



Root systems of some Chihuahuan Desert plants

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Root systems of 11 shrub or shrub-like species, 11 grass species, 19 perennial forb species and four annual forb species were excavated on the Jornada Experimental Range in the northern Chihuahuan Desert in southern New Mexico, U.S.A. Maximum radial horizontal spread of shrub root systems usually occurred above calcic and petrocalcic horizons at depths above 1 m. With one exception, all shrub species roots were traced through calcic and petrocalcic horizons to depths down to 5 m. Upward growing roots reaching very shallow depths (< 10 cm) were common for most shrub species. Thus, the shrubs can readily access soil water and nutrients from both surface and deep soil horizons. Grass root systems on sandy soils extended radially up to 1.4 m, perhaps an adaptation to capture more soil water from the frequent small rainfall events. Grass roots did not extend through calcic or petrocalcic horizons and none penetrated deeper than 1.6 m. Perennial forb root systems varied in depth of branching but often penetrated into or through calcic and petrocalcic horizons and, like shrubs, have an advantage over grasses during droughts. Root systems of the annual forbs, excavated at the end of a season of above average precipitation, reached depths of 0.5–1.2 m. At each of the 18 excavation sites the roots of all the plant life forms were highly intermingled in the upper soil horizons, indicating that competition for water and soil nutrients is intense. It is believed that the plasticity and architecture of the shrub root systems, enabling them to compete with the grasses for soil water in the upper soil horizons and also access soil water at depths beyond the reach of grass roots, has been a major reason for the increase of shrubs during the historical period in this arid environment.

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Introduction

The development of roots has been described as the most dramatic event in the evolution of the plant kingdom because it made possible the colonization of terrestrial environments (Harper *et al.*, 1991). The primary functions of root systems of terrestrial plants are anchorage and acquisition and conduction of water and nutrients from soil; other functions such as storage, synthesis of growth regulators, propagation and

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dispersal may be viewed as secondary (Fitter, 1991). Because roots are an indispensable pathway for water and nutrients much has been learned about the anatomical and physiological aspects of root systems, particularly those of crop plants (e.g. Drew, 1987). To some degree, universal physiological functions as influenced by anatomical details and resource levels may be extrapolated from crop plants to plants in natural ecosystems (Gregory, 1987). However, it was recognized at an early date that a detailed knowledge of root system architecture was essential for understanding the distribution of natural plant communities and the interactions between species within these communities (Cannon, 1911; Weaver, 1919).

Root systems are especially important in the collection of scarce soil resources, and it is interesting to note that some of the earliest descriptions of root systems in natural plant communities were made in the Sonoran (Cannon, 1911) and Chihuahuan (Markle, 1917) Deserts of North America where water is often limiting to plant growth. Many subsequent descriptions of root systems in arid environments world-wide have been made and a review of the structure and function of desert root systems (Rundel & Nobel, 1991) shows that the strong spatial and temporal heterogeneity of soil water in deserts has resulted in very divergent patterns of rooting architecture. A review of root biomass in biomes of the world (Jackson *et al.*, 1996) showed that tropical evergreen forests with 4.9 kg m^{-2} of root biomass were highest and deserts among the lowest. Cold deserts had three times more root biomass than warm deserts, 1.2 and 0.4 kg m^{-2} , respectively. A review of rooting depth on a world-wide basis (Canadell *et al.*, 1996) showed that maximum rooting depth ranged from 0.3 m for some tundra species to 68 m for a species in the Kalahari Desert in Africa. Rooting patterns are used to determine the storage term in terrestrial water balance models but may not always explain the distribution of plant communities. A study of vegetation along a rainfall gradient from 770 mm forest to 125 mm desert in Patagonia (Schulze *et al.*, 1996) revealed that total biomass decreased with decreasing precipitation but below-ground biomass decreased at a slower rate than above-ground biomass. Contrary to expectation, free water was available at 2–3 m depth throughout the transect. Thus, soil water accessibility by rooting depth and water balance alone could not explain the zonation of plant communities along the rainfall gradient and it was speculated that other factors, such as seedling establishment, were responsible for vegetation zonation.

The seemingly regular (as opposed to random or aggregated) spacing of shrubs in deserts, particularly creosotebush [*Larrea tridentata* (Sess. & Moc. ex DC.) Cov.] in deserts of the south-western United States and northern Mexico, was at first attributed to competition for water (Shreve, 1942) and toxins exuded by roots (Went, 1955). However, in a review of literature, Barbour (1973) showed that regular distributions of shrubs was an untenable dogma because field evidence of allelopathy has rarely been found and rainfall is not the sole determinant of plant pattern. Plant communities in the worlds driest deserts often have only one or two species and provide most of the evidence that competition for water results in regular spacing. A study by Gulmon *et al.* (1979) of pure stands of a stem succulent cactus in the Atacama Desert of northern Chile (mean precipitation 25 mm yr^{-1}) where the ratio of horizontal root area to surface area exceeded 1.0 suggested root systems might have saturated water uptake space. However, estimates of water use indicated that the plants depended on stem-stored water to survive rainless periods (up to 6 years). Thus, plant spatial patterns resulted from survival during rainless periods (larger plants favoured) rather than competition for soil water which the 3-cm-deep root systems would not access.

Recent studies have shown that root systems of some plants in both warm and cold deserts do compete for water, both on an intra-specific basis (e.g. Ehleringer, 1984; Nobel & Franco, 1986) and an inter-specific basis (e.g. Eissenstat & Caldwell, 1988a; Franco & Nobel, 1990). Differences in rooting depth by different life-forms as found by Cody (1986) in the Sonoran Desert can reduce the competition for water and

increase plant diversity. Competition between the same or different species may be influenced by differential root responses to soil temperature and nutrient patches, as well as fine root density (Nobel *et al.*, 1986; Eissenstat & Caldwell, 1988b; Caldwell *et al.*, 1991; Caldwell *et al.*, 1996). Models of root systems are proving to be helpful in explaining interactions of desert plants (Caldwell & Richards, 1986). Such models are often only two-dimensional and as yet do not reflect what Robinson (1991) called '... the three-dimensional dynamic mess that is a real root system'. Robinson also noted that rudimentary architectural limits of root systems are necessary for formulating realistic conceptual models.

This study was undertaken to obtain descriptions of root systems in plant communities of the Chihuahuan Desert, particularly of shrub species which have increased dramatically in the past 100 years (Buffington & Herbel, 1963; York & Dick-Peddie, 1969). It was hypothesized that success of shrubs depended on root systems with an architecture which could exploit soil resources, particularly soil water, more effectively than grasses. The importance of root system biomass, particularly to modelers of global carbon balance (e.g. Jackson *et al.*, 1996) is recognized but is not addressed. Even acquisition of elementary descriptions of root systems in natural plant communities is onerous, and as Cannon (1911) noted, a prosaic task. The following descriptions will be of value in interpreting the ecological role of plant species and serve as guides in designing studies to acquire further knowledge of underground biomass dynamics and competitive interaction of roots.

Study area

All root excavations were made in the northern Chihuahuan Desert on the Jornada Experimental Range (JER), (a 78,266-ha rangeland research facility established in 1912 and now administered by the Agricultural Research Service, USDA) located approximately 40 km NNE (32°37'N; 106°44'W) of Las Cruces, New Mexico, U.S.A. Mean annual precipitation is 247 mm with 53% of the total occurring in July, August, and September. Summer precipitation originates in the Gulf of Mexico and occurs as intense convective storms that are highly localized and of short duration. Winter frontal storms originate over the Pacific Ocean and yield low intensity precipitation which occurs over broad areas, occasionally in the form of snow. Temperature maxima of 40°C or greater occur in June and temperature is lowest in January when the mean maximum is 13.3°C. Temperatures below 0°C occur frequently in December and January. The effective growing season, when both precipitation and temperature are favorable, is normally July through September.

Most of the JER lies on the level-to-gently undulating floor of an intermountain basin with no external drainage. Standing water occasionally collects in scattered ephemeral lake basins (playas). Elevation of the basin floor is about 1260 m (Fig. 1). Soils have formed from fluvial materials deposited by the ancestral Rio Grande and washed in from the surrounding mountains. Deposition of calcareous dust has supplied calcium carbonate which has been leached downward in soil profiles to form calcic horizons, often rock-like or petrocalcic in nature, at depths of a few centimetres to a meter or more (Gile & Grossman, 1979). The calcic horizons can restrict penetration by water or roots.

Vegetation on the JER is usually classified as desert grassland (McClaran, 1995) although the so-called 'grassland' is actually a complex of vegetation types ranging from nearly pure stands of grass, through savanna types with grass interspersed by shrubs, to nearly pure stands of shrubs. Shrub density has not only increased in the past but is continuing to do so (Gibbens *et al.*, 1992). Mesquite (*Prosopis glandulosa* Torr.) is now a major dominant on sandy soils where broom snakeweed [*Gutierrezia sarothrae* (Pursh) Britt. & Rusby], and soaptree yucca (*Yucca elata* Engelm.) are also abundant. Extensive

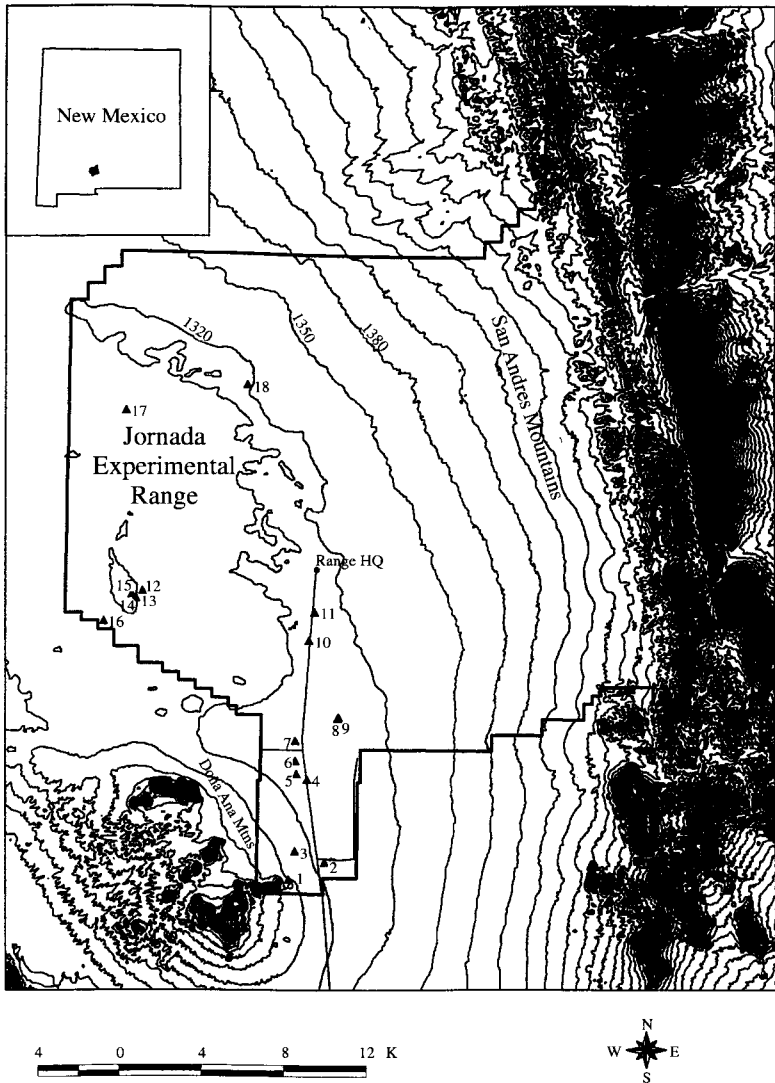


Figure 1. Map showing location of study sites (▲), numbers 1 to 18, on the Jornada Experimental Range in southern New Mexico, U.S.A. Contour intervals are in meters.

areas of coppice dunes (nebhka) have developed on areas dominated by mesquite. Common and once dominant grasses on sandy soils include black grama [*Bouteloua eriopoda* (Torr.) Torr.], mesa dropseed [*Sporobolus flexuosus* (Thurb.) Rydb.] and red threeawn [*Aristida purpurea* var. *longiseta* (Steud) Vasey]. Low-lying areas and ephemeral lake basins with finer textured soils, which receive surface runoff water, are usually dominated by tobosa [*Pleuraphis* (*Hilaria*) *mutica* Buckley] and burrograss [*Scleropogon brevifolius* Phil.]. Tarbush (*Flourensia cernua* DC.) is a frequent invader of these heavy soils. Creosotebush (*L. tridentata*) dominates gravelly soils on bajada slopes near the mountains and, like mesquite and tarbush, has greatly expanded its area of dominance during the historical period (Buffington & Herbel, 1965).

Methods

Roots were excavated at sites representative of various plant communities. Sites were chosen reasonably close to existing roads but at sufficient distance to avoid influence from drainage or accumulation of water along the roadways. Traditional methodology, also referred to as the skeleton method, was used to expose root systems (Bohm, 1979). Trenches (bisects) were located by selecting a target plant (usually a shrub) which had as many other species as possible accessible from the same trench. Trenches, about 1 m wide, were usually dug 1 m away from the base of the target plant and were initially about 5 m long and lengthened as necessary. The first three trenches were dug with a small backhoe which could reach only 3 m depth. A new backhoe reaching 4 m depth was used on subsequent trenches and reduced the amount of time and labor expended in following roots to depths of 5 m. Due to safety concerns involving trench wall stability roots were not followed deeper than 5 m. Roots were exposed at the first bisect (Fig. 1, Site 6) entirely with icepicks. Water was occasionally dumped into the trench to soften the soil and make digging easier. At Sites 8 and 9 (Fig. 1), water was piped in from a stock water tank so a low pressure water spray was available. At all other excavation sites a modified John Bean sprayer equipped with two spray wands which could be adjusted from a fine, gentle spray to a solid, high pressure stream of water was used whenever possible. Various spuding bars, chisels, punches, geologists hammers, air hammers, and occasionally a jack hammer were employed to expose roots in petrocalcic and other tightly packed soil horizons. Roots were exposed from origin on the plant to their end, thus eliminating all question as to root identity.

To facilitate mapping of root systems a base line was established with a tightly stretched cord at the soil surface running through the base of the target plant and parallel to the trench. All coordinate measurements (x, y, and z) were made from this base line. After exposure, roots were usually mapped at a scale of 10 cm = 1 inch on 17 × 22-inch sheets of graph paper which had 10 divisions per inch. Larger scales, e.g. 1 m = 1 inch, were used on very extensive root systems. Either a vertical or horizontal (sometimes both) projection was mapped with the appropriate z coordinate noted so that 3-D drawings could be made. A 1 × 1 m frame subdivided into 0.1 × 0.1-m squares with fine wires proved to be a handy reference tool when mapping. With one exception, the perspective of drawings is looking perpendicular to the long axis of the access trench with the trench in the foreground but not shown. Root diameters were measured with a vernier-scale caliper (early excavations) to nearest 0.1 mm and then with a digital caliper to nearest 0.01 mm although these readings have been rounded to nearest 0.1 mm for reporting.

Root excavations were made each year from 1989 to 1996. Soil series determinations at all sites were made by Dr Leland H. Gile while access trenches were open. Plant nomenclature follows Allred (1993, 1997). All drawings of root systems were made by the senior author.

Root systems at creosotebush-dominated sites

Root systems of creosotebush (*L. tridentata*) and tarbush (*F. cernua*) were excavated at a site on the upper reaches of a bajada slope (Site 1, Fig. 1). The site was dominated by creosotebush with a few scattered tarbush plants. Other species present included mesquite (*P. glandulosa*), broom snakeweed (*G. sarothrae*), bush muhly (*Muhlenbergia porteri* Scribn.), desert zinnia [*Zinnia acerosa* (DC.) Gray], desert Christmas cholla (*Opuntia leptocaulis* DC.), and fluffgrass [*Dasyochloa pulchella* (H.B.K.) Studel]. The site slopes 4% to the north-east and the soil surface was covered with gravel and stones. The loamy-skeletal soils lack an argillic horizon and are a Typic Petrocalcid, Delnorte series. This site is the same as Site C in Gile *et al.* (1998) where a detailed soil

description is given. The petrocalcic horizon occurred at depth of about 30 cm and was capped with a well developed laminar layer. Due to the high gravel content of the soil it was found that an icepick and paint brush were more efficient in exposing roots than a water spray.

Some roots of two creosotebush plants growing 0.8 m apart were excavated. Drawings of excavated roots may be found in Gile *et al.* (1998). Top of one plant was 1.1 m tall and 1.6 m in diameter, the other plant was 0.9 m tall and 0.8 m in diameter. Soil pedestals 5 and 3 cm tall were present under the large and small plant, respectfully. The root crown of the larger plant was 15 cm in diameter and 10 cm in length. There were 70 roots arising from the crown with diameters ranging from 0.7 to 22.1 mm with a mean diameter of 5.5 mm. In addition, there were six adventitious roots arising from stem branches in contact with the soil. The root crown of the smaller plant was 10 × 15 cm and 5 cm long. Originating from the crown were 23 roots ranging from 1.2 to 18.7 mm in diameter with a mean diameter of 5.7 mm. Although the crown and stem branches of both plants gave the appearance of a single individual, both crowns were segmented. The large plant crown had five segments with one to eight stems each. The small plant crown had six segments with one to four stems each. Crowns of other creosotebush at this site were found to be similarly segmented. One possible explanation is that the plants are very old and over time the once continuous vascular system of the root crown has degenerated, creating a number of physiologically independent systems. Bean-caper (*Zygophyllum dumosum*) shrubs growing in a habitat with 10–20 mm of available water in the Negev Desert show a similar fragmentation into autonomous entities (Evenari *et al.*, 1971). It is quite likely that these obviously old plants furnished the seed for establishment of downslope shrubs which have become established in historical times.

Radial spread of both root systems was > 2 m and roots of the two creosotebush plants excavated were highly intermingled. Most of the roots were found above the petrocalcic horizon and often they grew in contact with the laminar layer capping the petrocalcic horizon. At various distances from the root crowns, some roots angled upward to within 7 cm of the soil surface. Several roots were traced into the petrocalcic horizon for 5–10 cm but it was extremely time-consuming to follow roots in this medium so none were traced individually through the approximately 40 cm thick petrocalcic material. Examination of the walls of the 1.5-m deep access trench revealed that a fairly large number of roots 0.2–1.4 mm in diameter which had the coloration of creosotebush roots were found at 1.5-m depth. A mat of very fine roots (about 0.1 mm in diameter) often occurred on the surface of the large cobbles (10–20-cm diameter) found below the petrocalcic horizon.

