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President—Sir WILLIAM HALE-WHITE, K.B.E., M.D.

OCCASIONAL LECTURE.

Circulation and Assimilation in Plants.[1]

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ON two previous occasions I have been able to give, before this Society, demonstrations of various life reactions in plants. The imperceptible growth of the plant was magnified fifty million times; a moving spot of light indicated the rate of growth. Application of drugs produced very characteristic effects; stimulants caused great enhancement of the rate of growth, or awakened it when dormant. Under the action of poison a violent death-spasm was seen to occur corresponding to the death-throe of the animal. These and other reactions were demonstrated by the automatic record made by the plant itself; they showed that the fundamental mechanism in the life processes is the same in the plant and in the animal. From the establishment of this generalization, it follows that the intricate problems of animal life are likely to be solved by the study of corresponding problems in the life of the plant.

Far more important than external manifestations are the activities in the interior of the organism which are beyond our scrutiny. New instruments of great sensitiveness have therefore to be invented to bring the invisible within the range of the visible. I shall describe a new method and appliance I have devised, which enabled me to probe into the interior of the organism. The internal activities, hitherto unsuspected, thus became fully revealed. I shall describe other experiments which solved the great mystery of the ascent of sap in trees, which baffled inquiry for more than two hundred years. I will also exhibit my new apparatus by which the rate of carbon assimilation in plants becomes automatically recorded, and by which investigation on this subject has been greatly extended. The shortness of time available will allow only brief accounts being given of two very extensive lines of investigation. The subject will be found fully dealt with in my "Physiology of the Ascent of Sap" already published by Messrs. Longmans, and the "Physiology of Photosynthesis" shortly to be published by them.

THE ASCENT OF SAP.

The movement of sap inside the tree is invisible, and no accurate means have hitherto been available for the measurement of the normal rate of ascent of sap, and how that rate is affected by changes of the environment. I have overcome the difficulty by devising three different types of apparatus by which the normal rate and its modification are determined with the highest accuracy.

[1] Substance of an Address delivered before the Royal Society of Medicine, December 6, 1923.

Strasburger, from his experiments, imagined that poisoning did not affect the ascent of sap; hence he inferred that the movement of sap cannot be due to the physiological action of living cells. This view, which found general acceptance, had the most disastrous effect on investigation of this intricate problem. My results completely disprove Strasburger's conclusion. The records obtained by my apparatus show that a complete arrest of ascent takes place under the action of poison. A simple, yet most conclusive, experiment is to take two similar drooping stems; of these the cut end of one is placed in water, that of the other in a poisonous solution of formaldehyde. In the first case the drooping stem soon becomes turgid and fully re-erected by the ascent of sap, but there is no recovery in the poisoned stem, which droops still more and soon becomes a huddled mass of dying tissue. This offers a conclusive proof that the movement of sap is essentially due to the cellular activity in living plants. Further experiments prove that a definite active tissue extends throughout the length of the tree, the cellular pulsations of which in regular sequence cause, by their pumping action, the propulsion of sap. In the animal the circulation is maintained by the pumping action of the throbbing heart. Since the mechanism for the movement of sap is essentially similar, the tree may be regarded as possessing an elongated "heart."

The effects of various agents on the "heart beat" of the tree and that of the animal, exhibit most astonishing similarities, of which I shall mention only a few instances. In the case of the animal it is well-known that the frequency of heart-beat is quickened under a rise, and slowed down under a fall of temperature, till at a sufficiently low temperature the rhythmic activity becomes arrested. Under certain abnormal conditions when the beating of the animal heart is arrested, it can be renewed by adequate stimulation. Certain stimulants cause a great enhancement of the pulsatory activity, while poisons arrest it. Results in every way parallel to these are observed in the cellular pulsation of the tree. Rise of temperature, increasing as it does the pulsatory activity, enhances the rate of ascensional movement of the sap. Lowering of temperature, on the other hand, causes a depression of the rate, till, at a critical temperature, the ascent becomes arrested. A slight rise of temperature above the critical point, however, renews the ascent. Under a condition of sub-tonicity the cellular activity and the resulting movement of sap become arrested. Stimulus is now found to revive the activity and renew the ascent. Very striking results are produced by the action of anæsthetics, which in small doses act as a stimulant. A small dose of ether is thus found to enhance the cellular pulsation and cause a great increase in the rate of ascent. Chloroform causes a preliminary enhancement, followed by arrest caused by the toxic effect of a large dose.

