

to make up a typical spiral nebula. We do not actually know that the density of distribution of stars in our region of the stellar system is less than it is in some of the distant Milky Way cloud forms. If our sun and our neighboring stars are members of a rich local group of stars the mass of the group as a whole may be sufficient to account for an appreciable component of the motions which we have observed; but I must confess that this is carrying the speculative spirit very far indeed. Fortunately such speculations need do no harm, and they have been known to do good.

I have speculated concerning our stellar system as a spiral nebula, partly as a guard against the assigning of undue weight to the deduced motion of our solar system. The speed and direction of the sun's motion, as here determined, may or may not hold good for the stellar system as a whole. If our local group of stars to which the solution refers composes but a small part of one of the isolated masses in a typical spiral, a knowledge of our motion with reference to the observed group of 2,034 stars may not tell us much concerning our motion with reference to the spiral as a whole. And if our stellar system is not a spiral, but on the contrary a non-rotating, fairly symmetrical system, we should likewise be modest in drawing conclusions as to where our tour amongst the stars is going to carry us, and when we may expect to return. Shapley may be approximately correct in his estimate of 300,000 light years for the diameter of our system, and there may be merit in his surmise that our present place of abode and travel is in a locality situated about 60,000 light years from the center of the system, which center, he suggests, is in the rich Milky Way region of Sagittarius. Now the 2,034 naked-eye stars upon which our solution for the solar motion depends are nearly all within a sphere of radius 500 light years having our sun at its center, and certainly there were no stars used in the solution which are as much as 1,000 light years away. If we represent the stellar system in its greatest dimension by a circle, assuming that its radius is 150,000 light years, and if at some point about two fifths of the way from the center to the circumference we draw with radius 1,000 light years, we shall find that this latter circle is little more than a dot upon the picture. If we represent the stellar system by a circle 300 inches, or 25 feet, in diameter, a circle within it only 2 inches in diameter would in effect contain the 2,034 naked-eye stars used in our solution, and the overwhelming majority of these stars would lie within the central 1 inch⁵ of the 2-inch circle.

⁵ Assuming, with Eddington, a density of 10 stars, each equal to our sun in mass, per sphere of diameter 33 light years, a sphere 1,000 light years in diameter

We know to a degree of accuracy quite satisfactory our sun's motion with respect to a system of 2,034 stars, nearly all giant stars, in our own neighborhood. The elements of the sun's motion as here determined may be, and probably will prove to be, also quite satisfactory with reference to a vastly greater group of stars. That remains to be determined. We can report progress and feel assured that future astronomers, equipped with more powerful instruments and probably with more effective methods, will carry on with stars continually fainter and more distant. It is by the taking of such successive steps that great problems of this kind eventually reach their solution.

W. W. CAMPBELL

UNIVERSITY OF CALIFORNIA

WHAT IS THE SIGNIFICANCE OF TRANSPIRATION?

A LARGE number of research experiments have been carried on dealing with various phases of the subject of plant transpiration, and botanical literature on the subject is voluminous. Most of these experiments have been directed towards a determination of the amounts of water lost by plants and the factors, both internal and environmental, which affect the rate of this loss. It is rather surprising how relatively few have been performed to determine the possible function of transpiration or its influence on the various life processes of the plant. From an inspection of the literature and text-books in botany and allied subjects and from conversation with many teachers and advanced students of botany it is evident that many have given little thought to its significance or they have assumed certain functions without critical examination or thought. I have found that opinions as to the possible value of transpiration to plants vary all the way from those which assume that transpiration results in benefits on a par with those resulting from photosynthesis and respiration to those which ascribe to transpiration practically nothing but harm. Opinions obtained from a large number of advanced students in botany, students who have had their early botanical

would correspondingly contain 270,000 unit stars. A circular disk of space 300,000 light years in diameter and 10,000 light years thick, would similarly contain more than 300,000,000,000 unit stars! We do not seem to be in possession of any facts of observation suggesting that our most powerful telescopes, employed in the manner which enabled them to photograph the most distant star clusters used by Shapley in estimating the diameter of our stellar system, would record more than 3,000,000,000 stars in the system. Are there really good reasons for thinking that the star clouds, or the stars distributed with the same order of frequency as observed in the sun's neighborhood, extend out even to half the distance of the farthest globular clusters thus far observed?

training in many different institutions, indicate that a distinctly large majority consider that transpiration is primarily beneficial to plants and results in relatively little if any injury to them.

