

l. 45–9, *for* Though most Algae . . . contain it. *read* Since most lower organisms can do without it we must conclude that it is not an essential constituent of the proteids of protoplasm, although, it is true, differences may occur even in the most important chemical compounds in individual groups of plants.

l. 54—P. **85**, l. 16, *for* The appearance . . . for calcium, strontium would *read* Why it is essential and what its function is, we do not know. Were it possible to replace it by another metal, strontium would

85, l. 24, *for* as a consequence of *read* after

ll. 47–50, *for* MOLISCH (1892) . . . same fact. *read* MOLISCH (1892) and by WILLSTÄTTER (1906), who found that chlorophyll contained no iron. On the other hand, an older research of RAULIN'S (1869), showing that Fungi which have no chlorophyll cannot do without iron, has been confirmed by MOLISCH (1892) and BENECKE (1895).

l. 53, *after* effect. *read* Whether chlorosis is always to be regarded as an indication that iron is absent from the nutritive solution or that the plant has not access to it, is a question we must leave undecided. Doubtless, other differences in the nutritive solution may also induce chlorosis.

86, ll. 3–5, *for* hence it should . . . discussed here. *read* hence nitric acid, as an essential nutrient, capable of being absorbed from the soil or from water, must be referred to in this connexion, although, not being found in the ash of plants, it should not, strictly speaking, be discussed here.

l. 32—P. **89**, l. 4, *for* In addition to . . . the subject intelligible. *read* In addition to the six elements spoken of above as essential to all higher plants, there are others which, although they are absorbed in large quantities by plants growing in the open, are yet to be regarded as unessential. Sodium is the best example of these. Although in almost all the analyses given in the table on p. 80 it is present in greater amount than the essential constituent iron, still, with the aid of the water-culture method, it may be shown to be quite unessential, although it must not be assumed that it is, if offered, quite useless. For certain general purposes, e.g. neutralization of acids or osmotic

activity, it may, as we have seen, partially replace potassium. The non-essential nature of a number of other elements has not been proved with so much certainty as that of sodium. In the first place, we may mention chlorine, an element which we have spoken of as non-essential to the majority of plants that have been investigated, with the exception of buckwheat. According to BEYER (1869) the same is true of peas and oats. It would be specially interesting to know how marine and seashore plants behave in this respect, plants which always absorb large amounts of this element.

Just as halophytes absorb large quantities of chlorine, so other plants take up certain other elements abundantly, elements which are only sparingly absorbed by other plants and which may be regarded as unessential. It may be questioned in this relation whether here also specific differences may not exist—whether, in fact, these elements, e.g. Si, Al, Mn, are not essential to certain plants. Si occurs as SiO_2 in Diatoms, in grasses, and in Equiseta in large quantities (comp. Analyses 10 and 11, p. 80). In grasses it is localized in the cell-walls of full-grown organs, but is completely wanting in embryonic parts and in the seed. SALM HORSTMAR held that SiO_2 was an essential constituent of the plant, but SACHS (1862) showed that maize could be grown, without detriment, in a 'SiO_2-free' water-culture. The evidence is, however, not quite conclusive, for the ash of maize plants grown in the 'SiO_2-free' solution still contained 0·7 per cent. of SiO_2 (instead of 18–23 per cent.), which they very likely had absorbed from the glass of the vessel in which the culture was made. Similarly, JODIN (1883) cultivated four generations of maize one after the other in 'SiO_2-free' solutions, but he was not successful in completely excluding Si, for in the second generation there was even more SiO_2 present than SO_3. On the other hand, some observers, e.g. SWIECICKI (1900), have endeavoured to show that silicic acid has a favourable influence on the plant. At present all we can say is that the large quantities of silicic acid in grasses are certainly unnecessary, but that it has not been proved that they can get on equally well when silica is entirely absent. The question deserves a critical investigation, all the more since O. RICHTER (1906) has proved that Diatoms cannot really thrive without SiO_2. Again, it is worthy of note that, although silica may be quite superfluous from the chemical point of view, it may be of great service to the plant in the biological sense.

Just as SiO_2 is a plentiful constituent of the plants above mentioned, so aluminium occurs abundantly in other forms. In *Lycopodium complanatum*, *L. clavatum*, and *L. chamaecyparissus*, 23–39 per cent. of the ash consists of Al, and in species of *Symplocos* and in *Orites excelsa* it is present in quantity, while in the majority of plants, as also in many species of *Lycopodium*, only minute traces are demonstrable (comp. ROTHERT, 1905). It would not be astonishing to find as a result of further research that Al was essential to many species of *Lycopodium* and to *Symplocos*; nor would it be surprising if iodine, which occurs in such quantity in Marine Algae, were found to be essential to these plants, or that lithium was not superfluous in such types as always accumulate it (TSCHERMAK, 1899). The same is true of manganese, found especially abundantly in aquatic and swamp plants (GÖSSL, 1905).

Having now discussed the question as to essential and unessential minerals, we must next study those which are injurious to plants. It need scarcely be said that every salt, even the most essential one, may be sometimes injurious in high concentration, owing to its osmotic activity; but an injurious effect may also be produced by it owing to its chemical nature, and this is what we mean by a poisonous effect. The salts of the heavy metals, even in quite minimal doses, operate injuriously or may bring about a fatal result. Even the essential potassium salts are poisonous. According to STIEHR (1903) the root-hairs of *Phloeum* are killed by a 0·5 per cent. solution of KCl. The salts of

magnesium are much more poisonous; a 0·15 per cent. solution of $MgCl_2$ was fatal to *Phloeum*. Many of the nutrients, therefore, must be injurious even in the concentrations in which they occur in nutritive solutions, unless their poisonous influence be counteracted by other substances. Thus, according to LOEW (1892), the poisonous effect of magnesium salts is restrained by the addition of calcium carbonate. BENECKE (1904) demonstrated a corresponding action of chalk, and OSTERHOUT (1906) has brought forward similar evidence. One thus appreciates how difficult it is to arrive at accurate conclusions with regard to the functions of the individual elements with the aid of the water-culture method. Every withdrawal of an element may have two effects, one due to actual absence of the element itself, the other due to the poisonous activity of another element whose action was previously inhibited by the absentee.

Recently, it has been observed that poisons which even in weak concentrations are injurious, aid the development of the plant when administered in still weaker doses. RAULIN (1869) had already shown that manganese stimulates the growth of Mould Fungi, yet there is no doubt that these organisms can exist for generations without manganese, and that it must not be looked upon as a nutrient. Still more noticeable were RAULIN'S discoveries with regard to zinc, discoveries which have been recently completely confirmed by RICHARDS (1897). RAULIN showed that the addition of 0·0005 per cent. of $ZnSO_4$ to a nutritive solution materially aided the growth of Fungi, and that a 0·003 per cent. solution of the same salt brought about a doubling of the plant's weight. The greatest effect was observed with this concentration; any further increase not only inhibited growth but had a directly injurious effect. There are quite a number of substances which behave in a similar way, acting favourably in dilute solutions but injuriously in stronger. $CoSO_4$ gives an optimum effect with a concentration of 0·002 per cent.; $NiSO_4$ acts best in a 0·033 per cent. solution. ONO (1900) found that an acceleration of growth took place after the addition of minute quantities of $LiNO_3$, K_2AsO_3, and NaFl to Algae and of $HgCO_2$ and $CuSO_4$ to Fungi. In Phanerogams also similar results have been obtained with the use of $CuSO_4$, $ZnSO_4$, and NaFl (LOEW, 1903; KANDA, 1904). A comprehensive exposition of the whole phenomenon will be found in LAFAR'S *Mykologie* (I, p. 342), from the pen of BENECKE. Without going into a discussion of the original papers themselves, we may conclude from this account that such effects are produced by many kations, but that certain anions, e.g. Cl and SiO_2, are also potent. Organic poisons, such as morphine and amygdalin, have also the same effect, and a stimulating action has been shown to be possessed even by certain unknown metabolic products of certain Mould Fungi on the organisms excreting them (NIKITINSKI, 1904).

RAULIN, on account of the fact that they promoted development, regarded Zn and Si as direct nutrients to Fungi, a view which cannot be accepted nowadays. It is more probable (PFEFFER, 1895) that these substances act as stimulants only, and that they further growth, though in a manner as yet unknown to us (Lecture XXV). One thing is clear, however, that to decide whether a substance is a necessary food-stuff or only a stimulant is by no means an easy task; doubtless, the genuine nutrients also act as stimulants. The facts already quoted explain also the effect of copper on the higher plant, an effect which has been demonstrated in agriculture in the employment of the so-called 'Bordeaux mixture' (a mixture of copper sulphate and calcium carbonate). If plants like potatoes or tobacco, liable to suffer badly from diseases due to Fungi, are sprayed with Bordeaux mixture they are thereby rendered immune, for copper is extremely poisonous to the lower plants. NÄGELI (1893) has shown that it is fatal to *Spirogyra* even when in a solution so dilute that it cannot be detected chemically. The fungicidal effect of

Bordeaux mixture is thus patent; but it has often been observed to have another and unexpected effect on the sprayed plant, for plants so treated thrive better than control plants, even when the latter are kept free from infection by the fungus. This favourable influence expresses itself in a more vivid green, in the more abundant formation of chlorophyll, and a correspondingly increased production of organic substance. More recently, however, this favourable influence has been called in question (comp. SCHANDER, 1904; EWERT, 1905); at all events, it has not been conclusively proved to exist. Should it be really the case, and should the effect be shown to be connected with the copper in the Bordeaux mixture, one must assume that only minute traces could enter the leaves of the sprayed plants, for according to HATORI (1899) anything above a 0·00005 per cent. solution of $CuSO_4$ is injurious to peas, while a 0·000005 per cent. solution is the highest that maize will tolerate without suffering injury.

89, Bibliography, l. 27, *for* ologodynamischen *read* oligodynamischen.

90, l. 24, *for* Owing to *read* In accordance with

91, l. 5, *after* consist *read* for the most part

l. 11, *before* aluminium *read* hydrated, *and delete* while retaining water,

l. 51, *after* analysis *read* The water of other rivers, ponds, and lakes has a similar composition; if, as is often the case, the residue obtained from such after evaporation be greater than that from a river, originating in primitive rock, it is especially due to the large amounts of calcium carbonate dissolved in these waters. Hence it may be readily understood that many aquatics send their roots into the soil, and unless they can obtain nutrients from it, are unable to thrive (POND, 1903).

l. 54, *for* live in *read* colonize

92, l. 3, *for* unassuming *read* less exigent

l. 4, *before* lichens *read* Cyanophyceae and

l. 5, *before* Algae *read* other

l. 7, *after* slowly *read* or can exist under conditions where growth is slight.

l. 8, *after* lichens *read* and Cyanophyceae

l. 24, *for* and a maximum of 4·8 per cent. in summer *read* (compare STOKLASA, 1905).

93, l. 4, *for* transposition *read* double decomposition

l. 13, *after* sodium. *read* Absorption and solution are influenced by the mass of the substances acting on each other.

ll. 25–34, *for* The question of . . . by the plant *read* What we know in a word as 'absorption' takes place only if certain clays (zeoliths), chalk, or humus are present in the soil; it does not take place in pure quartz sand. Its importance to the plant lies primarily in the fact that a soil formed by weathering, which is originally poor in plant nutrients, is gradually rendered richer in these substances. Further, the substances so absorbed are, in a large measure, protected by it from being washed out by rain, although they are still capable of being taken up by the plant.

l. 37, *for* 36,600 *read* 36,000

l. 48, *after* lichens *read* and Fungi

94, l. 35—P. **96**, l. 9, *for* For a long time . . . carbon-dioxide in solution. *read* This is undoubtedly due partly to the fact that the root-hairs, like all other living cells, give off carbonic acid. CZAPEK (1896) thought he had proved that the solvent action of the root was *exclusively* or in great part due to the excretion of carbonic acid, but PRIANISCHNIKOW (1904) has shown that his arguments are not sound. As a matter of fact, the plant can extract from a soil much more nutrient material than we can with the aid of water holding carbon-dioxide in solution.

96, ll. 23–35, *for* What the materials are . . . mineral acids *read* Indeed KUNZE (1906) has recently clearly established the fact that acids are excreted from root-hairs, at least in many plants—a fact that previously had been often stated; in some cases he was able to show that formic acid was excreted, but in other cases the chemical nature of the excretion has not as yet been determined. Many plants indeed give off so little acid from their root-hairs that no red reaction is given by litmus. It must further be noted that it is not from living cells alone that substances are produced that are of importance in rendering the soil soluble. Dead root-hairs also add acid sap to the soil, and we know that root-hairs are very short-lived. Again, the exuviated and decomposing cells of the root-cap have similar effects on intractable minerals.

If substances which are soluble only with difficulty are to be absorbed by the plant they must be in an extremely fine state of division, and must be presented to a much more extensive absorbent surface than is the case with the plates above mentioned. Thus in CRONE's culture solution we have seen that finely pulverized calcium phosphate and ferric phosphate may serve as the source of iron and phosphoric acid to the plant, and similarly mica (PRIANISCHNIKOW, 1905b) may be employed if the plant be permitted to come in contact with it at many points. It should also be noted that a dissolution of nutrients may be effected by the root taking up certain kations from the medium, and thus rendering it acid, which acidity in its turn has a solvent effect. Thus PRIANISCHNIKOW (1901) showed that grasses could employ that very intractable mineral apatite as a source of phosphoric acid, only if the nitrogen was presented to them in the form of ammonium sulphate (instead of potassium nitrate). He explained this by supposing that the PH_4-ions were rapidly absorbed, thus releasing the sulphuric acid, which in its turn had a solvent action on the calcium phosphate. His more recent researches (1905a) have established the same solvent action for ammonium nitrate, but whether this salt operates in the same way must remain for the present undecided. It is very probable that under natural conditions Bacteria also frequently play a great part in the dissolution of soil (KOCH, 1906), but it cannot be at present estimated how far Bacteria co-operated in PRIANISCHNIKOW's experiments.

ll. 49–50, *for* possess none. Plants which . . . water-cultures *read* possess none, or, under certain circumstances, e.g. in water-cultures, do not develop any.

97, l. 7, *after* humus. *read* Statements are not wanting (e.g. MOEBIUS, 1904) according to which roots grown in a sandy soil poor in nutrients are more extensively branched than when grown in good soil, and this fact also can be readily explained biologically. Further research must, however, show whether or not the difference between these divergent observations is due to the fact that in one case the whole root, in the other only parts of it, occurred in bad soil. It must also be noted in this relation that an acceleration of growth has often been observed in roots (compare BENECKE, 1903) when grown in media which were deficient in nutrients—more especially in nitrogen.

98, ll. 9–10, *for* for no soil . . . from it. *read* for it is very improbable that ordinary sandy soils are so poor in calcium that some plants cannot obtain all that they require from them.

l. 31—P. **99**, l. 21, *for* very quickly; solutions . . . II, p. 124).] *read* very quickly. PAUL (1906) has shown that quite a number of species of *Sphagnum* cannot tolerate a solution of 0·03 to 0·008 per cent. of calcium carbonate, whilst they are practically indifferent to gypsum. OEHLMANN (1898) has obtained similar results, and the statements to the contrary made by WEBER (cited by SOLMS-LAUBACH, 1905) are not perfectly intelligible.

From the fact that $CaSO_4$ is not injurious, while $CaCO_3$ rapidly brings about death, it follows that it is not the Ca-ion that acts poisonously; it must be due, on the other hand, rather to a secondary effect of the lime, a view supported by the investigations of FLICHE and GRANDEAU (1873). These investigators analysed the ash of trees which had been grown in normal soil, and compared it with the ash of other specimens which had passed a miserable existence in a soil rich in lime. The result of this comparison was to show that the ash of those grown in a siliceous soil contained 40–45 per cent. of lime, while in those from a lime soil the percentage rose to 56–75 per cent.; at the same time, the absorption of potassium was much reduced (from 16–22 per cent. down to 4–6 per cent.). It is conceivable that the diminution in the absorption of potassium was due simply to the fact that the calcium carbonate rapidly neutralized the acid secretions of the root, and so interfered with its disintegrating action on intractable rock materials. It also appears probable that calciphobous plants have a considerable need for potassium. ENGLER (1901) says that the calciphobous chestnut can thrive on sandstone and marl rich in lime if these be at the same time rich in potassium. In addition to a diminution in potassium there is a deficiency in magnesium and iron. In support of this view one may cite the fact that calciphobous plants become chlorotic on lime soils (ROUX, 1900), and that this chlorosis (according to a verbal statement by Professor STAHL) can be rectified by spraying with a solution containing iron.

l. 36, *for* calciphobous *read* calciphilous

100, l. 34, *before* SCHIMPER *read* SOLMS (1905),

ll. 50–2, *for* and at the same time . . . in the soil *read* and thus draw attention to another aspect in which the minerals present in the soil are of fundamental importance.

101, ll. 9–12, *for* EBERMAYER . . . of the ash *read* According to a table compiled by CZAPEK (*Biochemie*, II, p. 842) a hectare of field crops or woodland abstracts from 50 to 350 Kg. of ash annually from the soil, e.g.

Pine	Wheat	Beech	Potato	Clover
49 Kg.	196 Kg.	210 Kg.	217 Kg.	343 Kg.

ll. 19–20, *for* and even . . . applications *read* by the use of different media, learnt from experience, which are easily explicable theoretically, or, better still, the exhaustion may be prevented by the employment of these media at the appropriate time.

ll. 43–4, *for* nitric acid *read* nitrogen

P. **103**, l. 7, *after* our attention. *read* We have to consider not only in what form and by what organs the carbon is absorbed from the environment, but also to show how it is combined after entering the plant. To this process of transmutation of a nutrient into plant substance we give the name of 'assimilation', and describe as 'assimilata' the first formed products. The reason why, in treating of the materials of the ash, we have not employed this terminology is because we know so little as to the changes which take place, and because what little we do know can be discussed more appropriately elsewhere (Lecture XI).

ll. 34–51, *delete* [Following PFEFFER . . . in so doing.]

104, l. 23, *after* water *read* (HANSEN, 1899)

l. 52, *for* forms a means of measuring *read* furnishes a measure of

105, ll. 17–19, *for* [If POLLACCI's criticism . . . worthless !] *read* (As to the method of working this apparatus see SCHMIDT (1902). A criticism, and,

apparently, a just one, of the accuracy of this method and a description of a better form of apparatus are given by POLLACCI, 1905 a.)

l. 22, *after* is produced *read* Thus BONNIER and MANGIN (1886) found the fraction $\frac{O_2}{CO_2}$ = 1·08 in ivy, and 1·06 in the horse-chestnut and *Syringa*; so that, as a matter of fact, somewhat more oxygen is given off than corresponds to the carbon-dioxide decomposed. This excess of oxygen, for reasons which will be given later (Lecture XVI), may be considerably greater in certain plants. Whether, in addition to oxygen, other gases also, e.g. hydrogen (POLLACCI, 1905 b), make their appearance during carbon-dioxide assimilation is as yet very doubtful.

ll. 40–1, *for* Another . . . has been more often employed *read* MOLISCH (1904) has carried out elaborate investigations with the aid of this method. Yet another physiological method has been very often employed,

106, l. 30, *after* number *read* exclusively ; *after* colour *read* only

l. 44—P. **107**, l. 2. *for* Recently EWART . . . quite inactive *read* It has been recently repeatedly stated that pure yellow etiolated chloroplasts can also decompose carbon-dioxide (ENGELMANN, 1881; EWART, 1897; KOHL, 1906). MOLISCH, however (1906), using the very sensitive luminous bacterium method, was unable to demonstrate any evolution of oxygen from such chloroplasts.

107, ll. 11–14, *delete* [MOLISCH'S . . . dead cells.]

ll. 20–1, *for* The dependence . . . assimilation. *read* Further, MOLISCH (1904) has, with the aid of the luminous bacterium method, observed carbon-dioxide assimilation in chloroplasts taken from dry dead leaves (compare BALDASSERONI, 1906).

ll. 35–8, *for* in the chloroplasts, and . . . Fig. 24 *read* in the chloroplasts. According to MOLISCH (1906) this is due to the fact that certain parts of the cell act as cloudy media, and obscure the fluorescence. The spectrum of crude chlorophyll is shown at the top of Fig. 24.

108, l. 1, *for* six *read* seven

ll. 2 and 5, *for* three *read* four

ll. 6–8, *for* The figure . . . product of it *read* The fourth band, just in front of line E, probably belongs not to chlorophyll itself but to a decomposition product of it.

l. 12, *for* dense *read* denser

l. 32—P. **109**, l. 10, *for* Great progress . . . This substance *read* Considerable progress has been made of recent years in the chemical investigation of true chlorophyll (compare MARCHLEWSKI, 1901 ; CZAPEK, *Biochemie*, I, p. 449). We know that it is an exceedingly complex organic body, containing, in addition to H, O, N, and C, magnesium in relatively large quantity (WILLSTÄTTER, 1906). Iron, on the other hand, as already mentioned, is absent from the chlorophyll molecule, and even phosphorus is only doubtfully present. On this latter ground it was held until recently that chlorophyll must be regarded as a lecithin compound, but WILLSTÄTTER (1906) has shown that this view is incorrect. It would appear that we have here to deal with an albuminous or proteid body, and, as generally in these cases, we must look to detailed researches into the decomposition products of the substance to furnish us with an insight into the complex structure of its molecule. Such decomposition products are obtained, by the action of acids and alkalis, in quantity, and have received names—very few of them can, however, be simple

chemical bodies, not even SCHUNCK's phylloxanthin and phyllocyanin, which are relatively well characterized. On the other hand, one other by-product, phylloporphyrin, has apparently been separated out in the pure state, and this substance,

l. 21, *after* to perform. *read* We cannot enter into a discussion here as to the pigments of the variously coloured chloroplasts of red, brown, and yellow Algae.

110, ll. 1–3, *for* (HERTZOG . . . *Bot. Ztg.* 62, I, i], *read* (HERTZOG, 1902; BERNARD, 1904, 1905; MOLISCH, 1904). Further, the statements of BACH (1898) as well as those of USHER and PRIESTLEY (1906) to the effect that a reduction of carbon-dioxide can be induced by the action of uranium salts with the co-operation of sunlight, still await confirmation; EULER (1904) was unable to obtain any such result.

ll. 10–11, *for* to our eyes . . . purpose. *read* which is still strong enough for one to see by.

ll. 14–16, *for* intensity of the light. We must first . . . what substances *read* intensity of the light; then only will it be possible to estimate the exact significance of light in carbon dioxide assimilation. On the other hand, we have still to inquire in the present relation what substances

ll. 41–52, *for* The variations from . . . beyond all doubt. *read* Indeed the development of carbohydrate in the process of carbon-dioxide assimilation in the green plant has been definitely observed. The necessity for the presence of water in this constructive process has, however, as yet been shown only indirectly. THEO. DE SAUSSURE (1804, p. 226) noticed that the increase in dry weight of the green plant was considerably greater than could be accounted for by the addition of carbon only, and this excess in dry weight must be due to combined water.

111, l. 12, *for* iodine-proof *read* iodine-test

ll. 16–30, *for* When leaves . . . Orchidaceae. *read* By using a leaf freed from starch it may be demonstrated very conveniently that it is only in light that this process takes place, and that, too, only in regions immediately exposed to it. It is sufficient to shade a part of the leaf by a piece of paper, cork, or something of that sort, when afterwards this region, i.e. where no starch has been formed, stands out clear on a dark background. Conversely, one may cover a leaf with an opaque stencil, from which has been cut out, say, the word 'starch'. After the leaf has been sufficiently illuminated, and after treatment with iodine, the letters will appear black on an otherwise colourless leaf surface. If we experiment with different species of plants we at once see that very variable amounts of starch are formed in the same time, and that not infrequently these amounts are the same for whole families. Thus, for example (A. MEYER, 1885), a large amount of starch is formed in Solanaceae and Papilionaceae, a considerable amount in Papaveraceae, Crassulaceae, Boraginaceae, Labiatae, &c., while only a little is formed in many Gentianaceae and Iridaceae, and none at all in *Asclepias Cornuti*, *Allium*, *Scilla*, and other Liliaceae and Amaryllidaceae.

l. 48, *delete* appearing

l. 49, *for* substances *read* sugars

l. 55—P. **112**, l. 1, *for* starch. [According . . . starch] *read* starch, and hence we may speak of 'amyliferous leaves' and 'saccharíferous leaves'.

112, l. 19, *for* from which the starch is formed *read* which leads to the formation of starch

l. 46—P. **113**, l. 4, *for* An optically inactive . . . (H_2CO_3). *read* The analogy

between chlorophyll and haemoglobin on which BAYER based his hypothesis cannot be maintained nowadays; but one may easily get over the difficulty of assuming a development of carbon-monoxide—which in itself suggests many criticisms—if we start, not as we have been doing from the anhydride CO_2, but from carbonic acid itself (H_2CO_3).

113, l. 6, *after* H_2CO_3 *read* or partly in the dissociated condition HCO_3

ll. 16–37, *for* Many arguments . . . be correct. *read* Should formaldehyde arise in this or in some other way (comp. CZAPEK, *Biochemie*, I. 503) its condensation to a sugar, outside the plant at least, presents no special difficulty. BUTTLEROW (1861) and LOEW (1886) successfully accomplished such a condensation by simple methods, and obtained formose—a mixture of sugars—with the fundamental formula $C_6H_{12}O_6$. That a similar condensation, however, takes place in the plant may be regarded even now as open to doubt. In the first place, it is by no means certain whether formaldehyde is demonstrable in the plant, although it has often been so asserted (POLLACCI, 1902; GRAFE, 1906; USHER and PRIESTLEY, 1906). That there are other aldehydes present has been established by CURTIUS and REINKE (1897), but these doubtless have nothing to do with carbon-dioxide assimilation. Still the absence of formaldehyde is no serious argument against the hypothesis, for if it really be an intermediate product in carbon assimilation it would naturally be at once transformed, and hence would never accumulate in any quantity. Such an accumulation would, indeed, be injurious, since formaldehyde is a virulent poison. This leads us to another objection made to BAYER's hypothesis. It has been clearly shown that formaldehyde in a concentration of 1 in 20,000 or even 1 in 50,000 is seriously inimical to green cells (BOKORNY, 1897), but TREBOUX (1903) has shown that a solution of 1 in 200,000 is not injurious to *Elodea*, so that one must admit that it may occur in chloroplasts if it be rapidly transformed. A third, and perhaps the principal, objection raised is that it has not been found possible to induce a formation of starch, either in light or darkness, by supplying formaldehyde to chloroplasts (TREBOUX, 1903), although this must certainly occur if the hypothesis be correct.

l. 45, *for* p. 341 *read* p. 326

ll. 46–9, *delete* Experiments . . . in the light.

114, ll. 16–43, *for* In the first place . . . in that form. *read* In the first place, we know that every part of the plant suffers considerable loss of organic substance owing to respiration acting in the reverse way to carbon-dioxide assimilation (Lecture XVI), and, further, owing to the continuous withdrawal into the stem of considerable quantities of soluble carbohydrate (Lecture XIV).

We cannot refer here to the way in which SACHS established a measure for the amount of this loss, but merely give the results he obtained, which were, that *Helianthus* formed 1·7–1·88 g. and *Cucurbita* 1·5 g. of dry weight per hour per sq. m. Taking these numbers as a basis, SACHS reckoned that a vigorous active sunflower can manufacture 36 g. and a cucumber 185 g. of dry weight in the course of a warm and bright summer day. More recently ARNO MÜLLER (1904) has carried out estimations as to the amount of assimilation in various leaves, using the same method, and has arrived at the following results :—

Carbohydrate formed per hour and per sq. m. in gr.

Amyliferous leaves:	*Nymphaea*	*Rumex*	*Petasites*	*Helianthus*	*Nicotiana*
	2·373	2·215	2·045	1·823	1·378
Sacchariferous leaves:	*Tulipa*	*Arum*	*Colchicum*	*Allium*	
	1·267	1·004	1·217	1·193	

The value given above for *Helianthus* agrees exactly with that obtained

by SACHS for the same plant. Other plants, however, exhibit far greater assimilatory activity, while in those enumerated in the second series assimilation is much lower than in *Helianthus*. These four plants, however, possess saccharíferous leaves (see p. 111), for under ordinary circumstances they form no starch ; it would appear that assimilation is, in general, more active in amyliferous than in saccharíferous leaves.

The mention of amyliferous and saccharíferous leaves leads us to follow out quantitatively also the carbohydrates appearing during assimilation, which we have previously spoken of from the qualitative point of view. Hitherto we have always spoken of the increase in dry weight or in carbohydrate. In SACHS's memoir, on the other hand, it is always 'starch-formation' that is spoken of, for at that time all products of assimilation were assumed to be deposited in that form.

l. 44, *after* experiments *read* with the half-leaf method.

l. 50—P. **115**, l. 1, *for* MEYER'S studies . . . in detail. *read* BROWN and MORRIS'S studies as to the nature of the sugars occurring in the leaf are for that reason of greater importance, and for such investigation they used the leaves of *Tropaeolum*. In what follows we will deal with the results of some of their experiments without discussing the methods they adopted to obtain them.

116, l. 36—P. **117**, l. 11, *for* We need not enlarge . . . with these relations. *read* We need not therefore enlarge on these results. GILTAY (1898) and BROWN (1899) have employed this method in a modified form. They worked with ordinary air whose percentage of CO_2 was accurately determined ; further, they used daylight and introduced only single leaves into the bell-jars, which leaves were still attached to the plant, so more easily guarding against wilting than was possible with severed leaves. GILTAY has experimented with a large number of plants, both European and Indian ; he calculated the value per hour per sq. m. and found it to be from 0·4 g. to 0·8 g. in the former and 0·4 g. to 1·4 g. in the latter. Assimilation, therefore, in tropical plants exceeded that in mid-European plants only to an unimportant extent. Exactly the same value, viz. 0·58 g., was obtained for the sunflower, whether grown in Europe or in Java. BROWN obtained quite similar values, and his experiments were published for the first time in detailed form in 1905. He made it out to be in the case of *Helianthus* 0·4–0·5 g., but in certain other plants it was somewhat less ; the maximum occurred in *Polygonum*, viz. 0·593 g. As we see, GILTAY'S and BROWN'S estimates are much lower than those obtained by SACHS and A. MÜLLER with the half-leaf method. BROWN, moreover, makes so many adverse criticisms on the half-leaf method that new experiments appear necessary before one can determine whether it can make any claim to accuracy.

118, ll. 9–10, *for* study first the amount . . . in the air. *read* study first how the plant manages to acquire the carbon-dioxide. In one of BROWN'S experiments (1905) a sq. m. of leaf surface of *Helianthus* took up 440 ccm. (or roughly ½ a litre) of carbon-dioxide in an hour. Our first inquiry must be how much CO_2 there is in the air, and whether the amount present suffices for the needs of the leaves.

l. 16, *after* average *read* in England ; *for* 2·8 read 2·94 ; *after* air *read* (minimum, 2·43 ; maximum, 3·60).

ll. 41–6, *for* will show. According to SACHS . . . and imagine the *read* will show (SACHS, 1884). A sunflower has a leaf surface approximately 1·5 sq. m. in extent. Taking as a basis the experiment referred to above it would absorb 660 ccm. of carbon-dioxide per hour, equal to about 1·3 g. Hence

we may conclude that the plant requires in round number 400 g. per month of CO_2, assuming a daily assimilatory period of ten hours. If we now imagine the

l. 49, *for* 135 billion kg. *read* 54 billion kg.

119, ll. 1–9, *for* twenty months. This is . . . exact analyses *read* fifty months. It would last somewhat longer if we took as our basis the CO_2 requirements of a wood. In any case it would appear that the supply of CO_2 in the air must in the course of a few years be entirely used up by the activity of green plants. Since, as a matter of fact, no decrease in the amount of CO_2 in the air has, according to the most exact analyses,

l. 21, *for* 279 *read* 298

ll. 32–3, *for* everywhere . . . present. *read* everywhere, in round numbers, 0·03 per cent. present.

l. 39, *after* 20° C. *read* Water at 15° C. in contact with the air has approximately the same amount of CO_2 dissolved in it, viz. 0·03 per cent.

l. 50—P. **120**, l. 37, *for* We owe our knowledge . . . though water cannot *read* To GODLEWSKI's (1873) and KREUSSLER's (1885) investigations, as also to those of BROWN and ESCOMBE (1902), PANTANELLI (1903), and of BLACKMAN and MATTHAEI (1905), we owe our knowledge of the fact that an increase in the amount of CO_2 in the air tends to an increase in assimilation. On the other hand, it is well known that a higher percentage of CO_2 induces closure of the stomata (DARWIN, 1898), and hence injures the plant, while a higher percentage still acts directly as a poison and destroys vitality (LOPRIORI, 1895). Hence there must be a certain medium percentage which induces an optimum effect. This optimum is not, however, constant, for the assimilatory activity depends on several other factors, e.g. light and temperature. Thus it arises that a percentage of CO_2 in the air which permits a maximum of assimilation when the light has a certain intensity, becomes a limiting factor at higher light intensities (BLACKMAN, 1905).

Let us now turn to the question how the carbon-dioxide reaches the assimilating cells of the leaf. Submerged plants are restricted entirely to carbon-dioxide, and gases generally, dissolved in water, and these gases manage to enter the plant by diffusion only through the continuous epidermis. Once the gases have penetrated the outer wall of the epidermis they can diffuse from cell to cell; moreover, they can also pass through the inner walls of the epidermal cells into the intercellular spaces, which are always exceedingly plentiful in aquatic plants, and can thus enter the individual cells from these spaces. Diffusion through the epidermal cells into the intercellular spaces takes place (DEVAUX, 1889) in accordance with the same law that EXNER established for the diffusion of gases through an aqueous film, i.e. the rate of diffusion of the gas is directly proportional to its solubility in water, and inversely proportional to the square root of the density of the gas. Hence it follows that the rate of diffusion of oxygen is twice, and of carbon-dioxide 55 times, as great as that of nitrogen. When the diffusion movement has produced an equilibrium, the intercellular spaces are found to contain air of approximately the same composition and at the same pressure as the atmosphere. Respiration (Lecture XVI) induces no essential alteration in this condition, but it is otherwise with carbon assimilation. Since the CO_2 streams rapidly from without inwards, in proportion as it is used up, while the oxygen arising from its decomposition diffuses outwards but slowly, increase of pressure results in the intercellular spaces, and finally an extrusion of air-bubbles from wounds produced intentionally or accidentally. This stream of air-bubbles we have already observed and used as a measure of CO_2-decomposition. That the air given off cannot be pure oxygen, but only a gaseous

mixture rich in that gas is readily understood, now that we have become acquainted with diffusion more in detail. The nitrogen diffuses continuously out of the water into the intercellular spaces, and all the more so the richer these become in oxygen owing to the decomposition of CO_2. Were the rate of diffusion not so slow the escaping gas would always exhibit the same proportion between oxygen and nitrogen as that which exists in air.

There is another reason for the evolution of air-bubbles from aquatic plants, which must be taken note of because it not infrequently may give rise to misconception. One notices often when using the bubble method for demonstration purposes that the stream does not cease in darkness. This is always the case when the water employed is previously supersaturated with gases, or when it becomes so by a rise in temperature. Under these circumstances, the surplus gas must come out of solution and air-bubbles appear on the walls of the vessel and on the outer surface of the plants; it diffuses also in bulk into the interior of the plant, causes a super-pressure there, and consequently a stream of bubbles to the exterior (DEVAUX, 1889; PANTANELLI, 1904). It is advisable, therefore, in all experiments in assimilation to employ water which has stood exposed, and not water direct from a tap.

The absorption of carbon-dioxide by the leaves of land plants is carried out in an essentially different manner from that seen in aquatic plants. In land plants the epidermis is covered by a corky layer—the cuticle—which is almost impermeable to water, although by no means so to carbon-dioxide; indeed carbon-dioxide can diffuse through a layer of oil, though water cannot.

121, l. 30, *for* 1·8 g. *read* 0·5 g.

l. 49, *after* opening *read* (BROWN and ESCOMBE'S experiments have been re-examined from the physical point of view by P. NELL (1905), but his results are by no means entirely confirmatory).

122, l. 12, *for* 0·134 ccm. *read* 0·447 ccm.

l. 13, *for* 1·8 g. *read* 0·6 g.; *for* 6 per cent. *read* 2 per cent.

ll. 46–8, *for* in carbon-dioxide, and it must . . . Assimilation is not lowered *read* in carbon-dioxide, for assimilation is not lowered

ll. 52–6, *for* It must not . . . water present *read* This, however, is by no means universally true, for a reduction in osmotic pressure produces an unfavourable effect on assimilation usually long before the plasmolytic stage is reached (PANTANELLI, 1903; TREBOUX, 1903). In addition to light and atmospheric moisture there are other factors still which affect the behaviour of the stomata. We need only refer to the carbon-dioxide itself, which, according to DARWIN (1898), induces closure of the stoma. DARWIN unfortunately does not mention the concentration of CO_2 which leads to this result.

123, l. 18, *read* For the formation of chlorophyll the temperature must not be

ll. 23–43, *delete* Even when . . . (comp. p. 114).

l. 44, *delete* only

ll. 48–50, *for* between such . . . indirectly *read* between external conditions as influencing this process directly and as influencing it indirectly.

ll. 51–2, *for* inhibit the action of the chlorophyll *read* bring about a closure of the stomata,

124, ll. 1–2, *for* it cannot be replaced . . . carbon-monoxide *read* it cannot apparently be replaced by any other compound of carbon. The compound which would first occur to us is carbon-monoxide, and from JUST'S researches (1882) it was supposed that this gas was indeed innocuous, but at the same time useless. More recently, quite contradictory statements have been made on the subject; on the one hand it has been asserted that CO might serve

as a substitute for CO_2 (BOTTOMLEY, 1903), on the other hand (RICHARDS and MCDOUGAL, 1904) this has been denied; at the same time CO has been stated to be a virulent poison.

ll. 4–5, *for* that, at the commencement . . . observable *read* that assimilation may start in the absence of demonstrable traces of oxygen,

l. 19, *after* inactive. *read* We speak of inactivity of the chloroplasts (EWART, 1896; PANTANELLI, 1903) when CO_2-decomposition is inhibited by any factors which do not suspend other processes in the plant, e.g. respiration, and which at the same time do not visibly injure the chloroplasts, so that when the inhibiting factors are removed, they are capable of again exhibiting their normal functions. A whole series of substances act in this way, anaesthetics and antipyretics, acids and alkalis. Carbon-dioxide itself in higher concentration has the same effect, and an accumulation of carbohydrates formed in the process of assimilation leads to temporary inactivity of the chloroplasts. Hence, quite incidentally, such an inactivity of the chloroplasts may occur in assimilation experiments, as, for example, when these are made on isolated leaves, where translocation of the assimilata is impossible (compare SAPOSCHNIKOW [1895] and the startling statements made by BROWN and ESCOMBE [1905, p. 50]). Finally, extremes of temperature and high insolation must be alluded to, but of these we shall speak presently. That the substances mentioned above, when present in small amount, may also act as stimulants, is not to be wondered at after what has been already said on the subject of poisons. Such a stimulatory action, e.g. due to ether and chloroform (KEGEL, 1905), dilute acids (TREBOUX, 1903), has been already demonstrated, and no doubt will be so for other substances also.

l. 20, *for* Heat *read* Temperature,

l. 27—P. **125**, l. 8, *for* KREUSSLER (1890) . . . still more sudden.] *read* MATTHAEI (1904). These were carried out with artificial light on isolated leaves by means of the method adopted by KREUSSLER. The leaves are, first of all, kept for 1½ hours at the temperature to be investigated, and then the amount of CO_2-decomposition taking place per hour is next determined. Fig. 25*a* gives the results in graphic form. The temperatures are indicated on the abscissa, while the ordinates give the amount, in milligrams, of CO_2 decomposed per 50 sq. cm. of leaf surface. The continuous line gives the results of the first hours of the experiment. It shows that the amount of CO_2 decomposed rises at first as the temperature rises and falls so rapidly above 37·5° C., that at about 45° no assimilation at all takes place; below 0° C. feeble decomposition goes on, and may be observed even down to −5° C. Many other functions in the plant depend in a similar manner on temperature, and SACHS (1860), who was the first to draw attention to the point, described the temperature at which the function in question began as the minimum, that which gave the best results as the optimum, and that at which the function ceased as the maximum. The minimum, optimum, and maximum he termed the cardinal points. Many investigations have been carried out since his time on carbon assimilation (the only function we are at present concerned with), especially by KREUSSLER (1890), with the view of determining the position of these cardinal points. From MATTHAEI'S researches it would appear that the cardinal points are by no means fixed. At all low temperatures the values obtained for CO_2-assimilation in successive hours on the whole correspond; the leaf, in other words, works with constant energy. Above 23·7° one notices, however, a steady fall in assimilation from hour to hour. This is expressed by the dotted lines II, III, and IV in the figure, which represent the assimilation taking place 1, 2, and 3 hours after the first determination. The result of this rapid fall at higher temperatures is that the optimum, which lay at 37·5° in the first reading, and which would certainly have been

found to be even higher had the reading been taken after the leaf had been subjected to that temperature for a shorter period, gradually shifted downwards : 30·5° in curve IV.

We owe an interesting theoretical interpretation of the curve of assimilation to BLACKMAN (1905). KANITZ (1905) independently drew attention to the fact that curve I between 0° C. and 27° C. agrees with VAN 'T HOFF's law on the dependence of the rate of reaction of chemical processes on temperature; BLACKMAN sought to show that this curve is the resultant of two antagonistic processes. CO_2-assimilation, being a chemical process, must increase with temperature somewhat in the way indicated by the curve AB in Fig. 25*b*, but the temperature has the further effect of rendering the chloroplasts inactive. The higher the temperature the more rapidly does this inactivity approach completeness, and we may express, very roughly, the curve of inactivity by the line CD (Fig. 25*b*). Owing to the combined stimulatory and retarding action of temperature then we arrive at the ' optimum curve ' AE, which, as a matter of fact, corresponds with that obtained by actual observation.

125, ll. 14–18, *delete* [Very often . . . experiment.]

ll. 31–2, *for* It is only . . . provided *read* —which indeed quantitative chemical methods cannot measure accurately in such a case unless

l. 35, *for* entirely when respiration *read* finally only when this diminution

l. 47—P. **126**, l. 20, *for* Further we are . . . environment increases.] *read* As the light increases in intensity CO_2-assimilation also increases. When the light is about as intense as ordinary sunlight, however, this relation is not maintained, and that for several reasons. In the first place, intense light, like high temperature, causes the chlorophyll to become inactive. PANTANELLI (1903) found that in *Elodea*, for example, when the intensity of the light was either 1 or $\frac{1}{4}$ (sunlight = 1) CO_2-decomposition went on for fifty minutes at a uniform rate, but that it decreased markedly after fifteen minutes' exposure to light of intensity = 4. In the second place, the CO_2-decomposition may remain constant in spite of an increase in light intensity, because the supply of carbon-dioxide is insufficient to render a further increase in assimilation possible. Thirdly, the temperature may exert a limiting effect on it. Owing to the factor first mentioned the curve representing the dependence of assimilation on illumination will take the form of an ' optimum curve ', and its apex will in due course approach those of lower light intensities. The effect of an insufficient supply of CO_2 or of a low temperature will express itself in a curve which at the beginning will rise proportionally to the light intensity, and will then proceed horizontally. Fig. 25*c* shows these relations diagrammatically. The law of minimum is thus appreciable here also; the factor operative in minimum degree determines the amount of organic substance formed.

BLACKMAN and MATTHAEI (1905) have shown that in nature, even in diffuse light, the deficiency in CO_2 never permits of the maximum of assimilation being reached. When they artificially increased the percentage of CO_2 in the air, the temperature of the leaves prevented the complete utilization of the sunlight—always in direct sunlight, but only on cool days in diffuse daylight. On warm days, on the other hand, the light intensity was insufficient when the light was diffuse to induce the maximum assimilation possible at such a high temperature.

Legend to Fig. 25c. The abscissa shows light intensities, the ordinates show amounts of assimilation. Curve I, assimilation with a sufficiency of CO_2, and high temperature; II, under the same conditions as I, but a later reading; III, Assimilation with sufficiently high temperature but a deficiency in CO_2; after reaching B the tracing becomes horizontal because higher assimilation values are prevented by deficiency in CO_2; IV, assimilation with a sufficiency of CO_2, but at a lower temperature; after reaching A, any rise in assimilation is rendered impossible by the lowness of the temperature.

126, l. 39, *for* TIMIRIASEF (1885) *read* TIMIRIASEF (1885, 1903),

127, ll. 10–12, *for* with the . . . be thrown *read* for instance, with the gas-bubble method, or in carrying out eudiometric researches, or in estimating the amount of starch formed ; on the other hand a microscopic spectrum may be thrown

l. 28, *after* points *read* of agreement

l. 33, *after* to us. *read* That ultra-violet light has also a feeble power in this respect is asserted by BONNIER and MANGIN (1886) only.

l. 35, *for* beyond *read* beside

l. 39—P. **128**, l. 10, *for* On the other hand . . . assimilation *read* 3. The principal apex of this curve lies in the less refrangible half of the spectrum.

Different views are held, on the other hand, as to the questions (1) in what wave-length region this chief maximum lies, and (2) whether, in addition, there is a second maximum in the region of less wave length. We will deal with the second question first.

If a plant be placed under a double-walled bell-jar filled with potassium bichromate or with ammoniacal cupric oxide, which allow yellow and blue light to pass through respectively, one sees that the plant assimilates almost as well in the yellow light as in white light, but only very feebly in the blue light. The experiment is more accurate if one dispenses entirely with absorbent glass vessels, and uses REINKE'S spectrophore. When the light, by its means, is spectrally divided, first the less refrangible rays (up to line D), and then the more refrangible ones, are severally concentrated by means of a biconvex lens. In this way one can subject the plant to the influence of either red or blue light. All authors are agreed that the red half has much greater effect than the blue. TIMIRIASEF (1903) states that the former has twice the assimilatory activity of the latter. One fact of great importance is established from these experiments, viz. that the light rays that play the chief part in CO_2-assimilation are other than those which induce the decomposition of silver salts. To describe, therefore, the blue-violet rays which are effective in the case of silver salts briefly as the ' chemically active ' rays is a quite erroneous generalization.

According to some authors (especially REINKE, 1884) the curve of assimilation continuously sinks in the course of the blue half of the spectrum, while according to ENGELMANN (1884) a second maximum is attained near FRAUNHOFER'S line F (comp. Figs. 27 and 28) ; this second maximum ENGELMANN demonstrated by means of the bacterium method, but PFEFFER (*Phys.* I, p. 345), on repeating the experiment with the same method, was unable to confirm this observation. KOHL (1903) has more recently studied the same question ; and from his experiments it may be concluded that although assimilation still occurs near line F, there is no second maximum then. Earlier statements of the same author (1897) appear to be even less securely founded.

128, first column of table, *for* upper side *read* under side directly illuminated ; and *for* lower side *read* upper side in transmitted light

129, l. 3, *for* why *read* in relation to which

ll. 35–40, *for* If relations . . . evidence. *read* Although then relations do exist between absorption and assimilation, still these are very complex and have yet to be made out in detail. A reinvestigation of this question is all the more desirable as other, partly biological, considerations have been put forward in support of a relation between absorption and assimilation. Thus ENGELMANN (1884) has made some interesting statements with regard to the non-green Algae. Since water absorbs the rays of greater wave length more rapidly than the blue ones, the rays of shorter wave length are more and more prominent (in the deeper layers of the sea). The colouring matters of

Marine Algae must thus be complementary to those of their environment, and hence this light, which is their optimal light, is absorbed by them. Confirmation of this view, which in our opinion, at least in relation to assimilation itself, is by no means sufficiently well founded, is given by the interesting results obtained by GAIDUKOW (1906). This investigator succeeded in inducing, experimentally, in certain Algae an alteration in colour, and that, too, in the sense of being a complementary coloration in relation to their surroundings (Chromatic Adaptation, compare Lecture XXIV). STAHL also (1906) has recently carried the matter a step further than ENGELMANN. He showed that in nature the plant is not affected merely by direct sunlight, as is the case when the heliostat is employed as a means of illumination, as is generally the case in assimilation experiments; for in addition the, quantitatively, by no means inconsiderable amount of light arising from diffuse atmospheric reflection must be taken into account. While, however, in the case of direct sunlight, the blue and violet rays are absorbed in their passage through the atmosphere, it is the red and yellow rays that are really lost in diffuse reflected light. According to STAHL, the chlorophyll proper has for its function the absorption of the red rays of direct light, while the accessory yellow pigment absorbs the blue rays of diffuse reflected light. That the green rays are as little absorbed as the ultra-red, STAHL explains in this way, viz. that these rays are present in so small an amount in diffuse light that the plant is unable to make any use of them, while they are so abundant in direct light as to injure the plant by causing an excessive elevation of temperature. Thus the vigorous absorption of light rays is prevented by the fact that the plant is not grey or black, but green. We must await proof, however, of this view. It would seem to us especially important to bring forward evidence of assimilation capacity in blue light of chloroplasts of yellow colour only, not of green. We cannot admit that KOHL (1906) has as yet proved this exactly.

l. 44, *for* possesses *read* possess

l. 45, *for* the end product, *read* an end product of combustion,

l. 52, *for* 1847, *read* 1845,

130, ll. 13–43, *for* It is possible . . . from that gas *read* It is possible to arrive at an approximate estimate of these amounts in the first instance theoretically, and for this purpose a knowledge of the following values is essential, viz. (1) the amount of carbohydrate formed per unit of time per unit of leaf surface; (2) the heat of formation of these carbohydrates; (3) the amount of solar energy falling on a unit of leaf surface in a unit of time. The first value, as we have seen, has often been estimated; the second may be regarded as equal to the heat of combustion; the third has been calculated by physicists, and more recently by BROWN and ESCOMBE (1905). These authors found that, in the case of *Helianthus*, only 0·66–0·72 per cent. of the light falling on the leaf was employed in photosynthesis. Similar results were obtained by PFEFFER (1871) and AD. MAYER (1897); they are less trustworthy, however, because these authors did not determine, as BROWN did, the value of the incident light in relation to assimilation.

Only a very limited portion of the solar energy at least is used up in photosynthesis. In addition to their theoretical determination an attempt has been made to estimate their value experimentally. DETLEFFSEN (1888) observed the absorption of light in a leaf with the aid of a thermopile, and placed the leaf alternately in air containing CO_2 (10 per cent.) and air with no CO_2.

l. 54, *after* solution. *read* As a matter of fact, much light is absorbed by the leaf that is put to other than photosynthetic uses. According to BROWN'S experiments the leaf of a sunflower exposed to a high temperature (27° C.)

absorbs 81 per cent. of the incident light, allowing only 19 per cent. to pass through, and of this 81 per cent., 80·3 per cent. is used in transpiration, and only 0·7 per cent. in photosynthesis. Since, however, the part of the solar energy employed in transpiration must, without doubt, be subject to continuous and great variations (due to temperature, atmospheric moisture, &c.), it must be a matter of considerable difficulty to draw any sound conclusions as to light energy used up in photosynthesis from observations on the variation of the amount of light passing through the leaf.

131, l. 4, *after* light, *read* e.g. chlorophyll (TIMIRIASEF, 1903),

l. 12, *after* sensitizer *read* in this sense. If, however, by the term 'sensitizer' we attach chief emphasis to the idea of a transfer of energy of the absorbed light to another substance, then one may well regard the chlorophyll as a member of the class of sensitizing substances (comp. MOLISCH, 1906).

l. 21, *for* 2nd ed. *read* I, p. 292.

ll. 24–5, *for* 2nd ed. 1, 289 *read* I, p. 308.

l. 42, *after* 'purification'. *read* He showed, further, that the CO_2 of the air was not only the source of the organic substance of the plant but also of the oxygen given off by it, and that the humus was of no nutritive value. He also had a perfectly clear conception of the extent of respiration. Hence he must be looked upon as the founder of our knowledge of nutrition; the facts that he established form the fundamental basis of all we know on the subject to-day.

ll. 46–54, *for* He showed . . . sound basis. *read* His studies, however, did not conduce to a marked advance in the subject (WIESNER, 1905); that we owe, in the first instance, to TH. DE SAUSSURE (1804), who by his accurate quantitative experiments provided that solid basis for the whole superstructure which it required.