Also excavated at Site 1 were roots of a tarbush plant 1.1 m tall and 1.0 m in diameter growing on a 2-cm-tall soil pedestal and 10 cm from the larger excavated creosotebush plant. A drawing of the root system appears in Gile *et al.* (1998). From a diameter of 54 mm at 3 cm depth the large taproot tapered to 34 mm diameter at 17 cm depth where it was deflected by a large stone and divided into two 17-mm-diameter roots. First-order branches with diameters of 8 and 10 mm arose at 7 and 7.5-cm depths, respectively. A 10 mm diameter root at 12-cm depth and two 13-mm diameter roots at 15-cm depth made up the rest of the first-order branches. All of the first-order roots branched extensively and attained a radial extension > 2 m. Like creosotebush roots, most of the tarbush roots were above the petrocalcic horizon but were traced into the petrocalcic layer at several points. Some roots angled upward to within 8 cm of the soil surface. Tarbush roots were darker in color and tended to be larger in diameter than creosotebush roots. Roots from 0.2 to 2.4 mm diameter with the coloration of tarbush roots were found in the access trench below the petrocalcic horizon. Roots of tarbush and creosotebush were highly intermingled, even at the bases of the respective plants. Also, roots of broom snakeweed, bush muhly, desert zinnia, fluffgrass, and desert Christmas cholla were intermingled with the shrub roots above the petrocalcic horizon.

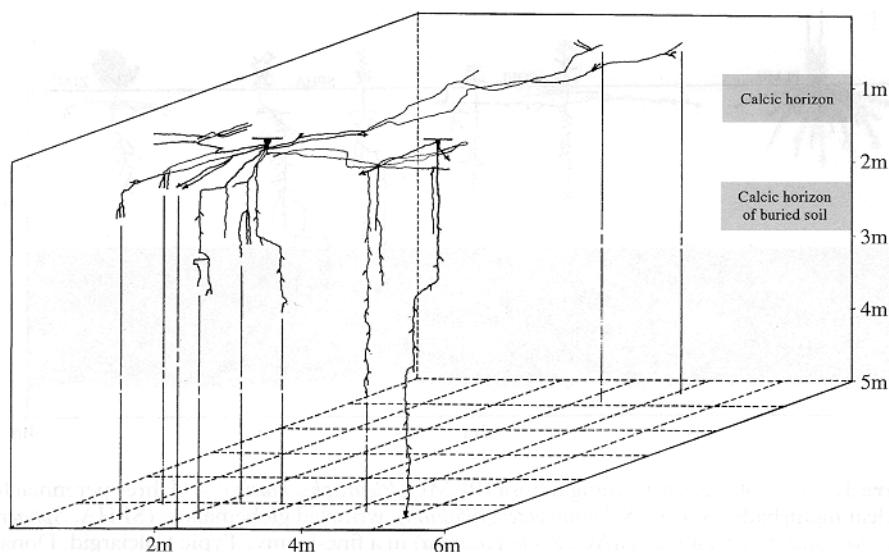


Figure 2. Roots of two creosotebush (*Larrea tridentata*) shrubs growing in a fine-loamy, Typic Calciargid, Dona Ana at Site 2. Soil surface is denoted by horizontal lines at tops of root crowns. Roots ending in arrows were not followed further. Position of calcic horizons is shown on back plane of figure. Drawing from Gile *et al.* (1998).

A trench was dug at the toe of a bahada slope where creosotebush abutted tobosa (*P. mutica*) grassland (Site 2, Fig. 1). Slope is 1% to the east and the fine loamy soil with an argillic horizon is a Typic Haplargid, Dona Ana series. This site is the same as Site A in Gile *et al.* (1998) where the soil is described in detail. It was very difficult to follow roots through the extremely compact B horizon. The calcic horizon extended from about 0.8 to 1.4 m depth and there was another calcic horizon of a buried soil extending from about 2.3 to 2.9 m depth.

Roots of two creosotebush plants were excavated (Fig. 2). Not shown in Fig. 2 are the soil pedestals about 4 cm in height and 30 cm in diameter under each plant which indicate some soil removal by overland water flows. Tops of the plants excavated were 0.9 and 1.4 m tall and 1.2 and 1.6 m in diameter for the left and right plants in Fig. 2, respectively. Root crowns of both plants were entire and not segmented and this site is one where creosotebush has become established in recent times (Buffington & Herbel, 1965). The plant on the left in Fig. 2 had a root crown 12 cm in diameter but at 10 cm depth it was only 6 cm in diameter and at that depth segmented into numerous roots. The root crown of the plant on the right in Fig. 2 was 6 cm in diameter and several large roots originated before the crown segmented into roots at 20 cm depth. Major first-order branches ranged up to 15 mm in diameter at point of origin. Roots of both plants extended through the calcic horizon and a root of one plant was traced to a depth of 5 m (Fig. 2) but a 1-mm diameter at this depth indicated it probably did not extend much further. There were many relatively fine roots (< 1–5 mm diameter) in the upper 30 cm of soil and some angled upward to within 8 cm of the soil surface. Two of these with beginning diameters of 8 and 10 mm were traced horizontally out to 4.2 and 4.5 m, respectively, from the plant. Roots of both plants were intermingled and roots of each were traced to the root crown area of the other.

A few roots of a tarbush plant 0.9 m tall and 1.2 m in diameter were excavated at Site 2. Like the creosote bush plants, there was a soil pedestal about 4 cm tall beneath the plant. The tap root was 6 cm in diameter at 10 cm depth and 2 cm in diameter at 30 cm depth.

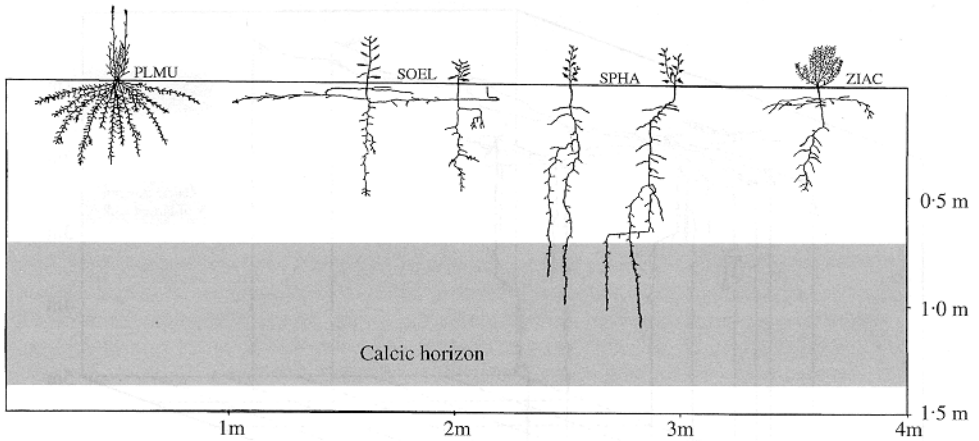


Figure 3. Roots of the sod-forming tobosa (PLMU, *Pleuraphis mutica*) and three perennial forbs, silverleaf nightshade (SOEL, *Solanum elaeagnifolium*), wrinkled globemallow (SPHA, *Sphaeralcea hastulata*), and desert zinnia (ZIAC, *Zinnia acerosa*) in a fine-loamy, Typic Calciargid, Dona Ana at Site 2. Plant tops are drawn at same scale as roots. The deeply penetrating roots of wrinkled globemallow indicate that it is better able to survive droughts than the other species shown.

Roots began arising from the tap root at 5 cm depth. Roots were traced to a depth of 3.4 m and horizontally 4.3 m from the plant base. Major roots tended to be larger in diameter and darker in color than those of creosotebush. A drawing of this root system appears in Gile *et al.* (1998).

Root systems of tobosa and three perennial forbs, silver-leaf nightshade (*Solanum elaeagnifolium* Cav.), wrinkled globemallow (*Sphaeralcea hastulata* Grey), and desert zinnia (*Z. acerosa*) were excavated at Site 2 (Fig. 3). Tobosa roots extended to a depth of 40 cm and had a lateral spread of 40 cm. Silver-leaf nightshade rhizomes occurred at 6–10 cm depths and had diameters ranging from 2.3 to 3.5 mm. The rhizomes gave rise to large numbers of mostly horizontally growing roots. Tap roots were associated with emergent plants and extended to about 54-cm depth. Wrinkled globemallow is a rhizomatous plant but the two plants which were excavated did not have rhizomes and both had a typical taproot system with upper diameters of 2.4–2.8 mm (Fig. 3). At 40-cm depth the tap roots were about 1.6 mm in diameter and at 60 cm depth root diameters were only 0.8 mm or less. The wrinkled globemallow roots did penetrate into the calci horizon, reaching depths slightly more than 1 m which would provide an advantage during droughts. The desert zinnia taproot was 6.9 mm in diameter at the top and at 5 cm depth horizontally growing roots arose which extended outward 20–25 cm (Fig. 3). The tap root extended to a depth of 49 cm. It is believed that the extremely compact B horizon contributed to the relatively shallow penetration of roots of tobosa and most of the forbs.

Another excavation was made in creosotebush dominated vegetation on a bajada slope (Site 3, Fig. 1). The slope is 2% to the east and there is evidence of recent erosion. The fine sandy-loam is a Typic Calciargid, Tres Hermanos, overwash phase. This site is the same as Site B in Gile *et al.* (1998) where a complete description of the rather complex geomorphology is given. Photographic and other JER records show that creosotebush has replaced black grama (*B. eriopoda*) on this site since the 1920s. Some roots of each of five creosotebush plants growing within a 0.4 × 1.1-m rectangle were excavated. Mean plant height and diameter was 1.1 m and 1.1 m, respectively. Two plants growing close together were believed to be one individual when top measurements were made. Number of stems per plant was highly variable, ranging from four

to 18. There were soil pedestals about 5 cm in height at the base of the plants. The non-segmented root crowns ranged from 5 to 7 cm in diameter and tapered into short tap roots which extended to 30–40 cm depths. The number of roots originating from each root crown and tap root was highly variable, ranging from 11 to 29. One plant had two adventitious roots arising from a branch base. Root diameters of first-order branches varied widely, ranging from 0.4 to 17 mm, with a mean diameter of 4.3 mm. Only 16 (17%) of the total of 93 first-order roots were traced and are portrayed in a drawing in Gile *et al.* (1998).

Most of the roots of creosotebush occurred in the upper 1 m of soil. Roots were traced laterally up to 3.6 m. Roots of the separate creosotebush plants were highly intermingled with each other and also with roots of mesquite, tarbush, broom snakeweed, desert zinnia, bush muhly, and fluffgrass. There were a few roots which grew vertically and others grew obliquely upwards, some to within 5 cm of the soil surface. Only one root was traced to a depth of 2 m. Close examination of the walls of the 3 m deep access trench did not reveal any roots below 2 m depth. It is quite likely that rapid runoff on the relatively steep slope did not allow water to penetrate below 2 m depth even during large rainfall events.

Roots of a tarbush plant 1.2 m tall and 0.9 m in diameter were excavated in the fine sandy loam soil at Site 3 and a drawing appears in Gile *et al.* (1998). The top of the plant was somewhat decadent, with several dead branches and major branches of the root system were also dead. Diameter of the top of the tap root was 7 cm and the major first-order roots had beginning diameters of 10–16 mm. At a distance of about 50 cm from the root crown one of the first-order branches grew upward from 60 cm depth to 19 cm depth before continuing horizontally. The tarbush roots had a lateral spread of about 2.5 m and extended into the matrix of excavated creosotebush roots. Tarbush roots were not traced below 1 m depth, although some were visible on the trench face between 1 and 2 m depth. As at Sites 1 and 2, tarbush roots were larger in diameter and darker in colour than creosotebush roots.

Roots of the perennial forb desert zinnia and the shrub-like broom snakeweed were excavated at Site 3 (Fig. 4). Both species had a relatively short tap root with a top diameter of about 20 mm. Relatively widespreading lateral roots at 10–20 cm depth

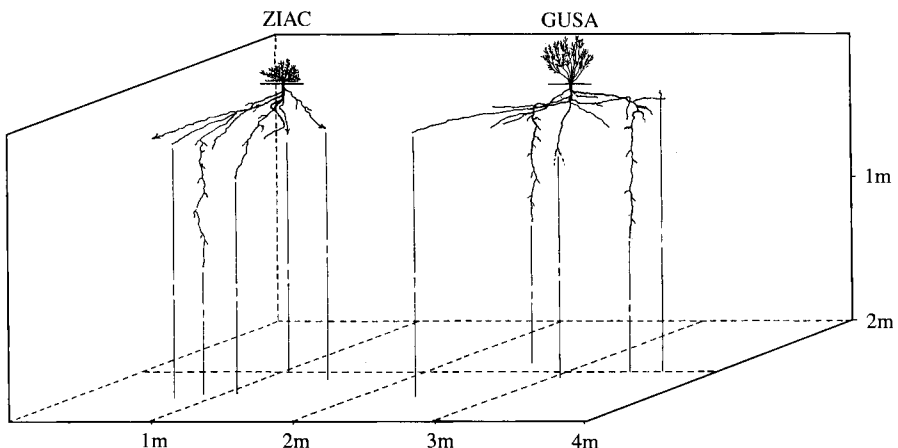


Figure 4. Roots of a perennial forb, desert zinnia (ZIAC, *Zinnia acerosa*) and the shrubby broom snakeweed (GUSA, *Gutierrezia sarothrae*) growing in a fine-loamy, Typic Calciargid, Tres Hermanos outwash phase at Site 3. Horizontal line at top of root crowns denotes soil surface. Roots ending in arrows were not followed further; roots ending in dashes were dead beyond that point. Plant tops are drawn at same scale as root systems. Roots of both plants were intermixed with those of creosotebush and tarbush.

occurred in both species. Roots of each species were traced to 1.1 m depth. The roots of both species were growing within the matrix of creosotebush and tarbush roots.

The root systems of creosotebush excavated at Sites 1, 2, and 3 exhibited a very high degree of overlap. Singh (1964), who did not specify diameter of mapped roots, and Brisson & Reynolds (1994), who mapped only roots > 2 mm in diameter, found very little overlap of creosotebush root systems at sites in the Jornada Basin. Because creosotebush roots < 2 mm diameter were found to extend horizontally 1–2 m at Sites 1, 2, and 3 it seems that this component of the root system should be considered. In Arizona, Chew & Chew (1965) found some overlap of creosotebush roots > 2 mm diameter and Cannon (1911) found considerable contact between root systems of neighbouring creosotebush plants on a bajada slope. Depths of creosotebush roots at Site 2 were much greater than those found in any of the studies mentioned above.

Roots systems at tarbush-dominated sites

Several excavations were made at sites dominated by tarbush or tarbush in combination with other shrubs (Sites 4, 5, 6, 8, and 9, Fig. 1). The fine-loamy soil with an argillic horizon at Site 4 is Typic Haplargid, Dona Ana and slope is 0.5% to the east. Two shrubs, winterfat [*Ceratoides lanata* (Pursh) J.T. Howell] and Berlandier's wolfberry (*Lycium berlandieri* Dunal var. *berlandieri*), shared dominance with tarbush. Tarbush roots spread laterally about 2.2 m and some grew at upward angles to within about 2 cm of the soil surface under the canopy of an adjacent wolfberry plant (Fig. 5). Several major tarbush root branches which were 6–7 mm in diameter at 50 cm depth were traced into and through the calcic horizon. At about 2.4 m depth there was a layer of fine

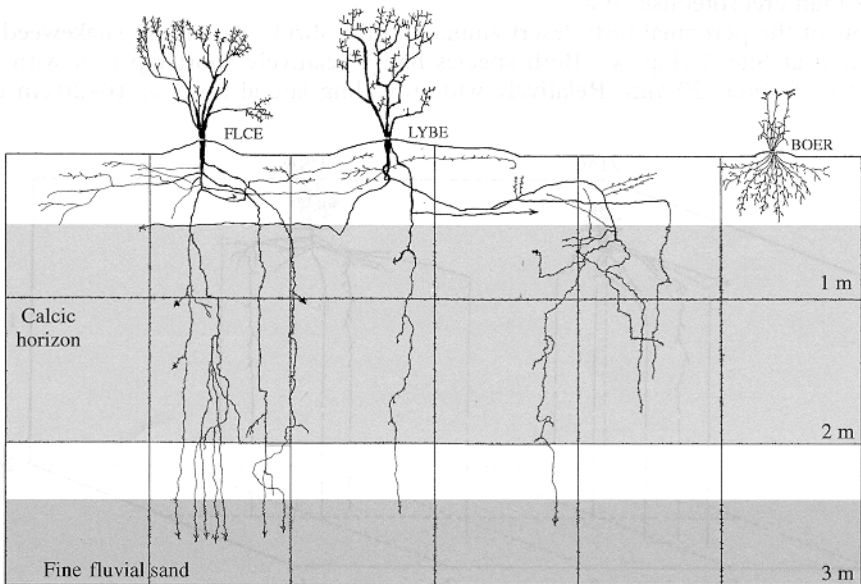


Figure 5. Roots of a tarbush shrub (FLCE, *Flourensia cernua*), a Berlandier's wolfberry shrub (LYBE, *Lycium berlandieri*), and black grama (BOER, *Bouteloua eriopoda*) grass growing in a fine-loamy Typic Calciorthid, Dona Ana at Site 4. Roots ending in arrows were not followed further. The layer of fine fluvial sand prevented following roots deeper. Horizontal distance between tarbush and wolfberry plants is as occurred in field. Plant tops are drawn at same scale as roots.

