The Transport of Water from Soil to Shoot in Wheat Seedlings

J. B. PASSIOURA

CSIRO, Division of Plant Industry, P.O. Box 1600, Canberra City, A.C.T. 2601, Australia

Received 13 July 1979

ABSTRACT

A technique is described for precisely measuring the drop in water potential, $\Delta \psi$, between the soil and the leaf xylem of wheat seedlings. The technique was used to explore the relation between transpiration rate and $\Delta \psi$ at various times during the monotonic drying of the soil in which the plants were growing. When the soil was wet, the relation was linear, but, as the soil dried, non-linearities appeared which were, in the main, explicable in terms of simple soil physical models describing the flow of water through the soil to the roots. There was no sign of the major hydraulic resistance at the root: soil interface that other people have recently found.

INTRODUCTION

When a soil is wet it has little direct influence on the uptake of water from it by a plant. When it is dry it has a large influence. When it is neither wet nor dry the extent of its influence is a matter of controversy. Some have argued that the conductivity of soil to water is often so small that the transport of water to the plant's roots may limit uptake even when much available water remains in the soil (e.g. Gardner, 1960; Carbon, 1973). Others have argued that the properties of the plant and of its aerial environment dominate the uptake unless the soil is so dry that there is virtually no available water left in it (e.g. Newman, 1969; Lawlor, 1972). Others again have argued that it is neither the soil nor the plant, but the interface between the two that dominates (Herkelrath, Miller, and Gardner, 1977; Faiz and Weatherley, 1978). Tinker (1976) has comprehensively reviewed many of the issues involved.

The controversy may have arisen for many different reasons.

(1) There is much confusion about the measurement of leaf water potential, $\psi_L$ (Neumann, Thurtell, and Stevenson, 1974; Bunce, 1978). Since $\psi_L$ is often used in calculating the gradients of soil water suction near the roots, these calculated gradients may be grossly wrong.

(2) Few experimenters have taken the trouble to measure carefully the hydraulic properties of their soils. Hydraulic conductivity decreases by several orders of
magnitude as a soil dries, and does so particularly rapidly in the light soils that many have used. The popular technique of measuring saturated conductivity and using it to calculate unsaturated conductivity (e.g. Hansen, 1974) may be too crude for our purposes.

(3) Salts build up at the interface between root and soil when their rate of uptake by the root is less than their convective inflow from the soil (Tinker, 1976). Such a build-up may vary widely between experiments, and, if large, could lead to large decreases in soil water potential close to a root even when none is expected from calculations based on the flow rate of water and the hydraulic properties of the soil.

(4) Roots may shrink when water-stressed (Huck, Klepper, and Taylor, 1970), thereby losing much of their hydraulic contact with the soil. A large difference in water potential presumably develops between root and soil (Cowan and Milthorpe, 1968). The shrinkage will depend on many factors, and may depend especially on

---

**Fig. 1.** Schematic view of a plant with its roots in the pressure chamber and its shoot in the cuvette.
the extent to which the roots are drought-hardened; roots that have experienced a rapid development of drought, such as is common in laboratory experiments, may be much more prone to shrink than those that have had time to adjust.

(5) The proportion of the total root length that is taking up water is generally unknown and may vary widely. Those who assume that most of the roots are active (e.g. Newman, 1969) predict minor gradients of \( \psi_s \) near the root; those who assume that few roots are active predict major ones (e.g. Caldwell, 1976).

