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Introduction: Water Movement Through Plants

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Introduction: water movement through plants

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Loss of water by leaves (transpiration) is inevitable if carbon dioxide is to be taken up for photosynthesis. The resulting flow of water through the plant gives rise to a water stress in the tissues which is explicable with reference to a simple model. The importance of this stress to the growth and physiology of the plant is indicated. Consideration of the soil–plant–atmosphere continuum as a series of resistances reveals that the major resistance lies in the gaseous phase where the stomata are strategically placed to control the rate of flow through the system. The stomata therefore play a key role in controlling stress in the plant as do the resistances within the plant. These 'plant resistances', e.g. that of the root and leaf, are not simple in that the resistance to flow through them can be a function of the flow itself. The physiological reason for this is still obscure. The water stress in the soil round the roots is clearly of major importance as the source from which water is drawn; thus flow of water to the root surface and perhaps the soil–root interface may play an important role.

In the notes for the guidance of contributions to Discussion Meetings of the Royal Society it is suggested that speakers should assume that the audience consists in part of scientists who have no special knowledge of the subject matter. It is to these that I address the following remarks hoping to provide for them a backcloth against which the more specialized contributions that follow can be seen.

May I start by describing a simple and as it turned out, rather a foolish experiment which illustrates the problem which was faced by the primitive land plants in becoming adapted to life on the land. A cylinder of potato tissue was sealed in to a potometer as shown in figure 1. The expectation was that evaporation would take place from the exposed surface of the tissue and water would be drawn in at the submerged end and the meniscus in the potometer would move to the left. In fact nothing of the sort happened. After 24 h the exposed part of the cylinder had lost water and had shrunk to an irregular mass of tissue shown by the dotted outline in figure 1 and the meniscus had not moved. The unexposed part of the cylinder remained turgid, but was unable to supply water to the flaccid exposed part.

The explanation is not far to seek. The rate of evaporation from a free water surface under well ventilated conditions can be as much as 10^{-5} cm^3 cm^{-2} s^{-1}. The permeability coefficients of plant cell membranes vary widely from species to species. For the alga *Chara* a value of 10^{-4} cm^3 cm^{-2} s^{-1} MPa^{-1} has been found, while for parenchyma cells it may be an order of magnitude less. If it is assumed that water moving towards the evaporating surface has to traverse two membranes in moving from one cell to the next, the difference in water potential $\Delta\Psi$ between adjacent cells to induce a flux equal to the rate of evaporation would be:

$$\Delta\Psi = \frac{10^{-5}}{10^{-5}} \times 2 = 0.2 \text{ MPa (2 bar) using the \textit{Chara} value}$$

or

$$\Delta\Psi = \frac{10^{-5}}{10^{-6}} \times 2 = 2 \text{ MPa (20 bar) using the parenchyma value.}$$

† 1 MPa = 10 bar.

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Since there are about 6 cells/mm in potato tissue a water potential gradient of between 1.2 and 12 MPa/mm (12 and 120 bar) would be necessary to supply the evaporating surface and the larger figure, referring to parenchyma, is likely to be more appropriate. In other words the permeability of the cell membranes is far too low to allow the evaporating layer of cells to be supplied with water from layers deeper than a fraction of a millimetre. Thus there is a drying out and collapse of the exposed cells which extends progressively to deeper layers, while the turgid cells in contact with the water supply a centimetre or more distant, remain unaffected.

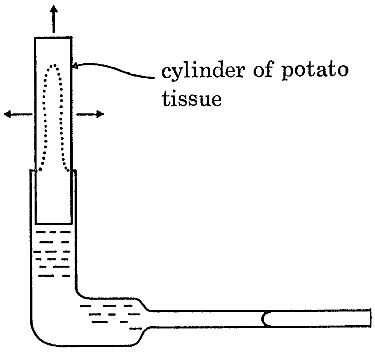

FIGURE 1. An attempt to demonstrate flow of water through a cylinder of potato tissue in response to evaporation. (→). After many hours the exposed potato tissue had shrunk (dotted outline) and the meniscus in the potometer had not moved.

