ABSORPTION OF WATER BY PLANTS

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INTRODUCTION

This review has been prepared as a supplement to Kramer's (1945a) paper, published in this journal. The intervening period has seen many old controversies renewed, particularly the osmotic versus non-osmotic theories of active absorption and the significance of water absorption by plants directly through their aerial organs. At the same time some aspects have received relatively little attention, particularly those concerned with the influence of soil physical conditions on absorption. Over the period several general reviews hav been prepared. Among these may be listed the two texts by Kramer (1949) and Crafts, Currier and Stocking (1949); the monogram on soil physical conditions and plant growth, under the general editorship of Shaw (1952); and the recent Encyclopedia of Plant Physiology, under the general editorship of Ruhland, of which Volumes I-III (1955, 1956a, 1956b) are of direct relevance. In addition to these valuable sources of reference, numerous reviews on specific aspects of water absorption have been prepared and the proceedings of several symposia have been published, all of which are cited in the text.

In some respects this relative abundance of material has tended to make the reviewer's task difficult, since it necessitates a different type of presentation in order to avoid unnecessary repetition. For this reason special emphasis is placed on the relative importance of the various factors affecting absorption, and these are evaluated in terms of the van den Honert (1948) hypothesis which regards the movement of water into, through and out of the plant as a catenary process, the rate of which is effectively controlled at the source of greatest resistance along its path. The implications of this hypothesis and the significance of the factors affecting absorption are discussed in detail.

Where possible, the material cited has been from papers published since Kramer's earlier paper was prepared, although in many cases earlier material has had to be referred to with reference to specific matters. Not only has the method of treatment deviated from the earlier paper; the subject matter has also been altered to some extent. In particular, some aspects of root pressure and guttation have not been considered, and a chapter on absorption through aerial organs has been added. The literature coverage pertaining to this review was completed in December, 1959.

TERMINOLOGY AND UNITS

At the present time, a variety of terms and units are utilised for discussions of absorption of water by plants. All of these are derived, in one form or another, from the fundamental thermodynamic principle concerning the movement of materials, that each molecule possesses a total internal energy equal to the sum of its internal kinetic and potential energies, and that the system is subject to spontaneous change if there is any process whereby the internal energy of the constituent molecules can be effectively reduced.

The terminology in most common use is that of Meyer (1938, 1945, 1956) which regards water movement as tending to occur along gradients of decreasing diffusion pressure. The basic unit involved is diffusion pressure deficit (DPD) which is defined by Meyer as the amount by which the diffusion pressure of water in a given state is less than that of pure water at the same temperature and under atmospheric pressure. The DPD difference (DPDD) between any two points is a measure of the driving force, so that the tendency of water to move, for example, inward into a plant or plant cell, can be expressed as the difference between the algebraic sum of the DPDs associated with internal factors and the algebraic sum of the DPDs associated with external factors, thus :–

$$\mathrm{DPDD} = (\Sigma \mathrm{DPD})\,i \quad -(\Sigma \mathrm{DPD})e$$

Meyer considers DPD to be an equivalent pressure directly related to the direction of transfer of water through a plant system, and the concept can be extended to include soil-plant water movement, since the commonly used soil water units, soil moisture tension and total soil moisture stress (TSMS), are identical in concept and dimensions with the DPD of soil water. In this case, tendency for water movement into a plant can be expressed by changing the last term of the above equation to TSMS.

Although this terminology has had general acceptance among plant workers, there has been a tendency in recent years to utilise alternative terms and units. This has been motivated, in part, by the fact that the use of pressure terms and units can be misleading. For instance, high equivalent pressures or suctions can frequently be measured in soil or plant water systems, but these values represent potential energies and do not necessarily imply the existence of actual pressure differences. Furthermore, the simple and straightforward equation relating DPD to osmotic pressure and turgor pressure ($DPD = OP - TP$) refers ideally to the completely vacuolated plant cell. In tissues in which the non-vacuolar volume reaches significant proportions, additional factors may contribute to the free energy status of the water in the system.

Among the studies which have considered alternative treatments may be cited those of Edlefsen (1941) who provided a generalized analysis of water absorption; of Edlefsen and Anderson (1943) who extended this analysis with more emphasis on the movement of soil water; and of Broyer (1947a, 1947b, 1950, 1951a, 1951b) who presented a series of valuable and lucid interpretations of the free energy function with special reference to the movement of water into, and within, the plant.

Edlefsen (1941) suggested the function "specific free energy" to describe the thermodynamic state of water in plant or soil. He proposed that the total specific free energy at any point in the soil-plant-atmosphere system is composed of several appropriately defined component free energies. These arise from the free energy possessed by the water because of the hydrostatic pressure it is under, because of the presence of dissolved material, because of its presence in a force field such as a gravitational or adsorptive field, or due to interfacial surface tension.

Broyer (1947a) defined "net influx specific free energy" (NIF) as the difference in action capacity between the algebraic sum of the specific free energies tending to cause water to move into the system and those tending to cause water to move out of the system. Thus the net influx specific free energy is equal to the sum of the influx specific free energies (ΣIF) diminished by the sum of the efflux specific free energies (ΣEF) as under :–

$$NIF = \Sigma IF - \Sigma EF$$

The principal partial specific free energies concerned in the movement of water through the plant are identified by Broyer as hydrostatic specific free energy, osmotic solute specific free energy, non-metabolic specific free energy and metabolic specific free energy. It is apparent that, while Broyer's NIF is analagous in form and application to Meyer's DPDD, not all the partial specific free energies contributing to NIF can be interpreted through diffusion pressure concepts. As a result, DPD and DPDD are only partially represented in the concept of NIF.

An alternative method of expression is in terms of the chemical potential of water, which is identical with the partial molal free energy. This procedure was adopted by Day (1942) who referred to it as "moisture potential." Schofield, cited by Owen (1952), suggested the term "water potential" for the same function, and more recently the 1959 UNESCO conference on plant water relations in arid regions favourably considered a terminology based on an evaluation of this function.

These considerations have been outlined by Slatyer and Taylor (in press). Briefly, the aim was to develop a terminology in which the primary components of the existing "hydraulic" terminologies can be identified but in which a more comprehensive description can be made of the state of water in the plant and soil system. Thus, the "water potential" is considered to comprise an osmotic potential, due to the concentration of solutes, analogous to the osmotic pressure term in common use; a pressure potential which can be identified with turgor pressure (actually, the pressure potential equals turgor pressure multiplied by the specific volume of water, which is unity) or hydraulic pressure in saturated soils; and a matric potential, which evaluates the water release relationship. In soils this is associated with soil suction or soil moisture tension; in plants it describes the condition of water within the cell walls or the colloidal system of the protoplasm, a factor which is not accounted for by turgor pressure or osmotic potential. As systems become more complex, and more independent variables are needed to describe the status of water, additional terms may be introduced so that they can be adequately described and interpreted. Likewise, external force fields, such as those of gravity, can be accounted for.

The question of units of expression is one of importance and interest. DPD is almost universally expressed as atmospheres; specific free energy is generally expressed in ergs.gm^{-1}, although Broyer uses volumed specific free energies expressed as litre atmospheres.litre^{-1} or atmospheres. The atmosphere is traditionally a unit of pressure and is used in this context by Meyer, since he regards DPD as a pressure unit. Since pressure is equal to energy per unit volume, it can be argued that to use atmospheres as energy units is valid but at the same time it must be recognized that to use an established pressure unit to express energy data can easily lead to confusion. After the procedure of Buckingham (1907), Owen (1952) suggested that water potential might be expressed in units of gravitational potential, as centimetres or metres of water. Such procedure provides a unit which is simple and can be made quantitatively and numerically comparable to the common pressure unit of atmospheres.

The terms and units which are adopted by individual researchers for the study of water absorption largely reflect their taste and training, but there is much to be said for the adoption by physiologists of more basic thermodynamic terminology. Several factors have contributed to the slow transition of thought to this more basic system. There has been a lack of direct methods for measuring free energy with convenience and precision, which has resulted in the expression of results in terms of equivalent pressures (pressure frequently being the component free energy applied to result in an equilibrium condition of zero movement). However, this has now been largely overcome by the application of hygrometric techniques to measurements of water potential (Spanner, 1951; Monteith and Owen, 1958; Richards and Ogata, 1958; Korven and Taylor, 1959). There is also the fact that the thermodynamic terminology is more complicated, so that scientists without training in physical chemistry are reluctant to use it. Moreover, the concept of DPD and of DPD gradients is widely accepted at the present time, and, since it is satisfactory for most purposes, there is a widespread tendency to retain it and to extend it, where necessary, to cover water movement beyond the plant (Meyer, 1956). In the present paper thermodynamic terms and units based on the chemical potential of water have been adopted. The term "water potential" is therefore used in place of DPD with reference to the free energy of plant water and in place of TSMS with reference to the free energy of soil water. "Osmotic potential" is used instead of osmotic pressure. Turgor pressure is retained when it is used as a pressure, but is referred to as a pressure potential where appropiate. The units of expression are ergs.gm^{-1}.

PROCESSES AND MECHANISMS

Renner (1912, 1915) distinguished between the two main groups of processes involved in the absorption of water by plants, on the basis that "active" absorption is associated with conditions maintained by actively metabolizing root cells, and "passive" absorption results from transpirational activity within the shoot. This division appears logical and satisfactory, since not only are the energy sources different in nature and origin, but under most conditions the two processes appear to be independent and do not operate at the same time. Thus, when atmospheric conditions favour very slow or negligible transpiration and little soil water stress exists, there is little tension in the plant system and active absorption proceeds. On the other hand, when the general stress level in the plant is high, as a result of either rapid transpiration or dry soil, or both, active absorption does not operate and passive absorption is the primary sorption mechanism.

Quantitatively passive absorption is of far greater significance than active absorption, and most water is absorbed by the plant in this manner. Active absorption finds expression mainly during nocturnal hours in the form of root pressure and guttation.

ACTIVE ABSORPTION

The recent controversy as to whether or not active absorption involves non-osmotic mechanisms has been due, in the main, to the fact that, although most absorption can be explained on the basis of simple osmotic theory, some aspects cannot adequately be explained in this manner.

In support of the osmotic theory, Eaton (1943) produced data which show that the amount of exudation from detopped cotton plants is proportional to the difference between the osmotic potential of the xylem sap and that of the solution surrounding the roots. This evidence confirmed and extended the results of Kramer (1941) who had found that rapid reversal from exudation to absorption through the stump could be demonstrated by transferring the roots to and from water and sucrose solutions. This behaviour could be produced in less than a minute and appeared to be similar to the responses of a simple osmometer.

Arisz, Helder and van Nie (1951) also concluded that active absorption is controlled by a diffusion or free energy gradient. They considered that absorption follows the active transport or secretion of salts into the xylem, and that, although development of the gradient involves energy expenditure through metabolism, the movement of water is primarily influenced by the slope of the gradient developed and the permeability of the tissue. These workers confirmed the results of Eaton (1943) that the concentration of the external solution is inversely proportional to the rate of exudation and directly proportional to the concentration of the exudate. Similar results were obtained by van Andel (1952). In general, workers supporting the simple osmotic explanation of active absorption agree with Levitt's (1954a) conclusions that negative gradients do not exist between the water-absorbing roots of plants and their environment and that experimental evidence claiming to prove that active water absorption is a non-osmotic phenomenon is due to error in determination or in interpretation of results.

