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# MEASUREMENT OF WATER FLUXES AND POTENTIALS IN A SINGLE ROOT–SOIL SYSTEM

## II. APPLICATIONS OF TENSIOMETER-POTOMETER SYSTEM*

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## SUMMARY

The usefulness of a tensiometer–potometer system in investigations of water flow in the vicinity of a plant root has been demonstrated. Measurements were made of the root–soil interface water potential, xylem potential and the distribution of water fluxes and root resistance along the length of a maize root. For a root growing in sand, the rhizosphere resistance was 3.5 to 8 times the radial resistance of the root at average rhizosphere potentials of −250 m bars. For a root growing in sandy loam such rhizosphere resistance was not achieved until the average rhizosphere potential is approximately −2 bars.

## INTRODUCTION

The importance of obtaining direct experimental measurements of the water potentials and fluxes in the vicinity of plant roots growing in soil has recently been emphasised[11 12]. At present most of the information available has been derived from indirect measurements or from mathematical models based on various assumptions.

Of particular interest is the relative magnitude of the resistance to flow provided by the soil and plant pathways respectively. While numerous workers have presented evidence to suggest that the rhi-

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zosphere resistance can be appreciable in relation to the resistance in the plant even at very high matric potentials[3 5 6 7 8], Newman has questioned the validity of many of the assumptions and interpretations used in previous work and has concluded that appreciable rhizosphere resistances generally only occur when the soil is near or beyond the permanent wilting point.

Much of the difficulty in resolving this question arises from the lack of a suitable method of measuring the water potential at the root-soil interface. In the preceding paper of this series[15] the construction and operation of a tensiometer-potometer system capable of measuring *in situ* and simultaneously the xylem water potential, the root-soil interface water potential and the flux of water into a single root growing in a soil was described. This paper presents three series of experiments carried out to evaluate the possible applications of this tensiometer-potometer system.

## MATERIALS AND METHODS

The construction and operation of the tensiometer-potometer system was described in the previous paper of this series[15]. Briefly, this apparatus consists of a tensiometer collar in series with one or more flow collars to make up a potometer system, in which a single plant root can be grown. The tensiometer consists of a ceramic cylinder of 0.6 cm ID cemented at its ends inside a perspex cylinder leaving a gap between the two materials which acts as a water reservoir. This reservoir is connected to a pressure transducer system and a calibrated capillary through a 3-way vacuum tap, such that it can be operated as a tensiometer or a flow collar for measuring the flux of water into the root. The inside of the ceramic cylinder of the tensiometer is packed with ceramic particles of 0.25–0.5 mm size, leaving a small channel in the centre for the root to grow through. The expectation is that the ceramic particles will act essentially as an extension of the ceramic wall of the tensiometer. The flow collars which are similar in construction (with the exception that they are not connected to a pressure transducer system) were similarly packed with either ceramic particles or soil.

At equilibrium the tensiometer will measure the xylem water potential of the root. The flow collars are used to measure the flux of water into the root under various suctions applied to the collar to simulate various soil suctions.

The soils used were a silicious sand from Jandakot, Perth, W. A. and a sandy loam from Harvey, W. A. Plants used were hybrid maize seedlings described in the first paper[15]. The transpirational demand on the plant was varied by controlling the environmental conditions of the aerial part of the plant within a perspex cabinet.

### *Measurement of the xylem water potential using the flux-estimation method*

As the tensiometer is limited in the range of measurement to −0.85 bars, it was hoped that xylem water potentials below −0.85 bars could be estimated by the flux estimation method, similar to the method employed by Brouwer[2] with his potometers containing nutrient solutions with various concentrations of an osmoticum. This would greatly enhance the range of usefulness of the equipment.

The resistance of the root tissues to water flow is known to change with the suctions applied to the root[2 10 13] but this change takes some time to complete. The flux immediately after a change in applied suctions will consequently be subject to the original root resistance before the change. An estimate of the xylem water potential can therefore be obtained by linear extrapolation to zero flux of the flux-suction relationship given by the fluxes measured before and immediately after the change in suction. For given environmental conditions including a constant root environment the xylem water potential will remain essentially constant and unaffected by the suctions imposed on a single root.

