and plus infinity, and its logarithm lies between $-\infty$ and $+\infty$.) No theory is metaphysical if it can be virtually either proved or falsified, because its log-odds would then become very large, positive or negative. According to this definition, it is a question of degree whether a theory is metaphysical.

For example, the theory of determinism is less credible than it was a hundred years ago, but is by no means disproved and never will be. A statistician can never prove that "random numbers" are not "pseudo-random," and likewise "pseudo-indeterminism" cannot be disproved (*10*).

We can consistently talk about physical probability without committing ourselves to the metaphysical theory that the universe is indeterministic, but only if we accept the existence of subjective probability or credibility. For if we assume determinism we can get physical probabilities only by having an incompletely specified physical setup. In this incomplete specification there must be probabilities. If we are determinists we must attribute these latter probabilities to our own ignorance and not merely to something basic in nature "out there." Whether or not we assume determinism, every physical probability *can* be interpreted as a subjective probability or as a credibility. If we do assume determinism, then such an interpretation is forced upon us.

Those philosophers who believe that the only kind of probability is physical must be indeterminists. It was for this reason that von Mises asserted indeterminism before it became fashionable. He was lucky.

References and Notes

1. J. M. Keynes, *A Treatise on Probability* (Macmillan, London and New York, 1921; St. Martin's Press, New York, 1952).
2. H. Jeffreys, *Theory of Probability* (Oxford Univ. Press, New York and London, 1939; ed. 2, 1948).
3. F. P. Ramsey, *Foundations of Mathematics* (Harcort, London, 1931; Humanities Press, New York, 1950).
4. B. de Finetti, *Ann. inst. Henri Poincaré* **7**, 1 (1937).
5. B. O. Koopman, *Ann. Math. Ser. 2*, **41**, 269 (1940); *Bull. Am. Math. Soc.* **46**, 763 (1940).
6. R. Carnap, *Logical Foundations of Probability* (Univ. of Chicago Press, Chicago, 1950).
7. B. Russell, *Human Knowledge, Its Scope and Limits* (Simon and Schuster, New York, 1948), part V.
8. I. J. Good, *Probability and the Weighing of Evidence* (Hafner, London and New York, 1950); *J. Roy. Statist. Soc. Ser. B* **14**, 107 (1952); in *Uncertainty and Business Decisions*, G. L. S. Shackle, Ed. (Univ. Press of Liverpool, Liverpool, 1957), ed. 2, chap. 3; *J. Inst. Actuaries* **82**, 249 (1956); "Significance tests in series and in parallel," *J. Am. Statist. Assoc.*, in press.
9. L. J. Savage, *Foundations of Statistics* (Wiley, New York and London, 1954).
10. I. J. Good, *J. Roy. Statist. Soc. Ser. B* **20**, 35 (1958).

Water Transport

This classical problem in plant physiology is becoming increasingly amenable to mathematical analysis.

James Bonner

Plant physiology, even though it has existed as an organized science for one hundred years, still has its classical problems—problems which have been studied by many investigators during this hundred years, and problems which are nonetheless still unsolved. Such a classical problem of plant physiology is that of water transport. It is not, in fact, unsolved in principle today. Certainly the question of how water ascends the trunk of the tree to supply the transpiring leaves has been solved in principle by Dixon (*1*) and by Renner (*2*). Although the tension-cohesion hypothesis of water transport proposed by Dixon (*1*) has been attacked from time to time, it has, I believe, thus far always turned out that the attackers have been barking up the wrong tree. In a broader sense, however, "water transport" can be used to mean material transport of water to, within, and from the plant, and in this sense water transport bristles with unsolved and even with unposed questions.

In this article I propose to take up the successive steps in the material transport of water and to comment for each step on recent contributions which appear to be of importance, as well as upon problems which appear to pose further interesting questions.

From Soil to Root

Let us first consider water movement from soil to root. As in all cases of water movement, this consists of water flow from regions of lower diffusion pressure deficit (DPD) to regions of higher DPD. The soil DPD is determined by soil moisture stress and by the content of osmotically active solutes in the soil water. But the solutes are, in general, salts which can be taken up by the root and increase the DPD of the root cells. It might therefore appear that such solutes would contribute little to the soil-plant DPD-gradient which determines water uptake by the root. Indeed Walter (*3*) many years ago declared explicitly that soil solutes which can permeate the root do not in fact play any role in moisture uptake by the plant.

