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# CHANGES IN ROOT HYDRAULIC CONDUCTIVITY FOR TWO TROPICAL EPIPHYTIC CACTI AS SOIL MOISTURE VARIES[1]

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The tropical epiphytic cacti *Epiphyllum phyllanthus* and *Rhipsalis baccifera* experience extreme variations in soil moisture due to limited soil volumes and episodic rainfalls. To examine possible root rectification, whereby water uptake from a wet soil occurs readily but water loss to a dry soil is minimal, responses of root hydraulic conductivity ($L_p$) to soil drying and rewetting were investigated along with the underlying anatomical changes. After 30 d of soil drying, $L_p$ decreased 50%–70% for roots of both species, primarily because increased suberization of the periderm reduced radial conductivity. Sheaths composed of soil particles, root hairs, and mucilage covered young roots and helped reduce root desiccation. Axial (xylem) conductance increased during drying due to vessel differentiation and maturation, and drought-induced embolism was relatively low. Within 4 d of rewetting, $L_p$ for roots of both species attained predrought values; radial conductivity increased for young roots due to the growth of new branch roots initiated during drying and for older roots due to the development of radial breaks in the periderm. The decreases in $L_p$ during drought reduced plant water loss to a dry soil, and yet maximal water uptake and transpiration occurred within a few days of rewetting, helping these epiphytes to take advantage of episodic rainfalls in a moist tropical forest.

The roots of tropical epiphytes generally experience extreme variations in moisture availability (Lüttge, 1989; Benzing, 1990). Despite high average yearly rainfall, many tropical forests have comparatively dry seasons (Windsor, 1990). Moreover, roots of epiphytes typically occur in small pockets of soil where tree branches join trunks, in bark crevices on trunks, or on bare limbs, all sites that dry more quickly than the soil of the forest floor (Antibus and Lesica, 1990). Aerial roots of epiphytes in several families are covered with a velamen (one or more layers of air-filled cells) that may limit water loss to dry air yet rapidly refill to permit water uptake during rainfall (Goh and Kluge, 1989). For roots of other epiphytes embedded in bark or humus, the physiological and structural responses to variations in moisture availability are less well known.

About 10% of the approximately 1,600 species in the Cactaceae grow as epiphytes in tropical forests (Gibson and Nobel, 1986; Kress, 1989). These epiphytes tend to occur in open sites high in the canopy (Benzing, 1989; Medina et al., 1989), where light, wind, and lower relative humidity can lead to desiccating conditions. Cacti in such forest canopies and in deserts are thus both subject to moisture stress. For desert cacti, the root-soil system has rectifier-like properties; that is, the roots rapidly take up water when the soil is wet, but succulent shoots lose little water through the roots to the drier soil during drought (Nobel and Sanderson, 1984; North and Nobel, 1992). Changes in the root hydraulic conductivity are important for reducing plant water loss in the early stages of soil drying (Nobel and Cui, 1992; North and Nobel, 1992).

Two species of epiphytic cacti, *Epiphyllum phyllanthus* (L.) Haw. (Cactaceae) and *Rhipsalis baccifera* (J. S. Mil.) Stearn (syn. *R. cassutha* Gaertn.; Cactaceae), were chosen to investigate whether their root systems, like those of desert succulents, are capable of rectification. The genera *Epiphyllum* and *Rhipsalis* comprise about half of the epiphytic species in the Cactaceae (Kress, 1989). *Epiphyllum phyllanthus,* with flattened leafless stems generally about 0.8 m long and 3 cm wide, occurs in moist tropical forests from Costa Rica to Colombia and Ecuador (Croat, 1978). *Rhipsalis baccifera,* with terete leafless stems up to 1 m long and 0.5 cm in diameter, occurs in moist forests in tropical America, Ceylon, and tropical east Africa (Croat, 1978). For both species, adventitious roots are produced at the base of the stem, at nodes where the stem contacts a substrate, and sometimes along aerial portions of the stem.

Plants were grown under conditions similar to those occurring in the forest canopy (Benzing, 1989; Windsor, 1990). Additional measurements were made for *E. phyllanthus* on Barro Colorado Island, Republic of Panamá, where this species is native (Croat, 1978). The hydraulic conductivity coefficient ($L_p$) relates the volume of water flow per unit time and area to a driving force, such as the difference in water potential (Nobel, 1991); it was determined for excised roots and whole root systems under wet, dry, and rewetted soil conditions. Changes in $L_p$ and its two components, radial conductivity (from the root surface to the root xylem) and axial conductance (along the root xylem), were determined, together with changes in the root tissues composing both radial and axial pathways for water flow.

## MATERIALS AND METHODS

***Plant material***—Stem cuttings were taken from three mature plants of *Epiphyllum phyllanthus* (L.) Haw. (Cactaceae) obtained from the Huntington Botanical Gardens, San Marino, California. Rooted plants and stem cuttings of *Rhipsalis baccifera* (J. S. Mil.) Stearn (Cactaceae) were

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obtained from a commercial nursery (Rainbow Gardens, Vista, CA). All plants were grown in 36-cm-long × 24-cm-wide × 6-cm-deep trays filled with equal parts of sphagnum peat moss, sand, and commercial epiphyte potting soil (humus, bark, and peat moss). Plants were maintained in a shaded, humidified enclosure in a glasshouse at the University of California, Los Angeles, with daily maximal/minimal temperatures of approximately 28 C/16 C, a mean relative humidity of 86%, and a mean photosynthetic photon flux density of 280 $\mu$mol $m^{-2}$ $s^{-1}$ (measured with a LI-Cor LI-190S quantum sensor).