The relevance of this to the colonization of the land by plants is that any plant body made up solely of living cells would need either to be flat with all cells close to the water supplying surface, i.e. little vertical extension, or need to be covered with a layer impervious to water or water vapour. The first solution restricts the size of the plant, the second would permit a considerable size to be achieved but a highly impervious covering would largely prevent the ingress of carbon dioxide as well as the egress of water vapour and so would preclude the possibility of photosynthesis. Plants might have solved this problem by evolving a differentially permeable cuticle – permeable to carbon dioxide but impermeable to water vapour. Instead, the aerial parts of plants are covered by a more or less water-impervious epidermis pierced by minute holes – the stomata. This is a compromise solution for if access is given to the inward diffusion of carbon dioxide, water loss must inevitably occur. The stomata are variable in aperture and, as they close, loss of water through them (transpiration) is reduced to a greater degree than ingress of carbon dioxide and this works to the plants' advantage. If, however, under conditions of water stress, loss of water is prevented by complete closure of the stomata, the plant is cut off from its essential supplies of carbon dioxide. Thus the plant is faced with a dilemma, the best answer to which would presumably be to find that stomatal aperture which allows the maximum uptake of carbon dioxide consistent with the least water stress.

This solution of having an impermeable epidermis pierced by stomata, would not in itself permit land plants to attain any great size, for even with the rate of transpiration so restricted, the low permeability of the cells to water would not allow any great spatial separation between the transpiring/photosynthesizing organs and the water absorbing surfaces in the soil. It was the development of the tracheid, an inert, rigid, empty conduit allowing relatively unimpeded mass flow which was, as Bruno Huber has said, the greatest single evolutionary step in the colonization of the land. The possession of such a low resistance pathway allowed the extensive development of the roots and shoots separated in the larger trees by a distance of many metres. Even here the transpiration stream has to traverse only a few cell layers as shown in figure 2. Between the vein ending and the transpiring mesophyll or epidermal cell there are only two or three cells while between the soil and the trachea in the root there are usually only a dozen or so. This is the basic structure of all the Tracheophyta and the only difference between a small herb and a giant tree is the length of the tracheal conduits connecting root and shoot.

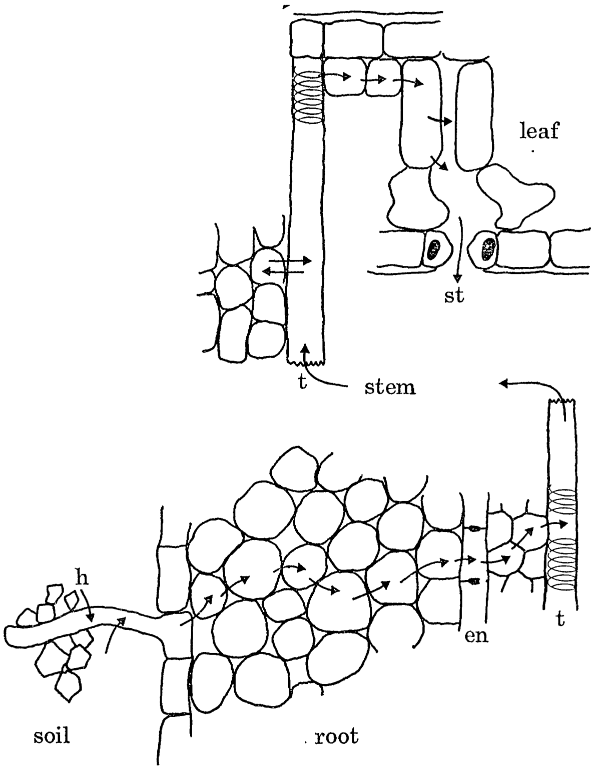

Figure 2. The pathway of the transpiration stream through the root, stem and leaf, en, endodermis, h, root hair, st, stoma, t, trachea.

Even with this restriction in the number of cells through which the transpiration stream must pass between soil and atmosphere, it seems that the drop in water potential within the leaf and across the root cortex is less than expected judging from established values of the permeability of cell membranes. Thus the whole root (i.e. cortex + stele) has a permeability coefficient equivalent to a *single* layer of cells. It would seem, therefore, that water has an alternative pathway to movement from vacuole to vacuole. This could be movement in the cell walls or in the cytoplasmic system which is continuous from cell to cell via the plasmodesmata – the so-called symplast. Inevitably water must pass along all three of these parallel pathways, the flow in each being a function of its hydraulic conductivity. It seems clear that the vacuolar pathway has a low conductivity, but the relative conductivities of cell walls and symplast are not yet known. If most of the water moves in the cell walls, it is interesting to note that between soil and atmosphere the water passes *through* one layer of cells only, namely the root endodermis in which the cell wall pathway is blocked by the impervious Casparian strips (figure 2) and here water must pass through the protoplast.

