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Root growth, developmental changes in the apex, and hydraulic conductivity for *Opuntia ficus-indica* during drought

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SUMMARY

Developmental changes in the root apex and accompanying changes in lateral root growth and root hydraulic conductivity were examined for *Opuntia ficus-indica* (L.) Miller during rapid drying, as occurs for roots near the soil surface, and more gradual drying, as occurs in deeper soil layers. During 7 d of rapid drying (in containers with a 3-cm depth of vermiculite), the rate of root growth decreased sharply and most root apices died; such a determinate pattern of root growth was not due to meristem exhaustion but rather to meristem mortality after 3 d of drying. The length of the meristem, the duration of the cell division cycle, and the length of the elongation zone were unchanged during rapid drying. During 14 d of gradual drying (in containers with a 6-cm depth of vermiculite), root mortality was relatively low; the length of the elongation zone decreased by 70%, the number of meristematic cells decreased 30%, and the duration of the cell cycle increased by 36%. Root hydraulic conductivity (L_P) decreased to one half during both drying treatments; L_P was restored by 2 d of rewetting owing to the emergence of lateral roots following rapid drying and to renewed apical elongation following gradual drying. Thus, in response to drought, the apical meristems of roots of *O. ficus-indica* near the surface die, whereas deeper in the substrate cell division and elongation in root apices continue. Water uptake in response to rainfall in the field can be enhanced by lateral root proliferation near the soil surface and additionally by resumption of apical growth for deeper roots.

Key words: Meristem, cell division, elongation zone, lateral roots, root primordia, water uptake.

INTRODUCTION

Roots of desert succulents endure extended periods of drought yet maximize water uptake when soil moisture becomes available (Nobel, 1988, 1996). In general, the structural changes enabling roots to survive drought and resume the uptake of water and nutrients depend on both the rate and the duration of soil drying (Jupp & Newman, 1987; Huang & Nobel, 1993). Various root tissues can survive prolonged drought; e.g., the exodermis, vascular tissues and endodermis in *Allium cepa* roots survive up to 200 d without watering (Stasovski & Peterson, 1993). Depending on the species and the rate of drying, root apical meristems can be more susceptible to drought than other root tissues (Jupp & Newman, 1987; Stasovski & Peterson, 1993) or less so (Stasovski & Peterson, 1991). In a root apex, drought can affect both cell proliferation and cell elongation (Sharp, Silk & Hsiao, 1988; Robertson *et al.*, 1990*a*, *b*), with both processes more likely to be inhibited by rapid, than by gradual, drying.

Most cacti have shallow root systems, with few roots deeper than 40 cm, yet few roots are found within 3 cm of the soil surface owing to the high temperatures and low water potentials in that region (Nobel, 1988, 1996; Rundel & Nobel, 1991). Although drying is more rapid near the soil surface, the light rains that interrupt dry periods in a desert are more likely to be utilized by shallow roots than by deep roots. Indeed, cacti and other desert succulents respond quickly to soil wetting after drought by resuming transpiration (Szarek, Johnson & Ting, 1973; Ehleringer *et al.*, 1991). The root properties underlying such recovery were examined in this study for the prickly-pear cactus *Opuntia ficus-indica*, a species whose root hydraulic conductivity has been investigated under various conditions (North & Nobel, 1992; Huang & Nobel, 1993).

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One hypothesis to be tested is that the apical meristem of roots of *O. ficus-indica* and hence root growth are more susceptible to rapid than to gradual drying. Under certain conditions, possibly including rapid drying, roots can exhibit determinate growth due to the cessation of cell production by the apical meristem (Dubrovsky, 1997*b*). Determinate growth occurs in the primary roots of some Sonoran Desert Cactaceae and represents an environmental adaptation favouring seedling establishment by early induction of lateral roots (Dubrovsky 1997*a*, *b*). A second hypothesis to be tested for *O. ficus-indica* is that changes in root apical growth in response to different rates of drying are accompanied by differences in lateral root initiation and development. Lateral root development is promoted by drought in a number of species (Jupp & Newman, 1987; North, Huang & Nobel, 1993; North & Nobel, 1994); e.g., when subjected to drought, roots of *Zea mays* and *Allium cepa* produce primordia in response to the death of the main root tip (Stasovski & Peterson, 1991, 1993).

