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**RESISTANCE TO WATER FLOW IN THE SOIL-PLANT SYSTEM – A CASE STUDY WITH  
INDOOR GROWN MAIZE PLANTS<sup>1</sup>**

**RESISTÊNCIA AO FLUXO DE ÁGUA NO SISTEMA SOLO PLANTA – UM ESTUDO COM  
PLANTAS DE MILHO CULTIVADAS SOB CONDIÇÕES CONTROLADAS**

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**SUMMARY**

The magnitude of the resistance to water flow in various parts of the soil-plant system was determined using indoor grown maize plants (hybrid United 108). The flux of water in the soil-plant system was measured by a weighing technique and the water status in the soil, root and leaf of transpiring plants was determined directly using the dew-point hygrometer technique. When the rate of water consumption for plant growth was accounted for, a linear relationship, passing through the origin was found between leaf-to-soil water potential difference and transpiration rate. Plant growth estimates varied from 0.0287 to 0.10g dm<sup>-2</sup> hr<sup>-1</sup>. Resistance to water flow in the plant increased with a decrease in soil water potential. The results indicated that the main resistance to water flow in the plant is located in the radial pathway for water movement from root cortex to root xylem. Plant resistance was larger than soil resistance until a soil water potential of -0.6MPa, below this value soil resistance became the limiting factor for water transport in the soil-plant system.

**Key words:** plant resistance, soil resistance, root resistance, water potential, transpiration rate.

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## RESUMO

A magnitude das resistências ao fluxo de água nos vários componentes do sistema solo planta foi determinada usando plantas de milho crescidas sob condições controladas. O fluxo de água no sistema solo-planta foi medido através da técnica de pesagem e o “status” da água no solo, raiz e folha foi determinado diretamente usando a metodologia do higrômetro de ponto de orvalho. Quando a taxa de consumo de água para crescimento vegetal foi considerada, encontrou-se uma relação linear, com centro na origem, entre taxa de transpiração e diferença de potencial da água entre folha e solo. As estimativas de crescimento vegetal variaram de 0,0287 a 0,10g dm<sup>-2</sup> h<sup>-1</sup>. A resistência ao fluxo de água na planta aumentou com o decréscimo no potencial da água no solo. Os resultados indicaram que a principal resistência ao fluxo de água na planta localiza-se no caminho radial para o movimento de água do cortex da raiz ao xilema. Para o tipo de solo usado no experimento a resistência da planta foi maior que a do solo até um valor de potencial da água no solo de -0,6MPa, abaixo deste valor, a resistência do solo torna-se o fator limitante no transporte de água no sistema solo-planta.

**Palavras-chave:** resistência da planta, resistência do solo, resistência da raiz, potencial da água, taxa de transpiração.

## INTRODUCTION

Water transport in the soil-plant-atmosphere continuum (SPAC) depends on the ability of the system to make water available at the evaporation sites, particularly in the leaves. The process of water evaporation from leaves is governed by the stomatal resistance and the water vapour concentration difference between the substomatal cavity and the surrounding air. The liquid flow from the soil through the plant up to the leaf mesophyll is mainly governed by: (1) the soil hydraulic conductivity; (2) plant internal resistance to liquid flow; and, (3) water potential difference from soil to leaves.

Water flow may be considered as a catenary process, and always related as an analogy to Ohm's law. This can be considered as true for steady state situations (BRUNINI & THURTELL, 1981; CARDON & LETEY, 1992). In transient cases the problem is complicated by storage in the soil or plant, and an analogy to a resistor-capacitor network better represents the system (COWAN, 1965; BOYER, 1971, 1974; MOLZ, 1981).

WILLIAMS (1974) and RUNNING (1980), suggested that the major resistance to water movement in the soil – plant system is not located in the soil, but in the radial pathway to water flow from root cortex to root xylem, with soil resistance becoming important only in dry soils. Changes in root resistance to water movement may be dependent on environmental factors (AZAIZEH & STEUDLE, 1991), or on the flow rate (WEATHERLEY, 1982; STEUDLE & JESCHKE, 1983). Variable hydraulic root resistance is probably associated with changes in root structures and consequently to the radial movement of water across the root as well as the transport along the vessels (PASSIOURA, 1988; MELCHIOR & STEUDLE, 1993).

