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Response of the water status of soybean to changes in soil water potentials controlled by the water pressure in microporous tubes

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ABSTRACT

Water transport through a microporous tube–soil–plant system was investigated by measuring the response of soil and plant water status to step change reductions in the water pressure within the tubes. Soybeans were germinated and grown in a porous ceramic 'soil' at a porous tube water pressure of –0·5 kPa for 28 d. During this time, the soil matric potential was nearly in equilibrium with tube water pressure. Water pressure in the porous tubes was then reduced to either –1·0, –1·5 or –2·0 kPa. Sap flow rates, leaf conductance and soil, root and leaf water potentials were measured before and after this change. A reduction in porous tube water pressure from –0·5 to –1·0 or –1·5 kPa did not result in any significant change in soil or plant water status. A reduction in porous tube water pressure to –2·0 kPa resulted in significant reductions in sap flow, leaf conductance, and soil, root and leaf water potentials. Hydraulic conductance, calculated as the transpiration rate/$\Delta\psi$ between two points in the water transport pathway, was used to analyse water transport through the tube–soil–plant continuum. At porous tube water pressures of –0·5 to –1·5 kPa soil moisture was readily available and hydraulic conductance of the plant limited water transport. At –2·0 kPa, hydraulic conductance of the bulk soil was the dominant factor in water movement.

Key-words: conductance; microporous tubes; sap flow; soil desorption relation; transpiration; water potential.

INTRODUCTION

An irrigation system has been developed that uses microporous materials to control the delivery of water and nutrients to plants. The system, as it was first conceived by Wright, Bausch & Knott (1988), used hydrophilic microporous membranes to maintain liquid and gas phase separation and control fluid flow in microgravity. Water was circulated around the membranes under a slight negative pressure and delivered to plant roots inside the membrane by capillary action through the pores. Since then the use of microporous ceramic or stainless steel tubes, with pore diameters in the 5–50 μm range, has replaced membranes, overcoming the difficulties of working with membranes (Dreschel & Sager 1989; Tibbitts, Cao & Frank 1995). The result of this research has been the development of several microporous tube culture systems for use on the Space Shuttle or Space Station (Dreschel *et al.* 1994; Morrow *et al.* 1994).

The use of microporous materials to control water delivery to plants is not new. Studies of plant response to drought have been limited by the ability to control the water potential of the soil in which plants are growing. In an attempt to control soil water potential, several researchers describe a system in which plants were grown in a thin layer of soil held within a membrane that was suspended in solutions of known osmotic potential (Painter 1966; Tingey & Stockwell 1977). The limitations of this system included the short life of the membrane and difficulties in maintaining low soil water potentials due to the correspondingly low hydraulic conductivity of the membrane and soil.

There have been other approaches to maintaining a constant soil water potential (Kramer & Boyer 1995). Suspension of pots over a column of water has met with variable success. Another approach has been the placement of plants in a nutrient solution containing substances such as NaCl or polyethylene glycol that lower the water potential to a predetermined level. Absorption by plants or toxicity to plants has been a problem with this technique (Tingey & Stockwell 1977).

Because of difficulties in maintaining a constant soil water potential, the most common approach to studying plant response to drought has been to grow plants in soil which is allowed to dry down over time. Roots are exposed to a variety of soil moistures, both in space and with time, during the drying process.

The development of the microporous tube irrigation system for plant production in bioregenerative life support systems has also created a new opportunity for the study of plant water relations in a situation where the soil water potential can be controlled, at tensions very close to zero. Until recently plants had been grown in this system using only hydroponic nutrient solution. Seeds were germinated directly on the tubes, and the subsequent root growth wrapped around the tubes. Berry *et al.* (1992) and Dreschel & Sager (1989) reported 30–40% reductions in wheat yield

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Conclusions

Although strong effects of soil CO_2 concentrations on root respiration and plant growth have been reported, the present data clearly show that there is no such effect for either citrus or bean. This was true for both short- and long-term effects as well as for the growth and maintenance components of root respiration. To prevent artifacts when using other species, it is necessary either to measure root respiration at natural CO_2 concentrations or thoroughly to evaluate the sensitivity of root respiration to soil CO_2 concentration, as shown in this study. Erroneous measurements can have a major impact on models describing carbon budgets of whole plants, ecosystems, and plant responses to stress.

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with porous tube water pressures below –0·4 kPa. It is likely that root water uptake was limited by the surface area of the tubes.

When soil is placed in contact with the microporous tubes in a closed system, the matric potential of the soil will equilibrate with the water pressure in the porous tubes within several hours. By adjusting the porous tube water pressure one can change, in a controlled manner, the matric potential of the soil. In reality, a true equilibrium may not exist for several reasons. On Earth, the effect of gravity on soil matric potential is 0·01 kPa mm^{-1} (Nobel 1991). Cao & Tibbitts (1996) measured the vertical gradient of matric potential in a 4-cm-deep soil profile and found it to range from –0·35 kPa at the bottom to –0·75 kPa at the top of the profile for a porous tube water pressure of –0·5 kPa. When plants are added to the porous tube–soil system, transpiration creates a gradient for water flow from the tubes to the roots. Lastly, the range of pressures for which the porous tube system can adequately control soil matric potential depends on the hydraulic conductance of the tube and soil.

There is still little detailed information on water transport within the porous tube–soil–plant continuum. Therefore, the primary objective of this research was to study the dynamics of water transport in the porous tube–soil–plant system and to determine operational limitations, if any. This required us to take a new look at an old issue, namely the role of soil water transport and physical characteristics in plant water relations and plant response to drying soil. More specifically, we re-examined the controversy of whether the plant (Blizzard & Boyer 1980), the soil (Gardner 1965; Passioura 1980), or the interface between the two (Herkelrath, Miller & Gardner 1977a,b; Faiz & Weatherly 1978) most strongly influences hydraulic conductance of the water transport pathway. These questions were addressed by measuring the change in soil and plant water relations in response to step change reductions in water pressure within the porous tubes.

MATERIALS AND METHODS

Irrigation system

The porous tube irrigation system was based on the design of, and operated in a similar fashion to, that reported by Tibbitts *et al.* (1995). It consisted of stainless steel porous tubes (Mott Metallurgical Corp., Farmington, CT, USA) with a pore diameter of 40 μm, and an air entry pressure of –2·2 to –2·8 kPa. Distilled water flowed through the tubes at 220 ± 7 cm^3 min^{-1} under a slight negative pressure which was maintained by use of a siphon.

