ROOT DEPLOYMENT AND SHOOT GROWTH FOR TWO DESERT SPECIES IN RESPONSE TO SOIL ROCKINESS[1]

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Soil texture, as well as the presence of rocks, can determine the water status, growth, and distribution of plants in arid environments. The effects of soil rockiness and soil particle size distribution on shoot and root growth, root system size, rooting depth, and water relations were therefore investigated for the Crassulacean acid metabolism leaf succulent *Agave deserti* and the C_4 bunchgrass *Pleuraphis rigida* after precipitation events during the summer and winter/spring rainfall periods in the northwestern Sonoran Desert. The soils at the field site varied from sandy (<3% rocks by volume) to rocky (up to 35% rocks), with greater water availability at higher water potentials for sandy than for rocky soils. Although *A. deserti* was absent from the sandiest sites, its shoot and root growth during both rainfall periods were greatest in comparatively sandier sites and decreased as the soil rock content increased. Furthermore, *A. deserti* had twofold greater root surface area, root : leaf area ratio, and mean rooting depth at sandier than at rocky sites. As for *A. deserti*, shoot growth was greater for *P. rigida* at the sandier sites than at the rockier sites, even though its root surface area and mean rooting depth did not vary significantly. After early spring rainfall events, the leaf water potential for *A. deserti* did not differ between rocky and sandy sites, but transpiration rates were almost twofold greater at rocky than at sandy sites. During the same period, *P. rigida* had lower leaf water potentials and 25% lower transpiration rates at rocky than at sandy sites. The greater variability in the deployment of the root systems of *A. deserti* in response to soil rockiness may reflect its evergreen habit and slower growth, which allow it to endure periods of lower water availability than does *P. rigida*, whose leaves die during drought.

Key words: *Agave deserti*; drought; *Pleuraphis rigida*; rocks; root plasticity; rooting depth; Sonoran Desert.

Root plasticity, as shown by the ability of root systems to make structural and physiological adjustments in response to varying resources, can be critical for plant success in environments with limited resources that are heterogeneous in time or space (Jackson and Caldwell, 1993; Fitter, 1994). Despite the general aridity of warm deserts, soil moisture can be spatially heterogeneous due to microhabitat differences in soil texture, depth, and rockiness (McAuliffe, 1994). At Agave Hill in the northwestern Sonoran Desert, USA, granite outcroppings and subsurface rocks create such heterogeneous soil habitats, and several species occur preferentially in either the rocky outcrops or the more sandy sites (Zabriskie, 1979). For example, several succulent species, such as *Agave deserti*, tend to occupy rocky microhabitats, whereas the bunchgrass *Pleuraphis rigida* occurs in both rocky and sandy sites but is the dominant perennial only in the latter (Zabriskie, 1979; McAuliffe, 1994). The disparity in distribution for the two species suggests that their root systems might vary in response to soil rockiness.

Rocks alter the physical properties of soils in ways that can increase water availability. Surface and subsurface rock fragments can act as mulch, reducing evaporation from the soil (van Wesemael et al., 1996). In addition, soil water potentials under and near rocks can be higher than in adjacent rock-free regions, due to condensation and reduced evaporation (Nobel, Miller, and Graham, 1992). In dry forests and chaparral, rocks themselves can store as much water as is available for plant use from the soil (Jones and Graham, 1993; Zwieniecki and Newton, 1996). On the other hand, rocks replace equivalent volumes of soil, thereby reducing the amount of space penetrable by roots. Fragmentation of belowground space, as can occur due to rocks, alters root architecture and deployment and may significantly reduce resource acquisition and plant growth (McConnaughay and Bazzaz, 1992). Possible differences in soil texture in association with soil rockiness, such as soil porosity, can also have far-reaching effects on root architecture and plant water uptake (Sperry et al., 1998; Hacke et al., 2000).

The effects of soil rockiness on root growth, distribution, and surface area and on leaf production were investigated after rainfalls during late summer and winter/early spring for *A. deserti* and *P. rigida* at Agave Hill. Along with differences in microhabitat preference, the species differ with respect to growth rate, metabolism, and phenology. *Agave deserti* is a slow-growing leaf succulent with Crassulacean acid metabolism (CAM) that does not take up water when the soil water potential is lower than about -1.0 MPa (Jordan and Nobel, 1984; Nobel, 1988). In contrast, *P. rigida* is a C_4 bunchgrass that can take up water when the soil water potential is as low as -2.8 MPa and whose leaves can have high transpiration rates (Nobel, 1981). Root surface area and root distribution with depth were measured, and plant success in the different microhabitats was assessed by measuring new leaf production and plant water relations after summer and winter rainfalls.