Field studies of plant resistance to water flow in soybean were carried out by JONES et al. (1982) under non-limiting soil moisture. Their results indicated that plant resistance increased with an increase in the transpiration flux at a non-linear relationship. For sorghum, MEYER & RITCHIE (1980), observed that radial root resistance was strongly dependent on transpiration rate. They have also observed that with moderate or high values of transpiration rate root resistance was higher than shoot resistance. On the other hand, for alfafa, ABDUL-JABBAR et al. (1984) observed that plant resistance to water flow remained constant throughout the day. Their results have also demonstrated that at higher values of transpiration rate plant resistance changed very little, but as the transpiration rate decreased substantially plant resistance increased up to five fold.

This paper presents some comparative results of the resistance to water flow in the soil-plant system for indoor grown corn plants (*Zea mays* L.; Hybrid United 108). It also indicates how plant resistance changes as plants undergo water stress, dealing with the possible causes of the non-linearity between transpiration rate and leaf-to-soil water potential difference.

## **MATERIAL AND METHODS**

Corn plants (*Zea mays* L.; Hybrid United 108) were grown in a greenhouse environment in plastic pots with dimensions 0.26 x 0.20 x 0.20m. Air temperature in the growth room was 25/20 ± 1°C (day/night cycle) and relative humidity 65% ± 5%. The plants were grown in two media: (1) a coarse silica sand with particle diameter of 2mm, and (2) a mixture (4:1) of soil (Guelph Loam) and Turface (soil amendment). Plants were supplied with a modified Hoagland's nutrient solution which had an osmotic potential of -0.08 MPa. Plants growing in the soil mixture were watered with this solution every two

days, whereas plants growing in the silica sand were watered daily during the morning with nutrient solution and every two days in the afternoon with pure water.

Four days before the experiments started, plants were transferred from the greenhouse environment to a growth cabinet. Air temperature inside the growth cabinet was  $25/22 \pm 1^\circ\text{C}$  for light/dark periods. The relative humidity was  $70 \pm 5\%$  and the duration of the light period was 12 hrs.

Plants used in the experiment were divided in two groups, one with 14 plants which were relatively older (55-70 days after emergence) and height 0.80 to 1.00 meters. The other group was formed by 25 plants with 45 to 50 days after emergence and height 0.50 to 0.60m.

Leaf water potential was measured with leaf hygrometers (NEUMANN & THURTELL, 1972). The hygrometers were attached to the distal end of the most expanded upper leaf and water potential was monitored continuously until plants showed wilting aspects.

Root water potential was measured with a modified version of the leaf hygrometer (BRUNINI & THURTELL, 1981). The hygrometers were attached to the roots, allowing continuous monitoring of the status of the water in the roots of a transpiring plant. All measurements of root water potential were made on the main roots which extended till the bottom of the pot and which diameters ranged from 0.3 to 0.5cm. Hygrometers were attached to the roots 10 to 15cm from the top of the soil surface.

Two kinds of root water potential measurements were taken. In one case the root cortex was left intact, and the corresponding values were named water potential of the root epidermis, ( $\Psi_{RO}$ ). For some plants part of the root cortex was removed by cutting a slice 1 mm thick and 2-3mm long, parallel to the root axis, and this part with the cortex removed was faced toward the hygrometer cavity. These values were named root water potential at the inner part of the root, or root xylem water potential ( $\Psi_{RX}$ ).

Soil water potential was measured with a soil hygrometer (BRUNINI & THURTELL, 1982). This device has a porous silver membrane as the hydraulic connection between the soil and the measuring cavity, allowing continuous monitoring of the water potential in the root zone and minimizes thermal gradient from soil to the measuring device.

## **Experimental Procedure**

In order to attain steady state situations the devices for measuring root, leaf and soil water potentials were attached to the plant or inserted into the soil one day prior to the beginning of the measurements. The relationship between water potential difference in the soil-plant system and transpiration rate was determined by submitting the plants to two conditions of water stress. One

treatment consisted of exposing the plants during light periods to a constant light intensity of  $200\text{W m}^{-2}$ , measured at the top of the plants and  $0.60\text{m}$  below the lights. Measurements of plant transpiration and water potential were taken daily in a 2 hours interval using plants which phenological stage were from 55 to 70 days after emergence. Every morning, before the lights were switched on, leaf and soil water potential were measured to determine if there was a non zero off-set on plant and soil water potential at zero transpiration rate.

