

SCIENCE

A WEEKLY JOURNAL DEVOTED TO THE ADVANCEMENT OF SCIENCE, PUBLISHING THE
OFFICIAL NOTICES AND PROCEEDINGS OF THE AMERICAN ASSOCIATION
FOR THE ADVANCEMENT OF SCIENCE.

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FRIDAY, DECEMBER 12, 1902.

ADDRESS OF THE PRESIDENT OF THE BOTANICAL SECTION OF THE BRITISH ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE.*

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THE visits of the British Association to a particular city recur with a certain irregular frequency and bring with them a temptation to the president of a section to dwell in his opening address on the progress made in the science associated with that section during the interval between such consecutive visits. This course possesses a certain fascination of its own, for it enables us to realize how far the patient investigations of years have ultimately led to definite advances in knowledge and to appreciate the difficulties that have involved disappointments, and that still have to be surmounted. We like to look back upon the struggles, to record the triumphs, to deplore the failures, and to brace ourselves for new efforts. The opportunity afforded hereby for criticism of methods, for reconsideration of what have been held to be fundamental principles, for the laying down of new lines of work based upon longer experience, shows us how desirable such a periodical retrospect may be.

Standing as we do almost at the threshold of a new century, it seems particularly advisable that we shall occupy our thoughts with some such considerations to-

MSS. intended for publication and books, etc., intended for review should be sent to the responsible editor, Professor J. McKeen Cattell, Garrison-on-Hudson, N. Y.

* Belfast meeting, 1902.

day. I do not wish, however, so much to dwell upon the past and to lead my hearers to rest in any way satisfied with the achievements of the last century, phenomenal as they have been, as to direct attention to the future and to place before you some of those problems which at the opening of the twentieth century we find awaiting investigation, if not solution.

I can only attempt to deal with a small portion of the botanical field. These are the days of specialization, and when anyone is said to be a botanist, the question which arises at once is, Which particular section of botany is he associated with? The same principle of subdivision which cut up the old subject of natural history into zoology, botany, and geology has now gone further as knowledge has increased, and three or perhaps four departments of botany must be recognized, each demanding as much study as the whole subject seemed to only fifty years ago. I shall therefore confine my remarks to-day to the field of vegetable physiology.

I should like at the outset to recommend this section of botanical work to those of the younger school of botanists who are contemplating original research. To my mind the possibilities of the living organism as such present a fascination which is not afforded by the dry bones of morphology or histology; valuable as researches into the latter are, they seem to me to derive their importance very largely from the past, from the possibility of indicating or ascertaining the line of descent of living forms and the relation of the latter to their remote ancestors. The interest thus excited seems to me to be rather of an academic character when compared with the actual problems of present-day life, its struggles, triumphs, and defeats in the conflict for existence waged to-day by every living organism. The importance of the study of physiology as bearing upon the prob-

lems of the morphologists has, I need hardly say, been fully recognized by the workers in that field. I may quote here a sentence or two from the address of one of my distinguished predecessors, who said at Liverpool, "There is a close relation between these two branches of biology, at any rate to those who maintain the Darwinian position, for from that point of view we see that all the characters which the morphologist has to compare are, or have been, adaptive. Hence it is impossible for the morphologist to ignore the functions of those organs of which he is studying the homologies. To those who accept the origin of species by variation and natural selection there are no such things as morphological characters pure and simple. There are not two distinct categories of characters—a morphological and a physiological category—for all characters alike are physiological."

But apart from the considerations of the claims of vegetable physiology based upon its own intrinsic scientific value and the interest which its problems possess for the worker himself, and upon the place accorded to it as its relationship to morphology, it must, I think, be recognized as being of fundamental economic importance, especially in these times of agricultural depression. For many years now it has been recognized that agriculture is based upon science; that it involves indeed properly the application of scientific principles to the cultivation of the soil. But when we look back upon what has passed for agricultural science since the alliance between the two has been admitted, we cannot but recognize how lamentably deficient in breadth it has been. The chemical composition of the soil and subsoil has been investigated with some thoroughness in many districts of the country. The effect of its various constituents on the weight and quality of the crops cultivated in it has been exhaustively inquired

into, and a considerable amount of information as to what minerals are advantageously applied to the soil in which particular plants are to be sown has been acquired. A kind of empirical knowledge is thus in our possession, in some respects a very detailed one, quantitative as well as qualitative records being available to the inquirer. But elaborate as have been the researches in these directions, and costly and troublesome as the investigations have been, they have been hardly, if at all, more than empirical. Till quite recently the physiological idiosyncrasies of the plants round which all these inquiries centered were almost entirely ignored. No serious attempt was made to ascertain the way in which a plant benefited by or suffered from the presence of a particular constituent of the soil. What influence, for instance, has potassium or any of its compounds upon the general metabolism of the plant? Does it affect all its normal nutritive processes, or does it specially associate itself with some particular one? If so which one, and how does the plant respond to its presence or absence by modifying its behavior? So with phosphorus again; hardly any investigation can be made into the nutritive processes of a plant without this element becoming more or less prominent. In some cases the empirical results already referred to show an enormous influence on the crop exerted by soluble phosphates in the soil or the manure applied to it. But what can yet be said as to the rôle played by phosphorus or by phosphates in the metabolic processes in the plant? Further, how do different plants show different peculiarities in their reaction to these various constituents of the soil? For the advance of agriculture the study of the plant itself must now be added to the study of the soil. The fact that it is a living organism possessing a certain variable and delicate constitution, responding in particular ways

to differences of environment, capable of adapting itself to a certain extent to its conditions of life, dealing in particular ways with different nutritive substances, must not only be recognized, but must be the basis for the researches of the future, which will thus supplement and enlarge the conclusions derived from those of the past, in some respects correcting them, in others establishing them on a firmer basis.

In pressing upon the younger school of botanists the importance of this line of research, I do not wish to minimize the difficulties that accompany it. Difficulties of method assume considerable magnitude, for we have here no question of section cutting and microscopic examination. Vegetable physiology is allied very closely to other sciences, and research into its mysteries involves more than a preliminary acquaintance with them. Especially must one point out the importance, indeed the necessity, of acquaintance with a certain range of organic chemistry and with chemical methods of work. In certain directions, too, physics are as much involved as chemistry in others. The bearing of these sciences in particular directions will be referred to later.

