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SOME PROBLEMS OF PLANT PHYSIOLOGY.

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In the present paper only a few of the many interesting and important problems of plant physiology can be mentioned. The time at my disposal forbids, for the most part, even the briefest outline of these much-needed investigations, and permits me to make little more than a mere enumeration. To be sure, many of these problems have been objects of research on different occasions and they have been investigated carefully from various points of view. The writer has studied and written contributions on many of these problems some of which will be referred to later.

As one attacks a problem he must cautiously feel his way as if in the dark, for that is his status for the most part, at the beginning. Step by step he can move forward if all goes well. Frequently he finds himself completely baffled from the very first and is compelled to retreat. This retreat, however, should not deter him but rather should act as a stimulus which will cause him to recharge the next time with more foresight and determination. After one such failure he must often adopt an entirely different line and point of attack, and marshal his forces in a new formation. Very often a difficult problem must be approached first from one angle and then from another in order to see where an entering wedge may be driven. Finally, after persistent, well generaled, and conscientious attacks an impression will finally begin to be made and when the first wall has crumbled, and the first trenches have been crossed the remainder of the resistances of the problem will often surrender more easily. Other problems, however, will only succumb or be conquered by a state of siege and this the writer declares after many attempts in the research field. It is therefore for the earnest research man a declaration of war in the cause of science. In this worthy procedure the physiologist as well as other scientists should ask no quarter and should give none. In some investigations he can bide his time, but often the nature of the problem surrounds him with conditions over which he has no control. He therefore may not be able to complete a problem at once or by continuous prosecution, but, like many an artist, must await the return of proper scenery or conditions from day to day or even sometimes from year to year with its sunlight, shadows, and colors in order that the advance may be made under the proper conditions.

The writer's aim and efforts have been to elucidate wherever and whenever possible those truths of nature which of themselves constitute sufficient reward. In many lines of research, no absolutely continuous line of attack on a problem can be predetermined. Therefore the investigation must proceed according to the manner in which the problem behaves and the way in which it reacts to the conditions that surround it. As none of the many problems have been exhausted all

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can be further studied with profit. It is often quite worth while to record one's failures as well as one's successes in an investigation. This is frequently valuable for guidance in further research.

Often what at first seemed to be of chief importance in a problem turns out to be of minor value in comparison with later developments. New points of view or new problems present themselves as he progresses with his problem and crowd upon his attention to such an extent that a limitless field for investigation sooner or later presents itself for solution. The writer realizes that work of enormous value has already been accomplished and that greater discoveries are in store for the future. With this view in mind he now ventures to mention a few at least of the problems in plant physiology for further study.

If we direct our attention to the root system of plants we find that this subject has by no means received the attention which its importance deserves, notwithstanding the large amount of study that its various phases have received. As a root grows older it gradually loses its ability to absorb water, which function is constantly relegated to the young roots. The rapidity, however, that marks this change and the specific modifications that occur both in cell walls and protoplasts are worthy of study. The well known cases of root contraction include a number of interesting lines of investigation. Since neither osmotic pressure nor the activity of secondary growth causes variation in root contraction in different plants, the question of the character of the active cells both as to elasticity and also localized transformation requires close attention (1, Bd. II p. 17).

A root of Faba will exert a pressure of from 300 to 400 grams and will grow in clay, where it meets a resistance of 100 to 120 grams, almost as rapidly as in water (2). The writer has recently found that root growth of seedlings is not stopped by a water pressure of 600 atmospheres and that, although the root is rendered transparent in a fraction of a minute, it recovers in a few days when replanted.

The statolith theory, ingenious as it is, requires confirmation notwithstanding the galaxy of able investigators who have made contributions in its behalf. Various attempts have been made to explain geotropism by chemical change, and this has created a field of special interest. Němec found that the geotropic stimulus caused certain changes in the protoplasm. Long ago Kraus (3) showed that the amount of sugar increased on the lower side of a horizontal stem while the acidity decreased and that later both sugar and acid decreased. Kraus (4) also states that the percentage of sugar is increased in active shoots that are continually shaken but this has been questioned. Czapek (5) opened up a field for investigation on the chemical side by proving the formation of homogentisinic acid by the oxidation of tyrosin that were geotropically stimulated.

The character of the soil is an object of more thorough study, particularly with regard to the needs of certain plants whose roots often undergo extensive development. Nobbe (6) has shown that the roots of a wheat plant will total a length of 500-600 meters, while the roots of a squash plant may attain 25 kilometers or 15⅜ miles. It may be readily seen that scarcely any part of the soil will escape penetration by one or more rootlets. Many relationships, symbiotic and otherwise, in connection with the root system await solution as are also various problems connected with the methods and effects of aeration.

The direction and rate of movement of water through the cortical cells of the root to the fibro vascular bundles still requires elucidation (7, p. 84). Roots generally are thicker the higher they arise from a stem (8, p. 126) but become smaller and smaller as they ramify through the soil. Here their function is chiefly one of absorption as can be shown by aniline dyes (1, Bd. I p. 134).

