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TRANSPIRATION AS ENERGY DISPERSAL.

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One of the subjects which receives considerable attention in our elementary textbooks of botany, but which continues to be presented in a manner more or less unsatisfactory from both the pedagogic and scientific point of view, is transpiration. While transpiration has received a large amount of attention in recent years, and while much valuable progress has been made in measuring and interpreting transpiration, this progress has not been sufficiently reflected in recent texts. In particular, the paragraphs which attempt to consider the significance of transpiration to the plant's own life are most unsatisfactory. And at the close of the discussion the important question as to why the plant transpires such a very large amount of water during the growing season has been left without an adequate answer.

Unfortunately, some of the best contributions to our knowledge of the meaning of transpiration to the plant itself have been published in magazines not generally available to secondary school men. This is true especially of the contributions of investigators whose work has appeared in foreign journals of far too limited circulation in America. The purpose of this discussion is to present a few of the salient facts which others have discovered, and to shift the emphasis from the material changes of the process of water loss to the energy changes involved.

One of the ways in which transpiration is frequently presented is that it is the unavoidable consequence of the need for the gases, oxygen and carbon dioxide, in two of the major processes of plant life. In leaving passageways for ingress and egress of gases which must dissolve in wet cell walls, the conditions leading to water loss were unavoidably produced. We all recognize the unavoidableness of transpiration so long as vapor pressure in the plant is higher than the vapor pressure of the surrounding air, and so long as water-permeable membranes exist. Moreover, this thing which cannot be avoided may even become dangerous at rare intervals when the life of the organism is threatened by transpiration proceeding more rapidly than root absorption can make good the water loss. But this presentation does not begin to reach the heart of the matter.

Another method of handling the subject is to point out the advantages accruing to the plant by virtue of its transpiratory process. One of the chief advantages pointed out is that the plant secures very rapid transportation and distribution of mineral nutrients needed for the growth of all living protoplasm. And it is true that the mass movement of solutes in the tracheae, which is the result of transpiration occurring at the upper end of the peculiarly constructed conducting system of plants, is a great advantage, particularly to tall plants. For if the salts needed by tall plants were obtainable only as a result of diffusion migration, there would probably be no tall plants. The migration of salts, even when the diffusion gradient is high, is very slow. For instance, as Haskell indicates, it would require six weeks for a molecule of barium nitrate to travel thirty centimeters by diffusion, with a concentration gradient running from saturation to zero in that distance. The length of time necessary for any given molecule to traverse the stem of a tree fifty meters tall by diffusion would require many years, for the concentration gradient for the soil minerals is quite low. It might conceivably require a century to make the same journey by diffusion that is accomplished in a few days by mass movement.

Another advantage sometimes suggested is the concentration of the salts in the leaves, as though the salts would be too dilute and inadequate for the plant unless transpiration were carried on with great rapidity. This view is entirely untenable, however, for it involves the false assumption that the more water which passes through the plant, the more salts the plant obtains from the soil solution. Experiments have shown that when plants are grown in sunshine, where transpiration is most rapid, they take in less salts than when grown in the shade, where transpiration is relatively much slower. The work of Hasselbring on Cuban tobacco and of Burns on white pine seedlings shows that the absorption of salts and water are independent processes and that water intake can be increased without accelerating the absorption of salts.

There is still another view of transpiration which regards it as a necessary process, so necessary that, if it were completely prevented on a bright warm day, it would be as serious to the plant as would deprivation of oxygen to a human being. And this view ascribes to it as its chief rôle the dissipation of energy. Some of the facts upon which this view rests are so valuable that every teacher of botany in secondary schools should be in possession of them. Disregarding the slight energy changes involved in condensation and digestion of foods, there are at least three ways in which energy may be accumulated in the plant: (a) the absorption of radiant energy; (b) respiration; (c) intake of energy from the atmosphere if the latter happens to be warmer than the plant.[1] There are also three ways in which the energy may be dissipated; (a) photosynthesis, which utilizes a small amount of the absorbed radiant energy; (b) dissipation into the atmosphere if the latter is cooler than the plant; and (c) evaporation of water, or transpiration.

These processes are all interrelated and the energy changes occurring at any given moment are somewhat complex. But for the purposes of this discussion we can leave aside the changes due to photosynthesis, which uses less than one per cent of the energy received from the sun, and to respiration, and thermal emissivity. These changes are all small under ordinary circumstances, although thermal emissivity may become important in special plants or under exceptional conditions, as in succulents in desert regions. The very large source of energy is of course the absorption of radiation from the sun, and most of this energy is dispersed by the evaporation of water.

In order to show that energy dispersal is vitally necessary, we must know the amount of energy absorbed per unit area per unit time, and the quantitative effects of the absorption if it were not dissipated. By means of a radiometer it has been found that about .8 calorie of energy falls upon a square centimeter of leaf surface in one minute during direct bright insolation. Of course, the amount will vary with atmospheric and seasonal changes. Not all of this energy is absorbed by the leaf. Part of the incident energy is reflected, and some of it passes on through the leaf. About 25 per cent of it passes through, but unfortunately we do not know how much light is reflected from the leaf surface. It would seem certain, how-

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[1] Intake and outgo of energy from one body to another due to conduction, convection, and radiation, is known as thermal emissivity.

ever, that the reflection is not negligible, since even a dead black surface will reflect perhaps one per cent of the light falling upon it. If we assume that reflection from the leaf is 10 per cent, then the energy absorbed would be 65 per cent of the total incident energy. The total absorption would then be .52 calorie per square centimeter per minute. At this rate enough energy is received by a square meter of leaf surface in one hour to evaporate more than half a liter of water. Therefore, the reason why the plant transpires so much water during the growing season is because it receives so large a supply of energy.