The soil water potential in the root zone ($\psi_{soil}$, determined with a Decagon thermocouple psychrometer) was maintained above −0.2 MPa by watering three times weekly. At 30 d of drying, $\psi_{soil}$ was −5.4 MPa and increased to −0.1 MPa within 8 hr after rewetting. Root age was determined by periodic excavation of representative rooted cuttings and measurement of their root lengths. Young roots (4–6 wk) were 5.5–6.0 cm long; the 6.0-cm-long sections at the base of 18–20-cm-long roots were designated older roots (5–6 mo).

***Field studies***—Additional cuttings of *E. phyllanthus* were obtained from recently dislodged plants that had fallen to the forest floor at Barro Colorado Island, Republic of Panamá (9°10′N, 79°51′W, 90 m elevation). These stem pieces were rooted in pots containing equal parts of soil and sand. They were grown in a screened enclosure with a mean photosynthetic photon flux density of 260 $\mu$mol $m^{-2}$ $s^{-1}$ and a mean relative humidity of 85%, similar to conditions at 15–20 m in the forest canopy (Windsor, 1990). The watering procedure was the same as for plants in the glasshouse.

Transpiration was determined hourly by weighing pots of *E. phyllanthus*. The soil surface was covered with plastic film and aluminum foil to minimize evaporation. To correct for residual soil water loss, pots without plants were simultaneously covered and weighed. Mean weight loss for pots of wet soil averaged 12% of the weight loss for pots with plants in wet soil; for pots of dry soil, weight loss averaged 62% of that for pots with plants in dry soil. The water potential of stem and root tissue was determined with a Decagon thermocouple psychrometer.

***Root hydraulic conductivity***—Root segments 5–6 cm long were excised and immersed in distilled water. All tissues external to the stele were removed from a 7-mm region at the proximal end, and the exposed stele was inserted into a 5-mm length of Tygon tubing attached to a glass capillary (internal diameter 0.8 mm) half-filled with distilled water. The Tygon tubing was appressed firmly to the stele by tightening a compression fitting (McCown and Wall, 1979; Lopez and Nobel, 1991), which microscopic examination indicated caused no distortion in the vascular conduits. For older root segments with excised tips, the distal cut ends were sealed with hydrophilic dental impression material (polysiloxane) and two coats of acrylic copolymer (Nobel, Schulte, and North, 1990).

Water flow through the root was induced by applying a partial vacuum to the open end of the attached capillary while the root segment was immersed in distilled water. The negative pressure was adjusted by a needle valve and monitored with a digital manometer. A traveling microscope capable of resolving 0.01 mm was used to observe the location of the capillary meniscus, and the distance traveled along the capillary per unit time was used to calculate the volumetric flow rate ($Q_V$, $m^3s^{-1}$). When $Q_V$ became constant at a given pressure (P, MPa), generally within 10 min, $L_p$ ($ms^{-1}MPa^{-1}$) was calculated as follows (Nobel, Schulte, and North, 1990):

$$L_p = (\Delta Q_V/\Delta P)(1/A) \quad (1)$$

where A ($m^2$) is the lateral surface area of the root (the projected area was determined with a Delta-T Devices area meter and multiplied by $\pi$ to yield A).

$L_p$ was also determined for entire root systems of *E. phyllanthus* grown at Barro Colorado Island. After the soil was washed away, the shoot was severed 15 mm above the most proximal root. The root system was then immersed in a tank of distilled water in a pressure chamber, and the cut stem was placed in a 20-mm length of tubing and inserted through a gasket in the chamber lid. The exudate induced by applying pressures of 0.1–0.3 MPa to the roots for 5 min at each pressure was collected on a preweighed piece of cotton (covered with plastic film to prevent evaporation during measurements). $Q_V$ was determined from the increase in weight of the cotton (measured to 0.1 mg), root area was determined as above, and $L_p$ was calculated using Equation 1. The mean osmotic pressure of the exudate from pressurized root systems (determined with a Wescor 5500 vapor pressure osmometer) was −0.04 MPa.

***Axial conductance***—To measure axial (xylem) conductance, the distal end of a root segment was cut and its terminal 2-mm portion was immersed in 100 mol $m^{-3}$ potassium chloride filtered through 0.22-$\mu$m pores to remove particles that might block pit membranes (Sperry, 1986). $Q_V$ was measured as for $L_p$ and was used to calculate the root axial conductance per unit pressure gradient ($K_h$, $m^4s^{-1}MPa^{-1}$):

$$K_h = Q_V/(\Delta P/\ell) \quad (2)$$

where the pressure drop $\Delta P$ was applied across the length $\ell$ (m) of the root segment (Gibson, Calkin, and Nobel, 1984). Measurements of $K_h$ were made before and after the root segment was pressurized in solution in a pressure chamber at 0.20 MPa for 20 min to dissolve air bubbles (emboli) in the xylem (Sperry, 1986; North and Nobel, 1991). Maximum values of $K_h$ were usually obtained after two pressurizations.