I fear another obstacle stands at the threshold of research which looks sufficiently formidable. The so-called fundamental facts of vegetable physiology have been laid down with sufficient dogmatism in text-books by many writers whose names carry with them such weight that it appears almost heresy to question their statements. We have been content to accept many things on the authority of the great workers of the past, with the result that the advance of knowledge has been hindered by such acceptance of what were deemed facts, but were really inaccuracies. We may refer, for instance, to the statement made by Boussingault, and accepted by most botanists ever since his time, that

the absorption of carbon dioxide from the air takes place by means of solution in the cuticle of the epidermal cells of plants and thence passes by diffusion to the seats of photosynthesis. Only comparatively recently has this been shown to be erroneous. If, however, it is once recognized that authority is fallible this apparent obstacle becomes the opposite. The more evident questions have not yet been solved, leaving only the more difficult ones for the present-day worker.

Recognizing the importance of work in this field, and realizing that with the advent of a new century new departures must be taken, I have thought I might venture to direct the thoughts of my hearers, many of whom I may call my colleagues, to the present position of certain problems which have long been the subjects of speculation and which offer the prospect, if not of complete solution, at any rate of considerable advance if investigated by modern methods.

I turn first to a few questions connected with the nutritive problems of plants in general.

There are several theories abroad as to the progress of events during photosynthesis, none of which can be regarded as entirely satisfactory. For many reasons it seems desirable that this question shall be thoroughly investigated in the light of the present condition of both chemical and physical science. I may perhaps venture to recall to you the principal hypotheses of carbohydrate formation which have been advanced, so that its present position may be properly appreciated.

The view that has met with the widest acceptance is that of Baeyer. On his hypothesis the carbon dioxide absorbed is decomposed under normal conditions to yield carbon monoxide and oxygen; a corresponding and coincident decomposition of water leads to the production of free hydrogen and oxygen. The oxygen from

both sources is exhaled, while the carbon monoxide and hydrogen combine to form formaldehyde. The formaldehyde gives rise by a process of polymerization to some form of sugar.

A modification of this hypothesis has been advanced, which suggests that the preliminary decomposition of the carbon dioxide and the water may not take place, but that by a rather less violent reaction between them the formaldehyde may be formed and the oxygen liberated.

Erlenmeyer has suggested a somewhat different course of reaction, yielding substantially the same results. He thinks it possible that the first interaction of carbon dioxide and water leads to the formation of formic acid and hydrogen peroxide, and that these subsequently interact with each other, yielding formaldehyde and water and giving off oxygen.

Many years after the views of Baeyer appeared, a hypothesis of a different nature was proposed by Crato. He suggests that the carbon dioxide after absorption becomes ortho-carbonic acid, and that this remains in solution in the cell sap. This acid has the structure of a closed benzene ring in which six molecules are linked together. This becomes decomposed, liberating six molecules of water and six molecules of oxygen, and forming a hexavalent phenol which subsequently undergoes a molecular rearrangement and becomes glucose.

Yet another suggestion was made by Bach in 1893. He points out that when sulphurous acid is exposed to light it becomes transformed to sulphuric acid, sulphur and water being split off, and he argues that a process analogous with this may take place in a leaf. The carbon dioxide uniting with water would form carbonic acid, and this might then split up in the same way as the sulphurous acid. The carbon and the water thus split off are on this hypothesis not set free sepa-

ately, but in combination as formaldehyde. The higher carbon acid, to which Bach ascribes the formula H_2CO_4 , splits up into carbon dioxide and hydrogen peroxide, and the latter is decomposed into water and free oxygen.

Lieben has still more recently put forward the view that formic acid and not formaldehyde is formed by the first decompositions. He has found that leaves of grasses and various trees yield formic acid among other products when mixed with their own weight of water containing a trace of sulphuric acid, and distilled with steam. Moreover, when carbon dioxide is acted upon by nascent hydrogen the only product is formic acid.

These speculations afford many points which might be well made the starting places of research. The views of Baeyer have met with most acceptance, though but little success has attended the few efforts that have been made to establish them by experiment.

They involve several definite stages of action, of which the most important seem the production of carbon monoxide and hydrogen, the formation of formaldehyde, and the construction of a sugar. The last two questions arise also in connection with the hypothesis of Bach.

If we examine the work that has been published bearing on the probability of the formation of carbon monoxide in the plant, we find little that is satisfactory. The statements that have been made are opposed to the idea that carbon monoxide is of value in nutrition; it is said that when supplied to a plant instead of carbon dioxide it does not lead to the formation of carbohydrates. It is further advanced that this gas is of a very deleterious nature, and if formed would result in the speedy death of the protoplasm of the cell in which it originates. This idea is, of course, specious; but it does not appear to be well

founded. The deadly character of carbon monoxide when inhaled by a human being depends upon a peculiar interference which it causes with the oxygen-carrying power of the red blood corpuscles. The pigment hæmoglobin to which these little bodies owe their usefulness forms a loose chemical combination with oxygen, the compound being formed in the blood vessels of the lungs and being decomposed with the liberation of the oxygen in those of the tissues of the body. It is evident, therefore, that the value of the corpuscles as oxygen-carriers depends upon their hæmoglobin. When this pigment is exposed to carbon monoxide it combines with it in the same way as it does with oxygen, forming, however, a more stable compound. The affinity for this gas which the pigment manifests is very considerable. Hence the poisonous nature of carbon monoxide. It is easily seen that the latter is a poison because it throws out of gear and temporarily paralyzes a most essential part of the mechanism of respiration, effectually preventing oxygen from reaching the tissues of the body. There is no evidence here that it exerts even a deleterious influence upon the living substance itself. The only poisonous effect it would be able to exert on the plant would necessarily be of the latter character, for there is no oxygen-carrying mechanism that could be interfered with. We cannot lay any stress, therefore, on the objection to Baeyer's view, based upon the action of carbon monoxide upon the human organism.

Another possibility may, however, be mentioned. As we shall see later, there are certain resemblances between hæmoglobin and chlorophyll, the vegetable pigment concerned in photosynthesis. May not carbon monoxide enter into some relationship with the latter, and thereby indirectly hinder its activity? Of that, however, there is no reliable evidence, the facts known to us rather pointing in the opposite direction.