Opposing this viewpoint, van Overbeek (1942) found that the osmotic concentration of the exudate from detopped tomato plants is significantly lower than the concentration of the external medium at which exudation ceases. Evidence for a non-osmotic factor in water absorption has also been obtained from other experiments. Bennett-Clark, Greenwood and Barker (1936) found that the osmotic potential of certain tissues is higher when measured plasmolytically than when measured cryoscopically on the expressed sap. This was regarded as evidence that the protoplasm secretes water into the vacuole instead of acting as a passive, differentially permeable, membrane. Similar discrepancies were noted by other workers (Mason and Phillis, 1939; Roberts and Styles, 1939; Bennett-Clark and Bexon, 1940; Currier, 1944), but, because of the possible inherent errors in the osmotic potential measurements, Levitt (1947) considered this evidence to be inconclusive.

Levitt (1947) also calculated the energy needed to maintain absorption gradients through respiration and concluded that the maintenance of a gradient of more than 2.10^6 ergs.gm^{-1} would rapidly deplete the carbohydrate reserves of a plant. Levitt's assumption of the need for respiration to provide the energy for non-osmotic absorption appears valid, as there is considerable evidence to link the processes, and water intake is reduced by factors which tend to inhibit respiration (Steward, Stout and Preston, 1940; van Overbeek, 1942; Rosene, 1944, 1947, 1950; Kelly, 1947; Hackett and Thimann, 1952; Bonner, Bandurski and Millerd, 1953). However, his conclusions were questioned on the basis that the permeability values used were incorrect and the thermodynamic calculation wrongly based (Bennett-Clark, 1948; Meyers, 1951; Spanner, 1952). A lively controversy commenced on these issues (Levitt, 1953, 1954b; Spanner, 1954), and Stiles (1956) considers this aspect of the question to be still open.

Active absorption of water is closely related to respiration, and this relationship, in turn, appears to be closely linked with auxin-induced water uptake (Reinders, 1938, 1942; Hackett and Thimann, 1952). In general, it was noted that auxin significantly promotes water absorption and that this absorption is inhibited by respiratory inhibitors. The latter authors, in common with Ketellapper (1953), also found that the increased water uptake is accompanied by a decrease in the osmotic potential of the cell sap and concluded that the effect of auxin on water uptake is not due to the formation of osmotically active substances in the cell. Hackett and Thimann (1952, 1953) subsequently concluded that the effect of auxin is on the cell wall, since respiratory inhibitors have a parallel effect on water uptake and on cell enlargement. They also showed that the effect of auxin on respiration parallels its effect on water uptake, which provides further evidence of the role of metabolic processes in active absorption.

Bonner, Bandurski and Millerd (1953) demonstrated that in the presence of auxin water absorption could take place, although at reduced rate, from mannitol solutions hypertonic to the cell sap. Again a close relationship between uptake and respiration was demonstrated throughout the range of solutions tested. However, this strong evidence of non-osmotic uptake, with respiration as a suggested energy source, was later found to be in error (Burström, 1953; Ordin, Applewhite and Bonner, 1956). These workers showed that in the presence of mannitol the osmotic potential of the cell sap increases rapidly and in approximate proportion to the concentration of added mannitol. They therefore concluded that a negative osmotic gradient does not exist and that it is unnecessary to invoke a non-osmotic mechanism to explain water uptake in these experiments. Although Mercer (1955) questioned Burström's (1953) interpretations on the basis that the increase in osmotic potential of the cell sap probably occurs as a result of decrease in hydration instead of permeation of mannitol, the conclusion remains valid that water uptake is osmotic. Mercer (1955) also pointed out that many of the experiments measuring water uptake by changes in tissue weight are subject to error because once the cells become plasmolysed the tissue weight fails to respond to changes in the volume of the protoplasts, i.e., to changes in apparent osmotic volume. For this reason the data of van Overbeek (1942) also lose their significance as evidence of non-osmotic absorption.

The mechanism by which auxin increases water uptake has been studied by numerous workers. Some of the earlier investigators attributed the effect to increased accumulation of osmotically active substances in the cell through starch hydrolysis or salt accumulation (Reinders, 1938, 1942; Commoner and Mazia, 1942; Commoner, Fogel and Muller, 1943), but later studies which found no increase in osmotic potential of the cell sap, in fact a decrease due to cell enlargement, showed this hypothesis to be in error (van Overbeek, 1944; Levitt, 1947; Hackett, 1952; Brauner and Hasman, 1952).

Three main effects of auxin have been suggested — increase in permeability of cell membranes, increased extensibility and plasticity of the cell wall, and direct stimulation of non-osmotic absorption. Brauner and Hasman (1949, 1952) concluded that the primary effect is to cause increased permeability and extensibility of the cell wall. A similar conclusion was reached by Levitt (1953) and Ordin, Applewhite and Bonner (1956), and this has the important corollary that auxin-induced water uptake follows osmotic principles.

Autonomic rhythms, which are frequently noticed in exudation of detopped root systems (Grossenbacher, 1939; Hagan, 1949), are sometimes cited as evidence of a non-osmotic control of active absorption. It appears probable that in these cases the endogenous rhythms are related to changes in respiration and other metabolic activity (Hagan, 1949). Van Andel (1953) found that water permeability and salt transport to the xylem varied with rate of exudation, and it is possible that these effects could also be interpreted through osmotic theory.

In conclusion, it appears that with present knowledge it is difficult to identify a non-osmotic factor in active water absorption, even though it is apparent that active absorption is closely linked to, and immediately affected by, changes in rate of respiration. As Kramer (1956b) pointed out, the fact that active absorption is linked with respiration does not prove that the process is non-osmotic. Even if it is an osmotic process, it will be affected by the permeability of the protoplasmic membranes and the concentration of solutes in the xylem—both of which are dependent on release of energy through respiration.

PASSIVE ABSORPTION

Of the processes involved in the absorption of water by plants, the most important is that which is initiated and controlled by transpiration from the shoot. It is generally attributed to evaporation of water from the mesophyll cells of the leaves, causing reduction of cell volume, which results in a decrease of water potential. This establishes a water potential gradient into these cells from the xylem of the leaf veins. Removal of water from the xylem reduces pressure on the water in the conducting system, and this reduction of pressure is transmitted through the xylem elements to the roots. In turn, a gradient develops across the root cortex and into the soil. Thus a water potential gradient is established extending from the soil water surrounding the roots, through the plant and into the atmosphere, and water tends to move along this gradient in the transpiration stream. While this explanation oversimplifies some of the processes involved, it serves as a model for more detailed discussion.

The operation of this process involves the cohesion theory of sap ascent. The literature on this subject has recently been reviewed by Greenidge (1957), his primary conclusion being that, although weaknesses in the theory exist and many aspects of the original theory are invalid, no satisfactory alternative mechanism has yet been proposed. Several recent studies, in particular, have demonstrated that the classical cohesion theory is inadequate. For instance, it has been shown that sap ascent has continued, virtually unimpeded, despite deep and overlapping incisions into the stem made from opposite sides of a bole (Elazari-Volcani, 1936; Preston, 1952; Greenidge, 1955a, 1955b), and Greenidge (1958) found that rate of dye movement up the stem of a number of tree species was virtually unaffected even when the bole had been severed. In addition, Scholander, Love and Kanwisher (1955) and Scholander, Ruud and Leivestad (1957) found that when vine or liana stems are severed and the plants placed in air, absorption continues when the stem is again placed in water, though at a reduced rate, and leaf turgor is regained. Introduction of copper sulphate to the absorbed liquid, in toxic concentrations, did not prevent water from being absorbed and transferred above atmospheric height. It can be appreciated that, while these experiments throw doubt on the cohesion theory as originally proposed, they also demonstrate that active processes are of little importance in sap ascent so that a predominantly passive process is involved. Certainly the evidence of continuous freely mobile sap columns, of tension in the stem during transpiration, and the transport of water through metabolically inert plants, are in accord with the broader aspects of the cohesion theory. In any case, from the viewpoint of the current discussion, perhaps the best evidence that absorption is controlled by transpiration is the close relationship which exists between these two processes (Lachenmeier, 1932; Kramer, 1937, 1938; Weatherley, 1951).

The whole pathway of water movement from soil to atmosphere is lucidly interpreted by considering the soil-plant-atmosphere system as a thermodynamic continuum. This procedure has been adopted, using different viewpoints, by Gradmann (1928) and van den Honert

(1948), and by Edlefsen (1941). The former authors applied an analog of Ohm's law to water transport, which implies that water transport across any part of the system is governed by the potential difference across the segment concerned and the resistance in between. On this basis van den Honert (1948) demonstrated that resistance to water movement across the gaseous phase from leaf cells to the free atmosphere, even with open stomates, is by far the greatest resistance encountered in the movement of water through a plant freely supplied with soil water. Edlefsen (1941) drew the similar conclusion that in transpiring plants the greatest free energy drop occurs in the region between the leaf cells and the outside air, even when the soil is as dry as the permanent wilting percentage.

These studies emphasise the importance of the factors controlling transpiration in the control of absorption. Notwithstanding this, however, the lag of absorption behind transpiration will be determined by the sum of resistances in the path of water movement. In dry soils this lag is caused primarily by lack of availability of water at the root surfaces, occasioned by inadequate water supply or the reduced potential of the soil water (Kramer, 1949; Richards and Wadleigh, 1952; Philip, 1957a), but in culture solutions or relatively wet soils the primary resistances are probably in the root (Kramer, 1956d). This is confirmed by studies in which it has been demonstrated that the absorption lag is reduced if the roots are detached (Kramer, 1938), and the association of the resistances with the living cells of the root is indicated by the inhibition of absorption which follows application of metabolic inhibitors (Crafts, Currier and Stocking, 1949; Kramer, 1955b, 1956a, 1956c) and by the increased absorption which follows death of the roots (Renner, 1929; Kramer, 1932; Brouwer, 1954; Ordin and Kramer, 1956; Mees and Weatherley, 1957b).

Although the factors affecting absorption will be discussed in detail in later chapters, it is pertinent at this stage to consider the pathway and mode of movement of water across the root. Several interesting studies have been conducted on this subject in recent years, using isotopically labelled water. With oat coleoptiles, Ordin and Bonner (1956) found that the cell walls presented a greater barrier to water movement than the cytoplasm, although the reverse situation was noted for bean roots (Ordin and Kramer, 1956), a tissue which was, in any case, much more permeable to water. Subsequently, Philip (1958b,c) and Bonner (1959) showed that in both previous experiments the time course of water diffusion through the tissue has followed closely the expectation based on resistance being uniform throughout. The only major barrier to diffusion appeared to be the cuticle, and in the tissue under study most of the exchange was presumably through the cut surfaces of the tissue cylinders.

The recent studies of Mees and Weatherley (1957a, 1957b) are of wider significance. These authors proposed that two permeability coefficients be considered in discussing the mechanism of water movement across the cortex, one being an index of permeability in relation to gradients of osmotic potential and the other to gradients of hydrostatic pressure. By establishing known osmotic and hydrostatic gradients across the root they were able to measure the change in flux per unit change in gradient and so evaluate the different coefficients. If the structure of the root had permitted diffusion only, the two coefficients should have been equal and a certain rate of water movement should have been caused by a given gradient of water potential, regardless of whether it was of osmotic or hydrostatic origin. The results obtained, however, showed that the rate of movement caused by a hydrostatic gradient is much greater than that caused by an equivalent osmotic gradient. This was attributed to two phenomena—firstly, that the osmotic permeability coefficient is increased considerably by the application of a hydrostatic gradient; secondly, that a mass flow component of water movement occurs in addition to diffusional movement.