132, l. 8, *after* starch *read* not only

133, ll. 3–4, *for* of which . . . here *read* e.g. the materials of the cell-wall, fats, and numerous organic acids.

l. 7, *for* every plant . . . percentage *read* these bodies form indeed but a small part of the dry substance, but they are never absent from it

ll. 10–11, *for* of whose . . . conception. *read* and thus complete our sketch of their absorption of nutriment.

l. 13, *for* than carbon. For *read* inasmuch as

l. 14, *delete* on the contrary

134, ll. 8–9, *for* reaches . . . ash *read* consequently must suffice for further development of the seedling than the amount of ash constituents present will permit.

l. 40, *delete* not to say the best possible

ll. 41–3, *delete* [How . . . say.]

ll. 47—**P. 135**, l. 32, *for* It is impossible . . . injurious effects. *read* After BOUSSINGAULT had furnished proof that the green plant thrived well with nitric acid as a nutrient, the older view that ammonia was the chief source of nitrogen to the plant, advocated especially by LIEBIG (1840), was overthrown. Indeed, some went further and affirmed that ammonia was far inferior to nitric acid as a source of nitrogen, believing that the earlier statements as to the favourable effect of ammonia were entirely due to the fact that the ammonia in the soil had become altered into nitric acid through the agency of micro-organisms (Lecture XIX). Apparently, however, this reactionary position as regards LIEBIG'S ammonia theory far overshot the mark. More recent experiments (PITSCH, 1887–96; MAZE, 1900; GERLACH and VOGEL, 1905; SOAVE, 1906)

have shown that ammonia is almost as good, and in some cases even a better nutrient than nitric acid. TREBOUX (1904) claims that ammonia quite generally leads to more favourable results, but he has not as yet furnished us with any evidence in support of his view. In cases where the results obtained with ammonia are poor, we may often put it down to the inability of the root to endure the presence of salts of ammonia in higher concentration. The poisonous effect of ammonium carbonate, coincident with its alkaline reaction, has been noted, while, on the other hand, a ½ per cent. solution of ammonium sulphate appears to have no evil effect at all.

Nitrites may be regarded as third in series, for MOLISCH (1887) has shown that in weaker concentrations they are plentifully absorbed, and are reduced in the plant, while in stronger doses they are markedly toxic. According to TREBOUX (1904) this toxic action disappears when the solution is alkaline, and then the nitrites are even better nutrients than the nitrates. This wants confirmation, however.

Finally, there are the humin substances to take account of, for they always contain abundant nitrogen, and are widely distributed in nature; that their nitrogenous constituents are, at least partly, made use of by the higher plants is not improbable but not definitely proved (NIKITINSKI, 1902).

136, l. 15, *after* itself. *read* In the tropics the amount of combined nitrogen present in rain is much greater than it is in our country; MUNTZ and MARCANO found as much as 16 mg. per litre at Caracas.

ll. 18–19 *for* [in tropical . . . 1889)] *read* in tropical countries as much as 6 kg.,

l. 24, *for* in general *read* at least in part,

l. 25, *for* XVII). This substance is greedily *read* XVII); the remainder appears in the almost insoluble humin substances. Ammonia is greedily

ll. 29–30, *delete* In this way . . . ammonia.

l. 50, *for* This evolution *read* A loss of this kind never occurs in the higher plant (CASTORO, 1904), for the plant is altogether more economical of its nitrogen than the animal; on the other hand, an evolution

137, ll. 10–12, *delete* Without doubt . . . soil.

l. 32, *after* soil. *read* We have now to investigate the amount of nitrogen present in the soil, and in the first place that present in uncultivated land.

138, l. 2, *after* in it. *read* We can scarcely go far wrong if we assume that the nitrogen is very frequently the limiting factor, and that on the amount of that element depends chiefly the amount of plant production in nature.

ll. 5–6, *for* Just as . . . removed. *read* For precisely the same reasons brought forward when speaking of the materials of the ash, so here also agricultural success depends on how much overcropping takes place so far as nitrogen is concerned.

l. 9, *for* is *read* are

ll. 22–3, *delete* traceable in its origin to vital activity.

ll. 26–30, *for* [Probably . . . detail later. *read* Further, those plants which fix the nitrogen of the air are of the greatest importance in agriculture, but of them we shall treat later (Lecture XIX). At present it must be noted that the artificial combination of atmospheric nitrogen has been accomplished, and the product, calcium cyanamide ($CaCN_2$), has been added to the soil as a substitute for other nitrogenous manures, where it undergoes decomposition

by micro-organisms, the resulting ammonia then becoming available for the higher plant (GERLACH, 1904; LÖHNIS, 1905; FRANK, 1905).

ll. 34–5, *for* As we remarked . . . defective. *read* These are problems, however, to which as yet we can give only very imperfect answers.

139, l. 4, *for* Nevertheless . . . which have *read* Their solutions have

l. 7, *for* This coagulation is permanent and *read* This coagulum is indeed capable of swelling, but

l. 47—P. **140**, l. 15, *for* Among the products . . . Pyridin group. *read* The further decomposition of peptone results in the formation especially of amino-acids, in addition to carbohydrates, ammonia, and humus substances. Many of these amino-acids have been prepared in the pure state, and their constitution determined; they have also been synthesized. The following summary is taken from ABDERHALDEN'S *Phys. Chem.* p. 1160:—

I. *Aliphatic series:*
   1. Monamino-acids: glycocoll, alanin, amino-isovalerianic acid, leucin, isoleucin:—serin:—aspartic acid, glutaminic acid.
   2. Diamino-acids: lysin, arginin.
   3. Sulphur-containing amino-acids: cystein, cystin.

II. *Aromatic series:* Phenylalanin, tyrosin.

III. *Heterocyclic compounds:* pyrrolidin-carbonic acid (prolin), tryptophan, oxyprolin.

140, ll. 21–2, *for* The classification . . . constitution *read* In all probability these amino-acids arise by hydrolytic decomposition without any profound alteration of the proteid molecules. In other words, the proteid consists essentially of a large number of linked amino-acids. The first step towards proteid synthesis has been already accomplished (E. FISCHER, 1906), for it has been found possible, by combining two to several amino-acids, to obtain so-called polypeptids, that is to say, substances which are very closely allied to peptones.

It will be the task of the future to arrange the proteids according to their synthesis from different amino-acids. Meanwhile we must still content ourselves with a provisional arrangement based on solubility, their capacity for precipitation, &c.

ll. 38–9, *delete* III. Glutinoids . . . wanting.

ll. 48–56, *for* Let us now . . . nitric acid. *read* Let us now return to our main problem, where and how nitric acid and ammonia are assimilated in green plants. There is no doubt that the nitric acid is easily absorbed by the root from the soil. The impermeability of the protoplasm to nitrates, which exhibits itself when KNO_3 is used to effect plasmolysis, is at least only relative, and does not come into play in solutions so dilute as those which are found in the soil. It is often possible by using diphenylamin to follow the absorption and migration of nitrates in the plant, but since many subsidiary circumstances interfere with this reaction one can draw no conclusion from negative results. In many plants the nitric acid absorbed rapidly disappears, because it obviously very quickly undergoes alteration, but in other cases it is first of all accumulated and then used up later, e.g. in the formation of the fruit.

141, l. 2, *for* contain large *read* store up

ll. 6, 7, *delete* The nitrate . . . takes place.

l. 13—P. **144**, l. 43, *for* Such storing of nitrate . . . in the *dark*. *read* No definite answer can as yet be given to the question as to where and under what conditions further metabolism of nitric acid and the construction of proteids take place, though, generally speaking, one is inclined to hold the view that all plant cells may be capable of carrying out these processes. For long it was thought that proteid synthesis took place only in the chloroplasts

and under the influence of light (SCHIMPER, 1888, 1890). This view can no longer be held, for the fact that further working up of nitrates may occur in non-green cells has been proved beyond a doubt by several investigators (ZALESKI, 1900; SUZUKI, 1898; GODLEWSKI, 1903). It has been shown, it is true (GODLEWSKI, 1903), that the amount of the proteid formed in light is markedly greater than in darkness, and doubtless the foliage leaf takes an important share in the synthesis. Further, it must be noted that the favourable effect of light in proteid formation is direct according to GODLEWSKI, and not merely conditioned by the contemporary carbon assimilation going on, although it cannot be doubted that the products of CO_2-assimilation are required in the synthesis. In the dark proteid synthesis takes place only when sugar is plentifully supplied.

We are as little acquainted with the seat of the working up of ammonia as we are with regard to that of nitrates. No ammonia is accumulated, as we have seen to take place often in the case of nitrates; on the contrary, it appears to be rapidly altered wherever it occurs, and this rapid transformation must be of importance, seeing that salts of ammonia are poisonous. Where it takes place, and whether light is an essential or helpful agent in the matter, we have no certain knowledge (LAURENT and MARCHAL, 1904; HANSTEEN, 1899).

In the absence of any positive data on the subject, we must content ourselves with hypotheses as to the nature of the chemical processes taking place in proteid synthesis. It is highly probable that the construction of proteid consists essentially in an inversion of hydrolytic decomposition. Amino-acids must first arise, and from them, through polypeptids, peptones, and albuminoses, arises the proteid. There is a possibility that the ammonia of the nitric acid at once unites with carbon in CO_2-assimilation, and then perhaps hydrocyanic acid might appear from nitric acid and formaldehyde as the first nitrogenous assimilation product, as TREUB (1895, 1905) has in detail attempted to show. Possibly also carbohydrates or their derivates may take up the nitrogen as ammonia, and so form amino-acids, and it must be remembered that ERLENMEYER junior (1912) has obtained glycocoll, the simplest amino-acid, from glyoxylic acid. ABDERHALDEN (*Phys. Chem.* p. 330) has shown how glycerose ($C_3H_6O_3$) may form a point of departure of the amino-acids, and he also shows how glucose may give rise to amino-acids through glycosamin. In every case, the nitric acid must first of all be reduced, and such reduction occurs in the plant not only frequently, but readily.

It seems natural to ascribe to the light a reducing power, especially as it has been certainly shown to possess such a capacity in CO_2-assimilation. Since, however, further metabolism of nitrates can take place also in darkness, and since, on the other hand, also, light is possibly useful in the assimilation of ammonia, the influence of light cannot be limited to the reduction of nitric acid, and it might be capable of being replaced by other sources of energy. Primarily, one thinks of the chemical energy released in the oxidation of carbohydrates, which we have discussed already in Lecture XVI. If that be so, then the carbohydrates are essential to proteid synthesis, not only because they take part as such in the construction of the proteid, but also indirectly, inasmuch as they supply the energy necessary for their actual construction. While CO_2-assimilation in the green plant is dependent on solar energy, N-assimilation can be carried out by means of chemical energy which the plant itself has accumulated. CO_2-assimilation is a photosynthetic process, while N-assimilation is a chemosynthetic one.

If we regard the amino-acids as the first stage in protein synthesis, we have then to find whether these bodies occur in the plant to any degree worthy of mention. As a matter of fact, they are found quite generally, wherever indeed one looks for them, but unfortunately we have no certain means of

deciding whether they are synthetic or decomposition products of proteid. That the latter are always present in the plant we have already learned; asparagin has been especially frequently found in plants, and in certain circumstances accumulates in very considerable amount. It is not one of the bodies arising from the hydrolysis of proteid, yet it is closely related to aspartic acid, which is never absent. The problem is whether the plant, if artificially supplied with amino-acids, amides themselves, or other allied substances, can form proteid from these compounds, and under what conditions that synthesis takes place.

Already in older researches on the subject (PFEFFER, *Phys.* I. 405), nitrates or salts of ammonia were replaced by urea, glycocoll, asparagin, leucin, tyrosin, guanin, creatin, hippuric acid, uric acid, and it was possible to deduce a synthesis of proteid from the increase in dry weight that ensued. It is certain, however, that the transformation of these bodies into proteid was not always a direct one, but, for the most part, subsequent to splitting. For example, there can be no doubt that hippuric acid is split into benzoic acid and glycocoll, and that the glycocoll only is made further use of. All these substances, however, are readily altered into ammonia by the action of micro-organisms. Although stress has often been laid on the fact that in certain experiments a formation of ammonia could not be proved to occur, it by no means follows that it did not take place.

It might have been that the ammonia, in such amounts as it occurs, was at once absorbed by the plant. Systematic exclusion of micro-organisms has only recently been effected (BAESSLER, 1887, and especially LUTZ, 1899, 1905), and as a consequence there appears to be no doubt that many amino-acids and other nitrogenous organic compounds may serve as a source of N to the green plant. It is by no means the case, however, that, as one would otherwise expect, proteid synthesis is carried on with special ease, for secondary factors, e.g. the feeble permeability of protoplasm to these compounds, often determine whether it shall or shall not take place. More recently, LEFÈVRE (1906) has attempted to show that green plants can increase their dry weight in light with the aid of a mixture of amino-acids, even when they are debarred from access to carbon-dioxide; but in all probability this result is possible only because carbon-dioxide is, in the first instance, split off from the amino-acids in the plant, which afterwards in light proceeds to form carbohydrate from it. Generally speaking, carbohydrates appear to be essential to the formation of proteid from amino-acids; all the same we must leave it undecided whether the carbohydrates act as the source of the material or of the energy. According to HANSTEEN (1898) different carbohydrates are essential for the formation of proteid when different sources of nitrogen are employed; thus with asparagin glucose only, but not cane sugar, is required. Hence one could conclude that this sugar was incorporated into the proteid molecule. The microchemical method employed by HANSTEEN is, however, so uncertain that we cannot attach any value to his results (compare REINHARDT and SUSCHKOFF, 1905). Further, MALINIAK (1900) found proteid synthesis took place in the dark from asparagin just as readily along with glucose as with cane sugar. Her results were, it is true, obtained by quantitative analysis, but all the same they are not quite convincing. Again, we are ignorant what part is played by the light and by the carbohydrate in the working up of amino-acids. In a series of recent researches ZALESKI (1901) and IWANOFF (1901 a), by accurate analytical methods, have shown that proteid synthesis takes place in the dark in resting and sprouting bulbs, tubers, and roots, without any absorption of N from the environment, and without any increase in nitrogen. ZALESKI (1905) has shown the same to be true of seeds. How these proteids arise is not quite certain, but in all probability they are produced from amino-acids.

144, ll. 49–51, *for* at present . . . to at all *read* here; we may refer, however,

to the comprehensive treatments of the question by MONTEMARTINI (1905) and SCHULZE (1906).

ll. 55–6, *for* to which elements . . . a discussion *read* to which organic substances employ the individual constituents of the ash in their constructive metabolism, a discussion

145, l. 31, *after* 1901 b) *read* According to more recent statements by IWANOFF (1904) one can only say that the assimilation of P obviously also takes place in darkness, and possibly only in living cells. According to BALICKA (1906) part of the phosphoric acid taken up must be utilized without becoming united into an organic compound.

ll. 40–2, *for* As we know . . . present *read* (comp. CZAPEK, *Biochem.*).

ll. 46–7, *for* from which . . . of note *read* among which carbohydrates starch is specially worthy of note;

146, l. 6, *for* nitrogen requirements *read* nutrition

147, *title of lecture, read,*

THE UTILIZATION OF THE PRODUCTS OF ASSIMILATION. I

DISSOLUTION OF RESERVES IN SEEDS; ENZYMES.

l. 7, *after* from it *read* and even in leaves it appears only in the course of development

ll. 11–24, *for* Migration . . . translocation. *read* Migration of substances, and especially of carbohydrates, out of the leaf may, as a matter of fact, be easily demonstrated.

ll. 31–3, *for* There is no fact . . . from the assimilating leaf *read* Proteid also becomes in general more or less broken down, and the more diffusible substances so produced then suffer translocation. Hence there arises a stream of organic plastic substances from the assimilating leaf

149, l. 34, *for* A similar decomposition *read* A rapid transformation of the starch into grape sugar

l. 50, *after* p. 155). *read* Starch grains from different plants are unequally resistant to this treatment.

150, l. 53, *for* separate *read* separates

last line—P. **151**, l. 1, *delete* It might . . . proteid.

151, ll. 6–7, *for* its action . . . substances *read* the action of certain substances on it.

l. 28, *after* obtained. *read* Doubtless this curve takes its special form in consequence of the fact that temperature affects diastase in two ways. In the first place, its hydrolytic power rises with temperature like other chemical processes; on the other hand, however, diastase is destroyed by higher temperatures in increasing ratio, so that its amount becomes diminished; the form of the optimum curve thus depends on these two factors (comp. DUCLEAUX, 1899).

152, ll. 1–4, *delete* HANSTEEN . . . asparagin.

ll. 16–19, *for* Those with . . . Lecture XVI). *read* (Exhaustive presentations of our knowledge of enzymes are given by CZAPEK, *Biochemie*; HÖBER, *Phys. Chem.*; DUCLEAUX, 1899, and GREEN, 1899). Enzymes may often be extracted from the organism by means of water or glycerine; but all enzymes are not so readily extractable as diastase. Since many enzymes cannot pass through the cell-wall, they can be obtained free only by thorough destruction and rupture of the cells.

l. 21, *for* always *read* generally

ll. 23–4, *delete* The enzymes . . . alcohol.

ll. 26–8, *for* We may distinguish . . . limited *read* Hence it is possible to classify enzymes according to the value of the effects they induce. Here we shall deal only with the hydrolytic enzymes—reserving other effects for treatment later on, and we must recognize at least six groups of these enzymes:—

ll. 37–8, *for* In addition . . . hydrogen *read* 6. Glucoside-splitting enzymes form grape sugar, in addition to other substances, from glucosides; thus amygdalin is split by emulsin into glucose, hydrocyanic acid, and oil of bitter almonds.

In each group of these enzymes there are several distinct types with quite specific activities; by these activities they have been characterized, and they have been asserted to have a general capacity for splitting off oxygen from H_2O_2. Apparently, however, in this we have to deal with an admixture of another enzyme, of which we shall speak later.

153, ll. 2–12, *for* platinum is . . . inhibitory *read* platinum (i.e. platinum particles of ultra-microscopic size in water) is, on the other hand, exceedingly active. BREDIG (1901) has obtained such colloidal solutions by kathodic spraying, and has shown that they exhibit close analogies with enzymes. The fact that enzymes are colloids has not been previously mentioned, but that they are so may be readily understood, since in all probability they are to be classified along with proteids. In the second place, colloidal platinum acts catalytically in quite minimum amount, just like an enzyme. BREDIG observed catalysis of H_2O_2 with a dilution of the platinum to 0·0000003 mg. per ccm. Thirdly, the analogy between the enzyme and a colloidal solution shows itself in the fact that both are affected by substances which act poisonously—bodies known as ' paralysers '.

ll. 16–30, *for* BREDIG finds . . . 1892) *read* The chief point, however, is the alleged similarity in the catalytic action of the enzyme and of the colloidal platinum. This, according to BREDIG, lies in the fact that, in addition to acting catalytically on H_2O_2, colloidal platinum can invert cane sugar and effect other fermentative reactions occurring in the organisms, while, on the other hand, enzymes, in addition to their own specific capacities, can induce a reduction of H_2O_2. We may leave it undecided whether really and truly colloidal platinum may be said to have an enzymatic influence (comp. *Zeitsch. f. phys. Chem.* 31, 212, note); we merely note that the H_2O_2-catalysis induced by the enzyme is, as already stated, exceedingly problematical. By heating up to a definite temperature (JACOBSON, 1892) the power of the enzyme to catalyse H_2O_2 becomes lost, while its own specific capacity remains unaltered.

l. 33, *for* very obvious *read* probable

l. 41—P. **154**, l. 42, *for* Further differences . . . 1902) *read* For all that, BREDIG has gone too far in describing colloidal metallic solutions as inorganic ferments. The similarity may possibly lie merely in the fact that both bodies are catalytic agents. Mineral acids also, which operate hydrolytically, are inorganic catalytic agents, and numerous instances of such acids are known. Many of them accelerate very many reactions, while others have more limited spheres of activity (examples are given by CZAPEK, *Biochem.* I, p. 59). Enzymes, on the other hand, are characterized obviously by their eminently specific functions, and in that fact lies their significance not only in the organism, but also in physical chemistry.

154, l. 54, *after* at present. *read* If we describe the action of catalytic agents by saying that they alter the rate of a reaction which takes place in their absence, it is equivalent to saying that they are unable to effect the final result of the reaction. The final result of a chemical reaction is, however, varied. In many cases it results in a complete transformation of the initial substances —thus cane sugar is entirely converted into glucose by means of acids. On the other hand, there are reactions which cease when an equilibrium is reached. Thus, for example, the splitting of the acetic ester into ethyl-alcohol and acetic acid by taking up water is not carried to completion, but ceases before all the ester is decomposed. This phenomenon is to be explained by regarding

the formation of the ester by separation of water and its decomposition by taking up water as occurring simultaneously, equilibrium being arrived at when splitting and synthesis proceed at the same rate. Since, however, the rate depends on the concentration of the materials present, it is possible to induce a splitting by increasing the concentration of acid and alcohol; in other words, the reaction is reversible. If the catalytic agent is unable to alter the equilibrium, hydrolysis of maltose to dextrose, for instance, which under the influence of acids is incomplete and reversible, must also lead to the same equilibrium and be reversible, when effected by an appropriate enzyme (maltase). As a matter of fact, HILL (1898) has proved this. At the same time, it must be noted that the activity of the enzyme must vary greatly according to the degree of concentration of the maltose and the dextrose; in one case it will induce hydrolysis, in another synthesis. (It is impossible to discuss in any further detail the fact that the product of the synthesis is isomaltose, which does not quite correspond to the initial substance, maltose.) If continuous removal of the product of the reaction from the mixture be effected, then a complete hydrolysis will be reached or a complete synthesis as the case may be. It is readily seen how important this double mode of working of the enzyme, demonstrated by HILL, must be to the organism.

Synthetic activities, similar to that exhibited by maltose, have been proved to exist in other enzymes also. As examples we may refer to the synthesis of fat out of glycerine, and a fatty acid by lipase, and of amygdalin from grape-sugar, and amygdonitrileglucoside by emulsin. On the contrary, emulsin is unable to form any amygdalin from the products of its complete hydrolysis.

Irreversible hydrolyses proceeding to total splitting must take place under the influence of enzymes just as completely as under that of acids, but, as a matter of fact, that is not always the case. For instance, the hydrolysis above mentioned, of amygdalin into hydrocyanic acid, oil of bitter almonds, and dextrose in presence of acids, is complete, but it is incomplete when induced by emulsin. The equilibrium in the latter case is described as a 'pseudo-equilibrium'; that it is distinct from the true equilibrium occurring in reversible actions is shown among other things by the fact that it depends not on the concentration of the amygdalin, but on its amount. Such pseudo-equilibria, which often appear in enzyme reactions, e.g. in that of diastase, are explained by the fact that the products of splitting act on the enzyme, destroying it or at least rendering it inactive. The splitting goes on again if the products of the reaction be removed or if more enzyme be added. It is obvious that one must not draw any conclusion from such 'pseudo-equilibria' as to the reversibility of the reaction or as to the synthetic activity of the enzyme concerned.

Several explanations of the accelerating action of the enzyme and of catalytic agents in general have been put forward; for these we must refer to the literature on the subject, more especially to HÖBER'S *Physical Chemistry*. It will be sufficient if we draw attention to the existence of this power on the part of enzymes. We might express the whole story in a word by saying that the catalytic agent acts as a lubricant to the machine (comp. BREDIG, 1902).

156, ll. 30–56, *for* Sufficient evidence . . . later on *read* More especially we must remember how protoplasm alters in its permeability, alterations brought about, as we know, in a variety of ways.

157, *Lecture XIII as far as p.* 161 *is combined with Lecture XII in the 2nd German Edition.*

l. 42, *for* in palms and many other Monocotyledons *read* in Palmaceae, Rubiaceae, Umbelliferae, Leguminosae, and Liliaceae,

l. 55, *for* Such celluloses . . . giving *read* In seeds especially we find certain celluloses deposited, which give

158, ll. 1–2, *for* on treatment . . . dilute. *read* on treatment with acids ; in quite dilute acids they are hydrolysable.

ll. 25–32, *for* The distribution . . . activity.] *read* That cytases are widely distributed is obvious (HÉRISSEY, 1903) ; they occur wherever hemicelluloses have to be dissolved. It is true that they often occur in very small quantities, and the slow dissolution, e.g. of the endosperm of palm seeds, may be thus explained. Owing to the fact that the products of hydrolysis, mannose and galactose, are usually not found in plants, it is very probable that they are rapidly altered and used up.

l. 42, *after* starch *read* ; BEIJERINCK (1904) also regards oil as a product of assimilation in Diatoms.

160, l. 4, *for* are always *read* become gradually

ll. 48–53, *for* the amido-compounds . . . 1905) *read* the amino-acids.

161, ll. 18–44, *for* [These have also . . . does not say] *read* In all probability there are several kinds of trypsin, each with its own specific mode of action (POLLAK, 1904). One difference between vegetable and pancreatic trypsin is that it operates best in an acid solution. Recently, the occurrence of erepsin in plants, and especially in seeds, has been affirmed (VINES, 1905, 1906 ; DEAN, 1900). This enzyme can act only on albumoses and peptones (not on proteid), breaking them down rapidly into amino-acids. Although it has not been possible hitherto to prove the general presence of proteolytic enzymes in seeds, it must not be concluded that they are absent ; but since in individual cases only peptones and proteid can be obtained from seedlings which empty themselves of their own accord (PURIEWITSCH, 1897), one must assume that hydrolysis of proteid is not always necessary in germination, and that proteid as such can also migrate through protoplasm and cell-wall, a possibility on which we have not hitherto reckoned, but which may be regarded as not improbable, more especially in view of the power which fats possess of passing through these walls.

From what has been already said, compounds of sulphur and phosphorus are set free by proteolysis during germination. Primary sulphur-containing products, such as cystin, cystein, &c., have not as yet been found in plants. Sulphates appear in their place, but how they arise is not known. The mode of origin of the phosphoric acid that appears in germination (IWANOFF, 1902) is also but imperfectly understood ; many albumins and proteids, and perhaps also lecithins, may take part in its formation. According to recent views (CZAPEK, 1907, p. 497), the lecithins and cholesterins are constructive units of the protoplasm, and not reserves, and hence no breaking down of these occurs in germination. Phytin finally may be regarded as a chief source of phosphorus, a body which plays an essential part in the formation of aleurone grains (POSTERNAK, 1903). Lastly, the aleurone grains contain a quantity of other ash constituents of special value to the plant (POSTERNAK, 1905), for the most part in organic combination ; in germination all these bodies are set free as inorganic salts.

161. *With the last paragraph a new lecture begins in the German edition with title*

THE UTILIZATION OF THE PRODUCTS OF ASSIMILATION. II

OTHER STOREHOUSES OF RESERVES. TRANSLOCATION AND FATE OF THE DISSOLVED RESERVES

P. **162**, l. 30, *after* recently *read* (GENAU, 1901)

ll. 43–5, *for* [Mucilage . . . 1903] *read* It must be classed with the mannates and galactates of the seed, and consists of hemicelluloses, which can be transformed into mannose and galactose, but which contain much more water than the corresponding substances in seeds (HÉRISSEY, 1903).

163, l. 13, *for* amido-compounds . . . also occur *read* several amino-acids, similar in composition to those which occur in seedlings, are also found (comp. SCHULZE, 1904),

l. 17, *for* amido-compounds *read* amino-acids

ll. 34–5, *for* of the wood fibres . . . in spring *read* of the cortical and phloem parenchyma, and often also of the wood fibres

l. 37, *for* amides *read* amino-acids

164, ll. 3–11, *delete* From a comparison . . . inactive.

l. 40—P. **165**, l. 8, *for* present say ; it will . . . higher plants *read* present say. As we have seen, diastase, generally speaking, transforms starch into maltose, i.e. a reducing disaccharide which is, by hydrolysis, broken up into two molecules of dextrose. We have already seen that dextrose is formed from starch by the action of certain diastases, and it might well be that we were really dealing with a maltase mixed up with the true diastases. That yeast possesses such a ferment has been definitely proved, but to what extent it occurs in higher plants is still doubtful. Cane sugar is closely related to maltose ; it splits on hydrolysis into one molecule of dextrose and one of levulose, and a splitting of this nature has also been often shown to occur in the germination of the beetroot, where doubtless the cane sugar is transformed into invert sugar. Further, the ferment invertase, essential to this splitting, has been proved to exist in various plant organs with sufficient certainty (comp. GREEN, 1899), e.g. in the leaves of *Tropaeolum*, the buds of trees, seedlings of barley, and in pollen grains, and so one can scarcely doubt that that invertase is widely distributed. It must not be supposed, however, that cane sugar is never employed directly.

165, ll. 14, 18, 19, *for* amides *read* amino-acids

l. 38, *after* BUSCAGLIONI *read* 1899

ll. 40–2, *delete* and it would . . . dispersed.

166, *The matter of Lecture XIV is continued as part of the preceding lecture.*

l. 52, *after* (1897 *read* comp. CZAPEK, *Biochem.* II. 209.

167, l. 7, *for* amides *read* amino-acids

l. 31, *after* leaf *read* and one must believe that proteid as well as amino-acids take part in the migration, probably after first undergoing hydrolysis.

169, ll. 1–26, *for* lies in roots . . . but we must *read* lies partly in the external layer of the protoplasm and partly also in the cell-wall. The important part played by certain cell-walls in preventing the exit of materials from the plant has been emphasized recently both from the anatomical (A. MEYER and his pupils) and the physiological point of view (WÄCHTER, 1905 ; BROWN, 1907). From WÄCHTER's researches it would appear that slices of onion and beetroot lying in water allow quantities of the cell contents to escape, while no extrusion of material worth mentioning takes place from the uninjured plant into damp soil. It is improbable that the actual wounding induced alteration in the permeability of the protoplasm ; on the contrary, it may be regarded as certain that the waxy cuticle of the onion and the corky covering of the beetroot must act as preventative agents. Since, however, the cell-walls of young roots are very permeable, it must be the duty of the protoplasm to prevent a loss of material by diosmosis. According to WILLFARTH (1906) part of

the ash taken up by a large number of cultivated plants must pass back again into the soil.

From the experiments of PURIEWITSCH, referred to in the last lecture, it is known that the permeability of the protoplasm in self-emptying stores of reserve is inconstant, and WÄCHTER has more recently investigated this point more in detail in the case of the onion. He finds that the emptying, the exudation of glucose and non-reducing sugar, is, as a rule, always incomplete, ceasing when the concentration within the cells has reached a certain value. That the concentration outside is of no importance is shown by experiments with varying amounts of water, and also with salt solutions ; certainly there was, as in PURIEWITSCH'S experiments, a retardation of the outflow in the presence of such salt solutions, but the amount showed no ratio to the concentration of the salt. In addition to salts, PURIEWITSCH says that chloroform and oxygen have an effect on the outflow, and CZAPEK has (1897) also shown that emptying is inhibited by chloroform in the case of the petiole. While granting the possibility of the alteration of the quality of the plasmatic layer by anaesthetics we must

ll. 39–40, *for* is quite as great in the latter as in water *read* is certainly not as great in the latter as in water (NELL, 1905).

169, *last line*—P. **170**, l. 15, *for* It must not . . . minute canals *read* Whether the cell-wall or the plasmatic layer presents the greater difficulties in the way of diffusion we do not know. The pits, however, which are never absent from a cell-wall, are at least adapted to further a transport of materials from cell to cell, and that in two ways : first, inasmuch as the membrane, where they occur, is generally much reduced in thickness, and secondly, because of the fine pores existent in the pit-closing membrane. Since adjacent protoplasts are by means of these canals placed in communication with each other, it might be supposed that fragments of the protoplasm or even starch grains might pass over by this means from cell to cell ;

ll. 32–4, *for* According to . . . short ones *read* In spite of the pits every transverse wall would appear, all the same, to offer a certain amount of opposition to the transport of materials, and hence we see this transport taking place more readily in long cells, in which there are only few transverse partitions to be passed through, than in short cells.

171, ll. 3–5, *for* Although CZAPEK . . . is the case. *read* CZAPEK brings forward the following experiment in support of his view.

l. 14, *after* necessary *read* (comp. HABERLANDT, *Phys. Anat.*; CHAVEAUD, 1897).

l. 27, *delete* [HABERLANDT . . . view.]

ll. 30–4, *for* The sugar . . . carbohydrates. *read* The sugar arising from the transformation of starch, after migrating through the assimilatory cells and the bundle-sheath, eventually reaches the sieve-tubes, more than half of whose dry weight often consists of sugar (KRAUS, 1885).

l. 32, *for* 592 *read* 580.

l. 40, *after* 363) ; *read* it is by no means easy to decide whether protoplasmic movement takes place in the sieve-tubes of the uninjured plant or not, for observations on isolated portions prove little ;

172, ll. 19–22, *for* It is more . . . evidence. *read* It is improbable that sieve tubes are aided in the performance of their functions by lacticiferous tubes (KNIEP, 1905).

l. 25, *for* from a few to more than *read* several to as many as

l. 36, *for* effected *read* effective

173, ll. 22–4, *for* A transference . . . taking place *read* Under certain conditions, however, storage of reserves may take place

l. 27, *for* consumption *read* storage

l. 31, *after* leaves. *read* The same thing takes place in cultures carried out under conditions of drought; the older parts dry up, since they surrender water to younger parts (PRINGSHEIM, 1906). In these cases the plant uses up some of the materials which one is accustomed to regard not as reserves but as constructive substances.

ll. 37, 50, *for* amides *read* amino-acids

ll. 48–9, *for* bodies whose constitution is very different from its own *read* amino-acids.

l. 56, *for* amide bodies *read* amino-acids

174, l. 1, *for* amides *read* amino-acids

ll. 4–20, *for* In the first place . . . by analysis. *read* Let us consider first the general nature of the mixture of amino-acids in different plants. The following table taken from ABDERHALDEN (*Phys. Chem.*) gives us such information; it shows us how many grams of each substance may be obtained from 100 g. of proteid :—

	Lupinus albus (Conglutin)	*Picea excelsa*	*Cannabis* (Edestin)
Glycocoll	0·8	0·6	3·8
Alanin	2·5	1·8	3·6
Amino-valerianic acid	1·1	(present)	(present)
Leucin	6·75	6·2	20·9
Prolin	2·6	2·8	1·7
Phenylalanin	3·1	1·2	2·4
Glutaminic acid	6·5	7·8	6·3
Aspartic acid	3·0	1·8	4·5
Tyrosin	2·1	1·7	2·1
Cystin	(present)	0·25 (?)	0·25
Histidin	0·65	0·62	1·1
Arginin	6·6	10·9	11·7
Lysin	2·1	0·25	1·0
Tryptophane	(present)	(present)	(present)

It would thus appear that the same amino-acids are everywhere present, but in varying quantities, and this conclusion remains practically unaltered when we take into account other proteids also. The same amino-acids (phenylalanin excepted) are obtained also in tryptic digestion; this much we do know, but there are no quantitative statements available. Those at least dealing with the analysis of the acids have more the character of rough estimates. These amino-acids (with the exception of glycocoll and alanin) also occur in etiolated plants, but in quite different proportions, and instead of glutaminic and aspartic acids, we find the amides, glutamin and asparagin. These amides often accumulate very markedly; thus glutamin, found in *Cucurbita, Ricinus*, and Cruciferae, may form 2½ per cent. of the dry weight, while in Papilionaceae, Gramineae, and other plants the asparagin found there may amount to 20 per cent. of the dry weight. There can be no doubt (SCHULZE, 1906; PRIANISCHNIKOW, 1904) that in the formation of asparagin we have to do with a secondary alteration in the substances produced by proteid hydrolysis, but it is out of the question that all the asparagin arises by an amide transformation of aspartic acid. Indeed it may be shown that in proportion as asparagin appears other amino-acids disappear; the formation of asparagin runs parallel, not with the progressive hydrolysis of proteid, but with the disappearance of these acids.

l. 30—P. **175**, l. 12, *for* Finally, it would appear . . . in the plant. *read* How asparagin and glutamin are formed from the amino-acids which disappear, e.g. leucin, tyrosin, &c., is unknown. SCHULZE assumes that these substances are either further split up hydrolytically, or that they are oxidized;

under any conditions ammonia must be split off, and from it first of all amides must be constructed. The formation of these bodies would thus be synthetic, and in the process probably some carbohydrate or other must take part. We ought to note in this relation the discovery by SCHULZE and WINTERSTEIN (comp. SCHULZE, 1906), that in *Ricinus*, monamino-acids, otherwise so common, do not make their appearance during germination. In place of them there occurs a body which bears the name of ricinin, and which possesses a pyridin group. Doubtless, it arises from primary or secondary decomposition products of proteid. It is probable that we have here a key to the interpretation of alkaloids, many of which also are characterized by the possession of a pyridin group. Alkaloids with other constituent groups also must be derived from products of proteid splitting. No accumulation of asparagin takes place in light, first because carbohydrate is under these circumstances abundant (PFEFFER, 1893), and also because light is directly favourable to the construction of proteid (BALICKA-IWANOWSKA, 1903; GODLEWSKI, 1903).

175, ll. 36–52, *for* It must be noted . . . of diastase. *read* Fat also appears, often at least in our native trees during winter, while starch disappears. The close connexion which one was led to assume between these two processes as a result of FISCHER'S (1890) work does not appear to exist (NIKLEWSKI, 1905; comp. also FABRICIUS, 1905). Where the fat comes from is not clear; on the other hand, it has been shown that the starch which disappears becomes transformed into sugar, and its accumulation is a direct result of low temperature. According to LECLERC (1904), fairly abundant accumulations of hemicelluloses arise during the winter as thickenings on the cell-walls. Conversely, it is possible at any time during the winter to induce a formation of starch by bringing amputated twigs into a warm room. A similar phenomenon has long been known in the 'sweetening' of potatoes at temperatures just above 0° C. (MÜLLER-THURGAU, 1882). The meaning of this starch-formation may perhaps be found in the lowering of the freezing-point, but the cause of it is as yet quite unknown; at all events it cannot be referred to the peculiarities of the diastase. It is as yet impossible to say how far our conceptions as to fat-formation in seeds and its relation to carbohydrates must be modified as a result of the observations of NIKLEWSKI on trees.

In addition to the storehouses of reserve mentioned we also find far-reaching transformations taking place in the materials stored in fruits, but into them we cannot enter (comp. e.g. GERBER, 1896; LECLERC, 1905).

176, ll. 20–2, *delete* [Many . . . (1904).]

ll. 31–41, *delete* We may at least . . . Naturw. 22).

177, *Lecture XV is XIV of the 2nd German Edition.*

177, *title, read* METABOLISM OF HETEROTROPHIC PLANTS

ll. 26–7, *for* chlorophyll, all . . . have seen that *read* chlorophyll, while

l. 29, *after* substances *read* and hence are heterotrophic.

ll. 31–44, *for* exclusively out of carbohydrates . . . adding sugar.] *read* exclusively out of assimilata formed by neighbouring leaves (JOST, 1895). By the artificial addition of organic compounds it has hitherto been possible only to a limited extent to induce growth in higher plants in darkness (LAURENT, 1903; LEFÈVRE, 1906). How that comes about we do not know. Lower plants, e.g. certain Algae, according to ARTARI (1904) and PAMPALONI (1905), even if they be adapted to the employment of carbon-dioxide, can frequently still grow perfectly well in the dark at the expense of glucose and peptone (or some other source of nitrogen). Indeed, many of these forms (*Euglena*, ZUMSTEIN, 1899; *Chlorella variegata*, BEIJERINCK, 1904, &c.) range themselves

alongside the purely heterotrophic Fungi, inasmuch as they habitually feed on organic substances, though still possessing chlorophyll.

178, ll. 28–9, *delete* [BENECKE . . . Fungi.]

ll. 32–4, *for* The only difference . . . require both. *read* The only difference is that Fungi can do without calcium, which higher plants require.

ll. 44–8, *for* REINKE (1883) . . . materials are *read* REINKE (1883) as well as many more recent investigators. These authors have shown that an extraordinarily large number of carbon-compounds may serve as nutrients to Fungi, e.g. carbohydrates, alcohols, organic acids, both of the aliphatic and benzol series (quinic acid), fats, peptones, and proteids. From these substances the Fungi construct first of all sugars, the materials which are formed by green plants in the process of carbon-dioxide assimilation. These sugars may thus be formed both by constructive metabolism from organic acids and by destructive metabolism from proteid; in both cases one may speak of a carbon-assimilation in Fungi. If, however, the carbon be offered in the form of sugar the primary process of assimilation is omitted, and only the further transformations of it are carried out. Among Mould Fungi there exist great differences in the capacity for assimilating carbon-compounds. In order to give some idea of these we may quote a few examples where the materials are

l. 54, *for* 372 *read* 384

179, ll. 4–7, *delete* LABORDE . . . *Aspergillus*.

ll. 10–13, *delete* [Certain Bacteria . . . many Fungi.]

l. 35—P. **180**, l. 3, *for* (CORRENS, 1889 . . . extraordinarily permeable. *read* (CORRENS, 1889; MOLISCH, 1893). The adaptation consists in the rise of the pressure within the cells in proportion to the rise in concentration in the culture fluid outside (Lecture XXXIII). Many Water-Bacteria which are adapted to life in quite weak concentrations of sugar behave conversely (KOHN, 1906).

180, l. 30, *for* their life *read* their entire life

l. 35—P. **181**, l. 1, *for* Many similar examples . . . differentiate; that *read Eurotiopsis gayoni* (LABORDE, 1897) can make use of lactic acid, but cannot thrive with tartaric acid and with sugar. The Bacteria which live in hay and are the cause of its 'heating', such as *B. calfactor* (MIEHE, 1907), prefer pentoses and dextrine to any other source of carbon. A certain species of *Penicillium*, according to RAHN (1906), can employ paraffines as sources of carbon, substances which are quite useless to most other organisms. BEIJERINCK (1903) has made us acquainted with a bacterium, *Bacillus oligocarbophilus*, which employs the mere traces of unknown organic compounds present in the atmosphere (compare KASERER, 1906, who has, it is true, only to a limited degree elucidated the physiology of this organism). Finally, we have come to know of Bacteria that use methane, and of some even that can work up carbon-dioxide—and that, too, without chlorophyll or light. In a word, we shall not go far wrong if we assume that every compound of carbon occurring in nature is employed as a nutrient by some organism or another.

Under these circumstances it is conceivable that NÄGELI'S (1879) attempts to refer its capacity for being assimilated to the composition of the compound must be unsuccessful, or, at most, may lead to definite results in individual cases only (comp. BENECKE in LAFAR'S *Mykologie*, I, p. 414).

Although, as we have said, a whole series of Fungi and Bacteria can thrive with the most varied food-stuffs, still they know how to distinguish between them, and that often with a degree of discrimination compared with

which our usual chemical methods appear remarkably rough. Take, for example, the case where

181, l. 9, *after* 1895 *read* ; vid. summary by EMMERLING in LAFAR'S *Mykologie*, I, p. 429).

l. 15, *for* is known to be rapidly *read* may be regarded as almost

l. 36—P. **182**, l. 32, *for* and we saw . . . glucose acts best. *read* and we have proved that the nitrogen can be assimilated in an inorganic combination. We have now to ask whether this is generally true. Our answer is ' by no means '. Certain Fungi are obviously heterotrophic so far as their nitrogen requirements are concerned ; they either directly require proteid, peptone, amino-acids, acid-amides, &c., or, at least, thrive better with these compounds than with inorganic ones. On the other hand, there are also organisms which are certainly autotrophic, and exist better with inorganically—than with organically—combined nitrogen. In the case of those that are preferably heterotrophic, as also in the case of those that are preferably autotrophic, the further question arises whether they select one definite nitrogenous compound from amongst others presented to them. It is impossible offhand to answer this question in relation to the fungus that has been most frequently investigated, viz. *Aspergillus niger*, for the literature on the subject, though very extensive, is often very contradictory ; it is very much less easy to formulate any general rules on the subject. Still, it appears to us permissible to separate Fungi and Bacteria into a number of classes in accordance with their preference for certain sources of nitrogen, on the lines adopted by BEIJERINCK (1890) and FISCHER (1903, p. 96). One must not, however, imagine that by classifying an organism in one of these groups we are expressing a generally valid conclusion. The nutritive value of a source of nitrogen is naturally dependent on many accessory factors, e.g. the reaction of the culture solution and the nature of the source of carbon presented at the same time. Since cultures in which the nitrogen is present as nitrate become gradually more and more alkaline, Fungi which are able to produce acids metabolically will grow better in these cultures than those which do not possess that power. These latter will, however, grow eventually in the presence of nitrate if we artificially combine the alkali which arises. Conversely, culture solutions containing ammonium are generally acid, and since various Fungi can tolerate acids in quite variable degrees, the nutritive value of the source of nitrogen in this case will be determined by another subsidiary factor, viz. the power of the fungus to resist these acids. As an example of the effect of the source of carbon on the metabolism of nitrogen we may note that in FISCHER'S experiments (1897, p. 53) *Bacillus coli*, *B. subtilis*, and *B. pyocyaneus* were able to live on nitrate in the presence of glucose ; if glucose were replaced by glycerine then *B. pyocaneus* alone could employ the nitrate, while the others required ammonia to meet their nitrogen wants. These facts limit very much the value of the following classification, which attempts to arrange Fungi and Bacteria in accordance with the suitability of the source of nitrogen :—

1. *Nitrogen-organisms.* These forms prefer the free nitrogen of the air to any nitrogenous compound (these will be treated of in Lecture XVIII).

2. *Nitrate-organisms.* These grow just as well as or even better with nitric acid than with other compounds. Among Fungi of this type we have *Alternaria tenuis*, *Mucor racemosus*, *Aspergillus glaucus* (LAURENT, 1889), *Monilia candida* (WENT, 1901), and among Bacteria, foecal Bacteria (JENSEN, 1898), *Bac. pyocyaneus*, and *B. fluorescens*.

3. *Nitrite-organisms.* BEIJERINCK (1893) has shown that *Bac. perlibratus* grows best with nitrite, and corresponding statements have been made for certain Fungi by WINOGRADSKI (1899) and RACIBORSKI (1906).

4. *Ammonia-organisms.* These forms develop also in presence of nitrates, but their growth is greatly furthered by ammonia. To this group belong *Eurotiopsis, Aspergillus niger, Saccharomyces albicans,* yeasts, and *Bac. subtilis.* With reference to *Saccharomyces albicans* it is stated (LINOSSIER, 1890) that it will have nothing to do with nitric acid, and that it develops more feebly with amino-acids than with ammonia; urea is even a worse nutrient than amino-acids.

5. *Amino-organisms. Bac. perlibratus, B. typhi,* and *Rhizopus oryzae* thrive better with asparagin than with ammonia; other amino-acids appear to have a similar effect.

6. *Peptone-organisms.* Growth is scarcely perceptible with asparagin or ammonia, and peptone cannot be replaced by proteid. Examples:—*Bac. anthracis, B. proteus*; lactic-acid Bacteria (BEIJERINCK, 1901).

7. *Proteid-organisms. Micrococcus gonorrhoeae* and *Bacillus diphtheriae* prefer proteid, and do not grow in peptone or other nitrogenous media. In nature, indeed, they are parasites and, strictly speaking, should not be included here.

Nothing is known as to the mode of manufacture of proteid out of the simpler nitrogenous compounds. We must assume, however, that amino-acids are first formed in this case also, which are afterwards combined into proteid. The fact that amides (urea, acetamide; SHIBATA, 1904) and amino-acids (RACIBORSKI, 1906) are first of all split up, and that it is only the resulting ammonia that is employed as the source of nitrogen, does not invalidate this hypothesis. Proteid can be formed only out of a number of different amino-acids; if, therefore, only one be present, then that must be first split up to give rise to the many required.

The question as to what is a good combination of carbon and nitrogen cannot naturally be answered in general terms. If proteid or peptone be the source of nitrogen the addition of a special source of carbon is often unnecessary; this is true in many cases of asparagin. Generally speaking, a culture solution containing peptone and glucose has hitherto been considered as the best medium.

182, l. 45, *after* in them *read* It is out of our power to give a detailed account of the more recent advances in this interesting department of our subject; a complete exposition will be found in LAFAR'S *Mykologie* (1904), by BENECKE, and also in CZAPEK'S *Biochemie*, Vol. II.

183, ll. 12–14, *for* REINITZER . . . humins *read* further, only part of the humus-nitrogen is assimilable. Possibly, certain 'specialists' may obtain their supply of carbon from humins, as these researches tend to show.

l. 31, *after* to exist *read* (comp. ITERSON, 1904; JONES, 1905).

l. 37, *for* etherial *read* ethereal; *for* (hadromal, comp. p. 70) *read* (lignin).

l. 38, *for* hadromal *read* lignin

184, ll. 7–9, *for* (on which . . . BRUNSTEIN, 1901) *read* a list of which is given by H. FISCHER in LAFAR'S *Mykologie* (I, p. 269)

l. 32, *for* Figs. 33–5 *read* botanical text-books

l. 33, *after* (1891–3) *read* and of FENNER (1904)

ll. 46–7, *for Sarracenia* . . . with others *read* epiphytes

l. 51, *after* by the plant. *read* Detailed investigations have still to be undertaken to determine whether the decomposition of the insects caught in the pitchers of *Sarracenia* is due merely to putrefactive processes or whether this plant should be classed with typical carnivores (FENNER, 1904).

185, ll. 2–10, *for* As yet . . . exist in them *read* The secretions appear frequently to have antiseptic properties, so that the co-operation of Bacteria in the digestion of the insects is excluded from consideration.

In *Drosera* the peculiar tentacles which arise from the lamina are tipped with glands which always give off a slimy substance, which by its stickiness holds the insect fast. When the glands are stimulated, however, by the presence of a nitrogenous organic substance a very copious secretion begins, and it can be shown that this secretion has an acid reaction and contains an enzyme. The latter has for long been recognized in glycerine extracts of the leaves. Glands similar to those of *Drosera* are met with in *Drosophyllum*, but only some of them are at the ends of tentacles; the majority are sessile on the leaf surface. It would appear that in this case only the sessile glands furnish the acid fermentative secretion, and this secretion begins only after the stalked glands have been stimulated chemically (FENNER, 1904).

The arrangements are essentially different in *Dionaea*. In the unstimulated condition the leaf is dry, and the sessile glands, which resemble those of *Drosophyllum*, give off their fermentative and acid secretion only after stimulation effected by the entrapped insect, but then in such quantity that it trickles away from between the closed halves of the leaf-blades.

Finally, in *Nepenthes*, the young pitcher secretes a slimy, tasteless fluid, giving a neutral reaction. This reaction becomes acid after stimulation, whether the stimulus be mechanical or chemical; after that, the secretion is in a condition to act digestively. According to CLAUTRIAU'S researches (1900) in the woods of Java, the absorption of proteid takes place extremely rapidly, and apparently without any very profound decomposition. On the other hand, according to VINES (1897–1902, 1906), in addition to a vigorous peptic enzyme, a more feebly active erepsin is secreted which decomposes the peptone formed by the peptic enzyme.

Whether these two enzymes are always distinguishable in carnivorous plants it is impossible to say; nor is the evidence conclusive with regard to the nature of the acids which are always present. Often it is formic acid that is recorded, but propionic, butyric, and other fatty acids have also been found, while nothing is known as to the occurrence of inorganic acids. These latter are not unlikely, seeing that in the animal hydrochloric acid is produced for a similar purpose.

l. 16, *after* three days. *read* In other cases, e.g. in *Drosophyllum* and *Nepenthes*, this process must take place much more rapidly; but comparative experiments on the subject are entirely wanting, and the chemical peculiarities of carnivorous plants in general, without doubt, deserve fresh and thorough investigation.

186, l. 19, *for* soil only. It is even *read* soil only; it would appear also that the root system of carnivorous plants is only moderately developed. It is even

l. 25, *for* perfectly obvious *read* exceedingly probable

187, ll. 36–43, *for* although isolated . . . history *read* although it contains chlorophyll. The amount of chlorophyll in *Cuscuta* varies. According to PIERCE (1894) an increase in chlorophyll occurs in amputated shoots; but according to a manuscript communication from PROFESSOR NOLL it is probable that this depends more on diminished intensity of light than on mere isolation. It may be assumed that the chlorophyll is functional, but that the products of assimilation are insufficient in quantity to maintain the plant in life. We must look upon the capacity for forming chlorophyll as an indication that *Cuscuta* has been evolved from chlorophyll-bearing plants; possibly, like *Lathraea*, it may in time entirely lose its power of forming chlorophyll.

l. 47, *after* studied *read* (HEINRICHER, 1897 onwards).

188, ll. 4–19, *for* HEINRICHER . . . such experiments *read* The meaning of the parasitism in these plants has not as yet been fully explained. HEINRICHER thought that they were completely independent in so far as carbon was concerned, and that they took up minerals only from their hosts. His conclusion was based on the abundance of nitrates in parasites, and on the demonstrable decomposition of carbon-dioxide which took place in light. He has not, however, shown that this latter process is quantitatively sufficient, and yet this is certainly necessary, after the very definite statements made by BONNIER (1893) that the activity of the chlorophyll is only very slight. One cannot, therefore, say with any certainty whether these plants, so far as carbon is concerned, are autotrophic or whether they withdraw carbohydrate from their hosts. SPERLICH (1902) postulates for them sometimes a greater, sometimes a less dependence on their hosts. There is a further possibility, viz. that nitrogenous compounds such as proteids and amino-acids must be taken up.

ll. 31–6, *delete* Exhaustive . . . PITRA (1861).

l. 49, *delete* when of no more use

189, ll. 3–5, *for* in Fungi, and among . . . no starch. *read* in Fungi. Among nitrogenous reserves, proteids claim the first place; they not infrequently appear in a crystalline form; further, volutin is very generally distributed in lower plants, a substance which A. MEYER (1904) regards as a complex body containing nitrogen and phosphorus. Among non-nitrogenous reserves fats are especially frequent; often, in addition, we meet with the alcohol mannite, and trehalose a close ally of cane sugar. On the other hand, since there are no chromatophores there is an entire absence in Fungi of the otherwise so widely distributed starch.

l. 22, *after* cell *read* (KOCH and HOSAEUS, 1894; comp. HEINZE, 1904).