In another treatment, plant transpiration rate was modified by changing the light intensity in the growth cabinet. Plants were exposed daily to three different irradiance levels ( $120$ ,  $250$  and  $400\text{W m}^{-2}$ ), and they were allowed to remain up to two hours at each new light regime, before transpiration and water potential measurements were made. Water potential and transpiration rate were recorded at 15 to 20 minutes intervals, obtaining at least four readings for each corresponding light intensity. Plants used in this experiment were 45 to 50 days old.

Watering was withheld at the beginning of both set of treatments and the plants were studied during a drying cycle, which generally lasted from 4 to 5 days depending on the media they were grown. Both set of studies (constant and variable light intensity) were performed using 14 and 25 corn plants respectively. Plastic pots were set in polyethylene bags, whose open end was sealed to the stalk with masking tape during the measuring periods and left open overnight to avoid an excess of  $\text{CO}_2$  accumulation around the roots. Total water loss was measured with the plants sitting on a scale which had an accuracy of  $0.1$  gram. Water loss was converted to transpiration rate per unit of leaf area per unit of time ( $\text{g dm}^{-2} \text{h}^{-1}$ ). Plant leaf area (TA) was the sum of the area of each individual leaf which was determined by the methodology proposed by FRANCIS et al. (1969).

Plant resistance to water flow in a steady-state situation was determined according to Ohm's law:

$$T = \frac{Y_L - Y_S}{R_G} \quad (1)$$

where  $T$  is the measured transpiration in a given time interval,  $\Psi_L$ , and  $\Psi_S$  are leaf and soil water potential respectively, and  $R_G$  resistance to water flow from soil to leaf.

Individual resistances in the soil plant system under steady state condition were based on

$$T = \frac{Y_L - Y_{RX}}{R_p} - \frac{Y_{RX} - Y_{RO}}{R_r} - \frac{Y_{RO} - Y_S}{R_s} \quad (2)$$

where  $\Psi_L$ ,  $\Psi_{RX}$ ,  $\Psi_{RO}$  and  $\Psi_S$  are respectively the water potential of the leaf, the root xylem, root epidermis and soil, and  $R_p$ ,  $R_r$  and  $R_s$  the hydraulic resistance to water flow within the plant, across the root and from soil to root surface.

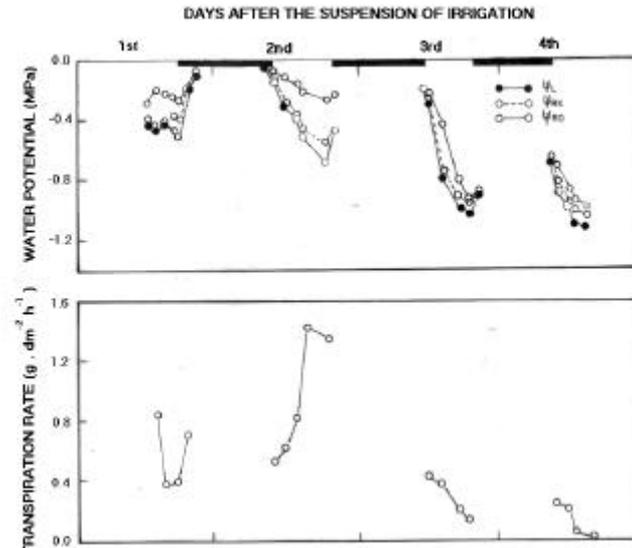
## RESULTS AND DISCUSSION

### Water potential difference and transpiration rate

The results indicated that the water potential difference from root xylem ( $\Psi_{RX}$ ) to root epidermis ( $\Psi_{RO}$ ) was much greater than the water potential difference from root xylem to leaf as (Figure 1). This is an indication that a high resistance to water flow was located in this pathway. It was also observed that leaf and root water potentials approached the same value after a few hours in the dark. Figure 1 indicates that when leaf water potential was greater than  $-0.8\text{MPa}$  transpiration rate increased probably due to an increase in the driving force.

