Mojave Desert Root Systems

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The roots of desert plants in North America, including in the Mojave Desert, have been studied since the late 1800s (Cannon 1911). The initial focus of these studies was to establish a general understanding of the differences between root systems in arid settings and those in wetter environments (Rundel and Nobel 1991). Studies focused on agricultural or horticultural applications (Dayton 1931), and little attention was paid to the form and function of individual root systems. A new wave of Mojave Desert root studies began in the late 1960s, motivated by a need to understand the fate of radioactive isotopes released during nuclear weapons testing at the Nevada Test Site (NTS) (Wallace and Romney 1972; Wallace et al. 1974; Wallace et al. 1980). Though these studies ultimately failed to answer fundamental questions about the uptake and transport of radionuclides, they provided detailed descriptions and quantifications of individual root systems for common plant species.

When, in the 1980s, Yucca Mountain on NTS (fig. 18.4) was suggested as a repository for high-level nuclear waste, a new cycle of root research began, this time with a focus on the role of root systems in the hydrologic cycle of desert soils (e.g., Hessing et al. 1996). Of particular interest was (and still is) whether or how much water can percolate past the root zone and potentially corrode buried storage containers filled with radioactive waste products, which could contaminate groundwater systems. Thus, evaluating the interaction between desert plants and soils became a critical factor in assessing the safety of long-term storage of buried wastes in arid lands. Recent advances in hydrological research suggest that the sparse and inconspicuous vegetation of the Mojave, North America's driest desert,

is responsible for regulating hydrologic fluxes on the scale of thousands of years (Walvoord et al. 2002; Scanlon et al. 2003).

Mojave Desert plants have also been ideal for testing some of the most innovative hypotheses in contemporary plant ecology regarding modes of communication between neighboring plants (Mahall and Callaway 1991). Results of recent root growth studies challenge our views of plants as largely passive site inhabitants. It has long been known that roots do not explore the soil randomly but have enhanced root growth in resource-rich soil microsites (Caldwell 1994). Roots of the same species appear to generate cooperative root system geometries that are more effective in nutrient and water extraction, while those of competing individuals appear to avoid one another. Some species are known to release chemical signals to which other roots respond by reducing root elongation rates, apparently to avoid overlap (Mahall and Callaway 1992). Nobody knows how pervasive such root signals are, but the implications of this phenomenon are potentially significant for entire plant populations and overall community structure. For example, Callaway and Aschehoug (2000) suggested that the success of some exotic plant invaders may, at least in part, be due to their chemical root signals, which strongly suppress the growth of neighbors in the invaded environment, but which elicit no response from the long-term neighbors in the invader's original environment.

There is no doubt that our understanding of root system organization is still in a formative state. A number of recent reviews have addressed the state of our knowledge on root ecology, notably a review by Schenk (2005) on the predictability of global patterns in root distribution, and one by Eissenstat (1997) on trade-offs in root form and function. Various commentaries and reviews point to deficiencies in our knowledge, especially regarding the measurement and function of fine roots (Pregitzer 2002; Waisel and Eshel 2002; Zobel 2003; Pierret et al. 2005). We will build upon these reviews to construct a coherent portrait of the root systems in the Mojave Desert's fluvial basins and to discuss management implications and questions for future research.

FORM VERSUS FUNCTION IN ROOT RESEARCH
Methods of Measuring Root Structure

A root system is a more heterogeneous collection of root types than meets the eye (Waisel and Eshel 2002). Even though individual roots may appear similar (e.g., in diameter), they can serve quite different functions. Structural roots (analogous to stems in a canopy) serve chiefly in providing structural support and in the transport of water and nutrients, while fine roots (analogous to leaves) serve primarily in resource uptake. There is possibly even greater specialization in roots adapted for nutrient and water uptake in an environment where these resources have unequal distribution. There are no sharp differences between transport and uptake roots; instead, there are varying degrees of efficacy for any

single function. Structural and fine roots are genetically different, with structural roots extending rapidly and indeterminately, while fine roots grow for a limited time and usually remain short, though they can continue branching and are shed when the surrounding soil becomes resource depleted (Eissenstat and Yanai 1997; Pregitzer 2002).

Structural roots are easily excavated, and in some cases three-dimensional images of entire structural root systems have been graphically reconstructed from observations recorded during excavation (e.g., Gibbens and Lenz 2001). However, as much as 90% of fine roots (usually defined as < 0.2 mm in diameter) may be lost in the process of physically separating roots from soil (Pierret et al. 2005). More accurate methods for root quantification do exist [e.g., X-rays, computed axial tomography (CAT) scanning, nuclear magnetic resonance imaging (NMRI)] but are rarely used due to the high cost. All common methods for root excavation and quantification are destructive and provide only a snapshot of the root distribution at a single point in time. Thus, destructive methods of root quantification cannot describe the dynamics of root growth and cessation over time, which are essential for understanding long-term root function in an arid environment (Fernandez and Caldwell 1975).

While structural roots are durable over the long course of a plant's lifetime, fine roots appear to be specialized for rapid response to changing resource availability on the scale of days to months. For example, "rain roots" can appear near the soil surface within a day of rainfall events (Lauenroth et al. 1994; Nobel 1994), aiding in the uptake of near-surface soil water that might otherwise be rapidly lost by evaporation (Nobel 2002). If the soil stays wet, fine roots may continue to grow for weeks. Fine root growth may also follow the downward movement of a wetting front in the soil and cede as the front passes (Fernandez and Caldwell 1975). Typically, when the soil dries, rain roots and other fine structures (e.g., root hairs—filamentous outgrowths of the root epidermis that develop in the root elongation zone and greatly increase root surface area) are shed, leaving behind only roots that show a degree of resistance to drying due to the deposition of hydrophobic substances like suberin and lignin in the cell walls of the endodermis. However, even suberized roots may senesce when drought conditions become severe enough.

A dynamic system of fine roots allows plants to continually adjust to shifting soil water and nutrient sources, placing new roots where resources are most freely available. Because of this, species with fairly different coarse root structures can have similar patterns of fine root growth (Fernandez and Caldwell 1975) and resource uptake (Schwinning et al. 2005), particularly as measured in the vertical dimension of the soil (fig. 13.1). For example, Fernandez and Caldwell (1975) showed that the fine root growth of three dominant Great Basin shrubs shifted vertically downward over the course of a growing season, following the extractable
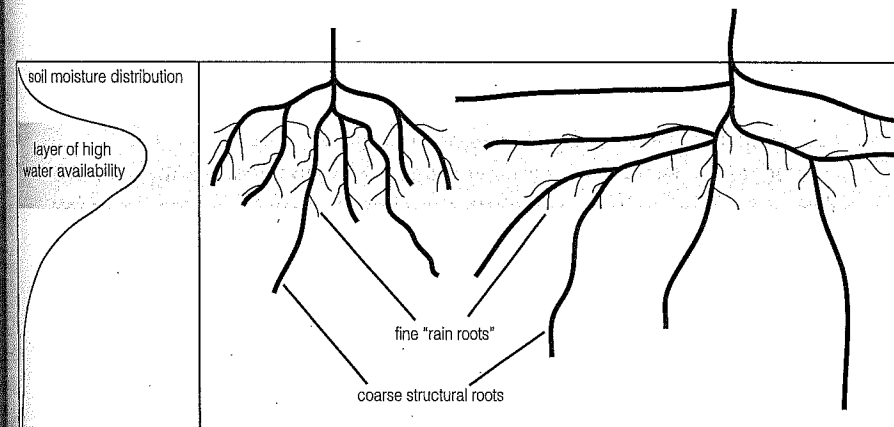

Fig. 13.1. Diagram of perennial plant species with different root structure and depth that can have similar vertical resource-uptake patterns, where both plants have fine root growth (indicated by the small, thin lines) on structural roots within the soil layer that has plant-extractable resources.

soil moisture as it receded from the surface. In this study, transparent root observation tubes called minirhizotrons were used to identify soil regions of enhanced fine root growth in situ. While this method allows nondestructive observation and quantification of root growth over time, one downside is that minirhizotrons provide extremely localized information on root dynamics and only a relative measure of fine root growth patterns (Wilcox et al. 2004).

