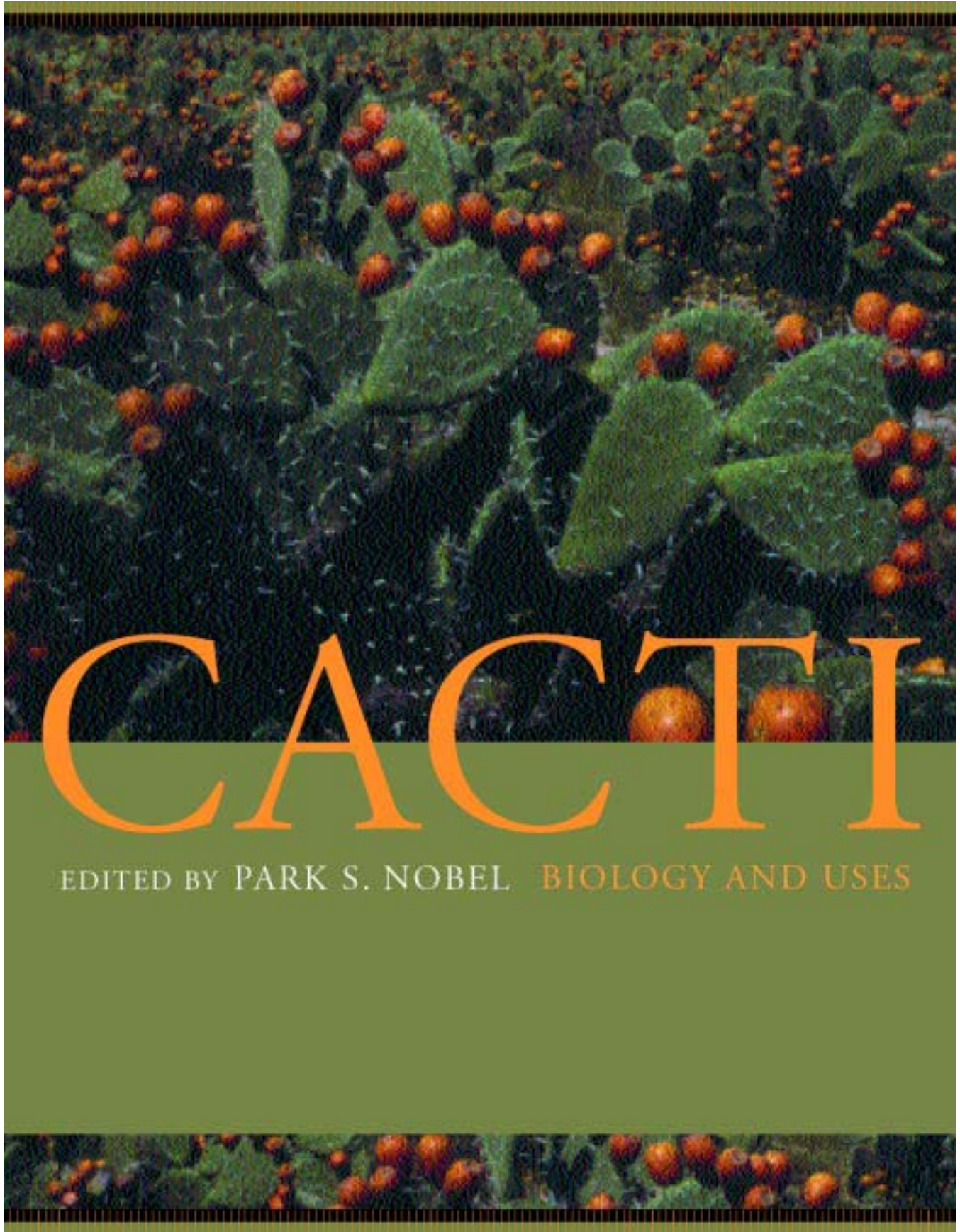


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ROOT STRUCTURE AND FUNCTION

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Introduction

From the first moments of a plant's life cycle, including germination, roots are essential for water uptake, mineral acquisition, and plant anchorage. These functions are especially significant for cacti, because both desert species and epiphytes in the cactus family are faced with limited and variable soil resources, strong winds, and frequently

rocky or sandy habitats. The goals of this chapter are to review the literature on the root biology of cacti and to present some recent findings. First, root structure, growth, and development are considered, then structural and developmental adaptations to desiccating environments, such as deserts and tropical tree canopies, are analyzed, and finally the functions of roots as organs of water and mineral uptake are explored.

Structure

Cactus roots are less overtly specialized in structure than are cactus shoots. Even so, root structural properties are fundamental to the ability of cacti to take up water and nutrients quickly, and to endure and recover from drought. An understanding of the relationship between root structure and function is essential to understanding how cacti are able to occupy some of the driest, most nutrient-poor habitats on earth.

Primary Structure

During embryogenesis, an embryonic root, or radicle, is formed. In most cactus species, the radicle is relatively small; for example, for *Echinocactus platyacanthus* the radicle is 320 μm long with a compact root cap of four cell layers covering the tip (Lux et al. 1995). Similarly, a small radicle is a typical feature in *Astrophytum myriostigma*, *Thelocactus bicolor* (Engelman 1960), and *Stenocereus gummosus* (Dubrovsky 1997b). Meristematic activity at the radicle apex begins approximately 12 hours after the radicle emerges from the seed coat for *S. gummosus* and *Ferocactus peninsulae* var. *townsendianus* (Dubrovsky 1997b). As a result of activity in the root apical meristem, roots grow in length, and the primary root tissues are formed (Esau 1977). The organization of the root apical meristem has been analyzed fully for *Opuntia basilaris* (Freeman 1969) and illustrated for a few other species. The roots of most cacti appear to have a closed apical organization in which each tissue can be traced to initial cells at the apex, as seen for *O. basilaris* (Freeman 1969), *O. arenaria* (Boke 1979), and *E. platyacanthus* (Lux et al. 1995).

Probably the best-studied species with respect to root development and structure is *O. ficus-indica*. The radial pattern of the primary root structure in *O. ficus-indica* does not differ significantly from that of most other dicotyledonous species (North and Nobel 1996). For this species, the external tissue—the epidermis—is composed of compact cells, some of which produce root hairs (Fig. 3.1A). Underlying the epidermis is the cortical tissue complex, which includes the hypodermis (the outermost cortical layer), the cortex proper, and the endodermis (the innermost cortical cell layer). The tissue complex located inward from the endodermis is the vascular cylinder. It comprises a two- or three-cell-layered pericycle and the vascular system, consisting of the xylem, the phloem, and the vascular parenchyma. The root vasculature is polyarch, usually with five to seven xylem poles in cylindropuntias (Hamilton 1970) and with four to eight xylem poles in platyopuntias (Freeman 1969). The pith is composed of parenchyma cells, as seen in *O. basilaris*

(Freeman 1969). Occasionally, mucilage cells are found in the primary root (Hamilton 1970).

Differentiation of primary tissues starts soon after cell division stops in the meristem. For *O. basilaris*, the protophloem is first evident at 340 μm from the root cap–root body junction; the protoxylem is first evident at 500 μm and is fully differentiated at 1,400 μm . Casparian strips in the endodermis occur at 500 μm from the junction. The metaxylem begins to develop at the base of the transition zone (region between the root and the hypocotyl) 4 to 5 days after germination and later can be found 1.2 mm from the root apex (Freeman 1969). Primary tissue development is unusually rapid in that as early as 6 days after germination the pericycle cells start to produce the periderm (Freeman 1969), which is the first secondary tissue to develop in platyopuntia roots.

Secondary Structure

For *O. ficus-indica*, *Ferocactus acanthodes*, and two epiphytic cacti, *Epiphyllum phyllanthus* and *Rhipsalis baccifera*, periderm layers (radially flattened cells just outside the pericycle) are well developed at about 150 to 200 mm from the root tip in young roots. Even young seedlings of cylindropuntias have roots with several corky (suberized) layers (Hamilton 1970). Such layers are more numerous and more heavily suberized closer to the tip of roots that have experienced drought than is the case for roots of well-watered plants (North and Nobel 1992). Back from the root tip, in regions approximately 2 to 4 months old, the cortex external to the periderm dies and is shed (Fig. 3.1B), a process that is also hastened by soil drying. Later in development, the outermost layers of the periderm are also shed as the vascular cylinder enlarges due to secondary growth. For the epiphyte *R. baccifera*, radial fissures open in the outer suberized layers of the periderm as roots swell upon re-watering after drought, thereby enhancing water uptake (North and Nobel 1994).