When leaf water potential values were below  $-0.8\text{MPa}$ , it is observed a negative effect over the transpiration, which decreases, probably not only due to an increase in the stomatal resistance related to the leaf water deficit but also probably due to the effects of low soil water potential on the stomatal behaviour which induces an increase in the resistance and a decrease in the transpiration rate.

Figure 2 represents the pattern of the resistance to water flow from root epidermis to root xylem, and from root xylem to leaf, according to Ohm's Law for a specific plant during one drying cycle under constant light level. On the first day, the resistance showed a small net increase indicating some cycling in root resistance, but the trend was not steady. As the water stress became more severe, this tendency to cycling disappeared and the resistance increased steadily throughout the day. This diurnal variation (cycling) in root resistance has already been observed for cotton plants (SKIDMORE & STONE, 1974) and coffee plants (MEINZER et al., 1990).



**Figure 1.** Daily variation in leaf ( $\Psi_L$ ), root ( $\Psi_{RO}$ ), root xylem ( $\Psi_{RX}$ ) water potential, and transpiration rate for indoor grown maize plant, at a constant irradiance level ( $250\text{Wm}^{-2}$ ). Horizontal bars represent night period (lights off).

The relationship between transpiration rate and water potential difference from leaf to root, root to soil, and, across the root for the variable irradiance experiments is shown on Figure 3 for 4 plants. The results indicated that a linear relationship could be fitted for a given set of values with a determination coefficient ( $R^2$ ) ranging from 0.80 to 0.90 (Figure 3). It is also observed that the slopes of the lines fitting water potential difference and transpiration rate change as plants undergo water stress. This may indicate that plant resistance to water flow was changing due to water stress or even due to metabolic processes.

From these set of treatments (constant and variable light intensity) it was possible to estimate the water potential difference from leaf to soil at zero values of transpiration rates. Under constant light intensity, this water potential difference was measured before the lights were switched on in the morning and for the variable light intensity treatment this value was estimated as the intercept of the regression lines fitting water potential difference and transpiration rate (Figure 3).

**Figure 2.** Daily variation of the resistance to water flow from root epidermis to root xylem for indoor grown maize plant at a constant irradiance ( $250\text{Wm}^{-2}$ ). Horizontal bars represent night period (lights off).

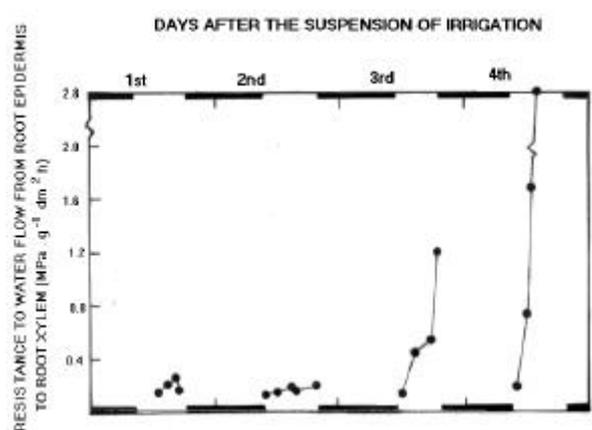
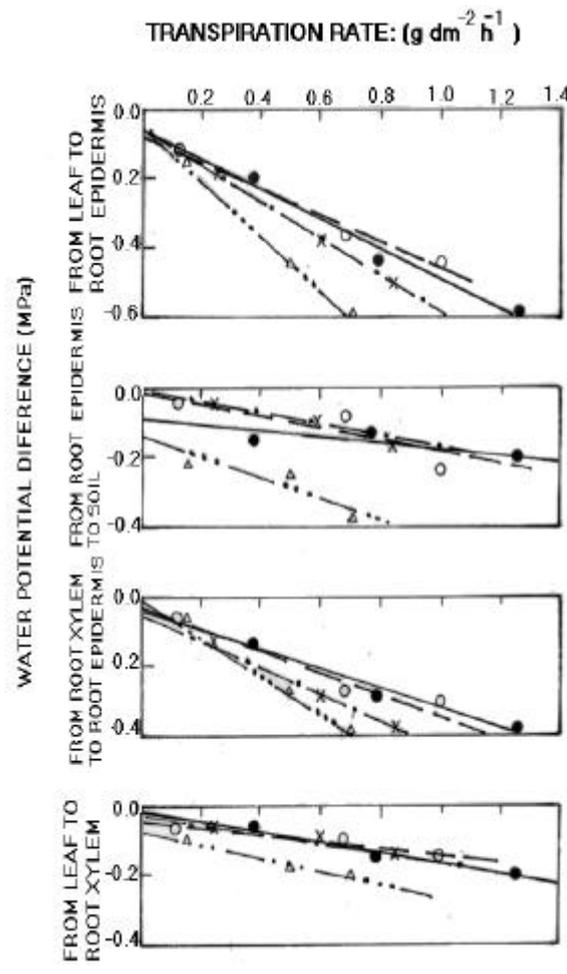