Wadleigh (*4*) and his colleagues at Riverside (California) have, however, developed the concept of total soil moisture stress, a total made up of physically and osmotically determined components. These workers have shown experimentally that the addition of salts to soil does in fact increase the effective soil DPD against which the plant must work. We have therefore a paradox—Walter's view based on sound plant physiological foundations and Wadleigh's view based on experiment.

The paradox has been resolved by John Philip (*5*) of the agricultural physics group of the Commonwealth Scientific and Industrial Research Organization's Division of Plant Industry (formerly at Deniliquin, now at Canberra). By applying recent advances in the quantitative theory of water movement in soils, Philip has shown that, during even moderate transpiration, removal of water

---

The author is a member of the staff of the Division of Biology, California Institute of Technology, Pasadena. This article is adapted from an address made 26 Aug. 1958 at the annual meeting of the American Society of Plant Physiologists, held in Bloomington, Ind.

Table 1. Rates of water movement through various media under an applied pressure differential of 1 atmosphere. [After Van den Honert (*14*)]

Object	Water movement (mg/cm² hr atm)
Water-air surface (still)	0.007
Water-air surface (strong wind)	0.191
1 meter of conifer wood	20,000
1 meter of young stem	100,000
Water-coleoptile surface	195
Water-root surface	about 2,000

from the soil by the roots results in a large moisture gradient close to the root surface. As a result, a large portion of the final transfer of water from soil to root takes place in the vapor phase across a narrow vapor gap. The vapor gap thus formed constitutes an effective barrier to the movement of salts; they cannot be taken up. The root is essentially surrounded by a membrane, the vapor gap, which makes it into an ideal osmometer, permeable to water, impermeable to solutes. Under these conditions the total soil-moisture stress concept is applicable. Under conditions in which the vapor gap is absent (conditions of low rate of transpiration and low soil-moisture stress), Walter's point of view —that salts, because they are taken up by roots, do not contribute to soil-moisture stress, does however obtain. The two views are both correct. They are merely two extreme expressions of plant-soil-water behavior.

Within Plant Tissue

Now let us consider the movement of water within plant tissue. Some interesting facts concerning this matter have come to light in recent years. Consideration of water movement within the plant can be simplified by discussion of movement within a tissue of isotopically labeled water. We take a tissue, give it some labeled water, and see how quickly and with what characteristics such water diffuses through the tissue. This is a diffusion process, and we can treat it in accordance with Fick's laws, just as we can the diffusion of a solute. Such experiments have been done by Buffell (*6*), by Ketellapper (*7*), by Ordin and Bonner (*8*) with oat coleoptiles (see Fig. 1), by Thimann and Samuel (*9*) with potato discs, and by Ordin and Kramer (*10*) with bean roots.

Now there are different ways in which the entry of water into and through a tissue might proceed. The water might find the principal barrier to diffusion in the cuticle of the tissue, in which case diffusion through the cuticle would be slow compared to diffusion within the tissue. Alternatively, water might enter the free spaces of the tissue and permeate the free spaces, thus surrounding each cell with a layer of labeled water, after which the labeled water would proceed to diffuse into the vacuole of each cell, the membrane of each cell constituting the principal diffusion barrier. In both of these cases the time course of diffusion should follow that expected for diffusion of the solute into a cell surrounded by a membrane with all resistance to diffusion located within the membrane. The kinetics of the diffusion should follow Fick's first law, given in Eq. 1, which predicts a particular and well-known time course:

$$\frac{dC_i}{dt} = \frac{D \cdot a \cdot (C_o - C_i)}{V \qquad q} \tag{1}$$

where C_i is concentration in the tissue, C_o is external concentration, D is the diffusion constant of water in the tissue, V is the volume of the tissue, a is the area through which the diffusion is taking place, and q is the thickness of the diffusion barrier.