MATERIALS AND METHODS

Field site and plant material—Agave Hill is in the northwestern Sonoran Desert in the University of California Philip L. Boyd Deep Canyon Desert Research Center at 33°38′ N, 116°24′ W, and 820 m elevation. The terrain is

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characterized by locally abundant rocky outcrops and subsurface rocks interspersed with coarse-sand flats. Rainfall, which annually averages 220 mm, is seasonally bimodal, with 20% more rain in the winter/early spring than in the late summer (Drennan and Nobel, 1997). *Agave deserti* Engelm. (Agavaceae) and *Pleuraphis rigida* Thurb. (Poaceae) [formerly *Hilaria rigida* (Thurb.) Benth. ex Scribn.] are codominant perennials, representing 33 and 15%, respectively, of the total ground cover at Agave Hill (Drennan and Nobel, 1997). In sandy microhabitats, *P. rigida* can compose over 50% of total ground cover, whereas *A. deserti* is absent from the sandiest sites (Zabriskie, 1979). Subsequent references to sandy sites for *A. deserti* refer to the least rocky sites where it occurred.

Small plants of similar size (range: 36 ± 2 cm height and 33 ± 2 cm width for *A. deserti*, with 13 ± 1 unfolded leaves; 50 ± 2 cm height and 28 ± 2 cm width for *P. rigida*, with 30 ± 3 culms) were selected in level areas. They were naturally isolated from other plants by at least 1.0 m. Categories of soil rockiness were initially identified based on visual estimation of aboveground rocks, defined as blocks of disintegrated granite having sides at least 10 cm in length. The percentage volume of rock in the soil in the rooting zone differed for each of the five rockiness categories ($P = 0.03$): (1) 0.5 ± 0.3% (sites termed sandy for *P. rigida*), (2) 3.3 ± 0.8% (sandy for *A. deserti*), (3) 9.7 ± 2.7%, (4) 20.5 ± 4.3%, and (5) 34.6 ± 3.7% (rocky for both species). Five to eight plants of *A. deserti* and six to eight plants of *P. rigida* in each of the five rockiness categories were identified during July 2000, prior to summer rainfall. Nine and 12 plants of *A. deserti* at sandy and rocky sites, respectively, and 12 and 15 plants of *P. rigida* at sandy and rocky sites, respectively, were identified during December 2000, prior to the winter rainfall.

Soil and rock physical properties—To determine the soil particle size distribution, six samples of 100–150 cm³ at the sandiest and the rockiest sites were obtained from the rooting zone of *A. deserti* and *P. rigida* at 10 ± 2 and 20 ± 2 cm below the soil surface. Sand fractionation was done by the sieving method; silt and clay were separated by the hydrometer method at the Utah State University Analytical Laboratory (Logan, Utah, USA). In agreement with previous results for Agave Hill soil (Young and Nobel, 1986), the distribution of particle size was not different at 10 and 20 cm at both sandy ($P = 0.25$) and rocky ($P = 0.27$) sites. Thus the results at the two depths have been pooled. Bulk density of the soil was determined in the field at the two site categories using the core method (Blake, 1965), which was adapted to rocky soil by inserting the cork borers horizontally in the soil at 10 and 20 cm below the soil surface.

The volumetric water content (θ_V, in cubic meters per cubic meter) and its value at field capacity (θ_V^s), which are used to fit the soil moisture characteristic, were also determined for soil samples taken between 10 and 20 cm below the soil surface (Campbell, 1985). The soil water potential (Ψ_{soil}, in megapascals) at various values of θ_V was obtained using a WP4 dewpoint hygrometer (Decagon Devices, Pullman, Washington, USA) following the manufacturer's protocol. The soil moisture characteristic was described by (Campbell, 1985):

$$\Psi_{soil} = \Psi_e(\theta_V/\theta_V^s)^{-b} \tag{1}$$

where Ψ_e (in megapascals) is the soil water potential at air entry and b is a parameter related to soil texture.

Twenty-eight rocks were collected in the field during root excavations. After removing soil from their surfaces with a brush, their volumes were determined using Archimedes' principle. The rocks were then dried to constant mass at 105°C, and their bulk density was calculated. The open porosity (pore volume available externally) of the rocks was determined after filling the pores using a vacuum method (Gras, 1994). To assess θ_V of rocks in the field, 15 air-dried rocks were placed in plastic pots, surrounded by 10 cm of field soil, and maintained in a greenhouse. The pots were watered to field capacity on alternate days for 2 wk. Five pots were then randomly selected, and Ψ_{soil} above and below the rocks was determined using the WP4 dewpoint hygrometer; the water content of the rocks was determined after oven-drying at 105°C to constant mass. Water was then withheld from the ten remaining pots until the average Ψ_{soil} was approximately −1.0 MPa, when five pots were randomly

selected and the water content of the rocks was determined. The soil water content of the rocks was also subsequently determined for the five remaining pots, when the average Ψ_{soil} was approximately −2.8 MPa.