In order that there may be no uncertainty with regard to terminology, transpiration as here used will mean the loss of water in vapor form from the plant. Since this loss of water by transpiration may have many distinctive effects on the plant, it may facilitate consideration of them if they are classified under different heads as follows:

(1) EFFECTS RESULTING FROM THE INFLUENCE OF
TRANSPIRATION ON THE WATER CONTENT OF
THE PLANT

(a) Since water lost by transpiration can not be instantaneously replaced there must always be at least a slight reduction of the water content and therefore a reduction in turgor. The slight reduction in water content will probably have little influence on the various processes of the plant if there is plenty of water available in the soil and the rate of loss does not greatly exceed that of absorption, but commonly the loss does exceed absorption and, especially when the soil moisture is somewhat deficient, this reduced turgor results in an appreciable check in growth even when no wilting is apparent. Under conditions when the soil moisture is deficient or when there is plenty of water in the soil but transpiration is excessive as on hot, sunny and windy days, this loss through transpiration is almost sure to result in a distinct check in growth and even causes many plants to die. Smith¹ has given a table of estimates which indicate that most crop plants suffer more from deficient water than all other factors combined.

The only conditions under which this reduced turgor may result in benefit to the plant would seem to be when the turgor is so high as to cause rupture or other injury to the tissues. This has occasionally been observed with certain fruits during excessively wet weather, but it seems that the possible occasional benefit resulting from such reduction is many times offset by the commonly injurious results of reduced water content.

(b) Several observers have found that when the water content of the leaf is reduced the stomates often close even before apparent wilting takes place. Loftfield² found that during periods of drought the stomates may remain closed much of the day, often closing an hour or two after sunrise. This closure of stomates, whether wilting takes place or not, would in

all probability distinctly reduce the rate of entrance of CO₂ and therefore interfere with photosynthesis. The high sugar content resulting from the loss of water would also tend to reduce photosynthesis. Iljin³ has reported a reduction in photosynthesis of 50 to 78 per cent. in wilting leaves, and Thoday⁴ has reported reduction of from 30 to 90 per cent. in leaves having deficient water. Though this reduced photosynthesis would not immediately reduce growth, for the actual sugar content at the time is probably usually high, yet the total sugar made would be so reduced that when water again becomes more abundant the loss can not be made good. This effect of reduced water content resulting from transpiration is evidently primarily harmful.

(c) Any marked reduction in water content of a tissue commonly results in a change in its composition. With some plants the sugar content of the leaves increases to a marked extent. There may be an accumulation of pentosans, a change in the form of protein and of other compounds both organic and inorganic. The types of such changes that occur probably vary greatly with the kind of plant, its stage of growth and also with the environmental factors. Whether the results are beneficial or harmful there is too little evidence to say. One possible benefit of such changed composition is that it makes some plants more resistant to injury from freezing. Plants frequently exposed to freezing weather might therefore be benefited by transpiration, but relatively few plants are exposed to freezes during the growing season and some of them seem to be just as resistant, whether transpiration has been rapid or slow. The check to growth resulting from high transpiration may also make a plant somewhat more resistant to injury during periods of drought, but one would hardly be justified in concluding that transpiration is for this reason beneficial unless one were justified in saying that typhoid is good for people because, if they survive, it makes them more immune to typhoid.

(d) It is sometimes suggested that the check in vegetative growth caused by excess transpiration may hasten maturity and thus enable the plant to escape early frosts. Very little direct evidence is available on this point. It seems that after a plant is well grown the check due to high transpiration might hasten maturity, but I know of no positive evidence showing this. There is some definite evidence avail-

¹ Smith, J. W., "Damage to Crops by Weather," U. S. monthly weather review, 48: 446, 1920.

² Loftfield, J. V. G., "The Behavior of Stomata," Carnegie Inst. Wash. pub., 314, 104 pp., 1921.

³ Iljin, W. S., "Der Einfluss des Wassermangels auf die Kohlenstoffassimilation durch die Pflanzen," *Flora*, 16: 360-378, 1923.

⁴ Thoday, D., "Experimental Researches on Vegetable Assimilation and Respiration. VI. Some Experiments on Assimilation in the Open Air," *Proc. Roy. Soc., London*, 28B: 421-450, 1910.

able, however, showing that drought, at least in the early stages of growth, distinctly delays maturity. Such data have been obtained by Miss Kibbe⁵ for mustard, beans, beets, barley and sweet alyssum and by Thompson⁶ for celery.