This paper reports experiments in which explicit attempts have been made to cope with these problems. The most important novel feature of the experiments is the use of a technique that enables the drop in water potential across the plant and soil to be very precisely defined. Plants are grown in small pots in such a way that a pressure seal can be made at the junction of root and shoot, and a whole pot put inside a pressure chamber (Fig. 1). If the soil atmosphere is pressurized so that a cut in a leaf vein is on the verge of exuding sap, the pressure of that sap is then precisely zero, and the difference in pressure between the sap and a hypothetical drop of free water inside the chamber is equal to the applied gas pressure. This technique is so sensitive that a decrease in gas pressure of as little as 10 kPa can arrest the growth of an exuded drop of sap and cause it to shrink. In addition to its great precision, the technique has several other important features. First, it is non-destructive. Second, it measures, in effect, the water potential of the xylem of the leaf, so that problems associated with a possible major variable hydraulic conductance in the mesophyll (Boyer, 1974) are avoided. Third, the water status of the shoot remains constant throughout an experimental run, even though the transpiration rate may vary greatly; complications due to the possible influence of the shoot on the conductance of the roots (Bunce, 1978) are therefore avoided.

The other problems discussed above were dealt with by (2) measuring the hydraulic properties of the soil throughout the full range of water content relevant to the experiment; (3) leaching the soil so that the osmolality of the soil solution was very small; (4) allowing the soil to dry slowly, over weeks rather than days, so that the roots would have time to adapt; and (5) making detailed observations on the appearance of the roots. The last is by no means satisfactory, but is perhaps the best that can be done until techniques are devised for measuring the water uptake by different parts of a root system growing in soil having a high matric suction.

**MATERIALS AND METHODS**

**Preparation of soil and plant**

Pots made of stainless steel tubes (50 mm diam. \( \times \) 150 mm long) having finely woven nylon cloth taped tightly across one end to form a bottom were packed with fertile loam to a bulk density of 1.27 g cm\(^{-3}\). The top of each pot was firmly attached with adhesive tape to a pressure-chamber cap. Each pot was then leached with 200 ml 10 mM NH\(_4\)H\(_2\)PO\(_4\) to ensure adequate supplies of N and P (the soil's only deficiencies) and to ensure that the soil solution would be very dilute. The pots were then drained on a tension table at 5 kPa suction. The final portion of leachate was collected for measurement of its osmolality by a vapour pressure osmometer.

Wheat seeds (Triticum aestivum L. cv. Gabo) were germinated on moist filter paper. When the primary seminal axes were about 10 mm long, they were fed into the holes in the caps of the pots and into matching holes of about 5 mm depth made with a pin in the soil below. The seedlings were kept in a humid atmosphere for 2 d to enable the roots to become established. The pots were then
Passioura—Transport of Water in Wheat

put in a glasshouse in approximately 14 h days with day/night temperatures of 21/10 °C. After a few more days, when the exposed parts of the roots had hardened, non-toxic silicone rubber (Sylgard 184) was poured into the wells in the caps to a depth of about 5 mm. After this had set, the retaining plugs were screwed into place, and the preparation of the plants was complete.

Measurements on the plants

Measurements were made on each plant from the time the third leaf emerged until the soil had almost run out of available water. The aim of the measurements was to define the relation between transpiration rate and the pressure required in the chamber to keep the leaf xylem at zero water pressure at various stages during the drying of the soil. Runs were made on each plant at about 2 d intervals. During a run the shoot was enclosed in a water-jacketed cuvette and was illuminated, horizontally, by a 1500 W quartz halogen lamp. The irradiance within the cuvette was varied, by shading, within the range 0.35–2.0 mE m⁻² s⁻¹ (400–700 nm wavelength). The humidity of the ingoing air was varied, within the range 6–16 mg l⁻¹, by injecting steam into the air supply after it had been brought to a dewpoint of 2 °C. The temperatures of both the cuvette and the pressure chamber were maintained at 19 °C. The cuvette contained a small fan that stirred the air sufficiently to produce slight waving of the leaves. The flow of air was varied within the range 0.7–10 l min⁻¹, depending on the transpiration rate, and was measured with Hastings mass flow meters. The humidities of the air entering and leaving the cuvette were measured, alternately, with a Cambridge 880 model dewpoint hygrometer. The transpiration rate was calculated as the product of the flow rate of the air and its change in humidity as it passed through the cuvette.