Leaf production—The number and length of newly unfolded leaves for *A. deserti* and of living leaves for *P. rigida* were counted 11 d (9 September 2000) and 51 d (19 October 2000) after the major summer rainfalls and 16 d (15 March 2001), 36 d (4 April 2001), and 53 d (21 April 2001) after the major winter rainfalls. No new growth was observed after the last sampling dates in the summer and the winter, which were thus used to give an estimate of the rate of leaf senescence for *P. rigida*. Prior to the rainfalls, the spiny tips of the three youngest unfolded leaves of *A. deserti* were clipped so that newly unfolded leaves could be identified. Leaf surface area was obtained by regression using leaf length. Data are based on total leaf surface area for *A. deserti*, whose leaves are crescent-shaped in cross section, and are based on the area of one side of the leaves for *P. rigida*.

Root excavation—Root growth in response to the late summer and the winter/early spring rainfalls was quantified on 9–10 September 2000 and 21–22 April 2001, respectively, for 3–5 plants of each species at both sandy and rocky sites. Roots were carefully excavated using a geologist's pick, a small brush, and a fine spatula. New main and lateral roots (identified by their whitish color and limited amount of lignification) were collected, and their lengths and mean diameters were measured and used to calculate root surface area. Root distributions with depth were determined on 4–6 November 2000; excavation of all roots for three plants of *A. deserti* and for four plants of *P. rigida* at both sandy and rocky sites was performed by removing sequential 5-cm thick layers of soil, and the lengths and mean diameters of main and lateral roots were measured for each layer.

Water relations—Soil samples of 20–30 cm³ were taken from the root zone of both species at 10 cm below the soil surface, and Ψ_{soil} was calculated using the moisture characteristic for soil from sandy and rocky sites. Leaf water potential (Ψ, in megapascals) and transpiration rate (E, in millimoles per square meter per second) were measured on the same plants on 18–21 April 2001. Transpiration rate was measured every 1–2 h from 2100 to 0600 (solar time) for *A. deserti* and from 0700 to 2000 for *P. rigida* using an LI-1600 steady-state porometer (LI-COR, Lincoln, Nebraska, USA). Leaf water potential for *A. deserti* was measured during maximum transpiration (2300–0100) as described by North and Nobel (1998) using an SC10X TruPsi thermocouple psychrometer (Decagon Devices, Pullman, Washington, USA). Leaf water potential for *P. rigida* was measured with a Scholander-type pressure bomb on three detached leaf blades per plant at predawn ($\Psi_{predawn}$, 0400–0500) and during maximal transpiration (Ψ_{max}, 1100–1300).

Statistical analysis—All statistical analyses were done using SigmaStat 2.03 (SPSS, Chicago, Illinois, USA). Data with nonnormal or inhomogeneous variance were log or square-root transformed. Differences due to soil rockiness were analyzed using one-way ANOVA followed by a Tukey's test. Paired and unpaired comparisons were made using Student's t test. Statistical differences were judged at $P < 0.05$.

RESULTS

Soil and rock physical properties—The proportion of particles smaller than 0.25 mm was lower at the sandiest than at the rockiest sites, whereas the opposite was true for particles larger than 0.25 mm (Fig. 1). The content of gravel (2.0–20 mm) of the bulk soil increased with the soil rockiness, being 14.0 ± 1.7, 26.3 ± 2.9, and 35.1 ± 2.9% at sites with rock contents of 0.5, 3.3 and 35% by volume, respectively. The coarse gravel (particle sizes 2.0–7.6 cm) represented <1% of the soil dry mass at the sandiest sites and 5% at the rockiest sites. The bulk density of the soil was not significantly different at the sandiest and the rockiest sites ($P = 0.31$), averaging 1.40 ± 0.04 Mg/m³ ($N = 6$). For the bulk soil, θ_V^s was 23.8
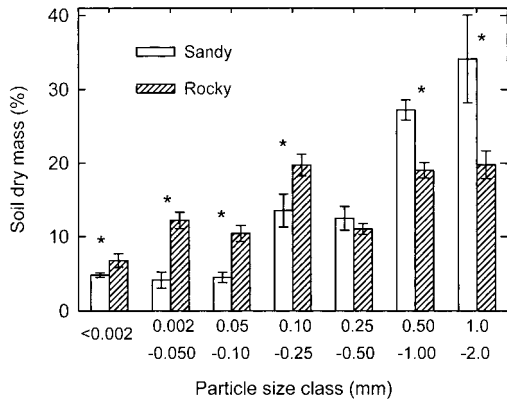
Fig. 1. Particle size distribution for fine soil (particles <2 mm) from the sandiest and the rockiest sites (0.5% and 35% of rock by volume, respectively). Data are means ± 1 SE (N = 6 soil samples). An asterisk indicates a significant difference using an unpaired Student's t test (P < 0.05).
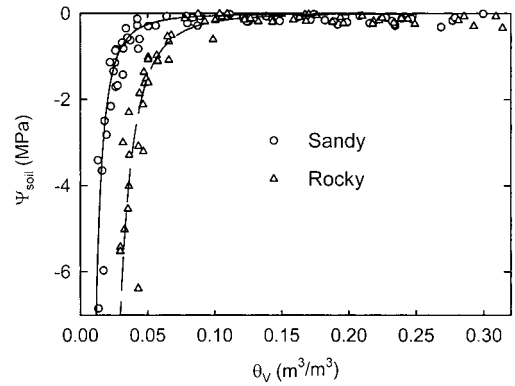

Fig. 2. Soil moisture for six soil samples from the sandiest and the rockiest sites. Solid line is fitted curve (Eq. 1) for the sandiest sites [$\Psi_{soil} = -0.0073(\theta_v/\theta_v^s)^{-2.28}$, $r = 0.93$, $P < 0.001$] and dashed line is for the rockiest sites [$\Psi_{soil} = -0.0096(\theta_v/\theta_v^s)^{-2.95}$, $r = 0.94$, $P < 0.001$].