(2) EFFECTS RESULTING FROM A MOVEMENT OF WATER INTO AND THROUGH THE PLANT

(a) A function frequently ascribed to transpiration is that it is supposed to increase the amount and rate of absorption of nutrients from the soil. It is generally recognized that the soil solution is very dilute and it is therefore natural to assume that rapid transpiration, by increasing the amount of this dilute solution absorbed and passing off the excess water, would correspondingly increase the intake of the needed salts. From theoretical considerations, however, it is evident that solutes and solvent may move through membranes independently. Within recent years a number of experiments have been carried out which tend to show that the amount of solute absorbed by plants bears no direct relation to the amount of water absorbed and lost through transpiration. Muenscher⁷ has summarized some of this evidence and has also given additional evidence which shows pretty clearly that transpiration by causing a movement of water into the plant has little or no influence on the absorption of salts. It seems probable that whatever effect transpiration may have on salt content results chiefly from its effect on the water content of the tissue and thereby on the types of chemical reactions occurring there rather than because its absorption mechanically affects salt absorption. Some have suggested that these effects would be different with inessential salts than with essential salts. Such a difference resulting from a mechanical flow of water is however hardly conceivable. Any differences in ash analyses observed could better be explained as resulting from the effects of a changed water content of the tissue on the types of chemical reactions occurring there and therefore on the absorption and accumulation of certain ions.

(b) Though a number have come to realize that nutrient absorption is practically independent of water absorption it is almost universally claimed that transpiration is essential for or at least plays an im-

portant part in transferring soil nutrients from the roots to the leaves. If the rate of removal of nutrients from the roots were largely determined by transpiration, then, since the removal of the solutes from the absorbing organ should increase absorption, increased transpiration ought to increase the absorption, but it evidently doesn't. Muenscher actually found on the other hand that plants with high transpiration rates induced by light had less ash in the tops and more in the roots than did those plants with low transpiration.

Still more conclusive evidence tending to show that transpiration has little effect in hastening the transfer of ordinary solutes I have reported in recent papers⁸ on the tissues concerned in translocation. This evidence, though perhaps not conclusive, at least clearly indicates that upward movement of solutes occurs chiefly in the phloem tissues. If solutes move upward chiefly through the phloem and are not carried in the water stream, the rate of transpiration can have little direct effect on their movement.

(3) ENERGY CHANGES RESULTING FROM THE CHANGE OF WATER FROM LIQUID TO VAPOR

The change in the physical state of water from liquid to vapor results in an absorption of an appreciable amount of heat, for its heat of vaporization is very great. The water vaporizing within a leaf therefore must tend to lower the temperature of the leaf. The absorption of light by leaves has been found to raise the leaf temperature considerably. It has been repeatedly shown that leaves exposed to bright sunlight may have a temperature of from 5 to 10 or, under special conditions, even 20 degrees centigrade above the air temperature. Tests have indicated that many kinds of leaves if exposed to temperature of 50° C or above for a few minutes are apt to be killed. If, therefore, the air temperature is fairly high, there is a possibility that the leaf may become so heated as to be injured or even killed. Realizing how hot some dark objects become when exposed to direct sunlight and knowing that transpiration has a cooling effect it has naturally been assumed that transpiration plays an important rôle by keeping the leaves cool. It has recently been found, however, that transpiration does not have as great a cooling effect as commonly sup-

⁵ Kibbe, Alice L., "Effect of Water Content of Soils on Relative Root and Top Growth of Plants," Thesis for M.S., Cornell, 1920, not published.

⁶ Thompson, H. C., "Factors influencing Early Development of Seed Stalk of Celery," *Proc. Am. Soc. for Hort. Sci.*, 1923, 219-224.

⁷ Muenscher, W. C., "The Effect of Transpiration on the Absorption of Salts by Plants," *Amer. Jour. Bot.*, 9: 311-329.