The ability of certain plant parts to again put out new roots is well known. "A leaf, however, of *Phaseolus multiflorus* cut off at the pulvinus" and put in water may form roots and live for months and this is also true of *Ficus elastica* (8, p. 164). This power is possessed by the cotyledons of various plants even if cut into pieces (8, p. 164). So we have here a line of study to ascertain the cause of these well known differences in plants. The germination of the seeds of citrus plants and the Cucurbitaceae within the closed fruit is not rare and may perhaps be due to temperature conditions. Even when the seeds turn green this may be due to pathogenic conditions, or to a disturbed state cf nutrition (1, Bd. I. p. 318). That some plants form active chlorophyll in darkness is well known. Cotyledons make but little or no food while filled with reserve materials even if green (9, p. 596). Although sometimes colored when exposed to light, roots generally are colorless. Nevertheless in Menyanthes a small amount of chlorophyll is produced (8, p. 166).

The importance of root-hairs merits further study. Schwartz (10) has shown that there may be as many as 230 root hairs per square millimeter and that these increase the absorbing surface as much as 12 times. The location and development of the root hairs give an excellent indication of the capabilities of the root for absorption. Various external conditions influence their development. According to Schwartz they are absent in *Allium cepa*, *Cicer arietinum*, *Cucurbito pepo*, *Helianthus annuus*, *Phaseolus multiflorus*, *P. communis*, *Ricinus communis* and *Zea mays* when the plants are grown in water. Some water plants do not produce root hairs except when they send their roots into soil (11, p. 194). Some root hairs may branch and remain unicellular (11, p. 25) as those of *Brassica napus*. There is the question whether new root hairs are ever produced between pre-existing ones or whether they always arise acropetally (11, p. 195). Snow (12) and others (13) have made valuable contributions to this topic.

Great interest attaches to the pegged and smooth rhizoids of Marchantia. If, according to one view, the pegged ones increase the absorbing surface and are of no mechanical assistance, we must also consider seriously the theory of Kamerling as to the service of the gas bubbles. At any rate this matter deserves thorough investigation (11, p. 202). The work on an individual root hair is small and it has been estimated that each hair will only absorb about .000,001 milligram (14, p. 242). However, their united action is great. Many problems await solution concerning the trichomes other than root hairs found in plants.

In Tortula the rhizoidal cross walls are oblique (11, p. 204) when first formed. It is by no means decided that in this plant and in other mosses this oblique position is for the purpose of offering the greatest amount of surface for diosmosis and conduction in the filament. Some roots that normally grow beneath the ground when cultivated in clear water are in certain instances positively heliotropic and in others negatively so. This shows an ability to respond to a stimulus and is not inherited by them according to Darwinian principles (14, p. 733). Notwithstanding the admirable researches of Czapek on the corrosive effect of roots, the nature of the various secretions is still undetermined (15, p. 107).

Such questions as the following have a physiological bearing: juxtaposed or superimposed apical cells; the length of time a procambium cell can produce new elements; the physiological significance of anthocyanin; and quantitative estimation of transpirational reduction by felted trichomes (11). The irritant of *Urtica dioica* formerly thought to be formic acid but now determined to be an albuminoid substance (11) should be studied in other representatives of the genus. Other problems are iridescent plates of the Rhodophyceae, velamen condensation, and the significance of oblique palisade tissue (11); and the cultivation of various embryos as shown by Hannig (16) and others.

The old question of the ascent of water is still unanswered notwithstanding all that has been done to solve it. Strasburger studied the problem and arrived at certain valuable conclusions (1, Bd. I, p. 207) but was not able to explain the situation and, like the "noteworthy experiments" of Dixon and Joly (17), left the question undecided. The theory of Sachs soon became untenable although the force of imbibition is sufficient for the purpose. The great force of imbibition is shown by the swelling of starch which according to Rodewald requires a pressure of 2,523 atmospheres to prevent it (1, Bd. I, p. 63). In dried seeds imbibition and osmosis work together. This force is sometimes made use of to split skulls for anatomical purposes (1, Bd. I, p. 63). This force is, however, small in comparison with the freezing expansion of water at —20° C. which would require a pressure of 13,000 atmospheres to keep ice from forming (1, Bd. I, p. 29). Thus, we have the reason for the formation of frost rifts in the wood of various trees. These rifts are mostly radial and along the lines of least resistance (1, Bd. I, p. 307). The loud pistol-like reports often heard in living timber during extended and very cold weather indicate the formation of these rifts. The question of pressure affects even the plant when growing for it was first shown by Hales and afterwards by Kraus (1, Bd. I, p. 74) "that tree stems and fruits swell slightly at night and decrease in the day time due to transpiration although such changes in tree trunks are generally less than one per cent."

Other questions that crowd themselves on our attention are: the pressure necessary to close bordered pits; the physiological importance of tyloses; certain functions of leptome parenchyma, especially in relation to the laticiferous system; the significance of the Casparian strips; and the meaning of guard cell fusion in Azolla and Funaria (11). Haberlandt was able to grow sporangia of Funaria in a culture solution for three weeks during which time normal spores were formed thus showing the efficiency of the chlorophyll system (11). The so-called secretion of wax by certain stomata requires further study (11). Uncertainty exists with reference to the secretions of certain glands as capitate and scutate ones (11) and elaioplasts (18). Objections have been offered to Tyndall's (11) interesting investigations concerning a layer of air saturated with ethereal oil which it is argued protects the parts concerned against heat, cold, or excessive transpiration. Do enzyme reservoirs contain protein material in addition to the enzyme (11)? Why are such large amounts of lime required for plants with cystolithic structures (11)?