190. *Lecture XVI is XV of the 2nd German Edition.*

l. 4 *from bottom*—P. **191**, l. 9, *for* On examining . . . dry weight *read* The increase in dry weight taking place in the course of the day in an assimilating leaf does not furnish us with a correct measure of the amount of assimilation; even if translocation of the assimilata from the leaf be prevented we still find that the amount of assimilation is too small because part of the material manufactured has, by evening, again become destroyed. Similarly with the increase in dry weight exhibited by the plant during the course of its entire vegetative period, all we have is the difference between the total amount constructed in assimilation, and the total amount destroyed in dissimilation. Under normal conditions, this difference is always on the plus side, i.e. in spite of dissimilation there is always an increase in dry weight. It is, however, by no means difficult to put the plant under conditions such that assimilation ceases or is reduced (e.g. cultivating an autotrophic plant in darkness or depriving a heterotrophic plant of its culture medium); since, however, under such circumstances dissimilation still goes on, the net result of growth now is a diminution in dry weight.

191, l. 33, *for* 3·38 *read* 3·88

ll. 39–40, *for* of a 0·003 . . . solution *read* of 0·003 to 0·03 per cent. solutions

ll. 43–50, *for* The deficit . . . organic materials *read* Destruction of organic substance is remarkably common in organisms, and is carried out in a variety of ways. Let us consider first that dissimilation process in the typical higher plant which is known as respiration. By this we mean the production of carbon-dioxide and water from organic materials.

192, l. 42, *for* oily *read* succulent

193, ll. 23–4, *for* because he . . . darkness *read* because they enable us to see how much greater respiration is in flowers as compared with foliage leaves.

ll. 38–40, *for* Finally, a few examples . . . respiration *read* With reference to this table it may be noted that some flowers investigated by Saussure, especially *Cucurbita*, are characterized by showing the maximum intensity of respiration at the time of opening, while in the majority of flowers respiration (in relation to their fresh weight) continuously diminishes from the young stage onwards (MAIGE, 1906). This fact leads us finally to consider two examples which show an alteration of this kind in the intensity of respiration during development ; the first of these is, at the same time, also of interest in relation to the absolute amount of respiration.

194, ll. 1–5, *for* If we express . . . daily in mg. *read* As a second illustration of the variation in respiration, according to the developmental condition, we may give in graphic form (Fig. 36) the results RISCHAVI (1876) has obtained for germinating wheat. A similar curve might be constructed from the numbers recorded for *Arum*. In both cases, respiration increases as time goes on until it reaches a maximum, when it once more falls.

ll. 12–17, *for* that it is the living . . . such a comparison *read* that in all probability certain enzymes are the immediate cause of respiration. Hence, it would be of especial interest to know whether any relationship exists between the amount of respiration and the amount of enzyme present ; but since the quantity of enzyme is probably regulated by the protoplasm, a knowledge of the amount of protoplasm in turn is of importance, and yet there are no data available either as to its volume or as to its weight.

l. 49, *for* masked *read* simply abolished

195, l. 11, *delete* by killing the cells

l. 17, *for* 1851 *read* 1852 ; *delete* (by means of baryta water)

ll. 51, 52, *for* cuticle (*bis*) *read* epidermis

l. 54, *for* equally *read* also adequately

196, ll. 1–3, *for* The matter . . . tension *read* There may be some doubt perhaps in this respect with regard to aquatics, for in their case the oxygen in the surroundings has a lower tension. HOPPE-SEYLER (quoted by OLTMANNS, *Algen*, II, p. 139) found 6·73 ccm. of oxygen in a litre of water from the Bodensee, at a depth of 2 metres, and at a temperature of 4° C., and at 725 mm. pressure, that is to say, only about 1/30 of that present in air. Roots and rhizomes living in mud are doubtless in the most unfavourable position for obtaining oxygen, and they attempt to counteract this by forming special organs, known as ' pneumatophores ', which grow upwards into the air, or at least into water layers richer in oxygen, and these carry out the necessary gaseous exchange.

l. 8, *after* spaces *read* (exceptions are recorded by CZAPEK, *Biochemie*, I, p. 331),

l. 12, *for* is *read* was

ll. 19–20, *for* are related . . . combustion *read* are dependent on the character of the respiratory materials.

ll. 33–5, *for* It would be . . . respiration *read* It would, however, be quite wrong to regard the frequent occurrences of unity as the value of the fraction $\frac{CO_2}{O_2}$ in higher plants as a proof that only carbohydrates were used up in respiration.

197, l. 23—P. **198**, l. 13, *for* Oxalic acid . . . oxidized by the fungus *read* Oxalic acid is especially frequently formed, and WEHMER'S (1891 and 1903) exhaustive studies, as also those of BENECKE (1907), have made us fairly well acquainted with the process. In the following account we shall follow BENECKE'S summary in LAFAR'S *Mykologie* (I, p. 317). Among Mould Fungi *Aspergillus niger* is known to produce oxalic acid vigorously, and it is on this fungus that almost all the experiments have been carried out. The most important result of these experiments is, perhaps, the discovery that the formation of the acid is by no means an essential phenomenon, but that it occurs under quite definite conditions. One might suppose that a deficiency in the supply of oxygen must be the primary cause of 'incomplete respiration' (as one might term the process when oxalic acid appears in place of carbon-dioxide), but that is not so, for the formation of oxalic acid is entirely independent of the amount of oxygen supplied. The first factor concerned in its production is temperature. At the optimum temperature (above 30° C.) the fungus produces oxalic acid just as at the ordinary temperature of a room, but it at once carries the combustion of the acid which arises a step further; by artificial addition of oxalic acid, one may show that it is able to induce a more vigorous oxidation at a temperature of that height. Further, by adding calcium carbonate one can induce an accumulation of the acid in the form of calcium oxalate, and so prove that it is always of the nature of an intermediate product. When cultivated at ordinary temperatures the fungus behaves according to the composition of the nutritive solution in which it is grown. Should this solution contain carbohydrate or salts of organic acids as the source of carbon, a vigorous formation of free oxalic acid takes place, which, however, goes on only until the solution has attained a certain degree of acidity, and this equilibrium generally results when the solution contains about 0·3 per cent. oxalic acid. When free acid is added to the culture, or after transformation of nutrients into acid by the fungus, the production of free acid ceases. On the other hand, the formation of free acid goes on uninterruptedly if substances capable of combining with the acid (e.g. carbonates or alkaline phosphates) are added, or if substances like these make their appearance as a result of the metabolic processes in the fungus, as when ammonia appears after the addition of peptone. WEHMER found that in one experiment *Aspergillus* formed 1·353 g. of oxalic acid out of 1·5 g. of sugar when the acid was neutralized as soon as formed. For this purpose, 0·8318 g. of sugar is used up, 0·290 g. being employed for the construction of fungal substance, and 0·3782 g. oxidized into carbon-dioxide. In a similar experiment with tartaric acid about half the amount of oxalic acid possible was formed, while the free tartaric acid was completely broken down into carbon-dioxide and water. In such an incomplete combustion as that leading to the formation of oxalic acid, obviously the respiratory material is not so fully made use of as when carbon-dioxide is formed, and hence one may ask whether this imperfect utilization of products does not make itself apparent in the growth of the fungus. The increase in dry weight is, however, the same whether oxalic acid is formed or not, hence from the nutritive and respiratory points of view the oxalic acid lost has no very great value; further, it is of no service as a source of carbon to the majority of heterotrophic plants. On the other hand, the acid given off, in the free state, has a very important biological significance, inasmuch as it acts as a poison to other organisms. Oxalic acid is employed by many Fungi as a protective weapon against other plants which, when dead, can then be made use of (DE BARY, 1886). It serves also as a deterrent to other Fungi that live in similar nutrient substrata (REINHARDT, 1892). It is of especial service when growth of the fungus is inhibited by unsuitable temperatures, but the fungus can do without it at optimal temperatures.

198, ll. 19–30, *for* In addition to . . . metabolism *read* According to MAZÉ (1904), however, the appearance of citric acid is not connected with the presence of oxygen, and does not arise from sugar, but from the proteid of decaying cells, from which younger cells take up nitrogen when other nitrogen compounds are deficient. WEHMER (LAFAR, *Mykologie*, IV, p. 248) contradicts these statements. It is worthy of note, however, that the constitution of citric acid, differing so much from sugar, makes its derivation from that substance difficult to conceive of. The formation of oxalic acid is also widely distributed among higher plants, as may at once be concluded from the frequency of the occurrences of calcium oxalate. While in earlier times the view was held that the purpose of the oxalic acid was to unite with lime, and so release the nitric acid which had been united with it to construct proteid, it appears from the researches of AMAR (1902) and BENECKE (1903) that the formation of oxalic acid arises in essentially the same way in green plants as in Fungi. It is an intermediate respiratory product, capable of being further broken down, but fixed in an insoluble combination when there is excess of lime in the cell. Hence it is possible to induce the formation or disappearance of oxalate in plants which normally contain it, if one presents to them not more than the essential minimum of $Ca(NO_3)_2$ (AMAR), or if the nitric acid be presented to them in the form of a salt of ammonia (BENECKE).

Apart from oxalic acid and oxalate the formation of acids takes place in almost all plants, and although these arise occasionally, perhaps, during synthesis, they appear frequently also in the course of hydrolytic splitting (of fats and proteid), and so, for the most part, are connected with respiration.

199, ll. 3–4, *for* at the moment when *read* where

l. 17, *after* disposal *read* Obviously there are among leathery leaves numerous transitions between normal leaves and the fleshy leaves of succulents. Although BONNIER and MANGIN (1886) found the assimilatory coefficients in *Ilex* to be 1·24 instead of approximately 1, that may be explained by supposing that part of the assimilata arose from the organic acids produced in decomposition.

ll. 27–8, *for* a convenient medium . . . normal *read* lies a simple means of tripling the osmotic pressure.

l. 38, *for* does not correspond to *read* far exceeded

l. 41, *for* leading to *read* leading even to

l. 46, *for* that seen only *read* that seen elsewhere

200, l. 21—P. **201**, l. 5, *for* in Fungi especially, and . . . contrasted with plants *read* in Fungi especially. *Aspergillus niger*, for example, grows remarkably well, as is well known, with peptone as the source of nitrogen and sugar as the source of carbon, and no indications are forthcoming that the peptone is at the same time employed as respiratory material. But the fungus is able to obtain what it needs, both of carbon and of nitrogen, when peptone is the only organic body presented to it. Under these circumstances duties even of the sugar must be undertaken by the peptone, but how that comes about we do not know. It is known that peptone is split into amino-acids (BUTKEWITSCH, 1902), from which again ammonia even is split off in varying quantities according to external conditions. Such a separation of nitrogen is indeed essential, because certain of the combustion materials used by the fungus contain no nitrogen. Whether the non-nitrogenous materials are alone used for respiratory purposes is not known ; it is not probable, however, for BUTKEWITSCH found much less ammonia formed in other Mould Fungi than in *Aspergillus*, and in this case also he was able to greatly restrain its formation by taking care that the culture did not become acid.

It is not easy to say whether proteid or other nitrogenous organic substances are employed as respiratory materials by the higher plants; it is, however, very probable that the changes which we saw taking place in the mixture arising from proteid hydrolysis when the seedlings were kept in the dark are due to oxidizing processes. Indeed, it has been suggested by BERTEL (1902) and CZAPEK (1906) that tyrosin becomes oxidized very generally in the plant into homogentisinic acid, nevertheless the observations of SCHULZE and CASTORO (1906) go to prove that there is no homogentisinic acid in the plants CZAPEK experimented with. Hence, it is impossible to make any definite statements at present as to the oxidation products of tyrosin. However it may be, one thing is certain, that the higher plant differs in one respect very greatly from the animal, viz. in that it does not excrete the decomposition products of its nitrogenous compounds, but uses them once more in constructive metabolism; it is able to re-employ as nutrients both the nitrogenous and non-nitrogenous end-products of metabolism. Since animals have no such power, they are dependent on plants to provide them with carbohydrate and proteid.

The question whether proteid may be used for respiratory purposes is not so easy to answer; we will confine ourselves to the question whether any of it must be used for that purpose. We shall return to this point again at the end of this lecture, after we have considered the dependence of respiration on external conditions.

201, ll. 11–13, *for* Since in other . . . MAXIMOW *read* The question cannot be considered as in any way settled, for MAXIMOW

l. 22, *for* vital processes. The plant must be *read* vital processes; in other words, the plant is

ll. 23–42, *for* If, however . . . beetroot *read* Other authors, e.g. ZIEGENBEIN (1893), KUNSTMAN (1895), STOKLASA (1903), demonstrated for respiration a typical optimal curve. The question has, doubtless, on the other hand, lost greatly in interest because in assimilation and respiration we must regard the part of the curve where the ascent is less, or where even a fall takes place, as under all conditions due to injury (BLACKMAN, 1905). The difference between respiration and assimilation would consist in the fact that in the former this injury first occurs at temperatures which paralyse every faculty in the plant, while assimilation is already retarded at lower temperatures.

ll. 53–5, *for* Respiration . . . during drought *read* Respiration ceases entirely in perfectly dry parts of plants, and seeds, mosses, lichens, and the like, which can tolerate desiccation, may remain alive during drought

202, l. 2, *after* (KOLKWITZ, 1901) *read* It appears not improbable that the diminution in respiration observed by LEWIN (1905) in seeds under pressure is only the result of a more limited water content.

l. 16, *after* poisons *read* (e.g. formaldehyde and the salts of certain metals)

l. 18, *after* 1899 *read* ; ZALENSKI, 1902

l. 21, *after* RICHARDS, 1896 *read* ; SMIRNOFF, 1903; KRASNOSSELSKI, 1905). That materials which in small quantities act as stimulants should inhibit in greater concentrations goes without saying.

l. 28, *for* in which . . . reduced *read* compressed

l. 55, *for* When glucose *read* If glucose,

203, l. 1, *after* and *insert* should ; *for* becomes *read* become

l. 2, *for* remains *read* would remain

l. 7—P. **204**, l. 4 *from bottom, for* Thus BREFELD . . . RACIBORSKI (1905) *read* One can arrange for the absence of oxygen, essential to intra-molecular respiration, by allowing seeds to soak under water. Thus, if large seeds of *Vicia Faba*, after being kept under water for two days, be crushed the pre-

sence of alcohol may be recognized by smell. According to DUDE (1903), however, all plants which usually live under conditions of access to air do not remain normal for long under those of intra-molecular respiration. Hence the large amounts of alcohol which LECHARTIER and BREFELD (1876) obtained from fruits and seeds after being for months deprived of oxygen doubtless did not arise from intra-molecular respiration, but were due to the action of lower organisms which had settled on them (comp. Lecture XVII). PALLADIN (1904) also finds that in the case of green plants the amount of CO_2 given off in a space free of oxygen rapidly decreases if micro-organisms are excluded. Specially interesting is PETRACHEWSKY'S (1904) statement that the respiratory coefficient of the alga *Chlorothecium* may rise to three times its normal value when its respiration changes from intra-molecular to the normal type, and then, after a short time, once more reaches its normal amount. LESCHTSCH (1904) has shown the same phenomenon to take place in *Saccharomyces* (see below).

It is well known that alcohol and carbon-dioxide are not the only products of intra-molecular respiration ; there are also higher alcohols, acids, aromatic compounds, and hydrogen. Whether these appear constantly we do not know. Naturally the products will alter according to the respiratory material ; hydrogen, for example, appears when mannite is abundantly provided. Different substances, again, are unsuitable for intra-molecular respiration. The results obtained by DIAKONOW (1886) were previously held to support this view, viz. that intra-molecular respiration in general only took place in presence of carbohydrates. More recently, however, KOSTYTCHEW (1904) has definitely proved that it occurred (in Fungi) when quinic acid, tartaric acid, and peptone were exclusively present, but it is not known whether carbohydrates are not first of all formed from these bodies. At all events, intra-molecular respiration goes on more readily and certainly in presence of sugar. GODLEWSKI (1904) has shown that in seedlings proteid splitting in absence of oxygen is carried out in a different manner than in its presence. There is none of that accumulation of asparagin, &c., which we have already recognized as due to secondary alteration of products of hydrolytic splitting.

We may now turn to the problem of the factors concerned in respiration (comp. BARNES, 1905). Respiration has been described as a combustion, and this, no doubt, it is, if we regard only the end-products to which it gives rise. If, however, we consider the chemical process itself we find it to be very different from ordinary oxidation, at least if we regard combustion as a direct union of oxygen and some other body. Sugar, starch, and fat, the substances which disappear in the cell during respiration, do not combine with oxygen at the low temperatures at which life goes on ; at least the formation of carbon-dioxide from them has never been observed under the sole influence of oxygen. Other reasons may be advanced, however, against the comparison of the combustion of sugar in the organism with that of coal in a furnace, especially this one, viz. that the amount of respiration is in great measure independent both of the amount of oxygen and of the amount of respiratory material present. Further, we have seen that the combustion is often by no means complete, and is not carried out to the end-products H_2O and CO_2, but stops at a definite intermediate product, although oxygen is still available in sufficient quantity to further oxidize these bodies. The best key to the real cause of respiration is to be found in the phenomenon of intra-molecular respiration. We may regard this as a new process which replaces normal respiration when oxygen is deficient, or—with PFEFFER—we may look upon the two processes as fundamentally the same. This second conception is supported by most of the more recent researches on the subject. In the first place, a splitting of organic materials must occur, which goes on whether oxygen be present or not, and

this results in the formation, on the one hand, of carbon-dioxide and on the other of an oxidizable body which, in presence of oxygen, is oxidized. We must not assume that this body is always the alcohol which appears in intra-molecular respiration—that, in other words, alcohol is always the intermediate respiratory product. There are many facts which contradict such a view, but the alcohol may indeed owe its existence to a subsequent alteration of the hypothetical primary oxidizable body. The essential point in this idea lies in the assumption that respiration consists of two processes, which are not necessarily inseparable—splitting and oxidation. What facts, then, can be advanced in support of there being two such processes concerned? In the first place, we must recall the results arrived at by PURIEWITSCH, which went to show that the formation of CO_2 and the absorption of O are in ordinary respiration much more independent of each other than we have hitherto been led to suppose; and in the second place, we would draw attention to the fact established by PALLADIN and PETRACHEWSKY that *Chlorothecium*, when kept for a long time in an atmosphere of hydrogen, gives off very much more CO_2 than usual when again placed in oxygen. That may be explained by assuming that a certain amount of readily oxidizable substance is produced, whose further decomposition is rendered possible on the addition of oxygen.

If respiration really consists in two processes, then the problem as to its cause would appear to be not simplified but rendered more difficult. This is not the case, however. Many more recent researches, which certainly have often the character of 'preliminary notes', and which are often contradictory, render it more and more probable that, as in the metabolic processes previously studied, enzymes play a chief part in this one also, and that these, independently of the living protoplasm, effect the formation of CO_2 from organic substances. These enzymes are, perhaps, not so readily extracted from the cell as so many other hydrolytic enzymes, for they are often unable to pass through the cell-wall (comp. however, RACIBORSKI, 1905), and perhaps, generally speaking, are not so soluble in water as they are. Hence we are even less able, in this case, than in that of the hydrolytic enzymes, to isolate them in the pure condition. The existence of a respiratory enzyme may be, indeed, clearly demonstrated in the following ways: (1) by vigorously grinding the cells, so that as many as possible are broken open, and subjecting them to great pressure (BUCHNER, 1903); (2) by rapidly killing the cells either by chemicals, such as ether and acetone (ALBERT, 1901), or by cold (PALLADIN, 1905). By the first method one obtains an expressed sap, by the second closed but dead cells. In both cases it can be shown that oxidation goes on though micro-organisms be carefully excluded. We may select from the abundant literature the experiments of MAXIMOW (1904) with the expressed sap of *Aspergillus niger*. This sap exhibits a gaseous exchange, after the addition of sugar, which entirely corresponds to that of respiration, oxygen being taken in and carbon-dioxide being given off. That this respiratory process is due to the action of two enzymes, however, one of which induces splitting and the other oxidation of the products of splitting, is proved by the fact that the evolution of CO_2 continues when oxygen is removed by a stream of hydrogen, and that the value of the fraction $\frac{CO_2}{O_2}$ rapidly falls. The latter fact is explained by the more rapid inhibition of the splitting enzyme than of the oxidizing one. There is nothing extraordinary in this destruction of the enzyme, since the sap contains a mixture of many bodies, from which digestive enzymes are never absent, and enzymes are in all probability digestible proteids.

One of these splitting enzymes inducing the formation of CO_2 (carbonases: PALLADIN, 1905) is exactly known, viz. the so-called zymase of BUCHNER,

which decomposes sugar into alcohol and carbon-dioxide, a body we shall have to consider in the next lecture. It need only be noted here that, as already said, probably no alcohol is formed in normal respiration. This compels us to assume the existence of another enzyme related to but not identical with zymase. Further statements, à propos of this subject, rest on too hypothetical a basis to justify the space their discussion would occupy. On the other hand, oxidizing enzymes in great numbers have been often demonstrated in the plant since the time of SCHÖNBEIN, and have been more recently very carefully studied. They ought not to be compared in their activity with ' active oxygen ', for this latter must, if present in the cell, attack all oxidizable bodies—it could not oxidize the sugar and leave the protoplasm and cell-wall untouched. The oxidizing enzymes, on the contrary, have specific actions. Most of them that have been thoroughly studied oxidize bodies which do not concern us here (comp. CZAPEK, 1907, 523), while the hypothetical oxidases of carbohydrates, &c., have as yet been but little studied.

Another conception of respiration has been suggested by BACH and CHODAT (1903). They liken it to the oxidation of self-oxidizing substances outside the organism, which apparently takes place by the taking up of molecular oxygen by the self-oxidizing bodies, with the formation of a peroxide. Peroxides (e.g. H_2O_2), however, readily give off ' active oxygen ' in the transition to simple oxides, and this active oxygen is able on its part to oxidize other bodies not easily oxidizable. In the plant, therefore, there would be one enzyme known as oxygenase, which plays the part of the self-oxidizing body, becoming a peroxide under the influence of atmospheric oxygen. This peroxide would then be similarly stimulated by a second enzyme (peroxydase) to a more vigorous evolution of oxygen, just as H_2O_2 is by salts of iron, and the oxygen atoms split off would bring about the combustion of the carbohydrate. The advantage of this conception is that it links respiration with the well-known processes of inorganic oxidation, but its disadvantage lies, as it appears to us, in failing to unite ordinary and intra-molecular respiration. It is to be noted that the existence of yet a third enzyme has been demonstrated in the plant, viz. a catalase. This enzyme splits off O_2 from peroxide, and destroys any excess without giving origin to any ' active oxygen ' (comp. BACH and CHODAT).

We note, in the first place, that both these conceptions are purely hypothetical ; both have this in common that they attribute respiration to enzyme action, and all that the protoplasm does is to construct these enzymes. Previously one had been usually accustomed to ascribe to the protoplasm another and much more important function. According to a view expressed by PFLÜGER, and emphasized from the botanical point of view by DETMER especially (1883), the protoplasm itself ought to be regarded as constantly undergoing oxidation, and as constantly being rebuilt. The disappearance of sugar in respiration would, according to this theory, be due not to its direct oxidation, but to its employment in the reconstruction of the oxidized plasma. This conception has never been proved, and it requires no express refutation. We need only remark that the phenomena discussed in Lecture XVI—the respiration of inorganic substances—may serve as a standing criticism of PFLÜGER's idea. Thus the question whether it is always proteid (protoplasm) that must be respired must be answered in the negative.

205, ll. 21–42, *for* in our next lecture . . . plant economy *read* As to special functions we may refer to Lecture XXIV, and only remark here that life itself is endangered by continuous withdrawal of oxygen. According to DUDE's (1903) experiments, *Aspergillus* lived only 4–4½ hours when it was supplied with sugar, and it died in an hour or even 40 min. when supplied with glycerine or tartaric acid—substances, that is to say, which are less suitable for support-

ing intra-molecular respiration. Hence, we may conclude that intra-molecular respiration at least delayed death, although it was insufficient to support the majority of the vital functions. According to many more recent statements, death does not at once take place after the stoppage of intra-molecular respiration. Seedlings remain alive without oxygen for 3–5 days, and seeds for as many as 15 days. In the next lecture we will become acquainted with plants which are better adapted to exist without oxygen altogether. The heat of combustion of the primary respiratory materials gives us a more accurate estimate of the amount of energy released in respiration ; if the material be oxidized to its end-products, CO_2 and H_2O, we reach bodies which have no heat of combustion at all, and the whole of the energy it contains has been used up in respiration ; if, however, organic acids or even alcohol are developed it is only the difference between the heat of combustion of the primary material and sum total of those of the end-products that is available for carrying on the work of the plant.

l. 46, *after* Although *read* INGENHOUSZ (WIESNER, 1905), and to an even greater extent

ll. 55–6, *for* many unending *read* an endless number of

207, *Lecture XVII is XVI of the 2nd German Edition.*

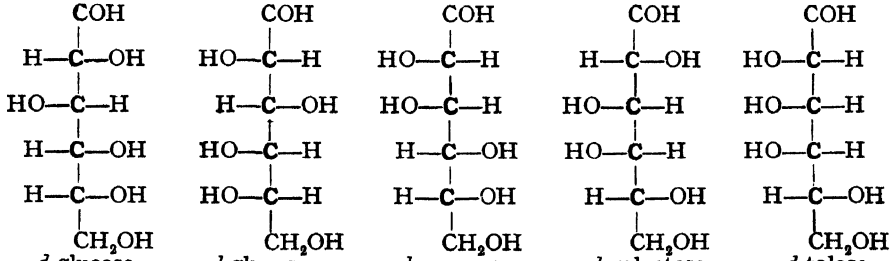
l. 20, *for* after *read* on

ll. 23–48, *for* As an example . . . ' alcoholic fermentation ' *read* In succulent plants also we may speak of acid fermentation. At present we will consider, in contrast to the oxidizing fermentative processes, as a type of splitting fermentations, alcoholic fermentation, which we are not entirely ignorant of. The term ' alcoholic fermentation '

208, l. 2, *after* organism *read* But there is no good reason for separating yeast fermentation from the alcoholic fermentation taking place in intra-molecular respiration, since GODLEWSKI (1901) has shown that alcohol and carbon-dioxide appear in the latter process in the same proportions as they do in the former, and that these bodies may also be formed in phanerogamic seedlings when supplied artificially with sugar.

ll. 21–3, *for* Fermentable carbohydrates . . . nonoses *read* Fermentable carbohydrates are characterized by possessing three or a multiple of three carbon atoms; thus trioses, hexoses, and nonoses are directly fermentable,

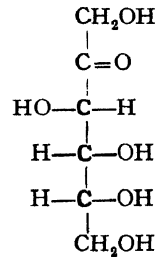
l. 28—P. **209**, l. 36, *for* These asymmetric carbon atoms . . . ferment at all *read* The structure of the aldohexoses is represented by the following formulae :—



The four central C-atoms, printed in heavy type, are the asymmetric ones ; the H and OH groups united to them may be arranged in 16 different ways, so that 16 stereoisomerous hexoses are possible, of which 12 are known. Of these 8 are perfect mirror-images of the other 8, as may be seen by comparing the formulae of *d*- and *l*-glucose. If a C-atom of the compound be

united on the left to H, on the right to OH, the corresponding C-atom of the enantiomorph has the H and OH arranged in exactly the reverse order. Along with the chemical structure runs an optical character, i.e. the way in which the compound affects polarized light; 8 hexoses (*l*-) turn the beam to the left, 8 (*d*-) to the right. It has been shown that only the dextro-rotatory isomers, but not all of them, are fermentable, viz. *d*-glucose, *d*-mannose, and *d*-galactose. Comparing their constitutional formulae, *d*-mannose shows an exchange of the H and OH groups attached to the first C-atom and *d*-galactose of those attached to the third, as contrasted with *d*-glucose. In *d*-talose, already referred to, an exchange of the groups attached to both first and third C-atoms takes place, and thus removes *d*-talose from the series of fermentable substances.

The structure of the ketohexoses is indicated by that of *d*-fructose (laevulose) :—



One sees that the groupings round the three asymmetric C-atoms entirely correspond with those round the three lower C-atoms of *d*-glucose and *d*-mannose; hence laevulose is also fermentable, but it is the only one of all the ketohexoses with this capacity. We have already called attention to the fact that, in spite of its being called *d*-fructose, it turns the polarized ray to the left.

There are altogether four fermentable hexoses known. *d*-Glucose (dextrose) and laevulose are almost equally fermentable, and mannose is apparently scarcely less so. On the other hand, the various species of *Saccharomyces* behave differently towards galactose. *S. pastorianus* (I) ferments it approximately as rapidly as it does the three other hexoses; *S. ellipsoideus* ferments it only slowly, and *S. productivus* and *S. apiculatus* not at all. As to the real connexion between constitution and fermentability we are still in the dark.

210, ll. 9–10, *for* which together can also hydrolyse maltose and saccharose *read* into *d*-galactose and *d*-glucose.

ll. 21–30, *for* There is another question . . . circumstances *read* On the other hand, the yeasts split up glycogen, and some of them also dextrine.

According to H. PRINGSHEIM (1907) a definite source of nitrogen must be present as well as a fermentable sugar, if fermentation is to take place. For this purpose ammonia, amino-acids, or peptone are suitable, but many other organic nitrogenous compounds, which in their structure are far removed from amino-acids, are quite unsuitable; still these substances often induce very apparent growth in yeasts.

l. 42—P. **218**, l. 23, *for* It is quite possible . . . by that gas *read* The splitting of sugar into alcohol and carbon-dioxide is remarkably thorough, as may be best seen by comparing the formula of *l*-glucose with those of its fermentation products :—

$$COH\,.\,(CHOH)_4\,.\,CH_2OH = (CH_2OH\,.\,CH_3)_2 + (CO_2)_2$$

This splitting can also be effected outside the cell by the action of caustic potash in sunlight on glucose (DUCLAUX quoted in LAFAR'S *Mycologie*, IV.

377). This is carried out in the cell, as BUCHNER (1897) has shown, by means of an enzyme, zymase or alcoholase. The existence of this enzyme can be as yet proved only in the same way as those concerned in respiration ; the sugar has been shown to split into alcohol and carbon-dioxide, on the one hand by sap expressed from yeast which has been subjected to great pressure and vigorous trituration, and on the other by intact and rapidly-dried yeast cells, killed by ether or acetone (ALBERT, 1901), just as well as by living yeast. The enzyme, so long as the cell-wall be complete, cannot diffuse out of either the living or the dead cell. As in the case of other enzymes, it loses its characteristic properties when treated with certain poisons. In all probability the enzyme is nothing more than a catalytic agent. Hence we meet here with a new type of enzyme, which differs from the hydrolytic and oxidizing ones by its reaction, viz. a profound splitting effect.

According to BUCHNER and MEISENHEIMER (1905) the splitting of glucose into alcohol takes place through the intermediate body, lactic acid :—

$$COH . (CHOH)_4 . CH_2OH = (COOH . CHOH . CH_3)_2$$
$$COOH . CHOH . CH_3 = CO_2 + CH_2OH . CH_3$$

Hence lactic acid when added to the expressed sap should be transformed into alcohol and carbon-dioxide. According to WOHL (1907) methylglycoxal and glycerine-aldehyde occur as intermediate products between sugar and lactic acid and the latter is further changed into methylglycoxal.

There can be no doubt that the determination of the existence of alcoholases by BUCHNER is one of the greatest advances as yet made in the physiology of fermentation ; it is worthy of note, however, that already E. TRAUBE (1858) had suggested that ' enzymes ' were the cause of fermentation, although he was not successful in isolating them from the living substance.

Although the existence of alcoholase has been proved, alcoholic fermentation by no means loses the character of a vital process, for zymases, as well as enzymes, are entirely dependent on the organism both in their origin and activity. If we could obtain alcoholase pure we would probably be able to demonstrate that its activity was dependent on external conditions in a quite different way than is fermentation in the living cell. Thus it is very probable that the optimal temperature for zymases is much higher than that for the fermenting cell. We cannot, however, prove that exactly, because the zymase in the expressed sap is destroyed by a proteolytic enzyme operative at the same time, all the more rapidly the higher the temperature is (BUCHNER and HAHN, 1903, p. 149). Further, it is known that zymase is active in sugar solutions of high concentration, while fermentation ceases entirely in a cane-sugar solution of at most 35 per cent. The most remarkable fact finally is the difference between enzymes and living cells in their dependence on oxygen. The enzyme splits the sugar independently of the presence of oxygen, while cells in this respect vary in their behaviour. Thus, in the last lecture, we got to know of higher plants and Fungi, where alcohol was formed only when oxygen was excluded, i.e. in intra-molecular respiration. In this case zymase has, perhaps, not yet been demonstrated with certainty (STOKLASA, 1904 ; MAZÉ, 1904), still its existence cannot be doubted. We do not know, however, in what relation it stands to the respiratory enzymes, whether it is in part identical with them or whether it is quite distinct from them. In the first case, the difference between intra-molecular and normal respiration must be that the primary products of splitting must be used up further in the presence of oxygen than in its absence ; in the second case, on the other hand, the absence of oxygen must increase the activity of the zymase, while in ordinary cases an oxidase would be operative.

Still all organisms do not behave in this way. We owe to PASTEUR (1861

and 1863) the proof that plants make very varied demands on oxygen. At the one extreme there are those which can go through their normal life only in its presence, and at the other those to which oxygen is a poison ; the former are termed aerobes or aerophiles, the others anaerobes or anaerophiles, but the difference is not so great as one at first sight might suppose.

213, ll. 29–36, *for* Since nothing . . . with a loss *read* Ordinary aerophiles can, as we have seen, support life for a long time by intra-molecular respiration. Alcoholic fermentation forms a substitute, though certainly a very inferior one, for respiration ; but in other organisms it forms a complete substitute. Thus *Mucor stolonifer*, when supplied with air, decomposes sugar completely into CO_2 and H_2O; when air is deficient, however, alcoholic fermentation begins which, in contrast with typical aerobes (e.g. *Aspergillus niger*), goes on for days (KOSTYTSCHEW, 1904a). Other species of *Mucor*, however, e.g. *M. racemosus*, *M. javanicus* (KOSTYTSCHEW, 1904a; WEHMER, 1906), never use up the sugar in presence of air uniformly, but always form alcohol. When air is deficient normal respiration is inhibited, but not the formation of alcohol. This behaviour certainly appears to support the view that there are two different enzymes, one for respiration and one for fermentation.

The yeasts are closely related to *Mucor racemosus*, for they possess, in addition to the power of inducing fermentation, the capacity for normal respiration, and if oxygen be present in the fermentable medium, part of the sugar is respired and the rest fermented. A definite amount of yeast produces all the more alcohol the less it is able to respire normally, and if oxygen be entirely absent all the sugar disappearing in metabolism is fermented. Since the energy in the sugar is available to a far greater extent in respiration than in fermentation, one would conceive that more sugar would be used up in the latter case. In one of GILTAY and ABERSON'S experiments (1894) 1 g. of yeast (dry weight) used up in the same time 7 g. of sugar when air was supplied, but 14 g. when it was excluded. The maximum formation of alcohol, however, is by no means coincident with the best vital condition of yeast. Growth and multiplication are in the higher degree dependent on the supply of oxygen. When the oxygen is greatly reduced vegetative growth ceases entirely, though fermentation continues for a longer time. Unfortunately there is no unanimity among authors as to the extent to which yeast increases in absence of oxygen ; some deny it altogether, while others (BEIJERINCK, 1894) state that the yeast may increase up to 20 or 30 times its original amount. Whichever view be correct, growth is certainly very limited when alcoholic fermentation alone goes on. but is unlimited when respiration ensues. Although, however, the amount of alcohol formed in a unit of time obviously depends on the amount of yeast present, still one cannot say *a priori* whether a minimal amount of yeast will produce in the long run more alcohol with or without oxygen. Experiments and empirical results teach us that if only a little oxygen be added the yeast increases greatly, and fermentation is so little retarded that a maximal production of alcohol may be observed. If a suitable nutritive solution be inoculated with a small amount of yeast, air being carefully excluded, the organism at first absorbs greedily the oxygen dissolved in the fluid ; it is able to appropriate even loosely-combined oxygen, tearing away oxygen from oxyhaemoglobin, although it is unable to decolourize indigo-carmine. Thus the yeast at first increases to a certain extent and alcoholic fermentation begins to be apparent, bubbles of CO_2 appearing in the fluid ; soon, however, the bubbles become smaller and smaller and finally cannot be seen at all. It is very remarkable how the addition of a minute air-bubble at once raises the intensity of fermentation and how visible bubbles of carbon-dioxide once more begin to come off

(DUCLAUX, 1900). If the oxygen be permanently excluded, however, the yeast in the long run dies, even though nutrients be still to hand (BEIJERINCK, 1894). Alcoholic fermentation itself must thus also be furthered in the long run by limitation of the amount of oxygen, but the statements in the literature on the whole question are perhaps more conflicting than in any other department of Physiology (CZAPEK, *Biochem.* I. 260).

By way of summary, we must say that the yeasts are neither genuine aerobes nor anaerobes. This statement, however, is, speaking generally, not quite in accordance with the facts, because different functions of the yeast are affected in quite different ways by oxygen. It is very desirable that the minimum, optimum, and maximum of oxygen needed for the carrying out of these functions in yeast should be determined as thoroughly as has been done by WUND (1906) for many Bacteria.

If the yeast forms alcohol under the conditions when normal respiration is possible, this indicates a loss of energy,

l. 50—P. **214**, l. 32, *for* This fact . . . higher alcohols *read* But this is true only under the artificial conditions of a pure culture; under natural conditions, where there is always a mixture of organisms, apparently such a suicidal action does not occur (BENECKE in LAFAR'S *Mycologie*, I. 330).

We thus see that yeast obtains an advantage by this habit of always forming alcohol, and we may suppose that other organisms that excite fermentation must behave in a similar way. By the term 'fermentation' we understand, therefore, a dissimilation process which does not lead to the formation of CO_2 and H_2O, and in which the products which are formed have a biological significance in relation to the organisms which produce them.

Alcoholic fermentation does not lead merely to the formation of alcohol and carbon-dioxide; there are always by-products as well, and the occurrence of lactic acid among these is quite intelligible since it is an intermediate stage between sugar and alcohol; but the case is otherwise with amyl-alcohol (fusel oil), glycerine, and succinic acid. The source of amyl-alcohol has been most satisfactorily explained by EHRLICH'S (1906) interesting demonstration of its origin from leucin. It has nothing at all to do with the real alcoholic fermentation, but arises from a nitrogenous substance which occurs already in the natural culture solution, or arises always as a down-grade product of proteids in the yeast. Its amount may be greatly increased, just as readily by the addition of more leucin to the culture as by a reduction in the concentration of the sugar, and hence it may be clearly seen that there is no relation between the formation of ethyl-alcohol and amyl-alcohol. The source of the glycerine is as yet unknown; it is very improbable that it arises from sugar, possibly the fat or lecithin of the yeast may be its source. Its amount varies and depends, in the first instance, on the species of yeast employed, and secondly, on the nature of the nutriment provided, not only the fermentable carbohydrate but also the source of nitrogen. LABORDE (1899) found that 2·5–7·75 g. of glycerine were formed from 100 g. of fermented sugar as the result of the action of various yeasts, and WORTMANN'S (1892) experiments with different wine-yeasts show a very variable formation of glycerine. Succinic acid comes next to glycerine in amount, and reaches about 0·5 g. per 100 g. of sugar, but the amount is liable to considerable variation. Since both these secondary products are also formed by yeast under conditions which exclude the formation of alcohol (UDRANSKI, 1889), we have obviously to deal with a special kind of metabolism whose significance is unknown, but which has nothing to do with alcoholic fermentation (WORTMANN, 1898). Into the question of the occurrence of other by-products such as aldehyde, volatile acids, &c., we will not enter; these are, doubtless, formed also in pure yeast fermentations, though not actually products of it. There are also other bodies present which give definite characters

to the fermented liquor, but these are not due to the yeast, but to the fermentable material—in the case of wine, for example, to the grapes.

215, l. 36—P. **216**, l. 22, *for* The researches . . . higher plants. *read* Still BEIJERINCK's theory does not appear to us to be sound ; the very accurate researches on butyric acid Bacteria argue against it. WINOGRADSKY (1898–1902) has isolated from soil a bacterium of this kind to which has been given the name of *Clostridium pasteurianum*, and which will occupy our attention later on (Lecture XVIII) on account of its power to assimilate free atmospheric nitrogen. *Clostridium* agrees morphologically in many points with BEIJERINCK's *Granulobacter butyricus*, e. g. in the spindle-shaped swellings of the cells and in its granulose reaction previous to the formation of spores. There are other and quite distinct differences between them into which we need not enter here ; the physiological activity of this organism is of more importance for our purposes. When supplied with suitable mineral and nitrogenous nutrients it ferments many, but not all, carbohydrates to acetic, butyric, and carbonic acids and hydrogen, about half of the sugar going to the formation of the acids and half to the formation of gases. This whole fermentation process is carried on, according to one of WINOGRADSKY'S experiments, for twenty successive generations, although oxygen was completely excluded.

Butyric acid-forming organisms have been frequently studied. They differ physiologically from *Clostridium* (apart from the absence of assimilation of free nitrogen) in their use of numerous fermentable materials (sugar-alcohols, polysaccharides, &c., besides sugar) and by other fermentation products, butyl alcohol being formed as well as butyric acid. Many of these forms are quite as strictly anaerobic as *Clostridium*, and the relation of two of them to oxygen has been studied in detail by CHUDIAKOW (1878). In the vegetative stage, these species (termed *C. butyricum* and *Bactridium butyricum* by CHUDIAKOW) are injured by a brief exposure to ordinary atmospheric air and killed by longer exposure, and even their spores are, in the long run, non-resistant to the action of oxygen. Low concentrations of oxygen can be tolerated, however, without injurious results ; thus *Bactridium butyricum* grows well in air of 5 mm. pressure, and *Clostridium* in air of 10 mm. pressure.

Again, there are forms, doubtless strictly anaerobic, which indeed are not injured by minute traces of oxygen, but which can thrive without it. Life without free oxygen is indeed possible only if some suitable material which can be fermented is supplied in its place, otherwise such an organism dies under all circumstances, or it requires free oxygen. If fermentation can take the place of respiration it may be concluded that the organism obtains oxygen in the process—certainly not free oxygen, but in the combined condition which it separates from its combination. In fact, it may be easily shown that all fermentations are reduction processes. Thus the loosely combined oxygen in oxyhaemoglobin is generally taken up by the fermentative organism, and the oxyhaemoglobin is, as in alcoholic fermentation, reduced to haemoglobin. Reduction of indigo-carmine and methylene blue to the colourless condition is also well known. Fermentable fluids which have such a colouring matter added to them lose their colour if they are excluded from oxygen, but become blue again after being shaken up with air. Further, atmospheric oxygen is absorbed in butyric acid fermentation, if it be presented in non-injurious concentrations (CHUDIAKOW, 1896). Many organisms which induce fermentation are also capable of splitting off oxygen which is very difficultly accessible ; thus nitrates and sulphates in nature are so reduced. Both of these processes must be considered in detail because they are of importance in the circulation of life on the earth.

Reduction of sulphates occurs in nature especially in the mud of fresh

water, of lakes, or of the sea (VAN DELDEN, 1903). *Microspora disulphuricans* and a closely related form living in such places produce sulphuretted hydrogen from sulphate ; in one of VAN DELDEN'S experiments the enormous amount of 0·952 g. was produced from 1 litre of culture solution. The oxygen so abstracted is found again in the carbon-dioxide which is obtained from the essential organic materials in absence of free oxygen. In addition to sulphates, thiosulphates are reduced by certain Bacteria, and yeasts also form sulphuretted hydrogen out of thiosulphates and sulphates.

One might imagine these reductions were the result of the action of the hydrogen produced in these fermentations, or of other similar reduced bodies, such as methane. When in the nascent state these substances can reduce sulphates, just as they reduce the easily-reduced bodies above referred to. However, the origin of H or CH_4 in the case of yeast is neither proved nor probable. On the other hand, Bacteria which form hydrogen abundantly and which decolourize indigo-carmine are unable to reduce sulphates. Finally, many Bacteria that are able to form H_2S from sulphates are unable to reduce the more readily reducible nitrate. All these facts suggest that we have here to do with quite specific reducing agents in living cells (OMELIANSKI, 1904, in LAFAR'S *Mykologie*, III. 217). That these substances must be of the nature of enzymes is supported by HAHN'S observations (comp. BUCHNER, 1903), according to which dead cells can induce the same reductions as living cells. His experiments were carried out with expressed yeast sap, dried yeast cells, and dead Bacteria.

Just as the combination of sulphur is aided by the reduction of sulphates into a form which is of no nutritive value to the majority of plants, so also by reduction nitrates are transformed into compounds which are of no value as nutrients to higher plants, or at least are in many cases of less value than nitrates. Nitrates may be transformed into ammonia through the intermediate stages of nitrites, or they may be reduced to free nitrogen, or, finally, NO and N_2O may be produced (comp. JENSEN in LAFAR'S *Mykologie*, III. 182 ; ITERSON, 1904). The last reaction is as yet little known, but ammonia formation is a quite common feature in the metabolism of micro-organisms. Since the ammonia in the soil is easily absorbed, its formation does not result in any loss of nitrogen in agriculture, but it is different when free nitrogen is formed. This process, 'denitrification,' in the limited sense, appears to be very common. JENSEN (1898, 1899) has studied some Bacteria which can split off nitrogen only when oxygen is absent, and which are able to live as anaerobes only when potassium nitrate is available. It is obvious that they take oxygen from potassium nitrate, and this view is supported by MAASSEN'S (1901) observation that bodies containing abundant oxygen, e. g. chlorates, inhibit the decomposition of potassium nitrate. Probably these chlorates take the place of nitrates, and oxygen is abstracted from them, so that they, to a certain extent, protect the nitrates. It has, however, been shown by several authors that denitrification is also possible in presence of oxygen, and this fact appears at first to be contrary to the conception of the process as above outlined. But when we bear in mind that yeast does not cease to produce alcohol when oxygen is plentifully supplied, we may well assume the possibility of the existence of Bacteria which can regularly split off oxygen from certain nitrogenous compounds, even when it is also supplied to them in the free state. From MAASSEN'S researches, indeed, it appears that certain Bacteria are specifically denitrifiers, i. e. always induce denitrification, while others develop such a power only under certain definite external conditions. The former are obviously limited in number, while the power of inducing ordinary denitrification is apparently widely distributed. The cause of nitrate—as of sulphate—reduction must be attributed to enzymes.

In general it is assumed that there is no great difference between the taking up of oxygen from oxides to effect combustion of sugar and to bring about a decomposition of sugar into alcohol and carbon-dioxide, or into butyric acid, hydrogen, and carbon-dioxide. Following PASTEUR, one may look upon these splittings as a transference of oxygen from one carbon atom to another in the same molecule. From that point of view, respiration and fermentation are to be considered always as cases of oxidation. While, however, in the so-called oxidizing fermentations, where different organic acids are formed, the fermentations go on without free oxygen, in normal respiration free oxygen is essential.

We must now strictly limit ourselves in any further enumeration of fermentation phenomena. Our most important work is to find out how the products of the animal and plant worlds are transformed into simple bodies by the fermentative agency of lower organisms, so that these may again become available for the nutrition of higher plants. (For all details see LAFAR'S *Mykologie*.)

216, l. 51, *after* organisms. *read* At least the special capacity of these Bacteria is in accord with enzymic action (BUCHNER and MEISENHEIMER, 1903).

217, ll. 25–53, *for* Butyric acid . . . cellulose, e. g. the *read* Among the fatty acids which arise from sugar through the activity of fermentative organisms we have, in speaking of *Clostridium pasteurianum*, already mentioned acetic and butyric acid. We should note, though quite briefly, that in addition formic acid and also higher fatty acids, such as propionic and palmitic acids, make their appearance in the so-called butyric acid fermentation. Probably we might increase the number of these acids considerably if more care were taken in looking for them. Further, it is of interest to note that there are also animal anaerobes, e. g. intestinal worms belonging to the genus *Ascaris*, which, according to WEINLAND (1901), induce propionic acid fermentation.

It was also noted above that many butyric acid formers are not restricted to sugar, but make use as well of polysaccharides, such as starch and cellulose. Since cellulose is one of the chief down-grade products of plant metabolism, its further utilization by micro-organisms is of the greatest interest. Among the forms which carry out this work is a

218, ll. 14–16, *for* become transformed . . . support of life. *read* in the form of humus, turf, and coal, become once more available for the support of life.

l. 19, *for* In a word *read* Recently,

l. 36, *after* OMELIANSKI *read* 1902,

l. 47, *for* [OMELIANSKI, 1904 b] *read* (Comp. LAFAR'S *Mykologie*, III. 269.)

l. 48—P. **219**, l. 36, *for* On studying . . . proteid fermentation *read* Just as the alcohol which arises in alcoholic fermentation is further worked up by other organisms, so the products of other fermentation processes are employed by yet other organisms still. We shall speak of the employment of greatly reduced bodies like H_2S, NH_3, H, and CH_4 in the next lecture. How butyric acid is broken down does not appear to have been investigated; but OMELIANSKI (1904) has made us acquainted with the anaerobic decomposition of formic acid. Calcium formate undergoes the following transformation:—

$$Ca(CHO_2)_2 + H_2O = CaCO_3 + CO_2 + 2H_2$$

The organism which brings aboutt his fermentation, viz. *Bacterium formicicum*, is able to make use of the simplest imaginable organic compounds, but it can use peptone as well. On the other hand, it can make no use of the closely allied fatty acids, although it can employ a whole series of sugars and sugar-alcohols. In OMELIANSKI'S cultures, in addition to CO_2 and H, there were

produced, from mannite and dulcite, also ethyl-alcohol, acetic, formic and lactic acids, and even succinic acid. We have thus established a fermentation for all these alcohols, and we may add that glycerine as well is known frequently to undergo fermentation.

Having referred to the most important non-nitrogenous organic materials which may be employed in fermentation, we must now turn to nitrogenous bodies. Plants, as we have already seen, are very economical of nitrogen; it is only when they are provided exclusively with substances rich in nitrogen that they give off that element in the form of ammonia. On the other hand, the excrement of animals always contains nitrogen, and in urine specially it is present in the form of urea, uric and hippuric acids. It has long been known, however, that these substances do not form suitable sources of nitrogen for autotrophic green plants, and hence it is all the more important that they should undergo transformation in the soil. In this process micro-organisms are concerned to a very large extent. Best known of all is the transformation of urea into ammonium carbonate, a process often termed ' urea-fermentation '. It takes place according to the formula:—

$$CO(NH_2)_2 + 2H_2O = CO_3(NH_4)_2$$

Here we have simply a taking up of water without any splitting, just like what occurs in so many enzyme actions. Since the gain in energy in this process is but limited, the formation of ammonia has, perhaps, rather the effect of making the medium alkaline, and so rendering the substratum unsuitable for other organisms. Still it is true that Uro-Bacteria are not very resistant to ammonia. Urea fermentation is, however, not the only source of energy to these Bacteria, for they are all strongly aerobic. A metabolic utilization of the ammonia so formed is not known; still one must not imagine that ammonia arises here in the same way as it does in genuine peptone nutrition. Since the urea does not serve as a source of carbon to the Uro-Bacteria, they cannot exist when supplied with it alone (BEIJERINCK, 1901); it serves as a source of nitrogen only. As regards their carbon requirements the various forms behave differently; those species which get on with acetic acid or oxalic acid make the most moderate demands, but they form only a little ammonium carbonate. More arises from such forms as grow in tartaric acid, and more still from those which employ malic acid. The greatest amount of ammonia is formed by *Urobacillus pasteurii* and *Urococcus ureae*, which employ meat extract as the source of carbon, for if a trace of them be added to the culture they can in a few days completely transform 10–12 g. of urea in 100 g. of fluid. The immediate cause of the formation of ammonia is an enzyme, urease, as to whose presence or absence there has been much controversy. Its existence cannot be doubted after BEIJERINCK'S recent discoveries, for this authority was able to show that Bacteria which had been killed by chloroform could attack the urea just as well as the living ones; he showed also that urease cannot diffuse out of the cells, so that the previous statements as to ' soluble urease ' must be attributed to minute Bacteria overlooked in the fluids under consideration. From uric acid ammonia at least arises; the fate of the hippuric acid we need not consider (comp. MIQUEL in LAFAR'S *Mykologie*, III. 71, as to that point, and also as to the morphology of Uro-Bacteria).

Another nitrogenous product, widely distributed in the animal kingdom, and also present in Fungi, is chitin. BENECKE (1905) has isolated a Schizomycete which is able to break down this exceedingly resistant body, although certainly only when well nourished and in presence of air.

The greatest interest centres round the nitrogenous bodies known as proteids, which are available for use by micro-organisms on the death of any

higher organisms. The mode of decomposition of these bodies (comp. HAHN and SPIECKERMANN in LAFAR, III. 85) appears to be as follows: they decompose into amino-acids, such as we have already met with in germination; from these ammonia is next split off and the remaining acid is transformed into simpler and simpler bodies by oxidation and reduction; finally, H, methane, carbon-dioxide, free nitrogen and ammonia are produced. Since, however, sulphur, and phosphorus as well, are present in proteids, sulphuretted hydrogen and phosphoric acid are also end-products. In the formation of these bodies numerous aerobic and anaerobic Bacteria and Fungi are concerned and many very characteristic by-products among the aromatic amino-acids make their appearance, the best known of which are indol and skatol. We need not go further into the matter, however, for the chief point we desire to establish is only that, in the long run, nitrogenous and non-nitrogenous organic bodies are transformed into simple inorganic compounds, which are in part directly, in part indirectly (due to the agency of micro-organisms which we shall study in the next lecture), made to serve once more as nutrients to the autotrophic green plant.