Two experiments were conducted using a two-collar arrangement (Exp. 1 and 2) to investigate the accuracy of this method. One collar was used as a flow collar whereas the other was used as a tensiometer collar to check the accuracy of the flux estimation method.

### *Measurement of the water potential at the root-soil interface and the root-soil resistance to water flow*

These measurements were conducted using three collar arrangements consisting of a 2 cm flow collar packed with Jandakot sand (sand collar), a tensiometer and a flow collar packed with ceramic particles (ceramic collar).

The fluxes of water through the sand collar were measured with various suctions applied to the collar. These valves thus constitute the suctions of the soil water at the outer boundary of the soil cylinder. Simultaneously the flux-suction curve for the same root was measured using the tensiometer and ceramic flow collar which was subjected to various applied suctions. As the resistance of the ceramic particle bed ($10^2$ mbar HR $cm^{-2}$) was very small relative to the root resistance ($10^4$ mbar HR $cm^{-2}$) the flux-suction curve essentially relates to the flow properties of the root only and the applied suction is essentially the inverse of the water potential at the root surface.

The water potential at the root surface that results in a flux similar to the flux of water through the sand collar can thus be found from the flux-suction curve. Once this was determined, it becomes a simple matter to calculate the root and soil (or sand) resistances.

Three experiments were carried out in this series (Exp. 3, 4 and 5).

### *Measurement of the distribution of fluxes and resistances along the length of a root*

These measurements were conducted using a three-collar arrangement consisting of a tensiometer collar (ceramic) sandwiched between two soil collars packed with a sandy loam from the Harvey region in W. A. Flux measurements were taken at the soil collars under a constant suction of 100 mbars and the xylem potential was monitored with the tensiometer. The soil resistance at this suction was very small relative to the root resistance and hence the root-soil interface potential measurements were not considered necessary. The length of root that had grown through the potometer was monitored with time so that any flux measured could be associated with a particular position on the root.

The sandy loam was used instead of the sand because its resistance to water flow is smaller, its resistance to root penetration is smaller and it appears that the root made better contact with the sandy loam than with the sand. Two experiments were conducted for this series (Exp. 6 and 7).

## RESULTS AND DISCUSSION

### *The flux estimation method*

A typical result of this method is shown in Fig. 1. The numbers on the points refer to the sequence of operation. For Exp. 1 the number

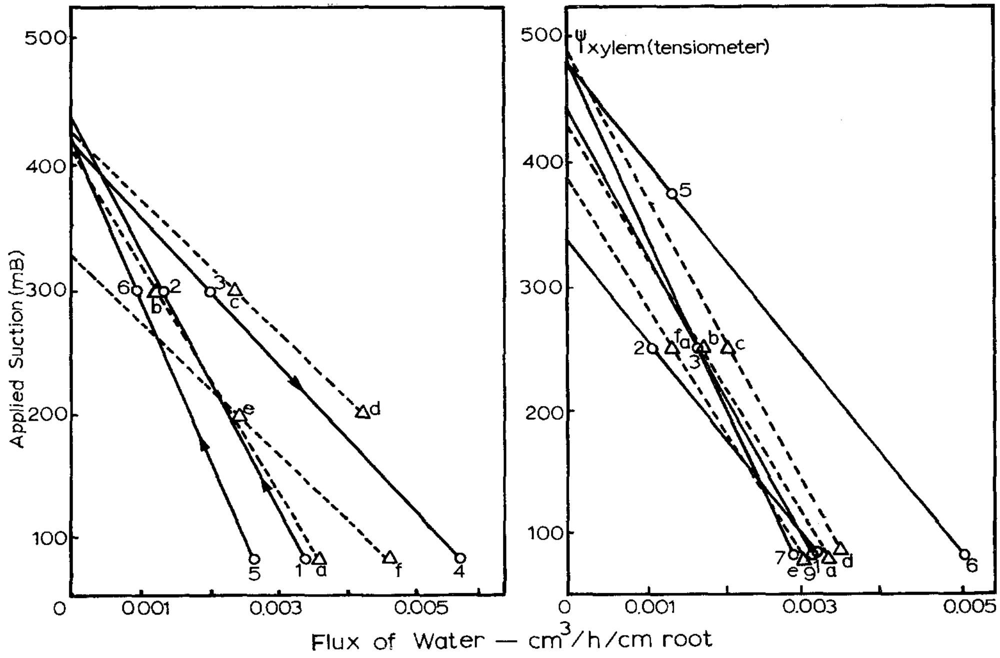

Fig. 1. Xylem tension estimated using the flux estimation method.