The siphon was created from a difference in height between the constant water level (head) in the supply reservoir and the outlet in the return reservoir (Δh_1) (Fig. 1). Water flowing through the porous tubes was under a tension because the water level in the supply reservoir (Δh_2) and the level of the outlet in the return reservoir were lower than the height of the porous tubes. The water pressure and flow rate were adjusted by the changing the height of the supply and return reservoirs with respect to the porous tubes, and to each other (Δh_1, Δh_2). Water was delivered to soil and/or plant roots by capillary action through the pores. For pressures of –0·5 to –2·0 kPa, water flux radially through the porous wall of a tube was measured by wrapping an 1800 mm^2 piece of dry absorbent paper around the tube and measuring the gain in water weight with time (Table 1) (Dreschel & Sager 1989).

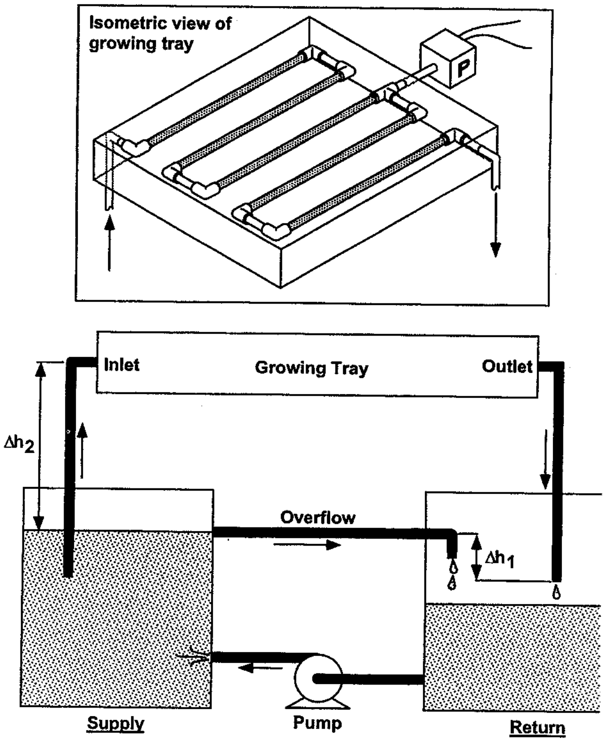

Figure 1. Diagram of the porous tube irrigation system. Water flows through the system by a siphon created from a difference in height between the water level in the supply and the outlet in the return reservoirs (Δh_1). The water flowing in the tubes is under a tension because the height of both the supply and return reservoirs is below that of the tubes. The water flow rate and pressure can be adjusted by changing the height of Δh_1 and Δh_2. Continuous pumping of water from the return to supply reservoir maintains a constant pressure head. Porous tubes are shown as shaded tubes. P = pressure transducer.

Because the system was operated in a siphon mode it was extremely sensitive to air bubbles breaking the suction. We connected the porous tubes in series (Fig. 1) so that any air bubbles entering the system were pushed through the tubes and were unlikely to collect in the corners of a manifold. The pressure drop from the centre of the five tubes in series to one end was 0·14 kPa at a flow rate of 200 cm^3 min^{-1}. During the experiment the water pressure within the tubes was checked daily using a pressure transducer (MPX2010, Motorola, Phoenix, AZ, USA) located near the centre of the series of tubes.

Polyvinyl chloride (PVC) trays with inside dimensions of 33 × 33 × 9·5 cm were used to grow plants. Each tray contained porous tubes, 5–28·5 cm long and 9·5 mm OD, held together by quick disconnects and polyethylene tubing.

Table 1. Comparison of soil hydraulic conductivity and the radial flow rate through microporous tubes for water pressures of –0·5, –1·0, –1·5 and –2·0 kPa

Porous tube water pressure (kPa)	Soil hydraulic conductivity[1] ($m\ s^{-1}$)	*Flow rate/unit tube surface area* ($m\ s^{-1}$)[2] Soybean transpiration[3]	Absorbent paper[4]
–0·5	$5{\cdot}7 \times 10^{-4}$	$8{\cdot}2 \pm 1{\cdot}3 \times 10^{-7}$	$2{\cdot}1 \pm 0{\cdot}19 \times 10^{-4}$
–1·0	$2{\cdot}5 \times 10^{-4}$	$1{\cdot}2 \pm 0{\cdot}17 \times 10^{-6}$	$6{\cdot}3 \pm 1{\cdot}3 \times 10^{-5}$
–1·5	$9{\cdot}0 \times 10^{-7}$	$9{\cdot}4 \pm 2{\cdot}1 \times 10^{-7}$	$3{\cdot}5 \pm 0{\cdot}52 \times 10^{-5}$
–2·0	$2{\cdot}9 \times 10^{-10}$	$4{\cdot}6 \pm 2{\cdot}2 \times 10^{-7}$	$1{\cdot}1 \pm 0{\cdot}42 \times 10^{-5}$

[1] Data from Fig. 2.

[2] Water flowed radially out of the tube in response to a water potential gradient between tube water pressure and the surrounding medium. Data are means ± 1 standard deviation.

[3] Transpiration data were taken from stem gauge measurements made between 1200 and 1300 h. Data were normalized on a tube surface area per tray basis ($n = 3$).

[4] Liquid flow through porous tubes into dry absorbent paper ($n = 9$).

The porous tubes were held in place 4–5 cm apart, 4 cm above the bottom of the tray by containing the ends and quick disconnects in 4 × 2·5 × 4 cm U-shaped PVC which rested on 2 × 2 cm PVC square tube. The tubes were connected to the supply and return reservoirs with 3·63 m of 9·5 mm OD black polyethylene tubing. The functional rooting volume of the tray was 7277 cm^3.

Growth conditions

Three trays were placed at one of three locations in the centre of a Conviron E15 growth chamber (Conviron, Asheville, NC, USA). Twenty-two Sierra slow release fertilizer tablets (16-8-12 + minors) (Scotts Sierra Horticultural Products Co., Marysville, OH, USA) were spaced evenly on the bottom of the trays to provide nutrients to the plants. The trays were filled with 7·5 dm^3 of Profile™, a porous ceramic aggregate 'soil' (AIMCOR, Deerfield, IL, USA), that had been thoroughly rinsed with distilled water. The soil was covered with white-outer-surface, black-inner-surface plastic that contained six small openings for plants. The water pressure in the tubes was initially set at –0·5 kPa, the highest pressure that could be used without excess water draining from the media. At this pressure the dissolved oxygen concentration in the soil, as measured by an Orion dissolved oxygen probe (model 840, Orion Research Incorporated, Boston, MA, USA), was at saturation. The soil and porous tubes were allowed to equilibrate until the soil matric potential and tube water pressure were in equilibrium.

Soybean (*Glycine max* cv. PI494·525) was planted at three seeds per location and thinned to six plants per tray, or a planting density of 60 plants m^{-2}. The plants were grown under a 14 h photoperiod with 26 °C light/22 °C dark and 70% relative humidity. The photosynthetically active radiation (PAR) (high-pressure sodium and metal halide lamps) at canopy height was 1150 ± 50 $\mu mol\ m^{-2}\ s^{-1}$. The metal halide lamps were turned off 10–17 d after planting to encourage elongation of the main stem for attachment of heat balance stem gauges. The PAR during this time was 600 ± 50 $\mu mol\ m^{-2}\ s^{-1}$.

