

Resistance of Plant Roots to Water Loss¹J. M. Baker and C. H. M. van Bavel²

ABSTRACT

In an attempt to resolve questions about the relative magnitudes of root resistance to uptake and exudation, an experiment was conducted in which the root zone of a bermudagrass (*Cynodon dactylon* × *Cynodon transvaalensis* L. Pers.) sod was divided by a barrier in such a manner that water could move from one side to the other only through the lateral stems of the connected plants. A large difference in soil water potential between the two sides was created by watering one side only. Under such circumstances nocturnal transfer of significant amounts of water from one side to the other, through the plant system, was observed repeatedly with a gamma probe. A separately measured resistance to uptake allowed calculations of the exudation resistance, which was found to be 1.2×10^7 MPa s⁻¹ m⁻¹, slightly larger, but of the same magnitude as the resistance to uptake. It was concluded that water will move from root to soil if the potential gradient is in that direction, though other factors such as soil hydraulic conductivity may become limiting.

Additional index words: Exudation, Root resistance, Root water uptake, Negative flow.

THERE is a fundamental and unresolved set of questions regarding the movement of water through plants. First, is there flow of water from roots to soil when the soil water potential is lower than that in the plant? Further, is the hydraulic resistance for outflow of the same magnitude as that for uptake? We have presented results that gave an affirmative answer to the first question, using bermudagrass [*Cynodon dactylon* (L.) Pers.] as a test plant (van Bavel and Baker, 1985). Here, we examine the question of resistance to exudation, relative to that to uptake.

These issues are of more than academic interest, being particularly pertinent to problems of water distribution in drip irrigation and other discrete applications of irrigation water, situations in which the water potential gradient in the root zone can be quite large. Other agronomic implications may be important. One is plant absorption of mineral nutrients from soil areas that otherwise would become and remain dry. Another would be the continued activity of microorganisms whose metabolism is often beneficial, if not essential, to the crop. Also, the local growth, renewal, and metabolic activity of the root system itself could be affected if water stress in the soil is alleviated by root transfer.

The literature contains many references that circumstantially support the notion that roots can exude water as well as absorb it. Kirkham (1983) has provided a thorough review. In addition to the citations therein, Hansen and Dickson (1979), Schippers et al. (1967), Shone and Flood (1980), and Mooney et al. (1980), among others, have reported observations of exudation in a number of plant species.

On the other hand, Molz and Peterson (1976) detected only negligible amounts of exudation in cotton (*Gossypium hirsutum* L.), despite large gradients in

potential favoring such movement. Dirksen and Raats (1985) obtained similar results with alfalfa (*Medicago sativa* L.).

The issue is particularly relevant to the mathematical prediction of water movement in the soil-plant-atmosphere system. As Molz and Peterson (1976) have pointed out, mechanistic models, in which the rate of water movement into the plant is assumed to be directly proportional to the potential gradient between root and soil, will predict exudation into dry areas of the root zone if evaporative demand is low, as is the case during the night, and if the roots have permeated wetter soil elsewhere in the profile. Whisler et al. (1968) noted this "shorting effect" in their model, recognizing the implications for transfer of water from wet to dry soil. Van Bavel and Ahmed (1976) showed similar behavior from their simulation model, mentioning it as a hypothesis in need of testing. Landsberg and Fowkes' model (1978) also predicted exudation under the appropriate conditions. They considered the effect to be real, but probably of minor significance due to a high soil resistance to flow away from the root, likely to be found in dry soils. Rowse et al. (1978) considered that predictions of negative flow were probably not reflective of true plant behavior and modified their uptake algorithm specifically to prevent it. In an attempt to resolve the questions surrounding this issue, we designed a split-root experiment in which the measurement of changes of water content and the possibility of transfer by the root system were facilitated.

MATERIALS AND METHODS

Physical details of the experiment are described elsewhere (van Bavel and Baker, 1985). Briefly, a split-root box was constructed as shown in Fig. 1, placed in a growth chamber, and filled with fritted clay, a rooting medium for which the hydraulic properties had been previously determined (van Bavel et al., 1978). A bermudagrass sod (*C. dactylon* L. Pers. × *C. transvaalensis* L. Burtt-Davy cv. 'Tifway') was established in the box such that plants on either side of the barrier were connected by stolons only.