± 1.1 and 26.1 ± 1.1% at the sandiest and the rockiest sites, respectively ($P = 0.009$, $N = 6$). Soil water potential decreased faster at the rockiest sites compared with the sandiest sites as θ_v decreased below 0.07 m³/m³ (Fig. 2). The available water capacity of the soil was 0.211 and 0.259 m³/m³ at the sandiest sites and 0.181 and 0.236 m³/m³ at the rockiest sites for *A. deserti* and *P. rigida*, respectively.

The bulk density of the rocks was 2.61 ± 0.04 Mg/m³ ($N = 28$) and their open porosity was 1.1 ± 0.2% by volume ($N = 13$). The open pore space of the rocks was 84% filled with water at $\Psi_{soil} = -0.01 ± 0.00$ MPa, 47% at $-0.96 ± 0.05$ MPa, and 33% at $-2.76 ± 0.05$ MPa ($N = 5$). The available water capacity, defined as the volume of water stored per unit volume between field capacity and the lowest Ψ_{soil} at which root water uptake occurs for a particular species, for the rocks was 0.0038 and 0.0054 m³/m³ for *A. deserti* and *P. rigida*, respectively.

Responses to late summer rainfalls—From August to October 2000, the daily average minimum air temperature decreased from 25°C to 15°C, and the maximum decreased from 35°C to 24°C (Fig. 3A). The year 2000 had only 115 mm total precipitation. No rainfall occurred from 8 March to 24 August 2000. The late summer rainfalls were relatively light (Fig. 3B), totaling 70 mm from 24 August to 6 November 2000 (date of the last field observations), 91% occurring by 29 August 2000. Soil water potential at 10 cm below the soil surface was higher at sandy than at rocky sites for *P. rigida* at 11, 51, and 68 d after the major summer rainfall events (Fig. 3C). In contrast, Ψ_{soil} was lower at sandy than at rocky sites for *A. deserti* on the dates when soil samples were collected, though not significantly so ($P \geq 0.12$).

At 11 d after the major late summer rainfall events (9 September 2000), the number of newly unfolded leaves for *A. deserti* was not significantly affected by the soil rockiness (Fig. 4A). However, at 51 d (19 October 2000), new leaf production was 64% higher at sandy than at rocky sites and decreased linearly with soil rockiness. Although the growth of *A. deserti* was higher at sandy sites, no isolated (presumably sexually produced) plants of *A. deserti* were found at the sandiest sites (0.5% of rock by soil volume). The root distribution with depth for *A. deserti* was greatly affected by soil rockiness (Fig. 5A); the mean rooting depth for *A. deserti* was twofold greater
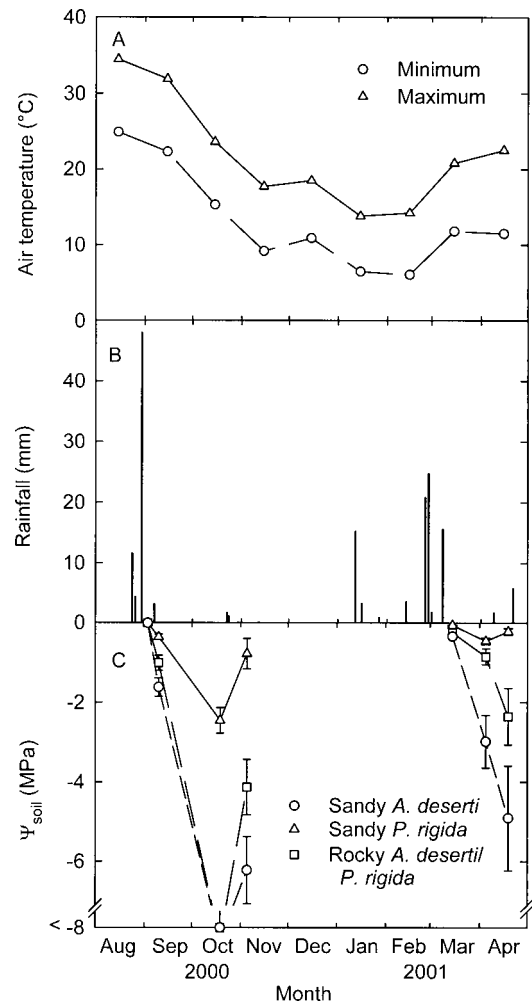