The plants were germinated and grown for 28 d at a porous tube water pressure of –0·5 kPa. Intensive measurements of plant water use and water status were made for 6 d (plant age 29–34 d). The intensive measurement period began when the diameter of the main stems was sufficient for attachment of heat balance stem gauges. Midway through the intensive measurement period, at 1330 h on day 3 (plant age: 31 d), the water pressure in the porous tubes was reduced from –0·5 kPa to either –1·0, –1·5 or –2·0 kPa. The intensive measurement period was intentionally kept short so that changes in plant growth, such as root:shoot ratio or root length, would not be an important factor in the response of the plants to a rapid step change in soil matric potential.

Plant water use and water status

The water use of all plants in each tray, reported on a leaf area basis, was measured from pre-dawn readings of the water level in the return reservoir (Fig. 1). Water loss from this reservoir is an indicator of plant transpiration and water stored in the plants; water gain in this reservoir occurs when water moves from the soil into the tube in response to a reduction in porous tube water pressure.

Individual plant water use, expressed on a leaf area basis, was measured using stem gauges (model SGA5, Dynamax, Houston, TX, USA) attached to the main stem of one plant in each tray. Sap flow was measured using a heating power of 0·08 W, the lowest pre-dawn values for the sheath conductance (Steinberg, van Bavel & McFarland 1989), and the average of beginning and ending values of stem diameter. Prior to the experiment, water use of soybean in individual pots measured gravimetrically was compared with that obtained from the stem gauges using sheath conductance values obtained pre-dawn or by enclosing the plant in a plastic bag (Steinberg *et al.* 1989). Use of the lowest pre-dawn value of sheath conductance to compute sap flow gave 24 h plant water use that was within ±10% of gravimetric measurements.

On days 1, 2, 4 and 5 of the intensive measurement period (plant age: 29, 30, 32 and 33 d) leaf and root water potentials were measured at 1200 h. At this time the transpiration rate had been stable for several hours after the beginning of the light period. Root water potential was measured using the isopiestic technique corrected for the heat of respiration (Boyer 1995). A small sample of root was quickly removed from each tray, gently shaken to remove soil particles and loaded into the thermocouple chamber. Small soil particles adhering strongly to the roots were not removed. In order to minimize disturbance to the plants, excessive digging to obtain roots from precise locations was not carried out. In all likelihood, most of the roots sampled were those growing in the upper half of the tray in between the porous tubes. Leaf water potential was measured with a pressure chamber (model 3000, Soil Moisture Equipment Corporation, Santa Barbara, CA, USA) on fully mature leaves from the upper canopy. It had previously been determined that leaf water potentials measured by pressure chamber and the isopiestic technique were not significantly different, a result also obtained by Boyer & Ghorashy (1971). Immediately after water potential measurements, the conductance of individual leaves from a similar location was measured with a steady-state porometer (LI1600, LICOR, Lincoln, NE, USA) on 5–7 leaves per tray. On days 3 and 6 (plant age: 31 and 34 d) root and leaf water potential measurements were made as described above at 0830 h (pre-dawn).

Hydraulic conductance (H_c) (m s^{-1} MPa^{-1}) through various segments of the tube–soil–plant continuum was calculated as:

$$H_c = \text{transpiration rate}/\Delta\psi, \qquad (1)$$

where $\Delta\psi$ was obtained from water potential measurements taken in the light described earlier (MPa), and the transpiration rate for the corresponding time period was taken from stem gauge measurements expressed on a leaf area basis (m s^{-1}). The porous tube water pressure and soil matric potential were used to calculate the potential gradients between the tube and soil, or within the soil. Water potential measurements were used to calculate potential gradients between the soil and plant, and within the plant. Hydraulic conductance of the roots and leaves was represented as soil-to-root and soil-to-leaf, because at porous tube water pressures of –2·0 kPa there were large gradients in soil matric potential within several mm of a tube, and root water potentials were not location-specific. Hydraulic conductances in the –1·0, –1·5 and –2·0 kPa treatments were measured on day 5 of the intensive measurement period, 2 d after the step reduction in porous tube water pressure.

Passioura (1984) discusses several inadequacies of Eqn 1, including non-linearity. Potential sources of error were minimized by using transpiration and water potential measurements taken at the same time every day when the transpiration rate had been steady for several hours. In addition, water transport properties of the soil were well defined.

Soil water relations

Physical, water-holding and water-transport characteristics of the soil are shown in Table 2 and Fig. 2. Saturated hydraulic conductivity was determined by the falling head method. The desorption relation was obtained by hanging column from 0·49 to 1·96 kPa, by tempe cell from 2·75 to 80 kPa, and by pressure chamber from 150 to 400 kPa. These measurements were made for us by Turf Diagnostics and Design (Olathe, KS, USA). Unsaturated hydraulic conductivity as a function of the volumetric water content was calculated according to the method of Jackson (1972). The pore size distribution and volumetric water capacity were calculated according to Hillel (1980).

In a separate experiment, soybeans planted in small pots were used to determine the percentage of extractable soil water as described by Turner, Schultze & Gollan (1985) (Fig. 2). The soil surface of well-watered and -drained potted soybean plants was wrapped in plastic and sealed with tape to prevent evaporation. The pots were weighed twice daily until no further water loss from transpiration was recorded. Soybeans were able to remove ≈0·5 m^3 H_2O m^{-3} soil before senescence occurred.

The matric potential of the soil was measured by miniature tensiometers (2100F, Soil Moisture Equipment Corporation, Santa Barbara, CA, USA) (±3% accuracy) placed either midway between two tubes (2–2·5 cm from a tube), or next to a tube, at a depth of 4 cm. The soil matric potentials were recorded twice daily, at 0830 and 1330 h. The water potential of the soil was calculated from the sum of matric and osmotic potentials. Osmotic potential (ψ_{osmotic}) was obtained from the relation: $\psi_{\text{soil}} = \psi_{\text{osmotic}} + \psi_{\text{matric}}$, where ψ_{soil} was measured by the isopiestic technique (Boyer 1995). During the first 28 d of the experiment when the porous tube pressure was –0·5 kPa, ψ_{osmotic} of soil next to a tensiometer was measured 4 times and found to be steady at 0·28 ± 0·05 MPa. Immediately after the soybean plants were harvested, five soil samples taken from the growing trays were placed in pots containing tensiometers and the osmotic potential was obtained for different matric potentials between 0 and 60 kPa ($n = 45$). Soil water potential was obtained in this fashion because, at a porous tube water pressure of –2·0 kPa, soil matric potential changed rapidly within several mm of a tube and we did not want to disturb the soil in the vicinity of the tensiometers during the intensive measurement period.