Methods of Measuring Root Function In Situ

One of the least intrusive methods of measuring root function involves the rates of water transport; heat-pulse flowmeters can be attached to main stems above ground to measure the quantity and direction of water flow in plants (Cohen et al. 1981; Hultine et al. 2003). To quantify nutrient uptake, leaf area growth rates can be combined with measures of tissue concentrations of nitrogen (N) and phosphorus (P) to estimate the rate of nutrient uptake. Additional methods, using stable isotopes, are available for estimating the spatial origin of water and nutrients taken up by plants. White et al. (1985) pioneered a method that uses the natural differences in the stable isotope composition of water at different soil depths to identify the water sources used by plants. This method has since been widely applied in the Americas, though not, to our knowledge, in the Mojave Desert. In a recent refinement of this method, data on the vertical distribution of stable isotope ratios in soil water are combined with data on the distribution of soil-water potential (a measure of soil water's free energy which determines the direction of

water transport and correlates with soil hydraulic conductivity) to estimate complete water extraction profiles for plants (Ogle et al. 2004). In another variant, water or nutrients with known, extreme (i.e., unnatural) stable isotope ratios are added to the soil to trace and quantify plant resource uptake from specific soil locations (Caldwell et al. 1985; Schwinning et al. 2002).

The overall lesson learned from in situ studies of root function is that patterns of resource uptake are extremely adaptable, largely due to the opportunistic growing patterns of the fine root system, though individual species may differ in the degree of fine root plasticity (Cui and Caldwell 1997). Patterns of resource uptake are not identical to the patterns of structural root distribution. However, the structural root distribution does constrain the space from where resource uptake is possible. For example, a more laterally extensive root system will be able to respond to water and nutrient pulses farther away from the main stem of the plant (Caldwell et al. 1996), and a deeper root system will be able to extract water and nutrients from deeper soil regions (Schwinning et al. 2005).

Linking Root Form and Function

The relationships among standing biomass, resource acquisition rates, and growth is central to any investigation of biological organization (Enquist 2002). The relationships between canopy photosynthesis, leaf area and placement, N content, and phenology are well understood (e.g., Aber et al. 1996). However, finding equivalent relationships among, for example, nutrient uptake rates and root area and placement is more difficult, not only because root form and function are more difficult to observe, but also because the soil is a more complex environment than the atmosphere, to which roots respond by undergoing more complex transformations than leaves typically undergo.

Young, actively growing roots have the highest capacity for water and nutrient uptake, aided by root hairs. These initially high water- and nutrient-uptake capacities can decline by an order of magnitude as roots grow older (Nobel et al. 1991), due to the loss of root hairs and the suberization of the outer cell layers of the root. However, not all root hairs are shorter-lived compared with the root. In shrubs of the Great Basin Desert, Fernandez and Caldwell (1975) observed that root hairs suberized along with the root epidermis, and persisted as long as the root itself. Suberization improves the longevity of roots, presumably by protecting the roots from adverse soil factors, but also reduces water uptake capacities. Suberization may not be uniform along a root and can be locally delayed under wet conditions in areas such as soil microsites that harbor water or in areas protected from evaporation, such as under rocks (North and Nobel 1998).

Roots can also adjust their nutrient uptake capacity in response to external ion concentrations (Ivans et al. 2003). In addition, if a plant's current demand for nutrients is low, or if its root system has access to higher nutrient concentrations

elsewhere, uptake rates may remain low even if nutrient supply is enhanced (e.g., Duke and Caldwell 2000; Gebauer and Ehleringer 2000). By adjusting their nutrient uptake capacity in time and space according to nutrient supply and demand, plants presumably optimize resource acquisition.

Nutritive and nonnutritive chemical uptake by plants involves complex interactions between plant roots and soil under various physical and chemical conditions. Nutrients and water are absorbed by the root, which creates a boundary zone with reduced resource concentrations that draws resources through the soil toward the root via mass flow and diffusion (Jungk 2002). Nutrient mobility across this gradient is influenced by nutrient solubility (a function of water volume, oxygen content, and pH), the buffering capacity of soil (i.e., interactions with charged particulate surfaces), interactions between ions in solute, as well as soil texture and compaction. For example, cation uptake generally decreases with increasing pH (particularly above 8.0), while anion uptake increases, and vice versa (Neumann and Römheld 2002). In the pH range of 4.0–8.5 (common for soils of North America), highly soluble nutrients such as nitrate, calcium, magnesium, and sulfate are readily extracted and move with water by mass flow toward the roots (Jungk 2002; Neumann and Römheld 2002). Less soluble ions, of generally intermediate or low mobility in soil, such as iron (Fe^{2+} and Fe^{3+}), potassium (K^+), ammonium (NH_4^+), and inorganic phosphorus (P_i), are transported primarily by diffusion (Glass 2002; Jungk 2002; Neumann and Römheld 2002), a slow process compared with mass flow. Plant roots can influence the local nutrient uptake potential by means of exudates that alter the pH in the soil immediately surrounding the root, thus improving the availability of certain ionic species (Jungk 2002). Mass flow and diffusion of dissolved nutrients are also influenced by soil capillary potential and the tortuosity of the pore spaces, which are, in turn, affected by soil texture and the degree of compaction (Jungk 2002).

Cost-Benefit Considerations for Root Design

While the theory of water and nutrient transport is well developed, and mechanistically elaborate models of root function do exist (e.g., Sperry et al. 1998), these models are too cumbersome to be employed in the prediction of community and ecosystem processes. Ecosystem models often sidestep the mechanistic characterization of root function, relying instead on the assumption of a simple relationship between soil resource uptake, root/shoot ratio, and the vertical distribution of root biomass (reviewed in Weltzin et al. 2003). One methodology that has helped in the development of a general quantitative framework in ecophysiology is cost-benefit analysis. Applied to root function, this approach is promising for root research and the effort to better understand root organization.

The basis of all cost-benefit considerations is the adoption of a common "currency" used to compare the costs and benefits of plant structures. Ideally, this

currency is fitness, but this is typically impractical, if not impossible, to measure. Perhaps carbon (C) is the second best choice as a common currency for plants, since many fitness components directly depend on C availability (e.g., biomass maintenance, growth, storage, and reproduction; Bloom et al. 1985). In this context, the "cost" of a root may be construed as the C requirement for building and maintaining the root, as well as for supporting root functions, such as nutrient transport, root exudation, and symbiotic associations. The "benefit" can be understood as the photosynthetic C "income" made possible by the existence of that root. The basic assumption is that natural selection would promote only those root growth patterns that optimize C capture efficiency. Eissenstat (1997) summarized the known root-related cost-benefit tradeoffs as follows:

1. When soil resources are more limiting, plants allocate a greater proportion of whole-plant C to root growth and maintenance. For example, plants growing in sites with higher water or nutrient limitations commonly have higher root/shoot ratios. This tradeoff applies not only to variation between sites, but also to phenotypic variation among plants within a site—ephemeral and drought-deciduous species should have smaller root/shoot ratios than evergreen species in the same site because the latter remain active during the more resource-limiting parts of the year. This generalization is widely applicable to desert plants (Smith et al. 1997).

2. Longer-lived (e.g., > 5 years) woody plants support a larger and more widespread system of structural roots, while shorter-lived (< 5 years) woody plants have smaller, compact root systems composed of thinner roots (Burgess 1995). The compact "herringbone" structure is better suited for the rapid and complete depletion of resources within the soil volume, while a spreading "dichotomous" structure leads to a more gradual depletion of soil resources via diffusion over longer distances (Fitter 2002).

3. Longer-lived roots have higher construction costs, lower maintenance costs, and reduced water and nutrient uptake efficiencies compared with shorter-lived roots. Many of these differences are due to variations in root thickness and in the degree of suberization and amount of tannin deposition in the cell walls. Thicker and more suberized roots are often more drought resistant, while tannins discourage herbivory. This allows roots to live longer, but also increases construction costs and reduces resource-capture efficiency. However, the lifetime C efficiency of longer-lived roots can still be high, because maintenance costs are low. In shorter-lived roots, construction costs may be relatively lower, but they require a major proportion of the lifetime resources of a shorter-lived root. Therefore, shorter-lived roots should be placed where resource levels are temporarily high, while longer-lived roots should be placed where the long-term prospect for resource uptake is high—for example, in competitor-free space in deeper soils that have more persistent water availability.