⁸ Curtis, O. F., "The Upward Translocation of Foods in Plants. I. Tissues concerned in Translocation," *Amer. Jour. Bot.*, 7: 101-124, 1920; "The Effect of Ringing a Stem on the Upward Transfer of Nitrogen and Ash Constituents," *Ibid.*, 10: 361-382, 1923; "Studies on the Tissues concerned in the Transfer of Solutes in Plants. The Effects on the Upward Transfer of Solutes of cutting the Xylem as compared with that of cutting the Phloem," *Ann. Bot.*, 39: 573-585, 1925.

posed. Miller,⁹ on measuring the temperature of leaves by the use of thermocouples placed on their surfaces, has found that transpiration reduces the temperature of leaves by only 1 to 5° C and Clum,¹⁰ on measuring the temperature of leaves by the use of thermocouples inserted into the leaf, has found that leaves in which transpiration was practically stopped by vaselining or withholding water rarely had temperatures that exceeded the normally transpiring leaves by more than 2 to 4° C. Air currents, the angle at which the leaf was exposed to the sun and the intensity of sunlight had effects on the temperature of the leaf greatly in excess of any cooling effect of transpiration. In no case even in direct sunlight on the hottest days did the temperature of the leaves approach the danger point when the plants were exposed to normal atmospheric conditions, even when transpiration was checked. The rapid loss of heat by conduction to the atmosphere seems sufficiently effective in preventing excessive heating.

The available data, therefore, indicate that the beneficial effects of cooling by transpiration have been greatly exaggerated, as the evidence seems to show that transpiration rarely lowers the temperature more than 2 to 5° centigrade. In fact the injury to plants that frequently occurs on hot days seems to be due chiefly to the injurious drying effects of transpiration itself. Transpiration therefore seems to be more harmful than beneficial on hot days when the cooling effects are most needed. It is notable that commonly those plants best adapted to hot regions are those which have modifications tending to reduce transpiration rather than those which favor it.

(4) EFFECTS RESULTING FROM A REDUCTION OF THE WATER CONTENT OF THE SOIL

Data from many sources are available showing that the water content of the soil is often appreciably decreased as a result of transpiration from the crops growing there. If the soil is so wet that root growth and activity are interfered with this type of drainage would probably be distinctly beneficial, but there is evidence which indicates that, if the soil has too much water, absorption is interfered with and therefore this type of drainage would not take place when most needed. That removal of water from the soil by transpiration often results in injury to the plants growing there is substantiated by abundant evidence.

⁹ Miller, E. C., and A. R. Saunders, "Some Observations on the Temperature of the Leaves of Crop Plants," *Jour. Agr. Res.*, 26: 15-43, 1923.

¹⁰ Clum, H. H., "The Effect of Transpiration and Environmental Factors on Leaf Temperatures," Thesis for Ph.D., Cornell, 1924. In press.

(5) EFFECTS OFTEN FALSELY ASCRIBED TO TRANSPIRATION

Though it might seem a waste of space to discuss false interpretations for which there are practically no grounds of support, it does seem worth while to touch briefly on a few of the points, for some of them are so frequently cited as functions of transpiration.

(a) It is surprising how frequently students, and teachers also, suggest that transpiration supplies a plant with water, or supplies the leaves with water for photosynthesis, or keeps the cells wet. Such a statement has even crept into a recently published and very reputable college text in botany. The water lost from leaves or from the plant as a whole tends to be replaced by more water entering the roots or rising through the stem. There is always, however, more or less of a lag in this replacement, and it is hardly conceivable that loss from the leaves can increase the supply to them.

(b) Students frequently have the idea that "fresh" water is needed. The only benefit that changing the water could have would be that "fresh" water contained solutes, either gaseous or otherwise, or that the water lost in transpiration carried solutes with it. As previously discussed, however, the available evidence seems to refute this.

(c) It is also often suggested that transpiration keeps the stomates open or that it hastens photosynthesis and respiration. There is, however, no evidence for such statements.

(d) It is sometimes stated that the poor or weak and succulent growth which occurs during cloudy and rainy weather is due to insufficient transpiration. It should be remembered, however, that this weak and succulent growth is probably due not to deficient transpiration but to the fact that photosynthesis has been very much reduced from lack of light. It may be that this failure to distinguish between the effects of high humidity and those of low light intensity accounts for the prevalent idea that drought hastens maturity and that moisture delays it as mentioned in paragraph (d) under the first heading. An unusually wet season at the time the plant approaches maturity is apt to be accompanied by low light intensity and perhaps low temperature which, through their effects on food manufacture, may account for the delay in ripening. If, on the other hand, the season is drier, there is a greater likelihood of higher light intensities and temperatures which, independent of their effects on transpiration or the water supply, may hasten maturity.