The gradient in soil matric potential extending radially outwards from a porous tube was calculated using a version

Table 2. Physical characteristics of Profile™, a porous ceramic aggregate

Bulk Density[1]	0·63 g cm^{-3}
Particle Density[1]	2·48 g cm^{-3}
Particle Size Distribution[2]	0·25–1·0 mm
Total Pore Space[1]	74·6%
capillary[2]	39·0%
non-capillary[2]	35·0%

[1] Physical characteristics measured by Turf Diagnostics and Design, Olathe, KS, USA.

[2] Information obtained from AIMCOR, Deerfield, IL, USA.

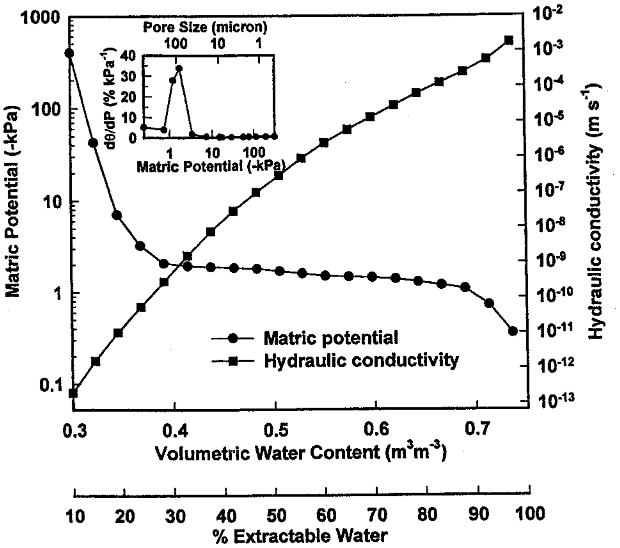

Figure 2. Matric potential (P) and calculated hydraulic conductivity as a function of water content (θ) and percentage extractable water for Profile™, a porous ceramic aggregate. The saturated water content was 0·75 m^3 m^{-3}; the corresponding hydraulic conductivity was $1{\cdot}7 \times 10^{-3}$ m s^{-1}. Inset: Volumetric water capacity ($d\theta/dP$) of Profile™ as a function of matric potential and calculated pore size.

of Darcy's law for the cylindrically symmetric case given by Nobel (1991):

$$P_{\mathrm{soil}} = \frac{\text{transpiration rate} \times r \times \ln(r_{\mathrm{soil}}/r_{\mathrm{tube}})}{K} + P_{\mathrm{tube}} \qquad (2)$$

where the transpiration rate is the same as that used to calculate Eqn 1, normalized on a porous tube surface area per tray basis (m s^{-1}), r is the radius of the porous tube (m), K is the hydraulic conductivity of the soil (m s^{-1}), P_{tube} is the matric potential of the soil (m) at the surface of the tube, P_{soil} is the matric potential of the soil (m) at various locations up to 25 mm away, r_{tube} is the radial distance (m) from the axis of the tube to the surface of the tube, and r_{soil} is the radial distance (m) from the axis of the tube to various locations in the soil up to 25 mm away. Equation 2 can be used if the transpiration rate and soil hydraulic conductivity are held constant for each applied porous tube water pressure. We also assumed that the soil matric potential at the surface of the tube equalled the water pressure inside. This equation is often used to describe water flow through the soil towards a root. In the present case it was used in reverse to describe the radial flow of water outwards from a porous tube to a distributed sink.

Biomass and root system characterization

On the third day after reducing the water pressure in the porous tubes (day 6 of intensive measurement regime; plant age: 34 d) the experiment was terminated due to severe leaf wilting and senescence in the −2·0 kPa treatment. The leaf area of each plant was determined using a leaf area meter (LI3100, LI-COR, Lincoln, NE, USA). The soil was removed from the roots and root length and volume were determined using the intersection and water displacement method, respectively (Böhm 1979). The dry weights of the leaves, stems and roots were then determined.

Data analysis

Each tray with its attending supply and return reservoir was an independent unit and represented one treatment (Jarrett & Chanter 1981). All plants were germinated and grown to experimental size at a porous tube water pressure of −0·5 kPa, which also served as the control. Each treatment, or reduction in tube water pressure, was blocked and replicated three times with time. Differences between treatments were analysed by analysis of variance.

RESULTS

During the time soybean was grown at −0·5 kPa, the matric potential of the soil was nearly in equilibrium with the tube water pressure (Fig. 3). The matric potential during the dark period was 0 to −0·5 kPa. In the light the matric potential ranged from −1·0 to −1·5 kPa due to transpiration rates of 110 ± 30 g m^{-2} h^{-1} (Fig. 4). It is possible that some of this diurnal change in matric potential may be due to heating and cooling of the water within the tensiometers. There was no significant difference in matric potential of the soil next to the tubes or between the tubes. Soil matric potentials, calculated from Eqn 2, similarly show no significant difference in matric potential with distance from a porous tube (Fig. 5). However, calculated matric potentials were not as low as those measured. This difference may be due to the accuracy of the tensiometers and unsaturated soil hydraulic conductivity.

At a porous tube water pressure of −0·5 kPa there was a small gradient in water potential from soil to root to leaf during the light period (Fig. 3). Soil water potentials were about −0·2 to −0·3 MPa, root water potentials were −0·3 to −0·4 MPa, and leaf water potentials were about −0·6 MPa. Pre-dawn measurement of water potentials showed that leaf water potential was commonly about 0·1 MPa lower than that of the soil.

A reduction in porous tube water pressure from −0·5 to −1·0 or −1·5 kPa did not change the water status of the plants. The soil matric potential was reduced to a slightly lower value of −1·5 to −2·0 kPa during the light period when plants were transpiring, but during the dark period it returned to 0 to −0·5 kPa. Matric potentials, calculated from Eqn 2, did not significantly change with distance up to 25 mm from a tube (Fig. 5). Leaf and root water potentials at −1·0 and −1·5 kPa were no different from those at −0·5 kPa. Sap flow rates were also unchanged. Leaf conductance was not affected by a reduction in tube water pressure from −0·5 to −1·0 or −1·5 kPa (Table 3). There was no difference in leaf conductance between plants at −1 or −1·5 kPa, nor were they significantly different from readings taken when the water pressure in the porous tubes was set to −0·5 kPa.