Changes in the root apex during drought can also be critical for the resumption of water uptake when the soil is rewetted. For most species, hydraulic conductivity is higher in the younger, distal region of the root than in the proximal region, despite the immaturity of the xylem near the root apex (Frensch & Steudle, 1989; North & Nobel, 1992). Thus, a capacity for rapid root growth upon the cessation of drought due to the elongation of existing roots and/or the production of new lateral roots can enhance water uptake (Nobel & Sanderson, 1984). A third hypothesis is that the hydraulic conductivity following drought and rewetting is greater for *O. ficus-indica* roots that produce numerous lateral branches than for roots that resume apical elongation only.

To investigate the three hypotheses regarding the interaction between drought-induced changes in the root apical meristem, lateral root development, and water uptake, plants of *O. ficus-indica* were subjected to relatively rapid drying in a shallow substrate, simulating conditions near the soil surface, or to more gradual drying in a deeper substrate, with both drying treatments followed by rewetting. Root growth, developmental changes in the root apex, lateral root development, and root hydraulic conductivity were measured under wet conditions and under the two drying conditions.

MATERIALS AND METHODS

Plant material

Terminal cladodes (flattened, succulent stem segments) *c.* 18 cm long and 10 cm wide were removed from mature plants of *Opuntia ficus-indica* (L.) Miller (Cactaceae) growing in a glasshouse at the University of California, Los Angeles (material was originally obtained at Chapingo, state of Mexico, Mexico; accession number 1279 of Texas A & M University, Kingsville). The basal third of the cladodes was placed in cylindrical polystyrene containers 15 cm tall and 10 cm in diameter, which were filled with vermiculite moistened with distilled water (water potential $> -0{\cdot}1$ MPa). In the glasshouse, daily maximum/minimum air temperatures averaged 28 °C/17 °C, daily maximum/minimum r.h. was 70 %/40 %, and the mean daily photosynthetic photon flux density was 30 mol m^{-2} d^{-1} (daily maximum instantaneous value of 1500 μmol m^{-2} s^{-1}). The vermiculite was kept moist by watering with one-tenth-strength Hoagland's solution on alternate days.

At 14 d, when cladodes had 10–20 main roots *c.* 90 mm long, the plants were divided into two groups: those transplanted to 32 cm × 28 cm × 14 cm plastic containers filled with vermiculite to a depth of 3 cm for a rapid drying treatment and those transplanted to containers filled with vermiculite to a depth of 6 cm for a gradual drying treatment. In both cases, roots were laid horizontally across a bottom layer, and then covered with an equal amount, of vermiculite; roots of *O. ficus-indica* are not strongly gravitropic and grew relatively horizontally. To determine durations for the drying treatments, the water-release characteristics for both the 3-cm and 6-cm deep vermiculite were measured. The water content of the vermiculite was determined by weighing small samples from the root zone of the containers before and after drying at 80 °C for 24 h; the water potential was measured after samples equilibrated for 3 h in a thermocouple psychrometer (True Psi, Decagon Devices, Pullman, WA). As the vermiculite water content decreased from 75 % to 20 %, the water potential for both 3-cm and 6-cm depths of vermiculite remained $> -0{\cdot}5$ MPa; at lower water contents, the water potential decreased sharply (Fig. 1*a*). Control plants were watered with distilled water on alternate days; for the drying treatments water was withheld. The containers with 3 cm of vermiculite decreased to a water potential of $-1{\cdot}3$ MPa in 7 d of drying whereas those with 6 cm required 14 d to do so (Fig. 1*b*). After the 7-d and the 14-d drying periods, plants in both groups were rewetted with distilled water, and the vermiculite water potential was maintained at $> -0{\cdot}1$ MPa.