***Radial conductivity***—Radial conductivity was equated to the volumetric flux density of water ($m^3m^{-2}s^{-1} = ms^{-1}$) at the root surface divided by the difference in water potential (MPa) from the root surface to the root xylem. Based on measured values of $L_p$ and $K_h$ together with the length $\ell$ and the radius ($r_{root}$, m) of root segments, root radial conductivity averaged over the root segment ($L_R$, $ms^{-1}MPa^{-1}$) was calculated as follows (Landsberg and Fowkes, 1978):

$$L_R = L_p\alpha\ell/\tanh(\alpha\ell) \quad (3)$$

where $\alpha(m^{-1})$ equals $(2\pi r_{root}L_R/K_h)^{1/2}$; $L_R$ was initially set

TABLE 1. Transpiration, root hydraulic conductivity ($L_P$), and water potentials ($\psi_{shoot}$, $\psi_{root}$) for *Epiphyllum phyllanthus* at Barro Colorado Island, Republic of Panamá. Data are means ± SE ($N = 4$ plants) for wet soil ($\psi_{soil} = -0.01$ MPa), after 30 d of drying ($\psi_{soil} = -4.7$ MPa), and after 4 d of rewetting ($\psi_{soil} = -0.01$ MPa). The total root surface area was 2.82 ± 0.31 × $10^{-3}$ $m^2$.

| Soil | Transpiration (mol $plant^{-1}$ $d^{-1}$) | $L_P$ ($10^{-7}$ m $s^{-1}$ $MPa^{-1}$) | $\psi_{shoot}$ (MPa) | $\psi_{root}$ (MPa) |
|---|---|---|---|---|
| Wet | 0.25 ± 0.02 | 1.92 ± 0.24 | −0.25 ± 0.03 | −0.10 ± 0.03 |
| Dry | 0.04 ± 0.01 | 0.52 ± 0.10 | −0.53 ± 0.06 | −0.61 ± 0.07 |
| Rewetted | 0.26 ± 0.02 | 1.87 ± 0.26 | −0.22 ± 0.04 | −0.10 ± 0.04 |

equal to $L_p$ and was then gradually increased to solve Equation 3 by iteration.

***Anatomical measurements***—To investigate anatomical features, roots were sectioned with a razor blade, stained with 0.05% (w/w) toluidine blue O in distilled water, and viewed with bright field and phase contrast optics at ×100–×1,000. Suberin was detected by staining with Sudan dyes and lignin with phloroglucinol in 1.2 mol $m^{-3}$ HCl (Jensen, 1962). Suberin and lignin were also assessed by their autofluorescence (Peterson, Emanuel, and Humphreys, 1981), viewed with an Olympus BH2 microscope equipped for epifluorescence with a DMU ultraviolet and a DMV violet filter system (excitation wavelengths between 370 and 420 nm). Mucilage was detected by staining with 0.42% (w/w) alcian blue in distilled water (Trachtenberg and Fahn, 1981). The presence of extracellular mucilage was checked by staining with 0.01% (w/w) Calcofluor White M2R and then viewing the sections with epifluorescence (Guinel and McCully, 1986). Unless otherwise stated, anatomical measurements were made on at least eight roots.

Changes in root diameter during drying were measured for five older roots of *E. phyllanthus*. The soil was removed from 10-mm zones for each root, root locations were marked by wires, and root diameter was measured with a traveling microscope capable of resolving 0.01 mm. After measurements, which were made at 0, 7, 14, and 30 d after water was withheld, the roots were re-covered with soil.

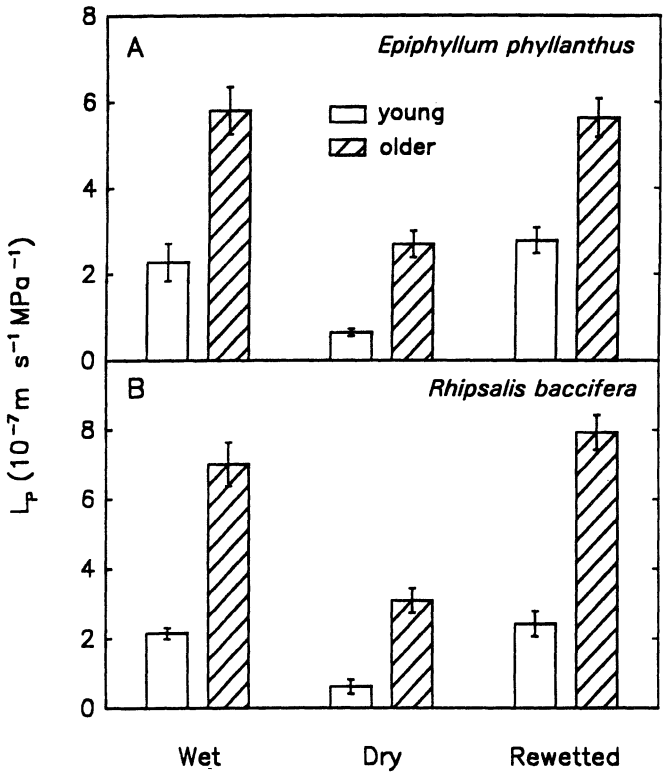



Fig. 1. Root hydraulic conductivity ($L_p$) for young roots (open bars) and older roots (cross-hatched bars) of *E. phyllanthus* (A) and *R. baccifera* (B). Data are means ± SE ($N = 5$ plants) under wet conditions ($\psi_{soil} = -0.1$ MPa), after 30 d of drying ($\psi_{soil} = -5.4$ MPa), and after 4 d of rewetting ($\psi_{soil} = -0.1$ MPa).

## RESULTS

***Field measurements***—For *Epiphyllum phyllanthus* growing in pots under wet conditions at Barro Colorado Island, transpiration measured by weight loss over 24 hr decreased 84% after 30 d of soil drying (Table 1). After 4 d of rewetting, transpiration was restored to its original value in wet soil. $L_p$ calculated (Equation 1) from measurements on whole root systems decreased about 70% during soil drying and fully recovered after rewetting (Table 1). After 30 d of drying, shoot water potential ($\psi_{shoot}$) became twofold more negative, and root water potential ($\psi_{root}$) became sixfold more negative (Table 1). Both $\psi_{shoot}$ and $\psi_{root}$ were restored to their original values after 4 d of rewetting. Water uptake calculated from $L_p$, root surface area, and assuming a root-soil water potential difference of 0.09 MPa was 0.24 ± 0.03 (mean ± SE for $N = 4$) mol $plant^{-1}d^{-1}$ under wet conditions. After 4 d of rewetting, the calculated water uptake was 0.28 ± 0.04 mol $plant^{-1}d^{-1}$, which was again within 10% of transpiration (Table 1).