P. **220**. *Lecture XVIII is XVII of the 2nd German Edition with title*

OXIDATION OF SULPHURETTED HYDROGEN, HYDROGEN, METHANE, AND AMMONIA BY BACTERIA. CARBON-DIOXIDE ASSIMILATION IN THE ABSENCE OF LIGHT AND CHLOROPHYLL

220, ll. 26–49, *for* At the conclusion of . . . 'sulphur-bacteria' *read* In the last lecture we became acquainted with certain processes which led to the formation of sulphuretted hydrogen, viz. the reduction of sulphates and the putrefaction of proteid; but there are other processes taking place in nature, which we need not go into here, which also lead to the development of sulphuretted hydrogen. We know, however, that this substance is quite unsuitable as a source of sulphur to higher plants, for these forms make use of sulphates exclusively.

221, ll. 7–8, *delete* [OMELIANSKI . . . sulphur-Bacteria.]

l. 38, *for* containing sulphuretted hydrogen *read* to which H_2S has been added,

222, l. 1, *for* a *read* an approximately

l. 7, *for* On the fluid being renewed *read* On ceasing to renew the fluid,

l. 11, *after* reach *read* rapidly

ll. 14–19, *for* In a mud swamp . . . its existence *read* In a mud swamp, just as in sulphur springs, it always attempts to find a region with an optimum oxygen tension, inhabiting level places subject to flooding and avoiding deeper hollows. Moreover, in determining its distribution not only oxygen but also sulphuretted hydrogen plays a part, for the organism can tolerate only a definite and not really high concentration of that substance.

l. 47, *for* diminished *read* accomplished

l. 54, *for* absent . . . cases *read* impossible for most living beings.

223, l. 5, *for* i. e. in infinitesimal quantity *read* i. e. infinitesimal quantities.

l. 22, *for* (p. 229) *read* (at least so we must suppose for the present; comp., however, p. 229).

ll. 26–33, *for* To *Beggiatoa* . . . with regard to them *read* To *Beggiatoa* is allied, in the first place, the genus *Thiothrix*, which according to WINOGRADSKY may be described simply as a fixed *Beggiatoa*. A reinvestigation of this form is desirable, however, for the presence of sulphur in it has recently been called

in question (WILLE, 1902; MOLISCH, 1903). Other colourless sulphur-bacteria have been discovered by OMELIANSKI (1905), HINZE (1903), and JEGUNOW (comp. OMELIANSKI in LAFAR'S *Mykologie*, III. 214). JEGUNOW'S observations on the movements of the forms he studied are of interest. When confined in a tall narrow vessel, these plants congregate at a certain distance from the upper surface of the fluid (as described above in the microscopic culture of *Beggiatoa*) and proceed to make incursions from thence into the deeper regions of the medium in what look like convection currents. Single cells migrate downwards into the middle of the stream and at the same time load themselves up with sulphur; they then move back again to the outer edge of the stream, upwards, and there oxidize the sulphur. The rapidity of the movement is considerable; they can traverse the whole distance back in five minutes.

Associated with the colourless sulphur-bacteria there is a whole series of so-called red sulphur-bacteria (Fig. 39, *d*, *e*), which physiological research has already shown to exhibit important differences from *Beggiatoa*, although no satisfactory conclusions have as yet been reached with regard to them.

ll. 43–5, *for* the question as to how . . . in association *read* it is incomprehensible how they manage to obtain the necessary oxygen. According to WINOGRADSKY (1888 b) they do so by always being in association

224, l. 5—P. **225**, l. 26, *for* It is to be hoped . . . nitric acids. *read* More recently MOLISCH (1907) has reinvestigated this question. He was unable to demonstrate any evolution of oxygen from purple Bacteria with the most varied methods, so that one must still regard the existence of such a process as open to the gravest doubt. It does not follow, however, that no CO_2-decomposition takes place. The oxygen produced might—indeed we might say must—be at once used up in the oxidation of sulphuretted hydrogen. A normal assimilation in these forms is all the more probable, since MOLISCH found that sunlight, though not essential, was at least helpful. In another aspect MOLISCH disagrees widely from WINOGRADSKY'S views. He finds that purple Bacteria can exist without peptone, and he unites with these organisms also those forms which contain the same colouring matter as the red sulphur-bacteria, though without the sulphur. It would thus appear that he attributes no special vital significance in these Bacteria to the sulphur. On the whole, we must admit that further research on the subject is still urgently needed.

A group of sulphur-bacteria with quite different peculiarities has been discovered by NATHANSOHN (1902) in the Gulf of Naples, and BEIJERINCK (1903) has shown that similar organisms occur in other seas, and are not wanting also in fresh water. The forms observed by NATHANSOHN oxidize thiosulphate to sulphuric acid and tetrathionic acid, according to the following formula:—

$$3Na_2S_2O_3 + 5O = 2Na_2SO_4 + Na_2S_4O_6$$

A separating out of sulphur occurs here also, but it does not take place within the organism and is perhaps, so far as its origin is concerned, quite independent of it. By the use of an agar-solution, to which has been added sea-water and $Na_2S_2O_3$, these organisms, like other Bacteria, may be cultivated and isolated; they do not exhibit that great sensitiveness to organic substances that *Beggiatoa* does. The addition of organic bodies, such as sugar or urea, is of no service to them, and does not enable them to do without thiosulphate; hence we must conclude that the oxidation of thiosulphate completely replaces the respiration of organic bodies, and that it cannot be replaced by them. *Thiobacillus thioparus*, studied by BEIJERINCK, differs widely from NATHANSOHN'S bacterium, inasmuch as it can decompose not only thiosulphate but also sulphides (calcium sulphide), sulphuretted hydrogen, and tetrathionate. The splitting off of sulphur which always takes place must, according to BEIJERINCK, be always

induced by the vital activity of the organism itself ; and the thiosulphate must be employed in the following way :—

$$Na_2S_2O_3 + O = Na_2SO_4 + S.$$

The sulphur is excreted by the *Thiobacillus* out of the cell and may be then oxidized by other Bacteria into sulphuric acid. These nitrates must be reduced and from them the oxygen needed for oxidation must arise :—

$$6KNO_3 + 5S + 2CaCO_3 = 3K_2SO_4 + 2CaSO_4 + 2CO_2 + 3N_2.$$

Hence we have here to deal with anaerobes whose metabolism yet awaits elucidation.

The different types of sulphur-bacteria are organisms of the greatest physiological interest. Inquiry is suggested as to whether other inorganic substances, as well as reduced sulphur, may serve as sources of energy in their oxidation by definite forms of life. As a matter of fact, quite recent researches have shown that many such organisms exist, and we have good grounds for assuming that we are far from having discovered them all. We may mention, first of all, the Bacteria studied by NABOKICH and LEBEDEFF (1906), as well as by KASERER (1905, 1906), SÖHNGEN (1906), and NIKLEWSKI (1906), which oxidize two widely distributed products of fermentation, viz. hydrogen and methane. (According to NABOKICH the oxidation of hydrogen was observed in 1892 by IMMENDORFF, and referred by him to the action of Bacteria.) This brief reference to these organisms must suffice ; we shall return to the subject and treat of it in greater detail later on. Iron-bacteria may also, perhaps, be considered in this connexion. According to WINOGRADSKY (1888) they are able to transform ferrous into ferric oxide and benefit thereby in the same way as the sulphur-bacteria do by the conversion of H_2S. Unfortunately, WINOGRADSKY'S short preliminary note has not been followed up by a detailed paper, and meanwhile his results have not been confirmed by MOLISCH (1892) ; hence we cannot as yet say anything definite as to the iron-bacteria.

Finally, the nitrifying Bacteria are of quite special importance, for to them is consigned the task of oxidizing the ammonia, which so often arises in nature, into nitrous and nitric acids.

225, l. 30, *delete* on them
l. 48, *delete* [WINOGRADSKY, 1904.]
l. 52, *for* varying *read* very different
l. 54, *before* experiments *read* previous
l. 55—P. **226**, l. 1, *for* require special conditions of investigation *read* have quite special requirements,

226, l. 31, *for* among these *read* in which

227, l. 47, *delete the first* and
l. 53–5, *for* to (in mg.) . . . 22·4 *read* to between 15 and 26 mgr.

228, l. 13, *for* HERAEUS (1886) and HÜPPE (1887) *read* HERAEUS (1887) and HÜPPE (1886 ; comp. also 1906),
l. 38, *for* four weeks later *read* at the end of four weeks
l. 39, *after* day *read* even after six weeks.
l. 48, *for* observed *read* held
l. 51, *for* observe *read* take into consideration

229, ll. 10–49, *delete* Respiration forms . . . nitro-bacteria.
l. 54, *for* previously *read* since

230, l. 1, *for* substances in *read* substances on
ll. 13–19, *for* In the first column . . . ordinary Bacteria. *read* In the first

column of each series are given the lowest percentages which merely retard development, and in the second the doses which completely inhibit it. The symbol > signifies 'more', but not much more than the number following (comp. also BOULLANGER and MASSOL, 1903, 1904). We may deduce several important conclusions from this table :—

1. The various organic substances are by no means neutral to the nitro-bacteria, but really operate directly as antiseptics, and their effect is not less intense than that of carbolic acid on ordinary Bacteria.

ll. 30–56, *for* All these facts . . . nitric acid. *read* Hence one would conclude that nitrate formation always began to take place in nature after the whole of the ammonia had been used up in nitrite manufacture. As a matter of fact, however, we always find nitrite and nitrate formation going on in the soil at the same time. This suggests that the ammonia has an injurious effect only on the *development* of the nitrate Bacteria and that the *full-grown* cells are much less sensitive to its influence (BOULLANGER and MASSOL, 1904). We must leave undiscussed the question as to whether the activity of the nitrite Bacteria begins to manifest itself markedly only after the organic substances (dead animals and plants, excreta) have been completely broken down by the ordinary fermentative forms so that their carbon has been transformed into CO_2 and their nitrogen into NH_3 or N (LÖHNIS, 1904). A clearly marked separation of nitrification from fermentation might indeed have special significance, since otherwise the nitrates formed would not become of service to green plants, but rather be broken down by the fermentative Bacteria which denitrify such bodies.

In this relation it should further be noted that the nitro-bacteria do not exhibit their activities merely in arable soils where ammonia is presented to them as a result of manuring, but that they also occur at the sea-bottom, where THOMSEN (1907) has shown the nitrite formers at least are generally distributed; he shows, however, that the nitrate Bacteria occur only near the coast-line. Further, as WINOGRADSKY has already clearly demonstrated, the nitro-bacteria also can establish themselves on bare calcareous rock. In such situations they are able to transform into nitric acid the small quantities of combined nitrogen brought to them in rain. They also decompose the lime and thus render the rocky substratum available for higher plants. Nitro-bacteria are thus the first colonists of calcareous rock, and so organic material is constructed by nitrate Bacteria entirely independently of light and of other organisms. Since ammonia is in reality always produced by organisms, that substance is not available for the nitrite formers; quantities of nitrite formed in the air by electric discharge are, however, at the disposal of the nitrate formers.

If now, having disposed of the nitro-bacteria, we glance back at the phenomena we met with in connexion with the colourless sulphur-bacteria, these show themselves in an entirely new light. Not only do we see a perfect analogy between the respiration of NH_3 on the one hand, and of SH, on the other, but we are led to reconsider the poor results obtained by feeding *Beggiatoa* with organic substances. It is in the highest degree probable that the sulphur-bacteria are also autotrophic organisms (WINOGRADSKY, 1890, p. 275), and that they thrive even better when organic food-stuffs are entirely excluded than when supplied with 'bad' nutrients. One can only wonder why this research was not carried out long ago. NATHANSOHN has shown in relation to the Bacteria that oxidize thiosulphate, that they exhibit a continuous increase in their dry weight when in the presence of CO_2 only and when organic substance is absent. Further, NATHANSOHN has also succeeded in proving that the addition of organic material is of no service to these Bacteria and in no way acts as a substitute for CO_2. Here also we have to deal with obligate autotrophic forms. The energy required for the further working up of CO_2, and

which green plants obtain from light, is in this case supplied by the oxidation of this sulphate.

Again, the methane-bacillus of SÖHNGEN (1906) is also autotrophic. Large quantities of carbon supplied in the methane are used up in the formation of its cells, but whether the methane is first of all transformed into CO_2, or whether the methane is assimilated as such, is not known; if the latter be the case, then this organism might be regarded as autotrophic. In a flask containing about 100 ccm. of pure mineral nutrients, 225 ccm. of methane were used up in fourteen days, of which 126 ccm. were employed in the manufacture of the Bacteria and 99 ccm. were transformed into CO_2; 149 ccm. of oxygen were taken up in the process.

Finally, as regards the Bacteria which oxidize hydrogen, investigations give as yet very contradictory results. If we disregard the somewhat fantastic statements of KASERER (1906) and confine ourselves to NIKLEWSKI's researches, we find that these organisms—which have not as yet been obtained pure—are without doubt capable of making use of CO_2 if they are able to oxidize hydrogen. They differ, however, from the majority of autotrophic Bacteria in having the power of becoming facultative heterotrophs. In a suitable nutrient medium (acetates and also other less effective salts of organic acids) they can exist without hydrogen; the organic material then serves as well for the manufacture of the substance of their bodies as for purposes of destructive metabolism.

Under these circumstances one may conclude that the hydrogen Bacteria practically never exist without respiring organic substance. With regard to the majority of the other Bacteria discussed in this lecture, the question is still an open one; certainly in no case can ' normal respiration '—although it generally takes place—replace the oxidation of specific inorganic materials. It has been definitely proved that respiration of organic substances does not, as a rule, take place in thiosulphate Bacteria. Further, it follows that the living matter itself does not suffer that continual destructive metabolism which would be necessary to the maintenance of life (p. 204).

231. *Lecture XIX is XVIII of the 2nd German Edition.*

l. 36—P. **233**, l. 3, *for* DENITRIFICATION . . . activity of Bacteria. *read*

NITROGEN FIXATION. SYMBIOSIS AND METABIOSIS. CIRCULATION OF CARBON AND NITROGEN

In Lecture XVII we have seen that through the agency of micro-organisms free nitrogen can be split off from nitric acid and from proteid. Since at an earlier date no organisms capable of combining nitrogen were known, it was thought that such continual loss of combined nitrogen must in the long run render the existence of living things on the earth an impossibility (comp. BUNCE, 1889). In reality, however, we have been long acquainted with the fact that a measurable accumulation of combined nitrogen does take place in certain arable soils, which could only have arisen from a combination of nitrogen in the gaseous condition, and by the year 1892 BERTHELOT had definitely shown that this combining of free nitrogen must be due to the activity of Bacteria, since the process came to an end when the soil was heated to a temperature of 100° C. It is to WINOGRADSKY that we owe the first comprehensive studies on the behaviour of these Bacteria.

233, ll. 41–3, *for* The isolation . . . in vacuo. *read* The isolation of *Clostridium* presented many and great difficulties, and was first successfully accomplished when it was sown on carrots in vacuo.

ll. 48–9, *for* When alone . . . nitrogen ; *read* It is only *Clostridium pasteurianum* that is able to combine nitrogen ;

234, l. 26, *for* One of . . . shows *read* The only statement made by WINOGRADSKY on the subject is to the effect

ll. 41—P. **235**, l. 19, *for* but he was unable . . . (KEUTNER, 1904)] *read* In connexion with WINOGRADSKY'S work it has been shown that there are many soil Bacteria similar to *Clostridium pasteurianum* in form, mode of life, and capacity (comp. HASSELHOFF and BREDEMANN, 1906 ; PRINGSHEIM, 1906), and that these are present also in the sea (KEUTNER, 1904). Further, BEIJERINCK (1901) has isolated from soil a colourless bacterium characterized by its large size and recalling in its habit a member of the Cyanophyceae (*Azotobacter chroococcum*), whose power of combining nitrogen has been fully established by GERLACH and VOGEL (1902), and by A. KOCH (1902). *Azotobacter* differs from *Clostridium* in being aerobic and in not being so exigent in its demands for organic nutriment as that form. It can live on sugar, but mannite or salts of propionic acid are in general more suitable to it, and these it employs in normal respiration. This bacterium's power of combining nitrogen exceeds that of *Clostridium* not inconsiderably. While *Clostridium* shows a gain of 2–3 mg. of nitrogen for every gram of sugar, different authorities give, for *Azotobacter*, 7–9 mg., or even as much as 12 mg. of nitrogen per gram of sugar (VOGEL, 1906, p. 40). *Azotobacter* is very widely distributed ; it is almost never absent from soil or sea water.

It is not possible to say with certainty whether or not other Bacteria in addition to those mentioned can combine nitrogen, but statements to that effect are not wanting (comp. VOGEL, 1906, p. 46 ; LÖHNIS, 1905, p. 594) ; how far these may be accepted must remain unsettled.

l. 25, *after* 559 *read* ; KOCH in LAFAR'S *Mykologie*, III. 12

ll. 29–51, *for* In spite of this . . . As already remarked, the Leguminosae *read* The market preparation ' alinite ' (a culture of this bacillus) is thus perfectly worthless. It has also been affirmed that Algae and Cyanophyceae have the power of combining nitrogen, but proof of the fact is entirely wanting. On the other hand, Leguminosae have this power to a marked degree, but we shall speak of these plants later.

It has not infrequently been observed that nitrogen combination goes on in the soil at a different rate from that in pure cultures of the nitrogen-combining organisms isolated from the soil ; the reason for this has not been clearly made out. It is possible that organisms accompanying *Clostridium* and *Azotobacter* play a part in the process. It is natural to think in this relation of the Algae which are assimilating carbon-dioxide in the uppermost layers of the soil, and which perhaps provide the Bacteria with sugar (KOSSOWITSCH, 1894), whilst obtaining in turn soluble nitrogenous compounds from the Bacteria. Further, the inorganic nutrients are of importance to the Bacteria, for it is known that they make great demands on chalk and phosphoric acid. Finally, it must be noted that nitrogen combination due to inorganic chemical processes is not impossible (WARMBOLD, 1906). In order to obtain an idea of the intensity of nitrogen combination in the soil, we may refer to the results obtained by J. KÜHN (1901). KÜHN obtained out of a certain field good and even increasing harvests, after being sown for twenty successive years with winter rye, without any nitrogenous manuring. This showed that more nitrogen was annually combined in the soil than was removed from it in the process of harvesting ; and since the rye is itself incapable of bringing about such a combination, and since, further, the amount of combined nitrogen precipitated on the soil nothing like makes up for the loss by harvesting (see p. 136), obviously atmospheric nitrogen must have been combined to a very large extent in the soil itself.

If as vigorous a combination of nitrogen occurs in all arable soils as took

place in KÜHN'S experiments then neither alinite nor any other artificial nitrogenous manure should be needed. Experience, however, teaches us the contrary; as a rule, nitrogenous manuring is essential and Leguminosae only are exceptional. The Leguminosae

236, l. 11, *for* 0·21 *read* 0·021

l. 32, *for* save . . . addition of *read* without added

l. 35, *for* other . . . soils *read* to be quite unable to use other sources of nitrogen than those present in soil,

ll. 39–40, *for* and an experiment . . . growth took place *read* when it was found that many behaved in precisely the same way as cereals, for growth took place

237, ll. 7–9, *for* since the extract . . . fruiting stage *read* since the extract of a sugar-beet soil, in which peas and various species of clover had been cultivated for a long time in regular rotation,

l. 18, *for* ' To show *read* ' In order; *before* make *insert* may

l. 30, *for* FRANK (1890), *read* NOBBE and HILTNER (comp. LAFAR'S *Mykologie*, II. 24)

ll. 32–55, *for* Without going into details . . . took place. *read* BEIJERINCK (1888) having isolated the bacterium (*B. radicicola*) and cultivated it by itself apart from the plant, PRAZMOWSKI (1890, 1891) succeeded in observing the mode of infection of the leguminous root. He established the fact that the Bacteria enter the root-hairs and, in the form of closed tubular masses, grow through first the hair and then the neighbouring cortical cells (Fig. 42). When these infection tubes have penetrated a certain depth into the root the Bacteria escape from them and fill the cells of the root. Just as we shall see in the case of gall insects, so the Bacteria exert a stimulus on the parenchymatous cells affected, and induce in them vigorous growth and division. A local hypertrophy is set up—the nodule or bacterial gall (Fig. 43, *a*, *b*). In the central cells of this gall the originally rod-shaped Bacteria swell and assume branched forms, rich in proteid, which have been long described as ' bacteroids '. In all probability these are degeneration forms, since they have also been observed in other Bacteria and described as involution forms. Several authors have succeeded in seeing the origin of these bacteroids in nutrient solutions apart from the plant (BEIJERINCK, 1888; HILTNER, 1900; STUTZER, 1901). According to HILTNER (LAFAR, III. 51) this result is easily obtained by providing a surplus of carbohydrates or organic acids in the culture. Many authors have made attempts to demonstrate a combination of nitrogen in pure cultures of *B. radicicola*. Ammonia was generally presented to the bacterium to act as a source of nitrogen, or no combined nitrogen at all was given in the hope that the combination of free nitrogen might be in this way all the more easily observed. All attempts of this kind were quite unsuccessful.

238, ll. 8–19, *for* MAZÉ'S results . . . view to take. *read* More recently his results have been called in question by HILTNER (LAFAR, III. 50), and so we must regard the nature of the symbiosis between *B. radicicola* and Leguminosae as not yet entirely cleared up, for the whole problem is by no means so simple as was previously supposed. It is not simply a case of the leguminous plant supplying the carbohydrate and the bacterium the nitrogen, thus making possible a mutually passive existence on the part of both organisms. HILTNER'S observations, on the contrary (LAFAR, III. 45), point to a constant parasitism of the bacterium, under certain conditions, or at least at first. How the host is able to accommodate a parasite as what might be termed a commensal we do not know; nor do we know what the exact rôle of the bacteroids is.

239, ll. 26–37, *for* Finally, we may note . . . same kind. *read* If we describe the association of Leguminosae with nodule-bacteria as a case of symbiosis, then, looking backwards, we may apply the term 'symbiosis' to the relationships that exist between *Clostridium pasteurianum* and the two associated Bacteria, and we may take this opportunity of drawing attention to some other cases of the same kind.

l. 53, *for* 1896 *read* 1906

240, ll. 10–23, *for* More recently . . . this relation. *read* From *Podocarpus* to the so-called Mycorhiza is only a step. We understand by the term 'Mycorhiza' a symbiotic union of fungus and phanerogamic root, widely distributed in nature.

l. 35, *after* host *read* (details will be found in GALLAUD, 1906).

l. 52, *for* digested *read* digestive

241, ll. 5–28, *for* Since the assimilation . . . (STAHL, 1900). *read* In this way the Conifer succeeds in obtaining nitrogen, and FRANK has suggested that *B. radicicola* and the bacteroids are also similarly digested by the Leguminosae. HILTNER (comp. LAFAR, III) alone denies the digestion process both in *Podocarpus* and by the bacteroids. At least, so long as the fungus continues to combine nitrogen it cannot be digested; only when the higher plant, being supplied with combined nitrogen, is rendered sufficiently vigorous, is it able to rid itself of the fungus by digesting it. Whatever the nature of the final answer may be to this problem, it is at least probable, after the behaviour of *Podocarpus*, that other endotrophic mycorhizae are also capable of combining nitrogen.

There are several experiments which tend to confirm this conception. Thus TERNETZ (1904) has stated that a fungus isolated from heather soil has the same power of combining nitrogen as that possessed by the mycorhiza-fungus of Ericaceae. Still, its identity has not as yet been proved, and the power of nitrogen-combination is not very evident. MÜLLER'S (1903) observations, which tend to show that the spruce can thrive in sandy soils, poor in nitrogen, only when it is cultivated in company with the mountain pine, would appear to support the view that the mycorhiza of the latter can combine nitrogen; still, MÜLLER'S (1906) researches do not provide us with any proof of this. Further, BEIJERINCK'S (1907) brief note suggests that the fungus isolated from Orchidaceae is also incapable of combining free nitrogen.

Under these circumstances it must be noted specially that there can be no doubt as to the utility of the endotrophic mycorhiza in many plants, if it be associated perhaps with metabolic processes other than nitrogen-combination. Thus N. BERNARD (1904, 1905) has shown that endotrophic Fungi are quite essential to orchids. Many seeds as a rule do not begin to germinate until they have been infected with the fungus, and in other species infection of the seedling must take place at earlier or later stages, otherwise development ceases. Further, it would be incorrect to suppose that the relation between the fungus and the flowering plant is to be interpreted generally in the sense that the duty of the latter is to provide carbohydrate, and of the former to collect nitrogen. Plants like *Neottia*, which exhibit no C-assimilation worth mentioning, prevent us from holding such a view; how their nutrition is carried out we do not know.

It seems to us important to differentiate clearly between endo- and ectotrophic mycorhizae. The latter type was first discovered by KAMIENSKI (1881) in *Monotropa*. Soon afterwards FRANK proved its very general distribution among our common forest trees (Cupuliferae, Betulaceae, Coniferae). In these cases the fungus—usually a member of the larger Agaricinae and Tuberaceae—does not as a rule enter the cells of the root, but forms a densely woven envelope over the root, not even excepting the growing point. Individual fungal cells

penetrate between the outer root cells, but confine themselves to the intercellular spaces. The presence of the fungus is associated with changes in the external form and anatomical structure, which enable the presence of mycorhiza to be recognized easily, and which must have some physiological significance. One point is especially noticeable, viz. that roots possessing fungus develop no root-hairs (Fig. 45), and hence the whole absorption of nutrient salts and water can be effected only through the mediation of the fungus. This is the chief difference between the ecto- and endotrophic types of mycorhiza, for in the latter most of the fungus lies in the interior of the cells, and is only connected slightly with living regions outside. While in many plants possessing endotrophic mycorhiza the fungus is essential, this does not appear to be the case in forest trees, for they occur both in the natural condition and also grow perfectly well in cultures without any fungus. NOBBE (1899) succeeded in obtaining excellent results with pine, spruce, larch, and beech grown in pure quartz sand, free of humus, without any fungus, during a period of twenty-five years. It is possible that in these cases the fungus is nothing more nor less than a parasite, for the fact that the plant does not suffer from the presence of the fungus must not be taken as evidence against parasitism. On the other hand, there is the possibility that the fungus aids the flowering plant in absorbing nutriment, and the three following possibilities may be considered: (1) the fungus might combine nitrogen; (2) it might absorb salts of ammonia from the humus and work them up so that the flowering plant would thus be a peptone-organism. Since, however, its behaviour in a water culture negatives this possibility, we must turn to the third alternative, viz. that the fungus does not meet the nitrogenous demands of the flowering plant, but that it aids it in taking up materials of the ash (STAHL, 1900).

l. 38—P. **242**, l. 13, *for* The part played . . . here also. *read* Obviously according to this view the function of the higher plant must lie in providing carbohydrate, and of the fungus in supplying minerals already built up (i.e. assimilated). This conception, however, which STAHL also considers to hold good for endotrophic mycorhiza, presents certain difficulties.

242, ll. 20–38, *for* Several problems . . . possesses]. *read* Again, MÜLLER'S (1902, 1903) studies on the pine have shown very clearly that the mycorhiza is absent in humus soils, but present in sandy soils; the tree grows, however, much better in humus without a mycorhiza than in sand with it. Many problems still await solution, and it is astonishing how little experiment has taught us in regard to this subject. Still, systematic experiments should not be considered as hopeless, for roots without the fungus are not difficult to obtain and the consequences of infection should make themselves apparent in some way or other.

244. *Lecture XXXI is made XIX in the 2nd German Edition and comes in here.*

247. *Lecture XX is incorporated in the 2nd German Edition partly with Lecture XXI and partly with Lecture XXIII.*

251, l. 3, *for* (1882, Vorlesungen über Pflanzenphysiologie, p. 618) *read* (Lectures on Plant Physiology, p. 509)

ll. 32–5, *delete* A detailed description . . . of these lectures.

l. 37, *for Basidiobolus read* an alga

l. 47, *for* of the original *Basidiobolus* remains *read* of an alga remain

252, l. 7—P. **253**, l. 13, *for* Numberless correlations . . . KERNER, 1891, &c.) *read* In addition to adaptation to function, the plant also shows adaptation to its environment. If we study plants which live together in the same kind of surroundings, we find they have the same general characters, even though they belong to different families, and have no phylogenetic relationship. Closer

study leads us to the conclusion that the structural traits they have in common are adaptations to their habitat.

253, ll. 38–44, *for* These brief notes . . . from each other. *read* It is a well-known fact that many plants can grow both on land and in water, and that they develop very differently in these two situations; as an illustration, we may refer to the land and water forms of *Polygonum amphibium*.

254, ll. 1–31, *for* Since it has been shown . . . to the conclusion that every change *read* Since then the water and the land forms are obviously organized in relation to the media they inhabit, we have here to deal with adaptations, or more correctly, self-adjustments, on the part of the plant; these, however, we cannot consider in greater detail at present. Just as in this case the adaptation arises in consequence of the influence of one or more external factors, so in other instances, which we will not speak of at present, a new and distinct function, differing from that ordinarily exhibited by the organ in question, may make its appearance.

What is of especial interest to us in all the phenomena referred to above, is the fact that the plant body does not possess a predestined form fixed once and for all, but that it is capable of modification, and it must be the task of physiology to discover the causes of such transformations. In very many cases it is possible to refer such changes to known external factors, while, in other cases, we must look for their origin in causes which are internal, and with which we have less acquaintance. It would, however, be quite incorrect to suppose that the plant reacts purposefully to every alteration in the environment. In numberless instances the question whether the reaction which takes place is purposeful or not depends very much on individual opinion. As far as the physiologist is concerned, the question is, generally speaking, rather a subsidiary one, for he deals only with the factors concerned in formation, while the biologist is more concerned with problems as to its aim and object.

Since, then, a purposeful reaction on the part of the plant very frequently cannot be denied, attempts have been made to see in this reaction something especially characteristic of the organism, and the question has of recent years been again put forward, with renewed interest, whether the phenomena of the organic world (more especially those of metamorphosis) have their origin in the same forces and obey the same laws as those of the inorganic world, or whether we must assume in their case conditions of a quite special nature. In order to decide between these alternatives, we must anticipate to some extent the conclusions of the lectures to follow. We shall see that every change (*follow on to* P. **256**, l. 29—plant physiology.])

256, l. 30—P. **257**, l. 28, *delete* From the examples . . . external factors.

258, l. 1, *before* The most simply, &c. *insert* In the second part of this course of lectures we have to discuss the change in form in plants, to inquire into the causes of growth, formation, and development. We have hitherto regarded the formative processes as something taken for granted, and treated them either only in a descriptive or comparative manner from the historical or hereditary point of view; but that it is possible to look at the subject causally also is a conclusion arrived at in recent times by morphologists and physiologists alike. SACHS, VÖCHTING, GOEBEL, KLEBS, and BERTHOLD may be reckoned as the founders of 'developmental physiology'. A comprehensive exposition of this branch of our science is as yet non-existent, and hence the following attempt cannot in any sense lay claim to completeness. Nevertheless we think that by separating this subject from 'transformation of energy' or 'physical physio-

logy ' we have taken a step in the right direction, and trust that our treatment of the subject will demonstrate the numerous gaps in our knowledge that have up till now existed, and at the same time lead to their being filled up. Indeed, there are still many problems unsolved—even unformulated—for much of the subject has been treated of only descriptively. We will commence with an essentially descriptive treatment, and endeavour to make ourselves acquainted first of all with the phenomena of growth (Lectures XX—XXIII). Afterwards we will endeavour to determine the external (Lectures XXIV, XXV), and internal (Lecture XXVI), factors concerned in growth, and finally discuss the phenomena of development(Lectures XXVII, XXVIII), reproduction, heredity (Lect. XXIX), variation and species formation (Lect. XXX).

Before beginning our studies, however, we will attempt to justify our position in devoting this section to the ' form ' of the plant, and so to a certain extent contrasting the ' form ' of the plant with ' the materials ' of which it is made, and which we have already considered. If the introduction to SACHS's famous treatise (*Ueber Stoff und Form*, 1880) be studied, our action in so doing may appear somewhat open to criticism. SACHS says ' plant morphology often suffers the misfortune that the form of the plant is looked at without any regard being had to its material characteristics '. ' A consideration of its material characteristics ' is most certainly essential, ' for it is in these only that the causes of its form may be sought for.' ' Just as the form of a drop of water or of a crystal is the necessary result of forces which bring the material in question under the influence of its environment, so also organic form can only be the outward expression of forces which transport materials, which make themselves apparent in the plant substance.'

Valuable as are the opinions which SACHS has put forward in this treatise, with the view of aiding in a revival of the subject of ' causal morphology ', we are nevertheless unable to agree entirely with the sentiments expressed in the sentences quoted. We cannot find that SACHS, or indeed any other author, has succeeded in referring the form of an organ to its material characteristics, and, keeping before our eyes the phenomena of non-living nature, we must confess that it is improbable that anything of the kind is ever likely to be established. Many chemical compounds have characteristic crystalline forms, and often these forms serve for the diagnosis of different bodies ; still the same form may be built up out of different materials. Thus it would be in the highest degree dangerous to refer the different forms of leaves to differences in the materials composing them. But even if that were possible, we must still, as in mineralogy, treat of the form of the plant by itself. Even although it were possible to prove that a definite form results from the presence of a definite material characteristic, still we should not know why it was so, any more than we should know why calcium oxalate crystallizes in a tetragonal form when three molecules of water are present, and in the monosymmetrical form when there is only one. Nowadays, when it is as yet impossible to refer form to chemical peculiarities, a section treating of ' change of form ' appears to us quite essential.

In discussing change of form in the plant, it would lead us away from our subject were we to consider also the corresponding researches in the domain of Zoology (Developmental mechanics) ; but the attempt must soon, however, be made, since, in spite of the agreement in fundamentals, there are still too few points of contact in individual cases ; for the mode of development of the typical animal differs widely from that of the typical plant. We must not, however, fail to draw attention to the brief general exposition of the results obtained in zoology, published by DRIESCH (1906).

l. 32, *after* organisms *read* i. e. such as possess neither protoplasm nor nucleus

259, ll. 36–41, *for* It is a viscous . . . characteristic *read* It is a viscous fluid whose external form, in the cases which interest us here, is determined by the cell-wall.

260, ll. 2–4, *for* In other cases . . . wall arises *read* The origin of the cell-wall by excretion is extremely common, and only in a few cases has it been definitely shown that it arises

l. 9, *for* an extremely *read* a more

ll. 10–11, *delete* Cell-wall formation . . . protoplasm.

ll. 40–1, *for* the cell-wall . . . thickness *read* the cell increases in length, but not in breadth.

261, ll. 24–36, *for* Surface growth . . . solution of tannin. *read* The growth in the cell has often been compared with the changes in shape observed in so-called artificial cells. Such artificial cells (TRAUBE, 1867) may be readily produced by taking a little gelatine, to which some sugar has been added, on the tip of a glass rod, allowing it to dry, and submerging it in a weak solution of tannin.

l. 49, *after* offhand. *read* In the living cell, surface growth takes place only in presence of protoplasm and nucleus, and, as a rule, such membranes grow only when the protoplasm is closely applied to them ; this application is maintained firmly by osmotic pressure, while at the same time the cell-wall is stretched by the same agency.

262, l. 41, *after* decreases. *read* This does not, however, appear to support the idea of purely passive stretching.

263, l. 27—P. **264**, l. 41, *for* We may certainly . . . STRASBURGER (1889). *read* In addition NOLL'S researches may be quoted, also the observations of ZACHARIAS (1891) and of REINHARDT (1899). ZACHARIAS showed in the case of the root-hairs of *Chara*, and REINHARDT in those of higher plants, that when growth had been stopped by artificial means it was possible to cause a deposition of a distinct thickening layer at the apex of the root-hair, and that when growth began again the older parts of the membrane which were incapable of growth were burst by the younger ones, which had that power. Both authors assume that in NOLL'S experiments the infiltration of prussian blue had induced an inhibition of growth in the membrane, and that the bursting followed only after that took place, and that when growth was uninterrupted, NOLL'S material could not exhibit a formation of lamellae any more than those referred to. On the other hand, NOLL believes that both in sections and in normally growing organs, like in those studied by ZACHARIAS and REINHARDT, such structural phenomena must be demonstrable.

Assuming that apical growth takes place in general by deposit of lamellae, that these grow and that the older ones burst, it doubtless follows that the individual lamellae, at the moment when they are ruptured, would cease to exhibit any surface growth, or at least would not grow as vigorously as the young lamellae. The old lamellae would, doubtless, be stretched passively ; whether, however, growth in the young lamellae is also passive, cannot be decided from these experiments. Should it be the case that we have to deal in these and similar instances, as also in the young membranes, with passive stretching, one would naturally look to osmotic pressure as the active agency. The fact, however, that this pressure is never sufficient of itself to stretch the membrane passively is of great importance, for it has been shown that a pressure even greater than it is incapable of extending the cell-wall beyond its limits of elasticity (PFEFFER, 1892, 241). Further, we never find membranes in the living cell which are stretched beyond these limits (comp. however,

LEPESCHKIN, 1907). One may, however, assume, with NOLL, that plastic stretching is also possible without exceeding the limits of elasticity. It should be remembered that a stretched wooden bow unbends itself gradually, a phenomenon which is possible only in consequence of internal changes; in this unbent condition, however, the bow is capable of being again bent at any moment. So also the cell-wall, stretched as a result of turgor pressure, might exhibit a relaxation, i.e. even a plastic extension, without, at the same time, necessitating a loss of elasticity on the part of the membrane It is often assumed that the protoplasm influences the elastic properties of the membrane, but there are as yet no data available to show us how that comes about.

The possibility that the young lamellae grow actively, that is, by intussusception, is at least not contradicted by these observations; on the other hand, ASKENASY (1890) and STRASBURGER (1889) have put forward a whole series of important facts in support of that view.

265, ll. 5–8, *for* We are doubtless . . . outer surface. *read* Since growth phenomena have been established also in the case of pollen grains (*Oenothera*; BEER, 1906), which correspond in all respects with those seen in *Isoetes* (comp. STRASBURGER, 1907), we have obviously to deal with a phenomenon which is very common in the course of origin of reproductive cells. Vegetative cells behave entirely differently. In their case the membrane grows in surface extent only so long as it is in contact with protoplasm, and the protoplasm proceeds to form a new membrane as soon as it is separated from the wall, e. g. by plasmolysis.

l. 16, *for* reduced by appropriate means *read* transferred to an adequate resistance,

l. 17, *for* contracted *read* retracted

ll. 20–1, *for* exhibited growth . . . vascular bundles *read* complete their surface-growth only after they have been relaxed by the resistance of the full-grown vascular bundles.

266, l. 55—P. **267**, l. 12, *delete* If this be . . . unlikely.

267, ll. 34–7, *for* It does not follow . . . without a nucleus. *read* But this is not universally true, for WISSELINGH (1904) and PALLA (1906) have definitely proved the formation of membranes round non-nucleated protoplasts.

ll. 41–2, *for* obviously occupies . . . conception *read* is far removed from the growing wall (KÜSTER, 1907).

269, l. 23, *for* built out from the spot where it originates *read* formed to the spot which it is to occupy permanently.

270, l. 2, *after* cells). *read* Many Flagellata also divide longitudinally; some do so obliquely (comp. OLTMANNS, *Algen*, I. 48).

l. 37—P. **271**, l. 7, *delete* NATHANSOHN'S . . . nucleus.

273, l. 17, *after* apex. *read* There are also sufficient instances of unicellular organisms with bipolar structure.

278, l. 24, *before* lateral *read* occasional; *for* both *read* as many

l. 25, *for* and leaves *read* as leaves

279, *under first cut, for* Fig. 64 *read* Fig. 74

280, l. 18, *for* The *read* These

284, l. 25, *for* (Lecture XXIII) *read* But it must not be supposed that the law of continuity of the embryonic substance is without exception. To preserve the general applicability of the law it would be necessary to ascribe the

character of embryonic substance to all protoplasm. It is a well-known fact that continuity of the plasma exists, and that protoplasm arises only from pre-existing protoplasm ; hence we will do better to draw another conclusion from the facts mentioned above, a conclusion which we may formulate by saying that protoplasm may exist in two conditions, one with a capacity for growth, the other without, in other words 'embryonic' and 'somatic' protoplasm, and further, that not only can the embryonic condition change into the somatic, but that the somatic state can become embryonic (comp. however, NOLL, 1903).

285. *Lecture XXIII is divided in the 2nd German Edition into two lectures, of which one, Lecture XXII, has the title* EXTENSION *and includes to p.* 295.

l. 48, *for* frequently exhibit, at a certain distance *read* begin to exhibit only at a considerable distance

P. **286**, ll. 38–9, *for* but varies . . . manner *read* but takes place in a special manner,

288, ll. 10–11, *for* each . . . apart *read* at intervals of 1 mm.

289, l. 41, *after* growth *add* in length,

l. 49, *after* aerial *insert* roots

290, ll. 2–3, *for* increases . . . one hour :—*read* hourly increments of growth :—

l. 15, *after* bud *read* (comp. BERTHOLD, 1904).

l. 19, *for* elongation *read* expansion

l. 23, *for* growth in length *read* expansion

l. 42, *after* period *read* and that the growth of the shoot, as a whole, shows the same thing.

l. 43—P. **291**, l. 2, *for* Let us now compare . . . growth in it. *read* Fig. 85a shows graphically the grand period in the development of the shoot of *Fritillaria*, but it also shows that it is by no means essential that the growth should always take place in this way. For example, the flower scape of *Taraxacum* (MIYAKE, 1904), which certainly is composed of one internode only, shows two grand periods of growth, separated by a retardation period which occurs at the flowering stage ; when fruit formation begins, renewed growth in the scape takes place. A strikingly analogous instance to this is exhibited by the unicellular sporangiophore of *Phycomyces* (ERRERA, 1884), which, when the sporangium begins to form, stops growing, but enters on another grand period afterwards, which is characterized by much more prominent elongation than the first.

When we compare such examples with a leafy tree, such as the horse-chestnut, we find in the axes of its buds as many growing zones as there are internodes, separated by nodes which grow by little or not at all. Each individual internode goes through its own grand period, but as to how growth is distributed in it, but little is known.

Fig. 85a. Graphic representation of growth in the scape of *Taraxacum* (after MIYAKE, 1904) ; and of *Fritillaria* (after SACHS, 1872). The abscissa indicates days, the ordinates the daily increment in growth in mm.

293, l. 39, *for* There . . . where, *read* In the more vigorous at least of the cases mentioned

l. 42, *for* cannot be expressed *read* is not given.

l. 44, *for* for *read* therefore

l. 45, *for* work out *read* express

294, l. 7, *for* If . . . may *read* Only if we know further the *duration of growth* can we

l. 39, *for* all cells, which *read* all living cells, especially parenchyma, which

l. 42, *after* may *insert* continue to
l. 43, *after* size *read* (URSPRUNG, 1906; SCHELLENBERG, 1907).

295, *after* l. 40 *read as title of new Lecture XXIII*

INTERNAL DIFFERENTIATION. ADAPTATION TO FUNCTION. FACTORS CONCERNED IN GROWTH

ll. 46–7, *for* which often . . . end *read* which always begins before the first has ended, but terminates after the second is complete.

P. **296**, l. 8, *for* p. 7 *read* p. 6

ll. 19–21, *for* may expand . . . other elements *read* can only be differentiated after reaching their full length, while, on the other hand, vessels generally become differentiated before all other elements; and as their walls are no longer, or only to a limited extent, capable of growth, they exhibit special arrangements which favour their passive stretching, and even their final rupture.

l. 28, *after* (1896) *read* As the embryonic cells of the growing point gradually alter into permanent tissue-cells, one notices changes taking place both in the cell-wall and in the cell contents. The wall takes on the final form by surface growth, and assumes its characteristic sculpturing in the course of secondary thickening, and also its definite chemical peculiarities.

l. 42, *after* passively *read* (ZIMMERMANN, 1893).

l. 52—P. **297**, l. 42, *for* This kind of . . . *Mucor. read* This kind of growth, which may, after KRABBE (1886), be termed 'sliding growth', is seen most clearly in elongated elements of the wood of trees, which, not infrequently, fork at their ends. So long as this growth is limited to the ends of the cells, it is quite comprehensible; and by such quite local separations of the cell-walls the compact tissue is loosened. Sliding growth is now known to be much more widely distributed than one was at first led to suppose (NATHANSOHN, 1898; JOST, 1901; STRASBURGER, 1901), and in certain situations cells must slide over neighbouring cell-walls for long stretches, and whole cells must force their way in between other cells whose walls were previously in contact. Since, however, there is always a firm connexion between the individual elements of a tissue, it is not readily seen how this sliding growth comes about. This difficulty of explaining the facts cannot, however, prevent us from acknowledging the existence of sliding growth. Indeed, we find that authors who previously argued against it now accept it (HABERLANDT, *Phys. Anat.* p. 70, where other good examples are given).

According to NATHANSOHN's statements (1898, p. 682), sliding growth may take place not only between individual cells, but also between entire tissues. Thus a root which has been enclosed in plaster of Paris shows, after the plaster has been removed, a vigorous growth of the central and peripheral parenchyma, while the reticulate vessels remain unaltered, so that the parenchyma must slide over the vascular strand. Phenomena such as these are, however, obviously not very common; but although neighbouring tissues exhibit, by no means infrequently, great differences in growth activity, this does not result in sliding growth, but only in a tension, known as 'tissue tension', which is very common in actively-growing young tissues.

A longitudinal tension may be easily demonstrated in solid growing internodes by separating, by means of a cork-borer, the pith from the peripheral tissues in *Sambucus*, *Dahlia*, or *Helianthus*. When the borer has been withdrawn, it may be seen that the pith is longer than the woody cylinder, and careful measurement shows that the latter has become shorter as well as the pith longer. If a median lamella, several millimetres thick, be cut out of such

an internode, it may be conveniently cut into longitudinal strips, each of which consists of one kind of tissue only. Epidermis, cortex, wood, and pith are easily separated from each other, and, by measurement, it may be determined what percentage of elongation or shortening each of these tissues undergoes. Assuming the original length to be 100, the following changes in length are shown, e. g. by *Nicotiana tabacum* (SACHS's Textbook, p. 297):—

No. of Internode.	*Percentage alteration in length.*			
I (youngest)	epidermis	cortex	wood	pith
III–IV	−2·9		−1·4	+3·5
V–VI	−2·9	−1·3	−0·8	+2·7
VII–IX	−2·7	−2·1	−0·0	+3·4
X–XII	−1·4	−0·5	−0·0	+3·4
XIII–XV	−1·05	−0·0	?	+4·0

It will be seen that all the tissues undergo contraction, save only the pith, which elongates. In the uninjured internode, therefore, the pith must have been compressed (positive tension), the remaining tissues are stretched (negative tension). The epidermis is stretched most, the cortex less, and the wood least of all, hence the epidermis is in a state of positive tension as contrasted with the cortex, and the cortex as compared with the wood, or, in other words, each layer is in a state of negative tension in comparison with that lying next outside. The above table is only one example of such tensions; in addition it should be stated that the maximal shortening in the cortex observed by SACHS was 5·9 per cent., and the maximal elongation of the pith 8·7 per cent. The following experiments show that these tissue tensions are the result of different degrees of turgidity in antagonistic tissues.

If a stem be split longitudinally by two cuts at right angles to each other, the four strips must necessarily curl up, so that the pith in consequence of its efforts to expand will occupy the convex side. If the same experiment be made with a hollow stem, such as the scape of *Taraxacum*, the same curvatures make their appearance, because here also the peripheral tissues are in a state of negative tension compared to those further in. If such a split stem be placed in water, the curvature increases, because the cells are now saturated with water, and are then able to follow out their efforts to stretch. Hollow stems treated in this way often exhibit curvatures of such an extent that the strips roll themselves up into spirals. If, on the other hand, the stems be placed immediately after splitting in a plasmolysing solution, the original curvature is undone, and the strips of tissue take on eventually a feeble curvature in the opposite direction. If, on the contrary, the split stem has, first of all, lain in water, and if it be then plasmolysed, it is not possible to remove the curvature entirely, because it has now become fixed by growth.

Let us now investigate the distribution of the tissue tension. Tissue tensions make their appearance in the manner above described just as prominently in vigorously-growing internodes as in petioles. As we pass from the parts where elongation is taking place towards the growing point, the tensions gradually disappear; they are first observable where tissues are differentiated. Further, they are almost completely absent from full-grown parts. The exceptions are the pulvini of many leaves, such as those of the Leguminosae and Oxalidaceae. These pulvini are cushion-like swellings, which we are very familiar with as occurring at the bases of the leaves of *Phaseolus*. A transverse section through such a cushion shows a central vascular bundle surrounded by parenchyma. If one cuts a longitudinal slice out of such a cushion, the effort on the part of the cortex to expand in opposition to the tension of the vascular bundle shows itself at once by the swelling of the originally straight upper and under surfaces of the section. If the cortex be separated from the vascular bundle, the former becomes concave inwards, and if it itself be halved longitu-

dinally, the two halves become convex to each other; thus, the median region of the cortex shows the greatest tendency to extension. Further, in the root also there exists a very obvious tissue tension at a certain distance from the growing point. If a longitudinal slice be taken from the full-grown region, one notes an effort to expand both in the central and in the peripheral regions; the cambial region is in a state of negative tension. If the lamella be cut into four pieces the curvatures correspond to those just recorded. The effect of the effort to contract on the part of the cambial layer has been already described.

In addition to longitudinal tensions one has to note also transverse tensions which exhibit themselves especially in such parts of the plants as develop secondary thickening. If one removes a ring of cortex down to the cambium and then endeavours once more to replace it in its old situation, it is found to be too short; it has, in fact, contracted.

The amount of tissue tension is not constant; on the contrary, it shows a striking periodicity which has been especially studied by KRAUS (1881, 1895). He found the maximum to occur early in the morning, and the minimum after midday. Since this periodicity is probably to be referred to the influence of external factors, we will not discuss it further at the present moment. In conclusion we may remark that tissue tensions contribute materially to the rigidity of plant organs; and this, too, for the same reasons that osmotic tension of the cell-wall induces an increase in rigidity in the individual cell. It may be assumed that herein lies the significance of tissue tension in the plant as a whole. Tissue tension has been studied in the past with great care, for it was expected that conclusions as to various physiological phenomena might be obtained from such studies. These expectations have not, however, been completely realized, and hence we shall not devote any more space to their consideration, but rather return to our discussion of the differentiation of cells at the growing point.

In addition to the form of the cells, the nature of their membranes is of importance. It is impossible to go into the question of the differences, both chemical and physiological, which show themselves in cell-walls during their formation, but we must study to a certain extent the sculpture of the cell-wall. It is very rarely the case that the cell-wall is thickened uniformly. We will not enumerate here the forms which this unequal thickening takes on, but pay attention more especially to the pits, that is to say, the regions which remain thinner than the regions immediately surrounding them. The most remarkable point about these pits is, undoubtedly, the fact that, generally speaking, in two neighbouring cells with one cell-wall, the pits on either side correspondingly placed, the closing membrane is common to both. If this common wall always arose by cell division, correspondence of the pits would not appear to be so very remarkable; for the pits would be formed at the same time that the wall was formed, and would have a certain relationship to the spindle threads which stretch from one pole of the dividing nucleus to the other. Corresponding pits, however, occur in cell-walls which, for the first time, come into contact with each other later in their history, as, for example, between latex tubes and their surroundings (and these latex tubes push their way into these environments by sliding growth); further, in the case of tyloses (STRASBURGER, 1901), how is it possible for a tylose to know where its neighbouring cell has formed a pit? In all probability the formation of pits comes about in another way, namely, by piercing of the young cell-wall by a whole series of exceedingly fine pores through which the protoplasts of neighbouring cells come into communication with each other. These protoplasmic bridges, which have been shown to occur with great frequency in higher and in lower plants, and also in the tissues of animals (compare especially KUHLA, 1900; STRASBURGER, 1891; A. MEYER, 1902), are

obviously of very great importance in the life of the plant. They render possible a very general interchange of materials between cells, and they must also be often the means of transmission of stimuli (Lecture XL). By their means the plant body, which is broken up by its cell-walls into thousands of individual compartments, once more becomes a unity. At least one is able to understand very much better the unity of response so often exhibited by the entire plant—a response conditioned by the various responses of the individual cells—if a single protoplasmic body permeates the whole plant (KUHLA, 1900).

Although many protoplasmic bodies penetrate through the unpitted wall, still most of them will be found in groups in the pits, and we are led to conclude that they are the cause of the correspondence of the pits. In addition to the fine communicating threads which penetrate the closing pit membrane, we find also coarser protoplasmic bridges which show themselves, e. g. in sieve tubes, after the dissolution of the entire closing membrane in certain cells. The difference between the two types is naturally a gradual one. One has, however, been accustomed to regard the sieve tubes as fusions of individual cells placed end to end ; one also assumes that the individuality of the cells is lost on account of these coarser intercommunications. Cell fusions are found also in the formation of tracheae, where the communication between the individual segments of the fused elements is much wider.