Fig. 3. Monthly average daily minimum and maximum air temperatures (A), rainfall events (B), and Ψ_{soil} (C). Soil water potential data are means ± 1 SE (N = 5–10 soil samples from different plant rooting zones).
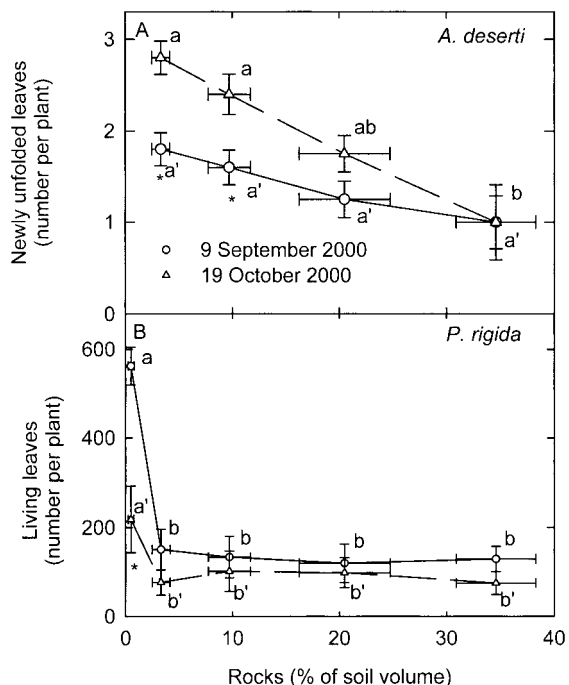
Fig. 4. The number of newly unfolded leaves for *Agave deserti* (A) or the number of living leaves for *Pleuraphis rigida* (B) vs. the volume of rock in the soil. Data are means ± 1 SE (*N* = 4–6 plants). An asterisk indicates a significant difference (*P* < 0.05) between 9 September and 19 October 2000 using a paired Student's *t* test. Different letters (a, b for 9 September 2000; a′, b′ for 19 October 2000) indicate a significant difference (*P* < 0.05) along the soil rockiness gradient using a one-way ANOVA followed by a Tukey's test.
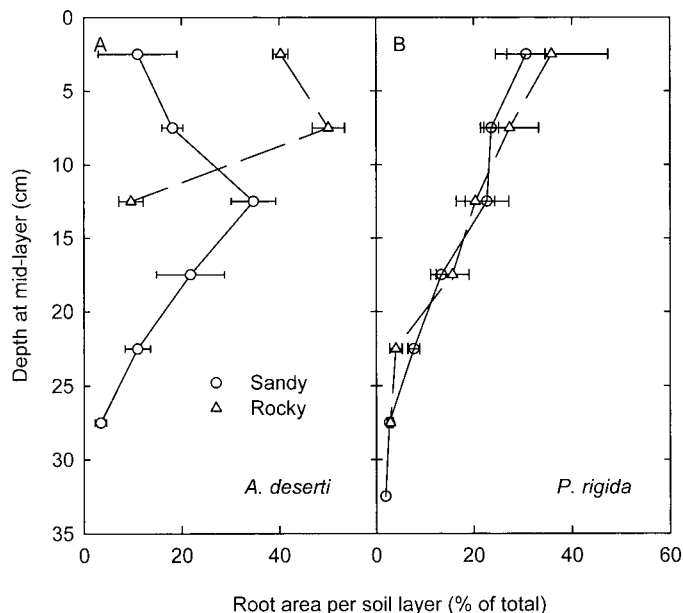

Fig. 5. Root distribution with depth for *Agave deserti* (A) and *Pleuraphis rigida* (B) excavated at sandy and rocky sites. Sandy sites had 3.3% and 0.5% of rock by soil volume for *A. deserti* and *P. rigida*, respectively, and rocky sites had 35%. Data obtained on 4–6 November 2000 are plotted at the middle of 5-cm thick soil layers and are means ± 1 SE (*N* = 3 for *A. deserti* and 4 for *P. rigida*).

at sandy than at rocky sites (Table 1); and the total root length and surface area of established roots per plant were 37 and 31% higher at sandy than at rocky sites, respectively (Table 1). New root growth for *A. deserti* represented only 5 and 1% of the total root surface area at sandy and rocky sites, respectively (Table 1). The diameter of established and new roots for *A. deserti* did not vary with depth (*P* = 0.56) or soil rockiness (*P* = 0.70) and averaged 1.59 ± 0.02 mm for essentially unbranched, established roots and 3.68 ± 0.18 mm for new roots, which occurred at the base of the shoot and as exten-

sions of established roots. The root : leaf area ratio for *A. deserti* was 60% higher at sandy than at rocky sites (Table 1).

