Root–soil contact for the desert succulent *Agave deserti* in wet and drying soil

BY GRETCHEN B. NORTH AND PARK S. NOBEL*

Department of Biology, University of California, Los Angeles, California 90095-1606, USA

SUMMARY

To investigate the extent and size of root–soil air gaps that develop during soil drying, resin casts of roots of the desert succulent *Agave deserti* Engelm. were made *in situ* for container-grown plants and in the field. Plants that were droughted in containers for 7 and 14 d had 24 and 34 % root shrinkage, respectively, leading to root–soil air gaps that would reduce the hydraulic conductivity at the root–soil interface by a factor of about 5. When containers were vibrated during drought, root–soil air gaps were greatly diminished, and the predicted conductivity at the interface was similar to that of the control (moist soil). For plants in the field (4 and 6 wk after the last rainfall), root shrinkage was greater than for container-grown plants, but root–soil contact on the root periphery was greater, which led to a higher predicted hydraulic conductivity at the root–soil interface. To test the hypothesis that root–soil air gaps would help to limit water efflux from roots in drying soil, the water potentials of the soil, root, and shoot of plants from vibrated containers (with gaps eliminated or reduced) and non-vibrated containers were compared. The soil water potential was lower for vibrated containers after 14 d of drought, suggesting more rapid depletion of soil water due to better root–soil contact, and the root water potential was lower as well, suggesting greater water loss by roots in the absence of root–soil air gaps. Thus, air gaps could benefit *A. deserti* by helping to maintain a higher root water potential in the early stages of drought and later by limiting root water loss at the root–soil interface when the water potential exceeds that of the soil.

Key words: Hydraulic conductivity, root shrinkage, root–soil interface, root water uptake.

INTRODUCTION

Root contact with the soil is essential for water and nutrient absorption by crops as well as native plants. Soil properties, such as the degree of compaction and the average particle size, and root properties, such as root diameter and relative hydration, can influence the extent of root–soil contact (Tinker, 1976; Nye, 1994). In heavily compacted or waterlogged soil, problems with root gas exchange may be exacerbated by the absence of air spaces between roots and soil particles (Veen *et al.*, 1992). Conversely, incomplete root–soil contact due to loose soil structure or root shrinkage can reduce the uptake of water and nutrients (Faiz & Weatherley, 1982; Veen *et al.*, 1992). The primary limitation on root water uptake in moist soils is the root hydraulic conductivity (Passioura, 1988; Hamza & Aylmore, 1992), whereas under dry conditions the conductivity of the soil is most limiting (Bristow, Campbell & Calissendorff,

1984; Nobel & Cui, 1992*a*). In soils of intermediate moisture levels, e.g. with water potentials of about -0.2 to -2.0 MPa in the case of desert succulents (Nobel & North, 1993), water movement is limited by the hydraulic conductivity of the root–soil interface, where air gaps between the root and the soil can arise due to root shrinkage (Faiz & Weatherley, 1982; Nobel & Cui, 1992*a, b*; Nye, 1994).

Roots can shrink radially by as much as 40 % in response to increases in transpirational demand (Huck, Klepper & Taylor, 1970; Faiz & Weatherley, 1982). Similar shrinkage can occur for roots under drying conditions caused by exposure to solutions of high osmotic pressures (Cole & Alston, 1974; Taylor & Willatt, 1983; Nye, 1994). Roots of the succulents *Agave deserti*, *Ferocactus acanthodes*, and *Opuntia ficus-indica* shrink by about 20 % after 4 or 5 d of exposure to an atmosphere with a water potential of -10 MPa (Nobel & Cui, 1992*a*). Although changes in root diameter with changing water status have been observed for roots in soil (Huck *et al.*, 1970; Taylor & Willatt, 1983), changes in root–soil contact

* To whom correspondence should be addressed.
E-mail: psnobel@biology.ucla.edu

in response to soil drying apparently have not been reported. Using resin casts of soil and roots *in situ*, the extent of root–soil contact and the dimensions of air gaps between the roots and the soil were investigated for the common desert agave *A. deserti* under various conditions of soil moisture in the field and in containers.

The effects of incomplete root–soil contact on plant water uptake have been explored through models that allow the hydraulic conductivity of the root–soil interface to vary with changes in soil water content and root diameter (Herkelrath, Miller & Gardner, 1977; Fernández & McCree, 1991; Nobel & Cui, 1992*a, b*; Jensen *et al.*, 1993; Nye, 1994). According to such models, the decrease in the conductivity at the interface due to poor soil contact can reduce water uptake by up to 99%. Vibrating containers of plants to eliminate air gaps between roots and soil increases water uptake, leading to higher leaf water potentials than for non-vibrated plants (Faiz & Weatherley, 1982). Air gaps can thus help to limit water loss from the roots to a drier soil, which is particularly important for desert species (Nobel & Cui, 1992*a*). Under drought conditions, the water potential of roots surrounded by air gaps should be higher than that of roots in full contact with the soil. Vibration experiments were therefore performed on container-grown plants of *A. deserti* to examine the relationship between root–soil contact and the water potentials of the soil, roots and shoot. Measurements of water potential, root diameter and gap width were then used to calculate the overall hydraulic conductivity of the root–soil pathway for field and container-grown plants under a range of soil moistures to help understand the role of the root–soil interface in controlling water movement between roots and soil.