Kramer (1932, 1940b) also found marked increases in water movement across roots when pressure gradients were applied, but, because of the absence of osmotic data, the comparative effects of osmotic and hydrostatic gradients are not known. Other workers have demonstrated that transpirational tensions result in increased root permeability (Brewig, 1936a, 1936b, 1939; Brouwer, 1953, 1954). Brouwer concluded that this reduction in resistance is due to decreased turgor pressure in the cells, which reduces the compression of the cytoplasm. Myers' (1951) conclusion that plasmolysed cells are more permeable than unplasmolysed cells supports this contention, although his data are in opposition to those of Levitt, Scarth and Gibbs (1936) and Aykin (1946). Mees and Weatherley (1957b), whose hydrostatic gradients were induced by externally applied pressure, rather than by tension, considered that the explanation may lie in the fact that reduced cell volume alters the permeability through differential extension of cell wall and cytoplasm. Dehydration alone normally reduces permeability (Kramer, 1955a), and the results of those workers who have noted reduced permeability when the osmotic potential of the external medium increases (Aykin, 1946; Arisz, Helder and van Nie, 1951; Mees and Weatherley, 1957b) support this point.

Apart from the effect of tension on the osmotic permeability coefficient, Mees and Weatherley's (1957b) evidence for a mass flow component is of special interest. They concluded that the mass flow pathway is probably located in the cell walls and most of the cytoplasm, thus comprising most of the free space (Briggs, 1957). The fact that they observed a 90 per cent reduction in the flux through the root due to metabolic inhibition is not inconsistent with this hypothesis, nor is the fact that the flux increased if the roots were killed. The cell walls are intimately connected with the underlying cytoplasm, and active aerobic metabolism appears essential for the maintenance of low resistance in this pathway. Although no studies of this type are available for movement of water across the leaf, it is possible that there is also a mass flow component to water movement across the leaf mesophyll. Water movement through the walls certainly occurs in this tissue (Strugger, 1943, 1949; Steubing, 1949).

FACTORS AFFECTING WATER ABSORPTION

In the following paragraphs, primary attention is paid to those factors affecting passive absorption, and in this regard van den Honert's (1948) treatment of water transport in plants has particular relevance.

As mentioned previously, van den Honert, following Gradmann's (1928) earlier analysis, applied an analog of Ohm's law to water transport considering the flux of water across any part of the soil-plant-atmosphere system to vary proportionately with the potential difference and inversely with the resistance to flow.

Van den Honert regarded water transport through the plant as a catenary process, in which the rate of the slowest partial process governs the velocity of the whole. This implies that the source of the greatest resistance to movement is the overall source of control, and that resistance elsewhere is of secondary importance.

Although van den Honert did not examine water movement through the soil to the root surface, or consider soils significantly drier than field capacity, these features can readily be included in the situation, as the whole path from soil to atmosphere forms a thermodynamic continuum, to points along which water potential or specific free energy values may be assigned, and for each segment of which the loss of free energy may be related to the flux of water and the resistance to the motion. This analysis can be applied strictly only to isothermal situations. Where temperature gradients exist, water movement can sometimes be observed in direction opposite to the gradient of water potential (Taylor and Cavazza, 1954). This phenomenon is not usually a factor of importance in the normal pattern of water absorption by transpiring plants but must always be borne in mind in non-isothermal situations.

From these considerations it can be seen that the primary factors affecting absorption are those which are responsible for the resistances developing along the transpiration path. The following discussion is directed towards an understanding of these factors and the extent to which they are significant.

SUPPLY OF WATER AT THE ROOT SURFACE

Two main phenomena are concerned with the supply of soil water to the surface of a root, namely, movement of the water to the root surface, and growth of the root into the soil mass.

RATE OF WATER MOVEMENT IN UNSATURATED SOILS. As water content decreases from saturation, rate of water movement decreases rapidly. Numerous studies have been made on this subject by soil physicists, and in recent years most aspects have been elucidated (Childs and Collis-George, 1948, 1950; Richards and Moore, 1952; Richards and Wadleigh, 1952; Klute, 1952; Staple and Lehane, 1954; Philip, 1954, 1955, 1957a, 1957b, 1958a). Philip (1957a) stated that, as water content decreases, unsaturated permeability decreases for the following reasons: (i) the total cross sectional area available for flow decreases with decreasing water content; (ii) as water content decreases, the largest pores are emptied first; since the contribution to permeability per unit area varies as the square of the pore radius, permeability may be expected to decrease much more rapidly than water content; (iii) as water content decreases, the chances of water occurring in pores or wedges, isolated from the general system of water films and channels, increases; once continuity breaks down there can be no flow in the liquid phase. In earlier years it was thought that unsaturated permeability would become zero as soil moisture tension approached a value equivalent to $1.0.10^6$ dynes.cm^{-2} (Richards, 1936; Richards and Wilson, 1936), but the investigations reported above indicate that some movement still occurs at much higher tensions. Experimental evidence supports this contention (Wilson and Richards, 1938; Richards and Weaver, 1944), the latter authors noting that, even at tensions equivalent to $1.0.10^8$ dynes.cm^{-2}, water movement could be achieved by application of pressure differences.

The proportion of vapour movement in the total movement of water increases as water content falls and probably constitutes the major proportion of water transfer in dry soils. Philip (1955, 1957b) has extended his work to include isothermal movement in the vapour and adsorbed phases, and Philip and deVries (1957) have examined the influence of temperature on water movement. This latter study included the interaction of vapour and liquid phases in total transfer of water and the differences between average temperature gradients in the air-filled pores and in the soil as a whole. Because of these considerations, neglected by some previous authors, good agreement has been obtained between experimental and theoretical data for water movement in response to temperature gradients. The extent of this movement can be quite appreciable (Edlefsen and Bodman, 1941; Hilgeman, 1948; Gurr, Marshall and Hutton, 1952; Taylor and Cavazza, 1954; Rollins, Spangler and Kirkham, 1954). As an example, the results of Hilgeman (1948) showed that, in a field study on bare soil in Arizona, a total movement of 9.8 inches of water in the top 8 feet of soil occurred over a period of 22 months.

An important aspect of vapour movement may arise if a vapour gap develops between root and soil. Philip (1955, 1957a) has shown that steep water gradients may develop near the root surfaces during transpiration and that, as a result, it is possible, even at fairly high mean soil water levels, for the soil immediately adjoining the absorbing surface to become so dry that the final transfer of water to the root could take place in the vapour phase. The discontinuity could be accentuated by soil and, more particularly, by root shrinkage during dehydration. Under these conditions absorption of water by the plant could be limited by the rate and extent of vapour transfer across the root-soil gap. A further effect of this discontinuity would be the accumulation of solutes at the evaporating soil surface. This would have two undesirable effects through a reduction in the free energy of the soil water and a cessation of nutrient absorption. The vapour gap hypothesis has been supported by Bonner (1959) but disputed by Bernstein, Gardner and Richards (1959) on the grounds that it is not necessary to invoke a vapour gap to explain observed phenomena and that, in fact, rates of vapour transport are inadequate to supply the amounts of water required.

RATE OF ROOT GROWTH INTO THE SOIL. Rates of water movement in unsaturated soils are slow, hence rate of root growth into the moist soil mass is an important agency in enabling the plant to obtain an adequate supply of soil water. This is particularly true of newly established plants for which rapid root growth is essential for survival. In such cases expansion of the absorption zone is observed to increase with increasing age and root development of the plant (Davis, 1940; Russell, Davis and Blair, 1940; Russell and Danielson, 1956). With established plants, such as orchard crops, a permanent and extensive root system exists and water extraction throughout the soil is more even (Hendrickson and Veihmeyer, 1929, 1934, 1942). In such cases maintenance of an adequate area of young and active roots and root hairs is more important than expansion of the whole root zone.

The factors which affect root growth are similar to those affecting plant growth generally—supply of growth materials and maintenance of a high degree of hydration—but in addition, temperature conditions, aeration and mechanical impedance are important factors. A discussion of the factors affecting growth materials in the form of mineral nutrients and photosynthetic products is beyond the scope of this paper. Only the effect of soil physical conditions will be mentioned here.

In general, it can be anticipated that root elongation decreases as water potential decreases and will cease when the water potential of the root tissue is reduced to the stage at which the turgor pressure in the enlarging cells reaches zero, just as stem elongation and normal cell enlargement usually cease at this point (Furr and Reeve, 1945; Blair, Richards and Campbell, 1950; Clements, Shigeura and Akamine, 1952; Ordin, Applewhite and Bonner, 1956; Slatyer, 1957a, 1957b). This implies that root extension will cease at approximately the same tissue water potential value as that at which permanent wilting occurs, as Slatyer (1957b) has shown that permanent wilting can be expected when the tissue water potential equals the osmotic potential of the cell sap. However, the fact that there is usually a gradient of osmotic potential through the plant (Stocking, 1956) may mean that root extension can be expected to cease at a water potential value slightly higher than that necessary to cause permanent wilting.

This general association of cessation of root extension with zero turgor pressure has been supported experimentally, several authors having shown that root growth is progressively inhibited with decreasing tissue water potential and ceases at approximately the permanent wilting percentage (Reed, 1939; Kaufman, 1945; Gingrich and

Russell, 1956, 1957). On the other hand, since the elongating zone of the root consists of incompletely vacuolated tissue, it cannot be expected that root extension will always follow these osmotic principles. In fact, some observations have shown that root growth may continue at much lower water potentials than are required to inhibit hypocotyl elongation (Ronnike, 1957). Also, if some roots are in moist soil, it is possible that the water potential through the root system will be reduced less than if all the roots are in dry soil, and extension may proceed even in those roots which are situated in the drier parts of the soil profile. This, too, is generally supported by experimental evidence (Breazeale and Crider, 1934; Hunter and Kelley, 1946; Volk, 1947; Kmock, Ramig, Fox and Koehler, 1957), although some investigators have not been able to demonstrate it (Hendrickson and Veihmeyer, 1931).

The association of cessation of root extension with permanent wilting is to be expected from the indirect effects of wilting on the supply of growth materials through photosynthesis and mineral absorption. It helps to explain why some investigators have observed that absorption of soil water appears to cease at the permanent wilting percentage (Veihmeyer and Hendrickson, 1927, 1928, 1934, 1949; Hendrickson and Veihmeyer, 1929, 1945). As Slatyer (1957b) has pointed out, there is no essential physical reason why absorption should stop at the permanent wilting percentage, but if root extension ceases as a result of decreasing water potential and water movement through the soil to the root is very slow, it is clear that absorption will be severely inhibited and for practical purposes could be considered as having stopped.

The effect of soil temperature on root growth is similar in most respects to the influence of temperature on growth generally (Hagan, 1952a). Within limits, increasing temperature results in increased cell division and cell elongation (Burström, 1941; Stuckey, 1941; Brown and Rickless, 1949); temperature is also of influence in the supply of other essential growth materials such as carbohydrates, mineral nutrients and water (Kramer, 1949; Hagan, 1952a). Optimal soil temperatures for root growth vary with species and the pre-conditioning of the plant, but for most species little root growth takes place below 5°C or above 40°C (Hagan, 1952b).