A second possibility is that water enters the tissue and diffuses continuously through it, across cell walls, across membranes, through vacuoles. According to this view, water would pass through a material with resistance to diffusion uniformly distributed through the tissue. Such diffusion, into a sheet of thickness x, should follow Fick's second law, given in Eq. 2, which yields a time course

$$\frac{\partial C_i}{\partial t} = D \frac{\partial^2 C_i}{\partial x^2} \tag{2}$$

different from that of Eq. 1. In Eq. 2 the symbols possess the same meanings as in Eq. 1, and x refers to the depth within the tissue. Work with oat coleoptiles and with roots has shown that movement of water into and through the tissue follows elegantly the time course expected if resistance to diffusion is uniform through the tissue. Water diffuses as a wave through a tissue of this kind. There is no special free space through which it quickly slurps. Nor is the outer boundary of the tissue a major barrier to water movement.

But material transport of water through a tissue is not accomplished strictly by diffusion. It is accomplished rather by differences in DPD. Water is moved from a cell of lower to a cell of higher DPD, and the way in which the diffusion constant of water enters into this, if it does so at all, is, so far as I know, totally obscure. The permeation constant used to describe movement of water under a DPD gradient contains a filtration constant (rate of movement of water through a membrane under unit hydrostatic pressure gradient), the elastic modulus of the tissue, and the osmotic concentration of the cell contents (*11*). However, the kinetics which characterize mass movement of water under the influence of a DPD gradient may be formally treated by the diffusion equations, and they have been so treated many times. For oat coleoptiles again, the time course for material transport of water under the influence of a DPD gradient follows elegantly the expectation based on resistance to flow uniformly distributed through the tissue.

The time characteristics of water movement in a tissue have been mentioned because, for some curious reason, plant physiologists in general treat the kinetics of water movement into or out of plant tissue in accordance with Fick's first law, just as one treats water movement into or out of a single cell. Plant physiologists thereby implicitly assume that resistance to water movement is located in a boundary layer in the case of a tissue just as it is in the case of a single cell. This, as we have seen above, is incorrect.

From Soil to Air

Let us now proceed to the movement of water through the plant from root, or indeed from soil, to air. Let us assume for the moment that root pressure contributes nothing to this process. We take a given mass of water, transport it through successive regions, and finally evaporate it into the air. In the steady state, Eq. 3 obviously holds.

$$\frac{d\left(\begin{matrix}\text{Amt. evaporated}\\ \text{from leaves}\end{matrix}\right)}{dt} = \frac{d\left(\begin{matrix}\text{amt. transported}\\ \text{through stems}\end{matrix}\right)}{dt} = \frac{d\left(\begin{matrix}\text{amt. transported}\\ \text{through roots}\end{matrix}\right)}{dt} = \frac{d\left(\begin{matrix}\text{amt. taken}\\ \text{up by roots}\end{matrix}\right)}{dt} \tag{3}$$

Now there is a further condition which applies universally to material transport, and this is given by:

$$\frac{d\ \text{Amount transported}}{dt} = \frac{\text{driving potential}}{\text{resistance}} \tag{4}$$

In electrical matters Eq. 4 is known as Ohm's law; in water matters we call it Van den Honert's law. It was first enunciated by Gradmann (*12*) in 1928, to be sure, but was first put to use by Van den Honert (*13, 14*). In the present case the driving potential is the difference in DPD between the supplying and the receiving regions, and the resistance to transport is that met by water in the liquid and vapor phases—that is, viscous and diffusional. Combining Eqs. 3 and 4, we obtain:

$$\frac{\mathrm{d}\ \text{Amt. transported}}{\mathrm{d}t} = \frac{\Delta\mathrm{DPD}_{\mathrm{Total}}}{R_{\mathrm{Total}}} = \frac{\Delta\mathrm{DPD}_1}{R_1} = \frac{\Delta\mathrm{DPD}_2}{R_2} = \ldots \qquad (5)$$

where $\Delta\mathrm{DPD}_1$, $\Delta\mathrm{DPD}_2$, and so on are the DPD differences for the individual steps in water movement and R_1, R_2, and so on are the resistances for the same steps.

We know something about the ΔDPD for each step in the process of water movement—for water movement from soil to root, from root to xylem, through the stem, from stem to leaf, and from leaf to air. And from this knowledge we can calculate the relative resistances of each step in water transport.

