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The gradient between pre-dawn rhizoplane and bulk soil matric potentials, and its relation to the pre-dawn root and leaf water potentials of four species

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ABSTRACT

Uptake of soil water by plants may result in significant gradients between bulk soil and soil in the vicinity of roots. Few experimental studies of water potential gradients in close proximity to roots, and no studies on the relationship of water potential gradients to the root and leaf water potentials, have been conducted. The occurrence and importance of pre-dawn gradients in the soil and their relation to the pre-dawn root and leaf water potentials were investigated with seedlings of four species. Pre-germinated seeds were grown without watering for 7 and 11 d in a silt loam soil with initial soil matric potentials of –0·02, –0·1 and –0·22 MPa. Significant gradients, independent of the species, were observed only at pre-dawn soil matric potentials lower than –0·25 MPa; the initial soil matric potentials were ≥ –0·1 MPa. At an initial bulk soil matric potential of –0·22 MPa, a steep gradient between bulk and rhizoplane soil was observed after 7 d for maize (*Zea mays* L. cv. Issa) and sunflower (*Helianthus annuus* L. cv. Nanus), in contrast to barley (*Hordeum vulgare* L. cv. Athos) and wheat (*Triticum aestivum* L. cv. Kolibri). Pre-dawn root water potentials were usually about the same as the bulk soil matric potential and were higher than the rhizoplane soil matric potential. Pre-dawn root and leaf water potentials tended to be much higher than rhizoplane soil matric potentials when the latter were lower than –0·5 MPa. It is concluded that plants tend to become equilibrated overnight with the wetter bulk soil or with wetter zones in the bulk soil. Plants can thus circumvent negative effects of localized steep pre-dawn soil matric potential gradients. This may be of considerable importance for water uptake and growth in drying soil.

Key-words: *Helianthus annuus*; *Hordeum vulgare*; *Triticum aestivum*; *Zea mays*; gradient; rhizoplane; root water potential; soil water availability; soil–root interface; water potential.

INTRODUCTION

The soil water potential at the soil–root interface appears to be the main soil characteristic controlling the availability of soil water to the plant (Slatyer 1967). The uptake of soil water by plants may result in gradients between the bulk soil and the soil in the vicinity of the roots. Composite mixed bulk soil samples only partially represent the actual situation of the plant. Therefore, correlations between average or bulk soil water availability and plant growth have to be interpreted carefully. It is necessary to determine the importance of gradients and whether they change our interpretation of average soil matric potentials with respect to plant growth.

Why do gradients occur? When the soil matric potential is high, mass flow is unrestricted and maintains a similar soil matric potential at the root surface. As the soil matric potential falls, the rate of water uptake by the roots may exceed the supply by mass flow, and the soil may dry out at the soil–root interface (Nye & Tinker 1977).

There is some uncertainty about whether roots induce large local gradients of soil matric potential in soil (Passioura 1982). Researchers who assume that most of the roots are active (Newman 1969) predict minor gradients of soil matric potential near the root; those who assume that few roots are active predict major gradients (Caldwell 1976).

Unless the soil is fairly dry and the rooting density low, the fall in water potential across the roots, from the epidermis to the xylem, will be much greater than the difference between the average water potential value in the soil and its value at the surface of the root (Newman 1969; Reicosky & Ritchie 1976; Passioura 1988). Molz *et al.* (1979) concluded from model calculations that movement of water in the cylinder of the root and adjacent rhizosphere will induce small gradients in the soil relative to the root even when the soil loses most of its available water.

In contrast, Faiz & Weatherley (1978) calculated a major drop in water potential between the soil and the root from experiments with sunflower growing in sand or soil. If the soil in the vicinity of the roots is in equilibrium with the water potential at the root surface, then the presence of a dry layer could contribute considerably to the radial resistance of water flow towards the root. The influence of such a layer is expected to increase as the bulk soil becomes drier. At low soil water contents, the water content at the root surface is much lower than in the bulk soil (Zur *et al.* 1982). If there is poor hydraulic continuity between the root and the soil, then there will be a large fall in water

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potential at the interface between them whenever there is a substantial rate of uptake of water by the root (Tinker 1976). Thus, contact between the root surface and soil by means of soil solution can be lost.

There are few experimental data about the size and significance of water potential gradients around roots. No experimental data exist which show the relationship between the soil matric potentials in the bulk and rhizoplane soil and the root and leaf water potentials. Theoretical calculations are frequently based on assumptions. In most of the experimental studies conducted so far, root and bulk soil compartments were separated by nets, allowing analysis of the soil at defined distances from the root surface. However, this has the disadvantage that planar rather than spherical distribution of water around roots was studied, and root growth was often restricted to a small volume. Recent non-destructive techniques, applying computer-assisted tomography to gamma- and X-ray attenuation measurements, were used to determine the spatial distributions of the soil water content (Hamza & Aylmore 1992). This technique, however, can only be applied to single roots. Gradients in water content can be shown by carefully separating roots from loosely adhering soil (rhizosphere soil) and closely adhering soil (rhizoplane soil) (Claassen 1990). This approach, also used in this study, does not give detailed information about the spatial distribution of water around roots, but has the advantage that it depicts average differences (gradients) between bulk soil and rhizoplane soil for a whole root system. We will use the term 'gradient' to denote a difference in matric potential between the bulk (> 2 mm from the root surface, average of the bulk soil) and the rhizoplane soil (0 to about 2 mm from the root surface).

The aim of this study is to evaluate the occurrence and importance of pre-dawn water potential gradients under drought stress conditions in four cultivars of four different species: barley, wheat, maize and sunflower. The relation between the pre-dawn soil matric potentials in the bulk and rhizoplane soil and the pre-dawn root and leaf water potentials of drought-stressed seedlings was investigated.