4. Roots that have high water-transport capacities relative to construction cost also have lower cavitation resistance (i.e., their ability to function under low suction pressures) and therefore a reduced range of operation with respect to soil-water potentials (Sperry and Hacke 2002). This trade-off should favor the construction of a denser, more costly xylem when most plant gas exchange takes place under relatively dry conditions (e.g., in drought-tolerant evergreen shrubs), and construction of a lighter wood with wide-diameter xylem elements and thinner cell walls when most gas exchange occurs under relatively wet conditions (e.g., in ephemerals or drought-deciduous shrubs). The tradeoff can also apply to roots of the same plant if roots are exposed to different soil moisture conditions. For example, in *Gutierrezia sarothrae* (broom snakeweed) the radial and axial hydraulic conductivities of deeper roots, which are exposed to more moderate soil-water potentials, are higher than those of the more suberized shallow roots, which are regularly exposed to much lower soil-water potentials (Wan et al. 1994).

5. Roots are shed when contributions to the plant's C income no longer justify maintenance costs. Fine roots are shed frequently, and longer-lived structural roots can also be shed during severe drought events when plants are in acute C deficit. This latter circumstance occurs when trade-offs associated with long-term C efficiency of longer-lived roots (which may still be high) are trumped by the immediate necessity for whole-plant survival. Short of shedding entire roots, plants can also shed just the outer layer (cortex) of the root, leaving the center (stele) intact. This reduces maintenance costs without losing all uptake and transport capacity, or the capacity to deploy new laterals when conditions improve (Jupp and Newman 1987).

6. Mycorrhizal associations increase nutrient uptake capacities of roots but also increase root maintenance costs. This symbiosis is more valuable for plants with coarse root systems in nutrient-poor environments. Mycorrhizal associations are usually reduced in fine roots and with high soil nutrient levels (Titus et al. 2002).

As we review the known rooting patterns of Mojave Desert plants, we will return to these cost-benefit principles and evaluate how well they describe Mojave Desert plants.

PATTERNS OF ROOT DISTRIBUTION
General Rooting Characteristics in Desert Biomes

In ecosystem models, the maximal rooting depth of plant communities is one of the more uncertain parameters, but has potentially significant effects on soil development, soil moisture fluxes (including moisture availability to plants), nutrient cycling, and community composition (e.g., Kleidon and Heimann 1999). Several recent studies have therefore focused on understanding prevailing vertical rooting patterns found within major bionomic associations on a global scale

(Canadell et al. 1996; Jackson et al. 1996; Schenk and Jackson 2002). In these global comparisons, desert biomes do not have the deepest root systems (Schenk and Jackson 2002), but they do have deeper root distributions than most other biomes. In addition, perennial plants in deserts have an average of 50% of their root biomass in the top 30 cm, as opposed to perennial plants in temperate grasslands and boreal forests, which have an average of 83% of their root biomass in the top 30 cm, and perennial plants in tundra, which have 93% (Jackson et al. 1996). This pattern might at first appear contrary to the typical view of deserts as places where water and nutrients are concentrated near the soil surface because of low rainfall and high evaporation. However, high soil surface temperatures in deserts tend to be lethal to roots, and generally low soil resource concentrations may drive desert plants to explore a greater portion of the soil volume, including marginal resource reservoirs at greater depth. Therefore, increasing water limitation in the environment tends to increase the average maximum rooting depth of shrubs relative to the size of their canopies (Schenk and Jackson 2002).

Soil resource levels are also quite variable horizontally in water-limited ecosystems, due to variable surface characteristics, biogeochemical conditions, and soil surface exposure (Breshears and Barnes 1999). Schenk and Jackson (2002) noted generally reduced lateral root growth by plants in arid environments compared with those in more mesic environments. However, lateral root spread and root response to horizontal resource heterogeneity (both temporally and spatially) vary dramatically among species. The lateral root spread of some woody perennials in the Mojave Desert is impressive, with lateral root lengths of up to 9 m, and commonly between 1 and 3 m (Hooten and Myles 2006).

Plant Communities in the Mojave Desert and their Overall Rooting Patterns

Compared with other North American deserts, the Mojave Desert has a relatively low diversity of perennial plants and summer annuals, and a fairly high diversity of winter annuals (Beatley 1969; Rundel and Gibson 1996). Among the perennial plants, woody shrubs, cacti, yuccas, and perennial grasses are dominant, while perennial forbs are relatively sparse. Nonsucculent trees are nearly all phreatophytic (with roots that obtain water from a permanent ground supply) and restricted to areas of shallow groundwater along desert riparian areas and near springs. Trees such as *Juniperus* ssp., *Pinus edulis,* and *Pinus monophylla* (juniper and pinyon) may be found at higher elevations (typically above 1,700 m) in the Mojave Desert, yet these species are typically considered landmark species for the Great Basin Desert bionomic province.

In an extensive survey of the northern Mojave Desert flora on the NTS, Ostler et al. (2000) listed 28 species of shrubs and trees useful for describing shrubland alliances and identified only three shrubland alliances in the northern Mojave Desert biome. Alliances were identified based on cluster analyses that required 75% similarity of species composition between landform units that were internally consistent with respect to soils, slope, geology, hydrology, vegetation, and resident animal species, and showed notable differences in plant species composition compared with neighboring units. One plant species may clearly dominate any given site, although one or more additional species may frequently occur. The strongest indicator of the Mojave Desert bionomic province was found to be the creosote bush–white bursage shrubland alliance, so named due to the predominance of the two species.

About one-third of the above-ground standing biomass of Mojave Desert plants is composed of these two species—*Larrea* and *Ambrosia* (Turner and Randall 1989). Of the total area of the Mojave Desert, 70% is inhabited by this alliance (Lathrop and Rowlands 1983), which typically occurs on gentle to moderately sloping bajadas, 800–1600 meters elevation, with soils composed of coarse, sandy loams. Within this alliance, *Larrea* and *Ambrosia* comprise, on average, 12.7% and 43.1%, respectively, of the shrub abundance, with considerable local deviation around the mean. Other perennial shrub species in the alliance with abundances over 5% are *Ephedra nevadensis* (Mormon tea, 7%), *Krameria erecta* (littleleaf ratany, 6.7%), and *Lycium pallidum* (pale desert-thorn, 5.2%).

Other Mojave Desert alliances on the NTS include the *Lycium shockleyi-Lycium pallidum* and *Atriplex confertifolia-Ambrosia* shrublands, each comprising about 1–2% of Mojave Desert plant communities. On average, the *Lycium shockleyi-Lycium pallidum* alliance is composed of 32.0% *Lycium shockleyi* (Shockley's thornbush), 29.2% *L. pallidum,* and 14.7% *Ambrosia,* and occurs exclusively in lowlands on clayey loams and loamy sand. The *Atriplex-Ambrosia* alliance (29.6% *Atriplex,* 20.3% *Ambrosia,* 10.1% *Ephedra*) occurs over the same wide elevation range as the *Larrea-Ambrosia* association, but predominantly on loamy soils (Ostler et al. 2000).

These distribution patterns illustrate the relatively low species diversity of the vast majority of the Mojave Desert and suggest that much of the rooting patterns of Mojave Desert communities can be studied by concentrating on relatively few key species. (For a more thorough review of the shrubland alliances of the NTS, see Ostler et al. 2000 and Hooten and Myles 2006.)

The most extensive observational analysis on root distributions of Mojave Desert shrubs was done in the late 1960s and early 1970s in Rock Valley on the NTS by Wallace et al.(1980), who excavated the top 50 cm of soil under 48 individual shrubs composed of 9 species. In their study, the top 50 cm were chosen because the greatest mass of coarse roots were located at those depths at the study site, which reportedly had an extensive hardpan (caliche) layer close to the soil surface. Other studies also reported the greatest abundance of structural and permanent roots in the top 1 m of soil (Wallace and Romney 1972; Gibbens and Lenz 2001). However, at another site in Rock Valley, without a restrictive caliche layer, Wallace and Romney (1972) found an abundance of roots well below 1 m.
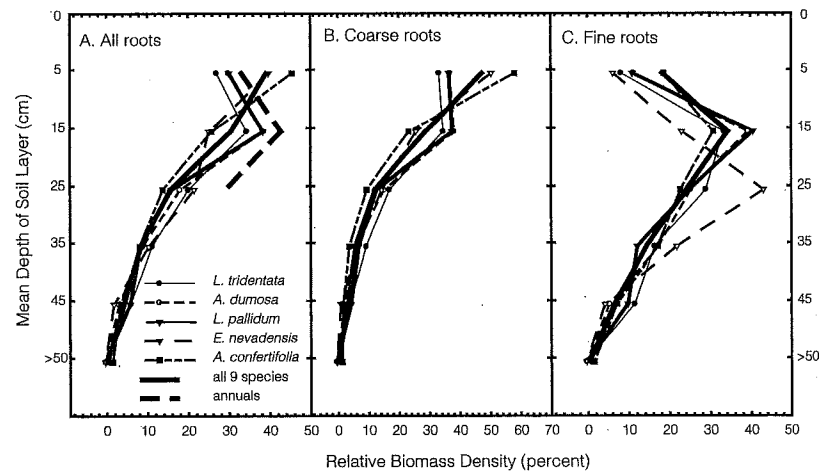
Fig. 13.2. Graphs comparing relative vertical root allocation of five different species [*Larrea tridentata* (creosote bush), *Ambrosia dumosa* (white bursage), *Lycium pallidum* (wolfberry), *Ephedra nevadensis* (Mormon tea), and *Atriplex confertifolia* (shadscale), all species combined, and a sampling of annuals. Note that *Ephedra* is the only species with maximum fine root density between 20 and 30 cm (data from Wallace et al. 1980).