It is well known that the bulk of the DPD gradient from soil to air is to be found at the step from leaf to air. This can be felt intuitively. We know that the leaf rarely possesses a DPD exceeding, say, 50 atmospheres, while air at 50 percent relative humidity possesses a DPD of close to 1000 atmospheres. The DPD gradient from soil to leaf may therefore be 50 atmospheres; from leaf to air, 950 atmospheres. It is quite clear, then, that the bulk of the resistance to water loss is located in the leaf-air couple. Resistance even of a free water surface to water movement from it as vapor is very large as compared to resistance to water movement through living tissue or through woody stems, as can be shown by actual measurements on rate of water movement under an applied DPD gradient. These rates of water movement and relative resistances to water movement are summarized in Table 1.

We can say in a general way that if the resistance to water movement from liquid water through and into the root is put at 1, then the resistance to water movement of a meter of stem is, say, of the order of 0.1 to 0.02, but that the resistance of water movement from water surface to water vapor in the air is 1 million or more. It is clear, then, that the leaf-air surface and the process of transpiration which takes place at it is of the greatest interest in the study of water relations.

Transpiration

We know of course a great deal about transpiration. During the past few years this knowledge has been increased by Bange (*15*), who has contributed to our understanding by working out the contributions to the resistance to water movement of the consecutive parts of the vapor path in the leaf—the resistance of the substomatal cavity, of the pore itself, and of the vapor cups over the pore. And Raschke (*16*) has made a contribution by his analysis of the radiation and heat balance of leaves in relation to transpiration. The rate of transpiration is in a great degree regulated by the temperature of the leaf, which in turn determines the vapor pressure of water at the leaf surface. The leaf temperature is in turn determined by the balance between rate of heat gain and rate of heat loss. The leaf absorbs light, degrades this to heat,

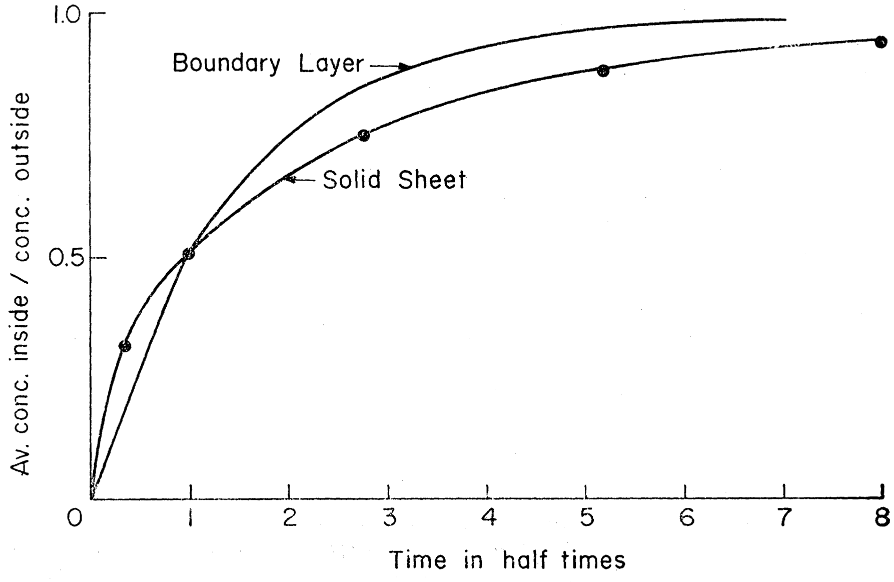

Fig. 1. Rate of equilibration of isotopically (DHO) labeled water, supplied externally, with the internal water of oat coleoptile sections. The average concentration of labeled water inside the tissue relative to the external concentration of the label is plotted as a function of time, expressed in half times. The two solid lines represent the expectations for boundary-layer (Fick's first law) and solid-sheet (Fick's second law) diffusion. The points are experimental. [Data from Ordin and Bonner (*8*)]