MATERIALS AND METHODS

Cultivation of plants

Barley (*Hordeum vulgare* L. cv. Athos), wheat (*Triticum aestivum* L. cv. Kolibri), maize (*Zea mays* L. cv. Issa) and sunflower (*Helianthus annuus* L. cv. Nanus) seedlings were grown for 7 and 11 d in a growth chamber [17 °C; 12 h day/night; 60% rH; 410 μmol m^{-2} s^{-1} (PPFD)] in pre-equilibrated illitic chloritic silt loam soil (fine mixed mesic Aquic Ustifluvent) with initial soil matric potentials of –0·02, –0·1 and –0·22 MPa. The soil was 9·1% clay, 59·5% silt, 31·4% sand and 0·85% organic matter (Schmidhalter, Selim & Oertli 1994). Gravimetric water contents were converted to soil matric potentials on the basis of a previously determined water retention curve (pF curve). Water retention characteristics were determined as described by Klute (1986) and are presented in Fig. 1. This analysis was carried out with soil of the same bulk density as the soil used in the experiments. The soil water retention model of van Genuchten (1980) was fitted to the measured data and used to predict soil matric potentials at water contents ranging from 0·21 to 0·04. Soil matric potentials at lower water contents were predicted according to an equation which best fitted the observed data in that range. Van Genuchten's retention function uses five parameters which must be fitted to experimental data. The function is given by

$$\theta = \theta_r + \frac{\theta_s - \theta_r}{[1 + (\alpha h)^n]^m},$$

where θ is the water content (g g^{-1}) at a given pressure head h (cm), θ_r is the residual water content, θ_s is the saturated water content, and α, m and n are equation-fitting parameters. The following values were determined for θ_s, θ_r, α, n and m: 0·293, 0·015, 0·0018, 2 and 0·5.

No fertilizer was added to the soil. Osmotic components of the initial soil water potentials were higher than –0·03 MPa. Further drying of this soil does not markedly lower the osmotic potential, because the salts in the soil solution, which consist mainly of $CaSO_4$ and $CaCO_3$, are increasingly precipitated as the soil dries out. This experiment did not contain a well-watered treatment, i.e. all plants were mildly to moderately severely drought-stressed.

Six seeds, pre-germinated for 1 d, were sown in 450 g dry soil (dry weight basis) and covered with 70 g soil (dry weight basis) which was covered by an 8 mm layer of sand (grain size 2 mm) to reduce evaporation. Seeds were grown for the first 3 d in closed transparent boxes (100 mm in diameter, 200 mm in height); thereafter the covers were removed from the containers.

Measurements of water relations

Pre-dawn water potentials in roots and leaves were measured by the pressure chamber technique (Schmidhalter,

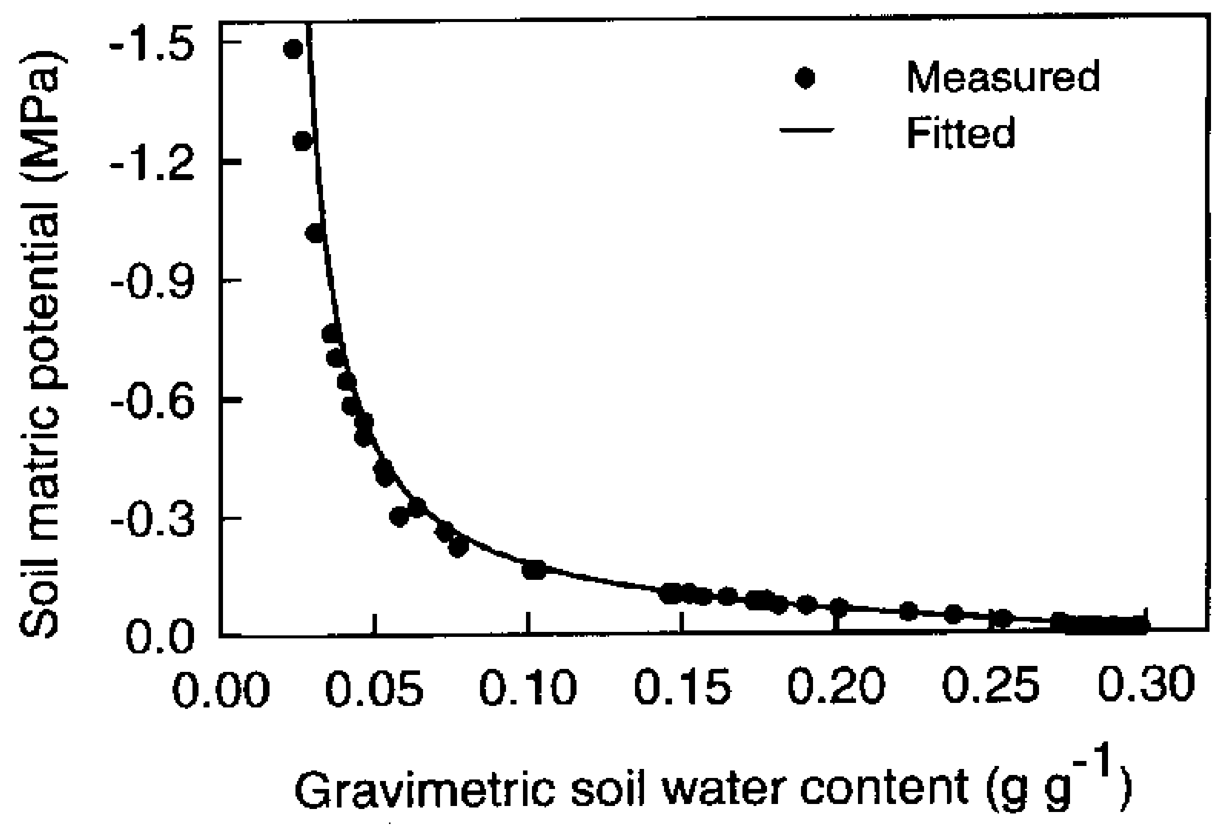

Figure 1. Soil water retention curve of Charrat silt loam. The Van Genuchten function was fitted to the water retention data. See text for details.