The effect of aeration on root growth is closely linked with the effect of temperature. With increasing temperature, the oxygen requirements for normal root growth increase rapidly. Cannon (1925) attributed this feature to the decreasing solubility of oxygen in the soil solution with increasing temperature, but increase in rate of respiration is probably more important in necessitating increased oxygen supply (Russell, 1952). Increased concentration of CO_2 likewise suppresses root growth (Whitney, 1942; Erickson, 1946; Leonard and Pinckard, 1946), and this effect appears closely related to the direct effect of CO_2 on aerobic respiration. In general, it appears that in most soils CO_2 concentration is seldom high enough to damage the roots of the majority of plants, but that the concentration of oxygen may frequently be too low for optimum growth (Kramer, 1949; Harris and van Bavel, 1957). Structural characteristics affecting oxygen diffusion are therefore of primary importance (Monselise and Hagin, 1955; Bertrand and Kohnke, 1957).

The effects of mechanical impedance on root growth are, in turn, closely related to those of aeration, both factors usually being operative at the same time if impedance is due to soil density. If, on the other hand, impedance is due to low soil moisture, aeration is usually optimal when soil water content is lowest. The apparent density of the soils is an important factor in preventing root elongation; and in most soils with an apparent density of greater than 1.9, no roots of any description are found (Veihmeyer and Hendrickson, 1946, 1948). These authors also noted, as would be expected, that a lower apparent density in fine textured soils had the same inhibiting effect as a high apparent density in coarse textured soils. As they found this effect to be independent of aeration, the size of the voids in the soil appears to be a more critical factor than density alone, except where density values are extreme. This hypothesis is confirmed by the work of Gill and Miller (1956) and Wiersum (1957).

The relative importance of water movement through the soil mass to the root and of root growth into untapped soil reserves, in determining the rate of supply of water at the root surface, depends on several factors, the primary ones being soil water content, soil water potential, root activity and root density. In soils drier than field capacity, it has been demonstrated (Hendrickson and Veihmeyer, 1931, 1941; Aldrich, Work and Lewis, 1935; Veihmeyer and Hendrickson, 1938; Richards and Loomis, 1942; Stocker and Kausch, 1952; Kausch, 1955; Peters, 1957) that water does not move in a root-free soil at a rate adequate to supply roots a number of centimetres way. This is to be expected from physical theory (Philip, 1957a), although it is also to be expected that if root density is high enough, for example, in potted plants, water could move through a few millimetres of soil at a sufficient rate to maintain adequate rates of supply (Richards and Weaver, 1944; Peters, 1957). Under field conditions, however, root density would normally be inadequate to enable this to occur, and continued root extension would appear to be necessary to maintain significant rates of absorption. This interaction between root density and rate of soil water movement is clearly of primary significance in assessing the relative importance of root growth in determining rate of supply of water to the root, and the influence of transpiration in determining rate of demand is likewise pertinent. Thus, while Weaver and Zink (1946) observed that removal of half the root systems of several grass species had little effect on growth, and Bialoglowski (1936) and Elazari-Volcani (1936) found that with slow rates of transpiration the root surface/leaf surface ratio of citrus could be reduced by about half without effect, many other investigators, particularly those concerned with field crops in drying soils, found that any significant reduction in root surface restricts absorption (Nutman, 1934; Grier; 1940; Leonard, 1944; Parker, 1949).

The fact that rates of flow of unsaturated soil water are very low in soils drier than field capacity emphasizes the importance of root extension for continued absorption. The figures of Kramer and Coile (1940), who computed from data of Dittmer (1937) that extension of the roots of a winter rye plant can provide up to three litres of water a day for absorption, highlight the importance of this feature. The apparent cessation of absorption at the permanent wilting percentage, which is probably related to the cessation of root growth, likewise demonstrates the point. In most cases it appears that the overall limitation to rate of water supply to the root surface will be the progressive effect, during soil water extraction, of the decreasing water potential in the plant-soil system inhibiting further root extension and reducing unsaturated soil water movement. Other factors affecting root growth, such as aeration, temperature and mechanical impedance, can be expected to become major sources of influence only under special circumstances.

ENTRY OF WATER INTO THE ROOT

Although the factors which influence water supply at the root surface are directly associated with the entry of water into the root, in some instances the mode of action differs. It is of value to discuss the factors affecting water entry in relation to zones of differential absorption at the root epidermis, permeability of the root cortex to water movement and the water potential at the root surface.

THE ABSORBING ZONE OF ROOTS. Examination of roots as absorbing organs has been an aspect of active physiological study for many years. Recent reviews by Kramer (1949, 1956d) provide comprehensive summaries of these investigations, and only the primary aspects will be mentioned here.

In general, it can be stated that the zone of most rapid absorption lies in the region where the xylem is fully mature, between the elongation zone close to the root tip and the suberized zone farther back. In the meristimatic region at the tip, absorption is slow because of the high resistance to water movement offered by the compact cell arrangement (Kramer, 1956e). Absorption is also restricted in the zone of cell elongation because the xylem is not completely differentiated. Maximum intake of water appears to occur in the region where the xylem is fully mature but where the endodermis and epidermis have not become impermeable. This region has been located from 1.5 cm to 20 cm from the root tip, although it is usually found between 5 and 10 cm from the tip (Sierp and Brewig, 1935; Brewig, 1936a, 1937; Hayward and Spurr, 1943; Brouwer, 1953, 1954). The length of the region is very restricted in slow growing roots and appears to increase rapidly with rate of growth (Kramer, 1956d). Beyond this zone of rapid uptake, rate of absorption decreases rapidly as permeability is reduced by increasing suberization and thickening of the walls of the endodermal cells and the suberization or lignification of the epidermal or hypodermal cells (Hayward and Spurr, 1943; Rosene, 1937, 1941; Esau, 1953).

The zone of most rapid absorption is observed to shift during transpiration. This phenomenon has been attributed by Brouwer (1953, 1954) to increased permeability in the older part of the root when turgor is reduced, although other explanations have also been proposed (Mees and Weatherley, 1957b). The significance of transpiration to root permeability is discussed in more detail elsewhere in this paper.

Although most studies have concentrated on zones of most rapid absorption, there is evidence that considerable quantities of water can be absorbed through suberized roots, at least under some conditions. Investigations on citrus trees have shown that, although few unsuberized roots are found on these species during winter, they are far from inactive at this time of year (Chapman and Parker, 1942; Hayward, Blair and Skaling, 1942). Direct studies have confirmed that absorption occurs through suberized roots (Crider, 1933; Nightingale, 1935; Addoms, 1946), and the fact that such a large proportion of the roots of all terrestrial plants are suberized makes it probable that significant quantities of water pass through such tissue.

The region of most rapid absorption appears to coincide with the normal zone of root hair development. This relationship is to be expected, knowing the importance of root hairs to absorption through their high permeability and their effect in increasing the total root surface (Rosene, 1943, 1954; Kozlowski and Scholtes, 1948; Dittmer, 1949). Estimates of the increase in root surface due to root hairs vary considerably. Some suggest that up to ten times the root surface is developed (Evans, 1938); others that the value is about 1.6 (Dittmer, 1937). With respect to permeability, Rosene (1943, 1954) has found that root hairs are about as permeable to water as the unsuberized epidermis of young onion roots. As is to be expected, their permeability decreases with age (Rosene and Walthall, 1954). Kramer (1956d) comments that root hairs are probably of little influence in total absorption from well watered soil, but whenever total root surface in contact with soil becomes a limiting factor in absorption, presence of root hairs may be of considerable importance.

MOVEMENT OF WATER ACROSS THE CORTEX. There are two main factors concerned with the movement of water across the root cortex: the water potential gradient across the root from the soil to the xylem, and the resistance to water movement caused by root permeability.

The water potential gradient across the root will vary with water potential at the soil-root surface and with fluctuations in the osmotic potential of the xylem sap and the tension developed in the xylem through transpiration. In the absence of transpiration the osmotic potential of the xylem sap alone will presumably determine the water potential at this point. The soil water potential will decrease as soil moisture tension increases (following water extraction) or as the concentration of the soil solution is increased (due to the effect of decreasing soil water or of added solutes). Both these effects will be of greater significance if water uptake by the root is more rapid than water supply to the root, in which case the water potential will decrease more rapidly at the root surface than in the soil mass.

Although the water potential gradient is the driving force causing water movement across the root, the rate of movement is also influenced by the resistance to flow; and as resistance increases, a steeper gradient is needed to maintain the same flux.

Evaluation of the water potential gradient from soil to root has recently aroused some controversy. For a number of years the views of the workers at Riverside (Bernstein and Hayward, 1958), that the soil water potential includes osmotic components, have been prominent. On the other hand, Walter (1955) considered that, since the solutes contributing to the osmotic potential of the soil water are diffusible into the plant, the ideal osmometer concept implicit in the Riverside hypothesis is invalid. Supporting the Walter contention, Philip (1958b) and Bonner (1959) proposed that the effects observed by the Riverside group could be explained, not on the basis of osmotically induced "physiological dryness" but, instead, by the development of a vapour gap which would effectively constitute the plant as an ideal osmometer, or by entry of the diffusible solutes into the plant in toxic quantities. The Riverside group (Bernstein, Gardner and Richards, 1959) disputed the occurrence of a vapour gap, and held that their experimental evidence is logically interpreted by the osmometer concept, a view supported, in general terms, by a number of other authors (see Crafts, Currier and Stocking, 1949; Kramer, 1949; Richards and Wadleigh, 1952). However, experimental data also are available to support Walter's basic premise that the solutes are freely diffusible (Maximov, 1929; Eaton, 1942).

It seems probable that the metabolic processes involved in salt absorption are of importance in this regard (Epstein, 1956a; Gauch, 1957; Robertson, 1958), particularly in view of the fact that respiratory inhibitors normally cause a severe reduction in uptake of both anions and cations (Ordin and Jacobson, 1955). Also, poisoning of the roots and elimination, not suppression, of the active processes has been observed to result in absorption of salts in proportion to their concentration in the external solution (Hoagland and Broyer, 1942).

Recently Scott Russell and Shorrocks (1959), repeating earlier work on ion uptake, have shown that when internal salt status of both the plant and the external medium are low, rate of transfer of ions to plant shoots is independent of the rate of transpiration. However, the combination of high salt status, internally and externally, can cause uptake to vary with rate of transpiration; and concentration of ions in the transpiration stream can be lower than that of the external solution. These results indicate the existence of a barrier which can offer high resistance to the passage of ions across the symplast of the plant roots.

Should such a barrier, also proposed by Bernstein and Hayward

(1958), exist, it seems that the controlling mechanism is located in, or external to, the endodermis, since once ions have entered the free space, their distribution through the rest of the plant would probably proceed rapidly. The possible special importance of the epidermis as an absorbing organ is suggested by the work of Sandstrom (1950) who demonstrated that removal of epidermis of wheat roots resulted in an increase in salt absorption which was wholly passive and proportional to water absorption.

Apart from this movement of water in relation to gradients of water potential, which is primarily passive, active absorption is rapidly inhibited as the water potential decreases below the reference level of pure free water. Most recent evidence indicates that it can proceed only when the soil water potential is not less than about -2.10^6 ergs.gm^{-1} (Eaton, 1943; McDermott, 1945; Hagan, 1949; Army and Kozlowski, 1951). Levitt (1947) calculated that active absorption could possibly maintain a gradient of $1\text{–}2.10^6$ ergs.gm^{-1} across the root. This is in close agreement with the values just cited, but as active absorption generally ceases when the external water potential is about -2.10^6 ergs.gm^{-1}, metabolism is presumably retarded and permeability decreased to such an extent by reduced hydration that no net transfer of water occurs.