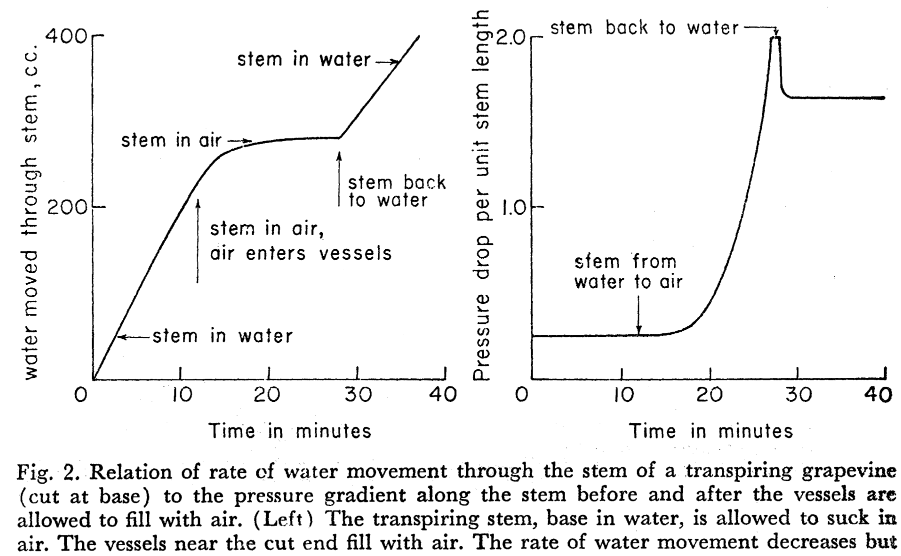

Fig. 2. Relation of rate of water movement through the stem of a transpiring grapevine (cut at base) to the pressure gradient along the stem before and after the vessels are allowed to fill with air. (Left) The transpiring stem, base in water, is allowed to suck in air. The vessels near the cut end fill with air. The rate of water movement decreases but is restored when the cut end is returned to water. (Right) Pressure drop along the stem (in arbitrary units) during the same experiment. The initially constant rate of water movement is attended by a constant pressure gradient. When air enters the vessels, the pressure gradient increases rapidly. When the stem is restored to water, the rate of water movement is restored, due to the greatly increased pressure gradient. [After Scholander *et al.* (*19*)]

and warms itself until its rate of heat loss equals its rate of heat gain. As Raschke (*16*) has so clearly shown, most of the heat gained by the leaf is dissipated by transfer to the surrounding air, and hence leaf temperature depends greatly on the rate of air movement over the leaf.

Movement of air across the leaf works at once in two directions, on the one hand cooling the leaf and hence decreasing the rate of transpiration, on the other, steepening the vapor-pressure gradient between leaf and air and hence increasing the rate of transpiration. And still another factor is of importance. Heat transfer from leaf to air is sensitive to the character of the air flow over the leaf. When the flow is turbulent, then the heat-transfer pattern is a modification of that which occurs when the flow is laminar. And we know next to nothing about the aerodynamics of leaves. At what speed does the air flow change from laminar to turbulent in the region of the leaf? How does leaf shape influence this process? In a real plant with many leaves—an assemblage of leaves—air flow through the plant is probably often irregular and hence turbulent. Is it possible that, despite this macroscopic turbulence, flow over the leaf on a microscopic scale remains laminar? These are unanswered questions. Raschke (*16*) has shown that it should be possible in principle to calculate and predict rates of transpiration of a leaf, a plant, or a crop, but that before we can do so we need to have additional physical information; we need a new science of phytoaerodynamics.

Ascent of Sap

Now let us return to the most classical aspect of water transport—namely, the ascent of sap. The basic idea of the tension-cohesion hypothesis is, roughly, that as water evaporates from the leaf-wall surfaces, liquid water moves into the pores thus emptied, keeping the wall wet. Thus, a tension is exerted on this water. This tension is transmitted all the way back to the roots through continuous water columns in the xylem. Many observations support this hypothesis, such as the fact that the water in the xylem is in fact under tension during transpiration. This tension has been calculated in various ways and can be measured simply by measuring the resistance of the stem to water flow under the influence of a known artificially applied pressure drop. If we then know also how fast water moves through the stem during transpiration and assume that the resistance is unchanged, we can calculate from Eq. 3 the tension needed to cause the measured flow. These tensions are considerable.

However, the principal difficulty with the tension-cohesion hypothesis has always been this: Why don't these fragile columns of water break and, if they do, why don't the breaks spread through the entire xylem and block transpiration? Recently, too, several people have expressed their dissatisfaction with the tension-cohesion hypothesis on the basis of xylem ringing experiments. Partial rings are made at intervals, inserted along a trunk with an appropriate phyllotaxy such that no linear longitudinal path for continuous water columns remains in the stem. But such a girdled plant continues to move water up its stem and does not wilt. Preston (*17*), Elazari-Volcani (*18*), and others have, on this basis, decided that the tension-cohesion hypothesis is wrong and must go.