Figure 3. Transpiration rate and water potential difference for indoor grown maize plants at variable light intensities (120, 250 and 400Wm<sup>-2</sup>). The lines represent 4 different plants (●----● plant 1; ○---○ plant 2, x---x plant 3, Δ---•---Δ plant 4).



Several researchers have dealt with this off-set at zero transpiration rate (JOSIS et al., 1983; MEINZER et al., 1990; ERDEI & TALERNIK, 1993). These authors have discussed the changes in water relations of plants concerning osmotic adjustment or internal changes in hydraulic conductivity of xylem vessels.

All estimatives of plant resistance to water flow were made considering that the water-absorbion rate (A) by the plant was always equal to the measured transpiration rate (T). This similarity can only be assumed at high values of transpiration where the absorbed water which plant uses for growth is negligible compared to the transpiration rate (BOYER, 1974).

In a general situation, the transport of water from soil to leaf may be expressed as a mass budget, described by:

$$A = T + G \quad (3)$$

when  $T \gg G$ ,  $T$  may be used to calculate the “true” plant resistance to water flow, and the denotation “true” refers to the value of the plant resistance which is closer to the real, because any error for not including the water used for growth is negligible. In the present situation the true resistance was estimated at high values of transpiration rate (irradiance levels above  $400\text{W m}^{-2}$ ) or transpiration rate recorded at leaf water potentials below  $-0.4\text{MPa}$ .

Using this technique, the water plant used for growth, could be estimated as:

$$G = Ae - T \quad (4)$$

where,  $G$ ,  $Ae$ ,  $T$  are the flux per unit of leaf area ( $\text{g m}^{-2} \text{h}^{-1}$ ), respectively of the water used for growth, water absorbed from the soil and the measured transpiration rate.

**Table 1.** Water potential difference from leaf to soil observed at zero transpiration rate for indoor grown corn plants, United 108.

Event	Dark measurements			Regression lines		
	N	X	$S_m$	N	X	$S_m$
$\Psi_L - \Psi_{RX}$	9	-0.006	0.004	25	-0.023 <sup>a</sup>	0.011
				25*	-0.026 <sup>a</sup>	0.013
$\Psi_{RX} - \Psi_{RO}$	10	-0.003	0.004	13	-0.067 <sup>b</sup>	0.021
				13	-0.016 <sup>a</sup>	0.011
$\Psi_{RO} - \Psi_S$	7	-0.016	0.013	19	-0.095 <sup>b</sup>	0.012
				19*	-0.017 <sup>a</sup>	0.015

N- number of events; X- mean;  $S_m$ - standard error of the mean;  $\Psi_L$ - leaf water potential (MPa);  $\Psi_{RX}$ - root xylem water potential (MPa);  $\Psi_{RO}$  – root epidermis water potential (MPa);  $\Psi_S$ - soil water potential (MPa)

\* - values obtained when the correction in the transpiration rate for plant growth was made

a- values not different from zero at 90% confidence level; b- values different from zero at 90% confidence level

Except in four cases where the estimated growth was greater than  $0.10\text{g dm}^{-2}\text{h}^{-1}$ , the results indicated that the average crop growth of the remaining 11 plants was  $0.0287\text{g dm}^{-2}\text{hr}^{-1}$ , with a standard error of the mean of 0.007. When this estimated growth was added to the transpiration rates, the intercepts of the regression lines fitting transpiration rate and water potential difference were no longer statistically different from zero (Table 1).