***Hydraulic and radial conductivity***—Root hydraulic conductivity ($L_p$) was similar for *E. phyllanthus* (Fig. 1A) and *R. baccifera* (Fig. 1B). Under wet conditions, $L_p$ was about threefold higher for older roots (5–6 mo of age) than for young roots (4–6 wk). Soil drying for 30 d caused $L_p$ to decrease about 70% for young roots and about 55% for older roots (Fig. 1). Rewetting for 4 d following the drying caused $L_p$ to increase to values slightly exceeding the initial ones for both root ages of both species (Fig. 1).

Radial conductivity ($L_R$) followed a pattern similar to $L_p$ for roots in all cases (Fig. 2). $L_R$ decreased about 80% during 30 d of drying for young roots and about 57% for older roots. During 4 d of rewetting, $L_R$ for all roots increased to values similar to those under wet conditions (Fig. 2).

***Structural changes in radial pathway***—Under wet soil conditions, young roots of both species had an epidermis,

a parenchymatous cortex, and a suberized endodermis at 10 mm back from the root tip. A periderm with 2.5 ± 0.2 ($N = 8$) cell layers was present at about 15 mm from the tip; at about 40 mm from the tip, the periderm was suberized and consisted of 5.4 ± 0.2 layers (Fig. 3). After 30 d in drying soil, a periderm with 9.0 ± 0.3 layers was present at midlength for young roots, and 2.4 ± 0.2 of these layers were heavily suberized and lignified (Fig. 4).

Under both wet and drying conditions, soil particles adhered to the surface of young roots starting at about 5 mm from the root tip, where root hairs and the outer cell walls of epidermal cells stained intensely with alcian blue, indicating the presence of mucilage. After staining with Calcofluor, this mucilage exhibited intense white fluorescence. Soil particles, root hairs, and mucilage formed soil sheaths that became thicker and progressively more difficult to remove from the root during soil drying (Fig. 5). Root tips became black and necrotic or absent after 30 d of drying. For such roots lacking tips, a suberized periderm extended up to the distal end. At the base of young roots, epidermal and cortical cells collapsed and pulled away from the periderm during drying (Fig. 6).

The epidermis and cortex were shed at about 3 mo of root age, so older roots of both species had a periderm as their outermost tissue. Soil sheaths were absent for older roots. For both wet and dry soil, the periderm consisted of several layers of phelloderm (parenchyma cells), often containing starch bodies and plastids (Fig. 7), with 19.1 ± 0.7 ($N = 8$) layers of phellem (suberized cells) on the outside. For both species, regions of heavily suberized, lignified phellem alternated with less suberized, less lignified regions. The heavily suberized, lignified regions were composed of radial files of cells (Fig. 7); after rewetting, radial breaks appeared between these files in the outer layers of phellem (Fig. 8).

Older roots of *E. phyllanthus* decreased in diameter in drying soil. Specifically, the diameter at the initiation of drying was 1.91 ± 0.13 mm ($N = 5$). The diameter decreased by 0.04 ± 0.01 mm, 0.18 ± 0.03 mm, and 0.24 ± 0.03 mm at 7, 14, and 30 d of soil drying, respectively.

***Axial conductance***—Axial (xylem) conductance per unit pressure gradient ($K_h$) tended to increase during 30 d in drying soil and 4 d of rewetting (Fig. 9). $K_h$ for older roots was about 11-fold greater for young roots of *E. phyllanthus* and about sevenfold greater for *R. baccifera*. Although average values of $K_h$ were similar for young roots of the two species, $K_h$ for older roots averaged 30% greater for *E. phyllanthus* than for *R. baccifera* (Fig. 9).

***Structural changes in the xylem***—During 30 d of soil drying, vessel number at least doubled for young roots of both species and increased about 40% for older roots (Table 2). Although mean and maximum vessel diameters also tended to increase during drying, such increases were generally not significant ($P > 0.05$ by ANOVA). For older roots, vessels were at least four times more numerous and about 35% greater in diameter than for young roots. As indicated by $K_h/K_h^{max}$, embolism decreased axial conductance by an average of 11% for roots under wet conditions (Table 2). After 30 d of drying, $K_h/K_h^{max}$ averaged 0.70, indicating more extensive embolism, although young roots of *R. baccifera* were not significantly more embolized than under wet conditions (Table 2). After 4 d of rewetting, $K_h/K_h^{max}$ increased to about 0.85 for all roots.