The procedure during a run was as follows: The pot was weighed (so that the water content could be determined), and the leaf area was measured, approximately, by ruler (Σ 0.75 × length × breadth of each leaf). The pot was put in the chamber and the pressure increased to 1.5 MPa with compressed air to ensure that there were no leaks. The pressure was then released. About 2 mm of the tip was cut off the youngest leaf that was long enough to be inserted in the capillary tube as shown in Fig. 1. The cuvette was placed over the plant, and the air supply and light were turned on. The initial conditions were always low light (0.35 mE m⁻² s⁻¹) and high humidity (16 g m⁻³). After about 1 h, when the transpiration rate had become steady, the pressure in the chamber was increased, using compressed air, until sap exuded from the cut leaf and formed a meniscus in the

![Fig. 2. Water-retention curve (△) and diffusivity of water as a function of water content (○), for the experimental soil at a bulk density of 1.27 g cm⁻³ and a temperature of 25 °C.](https://academic.oup.com/jxb/article-abstract/31/1/333/473180/313397)
capillary tube. The pressure was then adjusted until the meniscus became stationary. When the meniscus had been stationary for at least 10 min, the pressure and transpiration rate were noted, and the humidity of the ingoing air was decreased to 13 g m\(^{-3}\) while the pressure was increased to maintain the meniscus stationary. Again, once the meniscus had been stationary for at least 10 min, the pressure and transpiration rate were noted, and the evaporative demand increased, this time by increasing the irradiance to 0.85 mE m\(^{-2}\) s\(^{-1}\) and doubling the flow rate. Two further points were obtained, by decreasing the ingoing humidity to 6 g m\(^{-3}\), then increasing the irradiance to 2.0 mE m\(^{-2}\) s\(^{-1}\) and again doubling the flow rate. To these five points, four more were added by retracing the steps of increasing evaporative demand, thus enabling any hysteresis in the system to be observed. At the end of a run, which usually took about 5 h, the leaf area was measured again, and the pot was weighed and returned to the glasshouse. This procedure was changed slightly towards the end of the experiment, by decreasing the size of the increments in evaporative demand so as to avoid excessively large increments in pressure. After several runs, when there was almost no available water left in the soil, the pot was watered and a final run made. The shoot was then harvested and weighed (both fresh and dry) and the roots washed out of the soil and weighed (fresh). The roots were photographed, and the diameters of their xylem vessels measured at selected places. Their length was determined by line-intersection (Newman, 1966).

**Measurements on the soil**

The water-retention curve for the soil (Fig. 2) was measured using a pressure plate. The diffusivity of water (Fig. 2) was measured using the same technique as Rose (1968) except that the columns were drained at 40 kPa suction. The water content of the soil in a pot was calculated using the weight of the pot minus the fresh weight of the plant, which was estimated from the fresh weight at harvest assuming that the fresh weight at any given time was proportional to the leaf area at that time.

**RESULTS AND DISCUSSION**

Figure 3 shows the most comprehensive set of data for any of the plants studied. Other plants behaved similarly. There are several features of interest in the figure discussed under separate headings below.

![Figure 3. Transpiration rate, \(E\), as a function of balancing pressure, \(P\), for one plant at various times during the drying of the soil.](https://academic.oup.com/jxb/article-abstract/31/1/333/473180)
Hydraulic conductance of the plant

When the soil was wet (volumetric water content, $\theta_v > 0.2$) and presumably not influencing gradients of water potential in the system, the evaporation rate, $E$, was closely proportional to the balancing pressure in the chamber, $P$ (A, B, and G in Fig. 3). There was no sign of the variable hydraulic conductance that has frequently been observed in other plants (Hailey, Hiller, Jordan, and van Bavel, 1973) and no sign of any interactions between the flows of solutes and water as discussed by Dalton, Raats, and Gardner (1975) and Fiscus (1975), except that the intercepts of $E(P)$ on $P$ were slightly less than we would expect from the known soil water potential (see the next section). This feebleness of interaction is perhaps not surprising given the low osmolality of the soil solution (7 mosm kg$^{-1}$). But what is