MATERIALS AND METHODS

Field measurements

Field measurements were made at the University of California Philip L. Boyd Deep Canyon Desert Research Center near Palm Desert, CA at Agave Hill (33° 38′ N, 116° 24′ W, 850 m elevation). *Agave deserti* Engelm. (Agavaceae) is the dominant species at the site, which has a loamy-sand soil with a non-gravel portion consisting of 73% sand (particle sizes of 0·05–1·0 mm) by mass (Nobel, 1977). Out-croppings of disintegrating granite are abundant, resulting in numerous rocks at the soil surface and in the upper 20 cm of soil, where the roots of *A. deserti* are concentrated (Nobel, 1988; Nobel, Miller & Graham, 1992). Resin casts of roots and soil were made *in situ* in two undisturbed level locations on 24 April and 8 May 1995. The soil moisture content within the root zone was determined gravimetrically, and the soil water potential (Ψ_{soil}) was calculated based on moisture release curves for Agave Hill soil (Young & Nobel, 1986). No precipitation was recorded at Agave Hill in April or May 1995, and Ψ_{soil} at a depth of 10 cm was $-1\cdot7$ MPa on 24 April and $-3\cdot4$ MPa on 8 May.

Laboratory experiments

Ramets (vegetative offshoots) *c*. 10 cm tall with four to five unfolded leaves were removed from mature plants of *A. deserti* growing in a glasshouse at the University of California, Los Angeles, and grown in containers of equal portions of washed quartz sand and soil from Agave Hill. After 30 d, when each ramet had six to 10 roots averaging 12 cm in length, the plants were transferred to cylindrical polystyrene containers 15 cm tall and 10 cm in diameter, which were filled with Agave Hill soil sieved to remove particles larger than 3 mm across. An aquarium-type airstone had been placed in the soil near the base of each container and fitted to Tygon® tubing that extended through a hole drilled in the side of the container, allowing a partial vacuum to be applied to insure complete infiltration of the soil by resin. Plants were maintained in the glasshouse, receiving water twice weekly, with daily maximum/minimum air temperatures averaging 28 °C/16 °C, daily maximum/minimum r.h. of 70%/40%, and a mean photosynthetic photon flux density of 30 mol m^{-2} d^{-1}.

After 14 d, six plants were randomly assigned to each of five groups and maintained for an additional 14 d: (1) control, which was watered twice weekly; (2) vibrated, in which containers were watered twice weekly while placed on a thin aluminium plate that was struck four times with a mallet twice daily; (3) droughted by withholding water for the last 7 d; (4) droughted for the entire 14 d; and (5) droughted and vibrated. At the end of the treatments, two containers from each group were infiltrated with resin, and six were used for determinations of water potential. For the first and second groups, containers had been watered 3 d before measurements. The root water potential (Ψ_{root}) was measured by excavating roots, wrapping them in Parafilm®, and removing the distal 15-mm segments in a humidified chamber; Ψ_{root} was determined after the segments equilibrated for 2 h in a thermocouple psychrometer (Decagon Devices, Pullman, WA). Shoot water potential (Ψ_{shoot}) was measured for 9-mm cores removed from the base of unfolded leaves, also using the thermocouple psy-chrometer. Ψ_{soil} was determined gravimetrically (Young & Nobel, 1986), using a soil bulk density of 1·57 Mg m^{-3} as determined for containers of sieved soil; soil volume and hence bulk density were not changed significantly by withholding water or by vibration. Gravimetric determinations of Ψ_{soil} were within $\pm 8\%$ of Ψ_{soil} measured with the thermo-couple psychrometer.

Resin infiltration and sectioning

An acrylic resin that hardened in a few hours, even in the presence of moisture, was used to make sections of soil and roots, both in the field and in containers (Moran, McBratney & Koppi, 1989). For each batch, 34 g of Araldite GY 509 resin, 34 g of Araldite RD-2 diluent, and 32 g of HY 956 hardener (Ciba-Geigy, Hawthorne, NY) were used. Three batches of liquid resin were applied in sequence from a large syringe fitted with a pipette tip and suspended 2 cm above the soil surface, which dispensed the resin at approximately two drops s^{-1} (total time 1·5 h). For plants in containers, a partial vacuum was applied during the application of the third resin batch to improve infiltration. One hour after infiltration, the resin was sufficiently hardened to allow removal of the soil block, and the block was further infiltrated with two batches of resin under partial vacuum in the laboratory. Within 24–48 h, the blocks were trimmed and cut in 1-cm-thick transverse and longitudinal sections with a diamond lapidary saw. Sections were viewed and photographed under a dissecting microscope at magnifications of $\times 10 - \times 30$.