Root growth

Roots were covered by fine-mesh nylon fabric and then by a 1-cm-thick layer of moist vermiculite for containers with the 3-cm depth of vermiculite, and a 2-cm thick layer for the 6-cm depth. On day 0 the main roots (averaging 1·7 mm in diameter) were marked at 10 mm from the tip by loosely fitting circles of coloured thread, and root growth incre-

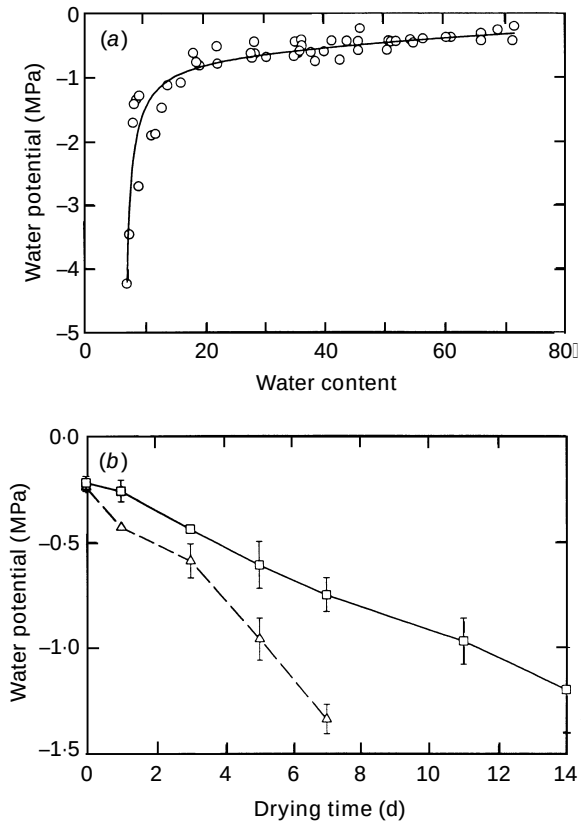

Figure 1. Water potentials of vermiculite. (*a*) Water potential vs. water content ((wet weight − dry weight)/wet weight). (*b*) Changes in water potential with drying time for containers with 3 cm (△) or 6 cm (□) depths of vermiculite.

ments were periodically measured after carefully raising the fabric. Root tips that shrivelled and became brown were considered dead. The visual criteria were confirmed by staining with 6-carboxyfluorescein diacetate (40 μg ml^{-1} in HEPES buffer, pH 7; Goodall & Johnson, 1982) or with acridine orange (0·001 % (w/w) in water; Henry & Deacon, 1981; Wenzel & McCully, 1991) for 2–5 min before rinsing and viewing with a BH-2® microscope (Olympus, Lake Success, NY) equipped for epifluorescence; live roots had bright fluorescence of nuclei and cytoplasm compared to the weak fluorescence of brown tips.

The number of lateral root primordia was determined in three root regions: distal, medial, and proximal. Each 40-mm-long segment was bisected longitudinally and incubated for 10 min in 0·001 % acridine orange. Sections were rinsed, mounted in water, and examined using the BH-2 microscope equipped for epifluorescence with a violet (DMV) filter; clusters of nuclei in lateral root primordia were detected by their bright yellow-green fluorescence.

Cell lengths, root zones, and cell cycle duration

Longitudinal sections were made with a razor blade, stained for 40 s in 0·05 % (w/w) toluidine blue O in water, infiltrated with distilled water under vacuum, and mounted in water. At various distances from the root cap-root body junction, cell lengths in the second to fourth cortical layers from the epidermis were measured using an ocular micrometer and the Olympus BH-2 microscope at $\times 200$ to $\times 400$. Intervals varied in length from 200 to 300 μm in the meristem and from 540 to 1000 μm in the elongation and differentiation zones; lengths were measured for 9–16 intervals per root and plotted at the midpoint distance of each interval. From such a cell-length profile, the lengths of the meristem and the elongation zone (where cells cease dividing and are elongating) were determined. The meristem length, as determined graphically, concurred with that based on cell size and internuclear distances in the cortex. Specifically, the latter meristem length (relative meristem height; Rost & Baum, 1988) was determined as the distance from the root cap-root body junction to the proximal region in the cortex where the distances between nuclei in neighbouring cells in a cell file became equal to or greater than the diameter of the nuclei (where the cell length along the meristem increased).