What would happen if this energy were not dispersed? If the energy intake could go on without any utilization for photosynthesis, without loss by thermal emissivity, and without evaporation of water, it would accumulate in the leaf as heat energy, and rapidly raise the temperature of the leaf. Just how rapidly would the rise in temperature proceed? A calorie is the amount of energy required to raise the temperature of one gram of water one degree from zero; and we can calculate the rate of rise which the leaf would undergo if we know the amount of energy received per unit time and the mass and specific heat of a square centimeter of leaf substance.

The mass of a square centimeter of leaf substance will vary from plant to plant, or from leaf to leaf, or in various parts of the same leaf. But in some cases a square centimeter of leaf substance weighs about .02 gram. The specific heat of the fresh leaf substance is high, since it is largely composed of water, and has been given as .879 as compared to water = 1[2].

The rate of rise in temperature of the leaf per minute can be computed by dividing the energy absorbed per minute by the mass times specific heat. In the form of an equation, $\frac{R \cdot a}{m \cdot s}$ = rate of rise in degrees per minute. In this equation R is the total radiant energy falling upon the unit leaf surface per unit time; a is the coefficient of absorption; m is the mass of the leaf unit, and s its specific heat. Substituting the given values of these quantities, we have $.52 \div .01758 = 29.6°$. The leaf is receiving energy fast enough to raise its own temperature almost 30° per minute. And since the leaf usually has an initial

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[2] The figures used in part, and the discussion, are based on "Researches on Some of the Physiological Processes of Green Leaves," Brown, H. T., and Escombe, F., Proc. Roy. Soc., Lond. B., 76:29-111. 1905.

temperature of 25° to 30° C., we see that it would approach 60° C. in a minute if no energy dispersal occurred. In other words, plants would reach the death temperature of their protoplasm in a minute or less if it were not for the constant dissipation of the radiant energy, the chief means of which is transpiration. There is no doubt that transpiration is vitally necessary, and that its chief function is energy dispersal.

Another problem connected with transpiration which is always handled in an unsatisfactory manner in elementary textbooks is the problem of stomatal movement. Most frequently stomata are represented as regulating to a certain degree the water loss, and this they no doubt do accomplish to a certain extent. But the main difficulty is that we have not thought sufficiently of water loss as energy dispersal. Instead of regulating water loss, they are regulating energy loss, the water evaporated merely measuring the quantity of energy. It is now generally recognized that stomata are usually open by day and at least partially closed at night in the majority of plants. Any student can convince himself of this fact by using the little porometer devised several years ago by Darwin and Pertz for such studies.

This diurnal movement of stomata is by far the most significant movement they have, and the mechanism by which they open and close has been described by Iljin. According to his account, when the sun goes down at night, or whenever the radiant energy is cut off artificially, certain soluble carbohydrates in the cell sap of the guard cells are condensed into insoluble form, and the osmotic pressure of the guard cells falls greatly. They lose part of their water to surrounding cells and are soon nearly closed. The following morning, or when light is renewed, the radiant energy reverses the condensation of the carbohydrates, the osmotic pressure is rapidly increased in the sap of the guard cells, they take in water from contiguous cells, and are soon wide open. The stomata open wide at the time energy receipt begins, and have energy dispersal as their chief function. At night, when energy receipt from the sun is at a minimum and when transpiration is mostly due to intake of energy by thermal emissivity, stomata may well be closed. Stomatal movement becomes most intelligible when thus linked up directly with the current of energy flowing through the plant. Of course, if transpiration goes on more rapidly than root absorption of water can supply the needs of the leaf, guard cells as well as other cells may lose their turgidity and collapse, thus partially closing the stomata. But this is not to prevent water loss. It is too late for that. It is to be looked upon rather as a temporary breakdown of the thermoregulative mechanism.

It is well known that a saturation deficit or incipient drying occurs in the leaf without bringing about the closure of stomata. If energy receipt continues while stomata partially close, or during incipient drying to such a degree as to decrease normal energy loss, then the temperature of the leaf must rise above that of the surrounding atmosphere, and thermal emissivity will supplement the ordinary means of energy dispersal.

There are some plants whose stomata do not close at night. This does not mean necessarily that such plants will transpire moré than if the stomata were closed. No more water will be evaporated than the energy received can vaporize. If conditions of relative humidity should lead to more rapid evaporation than sunlight energy makes possible, the leaf becomes cooler than the atmosphere and receives additional energy by thermal emissivity. The same would be true for plants with stomata open at night. Of one thing we can be quite certain, that the total energy received by the leaf from all sources and the total utilization of energy are on the average equal quantities, and it is very easy to determine what must happen in the leaf as the conditions affecting intake and outgo of energy are changed.

Such a treatment of transpiration and stomatal movement puts the emphasis where it belongs, on the energy changes involved rather than upon the material changes. It has proved to be a satisfying presentation of the subject to large numbers of students in college classes, and there is nothing in it too difficult for students in secondary schools if the instructor himself has a clear conception of the processes.

BULLETIN ON THE TRAINING OF TEACHERS OF MATHEMATICS FOR SECONDARY SCHOOLS.

There has just been issued by the Bureau of Education at Washington a Bulletin on "The Training of Teachers of Mathematics for Secondary Schools of the Countries Represented in the International Commission on the Teaching of Mathematics." This Bulletin has been prepared by Professor R. C. Archibald of Brown University. It is a work of nearly three hundred pages, giving in great detail the requirements set by the various governments for a teacher of secondary mathematics. The Bureau of Education has a limited number of copies of this Bulletin which it can send to those who are particularly interested in the work. After this limited number has been exhausted, copies can be obtained from the Superintendent of Documents, Government Printing Office at Washington, D. C., at thirty cents per copy.