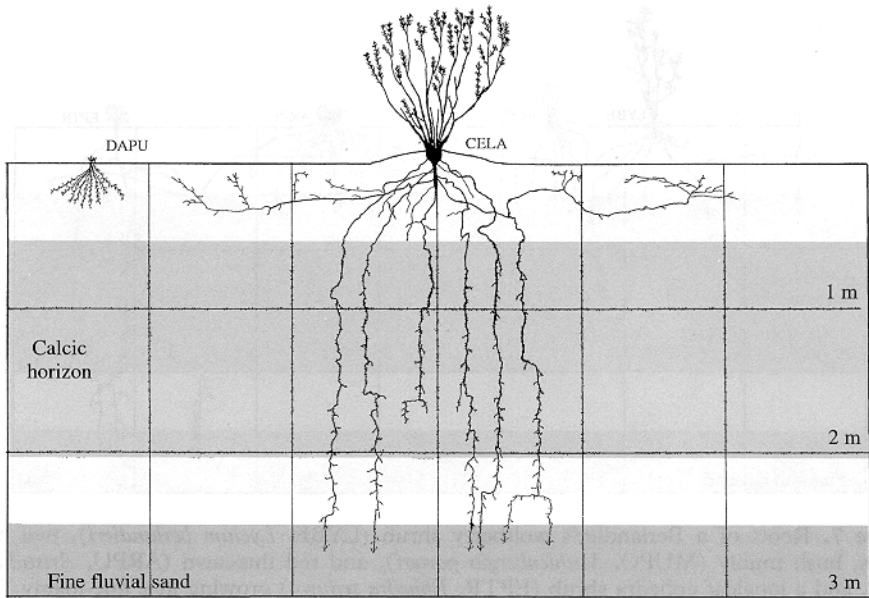


Figure 6. Root systems of a bunch grass, fluffgrass (DAPU, *Dasyochloa pulchella*) and a winterfat (CELA, *Ceratoides lanata*) shrub in a fine-loamy Typic Calciorthid, Dona Ana at Site 4. Roots ending in arrows were not followed further. The layer of fine fluvial sand prevented following roots deeper. Note upward growing roots of winterfat. Plant tops are drawn at same scale as roots.

fluvial sand which 'belled out' and prevented following roots further unless an unacceptable amount of time would have been invested in shoring. Tarbush roots were about 1 mm in diameter at 2.65 m depth in the sand. Wolfberry roots were traced laterally for 2.1 m and, like tarbush, had upward angling roots above the calciic horizon (Fig. 5). Wolfberry roots penetrated through the calciic horizon and into the fluvial sand. Radial extension of black grama (*B. eriopoda*) roots was about 40 cm and a few roots reached the top of the calciic horizon at 45 cm depth (Fig. 5).

Roots of a winterfat plant 0.95 m tall and 1.0 m in diameter were excavated at Site 4 (Fig. 6). The winterfat plant is portrayed separately for clarity but the plant was located between the bush muhly and red threeawn plant shown in Fig. 7. The plant had a bulbous root crown 10 cm in diameter and 6 cm long. A short tap root extended to 25 cm depth where the diameter was 4.5 mm. There were five roots arising from stems in contact with the soil, 14 roots arising from the root crown and 131 roots arising from the short tap root. Roots ranged in diameter from 0.3 to 6.4 mm and had an average diameter of 1.56 mm. Extensive branching of large and small roots gave the root system a fibrous appearing root distribution pattern. Roots were traced laterally for 2.2 m and there were upward growing branches which extended to within 4 cm of the soil surface (Fig. 6). Roots of fluffgrass (*D. pulchella*) were excavated at this site and are also shown in Fig. 6. They had a lateral spread of 29 cm and reached 30 cm depth.

Roots of another wolfberry plant were excavated at Site 4 (Fig. 7). One of the laterally growing roots had partially developed sprouts 15–25 cm from base of the plant and an emergent sprout at 1.2 m from the plant base. Emergent sprouts from roots are a common form of reproduction for wolfberry. The root extending to the right in Fig. 7 was traced out 3.1 m before it turned and ran into the access trench. Beginning diameters of the lateral roots were 4–5 mm and about 2 mm at distal ends. There were

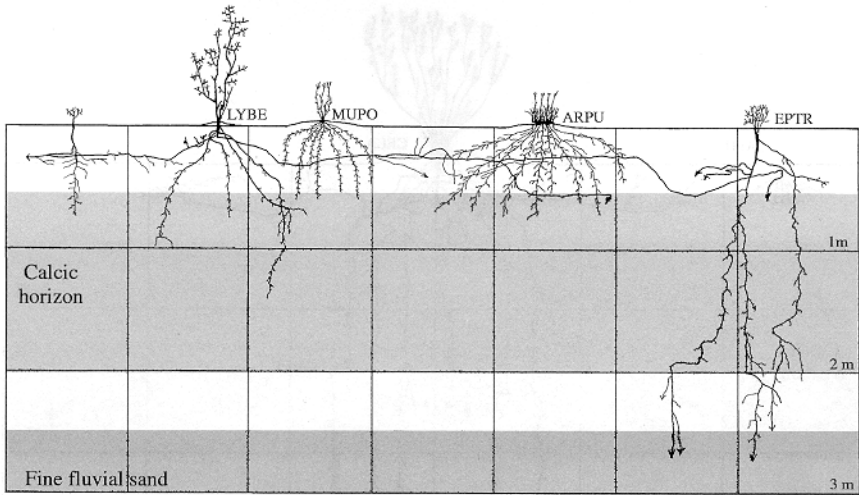


Figure 7. Roots of a Berlandier's wolfberry shrub (LYBE, *Lycium berlandieri*), two bunch grasses, bush muhly (MUPO, *Muhlenbergia porteri*), and red threeawn (ARP, *Aristida purpurea*), and a longleaf ephedra shrub (EPTR, *Ephedra trifurca*) growing in a fine-loamy, Typic Calciorthid, Dona Ana at Site 4. Horizontal spacing of LYBE, MUPO, and ARP plants are as occurred in field and the winterfat plant shown in Fig. 6 occurred between the MUPO and ARP plants. The EPTR plant was on opposite side of trench. Roots ending in arrows were not followed further and the layer of fine fluvial sand prevented following roots to greater depths.

some upward growing roots along the laterals. Roots extended into the calcic horizon but none that were followed extended beyond 1.4 m depth. Bush muhly roots extended laterally 40 cm and to 65 cm depth (Fig. 7). Individual plants of the 'bush' of bush muhly had up to 14 roots. Red threeawn roots extended laterally 94 cm and to the top of the calcic horizon (Fig. 7). Roots of a small (16 cm tall, 24 cm diameter) longleaf ephedra plant were excavated at this site (Fig. 7). Top of the tap root was 2 cm in diameter and at 50 cm depth diameter was 3.6 mm. The largest root at 2.8 m depth in the fluvial sand layer was 2 mm in diameter.

Site 5 (Fig. 1) is dominated by tarbush and the stoloniferous, sod-forming burgrass (*S. brevifolius*). The fine-loamy soil has an argillic horizon and is a Typic Haplargid, Dona Ana. Slope is 0.5% to the east. The calcic horizon extended from about 0.7 to 2.5 m. The excavation at Site 5 was made as much to determine soil series for other studies as for root excavations and only root systems of the perennial forbs desert holly (*Perezia nana* Gray), sicklepod (*Hoffmanseggia drepanocarpa* Gray), and flame-flower [*Talinum angustissimum* (Gray) Woot. & Standl.] were excavated (Fig. 8). Desert holly had extensive rhizomes 1.5–3.0 mm in diameter at 5–30 cm depths. Downward extending roots with diameters of 1–2 mm originated at erratic intervals along the rhizomes and were not always associated with an emergent plant top. Most of the roots terminated in the calcic horizon at about 1 m depth but one root entered a dead, decayed tarbush root at 1 m depth and was still going downward within the tarbush root at 2.8 m depth. There were no branches extending outside of the tarbush root channel. Sicklepod rhizomes occurred at depths of 8–15 cm and were 0.8–1.4 mm in diameter. Like desert holly, roots arising from the rhizomes were not always associated with an emergent plant top. Dark red, irregularly-shaped structures (after sectioning, believed to be tubers rather than nodules) from 8 to 25 mm long and up to 12 mm in diameter were found at depths ranging from 28 to 61 cm. Root diameters, ranging from 0.5 to 0.7 mm, were nearly identical above and below the tubers. Although not shown in Fig. 8 there were some small second-order branches scattered along the main roots both above and below

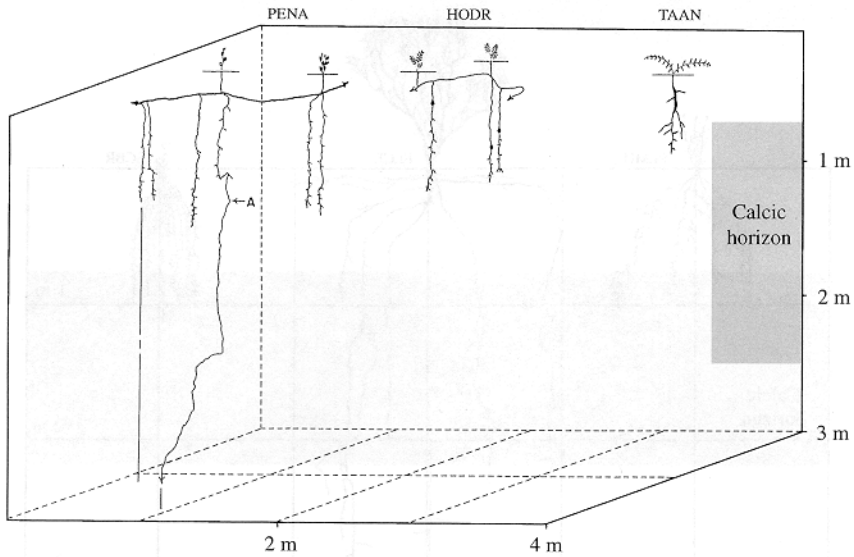


Figure 8. Roots of three perennial forbs, desert holly (PENA, *Perezia nana*), sicklepod (HODR, *Hoffmanseggia drepanocarpa*), and flameflower (TAAN, *Talinum angustissimum*), in a fine-loamy, Typic Calciorthid, Dona Ana at Site 5. Horizontal lines below the plant tops denote soil surface and plant tops are drawn to same scale as roots. Position of the calciic horizon is shown on the back plane of the figure. Most of the desert holly roots did not extend through the calciic horizon but at point A a desert holly root 0.45 mm in diameter entered a dead, partially decayed tarbush root and was still inside the old root at 2.8 m depth.

the tuber. The most extensive branching occurred at the ends of the downward penetrating roots.

Three flameflower tubers, one of which is shown in Fig. 8, were excavated and the upper end of the tubers occurred at 4–8 cm depth. The tubers ranged from 11 to 21 cm in length and 6–20 mm in diameter, tapering toward both upper and lower ends. A few extremely fine, < 0.1 mm diameter, roots originated on the tubers but larger roots arose from the lower end of the tubers. Roots of the plant shown in Fig. 8 were < 1 mm in diameter and did not penetrate below 55 cm depth. Although not illustrated, roots of burrograss were traced to a depth of 1 m at this site and live tarbush roots were found at 3 m depth.

At Site 6 (Fig. 1) the fine-loamy soil with an argillic horizon is a Typic Calcigrid, Dona Ana and slope is 0.5% to the east. Tarbush was dominant with an understory of burrograss and tobosa. This was the first excavation made and roots were exposed entirely with icepicks. The top of the tarbush taproot was 3 cm in diameter and at 25 cm depth diameter was 2 cm. Several major branches were traced through the calciic horizon, which extended from about 0.8 to 1.2 m, and one was followed to 5 m depth where the diameter was 1.4 mm (Fig. 9). Lateral spread of horizontal branches was about 1 m. Upward slanting branches reached to within 5 cm of the soil surface. Tobosa roots had well developed first-order branches and spread laterally about 60 cm, penetrating into the calciic horizon to just over 1 m depth (Fig. 9). Roots of burrograss had a lateral spread of about 20 cm and penetrated into the calciic horizon to 1.1 m depth (Fig. 9). This excavation was at the edge of a slight depression which accumulated runoff water and the additional water may account for the deeply penetrating roots of tarbush at this site.

Sites 8 and 9 (Fig. 1) were only 65 m apart and were in an area dominated by tarbush with an understory of burrograss and ear muhly [*Muhlenbergia arenacea* (Buckl.) A.S.

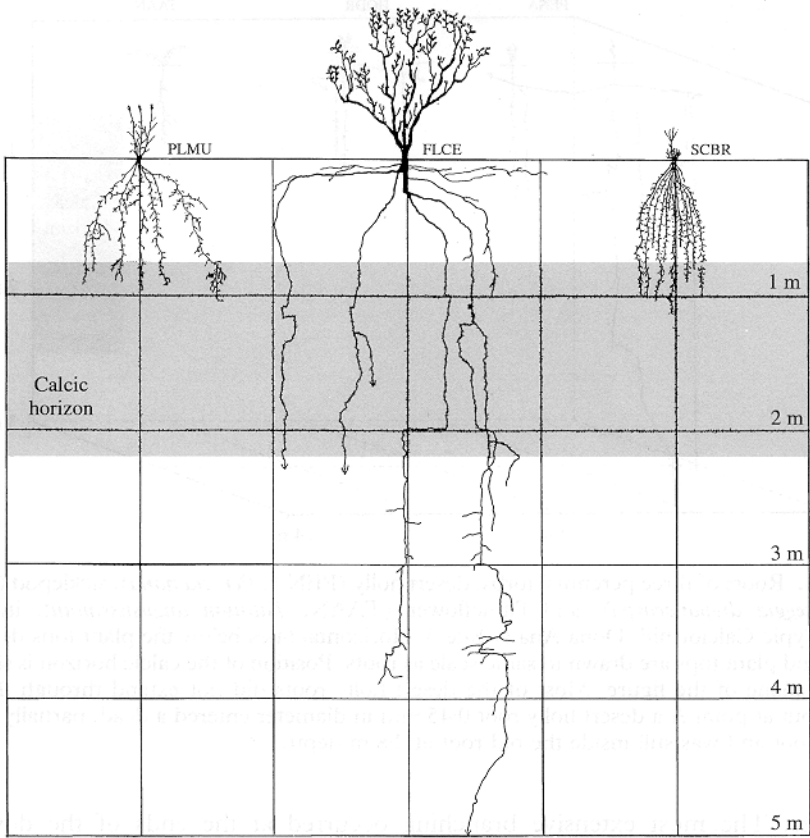


Figure 9. Root systems of the sod-forming tobosa (PLMU, *Pleuraphis mutica*), a tarbush shrub (FLCE, *Flourensia cernua*), and the sod-forming burrograss (SCBR, *Scleropogon brevifolius*) in a fine-loamy, Typic Calciorthid, Dona Ana at Site 6. Roots ending in arrows were not followed further. Plant tops are drawn at same scale as roots. Root systems are shown separately but root systems of both grasses were intermingled with roots of tarbush plants.

Hitchc.]. Scattered plants of crucifixion thorn (*Koerberlinia spinosa* Zucc.) and a few individuals of four-wing saltbush [*Atriplex canescens* (Pursh) Nutt.] also occur. The sites slope 0.5% to the west and the soil which has formed in the fan-toeslope deposits is a fine-silty, Ustic Haplocalcid, Reagan which contains abundant carbonate throughout the profile. A complete description of the fan-toeslope deposits and underlying river sediments by horizons to a depth of 5 m at Site 8 is given in Gile *et al.* (1995). Water was piped to the sites from a stockwater pipeline. Water pressure was moderate but with a garden spray nozzle roots in the upper soil horizons could be exposed fairly rapidly. It was found that continual soaking of the soil led to sluffing of the trench walls so below a depth of 3 m water was not used and excavation was accomplished with shovels and icepicks.

At Site 8 roots of a large crucifixion thorn plant 1.5 m tall and 2.5 m in diameter were excavated (Fig. 10). The prominent, very straight taproot was about 10 cm in diameter at the top but tapered rapidly and was only 3.1 cm in diameter at 1.73 m depth. The tap root was constricted to a diameter of 0.84 cm as it penetrated a compact soil layer at 3.25 m depth but it regained diameter and was about 1.5 cm in diameter when it made a loop and turned away from the trench at 3.64 m depth. A remarkable feature of the tap root was the absence of lateral branches on the upper portion of the root. A major first-

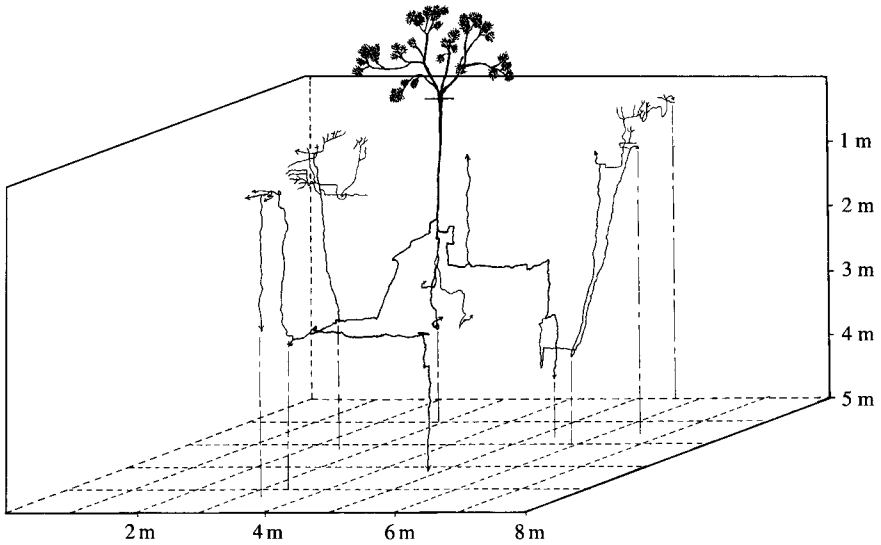


Figure 10. Root system of a large crucifixion thorn (*Koberlinia spinosa*) shrub growing in a fine-silty Ustic Haplocalcid, Reagan. Horizontal line at base of plant denotes soil surface and plant top is drawn to same scale as roots. Roots ending in arrows were not followed further. Upward growing roots extended to within 10 cm of soil surface. One root was traced into a layer of fine, fluvial sand at 5.2-m depth where its diameter was 1.85 cm. Drawing from Gile *et al.* (1995).

order branch with dimensions of 2.40×1.64 cm originated at 1.78 m depth. Another first-order branch originated at a depth of 2.1 m. All of the major branches were contorted and seldom round in cross-section.

Another remarkable feature of the root system was the large number of major roots which grew vertically upwards. At 3.55 m depth the upper first-order root gave rise to a second-order root with a diameter of about 1.65 cm which grew upward 2.6 m before branching. The second-order root extended to a depth of 0.35 m where it turned and grew horizontally but the 1-cm diameter root was lost when part of the trench wall caved in. At a depth of about 0.98 m a third-order branch arose which also grew upward. Above a depth of about 0.8 m branching of the roots was fairly diffuse and some fourth-through sixth-order branches with diameters ranging from 0.35 to 0.14 cm were traced to within 10 cm of the soil surface. Crucifixion thorn roots are relatively coarse in comparison to other shrubs but following the finer branches was difficult because the upper 1 m of soil was occupied by a mass of burrograss roots. Other second- or third-order roots with diameters ranging from 0.7 to 0.9 cm grew obliquely or vertically upward from depths of 2.3 to 3.8 m (Fig. 10). These upward growing roots had a striking absence of branches until they reached about 1 m depth.