TABLE 1

Accuracy of the flux estimation method

| Exp. | Tensiometer | Xylem potential (mbars) measured by flux estimation method* |
|---|---|---|
| 1 | — | −410, −416, −420, −426, −436 |
| 2 | −493 | −340(69), −483(98), −480(97½), −440(89½)<br>−340(69), −385(78), −430(87), −485(98½) |
| 3 | −312 | −290(93), −360(115), −315(101) |
| 4 | −312 | −291(93), −287(92) |
| 5 | −465 | −386(83), −394(85), −290(62½) |

* Numbers in brackets are the percentages of the tensiometer readings.

1 is the equilibrium flux at a suction of 80 mbars, 2 is transient flux immediately after the suction was changed to 300 mbars (after allowing 5 min for a drainage equilibrium to be achieved for the ceramic particles). 3 is the equilibrium flux at 300 mbars suction whereas 4 is the transient flux immediately after the suction was changed to 80 mbars. The intercept of line 1–2 or 3–4 with the Y-axis should give an estimate of the xylem water potential as measured by the tensiometer. The accuracy of these estimations varies widely as shown in Table 1. In this table this method was extended to include other experimental runs. It is obvious that the accuracy of this method was not satisfactory as the estimates range from 60–115% of the true value (tensiometer reading) with the majority being below 100%. Thus the method tends to over-estimate the xylem water potential. The poor precision and accuracy of this method was probably the result of the lack of accuracy of the flux measurements immediately after the suction change. Such a change was always accompanied by a change in water content of the ceramic particles which was completed within 5 minutes when no plant was present, and hence the 5 minutes delay before the first flux measurement was made. However, the change in root resistance caused by a change in suction was usually completed in about 30 minutes for maize which is in agreement with the findings of Hayward and Spurr[9]. This allowed only one or two transient flux measurements before the change in resistance was complete (approximately 25 minutes) which was not enough to make corrections for the first 5 minutes period after the change.

Brouwer[1] found that the change in resistance of broad bean roots associated with a suction change was completed in 3 hours which allows adequate time for reasonably accurate measurements.

It was concluded that the flux estimation method does not provide sufficient accurate estimates of the xylem tension of a maize root.