Evéquoz & Oertli 1992a). For the pressure chamber determinations (PMS Instrument Co., Model 1002, Corvallis, OR, USA), the youngest fully developed leaf blade (barley, wheat and maize), cut at one-third of the distance from the leaf base, or the intact leaf with its petiole (sunflower) were used. Measurements were first made on the detached leaf, leaving the remainder of the plant in the pot. Thereafter, only the bulk of the soil was gently shaken from the root/shoot system, and the intact root system, cut above the root–shoot junction, was used for the pressure chamber measurements. The time from excision to sealing in the pressure chamber was no longer than 10 s to avoid dehydrating the tissue. Measurements took 1 or 2 min, ensuring a true balancing pressure, previously checked with longer equilibration times, to obtain a stable, flat water film at the cut xylem surface (Boyer 1995). Pressure chamber readings were not corrected for the osmotic potential of the xylem sap; previous investigations showed that it was always higher than –0·05 MPa.

The pre-dawn water content was measured gravimetrically in the soil adhering to the roots (rhizoplane soil) and in root distant soil (bulk soil) and converted to soil matric potentials based on the soil water retention curve. Rhizosheaths had formed in all species and varied in thickness from ≈0·5 to 2 mm. The root system was carefully removed from the soil pots and gently shaken. The remaining soil adhering to the rhizosheaths, termed 'rhizoplane soil', was removed with a brush in a humidified chamber to prevent evaporation losses.

Dry weight of roots and shoots, root distribution and root morphology

Plants were harvested after 7 and 11 d to determine the dry weights of roots and shoots and the root/shoot ratio. For dry weight determination, the roots were carefully cleaned of adhering soil particles by washing gently. Dry weights of roots and shoots were determined gravimetrically after oven-drying for 48 h at 65 °C and the root/shoot ratio was determined.

Maximum root length, root distribution and root morphology were visually evaluated. The whole root system, as used for the root water potential measurements, was photographed. This information was used to determine the length, distribution and morphological development of the roots and was adequate to describe relations to the observed gradients. A more detailed analysis of maize root length could be conducted based on other information giving the relationship between root dry mass and root length; it is described in the 'Discussion' section.

Experimental design and statistical analysis

A completely randomized experimental design with four replications was used. Each replication repeated the experiment consisting of the four species, three initial soil matric potentials and two growing times (7 and 11 d). Measurements were performed after 7 and 11 d. The sequence of measurements was plant water status, soil water status and the determination of biomass. The mean values presented are based on four observations containing 1–2 subsamples of the four pots (plant water potential), four observations of the biomass (pot average) and three observations of the soil matric potential. The whole study was repeated with similar results. A logarithmic transformation was used to account for the increasing variance observed of lower soil matric potentials and, to a lesser extent, plant water potentials. Analysis of variance (ANOVA) was performed with type III sums of squares from the GLM procedure of SAS (SAS Institute 1991) in order to account for the unbalanced nature of the data. The experiment was analysed as a completely randomized design. Standard errors of the means and regressions were calculated using SAS. The general linear model procedure was used to detect significant differences at $P < 0{\cdot}05$. Regression analysis was performed with the corresponding individual replicate data from three pots of each treatment. Data were analysed for the whole set of data as well as separately for the determinations made after 7 and 11 d.

RESULTS

Shoot and root dry weights were significantly lower ($P < 0{\cdot}0001$) at lower initial soil matric potentials (Table 1). Shoot and root dry weight production was much higher in maize and sunflower than in barley and wheat. With increasing stress, the root/shoot dry weight ratio increased in maize and sunflower, especially at the second harvest (Table 1).

In treatments with initially high and moderately low soil matric potentials (–0·02 and –0·1 MPa), no significant difference in soil matric potential between rhizoplane and bulk soil was observed with bulk soil matric potentials as low as –0·28 MPa (Table 1). Pre-dawn gradients ranged from 0·01 to 0·12 MPa. At initial, moderately low bulk soil matric potential (–0·22 MPa), a steep pre-dawn gradient between rhizoplane and bulk soil was observed after 7 d in maize and sunflower (0·55 and 0·44 MPa), in contrast to barley and wheat (< 0·07 MPa). Differences in soil matric potential between rhizoplane soil and bulk soil increased very markedly and significantly ($P < 0{\cdot}0001$) from day 7 to day 11 and ranged from 0·21 to 2·27 MPa (Table 1). Pre-dawn gradients became large at bulk soil matric potentials around –0·3 MPa (Fig. 2). Standard errors for bulk soil and rhizoplane soil matric potentials were comparable (Table 1). They were relatively small down to –0·3 MPa and increased markedly at lower soil matric potentials. The latter is a consequence of drastically decreased soil matric potentials at low soil water contents. Small differences in low soil water contents will result in very different soil matric potentials (Fig. 1). This increases the likelihood that replicate measurements will show large deviations at low soil matric potentials.