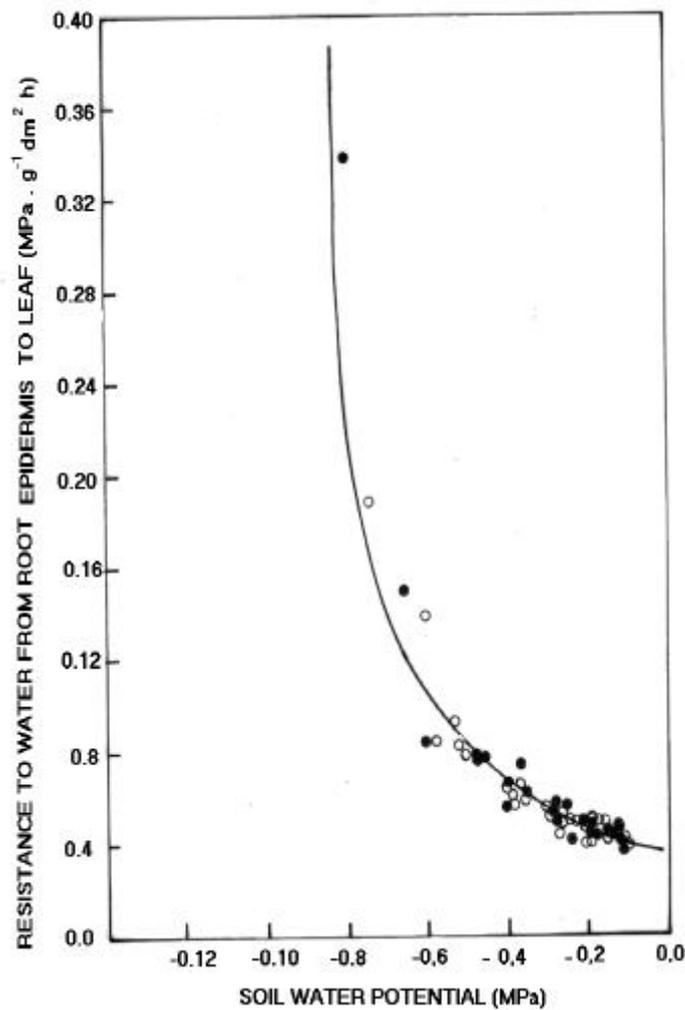
### **Resistance to water flow in the soil-plant system versus soil water potential**

The global resistance to water flow in the plant from root epidermis to leaf is presented on Figure 4. It shows an increase in plant resistance as soil water content decreases. The resistance to water flow from root xylem to leaf remained constant until a soil water potential of  $-0.2\text{MPa}$ , but increased markedly at soil water potential below this value (Figure 5).

The resistance to water flow from root epidermis to root xylem as soil water potential decreases, is described on Figure 6. The soil hydraulic resistance to water flow from soil to root surface also increased as the available soil water was depleted (Figure 7), indicating that the increase in resistance is mainly governed by the soil hydraulic conductivity which decreases exponentially as the soil water content decreases.

The results showed a large variation in soil resistance when soil water potential was greater than  $-0.2\text{MPa}$ . Some of these values correspond to the constant light experiments where most of the plants were grown in silica sand in which the decrease in hydraulic conductivity with decreasing water content is faster than in soils. RUNNING (1980), observed that for *Pinus contorta* soil and root resistance are both important in governing plant water uptake. Increase in plant resistance to water flow due to water stress might be related to root tissue suberization (PETERSON & STEUDLE, 1993) or due dry conditions in the region of soil surrounding the roots (PETRIE & HALL, 1992; PETRIE et al., 1992).