### Table 1. Leaf area of the plant and water status of the soil at the beginning and end of each run

| Run | Days after sowing | Leaf area (cm$^2$) | $\theta_v$ | $|\psi_m|$ (kPa) | $P_e$ (kPa) |
|-----|------------------|--------------------|-----------|----------------|------------|
| A   | 16               | 10                 | 0.271     | 20             | 0          |
|     |                  |                    | 0.266     | 30             | 10         |
| B   | 18               | 16                 | 0.221     | 190            | 170        |
|     |                  |                    | 0.214     | 50             | 220        |
| C   | 20               | 22                 | 0.146     | 190            | 170        |
|     |                  |                    | 0.140     | 210            | 220        |
| D   | 21               | 26                 | 0.121     | 330            | 330        |
|     |                  |                    | 0.117     | 370            | 470        |
| E   | 23               | 28                 | 0.098     | 580            | 700        |
|     |                  |                    | 0.092     | 720            | 980        |
| F   | 24               | 28                 | 0.084     | 950            | 1080       |
| G   | 24               | 28                 | 0.36      | 10             | -20        |

surprising is that the conductance, $K\mu g \text{s}^{-1} \text{MPa}^{-1}$, given by the slope of $E(P)$, barely changed throughout the duration of the experiment: $E(P)$ was virtually identical in A, B, and G, even though the size and age of the plant were substantially different (Table 1). This constancy of $K$ was perhaps fortuitous, but it simplifies and gives added confidence in the analysis of pressure gradients in the soil which is discussed later. The constancy might suggest that flow in the plant is dominated by a small and fixed conductance such as might occur in the xylem of the roots (Passioura, 1972; Landsberg and Fowkes, 1978). But measurements of the diameter of the xylem vessels showed that this was not so (assuming, that is, that Poiseuille's equation was applicable). Figure 4 schematically depicts the root system of the plant as it was at the end of the experiment, and shows the diameter of the main xylem vessels at selected points. Poiseuille's equation gives the conductance of the basal 2 cm of the root axis as $\sim 10 \mu g \text{s}^{-1} \text{MPa}^{-1}$ (assuming an effective radius of the main vessel of 30 $\mu m$); the collective conductance of the basal 2 cm of the laterals is also $\sim 10 \mu g \text{s}^{-1} \text{MPa}^{-1}$ (assuming an effective vessel
radius of 10 μm and that the flow is carried equally by all laterals). These conductances are so much larger than that of the plant as a whole (~300 μg s⁻¹ MPa⁻¹), that it seems most unlikely that the xylem of the roots is completely dominating the overall conductance. Figure 4 also shows that Landsberg’s and Fowkes’ (1978) interesting analysis of the conductance of wheat roots, in which they assume that the diameter of the main xylem vessels is constant in a given class of root, would have to be greatly modified to deal with more realistic root systems.

FIG. 4. Schematic diagram of the root system of the plant at the end of run G. The numbers refer to the diameters in μm of the main xylem vessels in the roots at selected points.

Soil water potential as perceived by the plant

The intercept of \( E(P) \) on the \( P \) axis, \( P_o \), gives an estimate of the bulk soil water potential. This estimate will be dominated by the matric potential, \( \psi_m \), of the soil water, but will also be influenced by the osmolality of the soil solution to the extent that the root system is behaving as an osmometer. Table 1 shows the intercepts from Fig. 3 together with values of \( \psi_m \) derived from Fig. 2. The agreement is close at low suction, but becomes increasingly poor at high suction, where the intercept shows a marked hysteresis. Perhaps the most likely explanation for the discrepancy at high suction is that it is due to an increasing concentration of the soil solution which is being manifested as an osmotic pressure. But the increase would have to be very large. Given the small initial osmolality of the soil solution (= 15 kPa osmotic pressure), one would have to assume not only that the bulk of the solutes initially present became concentrated in the remaining water (which would give a 3–4-fold increase and account for say 50 kPa of the discrepancy) but also that there was an additional concentration adjacent to the roots, as discussed earlier, or even within the roots, as discussed by Nulsen and Thurtell (1978). If this additional concentration were responsible for much of the discrepancy, its persistence is a puzzle. Any build-up of salts at the interface between root and soil should decay within a few hours once the flow of water into the root becomes small (Passioura
Passioura—Transport of Water in Wheat