The duration of the cell division cycle T (h) was determined for individual roots using the rate of cell-production method (Ivanov, 1974, 1994; Ivanov & Dubrovsky, 1997):

$$T = N_m l_e \ln 2/V, \quad (1)$$

where N_m is the average number of meristematic cells in a cell file, l_e (μm) is the average length of fully elongated cells, and V (μm h^{-1}) is the rate of root growth. Under both wet and drying conditions, no unusually large cells were observed in the meristem, suggesting that essentially all cells were in the cell division cycle, an assumption underlying eqn (1).

Root hydraulic conductivity

For measurements of root hydraulic conductivity (L_P), roots were detached, removed from the vermiculite, immediately immersed in water, and then cut with a razor blade to produce apical segments 50 mm long that included the root tip. At the proximal end of the segment, a 10-mm length of the vascular cylinder was exposed by stripping away outer tissues gently by hand, including any lateral roots. The exposed vascular cylinder was inserted into a 10-mm section of Tygon® tubing attached to a glass microcapillary (internal diameter 0·4 mm) that was half-filled with water. A silicone and brass compression fitting was then tightened around the tubing to prevent radial leaks (Lopez & Nobel, 1991). Dental impression material (polysiloxane) and two coats of an acrylic co-polymer (Nobel, Schulte & North, 1990) were applied to seal the junction between the tubing and the vascular cylinder before immersing the segment in distilled water.

A partial vacuum, which was regulated with a needle valve and monitored with a Validyne PS309® digital manometer (Validyne Engineering, Northridge, CA), was applied to the open end of the microcapillary to induce water flow through the segment. If leaks occurred at the compression fitting (detected by the appearance in the microcapillary of crystal violet dye added to the immersion water), the root segment was discarded. After the volumetric flow rate Q_V ($m^3 s^{-1}$) became constant at a given pressure P (MPa), usually within 10 min, L_P ($m s^{-1} MPa^{-1}$) was calculated as follows (Nobel *et al.*, 1990):

$$L_P = (\Delta Q_V/\Delta P)(1/A), \quad (2)$$

where A (m^2) is the root surface area, calculated from the root segment length and radius. To check for possible constriction of the vascular tissue by the compression fitting, axial conductance of the root segment was measured by cutting at the distal end; segments were discarded for which axial conductance was not at least five times greater than L_P for intact segments (Melchior & Steudle, 1993).

Unless otherwise indicated, data were statistically analysed using Student's *t*-tests and are presented as means ± SE ($n = 4$ plants).

RESULTS

Root growth analysis

Elongation rates of roots under both wet and rapidly drying conditions were the same for 3 d, after which the growth rate of roots subjected to rapid drying sharply decreased and became zero at 5 d ($P < 0.05$, Fig. 2*a*). The percentage of living root tips also declined after 3 d of rapid drying, becoming only 6 % at 5 d (Fig. 2*b*). Roots subjected to gradual drying had growth rates similar to those under wet conditions until 9 d, after which the growth rate decreased ($P < 0.05$). At 13 and 14 d, the growth rate averaged 55 % of the control (Fig. 2*a*). About 70 % of the root tips were alive at 14 d under gradual drying (Fig. 2*b*).