Fig. 13.3. Graph of vertical and horizontal variation in root biomass (including all diameter classes) depicted for three sites dominated by different species: *Larrea tridentata-Ambrosia dumosa, Ambrosia dumosa,* and *Lycium pallidum.* Only the site dominated by *Lycium* had greater biomass under the plant canopy (data from Wallace and Romney 1972).

The overall root distribution of the creosote bush–white bursage alliance is dominated by the coarse root fraction (i.e., roots > 2 mm diameter), which comprises roughly 64%–78% of total root biomass (Wallace et al. 1980) (fig. 13.2). Between 25% and 50% of all coarse root biomass is in the top 10–20 cm of the soil and coarse root density drops off approximately exponentially with an average decline of 5% per centimeter. Fine root biomass (i.e., roots < 2 mm diameter) peaks in the 10–20 cm soil depth interval for most species and drops off below this in an approximately linear fashion in relation to depth. Wallace et al. (1980) speculated, and Nobel (2002) confirmed, that the upper 10 cm of soil may frequently be too hot and dry to support water or nutrient uptake by fine roots, while the 10–20 cm layer has more moderate temperatures and is still shallow enough to be wetted relatively frequently by larger precipitation events.

Wallace and Romney (1972) found that while the relative vertical allocation of shallow root biomass was quite similar among shrub species, communities differed both in overall root density and in the horizontal placement of roots with respect to canopy and interspaces. In a *Larrea-Ambrosia* community, the top 30 cm of soil had four times more root biomass between than underneath shrub canopies (fig. 13.3). At another site, dominated by *L. pallidum,* root biomass below the shrub canopies was three times greater than in the interspaces, while an *Ambrosia*-dominated site had more evenly distributed, horizontally placed roots
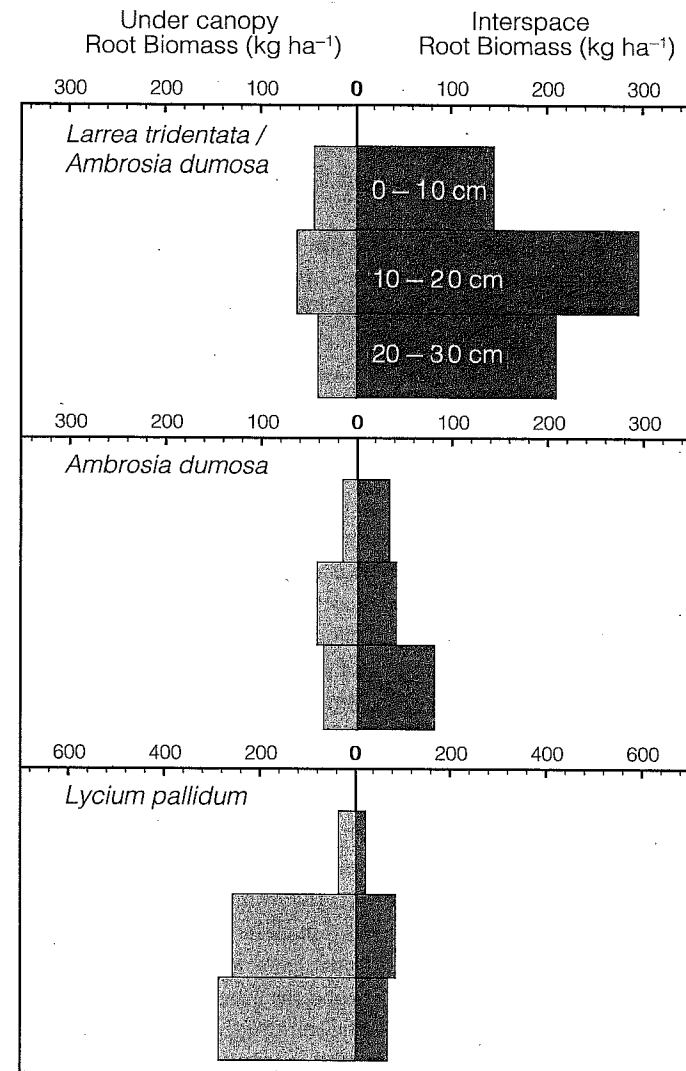
than at either of the two other sites. These differences suggest that shrub species may differ more in their horizontal than in their vertical root distributions, the latter being greatly constrained by steep resource gradients. Thus, to better understand the root structure and function of Mojave Desert plants, we have to consider the full three-dimensional configuration of the root systems.

Rooting Patterns of *Larrea tridentata*

The most common shrub of the Mojave, and arguably the most studied, is *Larrea tridentata*, a longer-lived sclerophyllous evergreen. It is thought that individuals of this species can live for centuries and, in some sites, perhaps more than a thousand years (McAuliffe 1988). The root distribution of this species has been studied in the Mojave (Wallace and Romney 1972; Stevenson et al. *this volume*), the Chihuahuan (Chew and Chew 1965; Brisson and Reynolds 1994; Gibbens and Lenz 2001) and the Sonoran Deserts (Yeaton et al. 1977). All excavations were conducted on basin and bajada soils, which are typically coarse gravelly loams, alluvial in nature, and with variable prominence of caliche layers at various depths. Parent materials are typically limestone sediments.

· Excavations portray the root system of *Larrea* in a generally consistent manner, with an extensive system of lateral roots, typically at 15–40 cm depth, depending on the location of the caliche layer (lateral roots stay above this layer). Stevenson et al. (*this volume*), working in dry sites of the Central Mojave Desert, found that root systems on young Holocene soils were deeper but had relatively less lateral spread than root systems developed in older Pleistocene soils.

Lateral roots grow outward at very low angles and even upward toward the soil surface, typically extending 3 m, and occasionally up to 4.5 m, from the central trunk (Gibbens and Lenz 2001). Several vertical sinker roots originate from laterals and penetrate deeply through breaks in caliche layers and highly compacted argillic horizons (Gibbens and Lenz 2001) (fig. 13.4). This was observed by Stevenson et al. (2006) in the Mojave Desert, though he deemed them rare.

At a relatively flat, sandy loam site in the Jornada Experimental Range, Gibbens and Lenz (2001) found taproots as deep as 5 m, though most roots ended at about 3 m (fig. 13.4). At a site where the slope of the terrain was 2%—slightly steeper than at the Gibbens and Lenz (2001) study site—Gile et al. (1998) found that taproots penetrated to no more than 2 m and thought that this was the result of increased runoff and reduced infiltration. Wallace and Romney (1972) sketched a *Larrea* root system from the NTS with essentially the same characteristics as those described by Gile et al. (1998), with sinker roots that reached into a gravelly layer 1.68 m deep (fig. 13.5), while Hooten and Myles (2006) observed *Larrea* roots below 3 m on the NTS. Thus, it appears that *Larrea* has the potential to grow roots to 5 m or more, but that individual site characteristics determine the actual depth, which is most likely constrained by the depth of water infiltration.
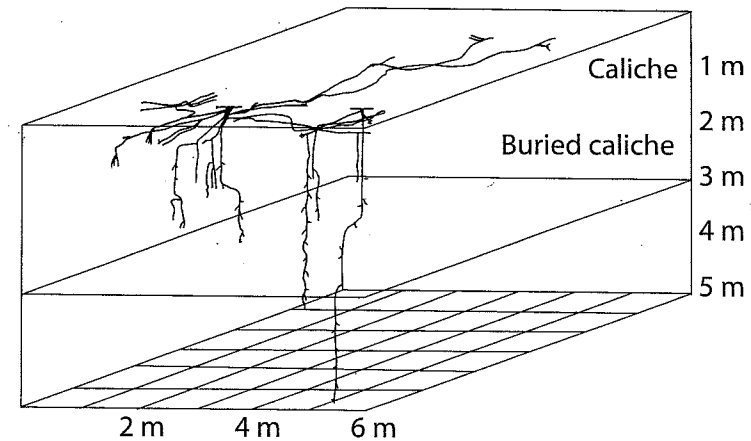
Fig. 13.4. Diagram of three-dimensional root structure of a *Larrea tridentata* plant in the Chihuahuan Desert showing the extensive system of lateral roots, which extend 3–4.5 m from the central trunk. Vertical taproots typically extend about 3 m deep, and sometimes as deep as 5 m (drawing from Gibbens and Lenz 2001; used with permission).