Measurements of root–soil contact characteristics were made from sections examined with the dissecting microscope using an ocular micrometer and from photographs enlarged to final magnifications of $\times 15 - \times 60$. Data were statistically analysed using one-way ANOVA followed by Student–Newman–Keuls pairwise testing (Sigmastat, Jandel Scientific, San Rafael, CA).

Hydraulic conductivity of roots, soil, and air gaps

The hydraulic conductivity (m s^{-1} MPa^{-1}) of the overall root–soil pathway (L_{overall}) for water movement was based on that of its three components (the soil, the root–soil air gap, and the root) in series (Fig. 1; Nobel & Cui, 1992 a):

$$\frac{1}{L_{\text{overall}}} = \frac{1}{L_{\text{soil}}^{\text{eff}}} + \frac{1}{L_{\text{gap}}} + \frac{1}{L_{\text{P}}}, \tag{1}$$

where $L_{\text{soil}}^{\text{eff}}$ is the effective hydraulic conductivity of the soil, L_{gap} is the hydraulic conductivity of an air gap between the root and the soil, and L_{P} is the hydraulic conductivity of the root (Fig. 1). $L_{\text{soil}}^{\text{eff}}$ was calculated as follows, assuming radial symmetry for Ψ_{soil} (Nobel & Cui, 1992 b):

$$L_{\text{soil}}^{\text{eff}} = \frac{L_{\text{soil}}}{r_{\text{root}} \log_e (r_{\text{distant}}/r_{\text{gap}})}, \tag{2}$$

where L_{soil} is the soil hydraulic conductivity, which is a function of Ψ_{soil}, as has been determined for Agave Hill soil (Young & Nobel, 1986); r_{gap} and r_{root}(m) are the radii of the air space and root, respectively (Fig. 1); and r_{distant} is set to the lesser of 30 mm and half of the inter-root spacing (Caldwell,
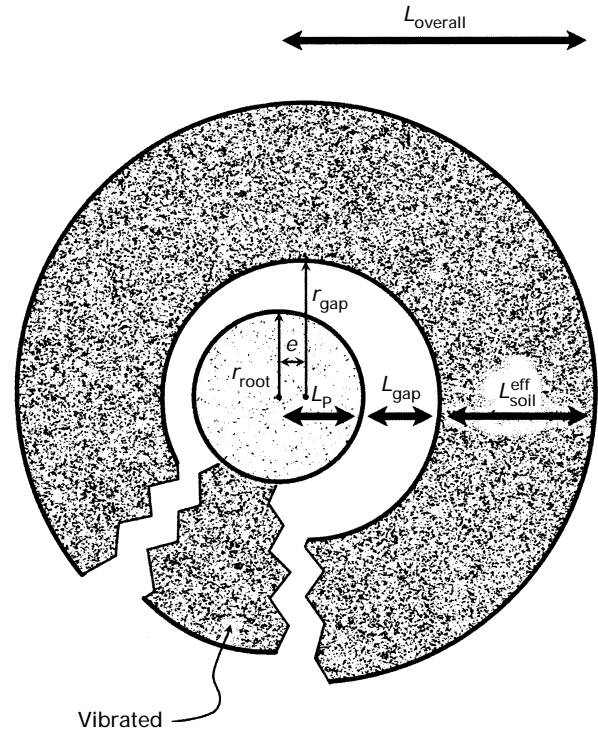
Figure 1. Cross section of root (light stippling) after shrinkage during drying, eccentrically located in an air space (no stippling) in soil (dark stippling). The radii of the root (r_{root}) and air space (r_{gap}) are indicated, along with the eccentricity (e, the distance between the centre of the air space and the centre of the root). Arrows indicate the components of the overall hydraulic conductivity (L_{overall}): the effective soil hydraulic conductivity ($L_{\text{soil}}^{\text{eff}}$), the hydraulic conductivity of the air gap (L_{gap}), and the root hydraulic conductivity (L_{P}). Wedge-shaped segment without an air gap shows probable effect of vibration.

1976), which was about 15 mm for plants in containers.