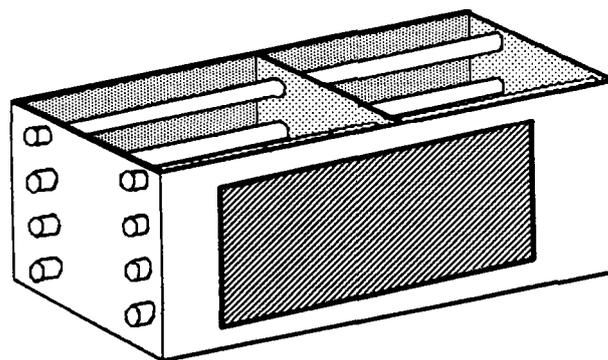


Fig. 1. Split root box. Dimensions are: height 0.4 m, depth 0.47 m, length 1.0 m, with a vertical, plywood barrier 0.4 m from the right end. The pairs of horizontal access tubes for the gamma densitometer measurements were installed at 0.10 m-depth increments from 0.05 m to 0.35 m. An observation window allowed examination of roots.

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After a complete root system had been established, a difference in water potential between the two sides was created by continued irrigation of the right side, while the left side was allowed to dry. The volumetric water content in all parts of the box was measured with a gamma probe twice daily, just before the lights came on and just after they were turned off. This entailed taking 30-s counts at 0.1-m intervals from one end of the box to the other, at each of the four depths. The resulting data were then compared with those obtained 12 h earlier, to compute changes in the water content of each portion of the root zone. The experiment was conducted over a period of 2 months, at the conclusion of which the stolons crossing the barrier were cut, and a final 24-h sequence of measurements was made.

An independent measurement of the crop hydraulic resistance on a ground-area basis was made in the following way. Pots (0.23 m diam, 0.20 m deep) of the same bermudagrass cultivar with well-established root systems and canopies were placed in the previously described growth chamber. Changes in the transpiration rate from one day to the next were induced by changing the irradiance level in increments from a minimum of 55 W m^{-2} to a maximum

of 500 W m^{-2} . Transpiration rates were determined by weighing, soil water potentials were monitored with tensiometers, and leaf water potentials were measured with a pressure chamber.

RESULTS

As the difference in water content between the two sides became large, overnight increases in the water content of the left (dry) side were consistently detected, as shown in Fig. 2. Figure 3 shows the average volumetric water content on the dry side vs. time, over the period of 19–27 September. It can be seen that overnight increases by exudation were about half the daytime transpiration losses. Thus, though the left side eventually required rewatering, it is evident that nightly transfer from the right side through the stolons delayed this event by several days. The fact that there was no transfer of water on 23 October after cutting the stolons indicates that the previously measured increases in water content were due to transfer through the plant system. The small, but significant, decrease in water content for that night was presumably due to nighttime evapotranspiration. Previous measurements in the absence of root water transfer (similar water potentials on both sides of the barrier) had indicated overnight losses of similar magnitude.

An error analysis based on radioactive decay statistics (Ostle and Mensing, 1975) showed that the standard error of measurement of the difference in absolute water content of the dry side between successive measuring times was 0.093 kg. The least significant difference (LSD) at a 5% significance level between two sets of measurements was 0.191 kg, which represents a difference in volumetric water content of 0.0017. It should be evident that the exudation process would have been undetectable with neutron attenuation equipment, time-domain reflectometry (TDR), or other less precise methods. Furthermore, if we had taken fewer readings at each measurement time, the content changes due to exudation might have been undiscernible from measurement error. A final point is that the water transferred overnight was lost in the transpiration flux of the following day, so that measurements over an extended time period could not be expected to yield useful information regarding the exudation process.

Figure 4 shows total exudation, summed over four nights, vs. distance from the barrier. Figure 5 is a similar treatment of exudation vs. depth. There are significant differences in both directions, perhaps due to variations in root density, but there is no consistent gradient, suggesting that the axial resistance to lateral flow through the stolons and roots was small relative to the radial resistance in the roots. The net loss of water at the 0.15-m layer is puzzling. Throughout the period, this layer had a somewhat higher water content than the layers above and below it, which may explain the lack of exudation, but the reason for this consistently higher water content is unknown.

To answer the second question, regarding the magnitude of resistance to outflow, it was first necessary to assess the resistance to uptake in bermudagrass. The results are shown in Fig. 6. From linear regression analysis, the estimated value is $0.83 \times 10^7 \text{ MPa s}^{-1}$