Within the vascular cylinder of most cactus roots, secondary growth produces wedge-shaped regions of vessels and fibers, separated by rays of parenchyma (Fig. 3.1C). For several species, including platyopuntias such as *O. ficus-indica*, large mucilage cells develop in the parenchyma rays, with a possible consequence for regulating water relations within the vascular cylinder (Preston 1901b; Gibson 1973; North and Nobel 1992; Loza-Cornejo and Terrazas 1996). Other characteristics associated with the parenchyma in the secondary xylem can be the occurrence of calcium oxalate crystals (Fig. 3.1D), the storage of starch, and the development of succulence. With respect to the xylem vessels themselves, secondary growth leads to a nearly

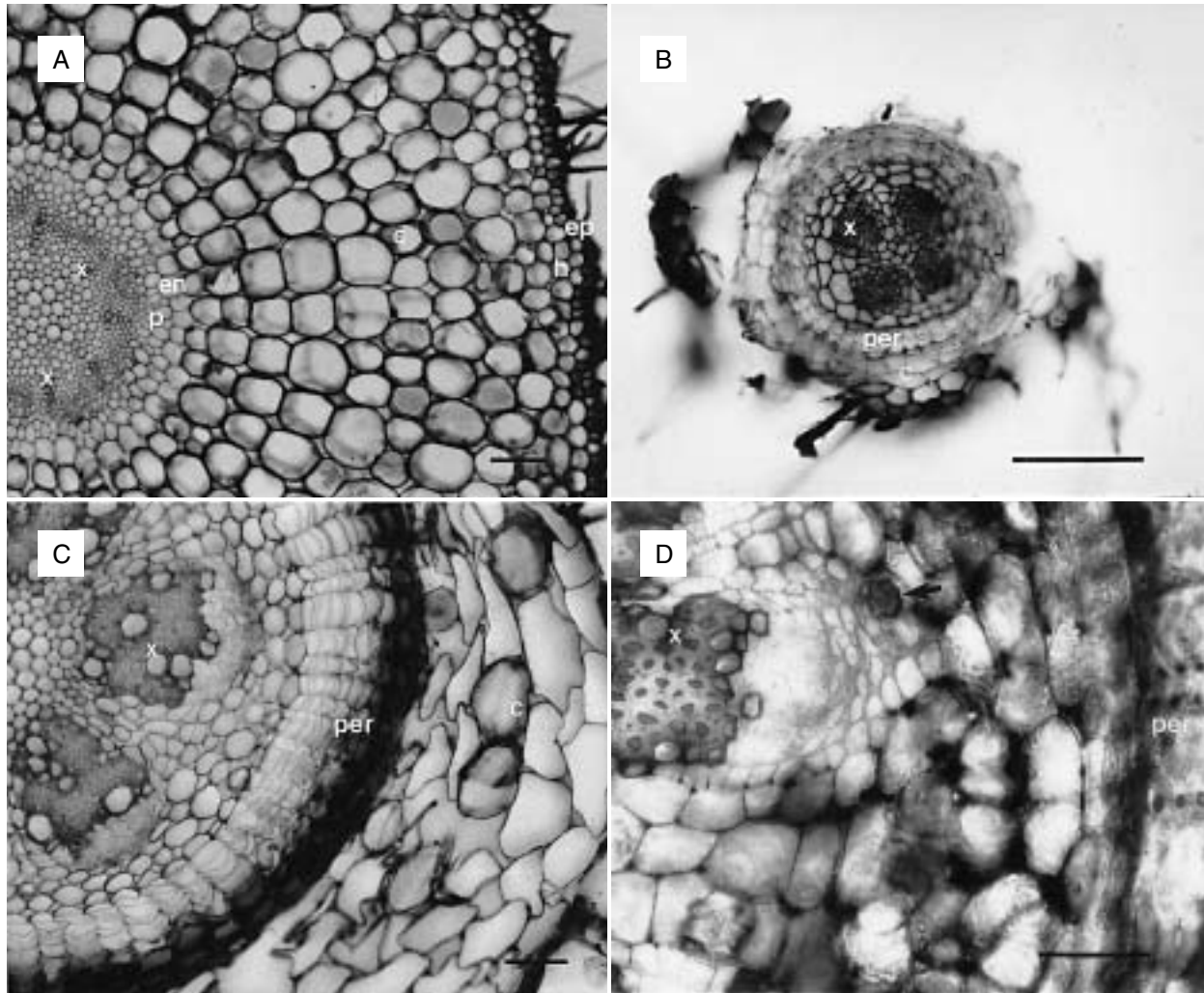


Figure 3.1. Median cross-sections of (A) a 1-month-old root of *Opuntia ficus-indica*, showing primary root tissues; (B) a 3-month-old root of *Epiphyllum phyllanthus*, with cortex separating from the periderm; (C) a 3-month-old root of *O. ficus-indica*, showing secondary growth; and (D) a 5-month-old root of *Rhipsalis baccifera*, with arrow indicating a calcium oxalate crystal. Cell types shown are epidermis (ep), hypodermis (h), cortex (c), endodermis (en), pericycle (p), periderm (per), and xylem (x). Scale bars: A = 50 μm , B = 500 μm , C–D = 100 μm .

threefold increase in mean vessel diameter for *O. ficus-indica* and *F. acanthodes*, and a seven- to tenfold increase in vessel number during 12 months of growth (North and Nobel 1992). For the epiphytes *E. phyllanthus* and *R. baccifera*, mean vessel diameter increases only slightly during 3 months of growth, but vessel number also increases about tenfold (North and Nobel 1994). Such increases in vessel diameter and number are accompanied by large increases in the rate of water transport in the xylem (North and Nobel 1992, 1994).

Root Types

Different types of roots can be classified according to their developmental origin. For example, a root that develops

from the embryonic radicle is termed a primary root. Later, when the primary root reaches a certain length, lateral roots are formed. Any root formed on another root is considered a lateral root. When a root is formed on an organ other than a root, it is termed an *adventitious* root. Cladodes of *O. ficus-indica* readily produce adventitious roots at or near areoles (Fabbri et al. 1996; Dubrovsky et al. 1998b), reflecting localized activity in the vascular cambium (Villalobos 1995). For *Pereskia*, adventitious roots can be formed on leaf petioles (Carvalho et al. 1989). Adventitious roots form along the stems of many decumbent, prostrate, and epiphytic cacti, most of which never develop elongated primary roots (Gibson and Nobel 1986). Adventitious rooting of fallen stem segments allows desert

species, such as *O. bigelovii*, to reproduce vegetatively, and the larger water storage capacity of such rooted segments assures greater drought tolerance than is the case for much smaller seedlings. For epiphytic cacti, adventitious rooting along stems can improve anchorage in the canopy, and enables dislodged stem segments to take root where they land on host species (Andrade and Nobel 1997). The ability to produce adventitious roots is also useful for clonal propagation of *O. ficus-indica* and other agronomic species (Le Houérou 1996).

Cactus roots can also be classified according to their function and position within a root system. A century ago, Carleton Preston from Harvard University defined anchoring versus absorbing roots in different cactus species and found some anatomical differences in these root types related primarily to the thickness of the vascular cylinder (Preston 1900, 1901b). William Cannon from the Desert Botanical Laboratory also used these terms, stating that anchoring roots can be: (1) vertically oriented, deeply penetrating, taproots; or (2) horizontally oriented, supporting roots (Cannon 1911). Cannon divided absorbing roots into two categories: (1) rope-like roots and (2) filamentous, relatively thin roots (Cannon 1911). This functional descriptive classification is not absolute, because each root type can have a few functions simultaneously (Preston 1900; Cannon 1911).

Two other root types with morphological modifications are succulent roots and tuberous storage roots, each of which can have some characteristics of the other. Cannon (1911) reported fleshy roots in *O. vivipara*, and first recognized water storage capabilities of the roots of some cactus species. Thick succulent roots (that occasionally include the hypocotyl–root transition zone) can be found in small cacti, such as species of *Ariocarpus* (Britton and Rose 1963; Bravo-Hollis and Sanchez-Mejorada 1978), *Aztekium* (Porembski 1996), *Leuchtenbergia* (Britton and Rose 1963), and *Lophophora* (Nobel 1994). For the columnar cactus *Pachycereus pringlei*, the fleshy taproot can be 18 cm thick near its base (J. G. Dubrovsky, unpublished observations). Succulence develops within the secondary xylem in *Maihuenia patagonica*, *Nyctocereus serpentinus*, *Opuntia macrorhiza*, *O. marenae*, *Pereskia humboldtii*, *Pterocactus tuberosus*, and *Tephrocactus russellii*, and in cortical ground tissue in *Neoevansia diguetii* and *Peniocereus greggii* (Gibson 1978). Generally, water storage capacity (capacitance) is relatively small in cactus roots compared to shoots (Nobel 1996). For succulent roots, however, the capacitance is greater than for nonsucculent roots, and may be comparable to that of the water-storage parenchyma in stems. Water-storage tissue in succulent roots has the abil-

ity to withstand a high degree of dehydration without irreversible damage, and may also help prevent water loss and decrease root shrinkage during drought.