Our discussion of protoplasmic bridges and cell fusions has gradually led us from the consideration of the cell-wall to that of the cell contents, to whose varied configuration is due the whole series of cell-forms functioning in different ways. We may note only that in the organs which subserve water carriage, namely, the vessels, the living contents entirely disappear, and are replaced by water and air, whilst in typical cells sometimes it is protoplasm and its apparatus, especially the chloroplasts, that is especially prominent, sometimes it is the vacuole. There is no need for us at present to discuss these relationships in detail.

The cells now unite together into tissues, in such a way that, as a rule, long stretches are composed of the same type of cell. In contrast to these there are the so-called 'idioblasts', which make their appearance as solitary units among otherwise homogeneous tissues. Examples of these are often met with in secretory receptacles, as isolated sclerotic elements, or finally as internal hairs. It should be the task of developmental physiology to elucidate the factors which induce the appearance of structures like these, and to determine why a definite cell, which to all appearance could have developed otherwise, should become an idioblast. The combination of cells into organs of higher rank, which is obviously subject to certain laws, should also be capable of causal explanation ; meanwhile, we can only say that the tissues, like the externally visible arrangement of the lateral members, co-operate in producing the symmetry of the whole body.

We have learned how the external subdivision of parts and the internal architecture of the complex plant come into being, so far as the main principles are concerned. If we now glance at the function of these parts, we discover, to begin with, that there is an intimate relation between function and structure.

298, l. 44, *for* 85 *read* 74

299, l. 21, *after* still *read* (40°, CATTERINA, 1904)

ll. 29–33, *for* of 75° . . . cardinal *read* of 70° (CATTERINA, 1904 ; MIEHE, 1907) ; Algae which grow in natural hot springs do not appear to be able to stand temperatures as high as that (LÖWENSTEIN, 1903). In general terms it may be said that, in the case of plants inhabiting cold regions, the two extreme cardinal

ll. 44, 49, *for* 91 *read* 80

300, l. 42, *after* thermotonus *read* (comp. A. MEYER, 1906);

l. 47, *for* killed rapidly . . . others may *read* killed rapidly, when kept for long in a state of cold rigour, others may

301, ll. 12–22, *for* [MEZ (1905) . . . of the question. *read* According to MEZ (1905), however, the freezing of frost-resisting plants is not due to the withdrawal of water, for death often takes place in these forms at a temperature which lies far below that at which all water must be crystallized out. In opposition to MÜLLER-THURGAU, who held that the formation of ice was continuously proportional to the decrease in temperature, MEZ attempted to show that at — 6° C. all water is crystallized; further research must determine whether that is the case or not. Further, according to MEZ, the formation of ice is a distinct advantage to the plant, inasmuch as ice conducts internal heat more slowly than the fluid cell-sap. The fatty oil which appears, e. g., in many trees in winter, must tend to prevent excessive cooling of cell-sap, inducing an opportune formation of ice, and therefore lowering the freezing-point in the plant.

Last line—P. **302**, l. 42, *for* Indirectly it is . . . rest of the protoplasm. *read* In the case of those organs on which light falls, especially the leaves, light would appear, at least at first sight, quite essential. As WIESNER has shown in a number of researches (1893–1905; summarized in 1907) the development of the shoot under natural conditions takes place only when the light is of a certain definite intensity, which varies very greatly according to the nature of the plant. WIESNER'S great service lies in his having accurately measured this intensity. For this purpose he employed the Bunsen-Roscoe method, which, it is true, is adapted to the study of the more highly refrangible rays, those, that is to say, which act on silver salts. WIESNER has determined both the absolute and the relative light intensity under which a plant will thrive in different surroundings. The light intensity, as measured by the Bunsen-Roscoe method, he terms the absolute 'photic ration'; the relative photic ration (L), on the other hand, is what range of the total light the plant can flourish in.

If the plant can live, for example, on the one hand in full illumination, and also in $\frac{1}{10}$ of that, WIESNER says that its relative photic ration lies between 1 and $\frac{1}{10}$.

Then read P. **307**, ll. 42–51.

Shade plants such as the beech can put up with $\frac{1}{10}$ of the light intensity that light-loving plants prefer. The beech can thus grow normally in diffuse light without any exposure to direct sun's rays (WIESNER, 1904).

Then read P. **307**, l. 52—P. **308**, l. 9 (For one . . . impossible). *and follow on* Branches of the plants above mentioned, however, grow under experimental conditions under light of much less intensity than what they are subjected to in nature. WIESNER (1904) has shown that in the case of the maple, no buds expand under natural conditions if the relative photic ration be less than $\frac{1}{55}$. Experimentally, however, buds do open with a relative photic ration of $\frac{1}{100}$, and indeed attain their normal form; they bud out as well in complete darkness, although they certainly assume at the same time an abnormal appearance, which has already exhibited itself when the relative photic ration $= \frac{1}{1000}$. This remarkable difference between the developmental behaviour of buds under experimental and under natural conditions is due, on the one hand, to the varying relationships existing between individual buds, and on the other to a certain stimulatory effect of light. Buds which are well illuminated sprout rapidly and prevent those less brilliantly illuminated from doing so. If, however, these relations be interfered with, as by darkening all the buds, it may then be seen that light is in no respect a condition of growth of the shoot.

Many other observations which appeared to indicate the dependence of

the leaf on sunlight may, on more careful reflection, be explained otherwise. It is well known (SACHS, 1863) that the leaves of many Leguminosae in the dark lose in a short time their special powers of movement in response to stimulus (Lect. XXXIX); they suffer from darkness-rigour and die off. Other leaves also which grow in light die rapidly when placed in the dark. Doubtless we have to deal in this case with a secondary destructive effect due to withdrawal of light, for if leaves are allowed to develop in the dark from their young state, and if suitable nutriment be provided, they reach their normal size and form and remain alive for a long time (JOST, 1895). It is, of course, obvious that an autotrophic plant cannot exist altogether without light, but its death is due to an absence of carbohydrate, for the formation of which light is essential.

Setting aside all the phenomena already spoken of, there remain but few facts which go to prove that light is an essential factor in development. Thus it has been proved that many seeds do not germinate, or do so badly, if they are kept perpetually in the dark; *Viscum album* (WIESNER, 1894), *Veronica peregrina* (HEINRICHER, 1899), and *Nicotiana* (RACIBORSKI, 1900) may be cited as conspicuous examples. That we have to deal in these cases not with an assimilatory effect of light, i. e. a renewal of the necessary food-stuff, but with a specific stimulatory effect, is proved by this fact amongst others, that in tobacco, for example, illumination for one hour of seeds soaked in water is sufficient to induce germination even in darkness.

In addition to the seeds above mentioned, there are also the spores of mosses and ferns which, according to BORODIN (1868), and LEITGEB (1876), germinate only in light. It has been shown, however, that a high temperature or material influences may be substituted for light in this case (GOEBEL, 1896; HEALD, 1898; TREBOUX, 1903). According to LAAGE (1907) the facts of the case may be expressed by saying that very many spores are able to germinate in darkness, but that they then make greater demands on the substratum; the accession of light enables them to overcome any unsuitable combinations in the substratum.

From these statements, it follows that a certain minimum intensity of light is a general condition of growth, just as is a minimum temperature, but that, all the same, any definite minimal intensity of light is not essential for the 'normal' elaboration of many plant organs. There is, however, a general maximum of light intensity which must not be exceeded, otherwise growth is retarded and the plant ultimately dies. The position of this maximum is, again, very different according to the species concerned. It lies low in shade-loving plants, such as inhabit woods, and such as are found specially abundantly in the sea. In direct sunlight such plants die. Many Bacteria also exhibit a similar sensitivity to light, for after a short exposure to its influence—even when nearly diffuse—they are killed. The light-maximum lies far lower when subterranean organs are in question; it is known, for instance, that buds on potato tubers readily germinate in the dark, though daylight—even if diffuse—retards the growth. A similar favourable influence of darkening has been established for many, though not all, roots, but these we shall discuss later on. Plants which are able to endure the highest light intensities, and which thrive under natural conditions in many situations, reach their maximum light intensity only when the sunlight is concentrated artificially by the aid of lenses. Not all organs of a plant are equally sensitive; the chloroplasts are often more rapidly injured than the protoplasm (PRINGSHEIM, 1879), and in this way may be explained a whole series of adaptations in the plant, aimed at the protection of the chlorophyll from excessive illumination (WIESNER, 1876, 1894).

Read P. **302**, ll. 43–55.

303, ll. 1–4, *for* Just as . . . optimum *read* Light intensities lying between

zero and the maximum affect the rate of growth in a variety of ways, as they do also the final form of the plant.

l. 28, *for* and KNY (1902) *read* KNY (1901), ILTIS (1903), BÜSGEN (1903).

305, l. 9, *after* way *read* they do not elongate their internodes, however, but form a greater number of them than when exposed to light; many trees also in absence of light show a precocious unfolding of the buds of the following year;

306, l. 5, *for* 102 *read* 90

l. 19–29, *for* The varied behaviour . . . means. *read* The varied behaviour of the individual organs of a plant, as well as of different species, shows indeed that in etiolation we are dealing with a stimulatory effect of darkening which leads to the most diverse results according to conditions. In the first place, there is always an alteration in the normal correlations among the organs; but it cannot be said with certainty whether the primary effect of darkening in Dicotyledons consists in an inhibition of the unfolding of the leaves, the result of which is a more vigorous elongation of the internodes, or whether, conversely, stem growth is accelerated in the first instance, the leaves in consequence remaining small. BEHRENS (1905) has shown in the case of hemp that darkening of the internodes only does not induce any super-elongation in them. In other cases, however, it has been shown that leaves in darkness may reach their normal size, if they be well nourished by removal of all buds, thus saving them from competition with these axes (JOST, 1895), or if vigorous elongation of these be prevented by suitable ligatures (PALLADIN, 1890), or if the leaves continue to develop after isolation (RIEHM, 1905).

l. 52, *for* and generally speaking *read* and plants which are accustomed to live in light of high intensity, such as *Sempervivum*, become etiolated in light which is still quite bright (WIESNER, 1893); generally speaking, we may say that

307, l. 18—P. **308**, l. 18, *for* Experimentally it may be shown . . . alteration in colour. *read* We can cite only a few out of the numerous examples which are known as to the formative influence of light of varied intensity. (*Then read* l. 51—P. **310**, l. 26.)

308, l. 18, *before* Etiolated plants *read* We shall take another opportunity of studying the effect of the intensity of light on flower formation; meanwhile, we may note that, in addition to the form, the colour of plants is greatly influenced by light.

ll. 43–50, *for* Similarly . . . for solution. *read* Further, the formation of the red pigment (anthocyan) is often, but not invariably, dependent on the presence of light (OVERTON, 1899: KÜHLBORN, 1904). Since the development of this pigment is affected in manifold ways by different substances (KATIC, 1905), it is conceivable that the light induces relatively simple chemical effects in this case as in that of chlorophyll.

l. 53, *for* produced . . . exposed to *read* correlated with

l. 54, *for* in older stages *read* is the adult form.

310, ll. 27–8, *for* We shall have . . . we have still *read* Having discussed the question of the intensity of light, we have now

311, l. 1, *after* dorsiventrality *read* in mosses (NĚMEC, 1906).

l. 8, *after* regions. *read* Closely related to dorsiventrality is the phenomenon of heterotrophy (WIESNER, 1892), where secondary thickening and leaf formation are different in character on the upper and under sides of a dorsiventral shoot. One especially remarkable case of heterotrophy is that of anisophylly, where the leaves are of different size; in extreme cases those arising on the upper side are

so small that careful searching is necessary to determine their presence. Such extreme cases appear certainly to be hereditarily fixed (habitual anisophylly), while less striking cases are conditioned by external factors, among which the direction of light is frequently one which plays a prominent part (NORDHAUSEN, 1901; FIGDOR, 1904).

l. 14, *after* darkness *read* (SACHS, 1864; WIESNER, 1893).

ll. 17–21, *for* The formation of . . . in red light.] *read* The influence of the quality of the light on the pigments of plants is of especial interest. The formation of chlorophyll, as REINKE (1893) has shown, can take place in light of all wave lengths between FRAUNHOFER'S lines A and H, but those between B and D are the most effective. Not all pigments, however, behave in this way; GAIDUKOW has recently made some very interesting statements as to the pigments which accompany chlorophyll in certain Algae. Several Algae have the capacity of showing chromatic adaptation by developing in their chloroplasts pigments which are complementary to the colour of the light which falls on them. Thus he has shown (1906) that a blue-green alga (*Phormidium tenue*) changed its colour to yellow-brown in the course of a few hours after being exposed to the more refrangible rays of electric light passed through a spectroscope, but that it remained blue-green when exposed to red rays. In similar experiments the red alga (*Porphyra*) took on a green colour where exposed to red and yellow rays. In consequence of the great importance of this discovery as regards the problem as to the relation between the colour of light and assimilation, it is highly desirable that GAIDUKOW should discuss certain pertinent criticisms which may be made on his observations; more especially he must tell us how these chromatically adapted cells behave later on—whether they do not die off as a result of this change in colour .

Rays beyond the visible part of the spectrum also have an effect on plant form.

313, l. 1, *for* the accessible . . . shown by *read* the effects of gravity accessible to

l. 20, *before* increasing *read* moderately

l. 22, *for* (MOTTIER, 1899) . . . expected *read* and an interruption of growth also takes place (ANDREWS, 1902).

l. 32, *after* (anisophylly). *read* Gravity is more concerned in anisophylly than light.

l. 47, *for* develop progressively . . . normal *read* spread further towards the opposite pole than when in the normal

314, ll. 13–15, *for* Growth in thickness . . . the under *read* Further, tissue formation takes place unequally as a consequence of the unilateral influence of gravity. In branches whose full-grown regions are placed obliquely, sclerenchyma and vessels on the upper side develop narrow lumina and thick walls, those on the under side wide lumina and thin walls (BÜCHER, 1906). Secondary thickening in such sloped branches is also eccentric.

ll. 22–4, *for* gravity. Further . . . HARTIG *read* gravity (comp., however, URSPRUNG, 1905, 1906). Further, the under side is distinguished not only by more vigorous growth in thickness, but also by a definite histological structure, and by special mechanical characters in the wood formed (SONNTAG, 1904). This wood, spoken of from its colour as 'red wood', is highly resistant to pressure, but its power of resisting tension is only half as great as that of the so-called 'white wood' formed on the upper side of the branch. Since the upper side is, for the most part, subjected to tension, and the under side to pressure, the object in forming these tissues is apparent. In all probability (EWART, 1906; HARTIG, 1901) this formation of different kinds of secondary

tissue is, in part at least, to be attributed to the action of gravity, although tension and pressure may also take part to some extent. This leads us to consider more in detail the influence of mechanical factors on growth.

l. 43, *before* Tension of necessity, &c. *read* Owing to mechanical stoppage of growth the meristem cells are able to remain for long unaltered, and to start growing again after the cause of stoppage has been removed. Cells which are in the act of elongating gradually turn into permanent tissue, and hence often remain smaller and less differentiated than under normal conditions (NEWCOMBE, 1894).

l. 49—P. **315**, l. 13, *for* The new cell-walls . . . surface. *read* In the second place we have to inquire whether tension and pressure have any effect on the formation of the tissues. Since it is possible to observe in ripening fruits an increasing differentiation of mechanically active elements (comp. KELLER, 1904), it might be supposed that this was due to the influence of tension or pressure; but many experiments (VÖCHTING, 1902; WIEDERSHEIM, 1902; BALL, 1903; KELLER, 1904) have shown that a uniform longitudinal tension or pressure has no such effect (comp. WILDT, 1906). It is all the more surprising that in violent curvatures and in geotropic curvings which are prevented from taking place (BALL, 1903; BÜCHER, 1906) peculiar anatomical changes do appear. In violent bending of shoots which have the power of growth, the walls of the collenchyma, sclerotic, and xylem elements on the convex side increase in thickness, and their lumina decrease; on the other hand, in stems whose geotropic curvature has been mechanically prevented, we meet with the same sort of formation of tissues on the upper side, i. e. on the side which would have become concave had it not been prevented from bending. Generally speaking, in both experiments the places where cell-wall formation is most vigorous are under tension, while on the opposite sides, under pressure, the tissue elements are thin-walled and have wide lumina. Although the plant does not react by special tissue formation to a mechanical influence in the longitudinal direction, when that influence is uniform, it does so if differences in tension are induced. Further, lateral organs frequently exhibit a contrast in structure on the concave and convex sides. In curved roots especially (NOLL, 1900) one sees the lateral rootlets appearing exclusively on the convex sides. NOLL believes that the difference in tension between the two sides is not the cause of the unilateral formation of secondary roots, and he considers that the plant must react to the curvature as such in the way mentioned. If, however, the diarch root of a lupin be divided longitudinally in such a way that each half contains one vascular strand, and hence one portion of the rhizogenic layer, one finds that the lateral roots develop in quite the same way whether the parent root be concave, convex, or straight. From this fact the conclusion must be, in our opinion, drawn that it is the difference in tension between the rhizogenic layers that leads to unilateral formation of lateral roots.

From what has been said already we know that cell division is also affected by mechanical influences; new cell-walls, unless prevented by other agencies, arrange themselves parallel with the line of pressure and at right angles to that of tension (KNY, 1901). Further, one very remarkable instance of stimulatory activity is met with when closely associated parts of the plant are affected by pressure acting with different intensity. A case of this kind is 'contact pressure' due to hard bodies, more especially such as have rough surfaces. Sensitivity to contact is a phenomenon which we shall meet with in certain cases of movement, but not a few examples of it are forthcoming in the formation of organs. Thus, for example, root-hairs have their growth inhibited by contact with soil particles, and they adapt themselves in the most intimate manner to the inequalities of the particles with which they are in contact.

315, l. 41, *after* plant. *read* More accurate investigations (GAUCHERY, 1899), especially from the point of view of anatomy, have certainly shown that the limited size of the branches is not due simply to dwarfing of all parts.

l. 54, *after* 1903 *read* SCHÖNE, 1906.

316, ll. 11–12, *delete* so that . . . concerned.

ll. 14–17, *delete* so that . . . conditions.

ll. 21–31, *for* After what . . . to them *read* The position of these cardinal points shows many specific differences. The maximum is very low in certain anaerobes: e. g. 0·001 of an atmosphere for *Bactridium butyricum*; 0·003 atm. for *Clostridium butyricum*; 0·01 atm. for *Bacillus carbonis*; 0·2 atm. for sulphur-bacteria; 0·7 atm. for thio-bacteria. In many facultative anaerobes and in aerobes it may rise as high as 9 atm. (PORODKO, 1904). Further, every organism has its specific minimum, which, on the whole, lies higher for Mould Fungi than for Bacteria; in the case of *Phycomices*, for instance, it is 0·6 per cent. of oxygen by volume.

l. 37, *after* 1901–2). *read* The distance between the maximum and minimum cardinal points is extraordinarily varied, and that distance by no means expresses a mean minimum and a mean maximum. For instance, according to PORODKO, facultative anaerobes are characterized by having their cardinal points very far apart, whilst obligate anaerobes have them very close together. In addition to specific differences, individual differences also show themselves in the position of the maximum and minimum, and WUND (1906) has shown that the different growth phenomena of the organism, such as spore formation, germination, and growth itself, are dependent in different ways on oxygen.

l. 52, *after* calcium. *read* As far as carbon-dioxide is concerned, it has been proved (CHAPIN, 1902) that it retards growth in roots when present in a concentration of 5 per cent., but inhibits it only when 25 to 30 per cent. is reached. The corresponding numbers for stems are: 15 per cent. and 20–25 per cent. A small percentage increase of carbon-dioxide in the air decidedly assists the development of green plants, and it is difficult to understand how BROWN and ESCOMBE (1902) arrived at an opposite conclusion. In nature certainly such an accumulation of CO_2 is not easily reached, since this gas is decomposed by green plants and so rendered harmless.

317, ll. 38–41, *for* That chemical . . . stimuli *read* In the germination of the seeds of aquatics also chemical stimuli play an important part (A. FISCHER, 1907).

That chemical stimuli also act in a formative manner may be concluded from the behaviour of *Basidiobolus*, a description of which has been given at p. 248: further examples of the same phenomenon will present themselves when we come to discuss gall-formation.

Among the other morphogenic effects of chemical stimuli we may note only the facts that in a concentrated sugar solution *Stichococcus* produced cells far more elongated than under natural conditions (ARTARI, 1904), and that *Spirogyra* may be made to transform its normally cylindrical cells into barrel-shapeds wellings (GERASSIMOFF, 1905).

l. 51, *after* state *read* (comp. RABE, 1905).

318, ll. 16–17, *for* by entry . . . follows *read* in many cases a reaction may follow either by penetration of the external osmotic substance into the cell, or by the new formation of osmotic substances therein,

319, ll. 46–51, *delete* According to . . . as it seems.]

l. 56, *after* conditions. *read* Again, mere extension growth is in nature affected by so many factors that the significance of a single one is often very difficult to

determine. BLACKMAN (1905; comp. also SMITH, 1906) has pointed out that one agent often acts as a limiting factor and so narrows the effect of others, and such limiting factors play a part in experimental investigations. Thus the curve of dependence of growth on temperature may assume a quite misleading form, inasmuch as from a certain point onwards the supply of the growing regions with water and organic material is no longer sufficient, although it is quite adequate at lower and also at higher temperatures. Graphic curves with truncated apices running level for a long range must always be attributed to the action of a limiting factor.

322, l. 20, *for* (*III*) *read* (Fig. 96, *III*)

324, l. 30, *for* 526 *read* 539

326, *for title of lecture read*

INTERNAL CAUSES OF GROWTH AND FORMATION

ll. 42–9, *delete* They stand . . . internal factor.

327, ll. 1–3, *for* each other . . . functions *read* each other reciprocally, because the specialization of one organ for the performance of a definite function necessitates specialization of other organs for the carrying out of other functions, although these organs may be quite capable in themselves of performing the function of the first.

ll. 16–37, *for* In only a few cases . . . [MASSART, 1898] *read* In order to study correlations it is best, in the first place, to isolate parts of the plant and to determine what alterations are induced in them. One may observe in this way isolated single cells or higher units such as stems, leaves, roots, or parts of these.

Plasmolysis may serve as the best means of separating a larger cell-complex into its individual cells, and the results obtained are extraordinarily varied. While in many plants the plasmolysed cells always rapidly die off, those of others, at least if the conditions be favourable, remain alive for a long time and exhibit changes of many kinds. Very commonly a new wall is excreted on the outer surface of the contracted protoplasm, much more rarely growth occurs before or after cell-wall formation. Cell-wall formation takes place most frequently in the lower plants, but it is not unknown in Dicotyledons (MANN, 1906), and we may regard it as replacing the membrane from which the protoplasm has become separated—as a case of regeneration. Growth after plasmolysis has taken place appears to be limited entirely to Algae (KLEBS, 1888; MANN, 1906). If plants are used for experiment, all of whose cells are in the embryonic state, as e. g. *Zygnema*, the newly formed wall takes on growth, just as in the old cell-wall—apart from certain irregularities, it elongates over its entire length. The case is otherwise with cell filaments which, like *Cladophora* (MIEHE, 1905), grow by means of an apical cell and hence exhibit a certain contrast between embryonic and somatic cells, between base and apex. After the formation of a new cell-wall round each isolated cell, there then takes place an apical growth at the base of each cell leading to the development of colourless undulating rhizoids; much later on the apical end also swells, becomes dark green, and develops into a normal straight-growing branch. Each cell of the filament has now assumed the polarity of the entire plant and becomes an independent individual.

These observations on isolated cells introduce us to the phenomenon of regeneration, essentially similar instances of which are to be met with in larger portions of the plant, and we learn to recognize that they possess certain capacities for cell-wall formation and growth which they do not exhibit when in

conjunction with others ; we regard these capacities in the normal condition as being correlatively inhibited.

Before proceeding to discuss the regeneration phenomena in larger organs, it must be briefly noted that there are other ways besides plasmolysis of separating a tissue into its individual units. In many Marine Algae the thallus breaks up into smaller branches, and even into single cells, when the culture conditions are unfavourable, and TOBLER (1906) has observed regene ration phenomena in single cells of *Griffithsia schousboei* similar to those described in *Cladophora*. In higher plants HABERLANDT (1902) has isolated assimilatory cells by teasing, and has cultivated these cells in various nutrient solutions. He found, however, that the resultant growth was only limited. WINKLER (1902 b) has isolated cells of higher plants in other ways, and was able to observe growth and division also, after adding small doses of certain poisons to the culture. No regeneration phenomena of any kind, however, are exhibited by cells so differentiated as these. Isolation of larger parts of the entire plant is effected by sectionizing, involving the infliction of a wound. The first result is always an effort on the part of the plant to heal the wound.

l. 46, *after* affected *read* (comp. MASSART, 1898).

328, l. 14—P. **329**, l. 11, *for* This is, however, . . . of this tree. *read* Other substitutional growths, however, also arise from callus, which are always of such a character as to replace the lost members. According to the way in which this takes place we may distinguish several types of regeneration :—

1. The lost organ is replaced by a new one formed from the cortical region of the lesion, and at the same spot.

2. The new organ arises in the neighbourhood of the wound, or in the callus arising from it.

3. The new organ is derived from primordia previously developed in the neighbourhood of the wound. Unfortunately the terms regeneration, reproduction, restitution, separation, have been applied by different authors to these various types of regeneration (linked together as they are by transitional forms), and that too in very different senses. It is perhaps preferable to apply the term regeneration to all three types, and to describe the first as restoration, the second as renovation, and the third as replacement.

Examples of restoration are comparatively rare in the plant world ; they are most common at the root apex. If about 0·5 mm. or less of the growing point be cut off (comp. SIMON, 1904), in a few days the apex is restored from cells bordering on the wound. Corresponding results have been observed on splitting longitudinally the growing points of certain ferns (GOEBEL, 1902 ; FIGDOR, 1906), and FIGDOR (1907) has noted the same phenomenon in longitudinally cleft leaves of Gesneraceae. Vegetative shoots of some of the higher plants also show a restoration of the missing halves, when these shoots are divided longitudinally (PETERS, 1897 ; KNY, 1905). The power of restoring organs which have been removed is always limited to embryonic tissue, but it is by no means a constant character of it ; it is not possessed, for example, by the majority of fern roots, or of vegetative growing points.

The second type of regeneration, renovation or re-formation in the neighbourhood of the wound, is much more common ; it is so closely connected with the third type, replacement, by transitional stages, that it is difficult to separate them in actual practice. If by primordium of an organ we mean only a cell mass already differentiated, then the two types must always be kept distinct. But there are primordia which, apart from macroscopic and visibly distinct primordia, are only microscopically distinguishable, and, further, even invisible primordia, groups of cells which, externally, give no indication of their capacity for giving rise to the organ in question, but which can perform the duty much

more quickly than cells in their immediate neighbourhood, both micro- and macroscopically identical. All these various forms of 'primordia' may be described as 'reserve organs' (GOEBEL, 1902). It is readily conceivable how by their presence the plant is saved the labour of forming renovations. Hence, when a large part of the apex of the root is cut off, the neighbouring lateral roots take on the function of the primary root, and, in the case of the stem, a number of buds shoot out, which were only waiting this opportunity to do so.

330, ll. 17–18, *for* Indeed VÖCHTING . . . (p. 333). *read* MIEHE'S experiments on *Cladophora*, described above, have shown us that the polarity exists in individual cells, and we shall meet with further illustrations later on.

l. 23, *after* factors *read* (VÖCHTING, 1906).

l. 39, *for* 1898–1901, p. 435 *read* Organography, II, p. 227.)

331, l. 4, *after* (peloria) *read* That peloric formations may also occur in lateral flowers does not contradict this statement, for lateral members only *may* be dorsiventral but *need not* be so.

Having now become acquainted with a series of examples, let us inquire into the conditions and causes of regeneration. Certain external factors, such as temperature, moisture, &c., are generally concerned in regeneration, and if these conditions be fulfilled we see, in many plants, some organ or other becomes regenerated, while in others only young cells have this capacity, or the capacity for regeneration may be wanting altogether; these differences in behaviour are specific, and no reasons can be given for them. Apart from this, however, we find that in lower plants generally, where only slight tissue differentiation exists, regeneration is much easier than in higher plants, and in the latter the capacity for regeneration decreases as tissue differentiation increases. Further, in plants with great powers of regeneration, such as Hepaticae, cells such as those which give rise to root-hairs, or to mucilage cells, are no more able to give origin to the entire plant than are the assimilatory cells. Hence it is probable, though not absolutely demonstrable, that all the cells of the organism when just formed have the power of reproducing the entire body, but that they gradually lose the power the more they become specialized to the performance of definite functions (comp. GOEBEL, 1905).

The causes of regeneration, which have been recently discussed comparatively from many points of view (GOEBEL, 1902, 1905; KLEBS, 1903; MACCALLUM, 1903; VÖCHTING, 1906), are as yet known rather negatively than positively. Thus we may say that the actual wounding does not of itself induce regeneration. An organ may often be very severely injured, e. g. by longitudinal sectionizing, without any regeneration taking place, while conversely a regeneration results from comparatively slight wounds, and even without any wounding at all. Shoots may arise from the leaves of *Begonia* or *Utricularia* not only when these leaves are cut off, but also after the growing point has been removed or rendered inactive. Such inactivity may be induced, mechanically, by enclosing it in plaster of Paris, by inhibiting its activity by chemicals, e. g. an atmosphere of hydrogen, and even by darkening; regeneration has been observed under all these conditions. In many cases all that is needed to induce regenerative structures is to separate the growing organ from the rest of the plant by ringing into the wood, though in the spruce, for example (ERRERA, 1905), this is not enough to induce the formation of an orthotropic lateral branch; on the other hand, this result may be obtained by sharply bending the terminal branch.

If the further question be asked, wherein essentially the influence of the growing or active organ lies, how its activity interferes with the development of other organs, it would appear that none of the various explanations offered are satisfactory; more especially we are not dealing here in general with dis-

turbances in nutrition, or in the supply of water. The buds in the axils of the cotyledon of *Phaseolus*, for instance, always shoot out if the growth in the epicotyl is inhibited; one cannot, however, ascribe this effect of the apical region to the withdrawal of water or nutriment. The formation of roots always takes place in shoots of *Phaseolus* above any transverse incision, but this is not because the cells concerned contain more water than before, for the same result takes place if the shoot be wilted, and it cannot be induced by longitudinal incisions, even if these be immersed in water. KLEBS (1903) believed that the root formation was due to water being supplied to the parts concerned, but MACCALLUM and VÖCHTING have shown that his view cannot be maintained. Hence there must exist varying relations of unknown nature between the different parts of the plant, the suspension of which induces regeneration. Relations of this kind are spoken of as correlations.

ll. 9–16, *for* which express . . . *multiflorus*. *read* since these parts have no longer any functions to perform. In fact, the usual result is the casting off of the leaf-stalk or the leafless stem, since regeneration cannot appear rapidly. The plant rids itself of useless organs. It is quite enough, under certain conditions, as WINKLER (1905) has found, to restore one of the functions of the leaf, transpiration, by placing a small block of plaster of Paris at the end of the petiole, to keep it alive for weeks, when under ordinary circumstances it would quickly drop off.

If the leaves be removed as fast as they unfold from the terminal bud, anatomical changes take place in the stem adapting it to carry out assimilation previously undertaken by the leaf. The stem develops more chlorophyll and stomata, and its cortical cells elongate like palisade cells (BOIRIVANT, 1897; BRAUN, 1899). The same sort of structure, only more pronounced, is permanently found in plants with small or evanescent leaves, e. g. *Genista*, *Sarothamnus*. Further, the vascular bundles in plants whose leaves have been removed become reduced and do not increase in thickness. Thus there is a relation between the leaf and the leaf-trace in the stem, a relation which may be studied very effectively in the epicotyl of *Phaseolus multiflorus*.

l. 22, *after* 1891 *read*, 1893

ll. 27–52, *for* In other cases . . . new functions. *read* Certain phenomena observed by the author in the years 1891–1893 are, doubtless, as MONTEMARTINI (1904) points out, results of wounding, which progress further towards the base than the apex. The reason for this is especially the feeble differentiation of the primary elements already laid down, while the inhibition of secondary growth may also be explained by the enclosure of the leaf in plaster of Paris. The author has no doubt that the differentiation of the leaf-traces might also be prevented by inhibiting the development of the leaf sufficiently early.

As in the cases mentioned the removal of an organ inhibited its function and at the same time caused another organ to develop feebly or to die off, so, conversely, an organ may be stimulated to new activities when some other function is transferred to it.

332, ll. 11–14, *for* The need for . . . demand. *read* Just as in the case of the potato tubers, one can make a petiole take its place in the general system of the plant, as, e. g., when *Begonia* leaves are planted with the bases of their petioles in wet sand. The petiole remains alive for a long time, and some of its vascular bundles exhibit conspicuous secondary growth (KNY, 1904). DE VRIES (1891) had previously observed the same phenomenon in the petiole of *Pelargonium*, which was stimulated to continued secondary growth by an anomalous leaf-bud on it.

ll. 26–33, *for* In this case . . . form them. *read* Neither structure is, however, of any use, for the plant has now no buds, and cannot produce any.

ll. 38–9, *for* throughout the year *read* for years

l. 41, *for* that roots swell into tubers since *read* that even roots swell into tubers if

ll. 46–53, *for* We have as yet . . . appropriate fusions, *read* When the scale-leaves of *Oxalis crassicaulis* subsequently swell and become reserve store-houses we have an instance of the transformation of an organ already apparently fully formed, a phenomenon at least by no means frequent (comp. however, WINKLER, 1902 a). The bulbs of other species of *Oxalis*, however, teach us that a change of function and accompanying change of structure may appear very late in their history. While, generally speaking, the formation of reserve scale-leaves may take place directly from as yet undifferentiated leaf primordia, the bases of normal foliage-leaves of many species of *Oxalis* swell out into scale-leaves (HILDEBRAND, 1888) and persist while their petioles and laminae die off. Similar phenomena are recorded by GOEBEL (*Organography*, Vol. I, p. 9 and Vol. II, p. 398) as occurring in certain Fumariaceae. How far these leaf-bases have developed when they receive the stimulus which causes them to swell, has yet to be settled.

As in regeneration phenomena, so also in the examples now given of inhibition and transference of functions, we have become acquainted with a whole series of correlations. Further illustrations are afforded us by a study of transplantation, to which we now turn. Transplantation—the artificial grafting of part of one plant on another—has long been practised in Horticulture, and has been interpreted scientifically in consequence of VÖCHTING's experiments. The simplest instances of transplantation studied by VÖCHTING (1892) were those in which he removed a cubical portion of beetroot by suitable incisions, and replaced it in the wound so formed in its original orientation. After ligaturing it in position in an appropriate manner, a rapid healing of the wound took place,

333, ll. 15–16, *delete* [MIEHE . . . manner.]

ll. 33–4, *for* as when . . . resorted to. *read*; thus, in 'budding' a single bud, in 'grafting' a small twig is transplanted.

l. 35, *for* the graft is *read* it is

334, l. 1, *for* grafting *read* budding; *for* cortex *read* rind with cambium cells attached

ll. 5–8, *for* Of the numerous . . . result. *read* Of the many types of grafting we need select only one, viz. cleft-grafting, where the end of the stock is split longitudinally and the bevelled end of the scion is sunk into the cleft. In this case, as in budding, scion and stock must be firmly bound together until a fusion is effected.

l. 17, *for Peireskia read Pereskia*

l. 18, *for* graft badly on *read* form unsuitable stocks for

335, l. 5, *for* for certain buds of *read* and then the buds of the scion close to

ll. 6–8, *for* In the course . . . do not *read* In forming these stola the tendency of the scion is clearly to form organs of storage which cannot

l. 11, *after* stock *insert* as that

l. 14—P. **337**, l. 27, *for* We have spent . . . of organs. *read* To refer so numerous and heterogeneous phenomena to the principle of correlation is only a step towards explaining the causes of plant form, and that too only a slight one. Although it is true we are able to demonstrate the existence of correlations we cannot, as yet, elucidate them further—the effect of one part on another remains a complete mystery. We do not deny that one organ may inhibit the growth of another by withdrawing nutrients or water from it, but it must be emphasized that we cannot altogether rest content with such simple assump-

tions. Since in the majority of cases we cannot demonstrate a physical effect of these organs on each other, and since further it has been already shown that NÄGELI'S idea of the transference of ' vibrations ' has proved valueless, we can scarcely do otherwise than assume that chemical processes play a great part in correlation. What the nature of the active material is, however, how it arises in the plant, how it moves from place to place and how it disappears, has yet to be settled. Still, note should be made of the antitoxins met with in the study of immunity, substances which are often characteristic of definite species. Certain phenomena in this aspect of plant life, especially self-sterility, have led us already to the belief in special materials of this kind (JOST, 1907). It is probable that we must look for the explanation of correlation in investigations of substances of this nature, though these are at present quite unknown. Just as species may possess special materials, so also may different kinds of cells or tissues. In reality, we have always assumed this, since one has, in the end, attempted to refer all differences between organisms to differences in the protoplasm. But if substances such as those which are required in correlations come out of individual cells and operate in some way or other at a greater or less distance, they must be diffusible, and cannot be part of the plasma which we know is confined within the cell itself.

Without following out any further these intentionally wide generalizations, and returning to the mere facts—i. e. the cases of correlation empirically determined—we have still to note in conclusion that these are demonstrated preferably by what are in reality experimentally induced variations in the typical mode of development of the plant—malformations, we might term them—but that they also doubtless play an important part in normal ontogenesis. A few examples will make this clear.

Looking first of all at organogenesis at the growing point, it must be said at once that the nature of this growing point (whether of stem or root) is already fixed in the egg-cell, and it must develop on these lines. At the apex of the stem-leaves appear—with free spaces between them. No one can doubt that any part of the merismatic cone is capable of forming a leaf in the same way, and hence if one region grows out into a leaf, that part must obviously inhibit leaf-formation in neighbouring parts ; in other words, we would explain leaf arrangements to a certain extent by assuming correlations in different regions of the growing point. Thus we are led to a subject as to which another theory, very widely accepted, has long held the field, a theory which has a mathematical basis, and hence, apparently, much more perfect than any other botanical conception—viz. the mechanical theory of phyllotaxis.

We are far from suggesting that the relations existing between plant organs are merely chemical in their nature, for reciprocal mechanical influences of organs touching each other are quite possible. Hence we must distinguish between a purely mechanical pressure and a stimulus effect, such as we saw in a previous lecture might result from pressure, contact, &c.

337, l. 52, *for* Since *read* Thus

338, l. 19, *for* for *read* from

l. 38, *for* do we gain much *read* do we obtain an exact explanation of the facts

l. 41, *for* to correlation, such as the *read* to correlation. We shall speak of these presently.

It is quite clear that correlations play an important part in the extension of organs, for otherwise all lateral buds must shoot out, since they are certainly all constructed on the same principle, nodes must develop in length to as great an extent as internodes, or one individual node must alone elongate, &c., &c.

We reach the same conclusion from a consideration of anatomical features.

Keeping at first general symmetry before us, we see the regularity of the arrangements on which even the position of organs is based. One naturally thinks of the

l. 49—P. **389**, l. 43, *for* The relations . . . demonstrated *read* Again, it is impossible to deal with the longitudinal interrelation of vessels, fibres, and sieve-tubes, without taking into account a mutual influencing of one by the other. The relations existing between the vascular bundles and the leaves introduce us to another set of correlations, and, finally, we meet with the same phenomenon in the relations subsisting between growth in surface and in thickness of the individual cell, and especially when we take into account the correspondence of pits.

There is yet another reason, not yet alluded to, which cannot be over-emphasized as explaining the significance of correlations in organogenesis. The growing point of the stem is not affected at all, or only to a slight extent directly, by many external factors such as light, water, &c.; when such do influence the formation of the plant, they can only directly affect full-grown parts; these must affect in turn the growing point, for the effect of external factors is often already apparent in the bud; where they come into direct contact with an organ, however, they produce no effect.

Numberless examples might be quoted, but these must suffice. Summarizing our discussion of correlations in a sentence, we might say that the structure of the plant under natural or experimental conditions is not fixed from the beginning, but is essentially determined by correlations existing between the whole and its parts.

We have divided the factors concerned in plant formation into internal and external; we have now to inquire in which of these categories the phenomena of correlation are to be included.

Looking at the plant as a whole—the most natural point of view to take—correlations are to be regarded as internal factors; but when one takes into account the relative independence of the individual cell or bud, the action of other cells or growing points on these may be regarded as external. But even in the single cell of a growing point we have a complex structure—we distinguish cell-wall, cell-sap, and protoplasm. We know that the essential formation of a plant depends on the protoplasm, and cell-sap and cell-wall are as much external environment to it as neighbouring cells are to the cell as a whole. Hence, following KLEBS (1903, 1904, 1905), one might assume three causes of plant formation: (1) external factors; (2) internal conditions; (3) specific structure. In 'specific structure', be it of a lifeless body or of an organism, KLEBS recognizes the factor concerned in determining the appearance of a definite peculiarity under definite conditions. Specific structure determines the 'capacities or potentialities of a body'. For instance, as water has the capacity of being solid, fluid, or gaseous, so the species *Sempervivum Funkii* has the capacity of growing leaf rosettes, offsets, or flowers. The internal conditions at the growing point determine which of these capacities shall become effective. By 'internal conditions' KLEBS (1905) understands 'the molecular affinities and forces which operate amongst the enormous mass of minute particles which go to make up the cell'. He goes on to say 'each cell is the product of another cell, and possesses, in consequence, from the very commencement certain peculiarities in its internal conditions, in relation to water-content, osmotic pressure, the presence or absence of certain substances, carbohydrates, proteid, acids, salts, &c. All this I include under the term internal conditions, and it depends on the special peculiarities present from the beginning which potentiality of the specific structure of the cell will become active, whether it grows, divides, alters its form in any one of many ways, &c.'

Internal conditions are, however, very variable, and the environment, inasmuch as it induces changes in them, has certainly only an indirect influence on the development of the plant.

We cannot accept this conception of KLEBS's because we look at the phenomena from an essentially different point of view. It appears to us that KLEBS has advanced no proof whatever that a cell really grows because certain materials, such as proteid, carbohydrates, and enzymes, are present or absent. On the contrary, we believe that it is not the presence or absence of a substance that determines the activity of protoplasm, but that the presence or absence is determined by the protoplasm. But what we generally understand by protoplasm cannot be identical with that which carries these potentialities. Only a part of it, to which has been given the name of idioplasm, can be the bearer of such potentialities, and what is left over, cell-sap, cell-wall, &c., might be an internal condition of the idioplasm. But ' internal conditions ' of this kind can scarcely be separated from specific structure, as we shall attempt to show by an example. According to KLEBS the polarity of plants is due to external factors or to internal conditions dependent on them. We have seen that no proof has been advanced in support of this view, but we have also pointed out that, even if it were so, we could not assume that polarity should make its appearance without a distinct capacity on the part of the plant to exhibit a polar structure. This capacity must, however, be specific, and dependent, as KLEBS says, on specific structure, for one cannot regard a higher plant as apolar. The oosperm of a willow divides into two polar segments, and though certain internal conditions may be the determining factors which settle which region of the oosperm must become one segment and which the other, one cannot regard these conditions as the agents in first inducing polarity. It would have to be shown that the plant, in the absence of these conditions, did not grow at all, or grew as an apolar sphere.

Further, it appears to us to militate against KLEBS's conception that his whole efforts are all the same directed towards destroying more and more the boundaries between specific structure and internal conditions. If KLEBS considers that by the appropriate action of external or internal conditions everything may be explained, why does he leave out potentialities, and regard them as invariably of service to the plant, even when a characteristic crops up, not noticed previously, but constant from the moment of its origin (compare ' Mutations ', Lect. XXX) ?

We dissent from the view that distinguishes between internal conditions and specific structure, because the view is quite untenable. Further, it is impossible to draw a hard and fast line between internal and external factors. Still, if we establish merely these two categories, we have only one line of distinction to draw, not two, as KLEBS has. Following PFEFFER, we regard as internal or autonomous causes of plant form, all factors which affect the development of the plant under constant external conditions, and amongst internal factors we naturally include also correlations. Certainly we are far from comparing these internal causes with the unchangeable causes of formation. It must always be our task to analyse, as far as may be, these internal causes. That we shall be able to do so but to a limited extent, renders it, unfortunately, often impossible for us to obtain a closer insight into the problems of development.

340, ll. 47–8, *for* Even plants, which . . . Siphonaceae) *read* Plants which increase by means of a growing point, no matter whether it consists of a part of a cell (as in the Siphoneae) or of many cells,

341, l. 21, *for* a very *read* an even more

ll. 35, 36, 37, *for* mmg. *read* mg.

ll. 53–5, *for* No generalizations . . . of respiration. *read* In such a desiccated condition respiration is doubtless so restricted that one is entitled to regard it as without any physiological significance. From these, as well as from certain recent researches of P. BECQUEREL (1906), we must conclude that respiration is not necessary to the maintenance of the capacity for germination, and that during the resting period it may exist in a condition of absolute physiological inactivity, comparable to a wound-up but motionless clock. Whether this is true of all desiccated seeds, we do not know.

342, ll. 19–27, *for* It is now . . . external conditions. *read* It is well known that these differences are in part due to the variable permeability of the testa to water, so that in the single individual the water required for development reaches the embryo at different times. On the other hand, however, seeds are known which, in spite of their permeability to water, germinate only after a certain rest period. This is the case, according to WINKLER (1898), in *Viscum*, and we must leave it undecided at present whether in this case internal change or removal of external inhibitives (poison from the fruit mucilage) is the effective agent. According to FISCHER (1907) the seeds of many aquatics do not germinate in spite of the presence of water ; in their case, apparently, chemical stimuli from without initiate germination.

343, ll. 35–6, *for* This must be . . . of the old. *read* We cannot conclude from this that the phenomena of periodicity in longitudinal growth is to be attributed to periodic changes in external conditions and their after-effect.

l. 55—P. **345**, l. 35, *for* The winter buds . . . worthy of notice. *read* Doubtless, there are trees and shrubs which go on unfolding leaves continuously under favourable external conditions. We should expect behaviour of this kind more especially in the tropics, where moisture and temperature show no variations worth mentioning. In Buitenzorg VOLKENS (1903) observed continuous leaf-formation in *Albizzia moluccana* and *Filicium decipiens*; probably *Ficus elastica* behaves in the same way (BERTHOLD, 1904), yet this plant under favourable conditions, as e.g. when grown in a room in this country, passes through a winter rest period. Apparently, we have to deal with the same phenomenon in roses, and many other shrubs ; they go on forming leaves in autumn if placed in a hothouse, but in the open their growth comes to a stop for other reasons. In all plants of this kind, as the shoot becomes higher and higher, the supply of water and nutrient salts to the apex, and of organic materials to the roots, becomes continually more difficult, and their growth, for internal causes of this nature, cannot be unlimited. It may be assumed, however, that the growing point might be maintained in a growing state for hundreds of years, if it could be arranged that new roots should be formed on the stem at a certain distance from the apex, and that these should be preserved under favourable vital conditions.

In the tropics, however, the majority of trees behave quite otherwise ; during leaf formation, times of vigorous activity alternate with periods of outward rest. Often in a few days buds become transformed into elongated twigs on which new buds are formed, and which, later on, unfold suddenly. An illustration of this phenomenon is seen in *Hevea brasiliensis*. In the ever warm and moist climate of the Brazilian rain forest near Para the main axis shoots intermittently a large number of times during the year. In one case, HÜBER (1898) noticed the commencement of new shoots on Dec. 10, 1896, Jan. 20, Mar. 12, April 25, June 6, 1897, each of which required about thirty days to unfold its leaves, followed by a quiescent period of about ten days. Besides these five shoots the plant formed three more during 1897. Each shoot began with

short internodes, then it produced longer ones, then shorter ones once more. It bore scale-leaves at the base, then foliage-leaves, and terminated in a bud, enclosed in scales, destined to be the next shoot. Further, from the fact that different plants of *Hevea* shoot at quite different times, it may be concluded that external factors do not bring about the closing and opening of buds. This conclusion seems all the more legitimate when we learn from SCHIMPER (1898) that many Javanese trees, which also often form shoots many times in the course of a year, exhibit variable behaviour on single branches. *Amherstia nobilis*, for example, may exhibit on the same tree, at the same time, branches with resting terminal buds and others which are in all stages of development. What the internal causes are of periodic opening out of buds we do not know for certain ; but it is quite possible that this periodicity is brought about either by nutritive relationships or by correlations. Whether it might be possible to induce a tree of this sort to produce leaves continuously, as is the case with *Albizzia* or *Ficus*, must be left for the future to decide. Nor are we able to say whether a certain periodicity is a permanent characteristic of protoplasm or not.

In this country also there are trees which during the summer lay down in the bud the whole of next year's shoot with all its leaves, buds, and even flowers, and these unfold in the following spring often in a remarkably short time (oak, beech, &c. ; comp. JOST, 1891 ; KÜSTER, 1898 ; BERTHOLD, 1904). Just as in the case of *Hevea*, the internodes, and often the leaves also, are characterized by regular differences in size, which may be present even in the bud. The initiatory impulse to development in spring is in this case, doubtless, temperature, and hence it is possible, at least from December onwards, to induce artificially unfolding of buds in most trees by raising the temperature. On the other hand, it is impossible that the inhibition of shoot-formation, which occurs as early as May, can be dependent on external factors. In the first place, the necessary leaf primordia capable of unfolding are simply wanting ; later on, in summer, they are present and able to unfold under various conditions, either as a second shoot—the so-called ' Lammas shoot ' which is not an infrequent phenomenon in many trees such as the oak—or in consequence of other circumstances which are recognizable and under experimental control. If the shoot be deprived of its foliage in early summer (GOEBEL, 1880), or if it be allowed to put out its leaves in darkness (JOST, 1893), thus interfering with the function of the leaves, a second shoot-formation appears quite regularly. Obviously correlations exist between leaves and buds of such a nature that fully functional leaves keep the buds from unfolding. Possibly, in many cases, withdrawal of water from the leaves (WIESNER, 1889) or of salts (BERTHOLD, 1904) inhibit the buds from growing, but this kind of correlation has not been exactly established. In the long run the inhibition may go on so far as to kill the apex of the shoot altogether (lime-tree). The same questions have to be solved in the case of these trees as in the case of the tropical ones above referred to. Their periodicity, is, as we see, not unchangeable, but we cannot tell whether it is possible to induce them to grow continuously. The latter view is, however, quite conceivable, for in many trees, e. g. *Acer* or *Forsythia*, every transition may be observed between those whose buds unfold intermittently, and those whose shoots grow continuously during the whole summer. The difference between our native trees with fitful unfolding of shoots, and tropical trees, lies in the fact that the former as a rule shoot only once a year, viz. in spring. There are certainly exceptions, one instance of which being the ' Lammas shoot ' already mentioned. We have to note also that many trees (especially *Aesculus*) form even a second shoot in autumn after they have lost their leaves owing to unfavourable climatic conditions, e. g. drought. In general, how-

ever, it is impossible to induce buds to open by means of external stimuli during most of the summer, and removal of leaves which, earlier on, led to such unfolding, is no longer effective. The buds remain in the resting condition, which under natural conditions continues until the following spring. It is possible—as already remarked—to stop it artificially from December onwards by raising the temperature ('forcing'); but all attempts causing premature shooting by raising the temperature between July and October lead to no result. In other ways it is, however, possible, not indeed to suspend, but still to shorten this resting period, as when the buds are treated with ether (JOHANNSEN, 1900).

l. 43—P. **347**, l. 32, *for* which is fatal, an action . . . relation to seasons. *read* which is fatal. Further, more recently HOWARD (1906) has succeeded in shortening the rest period by the action of frost and by darkening.

In many plants, however, the rest period remains for a definite time unaffected after the application of such stimuli, a fact all the more remarkable since the same bud which cannot be made to open out now was forced to develop prematurely—as we saw, e.g., by removal of the foliage-leaves. Some change inside the bud must first take place which results in inhibition of growth and which gradually fades away. As to the nature of this change, we have no certain information; we can only suppose that its seat is in the protoplasm. As an indication of such a change in the protoplasm we may perhaps regard the alteration of starch into sugar and other substances which takes place in autumn; it is at least worthy of note that one cannot successfully induce buds to unfold before the starch has diminished to its minimum.

At all events, this dissolution of starch in winter, followed later by its reconstruction, shows us very clearly that 'rest' in trees is only an apparent rest, and there are other evidences which confirm this. First of all, respiration is maintained in relatively higher degree in winter, or makes its appearance if the temperature be sufficiently high (SIMON, 1906); further, growth phenomena may be also induced during hibernation by wounding, e. g. cork and callus formation, root growth and even bud growth (JOST, 1893; SIMON, 1906). In contrast to one-year-old buds, buds several years old may often be made to open in autumn; they do not resist artificial forcing so well as the former. Under quite natural conditions also buds—and especially terminal buds—may commence growing in winter, as ASKENASY (1897) has shown in the cherry. This growth is, however, embryonic, and we do not know how it is that at one time it may be easily transformed into growth in length and at another time not at all. If the incapacity for development of the chief bud appears, from a purely physiological point of view, obscure, its biological significance is evident enough: the tree, owing to the fixity of its resting period, is unaffected by small climatic changes in winter, and thus saved from premature shooting.