The hydraulic conductivity of the air gap, L_{gap}, was calculated assuming isothermal conditions and allowing the root to be located eccentrically within the gap, where the eccentricity e (m) equals the distance between the geometric centre of the air space and that of the root (Fig. 1; Mills, 1992; Nobel & Cui, 1992 a):

$$L_{\text{gap}} = \frac{L'}{r_{\text{root}} \cosh^{-1} \left(\dfrac{r_{\text{gap}}^2 + r_{\text{root}}^2 - e^2}{2 r_{\text{gap}} r_{\text{root}}} \right)}. \tag{3}$$

L' equals $\bar{V}_{\text{w}}^2 D_{\text{wv}} P_{\text{wv}}^* / (RT)^2$, where $\bar{V}_{\text{w}}$ is the partial molal volume of water (m^3 mol^{-1}), D_{wv} is the diffusion coefficient of water vapour in air (m^2 s^{-1}), P_{wv}^* is the saturation partial pressure of water (MPa), and RT is the gas constant times the absolute temperature (m^3 MPa mol^{-1}); at 25 °C, L' equals $4·18 \times 10^{-12}$ m^2 s^{-1} MPa^{-1} (Nobel & Cui, 1992 a). When the root is concentrically located within the air space, e equals zero, and $\cosh^{-1}(r_{\text{gap}}^2 + r_{\text{root}}^2/2 r_{\text{gap}} r_{\text{root}})$ equals $\log_e (r_{\text{gap}}/r_{\text{root}})$; when e equals the gap width (a root touches the soil), eqn 3 is not applicable. For the intermediate cases considered here, mean values of e
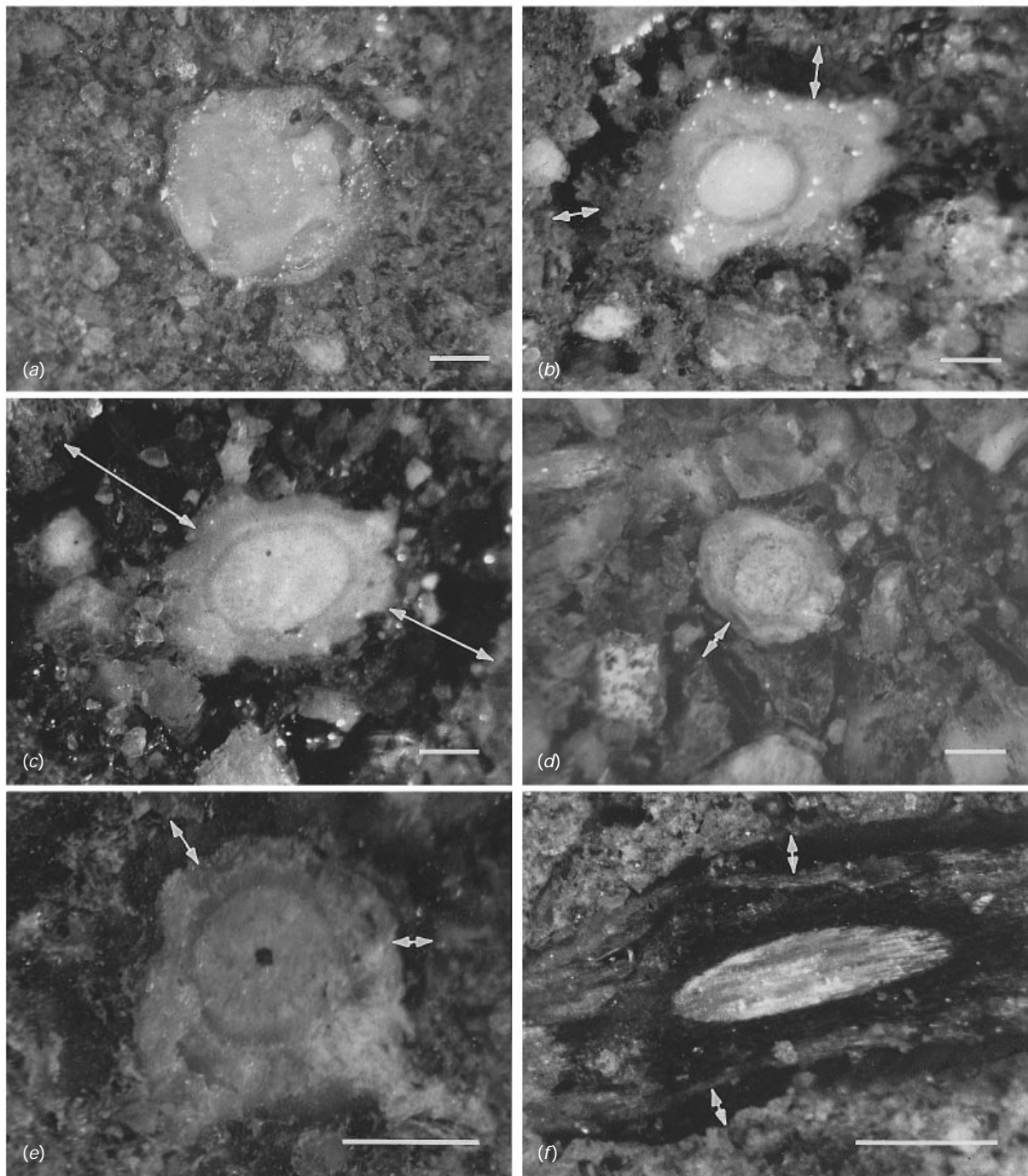
Figure 2. Micrographs of resin sections of roots of *Agave deserti* in soils. (*a*) Cross section from control container (moist soil). (*b*) Cross section from container-grown plant after 7 d of drying. (*c*) As for (*b*), but after 14 d of drying. (*d*) As for (*c*), but after vibration treatment. (*e*) Cross section from field on 24 April. (*f*) Longitudinal section from field on 5 May. Bars = 1 mm.

were always less than the mean gap width. L_P was based on previous measurements for young main roots of *A. deserti* (North & Nobel, 1995).