Some years ago van den Honert (1948) formulated an analysis of the relative resistances of the transpiring plant and its aerial environment which, though extremely simple, has had a profound influence on our thinking. The analysis was based on concepts discussed much earlier by Gradmann and Huber (Richter 1973). The transpiration stream through the plant and into the atmosphere is treated as a flow encountering a number of resistances in series. At a steady state, the flux of water through the plant (from soil: root interface to the evaporating surface of the leaf cells) and through the gas phase (from the leaf cell, through the stomata and through the boundary layer of air surrounding the leaf) will be equal and it is postulated that this flux of water through the plant and through the gas phase each obeys an Ohm-type law. Thus

$$F = \frac{\Psi_s - \Psi_l}{r_p} = \frac{\Psi_l - \Psi_a}{r_g} \tag{1}$$

where F is the transpirational flux of water through the system, Ψ_s, the water potential at the soil–root interface, Ψ_l, the leaf water potential, Ψ_a, the water potential in the air at large, r_p and r_g are terms representing the resistances to liquid flow in the plant and in the gas phase respectively.

Reasonable values can readily be assigned to the water potentials. If the soil is water saturated, $\Psi_s = 0$. The water potential of the leaf cells seldom falls below -2 MPa (-20 bar), while if the relative humidity of the air is 50% its water potential is around -100 MPa (-1000 bar). Thus from equation (1)

$$\frac{2}{r_p} = \frac{98}{r_g} \quad \text{therefore} \quad \frac{r_g}{r_p} = \frac{98}{2} = 49.$$

Thus the resistance of the gas phase is very much greater than that of the plant. The importance of this can be appreciated if the rate of transpiration (F) is expressed as the total drop of potential divided by the sum of the plant and air resistances:

$$F = \frac{\Psi_s - \Psi_a}{r_p + r_g} = \frac{100}{1+49}. \tag{2}$$

From this equation it is evident that the resistance of the gas phase being so much larger than that of the plant, will have a controlling influence on the rate of transpiration (doubling r_g will almost halve F) while a change in the plant resistance will have little direct effect (doubling r_p will reduce F by 2% only). Similarly when the water potential of the atmosphere is low, the water potential of the soil can have little *direct* effect on the rate of transpiration, for plants mostly wilt at Ψ_l values around -2 MPa (-20 bar) so that Ψ_s cannot be much lower than this if the plant is to survive. Now lowering Ψ_s by 2 MPa will reduce the numerator in (2) from 100 to 98 MPa only and will result in a mere 2% reduction in F.

The stomata are then strategically placed, being in the gas phase, to be effective in controlling transpiration. Furthermore, since the aperture of the stomata may be controlled by the leaf water potential (Ψ_l) any 'upstream' resistance such as that of the root system which leads to a fall in Ψ_l will cause stomata to close and therefore the rate of transpiration to fall as a secondary effect. Similarly the water potential of the soil may control the rate of transpiration as a secondary effect. In addition, the stomatal aperture and hence rate of transpiration may be linked to events in other parts of the plant, e.g. by hormones, the levels of which may change in response to water stress or other factors.

It is implicit in what is said above that high 'upstream' resistances in the plant, e.g. in the roots, or low potentials in the soil are harmful to the plant in that they lead to low water potentials (water stress) in the tissues of the plant. This sets up a train of complex and interrelated events which in a sense are the physiological equivalents of the physical concept of *strain*, i.e. deformation suffered in a physical system subjected to a stress (applied force). Examples of such *strains* are: loss of turgor which leads to slowing or cessation of cell expansion and hence growth; stomatal closure which leads to carbon dioxide starvation; reduction in cell volume which occurs especially with cells having very extensible cell walls and which will lead to an increase in osmotic pressure of the vacuoles and cytoplasm with its attendant dehydration of colloidal gels and organelles (Weatherley 1970).

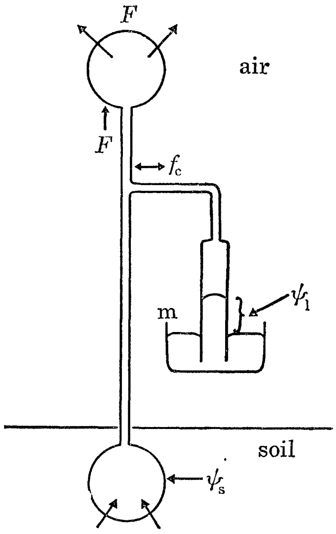

FIGURE 3. Model of transpiring plant. The upper and lower porous pots represent the leaves and roots respectively. The manometer (m) represents the cells of the leaf.