In addition to vessels, fibers were more numerous in the xylem of young roots for both species after 30 d of drying (Fig. 10) than under wet conditions, and they also developed closer to the root tip. In all cases, fiber devel-

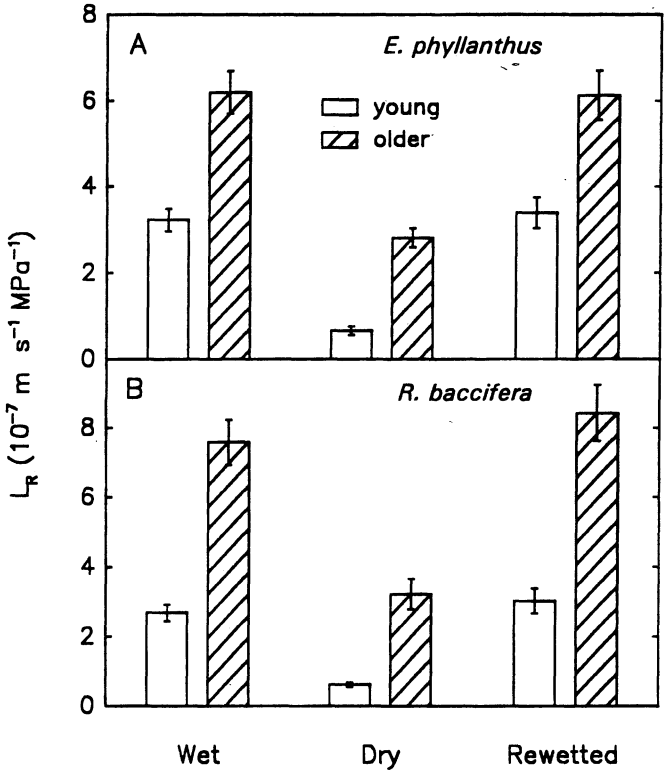
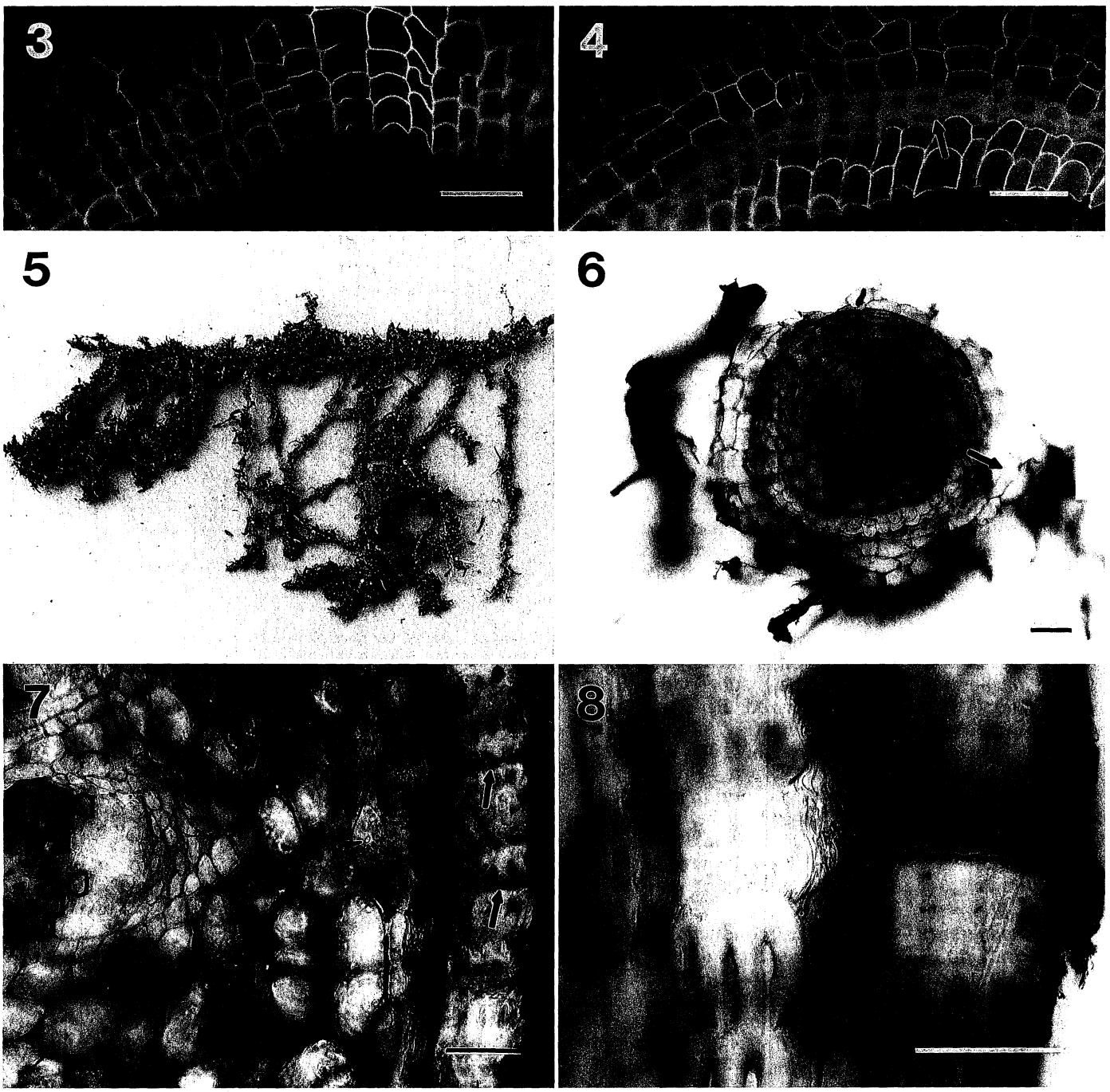



Fig. 2. Radial conductivity ($L_R$) for young roots (open bars) and older roots (cross-hatched bars) of *E. phyllanthus* (A) and *R. baccifera* (B). $L_R$ was calculated using Equation 2. Soil conditions were as for Fig. 2.