Stands of *Larrea* have a greater density of root biomass between canopies than under canopies (fig. 13.3). A recent study showed that fine root growth, as measured by microrhizotrons, is also higher in the interspaces between canopies (Wilcox et al. 2004). Lateral roots of *Larrea* tend to avoid spatial overlap with other species (Brisson and Reynolds 1994), suggesting that during root system development, roots preferentially grow into root-free spaces (Chew and Chew 1965). The result is that mature stands of *Larrea* leave virtually no horizontal soil space unexplored (Brisson and Reynolds 1994). Consistent with this rooting pattern, *Larrea* stands deplete soil moisture uniformly in horizontal space (Yoder and Nowak 1999).

In summary, *Larrea* has the extensive root system (in both vertical and horizontal dimensions) that one would expect from a longer-lived species. Furthermore, the presumably high construction cost of its long-lived, drought-tolerant lateral roots would call for a placement that maximizes average resource uptake over long time periods. Avoiding overlap with neighboring root systems may be a way to accomplish this. In addition, the release of allelochemicals, which suppress the growth of invading roots (Mahall and Callaway 1992), may additionally ensure that the resource return of structural roots remains high throughout their long lifetimes.

Several studies have found information that supports the idea that *Larrea* stands deplete soil moisture to the limit of their physiological tolerance. At a depth of 1–2 m, soil-water potential is consistently drawn down to an annual minimal level of between -6 and -7 MPa (Scanlon et al. 2003). Comstock and Sperry (2000)
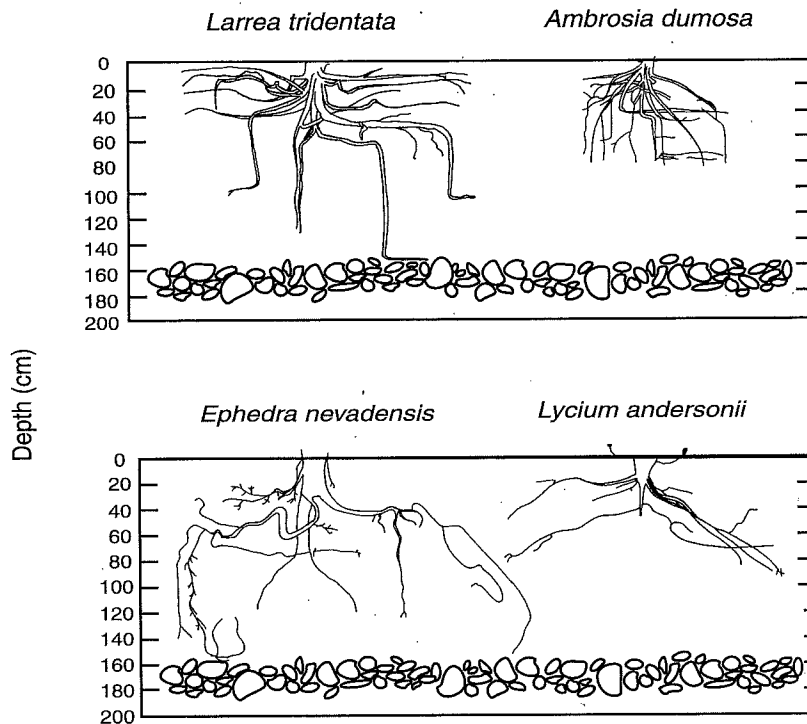
Fig. 13.5. Schematic diagram of the root systems of four common species found in the Mojave Desert scaled to size. *Larrea tridentata*, a longer-lived evergreen, has sinker roots that extend into a gravelly layer about 1.68 m deep. *Ephedra nevadensis*, also a longer-lived evergreen, has roots as deep as *Larrea*, but lacks the wide-reaching system of shallow lateral roots. *Ambrosia dumosa*, a shorter-lived drought-deciduous shrub, has a relatively compact root system. *Lycium andersonii*, another shorter-lived drought-deciduous species, also has relatively shallow, but more widely spread, roots (drawings adapted from Wallace and Romney 1972; used with permission.

found that, at this level, *Larrea* stems are about 80% embolized, or blocked, and are thus near the limit of their capacity for transporting water to support transpiration. Wilcox et al. (2004) found that *Larrea* responds to soil drying by increasing fine root growth, thus compensating for loss of hydraulic conductivity by increasing root surface area.

The existence of deep, extremely drought-tolerant roots may be an essential requirement for evergreen desert shrubs because they are more dependent on a continuous supply of transpiration water than other plant types (Canadell et al. 1996). Even though the soil surrounding *Larrea*'s deepest roots may frequently be near the water-extraction limit, the hydrologic connection to this soil layer may

allow plants to maintain physiologically viable tissue water potentials at a time of drought (see also Hamerlynck et al. 2002 and Nobel 2002).

Larrea is vulnerable to episodic drought mortality on substrates where deep root development is constrained by an impenetrable hardpan layer (McAuliffe 2003), which provides further evidence that *Larrea* depends on deep roots. This is presumably where *Larrea-Ambrosia* communities give way to *Atriplex-Ambrosia* communities. The only *Larrea* plants that may be able to survive drought at such sites are those few individuals whose roots were able to find gaps in the hardpan layer and extract water that may have accumulated below. *Larrea* is also excluded from surfaces with episodically reduced rates of gas exchange between soil and atmosphere (e.g., clay-rich soils) (McAuliffe 2003), from areas with high flood frequency (Wallace and Romney 1972), and from areas with shallow groundwater. These patterns are indicative of *Larrea*'s unusually high root oxygen demand, as determined by Lunt et al. (1973).

Rooting Patterns of *Ephedra nevadensis*

Ephedra nevadensis is a longer-lived, leafless evergreen gymnosperm and, like *Larrea*, may live for centuries (Bowers et al. 1995). Due to differences in the hydraulic architecture of gymnosperm wood (containing only short tracheids) and angiosperm wood (containing long vessels), gymnosperms attain relatively lower levels of hydraulic conductivity for a given level of cavitation resistance compared with angiosperms, or else have to invest much more carbon to achieve the same level of hydraulic conductivity (Hacke et al. 2004). This would suggest that gymnosperms are less well adapted to cope with the very low soil-water potentials near the soil surface. According to Wallace and Romney's (1972) sketch (fig. 13.5), *Ephedra* is as deep-rooted as *Larrea* but does not have a particularly wide-reaching system of shallow lateral roots. It does have a proliferation of roots below 50 cm, consistent with a description by Cannon (1911). Accordingly, fine root growth is more pronounced under the canopy than in the open (Wilcox et al. 2004). In Wallace et al.'s (1980) study, *Ephedra* stood out by maximizing fine root density in the 20–30 cm layer, while all other species investigated had their highest fine root density between 10 and 20 cm (fig. 13.2).

This rooting pattern affirms the association of deep roots with the evergreen life history and the association of spatially extensive root growth with longevity. However, unlike *Larrea*, *Ephedra* appears to avoid rooting in the top 20 cm of the soil, except close to the stem where there may be increased water infiltration from stem flow (fig. 13.5), and where shading from the main body of the plant offers protection to roots. This pattern may reflect the lower cavitation tolerance of gymnosperm xylem, which is incapacitated by the frequently low water potentials of the subsurface soil. As a consequence, *Ephedra* may depend primarily on precipitation events that result in infiltration well below 20 cm.