The idea of the poisonous nature of this gas may easily be subjected to experimental examination. It would appear easy to expose a plant to an artificial atmosphere made up to different partial pressures of carbon monoxide, to expose it in such atmosphere to various conditions of warmth and illumination and to note the effect produced. It would seem possible to examine a great variety of plants in that way, to try both aerial and aquatic forms, and indeed to test the matter exhaustively. It must be borne in mind, however, that the solubility of carbon monoxide in water is extremely small, and that there may be a great difficulty in getting it brought within the scope of the influence of the living substance on that account. It must necessarily be in solution in the cell sap before it can affect the activity of the chloroplast. Even the relations of solubility are not, however, outside the range of experiment, and it may be that the slightly acid cell sap has not the same peculiarities as water as a solvent for the gas.

It is important again to take into account in such work the factor of sunlight, on which the power of photosynthesis depends. Should carbon monoxide prove capable of serving as a basis for the formation of carbohydrates, the question would arise, Is the activity of the chlorophyll in sunlight confined to the preliminary formation of carbon monoxide from the dioxide, or is the energy derived from the light brought to bear upon the subsequent constructive processes? We have little or no accurate information as to the way in which the energy is utilized after absorption by the chlorophyll.

This opens up a very important but very difficult line of work, which brings home to us the intimate dependence of vegetable physiology upon physics. The absorption of energy from without, in the form of the radiant energy of the solar rays, is certainly

a fact, and to a certain extent we can picture to ourselves the way in which it is secured. The spectrum of chlorophyll shows us a number of absorption bands whose position corresponds with the position in the spectrum of the places where oxygen is liberated in photosynthesis. But the transformation and applications of energy in the body of the vegetable organism need much closer examination. The intimate relationship between the different manifestations or forms of energy and the ways in which they can be transformed into one another have been very minutely scrutinized in recent times. What then should hinder us from learning something much more definite than we at present know about these transformations in the rôle of vegetable life? The electrical phenomena connected with the movements of the leaves of the Venus's fly-trap (*Dionaea muscipula*) have been examined with considerable completeness by Burdon Sanderson, and we have learned that the vegetable and animal organisms show considerable similarities in this respect. Recently again Bose has made important contributions to the subject of the electrical responses to stimulation that can be observed under particular conditions. A promising beginning has thus been made, but only a beginning. The electrical condition of the normal plant under different conditions of rest and activity has still to be investigated. If we return to the subject of photosynthesis and the work done by the chloroplast, may we not hope to discover something about the transformation and utilization of the radiant energy associated somehow with this structure? Considering the relations between the manifestations of energy which we appreciate respectively as light and electricity, it does not seem wildly improbable to imagine that the energy absorbed as the former may lead to a possible electrolysis of carbonic acid under the influence of the

chloroplast, with the formation of carbon monoxide and oxygen. Pfeffer has suggested that perhaps the decomposition of the gas is not due to the light rays at all, and that they may exercise only a stimulating influence upon the chloroplast, the energy concerned being derived from heat rays directly absorbed, or heat vibrations derived from the more rapidly vibrating light rays. In this case is the decomposition brought about directly by the heat vibrations, or have we a transmutation into some other form of energy? The whole subject seems at all events a promising subject for inquiry.

Another problem connected with the action of chlorophyll is associated with the absorption of radiant energy by the different regions of the spectrum. Bands of considerable intensity are noticeable in the blue and violet, though the deepest absorption takes place in the red. Yet Engelmann's classic bacterium method shows us that very little evolution of oxygen takes place in the position of these bands in the blue and violet. The fact that absorption of radiant energy and photosynthetic activity show no quantitative relationship is of course not new, but the reason remains still to be discovered. Van Tieghem has suggested an explanation which recalls to us the hypothesis advanced by Pfeffer, just alluded to. This explanation is that there are two factors concerned in the action of chlorophyll, the elective absorption of light, shown by the occurrence of the absorption bands in the spectrum, and the calorific energy of the absorbed radiations. The failure of the rays of the blue and violet to effect photosynthesis, in spite of their absorption, would on this view be attributable to their possessing but little calorific energy. The latter is associated much more strongly with the deep band in the red, which is the seat of the maximum evolution of oxygen when the spectrum is thrown

upon a collection of active chloroplasts. The heating rays alone are ineffectual, as shown by the fact that there is no liberation of oxygen in the region of the infra-red, due no doubt to the fact that chlorophyll does not absorb these rays.

Timiriazeff, in his classical researches on the liberation of oxygen by the leaves of the bamboo when exposed in tubes of small caliber to a large spectrum, found that the amount of carbon dioxide decomposed by leaves is proportional to the distribution of effective calorific energy in the spectrum.

Van Tieghem's hypothesis that this is a matter of calorific energy may prove to be erroneous, and yet his views may rest on some sound basis. It may be a matter in which electrical rather than calorific energy may be concerned.

Returning now to the chemical steps demanded by Baeyers's hypothesis, there are certain considerations which may be urged in favor of the view that carbon monoxide really occurs in photosynthesis. It has been ascertained by Norman Collie that when a mixture of gases containing a large proportion of carbon dioxide is exposed at low pressures in a vacuum tube to the action of an electric discharge from an induction coil there is a very large formation of the monoxide, together with oxygen, in some cases as much as seventy per cent. of the gas undergoing decomposition.

Appealing to the experience of various observers, there seems on the whole to be a balance of evidence in favor of the power of plants to live and prosper in an atmosphere containing a very considerable percentage of carbon monoxide.

The question of the possibility of the latter replacing the dioxide, as the theory appears to require, is complicated very seriously by the differences of solubility between them. Carbon dioxide dissolves very readily in water and in cell sap; carbon monoxide is almost insoluble in either.

As the amount of a gas taken up by a solvent depends not only on its solubility, but upon its partial pressure, it is very evident that we cannot compare the two gases by admitting the same quantity of both to plants under simultaneous comparison. It is only necessary to supply the dioxide in the proportion of four parts in 10,000; but the almost insoluble nature of the monoxide makes it inevitable that from two to five per cent. shall be experimented with. The same question of solubility makes it almost out of the question to experiment with an aquatic plant.