and Frere, 1967). Runs E and F of Fig. 3 were each started early in the day after a night of presumably very low transpiration rate, and any build-up should have been dissipated. Further experiments, with variable osmolality of the soil solution, may elucidate the problem.

Another possible explanation for the discrepancy is that it was due to the soil water being unevenly distributed within the pot. This however seems unlikely, for it implies that some of the roots would be experiencing less than the average matric suction, and we would therefore expect, first, that \( P_0 \) would be less than, not greater than, this average, and second, that as \( E \) increased, there would be an apparent increase, not a decrease, in the conductivity of the system, that is, that \( d^2E/dP^2 \) would be positive (Landsberg and Fowkes, 1978).

A third possible explanation is that the discrepancy is an artefact. This also seems unlikely. Since water is effectively incompressible, changing the pressure in the chamber should do little more than change the water potential uniformly throughout the whole system, as was found by Nulsen, Thurtell, and Stevenson (1977) for corn. Gradients in the root:soil system should remain unaltered (providing there are no effects on stomatal conductance, which would change \( E \)) and therefore any strains should remain unaltered. Changing the pressure does affect strain in the shoot, but, since the experiment was run with a constant condition in the shoot, namely zero water pressure in the xylem, it is hard to see why an artefact would appear at high soil matric suction but not at low. Intercellular spaces in the root cortex may shrink temporarily when \( P \) is increased, for they are filled with gas that may have little continuity with the atmosphere. However, diffusion of dissolved air will be rapid over the short distances involved, and the pressures inside and outside the root should soon equalize.

A fourth possible explanation is that the sample of soil used in determining the water retention curve was slightly different from the soil used in the pots or that there were errors in determining \( \theta_v \). Because \( d\psi_m/d\theta_v \) is so steep when \( \psi_m \) exceeds 0.6 MPa, ranging from 20 MPa at 0.6 MPa to 100 at 1.5 MPa, a very small translation of the curve could have a big effect on apparent \( \psi_m \); the discrepancy between \( P_0 \) and \( \psi_m \) in run F corresponds to a difference of only 0.002 in \( \theta_v \). However, the discrepancies in run E correspond to differences of 0.005 and 0.009 in \( \theta_v \) in the rising and falling arms respectively, and it is hard to believe that these could arise from variability of the soil or from errors in determining \( \theta_v \). Pots were weighed to the nearest 10 mg, which corresponds to the nearest \( 5 \times 10^{-5} \) in \( \theta_v \), and errors in determining the fresh weight of the plant were unlikely to exceed 100 mg, or \( 5 \times 10^{-4} \) in \( \theta_v \).

**Suction gradients in the soil**

The linearity of \( E(P) \) breaks down as the soil dries beyond a matric suction of about 200 kPa. This breakdown is, at least qualitatively, what one would expect from simple soil physical models such as those discussed by Tinker (1976): as the soil dries, water flows through it less easily, and large gradients of suction develop near roots, the surfaces of which experience a larger suction than in the bulk of the soil, so that a correspondingly larger value of \( P \) is required.
Given good data on diffusivity (Fig. 2), the most useful model is that based on the cylindrical diffusion equation:

$$\frac{\partial \theta}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left( r D(\theta) \frac{\partial \theta}{\partial r} \right)$$  \hspace{1cm} (1)$$