TABLE 2. Xylem properties for roots of *Epiphyllum phyllanthus* and *Rhipsalis baccifera* under wet conditions and after 30 d of soil drying. The ratio of the axial conductance per unit length measured before ($K_h$) to that measured after pressurization ($K_h^{max}$) indicates the degree of embolism. Data are means ± SE ($N = 5$ roots).

| Species | Vessel number | Mean vessel diameter (μm) | Maximum vessel diameter (μm) | $K_h/K_h^{max}$ |
|---|---|---|---|---|
| *E. phyllanthus* | | | | |
| Young roots | | | | |
| Wet soil | 10 ± 2 | 7.8 ± 0.9 | 15.3 ± 0.8 | 0.88 ± 0.08 |
| Dry soil | 29 ± 4 | 8.9 ± 0.7 | 15.8 ± 0.8 | 0.67 ± 0.08 |
| Older roots | | | | |
| Wet soil | 94 ± 15 | 10.9 ± 0.5 | 17.8 ± 1.3 | 0.86 ± 0.11 |
| Dry soil | 124 ± 13 | 10.9 ± 0.4 | 18.2 ± 1.4 | 0.63 ± 0.09 |
| *R. baccifera* | | | | |
| Young roots | | | | |
| Wet soil | 11 ± 3 | 6.4 ± 0.4 | 11.5 ± 1.3 | 0.94 ± 0.08 |
| Dry soil | 23 ± 3 | 6.9 ± 0.7 | 14.3 ± 1.6 | 0.87 ± 0.10 |
| Older roots | | | | |
| Wet soil | 83 ± 16 | 9.5 ± 0.2 | 15.9 ± 0.9 | 0.88 ± 0.10 |
| Dry soil | 119 ± 13 | 9.7 ± 0.6 | 15.6 ± 1.7 | 0.61 ± 0.08 |




Figs. 3–8. Roots of *E. phyllanthus* and *R. baccifera*. Figs. 3, 4 are micrographs using epifluorescence optics to show white autofluorescence of suberized, lignified cell walls; Fig. 5 is a photograph of an entire young root system; and Figs. 6–8 are light micrographs of tranverse sections stained with toluidine blue O. **3.** Periderm of a young root of *E. phyllanthus* in wet soil. **4.** Periderm of a young root of *E. phyllanthus* after 30 d of drying; arrows indicate more heavily suberized, lignified cell layers. **5.** Young root system of *E. phyllanthus* (oldest main root is 3 mo of age) after 30 d of drying, showing extensive soil sheaths. **6.** Young root of *E. phyllanthus* after 30 d of drying; arrow indicates cortical cells that have pulled away from periderm. **7.** Older root of *R. baccifera* after 30 d of drying; large arrows indicate radial lines in phellem, and small arrows indicate starch bodies in phelloderm. **8.** Older root of *R. baccifera* after 4 d of rewetting, showing radial break in outer layers of phellem. Bars = 50 μm.

opment was synchronous with the development of a suberized periderm. For older roots in both wet and dry soil, fibers were much more abundant than vessels (Fig. 11).

***Branch root initiation***—The root systems of both species were highly branched under wet, dry, and rewetted conditions. For young roots in wet soil, branch root primordia began to form about 35–40 mm from the root tip, indicated as swellings along the main root axis; 8 ± 1 such primordia or short (<5 mm) branch roots developed per cm of main root axis for young roots of both species. Within 1 d of initiation, these primordia broke through the periderm of the main roots. During 30 d of drying, branch root primordia developed within 10 mm

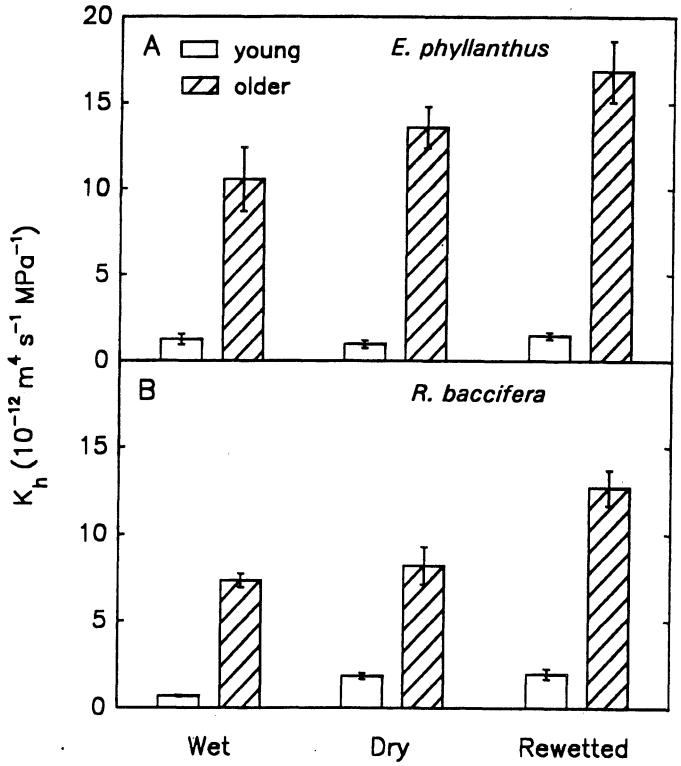



Fig. 9. Axial conductance per unit length ($K_h$) for young roots (open bars) and older roots (cross-hatched bars) of *E. phyllanthus* (A) and *R. baccifera* (B). Data are means ± SE ($N = 5$ plants) under wet conditions ($\psi_{soil} = -0.1$ MPa), after 30 d of drying ($\psi_{soil} = -5.4$ MPa), and after 4 d of rewetting ($\psi_{soil} = -0.1$ MPa).