It would be of considerable interest from this point of view also to inquire whether if carbon monoxide is liberated at the outset of the photosynthetic processes its combination with other groupings can take place apart from the action of chlorophyll. If so the fungi should be capable of carbohydrate construction if supplied under proper conditions with the monoxide and with hydrogen. The proper conditions, however, might be extremely difficult to establish.

The next stage in the constructive process affords still ample room for investigation. The presence of formaldehyde is not the hypothesis of Baeyer alone, but is demanded according to Bach's views, though the stages of its hypothetical construction are not the same. We have therefore to ask whether formaldehyde can be detected in plants, and if so whether the conditions under which it may exist admit of its being considered an up-grade product in photosynthesis. Objections to the theory of its formation may be advanced, based upon its undoubtedly poisonous nature. Of all the antiseptics now available to the bacteriologists it is perhaps the most potent, even traces being fatal to the form of vegetable protoplasm which is found in bacteria. We may argue that it must be equally deleterious in the cell containing chlorophyll

and to the chloroplast itself, as we have no reason to suppose that any difference in vitality exists between the protoplasm of different plants. At first sight this appears an almost insuperable difficulty in the way of the theory. Formaldehyde has, however, the properties of aldehydes in general, one of which is the power of condensation or polymerization. It passes with extreme readiness into a much more inert form, para-formaldehyde, a body in which three molecules of the formaldehyde are grouped together. It is therefore possible that it may be prevented from exercising its deleterious properties by a transformation at once into this comparatively harmless modification. This will slowly decompose under proper conditions, giving off the free aldehyde.

Pollacci has stated that it is possible to extract formaldehyde from leaves. In his experiments he took such as had been exposed to light for a very considerable period and then macerated them in water. After a sufficient extraction he distilled the leaves, together with the water in which they had been steeped. The first portions of the distillate yielded reactions indicative of the presence of formaldehyde. His experiments do not enable us to say that free formaldehyde was there, for the more stable *para*-form would be likely to decompose during the distillation, so that the reactions would be explained without demanding the presence of the free aldehyde in the leaves.

But little success has attended hitherto the attempt to show that formaldehyde, in the presence of chlorophyll, or preferably, we may say, of chloroplasts, can give rise to carbohydrates. We have nothing more satisfactory than Bokorny's experiments, in which, after failing to set up photosynthesis in a filament of *Spirogyra* fed with formaldehyde, he succeeded when he supplied the alga with its compound with

sodium-hydrogen-sulphite. Experiments on a more comprehensive scale, conducted on a variety of plants of different habits, are needed before we can regard the process as satisfactorily established.

We have further to pursue the problem by an inquiry as to the nature of the sugar first formed. Certain considerations lead to the view that it is probable that a sugar of the aldose type must be accompanied in the plant by a ketose. The hypothesis as stated by Baeyer, and so far accepted till quite recently, took no account of the latter. The aldose *grape sugar* was the one always suggested, and from this all others met with have been held to be constructed. The first appearance of a ketose, *levulose*, or *fruit sugar*, has been associated with the hydrolytic decomposition of *cane sugar*, itself constructed presumably from the grape sugar. I fear sufficient attention has not been paid to probability or to the normal course of chemical action in framing our hypotheses, for it is rather difficult to see how some of the transformations somewhat dogmatically affirmed can possibly take place. I may refer in passing to the statement that in the digestion of fat or oil during germination part of it is converted into starch or sugar.

But to return to the construction of sugar. The condensation of formaldehyde, which can be brought about by the action of basic lead carbonate, leads to the formation of several sugars, each yielding its characteristic osazone. How far the condensation in the plant follows this is still uncertain. It is quite possible that stages intervene between formaldehyde and sugar of any kind. It has been suggested that formaldehyde in the presence of water may under the conditions obtaining in the leaf give rise to glycolaldehyde, a body which forms sugar very readily indeed. The formation of sugar directly from formalde-

hyde is a much longer process and is attended with greater difficulty.

I may call your attention here to the views of Brown and Morris traversing the theory of the primary carbohydrate being grape sugar. In their classical paper on the chemistry and physiology of foliage leaves they have adduced strong evidence, based upon analyses of the sugar-content of leaves of *Tropæolum majus*, that in this plant at any rate the first sugar to be formed is cane sugar. Whether or no this is the case in plants generally cannot at present be said, though it appears from many considerations probable.

The part played by chlorophyll in photosynthesis has already been touched upon. Remarkably little is known about chlorophyll itself. It has so far been found impossible to extract it from the chloroplast without causing its decomposition, and hence our ideas of its constitution, such as they are, are based upon the examination of something differing in some not well-ascertained particulars from the pigment itself. A remarkable relationship is known to exist between the latter and iron, for unless this metal is supplied to a plant its chloroplasts do not become green. But the condition of the iron in the plant is uncertain; it seems probable that it does not enter into the molecule of the pigment at all. A remarkable series of resemblances between derivatives of chlorophyll and derivatives of hæmatin, the coloring matter of hæmoglobin, has been brought to light by the researches of Schunck and Marchlewski, which is very suggestive. The same leaning towards iron is found in the two pigments, but in the case of hæmatin our knowledge is further advanced than in that of chlorophyll. The iron is known to be part of its molecule. It can by appropriate treatment be removed, and a body known as *hæmatoporphyrin* is then formed, which presents a most striking similarity

to a derivative of chlorophyll which has been named *phylloporphyrin*. The two pigments are almost identical in their percentage composition, the hæmatoporphyrin containing a little more oxygen than the other. Both seem to be derivatives of pyrrol. The most striking similarity between them is their absorption spectra, their ethereal solutions both showing nine bands of identical width and depth, those of hæmatoporphyrin being a little more towards the red end of the spectrum. Their solutions in alcohol and ether show the same color and the same fluorescence. Though they differ in certain other respects, notably the facility with which they form crystals, it is impossible to deny that a close relationship seems probable. If this is established we may by analogy perhaps learn something about the part played by iron in the action of the chloroplast, which so far has proved as obscure as the relation of the metal to the pigment. It is very suggestive to recall the resemblances between the two pigments, the one playing so prominent a part in animal, the other in vegetable life. Both are associated with a stroma of proteid, or possibly protoplasmic, nature, in which a solution of the pigment is retained, apparently after the fashion of a sponge. Both are concerned in metabolic processes in which gaseous interchanges play a prominent part. Both are in some way dependent on the presence of iron for their individuality, even if iron is not actually present in the molecule of both. The iron being removed, the derivatives which are found are almost identical. Further researches may throw a light on this curious relationship, perhaps showing that chlorophyll may enter into a combination with carbon dioxide as hæmatin does with oxygen. Such a combination might well be the precursor of the decomposition of the carbon dioxide which has been already spoken of.