In reviewing the available evidence on the possible influences of transpiration on the life processes of a plant it seems that there is little evidence to support many of the supposed benefits and in fact consider-

able evidence tending to show that transpiration very frequently results in considerable harm and rarely if ever has any appreciably beneficial influence. When the water supply is adequate and transpiration is not excessive it probably has little influence on the life processes, but as is so very frequently the case the water in the soil is deficient or transpiration is excessive.

The question may naturally be raised as to why, if transpiration is harmful, natural selection has not eliminated it. This might be answered by saying that many types of modifications do occur tending distinctly to reduce transpiration, and that in many regions plants could not exist without these modifications, but that green land plants could not entirely eliminate transpiration and continue to carry on the essential process of photosynthesis, because for photosynthesis moist cell surfaces must be exposed to the atmosphere to allow for the absorption of CO_2 and the elimination of O_2 and wherever moist cell surfaces are exposed to the atmosphere transpiration must necessarily occur.

I do not advocate that teachers and text-books should dogmatically state that transpiration is primarily harmful and rarely if ever beneficial. I merely wish to point out the fact that statements to the contrary are frequently made and, though many teachers and text-books state that transpiration is probably a necessary evil rather than an advantage, my experience has shown that a large majority of students from many different institutions have the idea that transpiration is essential and primarily beneficial. Usually, however, they can offer but few reasons to uphold their conclusions. Transpiration is one of the most obvious and easily demonstrated processes, and it seems that usually, especially in courses in general botany, more experiments are performed and more discussion is taken up with various phases of transpiration than with any other one process. Often, however, little attention is given to its significance and because of such study the student without giving much thought to it is led to assume that transpiration is a primary function of plants, as is photosynthesis or respiration. That various other physiological processes, especially respiration, are sometimes studied with almost as little thought with respect to their possible functions or significance is also evident.

OTIS F. CURTIS

LABORATORY OF PLANT PHYSIOLOGY,
CORNELL UNIVERSITY

THE NAPLES ZOOLOGICAL STATION¹

RECENT reports from the Naples Zoological Station indicate great progress in the development of its

¹ An article on the reorganization of the zoological station was published two years ago in this journal, Vol. LIX, No. 152, February 22, 1924.

work since the reorganization in 1923-24. At the time Dr. Reinhard Dohrn resumed the directorship, after the inter-regnum caused by the war, most of the subscriptions for working-tables made by foreign countries had lapsed, the only tables still maintained being those of Italy, Belgium and England. Since then eight additional countries have resumed their ante-bellum subscriptions, namely, Russia, Japan, Austria, Hungary, Poland, Switzerland, Germany and the United States. The total number of tables has thus increased from 18 to 45, and a further increase is probable this year by subscriptions from other countries. During 1925 more than 100 biologists worked at the laboratory, nine of them Americans of whom several are now in residence at the station, while other applications have been received. An important factor in the recent development of the work at Naples has been a considerable grant from the international education board, used in part to establish traveling scholarships for the benefit of investigators from various countries who without such aid would have been unable to work at the laboratory. Information from various sources, including Dr. Dohrn himself, agree in showing that research at the laboratory is now progressing satisfactorily and that the station has gone far towards becoming once more a truly international center as it was before the war.

This encouraging situation emphasizes the importance of maintaining American support of the station. The extraordinary richness and variety of marine life in the Bay of Naples, together with the excellent equipment and service of the laboratory and library, offers unsurpassed advantages for biological investigation in many of its branches, above all, perhaps, in experimental work; and at least equally important is the unique opportunity offered by residence at the station for personal association with investigators of many nationalities representing the most varied interests. The United States is now maintaining three tables at Naples, one supported by the American Association for the Advancement of Science; one by the Rockefeller Institute for Medical Research, New York, in memory of Jacques Loeb; and one by the Association to Aid Scientific Research by Women. At the present moment all these tables are occupied, but vacancies will arise in the near future and it is also hoped that arrangements may be made whereby temporary overlapping of periods of occupancy by different workers may be provided for, so as to facilitate use of the American tables. Applications for use of the American Association for the Advancement of Science table may be made to Secretary Burton E. Livingston, Smithsonian Institution, Washington, D. C.; for the Jacques Loeb table to Dr. Simon Flexner, Rockefeller Institute, New York City; and for the Women's table to Mrs. Samuel F. Clark, Williamstown, Massachusetts. E. B. W.