Pre-dawn leaf water potentials were lower and root water potentials were about the same as the corresponding bulk soil matric potentials down to –0·5 MPa (Fig. 3). At

Table 1. Initial bulk soil matric potential, pre-dawn bulk soil and rhizoplane soil matric potential measured after 7 and 11 d and corresponding pre-dawn values of leaf and root water potential, dry weight of shoot and root, and root/shoot ratio. Standard errors are indicated in brackets ($n = 4$)

Species	Ψ_{mi}† (MPa)	Time‡ (d)	Soil matric potential (MPa)		Ψ_w (root) (MPa)	Ψ_w (leaf) (MPa)	Dry weight (mg)		Root/ shoot
			Bulk	Rhizoplane			Shoot	Root	
maize	–0.02	7	–0.09 (0.02)	–0.14 (0.03)	–0.13 (0.00)	–0.33 (0.03)	49.7 (5.4)	77.0 (7.1)	1.5
maize	–0.10	7	–0.22 (0.03)	–0.34 (0.03)	–0.25 (0.03)	–0.36 (0.03)	38.0 (2.4)	74.5 (1.5)	2.0
maize	–0.22	7	–0.26 (0.05)	–0.81 (0.25)	–0.31 (0.03)	–0.41 (0.03)	7.5 (1.0)	20.7 (0.8)	2.8
maize	–0.02	11	–0.57 (0.27)	–0.95 (0.62)	–0.46 (0.03)	–0.41 (0.01)	105.5 (9.9)	166.0 (5.5)	1.6
maize	–0.10	11	–1.10 (0.62)	–3.27 (0.97)	–1.82 (0.09)	–1.31 (0.11)	48.9 (1.9)	99.1 (8.1)	2.0
maize	–0.22	11	–0.30 (0.12)	–0.97 (0.12)	–0.49 (0.02)	–0.47 (0.04)	6.7	30.0	4.5
barley	–0.02	7	–0.07 (0.00)	–0.09 (0.01)	–0.34 (0.03)	–0.30 (0.03)	12.7 (0.8)	21.2 (3.4)	1.7
barley	–0.10	7	–0.15 (0.01)	–0.26 (0.01)	–0.37 (0.03)	–0.52 (0.05)	9.9 (0.4)	13.5 (2.3)	1.4
barley	–0.22	7	–0.42 (0.16)	–0.49 (0.16)	–0.34 (0.03)	–0.35 (0.04)	7.9 (2.1)	14.5 (2.3)	1.8
barley	–0.02	11	–0.26 (0.02)	–0.53 (0.26)	–0.43 (0.02)	–0.58 (0.06)	25.5 (0.3)	40.5 (8.0)	1.6
barley	–0.10	11	–0.58 (0.29)	–0.91 (0.56)	–0.55 (0.01)	–0.55 (0.02)	17.2 (0.5)	33.7 (2.9)	2.0
barley	–0.22	11	–1.06 (0.20)	–1.70 (0.44)	–0.43 (0.01)	–0.50 (0.04)	10.0 (0.0)	13.0 (0.5)	1.3
sunflower	–0.02	7	–0.10 (0.01)	–0.15 (0.03)	–0.19 (0.01)	–0.43 (0.01)	45.4 (1.1)	15.9 (0.4)	0.3
sunflower	–0.10	7	–0.28 (0.06)	–0.39 (0.05)	–0.22 (0.03)	–0.52 (0.03)	35.0 (1.0)	31.5	0.9
sunflower	–0.22	7	–0.28 (0.06)	–0.72 (0.03)	–0.25 (0.01)	–0.37 (0.05)	23.7	15.6 (0.6)	0.7
sunflower	–0.02	11	–1.06 (0.24)	–1.59 (0.85)	–0.52 (0.01)	–1.00 (0.03)	60.3 (1.4)	23.3 (1.0)	0.4
sunflower	–0.10	11	–2.35 (1.08)	–2.84 (0.79)	–1.33 (0.09)	–1.66 (0.06)	44.0 (2.5)		
sunflower	–0.22	11	–1.85 (1.09)	–2.37 (1.21)	–0.82 (0.03)	–1.20 (0.02)	34.4 (1.6)		
wheat	–0.02	7	–0.06 (0.00)	–0.08 (0.00)	–0.46 (0.04)	–0.77 (0.03)	12.1 (0.7)	11.2 (1.9)	0.9
wheat	–0.10	7	–0.16 (0.01)	–0.27 (0.07)	–0.39 (0.03)	–0.79 (0.04)	9.3 (0.1)	8.3 (0.4)	0.9
wheat	–0.22	7	–0.28 (0.06)	–0.29 (0.03)	–0.48 (0.03)	–0.64 (0.05)	5.1 (1.0)	10.2 (1.6)	2.0
wheat	–0.02	11	–0.27 (0.01)	–0.48 (0.03)	–0.44 (0.03)	–0.92 (0.04)	25.8 (0.3)	26.5 (0.4)	1.0
wheat	–0.10	11	–0.64 (0.28)	–1.34 (0.04)	–0.58 (0.01)	–0.68 (0.04)	18.0 (0.1)	19.9 (0.9)	1.1
wheat	–0.22	11	–0.31 (0.06)	–0.57 (0.23)	–0.39 (0.06)	–0.81 (0.09)	6.8 (0.4)	7.7 (1.2)	1.1

†Bulk soil matric potential at the beginning of the experiment.

‡Indicates time at which water status in plants and soil and biomass production were determined.

lower bulk soil matric potentials, plant water potentials were comparable or higher. A comparison with the rhizoplane soil shows that pre-dawn leaf water potentials were lower than the rhizoplane soil matric potentials down to –0·7 MPa; pre-dawn root water potentials were usually higher than the corresponding rhizoplane soil matric potentials in the same range, although lower values were found too. Leaf and root water potentials were higher at even lower rhizoplane soil matric potentials.