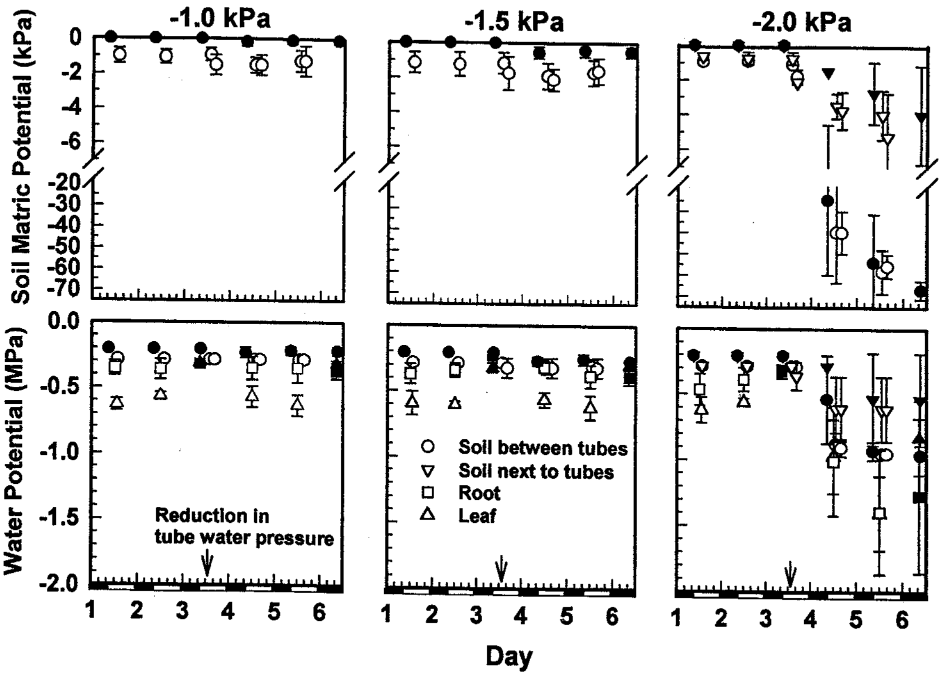

Figure 3. Soil matric potential (upper panels) and soil, root and leaf water potentials (lower panels) before and after a reduction in porous tube water pressure from –0·5 to –1·0, –1·5 or –2·0 kPa ($n = 3 \ldots 5$). Measurements of soil, root and leaf water potentials measured on days 1, 2, 4, and 5 were made in the light (open symbols); measurements on days 3 and 6 were made in the dark (closed symbols). Symbols represent means ± 1 standard deviation. The solid area indicates dark periods.

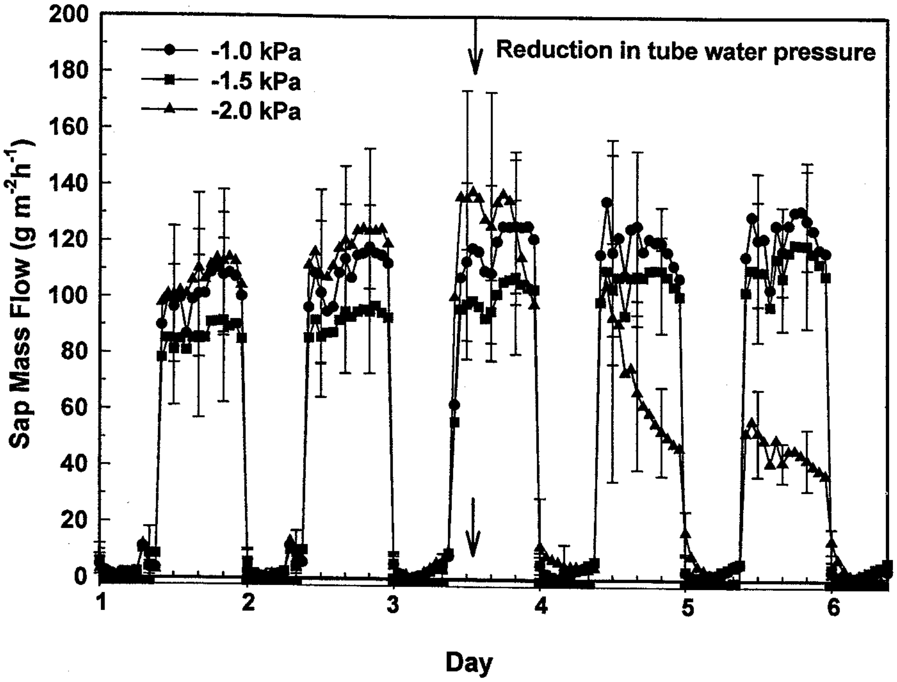

Figure 4. Sap mass flow rate through the main stem of soybean before and after a reduction in porous tube water pressure from –0·5 to –1·0, –1·5 or –2·0 kPa. Data are expressed on a leaf area basis. Symbols represent means ± 1 standard deviation ($n = 3$). The solid area indicates dark periods.

Total daily water use as measured by stem gauges on individual plants and the water level in the return reservoir representing the whole tray (Fig. 1) is compared in Fig. 6. The two measures of water use were not significantly different except on day 3, when porous tube water pressures were reduced. After the reduction in porous tube water pressure, water moved from the soil into the tubes and entered the return reservoir, offsetting that lost by transpiration. Hourly measurement of tray water use on day 3 of the intensive measurement regime is shown in Fig. 6. When the porous tube water pressure is reduced from –0·5 to –1·0 kPa, a small amount of water is pulled from the soil

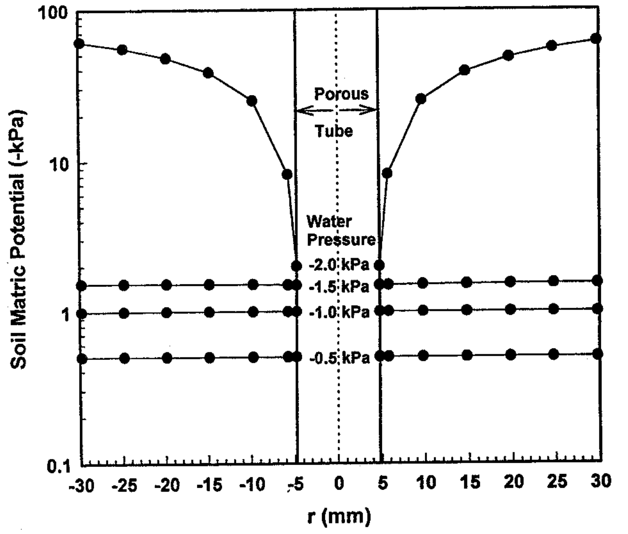

Figure 5. Variation in soil matric potential with radial distance from a porous tube assuming a constant flow rate and soil hydraulic conductivity for each porous tube water pressure. The porous tube radius was 4·75 mm. The gravitational potential of 0·01 kPa mm^{-1} was not included.

during the equilibration process. There was only a slight change in the volumetric water content of the soil for a change in matric potential from –0·5 to –1·0 kPa (Fig. 2). Daily water use, measured by either method, did not vary during the entire intensive measurement period (Fig. 6). The reduction in porous tube water pressure to –1·5 kPa on day 3 did not change the daily water use as measured by the stem gauges, but tray water use obtained from the return reservoir was reduced. This net increase in water in the return reservoir was of the order of 0·53 dm^3 over a period of several hours. The volumetric water content of the soil changed from 0·74 to 0·55 m^3 m^{-3} for a reduction in soil matric potential from –0·5 to –1·5 kPa (Fig. 2).