The matter has been approached again by Scholander and his colleagues (*19*). They have already shown (*20*) that a grapevine can transpire very well indeed even if all or nearly all of the xylem vessels are filled with air (Fig. 2). They have now shown that the xylem behaves as a continuous system made up of macropores (the vessel lumens), which are imbedded in a matrix of micropores (perhaps the cell walls). At full transpirational flow the large macropores, which offer the least resistance to flow, conduct most of the water. If air is allowed to enter the vessels or if a cavitational break occurs, the vessels concerned are emptied of water but the air cannot penetrate further—it cannot pass through the small pores, the micropore structure. Water flow continues past the air-blocked cavity but through the micropores. The situation is similar to the rise of water by capillarity up a piece of blotting paper; this rise is of course not blocked by the act of poking a small hole in the center of the paper. In the case of the xylem, resistance to flow is increased by the break. Full transpirational flow is maintained only at the cost of an increase in pressure drop along the stem.

These facts have been established by Scholander and his colleagues (*19, 20*) by the use of ingenious experimental devices for the measurement of pressure and tension in the xylem. These are all essentially hydraulic instruments and are well suited to their purpose. The conclusions are clear: water flow under tension can continue even in stems in which the xylem contains air; water flow can continue also in stems which have been subjected to multiple girdling and in which no direct longitudinal water columns can remain. In both of these cases, however, maintenance of flow rate is at the cost of increased tension in the xylem.

Even so, problems still present themselves in connection with the ascent of sap: How do vessels once emptied of water by cavitational breaks become refilled? What exactly constitutes the micropores? But in main outline we see that continuous columns of water under tension occur in the plant in spaces other than the lumens of the vessels. The tension-cohesion hypothesis of water transport remains unchallenged.

Phytobiophysics

These, then, are some of the problems of water transport. There are still many problems to be solved; the problems of water relations are increasingly of a physical nature—problems which lend themselves to mathematical formulation and analysis. They are problems that might properly be the concern of that branch of plant physiology which I like to call "phytobiophysics."

References

1. H. H. Dixon, *Transpiration and the Ascent of Sap in Plants* (Macmillan, London, 1914).
2. O. Renner, *Jahrb. wiss. Botan.* 56, 617 (1915).
3. H. Walter, *Ann. Rev. Plant Physiol.* 6, 239 (1955).

→ C. H. Wadleigh, *Soil Sci.* 61, 225 (1946).

5. J. R. Philip, *Proc. Intern. Congr. Irrigation Drainage, 3rd Congr.* 8, 125 (1957); *Plant Physiol.* 33, 264 (1958).
6. K. Buffell, *Mededeel. Koninkl. Vlaam. Acad. Wetenschap. Belg.* 14, No. 7 (1952).
7. H. J. Ketellapper, *Acta Botan. Neerl.* 2, 388 (1953).
8. L. Ordin and J. Bonner, *Plant Physiol.* 31, 53 (1956).

→ K. V. Thimann and E. W. Samuel, *Proc. Natl. Acad. Sci. U.S.* 41, 1029 (1955).

10. L. Ordin and P. J. Kramer, *Plant Physiol.* 31, 468 (1956).
11. J. R. Philip, *ibid.* 33, 271 (1958).
12. H. Gradmann, *Jahrb. wiss. Botan.* 69, 1 (1928).
13. T. H. Van den Honert, *Discussions Faraday Soc. No. 3* (1948), p. 146.
14. ———, *Studies on Rates of Physiological Processes in Plants* (California Institute of Technology, Pasadena, 1956).
15. G. G. J. Bange, *Acta Botan. Neerl.* 2, 255 (1953).
16. K. Raschke, *Planta* 48, 200 (1956).
17. R. D. Preston, "Movement of Water in Higher Plants," in *Deformation and Flow in Biological Systems* (North Holland, Amsterdam, 1952), pp. 257–321.
18. T. Flazari-Volcani, *Palestine J. Botany* 1, 94 (1936).
19. P. J. Scholander, B. Rudd, H. Leivestod, *Plant Physiol.* 32, 1 (1957).
20. P. F. Scholander, W. E. Love, J. Kanwisher, *ibid.* 30, 93 (1955).