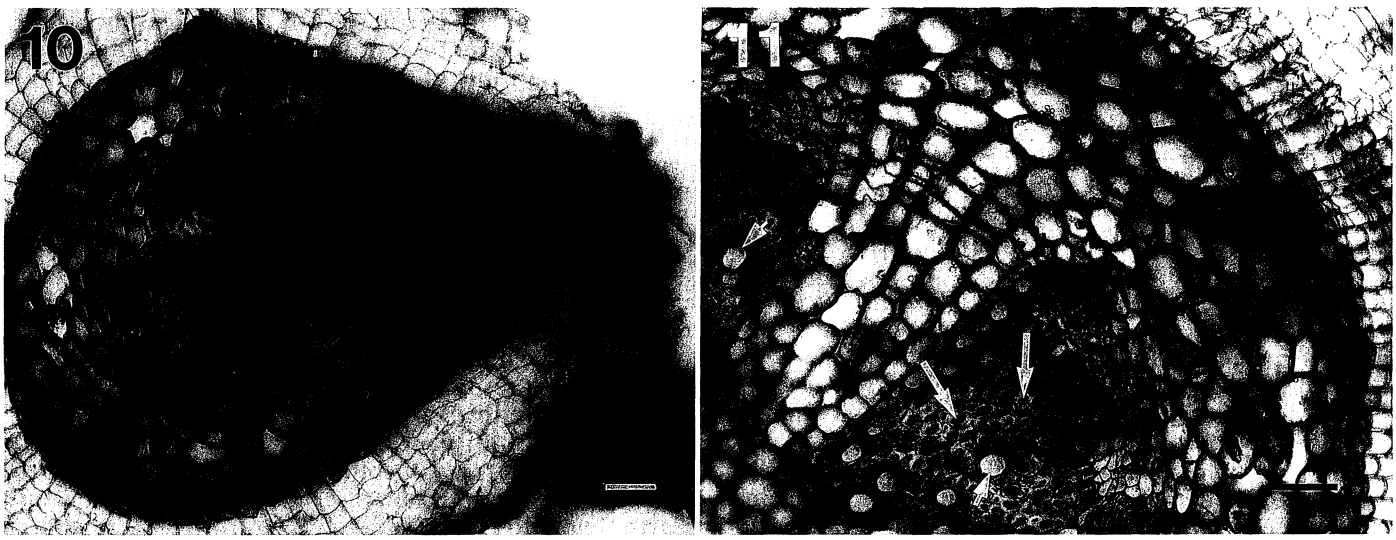
of the necrotic root tip of young roots of both species, and the number of primordia increased more than 50% ($P < 0.05$) to 13 ± 1 $cm^{-1}$ for *E. phyllanthus* and 14 ± 1 $cm^{-1}$ for *R. baccifera*. During 4 d of rewetting, several primordia (Fig. 10) elongated to form branch roots 2–5 mm long.

## DISCUSSION

Roots of the epiphytic cacti *Epiphyllum phyllanthus* and *Rhipsalis baccifera* changed during drought in a manner that helped limit plant water loss. Specifically, root hydraulic conductivity ($L_p$) decreased about 70% for young roots and 50% for older roots during 30 d in drying soil. Equally important, water uptake was fully restored within 4 d of rewetting, allowing transpiration for *E. phyllanthus* to return to its predrought level. The roots of these epiphytic cacti, like those of desert cacti (Nobel and Sanderson, 1984; Lopez and Nobel, 1991; North and Nobel, 1992; Huang and Nobel, 1993), thus help restrict water loss from roots to a drying soil yet readily take up water when the soil is rewetted.

During drying, soil sheaths composed of soil, root hairs, and mucilage helped limit desiccation for young roots of *E. phyllanthus* and *R. baccifera,* thereby allowing them to maintain a relatively high $L_p$. Comparable soil sheaths develop for roots of *Glycine max* (Sprent, 1975), *Oryzopsis hymenoides* (Wullstein and Pratt, 1981), *Zea mays* (McCully and Canny, 1988), and two cacti native to desert or semi-arid lands, *Ferocactus acanthodes* and *Opuntia ficus-indica* (North and Nobel, 1992). The water potential of young roots of *O. ficus-indica* with soil sheaths is about 30% greater during drying than that of roots with soil sheaths removed (Huang, North, and Nobel, in press). Besides preventing the desiccation of roots, copious root hairs and mucilage may also help anchor the young roots of *E. phyllanthus* and *R. baccifera* in sites exposed to wind and other disturbances.

In addition to soil sheaths, the increase in number and suberization of periderm layers for young roots of both species during drying helped limit water loss, as is the case for the stems of *Betula pendula* (Schönherr and Zieg-




Figs. 10, 11. Light micrographs of transverse sections of roots of *E. phyllanthus,* stained with toluidine blue O. **10.** Young root after 4 d of rewetting, with a new branch root primordium to the right. **11.** Older root after 30 d of drying; large arrows indicate fibers, and small arrows indicate vessels. Bars = 50 μm.

ler, 1980) and the roots of *F. acanthodes* and *O. ficus-indica* (North and Nobel, 1992). The tips of young roots of the epiphytic cacti, which lacked both soil sheaths and periderm, became necrotic and in many cases were absent after 30 d of drying. Perhaps due to death of the root apical meristem, more branch root primordia formed during drying than under wet conditions. After 4 d of rewetting, primordia lengthened into 2–5-mm-long branch roots that had no suberized layers and thus had a high $L_R$. Similarly, clusters of new lateral roots increase $L_R$ at junctions between main roots and lateral roots of *F. acanthodes* (North, Huang, and Nobel, 1993).

Older roots of *E. phyllanthus* and *R. baccifera* had higher $L_p$ than did young roots under wet, dry, and rewetted soil conditions, as is the case for root systems of *F. acanthodes* and *O. ficus-indica* (Huang and Nobel, 1992; North and Nobel, 1992). An increase in $L_p$ with root age is consistent with the proportional decrease in the length of the radial pathway for water flow, as older roots were composed of a vascular core surrounded only by periderm. The vascular core continued to expand with root age due to secondary growth; new layers were added to the periderm as well, but older, outer layers were shed.