Rooting Patterns of *Ambrosia dumosa*

Ambrosia dumosa is a shorter-lived, drought-deciduous perennial shrub. Its average life span is not known, but some argue that it may be close to the life span of its congener *Ambrosia deltoidea*—about 50 years (McAuliffe 1988). Rooting depth varies with plant size, and presumably age, but in unexpected ways. Jones (1984) found that small plants (< 40 cm height) had taproots extending to 1 m and frequently penetrating layers of hard-packed gravel, but that large plants (> 80 cm height) lacked these deep taproots and had dominant woody lateral roots no deeper than 50 cm. This suggests that *Ambrosia dumosa* sheds deeper taproots at some stage during development and begins to rely entirely on resource uptake from shallow soil layers. Wallace and Romney (1972) sketched *Ambrosia* with a relatively compact root system and many roots reaching a depth of 86 cm or more (fig. 13.5). Yoder and Nowak (1999) deduced from patterns of soil moisture depletion that stands of *Ambrosia*, like stands of *Larrea*, depleted soil moisture below 1 m, and therefore must support significant live root biomass at that depth.

Wallace and Romney's (1972) sketch of *Ambrosia* also suggests a relatively narrow root system in comparison to *Larrea*, and a notable absence of far-reaching laterals, consistent with the hypothesis that shorter-lived species have less extensive root systems. *Ambrosia* deploys a greater quantity of fine roots beneath its canopy than in the interspaces, and in the beginning of the growing season, *Ambrosia* depletes soil moisture below its canopy more quickly than *Larrea* (Yoder and Nowak 1999). Fine root growth is positively correlated with soil moisture, suggesting that fine roots track the wet portions of the soil horizon and deplete them rapidly. The rapid exploitation of temporarily high resource levels is consistent with the drought-deciduous life history; roots made only to survive the season should absorb resources rapidly and be shed, rather than reinforced, as resource levels drop. Nevertheless, *Ambrosia*'s ability to extract water from relatively dry soil does not lag far behind that of *Larrea* (Pockman and Sperry 2000; Hamerlynck et al. 2002).

Unlike *Larrea*, *Ambrosia* is not excluded from older, clay-rich surfaces, nor from soils with well-developed argillic horizons, which have extremely high soil strength and are virtually impenetrable by water or roots (Pockman and Sperry 2000; Hamerlynck et al. 2002). Being drought-deciduous, *Ambrosia* may be able to survive seasonal droughts without the support of a deep taproot. It would therefore be able to persist in sites with shallow hardpan soil layers or argillic horizons.

Rooting Patterns of *Lycium pallidum*

The lifespan of *L. pallidum* is about twice the presumed lifespan of *Ambrosia* (Bowers et al. 1995). The species is described as having an almost entirely horizontal root system (Markle 1917), which can extend up to 9 m from the main stem,

according to Mathews (1994). Unfortunately, Wallace and Romney (1972) did not provide a drawing of this species, only of its relative *Lycium andersonii* (Anderson desert-thorn), also a drought-deciduous species (fig. 13.5). Wallace et al. (1980) indicated a root distribution that is denser beneath the canopy than out in the interspaces (fig. 13.3), but Wilcox et al. (2004) observed a balanced fine root growth under the canopy and in the interspaces. *Lycium pallidum*, like *Ambrosia*, depletes soil water slightly more rapidly under the canopy than in the open early in the growing season (Yoder and Nowak 1999). On balance, the available evidence (Matthews 1994) suggests that *L. pallidum* develops a fairly spread-out system of relatively shallow roots (to about 50 cm deep) with few or no deep taproots.

Based on this assessment, *L. pallidum* appears to share with *Larrea* the prominence of long lateral roots, but shares with *Ambrosia* the absence of deep roots, as well as drought-deciduousness. This supports a general pattern that associates an extensive lateral root system with plant longevity, and a deep root system with the evergreen life history. The absence of deep roots in the longer-lived, drought-deciduous *L. pallidum*—as well as the shedding of deep roots in the shorter-lived, drought-deciduous *Ambrosia*—strongly suggest that deep root development is not limited by plant life span, and furthermore, that deep root maintenance is quite costly, so that a species that can get by without deep roots (i.e., a drought-deciduous species), and will not invest costly resources in the construction and maintenance of deep roots.

Rooting Patterns of Yuccas and Cacti

Nobel (2002) and Rundel and Nobel (1991) provide extensive reviews of the root structure and function of yuccas and cacti, which we need not repeat here. Briefly, yuccas and cacti possess relatively fine, fibrous, nonsucculent roots that are confined to the upper soil layers (≤ 0.15 m), with no roots in the top 3 cm of soil (Nobel 2002). An illustration of the roots of *Yucca schidigera* (Mojave yucca) by Rundel and Nobel (1991) shows the roots of this relatively large species at a depth of roughly 50 cm. Oddly, little is reported about the root depth and extent for the widely spread *Yucca brevifolia* (Joshua tree), although Tirmenstein (1989) mentions one variety with roots between 0.2 and 1.3 m in length. Given the relatively uniform nature of yucca root systems (as depicted by Rundel and Nobel 1991), one might expect the maximum depth of Joshua tree roots to be somewhere in the realm of 1.5 m, based on Tirmenstein's (1989) singular report. Cacti appear to have less extensive root systems than yuccas. Both groups are known for the extraordinarily fast growth of fine roots following rainfall events. For example, elongation rates of 6 mm in 5 hours after a rainfall event were observed in fine roots of *Agave deserti* (desert agave) (Nobel 2002).

Although yuccas and cacti are in some sense "evergreen," their high storage capacity for water makes them less dependent on a continuous water sup-

Table 13.1 *Spatial extent of the root system of two perennial grasses of the genus* Achnatherum *at the Nevada Test Site*

Species	Maximum depth (m)	Maximum width (m)
Achnatherum hymenoides	0.97 (0.16)	0.96 (0.19)
	$n = 11$	$n = 10$
Achnatherum speciosum	1.06 (0.34)	0.89 (0.11)
	$n = 6$	$n = 6$

Hooten *unpublished.*
Numbers in brackets are standard deviations.

ply compared with woody evergreens and, presumably, less dependent on deep roots. Yucca and cactus roots have rectifier-like qualities. That is, they transition between low hydraulic conductance (and therefore reduced water loss in dry soil) and higher hydraulic conductance (high capacity for water uptake in wet soil) (Nobel and Sanderson 1984). Some yuccas and cacti live for hundreds of years, but there is too little information to evaluate if a correlation between plant longevity and lateral root extension also holds for this group of plants.

Rooting Patterns of Perennial Grasses

Precious little has been published on the root systems of desert perennial grasses. On the NTS, Hooten (*unpublished*) excavated *Achnatherum hymenoides* (Indian ricegrass) and *Achnatherum speciosum* (desert needlegrass). Both of these common grasses have extensive fibrous root systems and may occupy soils that vary from coarse, gravelly loams to fine, silty loams. Average maximum root depth and spread of these two species are in the order of 1 m (table 13.1), and the deepest rooting depth observed was 1.58 m for *A. speciosum*. Grass roots were most abundant below 15 cm, where the root systems spread out with great uniformity, creating an urn-shaped root volume. Above approximately 15 cm, the observed roots were found primarily beneath the grass canopy.

Rooting depths and spreads of other perennial grasses may differ significantly from *Achnatherum* ssp. Nobel (2002) mentions three species of perennial grasses from both the Mojave and Negev Deserts that have mean rooting depths of only 10 cm. Nobel (2002) also mentions two *Agropogon* ssp. with mean rooting depth recorded at 35 cm. Although observations of perennial grasses are wanting, their delicate fibrous root systems are likely well adapted for rapid fine root growth under wet conditions. Their ability to tolerate dry seasons and drought is undoubtedly tied to seasonal dormancy.

Rooting Patterns of Annuals

The Mojave Desert has a rich community of spring annuals (Beatley 1969; Rundel and Gibson 1996). Annual plant abundance is highly variable between years, depending strongly on germination-triggering rainfall events at the right time of

year (Bowers 1996; Rundel and Gibson 1996). About every 5–7 years, concurrent with El Niño events (Bowers 2005), the Mojave Desert "greens up" with a lush carpet of annual plants. In other years, annual plants are spatially constrained to sites with considerable run-on and sites that receive adequate rainfall.