Data from the regression analysis, using logarithmically transformed values for the leaf and root water potentials and the soil matric potential, indicated a slightly more significant relation for the whole set of data between root water potential (RWP) and rhizoplane soil matric potential (RSMP) [RWP(kPa) = 2·45(0·03) – 0·17(0·02) × RSMP (kPa); $R^2 = 0{\cdot}49^{***}$; standard errors and units are given in parentheses] than between root water potential and bulk soil matric potential [RWP(kPa) = 2·48(0·03) – 0·23(0·03) × RSMP(kPa); $R^2 = 0{\cdot}41^{***}$]. The low slopes indicate that

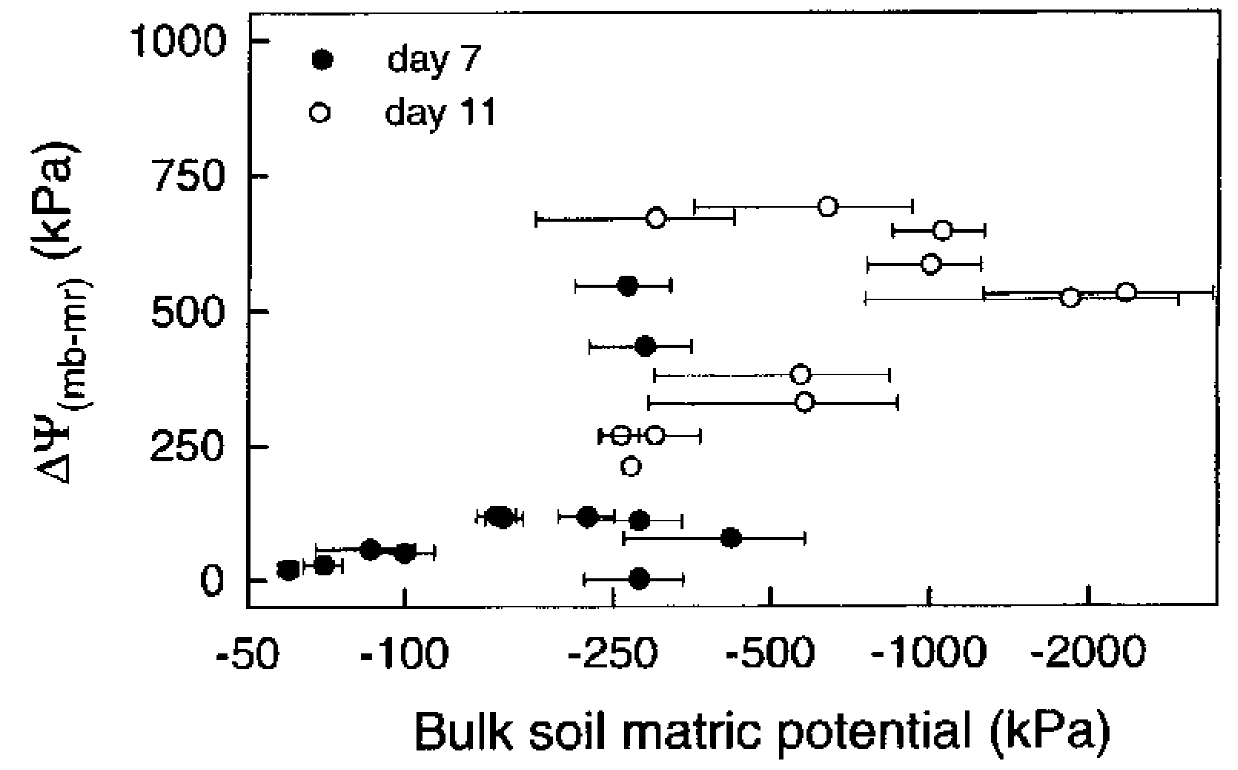

Figure 2. Mean values of the difference between bulk (Ψ_{mb}) and rhizoplane (Ψ_{mr}) soil matric potentials (logarithmic scale) plotted against mean values (± SE) of the bulk soil matric potential. Points represent means of four observations. Error bars are not shown if smaller than the symbol size. Data from seedlings of four species which were grown for 7 and 11 d in soil with initial soil matric potentials of –0·02, –0·1 and –0·23 MPa are presented together.