We meet with another pigment in many plants, the physiological significance of which has in recent years begun to attract some attention. This is the red coloring matter, *anthocyan*, apparently related to the tannins, which is developed especially in the young leaves of shade-loving plants when they become exposed to illumination exceeding the intensity which they normally encounter. The formation of this pigment is greatest in tropical plants, where it is found usually in the epidermis of the young leaves, though in some cases it extends to the mesophyll as well. The pigment seems in some way to be supplementary to chlorophyll, for its absorption spectrum shows that it allows all the rays useful in photosynthesis to pass through it. It is unlikely that it takes any share in photosynthesis. Several theories have been advanced to explain its presence; it may be simply to protect the delicate cells from the destructive action of too intense light, or to avert the evil of overheating from the solar rays. It has been suggested that certain rays hinder the translocation of starch, and that the pigment shields the cells from the incidence of such rays. Again the view has been advanced that the red color is important in accelerating the development of diastase from its antecedent zymogen, which has been found to take place under the influence of the rays of a certain region of the spectrum. While all these views have been advanced, however, there is little positive information bearing upon either the formation or the function of the pigment.

Very little progress has been made with the problem of the construction of proteid matter in the plant, which still confronts us. The question of its relation to the mechanism of photosynthesis has received some attention without leading to any satisfactory conclusion. Winogradski's success in cultivating the nitrate bacteria upon

purely inorganic matter reveals an unexpected constructive power in some forms of vegetable protoplasm. The question of the energy made use of in proteid construction is in an equally unsatisfactory condition. Laurent, Marchal and Carpiaux have stated that the rays of the violet and ultra-violet region of the spectrum are absorbed and devoted principally to the construction of nitrogen compounds from the nitrates, or the compounds of ammonia, which are absorbed by the plant, while the intervention of the chlorophyll apparatus is unnecessary for this purpose. The experiments which they give in considerable detail upon this absorption carry much weight and appear conclusive. Unfortunately other observers have failed to confirm them, so that at present the matter must be left open.

Among the problems connected with the nutrition of the plant, the part played by alcohol has recently come into prominence. Alcohol was originally associated only with the lower fungi, and especially with the yeast plant. Biological problems of grave importance arose in connection with the *Saccharomyces*, apart from what seemed at first the larger question, viz., the nature of fermentation. A prolonged study of the latter phenomenon led Pasteur to the view that alcoholic fermentation is only the expression of the partial asphyxiation of the yeast, and its efforts to obtain oxygen by the decomposition of the sugar. It is hardly necessary here to remind you of the controversies that centered about the question of fermentation and the theories held and abandoned as to its cause. The biological phenomena have, however, a claim now upon our attention in the light of some very remarkable researches that are calling for our attention and criticism to-day. Pasteur's explanation of the behavior of the yeast was, as we have seen, such as to connect it with the respiration

of the plant. When oxygen was withheld from active yeast sixty to eighty parts of sugar disappeared for one part of yeast formed. When oxygen was present not more than ten parts of sugar were decomposed for the same amount of yeast production. Undoubtedly the stimulus of asphyxiation materially stimulated the yeast metabolism.

But certain observations did not agree with Pasteur's explanation. An energetic fermentation takes place in the presence of oxygen, the plant multiplies extremely quickly, and its metabolism appears very active. Schützenberger argued against Pasteur's explanation with some force, emphasizing these points of disagreement between his hypothesis and the facts, and claimed that the matter rather concerned nutrition than respiration. He based his view on experiments carried out to ascertain how respiration was affected under changed conditions.

The results he obtained were briefly the following:

1. In a watery liquid without sugar, but containing oxygen in solution, the quantity of oxygen absorbed in unit time by a gram of yeast is constant, whatever proportion of oxygen is present.
2. In a saccharine liquid containing albuminous matter as well as sugar, and with oxygen in solution, the same result is obtained, except that the quantity absorbed in unit time is greater.
3. In two digestions carried on side by side for some time, one being supplied continuously with oxygen and the other deprived of it, the former produced most alcohol.

If the decomposition of the sugar had been the result of the respiratory activity of the yeast cells at the expense of the combined oxygen of the sugar, it would seem that fermentation should either not have taken place at all in the presence of free

oxygen, or that it should have been much less than in the other case, whereas the reverse is what is found. Hence Schützenberger advocated the view that the sugar is alimentary and not respiratory.

Certain facts more recently discovered support strongly the view that the nutrition of the yeast is the chief object of the process normally, though we cannot deny that when partial asphyxiation sets in fermentation is resorted to by the plant in its difficulty, that it may obtain the energy normally supplied by the respiratory processes. The mode of decomposition of the sugar, however, the formation of alcohol and carbon dioxide, raises a question as to the exact form in which the nutritive material is supplied to the protoplasm.

Of these more recent discoveries the work of Devaux on the trunks of trees may be mentioned first, as it seems to point to a similar problem to the one connected with yeast. Devaux examined the composition of the air in the interior of woody stems growing under normal conditions, and found that the proportion of oxygen it contains often sinks as low as ten per cent., while in a few cases, in the most internal part of the tree, he found this gas to be entirely absent. The disappearance of oxygen becomes easier with every increase of temperature. This partial asphyxiation is attended by the formation of alcohol in the struggling tissue, the spirit being detected by cutting up the branches of the trees and distilling them with a large excess of water. Devaux's experiments were made upon a considerable variety of trees, among which may be noted *Castanea vulgaris*, *Pyrus domestica*, *Alnus glutinosa*, *Ulmus campestris*, *Sambucus nigra* and *Ficus Carica*.