At 11 d after the major late summer rainfall events, the greatest leaf production for *P. rigida* occurred at the sandiest sites, and the production of new leaves was not significantly influenced as the volume of rock by soil volume varied from 3.3 to 35% (Fig. 4B). At 51 d after the major summer rainfall events, the number of green leaves had decreased by 66% at the sandiest sites, but it had not decreased significantly at the four rockier sites; nevertheless, the number of living leaves was then 2.5-fold greater at the sandiest sites. The root distribution with depth (Fig. 5B) and the total root length per plant (Table 1) for *P. rigida* were similar at rocky and sandy sites, although the mean rooting depth and the surface area of rel-

TABLE 1. Mean rooting depth, total root length, surface area of established roots, and root : leaf area ratio for isolated plants of similar size of *Agave deserti* and *Pleuraphis rigida* at sandy and rocky sites determined at the end of the summer wet period (4–6 November 2000) and new root surface area for *A. deserti* and *P. rigida* in the late summer (9–10 September 2000) and early spring (21–22 April 2001) at sandy and rocky sites. Sandy sites had 3.3 and 0.5% of rock by soil volume for *A. deserti* and *P. rigida*, respectively, and rocky sites had 35%. Data are means ± 1 SE (*N* = 4 plants).

Root system characteristics	Excavation	*A. deserti*		*P. rigida*	
		Sandy	Rocky	Sandy	Rocky
Mean rooting depth (cm)	4–6 Nov 2000	12.3 ± 0.9[A]	6.0 ± 0.1[B]	10.3 ± 0.7[A]	8.4 ± 0.6[A]
Total root length (cm)	4–6 Nov 2000	2182 ± 184[A]	1368 ± 184[B]	1261 ± 270[A]	1423 ± 322[A]
Surface area of established roots (cm²)	4–6 Nov 2000	1336 ± 109[A]	917 ± 99[B]	516 ± 82[A]	276 ± 53[A]
Root : leaf area ratio[a]	4–6 Nov 2000	0.42 ± 0.04[A]	0.26 ± 0.05[B]	0.4 ± 0.1[A]	4.0 ± 1.4[B]
Surface area of new roots per plants (cm²)	9–10 Sep 2000	63 ± 23[A,X]	8 ± 3[A,X]	9 ± 3[A,X]	2 ± 1[A,X]
	21–22 Apr 2001	244 ± 29[A,Y]	92 ± 5[B,Y]	296 ± 113[A,Y]	57 ± 16[B,Y]

Note: Different letters indicate a significant difference (*P* < 0.05) within a species between sandy and rocky sites using an unpaired Student's *t* test (A or B) and for surface area of new roots within a species and a site type between 9–10 September 2000 and 21–22 April 2001 (X or Y) using an unpaired Student's *t* test.

[a] The root : leaf area ratio was calculated using the maximal leaf surface area per plant, which was measured on 19 October 2000 for *A. deserti* and on 10 September 2000 for *P. rigida*.

TABLE 2. Number of newly unfolded leaves for *Agave deserti* and number of living leaves for *Pleuraphis rigida* at various dates after the major winter rainfall events for sandy and rocky sites. Data are means ± 1 SE (*N* = 7–9 plants).

| | Newly unfolded or living leaves (number per plant) | | | |
| | *A. deserti* | | *P. rigida* | |
Date	Sandy	Rocky	Sandy	Rocky
15 March 2001	1.3 ± 0.2[A,X]	0.7 ± 0.2[A,X]	23 ± 4[A,X]	23 ± 4[A,X]
4 April 2001	2.3 ± 0.3[A,Y]	1.2 ± 0.1[B,XY]	248 ± 27[A,Y]	111 ± 29[B,Y]
21 April 2001	2.4 ± 0.3[A,Y]	1.3 ± 0.2[B,Y]	214 ± 30[A,Y]	68 ± 10[B,Y]

Note: Different letters indicate a significant difference ($P < 0.05$) within a species between sandy and rocky sites using an unpaired Student's *t* test (A or B) and within a species and a rockiness category between different dates using a one-way repeated measures ANOVA followed by a Tukey's test (X or Y).

atively unbranched, established roots tended to be higher at sandy than at rocky sites (Table 1). As for *A. deserti*, the surface area of new roots was small, representing 2 and 1% of the total root surface area at sandy and rocky sites, respectively (Table 1). At sandy sites, the root diameter of *P. rigida* averaged 0.96 ± 0.02 and 0.56 ± 0.09 mm ($P < 0.001$) for the 0–5 cm and the 30–35 cm soil layers, respectively, and was 18% ($P < 0.001$) and 37% ($P = 0.024$) smaller at rocky sites for the 0–5 cm and the 30–35 cm soil layers, respectively. The diameter of new roots of *P. rigida* averaged 1.43 ± 0.04 mm at sandy sites and was 25% lower at rocky sites ($P < 0.001$). The root : leaf area ratio for *P. rigida* at sandy sites was only 10% of that at rocky sites (Table 1).