The first-order branches tended to grow horizontally along the top of very compact soil layers until a less compact zone was found for descent. There were several of these compact, root turning layers with a high percentage of very fine sand (Gile *et al.*, 1995) but the upper first-order branch was followed through all of them to a layer of non-compacted sand at a depth of 4.7 m. Sluffing of the sand prevented following the root below a depth of 5.2 m where the root was round in cross section and 1.85 cm in diameter. A few small branches < 0.1 cm diameter and 5–10 cm in length were found between 3.5 and 5 m depth. Roots were traced out 3.5 m from the base of the plant but the maximum horizontal spread was not determined even though about 28 m^3 of soil were removed in following the roots.

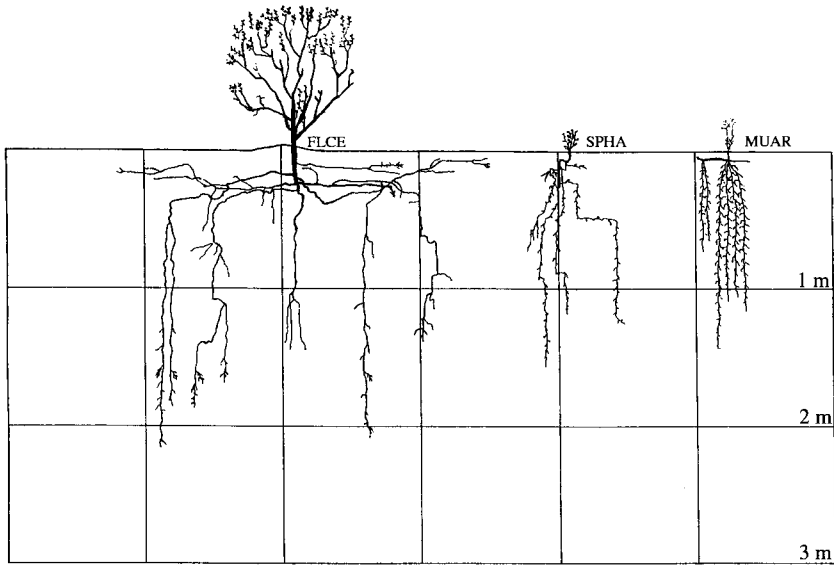


Figure 11. Roots of a tarbush shrub (FLCE, *Flourensia cernua*), a perennial forb, wrinkled globemallow (SPHA, *Sphaeralcea hastulata*), and the rhizomatous grass, ear muhly (MUAR, *Muhlenbergia arenacea*), growing in a fine-silty, Ustic Haplocalcid, Reagan at Site 8. Roots ending in arrows were not followed further and plant tops are drawn at same scale as roots. These root systems were growing within a matrix of crucifixion thorn roots.

Roots of a tarbush plant 78 cm tall and 65 cm in diameter were excavated at site 8 (Fig. 11). The top of the tap root was 5 cm in diameter and at 25 cm depth the tap root was 25 mm in diameter. The first major branch occurred at 17 cm depth and other major branches at 25 and 30 cm depths with diameters of 10–15 mm. The tap root divided into several branches at 1.2 m depth and none of these extended below 1.9 m depth. Some of the horizontally growing branches angled upward to within 10 cm of the soil surface (Fig. 11). Radial spread of horizontal roots was about 1.1 m. A few roots of another tarbush plant were traced and revealed a root distribution pattern very similar to that of the tarbush plant shown in Fig. 11.

Root systems of two wrinkled globemallow plants (*S. hastulata*) about 15 cm tall were excavated at Site 8, one of which is shown in Fig. 11. Tap root of the plant shown in Fig. 11 was 8.3 mm in diameter at the top, 3.4 mm in diameter at 13 cm depth and 0.5 mm in diameter at 1.4 m depth. Six large first-order branches originated in the first 10 cm. The deepest penetrating root entered a dead tarbush root at 40 cm depth and was still inside the tarbush root at 1.4 m depth. Another root entered a dead tarbush root at 90 cm depth and penetrated to 1.2 m depth. Both of the roots within the tarbush roots had two to three short, fine branches per centimeter. The tap root of the other wrinkled globe mallow plant was 44 mm in diameter at the top, 3.4 mm in diameter at 30 cm depth, and 2.4 mm in diameter at 55 cm depth. Nine major branches arose in the first 10 cm; deepest penetration was 1.6 m.

Roots of ear muhly at Site 8 originated in clusters from nodes on a stolon at 7 cm depth. Not all root clusters had an emergent top. Most roots ended between 0.8 and 1.1 m depths (Fig. 11). The deepest penetrating root followed a dead tarbush root to a depth of 1.25 m.

At Site 9, the roots of two small crucifixion thorn plants in a group of small plants were excavated. One plant was 35 cm tall and 25 cm in diameter, the other 56 cm tall and 70 cm in diameter. Cannon (1911) found that crucifixion thorn often grows in clumps

which arise from adventitious sprouting. However, no connections were found between the plants excavated although it is possible that connections had decayed. Drawings of the root systems appear in Gile *et al.*, 1995.

Tap roots of both crucifixion plants were well-developed. The tap root of the smaller plant was 1.6 cm in diameter tapering to 0.46 cm at a 1 m depth. Two of the three primary tap root branches of the small plant were followed to 3.3 m depth where horizontal branches extended along the top of an extremely compact soil layer. The larger plant had a tap root 5.4 cm in diameter but was only 2.9 cm in diameter at 45 cm depth where the first first-order branch originated. This branch grew away from the trench and was not followed. At 1.3 m depth the tap root was 1.9 cm in diameter and two major first-order branches originated, one of which was dead. The tap root of the larger plant reached 3.2 m depth and grew horizontally for 2 m on top of the hard layer before turning and growing vertically upward. The upper portion of this root had been destroyed when the access trench was dug. The living first-order branch arising at 1.3-m depth grew horizontally for 1.7 m before turning and growing upward. Branches from this root were traced to within 10 cm of the soil surface in areas covered by burrograss sod. Other branches were followed downward to the compact soil layer at 3.3 m depth. It was necessary to use a jackhammer to penetrate this 20-cm-thick compact layer. No roots were found below the layer.

The small crucifixion thorn plants differed from the large one excavated at Site 8 in that there were branches originating from the tap roots in the top 2 m of soil. However, the larger of the small plants had roots which grew upwards after encountering compact soil layers just like the large plant at Site 8.

Roots of a four-wing saltbush plant 1.5 m tall and 1 m in diameter with a 5 cm tall, 50 cm diameter soil pedestal under the plant were excavated at Site 9. The sharply tapered tap root was 6 cm in diameter at the soil surface but only 1 cm in diameter at 18 cm depth (Fig. 12). A large number of fine (1.5–1.7-mm diameter) first-order roots originated from the upper part of the tap root. Larger, about 10 mm diameter, first-order roots originated at 8 cm depth and below. Roots were traced to 3.3 m depth where they terminated in numerous branches on top of the very hard soil layer. One root about 3 mm in diameter was traced laterally for 3.5 m (Fig. 12). For 0.5 m of this distance the four-wing saltbush root grew inside of a dead tarbush root.

Roots of burrograss at Site 9 penetrated to 96 cm depth but were abundant only to 60 cm depth (Fig. 12). Maximum lateral spread of 16 cm occurred at 20 cm depth. Roots of a tarbush plant 1 m tall and 1.1 m in diameter were excavated but are not illustrated. Tarbush roots were traced to 2.1 m depth and radial spread was 1.4 m. Upper branches were often angled upward to within 10 cm of the soil surface.

Root systems at mesquite-dominated sites

Mesquite is the sole dominant at Site 17 (Fig. 1) where it occurs in coppice dunes with scant vegetation, principally fluffgrass and broom snakeweed, in interdune areas. The site slopes 2% to the north and a detailed analysis of soils at the excavation site (Gile *et al.*, 1997) revealed a mosaic of sandy or coarse-loamy soil types formed on the La Mesa surface including Typic Calcargids (Yucca series), Typic Haplargids (Sonoita series and its overblown phase), Typic Petroargids (Rotura series), Typic Petrocalcids (Harrisburg, Simona, and Tonuco series), Argic Petrocalcids (Hueco series and its overblown phase), Typic Haplocalcids (Whitlock series) and Typic Torripsammets (Bluepoint series and its overblown phase). Soil pipes or downward extensions of B and/or K horizon materials with less carbonate than adjacent horizons were unusually common (origin of pipes is discussed by Gile & Grossman, 1979: 185).

An entire coppice dune 6.3 m long, 4 m wide and 1.1 m in height was excavated. Mesquite stems having a mean height of 0.6 m covered the dune and near one end of the

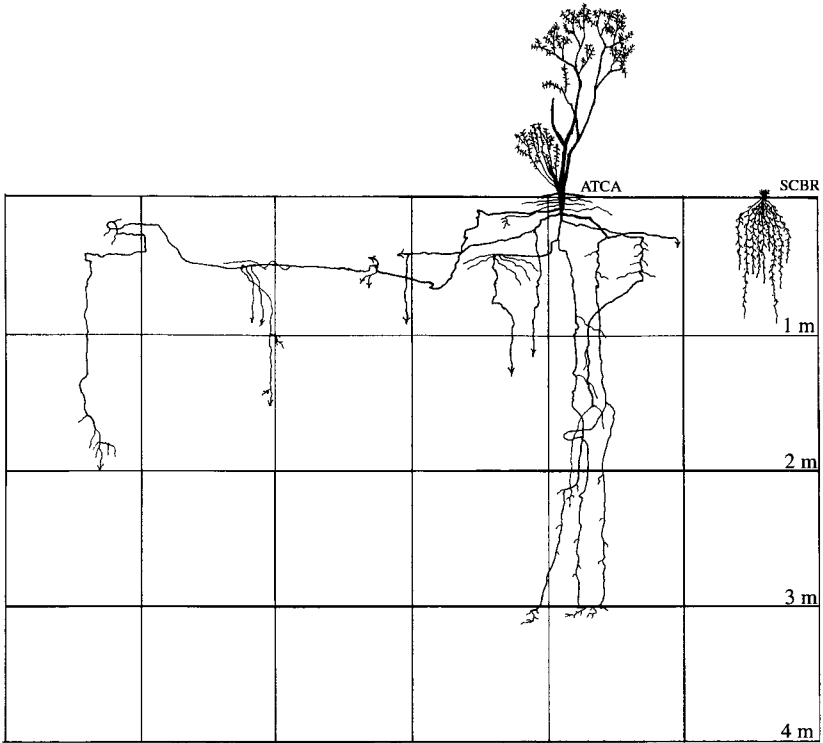


Figure 12. Root systems of a four-wing saltbush shrub (ATCA, *Atriplex canescens*) and the sod-forming burrograss (SCBR, *Scleropogon brevifolius*) growing in a fine-silty Ustic Haplocalcid, Reagan at Site 9. Plant tops drawn at same scale as roots. Roots ending in arrows were not followed further. An extremely compact soil layer at 3.3 m prevented deeper penetration of roots.

dune there was a large four-wing saltbush plant 1.6 m in height. A few mesa dropseed plants were growing on the dune. Live, above-ground mesquite biomass (oven-dry, 60°C) totaled 11.3 kg and above-ground dead mesquite biomass totaled 5.9 kg. Excavation of the dune revealed that there were four separate mesquite plants within the dune. Three of these were large and probably of comparable age while the fourth, found at the periphery of the dune, was small and probably much younger. As the dune formed mesquite branches were buried but continued to grow. These large buried branches gave rise to emergent branches which formed the above-ground part of the mesquite plants. It was impossible to remove all sand from the rough bark of the buried branches so ash-free weights were determined from subsamples. The live buried branches totaled 16.2 kg, exceeding the emergent live biomass. Dead, buried branch biomass was only 1 kg but it is likely that several kilograms of material had decayed during the life of the dune. The four root crowns weighed 6.4 kg. Trunks of the large mesquite plants were all decayed in the center and ring counts could not be made. Cross sections of the larger buried branches had very poorly defined growth rings and only an estimate of > 50 years of age could be made.

The four-wing saltbush plant growing in the coppice dune had above-ground live and dead biomass of 7.6 and 3.9 kg, respectively. There was a well-developed tap root which extended to a depth of 57 cm where it split into three branches. A very large (5 × 7 cm) horizontal branch arose at a depth of 10 cm. There were 370 first-order branches arising from the tap root and over half of these originated between depths of 20 and 40 cm. Only 32 of the first-order branches were > 2 mm in diameter. The larger, extensively

branched roots extended up to 5 m from the plant. Most of the first-order branches < 2 mm diameter were < 1 m in length.

The well-developed tap roots of the three old mesquite plants penetrated to the level of the petrocalcic horizon (1.5 m from top of dune) but, in every case, the lower portions of the tap roots were dead and decayed. The active mesquite root systems were composed of, collectively, about 230 roots ranging in diameter from 0.8 to 34 mm arising from the buried branches and a few roots originating from the root crowns. A mass of fine roots of mesquite and four-wing saltbush permeated the dune soil. It has been postulated that shrubs cause heterogeneity to develop in soil resources by creating self-augmenting 'islands of fertility' (Schlesinger *et al.* 1990). This hypothesis is supported by the abundance of roots in the elevated portion of the dune which indicate that the dune itself was a major source of water and nutrients for the shrubs.

Thirteen roots, originating primarily from buried branches, with diameters ranging up to 34 mm were traced outward from the dune and a vertical projection of these roots is presented in Gile *et al.* (1997). The roots extended from 4.5 to 16 m from point of origin. Measured along its path, the longest excavated root was 22 m in length. It was necessary to dig several additional trenches to receive wash water when following the long roots. The larger roots typically bi-, tri- or quadra-furcated into branches of slightly smaller diameter at varying distances from point of origin. Because only a few of the many branches could be traced, the policy was to continue excavation of the largest branch. The horizontally extending roots typically grew just above the petrocalcic horizons at depths ranging from 7 to 80 cm.

Roots from adjacent coppice dunes were frequently encountered when excavating the horizontal roots, indicating a great deal of overlap of root systems in the interdune areas. No roots from neighboring dunes were detected within the excavated dune but a root from the excavated dune was traced into an adjacent dune. There were many instances where roots within the dune had been severed by rodents burrowing into the dune. A number of dead branches of all diameters were found on the horizontally extending roots, indicating a fairly high rate of root turnover.

The horizontal roots all had a large number of small, relatively short branches. Many of these branches grew vertically upward rather than horizontally or downward. These upward growing roots originated from depths as great as 50 cm and ascended to within 4 cm of the soil surface. Upward growing roots were found on a mesquite tree in Texas but were largely confined to the area under the tree canopy (Heitschmidt *et al.*, 1988). The upward growing roots of mesquite suggests that the wide-spreading root systems are well adapted to take advantage of the relatively frequent small precipitation events that only wet the soil to a depth of a few centimeters.

In the access trench at the edge of the dune, roots of both mesquite and four-wing saltbush penetrated cracks in the petrocalcic horizon. These roots were traced through the petrocalcic horizon to a depth of 3 m. The roots had a diameter of about 5 mm at 3 m depth and undoubtedly penetrated to greater depths but were not followed due to time constraints. Mesquite roots were also traced downward to 1.5 to 2 m depths in some of the frequent soil pipes in the interdune area.

At Sites 12, 13, 14, and 15 (Fig. 1) mesquite is now the primary dominant in an area formerly dominated by black grama. The soils at the four sites are coarse-loamy with an argillic horizon and are an Argic Petrocalcic, Hueco. Average slope is about 0.5% to the south-west. At Site 12, roots of a rather small mesquite plant, 50 cm tall and 1 m in diameter, were excavated (Fig. 13). The prominent tap root was 37 mm in diameter at 2 cm depth and 21.5 mm in diameter at 50 cm depth. Calcic pebbles and blocks were found at 78 cm depth but the extremely dense and hard petrocalcic layer, capped with a laminar layer, occurred at about 1 m depth. The tap root entered a crack in the petrocalcic layer and became distorted and flattened to 3.2 × 2.4 mm at 1.03 m depth. The tap root regained a cylindrical shape and a diameter of 8.1 mm at 1.07 m depth. Following the root through the petrocalcic layer was an extremely slow and tedious

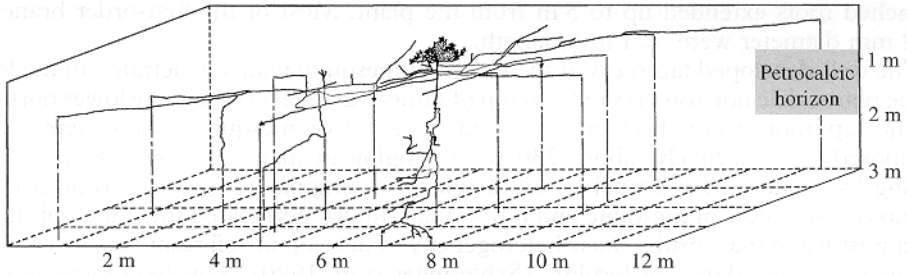


Figure 13. Root system of a relatively small mesquite (*Prosopis glandulosa*) shrub growing in a coarse-loamy, Argic Petrocalcic, Hueco at Site 12. Roots ending in arrows were not followed further. Position of petrocalcic horizon is shown on back plane of figure. Although most of roots were above the petrocalcic horizon, they did penetrate through the petrocalcic horizon in several places. Plant top is drawn at same scale as roots.

process as it was necessary to use chisels and sharpened punches. The petrocalcic horizon, which extended to about 2 m depth, became less dense and hard below 1.3 m depth where the taproot branched. At 2.7 m depth there were branches with diameters ranging from 0.3 to 0.8 mm and these were traced to a depth of 2.9 m in a compacted sandy layer with carbonate coated nodules. This access trench was later deepened for soil geomorphology studies and mesquite roots about 1.0 mm in diameter, apparently originating from large mesquite plants in the vicinity, were found at 5.2 m depth.

Only a few of the many lateral roots originating from the tap root above the petrocalcic horizon were traced. With beginning diameters ranging from 1.5 to 12.5 mm the well-branched lateral roots extended outward up to 6.4 m (Fig. 13). These roots were mostly found above 80 cm depth although some branches grew downward through the petrocalcic horizon. Upward growing branches were common, some extending to within 4 cm of the soil surface. On a 1 m section of a first-order lateral root, 15 upward growing branches were counted. The number of second-order branches per given length of first-order lateral varied widely ranging from none to over 1 per cm and the second-order branches often originated in pairs.

Roots of another small mesquite plant whose top had only two branches and a height of 36 cm were excavated at site 12 (Fig. 14). The tap root, with an upper diameter of 10.1 mm and 7.9 mm at 50 cm depth was well developed. The tap root was deflected horizontally by the petrocalcic horizon but branches of the tap root eventually penetrated the petrocalcic horizon through cracks and extended to a depth of 2.72 m where diameters were < 0.3 mm. There were only a few first-order horizontal branches from the tap root and none were traced further than 1.5 m.