Similar results have been obtained by Mazé in some researches on seeds. When a number of these are submerged in water, microorganisms being properly guarded

against, they do not readily germinate, but their weight nevertheless somewhat rapidly diminishes. In some of Mazé's experiments with peas he ascertained that this diminution was attended by a considerable formation of alcohol. Three parcels of forty peas were examined, weighing respectively 10, 17 and 27 grams, and the experiments lasted 6, 12 and 27 days. He found the proportion of alcohol to the original weight of the peas was 2.34, 4.63 and 6.56 per cent. As the peas were submerged, and so kept out of contact with air, it seems possible to suppose we have here again an effect of asphyxiation. Other experiments, however, make this view unsatisfactory. He germinated twenty peas at 22° C. for seven days under normal conditions, till their axes were about 1½ inches long. He then covered them with water, in some cases leaving the terminal bud exposed to air. The development of the submerged plants stopped at once, and at the end of five days the liquid contained 130 milligrams of alcohol. The seedlings whose terminal buds were exposed to the air continued to grow without showing any disturbance. Mazé concludes that the alcohol produced was utilized by them in their growth, and suggests that it is a normal and necessary product of the digestion of carbohydrate material in seeds in course of development.

He goes on to show that alcohol can be demonstrated to be present in plantlets that have germinated for forty-eight hours at 23° C. under normal conditions.

Another worker of great eminence who has found similar conditions to exist in normal vegetation is Berthelot. He put blades of wheat and leaves of the hazel in flasks, displaced the air by hydrogen, and distilled. In the case of the wheat he heated the flask to 94° C., in that of hazel he conducted the distillation by passing steam through the flask. In both he found

the distillate contained alcohol. The quantity was not large, but still measurable; from 10 kilos. of leaves he obtained 10 grams of alcohol.

Mazé claims to have found alcohol under normal conditions in the stems and leaves of the vine.

Mazé finds further that the weight of a seedling of maize approximates at any moment during the early stages of germination to half that lost by the reserve store in the endosperm.

From his experiments, and those of the other authors alluded to, he concludes that alcohol is formed in the living cells of seeds at the expense of grape sugar by virtue of a normal diastasic process, which makes them approach yeast cells more closely than has been suggested by any of the experiments hitherto published. We may inquire further how far the evidence points to the probability that the molecule of sugar is split up in that way into alcohol and carbon dioxide, and that the alcohol is the nutritive part of the sugar molecule. Certainly Mazé's experiments on the submerged seeds with the plumule exposed above the water are not inconsistent with that view. Duclaux has spoken more definitely still on this point, and has said that the alcohol formed becomes a true reserve material to be used for nutriment.

We have, however, further evidence that to some plants, at all events, alcohol is a food. Laborde has published some researches conducted upon a fungus, *Eurotiopsis Gayoni*, which point unmistakably to this conclusion. He cultivated it in a solution containing only the mineral constituents of Rawlin's fluid and a certain percentage of alcohol, usually from four to five per cent. The plant grew well, forming little circular patches of mycelium, which enlarged radially as the growth progressed. The mycelium became very dense in the center of the patches, and the

fungus evidently thrived well. As it grew the alcohol slowly disappeared, the rate being about equal to that of sugar in a similar culture in which this substance replaced the alcohol. The mycelium in some experiments was cultivated quite from the spores. Eurotiopsis is a fungus which has the power of setting up alcoholic fermentation in saccharine solutions. When cultivated in these alcohol is accordingly produced, and subsequently used, but the growth of the mold is not so easy under these conditions as when the alcohol is supplied to it at the outset.

Duclaux has shown that in the case of another fungus, the well-known *Aspergillus niger*, though alcohol kills it while it is in course of germination from the spore, it can utilize for nutrition 6.8 per cent. when it becomes adult, continuing to grow, and putting out aerial hyphæ. Eurotiopsis is more pronounced in its liking for alcohol, for it thrives in a mixture containing ten per cent.; even if submerged entirely it continues to grow and flourish in an eight per cent. solution.

The peculiarity relates only to ethyl alcohol; methyl alcohol will serve as a nutritive medium for only a little time, sufficient only for the commencing development of the spores into a mycelium and disappearing very slowly from the culture fluid. The higher alcohols, propyl, butyl and amyl, not only give no nourishment, but are poisonous to spores. A very small trace of any of them can be used by the adult mold.

Laborde claims to have established as the result of his investigations that Eurotiopsis normally makes alcohol from the sugar to nourish itself with it, just as yeast makes invert sugar from cane sugar because it is the nutritive material it likes best. The enzyme zymase is present in the fungus and plays the part of an alimentary enzyme. Its consumption lasts twice as

long as that of a corresponding weight of glucose; it can serve twice as long for the nutrition of the same weight of plant.

These remarkable results lead us to the consideration of the mode in which the carbohydrates, and particularly the sugars, are assimilated by the plant. We have held the view that the sugar molecule is capable of entering with little if any alteration into that of protoplasm. We have found no direct evidence bearing upon its fate. It is possible to detect sugar in the axis of a plant till quite near its growing point. Then the reaction ceases to be obtainable, and we know that assimilation is taking place. But we have still to investigate the steps, no very easy problem to undertake. May it possibly be that it is the alcohol moiety of the sugar which the protoplasm takes up, part of the carbon dioxide evolved by the growing organ being an expression, not of respiration, but of a fermentation preliminary to assimilation?

But I feel I have dealt at sufficient length with this question. I pass, therefore to consider briefly another nutrition problem of a rather different kind. The germination of seeds is a question that might be thought to have been fairly settled by the investigations of the latter half of the last century. We have come to the conception of the seed as fundamentally a young embryo lying quiescent within its testa, and provided with a store of nourishment deposited either within its own substance, or lying round it in the tissues vaguely named endosperm or perisperm. The nourishment has been held to be practically ready for its use, needing only a certain amount of enzyme action to be applied to it to convert the food store from the reserve to the nutritive condition. We have recognized here starch, proteids and glucosides, and have ascertained that the embryo can furnish the appropriate enzymes for their digestion. Each reserve store has apparently been

quite independent of the rest, and the embryo has had control of the whole.