Diurnal periodicity in intravascular pressure.—The cellular activity undergoes a periodic variation, in response to changes in the environmental condition during twenty-four hours. This causes a very interesting diurnal periodicity of the pressure exerted by the sap, as indicated by a self-recording manometer attached to the tree. It would no doubt be interesting to find out whether there is a diurnal periodicity of blood-pressure in the animal.

The "Milking" of the Palm Tree.

The water pumped up by the root causes intra-vascular pressure, and profuse exudation may thus take place when a hole is drilled into the tree. But the Indian date palm grows in a dry or even arid soil, and necessity compels the tree to exploit the scanty or precarious supply of water. The sap

is held very tenaciously in the trunk, and a hole drilled into it causes no exudation of sap. Yet, after certain special treatment, the tree yields quantities of sap containing sugar, as large as 20 litres per day. No explanation has hitherto been offered for this copious exudation in the absence of internal pressure to urge it. My experiments show that a dormant and inactive tissue is roused to intense activity under repeated irritation. When a slanting cut is made in the date palm at the upper end of the trunk, it does not cause any yield of sap. But when the wound is made for several days in succession, the cumulative irritation is followed by copious exudation of the sap. This drastic and harsh treatment cannot but cause injury; it is within bounds of possibility to devise other modes of irritation which are less injurious to the tree. In certain other varieties of palm the sugar-containing juice is yielded by the inflorescence, and the coercion employed here is as curious as it is interesting. The Malays inflict repeated blows for several days with a wooden hammer to the base of the flower stalk; after this an incision made at the tip of the spadix is followed by copious exudation. In Bengal the practice is perhaps a little more humane; the long spadix is held tightly between the fingers and kneaded downwards. This potential milking process is continued for about a week, after which the yield of sap becomes abundant. The two processes just described may be aptly described as "butting" and "milking," from the analogy of the action of the calf to make the cow yield her milk.

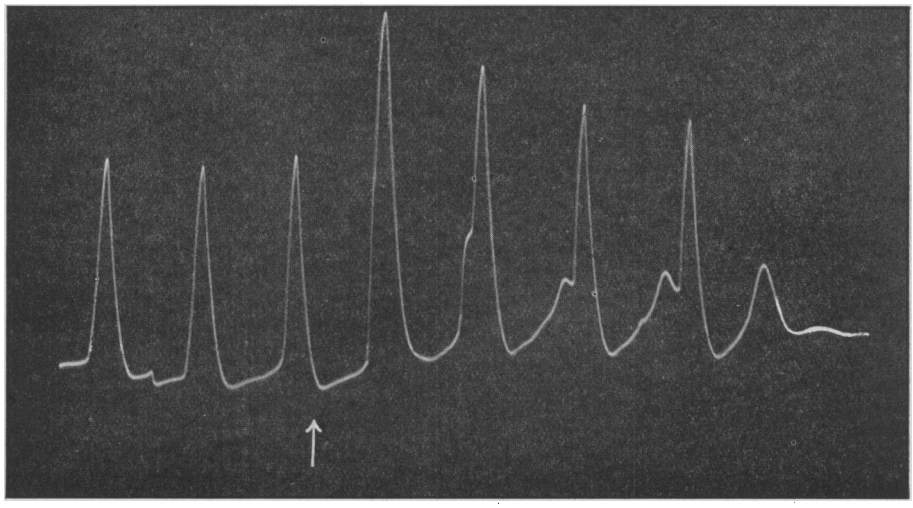

FIG. 1.—Electric record of cellular pulsations in the interior of the plant. Application of chloroform at arrow is seen to cause a preliminary enhancement followed by permanent arrest due to toxic dose.

THE ELECTRIC PROBE FOR RECORD OF THE INTERNAL PULSATION.