There is the difficult problem of the dehiscence and cohesion mechanism of anthers, sporangia and other structures (11) which has occupied the attention of so many observers and has been so often the topic of research. Although these cases are of a physical nature, they are also of physiological interest and are still partly unsolved. The immense amount of work done on living motor tissues in the Urticaceae, *Stylidium adnatum,* and *Cyclanthera explodens* leave many points in doubt (11). It is moreover, remarkable that tactile pits have thus far been found in the walls of sensory cells only in the Curcurbitaceae and possibly also the Sapindaceae and tactile papillae only in floral organs and tendrils (11). The work on tactile organs of carnivorous plants, first recognized by Edwards in 1804, (11) leaves much to be done. In *Drosera rotundifolia,* Darwin found that a hair weighing .000822 milligram produced a noticeable reaction (1, Bd. II, p. 461) while, according to Kemmler, the least weight that will produce a stimulus on a sensitive skin is .002 milligram (1, Bd. II, p. 423). The causes of certain changes in the rate of growth of tendrils are unknown (1, Bd. II, p. 443). The epidermal lens cells of the epidermis as studied by Haberlandt present an interesting field worthy of further study. His photographs of a portion of a microscope made in connection with one of the membrane lenses show their capabilities (19).

The transmission of stimuli varies according to the kind of stimulus. Thus, Czapek (20) and others state that geotropic and heliotropic stimuli travel two millimeters in five minutes. Traumatic stimuli, according to Kretschmar (21) travel one to two centimeters per minute and Fitting (22) gives the rate as one to two centimeters per second for the tendrils of *Passiflora coerulea.* In *Mimuosa pudica* the velocity is about 1.5 centimeter per second (11). Questions as to the exact part played by the protoplasmic threads between the protoplasts are unanswered. Chemical stimuli in Drosera are transmitted only about ten millimeters per minute. Darwin found that .000423 milligram of ammonium phosphate would cause curvature of a tentacle (1, Bd. II, p. 463). The question remains as to what response if any is due to external causes. The origin of certain stimulatory movements is also obscure. The quick movement of cilia after a stimulus shows its rapid propagation.

Physiologists differ as to the origin of excentric growth in roots and branches (11). The question of annual rings still awaits a solution (1, Bd. II, p. 274) along with certain ribbon shaped stems (11). On the subject of osmosis and plasmolysis, various questions remain for solution. How does a diatom retain its form in spite of the internal hydrostatic pressure (1, Bd. I, p. 122)? In the case of plants whose roots have been killed by heat the stems may remain living for several days but no experiments have as yet been made on their transpirational behavior. No exact work has been done to ascertain the influence of external agencies on the excretion of water pores. Similarly, doubt still surrounds the methods of sugar secretion by glandular cells and the means by which gland cells escape injury by high osmotic forces (1, Bd. I, p. 265) and other factors notwithstanding the large amount of excellent work that has been done on the subject.

The objections to the plasmolytic method are negatived in as much as verification of the method is easily obtained in various ways. Ostwald (23) has given an illustration of the membrane concerned and osmotic pressure in a theoretical way. The cryoscopic and other methods give results of great value. De Vries used the plasmolytic method to determine the molecular weight of raffinose and his results have since been confirmed (24). Moreover the work of Pfeffer has been confirmed again recently by Morse (25) and others who have made notable contributions to the subject. Among these the work of Fitting and Renner may be mentioned. Various questions arise concerning the conditions, under which natural plasmolysis occurs. Although a new cell wall may sometimes form around a plasmolysed cell which may remain living from a few hours to several weeks, nevertheless permanent plasmolysis produced and maintained artificially always finally causes death (1, Bd. II, p. 331). The specific difference in these cases deserves careful study. Taking the work of Pfeffer as a basis, Van Hoff founded his well known theory. Van Hoff also discovered the R. G. T. rule concerning chemical reactions and Kanitz showed its applicability for various cell activities (20). Recently much work has been done on osmotic pressure from a quantitative standpoint, on osmotic equilibrium, on permeability of organic membranes that are not protoplasmic in character, on the magnitudes of osmotic pressures and electrical conductivity and on osmotic pressure as it relates to distribution, morphology and growth (26).

With regard to the protoplasm numerous questions of direct physiological importance remain unsolved. For example, questions concerning cohesion and viscosity as well as the variation in surface tension need elucidation. Much interest also attaches to the various theories of protoplasmic streaming and much remains to be done concerning the effect of different chemical substances and other conditions (27). Temperature combinations with certain anaesthetics require attention. The locomotion of various diatoms and ciliated spores about which certain points are not clear is more rapid in proportion to their size than any of our vessels that move on water. The recent valuable list of papers by Haberlandt on "The Physiology of Cell-Division" deserves consideration in this connection.

Overton (28) presented a rather plausible theory concerning the permeability of the protoplasmic membrane which was afterwards supposedly confirmed (29). Later studies, however, have thrown a cloud of uncertainty over his rather ingenious theory and further study of this important subject is necessary. The question of the penetration of aniline dyes into the living protoplasm was worked out by Pfeffer (30). The exact way in which an accumulation of dye occurs in certain plants remains to be explained.

Pfeffer's (30, Bd. I and II) work on chemotaxis is also of far-reaching importance. From the osmotactic standpoint the question arises concerning a tactic or phobic response in strong solutions. Spermatozoids and bacteria (1, Bd. II, p. 813) were caused to enter a capillary tube containing only .00000001 milligram of malic acid or peptone. Relatively, these amounts are not so small as they would seem since the sperms weigh only about .00000025 milligram and a cell of "*Bacterium termo*" about .000000002 milligram. On the other hand stronger solutions having an osmotic value of 0.5 per cent KNO_3 produce negative osmotaxis (1, Bd. II, p. 813). Englemann has introduced an excellent method of demonstrating chemotaxis in which certain organisms such as "*Bacterium termo*," *Spirillum undula* and *Spirillum tenue* are used. By his delicate test .000000001 milligram of oxygen can be detected (1, Bd. I, p. 292).