*The root–soil interface water potential*

The results of three experiments are presented in Fig. 2 where the

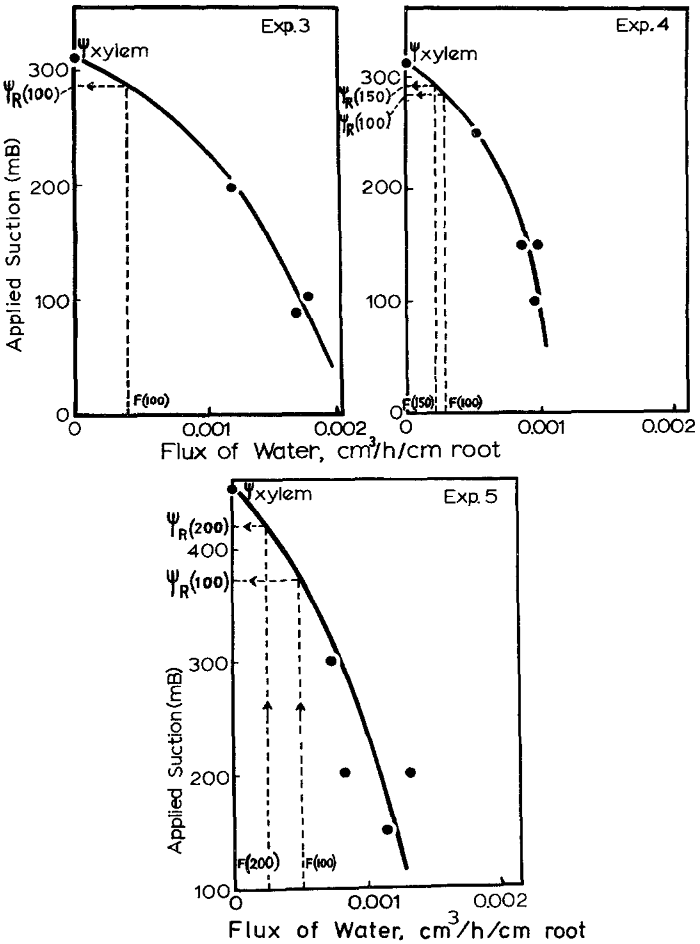

Fig. 2. Flux-suction relationships for the roots of Expts. 3, 4 and 5. Dotted lines with arrows show the method used for obtaining Ψ' root from the flux of water through the sand column. $F_{(100)}$ = flux of water through sand at 100 mbars suction. $R_{(100)}$ = Tension at the root surface at soil tension of 100 mbars.

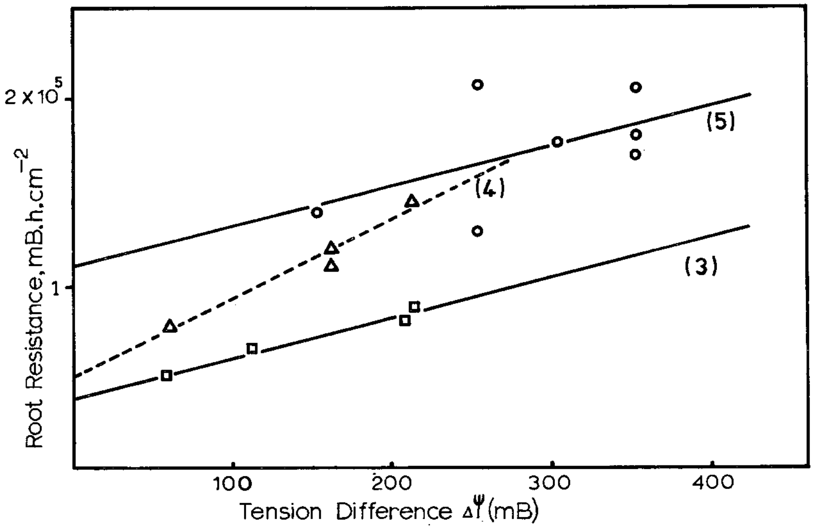

Fig. 3. Root resistance *versus* tension difference for roots in Expts. 3, 4 and 5.

flux was plotted against applied suction at the root surface. The solid curves were replotted from the regression lines in Fig. 3 which shows the root resistance plotted against the suction differences between the xylem and root surface[15].

The flux through the soil collar under applied suctions of 100 and 150 mbars (F100 and F150) were superimposed on this curve and the root-soil-interface tensions were found as shown by the dotted lines (100 and 150 respectively).

This allows the root and sand resistances ($R_R$ and $R_S$) to be calculated from the Ohm's law analogue

$$\text{Flux} = -\frac{\Psi_X - \Psi_R}{R_R} = -\frac{\Psi_R - \Psi_S}{R_S} \tag{1}$$

where $\Psi_X$, $\Psi_R$ and $\Psi_S$ are the water potentials of the xylem, root-soil-interface and the soil respectively.
Therefore the ratio

$$\frac{R_R}{R_S} = \frac{\Delta\Psi_{\text{root}}}{\Delta\Psi_{\text{soil}}} \tag{2}$$