In general, reduced hydration results in reduced permeability, and most studies which have related permeability to the concentration of external solution have obtained this result (Levitt, Scarth and Gibbs, 1936; Aykin, 1946). On the other hand, Bogen (1940, 1941) and Myers (1951) observed that plasmolysed cells are more permeable than those unplasmolysed. It seems probable that any marked and prolonged reduction in turgor, leading to disruption of normal metabolism, has a direct and severe inhibitory effect on permeability and hence on absorption. In this regard Mees and Weatherley (1957a, 1957b) noticed a decline in root permeability after several hours of induced hydrostatic pressure, even though the initial effect was to cause a marked increase in permeability. Kramer (1950) concluded that prolonged water stress causes an immediate decrease in permeability due to the increased resistance of dehydrated cell membranes and a delayed effect caused by changes in the structure of the protoplasm. It is clear that the tensions across the root resulting from the influence of transpiration must be interpreted differently to the effect of a general decrease in the water potential of the root tissue associated with decreasing soil water potential.

The permeability of the root to water is markedly affected by the metabolic condition of the root tissue and hence by factors which influence respiration, the energy source for metabolism. This is well illustrated by the inhibitory effect on absorption caused by respiratory inhibitors such as azide or KCN (van Overbeek, 1942; Rosene, 1944, 1947; Mees and Weatherley, 1957b). Under natural conditions the most important factors affecting permeability appear to be hydration, temperature and aeration. Active absorption, being wholly dependent on metabolism, is more severely inhibited than passive absorption when these factors are adverse.

The primary effect of low temperature on absorption appears to be to decrease the permeability of the tissue, directly through an effect on membrane permeability, and indirectly through increased viscosity of the protoplasm and of water (Kramer, 1949, 1956c). As much of the resistance to movement of water decreases if the roots are killed, the former factor is probably of greater importance.

The effect of low temperature on reducing absorption varies considerably with different species, plants native to warm environments being more affected than those from cold climates (Brown, 1939; Schroeder, 1939; Cameron, 1941; Kramer, 1942; Kozlowski, 1943). The effect of prolonged low temperature is more complicated than that of sudden chilling as conditioning to low temperature can result in an increase in permeability and hence in absorption rate (Levitt and Scarth, 1936; Levitt, 1941). High temperatures also influences absorption (Haas, 1936; Bialoglowski, 1936). As active absorption is more sensitive to high temperature than passive absorption (Kramer, 1940a), it would appear that the high temperature effect is also due to disruption of normal metabolism. Ellis and Swaney (1947) considered that inadequate oxygen supply is important at high temperatures, and Hagan (1952b) has suggested that direct heat injury to fine roots and root hairs could be important.

The effect of temperature on permeability is closely linked with that of aeration, since the oxygen requirements for respiration increase rapidly with temperature. Under field conditions marked differences in response to lack of aeration have been observed, some investigators finding that flooding markedly reduces absorption, others that it is little affected (Parker, 1950; Hunt, 1951; Kramer, 1951). Differences between species are also important, water plants being relatively unaffected by lack of aeration and many land plants showing extreme tolerance to flooding (Kramer, 1949; Russell, 1952). As might be expected, plants are usually less affected if dormant, and the degree of injury becomes more pronounced with increasing temperature (Kramer and Jackson, 1954).

Lack of aeration is probably of influence through the combined effects of low oxygen and high CO_2 concentrations, although the two factors have somewhat different modes of action. The effects of high CO_2 appear to be very rapid (Kramer, 1940b, 1945; Hoagland and Broyer, 1942; Chang and Loomis, 1945; Hagan, 1950; Kramer and Jackson, 1954) and are probably caused by the direct toxic effect of high CO_2 on permeability (Russell, 1952; Kramer, 1956c). Oxygen deficiency, on the other hand, is slower acting and may take hours or even days to become apparent (Whitney, 1942; Hoagland and Broyer, 1942; Rosene, 1950; Rosene and Bartlett, 1950; Mees and Weatherley, 1957b). This delay is closely related to the degree of oxygen deficiency, total absence of oxygen in small containers usually inhibiting absorption in several hours (Mees and Weatherley, 1957b). Kramer (1949) suggested that the longer delay normally encountered may be due to the fact that some oxygen is present in the tissues and that some may diffuse down from the shoots, thus deferring the onset of oxygen shortage and inhibition of aerobic respiration. He also suggested that if one of the primary effects of low oxygen is a build up of toxic end products of anaerobic respiration, some time may elapse before this accumulation becomes important. Probably both these explanations are valid.

Some investigators have noted an increase in absorption rate following the initial decrease caused by lack of aeration. This has been generally attributed to the breakdown of root tissue following permanent damage (Russell, 1952). The results of Mees and Weatherley (1957b) support this contention, and they concluded that, as the effect is not reversed by subsequent aeration, it is due to death of the cells. In general, lack of aeration appears to act through reduced oxygen supply, not through excess CO_2, particularly if it proceeds for several days. Whitney (1942) observed that even high CO_2 concentrations are of little consequence if the oxygen concentration is adequate. Russell (1952) concluded that, under field conditions, high CO_2 is likely to be of minor significance unless conditions also favour very low oxygen levels.

Most of the factors affecting movement of water through the root have been considered here with special reference to their immediate effects on absorption. It must be recognised that the indirect or longer term effects are also of significance. In particular the effects of adverse conditions—low water potential, lack of aeration, low or high temperature—on root growth and development are important in this regard. Resultant inhibition of root growth, increased suberization and death of root hairs all reduce absorption over a period of a few days. In addition, the conditioning of plants to, say, low temperature may result in changes in permeability which can affect rates of absorption.

The effect of the various factors on controlling absorption are varied, but all significantly affect absorption under certain conditions. Decreasing soil water potential inhibits active absorption at levels below about -2.10^6 $ergs.gm^{-1}$ (Eaton, 1941, 1943; Kramer, 1941; McDermott, 1945; Jannti, 1953; Jannti and Kramer, 1956) and progressively restricts passive absorption as it decreases over a wider range (Chung, 1935; Martin, 1940; Eaton, 1942; Hayward and Spurr, 1944; Army and Kozlowski, 1951; Corey and Blake, 1953; Bloodworth, Page and Cowley, 1956; Slatyer, 1956b, 1957a). Low temperature also severely inhibits absorption and transpiration, and frequently results in marked wilting of leaves (Döring, 1935; Brown, 1939; Schroeder, 1939; Kramer, 1942). Deficient aeration can reduce transpiration by more than 50 per cent, with associated wilting (Kramer, 1938, 1940b, 1945; Whitney, 1942; Parker, 1950). Although these factors, acting through reduced root permeability or decreased soil-xylem water potential gradients, frequently appear to be direct in action, the van den Honert hypothesis raises the possibility that they may be indirect, acting primarily through reducing the water potential in the leaves and hence causing stomatal closure and reduced transpiration. This subject will be discussed in detail below.

PASSAGE OF WATER IN CONDUCTING ELEMENTS

Aspects of water movement in the conducting elements have already been discussed. In these paragraphs the primary interest is to evaluate the resistance to movement in the conducting elements and understand the factors influencing it. The recent review by Greenidge (1957) may again be cited for a more detailed treatment of the general aspects of sap ascent.

Experimental work has proved conclusively that rapid longitudinal movement of water in plants can take place through the non-living elements of the xylem (Crafts, Currier and Stocking, 1949). This in itself is evidence of low resistance to movement; and the phenomena of guttation and root pressure, which are manifestations of active absorption processes, likewise demonstrate that little resistance occurs.

It is to be expected that such resistance as does occur may be attributed to breaks in the cohesive columns, to the physical effect of the height of the plant or to the conductive capacity of the elements. The occurrence of breaks in the elements appears to have surprisingly little effect on water movement, so is presumably a source of minor resistance in the system. Even drastic treatments, such as overlapping horizontal cuts in the stem (Elazari-Volcani, 1936; Preston, 1952; Greenidge, 1955a, 1955b, 1958), only slightly retard movement, and introduction of gas into the elements does not prevent large vine and liana stems from regaining their previous absorption rates when water supply is re-established (Scholander, Love and Kanwisher, 1955; Scholander, Ruud and Leivestad, 1957). The hypothesis that water moves freely around overlapping cuts in the bole has been substantiated by the recent demonstration by Postlethwait and Rogers (1958).

Although the evidence suggests that little resistance occurs, a hydrostatic gradient is to be expected through a transpiring plant due to the length of the stem and its gravitational head. Thus with increasing height the tension in the system needed to maintain a constant rate of movement can be expected to increase. Most studies reveal that only a small gradient occurs with height, usually 0.2–0.5 atm.metre^{-1} (Renner, 1911, 1912; Dixon, 1914; Eaton, 1941; Stocking, 1945), but Arcichovskij and Ossipov (1931) observed a gradient of as much as 44 atm.metre^{-1} in a desert shrub. Although the experimental technique used by these authors was subject to some errors, this general order of resistance presumably occurred and could possibly have been a result of the general degree of desiccation of the plant, resulting in almost complete absence of water columns.

The effect of adverse environmental conditions on resistance to water movement through the stem has not been extensively investigated, although Handley (1939) investigated the influence of low temperature on upward water movement in two tree species. He found little resistance to movement until the temperature was reduced below 2°C., when marked reduction of water supply to the leaves occurred and wilting ensued. More recently Johnston (1959) found no reduction in stem flow of *Pinus radiata* until freezing of the stem occurred, and he considers that Handley's data should also be re-interpreted in this manner.

Resistance to flow of water in the xylem elements increases rapidly when very small diameters are encountered, as, for example, in grass roots. Emerson (1954) and Wind (1955a, 1955b) studied this subject in some detail, and the latter author concluded that the resistance to flow in metaxylem elements of radius less than 20 μ is so great that it exceeds the resistance to unsaturated water movement through the soil. On this basis, Wind explains the absence of grass roots below about 20 cm in moist soils. Although these conclusions are open to question, particularly because his soil water data apply to capillary rise of water in moist soils and not to movement in dry soils, the significant resistance to water movement in small roots must be recognized. It is probable, however, that for most herbaceous plants the xylem and metaxylem elements are of adequate radius to permit movement at low resistances.

MOVEMENT OF WATER THROUGH AND OUT OF LEAVES

The primary factor causing water movement through the leaf, as through the plant, is transpiration.

Transpiration can, to a considerable extent, be regarded as a purely passive process, the rate of which is determined primarily by the vapour pressure gradient between the leaf and the outside air and by the various resistances to water movement in the transpiration path. Ordinary evaporation of water from porous materials is also affected by these considerations so that in general the effect of atmospheric conditions on transpiration will parallel their effect on evaporation. A valuable recent review on this subject is available (Milthorpe, 1959).

The important physiological factors influencing transpiration are those which cause resistance in the transpiration path and which directly or indirectly affect the vapour pressure gradient to the outer air. These can be arranged in two groups: those which cause resistance to movement in the gaseous phase and those which cause resistance through the cell walls.