For older roots of *E. phyllanthus* and *R. baccifera,* the heavily suberized, lignified layers of phellem developed radial breaks during rewetting. Such breaks probably accompany the normal process of phellem shedding, but they also help account for the changes in $L_R$ for older roots. During drying, no radial breaks were apparent in the suberized layers, which were most impermeable to water when dry (Vogt, Schönherr, and Schmidt, 1983). Upon rewetting, the phelloderm cells internal to the phellem took up water (perhaps facilitated by osmotica released by the breakdown of starch) and swelled, causing the phellem to break apart along radial lines. The channels thus formed could have increased the local $L_R$ and $L_p$. Such radial channels are not observed in the phellem of rewetted roots of *F. acanthodes* and *O. ficus-indica,* whose $L_p$ decreases more than 50% during 30 d of drying and increases to only 60% of its initial value after 7 d of rewetting (North and Nobel, 1992).

In contrast to the roots of desert cacti, for which axial (xylem) conductance per unit pressure gradient ($K_h$) decreases during drying due to embolism (North and Nobel, 1992), $K_h$ increased for the roots of *E. phyllanthus* and *R. baccifera* after 30 d of growth during drying. Such increases were due primarily to increases in the number of vessels per cross-sectional area of root, accompanied by a slight tendency for mean and maximum vessel diameters to increase as well. In addition, drying may have hastened the maturation of vessels and the developmental loss of end-walls, thereby increasing vessel conductivity, as occurs for lateral roots of the desert succulent *Agave deserti* (Huang and Nobel, 1992).

Embolism reduces $K_h$ more than 70% for older roots of *F. acanthodes* and *O. ficus-indica* during 30 d of drying (North and Nobel, 1992), but embolism reduced $K_h$ for roots of the epiphytic cacti only 30%. After rewetting, $K_h/K_h^{max}$ increased to predrought values, indicating that emboli had been removed. Although the relationship between embolism and vessel size is not clear (Tyree and Sperry, 1989), the small diameters of vessels in roots of *E. phyllanthus* and *R. baccifera* may reduce their susceptibility to cavitation (Zimmermann, 1983); for the older roots of the epiphytic cacti, mean vessel diameter was less than half that for *F. acanthodes* and *O. ficus-indica* (North and Nobel, 1992). The extremely narrow vessels in the young roots of *R. baccifera* and their relative lack of emboli during drying are also consistent with the tendency of this species to occur on bare limbs (Antibus and Lesica, 1990), whereas *E. phyllanthus,* with young roots more susceptible to embolism, is almost always rooted in pockets of soil or even in ant nests (Davidson and Epstein, 1989). The abundance of fibers in the vascular tissue of roots of both epiphytes may help prevent cavitation of vessels, as fibers can store and release water (Zimmermann, 1983), although their chief role is probably to provide the mechanical strength needed to secure the plants in precarious sites in the canopy.

For desert succulents, water flow into the roots in wet soil and in the early stages of drought is determined primarily by $L_p$ (Nobel and Cui, 1992). During the intermediate stages of drought ($\psi_{soil}$ of about $-0.5$ MPa to $-3$ MPa for desert soils), water flow is limited by the conductivity of an air gap that forms between the root and the soil as the root shrinks (Nobel and Cui, 1992). Similarly, the older roots of *E. phyllanthus* decreased in diameter by 10% during 30 d in drying soil, also potentially leading to air gaps. Along with reductions in $L_p$, such gaps may help limit plant water loss during the moderate droughts that can occur frequently for epiphytes in moist tropical forests. From $\psi_{soil}$ of $-0.01$ MPa to $\psi_{soil}$ of $-10$ MPa, the hydraulic conductivity of a sandy desert soil decreases by a factor of $10^3$ (Nobel and Cui, 1992). Such a decrease more than counteracts the greater tendency for water to move out of the root due to the increase in the water potential difference between the root and the drier soil. Although the hydraulic conductivity of the soils in which epiphyte roots typically grow may decrease somewhat less than that for desert soil, the movement of water between roots and soil should be limited by the low hydraulic conductivity of the soil during prolonged drought. When soil moisture is replenished after drought, root $L_p$ again limits water flow.

The development of soil sheaths and increasing suberization of the periderm during drying helped limit water loss from the roots of *E. phyllanthus* and *R. baccifera,* just as for the roots of desert cacti. The death of young root tips and the proliferation of branch root primordia increased radial conductivity after rewetting for the epiphytes, as also occurs for *F. acanthodes* (North, Huang, and Nobel, 1993). The radial channels that opened in the outer layers of phellem of older roots of *E. phyllanthus* and *R. baccifera* are not observed for desert cacti; and unlike roots of the epiphytes, older roots of the desert cacti do not fully regain radial conductivity after 7 d of rewetting (North and Nobel, 1992). Thus, older roots of the epiphytes responded more quickly and more completely to rewetting than do older roots of desert cacti. Under rewetted soil conditions, $L_p$ was higher for all roots of the epiphytes than for comparably aged roots of desert cacti. Periods without rain rarely last longer than 30 d on Barro Colorado Island (Windsor, 1990) but can last longer than 6 mo in the Sonoran Desert, where *F. acanthodes* is native (Nobel, 1988). Roots of epiphytic and desert cacti are thus similar in several of their responses to drying,

yet differences in their responses to rewetting reflect the greater probability of rainfall interrupting drought in a moist tropical forest than in a desert.

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