The broom snakeweed plant portrayed in Fig. 14 was 36 cm tall and 60 cm in diameter. The root crown was 5.4 mm in diameter and the largest first-order branch just below the soil surface had a diameter of 5 mm. Major root diameters at about 1 m depth ranged from 1.3 to 1.8 mm. The petrocalcic horizon deflected the major roots laterally but all that were traced eventually penetrated the petrocalcic layer and extended to 2.4 m depth. Most second-order roots were relatively short, < 5 cm in length. Lateral spread of the roots was 1.7 m and was greatest below the petrocalcic horizon. The root systems of the mesquite and broom snakeweed plants are shown separately in Fig. 14 for clarity but in fact were highly overlapped as the plants were only 40 cm apart. Roots from the mesquite plant shown in Fig. 13 which was 2.8 m distant were growing through both root systems.

Two very young mesquite plants believed to be in the third season of growth were found at Site 12 (Fig. 15). Both had been browsed by rodents or lagomorphs and were only 2.5 cm tall. The prominent taproots were 1.9 and 2.16 mm in diameter at the top

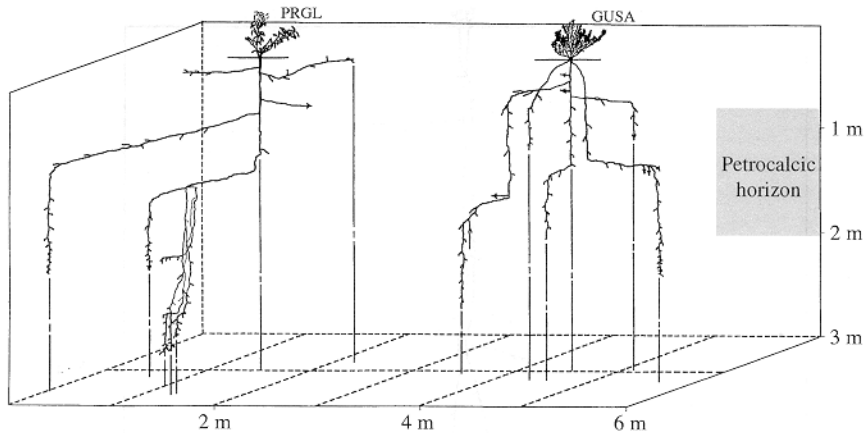


Figure 14. Root system of a small mesquite shrub (PRGL, *Prosopis glandulosa*) and a broom snakeweed shrub (GUSA, *Gutierrezia sarothrae*) growing in a coarse-loamy, Argic Petrocalcic, Hueco at Site 12. Horizontal lines at plant bases denote soil surface and position of petrocalcic horizon is shown on back plane of figure. Plant tops are drawn at same scale as roots. Roots ending in arrows were not followed further. Roots of both species extended through the petrocalcic horizon and were intermixed with the roots of the mesquite plant shown in Fig. 13.

and penetrated to 76 and 85 cm depths, respectively. At 40 cm depth tap root diameters were 0.4 and 0.7 mm. Ending diameters were about 0.2 mm. At a depth of 29 and 40 cm the smaller and shallower tap root had haustoria of the parasitic three fans (*Krameria lanceolata* Torr.) attached. The first-order lateral branches were small and short. From the mesquite plants excavated at this site it would appear that initially development of a deeply penetrating tap root takes precedence over the extensive horizontal roots which eventually develop.

The access trench at Site 12 provided an opportunity to excavate roots of a soap tree yucca (*Y. elata*) plant. The plant top was 1.1 m tall and 1.1 m in diameter. The caudex had a diameter of 18 cm at the soil surface. Below ground the caudex branched, with one branch extending to 95 cm depth and the other to 80 cm depth. Both branches extended into the calcic material overlying the petrocalcic horizon but neither branch penetrated into the indurated horizon. A large number of roots, many of which were dead, arose from the caudex. These roots were relatively uniform in diameter with diameters at origin ranging from 2.1 to 3.9 mm. The roots extended laterally, usually at 60–90 cm depths, above the petrocalcic horizon (Fig. 16). Maximum lateral extension of a traced root was 6.2 m and diameter at the end was 1.2 mm. The number of branches from the laterally spreading roots was relatively sparse. For example, the first and second meters of length of one root had 13 and 10 branches, respectively. Vertically growing branches were common and some were traced to within 9 cm of the soil surface. The large number of dead roots still attached to the caudex suggests that root turnover is relatively high in this long-lived plant. Sisson (1983) excavated seven soap tree yucca plants on the Jornada Experimental Range for biomass determinations. Six of the plants grew where depth to caliche was similar to Site 12 and had belowground:aboveground ratios ranging from 1.29 to 5.94 (mean = 3.31). Depth distribution of roots was similar to that at Site 12. However, horizontal spread was only 3 m.

A trench was excavated at Site 14 to access the roots of a four-wing saltbush plant. Top of the plant was 1.6 m tall and 2 m in diameter. The irregularly shaped root crown was 8–10 cm in diameter and about 30 cm in length, terminating on top of a large caliche nodule. Below 5 cm depth there were many fine branches from 0.6 to 0.8 mm in diameter arising from the root crown and extending outward 50 cm or less. Five large

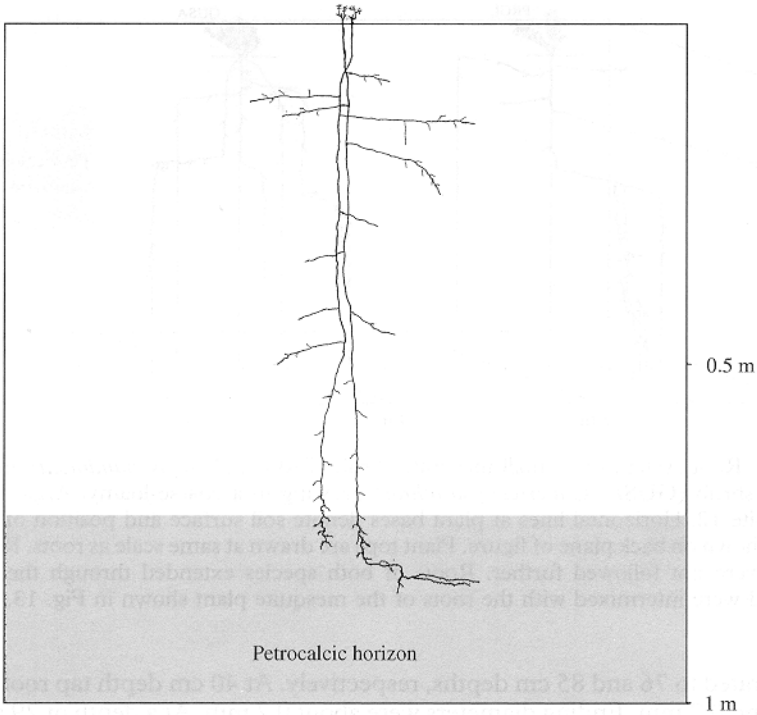


Figure 15. Roots of two young mesquite (*Prosopis glandulosa*) shrubs growing side-by-side which had penetrated into upper, fractured portion of petrocalcic horizon of the coarse-loamy Argic Petrocalcic, Hueco at Site 12. Tops of the plants, which were believed to be third growing season, had been browsed, probably by rabbits, and were only 2.5 cm tall.

horizontal branches 10–18 mm in diameter originated from the lower part of the root crown and these and their subsequent branches made up the extensive root system (Fig. 17). One large first-order branch and one of its second-order branches were traced through the petrocalcic horizon. The first-order branch was traced to a depth of 3.6 m where the root was still relatively large with a flattened cross section 1.7×3.3 mm and probably extended much deeper into the dense sand present at this depth. Another second-order branch with a beginning diameter of 2.3 mm was traced to a depth of 3.5 m where its diameter was 1.3 mm. This root entered a dead root channel (probably mesquite) in the dense sand at 2.9 m depth and continued downward without branches. The extensive

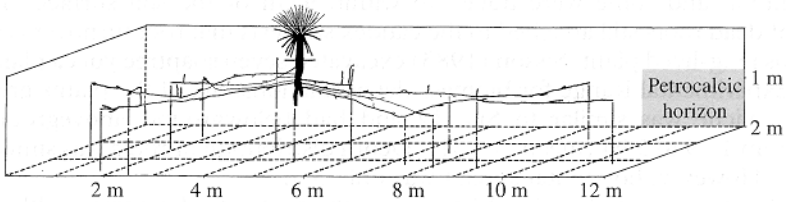


Figure 16. Roots of the shrub-like soap-tree yucca (*Yucca elata*) growing in a coarse-loamy, Argic Petrocalcic, Hueco at Site 12. Horizontal line through caudex denotes soil surface and position of petrocalcic horizon is shown on back plane of figure. Plant top is at same scale as roots. Neither caudex nor roots penetrated through the petrocalcic horizon. Note upward growing roots.

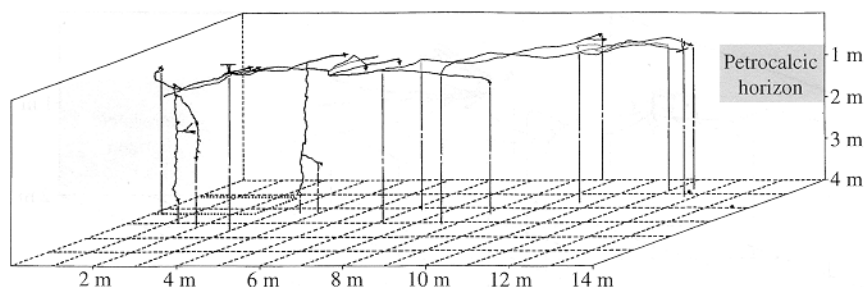


Figure 17. Root system of four-wing saltbush (*Atriplex canescens*) shrub growing in a coarse-loamy, Argic Petrocalcic, Hueco at Site 14. Horizontal line on root crown denotes soil surface and position of petrocalcic horizon is shown on back plane of figure. Dotted lines on base plane show location of access trench as this is the only drawing where the access trench is not in the foreground. Roots ending in arrows were not followed further. Dots on surface and base plane at right side of figure show origin of mesquite roots portrayed in Fig. 18.

horizontal branch shown in Fig. 17 had a diameter of 9.2 mm at 1.5 m from the root crown. It extended outward at depths of 30 to 60 cm to 9.1 m from the root crown. One of the terminal branches divided into four branches which extended upward from a depth of 68 cm to depths of 38–48 cm. These terminal branches were under a mesquite crown. Another of the distal branches was traced into a cluster of caliche nodules at 70 cm depth under the mesquite crown. This root still had a diameter of 3.4 mm but tracing it further would have required an excessive amount of labor and time.

The mesquite clump into which the saltbush roots were traced was a cluster of mesquite plants 4.0×4.7 m in diameter and an incipient dune 15 cm in height had formed. Portions of two mesquite roots from separate plants were traced because they had been partially exposed when the saltbush roots were excavated (Fig. 18). Both roots were traced horizontally at 20–60-cm depths out to 10 m from their point of origin. Beginning diameters were 26 and 19 mm. At 10 m out from the plant base one root turned downward near the base of the saltbush plant and was traced through the petrocalcic horizon to a depth of 1.5 m where the diameter was still 2.6 mm and undoubtedly the root penetrated to much greater depths. Vertically growing branches, a few of which are shown in Fig. 18, were traced to within 9 cm of the soil surface.

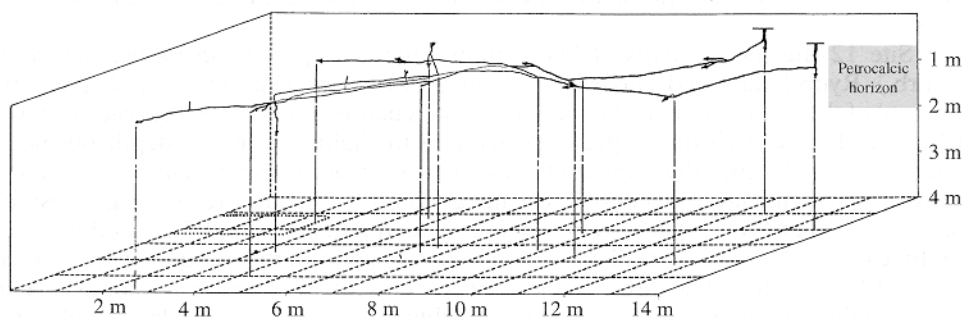


Figure 18. Mesquite (*Prosopis glandulosa*) shrub roots traversing the same area as the four-wing saltbush roots shown in Fig. 17. Horizontal lines at root crowns denote soil surface and position of petrocalcic horizon is shown on back plane of figure. Roots ending in arrows were not followed further. Dots on surface and base plane show position of four-wing saltbush plant portrayed in Fig. 17.

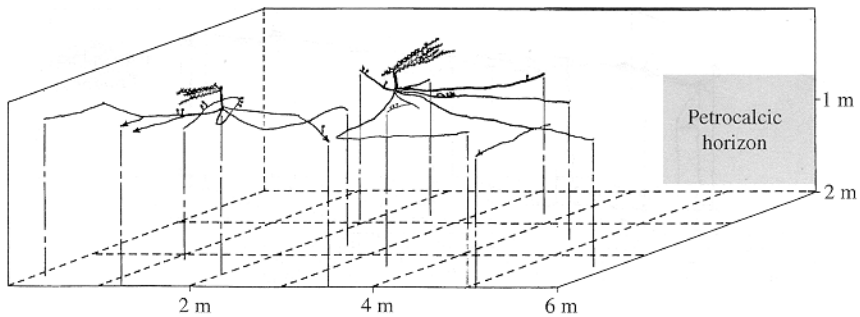


Figure 19. Two root systems of a perennial forb, three fans (*Krameria lanceolata*), growing in a coarse-loamy Argic Petrocalcic, Hueco at Site 13. Plants are spaced as in field and tops of plants are at same scale as roots and are prostrate on soil surface. Position of petrocalcic horizon is shown on back plane of figure. Roots ending in arrows were not followed further. Short roots ending in dots denote location of haustoria which were attached primarily to mesquite roots.

The four-wing saltbush and mesquite roots are portrayed in separate figures for clarity. In the soil the two root systems were interwoven and physical contact between the two root systems was not uncommon. About 2 m out from the mesquite plants roots of both species traversed a very large soil pipe which was about 2 m in diameter and > 2 m deep. No branches from traced roots extending downward into the pipe were found for either species.

Roots of two three fans (*Krameria lanceolata*) plants were excavated at Site 13 (Fig. 1). Tops of both plants were decumbent on the soil surface with branches up to 50 cm long. Root crowns were 17–20 mm in diameter and first-order, horizontally spreading roots originated at 17 to 20 cm depths (Fig. 19). At their origin the horizontal roots had diameters ranging from 5–12 mm and the rather soft, fleshy first-order branches were often still 3 mm or more in diameter at 1 m from the root crown. The plants were parasitic and large numbers of haustoria were attached to mesquite roots 20–30 mm in diameter. The haustoria on mesquite roots often occurred in clusters. Haustoria were also found on roots of black grama, tetraclea (*Tetraclea coulteri* Gray), and dwarf dalea (*Dalea nana* Torrey). Three fan roots were traced horizontally about 2.5 m at 20 to 60 cm depths but none were traced into or below the petrocalcic horizon. One first-order root grew upward from 40 to 10 cm depth before attaching to a mesquite tap root. The fine (< 1 mm diam.) second- and third-order branches often grew upward before ending. Some, but not all, of the fine roots ended with a haustoria attached to a root.

At Site 12 the root systems of black grama, mesa dropseed [*Sporobolus flexuosus* (Thurb.) Rydb.], and red threeawn (*A. purpurea*) were excavated. A diagrammatic portrayal of these root systems showing depth of penetration and lateral spread is shown in Fig. 20. Roots of all three species penetrated to slightly over 1 m depth but none penetrated very far into the indurated petrocalcic horizon. Careful examination of soil below the indurated layer failed to reveal any grass roots. Radial spread was greatest for mesa dropseed at 1.4 m. Black grama roots extended radially up to 95 cm and those of red threeawn had a radial spread of about 50 cm. Roots from the mesquite plant shown in Fig. 13 were threaded through the root systems of all three grass species. The widespreading root habit of the grasses is probably an adaptation for utilizing soil water from small rainfall events characteristic of the arid climate.

One of the common perennial forbs at Site 12 was rattlesnake weed (*Euphorbia albomarginata* Torr. & Gray). A few roots of this prostrate, rhizomatous plant are shown in Fig. 21. Rhizomes with diameters ranging from 0.7 to 2.5 mm occurred at 5–15 cm depths. Stems arising from the rhizomes had diameters ranging from 0.6 to 1.4 mm and

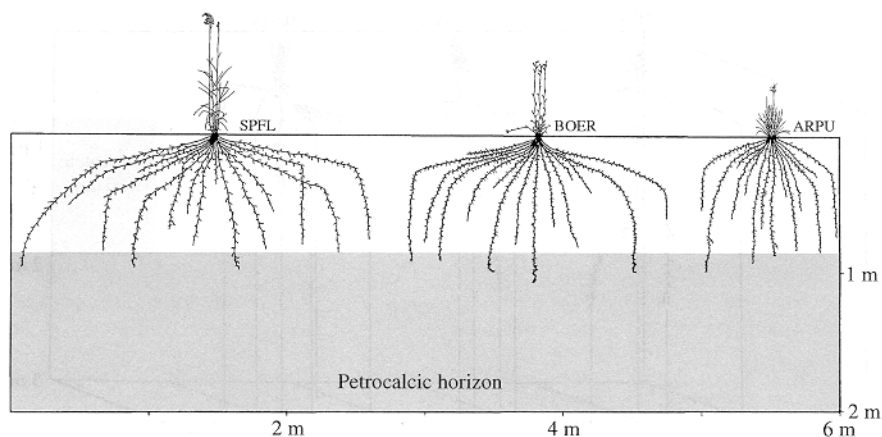


Figure 20. Root systems of the bunch grass, mesa dropseed (SPFL, *Sporobolus flexuosus*), the sod-forming grass, black grama (BOER, *Bouteloua eriopoda*), and the bunch grass, red threeawn (ARPU, *Aristida purpurea*), growing in a coarse-loamy, Argic Petrocalcic, Hueco at Site 12. Roots of all three grasses penetrated only a few cm into the petrocalcic horizon. Roots of mesquite plants were intermixed with the grass root systems.

often branched at about 2 to 3 cm depths. Roots arose from the rhizomes at irregular intervals and beginning diameters where 0.5 to 0.9 mm. Short second-order branches were rather sparse. Roots were traced to a depth of 83 cm which was the top of the indurated caliche.