In addition to storing water, cactus roots frequently accumulate starch. To accommodate starch reserves, the roots of some species acquire a distinct morphology. A relatively large, subterranean storage root is characteristic of cacti that are geophytes; such roots give rise to aboveground annual shoots that shrivel and die during drought and are regenerated the following year, when water is available (Gibson 1978; Gibson and Nobel 1986). Typical geophytes in North America are species of *Neoevansia*, *O. chaffeyi*, *Peniocereus*, and *Wilcoxia*, and in South America, *Pterocactus tuberosus* (Gibson 1978). Tuberous roots of *Wilcoxia poselgeri* and *W. tamaulipensis* are characterized by starch-storing parenchyma, primarily in the cortex, along with mucilage cells in the pith, the cortex, and the vascular tissue complex (Loza-Cornejo and Terrazas 1996). Tuberous roots can be sizable; e.g., those of *Peniocereus greggii* grow up to 60 cm in diameter, 15 to 20 cm long, and have a weight of 27 to 56 kg (Britton and Rose 1963). Non-geophytes can also develop one or a few tuberous or tuber-like roots. Groups of tuber-like roots 1 to 2.5 cm in diameter occur for *O. arbuscula* (Cannon 1911), *O. marenae*, and *O. reflexispina* (Felger and Moser 1985). Single tuber-like taproots occur for other non-geophyte species, such as *Ancistrocactus megarhizus* (Britton and Rose 1963), *Escobaria henricksonii* (Glass 1998), *Thelocactus mandragora* (Bravo-Hollis and Sanchez-Mejorada 1978), and *T. subterraneus* (Higgins 1948).

Another specialized root type—airial roots—are rarely produced by desert cacti. However, aerial roots can occur for *S. gummosus* in the Sonoran Desert (Dubrovsky 1999). This species has decumbent stems that form adventitious roots when branches touch the soil. Aerial roots can develop before such contact, on the lower part of the convex stem or on other portions of the stem (Fig. 3.2). These roots are short, succulent, and sometimes extensively branched, with secondary growth, and can be 3 to 4 mm or more in diameter (Dubrovsky 1999). A possible role for such roots in dew uptake remains to be studied. Under greenhouse conditions, *O. arenaria* is also capable of forming numerous aerial roots (Boke 1979). In epiphytic and climbing species, aerial root development is a common phenomenon, as in plants from the genera *Epiphyllum*, *Hylocereus*, and *Selenicereus* (Bravo-Hollis and Sánchez-Mejorada 1978).

Root systems can be composed of several different root types and in many combinations. Nevertheless, three basic morphological patterns of root systems are recognized



Figure 3.2. Aerial roots on the shoot of *Stenocereus gummosus* in the Sonoran Desert.

(Cannon 1911; Gibson and Nobel 1986). The first type is composed of a taproot with few or no lateral roots, as seen for geophytes and species with succulent roots, such as in the genera *Lobivia* and *Lophophora* (Gibson and Nobel 1986). The second type of root system is composed of a taproot and horizontal, subsurface lateral roots and/or adventitious roots, as occurs for most columnar cacti and species of *Ferocactus* (Cannon 1911; Gibson and Nobel 1986). The third type lacks a taproot and consists of roots of different lengths, with small species tending to have numerous branched roots directly beneath the shoot, and larger species tending to have long subsurface roots extended some length from the shoot, as seen in several species of *Opuntia* (Gibson and Nobel 1986).

Development and Growth

Root development and growth are important, both during the early stages of a plant's life cycle (particularly for seedling establishment) and, later, as continued shoot growth requires that roots invade new areas to obtain water

and nutrients. Increases in root surface area are the result of two processes: (1) root elongation, which involves cell production by the root apical meristem; and (2) root branching, or the production of lateral roots. Cells within the root apical meristem can proliferate for an indefinite period, exhibiting indeterminate growth, or they can lose such ability after a limited period, exhibiting determinate growth. The amount and pattern of root branching depends, in part, on whether main roots are characterized by indeterminate or determinate growth.

Indeterminate Root Growth

Indeterminate root growth is common in most flowering plants, including cacti. For example, adventitious roots of *Opuntia ficus-indica* are characterized by indeterminate growth, insofar as cell production by the root apical meristem continues for a relatively long period. The tips of main roots of *O. ficus-indica* generally die after a few months of growth; however, death occurs more quickly in dry soil than in wet soil (Dubrovsky et al. 1998b; G. B. North, unpublished observations). By analyzing the cell lengths along the root, three main root zones can be determined for *O. ficus-indica*: (1) the meristem (where cells are relatively small and are in the cell division cycle), (2) the elongation zone (where cells start and nearly complete rapid elongation), and (3) the differentiation zone (where cells complete their elongation and start to acquire certain tissue characteristics). The root apical meristem of a main adventitious root of *O. ficus-indica* is relatively large—on average 1.1 mm long—consisting of 82 cortical cells in a cell file (Dubrovsky et al. 1998b), comparable to the root meristem of most crop plants. The growing part of the root (the meristem and the elongation zone) in this species is 5 to 7 mm long. The primary root of a Sonoran Desert species, *Pachycereus pringlei*, exhibits indeterminate growth only

TABLE 3.1

Growth characteristics of species with determinate root growth (*Stenocereus gummosus* and *Ferocactus peninsulae*) and indeterminate root growth (*Pachycereus pringlei*) in the first week of the seedling stage

Quantity	<i>S. gummosus</i>	<i>F. peninsulae</i>	<i>P. pringlei</i>
Primary root growth rate ($\mu\text{m hour}^{-1}$)	93 \pm 9	111 \pm 9	178 \pm 7
Length of mature epidermal cells (μm)	98 \pm 2	85 \pm 3	176 \pm 5
Cell number in a file of epidermal cells			
in the meristem	12.0 \pm 0.2	20.9 \pm 0.4	20.8 \pm 0.4
Duration of the cell division cycle (hours)	9.7 \pm 1.1	11.7 \pm 0.9	14.5 \pm 0.6

The duration of the cell division cycle is estimated by the rate of cell production method (Ivanov and Dubrovsky 1997). Data are means \pm SE (n = 11) and are from Dubrovsky et al. (1998a).

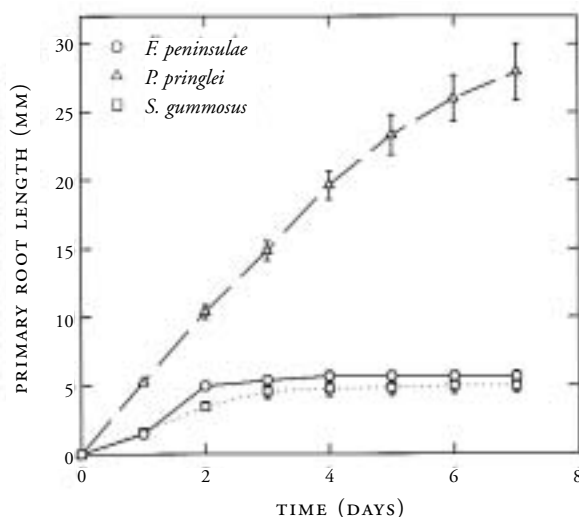


Figure 3.3. Primary root length for *Ferocactus peninsulae*, *Pachycereus pringlei*, and *Stenocereus gummosus* for 7 days after the start of radicle protrusion. Data are means \pm SE ($n = 12$) and are from Dubrovsky et al. (1998a).

during the first week after germination (Fig. 3.3) and then stops growing. The roots have much shorter meristems, averaging 21 epidermal cells in a cell file (Table 3.1). Smaller root meristems are more typical for young seedlings, because meristem size is correlated with root diameter, and primary and lateral roots are typically thinner than adventitious roots.

The rate of root growth depends on various factors. A primary external factor is temperature, which affects the duration of the cell cycle (cycle time). At an optimal temperature, the average cycle time in the root apical meristem for *O. ficus-indica* is 28 hours (Dubrovsky et al. 1998b) and for *P. pringlei* is 15 hours (Dubrovsky et al. 1998a). A primary internal factor is the final size of elongated cells. The cell length for *O. ficus-indica* averages 378 μm (Dubrovsky et al. 1998b) and for *P. pringlei*, 176 μm (Dubrovsky et al. 1998a). The average cell cycle time within the root apical meristem can vary within and among species, but, in general and assuming elongated cells are the same size, the shorter the cycle, the greater the rate of root growth (Dubrovsky et al. 1998a).

Determinate Root Growth

Determinate root growth is the result of a developmental program in the root apical meristem, in which a finite number of cell division cycles takes place. For cacti, determinate root growth was first described for lateral roots of *Opuntia arenaria* and *O. tunicata* var. *davisii* (Boke 1979).

Two types of determinate roots occur for these species. First, relatively long lateral roots (a few cm long) are developed as a part of the absorptive or feeder root system. The apical meristem of these roots has a normal organization, but functions for only a limited time. Soon the root tip dies, and a new meristem is formed behind the dead root tip, giving rise to a sympodially branched system of roots of various lengths. On relatively long roots, short determinate roots of a second type, called "root spurs," develop. The root spur is a cluster of sympodially branched roots less than 1 mm long. The root tip of such spur roots is atypical, lacking a root cap. All cells of the small apical meristem become differentiated, and the tip of the spur root becomes completely covered by root hairs. Spur roots may allow a rapid increase in root surface area, increasing water uptake during infrequent periods of rainfall (Boke 1979).

A determinate pattern of root growth in primary roots is highly unusual for flowering plants. Indeed, continuous elongation of primary roots seems generally more advantageous, particularly for seedling establishment. Surprisingly, determinate root growth is exhibited by the primary root of Sonoran Desert cacti belonging to two tribes, Pachycereeae (*P. pringlei*, *Stenocereus thurberi*, and *S. gummosus*; Dubrovsky 1997a,b) and Cactaceae (*Ferocactus peninsulae*; Dubrovsky 1997b). Determinate growth of primary roots is also shown by *S. pruinosus* and *S. standleyi* growing in the Tehuacán Valley of Mexico (Dubrovsky 1999). A similar pattern occurs for epiphytic cacti, including *Epiphyllum phyllanthus*, in which the radicle dies after elongating by only 200 to 400 μm (G. B. North, unpublished observations).