In the various processes of growth interest attaches in many ways. The position of the nucleus in growing parts such as root hairs may not always be in the most active part of the cell as the writer has shown. The rapid growth of certain plants or plant parts is well known. It is estimated that "a bacterium can under favorable conditions divide in 20 to 30 minutes. At this rate in three days 4,772 trillions of individuals would be produced."

Can all plants live when continuously illuminated? Plants in the polar regions do this and McKinney has shown that a certain amount of continued illumination is without effect (31, p. 222).

Growth may be checked locally by cold and still continue at other points. This was well shown by introducing the top of a defoliated clematis plant into a hothouse. Leaves were formed on the stem in the greenhouse while the part outside was still frozen and dormant (32). This development of transpiring leaves proved that in spite of the low temperature outside a large amount of water was absorbed by the roots from the frozen soil and carried through the stem. Knight long ago demonstrated that a plant exposed to transitory cold sprouted earlier than those maintained continuously in a greenhouse. The same phenomenon was observed by Pfeffer in various plants and by Müller-Thurgau in potato tubers (1, Bd. II, p. 266). Molisch reports that potato tubers placed at once in an ice box for 14 days at +1 to 3°C will grow at once if planted in a warm house. In case of an early variety one may thus obtain two crops in the same year (33, p. 272). Plants growing in northern regions, ripen as a rule in a shorter time and here the question of illumination or other causative factors requires further study.

Many deciduous plants continue to cast off leaves and form new ones even when removed from temperate zones to the tropics. Oaks and beeches never cease to do this, while others such as the cherry gradually become evergreen in Ceylon but cease to bear flowers. The peach, on the other hand, produces flowers and fruit during the entire year (1, Bd. II, p. 271). Experiments of this kind are much to be desired in temperate climates where artificial conditions could be supplied. It is difficult or impossible to cause many plants to bloom out of season while others lend themselves more or less to the process of forcing. However, artificial forcing causes abnormal development in some plants, as in the case of Lily of the Valley which is caused to develop the flowers before the leaves (7, p. 238).

A good many questions are concerned in the solution of certain points connected with periodicity. The experiments of Johannsen (34) show that treatment with ether or chloroform for 12 to 24 hours will cause the buds of such plants as *Syringa vulgaris* and *Prunus triloba* to open three to six weeks earlier than the plants not so treated and the activity of various functions was increased. Elfing and Lauren had observed before this that ether or chloroform increased respiration if the doses were not too strong, although this has been questioned. Molisch (35) has shown that if certain plants are immersed in water at 30° to 35° C, for 10 to 12 hours the resting period may be terminated. For example, a hazel branch one side of which was subjected to warm water bloomed in nine days while the other side which was untreated was still in the resting condition. *Forsythia suspensa* bloomed in 12 days after such treatment while the control was still unopen. Syringa bloomed 40 days after the warm bath while the control was still dormant. The responses shown in these experiments leaves certain questions unanswered.

Fitting's experiments (36) with *Erodium gruinum* and *E. ciconium* are interesting in this connection. He found that when, on a cool morning, deep blue flowers of these species were put in a box having a temperature of 40° to 42° there occurred quickly a sudden change of color. Within three seconds the blue flowers changed to a light rose and a few minutes later to a bright red. When returned to a cool place the blue color soon returned. Furthermore, the reaction of the cell sap is often indicated by the color of various living cells. Thus, the red color of rose petals and beet-roots shows that the cell sap is acid while the blue color of the hyacinth, blue bell, or cranberry shows that the sap is neutral or slightly alkaline (1, Bd. I, p. 490). We also have striking color changes caused by oxidases. Among these is the brown color assumed by the exposed flesh of apples, the prussian blue shown by Boletus when broken and the dark color of raw rubber (37, p. 390). The oxidation of the sap of Rhus to a black lacquer varnish in air by laccase is also well known.

Other properties of the enzymes are noteworthy. The dried substance of diastase, protease and ereptase of wheat and barley may retain its activity for 20 years and after the power of germination is lost (37, p. 390). Finely divided platinum and iridium among inorganic substances cause a catalytic action resembling that of enzymes. Buchner's discovery that the filtered sap of yeast plants can change sugar to alcohol and carbon dioxide, is interesting in this connection. The capability of diastase to hydrolize 10,000 times its volume of starch and invert 100,000 times its volume of sugar shows its great power. The yeast plant itself is active in various ways; thus it can reproduce 20 or 30 times in the absence of oxygen, it can produce alcohol up to 14 per cent before the yeast plant is killed, and it may produce a pressure of 25 atmospheres of carbon dioxide in a closed vessel before such action ceases (1, Bd. I, p. 576). Nägeli (38) estimates that the volume of a cell of beer yeast is about .000002 cubic centimeter and weighs about .0000005 milligram. The great numbers, however, make up for their diminutive size.