Roots of an infrequent perennial forb, wooly-white (*Hymenopappus flavescens* Gray var. *canotomentosus* Gray) were also excavated at Site 12 (Fig. 21). This 1.3 m tall forb

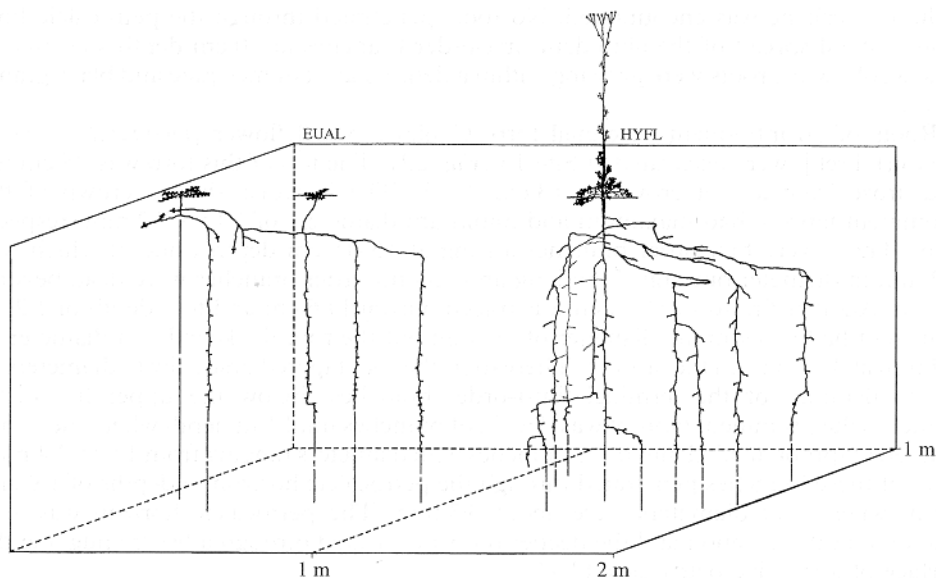


Figure 21. Root systems of two perennial forbs, rattlesnake weed (EUAL, *Euphorbia albomarginata*) and wooly-white (HYFL, *Hymenopappus flavescens*), growing in a coarse-loamy, Argic Petrocalcic, Hueco at Site 12. Horizontal lines at base of plants denotes soil surface and plant tops are drawn at same scale as roots. Roots ending in arrows were not followed further. Roots of both species penetrated into but not through the petrocalcic horizon.

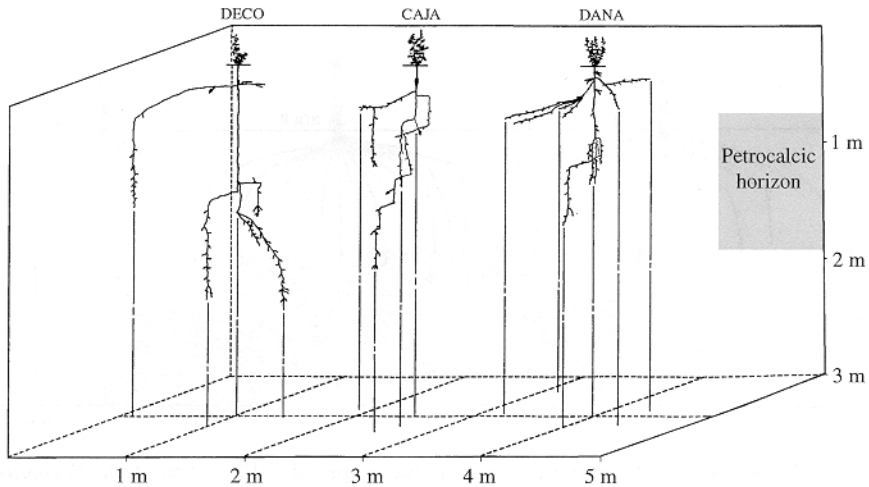


Figure 22. Root systems of three perennial forbs, Cooley's bundleflower (DECO, *Desmanthus cooleyi*), caesalpinia (CAJA, *Caesalpinia jamesii*), and dwarf dalea (DANA, *Dalea nana*), growing in a coarse-loamy Argic Petrocalcid, Hueco at Site 13. Horizontal lines at base of plants denote soil surface and location of petrocalcic horizon is shown on back plane of figure. Roots ending in arrows were not followed further. Plant tops are drawn at same scale as roots. Roots of all three species followed fissures and cracks into the petrocalcic horizon.

was growing within the canopy of the mesquite plant portrayed in Fig. 13. There was a large (14.7 mm diameter) tap root which tapered sharply to 1.9 mm diameter at 20 cm depth where the tap root forked. Only a few of the 40 first-order branches which arose from the tap root between 10 and 20 cm depth were traced. Both first-order branches and the two branches of the tap root were traced to about 86 cm depth where the indurated caliche was encountered. No roots penetrated through the petrocalcic horizon. Lateral spread of the abundant first-order branches at 30 cm depth was 50 cm. The woolly-white roots were growing within a dense matrix of mesquite and black grama roots.

Roots of an infrequent perennial forb, Cooley's bundleflower [*Desmanthus cooleyi* (Eaton) Trel.], were excavated at Site 13 (Fig. 22). The top of this forb was 25 cm tall and arose from a root crown at 13 cm depth. The irregular shaped crown of the prominent taproot had maximum and minimum diameters of 10.5×7.2 mm, respectively. There were first-order branches arising at 15–18 cm depths, one of which was 4.2 mm in diameter but only 5 cm long and second-order branches were dead beyond 20 cm. Another first-order branch was traced outward 86 cm and to a depth of 1.2 m. This root had a beginning diameter of 1.5 mm but the root thickened to a diameter of 2.4 mm at 40 cm from the taproot. Thereafter, the root tapered gradually to diameters of 0.1 to 0.4 mm for the terminal third-order branches. Below the upper first-order branches the prominent taproot was devoid of branches until 1 m depth where the 7 mm diameter taproot divided into three branches with diameters ranging from 1.9 to 2.4 mm. Two of these branches penetrated through the petrocalcic horizon to depths of 1.9 and 2.1 m where root diameters were about 0.3 mm. The petrocalcic horizon was very fractured at this location and the deeper roots penetrated through a fissure hugging the surface of a massive petrocalcic block.

The roots of a fairly common perennial forb, caesalpinia [*Caesalpinia jamesii* (Torr. & Gray) Fisher] shown in Fig. 22 were also excavated at Site 13. The plant top had three branches and a height of 31 cm. Stem diameter above the prominent corm was 8.1 mm with the top branches arising at 1 cm depth. The carrot-shaped corm, with a maximum diameter of 26 mm was about 7 cm long. Prominent first-order branches, 1.3 to 2.4 mm

in diameter originated between 17 and 25 cm depths. The tap root branched at 47 cm depth and one branch was traced into the petrocalcic horizon to a depth of 1.6 m where terminal branches were about 0.3 mm in diameter. The tap root of another caesalpinia plant was excavated at this site but is not illustrated. The corm was much larger than that of the plant in Fig. 22 with a maximum diameter of 32 mm and a length of 20 cm. The stem, originating from the top of the corm at 12 cm depth was 15 mm in diameter and seven top branches originated at 3 cm depth. A large first-order root arose at 24 cm depth. The tap root, which branched at 1.5 m, was traced through a fracture in the petrocalcic horizon to a depth of 1.95 m.

The access trench at Site 13 was positioned so that roots of a fairly frequently occurring perennial forb, dwarf dalea (*D. nana*), could be excavated. The plant was 16 cm tall with 16 stems. Top of the tap root was 5.3 mm in diameter and 1.3 mm in diameter at 60 cm depth where it divided into many branches (Fig. 22). There were numerous first-order branches from the upper 30 cm of the tap root and some of these extended outward > 80 cm. From 60 to 90 cm depth the numerous first- and second-order branches grew in all directions among the caliche nodules and were traced through fractures in the petrocalcic horizon to 1.3 m depth. Third-order branches usually arose in clusters of 3–5 roots with 4–5 clusters per cm of second-order root. Haustoria of three fans were found on two of the dwarf dalea roots at about 20 cm depth.

At Site 15, three root systems of a very common perennial forb, twin-leaf senna (*Cassia bauhinioides* Gray) were excavated, one of which is shown in Fig. 23. The

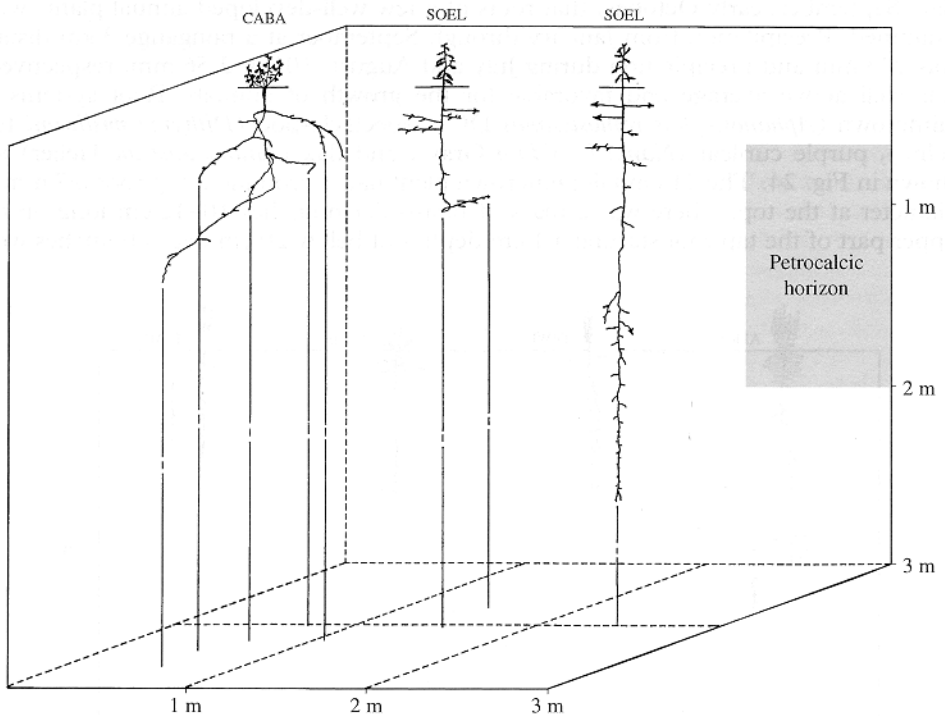


Figure 23. Root systems of two perennial forbs, two-leaf senna (CABA, *Cassia bauhinioides*) and silverleaf nightshade (SOEL, *Solanum elaeagnifolium*), growing in a coarse-loamy, Argic Petrocalcic, Hueco at Site 15. Horizontal lines at base of plants denote soil surface and position of petrocalcic horizon is shown on back plane of figure. Plant tops are drawn at same scale as roots. Roots ending in arrows were not followed further. The two-leaf senna roots and roots of one silverleaf nightshade plant penetrated into but not through the petrocalcic horizon. The other silver leaf nightshade root extended through the petrocalcic horizon to 2.3 m depth.

portrayed plant was 18 cm tall with five branches. The upper portion of the tap roots of all three excavated plants were fairly large and prominent. The tap root of the plant portrayed in Fig. 23 was 7 mm in diameter at the top and 6 mm in diameter at 12 cm depth where the first major first-order branch arose. At 35 cm depth the tap root was only 1.4 mm in diameter and below 50 cm depth roots were < 1 mm in diameter. The tap root of the plant shown in Fig. 23 were traced into a fissure in the petrocalcic horizon to a depth of 85 cm. Roots of one of the other dwarf dalea plants were traced to a depth of 1.7 m.

Four silverleaf nightshade (*S. elaeagnifolium*) plants were also excavated at site 15 and two of the plants are shown in Fig. 23. All of the excavated plants were about 20–25 cm tall with 1 to 3 stems. Stems originated from extensive rhizomes 2–3 mm in diameter, usually at depths between 6 and 12 cm. Roots originated from the same rhizomes and usually there was a prominent root associated with each top. Rhizomes originated from roots at depths up to 30 cm. Underground portions of stems were about 3 mm in diameter and upper portions of roots about the same diameter. Major roots had the characteristics of tap roots and penetrated downward with a very gradual loss in diameter. Of the four plants excavated, roots of two terminated in a very contorted manner on top of the petrocalcic material at depths of 68 and 90 cm. However, roots of the other two plants were traced through the petrocalcic horizon. The deeper rooted plant shown in Fig. 23 ended at 2.14 m depth with a terminal diameter of 0.2 mm. The root of the other plant was lost at a depth of 2.3 m with a diameter of 0.8 mm and could have reached greater depths.

Excavations at Sites 13 and 14 were made late enough in the 1993 growing season (late September, early October) that roots of a few well-developed annual plants were examined. Precipitation from January through September at a raingauge 3 km distant was 243 mm and precipitation during July and August, 101 and 56 mm, respectively, was well above average and favorable for the growth of annuals. Root systems of faintcrown (*Aphanostephus ramosissimus* DC.), spectacle-pod (*Dithyrea wislizenii* Engelm.), purple curleaf (*Nama hispidum* Gray), and flax (*Linum australe* Heller) are shown in Fig. 24. The 21 cm tall faintcrown plant had a prominent tap root 0.7 mm in diameter at the top. There was a mass of first-order branches 10–12 cm long on the upper part of the tap root starting a 1 cm depth but below 20 cm depth branches were

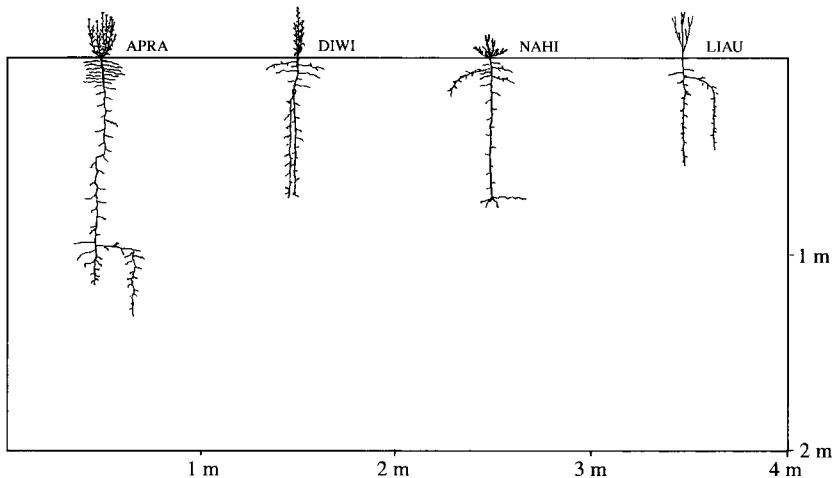


Figure 24. Root systems of annual forbs, faintcrown (APRA, *Aphanostephus ramosissimus*), spectacle-pod (DIWI, *Dimorphocarpa wislizenii*), purple curleaf (NAHI, *Nama hispidum*) and flax (LIAU, *Linum australe*), growing in a coarse-loamy, Argic Petrocalcic, Hueco at Sites 13 and 14. Plant tops are drawn at same scale as roots. Only roots of faintcrown penetrated into the petrocalcic horizon.

less numerous. The root was traced into the petrocalcic horizon to a depth of 1.3 m. The 24 cm tall spectacle-pod plant had a number of relatively short horizontal branches in the top 20 cm of soil and the 3 mm diameter, branched tap root was traced to the top of the petrocalcic horizon at a depth of 75 cm. The purple curleaf plant was only 10 cm tall but about 15 cm in diameter. Although the top of the tap root was 4 mm in diameter it was only 0.6 mm in diameter at 50 cm depth. The larger roots had a dark-colored, rough, bark-like outer layer which sloughed off easily. A 20 cm long first-order branch arose at 13 cm depth but most of the upper first-order branches were < 10 cm long. The tap root was traced to the top of the petrocalcic horizon at 74 cm depth. Another purple curleaf plant root (not illustrated) was traced into the petrocalcic horizon to 1.2 m depth. The flax plant was 23 cm tall and had a very sparse root system. The root was 2.3 mm in diameter at the top and 0.1 mm in diameter when it terminated at 64 cm depth. There was only one prominent first-order branch at 10 cm depth and other first- and second-order branches were short and only averaged about 4 per cm of root length. The depths attained by faintcrown and purple rolleaf roots indicate that annuals have the ability to exploit soil water in fissures of the petrocalcic horizon as well as at shallower depths. Root development of annual plants is undoubtedly greatly influenced by rainfall distribution during the growing season and for this reason only a few annual plant root systems were examined.

Site 16 (Fig. 1) is in an area where mesquite has invaded black grama grassland, very similar to the area where Sites 12 to 14 are located. Soils exposed by the access trench, which was excavated as much to determine soil type as for root studies, were primarily a coarse, loamy Typic Haplocalcid, Simona with a Typic Petrocalcic, moderately deep analog of Simona, also occurring. Slope is 0.25% to the east. Caliche nodules were common below 20 cm depth but an indurated petrocalcic horizon was not encountered until about 75 cm depth. A few roots from a mesquite plant 68 cm tall and 1.5 m in diameter were excavated and mapped (Fig. 25). The root crown was 42 mm in diameter and the taproot was 15 mm in diameter at 1.2 m depth where it divided into two branches 10 and 9 mm in diameter. The tap root branches were traced to 2.3 m depth but they undoubtedly penetrated much deeper. One first-order branch was traced from its origin at 15 cm depth outward 3.8 m at 15 to 20 cm depths to its end at 15 cm depth. Beginning diameter was 4.8 mm and ending diameter was 0.2 mm. Another first-order branch which arose at 25 cm depth with a diameter of 14.4 mm was traced outward to 6.5 m where, with a diameter of 3.6 mm it trifurcated into three branches with diameters of 1.3 to 1.6 mm. One of these branches was traced out to 8.4 m from the base of the plant where it ended at 51 cm depth. A large number of second-order branches originated from this long first-order branch. Some second-order branches grew upward and terminated at depths of 5 to 10 cm, with terminal diameters of 0.2 to 0.3 mm. At

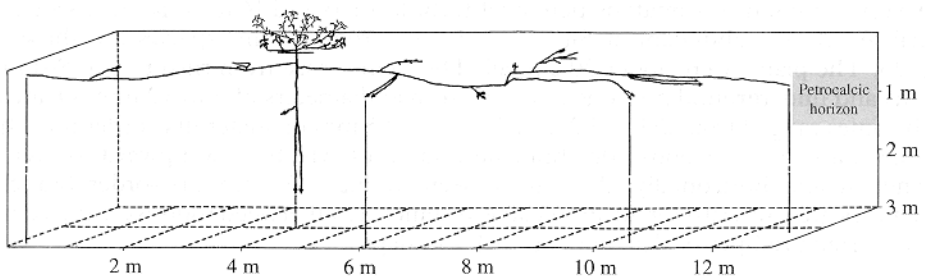


Figure 25. Roots of a small mesquite (*Prosopis glandulosa*) shrub, growing in a coarse, loamy, Typic Haplocalcid, Simona series and a Typic Petrocalcic, moderately deep analog of Simona, at Site 16. Horizontal line at base of plant denotes soil surface and position of petrocalcic horizon is shown on back plane of figure. Plant top is drawn at same scale as roots and roots ending in arrows were not followed further.