The root excavation study by Wallace et al. (1980) also included a sampling of annuals. Annual plant root growth was found to peak in the same 10–20 cm soil layer as the fine roots of perennial shrubs (fig. 13.2). However, annual plant roots were generally more densely distributed in this soil layer than shrub roots. Moreover, of all annual plant roots found in the 0–10 cm layer, approximately 60%–80% were concentrated in the top 5 cm, indicating a proclivity for rapid moisture removal following relatively small rainfall events. There was also a tendency for even shallower root placement at less productive sites. The root systems of annuals, more so than those of drought-deciduous species like *Ambrosia* and *L. pallidum,* are built to take advantage of short periods of mesic conditions, with no investment in root structures (such as deeper roots), which would prolong the plant's lifetime during drought.

SITE EFFECTS
Soil Texture

Soil texture affects how much water can be stored in soil, with fine-textured clay holding the most water per unit volume, and coarse sand holding the least. However, soils rich in fine particulates also readily hold water and create a greater resistance to root uptake through capillary force, rendering a larger portion of the stored water unavailable to plants. Finer soils tend to decrease the infiltration depth of rainwater and tend to dry out faster than coarser soils (McAuliffe 2003). Finer soils are also prone to developing argillic layers over time. In addition, oxygen diffusion rates can be reduced in finer soils because of the smaller pore size to the detriment of root growth (Armstrong and Drew 2002). In finer soils, root distributions tend to be shifted upward, as might be expected from the reduction in the infiltration depth. However, soil texture apparently does not affect below-ground to above-ground biomass ratios or maximum rooting depths (Schenk and Jackson 2002).

The inverse-texture hypothesis (Sala et al. 1988) states that in arid ecosystems, communities on coarse-textured soil are more productive than those on fine-textured soil (which is the inverse of trends in mesic ecosystems). Recent results from the Great Plains region of the United States showed that productivity was not strongly correlated with soil texture, but that shrubs under more arid conditions contributed more to community productivity on coarse-textured than on fine-textured soils (Dodd et al. 2002). Fine-textured soils also have greater pools of labile C and N, possibly producing larger nutrient pulses upon wetting (Austin et al. 2004). This should favor the faster-growing species

with thinner roots and shallower root systems, such as grasses, annuals, and herbaceous shrubs.

In accordance with the pattern outlined above, Mojave Desert populations of *Larrea* have the greatest proportions of large and, presumably, old clones on coarse-textured dune sites. On these sites plants are usually taller, have deeper roots, and have consistently higher predawn soil-water potentials (Hamerlynck et al. 2002; Stevenson et al. 2006). Populations of *Larrea* on old, fine-textured alluvial deposits are chiefly composed of small and, presumably, young individuals. McAuliffe (1994) observed a similar pattern for the distribution of *Larrea* in the Sonoran Desert. There, *Larrea* was practically excluded from mid- to late-Pleistocene alluvial deposits but formed quasi monocultures on sandy sites with low erosional disturbance. McAuliffe (1994) suggested that where *Larrea* can form large clones and remain undisturbed for millennia, other species may be effectively excluded by competitive suppression during their establishment. On clay-rich surfaces, *Larrea*'s lack of drought-deciduousness may make it more vulnerable during extremely low soil-water potentials, especially where an argillic horizon stunts taproot development through mechanical resistance, low oxygen levels, or both.

In contrast to *Larrea*, *Ambrosia* occupies alluvial surfaces of all ages, and its population density even increases with argillic horizon development (Hamerlynck et al. 2002). *Ambrosia*, which is less dependent on taproots and is dormant during the driest time of year, is also less sensitive to variation in soil texture.

Calcic Horizons

Hardened layers of calcium carbonate and silica, called calcrete, caliche, or petrocalcic layers, are common in the Mojave Desert. They form over thousands of years at a level that demarcates a persistent depth of precipitation infiltration, and therefore the transport limit of dissolved calcium carbonate and silica. Caliche layers are typically found at depths greater than 0.3 m. More than one caliche layer may be found at a given site, formed earlier in geologic time and buried at greater depths. Layers may be 0.5–1 m thick (Rundel and Gibson 1996; M. Hooten *personal observation*) and form effective barriers to root development. However, cracks in the caliche layer are almost always present, giving deep-rooted species the opportunity to grow through the layer and exploit the moisture that gathers underneath (Gibbens and Lenz 2001). Thus, while caliche layers may curb the dominance of species such as *Larrea*, they do not exclude them completely (Shreve and Mallery 1933).

Desert Pavements and Desert Varnish

Desert pavements, and desert varnish on surface clasts, are common on the bajadas and in the valleys of the Mojave. Desert varnish is formed by the amalga-

mation of surface particulates, probably due to near-surface evaporation of water, which leaves behind sodium-rich salts. These salts bind surface particles together (stones, sand, etc.) to a depth of several centimeters and give the desert surface a hard crust and a smooth, varnished appearance over time.

Desert pavement forms by the redistribution of surface clasts from wind and water action, and the addition of fine, wind-blown material over time. This results in heavy clasts that remain in place with depositional fines in between, and creates a surface that has an appearance similar to a cobbled road. Pavements occur on older soils that often also contain an argillic or caliche horizon, which further restricts root development. These conditions make it difficult for seeds to germinate; where plants do manage to establish, water limitations may be severe because of increased runoff from these surfaces. Pavement sites are generally unfavorable for all plant species, but if given the opportunity to establish, *Larrea* can survive on such surfaces, while *Ambrosia* is excluded (Hamerlynck et al. 2002).

Compaction and Preferred Flow Pathways

Compaction in soils dramatically limits root growth (Unger and Kaspar 1994). The more compacted a soil is, the more force is needed to push soil particles apart and make room for roots. Roots exert this force through positive turgor pressure in the expanding cells near the root tip, but there are upper limits to the magnitude of pressure that cells can sustain. Roots growing in compacted soils have thicker cell walls, are shorter, and grow more slowly, all of which translate into increased metabolic cost and reduced resource uptake. We know very little about the abilities of desert plants to grow through compacted soils, but the agricultural literature suggests that there is considerable species variation in this ability, which could also contribute to modifying species distributions in the desert landscape.

All soils have a tendency to become more compacted over time and with depth, either through natural causes (such as gravitational force) or repeated anthropogenic disturbance, and fine-textured soils are much more prone to compaction than coarse-textured soils. Burrowing animals and growing roots reverse this process by reestablishing macropore structure and mixing organic materials into the soil. Animals may actually burrow more vigorously in dense and disturbed soils (Arthur et al. 1987; Reynolds and Laundré 1988; Smallwood et al. 1998), thereby accelerating the recovery of compacted soil. However, caliche and argillic horizons appear to deter burrowing. Plant roots accumulate in burrows and channels of loose soil because the conditions for root growth in these features are improved. Burrows and other macropores constitute preferred flow pathways for water, and their reduced mechanical impedance makes it easier for growing roots to glide through the soil. Macropores also have increased gas exchange rates, thus improving the oxygen supply to growing tissues (Laundré 1993).

In the Mojave Desert, a number of species of ants commonly burrow 1–4 m deep, with some species [e.g., harvester ants (*Messor pergandei*)] exceeding 4 m (M. Hooten *personal observation*). Unlike mammalian burrowers, ants establish nests away from plants, and thus may help to prepare the ground for the establishment of seedlings. Ants do not appear to distinguish between geomorphic surfaces (Hooten *personal observation*), but may be limited by the abundance of foodstuffs in a given location. If plants make extensive use of macropores created by ants nesting on various geomorphic surfaces, then the primary limitation to maximum rooting depth may be the depths of the ant nests themselves. This agrees with Schenk and Jackson's (2002) observation that there was little difference in maximum rooting depths between substrates within specific desert biomes.

Irrigation experiments using dyed water showed that the main roots of shrubs and trees followed such preferred flow pathways, increasing the infiltration depth of water to at least 20 cm deeper than nonvegetated sites. However, these pathways affected less than 1% of the total soil volume (Martinez-Meza and Whitford 1996; Devitt and Smith 2002). Hydrological studies suggest that macropore flow does not significantly alter infiltration depth except in the wettest years (Dong et al. 2003). Nevertheless, the close association between macropores and plant roots could have a significant effect on the growth and survival of deep-rooted plants. Once deep roots are established, they could facilitate the transport of water into soils below the prevailing infiltration depth by means of hydraulic redistribution (Caldwell et al. 1998). The establishment of a deep water source created by hydraulic redistribution of near-surface water could give evergreens a better chance of survival during severe droughts. Additionally, it would remove water from the reach of more shallowly rooted competitors (Ryel et al. 2001).