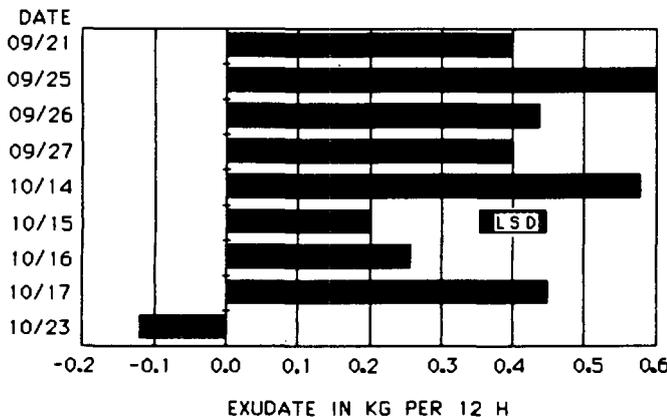


Fig. 2. Measured exudation of water in the split-root box. Amounts represent overnight transfer of water from the wet compartment to the dry compartment, and were calculated from sets of gamma counts taken at the beginning and the conclusion of the 12-h night period. The negative value on October 23 signifies a net decrease in water content overnight, following the severing of the stolons connecting the plants on either side. Mean soil water potential for the dry compartment on the 8 nights of exudation shown was $-1.00 \pm 0.16 \text{ MPa}$, while the mean value for the wet compartment was $-0.002 \pm 0.0005 \text{ MPa}$.

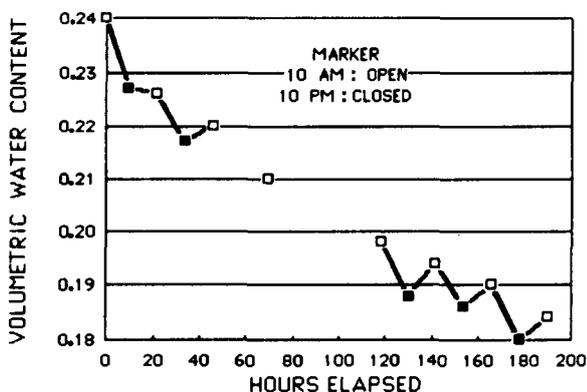


Fig. 3. Changes in volumetric water content of the left (dry) side, September 19–27. Missing data points are due to a malfunction in the charging circuitry of the gamma probe. AM readings were taken just prior to the beginning of the light period and PM readings were taken immediately after the lights were turned off.

m^{-1} , with a standard error of estimation of $0.15 \times 10^7 \text{ MPa s}^{-1} m^{-1}$. This number is similar to published values for other species and to the generic value proposed by Cowan (1965). A quasi steady state analysis of water transfer from the wet to the dry side can be stated as:

$$\text{TRATE} = \frac{[\text{PPOT}(R) - \text{PPOT}(L)]}{[R_{up}/\text{AREA}(R) + R_{ex}/\text{AREA}(L)]} \quad [1]$$

where TRATE is the rate of water transfer in $m^3 s^{-1}$, PPOT(R) and PPOT(L) are the average soil water potentials for the left and right compartments expressed in MPa, AREA(R) and AREA(L) are the areas of the two sides in m^2 , and R_{up} and R_{ex} are the hydraulic resistances to uptake and exudation, respectively, in $\text{MPa s}^{-1} m^{-1}$. Division of each resistance by the respective area, in m^2 , gives proper weight to each and converts them to absolute resistances so that the resulting transfer rate is in $m^3 s^{-1}$ rather than in depth units. Each resistance involves a crop and a soil component; in the case of uptake from the wet side, the soil was so near saturation that the soil resistance could be considered negligible (Newman, 1969), so R_{up} will be taken to be equal to the previously mentioned crop hydraulic resistance, which was measured under similar, well-watered conditions. The values for TRATE, PPOT(R), and PPOT(L) are taken from the mean values for the eight occurrences of exudation shown in Fig. 1, the transfer rate being corrected to account for nighttime ET losses as estimated from the content change on the night of 23 October, following cutting of the stolons. Insertion of all known values allows estimation of R_{ex} . The resulting value is $1.2 \times 10^7 \text{ MPa s}^{-1} m^{-1}$. This term contains both a crop and soil resistance, as in this case the soil resistance may not be negligible, since the water content was much lower on the exudation side of the box. It is tempting to conclude that the difference between the calculated resistances to uptake and exudation represents the increase in soil resistance associated with the drier soil, but we do not have the requisite data on root length density and mean root diameter to allow calculation of a soil resistance term.

In any case, the resistances (soil + plant) to uptake and exudation did not differ by much, and we did not observe the large interfacial resistance in the dry soil that Herkelrath et al. (1977) noted. Passioura (1980), working with wheat (*Triticum aestivum* L.) in a silt loam soil, also was unable to detect an interfacial resistance. A possible explanation in our case is that we used a rooting medium that contained, at a potential of -1.0 MPa , nearly 30% of the water contained at saturation. Bristow et al. (1984) showed that, in three soils of differing texture, increased resistance (whether one attributes it to the conductivity of the innermost ring of soil about the root or to the interface of soil and root) does not dominate until the water content drops $< 20\%$ of its saturation value. The data of Schippers et al. (1967) demonstrated the influence of texture-related soil hydraulic properties on the exudation process. They measured three times as much exudation in a silt loam, compared with that measured under similar conditions in a sand. This may account for the lack of consistent, measurable exudation in the work

of Dirksen and Raats (1985), who used a sandy loam soil in which the increasing resistance associated with decreasing soil water potential might be expected to be more pronounced.