The results of the 3 experiments in this series are presented in Table

TABLE 2

Water potentials and resistances to water flow observed during experiments on Jandakot sand

| (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | (10) | (11) |
|---|---|---|---|---|---|---|---|---|---|---|
| Exp. | $\Psi$xylem | $\Psi$soil (at r = 0.3 cm) | $\Psi$root surface | Flux of water per cm of root cc $HR^{-1}$ | $R_S$ calculated from $R_R$ | | | | $R_S$ calculated from $\Delta\Psi$soil | |
| | | | | | $\Delta\Psi_{root}$ | $R_{root}$ $\times$ $10^4$HR $cm^{-2}$ | $R_S/R_R$ | $R_S$ $\times$ $10^4$HR $cm^{-2}$ | $\Delta\Psi_{soil}$ | $R_S$ $\times$ $10^4$HR $cm^{-2}$ |
| 3 | −312 | −100 | −288 | $4.8 \times 10^{-4}$ | 24 | 5.35 | 7.85 | 41.9 | 188 | 39.2 |
| 4 | −312 | −100 | −285 | $3.6 \times 10^{-4}$ | 27 | 7.20 | 6.85 | 49.3 | 185 | 51.4 |
| | | −150 | −294 | $2.7 \times 10^{-4}$ | 18 | 6.85 | 8.00 | 54.9 | 144 | 53.4 |
| 5 | −452 | −100 | −372 | $6.0 \times 10^{-4}$ | 80 | 15.4 | 3.40 | 52.4 | 272 | 45.4 |
| | | −200 | −421 | $3.0 \times 10^{-4}$ | 31 | 14.1 | 7.21 | 100.4 | 221 | 74.0 |

2. $R_S$ was calculated from $R_R$ taken from Fig. 3 and multiplied by the factor $R_S/R_R$ (Column 9) and also directly using the Ohm's law analogue (Column 11). The agreement between the two $R_S$ values was good, indicating that the values of $\Psi_R$ were valid and accurate.

A comparison was made between these experimental values of $R_S$ with those calculated from conductivity (K) data of the Jandakot sand measured separately[15]. As K is a sensitive function of matric potential, it was averaged by the formula given by Crank[4].

$$\overline{K} = \frac{1}{\Psi_2 - \Psi_1} \int_{\Psi 1}^{\Psi 2} K d\Psi \qquad (3)$$

The geometry of the root is not a simple cylinder, as root hairs protrude out of the main cylinder. However, as the effective root radius is not known, maximum and minimum possible values of the average soil cylinder resistances can be calculated from $\overline{K}$ values of Equation (3). The maximum average soil cylinders resistances $\overline{R}_s$ were calculated using the dimensions of 0.6 cm O.D. and 0.16 cm I.D. which are the diameters of the root cylinders whereas the minimum average soil resistance $\overline{R}_s$* were calculated using 0.6 cm O.D. and 0.31 cm I.D. which is the diameter of the cylinder at the tip of the root hairs.

The agreement of the $R_S$ values of Table 2 being the resistance of the effective soil cylinder, with the values of $\overline{R}_s$ and $\overline{R}_s$* (Table 3)

TABLE 3

Calculated resistance of sand collar

| Exp. | Soil tensions (mbars) | k ($10^{-7}$ $cmHR^{-1}$) | $\Psi$ (mbars) | $R_S$ (.16cm ID) ($10^4 HRcm^{-2}$) | $R_S$* (.31cm ID) ($10^4 HRcm^{-2}$) |
|---|---|---|---|---|---|
| 3 | 100–288 | 8.1 | 243 | 65 | 32.5 |
| 4 | 100–285 | 8.1 | 243 | 65 | 32.5 |
|  | 150–294 | 4.3 | 254 | 80 | 40 |
| 5 | 100–372 | 5.7 | 285 | 130 | 65 |
|  | 200–421 | — | — | — | — |

was good. With the exception of experiment 5, the values of $R_s$ were all between the maximum $\overline{R}_s$ and the minimum $\overline{R}_s$*. The root of experiment 5 appeared to be diseased (brown spots were visible on the root when dismantling) and this may be the cause of the poor correlation between root resistance and suction difference (Fig. 3) and the poor agreement between the various soil resistance values.

It must be concluded that with the agreement between the two experimental values of $R_S$ and the calculated values of $\overline{R}_S$ and $\overline{R}_S$*, that the accuracy of the measurement of the root–soil interface water potential must be good.

Higher suctions were not used on the sand collar as the fluxes became too small for accurate measurements due to the rapid reduction of the conductivity K.