RESULTS

Root shrinkage and root-soil contact

Roots showed no evidence of shrinkage or distortion due to resin embedding (Fig. 2). Control roots

(maintained in moist soil) were white and generally circular in cross-section (Fig. 2*a*), whereas roots subjected to drought were more irregular in outline, with a darker endodermal cylinder evident within the cortex (Fig. 2*b–d*). Most roots in sections made in the field were older and darker (Fig. 2*e, f*) than the 4-wk-old to 8-wk-old roots of the container-grown plants. Air gaps between the roots and the soil appeared dark in the resin sections, which were kept wet under the microscope to improve contrast.

Table 1. *Characteristics of root–soil contact for* Agave deserti *in containers in the glasshouse and on two dates in the field*

Treatment	Gap width (mm)	Root radius (mm)	Root–soil contact (%)	Root shrinkage (%)
Control	0·07±0·02	0·86±0·15	94±2	8±2
Vibrated	0·05±0·03	0·89±0·13	95±6	10±3
Droughted 7 d	0·25±0·04 a	0·79±0·10	24±7 a	24±4 a
Droughted 14 d	0·34±0·05 b	0·64±0·06	21±7 a	34±3 a
Droughted/vibrated	0·07±0·03	0·71±0·13	90±3	9±2
Field (24 April)	0·11±0·02	0·36±0·05 a	59±9 b	26±3 a
Field (5 May)	0·12±0·02	0·26±0·04 a	46±8 b	40±5 b

Different letters within a column indicate significant differences from the control and between treatments ($P < 0.05$ for pairwise testing).

The width of the air gap was determined by averaging four measurements from the outer edge of the root in transverse section to the edge of the soil. The percentage of root contact with the soil was determined from photographs by outlining the perimeter of the root with thread and marking regions where no gap was evident. The percentage of root 'shrinkage' was calculated from the mean gap width divided by the sum of the gap width plus the root radius (= percentage difference between air space diameter and root diameter). Data are means ± SE for $n = 10$ roots.
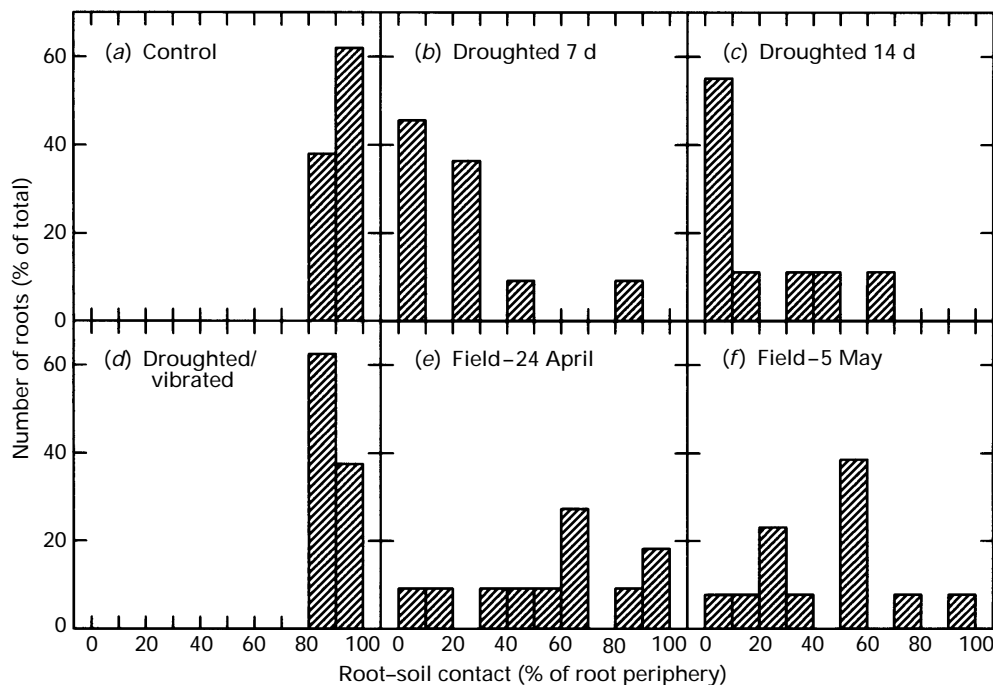

Figure 3. Root–soil contact for roots of *Agave deserti*. (*a*) Control (in moist soil). (*b*) After 7 d of drying in container. (*c*) As for (*b*), but after 14 d of drying. (*d*) As for (*c*), but after vibration treatment. (*e*) From field on 24 April. (*f*) From field on 5 May. Data represent $n = 12$ roots.