A reduction in porous tube water pressure from –0·5 to –2·0 kPa resulted in at least a 50% reduction in the transpiration rate, and in the root and leaf water potential. Sap flow rates rapidly declined over a 2 d period to a level of about 40 g m^{-2} h^{-1}. One day after a reduction in tube water pressure from –0·5 to –2·0 kPa, leaf conductance was reduced by 50%. Two days after the reduction leaf conductance had been reduced by ≈80% (Table 3).

Even though a significant amount of water (≈1·3 dm^3) was lost from the soil over a period of several hours immediately after the porous tube water pressure was reduced from –0·5 to – 2·0 kPa (Fig. 6), transpiration was not reduced until the following day (Figs 4 & 6). For this change in soil matric potential the volumetric water content was reduced from 0·74 to 0·4 m^3 m^{-3} (Fig. 2). At –2·0 kPa the porous tube water pressure and soil matric potential never come close to equilibrating. Plant water extraction reduced the soil matric potential to well below –2·0 kPa (Fig. 3, upper panels). A gradient in matric potential developed within the soil and ranged from about –5·0 kPa next to the tubes to –60 to –80 kPa in between tubes, a distance of ≈20–25 mm (Fig. 3). The matric potential did not change during the dark period. The soil matric potential profile calculated from Eqn 2 also shows a similar change with radial distance from a tube, ranging from approximately –7 kPa next to a tube to > 50 kPa in between tubes (Fig. 5).

As a result, the variability in measured soil and plant water potentials increased substantially (Fig. 3, lower panels). By the second day after the reduction to a porous tube water pressure of –2·0 kPa, leaves were severely wilted and senescence was beginning. Root and leaf water potentials were 0·3–0·5 MPa lower than the soil water potential between tubes, and were not significantly different. Roots sampled for water potential measurement were obtained with minimal disturbance to the system and probably reflect the potential of the large percentage of soil which was not in direct contact with the tubes. Visual observation of these roots showed them to be dry and wilted. Roots located next to a tube probably had a higher water potential and could continue to supply water to the leaves. Values of pre-dawn leaf water potential were intermediate between soil water potentials between and next to tubes. Pre-dawn leaf water potentials higher than water potentials of the soil between tubes indicates some water transport from the tube directly to the leaves.

Conductance between various points in the tube–soil–plant continuum showed that, at a porous tube water pressure of –0·5 kPa, conductance from tube-to-soil and within the soil was several orders of magnitude higher than from soil-to-root and soil-to-leaf (Fig. 7). Soil-to-leaf conductance was lower than conductance from soil-to-root. A reduction in porous tube water pressure to –1·0 or –1·5 kPa did not significantly change these conductances. Hydraulic conductance of both the soil and plant was reduced after the tube water pressure was reduced from –0·5 to –2·0 kPa. Conductance from soil-to-leaf declined slightly, but remained within the same order of magnitude. Soil-to-root conductance declined by about 1 order of magnitude. The greatest reduction, of > 2 orders of magnitude, occurred from the tube to the soil between tubes.

Table 3. Leaf conductance of soybean in response to a step change in the water pressure within a porous tube irrigation system

	Leaf conductance[2] (cm s^{-1})		
Intensive measurement period (day)	Porous tube water pressure[1] (kPa)		
	–1·0	–1·5	–2·0
1	1·05 ± 0·3	1·15 ± 0·4	1·20 ± 0·3
2	0·91 ± 0·3	1·00 ± 0·3	1·10 ± 0·3
4	1·23 ± 0·3	1·12 ± 0·4	0·55 ± 0·6*
5	1·04 ± 0·4	0·95 ± 0·3	0·18 ± 0·2*

[1] On days 1 and 2 the water pressure within the porous tubes was –0·5 kPa; on day 3 it was reduced to either –1·0, –1·5 or –2·0 kPa.
[2] Data are means are ± 1 standard deviation (n = 15).
*Means were significantly different across rows at the α = 0·05 level.

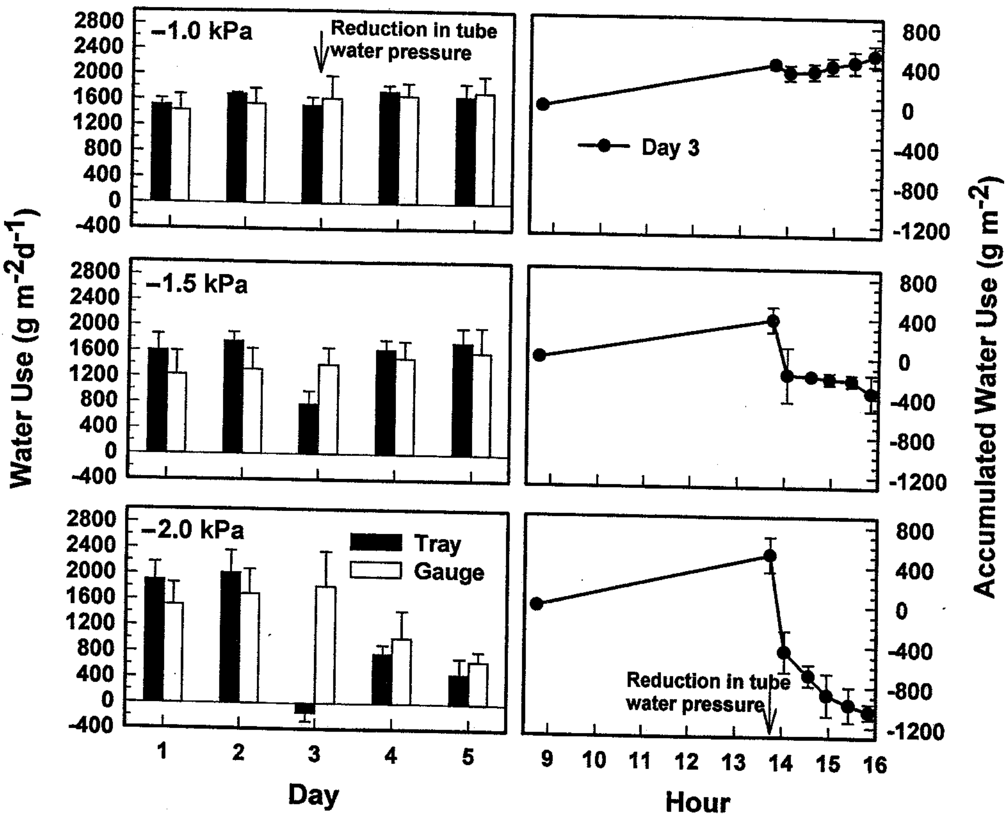

Figure 6. Water use per unit leaf area of soybean before and after a reduction in porous tube water pressure from –0·5 to –1·0, –1·5 or –2·0 kPa on day 3. Left: daily water use of soybean measured by stem gauge (individual plants) and the water level in the return reservoir (whole tray). Right: hourly water gain/loss in the return reservoir from the beginning of the light period until after the reduction in porous tube water pressure on day 3. Bars and symbols represent means ± 1 standard deviation ($n = 3$). Tray water use was measured from the water level in the return reservoir. Water is lost from the return reservoir due to plant transpiration. Water is gained in the reservoir as water moves from the soil into the tubes in response to a lower porous tube water pressure.