where $\theta$ is the volumetric water content of the soil, $t$ is time, $r$ is the radial distance from the centre of a root, and $D(\theta)$ is the diffusivity. This equation can be solved by making the reasonable assumptions (Tinker, 1976): (1) that each root has sole access to a hollow cylinder of soil of inner radius $a$, the radius of the root, and outer radius $b = (\pi L)^{-1}$, where $L$ is the length of root per unit volume of soil; (2) that there is no flow at $b$, i.e. that $\partial \theta / \partial r$ is zero at $b$; and (3) that the root withdraws water from the soil at an effectively constant rate that results in $\partial \theta / \partial t$ having an effectively constant value, $Q$. The solution is

$$b^2 - a^2 = QG$$

(2)

where $G = b (1 - \ln (b/a))$ and is derived by assuming that $a^2$ is negligibly small, which is usually true.

The non-linear data of Fig. 3 can best be analysed in terms of equation (2) by using it to calculate the rooting density, $L$, that would be required to give the inflated values of $P$. At a given transpiration rate, $E$, the pressure drop across the plant is $E/K$, where $K$, the hydraulic conductance of the plant, is taken to be equal to the slope of line $G$ in Fig. 3. The pressure at the surface of the roots is therefore $P - E/K$. If there are no complications due to the presence of solutes, then $P - E/K$ is also the matric suction of the soil water at the surface of the root. But we have seen in the previous discussion that there are complications, for $P_o$ and $|\psi_m|$ do not agree at high suctions. Let us assume for the moment that the discrepancy between $P_o$ and $|\psi_m|$ is due to an osmotic effect that remains constant at least during the first half of each run. If we now translate curves D, E, and F, so that $P_o$ coincides with $|\psi_m|$, then the translated $P - E/K$ gives us an estimate of the matric suction at the surface of the roots, and can be used to derive $\theta_a$ from Fig. 2. Because of the cylindrical geometry and the nature of $D(\theta)$, any major gradients in $\theta$ will occur close to the surface of the roots and will have a negligible influence on the average water content $\bar{\theta}$, which we can take to be the same as $\theta_a$. The integral in equation 2 can easily be evaluated numerically between $\theta_a$ and $\bar{\theta}$, and on dividing it by $Q$, which is simply $E$ divided by the volume of the pot and the density of water, we arrive at a value of $G$. From this we can calculate $b$, and hence $L$, given that the average radius of the roots was $\sim 150 \ \mu m$. The values of $L$ calculated in this way for the maximum $E$ in runs D, E, and F were 1.3, 1.5, and 1.4 cm cm$^{-3}$, respectively. The lesser values of $E$ during the first half of each run gave similar values of $L$, although the errors become very large when $\bar{\theta} - \theta_a$ is small. These values of $L$ are about 30% of the measured rooting density, which was 5.2 cm cm$^{-3}$.

Let us now assume that the pressure at the surface of the root contains a varying osmotic component; i.e. that $P - E/K = |\psi_m| + \sigma \sigma_s$, where $\sigma$ is the reflection
coefficient for the roots and $\pi_s$ is the osmotic pressure of the soil solution. We have no way of knowing precisely what $\pi_s$ might be, but if the discussion in the previous section is sound, a good estimate of $\pi_s$ at the beginning or end of a run would be $P_0 - |\psi_m|$. The value of $P_0 - |\psi_m|$ at the end of a run may also be a reasonable estimate for $\pi_s$ at maximum $E$, if the build-up of solutes at the root:soil interface had little chance to decay during the second half of a run. If we assume that $\pi_s$ at maximum $E$ is given by $P_0 - |\psi_m|$ at the end of the run, then we have values of 100 and 200 kPa, respectively for runs D and E. Decreasing $|\psi_m|$ at the surface of the roots by these amounts gives new values of $\theta_a$ (via Fig. 2) to apply in equation 2, and results in calculated values of $L$ of 1.6 and 2.2 for the maximum $E$ in runs D and E respectively.