Van den Honert (1948) considered that, for a plant freely supplied with soil water, under normal atmospheric conditions, the resistance to transpiration in the gaseous phase is of the order of 20 times the resistance through the rest of the plant. At first sight this may seem improbable, but the main source of resistance appears to be in the air layer adjacent to the evaporating surfaces of the cells, in which a steep diffusion gradient is found leading to the freely circulating air beyond the leaf surface. Van den Honert considered that, because of the magnitude of this factor, resistance to movement through open stomates is only about ten per cent of the gaseous phase as a whole. He subsequently concluded that the effect of stomatal closure on transpiration, and hence on absorption, cannot be expected to exert control until its resistance balances that of the gaseous phase itself. Van den Honert considered that such an effect arises only at small stomatal apertures.

The role of stomatal closure in controlling transpiration has been difficult to determine because of the fact that stomatal reactions are frequently associated with decreasing water content. Most recent studies tend to support van den Honert's hypothesis and show that stomatal control is relatively ineffective until the aperture is reduced by about half, beyond which point very effective control is exercised (Mendel, 1944; Brueckner, 1945; Crafts, Currier and Stocking, 1949; Bange, 1953; Hygen, 1953; Milthorpe and Spencer, 1957; Williams and Amer, 1957), although Kuipen and Bierhuizen (1958) have demonstrated effective stomatal regulation over a wide range of light intensities. Most of these studies have been conducted in the laboratory where resistance to diffusion outside the leaf can be a major factor in the total diffusion resistance in the gaseous phase. Under natural conditions, mobility of the leaf and turbulent eddy diffusion reduce the external resistance appreciably, and Philip (personal communication) considers that even the resistance of open stomates could be a significant factor.

In general, with decreasing water content, a constant rate phase of transpiration first occurs, during which little stomatal control is exercised. This is followed by a falling rate phase, during which stomatal closure progressively inhibits transpiration, and subsequently by a cuticlar phase when the stomates are completely closed. Superimposed on this picture is the effect of decreasing water content, in which loss of water follows the normal behaviour to be expected from water evaporating from porous materials (Gilliland, 1938). This also shows an initial constant rate phase followed by a sudden change to a falling rate phase in which the rate drops rapidly with decreasing water content. Although Gregory, Milthorpe, Pearce and Spencer (1950a, 1950b) and Milthorpe and Spencer (1957) maintained that leaf water content *per se* is of no consequence in controlling water loss, it is difficult to separate the direct and indirect effects of this factor.

The critical water content at which the falling rate phase commences is of obvious importance with respect to transpiration. Gregory *et al* (1950b) found that with the experimental material and conditions they used, it is about 90 per cent of the turgid water content. With more rapid transpiration it could be expected to be higher, and a wide variation in different types of plant and plant tissues could also be expected. Even so, a value of 90 per cent probably represents a water potential of only $-5-10.10^6$ ergs.gm^{-1}, a value commonly attained in transpiring plants under natural conditions, and the possible significance of low leaf water content must accordingly be recognized.

The mode of action of this factor on reducing transpiration is obscure. Although it is clear that any retreat of the evaporating surface, involving a lengthening of the diffusion path, will tend to increase the resistance in the gaseous phase, it is also possible that partial drying of the cell walls may be of influence. A reduction of water content in the leaf will be associated with a partial drying of the mesophyll cell walls, and Preston (1954) considers that this increases the resistance of the walls to water movement. Supporting evidence for this view is found in the work of Klemm (1956) who noted that evaporation from exposed cell surfaces, under conditions of low humidity, was much less than that from moist filter paper or multiperforate septa. In addition, the work of Boon-Long (1941) showed that any decrease in the water potential of the mesophyll cells is associated with greatly decreased cell wall permeability, and Meidner's (1955) studies demonstrate a marked increase in mesophyll resistance with decreasing water content.

Any significant increase in resistance to water movement through cell walls may be of importance in controlling transpiration if it is adequate to result in the difference in water potential across the wall being an appreciable fraction of the potential difference across the gaseous phase. Evidence of resistances of this magnitude is lacking at the present time (Milthorpe, 1959), although data that the external mesophyll cell walls are hydrophobic (Lewis, 1945, 1948) indicate that the water potential of the air adjacent to the walls could be appreciably lower than that of the cell. This effect could be expected to be most pronounced in xerophytic and sclerophytic species where cutinization of the walls may occur. Should cutinization be extensive, cell wall resistance in the sub-stomatal cavities could conceivably approach that of the leaf cuticle. This seems improbable for most cultivated plants and indeed for any physiologically active species, since the concommittant reduction in CO_2 exchange would severely limit photosynthesis and growth.

Regardless of the mode of action, it is apparent that in several cases marked changes in transpiration rate have been observed in the absence of measurable stomatal reactions (Went, 1944; Oppenheimer, 1951). It therefore appears that, while stomatal explanations of transpiration regulation are usualy adequate to explain observed phenomena, other factors may also be operative, and these will possibly be associated with phenomena such as those just discussed.

RELATIVE IMPORTANCE OF FACTORS AFFECTING ABSORPTION

If water transport through plants can be regarded as a catenary process, rate of transport dm/dt, through the whole of the soil-plant-atmosphere system, under isothermal and steady state conditions, can be expressed in a form analagous to that of an Ohm's law equation, so that:—

$$\frac{dm}{dt} = \frac{PD_s}{R_s} = \frac{PD_r}{R_r} = \frac{PD_x}{R_x} = \frac{PD_l}{R_l} = \frac{PD_g}{R_g}$$

where R_s, R_r, R_x, R_l, R_g are the resistances in soil, root, xylem, leaf cells and gaseous phase, respectively, and the PD symbols represent the reduction in water potential across each of the appropriate resistances. It must be appreciated that the potential difference in the gaseous phase is in reality the vapour pressure gradient from the evaporating surface within the leaf to the external air. Because of the non-linearity of the water potential/vapour pressure relationship, the magnitude of the resistance in this phase is not usually as great as may appear. However, this does not affect the general validity of this analysis, since under normal conditions the magnitude is the same.

Although, as shown in this expression, each of the partial processes in the system proceeds at the same rate, the general rule regarding catenary processes applies—that the limiting partial process (in this case the partial process encountering the greatest resistance) controls, for practical purposes, the velocity of the whole. Furthermore, in an Ohm's law equation, the resistance in any one of the partial processes is directly proportional to the potential difference, in this case the reduction in water potential. From these two generalisations the relative magnitude of the various resistances in the path of water movement through the soil-plant-atmosphere system can be evaluated and the primary source of control identified.

The water potential in the soil adjacent to the roots normally fluctuates from near zero to about -30.10^6 ergs.gm^{-1}, whereas the water potential in the atmosphere under normal conditions (air temperature 15-20°C, relative humidity 50 per cent) is equivalent to -800-$1{,}000.10^6$ ergs.gm^{-1}. The water potential in the leaf cells normally fluctuates over a range similar to that of the soil, and values below -50.10^6 ergs.gm^{-1} are unusual. From these figures it can readily be seen that the total reduction of water potential from soil to leaf cells seldom exceeds 50.10^6 ergs.gm^{-1}, while the reduction of water potential in the gaseous phase from leaf cells to free atmosphere may be 750-950.10^6 ergs.gm^{-1}. Therefore, the conclusion must be drawn that the resistance in the gaseous phase far exceeds the resistance in the rest of the plant and that, as a consequence, control of water transport is located at this point.

In essence, these are the interpretations and conclusions of Gradmann (1928) and van den Honert (1948), and they appear to be soundly based and logically derived (Edlefsen, 1941; Philip, 1957a). Consequently the question must arise as to the mechanism by which absorption can be controlled elsewhere than in the gaseous phase in the leaf, since, before any control can be exercised directly from another part of the system, the reduction of water potential across that zone must represent a significant fraction of the reduction of water potential across the gaseous phase.

It can be appreciated that, if air temperature is low and humidity high, such a phenomenon may occur. In winter, particularly, it seems possible that resistance elsewhere than in the leaf could be of major importance. Under atmospheric conditions favourable to plant growth, however, such as those defined above, it is difficult to envisage any resistance in the plant of adequate magnitude to be of direct influence because there does not appear to be any part of the plant within which such resistances could arise. The highest water potential values measured or estimated in plants have been about -200.10^6 ergs.gm^{-1} (MacDougal, 1926; Arcichovskij and Ossipov, 1931; Stone, Went and Young, 1950), and even the direct effect of such values as these, under the atmospheric conditions given above, would be to reduce water transport by only about one quarter.

Since the experimental data reported previously in this paper have shown that low soil temperature, inadequate aeration and low water potential can reduce absorption and transport virtually to zero, it seems probable that the mechanism by which such factors normally operate is not through their direct effect on resistance in the root but through their indirect effect on resistance in the gaseous phase in the leaf, through reduced leaf water content and stomatal closure.

As van den Honert (1948) has pointed out, the gaseous phase is the logical place for regulation of water transport, since regulation elsewhere could result only in rapid dehydration of the portion of the plant between the zone of regulation and the leaf surface. Thus the direct effect of increased root resistance on transport appears to be due to its effect on increasing the water potential difference across the root. Even if this results in only a small reduction of water potential in the rest of the plant, it causes a significant reduction in leaf turgor and probable stomatal closure. In this way the resistance in the gaseous phase is increased significantly, and rate of transpiration and of transport generally is reduced.

Experimental data bearing on this point support this explanation, the immediate effect of any of the factors known to reduce markedly absorption being to cause pronounced loss of leaf turgor and onset of wilting. It is apparent that in order for the maximum reduction in absorption to occur, complete stomatal closure would have to be achieved. Regardless of plant species, it is probable that stomatal closure is complete when the leaves are severely wilted and the water potential in the leaves has dropped to the stage at which there is zero turgor pressure in the active tissue. In most sun plants this represents a water potential of about -15.10^6 $ergs.gm^{-1}$ (Slatyer, 1957b). There are very few quantitative data on the effect of decreased root permeability on the water potential in the leaves, but the fact that severe wilting can follow exposure to low temperature and inadequate aeration or introduction of metabolic inhibitors is evidence that the drop in water potential across the root, in such cases, is of this magnitude. The data of Long (1943) provide evidence of the decreased root permeability which follows a decrease in the osmotic potential of culture solutions. Long observed that plants in substrates of $-0.7.10^6$ $ergs.gm^{-1}$ had a water deficit in their leaves of 15 per cent; in solutions of $-4.8.10^6$ $ergs.gm^{-1}$ the water deficit was 25-30 per cent. Approximate plant water potential values for these deficits (Weatherley and Slatyer, 1957) could be -10 and -20.10^6 $ergs\text{-}gm^{-1}$, respectively, so that the reduction in water potential across the root in the former case could have been 9.10^6 $ergs.gm^{-1}$, in the latter 15.10^6 $ergs.gm^{-1}$. It can be appreciated that a water potential of -20.10^6 $ergs.gm^{-1}$ would almost certainly be associated with severe wilting, complete stomatal closure and reduced water transport. A reduction in transport of 88 per cent was in fact observed in an experiment with substrates of similar concentration conducted by Hayward and Spurr (1943).

The efficiency of stomatal regulation of water transport varies considerably from species to species and with different environmental conditions. If continued water loss occurs in the form of cuticular transpiration, even when the stomates are completely closed, there is a danger of continued dehydration and possible death of the plant. This can occur if the rate of cuticular transpiration is rapid enough and root resistance high enough to result in a considerable reduction of water potential across the root and a resultingly low water potential in the rest of the plant.