Some of the causes of water stress in transpiring plants have been indicated above. They are readily understood with reference to a simple physical model which is essentially that used by H. H. Dixon in his Royal Society Croonian Lecture in 1938. Two porous pots filled with water are joined by a tube (figure 3). The upper one represents the leaf, the lower one which is semipermeable is buried in the soil and represents the roots. The manometer represents the cell vacuoles (off the main pathway if movement is through the cell walls) and the cells of the tissues adjacent to the pathway, e.g. parenchyma of the xylem in the stem. At a steady rate of transpiration the manometer will register the reduction in pressure arising in the pathway. If, however, the rate of transpiration changes from one steady value to another there will be a period of adjustment of the manometer during which water will be added to or abstracted from the transpiration stream. During this period.

$$F = f_a \pm f_c, \tag{3}$$

where F is the rate of transpiration, f_a, the rate of absorption through the roots and f_c, the adjustment of the water content of the tissues. This last is greatest immediately after the change in F and declines to zero when the adjustment ceases. The volume of water displaced by the rise in level of the mercury represents the water deficit of the plant. It is often said that a water deficit develops in a plant when transpiration exceeds absorption. Numerically this is of course true. But it seems to imply that a water deficit arises *because* transpiration exceeds absorption, and this

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is surely a misconception. If the rate of transpiration F increases, the tension in the plant increases because of the resistance in the lower pot and there is a flow f_c into the main stream as the mercury rises in response to the increased tension. It is *because* of this contribution (f_c) that absorption (f_a) is less than transpiration (F) and the more extensible the cell walls, the greater the volume change of the cells and the greater will be the transient discrepancy between transpiration and absorption. If the cells were completely rigid (i.e. no manometric adjustment) transpiration and absorption would remain equal throughout the transition.

What are the contributory factors which define the magnitude of the water potential in a leaf as represented by the manometer in the model? Even in the absence of transpiration and with a water saturated soil the manometer will register a lowering of pressure in relation to its height above the free water surface. Since the height of the water barometer is approximately 10 m, there will be a reduction of pressure of 10 kPa/m (0.1 bar/m) which will be manifest as a decrease of Ψ_l of this magnitude with height.

A second factor which will cause a lowering of the water potential in the plant in the absence of transpiration is the water potential of the soil (Ψ_s) surrounding the roots. In this situation the plant is acting like a tensiometer and this static value of Ψ_s would contribute equally during transpiration. However, water flowing through the system must move towards the root surface and if the rate of this movement were sufficiently great in relation to the hydraulic conductivity of the soil, gradients of water potential might arise. Then Ψ_s at the root surface would fall below the static value and this lowering would be a function of the rate of transpiration.

The last factor is the drop of water potential consequent on the flow of water encountering the resistances in the pathway within the plant. As mentioned in discussing van den Honert's analysis it is reasonable to assume this obeys an Ohm-type law so that $\Delta\Psi = Fr_p$.

The water potential of the leaves (Ψ_l) is the sum of these three terms:

$$\Psi_l = \Psi_s - Fr_p - 0.1h. \tag{4}$$

Each can be studied separately. If a small plant is used $0.1\,h$ is negligible and if the plant is rooted in moist soil $\Psi_s = 0$. Under these circumstances $\Psi_l = -Fr_p$ and the validity of this expression can be tested by measuring steady state values of Ψ_l at various steady rates of transpiration. If Ψ_l is plotted against F a straight line should be obtained, the slope of which is a measure of r_p. Experiments of this kind have yielded widely different results for different species and for the same species at the hands of different experimenters (Macklon & Weatherley 1965, Tinklin & Weatherley 1966, Stoker & Weatherley 1971, Barrs 1973, Neumann, Thurtell & Stevenson 1974, Black 1974). My colleagues and I have always found with *Ricinus*, *Gossypium* and *Helianthus* that Ψ_l is constant over a wide range of transpiration rates. Such constancy means that the hydraulic conductance of the transpiration pathway in these plants is, over this range, a linear function of the rate of flow through the plant as illustrated in figure 4. In contrast Neumann (1974) and his colleagues have found linear relations between Ψ_l and transpiration rate indicating a *constant* hydraulic conductance. The contrast between our findings and those of Neumann both for sunflower, is shown in figure 5. The reason for this discrepancy is difficult to see. Barrs (1973) found with tomato, cotton and pepper that the resistance to flow declined with increasing rates of transpiration though not sufficient to give a constant value of Ψ_l with changing rate of transpiration. With maize, however, plants grown in water culture showed a linear rise of hydraulic conductance with increasing transpiration, whereas similar plants a few days after being transferred from culture solution to pure water showed a constant hydraulic conductance with changing transpiration. The explanation of this change in the physiological mechanism of the decline in resistance is not yet understood. However, such a drop in resistance with increasing rate of transpiration may be of ecological significance for, over a wide range of transpiration rates, the water stress in the plant remains constant, and no extra 'strain' reactions will develop.