A typical characteristic of cactus roots with determinate growth is the relatively short duration of primary root growth and early meristem exhaustion. For example, *F. peninsulae* and *S. gummosus* grow for only 2 days after the start of radicle protrusion (Fig. 3.3). When seedlings are grown on filter paper, the radicle does not exceed 10 mm, similar to its length in soil (Dubrovsky 1997a,b). When seedlings are grown on sterile medium supplemented with 2% sucrose, the pattern of growth is the same, even though the final size of the roots is greater (Dubrovsky 1997b). During the period of steady-state growth (24–36 hours), meristematic activity is maintained and the size of the root apical meristem remains unchanged. After this period, meristematic cells cease dividing, leave the meristem, and undergo rapid elongation. Because no new cells are produced, the meristem rapidly decreases in size and becomes exhausted. As epidermal cells elongate and differentiate producing hairs, the root hairs grow to the tip of the

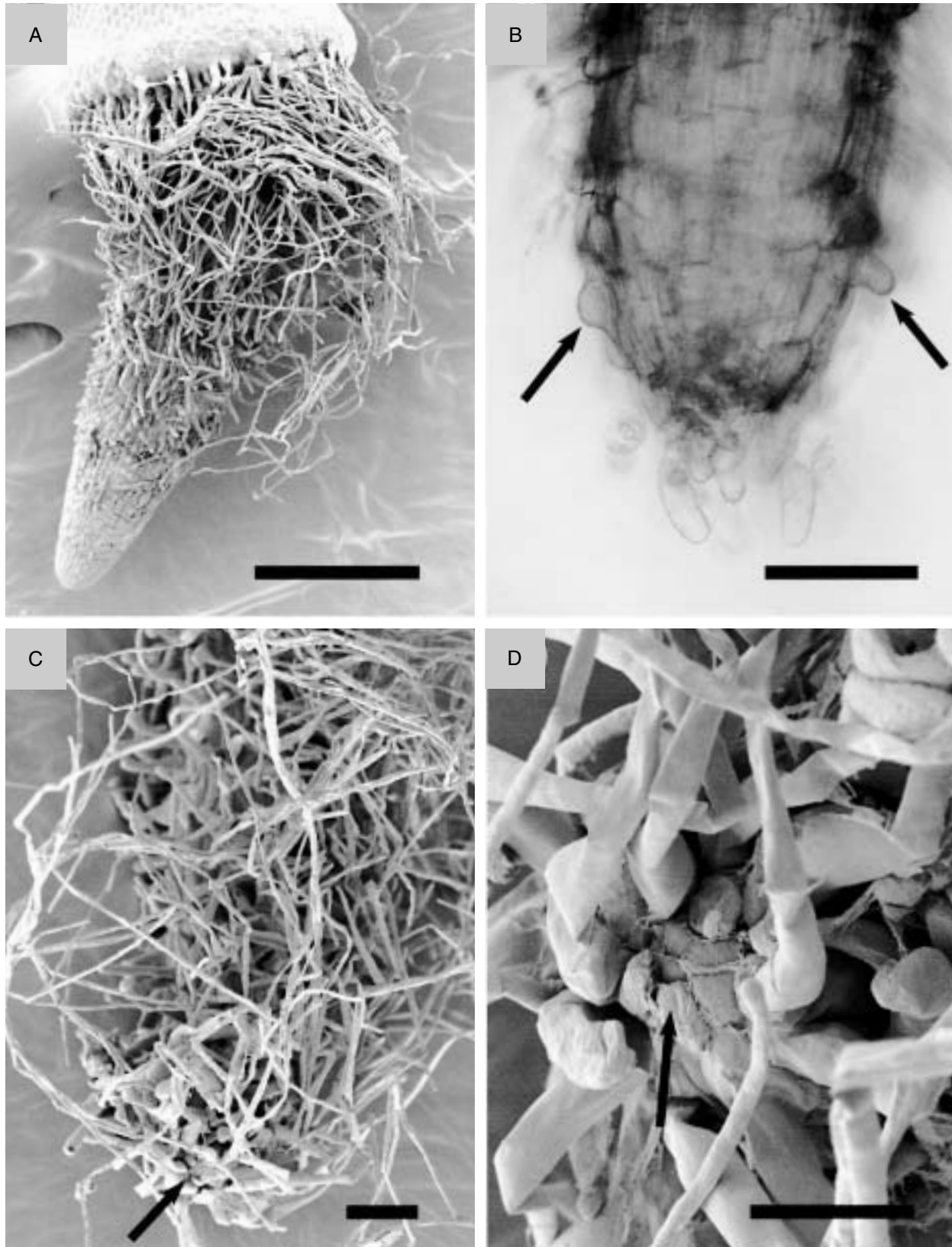


Figure 3.4. Root tips of *Stenocereus gummosus* at (A) 24 hours, (B) 36 hours, and (C) and (D) 48 hours after the start of radicle protrusion. Root hairs (arrows) approach the tip in (A) and (B) and later cover the tip completely in (C). In (D), the five most apical cells (arrow) have not formed root hairs. Scale bars: A = 400 μm , B–C = 100 μm , D = 50 μm .

root and subsequently cover it completely (Fig. 3.4; Dubrovsky 1997b).

The size of the root apical meristem for cacti with determinate root growth is relatively small, with 12 to 21 cells in a cell file (Table 3.1). The cells in the root apical meristem divide relatively quickly, every 10 to 14 hours for *Stenocereus gummosus* and 12 to 17 hours for *Ferocactus peninsulae* (Dubrovsky et al. 1998a). A comparison of the duration of the period of steady-state growth (Dubrovsky 1997a,b) and the duration of the cell division cycle in the root apical meristem (Dubrovsky et al. 1998a) shows that, on average, only two cell division cycles occur in the root apical meristem in both species. Assuming that meristematic activity is maintained until the meristem is exhausted, the maximum number of cycles is four in *S. gummosus* and five in *F. peninsulae*. Thus, the determinate pattern of root growth in these cactus species represents a normal developmental path, during which only a few cell division cycles take place.

Lateral Root Development

For angiosperms, lateral roots originate mainly from the pericycle of a parent root. For *O. basilaris*, the pericycle cells opposite the protoxylem give rise to lateral root primordia early in seedling development (Freeman 1969). For *F. peninsulae* and *S. gummosus*, lateral root primordia can be detected 4 to 5 days after germination (Dubrovsky 1997a,b). The time from primordium initiation to lateral-root emergence is relatively short for these species and comparable to that of other angiosperms (Dubrovsky 1997b). During lateral root development, a vascular junction between the parent root and a lateral root is established, consisting of relatively short tracheary elements with large areas of non-lignified primary cell walls (North et al. 1992), phloem elements, and vascular parenchyma cells. Early in development, lateral root primordia are internal to the periderm, cortex, and epidermis of the parent root (North et al. 1992; North and Nobel 1992). For *Ferocactus acanthodes*, the inner layers of the periderm (the phelloderm layers) of the parent root are continuous with the base of the lateral root, whereas the suberized layers of the periderm (the phellem layers) of the parent root are ruptured as the lateral root elongates (North et al. 1992).

The initiation of lateral root primordia is apparently promoted by drought. For example, the number of second-order lateral root primordia for *F. acanthodes* is significantly greater for plants subjected to drought than for plants under wet conditions (North et al. 1993). In distal root segments of *O. ficus-indica*, four to five more lateral root primordia develop during soil drying than under

wet conditions (Dubrovsky et al. 1998b). Similarly, the initiation of lateral root primordia in the epiphytes *E. phyllanthus* and *Rhipsalis baccifera* is stimulated by soil drying (North and Nobel 1994). Because the rate of root growth decreases during drought (Dubrovsky et al. 1998b), the occurrence of primordia closer to the root tip than under wet conditions may reflect reduction in parent root growth, induction of lateral roots, or both. The developmental signals for lateral-root initiation may also include changes in hormone levels due to the death of the parent root tip.

Lateral root elongation after drought is induced by rain or watering, and such lateral roots have been called "rain" roots, although a more general term is "ephemeral roots," because such roots tend to be short-lived (Nobel 1988). Ephemeral roots can emerge rapidly, for example, within 8 hours of watering for both *Opuntia puberula* (Kausch 1965) and *F. acanthodes* (Nobel and Sanderson 1984). Within 24 hours of watering *O. ficus-indica* after 14 days of drought, lateral roots are 2 to 4 mm long, and lateral root growth rate during the second day after emergence is 9.7 mm day⁻¹ (Dubrovsky et al. 1998b). Apparently these roots emerge from primordia formed during drought, but further analysis is needed. Ephemeral roots are important for a rapid increase in absorbing surface area without a substantial increase in the distance for water transport (Cannon 1911; Jordan and Nobel 1984; Dubrovsky et al. 1998b). For example, for *F. acanthodes* the total root length increases by 27% because of ephemeral root formation (Jordan and Nobel 1984). During subsequent drought, fine lateral roots can abscise (North et al. 1993), and have thus been called "deciduous roots" (Cannon 1911).