Certain considerations, however, lead us to the view that for albuminous seeds at any rate this mode of looking at the matter is no longer satisfactory. We may first ask how far the embryo is the controlling factor in the digestion. Putting the matter in another form, is the influence of the parent plant lost when a stable store of food has been provided for the offspring, and does it leave its utilization entirely to the latter? Is the gametophyte prothallus merely to become a dead or inactive structure as soon as it has developed its young sporophyte, or may its influence extend for the longer period of germination? There are many reasons for thinking this is the case. Indeed the view has been put forward by some observers at intervals for some years. Gris claimed to have shown it in 1864; but it was opposed by Sachs, who said that the enzymes which cause decompositions in the reserve materials are always formed in the young plant or embryo and are excreted by the latter into the endosperm. Some careful experiments on the point were conducted by Van Tieghem and were published by him in 1877. His work was carried out on the seeds of the castor-oil plant. He deprived the seeds of their embryos and exposed them for some weeks on damp moss to a temperature of 25–30° C. After several days of this exposure he found the isolated endosperms were growing considerably, and at the end of a month they had doubled their dimensions. In the interior of the cells he found the aleurone grains to be gradually dissolving, and the oily matter to be diminishing, though slowly. The dissolution extended throughout the mass of the endosperm, and was not especially prominent in the side that had been nearest to the cotyledons. He noted, too, that though starch did not normally appear in the germinating endo-

sperm, under the condition of non-removal of the products of the decomposition, it did appear in the cells in the form of small grains, though not till after several days had elapsed. Van Tieghem also observed that the progress of the decompositions could be arrested and the endosperms made to reassume a quiescent condition, and that then the aleurone grains again became formed, though in less quantity than before.

In some experiments on *Ricinus* which I carried out in 1889 I found much the same sequence of events as Van Tieghem had described. The endosperm unquestionably became the seat of a renewed metabolism, in the course of which many interactions between the various reserve materials became noticeable. It was remarkable that the activity of this metabolism was much more pronounced when the embryo or parts of it were left in contact with the endosperms.

An observation of a similar character has been made by Haberlandt and by Brown and Morris in the case of the seeds of grasses. The conversion of the reserve cellulose of barley grains has been shown by these observers to be the result of the action of an enzyme *cytase*, which is secreted largely by the so-called aleurone layer, which is found surrounding the endosperm, immediately underneath the testa.

Recently my own work has been bearing on this question, particularly as regards the behavior of the seeds of *Ricinus* during germination. The reserves of this seed are mainly composed of oil and aleurone grains, hardly a trace of carbohydrates being present. At the onset of germination there is a remarkable appearance of both cane sugar and glucose, which increase as the oil diminishes. The old view advanced to explain this fact has been the transformation of the oil directly into the sugars or one of them, a theory which it was difficult to

reconcile with the chemical possibilities of oil. I have found that side by side with the appearance of the sugar we have also the formation of a considerable quantity of lecithin, a fatty body containing nitrogen and phosphorus. The seed contains a comparatively large amount of phosphorus in the form of the well-known globoids of the aleurone grain, a double phosphate of calcium and magnesium. The occurrence of this body points to a considerable interaction of various substances existing in the seeds, the phosphorus apparently coming from the globoids and the nitrogen from the proteids. Instead therefore of the fat being transformed into sugar it seems certain that a very considerable metabolism is set up, in which the various constituents of the endosperm interact very freely together. I am informed by Mr. Biffin, who has investigated the histological changes accompanying the germination, that the protoplasm of the endosperm cells appears to increase in amount very greatly during the early stages. The observations suggest a very vigorous resumption of metabolic activity by the cells of the endosperm, in the course of which the various reserves are brought into relation with the living substance of the cells and a number of new products are formed to minister to the nutrition of the growing embryo. The formation of the sugars may more probably be referred to the renewed activity of the protoplasm of the parent gametophyte than to a direct transformation of the fat under the influence of the embryo. Further researches upon a large variety of seeds appear necessary to give us a true idea of the chemical processes of germination. What now appears probable in the case of fatty seeds may prove to be true also in the case of those which have other varieties of reserve material.

I have already alluded to the problems concerning the electrical phenomena pre-

sented by the plant at rest and during activity. Very little work has so far been done in this direction, and our knowledge of the subject is materially less than that concerning similar phenomena in muscle and nerve. Still a beginning has been made, and we have observations on record due to Waller and to Bose which are of the greatest interest, not only because they show a great correspondence in behavior between animal and vegetable structures, but on account of their possible importance in determining the character of many of the metabolic processes and the forces at work in the tissues.

Some very striking results were only a few months ago published by Bose on the electric response in ordinary plants to mechanical stimulation. He arranged a piece of vegetable substance, such as the petiole of the horse-chestnut, or the root of a carrot or a radish, so that it was connected with a galvanometer by two non-polarizable electrodes. The uninjured tissue gave little or no evidence of the existence of electrical currents; but if a small area of its surface was killed by a burn or the application of a few drops of strong potash, a current was observed to flow in the stalk from the injured to the uninjured area, just as is the case in animal tissue. The potential difference in a typical experiment amounted to .12 volt. The tissue was then stimulated, either by tapping or by a torsion through a certain angle, and at once a negative variation or current of action was indicated, the potential difference being decreased by .026 volt. Very soon after the cessation of the stimulus the tissue recovered and the current of rest flowed as before. Bose's investigations extended considerably beyond this point, and established a very close similarity in behavior between the vegetable substance and the nerves of animals. Summation effects were observed, and

fatigue effects demonstrated, while it was definitely shown that the responses were physiological. They ceased entirely as soon as the piece of tissue was killed by heating.

This remarkable demonstration of similar electrical properties to those possessed by nerve strengthens very greatly the view of the conduction of stimuli in the plant by means of the protoplasmic threads which have been demonstrated by Gardiner and others to exist throughout the plant, uniting cell to cell into one coherent whole.

Much remains to be done in this field; indeed, not more than a beginning has been made. The electrical accompaniments to response to stimuli have been investigated by Burdon Sanderson in the case of *Dionæa*, but many other instances are still awaiting examination. The peculiar phenomena of electrotonus and their relation to stimulus have so far only been observed in animals.

These observations strengthen considerably the view of the identical nature of animal and vegetable protoplasm which has in recent years come into prominence, and which is receiving more and more support in all directions.