Reviewing what has been said, we see that the periodicity in leaf-formation in trees is conditioned in the first instance by internal factors, but that it bears a certain relation to seasonal periodicity in countries where plant growth is not possible the whole year through. Periodic phenomena in plants may, however, be made to accord with another distribution of seasons, though not equally easily or successfully in the case of all plants. The transference of the shooting period to another time of the year is most readily accomplished in cases where, by employing ice, development may be delayed, as is done on a large scale with elder or lily of the valley. When plants from a temperate climate are transferred to the tropics, however, where the conditions are continually favourable for growth, the plants retain their periodicity, but it no longer shows any relation to the environment.

347, l. 39—P. **348**, l. 35, *for* In other tropical climates . . . very well marked. *read* Looking now at other periodic phenomena in plants, we come first to those

of root-growth. Owing to the obvious difficulty of research the problems connected with root-growth have been as yet little elucidated, and investigators (RESA, 1877; WIELER, 1893; BÜSGEN, 1901; HÄMMERLE, 1901; A. ENGLER, 1903) are not in accord on the subject. This much is certain, however, that in many roots growth begins in March and continues till November or December; in the middle of summer a marked decrease in growth may be frequently observed, which scarcely amounts, however, to a complete stoppage. No experimental researches are as yet forthcoming, especially on the influence of external conditions, such as heat and moisture, but such researches are absolutely essential before we can arrive at any decision on the periodicity of growth in the root. In all probability this periodicity is much more dependent on external factors than that of buds.

Perennials also often exhibit a marked periodicity, and many agree with trees as regards the mode of development of the leafy shoot. A peculiarity, however, appears in our spring flowers, where apparently the resting period is transferred to the dry season of the year, the actual summer. The commencement of the new growing period generally occurs in these plants in autumn, and shows itself first in the formation of new roots. The buds also begin to develop in October and November, but do not as yet come above ground. Further development is retarded by the winter cold, and may be temporarily brought to a standstill. This hibernation is, however, an induced one, and if the temperature be raised, all these plants are easily induced to shoot in winter. In nature the formation of flowers and foliage takes place in the early spring, according to the species, from February to May. Early in the summer the leaves fall away, so that in midsummer the plant is reduced to its subterranean parts only.

More exact investigation shows us that the differences between spring plants and trees are by no means deep-seated. The summer rest of the former may be readily compared with the absence of leaf-unfolding in summer in all intermittently-budding trees; the foliage-leaves of such plants die off much sooner than in the case of trees, but it can scarcely be doubted that embryonic growth continues during the whole summer in the subterranean organs. Nor is the early commencement of vigorous growth in the buds in autumn so very extraordinary, since, according to ASKENASY, the buds of trees do not cease developing during the winter. The characteristic feature of spring plants lies only in this, that their periods are somewhat moved forward and that their leaves are very short-lived. They also exhibit a resistance at certain times to artificial forcing; thus tulips and hyacinths cannot be made to flower before December, and many kinds of potato cannot be made to shoot in autumn. But in their case also it is possible to induce an early development, if the organ in question be in the first instance prevented from hibernating, as SCHMID (1901) has succeeded in doing in the case of the potato and KLEBS (1903) in the hyacinth.

What conclusion then may we draw from the fact that it is possible to shorten considerably the resting period in trees and perennials in which a well-marked resting period occurs? KLEBS appears to think that it is possible to induce a continuous leaf-formation quite generally by using the appropriate means, but we cannot agree with him in this. It appears to us that in many plants the periodicity is unchangeable because in their case there is no continuous and uniform formation and evolution of foliage-leaves. Although it is possible, perhaps, to induce a tree like the beech, which shoots periodically, to go on doing so continuously, it does not necessarily follow that there is any prospect of making a bulbous plant do so. The formation of a certain number of foliage-leaves must always lead to the evolution of scale-leaves at the terminal

or lateral growing point, and hence an unchangeable periodicity would be established for internal reasons. Were it possible to compel a bulbous plant to go on forming leaves continuously, or a potato to form only orthotropic shoots with foliage-leaves and to cease the production of stolons with tubers, we should have altered the essential characters of the plant and produced a new species altogether.

Reference to the alternating origin of foliage and scale leaves suggests the qualitative changes in the productive capacity of the plant, while those we have already discussed, though closely related to this series, have rather been quantitative in character.

349, l. 33, *for* tracts *read* bracts

350, l. 5, *for* pass to *read* accumulate in
l. 9, *for* 234 *read* 187.
l. 25, *after* 1893 *read*; URSPRUNG, 1904).

351, l. 38, *after* leaf-formation *read* (WIESNER, 1906).

353, l. 43, *for* in the form of *read* enclosed in
ll. 44–5, *for* and the cell-mass . . . or bud *read* and this cell-complex may, to a certain extent, take the form of a growing point or of a bud.
l. 47—P. **355**, l. 45, *for Ulothrix zonata* . . . uniform system. *read Vaucheria repens* is an alga forming green layers on moist earth. Examined under the microscope it is seen to consist of long cylindrical, occasionally branched threads, in which usually no transverse walls occur; the plant is unicellular. Reproduction is effected by two kinds of organs, by swarmspores and by ova. In the formation of swarmspores the end of a branch is cut off by a transverse wall, and the contents of the abstricted portion contract, escape through an aperture in the membrane, and move about by aid of minute cilia arising over the surface of the, as yet, naked protoplasmic mass. Formation and movement of these swarmspores takes place only in presence of water. After a certain time the spore comes to rest, fastens itself firmly to the substratum and germinates into a new filament, which, later on, branches, and which can live both in water and in moist air. In the other mode of reproduction two kinds of organs are formed, known as oogonia and antheridia. Both organs are separated from the thallus by transverse walls, and both open later by apertures at their apices. The antheridia only permit their contents to escape after these have divided into numerous small, colourless spermatozoa, which hasten to the oogonium and penetrate through the opening. One of these sperms then fuses with the protoplasm of the oogonium, which has meanwhile contracted into an egg-cell. Thereafter the ovum excretes a new, thick wall, and becomes an oosperm, which, after a resting period, germinates into a new *Vaucheria* filament.

A quite similar kind of reproduction occurs in many Fungi belonging to the genus *Saprolegnia*. Here also we have a unicellular branched vegetative body, though it contains no chlorophyll. *Saprolegnia* occurs usually on dead aquatic insects, and the thallus permeates in the first instance the body of the insect. After a certain time it grows out on the surface, and forms all round it a series of radiating threads. The ends of these filaments are, as a rule, segmented off, and form, not one swarmspore, as in *Vaucheria*, but many, which escape and move about. Later there appear oogonia and antheridia, whose structure we need not describe. We need only note that such an oogonium contains several ova, each of which becomes an oosperm, in certain types at least, only after fusion with the contents of an antheridium. The fact that in many cases the ovum can germinate directly is of less importance in this relation.

As in these two cases so also in numberless Algae and Fungi, two methods of reproduction have been discovered, viz. sexual, i. e. by fertilized ova, and asexual, i. e. by swarmspores. Not infrequently it happens that in certain species several types of reproductive organs make their appearance, all of which subserve asexual or ' vegetative ' propagation.

l. 52—**P. 358**, l. 24, *for* It is owing . . . permit of more. *read* More especially in *Saprolegnia*, vegetative growth, formation of swarmspores, and then sexual reproduction follow one after the other, under natural conditions, with such regularity that we might well conclude that the cycle of development was unchangeable. Thanks are due primarily to G. KLEBS (1889; summary in 1896 and 1904) for his efforts, carried out over many years, to extend and improve our knowledge of this subject. The principal result of his labours may be briefly expressed by saying that the normal cycle of development of an alga or a fungus represents only one of many possibilities, and that it is often possible by altering the culture conditions to induce a definite change in the cycle, with the certainty of a chemico-physical experiment. External factors determine, in other words, which of the different developmental possibilities which the organism exhibits under natural conditions shall show itself. Even the normal cycle is determined by external conditions, and so long as these remain constant the organism goes on growing in the usual way.

KLEBS (1903, p. 41) has succeeded in inducing variations in the life cycle of *Saprolegnia mixta* in the following way :—

1. The mycelium grows for years in a purely vegetative manner if supplied continually with fresh and suitable nutrients.

2. If such a well-nourished mycelium be transferred to pure water it proceeds rapidly to form abundant sporangia.

3. In solutions of leucin (0·1 per cent.) and haemoglobin (0·1 per cent.) active growth first of all takes place, followed by the formation of sexual organs. Swarmspores are not formed, but these make their appearance subsequently to the sexual organs if a more dilute solution of haemoglobin (0·01 per cent.) be employed. Similar experiments with *Vaucheria repens* give the following results :—

1. Continuous vegetative growth took place in fresh inorganic nutritive solutions in bright light, and even in weak light when the nutritive solutions were seldom changed.

2. Continuous zoospore formation until the thallus was completely exhausted, when placed in darkness after being previously well nourished in water, in light.

3. Regular alternation of growth and zoospore formation when grown in water, in alternate light and darkness.

4. Growth and continuous oosperm formation when cultivated on moist soil in light.

5. Growth, then swarmspore formation and later oosperm formation, if grown first in a nutritive solution and then placed in water in bright light.

6. Growth, then oospore and, later, swarmspore formation, if grown first on damp soil, then in water or a dilute nutritive solution.

From these experiments it is evident that in nature also the life-history must vary from the normal in accordance with changes in the environment, and this has actually been observed to take place.

KLEBS, partly in conjunction with his pupils, has investigated a large number of Algae and Fungi in the same way as in the case of the examples quoted.

The principal result arrived at was in all cases the same, viz. that the developmental cycle was in no sense determinate or invariable. In every case

it was possible by appropriate means to affect both growth and reproduction. In individual cases certainly the effective stimuli necessary were extremely varied, and, when we take a general view of all the organisms studied by KLEBS, we can only say that the development of reproductive organs in place of mere vegetative growth is determined by alterations (by way of increase or decrease) in the general vital conditions (temperature, light, moisture, oxygen, organic or inorganic nutrients). It is not essential that a stimulus previously absent should be applied to produce such a result ; it is quite sufficient that quantitative alterations be made in stimuli already present (KLEBS, 1904, p. 487).

Before inquiring more closely how the environment really acts we will investigate, in a single instance, the various stimuli by which one and the same process in a selected species can take place. Let us glance at the formation of swarmspores in *Vaucheria repens*. KLEBS (1904, p. 497) observed this to take place under the following conditions :—

1. On transferring the filaments from more to less concentrated nutritive solutions or to water.
2. By transferring filaments from air to water.
3. By transferring filaments from flowing to stagnant water.
4. By reducing illumination, or best of all by darkening completely.
5. By reducing temperature nearly to the minimum.
6. By increasing the amount of salts present nearly to the maximum.

The same result, however, does not take place in the same way when these six different agencies are allowed to operate. It is possible, on the other hand, to divide them into three series (KLEBS, 1904, p. 497) :—

(*a*) The external condition operates so as to cause a sudden change in the first 24 hours, when thereafter normal growth ensues, as in cases 1–3, when the filaments are transferred from air to stagnant water, nutritive solution, or flowing water.

(*b*) The external condition operates at once, but continues only as long as sufficient nutriment is present. Thus zoospore formation begins, e. g. after the filaments are darkened. After the spores are shed growth begins again, and then the ends of the filaments are once more changed into sporangia and so on. The whole process comes to an end when the filaments become exhausted or when the nutriment gives out.

(*c*) The external condition operates only after a certain time, as in cases 5 and 6. Lower temperatures and increase of salts operate on the cells in such a way that, after a few days apparently, zoospore formation takes place spontaneously, continuing for weeks.

It is sufficient for us to note that certain of these reactions are readily explicable from the biological standpoint, i. e. that they are purposeful and essential to the existence of the alga. Swarmspore formation, which results from the application of the agencies 1, 2 and 3, is the way in which the alga adapts itself to the new life conditions ; the old cells can no longer live under the new conditions ; the plants which arise from these swarmspores, however, go on living under them for an unlimited time.

A comparable case would be the dying off of the aerial leaves and the formation of aquatic leaves in an amphibious plant when transferred from land to water. The fourth condition (darkness) never occurs as a possible state of existence, and hence no adaptation to that condition can take place. The plant is always making fresh efforts to reach a more suitable environment by means of swarmspores. The two last agencies are more difficult to explain, but it would take us too far to formulate any suggestions as to their significance.

Still, the biological meaning of the external factors in zoospore formation is not really at present under consideration, but the physiological aspect of the

problem must be elucidated. As we have previously seen, KLEBS assumes that the external factors always effect certain internal changes which in their turn operate on the specific structure of the plant. KLEBS attempted earlier (1903, p. 67) to prove that different external factors which induce the same morphogenic results affect the internal conditions in the same way. Thus, for example, a reduction of osmotic pressure in *Vaucheria* should in general be followed by the formation of swarmspores. More recently, however (1904, p. 492), KLEBS rightly discards this idea and admits that the first internal changes in the cases 1–6 may be very distinct. At the same time we must confess that we know absolutely nothing as to the mode of operation of external factors. To us it does not appear to be at all certain that these agents must always, in the first instance, influence internal conditions ; we cannot see why it should not be possible that the influence of the determinating part of the protoplasm in such simple cells living in water should be direct.

We suggested in the first edition of this book that external factors operate as releasing stimuli. This view was based on the comparison of an organism and a machine. What KLEBS has put forward against this comparison (1904, 1905) appears to us to be both correct and worth noting. The comparison is, like all comparisons, imperfect, and perhaps very much so ; still, we must continue to employ it, if we would seek to acquire any essential knowledge of the effect of external factors on plant organogenesis. Let us assume that we are dealing with a machine with threefold powers, e. g. a machine that can stitch, embroider, and knit, and that it is driven by steam. The fly-wheel set in motion by the steam can render one or other of these powers operative by bringing into or throwing out of gear a certain small wheel, and this latter action may be brought about by external forces such as heat, light, gravity, chemical forces, &c. The external forces do not actually perform the work, but merely permit the manifestation of this or that activity. Similarly, in the organism certain external factors operate as releasing agents ; they subtract or add something, and in consequence the activity of the protoplasm responds in a definite way. This is the idea we have in mind—though we would willingly replace it with a better if we had one.

Although studies hitherto undertaken on these fundamental problems have not led us to any explanation of them, still we must not underestimate their results ; the knowledge of the fact that the developmental cycle in lower plants is determined by the environment is of importance.

358, l. 30, *after* entirely different. *read* By altering external conditions we can, at least in many plants, fundamentally alter the typical life-cycle. Changes of this kind have been effected by KLEBS on *Sempervivum Funkii*.

359, l. 3, *for* 1898–1901, p. 430 *read Organography*, p. 607).

362, l. 9, *after* these *read* buds
l. 28, *for* water *read* materials

363, l. 42. *after* (1893) *read* and KLEBS (1903–1906) ; *for* has *read* have
ll. 43–4. *for* The plant . . . which left off *read* One may either start from the vegetative stage and determine what changes in the environment lead to flower formation or, conversely, under what conditions a plant at the flowering stage may be induced to return to the vegetative stage. Hitherto no conclusions of general applicability have been established, for a factor which leads to one result in one plant is often in another without any effect.

Taking *Sempervivum Funkii* as an illustration (a plant already referred to), KLEBS (1906, p. 116) has summarized the results of his experiments as follows :—

1. When carbon assimilation is active in bright light, and when water and

salts are absorbed in abundance, the plant goes on growing in a purely vegetative manner; either the rosette as such continues growing or lateral offsets are produced, which behave in the same way (KLEBS, 1904, p. 266).

2. When carbon assimilation is active in bright light, but when the absorption of water and salts is limited, flower formation takes place.

3. When the absorption of water and salts is moderate in amount, it depends on the intensity of illumination whether flowering or vegetative growth ensues. If the intensity of the light be low (or if blue light be employed), growth only follows; if the intensity of light be increased (or if red light be used), flowering takes place.

There are many observations and experiments available which teach us that light, nutrient salts, and other factors also are of significance in flower formation. The significance of light in flower formation is shown by the well-known fact that ivy forms flowers only in brightly illuminated situations, but not in shady woods, although it grows well there. VÖCHTING has obtained similar results from experiments on *Mimulus Tilingii*. This plant left off

l. 50—P. **864**, l. 25, *for* This illustration . . . environment.] *read* KLEBS (1904, 548) has made corresponding experiments on such plants as *Lobelia erina* and *Veronica chamaedrys*, and he shows that, in all plants that have no reserves worthy of mention, diminution in light inhibits flower formation. He regards the carbon assimilation induced by light as primarily responsible for its effect on flower formation. This view is supported by the fact alluded to above that blue light, under which assimilation is weakened, operates like light reduction, while red light, which is more favourable to assimilation, permits flowering to take place. It may further be concluded that blooming may occur in darkness if only a sufficiency of organic materials be present, and that flowering can also be induced by ringing, i.e. by preventing the flowing away of organic materials. In addition to this assimilatory action of light, which has been noted by other authors (LOEW, FISCHER, 1905), other effects, doubtless, must be taken account of, e.g. its effect in promoting synthesis of proteids and other processes whose nature is still obscure.

Temperature also obviously plays an important part; a continuous high temperature retards flowering. Thus temperate plants remain in the vegetative stage in the tropics, and biennial native plants such as beetroot or *Digitalis* may be prevented from flowering in the second year, if they be kept warm during winter and allowed to continue vegetative growth. Thus KLEBS (1904) has succeeded in making beetroot go on growing vegetatively for several years; similarily, *Glechoma* and *Sempervivum* grew for years in the vegetative state, when they were prevented from passing into the winter resting condition.

That air is essential to flower formation is shown by many aquatics, in which only aerial shoots form flowers. It is quite probable that transpiration is of considerable importance, for in land plants also transpiration appears to promote flowering (MOEBIUS, 1897).

Finally, we must note the effect of nutrient salts. Many seedlings may be induced to become dwarf and starved plants by withdrawal of nutrient salts, and in these flowering often begins after a few stunted foliage-leaves have been formed (p. 316). Experiments carried out by MOEBIUS (1897) have also shown that grasses and *Borago* flower better when less mineral matter is supplied than when they are richly manured. The increase in yield of fruit trees obtained after pruning their roots must also be due to diminution in the mineral supply. BENECKE (1908) especially has pointed out that all minerals do not operate in the same way and from his own experiences and from the records published by others he has proved that a diminution in the supply of nitrogen and an increase in that of phosphorus lead to flowering.

l. 39, *after* versa. *read* This is just as apparent in plants which flower once only as in those which do so often, e. g. our native trees. In the case of the latter we see the flowers produced on the feebly-developed short shoots, and all factors which aid in inducing the formation of short shoots also promote flowering, while, conversely, the transformation of a short into a long shoot deprives such a shoot of its capacity for blooming (comp. VÖCHTING, 1884).

ll. 45–8, *for* It is always . . . very suggestive. *read* The question now before us is whether the external factors operate directly on the growing point or through other parts, so as to cause this growing point to become a flowering axis. KLEBS (1904, 1908) has endeavoured to refer to one general principle the effects of external factors of various types which induce flowering. He points out that flowering and vegetative growth take place under the same external conditions, and that only quantitative changes in these factors decide what the result shall be ; new stimuli acting specially on flower formation need not affect the plant, but only a variation in degree of factors already operating. KLEBS regards the most important of these changes to be an increase in the organic substance ; the absolute amount need certainly not be increased. A seedling beetroot arising from a dense sowing in autumn proceeds to flower in spring (KLEBS, 1906, pp. 74, 113), although it does not contain one-hundredth part of the organic nutriment that the autumn beet that has been kept warm during the winter shows in spring ; yet the latter does not flower. Thus, the most important factor is the concentration of the organic nutrients, as also their relation to the inorganic. This high concentration, however, must arise from the fact that dissimilation is far exceeded by assimilation. The attainment of such a high concentration may be combined under certain conditions with long-continued vegetative growth, as in *Agave* or trees. Once attained, however, we observe flowering taking place universally even on slips taken from such a plant. KLEBS quotes certain apposite and interesting observations of SACHS (1892).

365, ll. 1–5, *for* Such facts . . . taken from it. *read* KLEBS himself has (1905) obtained similar results with *Sempervivum*.

In this relation we must point out that SACHS interpreted his observations in quite a different way, viz. by his hypothesis of specific organ-forming substances. According to him flowering resulted not from the effect of a certain quantity or concentration of ordinary nutrients on the growing point, but from the presence of materials of a certain quality. Wherever these were present the formation of flowers took place.

ll. 13–16, *for* The conditions . . . of flowers. *read* WINKLER's experiments just cited argue not only against SACHS's but also against KLEBS's view, in opposition to which many other arguments may be advanced; we will limit ourselves to the following remarks. When we inquire how, essentially, this alteration in the relationship of assimilation and dissimilation which leads to flower formation arises, we must admit that we have in many cases no answer available. Most instructive is the increase in respiration over the normal in beetroots or rosettes of *Digitalis*, kept warm through the winter. One might be doubtful, even in the case of the favourable effect of light on flowering, whether an excessive concentration of assimilata really takes place ; at all events, the concentration would not occur if active vegetative growth used up these materials. One would naturally think of the absence of ash materials which might lead to diminished use of the assimilata in growth. But we cannot co-ordinate this, in itself, very hypothetical explanation with the fact that many flowering plants form both flowering short shoots and vegetative long shoots. If one bud has a sufficient supply of salts to enable it to grow vigorously, how does it come about that another has not ? If the concentration of the assimilata in a bud becomes so great that it forms flowers, how does a dilution arise in the buds

of long shoots ? It is easily seen that the problem is much more complex, and it would appear to us that a certain condition of the protoplasm is essential for determining the nature of the resulting formations. This condition of the protoplasm might, on its part, be due to the primary changes in the ' internal conditions ', emphasized by KLEBS—and indeed there cannot be the slightest doubt that KLEBS admits profound subsequent changes of this kind, and regards them as essential. But this state of the protoplasm might be primary, and it might induce one cell to grow only moderately, and so store up abundant reserves, while it induced another to grow rapidly, and to go on using up the materials brought to it. This condition of the protoplasm is not the specific structure in KLEBS's sense of the term, but it is the final result of its ' internal conditions '. It would appear to us that this factor had a special significance over other more external factors, such as the concentration of cell-sap, amount of enzymes present, &c., a significance which in KLEBS's argument is not made sufficiently prominent.

366, ll. 4–5, *for* As above observed . . . mode of origin. *read* It would be very convenient if it were possible to replace the usual classification of reproductive organs into sexual and asexual by a better ; for organs such as swarmspores and sexual cells of Algae, despite their well-known relationship to each other, are grouped into two categories, while, on the other hand, bodies so distinct as swarmspores, propagative bulbs, isolated leaves or twigs, &c. are grouped together as asexual organs. HANSTEIN (1877) has already attempted such a classification, viz. into ' germs ' and ' buds ', and more recently MOEBIUS (1897) has striven to carry out this distinction further by distinguishing these bodies by their mode of origin.

367, *title of lecture, delete note in square brackets.*

ll. 11–17, *for* In endeavouring . . . 1899). *read* We will now endeavour to examine more closely into the significance of fertilization.

l. 34—P. **370**, l. 14, *for* It is probable . . . stimulus, *read* The nuclei of ova, as also of spermatozoa, exhibit one remarkable difference from those of vegetative cells. In the development of the sexual cells a special kind of mitosis takes place which has been termed reduction division. The essential features of this mitosis are surprisingly similar throughout the whole organic world, and its principal characteristic lies in the fact that the daughter cells have only half the usual number of chromosomes. In ordinary mitosis longitudinal splitting of the chromosomes takes place, and each of the longitudinal halves passes to a daughter cell, but in reduction division the unsplit chromosomes pass to the daughter cells (comp. STRASBURGER, 1905 b).

Since the ovum and the sperm cell have only half as many chromosomes as the ordinary cell nucleus, it is reasonable to assume that their individual incapacity for development is bound up with this fact and that, conversely, the development that ensues subsequently to fusion is the result of the reappearance of the normal number of chromosomes. This view at first sight appears to be confirmed by the phenomena of Parthenogenesis. By this we mean the development of the egg without previous fertilization (STRASBURGER, 1904 and 1907 ; FARMER and DIGBY, 1907 ; WINKLER, 1906). Parthenogenesis has been found to occur in many ferns, species of *Marsilia, Alchemilla, Wickstroemia,* and many other plants.

Many of these have entirely lost the male cells necessary for bringing about fertilization, and in all of them parthenogenesis has become the normal mode of development ; it does not take place merely when, by some accident, fertilization has not been effected. In all these cases where accurate cytological investigations were possible it has been found that the ovum exhibits

the unreduced number of chromosomes. In other cases certainly, as in *Hieracium* (ROSENBERG, 1906, 1907), normal fertilization takes place as well as parthenogenesis, but it has been shown in this genus that there are two kinds of ova, some with the reduced number and some with the double number of chromosomes, and it is very probable that the former develop only after fertilization, and that the latter are parthenogenetic.

Since, therefore, it cannot be denied that there is some connexion between parthenogenesis and the number of chromosomes, still it appears to us by no means proved that fertilization removes the inhibition of development by increasing the number of chromosomes. We would draw attention to three groups of phenomena which go to prove that growth is also possible where the reduced number is present. Take first the prothalli of Pteridophyta. In this group of plants, the reduced number of chromosomes is not limited, as it is in Angiosperms, to the ovum and its sister cells, but is characteristic of the whole sexual generation, capable in itself of unlimited growth and of propagating itself vegetatively. Since then one cell of this generation, i.e. the ovum alone, shows inhibited development, this must be due to some special reason. Further, in Angiosperms also, growth of cells with the reduced number of chromosomes is not impossible ; as, for instance, in the pollen-tube, which it is true does not show unlimited powers in this respect.

Secondly, we may note the cases of artificially induced parthenogenesis, i.e. parthenogenetic development of normal ova which possess the reduced number of chromosomes, and which are usually fertilized. In the animal world the experiments of LOEB (summarized 1906) are especially noteworthy, and from these it would appear that ova capable of fertilization may be induced to undergo parthenogenetic development when treated with salt solutions of definite concentration and by withdrawal of water. It is probable that there are plant ova also which may be induced to act in the same way by using appropriate agents. At present none such are known, for STRASBURGER (1907) has shown that NATHANSOHN'S (1900 a) statements as to artificial parthenogenesis in *Marsilia* are erroneous. We must, therefore, consider lower plants where not infrequently sexual cells are able to develop without fertilization. A case of this kind has been investigated by KLEBS (1893), i.e. in *Protosiphon*, where development, without fertilization, is induced by high temperature.

Lastly, we have the phenomenon of so-called ' merogeny '—the development of portions of ova, more especially those which are without nuclei. Thus WINKLER (1901) observed normal development taking place in fertilized but non-nucleated ova of *Cystoseira barbata*, and it can scarcely be doubted that they contain only the reduced number of chromosomes brought to them by the spermatozoid. This is quite definitely proved in the case of BOVERI'S experiments with the eggs of sea-urchins, in which the larvae were smaller, but in every respect normal, although the nuclei of these cells contained only half the number of chromosomes present in the cells of normal individuals.

From all these considerations we may conclude that the initiation of development in fertilization is of the nature of a stimulus, which we may associate with the effect of ether on the unfolding of resting buds. Such developmental stimuli have been the subject of previous consideration, so that we may limit ourselves at present to recording a few examples of stimuli actually provided by pollen-tubes, which have nothing to do with the actual process of fertilization, i.e. the fusion of the two sexual cells. The best known case is that of the Orchidaceae, where indeed the ovule is formed only after the pollen-tube has germinated on the stigma. This stimulus,

370, l. 16, *after* orchids. *read* According to STRASBURGER (1886) in the case of *Fritillaria persica* it may also be induced by the pollen-tube.

ll. 47–51, *delete* All stages . . . cells concerned.
l. 55, *for* similar stimulus, *read* stimulus in this connexion

371, ll. 3–12, *delete* Bearing on . . . non-nucleate egg.

372, ll. 10–14, *for* If we now . . . studied. *read* Fertilization need not, however, have everywhere the same significance. It must have a special and abnormal purpose in cases like the Diatomaceae, which consist of two half shells, and which at every successive division must necessarily become smaller and smaller. In this case the enlargement of the cell is the immediate result of conjugation.

If we now desire to investigate more closely the complete fusion of primordia in fertilization we find ourselves face to face with the problem of the 'physiology of heredity'; we have to inquire what characteristics of the father and what of the mother reproduce themselves in the offspring, and in order to study the subject it is necessary to cross two individuals which exhibit marked differences.

ll. 26–7, *for* for *read* from; *for* Among botanists . . . to conduct *read* LINNAEUS was the first to raise a hybrid between *Tragopogon pratensis* ♀ and *T. porrifolius* ♂, while later on KÖLREUTER (1761) conducted

ll. 32–6, *for* purposes; . . . 1905]). *read* purposes. The nature of the laws which govern hybridization did not appear in FOCKE's general summary of observations on the subject, published in 1881. These laws were first discovered when, following MENDEL (1866–70), one began to investigate statistically the whole preliminary history of a hybrid. MENDEL's numerous experiments—which had almost been forgotten—were brought to light again in 1900 almost simultaneously by DE VRIES, CORRENS, and TSCHERMAK, and the principal results of these experiments have been clearly enunciated by these authors. In the six years which have elapsed since then, numerous investigations have been made which have been several times summarized (CORRENS, 1901 a, 1903, 1905 b; DE VRIES, 1903; BATESON, 1907). A new branch of science has sprung into being, common to Zoology and Botany. In order to gain some acquaintance with its results it will be possible for us to mention only a few facts, and these we may take especially from the treatise published by CORRENS (1903 b).

l. 49—P. **373**, l. 3, *for* It is usually . . . may be induced. *read* The pollen-tubes find on the stigma a chemical substratum which as yet has been insufficiently investigated, and which we as yet have been unable to imitate artificially; but we may say with certainty that the germination of the pollen-grains is determined by the conditions obtaining on the special kind of stigma in question. The pollen-tubes of *Mirabilis longiflora* are perfectly adapted for germination on the stigma of *M. Jalapa*, but the converse is not the case (comp. JOST, 1907).

ll. 11–46, *for* No general rule . . . show variations. *read* If two breeds, which differ in one point only, be crossed, one would think the hybrid must be intermediate in this character between its parents; but this is by no means the rule. When MENDEL crossed a white-flowered with a red-flowered pea the hybrid was not pink but red. As we have already seen, however, white initials are not obliterated but are only inhibited from appearing by the red, hence MENDEL spoke of the red as dominant and the white as recessive. Although the domination of one initial over another is so frequent that one may speak of it as the 'rule of prevalency', still it is not so general as one at first thought (CORRENS, 1903). We know of cases in which the one initial inhibits the other only to a certain extent without actually suppressing it, and we know of hybrids where both initials are equally active, so that forms

intermediate between the two parents arise. Further, the individual members of the hybrid race may show differences, some being more like the father, some more like the mother, and finally parts of the single individual may show differences among themselves, one part displaying paternal, the other maternal characteristics.

l. 51—P. **374**, l. 51, *for* Although the hybrid . . . white-flowered. *read* As an instance of an intermediate hybrid we may quote what KÖLREUTER wrote as to the first ' botanical cross ', the hybrid *Nicotiana rustica* ♀ × *N. paniculata* ♂ : ' I was gratified to find that the hybrid took a median place between the two parents not only in the arrangement of the branches, and in the position and colour of the flowers, but also in all the parts of the flower (the stamens alone excepted), which exhibited an almost geometrical mean.'

In studying the hybrids of the second generation, i.e. the plants arising from self-fertilized hybrids of the first generation, we will select a pea hybrid which has sprung from a white- crossed by a red-flowering form, and which, as we saw, has red flowers.

375, ll. 36–45, *for* MENDEL's law . . . fertilization. *read* This so-called ' law of segregation ' has a wide but not a universal application ; perhaps it is truer of hybrids between closely-related varieties than of specific hybrids. The segregation may appear in one character though it is lost in another, and segregation may result in the characters which are subject to the law of prevalency as well as in others which lead to an intermediate hybrid.

In the last case the results of segregation are exceedingly instructive. If a white-flowered plant of *Mirabilis Jalapa* be crossed with a red-flowered, the hybrid has light rose-coloured flowers. In the second generation, however, 25 per cent. of the flowers are pure white, 25 per cent. rose, and 50 per cent. light-rose. It is possible here also to distinguish the individuals which are still hybrids, and which segregate further from those which revert to the pure type.

Besides the laws of prevalency and of segregation, MENDEL has advanced a third and very important observation, which may be termed the law of ' independence of characters '. This shows itself when the two crossed races differ in more than one point. If the white-flowered peas have yellow cotyledons, and the red-flowered, green, the colour of the cotyledons of the hybrids is yellow. Hence one sees that it is not simply a case of one type maintaining a struggle for supremacy against another, but that individual characters struggle among themselves, sometimes one and sometimes another being successful. Hence also each character of the plant must have a distinct initial in the germ, and we cannot rest satisfied with the assumption of ' a specific structure ' in a race from which its various characteristics arise.

From the law of independence of characters it may be further assumed that on the commencement of segregation in the second generation, forms must also arise which possess a combination of characters not possessed by the original races, e.g. white-flowered peas with green and red-flowered with yellow cotyledons. If the parents differ in more than two characters the complexity rapidly increases. CORRENS says that, with ten different characters, the second generation must present thousands of externally different, and almost 60,000 internally different, individuals.

Such new combinations are readily comprehensible ; but the fact that entirely new characters not possessed by the parents may appear in hybrids is not explicable at the first glance. Thus *Datura ferox* × *D. laevis* has brown stems and violet flowers, while both of the parent stocks have green stems and white flowers. The hybrid between two races of *Mirabilis Jalapa*, one of which possesses white and the other bright yellow flowers, is distinguished by

having bright pink flowers with red streaks. In the second generation we find, on the whole, eleven different kinds of flowers which show transitions from white to red or white to yellow. The pigment appears in solitary streaks on a white ground, as a 'pure' self colour of brighter or darker shade, or finally as dark streaks on a brighter ground. Since we know that in races which follow the law of prevalency a character may appear, externally, to be lost in the first generation, but makes its appearance again in the next, we must assume that in the case of *Mirabilis* also the red initials lie latent both in the white and yellow forms, and we are strengthened in this belief when we learn that both forms arise from a red type. Similarly, the above-mentioned species of *Datura* are doubtless descendants of pigmented forms. In a word, we have here to deal with atavistic characters or reversions (comp. CORRENS, 1905 a). It is also probable that characters which make their appearance for the first time arise as initials, and that these may most easily show themselves in visible forms by appropriate crossing.

The large number of so-called new characters which have been observed in hybrids spring, no doubt, from combinations of old characters and from atavistic initials which become active. Other differences between hybrids and their parents can scarcely be regarded as distinct 'characters'. Thus hybrids are often distinguished from the pure races by their power of 'vegetative growth'. This energy may be feebler than that of the parent plants when the parents are not closely related forms. In this case the seeds germinate badly, and the seedlings are difficult to rear. Or—and this is particularly applicable to hybrids between nearly-related races—they are remarkable for their size, rapid growth, early blooming, free flowering, longer period of life, great capacity for multiplication, abnormal size of individual organs, and similar characters (FOCKE, 1881, p. 475). If, for instance, the hybrid *Datura Tatula* × *D. Stramonium* attains a height of two metres, while the parents only attain a height of about one metre, we may say that the hybrid has acquired a new character, nevertheless it is only a quantitative and not a qualitative variation; such as we might obtain otherwise, e.g. by over-nutrition in seed-formation or good manuring in germination. One may look just as little upon the increased growth-energy of the hybrid as on the other, at all events, frequent characteristic, its diminished fertility, as a serious objection to the view that hybrids show no new characters. This diminished fertility is usually manifested in partially or completely unfertile pollen, more rarely in immature ovules. For this reason it is often possible to rear fruits and seeds only by pollinating from the parental line, although there is a class of hybrids whose ovules are quite fertile with their own pollen (*Salix, Hieracium*). At the extreme limit of sterility are many species of *Rhododendron, Epilobium*, &c., hybrids of which, in general, do not even form flowers.

Before proceeding to study hybrids from an entirely different aspect, we will inquire what criticisms as to the phenomena of fertilization are suggested by the results hitherto arrived at from experimental hybridizing.

376, l. 11, *for* II, 180]. *read* II, Chapter xix].

l. 20, *after* polymorphic. *read* Possibly under certain circumstances both may take place. Since further segregation may, without doubt, occur not only among hybrids but also in fertilization of similar races, it is possible that a fusion which has occurred may break down again in its units in the offspring.

Heredity, the laws of which we have become acquainted with in hybrids, is a peculiarity of organisms which shows itself both in the simplest form of reproduction, viz. division, as in the most complicated sexual act.

l. 45—P. **381**, l. 36, *for* It is impossible . . . kind of hybrid. *read* The pheno-

mena of regeneration show us also that not only propagative but almost all cells—indeed we might say all cells originally—bear all initials of the organism ; hence the quite special question arises what are really these initials, and where are they to be looked for ?

Hitherto we have used the word ' initial ' to signify briefly that the plant possesses a quite definite developmental capacity. We have not suggested, as the word ' initial ' might be thought to indicate, that the character in question was represented in the plant by some structure of microscopic or ultra-microscopic size. For a long time one has felt the necessity of attempting a more accurate determination of the nature of these initials, and recently special hypotheses, based on certain histological evidence, have gained ground. All these hypotheses have this in common, that they postulate a definite part of the cell as the material substratum or seat of heredity. While, to commence with, the nucleus as a whole (HAECKEL, 1866 ; STRASBURGER, 1884 ; DE VRIES, 1889) was invested with this duty, more recently it has become more and more the custom to ascribe the function to a part of it, viz. the chromosomes. It is assumed that the chromosomes are permanent organs of the nucleus, multiplying by longitudinal division. In fertilization the same number of chromosomes are contributed by father and mother, and by the fusion of these it is believed that both parents may thus have an equal influence on the form of the resulting offspring. During the entire vegetative life of an organism the chromosomes of its nuclei are always half paternal and half maternal, but only just before the formation of new sexual cells, at the commencement of reduction division, a fusion of homologous chromosomes in pairs takes place, after which longitudinal splitting begins once more. The fusion must permit of an exchange of the very minute bearers of individual initials, and the renewed longitudinal splitting must then furnish the basis for the law of segregation.

These few remarks must suffice at present, and the reader interested in the subject is referred for further details to STRASBURGER'S monograph (1905 b). It is obvious that we have here to deal with doubtless very ingenious interpretations of the observed facts of karyokinesis. There are many points, however, in this most recent branch of science which to the physiologist appear open to criticism. In the first place, the observations made in recent years as to the changes going on in the nucleus have led to very diverse conclusions. Although nowadays these have become more harmonized, still it must be remembered that this harmony has arisen under the influence of a hypothesis which has yet to be proved ; it would appear possible that, sooner or later, we shall be provided with explanations of reduction division other than those we are as yet familiar with. In view of the great difficulty of the subject this is only what might be expected. Not only are the actual facts of mitosis not as yet perfectly settled, but their interpretation is uncertain. We are ignorant whether the interchange of characters is exclusively associated with the nucleus, and with the chromosomes more especially ; there are many grounds for believing that the protoplasm also has a share in heredity. Further, there is no experimental evidence available in any part of the subject ; the explanations offered take into consideration, in a one-sided manner, certain simple possibilities without excluding others ; hence, in spite of the great interest it has aroused, the subject has not received the attention it deserves in treatises on Physiology. While referring to the special literature on the subject quoted in STRASBURGER'S works (1905 a, 1905 b, 1907), we need only put forward one reason which appears to negative the view that only the nucleus is the bearer of hereditary characters, and we do this because we come to know in this way of new and important facts bearing on the subject.

It has been stated above that in hybrids, in the long run, in single parts

of the individual, it is a matter of chance whether the paternal or the maternal initials make themselves evident. One cannot assume, however, that only one initial is present in a single twig—on the contrary, all cells of such a mosaic hybrid must carry both paternal and maternal initials, since, according to the chromosome theory, segregation can make its appearance only in reduction division, i. e. when the sexual organs are formed. There is a plant which is doubtless a hybrid between *Cytisus Laburnum* and *C. purpureus*, and which is essentially intermediate between the two parent species. In this hybrid—*Cytisus Adami*—we find, extremely frequently, branches which have taken on completely the characters of *C. Laburnum*, more rarely those of *C. purpureus* (comp. Figs. in the Bonn Text-book). These reversions are really segregations; the *Laburnum* twigs are perfectly fertile (while *C. Adami* is sterile), and from their seeds the pure *Laburnum*-type arises, without any suggestions either of *Adami* or *purpureus*. Now the reversion in question cannot very well be associated with a reduction division, and hence segregations must obviously take place independently of such divisions. We must go still further and say that the reversions in this case have no connexion with either nuclear or cell division. Occasionally one notices that only one half of a bud has reverted; and then the branch arising from it has on one side the characters of *Laburnum*, on the other of *Adami*; further, the boundary between these may be in the middle of a leaf or a flower (BRAUN, 1851); in such cases it is perfectly obvious that the segregations are not limited to derivatives of one cell (BEIJERINCK, 1901). Owing to this fact it would appear certain that the distribution of the initials in the cells is not dependent on nuclear division.

The origin of *Cytisus Adami* is obscure. Since its first description by ADAM it has been found impossible to produce the hybrid anew. We do not know whether it is an ordinary hybrid or a so-called graft-hybrid, i. e. a hybrid arising from a vegetative union of two parents. As it is not possible at all to produce such graft-hybrids (VÖCHTING, 1892), statements as to their existence have been sceptically received. KÖHNE (1902), however, has drawn attention to a hybrid produced at Bronvaux between *Crataegus* and *Mespilus*, which arose close to the point of concrescence of a *Mespilus* scion on a *Crataegus* stock. According to NOLL (1905) it is scarcely possible to doubt that in this case we are dealing with a genuine graft-hybrid. NOLL assumes that the bud from which the hybrid was formed might be referred back to a fusion of two vegetative cells which had accidentally entered the callus. According to MIEHE (1901), KÖRNICKE (1901), and NĚMEC (1904), a transference of nuclei from one cell to another in the neighbourhood has been observed to take place in other cases, and that this occurs frequently after certain stimuli have been applied. But without such a stimulus it has been shown to take place in certain apogamous fern prothalli (FARMER and DIGBY, 1907), and in that case, after the transference, a fusion of the nuclei and the formation of a fern-sporophyte followed. Hence we cannot deny that in a callus of two graft-symbionts such a fusion may occasionally take place leading to the formation of a vegetative hybrid. But because the chances are so greatly against such fusions, graft-hybrids must be correspondingly rare.

The Bronvaux hybrids (comp. NOLL, 1905) are distinguished in two points from ordinary hybrids produced by crossing. In the first place, they showed segregations similar to those of *Cytisus Adami*, and secondly, the three shoots formed on the callus differed among themselves, although they were all intermediate in character between their parents. One of them (*forma Jouini*, NOLL) is of especial interest because it had at first quite the characters of *Crataegus*, and then gradually assumed those of the hybrid. This shows that the initials of a character can appear in cells after these are adult, and hence must be independent of the nucleus. One might indeed say that protoplasmic

particles wander through the protoplasmic bridges from cell to cell, and so might be the means of conveying the initials of characters. That nuclei are of no significance in the transference of characters in graft-hybrids, is shown also by the histological researches of STRASBURGER (1905 a) on *Cytisus Adami*, and by NOLL (1905) on *Crataegus* × *Mespilus*: in both cases the hybrids do not possess the double number of chromosomes possessed by their parents, as might have been expected from a nuclear fusion (comp. NOLL, 1905, p. 19).

We may still expect a far-reaching insight into the problems of heredity from a searching study of graft-hybrids, more especially if the experimental treatment of the subject be successful. For the moment the known data are too few to enable us to come to any definite conclusion.

Still it may be noted, in conclusion, that it is quite possible that to employ them, as we have done, in opposition to the 'chromosome theory of heredity' is not quite free from possible criticism. As STRASBURGER (1907) correctly points out, there are many phenomena which appear at first to stand in opposition to this hypothesis, but which on closer study may really be brought to support it, though superficially. The same may be true of graft-hybrids.

383, *title of lecture, delete* ADAPTATION *and note.*

ll. 18–24, *for* Two questions . . . par excellence, *read* Doubtless, however, hybridization is not the only mode of origin of new species; it must now be our task to investigate other possible factors.

We are thus led to consider a problem

384, ll. 48–9, *after* generations *read* by multiplying vegetatively or by self-fertilization.

386, ll. 22–4, *for* At the same time . . . obviously two *read* We must obviously recognize two

387, ll. 1–3, *for* three (DE VRIES . . . fourth type, *read* two, fluctuating variations and mutations. To these may be added a third type,

l. 36—P. **388**, l. 17, *for* It should be noted . . . KLEBS, 1903.] *read* Although the curve takes this form very frequently, still there are other forms of variation curves also. Thus, for instance, a character may vary only in one direction, and hence half-Galtonian curves present themselves; or, again, curves may appear with two or more apices. The latter phenomenon may be associated with the fact that a certain number occurs more readily than those close to it, but it may be due to the material under investigation not being all of one kind —to the mixing of two forms whose averages are different, but whose rarer numerical values merge into each other (transgressive curves). We cannot deduce from this that a variation curve with a single apex is an indication of the uniformity of the material, for a mixture of many forms may indeed present a Galtonian curve with one apex.

The reason that the characters of a species vary round a certain average is that, even with the most careful cultivation, irregularities in the growth conditions ('nutrition' in the widest sense of the word) must occur.

l. 38—P. **393**, l. 2, *for* If individual variations . . . is formed. *read* That the variations from the mean follow, however, certain laws is associated with corresponding variations in the external conditions round a certain mean (comp. KLEBS, 1903). There is no reason for regarding the variations in quantitative characters, which are demonstrable statistically, in any way differently from the variations induced in the course of experiment which we have studied in Lectures XXIII and XXIV. Variations are induced in the present instance by the sum of the factors which we have termed collectively 'nutrition', as they were in that case by one individual factor. Since,

however, in an experiment the external factors very often vary from the average much more than they do in nature, so also do the variations so experimentally induced; we have not in every case to deal with simple quantitative variations from the mean—qualitative variations may also make their appearance. The effect of intense light on the one hand and of complete darkness on the other, or of cultivation on land or in water, in dry or damp air, must be borne in mind in this connexion. It is quite impossible to express in a determinate manner such variations as exhibit themselves under conditions apparently constant and capable of statistical expression. Hence the statistical method cannot give us any sort of picture of the possibilities of variation in plants (KLEBS, 1903); it is only when one has cultivated a species under every conceivable variety of external condition that one can obtain a notion of the range of variation or the limits of the power of varying—from the statistical point of view it is only the range of variation under ordinary conditions that is disclosed.

The question now before us is whether the individual variation can play a part in the formation of species; and this question is associated with another as to the inheritance of such variations. Certain agricultural experiences do appear to support such an inheritance. By careful selection of individuals which exhibit in a high degree a certain feature and by breeding from such forms one can accentuate this character by continued selection. Thus, in the sugar-beet industry, the selection and employment for propagation of the seeds of those plants which are richest in sugar leads to a marked rise in the general average of the sugar percentage in the beet. Fifty years ago the percentage was 7–8 per cent., now it has been raised to about 15 per cent. In the same way, by rigorous selection, races may be produced which will exhibit especially large flowers or fruits, better flavour, increased succulence, &c. So far as we know, no new characters arise spontaneously, although those already existent may be added to or reduced. The limits of such variations are usually reached in a few generations (3–5); further selection merely serves to fix the character which has been acquired. It must be specially noted, however, that such characters are liable to fade away quite as rapidly as they appear; after a few generations, if selection be discontinued, the original condition is reverted to. Herein lies a great distinction between artificially produced races and natural species: the former are transitory, the latter are constant.

If then every variation which is the result of some external influence is really to be referred to an impression made on the protoplasm of the sexual cells, in consequence of which these are able in the next generation to cause the appearance of a similar variation without the external stimuli being to hand, and to accentuate that variation when the stimulus is present, then it is difficult to see why such an effect should not be still more capable of accentuation in the third generation. In fact, other experiences have shown that such external impressions are not inherited. KLEBS notes that *Saprolegnia*, after growing for years in a vegetative manner, proceeds to form reproductive organs just as readily as a specimen grown in the ordinary way, as long as the conditions necessary for the construction of such organs are granted. The same is true of yeast which, in spite of continued vegetative multiplication, has not lost its power of producing spores. Finally, we may draw attention here to the fact that plants which have lived in the high Alps for thousands of years, and which have adapted themselves to their surroundings by taking on very characteristic forms, lose all these peculiarities when they are cultivated in the plains below. Conversely, lowland plants transplanted to an alpine habitat take on an alpine form, but lose the adaptations which they thus acquire when once more brought back to their original home (BONNIER, 1895). The results of selection in cultivated plants may also be otherwise

explained. JOHANNSEN'S (1903) researches at least form an important advance towards the interpretation of the subject. This investigator shows that it is possible by selection of the largest seeds of a certain type of bean to increase rapidly the average weight. When, however, he employed not the offspring of a whole field but that of a single individual, he always obtained the same average value whether he started from small or from large seeds. He concludes from these experiments that an apparently pure variety still includes sub-varieties (JOHANNSEN calls them 'lines'), which differ in the average weight of their seeds. When specially large beans are selected from a mixture of such 'lines' as the point of departure for further cultures, they may be extreme forms of the small-seeded lines, but probably they belong to the large-seeded lines. If selection be carried on in the same way for two or three generations a selection of the large-seeded lines will be the result. Similarly, in the case of other selections there will not be any isolation of varieties which have newly arisen, but of already existing races from a general mixture of these. This explanation is not satisfactory in all respects, because it does not account for rapid reversion, associated with the cessation of selection.

393, l. 3, *for* third *read* second

l. 9, *for* or a single bud *read* or in a single bud. Still it is not the amount of the leap but its hereditary constancy that is the essential characteristic of a mutation.

ll. 33–4, *for* (e.g. white-flowered . . . characters. *read* ; they have either lost a feature possessed by the type species (retrogressive varieties), such as a pigment, hairiness, &c., or exhibit a character which occurs in allied forms, and which they once possessed and have again assumed (degressive varieties). These sub-species, however, are distinguished from each other in all features, and arise by the formation of new characters (progressive varieties).

l. 40, *after* characters. *read* [That DE VRIES'S mutation theory is really founded on a garden escape is for many reasons unfortunate. The purity of the breed may be all the more questioned since the plant is no longer to be found in its original home (Texas).]

394, ll. 9–11, *for* predominant ; . . . previously *read* predominant, if MENDEL'S laws of prevalency and segregation hold good. In the case of the *Oenothera* mutations, and in progressive mutations generally, that is not the case, however (DE VRIES, 1903) ; the hybrids with the principal type or with another mutation even in the first generation take on many forms.

In the following generations the forms arising in this way remain quite constant ; in other words, the mutations are not obliterated by crossing. In an extreme case it is obvious, however, that the first hybrid generation may be uniform, so that the new mutation alone makes its appearance.

l. 13, *for* 1891 *read* 1791

395, l. 19, *after* itself *read*

We have regarded mutation as something totally distinct from variation ; this is true, no doubt, for certain cases, but not for all. DE VRIES has observed a great number of races which must have arisen by mutation but which nevertheless transmit their characters entirely ; into the discussion of these half and intermediate forms we cannot enter, but content ourselves with noting the existence of transitions between mutations and variations. Again, this must be the case from another aspect, viz. in relation to origin, in so far as the variations appearing may be the result of external factors.

The better known cases of interest in this relation occur among micro-organisms. It has been found possible with the aid of high temperature and by use of poisons to deprive certain Bacteria of the power of forming

colouring matters and of producing spores, and this loss of power has become hereditary, i. e. many generations of cells, increasing vegetatively, have, in spite of normal culture conditions, failed to regain the capacities mentioned. The characteristic point in this process is the gradual fixation of the loss of power ; for at temperatures of definite height the formation of spores ceases at once, but on cooling it recommences, and it is only after long-continued exposure to high temperature that a permanently asporous race is produced. Should the loss of capacity be actually final—a point as yet requiring proof—the question would be whether it might not be that in this case a mutation had appeared better adapted to the unsuitable environment, and which had, for that reason, killed out the original forms. It is possible, however, that the loss of capacity is still not absolutely final, but that it lasts longer than the operating cause of loss. We know indeed of changes in the plant of which this is true, and in speaking of periodicity we got to know of so-called ' after-effects ' which it is possible to correlate with the after-effects of a high temperature as affecting loss of spore-forming capacity.

If in these and similar cases we have to deal with heredity in the true sense of the term, then we would have before us cases of what the zoologist terms ' inheritance of acquired characters '. WEISMANN (1892) attempted to show that the inheritance of such characters is theoretically impossible, and that it has never been proved in practice. This view of acquired characters is, in the first instance, based on a study of the animal world, where there is frequently a sharply marked demarcation between germ and somatic cells from the very commencement of the divisions in the egg-cell. The peculiarities which occur in the somatic regions induced by external influences or functional stimuli are regarded as acquired, or originating during the life of the individual, in contrast to those which are inherent, that is, whose initials were already present in the ovum.