It must also be noted that crop characteristics cannot be ignored in studies of this nature. *Gramineae*

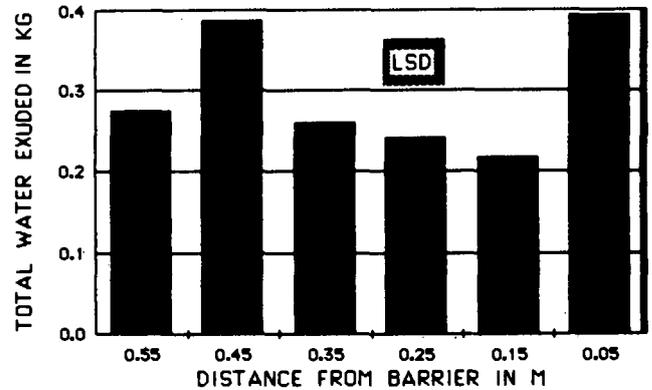


Fig. 4. Exudation vs. distance from the barrier. Each bar represents total measured exudation at a given distance from the barrier over a 4-night period, averaged from two such measurement series.

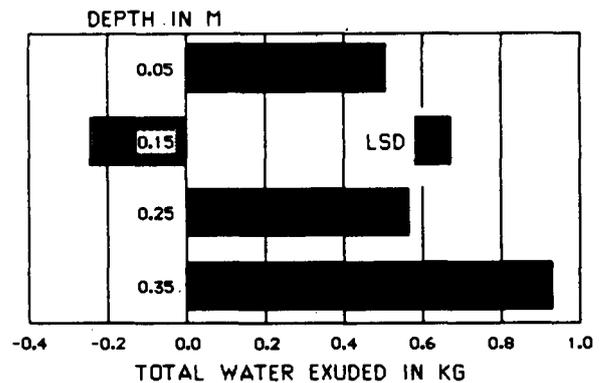


Fig. 5. Exudation vs. depth. Each bar represents total measured exudation depth over a 4-night period, averaged from two such measurement series.

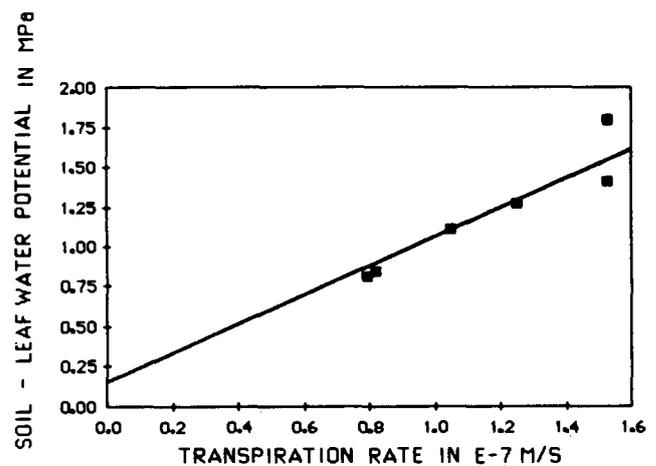


Fig. 6. Determination of crop hydraulic resistance. Different transpiration rates were induced by varying the irradiance level. Calculated resistance (slope) is $0.83 \times 10^7 \text{ MPa s m}^{-1}$. Coefficient of determination = 0.89.

species, as noted by Newman (1969), typically have rooting densities greater by at least an order of magnitude than many dicotyledonous field crops. Therefore, soil or interfacial resistances may be less important in bermudagrass than in alfalfa or soybean [*Glycine max* (L.) Merr.]

CONCLUSIONS

Our experiment was designed to demonstrate conclusively the presence or absence of water movement from roots to soil, using bermudagrass as a test plant. The outflow detected was consistent with the concept, originally demonstrated by Jensen et al. (1961), that the plant hydraulic resistance is independent of the direction of flow. There was no evidence of a large increase in resistance associated with drying soils that has been noted by others, but this could be explained from differences in soil hydraulic properties and/or plant root system characteristics. The potential significance of water loss from roots to dry soil cannot be readily assessed until a unified theory of the effects of drying soil on soil-root flow processes has been proposed and tested. We concur with Landsberg and Fowkes (1978) that this probably requires a time-dependent synthesis of the *macroscopic* and *microscopic* concepts of root water uptake.

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