It is probable that such a phenomenon frequently occurs when plants die or become extremely desiccated in drying soils. Unless transpiration can be reduced almost to zero, the resistance across the soil-root surface zone in drying soils increases very rapidly, and a steep enough water potential gradient across this zone cannot be developed without severe dehydration and probable death of the top of the plant. Kramer (1942, 1956c) considers that "winter injury" is brought about by a mechanism such as this, since in cold soils (particularly if frozen) considerable resistance to water movement in the soil-root surface and root surface-xylem zones develops; and if a period of warm sunny weather occurs, dehydration of the top of the plant takes place.

From this analysis the relative importance of the various factors affecting absorption can be seen to depend very largely on the "filtration" resistance which they cause, for this determines the water potential further along the path of water movement and ultimately affects the resistance in the gaseous phase. On this basis the only segment of the transpiration path in which major sources of resistance appear likely to occur are in the soil-root surface and root surface-xylem regions. In the stem it appears that little resistance to water movement occurs except in tall trees or in cases where the stem is at freezing temperatures. The latter effect appears unlikely to arise in practice, as under such temperature conditions it is highly probable that transpiration would be near zero or that, in such cases, resistance in soil and root would be even higher than in the stem. Resistance in the leaf also appears to be low in most cases, even though the indirect evidence reported previously suggests that under some conditions it could be of significance.

In the soil-root surface zone, low resistance to movement exists only while the soil water is at very low tension or while root extension continues. As soon as drying commences and root extension ceases, very high resistance to movement develops. In the root surface-xylem zone, resistance is low also in the absence of adverse environmental conditions and other factors adversely affecting metabolism, and as long as root surface area is adequate. The onset of adverse conditions has a direct effect on metabolism and an indirect effect on the absorbing surface of the roots, both these features contributing to a rapid increase in resistance to water movement across the root. Although low temperature or deficient aeration can reduce transpiration almost to zero, the most important overall factor affecting water transport appears to be low soil water potential at the root surface. This can be of influence in three ways. It has a direct effect on the water potential in the plant, since, in order to maintain a gradient favouring absorption, the water potential in the plant must always be lower than that in the soil. It has an indirect effect on root resistance through the effect of hydration on permeability and suberization. Finally it has a direct effect on resistance to water movement through the soil-root surface zone, which influences the water potential gradient needed to maintain transport across the zone. It can be appreciated that resistance to water movement through the soil can become of sufficient magnitude to limit directly water transport. However, this rarely occurs in living plants, since plants die of dehydration before the resistance reaches a high enough level.

To conclude this portion of the paper it may be stated that examination of water absorption by plants in terms of the van den Honert hypothesis leads to the conclusion that most of the factors which result in decreased absorption act indirectly through the effect of reduced water potential on decreasing transpiration by the leaf instead of directly in the region in which they occur. The van den Honert hypothesis appears sound, although its application may need more attention. In this regard a fuller realisation is needed of all the sources of resistance and their potential orders of magnitude. The latter factors may be of special significance if, as Preston (1954) has suggested, resistance in the leaf mesophyll cell walls be of an order similar to that of the gaseous phase. If such resistance were to develop, direct control of absorption at the root would be much more probable. At present, however, the evidence for such a source of resistance is inadequate.

ABSORPTION OF WATER BY LEAVES AND OTHER AERIAL ORGANS

Studies of the absorption of water and of water vapour by the above ground parts of plants have been conducted for many years, yet present knowledge of the extent and significance of such absorption is inadequate, and considerable controversy still exists concerning some aspects of the phenomenon.

The present discussion is concerned with the processes involved in the absorption of water in this manner, the extent to which absorption occurs and the significance it has to the water economy of the plant. Two recent reviews are available for more extensive coverages of this literature (Gessner, 1956; Stone, 1957a).

PROBABLE MECHANISMS INVOLVED

The factors associated with the entry of atmospheric water into, and its passage through, a plant appear to be those which determine the surface characteristics of the leaves, the resistance to movement within the plant and the water potential gradient across the atmosphere-plant-soil system. As with normal absorption, rate of water uptake will depend on the gradient developed and the resistance to flow.

ENTRY OF WATER INTO THE LEAF. Wettability of the cuticle appears to be an important prerequisite for absorption. The ability of a liquid to wet a surface is a function of its contact angle on the surface; in turn this depends on the surface tension of the liquid and the nature of the surface. As would be expected from the work of Wetzel (1924) and Marloth (1926) who showed that pubescence and the presence of hydrophobic surface agents reduced water uptake, Fogg (1947) noted that marked differences exist in the contact angles of water on several species, and that the contact angle is influenced by age of leaf and water content. Fogg attributed these differences primarily to variations in surface conformation, pubescence and the composition of the cuticle. As contact angle is reduced by the addition of wetting agents (Ebeling, 1939), it could be expected that the addition of such materials would materially improve absorption at least on some types of leaves. In this connection the addition of detergents to foliar sprays (Guest and Chapman, 1949; Cook and Boynton, 1952) has been found to materially increase nutrient uptake, and, although no studies dealing with water absorption have been made so far as the author is aware, a similar result could be expected in such cases.

Although a considerable amount of data is now available on foliar applications of nutrient sprays (Boynton, 1954), the fact that nutrient uptake takes place even when the leaf appears to be dry is evidence that other mechanisms are operative besides those associated with water absorption. Even so, some of this work is of considerable value in understanding the path of entry of water into the leaf. Thus, Roberts, Southwick and Palmiter (1948) found that in apple leaves the cutin of the epidermis was in discontinuous lamellae parallel to the outer epidermal wall. Interspersed with the cutin lamellae, pectinaceous substances were found to occur in intermittent layers in the outer epidermal walls and appeared to form a continuous path from the layers in the cuticle through the anticlinal walls of the epidermal cells to the cell walls of the vein extensions and bundle sheaths surrounding the larger veins of the leaves. These authors considered that this could provide a pathway for water movement from the cuticle to the living cells surrounding the vascular tissues. A separate study by Palmiter, Roberts and Southwick (1946) demonstrated that solutes did move along this pathway; and Steubing (1949), using flourescent dyes, observed water movement through the walls in a similar manner. On more recent considerations it seems probable that most of the free space would be available for the rapid transfer of both water and solutes once they have crossed the epidermis (Epstein, 1956b; Kramer, 1957).

The relative importance of stomates as the points of initial water entry is still obscure, although it is clear that absorption of nutrients and insecticidal oils frequently occurs in this manner (Knight, Chamberlain and Samuels, 1929; Ginsburg, 1930; Kelley, 1930; Rohrbaugh, 1934; Cook and Boynton, 1952). Crafts (1933), however, regarded absorption through stomates as negligible; and Turell (1947), arguing on the basis of contact angle and capillarity, supported this contention, although he considered that addition of wetting agents could result in some absorption. Gessner (1956) thought that in most cases water penetration occurs directly through the cuticle, and the studies of Zamfirescu (1931) and Meidner (1954) raise the possible importance of specialised epidermal cells in water uptake. The latter author, in particular, noted that most of the water absorbed by *Chaetacme aristata* leaves occurs through specialised cells in the epidermis. He also noted that absorption by the upper leaf surface, where most of the cells are located, is much greater than on the under surface where stomatal frequency could be expected to be highest, and this observation may also provide some evidence as to the significance of stomatal absorption.

In general, and with the present state of knowledge, it appears that most of the water absorbed by leaves is through the cuticle. If this is so, a marked increase in cuticle permeability must occur on wetting in order to explain the paradox of high cuticle resistance to water transport during transpiration. The evidence for any conclusive remarks is inadequate and this question must still be regarded as open. Little work has as yet been conducted on water entry through organs other than the leaf.

Rate of absorption is markedly affected by the potential gradient from air to leaf (Krause, 1935; Slatyer, 1956a), and it is to be expected that initial rates of uptake would be greatest, the rate decreasing progressively as the leaves regain turgor and the gradient is reduced. Eisenzopf (1952), however, observed a peak rate of absorption after 90 minutes immersion in water, following which rate of uptake decreased fairly rapidly. It seems probable that the increased rate for the first 90 minutes was caused by a progressive increase in cuticle permeability as a result of increased cuticle hydration. The decreased absorption after this time was attributed by Eisenzopf (1952) to decreased permeability of the cuticle, although a more probable explanation is that the water potential gradient had been progressively reduced.

TRANSFER OF WATER THROUGH THE PLANT. As has been mentioned previously in this paper, movement of water through the plant may be validly interpreted by regarding the soil-plant-atmosphere system as a thermodynamic continuum. Such considerations apply equally well to the movement and redistribution of water which is absorbed through the leaves. However, experiments conducted on this subject have to date given conflicting results, and it appears that in many cases resistance to movement is such that the gradients established are inadequate to cause movement.

The most frequently cited experiments concerning negative transport through the whole atmosphere-plant-soil system are those of Breazeale, McGeorge and Breazeale (1950, 1951) and Breazeale and McGeorge (1953a, 1953b). In addition to these studies, Haines (1952, 1953), Stone, Shachori and Stanley (1956) and Slatyer (1956a) observed negative transport when roots were placed in empty flasks and a steep water potential gradient had been established. Although these experiments appear to provide a sound physical explanation for water absorption and transfer, several other experiments conducted along similar lines have not demonstrated transport. Thus with plants rooted in soil, even when the soil was as dry as the permanent wilting percentage and an adequate gradient should have been established, no accumulation of water in the soil has been observed by some investigators, even though the leaves of the plants under study regained turgor (Hohn, 1954; Janes, 1954; Stone, Shachori and Stanley, 1956). This is somewhat surprising in view of the fact that Hagan (1949) and Bormann (1957) demonstrated sufficient cross transfer of water through inter-twined root systems to maintain growth of plants with no other water source. Hagan observed rapid negative transport when plants in dry soil had been detopped and the stumps connected to potometers.

It seems probable that several factors are of influence in causing these conflicting results. In the first place absorption of water by leaves, although occurring in most species if a favourable gradient exists, generally appears to be very slow because of the resistance of the cuticle to water entry, and the quantities of water absorbed may be quite small. Transfer of this water to other branches and to the roots has also been observed (Dixon, 1924; Brierley, 1934, 1936). However, because of the small amounts of water absorbed by the leaves, and because the rate of transfer also appears to be fairly slow, the amount of water transferred is in some cases not sufficient to enable recovery of turgor by other parts of the plant. Because such small amounts of water are involved, it seems probable that in many instances the lack of accumulation of water in the root medium may be due to inadequate rate of water intake by the leaves.

This could be expected to be more noticeable when the roots are in soil than when they are in air, since the water potential gradient from root to soil will not normally be as great as that from root to air, particularly if in the latter case the temperature of the flask containing the roots is permitted to fluctuate appreciably. The fact that Hagan (1949) observed rapid negative transport into soil when rate of supply was non-limiting supports this contention; and the data of Hohn (1954), which showed that negative transport into the vapour surrounding the roots does not occur until the relative humidity falls to 85 per cent, is evidence of the gradient needed, in some cases, to cause water movement through the system. Stone, Shachori and Stanley (1956) also noted that the relative humidity in the flask containing roots falls to about 85 per cent on warm days. This is equivalent to a water potential of about —200.10^6 ergs.gm^{-1} at the temperature employed, and is considerably in excess of the probable root-soil gradients which develop with plants rooted in soil. It must again be recalled that in dealing with vapour transport it is the vapour pressure gradient, not the water potential gradient, which determines the rate of water movement. As in transpiration, however, use of water potential considerations does not appear to affect the validity of the conclusions which are drawn in this discussion.