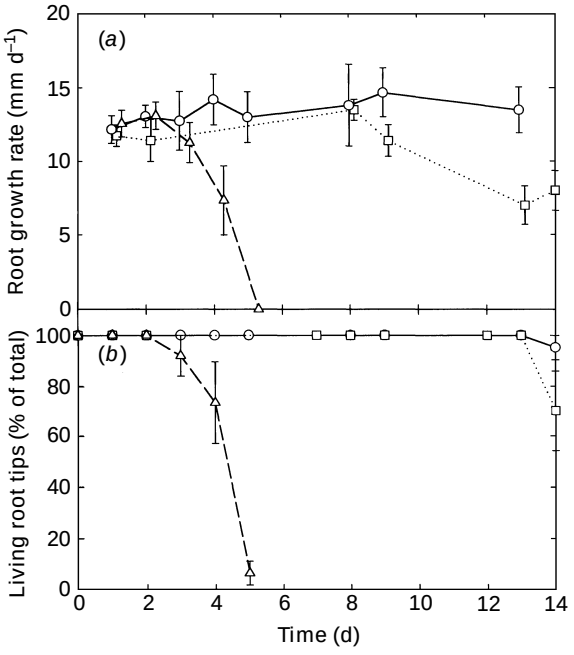

Figure 2. Root growth rates and percentage of living tips for roots of *Opuntia ficus-indica* under wet conditions (○) and subjected to rapid (△) or gradual (□) drying. (*a*) Root growth rates. (*b*) Percentage of living root tips per plant. Data are means ± SE ($n = 4$ plants, 3–4 roots each).

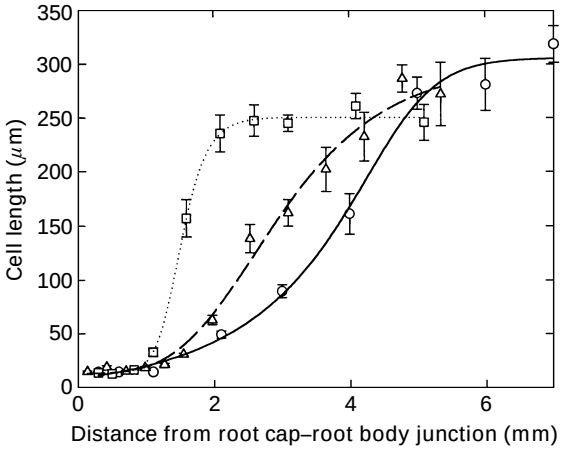

Figure 3. Representative cell-length profiles: cell length as a function of the distance from the root cap-root body junction for roots of *Opuntia ficus-indica* under wet conditions (○) and those at 3 d of rapid drying (△) and at 14 d of gradual drying (□). Data are means ± SE (n = 10–14 cells).

The cell-length profiles determined for roots under wet conditions and those subjected to 3 d of rapid drying and to 14 d of gradual drying were sigmoidal (Fig. 3). The meristem length was shortest under gradual drying. Cell length reached 95 % of the maximum, indicating the approximate extent of the growing part of a root, at 5·4 mm from the root cap-root body junction under wet conditions, at 4·5 mm for roots subjected to 3 d of rapid drying, and at 1·8 mm for roots subjected to 14 d of gradual drying (Fig. 3).

The meristem length was similar under wet conditions and at 9 d of gradual drying, but decreased by 25 % at 14 d of gradual drying (Table 1). Under gradual drying, the number of cells in the cortex within the meristem (N_m) decreased by 16 % at 9 d and by 30 % at 14 d compared with wet conditions (Table 1); N_m did not vary over 14 d under wet conditions. The duration of the cell division cycle in the meristem was similar under wet conditions and 9 d of gradual drying but increased by 36 % at 14 d of gradual drying (Table 1). The length of the elongation zone decreased by 56 % at 9 d of gradual drying and by 69 % at 14 d (Table 1). The length of fully elongated cells was greatest under wet conditions, decreasing by *c.* 30 % at 9 and 14 d of gradual drying (Table 1).