The values of $R_S/R_R$ ranged from 3.5 to 8 for Jandakot sand under suctions of 100 to 200 mbars applied at a distance of 0.3 cm from the root axis. The sand within this area is considered as the rhizosphere[14]. Thus the resistance of the sand rhizosphere was much higher than the root resistance. The rhizosphere in these experiments is equivalent to that of a root system with a density of 3.5 cm root /cm$^3$ of soil, ($= 1/\pi R^2$, $R =$ inner radius of tensiometer cylinder) where the root system is assumed to be an array of parallel roots.

Newman[11 12] developed Gardner's model further and predicted that the development of an appreciable rhizosphere resistance was rare at soil suctions as low as 1 bar and claims that such a high rhizosphere resistance is only possible with very low root densities such as those used by Cowan[3] which ranged from 0.125 to 0.5 cm/cm$^3$. In his treatment of the radial flow of water to a single root, Gardner[7] gives the solution of the steady state flow of water in a hollow cylinder as

$$\Delta\Psi = \Psi_a - \Psi_b = \frac{\Phi}{4\pi K} \ln \frac{(b^2)}{a^2} \qquad (4)$$

where: $\Psi_a$ and $\Psi_b$ are the water potentials at $r = a$ (root radius) and $r = b$ (outer radius of soil cylinder), $\Phi$ = volume flux of water (radial flow) and $K$ = soil's conductivity.

Using this solution and extrapolating to a soil–plant system, Newman obtained an expression for the soil conductivity K when the rhizosphere resistance becomes appreciable or when the soil resistance ($R_S$) equals the plant resistance ($R_p$):

$$K = \frac{1}{2\pi\, L_A R_P} \ln \frac{b}{a} = \frac{E}{2\pi\, L_A(\Psi_R - \Psi_e)} \ln \frac{b}{a} \qquad (5)$$

Where E = transpiration rate, $\Psi_R$ and $\Psi_e$ are the water potentials at the root surface and evaporating sites in the leaves respectively and $L_A$ = length of root per unit ground surface area. Therefore, the value of K is dependent on $L_A$. From his examination of observed $L_A$ values Newman concluded that the rhizosphere resistance rarely becomes appreciable until the soil moisture potential is near wilting point except at very low values of $L_A$.

If we assume a rooting depth of 15 cm for a 3 week old maize (actual root lengths range from 0 to 50 cm) this will give a value for $L_A$ of approximately 50 (15 cm × 3.5 cm/cm$^3$) which is within the range of observed $L_A$ values[12] (5 to 4000 cm/cm$^2$). The values of ln (b/a) in this experiment range from 0.66, if the tip of the root hairs is considered as the root cylinder, to 1.40 if the root cylinder itself is used. Therefore a value of 1.00 was used. The value of $R_p$ of $5 \times 10^3$ days used by Newman was used, considering the leaf water potential under the experimental conditions was approximately 3 bars and the potential transpiration rate of 0.6 cm/day which gives an $R_P$ of $5 \times 10^3$ days. Using Equation (5) K was calculated to be $2.7 \times 10^{-8}$ cm h$^{-1}$ which corresponds to a suction of 260 mbars in the Jandakot sand and approximately 2 bars in the Harvey sandy loam.

The experimental results show that at average rhizosphere suctions of 240 to 285 mbars (Table 3) the rhizosphere resistance is several times the root resistance. The ratio $R_S/R_R$ would remain the same for a whole root system as well as a single root assuming water flows predominantly in the radial direction. However, the plant resistance would be 2 to 3 times the root resistance. Hence, the results show that appreciable rhizosphere resistance can develop at suctions well before wilting point is approached and this will depend on the conductivity – water potential relationship of the soil used.

The uncertainties in the calculations are the values of $L_A$ and $R_P$ which are inversely related to K. However the magnitude of the average soil potential is insensitive to changes in the magnitude of K. A change in K by factor of $10^3$ will produce a change in soil potential of approximately 100mbars in the sand and 0.9 to 1 bar in sandy loam[15]. Therefore unless $L_A$ and $R_P$ are in error by several orders of magnitude the above conclusion will not be significantly affected.

Thus Newman's generalisation should be viewed with caution and a consideration of the soil type should be included.