Root System Development

The type and extent of root systems in cacti can vary in response to both external and internal factors. For example, cladodes of *Opuntia versicolor* planted in adobe (clay-containing) soil produce some vertically oriented anchoring roots and some horizontally oriented absorbing roots, whereas cladodes planted in sand produce roots at seemingly random angles (Cannon 1925). The formation of a root system is not necessarily a continuous process in a desert. For example, a seedling may develop roots, then lose them during a subsequent drought, and develop another root system upon re-watering. The duration of drought, the shoot biomass (and thus water storage capacity), and the ability to form sequential root systems all affect seedling survival for *Stenocereus thurberi* (Dubrovsky 1996, 1998, 1999). Most seedlings having fresh weights of 25 to 75 mg lose their root systems completely during a 40-day drought. After rehydration, adventitious roots grow

from the basal portion of the hypocotyl, forming a new root system that is larger than the original one (Dubrovsky 1999). Seedlings and young plants in the desert may develop a number of root systems before forming a lasting, adult root system.

The architecture of a root system is partially determined by whether roots exhibit determinate or indeterminate growth. For plants with determinate primary root growth (e.g., *S. gummosus*), some lateral roots appear to have indeterminate growth. In an adult plant of this species, long rope-like roots can be found, extending 5 to 6 m away from the plant (Dubrovsky 1999). Upon closer inspection, however, such roots are not formed by continuous growth of the root apical meristem, but instead represent a series of interconnected lateral roots (J. G. Dubrovsky, unpublished observations), similar to sympodially branched roots described by Boke (1979).

Adaptations to Deserts and Other Arid Environments

Root Distribution in the Soil

Most desert cacti can be classified as shallow-rooted perennials (Rundel and Nobel 1991). In the Sonoran Desert, the roots of most cacti usually grow no deeper than 15 to 30 cm below the soil surface, although the roots of some species can extend laterally more than 10 m away from the plant base (Cannon 1911). Not surprisingly, the deepest roots are found for columnar cacti. A young plant of *Carnegiea gigantea*, 1.2 m tall, had a stout taproot that penetrated 30 cm and lateral roots that extended 1.5 to 5 m away from the plant, whereas an older, 6.8-m-tall plant had lateral roots up to 9.7 m long that penetrated to a depth of 77 cm (Cannon 1911), perhaps the deepest cactus roots on record.

Root proliferation and elongation is essential for continued water and mineral uptake, and for competition for these resources with other plants. For *Ferocactus acanthodes* at a site in the Sonoran Desert, the dry weight of the whole root system averages only 14% that of the shoot; however, the total surface area of the root system is about 3 times greater than that of the shoot, and the total length of the main roots in the root system per plant averages 182 m (Jordan and Nobel 1984). Roots of *Opuntia polyacantha* growing in the shortgrass steppe of Colorado have a median root depth of less than 2.5 cm (Dougherty et al. 1996). For *O. polyacantha*, as little as 2.5 to 5 mm of precipitation significantly increases cladode biomass. Indeed, the frequency of rain is more important than the absolute amount of rain, due in part to competition with more deeply rooted grasses that capture water from deeper soil

levels (Dougherty et al. 1996). In this case, a shallow root distribution not only helps to exploit light rainfall, but also gives the cactus an edge in competition with other plants.

Environmental Effects on Root Development

The root elongation rate depends on temperature. For *F. acanthodes*, root growth in response to temperature can be described by a bell-shaped curve, with maximal elongation at 30°C (Jordan and Nobel 1984). Cactus roots in natural environments are frequently exposed to temperatures higher than optimal; for example, in the northeastern Sonoran Desert, the maximum temperature 5 to 10 cm below the soil surface can be 40 to 50°C (Jordan and Nobel 1984). Cannon (1916) reported that at 43°C, roots cease growing. At 60°C, the root cells of *F. acanthodes* die, although high temperature tolerance of roots in this species can be increased by acclimation. Roots of plants acclimated at day/night temperatures of 45/35°C survive at temperatures 4°C higher than those of plants acclimated at 30/20°C (Jordan and Nobel 1984).

Boulders and subterranean rocks, which are common in desert environments, can provide favorable microsites for cactus root systems. Cannon (1911) observed that rocks stimulated root branching of *Opuntia phaeacantha* var. *discata* in the Sonoran Desert. Similarly, roots of *Echinocereus engelmannii* are more commonly found alongside boulders than at increasing distances away, and lateral roots of *F. acanthodes* are 5.5 times longer and 3 times more numerous under rocks than in regions of the soil without rocks (Nobel et al. 1992b). Such increased growth and branching are explained primarily by a longer period of water availability, as the soil water potential decreases sharply with distance away from rocks and, after soil wetting, remains higher under rocks than in rock-free soil (Nobel et al. 1992b). In addition to creating locally moist microsites, rocks may also be associated with regions of higher nutrient concentrations. During active growth, roots exude carbohydrates to the soil (Huang et al. 1993) and, during subsequent drought, ephemeral roots die. Organic matter may thus accumulate in the vicinity of rocks, promoting new root growth near the rocks when water is again available.

Soil drying generally decreases the rate of root growth, although the rate of drying is critical in determining whether apical elongation can continue. For example, when *Opuntia ficus-indica* is subjected to gradual drying of the substrate, roots have sufficient time for developmental changes to occur, whereas rapid substrate drying leads to death of the apical meristem. The meristem and elongation zone become shorter when the substrate dries gradually,



Figure 3.5. Root system of *Epiphyllum phyllanthus* after 21 days in drying soil, in which all roots are covered by rhizosheaths.

whereas under rapid drying roots die because insufficient time for such rearrangements is available (Dubrovsky et al. 1998b). Similarly, plants of *F. acanthodes* that have been previously exposed to drought suffer less inhibition in root growth under newly imposed water stress than do plants that have not previously been so exposed (Jordan and Nobel 1984).

For a number of desert and epiphytic cacti, soil drying also appears to enhance the development of rhizosheaths, which are rough cylinders around the roots, composed of soil particles that are bound to root hairs and other epidermal cells by mucilage exuded by the roots (Fig. 3.5; Huang et al. 1993; North and Nobel 1992, 1994). Such rhizosheaths become thicker and more cohesive during drought and help improve root water relations, both by ensuring good contact between the root and wet soil and by helping to reduce water loss from the root to a drier soil (North and Nobel 1997).

Developmental Adaptations

Determinate root growth can be viewed as a developmental program well suited to desert conditions. For example, meristem exhaustion in the primary root of *Stenocereus gummosus* coincides with or perhaps triggers the initiation of lateral root primordia. The percentage of roots bearing lateral root primordia is correlated with the percentage of roots in which the root apical meristem is exhausted (Dubrovsky 1997a, 1997b). Determinate primary root growth is thus a developmental mechanism leading to the rapid induction of lateral root formation and root system development. In most desert habitats, the optimum period for seed germination is extremely brief; thus, the rate of root-system formation is a critical factor for successful seedling establishment. Because many of the lateral roots of *S. gummosus* also have determinate growth, a compact

root system is formed that requires limited carbon input but is sufficient for water and mineral uptake (Dubrovsky 1997b, 1998).

A related developmental feature with adaptive significance is the relatively short duration of the cell cycle in the root apical meristem for cacti with both determinate and indeterminate root growth. Rapid root elongation and root branching are possible only when new cells are produced rapidly. A relatively short cell cycle can thus be advantageous, particularly during the critical stage of seedling establishment. At a later stage, when established roots resume both apical growth and branching after a drought, a relatively short cell cycle with its high rate of cell production should also enhance the rate of colonization of new soil regions by the roots.

Early root hair production, as seen for *S. gummosus*, represents another developmental adaptation. For this species, root hairs develop almost at the onset of seed germination. When the radicle is still very small, root hairs are evident and are frequently longer than the radicle itself (Fig. 3.4A). The basal epidermal cells, embryonic in origin, average 18 μm in length, whereas the root hairs formed by these cells average 100 times longer (1.8 mm). Each epidermal cell is capable of forming a root hair, unlike the usual case for plants. Later, the epidermal cells that are formed due to root meristem activity average 98 μm in length (Table 3.1). Such early root hair formation, occurring even before germination is completed, can maximize the root surface area available for absorption, thereby increasing water and mineral uptake during the relatively short optimum growth period in a desert (J. G. Dubrovsky, unpublished observations).