Table 1. *Morphometric features for roots of* Opuntia ficus-indica *growing under wet or gradual drying conditions*

Condition	Meristem			Elongation zone length (mm)	Length of fully elongated cells (μm)
	Length (mm)	Number of cells (N_m)	Cell cycle duration (h)		
Wet	1·10 ± 0·03 a	82 ± 4 a	28·0 ± 3·1 ab	5·95 ± 0·84 a	378 ± 16 a
9 d of gradual drying	1·12 ± 0·05 a	69 ± 3 b	27·0 ± 1·9 a	2·64 ± 0·06 b	252 ± 18 b
14 d of gradual drying	0·82 ± 0·06 b	57 ± 1 c	38·0 ± 1·9 b	1·83 ± 0·43 b	269 ± 20 b

Data are means ± SE (n = 3–4 plants, one root each); length of fully elongated cells was measured for 40–50 cells per root. Means denoted by different letters within a column differ at $P < 0·05$.

Table 2. *Number of lateral root primordia initiated in main roots of* Opuntia ficus-indica *under various conditions*

Condition	Number of lateral root primordia		
	Distal	Middle	Proximal
Wet	0·5 ± 0·3	4·2 ± 0·5	5·0 ± 0·9
7 d of rapid drying	3·0 ± 1·1	8·5 ± 0·3	7·5 ± 0·9
7 d of rapid drying, 2 d of rewetting	4·0 ± 1·0	8·8 ± 1·0	7·5 ± 1·0
14 d of gradual drying	2·2 ± 1·4	8·0 ± 0·9	10·8 ± 1·7
14 d of gradual drying, 2 d of rewetting	3·0 ± 1·6	8·5 ± 1·5	12·2 ± 1·8

Data are means ± SE (n = 4 plants, one root each); the distal 120 mm of a root was cut into three 40-mm segments (distal, middle, and proximal), which were bisected longitudinally, stained with acridine orange, and examined microscopically.

Lateral root development

For distal, medial and proximal segments of main roots, the number of lateral root primordia was greater after 7 d of rapid drying and 14 d of gradual drying than under wet conditions, and greater still after 2 d of rewetting (two-way ANOVA, $P < 0·001$ for both the position of a segment along a root and the moisture condition; Table 2). Under all conditions, the number of lateral root primordia increased from the distal to the middle to the proximal root segments ($P < 0·05$), and no interaction occurred between the condition and the position of a segment along a root ($P > 0·05$). Roots subjected to gradual drying had more lateral root primordia in proximal segments than did roots subjected to rapid drying, both before and after rewetting ($P < 0·05$; Table 2).

Lateral root emergence in plants rewetted at 8 d of rapid drying was extremely rapid. The lateral roots were 2–4 mm long and 0·7 mm in diameter 20 h after rewetting. At this stage, N_m was 49 ± 1, which 24 h later decreased to 35 ± 2. The growth rate of lateral roots was 9·7 ± 1·0 mm d^{-1}, the length of fully elongated cells in them was 327 ± 12 μm, and the duration of the cell division cycle was 23·3 ± 4·0 h.

Root hydraulic conductivity

Root hydraulic conductivity (L_P) decreased to *c.* 50 % of its value under wet conditions during both 7 d of rapid drying and 14 d of gradual drying (Fig. 4). No emerged lateral roots were present for the segments on which L_P was measured (the distal 50 mm) under wet conditions or during drying. After 2 d of rewetting, L_P for roots subjected to either rapid or gradual drying was restored to the control value; after 4 d of rewetting, L_P exceeded the control value by 10–20 % ($P > 0·05$; Fig. 4). Following 7 d of rapid drying, root segments had 12·5 ± 3·9 emerged lateral roots with an individual mean length of 5·6 ± 0·9 mm after 2 d of rewetting and 11·0 ± 3·0 lateral roots with a length of 18·2 ± 3·1 mm after 4 d of rewetting. Following 14 d of gradual