The results obtained in this study agree with the results of PETERSON et al. (1993), who affirm



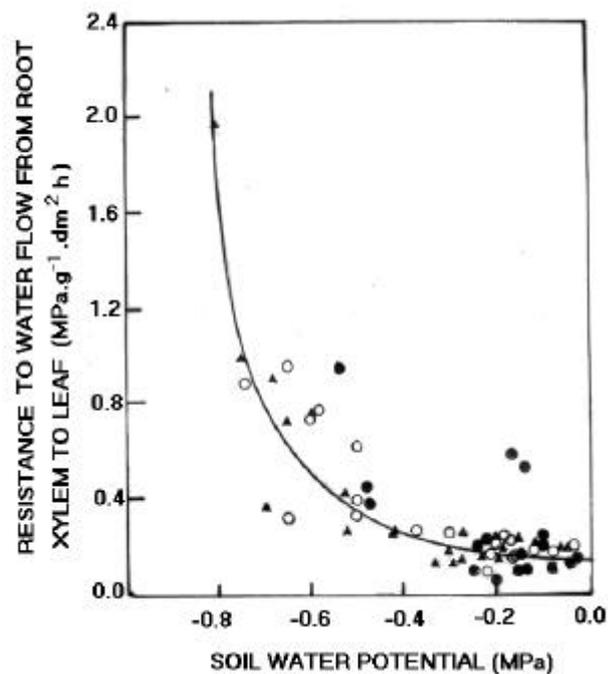
**Figure 4.** Resistance to water flow from root epidermis to leaf, as a function of the soil water potential for indoor grown maize plants. (Symbols represent different combinations of  $\Delta \Psi$  and T).

that the main barrier to radial flow in maize and onion roots is located in the endodermis. MELCHIOR & STEUDLE, (1993) have also observed that the radial movement of water in the roots is the major constriction to water uptake by plants. The variable root resistance is closely correlated to changes in root structure and to changes in both pathways used for water movement: the axial transport in the vessels or the radial movement across the root (BIZZARD & BOYER, 1971).

Plant resistance is mainly the resulting of the combination resistance from root xylem to leaf and to the radial movement across the roots. The comparative resistances to water flow in the SPAC are presented in Figure 8. These values indicate that resistance to water flow throughout the plant was greater

than soil resistance until a soil water potential of 0.60MPa, below this value soil resistance became more important

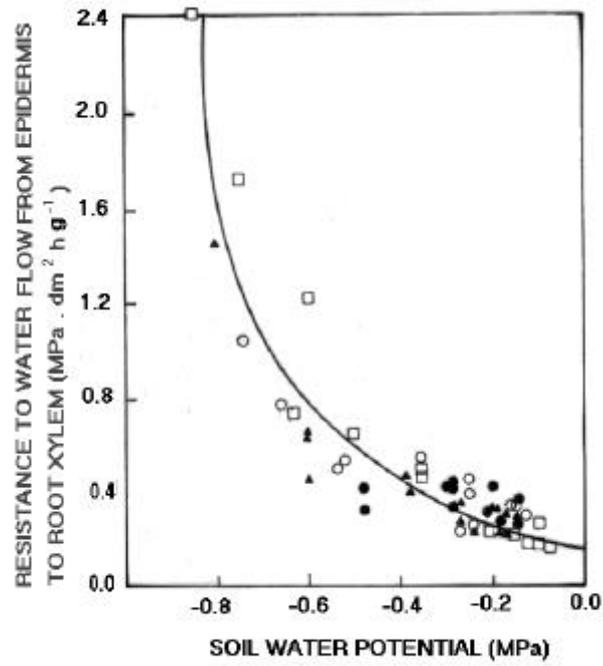
than plant resistance. There is an indication that when soil water potential is  $-0.40\text{MPa}$  or higher, the resistance to water flow radially across the root (from root epidermis to root xylem) was greater than soil resistance, but below this value ( $-0.40\text{MPa}$ ) soil resistance became the limiting factor. Similar observation were also pointed out for millet and cowpea (PETRIE et al., 1992), as well as in a general discussion on computer simulation models used to describe water uptake by plants (HAINSWORTH & AYLMOORE, 1989).