### *Distribution of the flux and resistance along the root*

The results of the 2 experiments are presented in Fig. 4 where the flux of water is plotted against distance from the root tip. These fluxes were measured subject to a constant suction of 100 mbars. The xylem potentials were not constant, decreasing progressively from —645 to —690 mbars for the first experiment and from —700 to —710 mbars for the second experiment over the 3 days of the measurements. As the flux varied with xylem potentials, the data had to be standardized assuming that $R_R$ remained constant over the relatively small changes of xylem potentials. This was achieved by using the equation:

$$R_R = \frac{-\Psi_X^S - 100}{F_S} = \frac{-\Psi_X^i - 100}{F_i} \qquad (6)$$

where:

$F_i$, $F_S$ = measured and standardized fluxes of water,
$\Psi_X^i$, $\Psi_X^S$ = measured and standard xylem potentials, and the number 100 refers to the suction applied to the collars.

Thus:

$$F_S = F_i \frac{\Psi_X^S - 100}{\Psi_X^i - 100} \qquad (7)$$

The fluxes of the first experiment were standardized to a xylem

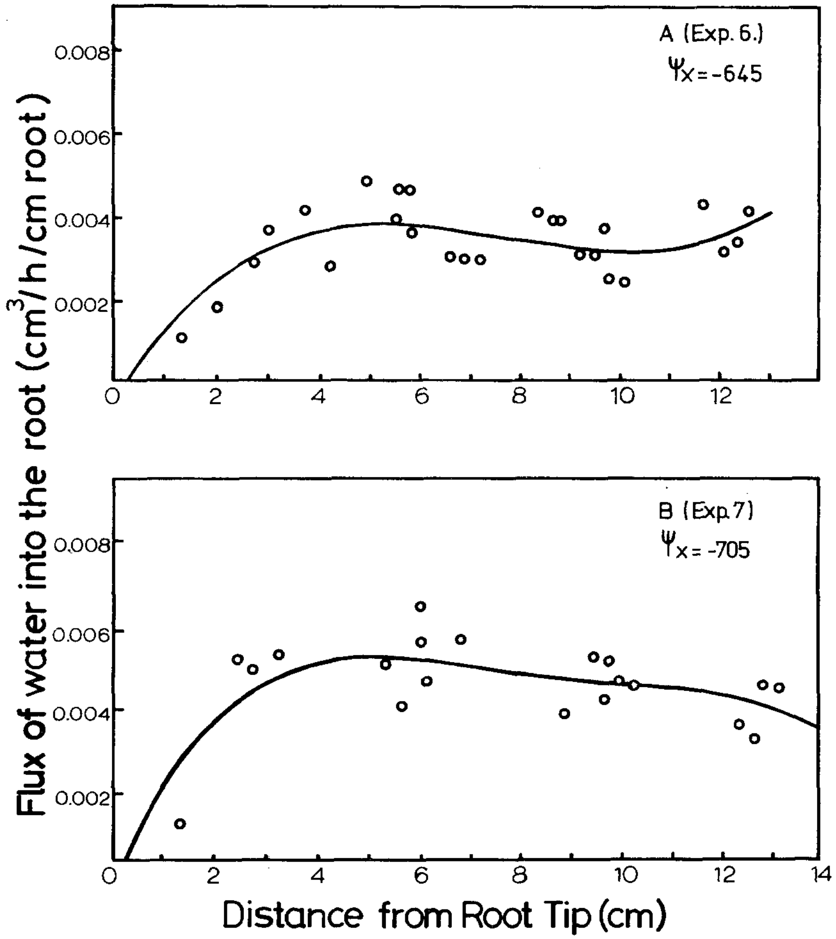

Fig. 4. Distribution of water fluxes along the root.

potential of —645 mbars whereas an average xylem potential of —705 mbars was used in the second experiment as the range was small and therefore the fluxes were not corrected. The curves were fitted to the data using the polynomials of the type $Y = a_0 + a_1X + a_2X^2 + \ldots\ldots$ etc. The best fitting curve was considered the polynomial with the minimum order that had the following characteristics: (a) A negative intercept with the Y-axis and consequently a positive intercept with the X-axis as the root tip would most probably show very little water uptake, and (b) The mean square of the residuals should not change significantly with an additional increase in the order of the polynomial.