Water and Mineral Uptake

Root Hydraulic Conductivity

For both desert and epiphytic cacti, soil moisture varies greatly in both time and space. The success of cacti faced with such heterogeneity in water availability depends on the ability of their roots to conduct water quickly when it is available, to resist water loss when the soil becomes dry, and to resume water uptake upon the cessation of drought. The ability of roots to absorb and transport water is quantified by the root hydraulic conductivity, or L_p . The units of L_p ($\text{m s}^{-1} \text{MPa}^{-1}$, where MPa is 10^6 pascals) indicate that a volume of water moves across the root surface area per unit time in response to a difference in pressure (such as the difference between the water potentials of the plant and the soil; Nobel 1999). For roots, L_p has two components, the radial conductivity, which determines the rate of

TABLE 3.2

Hydraulic conductivity (L_p) for young (1-month-old) and older (3- to 5-month-old) roots of two terrestrial cacti (*Ferocactus acanthodes* and *Opuntia ficus-indica*) and two epiphytic cacti (*Epiphyllum phyllanthus* and *Rhipsalis baccifera*) under wet conditions, at 21 to 30 days in drying soil, and at 3 days after soil rewetting

Species	Root age	$L_p (\times 10^{-7} \text{ m s}^{-1} \text{ MPa}^{-1})$		
		Wet soil	Drying soil	Rewetted soil
<i>F. acanthodes</i>	young	2.4	1.8	2.0
	older	4.2	1.6	2.6
<i>O. ficus-indica</i>	young	1.7	1.4	1.9
	older	5.4	1.3	1.4
<i>E. phyllanthus</i>	young	2.3	0.7	2.8
	older	5.6	2.6	5.4
<i>R. baccifera</i>	young	2.1	0.7	2.5
	older	7.0	3.2	8.0

Data are from North and Nobel (1992, 1994).

water flow across the root tissues up to the xylem (and which generally is similar in value to L_p), and axial conductivity, which determines the rate of flow through the xylem.

Despite the ability of most cactus roots to endure drought, their L_p under wet soil conditions (Table 3.2) is comparable to that of many mesophytic species, such as *Zea mays* ($1.0\text{--}2.8 \times 10^{-7} \text{ m s}^{-1} \text{ MPa}^{-1}$; Steudle et al. 1987) and *Phaseolus vulgaris* ($1.4\text{--}4.0 \times 10^{-7} \text{ m s}^{-1} \text{ MPa}^{-1}$; Sands et al. 1982). Three- to 5-month-old roots of both terrestrial and epiphytic cacti have a higher L_p than do 1-month-old roots under wet conditions, due to the higher resistance of the cortex and the immaturity in the xylem of younger roots (North and Nobel 1992, 1994, 1997). During 3 to 4 weeks of soil drying, L_p decreases to about 50% of its value under wet conditions, averaged for young and older roots of the four cactus species (Table 3.2). The decrease is primarily due to reductions in radial conductivity, caused by increased suberization in the periderm, and secondarily to decreases in axial conductivity, due to embolism in the xylem (North and Nobel 1992, 1994, 1996). During the same period of soil drying, root diameter shrinks by 19% for roots of *Opuntia ficus-indica* with rhizosheaths, by 26% for bare roots of this species, and by 13% for older bare roots of *Epiphyllum phyllanthus* (North and Nobel 1992, 1994). Such shrinkage causes air gaps to develop between the root and the soil, which decrease water loss from the root that would otherwise occur due to the higher water potential of the root than of the soil during drought (Nobel and Cui 1992).

In response to soil rewetting after drought, L_p 's for roots of both terrestrial and epiphytic cacti increase to equal or exceed their pre-drought values, with the exception of older roots of *Ferocactus acanthodes* and *O. ficus-indica* (Table 3.2). The layers of periderm in these older roots increases in number and in extent of suberization during drought, with a concomitant reduction in their permeability to water (North and Nobel 1992, 1996). Younger root regions lack a periderm, and their permeability is restored by simple rehydration of tissues that, in addition, are protected during drought by the rhizosheaths (North and Nobel 1997). For the younger roots, and for root regions near the junctions between main and lateral roots, numerous lateral root primordia arise during drought and elongate upon rewetting. As these new lateral roots emerge from the parent root, they break through the suberized layers of periderm, thereby increasing root permeability and L_p (North et al. 1993; Dubrovsky et al. 1998b). Once new lateral roots have emerged, the root system for these cacti is capable of rapid water uptake, allowing depleted storage reservoirs to be refilled.

Mineral Uptake

The ability of roots to take up minerals is directly related to their growth. In addition, root growth depends on the nutrient status of the soil. When a mineral resource is in limited supply in the soil, root systems increase in length to explore more area around the plant. As a consequence, relative root biomass (or the root/shoot ratio) tends to be higher in poor soil than in richer soils (Marschner 1986).

Such is the case for cactus plants. In the Sonoran Desert, trees with relatively large canopies (e.g., *Prosopis articulata*) that serve as nurse plants for many cactus species (Nobel 1988) tend to be “islands” rich in nutrients. The concentration of nitrogen (N), phosphorous (P), and carbon (C) in such island soil is 1.4, 1.6, and 1.8 times greater, respectively, than in a treeless region; correspondingly, the root/shoot ratios for plants of *Pachycereus pringlei* grown in island soil are smaller than for plants grown in soil from a treeless region (Carrillo-Garcia et al. 2000).

Mineral uptake by roots can be assessed indirectly from an analysis of the contents of different elements in cactus stem tissues. By abundance, the elements in the stem tissue rank as follows: Ca > K > N > Mg > Na > P > Fe ≥ B > Mn ≥ Zn > Cu > Mo, with the chlorenchyma having higher levels of Ca, Mg, B, and Zn than are found in most agronomic plants (Berry and Nobel 1985). Element concentrations in the cactus stem tissues can be more than 10³ times greater than in the root substrate, implicating active uptake and transport of ions by the roots (Berry and Nobel 1985; Kolberg and Lajtha 1997). Like cactus stems, roots also accumulate certain elements in their tissues. For example, when boron (B) is applied at a concentration of 15 ppm to soil in which *O. ficus-indica* and *F. acanthodes* are grown, the content of the element in the roots of both species is about 145 ppm. Interestingly, the level of B increases to 2,000 ppm in stem tissues of *O. ficus-indica* and to only 220 ppm in *F. acanthodes* (Berry and Nobel 1985), indicating species differences in element translocation from the root to the shoot. Different species can also vary in their sensitivity to heavy metals. For example, when high concentrations of copper (Cu) and zinc (Zn) are added together to a substrate, the root dry weight of *O. ficus-indica* is reduced more than that of *F. acanthodes* (Berry and Nobel 1985).

Mycorrhizal and Bacterial Associations

Mineral acquisition is frequently related to the activity of fungi and bacteria in the rhizosphere. Mycorrhizal associations, important for mineral uptake in many plant species, occur in the root systems of a number of cacti. The characteristic structures indicating infection by vesicular-arbuscular mycorrhizae can be detected in a cleared, longitudinally dissected root of *P. pringlei*. During the first stages of root colonization, the fungus forms an adherent apressorium on the root surface. Subsequently, fungal hyphae penetrate the root, apparently multiplying the internal surface area available for the absorption of limiting mineral nutrients such as P and iron (Fe). In the Sonoran Desert, the level of mycorrhizal colonization ranges from

less than 10% of the roots examined in *Mammillaria dioica*, *P. pringlei*, *Stenocereus gummosus*, and *S. thurberi*, to 30 to 70% in *F. peninsulae*, to more than 70% in *Cochemia poselgeri*, *Lophocereus schottii*, *Opuntia cholla*, and *O. lindsayi* (Carrillo-Garcia et al. 1999). Extensive colonization by three different fungal species in the genus *Glomus* also occurs for roots of *Echinocactus acanthodes*, *Echinocereus engelmannii*, *O. acanthocarpa*, *O. basilaris*, *O. bigelovii*, and *O. echinocarpa* (Bethlenfalvay et al. 1984). Mycorrhizal associations are found in tropical forest cacti as well, including *Nopalea karwinskiana*, *O. excelsa*, and *O. puberula* (Allen et al. 1998). For these forest species, mycorrhizal infection increases in proportion to fine root production, which, in turn, is determined by the rainfall pattern (Allen et al. 1998).

Free-living nitrogen-fixing bacteria from the genus *Azospirillum*, present in the rhizosphere of many plant species (Kapulnik 1996), have been isolated from cactus roots as well. For example, *A. lipoferum* occurs in the rhizosphere of species of *Opuntia* growing in India (Rao and Venkateswarlu 1982) and Mexico (Mascarua-Esprarza et al. 1988). Another species, *A. brasilense*, which occurs in the rhizosphere of *O. ficus-indica*, *S. pruinosus*, and *S. stellatus*, shows nitrogenase activity (ability to fix atmospheric nitrogen) and also exudes the plant hormone auxin, which may induce root branching (Mascarua-Esprarza et al. 1988). When young seedlings of *P. pringlei* are inoculated with *A. brasilense*, the bacteria survives in the plant rhizosphere for up to 300 days (Puente and Bashan 1993). In another experiment, inoculation with *A. brasilense* increases root length but not shoot size, and nitrogenase activity is not detected (Carrillo-Garcia et al. 2000). However, bacteria showing acetylene reduction activity (indicative of nitrogenase activity) are eleven times more abundant in the rhizosphere of ten species of cacti in Mexico than in adjacent bare soil (Loera et al. 1996). A likely role for rhizosheaths in providing conditions favorable to the growth of beneficial bacteria has yet to be explored for cacti.