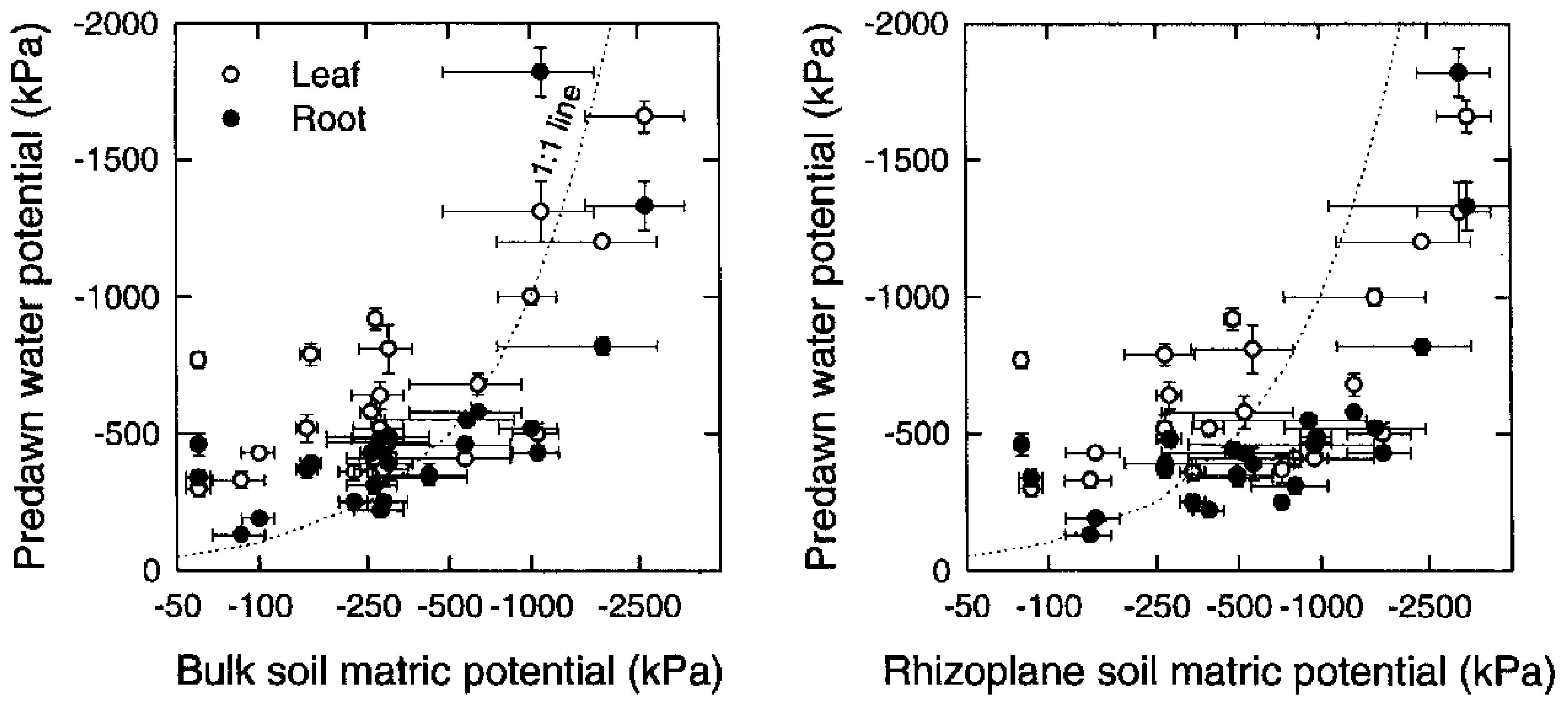

Figure 3. Pre-dawn root and leaf water potential plotted against bulk soil and rhizoplane soil matric potentials (logarithmic scale). Points represent mean values ± SE of four observations. Error bars are not shown if smaller than the symbol size.

there was no agreement. Root water potentials may approximate neither the average bulk soil matric potential nor the average rhizoplane soil matric potential. The assumptions of a correspondence and a linear relationship between average soil matric potential and root water potential in such a large soil matric potential range may be incorrect. In the investigated experimental system, all plants were subjected to water deficit. With increasing drought stress it becomes increasingly likely that gradients in water potential between soil and plant will occur and that drought-induced cavitation events will increase the risk that the plant water potential will not become equilibrated overnight with the soil water potential. The data also suggest that species may behave differently (Table 1). Steeper pre-dawn soil matric potential gradients, with a difference of up to 0·8 MPa between the rhizoplane and the bulk soil matric potentials, did not decrease pre-dawn water potentials of roots and leaves (Fig. 4).

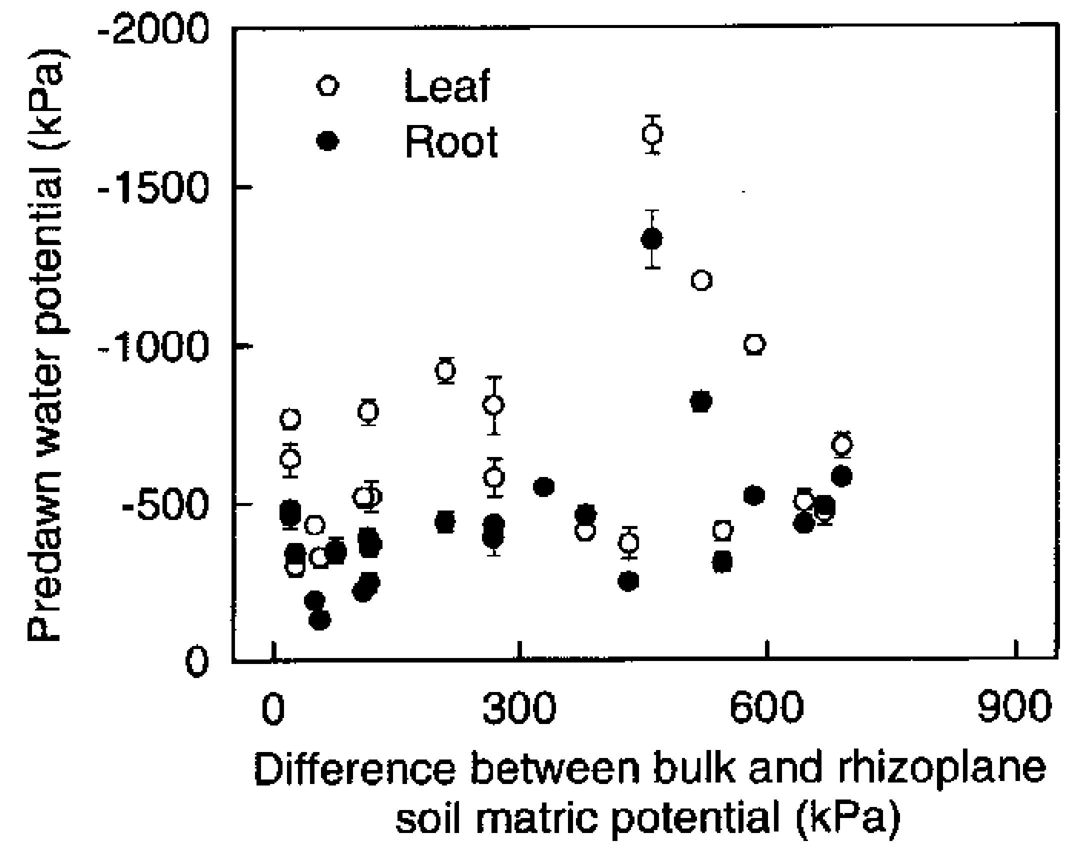

Figure 4. Pre-dawn root and leaf water potential plotted against the difference between bulk and rhizoplane soil matric potentials. Points represent mean values ± SE of four observations. Error bars are not shown if smaller than the symbol size.