The experiments already described prove that the movement of sap is maintained by the pulsating activity of certain cells. The next problem was the localization of the pulsating layer, and to obtain an actual record of the individual pulsation and watch its responsive variations under drugs and other agents. For this we have to get access to the smallest unit of life, the

individual cell or the "life atom," a congregation of which constitutes the living organism. But the pulsatory movement of a cell is ultra-microscopic and its detection may well appear to be beyond the range of possibility. This has, however, been accomplished by my electric probe in circuit with a recording galvanometer. The probe is gradually introduced across the tree, its tip thus coming in contact with successive layers of cells. The record thus obtained is thrown on the screen, from which it will be seen that the galvanometer remained quiescent till the probe came in contact with the active layer, the throbbing pulsations of which gave rise to corresponding electric pulsations recorded by the galvanometer. In dicotyledonous plants it is the inner layer of cortex which functions as the organ for the propulsion of sap. Moreover, any agent which quickens or arrests the heart-beat of the animal is also found to enhance or inhibit the electric heart-beat of the tree. The automatic records given by the tree are thrown on the screen; under the action of a stimulant we find the cellular pulsations become very greatly enhanced. The effect of a poisonous dose is soon seen in the permanent abolition of the throbbing activity (fig. 1). We thus find that the tree which appears so insensitive and inactive is not so in reality, but that notwithstanding its placid exterior intense and ceaseless pulsations are taking place within it—pulsations which are modified in response to changes in the environment. The fluctuations of the life-activity in the interior of the tree are thus revealed by the waxing and waning of its pulse-records. We are now in a position fully to realize the essential similarity of physiological mechanism in the maintenance of circulation in the plant and in the animal.

Assimilation in Plants.

It is through these incessant internal activities that the tree is enabled to raise large quantities of water to a height sometimes as great as 450 ft., as in the giant eucalyptus. The energy for doing this work resides in the breakdown of complex chemical substances in internal combustion or respiration. Energy must therefore be stored in meeting this loss; green leaves function in storing the energy of sunlight, CO_2, which is the gaseous food of the plant, being built up by photosynthesis into carbohydrate. The phenomenon of CO_2 assimilation in plants is of great thoretical interest, as an example of the simplest type of assimilation. In normal photosynthesis a certain volume of CO_2 is absorbed and an equal volume of oxygen evolved. Photosynthetic activity may therefore be measured from the rate of absorption of CO_2 or of evolution of oxygen. The method that has been generally employed is the absorption of CO_2, necessitating complicated chemical analysis, which is therefore a very prolonged and laborious process. It is not a very sensitive or a highly accurate method. The evolution of oxygen by water plants is a more sensitive indicator of photosynthesis, but numerous sources of error had hitherto stood in the way of its employment for quantitative measurements. These difficulties have been completely removed by the new method which I devised, by which the evolution of equal volumes of pure oxygen becomes automatically recorded (fig. 2). The photosynthetic recorder is seen at work; the record of successive evolution of equal volume of oxygen is obtained by the electric device which actuates the electro-magnetic writer to inscribe successive dots on a revolving drum (fig. 3). It also gives independent audible signals. This method being automatic all personal errors of observation are completely eliminated. It is also so extremely sensitive that it is possible to measure photosynthetic deposit of

carbohydrate as minute as a millionth of a gram. The extreme sensitiveness and accuracy of this new method has led to the discovery of several important phenomena which otherwise would have been impossible. Stimulation is

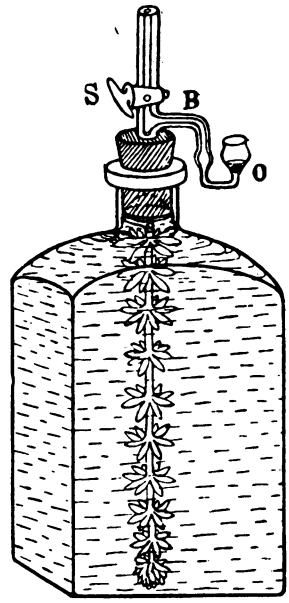

FIG. 2.—The vessel containing the water-plant, *Hydrilla*. S, stop-cock; B, bubbler; O, oil-valve. Photosynthetic evolution of oxygen lifts the oil-valve, successive bubbles of the bubbler representing evolution of equal volumes of gas.