Carbon Relations

In comparison with most other plants, cacti invest relatively little carbon into the construction and maintenance of roots. This is partly due to the extremely small root/shoot ratio of most succulents (Nobel 1988; Rundel and Nobel 1991), particularly when expressed on a fresh weight basis. It is also due to the relatively low rates of root respiration. Specifically, root respiration, as measured by total CO₂ efflux, is 0.7 and 0.3 mol CO₂ kg⁻¹ day⁻¹ for young and older roots, respectively, of *Ferocactus acanthodes*, and

1.1 and 0.5 mol CO₂ kg⁻¹ day⁻¹ for young and older roots of *Opuntia ficus-indica* (Palta and Nobel 1989). Comparable rates for the roots of twelve nondesert angiosperms average 4.8 mol CO₂ kg⁻¹ day⁻¹ (Lambers 1979). Under drying conditions, root respiration for *F. acanthodes* and *O. ficus-indica* declines even further, averaging 14% of the rate under wet conditions 8 days after water is withheld (Palta and Nobel 1989). The rate of growth respiration, measured as CO₂ given off by newly initiated roots, is also low for cacti in comparison to other plants, averaging about 9 mol CO₂ kg⁻¹ day⁻¹ for *F. acanthodes* and *O. ficus-indica* (Nobel et al. 1992a), in contrast to 24 mol CO₂ kg⁻¹ day⁻¹ for nondesert angiosperms (Lambers 1979). Carbon costs are also involved with maintaining mycorrhizal associations and with the creation of rhizosheaths, although young sheathed roots of *O. ficus-indica* exude only about 1% of newly fixed carbon to the soil (Huang et al. 1993).

Conclusions and Future Prospects

Roots and root systems of cacti have evolved structural and physiological features that permit them to withstand environmental stresses, such as high temperatures, prolonged drought, nutrient-poor soils, and strong winds. Developmental adaptations, such as the early formation of root hairs, lateral roots, and periderm, are most significant during the critical period of seedling establishment. The development of rhizosheaths is important for taking up water from moist soil and reducing water loss to dry soil, and the formation of lateral root primordia during drought hastens plant recovery when soil moisture is restored. The shallow distribution of roots in desert and grassland soils helps cacti to exploit limited rainfall, at times in competition with more deeply rooted neighboring plants. Root associations with fungi and bacteria can help in the efficient capture of limited mineral nutrients.

A number of structures and processes in roots of the Cactaceae deserve further investigation. For example, a century ago it was known that roots of *Opuntia arbuscula* are capable of producing shoots (Preston 1901a), and similar "root buds" have been described for *O. arenaria* (Boke 1979). New shoots also appear to arise from the roots of *Myrtillocactus geometrizans* (J. G. Dubrovsky, unpublished observations). Although root buds are a known phenomenon in angiosperms (Peterson 1975), their occurrence in cacti has not been studied. Despite many accounts of ephemeral roots, little is known about root phenology and root plasticity in cacti. The relationship between root growth and shoot activity and how it is affected by environmental variables, such as precipitation, needs to be investigated, particularly in the field. As an example, an un-

derstanding of how cactus roots respond to rain occurring in the middle of a summer drought is important for predicting how desert communities will respond to possible climate changes. Studies of mycorrhizal and bacterial associations with cactus roots will also help elucidate phenomena that are less well known for deserts and for tropical canopies than for other plant communities. The nurse-plant association between cacti and other perennial species deserves to be investigated from the perspectives of root competition and root communication, both processes that may also be influenced by fungal and bacterial activity.

In addition to the ecological questions remaining to be addressed for cactus roots, certain basic developmental and physiological processes should be explored for species that can withstand prolonged water stress, such as *Opuntia ficus-indica*. For example, the effects of soil drying on proteinaceous water channels (aquaporins) in the cell membranes of cactus roots can add to the current understanding of such channels in more mesophytic species. The external and internal signals that trigger the initiation of lateral root primordia and other developmental processes, such as determinate root growth and early root hair formation, can be studied in cacti from a wide range of habitats. The role of cactus roots as intermediaries between relatively stable, succulent shoots and heterogeneous, often desiccating soil suggests numerous stimulating possibilities for future research.

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Literature Cited

- Allen, E. B., E. Rincón, M. F. Allen, A. Pérez-Jomenez, and P. Huante. 1998. Disturbance and seasonal dynamics of mycorrhizae in a tropical deciduous forest in Mexico. *Biotropica* 30: 261–274.
- Andrade, J. L., and P. S. Nobel. 1997. Microhabitats and water relations of epiphytic cacti and ferns in a lowland neotropical forest. *Biotropica* 29: 261–270.
- Bethlenfalvay, G. J., S. Dakessian, and R. S. Pacovsky. 1984. Mycorrhizae in a southern California desert: Ecological implications. *Canadian Journal of Botany* 62: 519–524.
- Berry, W. L., and P. S. Nobel. 1985. Influence of soil and mineral stresses on cacti. *Journal of Plant Nutrition* 8: 679–696.
- Boke, N. H. 1979. Root glochids and root spurs of

- Opuntia arenaria* (Cactaceae). *American Journal of Botany* 69: 1085–1092.
- Bravo-Hollis, H., and H. Sánchez-Mejorada. 1978. *Las Cactáceas de México*. Universidad Nacional Autónoma de México, Mexico City.
- Britton, N. L., and J. N. Rose. 1963. *The Cactaceae*. Dover, New York.
- Cannon, W. A. 1911. *The Root Habits of Desert Plants*. Publication 131, Carnegie Institution of Washington, Washington, D.C.
- Cannon, W. A. 1916. Distribution of the cacti with especial reference to the role played by the root response to soil temperature and soil moisture. *American Naturalist* 50: 435–442.
- Cannon, W. A. 1925. *Physiological Features of Roots, with Especial Reference to the Relation of Roots to Aeration of the Soil*. Publication 368, Carnegie Institution of Washington, Washington, D.C.
- Carrillo-García, A., J.-L. León de la Luz, Y. Bashan, and G. J. Bethlenfalvay. 1999. Nurse plants, mycorrhizae, and plant establishment in a disturbed area of the Sonoran Desert. *Restoration Ecology* 7: 321–335.
- Carrillo-García, A., Y. Bashan, E. Díaz-Rivera, and G. J. Bethlenfalvay. 2000. Effects of resource-island soils, competition, and inoculation with *Azospirillum* on survival and growth of *Pachycereus pringlei*, the giant cactus of the Sonoran Desert. *Restoration Ecology* 8: 65–73.
- Carvalho, M.-A. M., W. R. Monteiro, and S. M. C. Dietrich. 1989. Histological aspects of root formation in petioles of detached leaves of *Pereskia grandifolia* (Cactaceae): Natural conditions and effects of GA₃ and dark. *Annals of Botany* 63: 505–514.
- Dubrovsky, J. G. 1996. Seed hydration memory in Sonoran Desert cacti and its ecological implication. *American Journal of Botany* 83: 624–632.
- Dubrovsky, J. G. 1997a. Determinate primary root growth in *Stenocereus gummosus* (Cactaceae), its organization and role in lateral root development. In *Biology of Root Formation and Development* (A. Altman and Y. Waisel, eds.). Plenum, New York. Pp. 13–20.
- Dubrovsky, J. G. 1997b. Determinate primary-root growth in seedlings of Sonoran Desert Cactaceae; its organization, cellular basis, and ecological significance. *Planta* 203: 85–92.
- Dubrovsky, J. G. 1998. Determinate root growth as an adaptation to drought in Sonoran Desert Cactaceae. In *Radical Biology: Advances and Perspectives on the Function of Plant Roots* (H. E. Flores, J. P. Lynch, and D. Eissenstat, eds.). American Society of Plant Physiologists, Rockville, Maryland. Pp. 471–474.
- Dubrovsky, J. G. 1999. Desarrollo de sistema radicular durante la ontogénesis de plantas del género *Stenocereus* (Cactaceae). In *El Pitayo en Jalisco y Especies Afines en México* (E. Pimienta-Barrios, ed.). Universidad de Guadalajara, Fundación Produce Jalisco, Guadalajara, Mexico. Pp. 133–146.
- Dubrovsky, J. G., L. Contreras-Burciaga, and V. B. Ivanov. 1998a. Cell cycle duration in the root meristem of Sonoran Desert Cactaceae as estimated by cell-flow and rate-of-cell production methods. *Annals of Botany* 81: 619–624.
- Dubrovsky, J. G., G. B. North, and P. S. Nobel. 1998b. Root growth, developmental changes in the apex, and hydraulic conductivity for *Opuntia ficus-indica* during drought. *New Phytologist* 138: 75–82.
- Dougherty, R. L., W. K. Lauenroth, and J. S. Singh. 1996. Response of a grassland cactus to frequency and size of rainfall events in a North American shortgrass steppe. *Journal of Ecology* 84: 177–183.
- Engelman, E. M. 1960. Ovule and seed development in certain cacti. *American Journal of Botany* 47: 460–467.
- Esau, K. 1977. *Anatomy of Seed Plants*. Wiley, New York.
- Fabbri, A., A. Cicala, and A. Tamburino. 1996. Anatomy of adventitious root formation in *Opuntia ficus-indica* cladodes. *Journal of Horticultural Science* 71: 235–242.
- Felger, R. S., and M. B. Moser. 1985. *People of the Desert and Sea. Ethnobotany of the Seri Indians*. University of Arizona Press, Tucson.
- Freeman, T. P. 1969. The developmental anatomy of *Opuntia basilaris*. I. Embryo, root, and transition zone. *American Journal of Botany* 56: 1067–1074.
- Gibson, A. C. 1973. Comparative anatomy of secondary xylem in Cactoideae (Cactaceae). *Biotropica* 5: 29–65.
- Gibson, A. C. 1978. Structure of *Pterocactus tuberosus*, a cactus geophyte. *Cactus and Succulent Journal (U.S.)* 50: 41–43.
- Gibson, A. C., and P. S. Nobel. 1986. *The Cactus Primer*. Harvard University Press, Cambridge, Massachusetts.
- Glass, C. E. 1998. *Guide to the Identification of Threatened Cacti of Mexico*. Fidecomiso Fondo para la Biodiversidad, Mexico City.
- Hamilton, M. W. 1970. The comparative morphology of three *Cylindropuntias*. *American Journal of Botany* 57: 1255–1263.