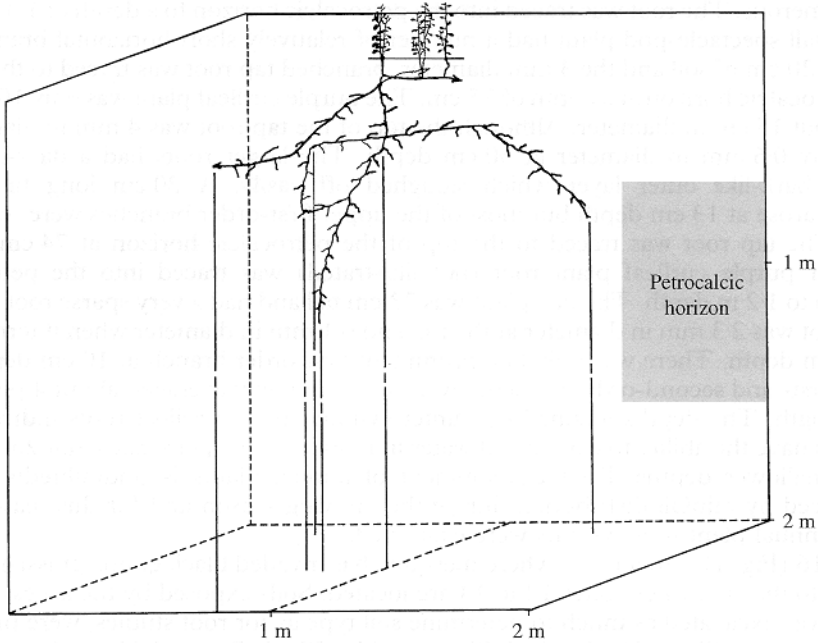


Figure 26. Roots of the rhizomatous perennial forb, leatherweed (*Croton pottsii*), growing in the coarse, loamy, Typic Petrocalcid at Site 16. Horizontal line at base of plants denotes soil surface and position of petrocalcic horizon is shown on back plane of figure. Roots ending in arrows were not followed further. Roots penetrated into the petrocalcic horizon and were intermixed with those of soaptree yucca and mesquite.

2.1 m from the base of the mesquite plant the long first-order branch grew within about 2 cm of the caudex of a soaptree yucca plant. The caudex supported two stems which were 87 and 66 cm tall. With beginning and ending diameters of 57 mm, 30 cm, respectively, the caudex extended to 73 cm depth. Roots of the yucca plant were not mapped in detail but tracing the mesquite roots exposed a root system very similar to that shown in Fig. 16. Yucca roots were interwoven with the mesquite roots and were traced outward to 4.6 m from the yucca plant base. One second-order branch 37 cm from the caudex was traced upward to within 4 cm of the soil surface. No yucca roots were observed below 70 cm depth. Although not mapped in detail roots of mesa dropseed and black grama were traced to depths of 1.1 and 1.0 m, respectively.

A very common rhizomatous perennial forb, leatherweed [*Croton pottsii* (Klotzsch) Muell.-Arg.], was abundant at Site 16 and a few roots of this species are shown in Fig. 26. The plants were about 20 cm tall. The stems arose from rhizomes at 8–11 cm depths and underground portions of the stems had diameters of 3 to 12 mm. Diameter of rhizomes ranged from 2.3 to 3.2 mm. The 1.5–2.5 mm diameter first-order roots had a large number of second-order branches, some of which grew upward as well as downward and horizontally. As can be seen in Fig. 26 even first-order branches sometimes grew upward for an appreciable distance. Leatherweed roots were traced into the very fractured petrocalcic horizon to 1.4 m depth.

Root systems of plants in miscellaneous dominance types

At Site 11 (Fig. 1) mesquite is invading a tobosa and burrograss dominated ephemeral lake basin. Soils at this nearly level site are fine-silty, Ustic Haplocalcids, Reagan.

A buried soil occurred at 3.2 m depth and is discussed briefly in Gile *et al.* (1997). Reagan is the same soil series in which crucifixion thorn roots were excavated and morphological details can be found in Gile *et al.* (1995). Roots of a small mesquite plant 60 cm tall and 90 in diameter growing in a dense tobosa sod were excavated. Water sprays were used to expose a portion of the upper part of the root system but continual soaking led to trench wall instability so icepicks were used to trace the majority of the roots excavated at this site.

The very prominent tap root of the mesquite plant (a drawing of this root system is in Gile *et al.*, 1997) had a beginning diameter of 29 mm and was traced to a depth of 5.5 m. At this depth the root turned horizontally and began growing away from the trench and was not traced further although it still had a diameter of 2.9 mm. In the upper 1 m of soil horizontal first-order branches were fairly well developed and were traced outward to nearly 3 m. At 70 cm depth a first-order branch originated which had an upward growing second-order branch and subsequent fourth- and fifth-order branches extended to within 5 cm of the soil surface. There were also upward growing second- and third-order branches from first-order roots originating at shallower depths close to the base of the plant. The soil was occupied with a mass of tobosa roots to a depth of 60 cm and these extended downward at reduced density to 1.4 m depth. Tobosa roots had no apparent influence on the mesquite roots. Below 1 m depth the first-order mesquite roots grew downward rather than horizontally. Between depths of 1.5 and 3.2 m the soil was very compact and there were very few fine branches on the tap root and the first-order branches. Below 3.2 m fine roots were more abundant even though the soil was still compacted. From 4.2 to 5 m depth the tap root extended downward within a krotovina (fill of tunnel made by rodents) and fine branches were very abundant.

Roots of a mesquite plant only 17 cm tall and with what appeared to be about nine growth rings were excavated at Site 11 (Fig. 27). This plant also had a prominent tap root which was 2.7 mm in diameter at 65 cm depth where a major first-order branch arose. At 1.6 m depth the tap root divided into two branches with diameters of 1.0 and 1.3 mm. One of these branches was traced to 2.7 m depth and the other to 3.2 m depth where the 0.3 mm diameter root was broken off and lost. It appears that the rooting strategy of mesquite in this grass-dominated site is to develop deeply penetrating roots first and later develop horizontally spreading roots.

Roots of a fairly common perennial forb, wooly sumpweed (*Iva dealbata* Gray), were excavated at Site 11 (Fig. 27). Excavation was done in June when the plants were only about 8 cm tall but mature plants are 30–70 cm in height. Thick rhizomes 5.4 mm in diameter occurred at about 7 cm depth and there were vertical extensions about 9 mm in diameter up to 2 cm depth where the above ground stems originated. Roots ranging in diameter from 6.3 to 3.4 mm in diameter extended downward from the rhizomes. A few first-order branches originated above 1 m depth but there was a notable lack of branches at greater depths. The two roots traced downward had diameters of 1.0 and 1.4 mm at 2.6 m depth. Roots were traced to 3 m depth but some probably extended further. A good deal of time was spent working at this site and it was noticed that where wooly sumpweed roots were severed and exposed on the sides of the trench new tops developed, even below 2 m depth. This unusual event was not observed for any other plant excavated.

At Site 7 (Fig. 1) the soil is a coarse-loamy Typic Calcicargid, *Yucca* with carbonate-free upper horizons overlying a calcic horizon extending from about 0.6 to 2 m depth. Slope is 1/4% to the south and the site is dominated by red threeawn (*A. purpurea*), with longleaf ephedra (*E. trifurca*) occurring as a codominant. A trench was dug beside what appeared to be a single longleaf ephedra plant growing from a soil pedestal about 10 cm in height. The top of the 'plant' was 60 cm tall and 1.6 m in diameter. As excavation proceeded it was found that the 'plant' was made up of four separate and distinct individuals believed to have originated from a like number of seedlings. The root crowns as well as the aerial branches were closely intertwined. Root crown diameters were

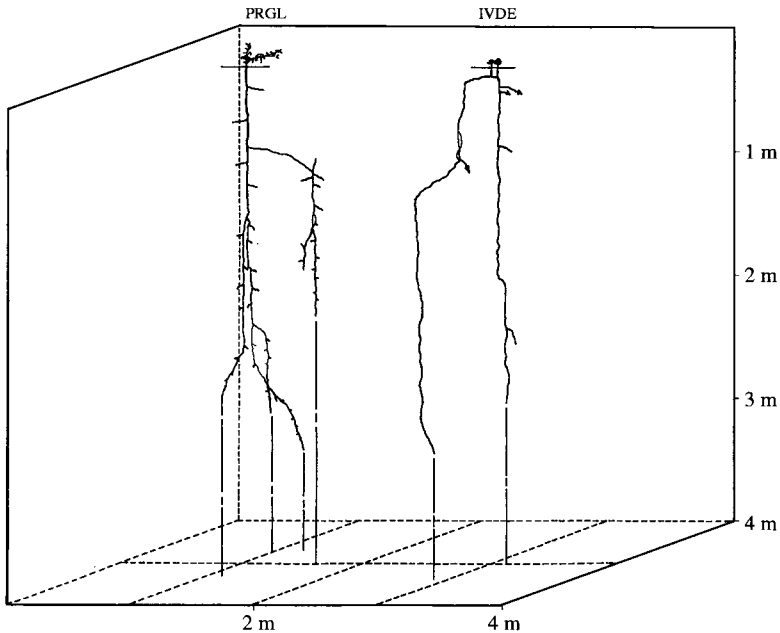


Figure 27. Roots of a small mesquite (PRGL, *Prosopis glandulosa*) shrub, and a perennial forb, woolly sumpweed (IVDE, *Iva dealbata*), growing in tobosa (*Pleuraphis mutica*) sod on a fine-silty, Ustic Haplocalcid, Reagan at Site 11. Horizontal lines at base of plants denote soil surface and plant tops are at same scale as roots. Roots ending in arrows were not followed further.

10 cm, 6 cm, 5 cm and 2 cm. Whether the plants were of the same or different ages is not known. There were no prominent tap roots and the root crowns all divided into numerous large roots at 25–30 cm depths (Fig. 28). One aerial branch 58 mm in diameter in contact with the soil 20 cm out from the crown had given rise to one small and one large (14 mm diameter) root.

Most of the roots were found between 20 and 50 cm depths. Even the major first-order branches often grew upward, e.g. from 71 to 43 cm depth, from 41 to 19 cm depth, and from 60 to 11 cm depth. Second- and third-order branches were found which grew directly upward to within 7 cm of the soil surface. Roots were traced outward 7.1 m from the root crowns and one second-order branch was traced downward through the calcic horizon into fine alluvial sands at 5 m depth. From 3.7 to 4.5 m depth there were hard calcium coated plates imbedded in dense sand and fine roots proliferated on the surface of the plates.

Roots of a purple threeawn plant 20 cm tall were excavated at Site 7. Roots were traced to 1.3 m depth (Fig. 29). Maximum horizontal spread of 1.1 m occurred at 40 cm depth. Roots of the rhizomatous wrinkled globemallow arose from a 2.6 mm diameter rhizome at 6 cm depth (Fig. 29). Tap roots of about 3 mm diameter gave rise to major first-order branches at about 90 cm depth. One tap root was traced to 1.7 m depth where it terminated with a diameter of 0.3 mm. Another tap root was traced to 3.3 m depth. From 2.5–3.3 m depth this root followed an old root channel. A 20 cm tall plant of the fairly common forb, plains zinnia (*Zinnia grandiflora* Nutt.), with two major top branches originating at 3 cm depth occurred at Site 7. The tap root, with an upper diameter of 3.3 mm, was traced to 1.5 m depth (Fig. 29). Fine, 0.2–0.4 mm diameter, first-order branches began at 24 cm depth and were quite numerous to 50 cm depth. A group of fairly long first-order branches occurred at about 1.2 m depth. One plant of the rhizomatous leatherweed (*C. pottsii*) was excavated at Site 7 (Fig. 29). The crown of

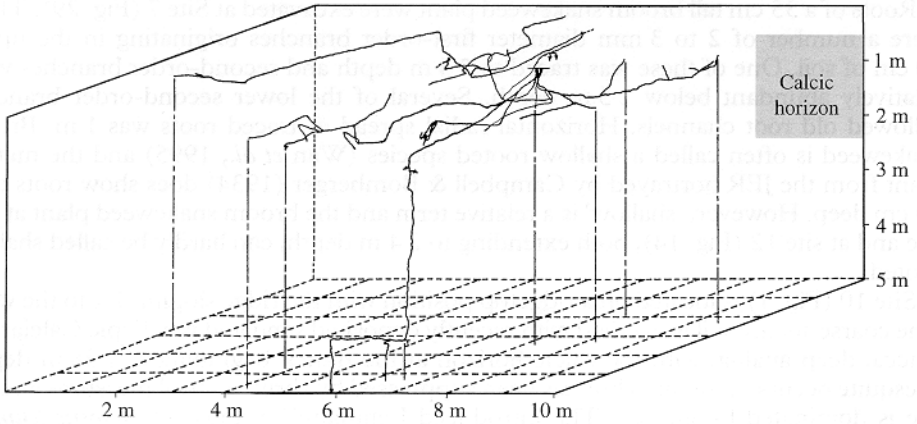


Figure 28. Root systems of the shrubby longleaf ephedra (*Ephedra trifurca*) growing in a coarse-loamy, Typic Calciorthid, Yucca at Site 7. Horizontal line at top of root crowns denotes soil surface and position of calcic horizon is shown on back plane of figure. Roots ending in dashes were dead beyond that point and roots ending in arrows were not followed further.

the tap root occurred at 5 cm depth and had a diameter of 6 mm. A rather fine rhizome (1 mm diameter) arose at 19 cm depth and extended upward to 9 cm depth where another plant occurred. Numerous short roots arose from the rhizome. There were a mass of small first-order branches arising from the tap root between 20 and 40 cm depths. At about 55 cm depth two first-order branches 0.5 mm in diameter extended outward about 45 cm. At 77 cm depth the tap root divided into several branches about 1 mm in diameter. One of these was traced to 1.6 m depth.

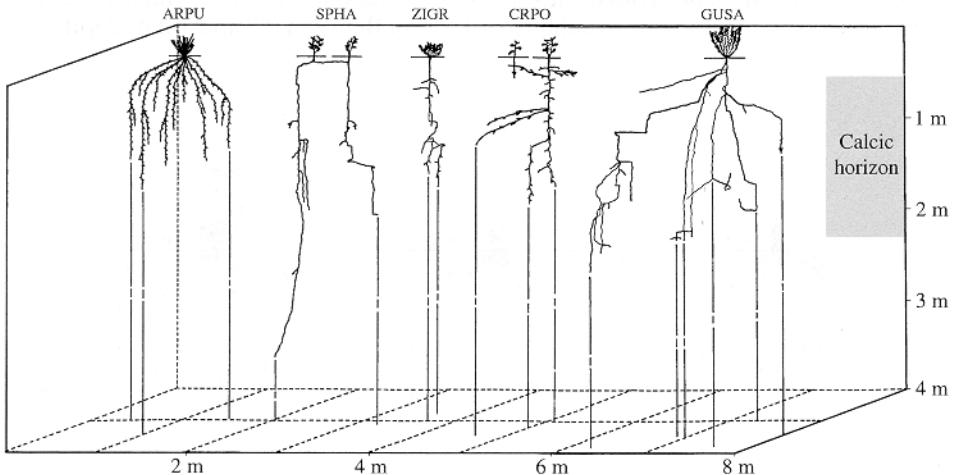


Figure 29. Root systems of a bunch grass, purple threeawn (ARPU, *Aristida purpurea*), three perennial forbs, wrinkled globemallow (SPHA, *Sphaeralcea hastulata*), desert zinnia (ZIGR, *Zinnia grandiflora*), and leatherweed (CRPO, *Croton pottsii*) and the shrubby broom snakeweed (GUSA, *Gutierrezia sarothrae*) growing in a coarse-loamy Typic Calciorthid, Yucca at Site 7. Horizontal lines at base of plants denote soil surface and position of calcic horizon is shown on back plane of figure. Plant tops are drawn at same scale as roots. Roots ending in arrows were not followed further.

Roots of a 35 cm tall broom snakeweed plant were excavated at Site 7 (Fig. 29). There were a number of 2 to 3 mm diameter first-order branches originating in the upper 20 cm of soil. One of these was traced to 2.4 m depth and second-order branches were relatively abundant below 1.5 m depth. Several of the lower second-order branches followed old root channels. Horizontal radial spread of traced roots was 1 m. Broom snakeweed is often called a shallow rooted species (Wan *et al.*, 1995) and the mature plant from the JER portrayed by Campbell & Bomberger (1934) does show roots only 60 cm deep. However, 'shallow' is a relative term and the broom snakeweed plant at this site and at site 12 (Fig. 14), both extending to 2.4 m depth, can hardly be called shallow rooted.

Site 10 (Fig. 1) is located on a ridgetop position with the ridge sloping 1% to the west. The coarse-loamy soil is overlaid with recently deposited sand and is a Typic Calciargid, Yucca, deep analog, with the calcic horizon at the trench beginning at 1.38 m depth. Mesquite occurs in this area but has been suppressed by shrub control measures and the site is dominated by grasses. The introduced Lehmann lovegrass (*Eragrostis lehmanniana* Nees.), black grama, and spike dropseed (*Sporobolus contractus* A.S. Hitchc.) are most abundant. Root systems of the above species are illustrated in Fig. 30. Roots of Lehmann lovegrass and spike dropseed were traced to depths of 1.2 and 1.3 m, respectively. Black grama roots were traced to 1.6 m depth. Roots of all three species had large radial extensions in the top 40 cm of soil. Maximum radial spread was 0.8, 1.25, and 1.35 m for black grama, Lehmann lovegrass, and spike dropseed, respectively. Root diameters within 1 cm of origin were determined for 150 roots of each species. Black grama and Lehmann lovegrass roots had a mean diameter of 0.33 and 0.42 mm, respectively, and did not differ significantly ($p > 0.05$). Spike dropseed roots, with a mean diameter of 0.44 mm, were significantly larger than both black grama and Lehmann lovegrass roots ($p < 0.05$).