![Fig. 5. Calculated pressure drop within the soil, $\Delta\psi_m$, as a function of rooting density, $L$, for maximum $E$ in runs D, E, and F.](https://academic.oup.com/jxb/article-abstract/31/1/333/473180/download)

The consistency in the calculated values of $L$, and the minor effects of the osmotic corrections, are not surprising when we examine the relation between $L$ and the calculated pressure drop in the soil, $\Delta\psi_m$ (Fig. 5): any deviations of $P$ from $P_0 + E/K$ that are greater than about 300 kPa will lead to estimates of $L$ that lie between 1 and 2. Figure 5 also shows that if the total root length of the plant were effective in taking up water ($L = 5$ cm$^{-2}$), then $\Delta\psi_m$ would never exceed 100 kPa. That $P - P_0 - E/K$ does often greatly exceed 100 kPa is strong evidence that well over half of the root length is ineffective (unless any osmotic effect is much greater than the above discussion suggests, which seems unlikely). The microscopic examination of the roots showed that there were two distinct types of root. One was smooth and white, and looked as though it could have been grown in nutrient solution. The other, which accounted for 30% of the total root length, was darkly stained by strongly adhering soil particles and was highly contorted, apparently from being pressed hard against the soil (Plate 1). The contorted roots were the youngest and had presumably grown after $|\psi_m|$ had become large. The smooth pieces at their tips were probably formed after the pot was watered, which was 16 h
before the roots were washed out. It is tempting to equate the contorted root length with the calculated active root length.

**Plate 1.** Photograph of a typical secondary lateral root attached to a primary lateral (×10 magnification).

**Hysteresis in E(P)**

The previous section concentrated on the rising arms of the $E(P)$ curves. In runs D and E a marked and puzzling hysteresis is apparent in the falling arms. Two possible but not very convincing explanations come to mind.

The first is that the relaxation times for the putative gradients in suction near the root are such that little recovery has occurred before the first measurements on the falling arm have been made. This is not convincing, for we would expect the relaxation time, $\tau$, to be much less than $0.2 \frac{b^2}{D}$, the approximate time taken to
establish steady state flow across a hollow cylinder (Crank, 1956). If \( L = 1.5 \text{ cm}^{-2} \), then \( b^2 = 0.2 \), so that for \( D = 1.5 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1} \), \( \tau \ll 3 \times 10^3 \text{ s} \). Thus substantial recovery in \( \theta_a \), and therefore in \( P \), is likely to have occurred in the half hour needed to make the first measurement on the falling arm. Furthermore, if steady rates had not been established, \( P \) would have been drifting markedly, which it was not.

The second possible explanation is that of the salt build-up mentioned previously. The diffusivity of solutes in soil having a high matric suction is much less than that of water, so relaxation times of several hours are possible. Indeed, a slow build-up of solutes may have been continuing during the measurement of the first point on the falling arm of run \( E \). But although this explanation seems possible for the first half of the falling arm, the second half remains a puzzle: the falling arm should continue to approach the rising one as \( E \) is decreased, and should not be parallel to it. Perhaps the sustained hysteresis is due to a build-up of solutes not in the soil, but in the cortex (Nulsen and Thurtell, 1978)? If hydraulic connections between soil and root become scarce as the soil dries, they may remain adequate to allow the soil solution to flow into the root, but may become inadequate for the solute to diffuse back into the soil.

**CONCLUSION**

Apart from the puzzling hysteresis, the plants in these experiments behaved rather simply. Their behaviour in wet soil was linear, and the non-linearities that appeared as the soil dried were consistent with what one would expect from simple soil physical models. This behaviour was markedly different from that described in recent papers by Herkelrath et al. (1977) and Faiz and Weatherley (1978), in which the uptake of water by the roots appeared to be dominated by a large hydraulic resistance at the root:soil interface. This difference in behaviour may have been due to one or more of the problems discussed in the Introduction, but detailed exploration of these would be needed in order to be certain.

**ACKNOWLEDGEMENTS**

The author wishes to thank Mr. R. A. Sageman for his technical assistance.

**LITERATURE CITED**

——— 1969. Ibid. 6, 1–12.