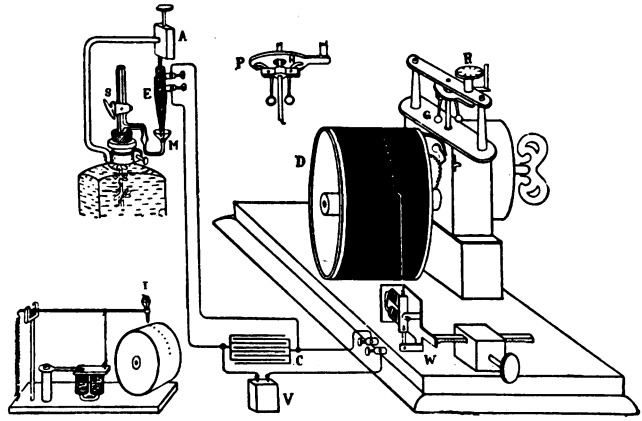

FIG. 3.—The photosynthetic recorder. E, the electric pencil for completing contact through drop of mercury, M; A, adjusting screw; V, voltaic cell; C, condenser; D, revolving drum; W, electromagnetic writer; G, governor (shown separately at P, with pair of hinged levers, H). I, ink recorder.

found to produce characteristic modification in the assimilation. A moderate stimulation enhances this power, but stronger stimulus inhibits it, the period of inhibition depending on the strength of stimulus. Still more interesting are

the actions of different chemical agents, the effects of which are strikingly modified by the strength of the dose.

Derangement of normal assimilation.—In normal cases the various co-efficients for the activity of assimilation in a particular season of the year are fairly constant. The respiratory quotient is in normal cases very nearly equal to 1. But a sudden derangement occurred in the physiological condition of the plant during the passage of heat wave in Bengal in April last. The respiratory quotient was then found to be very much lowered and less than unity. Further examination showed that the juice of the normal plant was practically neutral, but under the excessively high temperature in April the plant becomes markedly acid, this physiological derangement being probably associated with the abnormal variation in the respiratory quotient.

Effect of Infinitesimal Traces of Chemical Substance on Assimilation.

During the course of another investigation I discovered the effect of minutest traces of certain chemical substances in inducing an extraordinary enhancement of assimilation by plants. The dilution employed was one part in a billion (billion in French measure is equal to 1,000 millions). With certain substances a dilution of one part in two billions produced an increase of activity of more than 200 per cent. The activity declined when the strength of the solution was raised above a critical dose. Dilute extract of thyroid gland, in a dilution of one part in a billion produced a maximum increase of activity of about 70 per cent. The noticeable fact in the action of thyroid extract is that no diminution of activity below normal took place for a considerable range in the dilution. The effect of traces of iodine was more or less similar. At first sight it is inconceivable that infinitesimal traces of certain chemical substances should have such a potent influence on life-activity. There is, however, no doubt about the reality of the phenomenon. The immediate and concrete demonstration of the effect of minute traces of chemicals on assimilation of plants is of special interest, since it enables us to understand the effects of ultra-measurable quantities of vitamin on general assimilation and of hormones on physiological reaction.

The plant is a multicellular organ and hence necessity arises for inter-communication and interaction between more or less distant organs; this is accomplished in two different ways: the first is exemplified by the hydraulic convection of liquids carrying chemical substances in solution such as occurs in the circulation of sap. The second mode of intercommunication is the conduction of excitatory change along certain tissues in the plant which function as nerves.

The ultimate result of investigations such as these and others which I have been able to complete, is the establishment of the important generalization of the unity of physiological mechanism in all life. For we find in the plant and in the animal, similar contractile movement under stimulus, similar reaction under particular drugs, similar cell-to-cell propagation of pulsatory movement, similar circulation of fluid by pumping action, similar nervous mechanism for the transmission of excitation, and similar reflex movements at the distant effector. The simpler type of plant organization offers a unique advantage in investigation, the pursuit of which will no doubt lead to the solution of many perplexing problems of animal life.