Bacteria also show activity in some of these directions. A closed flask, for example, containing a nutrient solution colored with indigo carmine and inoculated with certain bacteria will lose the blue color due to the removal of every trace of oxygen by the bacteria. On readmitting oxygen the blue color will return. In proportion to their bulk some bacteria may use oxygen 200 times as fast as man (1, Bd. I, p. 526). Certain bacteria will live in carbon dioxide under 50 atmospheres of pressure and may burst tin cans of conserves by developing such gas pressures. Small amounts of carbon dioxide thus given off may be estimated conveniently by a method given by Hempel (39) and extremely small amounts of carbon dioxide can be detected by the biometric method for seeds and other objects as devised by Tashiro (40).

The subject of phosphorescence presents an interesting field for investigation. For the already voluminous literature, one is cited to the recent work of Czapek (41), Molisch (42), and other contributors. Whether one holds to the extracellular, intracellular, or other theory regarding the production of light in different plant forms, various questions arise. The sudden increase or decrease in the strength of the light emitted requires explanation, as does the effect of different pressures of oxygen and the actual oxygen consumption by the organism in its formation of light. The light intensity may be sufficient to produce clear photographs of various objects, to produce heliotropic curvatures, and to read by, especially when "bacterial lamps" (42) are used, and is equivalent to about .000785 of a Hefner unit per square meter. The meaning of the necessity of a large amount of sodium for luminous bacteria is important as is also non-motility and light production in certain forms (31, p. 213).

Many interesting points regarding diffusion await solution. The diffusion of gases ordinarily takes place comparatively slowly as shown by Clausius (43, Bd. 3, p. 753) in connection with whose work the theory of diffusion by Maxwell was founded. Ewart (44) has shown that in certain cases diffusion causes the distribution of substances more rapidly than streaming. Osmotic pressure varies only slightly

(45) in plant cells within the temperature range ordinarily present, for a rise of only 15° C. causes a pressure change from 100 to 105.5 (1, Bd. I, p. 120) and this, to a degree, follows the laws of gaseous pressure (46). Brown and Escombe have opened up an interesting field in showing that the diffusion of CO_2 is not dependent on the size of the leaf pores but is proportional to their diameter (47). In like manner the diffusion of CO_2 as first shown by Graham constitutes an interesting topic. A study of diffusion in gelatine as investigated by Hüfner and Hagenbach (43, Bd. I. p. 445) and compared to protoplasm would be of value. Further studies are needed concerning the behavior of certain cell walls to the diffusion of liquids and gases. Conduction of food materials takes place rapidly in some parts, but is prevented entirely by girdling. The length of life, however, of that part of a tree above the girdle varies.

Many problems remain concerning the storage of food. Trees for example, are distinguished from annuals because the latter store their reserves permanently only in the seeds, and they differ from perennials because the latter store their reserves subterraneanly (48, p. 225). Many problems arise concerning the nitrogen question, particularly regarding autotrophic plants. There is the question of nitrites and nitrates and especially a question of nitrites in developing green plants. Questions arise concerning vegetable proteids and their synthesis, under certain conditions and points relating to sulphur. Plants of *Chenopodium vulvaria* and flowers of *Crataegus oxyacantha* evolve a nitrogenous compound in such quantity that a glass rod dipped in hydrochloric acid emits fumes when brought under a bell jar with such specimens. Wicke says this substance is trimethylamine in Chenopodium (49). The nitrogen problem is one requiring investigation by both physiologist and chemist.

Ethereal oils constitute a question. In *Dictamnus albus* the oil may vaporize to such an extent as to ignite when a flame is brought near it and hence many such flowers may be more fragrant at night (1, Bd. I, p. 502). In the daytime, however, the change in the diathermanicity of the air which would assist in reducing the heat of the sun's rays would be slight notwithstanding the efficiency of these vapors in that respect as mentioned above (50 and I, Bd. II, p. 848). Green and other colored leaves can absorb 50 to 90 per cent of the sun's energy (50). Certain species of Citrus possess highly inflammable oil. Among cryptogams the oily nature of certain parts is well known. In Lycopodium the spores flash into a beautiful array of scintillations on ignition, hence their frequent use in pyrotechnical displays.

Oligodynamic studies will bear further inquiry. Grafe has made valuable studies on cell chemistry and Haas and Hill have recently mentioned various metabolic problems (51). Electro-culture and the physiology of seedlings are worth-while problems. In 1878 Sachs stated that an electric current passed from the stigma to the ovary pedicel of Berberis stimulated all the stamens, but when sent in the reverse direction no stimulation was produced (14, p. 685). Other stimuli produce comparable results, for when plants are passed from dark to light and vice versa the stimulation is different (1, Bd. II, p. 504).

A stimulus may be positive at one intensity and negative at another. Geotropism is positive for most roots although moisture conditions may reverse this reaction. Most stems are positively heliotropic but in Linaria this undergoes a natural reversal since the young flower stems are positively heliotropic, becoming negative as they elongate (52, p. 318). Agapanthus and Papaver are similar examples.

Questions of symbiosis and metabiosis also arise. Just as numerous questions presented themselves concerning photosynthesis, we also have the field of chemosynthesis with many unsolved problems. Sugar may constitute a product both in constructive and in destructive metabolism and hence a physiological and chemical classification will not agree (48, p. 262). Questions have arisen concerning the wave length of light best for green plants. Pfeffer gives it as between Frauenhofer's lines C and D of the spectrum and of 660-680 uu wave length (1, Bd. I, p. 330). Reinke's (53) spectrophore can displace diffraction grating in certain experiments of this kind. The growing of lichens on windows of houses and their mechanical action shows unusual capabilities (54).