In some cases where air gaps were present, some soil particles still adhered to the root surface but had separated from the bulk soil (Fig. 2*b, c*).

Only small air gaps were present between roots and the moist soil for the control, as average root contact with the soil then exceeded 90% (Table 1, Fig. 3*a*). Such control roots showed only 8% shrinkage (which for all treatments is more accurately described as the percentage difference between air space diameter and root diameter; Table 1), and all of the roots had at least 80% contact with the soil along their cross-sectional perimeter (Fig. 3*a*). Roots from plants maintained in moist soil and

vibrated were similar to the control roots with respect to gap width, root–soil contact, and root shrinkage (Table 1).

After 7 d of drought, a significantly larger air gap developed between roots of container-grown plants and the soil, along with a loosening of soil particles in the vicinity of the root (Fig. 2*b*), and root shrinkage increased to 24% (Table 1). Mean root–soil contact decreased to 24%, with 45% of the roots having less than 20% root–soil contact (Fig. 3*b*). After 14 d of drought, the mean width of the root–soil air gap increased to 0·34 mm (Table 1), and 66% of the roots had less than 20% root–soil contact (Fig. 3*c*).

Table 2. *Water potentials of the soil and organs of* Agave deserti *in containers in the glasshouse*

	Water potential (MPa)		
Treatment	Soil	Roots	Shoot
Control	-0.1 ± 0.1	-0.45 ± 0.02	-0.42 ± 0.03
Vibrated	-0.1 ± 0.1	-0.47 ± 0.03	-0.44 ± 0.02
Droughted	-4.2 ± 0.4 a	-1.04 ± 0.03 a	-1.01 ± 0.06 a
Droughted/vibrated	-6.4 ± 0.7 b	-1.13 ± 0.02 b	-0.96 ± 0.06 a

Different letters within a column indicate significant differences from the control and between treatments ($P < 0.05$ for pairwise testing).

Data are means $\pm$ SE for $n = 6$ plants treated for 14 d.

Table 3. *Hydraulic conductivities of the soil ($L_{\text{soil}}^{\text{eff}}$), root–soil air gap ($L_{\text{gap}}$), root ($L_{\text{P}}$), and overall root–soil pathway (L_{overall}) for* Agave deserti

	Hydraulic conductivity (10^{-8} m s^{-1} MPa^{-1})			
Treatment	$L_{\text{soil}}^{\text{eff}}$	L_{gap}	L_{P}	L_{overall}
Control	2458	6.21	20	4.65
Droughted 7 d	12.7	1.95	8	1.40
Droughted 14 d	5.64	1.52	5	0.97
Droughted/vibrated	2.22	6.26	5	1.23
Field (24 April)	33.1	4.22	10	2.72
Field (5 May)	12.6	4.21	5	1.94

Data were calculated using Ψ_{soil} from the text and Table 2, root and gap radii from Table 1, and L_{P} for young main roots of *A. deserti* (North & Nobel, 1991) in eqns 1–3, assuming isothermal conditions and concentric location of the roots within the air spaces.

Roots from containers that were vibrated daily during 14 d of drought did not differ from the control roots with respect to gap width or root shrinkage (Table 1), and all had at least 80 % contact with the soil (Fig. 3*d*).

For plants in the field, resin sections made on 24 April and 5 May (*c.* 4 and 6 wk after the last rainfall, respectively) included roots that were thinner on average than the roots from container-grown plants (Table 1). On both dates the gap width represented a greater fraction of the air space occupied by the roots, as reflected in the greater root shrinkage (Table 1). The mean root–soil contact for field roots was intermediate to that for control roots and droughted roots for the container-grown plants (Table 1). On both field dates, root–soil contact of individual root cross sections ranged from 0 to 100 %, with more than 50 % of the roots having at least 60 % contact on the earlier date, compared with only 15 % on the later date (Fig. 3*e, f*). In many cases, roots were located adjacent to rocks, usually with full contact between root and rock.

Water relations

Soil water potential (Ψ_{soil}) for the control treatment did not differ from that for watered containers that were vibrated (Table 2). After 14 d of drought, Ψ_{soil} decreased to -4.2 MPa for containers that were not vibrated and to -6.4 MPa for those that were (Table 2). Vibration had no effect on root water potential (Ψ_{root}) for containers of moist soil, but Ψ_{root} was about 8 % lower for vibrated than for non-vibrated containers after 14 d of drought (Table 2). Shoot water potential (Ψ_{shoot}) was unaffected by vibration. For droughted, non-vibrated plants Ψ_{root} and Ψ_{shoot} were similar, whereas for droughted, vibrated plants Ψ_{root} was lower than Ψ_{shoot} ($P < 0.05$; Table 2).