That the majority of such reactions do not make themselves evident in the offspring under normal conditions is self-apparent. If an organism became deformed by injury or by a parasite, and if that deformation reappeared in the offspring without any injury or the presence of any fungal parasite, its reappearance would be indeed extraordinary. On the same supposition we would expect the offspring of plants grown in shade to exhibit ' shade-leaves ' when grown in light. The question comes to be, whether any fundamental considerations can be advanced against the assumption of their transmissibility. That would be the case if we conceived of the origin of the adaptations in the individual as the zoologists often appear to do ; for they assume that any alterations in the somatic cells must be appreciated by the germ-cells, but that can scarcely occur unless by a transference of idioplasm from the somatic to the germ-cells. Such an assumption (Pangenesis, DARWIN, 1868) verges too near to empiricism, and it would appear to us that such an idea is not only unessential for the explanation of the phenomena as presented by the vegetable kingdom, but is in itself quite incorrect. Let us study a single example of adaptation in the plant. If we place a land plant in water we do not find that leaves already present change their shape and structure, but die off just because they no longer possess the power of adapting themselves to their new surroundings ; on the other hand, adaptations appear in the quite embryonic leaf-primordia, close to the growing point, where germ-plasm or idioplasm is much more abundant than in the full-grown parts. We find, that is to say (and this is of general significance), that the adaptation does not take place in the soma proper, but in the growing point. It is from the growing point, however, that the reproductive cells are also derived, and they are able to receive adaptative impressions without the inexplicable transference of a material basis from the soma. Certainly we must assume the transference of

a stimulus, inasmuch as the growing point is not itself in contact with the water, and can only be indirectly affected by it (p. 339). Similarly, in other cases, as when leaves take on forms adapted to light or to shade, the relationship of light to the growing point enclosed in its scales must be the same in both cases, although a quite different type of leaf is differentiated in the bud of the shaded branch from that of the illuminated one. Experimental investigations on this subject are, however, much required. As NORDHAUSEN (1903) has shown, the characteristic anatomical differences between light- and shade-leaves of the beech are already established in the bud, and the light relations concerned in the unfolding of the bud play only a limited part in the process. If we arrange that the primordia of the light-leaf are allowed to develop in the dark, the typical double row of palisade-cells (Fig. 115, I) is retained, whilst the shade-leaf retains its own characters, although it be developed in bright sunlight (Fig. 115, II). The growing point, in this case, undergoes adaptation, and the effect outlasts the stimulus, so that one may readily conceive how hereditary races may in this way come into existence. As a matter of fact, this is not the case in the beech; further research is needed to show how far the after-effect is continued—whether the branches which have been exposed to light for ten years form leaves of the light-type, after shading, longer than those which have been exposed to intense light for one year. The conception we hold as to inheritance of acquired characters may be more briefly expressed by saying that there are no acquired characters in the sense indicated; the characters do not appear in the soma (compare GÖTTE, 1898), but in the growing point, and hence their inheritance is taken for granted. In lower organisms, which, as a rule, show no distinction into somatic and germ-plasma, this is quite obvious, and it is just on these forms that the observations quoted above have been made as to the inheritance of effects of external factors. According to KLEBS (1906) it would appear not improbable that phenomena of a similar nature must occur among higher plants also.

We have already considered the origin of races or sub-species by mutation. The formation of species further apart out of the fundamental type is, according to DE VRIES, easily understood, since many 'petite espèces' disappear in the struggle for existence. Of course the mutation may be so great that a new genus or a new family may come into existence. *Capsella Heegeri*, for example, would scarcely have been placed in the genus *Capsella* were it not that its origin was known. It is also quite possible that whole genera and families may be referred back in their chief features to monstrosities. HILDEBRAND (1890) has found *Fuchsia* to produce zygomorphic flowers arising by mutation (Fig. 118), so that the allied genus *Lopezia* may have arisen from a malformation (compare SACHS, 1893).

HOFMEISTER long ago (1868, p. 564) ascribed to mutation a very prominent part in the formation of species. He said: 'New forms do not come into existence by the summation in successive generations of small differences from the customary form, all tending in the same direction; they appear suddenly, and are widely different from the parent.'

In addition to individual variations and mutations, a third type of variation in plants has often been assumed to occur, i.e. the so-called 'adaptations'. By adaptations are understood changes which subserve special purposes in the organism. Such adaptations do not differ, it may be said, from other variations in their mode of origin, but only in the way we look at them. From a purely physiological standpoint, and looking at causal relation only, there are no such things as adaptations; they exist only as ecological (biological) phenomena, when the question of purpose is under consideration. Although we regard this way of looking at the subject as quite permissible, still we may

set on one side the discussion of such adaptations in dealing with the physiology of formation, and refer to DETTO's (1904) exposition of the subject. We will note only that we have not to deal here with such purposeful adaptation in structure and function as every organism constantly exhibits, but such reaction and regulatory responses as result from the operation of external factors. The changes which appear in the application of external stimuli are doubtless as a rule to be regarded as individual variations, and hence are not inherited; but if, perchance, mutation or inherited variation also makes its appearance as a result of environmental causes, it is not obvious in the face of it why adaptations should not be included under this head. Physiology cannot explain causally why the plant often replies in a purposeful manner to such stimuli; the most it can do is to suggest how this capacity has been developed historically.

In this lecture we have not been able to give more than the briefest sketch of the theory of the origin of species, and have been compelled to omit consideration of very many most important observations and views. We must therefore refer to the special literature on the subject, and especially the writings of the following authors :—CORRENS (1904); DETTO (1904); ERRERA (1904); GOEBEL (1904); KLEBAHN (1904); KLEBS (1903 and 1906); LOTSY (1906); PLATE (1903); REINKE (1901); SOLMS-LAUBACH (1905); DE VRIES (1901–3 and 1906); WALLACE (1891); WEISMANN (1902); WETTSTEIN (1903). The *Archiv für Rassenbiologie* should also be alluded to, a journal which is specially devoted to the subject of species formation.

By way of summary we must say that mutations, doubtless, do not form the only or even the chief mode of origin of species, and hence further investigations are urgently needed both as to mutations themselves, and especially as to their causes.

397. *Lecture XXXI is XIX in 2nd German Edition.*

397, ll. 1–42, *for* Side by side . . . of such cases; *read* We have now obtained a general idea of the metabolism of a green plant and have seen that, notwithstanding its endless variability in detail, two chief processes make themselves evident, viz. assimilation and dissimilation. The significance of assimilation is obvious on the face of it; the plant goes on growing, and its continued growing involves a continuous absorption of materials from without and a transformation of these into the constituent units of its body. The meaning of dissimilation is not quite so apparent, for it appears to undo what assimilation has done. We have, however, learnt that destructive metabolism results in a gain in energy; hence we must naturally discuss the gain in energy in connexion with the problems of metabolism.

Any considerations of this sort must obviously take into account the law of conservation of energy. The plant can as little create matter as it can create energy; it must obtain both from without, and can only alter them within itself.

The sources of energy available are, in the first instance, kinetic, e. g. electric energy, heat, light; there is also the energy potential in substances containing it. It is improbable that the plant can make any use of the electric energy presented to it in the free state; at least, we do not know of any instance of it.

398, ll. 12–17, *for* Probably . . . within it. *read* As to the third form of kinetic energy, the answer is entirely different. We know that the green plant requires luminous energy in order that it may grow, that it develops large leaf surfaces in order to intercept light and absorb it. Part of the light energy absorbed is transformed into chemical energy which reappears in the assimilata,

and it is this chemical energy, as well as direct sunlight, that is employed in carrying out the work of the plant. This is true both of the green and the non-green plant; for the latter is, as we have seen, dependent on the products of assimilation manufactured by the green plant, so that light energy also plays an important, though indirect, part in the nourishment of heterotrophic plants. Keeping in view, however, the immediate sources of energy, we are bound to admit that these are partly light, partly that locked up in nutrients.

What we have now to inquire into is how the energy so provided is transformed. The final expressions of energy appearing externally are those most accessible to investigation, while we can form only a vague conception of the changes taking place within the organism. Of these final manifestations of energy, by far the most important is mechanical energy. The movements carried out by the organism or by parts of it are manifestly amongst its most remarkable, and hence also most thoroughly studied, activities. Thus the production of heat is to be recognized as a phenomenon of very common occurrence, as to the significance of which we can, it is true, say but little, although we are more accurately acquainted with its causes. In addition to the evolution of heat, mention must be made of the evolution of electric currents and of light, two phenomena which as yet are of but minor importance in plant physiology.

398, ll. 33–6, *for* This third section . . . electricity. *read* It must now be our task to study more in detail the origin of these forms of energy and to elucidate their relationship to metabolism, and we may commence our inquiry with a study of the evolution of heat.

399, l. 43, *after* (COHN, 1893). *add* The considerable rise in temperature often observed in piled-up hay is due to the agency of such thermophilous Bacteria. According to MIEHE (1907) *Bacillus coli* and *Oidium lactis* raise the temperature up to 40° C. and thus render it possible for *B. calfactor*, a genuine heat-producer, to develop. The minimum temperature for this bacterium is about 30° C., and it is capable of raising the temperature of the hay up to 70° C., which is its maximum. No such heating up takes place in sterilized hay.

l. 48, *after* attained. *read* The heat produced is thus not a protection against frost.

l. 53, *after* plant *read* ; apparently this is not the case.

400, l. 3, *for* just *read* however

l. 12, *after* night *read* (KRAUS, 1896).

l. 21, *for* (1857) *read* (1851)

ll. 27–9, *for* an excess of . . . Again, in cases *read* an excess of only 0·3° C. as against 16·5° C. in normal respiration, and in *Raphanus* seedlings, 0·2° C. as against 5·7° C. On the other hand, in cases

l. 38, *for* increase . . . observed *read* increased production of heat accompanies increase in respiration (p. 202)

ll. 44–5, *for* or other . . . explanation *read* also by many other molecular splitting processes, and in just this liberation of energy lies the importance

l. 54, *after* heat *read* (often twice as much)

401, l. 1, *for* and friction *read* mixing of fluids, imbibition, and finally friction,

ll. 14–16, *for* This holds . . . many flowers *read* Indeed in BONNIER'S experiments mature organs always gave off much less heat than could be accounted for by the amount of respiration going on. The energy evolved in

respiration in these cases was thus not transformed into heat, or else the heat produced was at once used up in metabolism.

l. 33, *after* suggested. *read* In Palms the heat serves, perhaps, to bring about bursting of the spathe (KRAUS, 1896).

l. 51, *after* luminous *read* and to be given off by many animals

l. 55—P. **402**, l. 3, *for* bears the same . . . permanently. *read* is manifested only when oxygen is present, and that it is due to an oxidation process. It cannot, however, be directly referred to respiration (MOLISCH, 1904), for, under certain circumstances, especially at high temperatures, the luminosity ceases, while respiration increases. Frequently the capacity for giving off light in a certain species is lost as a result of high temperature or some other influence, although growth and respiration continue unimpaired.

402, *last line, after* 1888 *read* ; comp. FITTING, 1906).

403, ll. 13–14, *delete* The rest . . . movements.

ll. 17–18, *for* We have now to *read* Later on we shall

ll. 34–46, *for* we need only . . . mechanical energy *read* we have only shown that respiration is an indispensable condition of protoplasmic movement, not that it furnishes the energy necessary for it to take place (PFEFFER, 1892). It is, however, very probable that respiration often has a direct energizing significance, or, in other words, that the chemical energy released is transformed directly into mechanical energy.

404, ll. 8–12, *delete* 1. The transformation . . . cells, &c.

l. 13, *for* 2. *read* 1.

ll. 25–7, *for* 3. Quite independently . . . in plants. *read* Independently of chemical energy, there are all the phenomena associated with 'surface energy'. To these belong, amongst others, the phenomena of imbibition and surface tension; to whose, frequently not inconsiderable, activities as a means inducing movements in plants, our attention will be directed presently.

ll. 28, 29, *for* 4, 5. *read* 3, 4.

l. 30, *for* frequently *read* obviously

ll. 44–5, *delete* In the following . . . by the plant.

405. *Lecture XXXII is XXXI in 2nd German Edition.*

405. *title of lecture,* HYGROSCOPIC MOVEMENTS

405, l. 32, *after* situations. *read* Cell contents which possess a greater specific gravity than the protoplasm, such as, e.g., starch-grains and crystals, collect, in obedience to gravity, at the lower ends of the cells (comp. Lecture XXXIII).

406, l. 3, *for* orthotropic *read* rectilinear

ll. 39–41, *for* Hygroscopic . . . cell-wall ; *read* Hygroscopic movements are due mainly to imbibition, and especially to changes in the water-content of the cell-wall ;

407, ll. 23–6, *for* with the best lenses . . . capable of swelling. *read* with the best lenses. It does not follow, however, that such pores do not exist. Again, the transparency, which is often put forward as an argument against the existence of such pores, might be due to the fact that these spaces were of ultra-microscopic dimensions (comp. BÜTSCHLI, 1900, p. 318). There is, however, another essential difference between finely porous bodies and bodies capable of swelling, apart from the size of the pores.

ll. 33–4, *for* in deposits on *read* in a pile of

408, ll. 3–4, *for* the former being . . . the latter *read* the former being inversely proportional to a higher power of the separating distance than the latter.

409, ll. 1–2, *for* swelling . . . protoplasm *read* imbibitional swelling, and so also both in cell-walls and in protoplasm.

410, ll. 30–1, *for* again. Movements . . . that the bending *read* again, even in the dead plant. Similar bendings take place, however, in living branches of native trees. GANONG (1904) has shown that these curvings are obviously due to variation in water-content, but it has yet to be shown whether the cell-wall can really exhibit such variations in water-content while the protoplasm remains alive. In *Anastatica* it may be readily shown that the bending

l. 42, *after* manner *read* (compare WEBERBAUER, 1901; STEINBRINCK, 1906).

ll. 47–8, *for* layering . . . striation *read* different orientation of the axes of the contraction-ellipsoids, which manifests itself externally in the layering of the cells in the course of the lamination or direction of the striation

l. 50, *for* 1. Differential contraction due to arrangement of cells *read* Differential layering of antagonistic cells.

411, l. 14, *for* 2. Differential contraction, &c. *read* Differential lamination of the cell-wall.

l. 39, *for* 3. Differential contraction, &c. *read* Differential striation of the cell-wall.

412, ll. 53–4, *for* Let us assume . . . pulled out. *read* This effect may be made clear by using a piece of ordinary writing-paper, which exhibits different powers of contraction longitudinally and transversely. The lengthways and breadthways of the paper are indicated by the ruled lines. If, now, two right-angled strips of equal size be cut out parallel and at right angles to the rulings, and if these be gummed together when wet, on drying the whole simply curves inwards; but if one of the rectangular pieces be gummed to the other so that the rulings cut each other at acute angles, on drying the whole assumes a spiral form (STEINBRINCK, 1906).

414, ll. 49–50, *for* hygroscopic movements *read* movements due to shrinkage.

415, ll. 32–3 and 54, and P. **416**, ll. 46 and 52, *for* imbibition water *read* water-content

417, ll. 13–17, *for* Into the discussion . . . appear. *read* It is impossible to discuss all these cases, and hence we limit ourselves to one only to which we have previously referred. We found that certain Bromeliaceae were able, by means of peculiar hairs on their leaves, to absorb water. These hairs, as seen on surface view, appear as multicellular, shield-like protuberances of the leaf epidermis. In section one notices two protoplasmic pedicel cells from which spring the cells composing the plate (MEZ, 1904), and their lumina are more or less filled with water. Should they lose this water to such an extent that it is abstracted from the pedicel cells and the underlying water tissue, their thin walls approximate in consequence of the cohesion of their water-content so as to completely obliterate the cell lumina. When again wetted the walls swell, the lumina reappear, and in so doing suck water in like pumps. Finally, it must be noted that the cohesion of the water-content may also possibly play a part in phenomena of swelling, so that the contrast between those two sets of processes may not be so marked as would at first sight appear.

l. 24, *after* anther-wall. *read* The phenomena discussed in this lecture

have recently received comprehensive treatment at the hands of STEINBRINCK (1906). It is all the more important to draw attention to this treatise, as it is due to STEINBRINCK, in the first instance, that the detailed facts have become established.

418. *Lecture XXXIII is XXXII of the 2nd German Edition.*

418. *Add to title of lecture* SLINGING MOVEMENTS

ll. 8–10, *delete* [The branches . . . 1904).

ll. 13–14, *for* yet to tension . . . water *read* yet to the cohesion of the evaporating water-content.

ll. 25–6, *for* the osmotic . . . solution is *read* the cell membrane is unstretchable by osmotic pressure we may conclude that a solution which just causes plasmolysis is

l. 37, *for* 3·5 *read* 4·67

419, l. 33, *after* atmospheres. *read* Still more remarkable are the regulatory phenomena seen in cells cultivated in concentrated media; while higher plants possess only a very limited power of adapting themselves to higher concentrations of the substratum, Mould Fungi behave totally differently. ESCHENHAGEN (1889) showed that *Aspergillus niger, Penicillium glaucum,* and *Botrytis cinerea* were still capable of growing in 51–55 per cent. solutions of common salt. RACIBORSKI (1905) noted growth still taking place in *Aspergillus glaucus* in saturated salt solutions and in a species of *Torula* in concentrated lithium chloride. Since the osmotic value of the cell-sap must be greater than that of the environment, the pressure in these fungal cells amounts to 300 atmospheres or more. In many cases such pressures must be caused by the entry of the nutrient solution into the cells; Bacteria and Cyanophyceae especially have very permeable protoplasm. On the other hand, a formation of osmotically active materials often takes place within the cell, but the chemical nature of the substances so produced is as yet doubtful (HEINSIUS, 1901; PANTANELLI, 1904; RACIBORSKI, 1905).

l. 40, *after* up to *insert* a point within

ll. 45–6, *for* insoluble . . . (e.g. starch) *read* insoluble (e.g. starch) or if soluble have large molecules,

420, ll. 3–4, *for* elasticity . . . deformation *read* elastic reaction equals the pressure; the stretched wall resists now all further deformation more strongly than before,

ll. 37–8, *for* only in the seeds . . . 1900), *read* further, the joint cells of hairs of *Aristolochia,* already alluded to, are very extensible, for they may be increased as much as 30 per cent. in length by osmotic pressure, and may be stretched mechanically a further 30 per cent. without the deformation becoming permanent.

l. 42, *for* occurrence *read* amount

ll. 44–5, *for* The value . . . of that *read* The value of the original osmotic pressure must have been only half the pressure actually observed.

ll. 54–5, *for* accompanied by contraction *read* or of extensibility

421, l. 31, *after* contract *read* when isolated

422, l. 10, *for* excretion- (*bis*) *read* secretion-; *for* may *read* might

l. 12, *before* According *insert* Nevertheless; *delete* although

ll. 23–8, *for* the wall is extended . . . above the normal. *read* the stretching of the wall is made permanent by growth, and as this progresses osmotic pressure becomes more and more directed against the external resistance. When the tension of the wall has completely disappeared, in the long run the

whole internal pressure is devoted to the performance of external work ; in many cases, as the external resistance increases, not only does the cell-wall go on relaxing, but a rise in osmotic pressure over the normal also may arise.

ll. 42–3, *for* imbibition water *read* water-content

424, l. 9, *for* it *read* the peduncle

426, l. 51, *for* 1877 *read* 1862

427, l. 43, *after* organ *read* (Statements of another nature made by HART in the Botanical Gazette, vol. XXII, p. 505, appear to us, after an examination of several species of *Catasetum* in the Strassburg Gardens, to be erroneous.)

429. *Lecture XXXIV is XXXIII of the 2nd German Edition.*

ll. 42–4, *for* if the lie . . . suspended *read* the operation of gravity would become suspended by constant and rapid change of the position of the germinating seed, and that it might be counteracted by the agency of centrifugal force.

431, l. 18, *after Cordyline, read* plumules of many Liliaceae,

ll. 27–8, *delete* and in unicellular . . . *Phycomyces.*

l. 29, *after* at all. *read* Finally one part of a cell may react geotropically, while another part does not ; thus the sporangiophores of Mucorinae are negatively geotropic, while the remainder of the mycelia of these Fungi does not react to gravity.

l. 35, *after* both ways, *read* at least in multicellular structures,

ll. 42–3, *delete* Almost all . . . SACHS.

433, ll. 14–31, *for* In order to . . . in the middle line] *read* In all probability the second alternative is the correct explanation, and the growth of the axis remains unaltered. The question is not decided, however, because the intensity of growth is so different in different individuals (LUXBURG, 1905).

ll. 51–2, *for* and for other . . . later on. *read* Every geotropic curvature is neutralized, however, on the klinostat also, and this, as VÖCHTING (1882) has shown, is the result of so-called 'autotropism'. This autotropism makes itself evident after every curvature and after every vigorous mechanical bending in such a way that the concave side is stimulated to more energetic growth ; as a consequence the organ straightens itself, unless growth has during the initial curvature come to an end. Autotropic curvature takes place, however, not merely if the geotropic stimulus is eliminated on a klinostat, but when gravity continues to act; in the latter case, however, it leads to a flattening of the curvature which has arisen, and not to complete neutralization of it (compare also BARANETSKY, 1901).

434, ll. 3–32, *for* In order that . . . growth occurs] *read* According to Count LUXBURG'S (1905) measurements, geotropic curvature is brought about in stems also by decreased growth on the concave side, without any alteration of growth in the axis. This statement, however, is not of universal application ; the joint-like swellings seen on stems or at the leaf bases of many plants (*Tradescantia, Dianthus*, grasses) exhibit, on the contrary, a markedly increased rate of growth in the axes after geotropic stimulation.

435, ll. 40–2, *for* More recently . . . geotropic stimulus *read* With the nodes of Gramineae—which are in reality leaf bases—are associated a whole series of cushion-like thickenings occurring at the basis or apex of petioles ; all of which retain the power of growth for a longer time than the adjacent stalk

regions, and they recommence longitudinal growth on application of exter stimuli (MOEBIUS, 1899).

l. 48, *after* BARANETSKY, 1901 *read* ; HARTIG, 1901

l. 54, *for* grows at first in a straight line *read* straightens itself again ;

436, l. 8, *for* cell-walls. *read* cell-walls ; the convex side becomes more extensible, and in unicellular organs the curvature must indeed depend on an alteration in the extensibility of the cell-wall.

437, ll. 20–1, *for* to obtain . . . phenomenon *read* from what has been said on p. 422 about the amount of external work that can be done by turgid growing organs.

l. 23, *for* is about . . . purpose *read* requires about all the energy that is actually available,

l. 36, *for* latent *read* reaction

ll. 39–44, *for* As CZAPEK . . . klinostat *read* If after the end of this period of stimulation the structures be placed in a vertical position, or, preferably, rotated on a klinostat, geotropic curvature results later on.

l. 48, *for* latent *read* presentation

l. 49—P. **438**, l. 7, *for* It has in no case been found . . . twenty minutes. *read* The presentation period in flower shoots of *Capsella* is about two minutes ; in flower shoots of *Sisymbrium* and *Plantago* and in hypocotyls of *Helianthus*, three minutes ; in other cases (plumules of *Phaseolus*, *Vicia*, *Cucurbita*, and grasses) it may last from four to twelve minutes, and more rarely, e.g. hypocotyl of *Lupinus albus*, it may amount to 20–25 minutes (BACH, 1907). As to the time which elapses before the initiation of the reaction (latent period) it is immaterial whether the organ be stimulated continuously or only until the presentation period has been reached ; as soon as the geotropic stimulus has operated for a period corresponding to the presentation period the minimum latent period is obtained (BACH, 1907).

438, l. 8, *for* latent *read* presentation

l. 11—P. **439**, l. 12, *for* If the root . . . klinostat. *read* Intermittent stimulation may be brought about in a very simple manner by laying the object in a horizontal position, then placing it upright and repeating the processes at stated intervals. The klinostat may, however, be employed for this purpose. First of all, DARWIN (1892), and later FITTING (1905), have used such intermittent klinostats. FITTING'S apparatus permits of altering the period of stimulation and the period of rest at will, and further enables one to place the object not only alternately in the vertical and horizontal position, but to combine any two selected orientations—a point which will be found of interest later on. Practically the same result may be attained, however, by means of the ordinary klinostat, if the plant be placed so that its axis forms an angle of 45° with that of the instrument, the latter itself forming an angle of 45° with the horizontal. When rotated the plant thus describes a cone in space, and assumes alternately a horizontal and a vertical position. If the klinostat be made to revolve as rapidly as possible without allowing disturbances due to centrifugal force to take place, still geotropic curvature always occurs. FITTING found that curvature took place even when the revolutions were one per second, i.e. when the duration of the single gravitational stimulus lasted only a fraction of a second. As yet it is uncertain whether it may, in the long run, be possible to subject the plant to the action of gravity for so short a period that no effect is produced, i.e. that no movement follows in consequence of summation of individual stimuli.

If summation of stimuli should finally lead to a curvature which the solitary stimulus never induces, it may be interpreted only by assuming that the solitary stimulus produces a certain change in the plant which persists for

a certain time, and which is accentuated by the next application of the stimulus. This view is supported by the results obtained by FITTING in intermittent stimulation. If the duration of the stimulation be first of all equal to that of the alternate rest period, stimulation, in order that curvature may follow, must be continued until the sum of the individual stimuli is equivalent to the presentation time. If the rest periods be increased until they are five times as long as the stimulation periods, the result follows, and the reaction still occurs after the same time of stimulation as it would if the stimulation had been continuous. Hence the absolute duration of the individual stimulation is of no significance. The rest periods between the individual stimuli cannot, however, be lengthened indefinitely, for the effect of the individual stimulus gradually wears off, and this takes place when the rest period is twice as long as the stimulation period. The effect of lengthening the rest periods, however, makes itself felt in an increasing of the presentation period: e.g. 12–15 minutes, as opposed to 6–7 normal time, when the presentation period is to the rest period as 1 : 11. It is obvious that lengthening of the rest periods also delays the commencement of curvature, i.e. the latent period is lengthened. The ' change ' which a single stimulus induces in the plant is termed the ' excitation ', and this excitation must reach a certain intensity before any visible reaction takes place ; what excitation consists in, however, is unknown.

439, l. 20, *for* latent period *read* latent and presentation periods

ll. 20–39, *for* If we vary . . . liminal intensity *read* When the centrifugal force is less than gravity the latent period is lengthened ; if, as in *Vicia Faba*, the latent period amounts to one and a half hours when the force = 1 g., it rises to four and a half hours when the force = 0·014 g. (BACH, 1907). This figure is far from expressing the lower limits of the centrifugal forces which produce a geotropic effect. CZAPEK (1895) observed geotropic curvature taking place after 8 hours with a force = 0·0005 g. ; BACH, in opposition to CZAPEK, found that there was no shortening of the latent period when the centrifugal force was raised from 1 to 100 ; on the contrary, he found that the dependence of the presentation period on the intensity of the stimulus was quite different in nature from that of the latent period, as is shown by the following table :—

Centrifugal force in g. . . .	27	19	10	6	3	2	1	0·7	0·6	0·4	0·15
Presentation period in minutes .	0·25	0·5	1	2	3	4	8	10	25	30	50

It is possible also to shorten very considerably the presentation period, more especially by employing high centrifugal forces—probably much more than is indicated in the above table. From a practical point of view it is not possible, however, to apply high centrifugal force suddenly and permit it to act only for a few seconds, otherwise one should certainly find that stimuli of a few seconds' duration should suffice to induce a geotropic movement. There can be no doubt that more vigorous stimulation brings about more vigorous excitation, but why a more vigorous excitation does not lead to a shortening of the latent period cannot be investigated here (comp. FITTING, 1905).

l. 51—P. **440**, l. 6, *for* Recent researches . . . shoots upwards. *read* Recent researches (FITTING, 1905) have indeed established this view. The point may be most clearly shown by stimulating intermittently two opposite sides of a plant, when it is seen that whenever the two positions of stimulation show the same deviations from the horizontal, curvature does not exhibit itself, but that a reaction follows if the angles with the horizontal be unequal. The curvature which takes place, indeed, is just that which is aimed at when the lie of the plant is nearest to the horizontal, and which overrides the contrary curvature in the opposite lie. It is possible also to show both for the root and the shoot that the inverse, as well as the normal, lie is a rest position, although

certainly, in a short time, inverted roots curve downwards and inverted shoots upwards.

440, l. 23—P. **441**, l. 38, *for* Any attempt . . . affects it ? *read* Since a geotropic stimulus reaction follows in an obliquely placed axis on the klinostat, it must be concluded that the stimulus is perceived also in an axis laid quite horizontally, but that this perception cannot lead to curvature because it is the same on all sides, i.e. the klinostat does not prevent stimulation, but only the visible reaction. This conclusion could be arrived at, before the publication of FITTING'S researches, only from the behaviour of the nodes of grasses. These structures when laid horizontally were induced not only to curve but to start growing afresh. When they were placed on a klinostat, they began to grow there also (ELFVING, 1884), but the growth was naturally uniform on all sides.

From the work which has hitherto been carried out on this subject it may be deduced with perfect certainty that between the application of the gravitational stimulus on the one side and the geotropic curvature on the other, a whole series of processes takes place as to whose nature we are certainly at present very much in the dark. It is obvious that in the first instance gravity must have a certain purely physical effect on the plant. Gravity must exert a pressure due to weight on some part of the plant or of the cell, but to this point we shall return later. The effect of this pressure is to cause a change of unknown character in the protoplasm, possibly of the nature of a compression. Although it has not as yet been proved that this change is dependent on the persistence for a certain time of the action of gravity, still we are forced to believe that it is so ; we must assume that gravity must act for a certain time in order to induce this change. After the primary purely physical action of gravity (assuming it to be of sufficient intensity and duration), there follows the physiological result spoken of as ' excitation '. When excitation has begun we say that the plant has ' perceived ' the gravitational stimulus. While, however, the physical change must pass off as rapidly as it arose after the removal of its determining cause, the excitation lasts longer—it persists even for as long as twelve times the period of stimulation. If now, after a period of rest, but before the excitation has quite faded away, we apply a second stimulus of like duration and intensity to the first, the same physical change will be produced, but the excitation which follows from it will be added to what remains of the first excitation. In this way a degree of excitation is gradually reached by continuous summation, which will lead in the end to movement ; the excitation has now overstepped the liminal value needed to induce response.

That excitation and reaction are two very different processes may be deduced not only from the fact that there may be excitation without reaction, but also from the fact that the two processes depend on external conditions in entirely distinct ways. Excitation often still takes place when growth—geotropic movement—is no longer possible. Thus at 2° C. a geotropic response may be induced after a sufficiently long exposure to the stimulus of gravity, but the movement is carried out only when the plant is exposed to a higher temperature. Again, the stimulus of gravity may be appreciated in an atmosphere free from oxygen, but that gas is essential for the carrying out of the movement. The processes which intervene between excitation and reaction are, generally speaking, unknown. In certain cases, however, we can convince ourselves of their existence with ease, e.g. when the reaction takes place in some other situation than perception or excitation. Obviously in such a case conduction must occur between the two regions. Conduction of this kind—usually spoken of as conduction of stimulus, but more accurately,

of excitation—has been definitely established in heliotropism, but is only probable in the case of geotropism. DARWIN (*Movements of Plants*) concluded from experiments (similar to those already carried out by CISIELSKI) that the perception of the gravitational stimulus took place, in the case of the root, in the growing point at a distance of a few millimeters from the region of curvature. When 0·05–1 mm. of the extreme apex of the root was removed, the root when placed horizontally—although it grew—showed no geotropic curvature. If, however, the root was first of all placed horizontally and then decapitated before any curvature began to show itself, the geotropic reaction took place quite normally.

The interpretation of DARWIN'S experiment has led to an extensive controversy (comp. ROTHERT, 1894), the net result of which is that proof of apical perception is not forthcoming, for the wounding itself exerts an injurious influence on the responsive powers of the plant. Hence CZAPEK (1895) attempted to solve the problem by using a new method of experimentation, where wounding was unnecessary. He allowed the root apices to grow into short capillary tubes, closed at one end, and bent at right angles, while the plants were on the klinostat, so that about 1 mm. of the end of the root formed a right angle with the remainder. When these bent apices were placed horizontally so that the growing region was in the rest position, a geotropic curvature made its appearance. This curving did not occur, however, when the apex was in the rest-lie and the growing region in the stimulus-lie. WACHTEL (1899) and RICHTER (1902) have shown that the compulsory curvature induced in this experiment is not without effect on the root, and that it leads to curvings which CZAPEK was misled into regarding as geotropic curvatures. Although CZAPEK has again put forward a plea for his method, his arguments can scarcely be regarded as of any great weight, especially after CHOLODNYI'S (1906) quite recent researches. By another method, which cannot be described here, but which is very like in principle to that already used in discussing grass seedlings, F. DARWIN (1902) has attempted to show that the seat of perception lies in the apex of the root. This method also is not above criticism, and hence, taking the most favourable view of the case, we can only say that, in view of all these statements, apical perception is probable; that, however, it is not absolutely proved may be concluded from the fact that, on the other hand (PICCARD, 1904), several methods have been employed to show that perception must take place in the region of curvature. These experimental methods also require reinvestigation, however, so that we need not discuss them further.

Those authors who assume that the perceptive capacity lies in the root apex are, however, by no means unanimous as to how far this perceptive capacity reaches, and yet, for reasons which we shall appreciate later, this is a point of great interest. At present we will only note that, according to NĚMEC (1901), perception is limited to the root-cap, while CZAPEK (1906) considers it as extending along the root for about 2 mm.

In addition to the root, the shoots of seedling grasses (especially Paniceae) have been shown to possess an organ to which has been ascribed the power of geotropic perception. We may note at once that there can be no doubt as to the perceptive powers of this organ for heliotropic stimuli; of the perception of geotropic stimuli, DARWIN'S experiments (1899; comp. also MASSART, 1902) offer only probability; they do not exclude the possibility of the region of movement being also a region where geotropic stimulation may be perceived. If, following DARWIN, we lay the apices of seedlings of Paniceae horizontally, curvature takes place in the growing region; this, however, does not cease if the basal region is placed in the vertical position, but continues as long as the power of growth is retained. Hence the basal region finally exhibits spiral windings.

By way of summary we must admit that in this latter case, as also in the case of the root, apical perception has been shown to be extremely probable. In most stems it is by no means generally established, however, for often portions of stems deprived of their apices may exhibit geotropic curvatures. Certain shoots studied by MIEHE (1902) are of special interest in this connexion, for in them it was apparent that there existed a very obvious dependence of geotropic sensitivity on their apices, although doubtless geoperception did not take place in them; the apices were of import in these cases only in as much as they determined the sensitivity of the whole organ.

We may now turn to the wider question as to what the primary effect of gravity is and how that leads to perception.

443, ll. 7–8, *for* movement, for . . . (1898), it is *read* movement. CZAPEK (1898) has shown that it is possible to remove a large part of the root apex without destroying perception. This takes place quite normally, e.g. if only one longitudinal half be retained, and it is then quite immaterial how this half is orientated. Hence it is

ll. 13–16, *for* Many of the . . . hypothesis *read* Another statocyst hypothesis has been simultaneously elaborated by HABERLANDT (1900) and NĚMEC (1900).

l. 28—P. **444**, l. 41, *for* observations (HABERLANDT, &c. . . . CZAPEK, 1905.] *read* observations, so that this theory must doubtless be granted a high heuristic value, although it has not as yet been uniformly adopted. Investigators whose forte lies more in anatomical studies have accepted it with enthusiasm, and in cases where difficulties were met with, have sought to surmount them with the aid of supplementary hypotheses. They draw attention more especially to the fact that such mobile starch-grains are never absent from the higher plants, that they are to be found nowhere else in such plants. Conversely, no starch, or at least no mobile starch, is found in organs which do not react geotropically. Still, however, there are geotropic organs without starch (e.g. certain Fungi, root-hairs) or without mobile starch (*Caulerpa*); in such cases other known or hypothetical bodies must be regarded as statoliths, or the statolith function must be accorded to non-mobile starch-grains. In fact, every starch-grain imbedded in sensitive protoplasm must be able to induce perception, and that too without change of position. To regard such apparatus as reduced or rudimentary, and to claim that statocysts with mobile starch have a greater functional capacity, is to look at the matter with the eye of faith!

Regarded more from the physiological standpoint, the hypothesis must be more sceptically received. In the first place, it must be noted that, in its original form, it is contradicted by physiological experiment; for it could be shown, both by rotation experiments and by intermittent stimulation, that a geotropic curvature arises when there is no unilateral accumulation of starch-grains. Since, however, HABERLANDT has more recently suggested that such an aggregation is unnecessary, and since he has laid the chief stress on a unilateral pressure excited by the starch-grain, his theory can no longer be attacked experimentally. We cannot see that this improves matters, for the theory at the same time becomes incapable of demonstration. Certainly attempts have been made to show that the unilateral pressure must proceed from starch-grains, not from any other constituents of the cell; but the methods (e.g. high or low temperatures) which are employed in removing the starch-grains are all open to the suspicion of affecting at the same time the sensitivity of the protoplasm.

We must content ourselves with these few observations on the voluminous literature which has gathered round HABERLANDT's and NĚMEC's hypothesis:

the principal treatises are: BACH (1907); CZAPEK (1906); DARWIN (1903, 1904 a, 1904 b); FITTING (1905, 1907); GIUS (1905); HABERLANDT (1902, 1903, 1905, 1906 a, b); JOST (1902); LINSBAUER (1907); NĚMEC (1902, 1904, 1905); NOLL (1902, 1905); SAMUELS (1905); SCHRÖDER (1904); TISCHLER (1905); ZACHARIAS (1905). Were we to attempt to state the pros and cons in full detail, we should have to devote a whole lecture to the subject.

The change in position of the starch-grains is not the only change which has been observed in geotropic organs, for NĚMEC (1901) has shown that peculiar rearrangements take place in the protoplasm of geotropically stimulated cells, but this phenomenon can scarcely be regarded as a direct effect induced by gravity. Chemical as well as histological research on this subject has led to certain results. G. KRAUS (1880, 1884) was the first to show that the amount of sugar present in the under side of horizontally laid shoots at first increased, while the amount of acid decreased; later on both decreased. Neither phenomenon occurs in absence of oxygen, so that they may perhaps be connected with the process of curving, and not with the perception of gravity, for the perception may take place in absence of oxygen. CZAPEK (1898, 1906) has recently attempted to show that a phenol derivative accumulates in geotropically stimulated root apices, the identification of which with homogentisinic acid has at least not been confirmed (SCHULZE, 1907). The accumulation of this substance may arise from the fact that its destruction under normal conditions by an enzyme is inhibited by an anti-enzyme, but the fact itself is as yet not perfectly established (comp. FITTING, 1907), and its interpretation opens up still greater difficulties. Since this same substance increases also after phototropic and hydrotropic stimulation, it is obvious that it can have no special relationship to the perception of the gravitational stimulus. Again, it can have nothing to do with the curving, for it takes place above all in apices which remain straight.

445. *Lecture XXXV is XXXIV in 2nd German Edition.*

446, l. 15, *for* bent *read* directed

447, l. 12, *for* branches *read* many branches

448, ll. 28–9, *for* especially is evidence . . . compensated *read* further, PORTHEIM'S (1904) results do not altogether support WIESNER'S view.

l. 36—P. **450**, l. 16, *for* A corresponding experiment . . . basal nodes *read* SACHS has carried out a corresponding experiment on the root. As in other correlations so here also it is seen that an alteration in the lateral organs takes place not only after removal of the chief axis, but also after inhibition of its functions. Thus the principal root is replaced by a lateral one when the growing point of the former is encased in gypsum (BRUCK, 1904).

The question now is whether the plagiotropism of the lateral branches is an inherent character of these branches, or whether the rest position is the result of two directive forces, so that, though naturally orthotropic, they are diverted from the perpendicular by influences emanating from the chief axis. The influence of the chief axis is most clearly demonstrated when geotropism is excluded by rotation on a klinostat. Under these conditions the lateral root does not assume casual and irregular orientation in relation to the chief axis, but forms a definite angle with it known as the 'special angle'. In roots this 'special angle' is, in general, greater than the limiting angle induced by positive geotropism: the lateral roots, that is to say, when on the klinostat stand out more at right angles from the primary root. The limiting angle observed when the roots are subjected to the influence of gravity is not constant, but may be reduced by employing greater centrifugal force (SACHS,

1874). This fact indicates clearly that the angle is the resultant of two forces. The relationships of lateral branches are of the same nature, for they also assume a special angle on the klinostat, and this is subject to alteration by negative geotropism. Negative geotropism has the effect of changing this special angle, so as to make it sometimes less, sometimes greater, according to the stage of development of the branch. Thus one often finds the axis of inflorescence directed quite perpendicularly upward (e.g. in *Aesculus*), while in *Pinus* all the young shoots at first stand up vertically, just like the candles on a Christmas tree, and then gradually assume an oblique or horizontal position.

Taking all these facts into account the question arises whether plagiotropism is, generally speaking, determined by correlation influences. This is certainly not so, since we shall learn presently that the main shoots and primary roots may become plagiotropic in consequence of external influences. On the other hand, we must note at this point that not only do the relations between axes and lateral branches affect geotropism, but that other correlations also play a part. Thus MIEHE (1902) has shown that the power of geotropic response of many shoots depends on the presence of the growing point. After that is removed no geotropic curvature takes place, although geoperception does not occur in the growing point.

Although we have previously stated that correlations, as well as geotropism, determined the lie of the lateral branches, we have not exactly indicated the force that operates in opposition to geotropism. According to BARANETSKY (1901) this force is that of autotropism, which attempts to undo curvatures induced by geotropism. It can scarcely be doubted that we should attribute a significance of this kind to autotropism, the nature of which we have already defined. Still there is another phenomenon which plays an important part—the so-called 'epinasty' (WIESNER, 1902; PFEFFER, Phys. III. 253). Under the influence of gravity there gradually arises the peculiarity that the upper side of the branch exhibits a more vigorous growth in length than the under side. Should epinasty be the only active agent, the branch must bend so that the upper side becomes convex, while, owing to negative geotropism, the under side should become convex. As a matter of fact, the former curvature takes place on the klinostat, for although epinasty arises from the unilateral influence of gravity, yet it does not cease at once if the influence of gravity is put out of account, but operates for long afterwards.

In addition to autotropism and epinasty, we must note finally the purely physical action of the weight of the branch itself, which must produce an effect in bending the later shoots. To these mechanical bendings are certainly often to be attributed the vigorous reactions on the part of the plant which again induce a lifting up of the shoot. Such weight curvatures are very obvious in certain 'weeping trees', such as *Fagus* and *Salix babylonica* (VÖCHTING, 1884).

450, l. 23, *after* plagiotropic. *read* (According to HABERLANDT (1903) a low temperature should quite inhibit geotropism. Further research is required to show whether, in VÖCHTING'S and LIDFORS'S experiments, the shoots were geotropic.)

452, l. 55, *after* downwards. *read* BARANETSKY (1901) has in many cases arrived at results contrary to those of FRANK; the whole question wants thorough investigation.

454, l. 24, *for* stand *read* strand

455, l. 1, *for* weight *read* gravity

457, ll. 39–42, *for* If it were . . . counteracted. *read* If, after a certain time, for internal reasons, another surface should grow more vigorously, the apex of the shoot must first of all be elevated, later on the side applied to the stick would grow more rapidly, and hence the tension would be relaxed.

458, l. 18, *for* 1882 *read* Lectures

l. 46, *for* AMBRONN, NOLL, and KOLKWITZ *read* AMBRONN (1884), NOLL (1892, 1901), and KOLKWITZ (1895).

459, l. 2, *after* of them. *read* If, after decapitation, the apical end of a suitable twiner be fixed, the free base performs twinings in a direction the reverse of the original; a left-handed twiner becomes a right-handed. This phenomenon is analogous with that discussed on p. 440.

460. *Lecture XXXVI is XXXV in 2nd German Edition.*

ll. 26–39, *for* From the analogies . . . with a window. *read* In order to study heliotropism by itself it is necessary to exclude geotropism. This may be done by allowing the plant to rotate in a vertical plane on a klinostat whose axis lies horizontally, and at the same time arranging that light falls on it on one side only, by placing the plane of rotation parallel to a window.

462, l. 15—P. **463**, l. 10, *for* Before considering . . . Fig. 146. *read* If we represent this conclusion in the form of a curve where light intensities are indicated on the abscissa and heliotropic curvature (as measured by the angle of curvature) on the ordinates we arrive at a diagram such as is represented at Fig. 146.

463, ll. 21–4, *for* The problem . . . internal conditions. *read* The determination of the position of the other cardinal points of this curve has been only partly settled. Thus FIGDOR (1893) has attempted to determine the lower limits of light intensity which are still able to induce heliotropic curvature when applied unilaterally. He found that in etiolated seedlings of *Vicia Faba* this lower limit was about 0·002 normal candle-power. Still, other flowering plants give other results; *Lepidium sativum* still showed heliotropism when the light was equivalent to 0·0003 candle-power, while 0·016 candle-power was insufficient to induce curvatures in *Raphanus sativus*.

Exhaustive research on other plants should be able to determine the minimum light intensity impinging unilaterally, and, further, should allow of the position of the other cardinal points being settled. So far, we know that we have no constants to deal with; on the contrary, the cardinal points vary both according to external factors and internal processes.

l. 36, *for* negative *read* a negative

464, l. 5, *for* unilateral *read* artificial unilateral

ll. 28–48, *for* It was already . . . relationship. *read* Over and above the direction and intensity of light the wave length is of importance. It has long been recognized that rays of different wave length do not act in the same way. The more highly refrangible rays which are more especially concerned in the formative activity of light (p. 310) have been found to be also those especially concerned in heliotropism. WIESNER (1878) found that the rays at the limits of the violet and ultra-violet regions were the most active, and that the activity decreased from that point, so that, in yellow light, practically no heliotropic curvature took place at all. The movements began again, however, in red light and increased towards the ultra-red, although this was not true of every plant examined. Negatively heliotropic organs, according to WIESNER, behave like positively heliotropic ones.

If unilateral light be allowed to impinge horizontally, seedlings also take up a completely horizontal position if the light be of a certain intensity (WIESNER, 1878). Since, under weaker illumination, they do not succeed in reaching this plane, but grow obliquely upwards, we must assume that geotropism is co-operating in the movement, and that the light stimulus is too weak to overcome completely the stimulus of gravity. Autotropism, however, has something to do with the result here as well as in geotropic curvature, and it also might aid in preventing the shoot from orientating itself fully in the direction of the incident ray. The case is otherwise with negative curvatures induced by intense light, as OLTMANNS has observed in *Phycomyces*. Here the plants always grow obliquely, and it is very probable that it is due to the fact that they are no longer orthotropic but plagiotropic. There are other organs, however, which always behave plagiotropically, and of these we may select foliage-leaves as an illustrative example.

465, ll. 12–13, *for* These phenomena . . . Fig. 147. *read* Not all plants behave in this way. In *Calystegia* it may be seen that the leaves placed on the stem laterally and posteriorly (as regards the incident light) twist and curve their petioles until the laminae succeed in regaining the same position in relation to light as those which arise on the front of the stem.

ll. 44–9, *delete* we need only . . . p. 438).

468, ll. 11–13, *delete* It was pointed out . . . rejected.

ll. 53–5, *for* and heliotropic . . . (p. 444) *read* and excitation, which are regarded previously as identical, are in this case two distinct phenomena

470, l. 6, *after* excitation. *read* What we know as to the transmission of the stimulus in the Gramineae may be also applied to other relations. At present it need only be noted that this transmission is doubtless carried out by living parenchyma (ROTHERT, 1894; FITTING, 1907). One must suppose that the intercellular protoplasmic threads are the media for the transference from cell to cell; the special fibrillae described by NĚMEC (1901) cannot play any important part in the conduction of the excitation (HABERLANDT, 1901).

ll. 36–49, *for* The perceptive power. . . . Neither is it true *read* According to HABERLANDT'S (1905) researches, the movements in the petiole in other plants, e.g. *Tropaeolum, Humulus*, &c., are to be accounted for by the perceptive powers of the lamina. Probably (KOHL, 1894) the negative heliotropism of many roots is to be attributed to perception in their apices. It is not the case, however,

471, ll. 10–31, *for* in this case . . . establish the fact *read* i.e. purely mechanically, and this possibility must not be entirely excluded from consideration, seeing that, according to MAXWELL, a pressure amounting to about 0·5 mg. per sq. m. is induced in any medium through which a light wave is propagated, in the direction of the path of propagation. The existence of this pressure has been more recently confirmed experimentally by LEBEDEW. Apart altogether from its limited amount, however, there are other reasons for doubting whether heliotropic perception is at all dependent on this pressure. It is more probable that light induces certain chemical changes; but an action like that which takes place in silver salts is inconceivable, because the red rays, which perform no function in photography, were found to be active in WIESNER'S experiments. It is certainly possible that heliotropic curvature in red rays is a phenomenon *sui generis*, which may be compared with thermotropic processes, which we shall consider later on (Lecture XXXVII); and if that be so, heliotropism might be, in the restricted sense, included amongst those light effects which, for the sake of brevity, may be termed photographic. On the other hand, it is also conceivable that definite chemical reactions are rendered possible

owing to the action of those kinds of rays which WIESNER found to act heliotropically.

Meanwhile we need not consider further the so-called chemical effect of light. If it can be proved that the plant reacts, as we may say, not to light but to an effect produced by light, then heliotropism may be regarded as a special instance of chemotropism (Lecture XXXVII), and would, for that reason, be still further removed from the category of phenomena that geotropism belongs to, where, as we have seen, it is not gravity itself as such, but the actual weight associated with gravity that is perceived. That geotropic and heliotropic perception are not identical is shown by the quite different relationship in which they stand to external conditions, especially to oxygen. Thus CORRENS (1892) has shown

l. 39—P. **477**, l. 37, *for* Although it follows . . . summary only. *read* On the other hand, RICHTER (1906) has shown that so-called ' laboratory air ' inhibits geoperception, while photoperception is at least not affected, possibly even increased.

In order that a heliotropic excitation should follow on a light impact, the light, as we have seen, must affect the plant unilaterally. We speak of light in heliotropism as the stimulus-medium, and its unilateral incidence as the stimulus-impact. Just as we were able to prevent geotropic curvature by continuously rotating the plant on a klinostat, so we may also prevent heliotropic response by rotating the plant or the source of light. Again, geoperception takes place on the klinostat, and similarly photoperception occurs in a plant illuminated on all sides. Perception is followed by excitation, and excitation by a reaction, but since in orthotropic organs this will occur equally on all sides, no curvature can result. When we inquire more closely as to the significance of unilateral light incidence, we find that it has been differently interpreted by different authors. SACHS laid special stress on the fact (compare MÜLLER-THURGAU, 1876, and SACHS'S Lectures) that the light rays penetrate the plant body obliquely. He assumed that an orthotropic organ is in a heliotropic rest position when the light rays impinge on it in the direction of its axis, whilst plagiotropic organs take up a definite angle to the line of incidence of light. On the other hand (DARWIN, 1881 ; OLTMANNS, 1892), it was held that the reaction depended on unequal light intensity in different parts of the plant. Neither view has as yet been exactly established, and it is questionable whether it is possible to place the plant under such conditions that different parts may be illuminated unequally without passing from the more to the less luminous light rays. Although, therefore, it is not at present possible—and perhaps may never be possible—to come to a decision as to these two views, still, in consequence of more recent experiments carried out by FITTING (1907), the idea we previously brought forward may be set aside, viz. that the stimulus which induced heliotropic curvature lay in the inequality in illumination on different flanks of the perceptive organ. We fancied, more especially, that a seedling *Avena*, one half of which, say the left, is shaded, would exhibit curvature to the right if the right half were illuminated equally brightly from before and behind. One of FITTING'S experiments renders that view improbable. If the apical region of the cotyledon of *Avena* be split longitudinally, and if one half be darkened while the other half is illuminated on both sides, no curvature follows, neither in the apex itself nor in the darkened base. On the contrary, curvature always takes place in the direction of the light when the light impinges unilaterally on the half cotyledon, and it is perfectly immaterial whether the other half be darkened or entirely removed. The darkened base also in this case curves in the direction of the light impinging on the apex, whether this be on the outside, the inside, or a flank of the segment of the cotyledon. Further still, FITTING was able to show that the transference

of the stimulus to the darkened base took place with scarcely diminished rapidity and in a perfectly normal manner, when the continuity of the tissues was interrupted by incisions made at adjacent regions of the cotyledon from opposite sides, and reaching beyond the middle. It may be deduced from this that the stimulus can be transmitted transversely as easily as longitudinally, and one can only conclude, as FITTING does, that a polarization of the cells or of the constituents of the cells of the perceptive organ arises from the impinging light, a polarization which is then continued downwards to all other cells. We are, however, entirely ignorant as to the nature of this polarization, whether it consists in the arrangement of definite protoplasmic particles, or whether it lies in the accumulation of certain chemical substances which must possess different characters at the two poles created by the light rays. At all events from all the experiments which have been carried out there is evidence showing that the response in the darkened base of the cotyledon is not a consequence of excitation transmitted straight downwards from two unequally excited parts of the apex, being differential on the concave and convex sides.