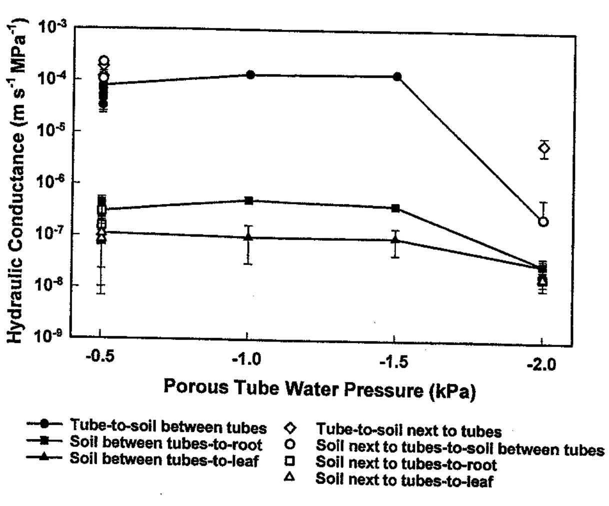

Figure 7. Hydraulic conductance between various points in the tube–soil–plant system as a function of porous tube water pressure was calculated as: transpiration rate/$\Delta\psi$. The transpiration rate was obtained from sap flow measurements on the main stem, expressed on a leaf area basis. All measurements were taken during the light period when the transpiration rate was steady. Symbols represent means ± 1 standard deviation ($n = 3\ldots5$).

The tube–soil pathway included conductance of the tube and bulk soil. The greatest reduction in conductance occurred from the soil next to tubes-to-soil between tubes, although there was some reduction from tube-to-soil (Fig. 7). A change in conductance of the tube with decreasing water pressure is also shown in Table 1 in terms of radial water flux through the porous tube to absorbent paper. Although water flux decreased by 1 order of magnitude as the water pressure was reduced from –0·5 to – 2·0 kPa, it remained 1 or more orders of magnitude higher than the transpiration rate.

The short duration of the intensive measurement regime, including the reduction of tube water pressure on day 3, had little effect on leaf area, biomass production or rooting characteristics (Table 4). There was no significant difference between treatments in biomass production of roots, stems or leaves. Root volume was slightly less in the –2·0 kPa treatment, perhaps because at harvest most of the roots were dry and wilted. Differences in root length between treatments were not significant. The rooting density in 7277 cm^3 of soil was ≈30 cm root cm^{-3} soil. In all treatments the roots had explored the whole volume of the soil and did not preferentially wrap around the tubes. The majority of the roots were located on the bottom of the tray.

Table 4. Biomass and rooting characteristics of soybean as a function of the water pressure in a porous tube irrigation system

	Water pressure in porous tubes (kPa)		
Variable[1]	–1·0	–1·5	–2·0
Leaf area (m^2)	0·96 ± 0·28	0·97 ± 0·06	0·77 ± 0·15
Dry matter (g)			
leaves	42 ± 13	44 ± 7	38 ± 7
stems	11 ± 5	10 ± 1	10 ± 2
roots	13 ± 2	14 ± 1	12 ± 1
Root volume (cm^3)	320 ± 69	307 ± 8	219 ± 24*
Root length (m)	2350 ± 370	2468 ± 199	2068 ± 207
Root density (cm root cm^{-3} soil)	32·5 ± 5	33·9 ± 3	28·4 ± 3

[1] Data are reported on a per tray basis (six plants per tray). Date are means ± 1 standard deviation.

*Means were significantly different at the $\alpha = 0{\cdot}05$ level.

DISCUSSION

Soybean was grown in an irrigation system where the water pressure within microporous tubes was used to control soil matric potential. When the porous tube water pressure was –0·5 kPa, the soil matric potential was never lower than –1·5 kPa during periods of rapid transpiration. The results also show that soil matric potential remained within about 1·0 kPa of porous tube water pressure, and the transpiration rate and water potential of soybean did not change in response to a step reduction in tube water pressure until a threshold value of –2·0 kPa was reached (Figs 3, 4 & 6).

A threshold response of plant water use to soil moisture has been documented by others. Gardner (1965) reported that plant transpiration remained constant or was controlled by meteorological factors until a critical value of soil matric potential was reached. In a growth chamber study, Gollan, Passioura & Munns (1986) also reported little change in leaf conductance with declining soil water content until the matric potential also began to decrease substantially. Others have found that leaf conductance or transpiration begins to decline when about two-thirds of the available soil water has been depleted (Ritchie 1974; Turner *et al.* 1985). A porous tube water pressure of –2·0 kPa corresponded closely with the point in the soil desorption relation where about two-thirds of the extractable water was depleted and there was a rapid reduction in soil matric potential for small changes in volumetric water content (Fig. 2).

The major reason why the present data so clearly illustrate a threshold response of plant transpiration and water status to soil water content is that the porous tube irrigation system allows control and maintenance of nearly uniform soil matric potentials at potentials very near zero. The ceramic aggregate of the particle size used in this study is somewhat similar to sand in that it has a wide range of water contents for which the matric potential does not change appreciably due to the number of large pores (Hillel 1980). For Profile™ most of the water is held in pores with radii of ≈100 μm (Fig. 2). By comparison, field capacity in most soils is commonly considered to be –0·01 to –0·03 MPa; the corresponding range in pore size is 5–14 μm. Because of the control of soil water content allowed by the porous tube system, plant and soil water status data could be collected from several points in this plateau region of the desorption relation.

Others have interpreted their results as indicating that transpiration is very sensitive to soil water content. Eavis & Taylor (1979) describe the transpiration rate of soybean decreasing linearly with soil water content. Turk & Hall (1980) found that relative ET (ET/Et_{pan}) began to decline when the soil water content was as high as 0·90. In a later study, Bates & Hall (1981) found that leaf conductance of fully irrigated cowpea began to decline when the available soil water content was greater than 0·7. Herkelrath, Miller & Gardner (1977a) found that plant water uptake decreased with soil moisture content when the soil water potential dropped below –0·01 MPa. However, their data do show that soil moisture diffusivity and water potential decline rapidly at water potentials below 0·01 MPa.