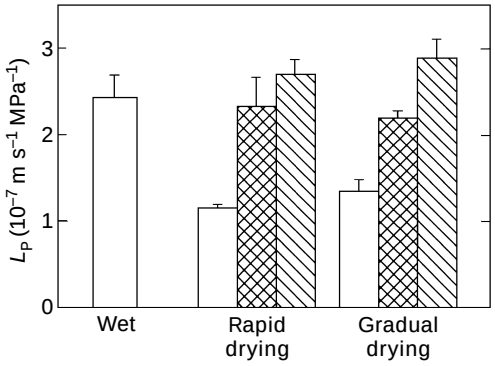

Figure 4. Root hydraulic conductivity (L_P) for *Opuntia ficus-indica* under wet conditions and after 7 d of rapid drying and 14 d of gradual drying (□), followed by rewetting for 2 d (⊠) or 4 d (▨). Data are means ± SE (n = 4 plants, 1–2 roots each).

drying, root segments had $2{\cdot}9 \pm 1{\cdot}7$ lateral roots with a mean length of $3{\cdot}5 \pm 0{\cdot}6$ mm after 2 d of rewetting and $9{\cdot}1 \pm 1{\cdot}7$ lateral roots with a mean length of $10{\cdot}0 \pm 2{\cdot}4$ mm after 4 d of rewetting. Such measurements were used to determine the root surface area needed for calculating L_P (eqn (2)).

DISCUSSION

During rapid drying, the root growth rate for *Opuntia ficus-indica* decreased rapidly to zero in 5 d, but during longer periods of gradual drying (14 d), the rate was at least half of that under wet conditions. Growth was thus maintained under gradual drying despite lower water potentials than occurred for rapid drying, indicating that some adaptation to drought developed within the root apex. Decreased steady-state growth rates also occur at decreased water potentials for roots of *Allium cepa*, *Zea mays* and *Triticum durum* (Sharp *et al.*, 1988; Bitonti *et al.*, 1991). A cessation of root growth, as occurred for *O. ficus-indica* under rapid drying, is typical for determinate growth and occurs for pea roots under high temperatures (Gladish & Rost, 1993), for sunflower roots under drought (Robertson *et al.*, 1990*a*), and for some semi-desert shrubs under field conditions (Fernandez & Caldwell, 1975). In the first two cases, root growth resumes under favourable conditions, so meristem function is not affected. For *O. ficus-indica*, determinate growth was environmentally induced and was a consequence of root-meristem mortality, contrary to developmentally controlled meristem inactivation in other Cactaceae (Dubrovsky, 1997*a*, *b*). High root tip mortality during rapid drying suggests that insufficient water was available to maintain cell hydration and hence viability.

The rate-of-cell-production method for estimating the duration of the cell division cycle assumes steady-state growth (Ivanov, 1994; Ivanov & Dubrovsky, 1997), which was generally the case for *O. ficus-indica* during a measurement interval. Both increased cell cycle duration and the decreased number of meristematic cells (with a consequent decrease in meristem length) can explain the decline in root growth rate under gradual drying. In this regard, the root meristem length progressively decreases under continuous drought for sunflower (Robertson *et al.*, 1990*a*); its root mitotic activity sharply decreases 6 h after the onset of drought and partially recovers after 3 d (Robertson *et al.*, 1990*b*). Osmotic stress results in a similar decrease in root meristem mitotic activity for *T. durum* (Bitonti *et al.*, 1991) and an increase in the duration of the cell division cycle in the root meristem of *A. cepa* (González-Bernáldez, López-Sáez & García-Ferrero, 1968).

In roots growing at a steady-state, the rate of cell production in a cell file equals V/l_e, where V is the rate of root growth and l_e is the length of a fully elongated cell. For *O. ficus-indica*, 48 cells were added to a meristem cell file per day under wet conditions but only 25 cells at 14 d of gradual drying, showing that cell production in the meristem was indeed affected by water stress. The number of cells in a meristem file equals 2^n, where n is the number of division cycles a cell passes through from the distal to the proximal border of the meristem. A meristem cell file for *O. ficus-indica* contained 82 cells under wet conditions and 69 and 57 cells at 9 d and 14 d, respectively, of gradual drying, so n is *c.* 6 in all cases. Multiplying the duration of the cell division cycle by the number of cycles, the life-span of cells in the meristem is found to equal 7 d under wet conditions and at 9 d of gradual drying, and to equal 9 d at 14 d of gradual drying. Thus, developmental changes had sufficient time to occur in the root apex during gradual drying.