Of the resistances to flow in the whole plant, that of the roots has been considered to be the

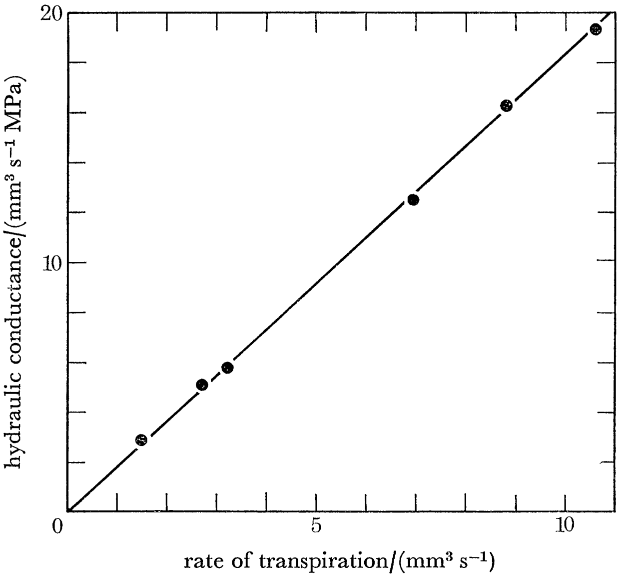

FIGURE 4. Relation between the hydraulic conductance of the whole plant and the rate of transpiration.

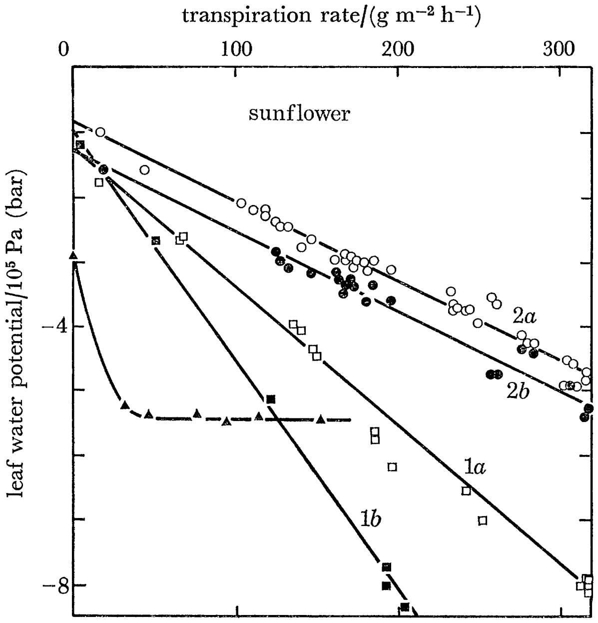

FIGURE 5. Relation between leaf water potential and rate of transpiration for sunflower plants. Data of Neumann *et al.* (1974): ○, ●, □, ■; data of Black (1974), ▲, Figure from Neumann *et al.* (1974) with Black's data added. (Reproduced with permission of the publishers.)

major one and therefore recognized as the site of the variable resistance. This was supported by the demonstration (Stoker & Weatherley 1971) that when the root system was killed by a short immersion in hot water, the resistance of the whole plant declined and was constant (i.e. there was a linear relation between F and Ψ_1). Further, the frequently demonstrated fact that lowering the temperature of the root system leads to increasing water stress in the leaves points to the root system having a high resistance (Abel El Rahman, Kuiper & Bierhuizen 1959; Boyer 1968; Kramer 1969; Hsiao, Avevado & Henderson 1970; Anderson & McNaughton 1973).

However, recent work indicates that the resistance of the leaf lamina is not negligible. This is indicated by there being a difference of several bars water potential between stem and lamina (Rawlins 1963; Begg & Turner 1970) and within individual leaves (Bliss, Kramer & Wolf 1957; Campbell, Zollinger & Taylor 1966; Gavande & Taylor 1967; Hoffman & Splinter 1968). Moreover, it appears that the resistance of the lamina declines with increasing transpiration rate (James 1970; Pospisilova 1972) and indeed detached leaves of sunflower freely supplied with water, maintain a constant water potential over a wide range of transpiration rates just as with whole plants (Black 1974). The mechanism of this adjustment of resistance is no more understood with leaves than it is with root systems.