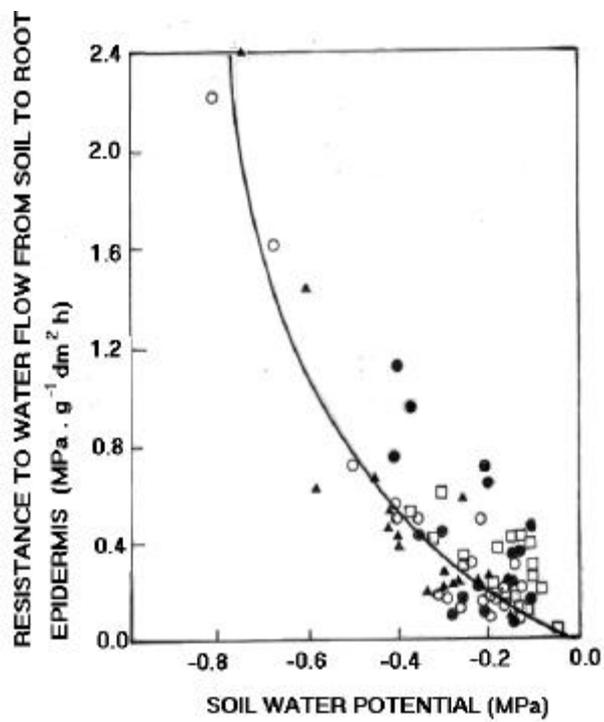
**Figure 5.** Resistance to water flow from root xylem to leaf as a function of soil water potential for indoor grown maize plants ( $\bullet 400 \text{ Wm}^{-2}$ ,  $\circ 250 \text{ Wm}^{-2}$ ,  $\blacktriangle 120 \text{ Wm}^{-2}$ )

### Acknowledgements

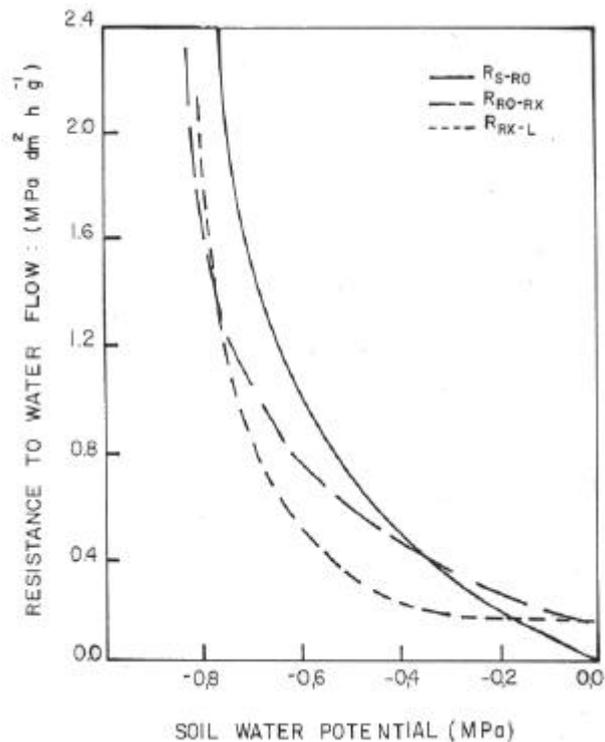
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**Figure 6.** Resistance to water flow from root epidermis to root xylem as a function of the soil water potential for indoor grown maize plants ( $\bullet$ 400Wm<sup>-2</sup>,  $\circ$ 250Wm<sup>-2</sup>,  $\blacktriangle$ 120Wm<sup>-2</sup>,  $\square$  constant light irradiance).



**Figure 7.** Resistance to water flow from soil to root epidermis as a function of the soil water potential for indoor grown maize plants ( $\bullet$ 400Wm<sup>-2</sup>,  $\circ$ 250Wm<sup>-2</sup>,  $\blacktriangle$ 120Wm<sup>-2</sup>,  $\square$  constant light irradiance).



**Figure 8.** Comparative resistances to water flow in the various part of the soil plant system as a function of the soil water potential for indoor grown maize plants ( $R_{S-RO}$  – resistance from soil to root epidermis;  $R_{RO-RX}$  – resistance from root epidermis to root xylem, and  $R_{RX-L}$ , resistance from root xylem to leaf).

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