DISCUSSION

Experimental findings support theoretical calculations

The results of this study do not give an exact description of pre-dawn gradients in the vicinity of roots. They are, nevertheless, useful, because they describe the driest situation averaged over the whole root system and allow us to draw some general conclusions. The main result of this study is that significant pre-dawn gradients, independent of the investigated species, were observed only at soil matric potentials lower than –0·25 MPa (initial soil matric potentials ≥ –0·1 MPa). Our experimental results show good agreement with theoretical findings of Gardner (1960), Cowan (1965) and Passioura & Cowan (1968). These researchers showed that gradients in the vicinity of roots are small if the soil is not drier than –0·2 to –0·3 MPa. Data presented by Molz *et al.* (1968) and McCoy *et al.* (1984) showed that, for large gradients, most of the decrease in soil matric potential during water absorption occurs within 1 mm of the plant root. Rhizosheath soil typically extended no more than 2 mm from the root surface of wheat roots (Young 1995). The thickness of the rhizosheaths observed in this study shows good agreement with theoretical calculations and other experimental observations (Hamza & Aylmore 1992).

Factors accounting for soil matric potential drawdown around roots

Root radius, root distribution and root morphology

Visual observation of the root system showed finer roots for barley and wheat than for maize and sunflower. In this study, we observed a bigger soil matric potential drawdown around the thicker maize roots than around the thinner barley roots. McCoy *et al.* (1984) calculated that roots with smaller radii exhibit greater drawdown of the soil matric potential as the total surface area decreases and the flux of water at the root surface increases. The flux at the root surface increases for equivalent root length density, because the volumetric water uptake rate is maintained, while the surface area for water uptake is reduced. If the water uptake per unit length root is small, then a low gradient is required to transport water at the necessary rate even in relatively dry soil. After 7 d in the treatment with –0·22 MPa initial soil matric potential, we observed only three seminal roots in maize (one primary root without laterals and two basal roots). In contrast, the root system of barley plants in the same treatment had two more basal roots. The tap root and basal roots were comparatively long in both species. Hence, the gradient which resulted in maize plants can be partly explained by a lower root length density. Rhizosheaths around maize roots were clearly thicker than around barley roots. After 7 d the primary root was about one-third shorter in the treatment with the lowest initial soil matric potential compared to the treatments with higher initial soil matric potentials. Although this may have contributed to the steep gradient observed in maize plants, it hardly affected the size of the gradient in the other investigated species. Treatments with initial soil matric potentials of –0·02 and –0·10 MPa differed at 7 d in all investigated species, mainly in the length of the lateral roots. These were 10–20 mm long in the initially well-watered treatment and were only about 5 mm long in the moderately dry treatment (–0·1 MPa). Results in Table 1 show that root development in the moderately stressed treatment was sufficient to prevent the development of steep gradients. The root system after 11 d showed the same maximum extension in depth for all treatments, and visual observation indicated a uniform distribution within the pot which was also favoured by the high number of seedlings. After 11 d, more, shorter laterals were found in the initially moderately stressed treatment as compared with the initially well-watered treatment which showed longer laterals. However, at this stage of the experiment steep gradients were found in all treatments. No relation to species and root dry mass was observed. This makes it very likely that no relation to the root length will be found.

This is supported by results from another study with a similar experimental system. In this work we found a very close correlation between root dry mass and root length and root surface ($R^2 = 0{\cdot}90^{***}$ and $0{\cdot}88^{***}$, respectively) in 11–18-d-old well-watered and drought-stressed maize seedlings. These results agree very well with findings that maize roots develop within a relatively narrow range of diameters and change very little in root length distribution by diameter with environment and plant age (Pallant *et al.* 1993). From this study and previous findings it is clear that fine roots (< 240 μm) make the largest contribution to the total root length. However, this cannot be definitively concluded by visual estimation but requires more sophisticated equipment, such as image-processing systems with a very high maximum resolution of at least 80 μm, to obtain accurate measurements of total root length, as well as root length by diameter distribution, and detailed investigations of the lateral proliferation along the root axes. However, as shown before, this information will probably not help to explain the observed gradients in the investigated low soil matric potential range. In this range the water flux becomes extremely slow and root growth decreases too, so that large gradients inevitably result. The less water there is, the more likely it is that gradients will be found between bulk soil and rhizoplane soil. At low soil matric potentials, small amounts of water taken up by plants will result in drastic decreases in the rhizoplane soil matric potential. It is reasonable to assume that some of these gradients will still be found at pre-dawn.

The drier a soil becomes, the more important it is to know the fraction of the root system which is active. Under these circumstances this information is more important than an exact knowledge of the root length. Large numbers of roots can be present in dry soil which no longer contribute to water uptake. Heterogeneous soil water distribution will usually result in drying soil and require a much more detailed analysis of the activity of the root system which cannot be described by root length alone.

Development rate

At an initial soil matric potential of –0·22 MPa, a significant pre-dawn gradient was observed in maize and sunflower but not in barley and wheat after 7 d. Differences in the rate of development in the root system and in transpiration rate per unit root length, resulting from different root/shoot ratios, may account for these differences. Faster root growth resulting in higher root length density will lead to smaller pre-dawn gradients. Shoot and root dry weight production (Table 1) was much higher for maize and sunflower than for barley and wheat. More rapid development might automatically lead to faster depletion of water. However, the results show that a high shoot dry weight in sunflower may have contributed to steep gradients, but not in maize. No relation was found among species at the two harvest times.