A consideration of MASSART'S experiments (1888) has led one to a similar conception. This investigator has illuminated unequally opposite sides of the sporangiophores of *Phycomyces*, and has determined what difference in light intensity induces curvature towards the more illuminated side. Curvatures took place when the light intensities differed in the proportion of 100 to 118. This ratio was found to be constant for light of varying intensity. Thus MASSART was enabled to prove in the case of heliotropism the validity of WEBER'S Law as to the relation subsisting between the amount of the stimulus and sensitivity, a law which we shall have to refer to later on in reference to other stimulus phenomena, and thus he was able to confirm an earlier suggestion made by PFEFFER (1884). Further investigations are urgently needed, however, in order to show whether this relation is really true of all light intensities; this, we think, is scarcely likely. Be it as it may, MASSART'S experiment is not to be compared with an ordinary heliotropic experiment, for here we are dealing with two antagonistic stimuli acting on the plant, as in intermittent geotropic stimulation, and it is able to respond to the stronger of these only if the difference between them is appreciable to the plant. In accordance with what has been said, we must not, on the contrary, look for the cause of the stimulus in ordinary unilateral stimulation in the difference between the illumination of the side facing the source of light and that facing away from it; in this case we have to do only with a single stimulus.

To HABERLANDT (1905) we owe a new conception as to the stimulus impact in heliotropic curvature. The epidermal cells of many leaves bear conical papillae, which split up the impinging light like lenses, so that a median region of the inner walls of the epidermal cells is more brightly illuminated than the margin. This difference in illumination must, according to HABERLANDT, induce a heliotropic stimulus, the leaf being in the rest position when the spot of light lies in the centre of the cell, and a movement being induced when the spot is eccentric. It is not altogether easy to apply this hypothesis to orthotropic organs, and further, the theory has no sense in it, for orthotropic organs which are most sensitive to light, such as grass seedlings, have no papillose epidermis. Again, FITTING has shown sufficiently clearly in the experiments quoted above that the inner side of the epidermis of the cotyledon, or any layer of epidermal cells which may be exposed by wounding, plays exactly the same part in the reception of the heliotropic stimulus as the external epidermis under normal circumstances. It has yet to be proved that the upper epidermis of a foliage-leaf has any determinative significance in this relation; and it is well known that not every leaf sensitive to light is papillose.

Again, KNIEP (1907) has shown that when the convergent lenses of the epidermis are transformed into dispersing lenses by smearing the epidermis over with paraffin oil the leaves react heliotropically just as before, although the centre of the cell in the rest position is darker than the margin. HABERLANDT (1906–7) has entirely neutralized the lens action of the epidermis by covering the leaf with water, and found that the heliotropic sensitivity of certain leaves was then inhibited. Further research has still to show, however, whether this was due to the injurious effect of the water or to the suspension of the action of the lenses.

Whatever may be the special stimulative impact that induces heliotropic curvature, this stimulus must have operated for a certain time before curvature follows as an after-effect. Here, as in geotropism, we can recognize a presentation period. According to CZAPEK (1898 a) it amounts to 7 minutes in the cotyledons of *Avena* and in *Phycomyces*, 10 minutes in the hypocotyls of *Sinapis alba* and *Beta vulgaris*, 20 minutes in the hypocotyl of *Helianthus*, and 50 minutes in the epicotyl of *Phaseolus*. Since, however, CZAPEK's estimates have been shown to be too high as regards the geotropic presentation period, so the same may be true here also ; nor has it been determined whether and to what extent the presentation period is dependent on the intensity of light. According to PFEFFER (*Phys.* III, p. 210) flashes of light of the very shortest duration but of sufficient intensity lead ultimately to heliotropic curvature by summation, and the pauses between individual stimuli may be in this case 15–30 times as long as the stimuli. According to WIESNER (1880) the sum of the individual stimuli may even be less than the presentation period of the continuous stimulus—that is, the intermittent stimulation may be more effective than the continuous ; but this wants confirmation.

Although, as we have already seen, geotropic differs from heliotropic perception, we cannot say the same of the excitation which is induced after the expiry of the presentation period. It is quite possible that it may be identical for the two stimuli, just as the process of curvature is identical in both cases. How transference of the excitation is brought about is as yet unknown. All that need be said as to the path followed has been indicated above, still it may be added that it is restricted to one direction, viz. towards the base.

Having now discussed heliotropic and geotropic movements separately, we have still to glance at movements which result from the simultaneous or rapidly consecutive stimuli of light and gravity. It must be noted more especially that the plant frequently does not assume the orientation which should be arrived at as a resultant of antagonistic geotropic and heliotropic curvature. This fact may be illustrated by a few examples (CZAPEK, 1895).

477, l. 38, *after* falls *read* horizontally

478, ll. 4–30, *for* It is obvious . . . presented by them. *read* These results show that differences in the plants in the first instance make themselves apparent, so that obviously in some cases geotropism, in other cases heliotropism is predominant. This is perfectly conceivable, for we already know that sensitivity to gravity may be affected by light, and so also heliotropic sensitivity might be altered by the action of gravity. Quite other factors still, however, play a part in the positions of equilibrium that have been observed. Thus especially there is the cessation of geoperception induced by the air of a laboratory. MOLISCH's (1905) and RICHTER's (1906) experiments which have demonstrated this effect render necessary in our opinion an entirely fresh investigation, from top to bottom, of the whole problem of the simultaneous action of geotropism and heliotropism. That CZAPEK (1898), to whom we owe the latest

exhaustive researches on the subject, must have carried out his experiments in very impure air, may be deduced from his own statements (1906). Since it is impossible to say what part this factor played in other researches, it would appear to us useless to go into the results previously obtained by MOHL (1856), MÜLLER-THURGAU (1876), VÖCHTING (1888), and NOLL (1892), and to attempt a discussion of the question as to whether the effect of one directive force on the other makes itself evident at the perceptive stage, in the excitation or only in the response.

478. *Lecture XXXVII is XXXVI of the 2nd German Edition, and, under title of* THERMOTROPISM AND OTHER TROPISMS, *begins with last paragraph on p.* 478.

479, l. 45, *for* can be fully *read* can be somewhat more firmly

480, ll. 28–42, *for* Obviously, growth . . . WORTMANN *read* Since we do not know whether we have to deal with a difference of temperature in the individual cells or in the entire organ, it is impossible to say how great the difference in temperature must be before the liminal intensity of the stimulus is reached. Nor have any investigations been made as to how the height of the absolute temperature affects the stimulus threshold or how the stimulus increases as the temperature rises. There is ample room here for experimental inquiry.

As to the purely physical or chemical action of heat which leads to perception we know nothing. It is not very probable that thermotropic perception is fundamentally similar to geotropic perception ; one of the facts which WORTMANN

481, ll. 26–7, *for* in all probability . . . XLIII). *read* in all probability it is some effect induced by the current that is perceived. It has not as yet been clearly made out whether we have to deal with a unilateral injury to the root apex, as GASSNER (1906) thinks, or a local accumulation of electrolytic decomposition products, as BRUNCHORST (1884) and EWART (1905) assume. If the first view be correct, galvanotropism would be allied to traumatotropism; if the latter, the phenomenon should be associated with chemotropism, of which we have now to speak.

l. 39, *after* Fungi *read* (compare, however, FULTON, 1906)

l. 52—P. **482**, l. 9, *for* Whenever . . . current. *read* The fungal hyphae then grew in the direction of the diffusion flow and toward the greater concentration.

482, l. 44, *for* doubfully *read* doubtfully

l. 54—P. **483**, l. 2, *for* The determination . . . concentration ? *read* Just as in heliotropism we established, in addition to a liminal intensity for unilateral stimulation, a liminal intensity for bilateral, but unequally vigorous, stimulation, MIYOSHI has also investigated, in the case of chemotropic stimulus, how great the difference in concentration must be, if the same stimulant operates on a fungal cell from two sides.

483, l. 23, *after* XLIII, p. 542). *read*

The question now comes to be whether MIYOSHI's experiences from stimulation on two sides may be applied to stimulation arising from a single diffusion flow. Does the cause of stimulation in this case also lie in the fact that the side of the fungus hypha nearer to the diffusion centre borders on a higher concentration of the stimulant than the opposite side ? It can scarcely be conceived that in a diffusion area with constant flow the fall in concentration can be so rapid as to sink from 5–10 on one side to 1 on the opposite side

of a fungal hypha. Further investigations are needed to clear up this poin
In regard to chemotropism also it is not known in what the primary act
perception consists ; it is not known whether the stimulant must first of a
enter the plasma or whether bodies which do not so enter may act as stimulan
(PFEFFER, *Phys.*).

l. 33, *for* glucose *read* a glucose
l. 35, *for* or *read* and
ll. 44–55, *delete* Starting from . . . 10 per cent.

484, ll. 14–15, *for* [As to the . . . (1904).] *read* Chemotropic sensitivity occu
also in roots as well as in the structures named ; this has been demonstrate
by SAMMET (1905) and LILIENFELD (1905). We cannot enter here into
description of the substances which induce positive or negative curvatur
Since numerous bodies which are quite useless to the root induce positiv
curvature, chemotropism in the root can have no great biological significance
it appears to play an important part, on the other hand, in the search for th
oogonia by the antheridia in *Saprolegnia*, and in the process of conjugatio
in the Conjugatae.

ll. 23–54, *for* MOLISCH's method . . . root apex, *read* MOLISCH's metho
of experimentation does not indeed exclude stimulation as the result of unequ
atmospheric moisture (hydrotropism) (BENNET, 1904), still, after SAMMET
experiments (1905), there is no reason to doubt the existence of aerotropism
SAMMET has placed roots and shoots on the one hand in a gaseous diffusio
flow, and on the other allowed gaseous currents to play on them unilaterall
He found that roots always exhibited positive curvatures at first both i
oxygen, carbon-dioxide, and hydrogen, as well as to alcohol, ether, ammoni
but these curvatures gradually become negative, for instance, with carbo
dioxide. The shoots investigated show no curvatures when carbon-dioxid
and oxygen are used, but react negatively with the alcoholic vapour, &
The biological significance of the whole phenomenon is very doubtful
and as there are many discrepancies in the results obtained by MOLISC
BENNET, and SAMMET, a reinvestigation of the whole problem seem
desirable.

MOLISCH noticed that aerotropic movements took place in roots aft
decapitation, and SAMMET has confirmed this; hence

485, l. 25, *for* in the growing zone. *read* no matter under what psychrometr
conditions the growing region be placed.
l. 37, *for* lead . . . this case. *read* exhibit quite peculiar phenomena.
l. 46, *after* 1892 *read* and 1906

486, l. 1, *for* the saturation . . . sufficiently *read* there is always a gradier
in the concentration of the water vapour sufficient
l. 22, *after* nature *read* (compare also FITTING, 1907).
l. 45, *for* (Lecture XXXVIII). *read* These movements are certainly
a rule not very conspicuous (NEWCOMBE, 1904), and hence, after their firs
discovery by SACHS (1873), their existence was often denied, or they wer
regarded as traumatotropic reactions. In the next lecture, however, we sha
get to know of unmistakable movements in response to contact in othe
cases.

487. *Lecture XXXVIII is XXXVII of the 2nd German Edition.*
l. 49, *for* 1903 a *read* 1903

488, ll. 15–16, *for* Organographie, p. 610); *read Organography*, II, p. 426);

489, l. 1, *for* curve *read* surface

l. 2, *for* affects successively *read* is continuously passing round to
ll. 38–9, *for* base to the apex, *read* apex to the base,
l. 49, *for* (1903 a) had *read* (1903) has
l. 52, *for* side only a short distance away *read* side for only a short stretch

490, ll. 37–8, *for* placed in position simply by *read* merely stirred by

491, l. 2, *for* fix bodies to *read* hold firmly
ll. 26–9, *for* The tendril . . . to them, *read* It is not, however, usual that repeated contact is a condition of stimulation ; a single contact, which indeed certainly always consists of several individual stimuli, induces this result, if the contact be sufficiently vigorous.
ll. 53–5, *for* Still it must . . . so that *read* Since, however, these 'pits' occur only in Cucurbitaceae and Sapindaceae, while, on the other hand, the tendrils of *Passiflora*, in spite of the absence of such arrangements, are extremely sensitive,

492, l. 8, *after* to say. *read* HABERLANDT'S view apparently is that mechanical bending of the tendril is not operative, because the tangential tensions, which arise in consequence, are too feeble. The illustration on which he bases his argument is not, however, very satisfactory. As a matter of fact, it is possible to bend the tendrils much further and to induce, therefore, much greater tangential tensions without any response ensuing (FITTING, MS.).
l. 19, *after* stimuli *read* ; FITTING has also obtained response by wounding.
ll. 23–5, *for* curvatures due . . . wild state. *read* curving is the only kind of reaction which tendrils exhibit.
l. 30, *for* (1903 a) *read* (1903)

494, ll. 7–11, *delete* It is very . . . present case.
ll. 15–16, *for* in an effort . . . instance in *read* in the preliminaries to curvature, in the mere tension of the parts concerned, and not be due only to
l. 46, *for* proximately *read* proximally
l. 57—P. **495**, l. 1, *delete* which are . . . support.

495, l. 18, *after* region.] *read* The cause of this phenomenon is not quite clear. It does not depend, at all events, on the strain to which the tendril is subjected, but is in some way or another caused by the twining round the support.

497, l. 12, *after* concentrate. *read* Fig. 156 (left) shows the result of a single eccentric stimulation.
ll. 25–6, *for* In all these . . . tendrils. *read* In this respect *Drosera* differs from a tendril, for in the latter case a single contact is sufficient, but that contact consists of numerous single stimuli.

498, ll. 4–8, *for* found that many . . . were first digested *read* many that were obviously neither useful nor harmful to the leaf, and, on the other hand, some that were well-known poisons, e.g. sublimate, and finally nutrients also, which, like ammonium salts or phosphates, were absorbed at once, or which, like proteid and proteinaceous animal compounds, had to be first digested
l. 30, *for* movements . . . take place *read* movement increases markedly
l. 43, *for* i.e. in *read* which is
ll. 45–9, *for* and we further . . . tentacles. *read* moreover, the aggregation occurs also in *Drosophyllum*, where no curving movements take place. It is worthy of note that, according to DARWIN, aggregations, though certainly much feebler in character, occur in decapitated tentacles ; PFEFFER assumes that this aggregation is transmitted from a directly stimulated tentacle. The question requires reinvestigation.

499, ll. 23–7, *for* [The mechanics . . . 1903 b).] *read* This proves that these tendrils also possess a certain degree of dorsiventrality.

Further, in the tendrils studied by FITTING (1903 a), curvatures followed wounding, not in all species, but always in the same direction. These curvatures may be induced by decapitation or by incisions as deep as the central cylinder. It is worth noting that, after basal incision, inrolling still takes place at the apex, and that the transmission of the stimulus is unusually rapid and far-reaching.

500. *Lecture XXXIX is XXXVIII of the 2nd German Edition.*

l. 10, for NYCTITROPISM *read* NYCTINASTIC MOVEMENTS

l. 21, *for* speaking generally, we may employ the terms *read* we may employ the more general terms

l. 44—P. **502**, l. 47, *for* These same . . . decreased. *read* Since in nature photonastic and thermonastic movements take place especially in relation to the alternation of night and day, we may also speak of them collectively as 'nyctinastic movements'. Under this term may be also included the less important reactions which result from changes in degree of moisture—'hydronastic movements'.

The reason why we associate nyctinastic with haptotropic movements is that the mechanics of the former often entirely correspond to those discovered in tendrils, and this is true of all nyctinastic movements which are carried out by growth agency. We may commence with the thermonastic movements seen in many flowers.

If a spring flower (such as a tulip or crocus) be subjected to increased temperature, e.g. in a warm room, more vigorous growth at once takes place on the upper sides of the perianth leaves, and so the flower opens. Indeed the upper sides become more or less convex, and the flower opens more or less according to the height of the temperature. Curvatures visible to the naked eye appear in the crocus even when the temperature has been raised only half a degree. If the temperature be raised considerably (e.g. 10°–20°) the curvature does not remain constant when the temperature is maintained at that height; on the contrary, an incurving or closing follows. This occurs in the tulip within two hours, but later in the crocus. This closing movement, however, by no means brings the flower back once more to the state in which it was when in the cold; the leaves take up a new position of equilibrium, corresponding to the increased temperature. If the temperature has been slowly raised the opening takes place more slowly, and the supra-curvature is not so great.

In endeavouring to elucidate the cause of the curvature and recurvature we must determine the growth on the upper and under sides of the perianth leaves during these movements by the aid of marks whose distances apart have been measured by a micrometer. The marks are made on the basal part of the leaf, for it is there that the most vigorous growth and greatest curvature take place. The results of such measurements are expressed graphically in Fig. 157 *a*. We see that in the tulip, as soon as the rise in temperature begins to operate, growth sets in on the upper side of the leaf, and it shows a very considerable extension (about 7 per cent.) in the course of one hour. At the same time the under side decreases in length, while the median region shows growth which is markedly more rapid both as contrasted with that occurring at 7·5° and that later on at 26°. In the second hour the under side of the perianth, however, begins to grow with considerable acceleration in the median region, and thus the backward curvature is brought about. A comparison of Figs. 154 and 157 *a* shows at once how remarkably similar this curving process is in its mechanics to that observed in tendrils. The only difference is that in the tulip the reverse action on the under side begins before growth

on the upper side has returned to the normal state ; the pause which FITTING (1904) observed to occur in tendrils between the two periods of accelerated growth is absent. The fact that in the crocus (Fig. 157 *a*) a pause occurs just as in tendrils shows that no special importance attaches to this point. The backward movement takes place here very much later than in the tulip, often, in fact, about three hours.

Fig. 157 *a*. Growth in thermonastically stimulated flowers (after WIEDERSHEIM, 1904). Percentage increase in growth of the upper (thick line), under (thin line), and median (dotted line) regions. *A*, tulip, after transference from 7·5° to 26° C. ; *B*, crocus, after transference from 9·3° to 20·8° C. The abscissa shows time in hours from the commencement of stimulation ; the ordinates, growth increments.

The similarity between thermonastic floral movements and tendril movements is much increased if the behaviour of the two types of organ be observed under conditions which do not permit of curvature taking place. WIEDERSHEIM (1904) was able to establish a pause between two successive periods of growth acceleration in floral leaves which were fixed, as FITTING had found in tendrils. From this it must be concluded that a reverse movement takes place in flowers not only after an accomplished curvature but also after the effort to curve. A further analogy with tendril movements shows itself in the fact that in floral movements also every time the temperature is raised a new stimulus is administered, both at the period of incurving and of recurving also ; the plants do not become accustomed to the stimulus, or do so only quite gradually, and it is possible to induce opening movements with appropriate elevations of temperature for many hours (JOST, 1898).

In spite of all these analogies, one must not forget the differences which exist between tendril and floral-leaf movements. These stand out prominently when we consider the effect of cooling on the perianth leaves. Cooling acts precisely in the reverse way to heating, i.e. it accelerates growth on the under sides of the leaves and induces closure of the flower. In tendrils, however, even in those which are haptotropically sensitive all round, a rise in temperature induces the same curvature as a fall. Apart from the direction of curvature, the stimulus movement in flowers, after cooling, is of the same character as that after heating ; it is the result of more vigorous growth in the middle zone. This is seen from the following measurements made by PFEFFER (1875) of the growth in length of the middle zone of the crocus in percentages per hour :—

	At 17°–18° C.		At 7°–7½° C.		
	4 p.m.–9 a.m.	9 a.m.–12 noon.	1st hf. hr.	2nd hf. hr.	next 3 hrs.
Crocus No. 1	0·64	0·70	4·65	1·87	0·41
Crocus No. 2	0·67	0·74	6·21	3·27	0·34

It is not known whether an opening movement, i.e. an autotropic reverse action, takes place at continued lower constant temperatures, but it is very probable that that is the case.

Summarizing, we have established that the act of changing the temperature causes the average growth of the perianth leaves to exceed quite markedly the amount attained in the long run when the temperature is constant. A temperature so high or so low that it at last stops growth may indeed, at the moment of application, even induce a growth acceleration (comp. BURGERSTEIN, 1902). This acceleration is partial and occurs indeed on the under or upper side of the perianth, according as the temperature is lowered or raised. When the stimuli are vigorous the acceleration overshoots the mark—the new position of equilibrium—and it is then compensated by a second growth movement setting in on the opposite side.

ll. 48 and 50, *for* nyctitropic *read* nyctinastic

ll. 51–2, *delete* [As to other . . . 1905).]

503, l. 11, *for* Nyctitropic *read* Nyctinastic

ll. 24–47, *for* Certain conclusions . . . this subject. *read* The measurements made by PFEFFER (1875) and WIEDERSHEIM (1904) teach us something as to the mechanism of this curvature. The distribution of growth corresponds completely with that in thermonastic flowers. In *Impatiens parviflora*, for instance, a marked growth acceleration on the upper side follows a darkening of the leaf about midday. After a pause, when no growth takes place, an acceleration on the under side occurs about two hours after the darkening begins. If growth on the upper side has placed the leaf in a depressed lie, it is now raised again by growth on the under side, without, however, quite reaching the position it holds in light. That both movements are associated with growth acceleration scarcely requires statement.

For reasons which we shall soon learn, it cannot be said with certainty, as in the cases of tendrils and the tulip, whether the retrograde movement is due to autotropism or is a more complicated phenomenon.

ll. 52–3, *delete* [Evidence . . . (1904).]

l. 54 and P. **504**, ll. 3 and 8, *for* nyctitropic *read* nyctinastic

505, l. 23, *after* temperature *read* (about 30° C., KOŠANIN, 1905)

l. 37, *after* intense light. *read* After KOŠANIN'S (1905) researches there can no longer be any doubt that this is the correct view.

l. 44, *for* nyctitropic *read* nyctinastic

506, l. 12, *for* nyctitropic *read* nyctinastic; *after* movement *read* (comp. PANTANELLI, 1904, p. 316)

507, ll. 4, 18, 25, 28, 43, 55, *for* nyctitropic *read* nyctinastic

ll. 20–3, *for* [WIEDERSHEIM . . . conclusion.] *read* WIEDERSHEIM'S (1904) experiments have, however, shown that the dissimilar results obtained by extirpating half-articulations are due to the unequal severity of the operation. The observations carried out by WIEDERSHEIM still, however, clearly show that the effect described by PFEFFER takes place only in certain cases, and that, too, often very incompletely.

l. 31, *for* moderates *read* leaves

l. 39, *after* 506 *read* and WIEDERSHEIM, 1904, p. 27).

l. 44, *for* 1876 *read* 1875

ll. 48–50, *for* Whether this . . . to determine. *read* It is not very probable, however, that such a decrease in the resistance to flexion is generally and necessarily bound up with 'day sleep', for KOŠANIN found no change in the resistance to flexion both in the 'day sleep' induced by high temperature and generally in all thermonastic movements. It must be left for further research to settle whether this is really a point of difference between photo- and thermonasty.

l. 54, *for* nyctitropism *read* nyctinasty.

508, *for* nyctitropic *throughout read* nyctinastic

l. 48, *after* function *read* (JOST, 1895).

509, ll. 4, 13, 49, *for* nyctitropic *read* nyctinastic

510, ll. 30–3, *for* [As a . . . movements.] *read* A recently published work of SEMON (1905) does not settle the question.

l. 48, *after* too far, *read* (comp. also HENSEL, 1905)

511, ll. 29, 38, 45, *for* nyctitropic *read* nyctinastic

l. 51, *after* against cold *read* ; it may also protect pollen from rain.

512, *Lecture XL is XXXIX of the 2nd German Edition.*
l. 33, *for* nyctitropic *read* nyctinastic
l. 37, *for* nyctitropism *read* nyctinasty

513, l. 5, *for* nyctitropic *read* nyctinastic
l. 21, *for* nyctitropism *read* nyctinasty

515, ll. 35–7, *delete* As PFEFFER . . . swelling.
l. 53, *after* at the same time. *read* Less than a second intervened between stimulation and movement.

516, l. 16, *for* hapto- and nycti-tropism *read* haptotropic and nyctinastic movements.
l. 20, *for* excessive *read* abundant
l. 45, *after* movement. *read* This stimulus-movement may be termed 'seismonastic' (PFEFFER, *Phys.*).

517, ll. 20–4, *for* The sensitivity . . . need not enter. *read* Not only in the mode of perception, but also in the rate of reaction, the sensitivity of these plants is closely related to that of tendrils; hence sensitivity to contact is not sharply distinguished from sensitivity to shocks, and between *Mimosa* and tendrils as extremes there are many transitional stages. It is impossible for us to discuss all these cases; we will merely glance briefly at *Biophytum*, for this plant exhibits many points of interest worthy of note.

The leaves of this member of the Oxalidaceae are simply pinnate, and a pulvinus occurs at the base of the petiole of each leaf and of each pinna. The latter only, however, are capable of seismonastic movement, by which depression is effected. A few minutes after depression the leaf begins to rise again, but this erection is very soon interrupted in a very remarkable manner, and a renewed depression commences. As this depression is not carried so far, however, and soon neutralized by a second erection, the leaf, after a number of periodic oscillations, reaches again its rest position (DARWIN, 1881; HABERLANDT, 1898). Similar oscillations are also known to occur in the stimulus-movements (e.g. after thermonastic movements) of many Oxalidaceae, e.g. *Averrhoa* (DARWIN, 1881).

In conclusion let us briefly glance at the movements seen in the carnivorous plant, *Dionaea muscipula*, with which may be associated in all essentials *Aldrovanda vesiculosa*. The lamina of *Dionaea* consists of two semicircular half-blades, which are united medianly by an articulated mid-rib, and whose margins are fringed with peculiar teeth. On the upper surface of each half-lamina arise three long bristles, each with an articulation at its base. When one of these bristles is touched the leaf closes instantly, the upper surfaces approximating and the marginal teeth interlocking. The curving necessary to effect this movement takes place more especially in the mid-rib or in its immediate neighbourhood. As yet it has not been determined whether the cause of the curving is due to a relaxation of cells or whether it is a growth phenomenon. It would be remarkable if the latter were true, because, as a rule, growth curvatures arise from contact, while shocks give rise to contraction curvatures. In *Dionaea* we have undoubtedly to do with a shock stimulus, for a stream of water or a moist gelatine rod is able to effect stimulation. Further, the whole leaf surface, both upper and under side, is competent to receive such a stimulus, and not the sensitive hairs only. Again, the rapid transmission of the stimulus from the point of application of the stimulus to the motile zone is worthy of note. This plant still requires most careful investigation (Literature in PFEFFER, *Phys.*; FITTING, 1905).

l. 33, *after* in pairs. *read* As a rule this phenomenon is limited to the single secondary petiole; only when the leaf is especially sensitive is the movement

propagated to the other secondary petioles, the leaflets of which fold together, the movement being from the base to the apex. Exceptionally the shock stimulus may be transmitted as far as the primary articulation in which a depression is induced.

l. 42, *after* itself *read* from the primary root or from a lateral root.

518, l. 4, *after* concerned *read*; when these organs are stimulated by wounding the rate of transmission of the stimulus is, according to FITTING (1903), 10 mm. per second. Haptotropic stimuli are transmitted over the same distance, in the most favourable instance, in 1–3 minutes.

ll. 6–17, *for* seeing that . . . vascular elements. PFEFFER *read* Careful investigations into this highly remarkable phenomenon have been carried out only with reference to stimulation by wounds. The stimulus in this case appears to be transmitted solely by the vascular bundle. An incision made into the stem has no effect unless the central cylinder in which the vascular bundle lies is affected, but after every wound capable of inducing stimulation one sees a drop of fluid escaping from the central cylinder. On the basis of such observations PFEFFER

ll. 24–7, *for* If an incision . . . place in them. *read* The effect of anaesthetizing and killing short stretches of the conductive strands supports the view that the stimulus is transmitted by means of mechanical media of this kind. As PFEFFER (1873 b) and HABERLANDT (1890) were able to show, stretches thus altered could still transmit the stimulus, a fact which completely excluded the co-operation of living cells in the process. According to FITTING's more recent results, however, there is a difference between stimulus conduction in uninjured stems and in those subjected to the temperature of boiling water: in the latter case the stimulus is transmitted backwards only, in the former both ways, and hence it follows that the conduction is effected in dead cells in another manner than in living ones. PFEFFER believed in a variation in pressure in the vessels, and regarded the fluid exuded from them as water. He based his view on an experiment of DUTROCHET's (1837), in which the stimulus was still transmitted through regions of the stem from which the cortex had been removed.

l. 41, *for* hyphae *read* cells

l. 43—P. **519**, l. 41, *for* The one criticism . . . in dispute.] *read* Several criticisms may be advanced against HABERLANDT's conception, of which the following are the most important (FITTING, 1903, 1906). The tubular cells with their closed walls, which are pierced only by very fine protoplasmic threads, are not well adapted for the rapid transmission of streams of water, nor has it been found possible to accelerate such streams artificially by subjecting them to greater pressure. More important still is the fact that many plants, more especially *Neptunia*, a genus very closely allied to *Mimosa*, possess no such tubular cells, and the secondary roots of *Mimosa* itself are also destitute of them, although they are capable of transmitting a stimulus induced by wounding. Finally, it appears, according to FITTING's observations, that the wound stimulus in tendrils corresponds exactly with that in *Mimosa*—here also stimulation takes place only if the central cylinder be cut into, and here also drops of fluid escape. The fluid in the case of the tendrils, however, escapes from the sieve-tubes—tubular cells are entirely wanting. It would thus appear as though the sieve-tubes were the conductive agents in *Mimosa* also, and their distribution in the plant is not out of accord with that view, and, further, their open pores would appear to adapt them much better for such a function.

If, then, the transmission of the stimulus in *Mimosa* and related cases is effected by fluid currents in sieve-tubes, we should have to deal with a mode

of transmission widely different from that already met with, e.g. in heliotropic stimulus conduction. In that case what was transmitted from cell to cell was the protoplasmic condition induced by the stimulus at some particular region; here it is the stimulus itself that is transmitted; the movement of the fluid can scarcely operate in any other way than by affecting the sensitive pulvinus and causing a vibration in it, like a shock from without. There are not wanting arguments against this conception, however. First of all it must be noted that tendrils are quite insensitive to blows striking them from without, and it is not quite conceivable why blows arising internally, associated with the water displacement, should induce a stimulation (FITTING, 1906). Further, HABERLANDT has found that the stimulus is propagated over a stretch of tissue which really includes the whole rind with sieve-tubes and tubular cells. HABERLANDT has attempted to harmonize this at first sight somewhat inconvenient observation with his own theory, by aid of a subsidiary hypothesis, but it is first of all necessary to determine whether the observation itself is correct—FITTING was unable to confirm it. FITTING, however, advances another observation which tells against the view that a displacement of fluid in the sieve-tubes is the cause of the conduction of the stimulus. There are many plants (*Neptunia*, *Biophytum*, tendrils of many Cucurbitaceae) where no extrusion of drops can be observed in spite of vigorous and rapid stimulation, but such an extrusion must be demonstrable if there be a streaming in the sieve-tubes. Hence we are unable to offer any final and logical explanation of this process, notwithstanding the frequency with which it has been studied.

We cannot say whether the conduction of a stimulus after rubbing corresponds with that after wounding, but FITTING (1906, p. 246) has shown that to assume that here also there is a purely mechanical transmission of the stimulus lands us in even greater difficulties than those we met with in discussing stimulus due to wounding.

519, l. 55, *after* stimulus. *read* According to LISBAUER (1905) the contraction begins in less than a second after contact in the very sensitive filaments of *C. americana*. The contraction is completed in 7–13 seconds, and in 50–60 seconds afterwards the filaments have regained their original length, and have again become capable of stimulation.

520, l. 48, *for* 1897 *read* 1887

521. *Lecture XLI is XL of the 2nd German Edition.*

l. 51, *after* yet done *read* (comp. especially PFEFFER, 1893; NOLL, 1896; FITTING, 1905–7).

522, l. 7, *for* I, 9 and II, 80 *read* I, 10 and II, 74

523, l. 45—P. **524**, l. 21, *for* Just as we . . . etiolation. *read* The plant is, however, more complicated in many ways than the simple machine, the electric arrangement, which has served as our illustration of a releasing stimulus. Should we desire to pursue the comparison with the plant further still, we must not only suppose that our model has different keys corresponding to different external influences, but we must also assume that the released current can do something more than set a bell in motion; we must grant the possibility of its acting on a glow lamp or a voltameter. If we assume that the current may at one time pass through one, at another time through another of these pieces of apparatus, our mechanical model will perform quite different work according to the conditions. The introduction of one or other of the three pieces of apparatus in the circuit might be effected by external agency or by internal conditions of the mechanism itself. As regards external agencies,

it might be either the releasing stimulus itself or some other factor that brought about the insertion ; internal agencies might, for instance, operate so that, in accordance with the construction of the mechanism, the voltameter might first of all be in circuit, and that when a certain amount of silver had been deposited the bell would then begin to ring ; after a certain period of action of the bell or of the voltameter, the lamp would finally begin to glow, &c.

Even assuming all this, we are yet far from having reached the degree of complication seen in the organism. More especially we must remember that the same external factor may operate on the plant in very diverse ways. Thus light, when affecting the plant generally, with constant intensity, may act as a stimulant, and the response on the part of the plant shows itself in the rate of growth ; a quite different stimulatory effect follows when the light falls on one side only, for the plant then responds generally with heliotropic curvatures. In contrast to these regional differences we have the periodic variations in light intensity which lead to nyctinastic movement. The preliminary phenomena of stimulation in heliotropism, nyctinasty, and etiolation doubtless differ from each other, however, not merely in the fact that one and the same perceptive organ is associated with different reactions ; in addition there must be differences both at the beginning of the stimulation process and in the perceptive process. We will attempt to show this at least for etiolation and heliotropism. We may perhaps express the stimulus action of light intensity by saying that certain materials arise in each cell proportional in amount to the light intensity. Should each cell react independently, darkening of the plant would result in similar elongation in all organs, but experience teaches us that leaves behave quite differently from stems. In spite of, apparently, the same kind of perception in both organs, the reactions are quite distinct and are conditioned by correlations between the parts concerned.

The matter is different, and more complex in the case of heliotropism.

l. 30—P. **525**, l. 22, *for* Although . . . response. *read* That heliotropic curvature is not induced by unequal-sided etiolation may be concluded from the behaviour of the hypocotyls of the Paniceae. These structures certainly react with etiolation phenomena to diminution of light (FITTING, MS.), but they are able to carry out heliotropic curvature only after excitations which proceed from the apex. Other experiments carried out on grass seedlings show clearly that unequal illumination of opposite halves is by no means a necessary condition of heliotropic stimulation. According to FITTING we must assume that the heliotropic action of light is to induce a ' polarized ' state in the sensitive organ. The plant must then have the power of appreciating the direction of the polarity induced by the unilateral light impact ; it must obviously perceive the degree of divergence of this newly induced polarity from that already existing in its complete structure, that is to say, we ascribe to it the power of comparing two conditions one with the other. We are forced to admit this power of comparison from other heliotropic phenomena. Thus if we allow light to fall on a plant from two sides, we find that there must exist a quite definite relationship in the intensities of the light, if a heliotropic movement is to result. There can be no doubt that, in general, the same relations repeat themselves in all tropisms—that, in other words, a ' differential sensitivity ' exists in the plant in all cases. This phrase, as also the term ' comparison ', might suggest that we here have to deal with psychical capacities on the part of the plant. Although psychical capacity suggests consciousness, still we must dismiss such an idea at once from our minds, for there is nothing in the plant in the nature of even the most primitive form of consciousness. One would rather think of comparing such movements in plants

with those animal movements which, though they take place through the agency of nerves and a central nervous system, yet awake no consciousness, viz. with so-called 'reflex actions', and, as a matter of fact, this comparison has often been made (OLTMANNS, 1892; CZAPEK, 1898). Indeed the characteristic feature of a reflex action, the transformation in the central organ of a sensory excitation transmitted to it into a motor excitation, is doubtless entirely absent in the plant, where any central organ comparable with a ganglion cell is non-existent (comp. FITTING, 1906, p. 239). Although we deny the occurrence of genuine reflexes in the plant, still we must all the more emphasize the existence and very wide distribution of the more simple forms of sensory conductivity.

After directing attention to FITTING's admirable exposition of the phenomena of stimulus conduction and to the statements on the subject made already in many places, we need only say in a word that there are obviously two types of stimulus conduction in the vegetable kingdom, neither of which ought to be compared with conduction in an animal nerve; the one type is that which takes place along the course of a vascular bundle for long reaches and with conspicuous rapidity; in that case we have doubtless to do with a comparatively rough mechanical conduction. On the other hand, the stimulus in other cases is propagated from cell to cell in all directions in ordinary parenchyma. Perhaps, if the reaction consists of relatively simple phenomena, a chemical alteration may be transferred through the tissues, and originate an excitation in the protoplasm of every part that it reaches. If a tropistic curvature is the result of the stimulation, a 'polarized state', about which nothing is really known, must be transmitted from cell to cell from the perceptive organ where it originated.

A glance at these cases of stimulus conduction, as generally at the last-mentioned phenomenon of stimulation, shows how simple the mechanism which we employed as an illustration is as compared with the living plant. In the latter there exists a whole chain of releasing actions between the first application of the stimulus and the final visible response.

526, l. 4, *for* 76 *read* 68

ll. 29–35, *for* also 'optima' . . . temperature *read* there are also processes in which well-marked minima, optima, and maxima may be recognized (comp. ERRERA, 1896).

ll. 41–5, *for* appearance . . . true of others. *read* appearance in a unit of time at that than at other temperatures. It is certainly questionable whether phenomena of this sort bear more than a superficial resemblance to the dependence of the organism on the outer world. It appears to us more probable that the optimum curves which have so often been found to express this relationship to external factors arise generally in the way which has been discussed under the curve of assimilation, where it was shown that the optimum curve was the resultant of two curves, one expressing the injurious action and the other the stimulatory action of the same factor on the organism.

If then in a single process, such as assimilation, temperature plays a double part, we cannot wonder that the curves for other processes dependent on temperature, e.g. of respiration or growth, are quite different in appearance from the assimilation curve, and we cannot doubt that the same is true of other formal conditions also.

527, ll. 23–30, *delete* An example . . . occurrence.

528. ll. 8, 19, 33, 38, 39, *for* nyctitropic *read* nyctinastic

ll. 40–7, *for* (minimum . . . petiole. *read* become so rapid that they may be readily followed with the naked eye. At 30–35° C. a to-and-fro oscillation is completed in half a minute. The rate of movement above and below this

optimum temperature is less, and at 16° or 37° C. rigor sets in (HOSSEUS, 1903). While the change in expansion in the articulations takes place alternately on opposite sides at lower temperatures, at higher temperatures it progresses round in a circle and affects one longitudinal area after another.

As the temperature gradually increases the leaf apex first of all performs a pendulum movement, and then describes an ellipse whose long axis is parallel to the principal petiole ; finally, the curve becomes a circle (HOSSEUS, 1903).

529, l. 1, *for* perhaps *read* obviously
l. 11, *for* HOSSENS *read* HOSSEUS

530, l. 24, *after* autonomous movements. *read* From the fact that tendrils also, when rotated on a klinostat, exhibit regular circumnutatory movements PFEFFER (*Phys.* II) draws the conclusion that geotropism plays a part in these movements as in those of twiners. According to WORTMANN (1887) the behaviour of tendrils on the klinostat is to be explained otherwise ; the successive bendings towards all sides due to weight render rotating movement impossible. Undoubtedly the question requires reinvestigation.

l. 38, *for* entirely autonomous. *read* partly autonomous, partly determined by space relationships in the embryo-sac (HANNING, 1906).

531, l. 3, *for* p. 508, Fig. 336). *read* II, p. 310, Fig. 202).
l. 27, *after* nature. *read* Further, it has been recently shown (NEUBERT, 1902) that the curvatures exhibited by many plumules (*Allium*) are not purely autonomous, but that geotropism co-operates in their production.

532. *Lecture XLII is XLI of the 2nd German Edition.*
l. 46, *after* in form *read* of the cell as a whole

533, ll. 50–1, *for* The apex . . . with *read* The head of the arrow indicates
l. 53, *for* the withdrawal *read* the return to the original position of the cilium

536, l. 15, *after* at rest. *read* According to JENNINGS (1904), however, the streaming movements in *Amoeba* are carried out in an entirely different manner. Fig. 168*a* (*A*) shows *Amoeba* seen from the side ; it shows that it is only the thin anterior end (from *x* to *a*), and not the thick rounded posterior region, that is applied to the substratum. Streamings in the direction of the arrows may be noted through the entire body. On the whole, streaming takes place only in the direction of the forward movement—there is no backward streaming of any kind. If a foreign body be stuck to the outer surface of *Amoeba* one sees it mounting the rear end, and moving forward over the upper surface. When the body has reached *a* it remains fixed to the substratum, while the protoplasm flows over it, and after it arrives close to the posterior region again, it is sucked up by the stream and carried forward once more. Fig. 168*a* (*B*) shows this movement diagrammatically ; it may be noticed that the particle *K* remains in the same place from stage 3 to stage 5. Whether JENNINGS's observations have been confirmed on other hands we do not know, but these observations have been carried out with such minuteness that mention of them must not be omitted.

537, l. 11, *for* 1868 *read* 1886

538, ll. 13–15, *delete* According to . . . FISCHER, 1901).
l. 38, *after* details. *read* If JENNINGS's observations be correct, then the analogy between an *Amoeba* and an oil-drop completely fails, and one must admit that amoeboid movement cannot be determined by an alteration of surface tension of the kind indicated.

539, l. 53, *after* weeks *read* (EWART, 1903).

540, ll. 47–50, *delete* Since, however, . . . protoplasmic movement.

541. *Lecture XLIII is XLII of the 2nd German Edition.*

543, ll. 38 and 39, *for* mg. *read* g. ; *for* $\frac{1}{3}$ *read* by $\frac{1}{3}$ g. ; *for* $\frac{1}{30}$ *read* by $\frac{1}{30}$ g.
l. 45, *delete* after

544, ll. 27–42, *for* The antherozoids . . . solution. *read* The spermatozoids of Pteridophyta that have been investigated react to malic acid, as do those of ferns. There is, however, a difference between the three great groups, viz. that the sperms of Equisetaceae are sensitive to malic acid only (SHIBATA, 1905 c), whilst in the Filicinae malic acid may be replaced by maleic acid (SHIBATA, 1905 a), and in Lycopodinae fumaric acid may take its place (SHIBATA, 1905 b). Sperms of all three divisions are further sensitive to many kations, of which Ca, Sr, and Ba, e.g. in *Equisetum*, are specially active. In addition to the capacity for responding to the dissociating salts already mentioned, *Equisetum* has a marked sensitivity to alkaloids.

In contrast to the uniformity of behaviour of the sperms of Pteridophyta to malic acid, it is very remarkable to note how differently the chief divisions of the Bryophyta behave in this relation. While sugar is the chemotactic substance in the Musci (PFEFFER, 1884), proteid is the chemotactic body in the Hepaticae, e.g. *Marchantia* (LIDFORS, 1905).

545, l. 12, *for* again halt *read* now halt in their backward movement.

ll. 13–19, *for* They are to be . . . backwards. *read* Thus they remain trapped within a definite zone about the centre of the opening of the tube, but their entry into this area is purely accidental, and the stimulus experienced there is not one of attraction but of *repulsion* induced by the transition to lower concentrations; the *response* consists not as in fern spermatozoids in a turning round movement of the anterior end, a consequent change in direction of the movement, but in *locomotion backwards*.

ll. 25–7, *for* hence ROTHERT . . . chemotaxis. *read* We will, following PFEFFER (*Phys.* III), speak of a topotactic response when the movement consists in a swimming to a definite place after a previous reversion of the long axis, and of a phobic response when it is in the nature of a recoil into a different concentration.

l. 29, *for* strophic *read* topotactic

l. 45, *for* apobatic *read* phobic

546, l. 1, *for* apobatic and strophic *read* phobic and topotactic

l. 4, *for* strophically *read* topotactically

l. 5, *for* apobatic *read* phobic

l. 9, *for* apobatic and strophic *read* phobic and topotactic

l. 14, *for* strophically and apobatically *read* topotactically and phobically

ll. 15 and 23, *for* strophic *read* topotactic

ll. 18 and 25, *for* apobatic *read* phobic

l. 27, *delete* from it.

l. 29, *for* (1905 b) *read* (1905)

l. 46, *after* chemotaxis. *read* or the individual ions may be partly attractive, partly repulsive.

547, ll. 15–18, *delete* Further investigations . . . these.

ll. 23–5, *for* On the other hand . . . 1905 b).] *read* On the other hand, we have to deal with quite distinct perceptive processes in the chemotactic phenomena induced by such kations as K, Ru, Ca, Sr, &c., for solutions of these bodies do not affect the capacity for perception of malic acid.

Similar statements have been made as to two Bacteria by KNIEP (1906). He has shown that ' bacillus Z ' possesses at least three distinct sensitivities,

one for phosphoric acid, one for ammonium, and one for asparagin. While the last-mentioned sensitivity is quite independent of the reaction of the culture fluid, the two former sensitivities do exhibit such a dependence, inasmuch as the response to phosphate takes place only in an acid solution, and to salts of ammonium only in an alkaline solution. A certain ' tuning ' to the operative factors is thus recognizable. Such ' tunings ' occur very frequently in lower organisms, and that too without any recognizable cause, and often create great difficulties in experimenting with them.

l. 29, *for* strophic *read* topotactic

l. 36, *for* chemotactica *read* chemotactical

l. 54, *for* The same result takes place *read* A similar explanation holds

548, l. 1, *for* yet *read* further ; *after* case *insert* also

l. 23, *for* positively chemotactic in *read* chemotactically attracted to

ll. 24–5, *for* after being . . . activity ; *read* on entering these solutions, being plasmolysed by them ;

l. 50, *after* organisms *read* (for literature see PFEFFER, *Phys.* III, 358).

549, l. 3, *for* graduated *read* varied,

ll. 5–6, *delete* so that we may dismiss the subject in a sentence.

l. 43, *after* same time raised *read* (also after the action of acids ; LOEB, 1906)

ll. 46–7, *for* exposed . . . intensity *read* in which the illumination is not uniform

l. 54, *after* indifferent condition. *read* This is one of those cases of changing in ' tuning ' which have already been mentioned in speaking of chemotaxis of Bacteria.

550, l. 40, *after* p. 472). *read* Much more doubtful still are the experiments which have been carried out with drop cultures under the microscope, for the actual distribution of light in these drops (CHMIELEWSKY, 1904) is quite different from what the experimenters generally assume.

l. 42, *for* strophic and apobatic *read* topotactic and phobic

ll. 44, 50, *for* apobatic *read* phobic

551, l. 5, *for* apobatic *read* phobic

ll. 6–10, *for* is apobatically . . . movements. *read* reacts phobically, for on sudden darkening the colonies at once sink to the bottom. How this phobic sensitivity is combined with topotactic sensitivity has yet to be explained. Only after further investigations have been carried out will it be possible to say how far light intensity and the direction of the rays affect phototactic movements.

l. 19, *for* strophic *read* topotactic

l. 20, *for* apobatic *read* phobic

l. 38, *for* anode end of . . . negative *read* anode, and this induces in the organism negative

552, l. 20, *for* correspondnig *read* corresponding

l. 53—P. **553**, l. 39, *for* It must be noted, . . . chloroplasts. *read* This change in position is often expressed externally on the leaf, for in the profile position of the chloroplasts the leaf is a paler green. The profile position is assumed in different plants under quite different light intensities ; in shade-loving plants this intensity is low, and high in those which prefer bright sunlight. Even in the cells of the same leaf differences manifest themselves ; thus the chloroplasts in the lower layer of cells in *Elodea* take up the surface position in light of higher intensity before those of the upper layer (MOORE, 1887). As to the mode of origin of both positions, what has been said of *Mesocarpus* holds good ; we have no certain knowledge whether the movements are passive or active, although if the former, the phenomena would be more easily explicable.

The significance of the profile position in bright light is on the whole intelligible, for we have here to deal with a directive movement of individual chloroplasts comparable with that we found in a motile leaf; it enables the chloroplast to obtain just the amount of light it requires.

In addition to profile and surface positions the chloroplasts may, in many, but by no means in all plants, take up a third, which has been termed the night position (Fig. 172, *N*). The chloroplasts retreat from the outer walls, and cover the inner and lateral ones, i. e. some are in the profile, some in the surface condition. Obviously chemotactic movements co-operate here, for carbon-dioxide more especially must have an attractive effect on the chloroplasts. When assimilation ceases on darkening the carbon-dioxide must, according to SENN (1904), accumulate on the inner and lateral walls, diffusing rapidly through the outer walls. Owing to the influence of light, chemotactic movements may be completely masked.

Other movements of the chloroplasts, such as their aggregating round the nucleus and in the corners of the cells, we need not discuss, for they are as yet but little understood (comp. KÜSTER, 1905). We need only note that, in addition to regional changes, changes in form also occur. Thus chloroplasts on the narrow sides of palisade cells have the power under light of bright intensity of changing from a hemispherical to a lenticular shape (STAHL, 1880). They thus offer a reduced surface to the light, and hence their change in shape has the same biological significance as the profile position in other cases.

In conclusion a word or two may be said as to the nucleus.

l. 50, *for* traumotaxis *read* traumatotaxis.

554, ll. 3–8, *for* We mention . . . nature. *read* It is a question whether their nuclei may not have been passively squeezed into the neighbouring cells by pressure exerted during the preparation of the object, but according to FARMER and DIGBY (1907) the nuclei of certain fern prothalli may wander actively into neighbouring cells.

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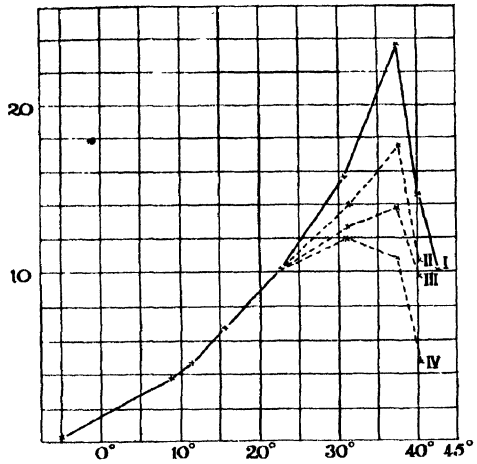


FIG. 25*a*. (*See* p. 34.) Dependence of assimilation upon temperature. After Matthaei (1904).

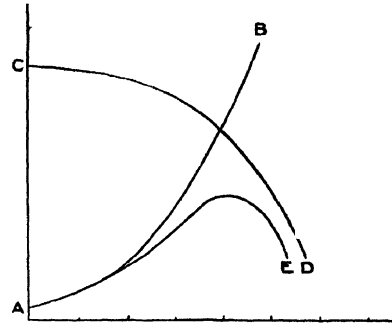


FIG. 25 *b*. (*See* p. 35.)

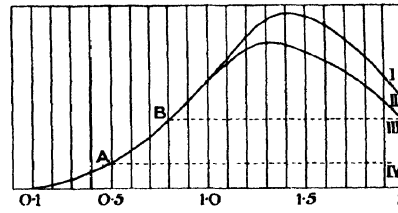


FIG. 25 *c*. (*See* p. 35.)

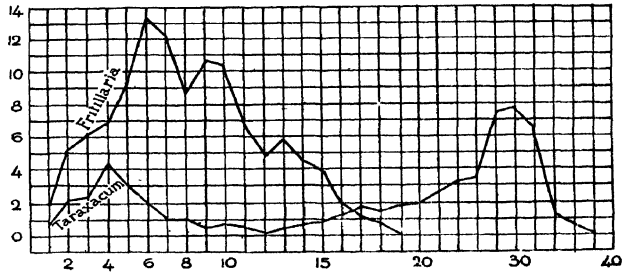


FIG. 85 *a*. (*See* p. 87.)

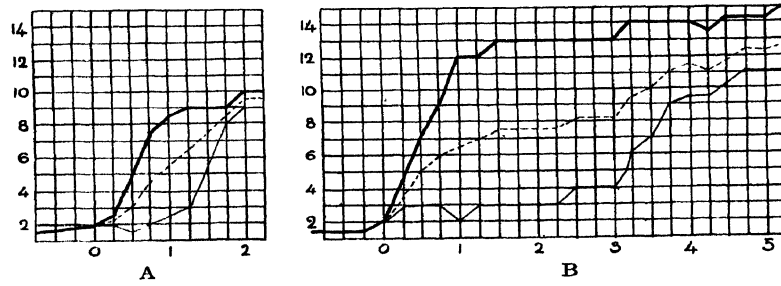


FIG. 157 *a*. (*See* p. 148.)

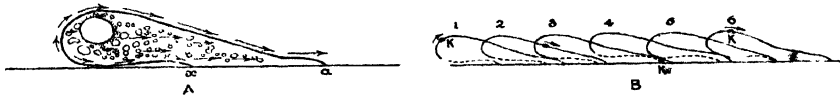


FIG. 168 *a*. (*See* p. 155.) Amoeba seen from the side. After Jennings (1904). *A*. Mode of resting on substratum : *B*. Scheme of forward movement.