Leatherweed was common at Site 10 and roots of one plant are shown in Fig. 31. Although the upper portion of root systems of a cluster of five plants were exposed, no evidence of rhizomes as at Sites 7 and 16 was found. The root crown had a diameter of 3.3 mm and one major branch with a diameter of 0.09 mm arose at 8 cm depth. At 19 cm depth the tap root divided into two major branches, both of which were traced into the calcic horizon and one to a depth of 1.78 m. Between 0.7 and 1.2 m depths there

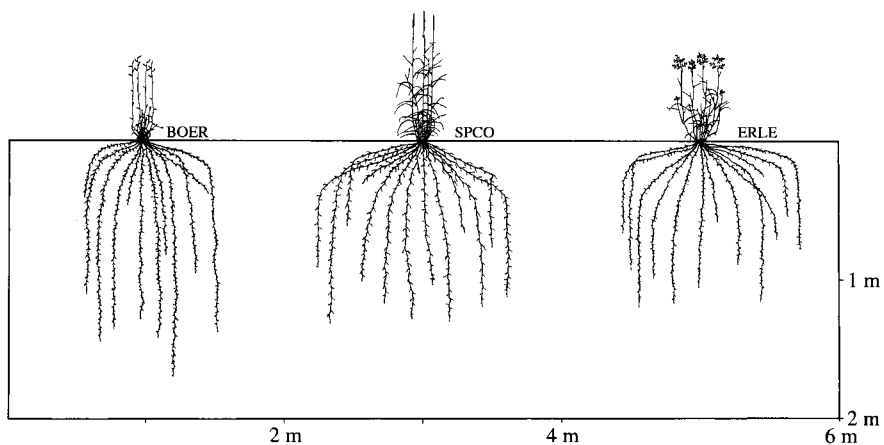


Figure 30. Root systems of a sod-forming grass, black grama (BOER, *Bouteloua eriopoda*), and two bunch grasses, spike dropseed (SPCO, *Sporobolus contractus*), and Lehmann lovegrass (ERLE, *Eragrostis lehmanniana*), growing in a coarse-loamy Typic Calciargid, Yucca deep analog at Site 10. Top of calcic horizon is at 1.38 m.

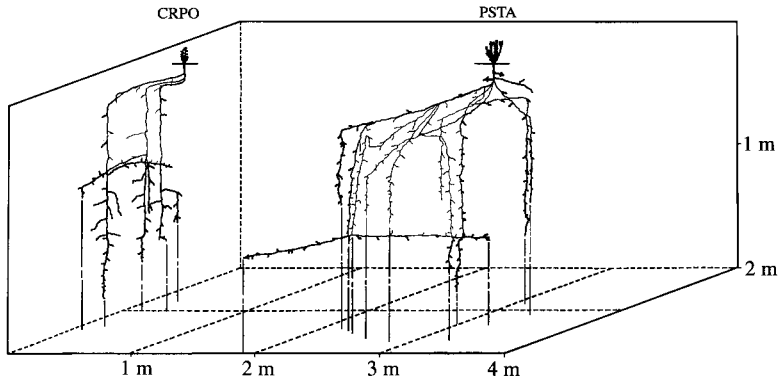


Figure 31. Root systems of two perennial forbs, leatherweed (CRPO, *Croton pottsii*) and paperflower (PSTA, *Psilostrophe tagetina*), growing in a coarse-loamy, Typic Calciargid, Yucca deep analog at Site 10. Roots ending in arrows were not followed further. Roots of both species penetrated into the calcic horizon which began at 1.38 m.

were about two second-order branches per cm of first-order root length and some grew horizontally for up to 40 cm.

Roots of paperflower [*Psilostrophe tagetina* (Nutt.) Rydb.], a perennial forb, were also excavated at Site 10 (Fig. 31). The rather massive root crown had a diameter of 11.4 mm and the tap root was still 11 mm in diameter at 14 cm depth where it divided into 3 branches with diameters ranging between 3.2 to 4.5 mm. Root diameters decreased rapidly with increasing depth and below 50 cm all roots were < 1 mm in diameter. One third-order branch divided at 1.2 m depth and the 0.3 mm branches grew horizontally on top of the calcic horizon (Fig. 31). Most of the profusely branched root system was above the calcic horizon but roots did penetrate into the calcic horizon to 1.76 m depth.

At Site 18 (Fig. 1), which slopes 1/2% to the north-west, a Typic Petrogypsid soil is dominated by gypgrass (*Sporobolus nealleyi* Vasey). Roots of Torrey's ephedra (*Ephedra torreyana* Wats.), a shrub characteristic of gypsiferous areas, were excavated (Fig. 32). The top of the excavated plant was 33 cm tall and 65 cm in diameter and branches were decumbent upon a soil pedestal about 3–4 cm in height. The root crown was 4.5 cm in diameter and large first-order branches with diameters ranging from 8 to 18 mm arose between 15 and 27 cm depths. These first-order branches lost diameter slowly but followed extremely contorted paths (Fig. 32). Overall, the gypsum was dense but some areas were so dense that roots did not penetrate. No roots were traced below 70 cm

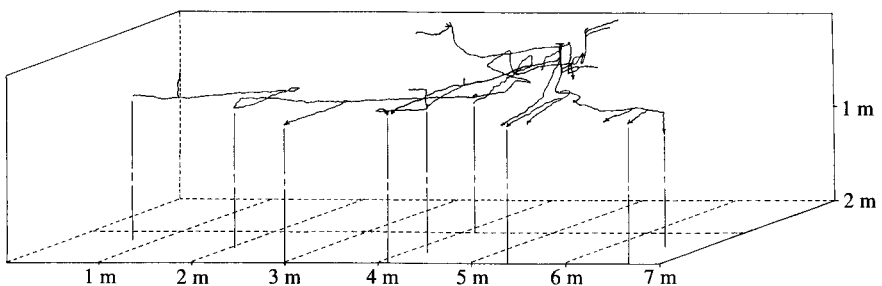


Figure 32. Root system of a Torrey's ephedra (*Ephedra torreyana*) shrub growing in a Typic Petrogypsid at Site 18. Horizontal line at top of root crown denotes soil surface. Roots ending in arrows were not followed further. Note upward growing roots.

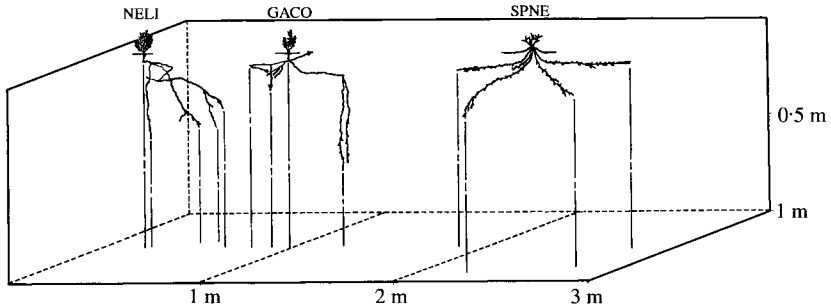


Figure 33. Root systems of two perennial forbs, White Sands mustard (NELI, *Nerisyrenia linearifolia*), and scarlet gaura (GACO, *Gaura coccinea*), and a bunchgrass, gypgrass (SPNE, *Sporobolus nealleyi*), growing in a Typic Petrogypsid at Site 18. Horizontal lines at base of plants denote soil surface. Gypgrass plants were almost always pedestaled. Roots ending in arrows were not followed further. Plant tops are drawn to same scale as roots.

depth, the 2 m depth shown in Fig. 32 is to provide visual clarity only. It is likely root depth was limited by water penetration rather than soil density. One root with a terminal diameter of 0.2 mm was traced horizontally 4.4 m. Roots frequently grew vertically, e.g. from 35 cm depth to within 4 cm of the soil surface.

Gypgrass crowns occurred on soil pedestals 2–7 cm tall and the centers of the crowns were often dead, so that the plant looked like a bird's nest. Height of plants was about 7 cm. Roots of gypgrass were traced to 19 cm depth but most spread horizontally up to 53 cm between 4 and 10 cm depths (Fig. 33). Main roots had an average diameter of 0.33 mm with first-order branches being 0.14–0.16 mm in diameter and the fine second-order branches had diameters of 0.02–0.03 mm. There were usually 10–15 roots originating from each crown segment.

Scarlet gaura (*Gaura coccinea* Pursh) and White Sands mustard [*Nerisyrenia linearifolia* (Wats) Greene] are two perennial forbs commonly found on gypsum areas. Roots of both species were excavated (Fig. 33). The scarlet gaura plant was 12 cm tall with a root crown 2.7 mm in diameter. Major roots had beginning diameters of about 1.3 mm but terminal portions were only 0.3 mm in diameter. Roots were traced horizontally 28 cm and to 62 cm depth. Most of the roots occurred between 8 and 12 cm depths. The White Sands mustard plant was 13 cm tall. The tap root had a diameter of 1.65 mm and the major branches diameters of about 1.2 mm 30 cm from their origin. Roots extended outward 42 cm from the base of the plant and were traced to 47 cm depth. There were few branches except on the distal portions of major roots.

Discussion and conclusions

The foregoing descriptions of root systems provide evidence that the extent and plasticity of shrub root systems is a contributing factor to the success of this plant life form in this arid environment. The root systems of creosotebush, mesquite, and tarbush, all of which have increased their area of dominance in recent times (Buffington and Herbel, 1963), have several common characteristics. (1) Roots spreading horizontally from a few to many meters at shallow soil depths and can access soil water resulting from the common small rainfall events; (2) A small but significant number of roots penetrate through calcic and petrocalcic horizons, accessing soil water from soil horizons where recharge is infrequent but may be crucial in sustaining plants during extended droughts; (3) All three species exhibit similar root systems in a wide variety of soils although mesquite is the most ubiquitous of the three in this respect. Root systems

of other shrubs, crucifixion thorn, fourwing saltbush, longleaf ephedra, Berlandier's wolfberry, winterfat, and broom snakeweed also are both widespreading and deeply penetrating. Soaptree yucca was the only shrub-like species which did not penetrate deeply. Only Petrogypsid soils restricted rooting depth of shrubs to less than 1 m.

It has been hypothesized that resource islands which develop under the canopy of the deeply rooted shrubs contributes to their success (Schlesinger *et al.*, 1990). It is not known whether the upper soil layers in these resource islands are irrigated through the upward nocturnal transport and release of water by roots, the 'hydraulic lift' phenomenon which has been documented for shrubs in arid environments (Richards & Caldwell, 1987; Caldwell & Richards 1989) and for trees in a mesic environment (Dawson, 1993). Hydraulic lift has been found to occur in broom snakeweed (Wan *et al.*, 1993) and it is a distinct possibility for the other shrub species examined. The shrub roots which penetrated to 5 m or more are presumed to result from roots following deeply penetrating wetting fronts since roots do not normally grow into dry soil (Portas & Taylor, 1976). However, both upward and downward transport of water to dry soil layers has been demonstrated for trees (Burgess *et al.*, 1998) and it is possible that a reverse hydraulic lift would allow roots to penetrate dry soils (Caldwell *et al.*, 1998). Reverse hydraulic lift has been demonstrated in dry Kalahari sands (Schulze *et al.*, 1998) where the deepest recorded roots (68 m) occur (Canadell *et al.*, 1996). Mesquite roots have been found at 53 m depth on a mountain slope in the Sonoran Desert (Phillips, 1963) and mesquite roots often reach relatively shallow (< 10 m) permanent water tables allowing the plant to function as a phreatophyte (Rundel & Nobel, 1991). However, given the relative small diameters of roots found at 5-m depth and the fact that it is necessary to drill to about 90 m deep to reach permanent water tables in the Jornada Basin it is unlikely that roots of any of the shrubs examined have reached permanent water. Also, the energetic costs of root construction (Lambers, 1987; Eissenstat, 1992) make such extension unlikely.

Fine roots have been variously defined as those with diameters < 1 mm (e.g. Fahey & Hughes, 1994), < 3 mm (e.g. Burke & Raynal, 1985), or, most commonly, < 2 mm (e.g. Hendricks *et al.*, 1993). Irrespective of diameter, the fine root component is recognized as critical in acquisition of essential plant resources. Minirhizotron studies in the Chihuahuan Desert indicated that the fine roots of creosotebush and mesquite have a low turnover rate with calculated life spans of about 3–8 years and 2–5 years, respectively (Reynolds *et al.*, 1999). Given such longevity, it is likely the fine roots probably display the 'rectifier-like' properties preventing water loss from roots to soil as has been found for desert succulents (Nobel & Sanderson, 1984). During the root excavations, which in the case of shrubs often took two or more weeks, it was noted on several occasions in spring and early summer when soils were very dry that shrub species initiated new roots after the application of water in the excavation process. This is an indication that a flush of root growth may occur after rainfall events, analogous to the 'rain roots' documented for other species (Jordan & Nobel, 1984).

The presence of upward growing roots, particularly common for mesquite and soaptree yucca but also found on tarbush, Berlandier's wolfberry, winterfat, and the ephedra's and with an extreme example in crucifixion thorn, is an interesting adaptation allowing the plants to capture soil water at shallow depths. A logical assumption is that these roots develop due to a hydrotropic response overriding the normal positive geotrophic response. That a positive geotrophism is not universal for roots is shown by roots which grow upslope (Cannon, 1911; Hellmers *et al.*, 1955) and like a shrub in the Negev Desert exploit the higher soil water present in the upslope position (Herwitz & Olsvig-Whittaker, 1989). A hydrotrophic root response was noted at a very early date Darwin (1881) and Hooker (1915), both quoted in Loomis & Ewan (1936), who tested many species from 29 genera and 14 families for hydrotropic responses and concluded that hydrotropic responses are not universal and probably genetically controlled. Recent experiments using a pea mutant with ageotropic roots have demonstrated that

hydrotropic responses are real and separate from geotropic responses (Jaffe *et al.*, 1985; Takahashi & Suge, 1991; Stinemetz *et al.*, 1996). Although all of the details have not been elucidated, it is well established that trophic responses originate in the root cap (Sievers & Hensel, 1991) and this is true of hydrotropism as well (Takano *et al.*, 1995). The shrub root systems excavated all show some evidence of hydrotropic responses. It is easy to envision soil wetting fronts which would cause upward or horizontal growth. However, it is not clear what would cause a root which has traveled several meters in a horizontal direction to suddenly turn and grow downward although a change in soil temperature is one possibility (Rundel & Nobel, 1991). Roots have evolved to become sophisticated biological probes (Atwell, 1993) and it is the accumulated tropistic responses of individual roots which determines the ultimate shape of root systems (Takahashi, 1994).

The grass root systems excavated in sandy soils, e.g. black grama, mesa and spike dropseed, and red threeawn, had a large radial spread which is assumed to be an adaptation to capture more of the soil water resulting from small rain fall events. The horizontal extension was similar to the 50–100 cm extension given as an average for grass root systems in arid Russian steppes (Titlyanova *et al.*, 1999). Root systems of grasses in the lowland sites were usually not so widespread and resembled those of grasses growing in wetter environments where roots tend to grow straight down from crowns (Weaver & Darland, 1949). It is likely that soil texture and soil water retention time has a major influence on horizontal spread of grass roots. Grass roots penetrated into but not through the calcic horizons, particularly the petrocalcic ones. It has been hypothesized that black grama was able to survive severe droughts such as that of the 1950s on shallow soils because the petrocalcic horizons held soil water within reach of the grass roots while on deeper soils the water percolated to depths below the reach of grass roots (Herbel *et al.*, 1972). This may be the case. However, petrocalcic caliche can absorb 13% by weight of water (Hennessy *et al.*, 1983). It can be hypothesized that this water is slowly released by evaporation and subsequent condensation makes it available to plants and thus it might be a more important source of water than that held temporarily in a 'perched' position. The interaction between roots and the petrocalcic horizons certainly needs further exploration.

Root systems of perennial forbs were quite variable between species and sites but tended to be relatively deep-rooted at most sites. Some, like leatherweed, were well equipped with horizontal roots close to the surface as well as deeply penetrating roots. Others, such as wrinkled globemallow, had extensive branches only at considerable depths, an advantage during droughts. The root systems of the few annual forbs excavated reached rather surprising depths but too few specimens were studied to allow any generalizations to be drawn. More extensive studies of summer and winter annuals show rooting depths are usually less than 0.5 m (Cannon, 1911; Forseth *et al.*, 1984).

In all of the plant communities where roots were excavated in this study the roots of shrubs, grasses and forbs were highly intermingled and inter- and intra-specific overlap and even contact was common in the upper soil horizons. Many factors other than mere proximity can affect root competition for soil resources (Caldwell, 1987). However it seems safe to assume that the high degree of root intermingling means that competition for soil water and nutrients occurs in upper soil horizons. Neighbor-removal experiments have shown that competition for soil water occurs in some desert communities (Fonteyn & Mahall, 1981; Robberecht *et al.*, 1983) but not between all co-occurring species due to stratification of root systems (Manning & Barbour, 1988). The only obvious stratification of the root systems examined here was that grass roots rarely extended below 1.5 m depth while shrub and some perennial forb roots usually penetrated to much greater depths. Mahall & Callaway (1992) have demonstrated that the interactions between roots of creosotebush and the co-occurring shrub *Ambrosia dumosa* are more complex than simple competition for a limiting resource. Also, subtle differences were found in the differential response of a clonal grass when rhizomes and

roots contacted different neighbor grass species (Huber-Sannwald *et al.*, 1999). In the plant communities studied here detailed studies might detect specific interference patterns among the highly intermixed root systems although there were no obvious avoidance patterns. Given the high degree of inter- and intra-specific overlap of creosotebush and tarbush root systems which was found, a plausible hypothesis is that such overlap, particularly under the canopy of neighbors is advantageous. Stem flow enhances water and nutrient status under shrub crowns (Mauchamp & Janeau, 1995; Martinez-Meza & Whitford, 1996; Whitford *et al.*, 1997) and the more of these enhanced sources an individual has access to in addition to its own would be a competitive advantage.

With the exception of the parasitic *Krameria lanceolata*, no examples of intra- or inter-specific root grafting were encountered. Significant populations of mesquite nodulating rhizobia have been found at 1–4 m depths in Jornada Basin soils, including mesquite dunelands, (Jenkins *et al.*, 1988) but nodules were found on mesquite roots only below 3 m depth in a playa where soil water content was relatively high. No nodules were found on any mesquite roots excavated in this study. It is quite possible that all of the root systems are linked through fungal hyphae (Reed, 1997). Fungi have been found associated with many desert plants (Bloss, 1985) and play an important role in water and nutrient acquisition (Cui & Nobel, 1992; Barrow *et al.*, 1997).

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