The prevention of flower wilting by the use of $PbNO_3$ deserves further study (55). The change of color of flowers due to a change of temperature, as above referred to, has a partial parallel in the enantiotropic substance, mercury iodide, and a further striking parallel in the double salt Cu_2 I_2 2HgI which changes color from red to brown and to red again on cooling (56). Though not analogous the sudden darkening of the pulvinus of Mimosa after stimulation shows that water has taken the place formerly occupied by air (57). A continued study of Schumann, Roentgen and other rays as well as different colored lights in various combinations of temperature and gases would net further valuable results.

Certain problems concerning the chemical action of different plants need further attention as that of wood destroying fungi; the penetration of structures by bacteria as egg-shells (58); the reported corrosion of stone, mollusk shells, oyster shells, and oolitic iron by algae (41, 1920, Bd. II, p. 360); and the penetration of membranes by fungal filaments (59). The unusual reported case of algae growing on a painting for about 200 years shows the capabilities in certain directions (60). Of the halogen group iodine and bromine are found in marine plants, as would be expected and probably in land plants (1, Bd. I, p. 433) though the latter is contradicted by Fresenius (61, p. 542). Other questions arise on this point. Lead is often present in plants but a practical method for its volumetric estimation is lacking according to Fresenius (62) and Sutton (63) advises weighing for its accurate determination. The chemist can assist in the many plant problems by determining substances in plants, but he cannot tell what ones and the amounts necessary for the proper functioning of the metabolic processes. This the plant physiologist must determine by actual experiment.

Facts in physiology once established are often disbelieved or forgotten. For example, the neglected work of Ingenhousz on the obtaining of carbon by green plants was afterwards brought to light by Liebig; the water-culture method first used by Woodward was subsequently resuscitated by Sachs (1, Bd. I, p. 412). Many such examples in physiology could be mentioned. The forgotten work of Mendal was resuscitated by de Vries, Correns and Tschermak almost simultaneously (48, p. 504) and also the restoration of the now famous work of Conrad Sprengel by C. Darwin.

Then there is the physical question of the Brownian movement, long known and of interest to all scientists. The chemist also looks for forms of energy in the atom by a rearrangement of the protons and electrons and the energy of radioactive substances (64). The determination of Hydrogen Ions much referred to, especially of late, presents many questions which the botanist would do well to work in conjunction with the chemist. The sensitiveness of the bacteria method, above referred to, exceeds that of various chemical methods ordinarily employed (65) and hence its extreme usefulness to the physiologist.

The chemistry of plant odors presents many problems. Many plants, such as *Ageratum mexicanum*, have no special odor during life but when killed by drying, freezing, or heating to 60° C., they give off a very pleasant odor of cumarin (33, p. 274). Similar odors appear in *Asperula odorata*, *Anthoxanthum odoratum*, *Prunus cerasus* and vanilla plants and the well known instances of hay and other plant odors. We can smell .000002 milligram of oil of roses and .000000002 milligram of mercaptan (66, p. 97). The topic of transpiration presents many problems. Hales (67) proved that the flow of water may be reversed in a stem and Strasburger verified this by cutting off a tree trunk near the base and which was naturally grafted about one meter above the cut. The cut-off stem remained fresh for years (68). A summarization of transpiration and the literature is given by Burgerstein (69) up to 1920.

There remain questions about carbohydrates and fats. In some plants no starch is formed in the chloroplast (52, p. 223) and in others cane sugar formation precedes that of starch. Questions arise concerning the absence of some polysaccharides in certain plants and some doubt still exists on the functions of mono-di- and poly-saccharides (1, Bd. I, p. 468).

Carbon is necessary for the metabolism of plants and as Noll says, no other element can enter into the formation of so many and such a diversity of substances in the organism or in the chemical laboratory (70). A reference to the works of Richter and Beilstein will substantiate this fact. According to Chamberlain (71) the number of carbon compounds now exceeds 200,000.

The well known process of abscission or leaf-fall can be brought about in various ways. Further research is needed to determine whether the production of organic acids is actually operative at the end of the summer according to Wiesner's view or if organic acids may have any influence (1, Bd. II, p. 278). In this connection it is interesting to recall the work of E. Hannig on the casting off of flowers as a result of external conditions and the field for investigation brought to light by his experiments. Several points concerning the action of poison by increasing the temperature as well as the differences in the resistance of plants to heat require study. Pouchet found that the seeds of Medicago would germinate after boiling in water for four hours (1, Bd. II, p. 294) while the seeds, from stone fruits that have been made into jam, germinated (9, Vol. II, p. 230). The subject of desiccation leaves numerous questions to be settled. Much attention has been given to a study of the effect of freezing on plants but still it is not known why freezing kills some plants and does not affect others. The resistance of bacteria to freezing requires further explanation (1, Bd. II, p. 314). The resistance of trees which form oil in cold weather as well as the ability of the same plants to withstand cold at different stages of their development needs solution (1, Bd. II, p. 317). A single reference to the work of Müller-Thurgau, Molisch, Göppert, Winkler and Kylin must suffice here. This topic forms a subject of great interest and its value can hardly be over-estimated. Even in reasonably cool situations plants may sometimes be injured by drops of water which concentrate the sun's rays. The resistance of certain marine algae which grow at -1.8° C. requires attention, as does the statement that the spores and mycelia of Mucor are equally resistant, and whether or not ice forms in turgid bacterium cells (1, Bd. II, p. 310).