Responses to winter/early spring rainfalls—The daily average minimum and maximum air temperatures were relatively constant for March and April 2001, the months of field observations, averaging 12°C and 22°C (Fig. 3A), respectively. The rainfall from 13 January to 22 April 2001 (date of the last field observations) was similar to the late summer rainfalls, totaling 79 mm, 58% occurring on 25–27 February. Soil water potential at 10 cm below the soil surface was higher at sandy than at rocky sites for *P. rigida* at 16, 36, and 53 d after the major winter rainfall events (Fig. 3C). In contrast, Ψ_{soil} was lower at sandy than at rocky sites for *A. deserti* at 36 and 53 d after the major winter rainfall events.

At 36 d (4 April 2001) and 53 d (21 April 2001) after the major winter rainfall events, the number of leaves unfolding for *A. deserti* at sandy sites was nearly double that at rocky sites (Table 2). New root growth in response to the winter/ early spring rainfalls was threefold greater at sandy than at rocky sites and represented 18 and 10% of the total root surface area at sandy and rocky sites, respectively (Table 1). At 53 d after the major winter rainfall events, Ψ_{max} for *A. deserti* was similar at sandy and rocky sites, but E_{max} was 43% higher at rocky than at sandy sites (Table 3).

At 36 d after the major winter rainfall events, the number

of living leaves for *P. rigida* was more than twofold higher at sandy than at rocky sites (Table 2). At 53 d, the number of living leaves decreased 14% from the value at 36 d at sandy sites but decreased 39% at rocky sites. New root growth in response to the winter/early spring wet period was five times greater at sandy than at rocky sites, although not significantly, and represented 57 and 21% of the total root surface area at sandy and rocky sites, respectively (Table 1). At 53 d after the major winter rainfalls events, $\Psi_{predawn}$, Ψ_{max}, and E_{max} for *P. rigida* were higher at sandy than at rocky sites (Table 3), all indicating greater water stress for *P. rigida* at rocky than at sandy sites.

DISCUSSION

Agave deserti and *Pleuraphis rigida* differed substantially in shoot productivity and root deployment in response to soil rockiness at Agave Hill. The two conformed to the expectation that slow-growing evergreen species, such as *A. deserti*, exhibit greater root variability in response to heterogeneous soils than do fast-growing species such as *P. rigida* (Fitter, 1994; Grime, 1994). Although both shoot and root growth for *A. deserti* increased as the soil rockiness decreased, this species was absent from the sandiest sites. *Pleuraphis rigida* also had greater leaf productivity at sandy sites, although its root distribution and root surface area were not significantly affected by soil rockiness. Thus, although the two species responded quite differently to soil rockiness and soil texture, both had greater leaf production at the sandiest sites where they occurred.

Soil characteristics—At Agave Hill, the soils at rocky and sandy sites differed not only in rock content but also in texture. The total available water capacity of the rocks plus the surrounding soil was 0.204 and 0.257 m³/m³ for *A. deserti* and *P. rigida*, respectively, at sandy sites, and 0.120 and 0.159 m³/ m³ for *A. deserti* and *P. rigida*, respectively, at rocky sites. At

TABLE 3. Leaf water potential measured predawn ($\Psi_{predawn}$) or measured concurrently with maximum transpiration rate (Ψ_{max}, E_{max}) for *Agave deserti* and *Pleuraphis rigida*. E_{max} occurred from 2300 to 0100 for *A. deserti* and from 1100 to 1300 for *P. rigida*. Data were obtained on 18–21 April 2001 and are means ± 1 SE (*N* = 5–7 plants).

| | *A. deserti* | | *P. rigida* | |
Characteristic	Sandy	Rocky	Sandy	Rocky
$\Psi_{predawn}$ (MPa)	—	—	−0.86 ± 0.09[A]	−1.33 ± 0.05[B]
Ψ_{max} (MPa)	−1.42 ± 0.08[A]	−1.35 ± 0.04[A]	−1.48 ± 0.10[A]	−2.10 ± 0.13[B]
E_{max} (mmol · m⁻² · s⁻¹)	0.17 ± 0.02[A]	0.30 ± 0.02[B]	2.67 ± 0.22[A]	2.04 ± 0.06[B]

Note: Different letters indicate a significant difference ($P < 0.05$) within a species between sandy and rocky sites using an unpaired Student's *t* test.

sandy sites, the rocks decreased the total available water capacity of the soil by less than 1% for both species, as calculated by subtracting the available water capacity of the rocks themselves; in contrast, at rocky sites, the rocks decreased the total available water capacity of the soil by about 33% for both species. During both the late summer/fall and the winter/early spring, the moisture characteristic of the soil at the sandiest sites (where only *P. rigida* occurred) led to a higher soil water potential (Ψ_{soil}) for a longer period than at the rockier sites. When soil moisture content was low at Agave Hill, the coarser soil at the sandiest sites had greater water availability than did the finer soil at rocky sites; thus, the soil texture appeared to be more important in determining Ψ_{soil} after a rainfall event than did the retention of water under rocks. Nevertheless, at rocky sites the presence of rocks in the soil delayed the decrease of Ψ_{soil} during both the late summer and the winter/early spring, consistent with previous results (Nobel, Miller, and Graham, 1992).