Cell length in roots of *O. ficus-indica* increased 26-fold from meristematic to fully elongated cells. At 14 d of gradual drying, the length of fully elongated cells was less than under wet conditions. In other species, cell elongation is also suppressed under water stress, and the length of the root elongation zone decreases (Sharp *et al.*, 1988; Fraser, Silk & Rost, 1990; Spollen & Sharp, 1991). Partly as a consequence of the cells being 30 % shorter, at 14 d of gradual drying the length of the elongation zone for *O. ficus-indica* was reduced by 69 %. Paradoxically the rate of cell elongation apparently increased, perhaps because of a loosening of the cell wall, as can occur for other species owing to increased expansin activity under water stress (Wu *et al.*, 1996).

Root hydraulic conductivity (L_P) was *c.* halved during both rapid and gradual drying, similar to previous results for young roots of *O. ficus-indica* (Huang & Nobel, 1993). For distal root segments of this and other cacti, axial conductivity in the xylem can limit L_P, particularly because of embolism (North & Nobel, 1992). The dehydration of non-vascular root tissues is likely to account for the remainder of the decrease in conductivity (North & Nobel, 1996). At 2 d after rewetting, L_P was restored to its value under wet conditions following both rapid and gradual drying, but for different reasons. During rapid drying most root apices died; subsequent rewetting caused a proliferation of lateral roots, with a total surface area of 165 mm² in 2 d, representing *c.* 30 % of the total surface area used to calculate L_P. Due to the greater hydraulic conductivity of young lateral roots of *O. ficus-indica* than of its main roots (Huang & Nobel, 1993), L_P after 2 d of rewetting increased despite drought-induced changes in main roots. By contrast, during gradual drying, most root apices remained alive, rehydrated during subsequent rewetting, and resumed apical elongation (only 24 mm² of lateral root surface area at 2 d of rewetting). The death of the root apex

during rapid drying apparently stimulated the emergence of lateral roots, although a similar number of lateral root primordia were initiated under both drying treatments (and this was at least 6-fold greater in the distal root region than under wet conditions). At 4 d of rewetting, the surface area of new lateral roots for roots subjected to gradual drying averaged 214 mm^2, resulting in a higher L_P than after 2 d of rewetting.

In summary, the first hypothesis that rapid drying would be more detrimental than gradual drying to root growth for *O. ficus-indica* was supported: gradual drying of roots of *O. ficus-indica* allowed developmental changes in the root apex to occur, resulting in continued cell division and elongation, whereas rapid drying led to death of the meristem. The second hypothesis, that differences in drying rates would lead to differences in lateral root initiation and development, was supported to a certain extent: both drying treatments increased the number of lateral root primordia per length of root, but lateral root emergence in response to rewetting was greater for roots whose apices had died during rapid drying. The third hypothesis, that root hydraulic conductivity would be greater for roots with numerous lateral branches than for roots with only renewed apical elongation, was not fully supported: root hydraulic conductivity decreased during both rapid and gradual drying, and increased upon rewetting, owing to the emergence of new lateral roots after rapid drying and to both new lateral roots and renewed apical growth after gradual drying. The differences in meristem mortality and lateral root emergence between roots exposed to rapid vs. gradual drying suggest a differential response to drought by roots of *O. ficus-indica* in the field depending on their location in the soil. For shallow roots, drought might lead to the death of the apical meristem, yet a rainfall event might stimulate the proliferation of lateral roots to renew water uptake. For deeper roots in more slowly drying soil, continued meristematic activity might allow root extension into lower soil layers where moisture is still available; in addition, the maintenance of the apical meristem implies that a more substantial rainfall will be required for the deeper roots to produce new lateral roots.

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