In most instances the chief source of resistance to negative water movement appears to be in the leaves, and rate of movement across the cuticle may be the limiting process (Slatyer, 1956a). Although Hagan's (1949) data indirectly support this hypothesis, the fact that other studies have failed to demonstrate negative transport suggests that significant resistance to water movement may also occur at the root surface. Slatyer (1957a) suggested that the death of small roots and root hairs in dry soil, together with rapid suberization, could markedly reduce the root surface available for transfer and hence increase the resistance to movement across this zone. If, as a result of soil and root shrinkage, a vapour gap were to develop between root and soil, a further important resistance could arise. If such phenomena occur, the failure in some experiments to observe negative transport, while at the same time recovery of turgor by the plant tops is noted, could be largely explained. An alternative explanation for the lack of transport into dry soils might be that if some exudation occurred into the soil layer directly adjacent to the root surface, the soil water potential in this layer would be effectively raised to a value approximating that at field capacity, and the gradient from atmosphere to soil would be eliminated. Unless the soil became completely saturated, water movement from this zone into the soil mass would not be expected because of the very slow rates of unsaturated water movement.

As a result the water in this narrow zone would be at a water potential close to field capacity, but the bulk of the soil mass would remain dry.

Because most studies involving roots in air have demonstrated negative transport (as long as the temperature of the flask containing the roots has been permitted to fluctuate) and most studies with roots in soil have not given this result, it seems that the main reason for lack of transport into soil is lack of an adequate gradient. In addition, in some cases when plants were rooted in soil, not only has there been no accumulation of water in the soil, but, on the contrary, continued transpiration has occurred and resulted in further soil water depletion (Hohn, 1954; Janes, 1954). This throws some doubt on the efficacy of the experimental methods in establishing water vapour saturation around the aerial parts of a plant, or in preventing leaf temperature from rising significantly above air temperature. Such contol is not as important in the case of plants rooted in air because of the much lower water potentials around the roots.

With roots in air, transpiration is greatly restricted by the absence of a water source around the roots. It seems possible that in some experiments with plants rooted in soil, negative transport may occur to a limited extent at night, but transpiration during the day results in a net loss over 24 hours. Any negative transport which occurs with plants in air results in accumulation of water in the bottom of the flask, and only a very small proportion of this water is subsequently available for transpiration.

While most evidence points to transport being subject to controls which are predominantly physical in origin, some experiments are not directly explicable on this basis. Breazeale, McGeorge and Breazeale (1951) observed transport into culture solutions of low osmotic concentration and in soils wetter than field capacity. To explain these results, Breazeale and McGeorge (1953a) proposed that an exudation pressure is developed, presumably in the leaves or roots, during transport. Haines (1952, 1953), in a repetitive experiment, was unable to find any evidence of a non-physical system, and Wiersma and Veihmeyer (1954) found that the exudation pressure measured by Breazeale and McGeorge could be explained solely on the basis of gases produced by decomposition of the plant roots. In the absence of further experimentation, a satisfactory explanation of the original results of Breazeale, McGeorge and Breazeale (1951) and of those workers who have observed continued transport of water into soil at field capacity must be deferred.

SIGNIFICANCE OF ABSORPTION IN NATURE

It seems that absorption of water by the tops of plants can be of possible influence to the water economy of the plant, either directly by increasing the amount of water in the plant, or indirectly by reducing transpiration. Both these factors tend to reduce the absorption lag behind transpiration, increase turgor and promote plant growth. Under natural conditions such phenomena could possibly occur as a result of wetting of the leaves by rain, dew or sprinkler irrigation or by the presence of very humid air. Greatest interest is centered around the possible utilisation of dew because the presence of rain or irrigation implies water abundance and minimises the importance of absorption through the aerial organs; also because in arid regions the amount of dew can be quite an appreciable proportion of the total precipitation (Duvdevani, 1953).

There are two main reasons why dew, which never comprises more than a small proportion of the water requirements of a normal plant, could be an important water source. These are that it occurs at night when transpiration is negligible and when the effect of increased leaf turgor is likely to have the greatest effect on leaf expansion, and that it frequently remains on the leaves for several hours after sunrise, thus reducing transpiration while permitting photosynthesis.

Most experiments designed to evaluate the significance of dew have shown that the beneficial effects observed could be attributed solely to the presence of surface water on the leaves and that it is not necessary to consider the possibility of absorbed water. Thus Walter (1936, 1951) concluded that the primary effect of dew in the South West African deserts is in reducing transpiration, while the leaves remain wet in the mornings following dew nights. Duvdevani (1953) reported that plants exposed to dew develop greater length and number of branches and greater leaf area than those not exposed. Although Duvdevani considered that this is due in large measure to the effect of dew absorption by the plants, it is apparent that similar responses could be expected from increased humidity and the lower transpiration of the exposed plants. That dew on the leaves does reduce transpiration is to be expected on physical grounds and has been confirmed experimentally (Pisek and Cartellieri, 1939; Jones, 1957). Some investigators have, however, observed direct absorption of dew by plants (Gates, 1914; Michaelis and Michaelis, 1934; Rouschal, 1938, 1939; Arvidsson, 1951; Meidner, 1954; Waisel, 1958), and the previously reported experiments on water absorption confirm the occurrence of this phenomenon. The amount of water absorbed is frequently quite small, sometimes serving only to raise the leaf water content a few per cent (Wetzel, 1924; Krause, 1935), although on occasions it appears to be enough, in winter at any rate, to balance transpiration losses on the following day (Gates, 1914; Rouschal, 1938, 1939; Arvidsson, 1951).

If absorbed water is to make a contribution to the water economy of the plant, it would seem that it must be sufficient to cause greater growth or production than would otherwise be the case, or to enable plants to persist longer during protracted periods of dry weather. Direct evidence of the former factor is lacking, although Duvdevani's (1953, 1957) results of increased growth and production almost certainly reflect some direct effect of absorbed water. Evidence for the latter factor is much stronger (Stone and Fowells, 1955; Stone, Shachori and Stanley, 1956; Stone, 1957b). These authors have noticed that artificial dew at night can prolong the life of seedlings of *Pinus* spp. rooted in dry soil by a month and a half. As soil water levels did not change in these experiments, these results provide clear evidence of the direct effect of applied water in enabling resaturation of leaf tissues and maintenance of normal metabolic functions.

The effect of humid air on plant survival is less clear. Stone, Went and Young (1950) and Slatyer (1956a) have noticed absorption of unsaturated water vapour by some species when a favourable water potential gradient existed, and it is possible that such absorption could, to a limited extent, enable prolonged survival of plants under certain conditions. As Slatyer (1957a) has pointed out, however, there can be no real physiological benefit to the plant unless positive turgor pressure can be re-established in the active tissues. Thus the water potential of the water in the atmosphere has to be high enough to raise the plant water potential to a level above that at zero turgor pressure. If this occurs, it is conceivable that sufficient photosynthesis might proceed in early morning, before transpiration re-establishes severe water deficits, to enable the plant to balance its respiratory losses. In such instances, plants could possibly persist for some time without further re-charge of soil water.

In conclusion it may be stated that the primary significance of dew is probably through its effect in reducing transpiration and generally creating a more humid environment for plant growth. Although some absorption of dew appears to be of general occurrence, the amounts involved are usually small and it is difficult to separate the effect on the plant of this absorbed water and of the unabsorbed water on the leaf surfaces. In general, dew does appear to exert a favourable effect on plants, with the possible exception of its influence on the spread of some plant diseases, but it must be appreciated that, even in regions of heavy dewfall, the total amounts of dew received comprise only a very small proportion of the overall water requirements for active plant growth and development.

GENERAL SUMMARY

The main development in terminology in recent years has been a tendency to replace the established "pressure" terms and units with more basic terminology involving thermodynamic units. This has been motivated, in part, by the fact that the use of pressure terms and units can be misleading. For instance, high equivalent pressures or suctions can frequently be measured in soil or plant water systems, but these values represent potential energies and do not necessarily imply the existence of actual pressure differences. Furthermore, the simple and straightforward equation relating DPD to osmotic pressure and turgor pressure (DPD = OP–TP) refers ideally to the completely vacuolated plant cell. In tissues in which the non-vacuolar volume reaches significant proportions, additional factors may contribute to the free energy status of the water in the system.

An active controversy has been in progress as to the existence of a non-osmotic factor in active absorption. Following a group of early studies which provided strong evidence of a non-osmotic factor, it now appears that all this evidence can be reinterpreted in terms of standard osmotic theory. As a result, it is difficult at the present state of knowledge to identify a non-osmotic factor, even though it is apparent that active absorption is closely linked to, and immediately affected by, changes in metabolic activity, particularly in rate of respiration.

Of the two major processes involved in absorption, passive absorption is by far the more significant, almost all the water which passes through the plant being transported in this manner. In a discussion of water movement through plants, van den Honert (1948) and others have shown the value of interpreting these phenomena through a consideration of the whole path of water movement through the soil-plant-atmosphere system. Van den Honert treated water movement through the system as a catenary process, the rate of which was controlled at the source of the greatest resistance. In addition, he applied an analog of Ohm's law to movement, so that the resistance was directly proportional to the reduction in free energy across any point in the system. This interpretation emphasizes the fact that the resistance in the gaseous phase, from sub-stomatal cavities to outside air, is far in excess of any other resistance that is likely to develop in a living plant. This provides the logical result that the stomates occur in the system at the only points where they could be of influence.

An important conclusion drawn from this analysis is that, because of the large resistance in the gaseous phase, resistance anywhere else in the plant can have little direct effect on transport. The mode of action of factors such as those which affect soil water availability or root permeability appears to be through reducing the water potential in the rest of the plant, with consequent reduced leaf water content, stomatal closure and retarded transpiration.

Of the factors affecting absorption, low soil water potential appears to be the most potent. It has a direct effect on the water potential in the plant, since the plant water potential must remain lower than the soil water potential in order to maintain an absorption gradient. It also has an indirect effect on root resistance through the effect of decreased hydration on permeability and suberization. Finally it has a direct effect on resistance to water movement through the soil-root surface zone, which influences the water potential gradient needed to maintain transport across this segment of the water transport path. It is probable that resistance to water movement through the soil can become of sufficient magnitude to parallel the resistance across the gaseous phase in the leaf and so directly influence transport. However, this could rarely occur in living plants, since a plant would die of dehydration before the resistance reached a high enough level.

Absorption of water by aerial organs and its subsequent transfer through the plant is also discussed in terms of the whole soil-plant-atmosphere system. Present knowledge indicates that the leaves of most plants can be expected to absorb limited quantities of water, either from liquid water or from saturated vapour, as long as a significant water potential gradient exists from atmosphere to leaf favoring such movement. Most of the water appears to be absorbed through the cuticle, and the rate of absorption varies considerably with the wettability and surface characteristics of the epidermis. Subsequent transfer of water within the plant appears to depend primarily on the water potential gradients established, and if the gradient extends into the root medium, negative transport of water into the medium is sometimes observed. When the plant is rooted in soil, the general observation is that no net negative transport is found. Several explanations are offered for this phenomenon.

Application of studies dealing with absorption of water by leaves, and with negative transport, to the significance of dew and its possible importance to the water economy of the plant must be undertaken with caution. Although some absorption of dew appears probable under field conditions, the primary effects seem to be to minimise transpiration while the leaves are wet and generally to create a more humid environment for plant growth. This enables more rapid turgor recovery at night and permits photosynthesis in the early morning hours.

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