These electrical currents, following mechanical action, which no doubt is accompanied by chemical change, make us ask whether electrical phenomena do not in all probability accompany the slow chemical actions which we call metabolism. The view that electrical energy is concerned in the processes of photosynthesis, suggested in an earlier part of this address, is certainly not weakened by a consideration of these phenomena.

The probability of the transmission of stimuli through vegetable tissue along the protoplasmic threads, extending from cell to cell, has been supported during the last year or two by some remarkable observations claimed to have been made by Némec on certain roots and other organs. He says he has succeeded in demonstrating a

continuous fibrillar structure in the protoplasm of the cells, fibrils passing along it in a longitudinal direction and apparently connecting the protoplasm of a longitudinal series of cells into a conducting chain. These conducting strands extend between the sensitive region—*e. g.*, the tip of the root—and the region which is growing, and which is caused by the stimulus to curve. Nêmec says that these conducting strands can be made evident by the use of appropriate staining reagents. They vary in number and position, but appear to be confined to sensitive and motile organs.

It is clear that the matter cannot rest where it is. The statements made by Nêmec call for investigation by both histological and physiological methods. It is possible that appropriate reagents may lead to the recognition of structure in what has been hitherto regarded as undifferentiated protoplasm.

Before concluding this address I may call attention to the vast field opening up in connection with the pathology of plants. The work done by our predecessors has been more largely work on the morphological peculiarities of various fungi than upon the physiological changes which constitute pathology, properly so called. It is only recently that attention has been given to the broad questions of disease in plants. Even now, however, certain advances have been made, and the direction of research is taking shape. In the science of pathology little in recent years has been so fascinating as the question of immunity against the attacks of certain diseases, either hereditary or acquired. It has been bound up with the very large question of toxins and their attenuation, their opposites, the anti-toxins and matters of a similar nature.

Great results have been obtained in human pathology, with which it is not for me to deal. I mention them here because we are face to face with the possibility of

treating some of the diseases of plants in a similar way, and perhaps on the threshold of very far-reaching discoveries.

I may call attention to the researches of Ray and of Beauverie upon the general question of plant infection, and especially upon a disease set up by a fungus known as *Botrytis cinerea* which attacks grapes, begonias, and other plants. The fungus exists in three forms, one of which is a harmless saprophyte, another a destructive parasite, and a third intermediate between the two. The first is a very common fungus, developing on decaying plants and bearing ordinary gonidia or spores. The second is completely filamentous and bears no reproductive organs. It is produced when the air is heavily charged with moisture and the temperature high, conditions of common occurrence in forcing houses. The third is an attenuated form intermediate between the other two. It bears gonidia like those of the first, and in addition others which germinate without falling off the parent plant and elongate into threads. Many plants can bear the invasion of this plant without suffering greatly, though it cannot be called harmless. It occurs chiefly when a high temperature is associated with a considerable amount of moisture in the air.

It is not difficult to cultivate this attenuated form of the *Botrytis* in sterilized soil. Beauverie describes one experiment made with it which is very striking. Damp earth was sterilized in a Petri dish of large surface, sown with spores of the *Botrytis*, and kept at a temperature of about 16° C. After three days the surface of the dish was covered with a loose mycelium, which bore numerous gonidiophores. The fungus was allowed to grow for some time under these conditions, and the infected earth was then transferred to fresh pots in which were placed cuttings of begonias. The plants grew well and were

not sensibly affected by the presence of the fungus in the substratum or in its surface. Placed subsequently in conditions which were eminently suitable to the development of the parasitic form, they resisted its action perfectly, though control plants which had not been cultivated in the ground infected by the attenuated form were killed very quickly. From their experiments the authors claim to have shown that the form of *Botrytis cinerea* intermediate between the gonidial and the sterile form can make plants immune to the attacks of the latter.

Researches of a somewhat kindred nature dealing with the infection of particular plants by specific fungi have been communicated recently to this section by Professor Marshall Ward in his paper read last year on the bromes and their brown rust. They brought to light many very important facts connected with the question of adaptive parasitism and immunity. Few questions in vegetable physiology can compare in economic importance with these when we think of their possible development in relation to agriculture.

I have now somewhat hurriedly surveyed certain parts of the field of vegetable physiology. It has been impossible in an address like this to do more than indicate what seem to me some of the more important problems awaiting investigation. May we hope that all such work will be vigorously conducted, but that the conclusions reached will be scrutinized with the greatest care and subjected to repeated examination? Great hindrances to the advance of the science resulted from dogmatic assertions made by eminent men in the past, their personal influence having led to their conclusions, not altogether accurate, being nevertheless almost universally accepted. Many years subsequently these conclusions have needed reexamination, the result being the destruction of a whole fabric that

had been reared upon this unworthy foundation. I may close, as I began, by an appeal to the younger school of botanists to take some of this work in hand, and by assiduous and critical experiment and observation to contribute to the solution of the problems pressing upon us in this field.

J. REYNOLDS GREEN.

CAMBRIDGE UNIVERSITY.

AMERICAN ORNITHOLOGISTS' UNION.

THE Twentieth Congress of the American Ornithologists' Union convened in Washington, D. C., Monday evening, November 17. The business meeting of the fellows was held at Dr. Merriam's residence, and the public sessions, commencing Tuesday, November 18, and lasting three days, were held at the U. S. National Museum.

Dr. C. Hart Merriam, of Washington, D. C., was reelected president; Charles B. Cory, of Boston, and C. F. Batchelder, of Cambridge, Mass., vice-presidents; John H. Sage, of Portland, Conn., secretary; William Dutcher, of New York City, treasurer; Frank M. Chapman, Ruthven Deane, E. W. Nelson, Witmer Stone, Drs. A. K. Fisher, Jonathan Dwight, Jr., and Thos. S. Roberts, members of the Council.

The ex-presidents of the Union, Dr. J. A. Allen and Messrs. William Brewster, D. G. Elliot and Robert Ridgway, are *ex-officio* members of the council.

Harry C. Oberholser, of Washington, D. C., was elected a fellow; Ernst Hartert, of England, and John A. Harvie-Brown, of Scotland, honorary fellows; A. J. Campbell, of Melbourne, W. P. Pyecraft, of London, Dr. H. von Ihering, of Brazil, and Alfred J. North, of Sydney, N. S. W., corresponding fellows. Thirteen associates were elected to the class known as members, and eighty-four new associates were elected.