Since then the resistances of the roots and leaves can be functions of the transpiration rate, it is clearly pointless to give a figure for either in absolute terms. Nor are the *ratios* of the component resistances within the plant necessarily constant, indeed they cannot be so if the xylem resistance remains constant while the resistances of root and lamina decline with increasing flux. It is rather surprising therefore that a close linear relation between hydraulic conductance of the whole plant and the rate of transpiration is demonstrable (figure 4). This suggests that in these plants the xylem resistance was negligible. In contrast the data of Neumann (figure 5) suggest that the resistance of the whole plant was constant and any variable resistances must have been negligible.

So far our analysis has been confined to plants grown in water culture or to conditions where the soil is saturated with water. In those cases where $\Delta\Psi_1$ is a constant over a wide range of transpiration rates it is relatively easy to detect any departures from this pattern when plants are growing in unsaturated sand or soil. In studies referred to above by Macklon, Tinklin, Stoker & Black, it has been shown that while with low rates of transpiration the value of Ψ_1 is identical with those of water culture plants (say -0.7 MPa) with higher rates of transpiration Ψ_1 falls considerably (to say -1.2 MPa). On reducing the rate of transpiration to a low value again, Ψ_1 rises to its former value. This cycle can be repeated several times with similar results.

These results are interpreted as a fall in Ψ_s at the root surface. In the example cited above Ψ_s would be -0.5 MPa (-5 bar). This cannot be the result of a general drying out of the soil, since there is complete 'recovery' on reducing the transpiration. Also it seems that the fall in soil potential occurs near to the surfaces of the individual roots since such cycles can be obtained in pots in which the dense root system ramifies throughout the soil mass (Faiz 1974). One possible explanation of these results is that the hydraulic conductance of the soil is sufficiently low to allow steep gradients of soil water potential to arise round the individual roots (perirhizal gradients). Similar patterns of results were obtained with sand, loam and clay soils. This interpretation has been critized by Newman (1969) who points out that the usually accepted values of the hydraulic conductance of soils are too high to give rise to such perirhizal gradients. If this is true, and we have some evidence that it is (Faiz 1974), then the large drop of water potential outside the root must have a different origin. It is suggested therefore that it is the soil–root interface which constitutes the high resistance barrier. The soil particles and the roots are different in shape so that the pattern of the points of contact at the interface are probably very different from that within the soil itself. This difference might be such that at high water fluxes a sharp gradient arises across the interface while only a slight gradient arises within the soil.

Finally there is the possibility, first suggested by Philip (1957), that with increasing water stress there might be a contraction in volume by the soil and the root with the formation of a gap between the two. Such a gap would be air filled and water could move across it only in the vapour phase. With the range of water potentials likely, movement of water across such a gap would be very slow and would constitute a very high resistance barrier. That such shrinkage does in fact take place has been demonstrated by a number of workers (MacDougal 1936 with Pinus; Huck, Klepper & Taylor 1970 with cotton; Cruiziat 1974 with sunflower; Faiz 1973 with sunflower). It appears that the roots may contract by as much as 40% in diameter. It is unlikely that such a contraction would leave the root concentrically placed in a cylindrical cavity, rather would it be irregularly in contact with the soil over a much reduced area. Alternatively and perhaps more likely, the soil particles in contact with root and root hair surface would be adherent by virtue of mucilagenous substances which are known to invest the root surface. On contraction of the roots the adherent soil particles would be pulled away from their neighbours causing a loosening of the perirhizal soil which would result in its hydraulic conductance being drastically reduced. That such contraction seems to be of significance in the water relation of the plant has been suggested by Faiz (1973); sunflower plants were grown in sand contained in a polythene bag and subjected to conditions favouring rapid translocation so that the water content of the leaves monitored by a β gauge steadily declined. If the bag was squeezed, a marked though transitory increase in leaf water content followed. Faiz also found that placing a transpiring plant on a mechanical shaker led to reduction of water stress in the leaves. These results were interpreted as resulting from a closing up of perirhizal gaps. Of course these gaps must result from a stress developed initially in another way. This may be the resistance of the intact soil–root interface which causes a stress to develop in the plant and this, with its attendant fall in water content would lead to a contraction of the roots. There is therefore a positive feed-back leading to a rapidly rising stress in the plant which could be mediated by stomatal closure.

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