Except for plants that were both droughted and vibrated, the hydraulic conductivity of the air gap (L_{gap}) was the lowest and thus the most limiting conductivity in the root–soil pathway (Table 3). The hydraulic conductivity of the soil ($L_{\text{soil}}^{\text{eff}}$) was the least limiting conductivity, except for container-grown plants droughted for 14 d; as Ψ_{soil} decreased from -0.1 MPa (control) to -6.4 MPa (droughted 14 d/vibrated), $L_{\text{soil}}^{\text{eff}}$ decreased by more than 10^3. Root hydraulic conductivity (L_{P}) decreased by a factor of 4 after 14 d in drying soil, and L_{overall} decreased by a factor of 5 (Table 3).

To quantify the effect of eccentric location of roots within air spaces on hydraulic conductivity, the eccentricity (e) was measured. For three roots from containers droughted for 14 d, the mean e was 0.19 mm. Using this e in eqn 3 along with values for root and gap radii from Table 1, L_{gap} for eccentrically located roots was 1.84×10^{-8} m s^{-1} MPa^{-1}, which is 21 % greater than L_{gap} for concentrically located roots after 14 d of drought (Table 3). For three roots in the field (5 May), an average e of 0.10 mm led to an L_{gap} of 7.63×10^{-8} m s^{-1} MPa^{-1}, which is 81 % greater than for the concentric case (Table 3). Averaged for all treatments, incorporating measured values of e into eqn 3 led to values of L_{gap} that were $29 \% \pm 10 \%$ higher than L_{gap} for concentrically located roots.

DISCUSSION

Resin casts of *Agave deserti* roots *in situ* demonstrated progressively greater root shrinkage and loss of root–soil contact during soil drying. Based on the root radius and the average width of root–soil air gaps, root diameter during drying apparently decreased by up to 34% in containers and 40% in the field. Such shrinkage was somewhat greater than the 20% reduction measured for roots of *A. deserti* in a drying atmosphere (Nobel & Cui, 1992*a*), in part, presumably, because of incorporation of air gaps (accounting for *c.* 8%) that were present even for well hydrated roots, such as the control. After 14 d of drying, the mean root diameter of container-grown plants was 26% less than the control root diameter, representing a decrease similar to that measured previously. The greater shrinkage for roots in the field than in containers might partly reflect greater average root age in the field, as cortical cells shrink and die during ageing, a process that is hastened by drought (North & Nobel, 1995).

Models of radial water uptake by roots in soil assume that the hydraulic conductivity of the root–soil interface is inversely proportional to the width of a root–soil air gap, whether water moves as a liquid or a vapour (Cowan & Milthorpe, 1968; Nobel & Cui, 1992*a, b*; Nye, 1994). Assuming isothermal conditions and a concentric location of roots within air spaces, the hydraulic conductivity of the gap (L_{gap}) for container-grown plants of *A. deserti* was predicted to decrease by a factor of 4 as the gap width increased by a factor of 5. For plants droughted in containers, as well as for plants in the field, L_{gap} was the lowest and therefore the most limiting hydraulic conductivity in the root–soil pathway, in agreement with previous calculations of L_{gap} for soils of similar water potentials (Nobel & Cui, 1992*a*). Despite greater relative shrinkage for roots in the field, the smaller gap widths and smaller root radii led to a predicted L_{gap} that was more than double that for droughted container-grown plants. Similarly, thinner roots of *Zea mays* maintain better contact with a drying soil and therefore take up more water per unit area according to a model based on changes in the root–soil contact angle (Nye, 1994). For *A. deserti* in the field, thin roots should be more effective in water uptake than thick roots during the early stages of soil drying, but they would also tend to lose water more readily to the soil when the soil water potential decreased below that of the roots.

Roots of *A. deserti* that were eccentrically located in air spaces had values for L_{gap} that were on average *c.* 20% higher than L_{gap} for the concentric case for container-grown plants. For roots of *A. deserti* in the field, a greater relative eccentricity than in containers resulted in a predicted increased in L_{gap} about 50% greater. In most field situations, roots are eccentrically located within air spaces, particularly when growing in pre-existing channels or macropores (Tinker, 1976; van Noordwijk *et al.*, 1992; van Noordwijk, Schoonderbeek & Kooistra, 1993). The most extreme case of eccentricity, in which the root touches the soil along its periphery, can occur more frequently than would be predicted assuming the random positioning of roots within air spaces (Kooistra *et al.*, 1992). When the root touches the soil, the eccentricity equals the mean gap width, and L_{gap} becomes infinite according to eqn 3 (actually, the isothermal assumption is then not valid, and eqn 3 is no longer appropriate). In this regard, measured L_{gap} for roots of *A. deserti* touching a filter-paper cylinder (simulating the soil) at one point on their perimeter is only 2·4-fold greater than for roots concentrically located in the cylinder, similar to the increase predicted by a graphical flux–plot method that allows for non-radially symmetric pathways for water movement from the soil to a root (Nobel & Cui, 1992*b*).