Neighbors

There are potentially fascinating interactions between the roots of neighboring plants, which must in some way affect the outcome of competition between neighbors. However, we can only speculate on the mechanisms governing these interactions on the basis of the spatial distributions of competing root systems. *Larrea tridentata* root systems, for example, are highly asymmetrical, suggesting compensatory patterns whereby structural root growth is enhanced in competitor-free space and suppressed elsewhere (Winkel et al. 1995; Brisson and Reynolds 1994). Chew and Chew (1965) also noted that the lateral structural roots of *Larrea* were thicker and longer if growing in the direction of competitor-free space.

There is increasing evidence that this rooting pattern emerges not just from resource-mediated feedback control, where preexisting roots deplete resources and thereby suppress the intrusion of new roots, but also by feed-forward control, where the growth of new roots is suppressed by growth inhibitors exuded by resident roots (Mahall and Callaway 1992). For example, *Larrea* roots have been shown to exude allelochemicals that suppress the growth of both *Larrea* and of *Ambrosia* roots. Interspecific root communication of this sort requires the coevolution of the species that send and receive the signal, with both species presumably gaining advantage through signal emission and reception. Thus, *Ambrosia* plants that respond to the presence of *Larrea* roots by ceasing to grow towards them (and presumably enhancing growth in another direction) are likely to be fitter, on average, than *Ambrosia* plants that ignore the signal (this has yet to be tested). Cessation of growth may not be the universal response to receiving a signal of another species' root presence. For example, Gersani et al. (2001) reported the overproduction of roots in response to the presence of competing root systems in the crop plant *Glycine max* (soybean), and Callaway and Aschehoug (2002) demonstrated that the novel North American neighbors of an invasive European forb responded more strongly to allelochemicals released by the forb than long-term Eurasian neighbors. This suggests that species may evolve to "ignore" the allelochemical root signals released by some community members.

Such differences in the reception of root signals between novel and long-term neighbors can, in part, explain the successes of some exotic invaders, which are typically less abundant in the native than in the novel community, even if both communities have similar plant functional composition and suites of herbivores that feed upon them.

SYNTHESIS, MANAGEMENT IMPLICATIONS, AND QUESTIONS FOR FUTURE RESEARCH

Roots are the great unknown in desert ecosystems. In theory, root systems are expected to have major effects on ecosystem carbon fluxes, soil food webs, plant community assemblages, population and community dynamics, and hydrologic fluxes over short and long timescales. Increasingly more is known about the organization of root systems, but major knowledge gaps remain. In this review, we tried to establish the state of knowledge regarding the root system structure and function in plants of the Mojave Desert, and to interpret old and new root data in the light of a developing theory of adaptive root design. We identified four particularly promising areas of research:

1. There appear to be correlations between a species's overall life history strategy and the structure of its root system, consistent with principles of optimal root design. For example, longer-lived, nonsucculent evergreen perennials, like *Larrea* and *Ephedra*, appear to depend more on deep roots than drought-deciduous species, and are less abundant on surfaces where deep root growth is severely restricted. Shorter-lived perennials appear to avoid the costs of building a horizontally and vertically extended root system, and instead build a compact system with a higher root density. Longer-lived perennials, whether evergreen or

drought-deciduous, tend to build extensive lateral root systems. The absence of deep roots in drought-deciduous species, whether long- or short-lived, suggests that the maintenance of deep roots, which operate in soil layers that are quite dry most of the time, appears to have a significant cost that only plants depending on them for survival are likely to pay.

We do not know how general these patterns are or whether they hold for plant groups other than woody shrubs. Root excavation studies, coupled with morphological and physiological measurements of root function, are clearly needed to establish a reliable pattern. In addition, largely theoretical concepts of root costs and benefits need to be verified, and the consequences of different root designs for competitive interactions need to be further explored. Only manipulative studies in conjunction with theory development will be able to address these complex issues.

2. There are potentially fascinating interactions between coarse structural roots and fine uptake roots. While many recent reviews have focused on the fine root system itself, most did not address the interplay between structural root location and fine root growth, which ultimately determines the spatial patterns of resource uptake by individual plants. The extent of the structural root system clearly constrains the influence of fine roots, but what about the converse: can fine root growth also direct the development of the structural root system? Optimal design principles would demand that structural roots are reinforced in soil regions where ephemeral uptake roots grow often and return water and nutrients in larger-than-average quantities, while structural root development should decline where ephemeral uptake roots seldom find resources. Structural root distribution consistent with compensatory root growth patterns have been observed (e.g., Chew and Chew 1965; Brisson and Reynolds 1994), and while root-to-root signaling between growing structural roots has been suggested as one mechanism leading to this pattern, other mechanisms better suited to respond to temporally variable microsite quality should also be explored.

3. We know that preferential flow pathways can affect the development of structural root systems, especially by the growth of sinker roots through cracks in highly compacted horizons or caliche layers. We do not know, however, how pervasive or important the relationship between preferred flow paths and root development is. Does the density of preferential flow pathways set an upper limit to the population density of functional plant types that depend on deep roots (e.g., evergreens)? Do species differ in their intrinsic ability to locate cracks through impenetrable soil horizons? Similarly unresolved is the importance of burrowing animals in establishing preferred flow pathways.

4. Recent ecohydrologic studies (reviewed by Porporato and Rodriguez-Iturbe 2002) have drawn renewed attention to the fact that root distributions are as much a cause of soil moisture patterns as they are an effect, yet we often ignore

this interaction when explaining rooting patterns. Statements such as "roots grow only as deep as precipitation water infiltrates" are circular explanations of the observed rooting patterns, since roots also control infiltration depths. We have little information on the way in which root systems respond to annual to multidecadal climate fluctuations. We know that wet winters and springs stimulate the growth of annual plants. This increase in primary production results in a proportional increase in evapotranspiration, which buffers fluctuations in soil-water content below the rooting depth of the annuals (Scanlon et al. 2005). At these greater depths, shrubs absorb the remaining soil moisture, which returns the soil-water potential to the extraction limit of the most tolerant species in the community (Scanlon et al. 2003; Seyfried et al. 2005).

In the Mojave Desert, the key species in this process is probably *Larrea*, because it is most common, remains active all year, and combines a deep root system with extreme drought tolerance. However, one must ask whether there are limits to the hydrological buffering capacity of Mojave Desert communities. What would happen if some change in land use or climate suddenly allowed water to infiltrate deeper? Do deep-rooted plants respond by growing even deeper roots? Or do rooting depths stay constant while plant and root abundance increase? Alternatively, will the community be invaded by more deeply rooted species? Considering that precipitation fluctuations may become more extreme as a consequence of global warming, we need to understand whether average maximal infiltration depths can change due to precipitation changes, and how communities respond to this change. Therefore, the question remains: how do the root systems of desert plants control hydrologic fluxes at annual to millennial time scales?

These research areas are not only of academic interest, they are also important for the long-term management of Mojave Desert sites, whether for restoration, preservation, or human use. Nowhere is the need for better understanding more critical than in the use of arid lands for waste deposition (Hakonson et al. 1992; Hooten and Myles 2006). Numerous toxic and radiological waste disposal facilities and dumps are found in the arid southwestern United States. Without proper planning and closure, these sites pose a potential threat to humans and the natural environment due to the pedoturbation of soils by plants and animals. In the natural course of nutrient uptake, plants may absorb some contaminants (radionuclides, metals, and organic wastes) from the soil and redistribute them to tissues elsewhere, either below ground or above ground or both (MacKay et al. 1998a, 1998b). This redistribution process can create or exacerbate surface contamination (Garbisu and Alkorta 2001; Wallace and Romney 1972). To better understand the uptake and redistribution of nonnutrients by plants, more attention needs to be paid to studying root distributions, fine root dynamics, and root-soil interactions.

The Mojave Desert has also been suggested as a site for storage of new high-level nuclear waste. The question of safe storage is inseparable from the question of how plants control hydrological fluxes over the course of millennia. Future research will have to ascertain to what extent the interplay of the annual plant community and the few shrub communities govern the unique ecohydrological characteristics of the Mojave Desert, and whether communities created by disturbance and invasion are capable of sustaining these basic characteristics.

While undisturbed sites in the Mojave are extraordinarily stable over the course of millennia, disturbed sites where vegetation has been removed and/or the soil has been compacted return very slowly to their original state (Lovich and Bainbridge 1999). For restoration and reclamation, questions of root development in soils with altered soil structure are paramount, as is the nature of root competition between native and exotic plants.

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