Dry spores such as those of Aspergillus and yeast are only slightly or not at all injured by submergence in absolute alcohol, ether, benzol or carbon dioxide. The point now arises how they would compare with spores in air (1, Bd. II, p. 324). Do roots of seedlings require gradual moistening to recover and live after drying (1, Bd. II, p. 324)? A further comparative study of the spores of bacteria and seeds would net additional worthy results. Notwithstanding what has been done on the effect of different alkaloids and on the various poisonous plant substances, there remain many problems for investigation by the physiologist.

Certain questions concerning the germination of seeds and the subsequent transfer of materials require investigation. There are questions of cortical and medullar functions which need attention. Schimper (72) has shown that the bundle sheaths in Plantago could convey substances, but less rapidly, after the removal of the fibro vascular bundles. In young tissues the Biuret reaction is useful in showing the disappearance of certain substances, as soluble proteids. Companion cells need study and the questions concerning latex are by no means settled. The writer by depriving the seedlings of Papaver of their latex checked the growth but did not kill the seedlings. The same experiment the author has performed on certain sieve tubes with similar results. Schwendener states that no latex escapes from withered plants or old parts when cut (1, Bd. I, p. 594).

If nine tenths of all phanerogamic seeds possess oil, as Nägeli states, it can be seen that this does not necessarily protect them from desiccation. (1, Bd. I, p. 609.) Puriewitsch and others planted grains of certain plants from which the embryo had been removed and the endosperm was neither changed to sugar nor removed. When, however, the place of the embryo was taken by substituting a small cylinder of gypsum whose lower end reached into water, to remove the forming

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sugar, the starch was completely removed from grains of maize or other plants (73).

In the field of microchemistry much of interest to the plant physiologist remains to be done. This work has been ably carried out, especially by Tunmann (74) and Molisch (75). The application of chemistry should go hand in hand with plant physiology. As we glance through the latter subject we see, as a rule, far too little of the use and knowledge of chemistry. The masterful work of Czapek (41) and others have rendered service of great value along this line. With this brief idea of physiology's great helper we turn our attention in conclusion to some special problems where it is concerned.

A change took place in chemistry when Wöhler in 1828 obtained urea from ammonium cyanate and thus produced for the first time an organic from an inorganic compound. Then Kolbe synthesized trichloracetic acid in 1845 and Berthelot synthesized alcohol from formic acid thus removing the boundary between organic and inorganic chemistry (76). Organic chemistry, the chemistry of carbon compounds, has tried to do what plants do, and in many cases has apparently succeeded. The plant no longer furnishes alizarin and indigotin for commerce which are now obtained from coal tar and even some alkaloids have been prepared artificially.

Since colloids were first investigated by Graham the similar nature of protoplasm has given their study a significance. Later the principle of Tyndall's phenomenon was applied by Zsigmondy to the so-called ultramicroscope so that protoplasm and living cells can be studied to advantage. Recently Czapek (77) has investigated the question of surface tension in plant cells and has called attention to the application of Richardson's Law. We have to do here especially with the behavior of two important substances in the plant cell, protoplasm and chlorophyll. Their activities go hand in hand in green plants. We shall now turn our attention to the behavior of the chlorophyll in particular. Glancing backward we recall that the green coloring substance of plants was recognized by Nehemiah Grew (78) in 1682 and that it was given the name of chlorophyll in 1817 by Pelletier and Caventon (41, Bd. I, p. 556). Numerous and valuable contributions have been produced in rapid succession and yet almost 250 years after Grew's work the performances of this riddle are unsolved. Colored lights have an effect on certain plants, for it is claimed that in red light specimens of Oscillatoria become green, in green light they turn red and in blue light assume a yellow hue (79, p. 245). Problems in great number remain to be answered as questions concerning a chloroplast membrane and the influence of chloroplasts on various cytoplasmic movements (79, p. 251). The positions assumed by chloroplasts so ably investigated by Stahl and Senn (80) still leave many points to be solved. The question of structure in certain respects is still doubtful as is the exact form of the chlorophyll in the chloroplast and points concerning yellow pigments (1, Bd. I, p. 297).

The greatest advances on the subject of chlorophyll so far are the investigations of Willstätter and Stoll (81). Their published papers deal with the chemical side of the question and are of such great importance that they are indispensable to an understanding of the subject. But the function of chloroplasts interests us most. Among the questions are the formation of starch and other substances; the first-formed products; is the same course always followed in sugar production; and the chemistry of pigments. Can oil produce starch or vice versa in the chloroplast independently of the cytoplasm? Are glucosides direct products of photosynthesis? Further studies should be made on the retarding influence of higher carbon dioxide percentages and on the more or less complete loss of photosynthetic power by normal chloroplasts. Is the protoplasm of heliophobic plants more sensitive to light than the chloroplast? (1, Bd. I, p. 285.)

The evolution of oxygen from water plants directed the attention of Ingenhousz to the photosynthetic processes in green plants and his work in connection with that of Senebier and De Saussure constitutes one of the most important scientific discoveries. Iron is necessary to chlorophyll formation, but the action of iron and alum in causing the reddish flowers of Hydrangia to become blue is uncertain (1, Bd. I, p. 421). Chemical reactions often occur with great velocity. So we may have an immediate cessation or recommencement of oxygen evolution in green plants as shown by the extremely sensitive bacteria method. In light, starch (1, Bd. I, p. 303) is produced in five minutes in considerable amount in Spirogyra which previously was starchless (82). Detmer has shown that the iodine reaction of starch can not be obtained in distilled water (83). No means of stabilizing this reaction is known. We have a great many chemical changes occurring in tiny green cells whose total volume often does not equal 0.1 cubic millimeter. Since the air contains only .03 to .04 per cent of carbon dioxide the work necessary on the part of the green plant to make its food will be easily understood.