Root/shoot ratio

With increasing water stress, the root/shoot dry weight ratio increased in maize and sunflower, especially at the second harvest (Table 1). However, we did not observe that increased root/shoot ratios counteracted increased soil matric potential gradients in the vicinity of the roots. Instead, it seems that increases in the root/shoot ratio represent an adaptive mechanism to decreased water availability which is reduced even more, when steep gradients develop in the vicinity of roots. Differences in root/shoot ratios have to be interpreted carefully. In an other study, we found that root/shoot ratios of maize seedlings decreased during early development, independent of the water and nutrient supply (C. Studer & U. Schmidhalter, unpublished results). Delayed development, brought about by withholding water, will automatically increase the root/shoot ratio in a stressed treatment compared with a non-stressed treatment if it is plotted against time after imposing stress. At an initial soil matric potential of –0·22 MPa, root/shoot dry weight ratios of sunflower, maize, barley and wheat were as follows after 7 d: 0·66, 2·76, 2·19 and 2, respectively. The low root/shoot dry weight ratio in sunflower may have contributed to the steeper gradients. However, a high root/shoot ratio in maize did not prevent the formation of steep gradients.

Relationship between pre-dawn bulk and rhizoplane soil matric potentials and pre-dawn root and leaf water potentials

Steep pre-dawn gradients between rhizoplane soil and bulk soil matric potentials may be reflected in decreased leaf and root pre-dawn water potentials. Pre-dawn gradients in soil matric potential are the consequence of a preceding transpirational demand during the day which could not be met by the water uptake of roots. If gradients persist at pre-dawn, it is expected that they will increase the following day in a drying soil, thus affecting the plant water relations. Increased interfacial resistance would decrease water flux to the plant, thus lowering its water potential. In general, the results of this study do not show lower root and leaf water potentials at steep gradients of 0·8 MPa soil matric potential difference between bulk and rhizoplane soil (Fig. 4). However, steep gradients between the bulk soil and rhizoplane soil matric potentials are not necessarily reflected in decreased pre-dawn water potentials. It has been observed that root and leaf water potentials tend to become equilibrated with moister zones of the soil (Schmidhalter, Besson & Oertli 1992b). This effect is most clearly observed with heterogeneous soil water distribution, for example when roots are found in dry surface soil and in wet subsoil. A gradient between soil and root water potentials was observed in barley and wheat, even at high soil matric potential (Table 1). This probably reflects higher radial resistance. In contrast, only a very small gradient was observed in maize and sunflower plants. After 7 d, no significant soil matric potential gradient existed between rhizoplane soil and bulk soil in barley and wheat. After 11 d, root and leaf water potentials decreased only slightly in barley and wheat, but strongly in maize and sunflower. The latter was probably a consequence of the severe water stress which did not allow sufficient recovery of the water potential overnight.

Do plants respond to the higher pre-dawn bulk soil matric potential or to the lower pre-dawn soil matric potential in the vicinity of the roots? Figure 2 shows that root and leaf pre-dawn water potentials are, in general, comparable or lower than the corresponding bulk soil matric potential but higher than the rhizoplane soil matric potential. In the latter case, water could flow in the opposite direction from the plant into soil. Exceptions to these general observations are usually found at high soil matric potentials, where bulk and rhizoplane soil matric potentials are similar, or when a gradient between root and shoot water potential is maintained. This means that root water potentials tend to equilibrate overnight with the bulk soil matric potential or with wetter zones in the bulk soil. Water is seldom uniformly distributed in soil where water uptake occurs, and it is likely that zones with soil matric potentials higher than the average bulk soil matric potential exist. Two situations can be observed at high soil matric potentials: either plants tend to equilibrate with the soil matric potential or a gradient is maintained.

Pre-dawn values represent the most favourable situation to which a plant will be subjected with regard to water status. As the day progresses, the situation will become increasingly unfavourable. However, daytime stress can be partly circumvented by root growth occurring during the night. The exploration of new wetter soil and the supply of water from there to the roots in drier regions may be of fundamental importance, not only for continued growth, but also for maintaining the activity of the old roots.

General conclusions

The results from this study, obtained with seedlings of four species, support a previous suggestion that gradients in the vicinity of roots are small if the soil is not drier than –0·25 MPa. The circumstances under which we demonstrated gradients for two species represent a very unfavourable situation, namely the establishment of seedlings in very dry soil. The delay in root growth which results can cause the build-up of significant gradients. With a more developed root system, it becomes unlikely that a significant gradient will develop in the investigated silty soil.

Laboratory experimental systems which use aggregated soils will tend to increase gradients because, at lower water contents, the unsaturated hydraulic conductivity will decrease more markedly than would be the case near the absorbing root surface of plants grown in field soil (Hsieh, Gardner & Campbell 1972). If root growth is physically confined to a small volume, the likelihood of gradients increases. It is possible that, in many experimental systems used previously for the demonstration of gradients in the vicinity of roots, answers obtained apply only in part to field situations.

To the best of our knowledge, no investigation exists which shows the importance of soil matric potential gradients in the vicinity of roots in field soils. There is a special need to show the importance of soil matric potential gradients in the vicinity of roots under field conditions as compared to laboratory studies. We expect that soil matric potential gradients may be strongly dampened as long as there is a sufficient number of roots present in moist subsoil. Steep soil matric potential gradients may thus be less important under field conditions. It can be argued that seedlings may be less prone to the development of gradients due to increased root growth and their high plasticity in growth in drying soil. However, a more extended root system can circumvent negative effects of steep gradients in part of the root system, because roots are hydrodynamically interconnected and can compensate by taking up water from wetter sites, for example from the subsoil (Hunter & Kelley 1946; Slavikova 1967; Schmidhalter *et al.* 1992b).

This situation may thus differ from that for nutrients, which are primarily located in the top soil, where there is less chance of avoiding the negative effects of nutrient depletion around roots. Even if gradients exist in part of the root system they may no longer be related to the plant water status, because root activity has stopped, for example at very dry sites. Therefore, it is more important to know the activity of roots than merely their distribution in soil (Schmidhalter *et al.* 1994; Dalton 1995).

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