Substantial root–soil contact, such as for the control roots, might thus greatly increase the hydraulic conductivity of the root–soil interface compared with that predicted based on mean gap width, thereby leading to a greater overall hydraulic conductivity ($L_{overall}$). However, the value of $4·7 \times 10^{-8}$ m s^{-1} MPa^{-1} for $L_{overall}$ for the control agrees well with a value of $4·8 \times 10^{-8}$ m s^{-1} MPa^{-1} calculated using a model of water uptake incorporating root–soil contact (Herkelrath *et al.*, 1977), in which the root hydraulic conductivity (20×10^{-8} m s^{-1} MPa^{-1}) is multiplied by a contact fraction equal to the volumetric soil water content (0·24 for saturated Agave Hill soil; Young & Nobel, 1986). Large decreases in root–soil contact occurred during soil drying for *A. deserti* in containers, with over 50% of the roots having less than 10% contact with the soil after 14 d. Greater root–soil contact was maintained in the field, probably because of relatively smaller root diameters and greater soil heterogeneity. In particular, roots were appressed against rocks, where greater water availability occurs due to condensation and water channelling (Nobel *et al.*, 1992).

Another assumption, that the temperature was constant from the root surface to the soil, led to an over-prediction for L_{gap}. Because of evaporative cooling at the root surface when water is leaving, the actual driving force for water vapour movement across air gaps to the soil is less than that predicted on the basis of root and soil water potentials (Cowan & Milthorpe, 1968; Nobel & Cui, 1992*b*). To allow for thermal effects, L_{gap} should be reduced by *c.* $65–70\%$ (Cowan & Milthorpe, 1968, Nobel & Cui, 1992*b*; Nye, 1994). When combined with the average 30% increase in L_{gap} caused by the average eccentric location of roots, L_{gap} calculated for the isothermal, concentric case should be multiplied by 0·6 to predict water conduction across a gap better.

Whatever the exact value of L_{gap}, root–soil air gaps had a major impact on water exchange between roots of *A. deserti* and the soil, as demonstrated by differences between plants in vibrated and non-vibrated containers. The soil vibration treatment had no effect on well hydrated plants, but plants vibrated during 14 d of soil drying had substantially smaller root–soil air gaps and greater root–soil contact than non-vibrated plants. The soil water potential (Ψ_{soil}) was lower for vibrated plants, in agreement with results for water-stressed *Helianthus annuus* (Faiz & Weatherley, 1982), and might reflect the greater water uptake by roots with greater soil contact, at least in the early stages of soil drying when Ψ_{soil} exceeded Ψ_{root}. In the transitional period of soil drying when Ψ_{soil} became less than Ψ_{root}, water loss by the roots was apparently retarded by root–soil air gaps, leading to a higher Ψ_{root} for plants that were not vibrated. Alternatively, the lower Ψ_{root} for vibrated plants could have resulted from the quicker depletion of soil water, exposing roots to a larger soil–root water potential gradient for a longer period. In any case, Ψ_{root} decreased below Ψ_{shoot} for vibrated plants, favouring water movement from the shoot to the root. Such a shoot–root gradient did not occur for non-vibrated plants, suggesting that wider air gaps (and a smaller L_{gap}) might help to limit water loss from the roots and thus from the shoot. No difference in Ψ_{shoot} occurred for the succulent shoots of vibrated and non-vibrated *A. deserti*, perhaps because greater water uptake by vibrated plants in the first few days of drying was counterbalanced by greater shoot water loss later. For desert succulents in the field, as for many plants in drying soil, root–soil air gaps might initially reduce water uptake but might also postpone root dehydration, thereby prolonging the period of root extension into wetter soil regions.

In summary, an increase in the width of root–soil air gaps and a decrease in root–soil contact were demonstrated for roots of *A. deserti* in drying soil. The overall hydraulic conductivity of the root–soil pathway for plants after 14 d of drying was a factor of about 5 lower than that of the control, or a factor of 3 lower when taking into consideration thermal effects and the eccentric location of roots. Similarly, water uptake is reduced by a factor of 3 in a model incorporating root shrinkage and a decrease in the root–soil contact angle (Nye, 1994). When gap formation was reduced by vibrating the containers, soil water was depleted more rapidly and root water potential was lower than for non-vibrated containers. For succulent plants such as *A. deserti*, the potential benefit of higher relative root water potential might outweigh the drawback of reduced water uptake caused by root–soil air gaps in the initial stages of soil drying, and the lower overall hydraulic conductivity due to gaps can help to limit its water loss in the subsequent stages of drought.

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