- Higgins, V. 1948. Root system of desert plants. *Cactus and Succulent Journal (U.S.)* 20: 71–73.
- Huang, B., G. B. North, and P. S. Nobel. 1993. Soil sheaths, photosynthate distribution to roots, and rhizosphere water relations for *Opuntia ficus-indica*. *International Journal of Plant Sciences* 154: 425–431.
- Ivanov, V. B., and J. G. Dubrovsky. 1997. Estimation of the cell-cycle duration in the root meristem: A model of linkage between cell-cycle duration, rate of cell production, and rate of root growth. *International Journal of Plant Sciences* 158: 757–763.
- Jordan, P. W., and P. S. Nobel. 1984. Thermal and water relations of roots of desert succulents. *Annals of Botany* 54: 705–717.
- Kapulnik, Y. 1996. Plant growth promotion by rhizosphere bacteria. In *Plant Roots: The Hidden Half*, 2nd ed. (Y. Waisel, A. Eshel, and U. Kafkafi, eds.). Marcel Dekker, New York. Pp. 769–781.
- Kausch, W. 1965. Beziehungen zwischen Wurzelwachstum, Transpiration und CO₂-Gaswechsel bei einigen Kakteen. *Planta* 66: 229–238.
- Kolberg, K., and K. Lajtha. 1997. Population dynamics and trace metal biogeochemistry of the saguaro cactus (*Carnegiea gigantea*) in the Sonoran Desert. *Ecoscience* 4: 223–231.
- Lambers, H. 1979. Efficiency of root respiration in relation to growth rate, morphology and soil composition. *Physiologia Plantarum* 56: 18–22.
- Le Houérou, H. N. 1996. The role of cacti (*Opuntia* spp.) in erosion control, land reclamation, rehabilitation and agricultural development in the Mediterranean Basin. *Journal of Arid Environments* 33: 135–159.
- Loera, T. M. L., J. M. Sánchez-Yañez, and J. J. Peña-Cabriaes. 1996. Acetylene reduction activity on the root of cactaceous plants. *Revista Latinoamericana de Microbiología* 38: 7–15.
- Loza-Cornejo, S., and T. Terrazas. 1996. Anatomía del tallo y de la raíz de dos especies de *Wilcoxia* Britton & Rose (Cactaceae) del Noroeste de México. *Boletín de la Sociedad Botánica de México* 59: 13–23.
- Lux, A., Mikuš, M., Hanáčková, Z., and J. Křištín. 1995. Radicle of *Echinocactus platyacanthus* (Cactaceae). *Plant and Soil* 167: 17–21.
- Marschner, H. 1986. *Mineral Nutrition of Higher Plants*. Academic Press, London.
- Mascarua-Esparza, M. A., R. Villa-Gonzalez, and J. Caballero-Mellado. 1988. Acetylene reduction and indoleacetic acid production by *Azospirillum* isolates from Cactaceous plants. *Plant and Soil* 106: 91–95.
- Nobel, P. S. 1988. *Environmental Biology of Agaves and Cacti*. Cambridge University Press, New York.
- Nobel, P. S. 1994. *Remarkable Agaves and Cacti*. Oxford University Press, New York.
- Nobel, P. S. 1996. Ecophysiology of roots of desert plants, with special emphases on agaves and cacti. In *Plant Roots: The Hidden Half*, 2nd ed. (Y. Waisel, A. Eshel, and U. Kafkafi, eds.). Marcel Dekker, New York. Pp. 823–844.
- Nobel, P. S. 1999. *Physicochemical and Environmental Plant Physiology*, 2nd ed. Academic Press, San Diego, California.
- Nobel, P. S., D. M. Alm, and J. Cavelier. 1992a. Growth respiration, maintenance respiration and structural-carbon costs for roots of three desert succulents. *Functional Ecology* 6: 79–85.
- Nobel, P. S., and M. Cui, 1992. Shrinkage of attached roots of *Opuntia ficus-indica* in response to lowered water potentials—predicted consequences for water uptake or loss to soil. *Annals of Botany* 70: 485–491.
- Nobel, P. S., P. M. Miller, and E. A. Graham. 1992b. Influence of rocks on soil temperature, soil water potential, and rooting patterns for desert succulents. *Oecologia* 92: 90–96.
- Nobel, P. S., and J. Sanderson. 1984. Rectifier-like activities of roots of two desert succulents. *Journal of Experimental Botany* 35: 727–737.
- North, G. B., F. W. Ewers, and P. S. Nobel. 1992. Main root–lateral root junctions of two desert succulents: Changes in axial and radial components of hydraulic conductivity during drying. *American Journal of Botany* 79: 1039–1050.
- North, G. B., and P. S. Nobel. 1992. Drought-induced changes in hydraulic conductivity and structure in roots of *Ferocactus acanthodes* and *Opuntia ficus-indica*. *New Phytologist* 120: 9–19.
- North, G. B., and P. S. Nobel. 1994. Changes in root hydraulic conductivity for two tropical epiphytic cacti as soil moisture varies. *American Journal of Botany* 81: 46–53.
- North, G. B., and P. S. Nobel. 1996. Radial hydraulic conductivity of individual root tissues of *Opuntia ficus-indica* (L.) Miller as soil moisture varies. *Annals of Botany* 77: 133–142.
- North, G. B., and P. S. Nobel. 1997. Drought-induced

- changes in soil contact and hydraulic conductivity for roots of *Opuntia ficus-indica* with and without rhizosheaths. *Plant and Soil* 191: 249–258.
- North, G. B., B. Huang, and P. S. Nobel. 1993. Changes in structure and hydraulic conductivity for root junctions of desert succulents as soil water status varies. *Botanica Acta* 106: 126–135.
- Palta, J. A., and P. S. Nobel. 1989. Influences of water status, temperature, and root age on daily patterns of root respiration for two cactus species. *Annals of Botany* 63: 651–662.
- Porembski, S. 1996. Functional morphology of *Aztekium ritteri* (Cactaceae). *Botanica Acta* 109: 167–171.
- Peterson, R. L. 1975. The initiation and development of root buds. In *The Development and Functions of Roots* (J. G. Torrey and D. T. Clarkson, eds.). Academic Press, London. Pp. 125–161.
- Preston, C. E. 1900. Observations on the root system of certain Cactaceae. *Botanical Gazette* 30: 348–351.
- Preston, C. E. 1901a. Non-sexual propagation of *Opuntia*. *Botanical Gazette* 31: 128.
- Preston, C. E. 1901b. Structural studies on southwestern Cactaceae. *Botanical Gazette* 32: 35–55.
- Puente, M.-E., and Y. Bashan. 1993. Effect of inoculation with *Azospirillum brasilense* strains on the germination and seedling growth of the giant columnar cardon cactus (*Pachycereus pringlei*). *Symbiosis* 15: 49–60.
- Rao, A. V., and B. Venkateswarlu. 1982. Associative symbiosis of *Azospirillum lipoferum* with dicotyledonous succulent plants of the Indian Desert. *Canadian Journal of Microbiology* 28: 778–782.
- Rundel, P. W., and P. S. Nobel. 1991. Structure and function in desert root systems. In *Plant Root Growth. An Ecological Perspective* (D. Atkinson, ed.). Blackwell Scientific, London. Pp. 349–378.
- Sands, R., E. L. Fiscus, and C. P. P. Reid. 1982. Hydraulic properties of pine and bean roots with varying degrees of suberization, vascular differentiation and mycorrhizal infection. *Australian Journal of Plant Physiology* 9: 559–569.
- Steudle, E., R. Oren, and E.-D. Schulze. 1987. Water transport in barley roots. Measurement of hydraulic conductivity, solute permeability, and of reflection coefficients of excised roots using the root pressure probe. *Plant Physiology* 84: 1220–1232.
- Villalobos, A. V. M. 1995. Tissue culture application for *Opuntia* sp. pl. micropropagation. In *Agro-Ecology, Cultivation and Uses of Cactus Pear* (G. Barbera, P. Inglese, and E. Pimienta-Barrios, eds.). FAO Plant Production and Protection Paper 132. FAO, Rome. Pp. 71–77.