The polynomials for the two curves are:

1st exp: $Y = -0.000475 + 0.0019\,X - 0.000275\,X^2 + 0.000012\,X^3$

2nd exp: $Y = -0.00028 + 0.0028\,X - 0.00053\,X^2 + 0.000041\,X^3 - 0.0000012\,X^4$

where Y is the flux of water into the root in $cm^3/HR$ cm root and X is the distance from the root tip in cm.

It is interesting to note that although the data show a considerable amount of scatter, both curves have the same shape except for the increasing uptake rate at the base of the root of curve A. This was undoubtedly a result of the branching of the root at the top collar which was observed when dismantling the potometer at the end of the experiment. Although the absolute values of the fluxes were different, the distribution patterns along the roots were very similar with a maximum uptake rate at 5 to 5½ cm from the root tip. The rate of uptake increased sharply from the tip to the maximum and decreased slowly thereafter. When the root resistances were calculated using the Ohm's law analogue, two similar distributions of root resistances were obtained for both experiments (Fig. 5). Thus the

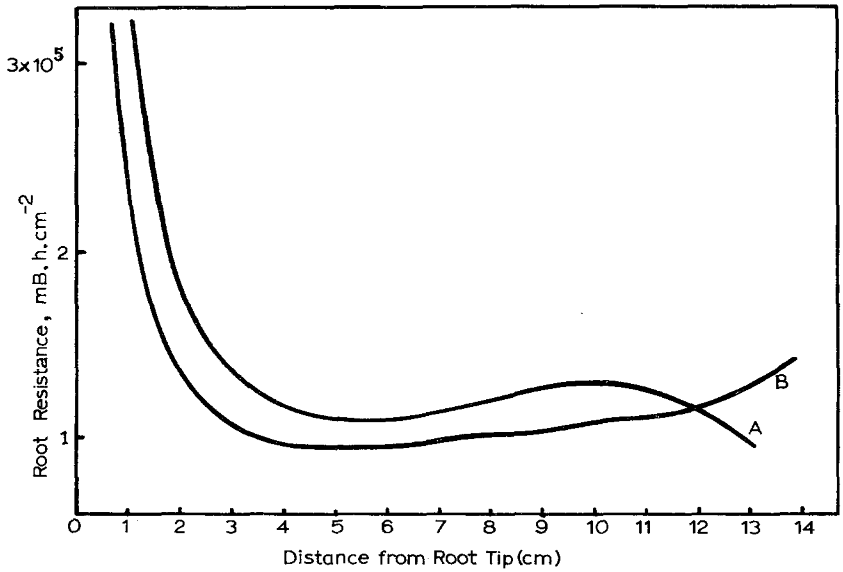

Fig. 5. Distribution of root resistances along the root.

differences in uptake rates resulted from differences in root resistance as well as observed differences in xylem potentials. These resistances are lower than those found by other workers on maize roots[16].

The assumption used that the rates of uptake or root resistances were uniform along the root is acceptable if measurements were taken some 4 cm or more away from the root tip. In the preceding experiments measurements were not started until the root has penetrated past the potometer by some 3 to 4 cm.

In conclusion, it has been shown that the tensiometer-potometer, described in a preceding paper[15] will be a useful research tool in plant soil water relationships. It is limited in the range of root xylem potentials that can be measured with this instrument. However, it may be possible to extend this range by using the flux estimation method on a root that requires a longer period than maize to change its resistance when subjected to a sudden change in applied suction, such as a broad bean root[1]. This instrument is capable of measuring the root-soil-interface water potential, the xylem potential and the flux of water simultaneously under various applied soil water potentials. Therefore it makes possible the direct measurement of root and rhizosphere resistances. Note that in these experiments good root–soil contact was maintained. It is also a useful tool for measuring the distribution of water flux or root resistances to water flow along the root length. If the variation of the tensiometer readings during the last experiments can be taken to be the result of xylem resistance, then it must be concluded that the xylem resistance of the nodal roots of maize is relatively small compared to its radial resistance.

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