There are several reasons why the results of these and other studies may not agree with those presented here. The first is that other soils, such as those containing clay, have a wide range of pore sizes containing water available to plants, resulting in a more gradual decrease in water content with matric potential (Hillel 1980). The likely result is a more linear response between transpiration rate and soil water content. Secondly, in many studies complete information about the physical water-holding and water-transport characteristics of the soil is rarely given. In many cases there is insufficient information to relate extractable soil moisture to soil water content or water potential. Undoubtedly, many studies were conducted in soil where soil matric potential had begun to decrease with water content. And lastly, there is some evidence that the soil moisture content at which water becomes limiting to plants depends on the potential transpiration rate, which in turn is highly dependent on environmental conditions (Denmead & Shaw 1962). Denmead & Shaw (1962) showed that either a linear or plateau relationship between transpiration and soil moisture content was possible depending on soil type and evaporative demand. These three factors alone could contribute to the differing interpretation of results found in the literature.

Implicit in the work of Denmead & Shaw (1962) is the importance of soil hydraulic conductivity in determining the point in the desorption relation at which soil moisture becomes limiting to plants. For transpiration rates measured in this study (Table 1; Figs 4 & 6), a reduction in soil hydraulic conductivity from $5{\cdot}7 \times 10^{-4}$ to $9{\cdot}0 \times 10^{-7}$ m s^{-1} had little effect on the soil matric potential profile between tubes (Fig. 3 and 5). Only a reduction in conductivity to $2{\cdot}9 \times 10^{-10}$ m s^{-1}, 2 orders of magnitude lower than the transpiration rate, significantly changed the matric potential profile. At this hydraulic conductivity the matric potential of the soil rapidly decreased from – 2·0 to > 50 kPa within 25 mm of a tube.

The role of soil hydraulic conductivity on water transport can also be seen in Fig. 7, where hydraulic conductance between various points in the tube–soil–plant continuum is displayed. At a porous tube water pressure of –0·5 kPa conductance from soil-to-leaf was slightly lower than that from soil-to-root, and both were several orders of magnitude lower than conductance within the soil. Blizzard & Boyer (1980) similarly showed that root-to-leaf conductance was lower than soil-to-root conductance when the soil water content was not limiting.

Blizzard & Boyer (1980) also reported that plant hydraulic conductance declined with soil water content and limited conductance in the soil–plant continuum over the range of available soil moisture. Saliendra & Meinzer (1989) hypothesized that large decreases in root conductance for relatively small decreases in soil matric potential were due to changes in conductance within the root. On the other hand, Faiz & Weatherly (1978) measured a perirhizal drop in water potential of –0·8 MPa in rapidly transpiring plants and suggested that the abrupt change in the hydraulic pathway from soil-to-root limited conductance. Herkelrath, Miller & Gardner (1977b) concluded that decreasing contact between the root and soil, rather than changes in soil hydraulic conductivity or potential, were responsible for decreases in plant water uptake with soil water content. However, Bristow, Campbell & Calissendorf (1984) showed that, in soils of differing texture, a reduction in interfacial conductance was not observed until the water content was < 20% of saturation, a condition not reached in the present study.

We found that soil-to-root and soil-to-leaf conductance, which would have included both interfacial and within-root conductance, did not change when the porous tube water pressure was reduced from –0·5 to –1 or –1·5 kPa. This result seems to agree with the work of Newman (1969) who hypothesized that soil-to-root conductance will remain greater than plant conductance until soil moisture contents are at or beyond the wilting point. The data show that the water potential of the roots was only 0·1 MPa lower than that of the soil for porous tube water pressures of –0·5 to –1·5 kPa (Fig. 3). Root densities found in the present study (Table 4) were approximately 3 times higher than reported by Blizzard & Boyer (1980) or Eavis & Taylor (1979), but were within the range reported by Newman (1969) for herbaceous plants. In our system the maximum distance soil water travelled was 20–30 mm, but was probably much less. Figure 5 shows that water transport through the soil was adequate to meet demand at any location for porous tube water pressures of –0·5 to –1·5 kPa.

It was only when the porous tube water pressure was reduced to –2·0 kPa that soil-to-root and soil-to-leaf conductance declined by an order of magnitude or less to the same level. At the same time, conductance through 25 mm of the bulk soil declined by over 2 orders of magnitude to approximately the same level as within the plant. The hydraulic conductivity of Profile™ at –2·0 kPa is 3 orders of magnitude lower than at –1·5 kPa (Fig. 2). Although hydraulic conductance of the tube declined by about 1 order of magnitude, it still remained significantly higher than water flow elsewhere in the tube–soil–plant system (Table 1; Fig. 7). The data simply indicate that the hydraulic conductance of the bulk soil, no matter on what basis it is calculated, must be higher than that of the plant or water stress will result.

It is possible that the rapid rate of change in soil water status resulting from a step reduction in porous tube water pressure influenced the observed plant response. Soil-porous tube water potential equilibration generally occurred within several hours of the reduction in water pressure (Fig. 6). A reduction in transpiration and leaf water potential occurred within 1 d of the reduction in tube pressure from –0·5 to –2·0 kPa. Jones & Rawson (1979) note that leaf conductance declined over a range of leaf water potentials greater than 1·0 MPa, the range being narrower for rapid onset of stress. Davies & Zhang (1991) provide evidence that during soil drying chemical signals originating in the root influence stomatal conductance. In the present study, leaf water potential fell concurrently with leaf conductance making it difficult to draw any conclusion about root-to-shoot signalling. However, in many water stress studies plants are allowed to dry down slowly and roots are subjected to a variety of soil moistures during the drying process. With a slower onset of stress, factors such as root–shoot signalling, osmotic adjustment, root exploration, and changes in biomass partitioning could play a greater role in mediating the plant response to drying soil. In the present study, biomass, root length and density were not significantly different between treatments (Table 4).

The results indicate that, when soybean was grown in soil maintained at a nearly constant matric potential by the water pressure in microporous tubes, and then subjected to a rapid reduction in tube water pressure, hydraulic conductance of the plant dominated water transport as long as soil moisture was readily available. When the porous tube water pressure was reduced to a threshold value of –2·0 kPa, soil matric potential began to decline significantly with water content and hydraulic conductance of the bulk soil limited water transport in the tube–soil–plant system. These results may be specific to the unique water-holding and water-transport properties of the porous ceramic aggregate. Because other soils have different water-holding and water-transport characteristics, optimal porous tube water pressures for plant growth will vary with the soil and environmental conditions.

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