Light we know is necessary for chlorophyll action, therefore it is not surprising that moonlight which is about 1/600000 the strength of sunlight would prevent the handling of CO_2 and even with light of 0.1 to 0.025 the strength of sunlight respiration and photosynthesis about balance (1, Bd. I, p. 323). Plants in dwellings often suffer from deficient light since at 0.5 meter from a window the plant gets only 0.3 and at a distance of two meters only 0.08 of the light it would get in the open sunlight (1, Bd. I, p. 323). When the sunlight falls on a thin green leaf most of the energy is usually absorbed so that the light which passes through would not cause the formation of starch nor an evolution of gas (1, Bd. I, p. 329). Copper beeches due to their color and light interference grow more slowly than vividly green species, other conditions being equal (84). An oleander leaf will produce per square meter in sunlight about 0.000535 gram of starch in one second, obtaining thereby energy equivalent to 2.2 caloric units, which is less than one per cent of the energy of the sunlight (84). Under good conditions other plants such as the pumpkin may produce in 15 hours 25 grams of starch per square meter (85) which necessitates the removal of the carbon dioxide from 50 cubic meters of air. The quantitative activity of the green plant is therefore easily realized. Recently studies have been made concerning carbohydrate substances of Thallophytes, Bryophytes and leaves of Angiosperms and methods for their estimation in the extracts (86). The amount of chlorophyll is really very small per unit area and Tschirch has estimated that only 0.1 to 0.2 gram is usually present per square meter of green leaf surface. Much work remains to be done on chlorophyll activities with various autotrophic plants of different colors and under different conditions of light composition. Marine plants suffer from light conditions as the water deepens and at a depth of 400 meters in the sea autotrophic plants cease to exist (1, Bd. I, p. 337). The chloroplasts of some plants can continue to live and carry on the process of photosynthesis for a short time when removed from the cell (87), but all attempts to grow them outside of the cell permanently have failed. The chlorophyll of green plants breaks down in solution. Wahmsley (88) states that he has preserved a specimen of Draparnaldia in camphor water for 20 years and that the chlorophyll remains unchanged. This, however, says nothing as to the actual preservation of the chlorophyll itself. Concerning those substances which form the chlorophyll only a faint intimation exists which creates a wide field for study.

A large field for investigation is brought out by Fitting in his interesting paper on a new branch of physiology which he names "Geographical Physiology" (89). The various theories concerning carbon dioxide assimilation have been well summarized by Schroeder (90). One which is much quoted may be mentioned, namely Bayer's Theory "according to which formic aldehyde is produced from carbon dioxide and water in the chloroplast, oxygen being evolved, and carbohydrates resulting by polymerization" (1, Bd. I, p. 340). Doubt attaches to this theory. More recently Ewart states "that not formaldehyde but a biose sugar is the first product in photosynthesis and the traces of formaldehyde which have been detected in green plants are the result of the destructive photo-oxidation of chlorophyll and are formed equally well in the entire absence of carbon dioxide when extracted chlorophyll is exposed to light" (91). Attention is also directed to the question of photosynthesis and the Electronic Theory (92).

Professor Giacomo Ciamician of Bologna, Italy, made an interesting address some years ago in New York which has a bearing in this connection. He asked "why use only the fossil energy of the sun—for that is what we do when we burn coal! Why should not man use sun power, direct, as do plants and trees?" (93) According to one estimate he made, the sun delivers in energy by means of its rays enough power in six hours to equal 2,500 tons of coal per square mile. We mine in the U. S. about 600,000,000 tons of coal per year while the Sahara Desert receives daily in solar energy the equivalent of 6,000,000,000 tons of coal every day. He indicated by a long list of chemical processes the probability of the consummation of his ideas and prophesied a trend toward the tropics which would on this account become thickly populated in time. Slosson says "man takes a 1,000 horse power engine and an electric furnace at a temperature of several thousand degrees to get carbon into combination with hydrogen, yet the little green leaf in the sunshine does it quietly and without getting hot" (66, p. 239).

One of the tasks of the future is to ascertain, therefore, if possible, the various ways by means of which green plants make their food substances and to follow out the chain of processes completely. Green plants get their energy from the sunlight and build up their structure. They have done this in past ages, and of this we have an expression in coal deposits, which are of proved vegetable origin (94). A knowledge of these various plant processes is all the more important since our timber supply is virtually gone. When we burn wood we release the energy of the sunlight which was stored up in the plant by the process of photosynthesis. By this transformation of potential into kinetic energy the activities of the green plant are reversed. And when we burn coal, formed as above indicated by green plants, which collected the sun's rays of many thousands of years ago and stored them, we release this energy in the form of heat by the process of combustion. And so with our forests, nearing exhaustion as a fuel resource and the end of our available coal in sight we realize that some other source of energy must ultimately be obtained. The recent coal strike furnished sufficient evidence to convince the railroads and other industries that coal was necessary to keep them in operation. Possibly a successful study of the various chemical and other processes of the chloroplast will later assist in throwing some light on this very important subject. With these suggestions and indicated problems some of which are old, many recent, and others in progress, some idea may be gained of the numerous opportunities for study which the subject of plant physiology offers.

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