Performance of Agave deserti—The texture of the bulk soil where *A. deserti* occurred did not differ greatly from site to site, thus its decrease in leaf productivity reflected the increase in soil rock content from 3.3 to 35% by volume. Along with lower leaf production, the total root length and the surface area of established roots of *A. deserti* were 37 and 31% lower, respectively, at rocky than at sandy sites, and its new root production during the winter/early spring was 62% lower. Similarly, plant productivity is negatively correlated with soil rock content for both *Malus sylvestris* (Magier and Ravina, 1984) and *Triticum aestivum* (Kosmas et al., 1994). Just as rocks reduced the available water capacity of the soil, they also decreased the space penetrable by roots. However, transpiration for *A. deserti* in drying soil during the early spring was greater at rocky than at sandy sites, implying that the reduced available water capacity at rocky sites was probably not limiting. In addition, Ψ_{soil} decreased more quickly after rainfall at sandy than at rocky sites where *A. deserti* occurred, perhaps allowing water uptake to occur at rocky sites for longer periods. Thus, the reduced space penetrable by roots was apparently responsible for much of the observed decrease in root growth for *A. deserti*.

The smaller root surface area for *A. deserti* at rocky sites resulted in a 38% lower root : leaf area ratio than at sandy sites, which can affect water uptake independently of rooting depth. The root system of *A. deserti* exhibits redundancy with respect to water uptake under wet conditions, but not during recovery from drought. Specifically, when the distal 50% of the root system of *A. deserti* is rewetted after 90 d of drought, recovery of half-maximal daily net CO_2 uptake is delayed by 40% compared with wetting the entire root system (Graham and Nobel, 1999). Thus, the lower root : leaf area ratio at rocky sites may limit the amount of water that can be captured before it evaporates, especially during the late summer when temperatures are high. On the other hand, the lower root : leaf area ratio for *A. deserti* at rocky sites can also be interpreted in terms of root efficiency. For example, 53 d after the last spring rainfall, nearly three times as much new root surface area at sandy sites as opposed to rocky sites was accompanied by only an 8% increase in leaf surface area. At the same time, transpiration (E_{max}) was higher for *A. deserti* at the rockier sites. The finer texture of the nonrock fraction of the soil at the rocky sites may also be associated with greater root efficiency for *A. deserti*, similar to the lower root : leaf area ratios

for *Pinus taeda* in loamy soil than in sandy soil (Hacke et al., 2000). Thus, greater leaf productivity for *A. deserti* at sandy sites was achieved at a relatively greater investment in root construction, whereas greater root efficiency at the rocky sites may lead to longer term leaf production.

Performance of Pleuraphis rigida—During the late summer, leaf productivity for *P. rigida* decreased sharply as soil rock content increased from 0.5 to 3.3% yet did not decrease further as rock content increased to 35%. Thus, leaf growth for *P. rigida* was highly sensitive to changes in soil texture and gravel content at relatively sandy sites, but insensitive to large changes in soil rock content. The productivity of other species, such as *Prunus persica* and *P. avium*, is also not affected by a soil rock content of up to 60% by volume (Gras, 1994). The higher leaf productivity for *P. rigida* at the sandiest sites was probably due to more favorable soil moisture characteristics at those sites, as indicated by the changes of Ψ_{soil} during both the late summer and the winter/early spring and by the greater E_{max} and higher leaf water potential (Ψ_{max}) in drying soil at the sandiest sites during the early spring.

The insensitivity of leaf growth for *P. rigida* to soil rockiness between 3.3 and 35% by volume was associated with little change in its root architecture. The ability of *P. rigida* to deploy roots in very rocky soil may be linked to its small root diameter (Zwieniecki and Newton, 1995) and to plasticity in diameter in response to depth and to soil rockiness. Indeed, the average diameter of new roots of *P. rigida* was 42% lower in the 30–35 cm soil layer compared with the 0–5 cm layer, and it was 25% lower at rocky than at sandy sites.

The root : leaf area ratio for *P. rigida* during the late summer was tenfold higher at rocky than at sandy sites, primarily due to greater leaf area at the latter sites. Thus, in contrast to *A. deserti*, root efficiency for *P. rigida* was greater in sandy soil. However, the earlier leaf senescence for *P. rigida* at sandy sites during the late summer may reflect its low root : leaf area ratio at those sites. *Pleuraphis rigida*, which has a high transpiration rate for a C_4 species (Nobel, 1981), is physiologically active for only a short period during the summer and autumn (about 30 d in the year 2000), when rainfalls are extremely limited and variable in the northwestern Sonoran Desert. Thus, it could be advantageous for this fast-growing species to allocate most of its carbon to leaf and inflorescence production during the short wet period in the late summer.

In conclusion, sandy soil, with its quick water release, was the more favorable substrate for *P. rigida*, a rapidly growing bunchgrass that loses its leaves during prolonged drought and exhibited little variability in root deployment in response to soil rockiness. For the succulent *A. deserti*, greater root system variability with soil type may be related to its longer periods of metabolic activity. Although more root growth and greater root : leaf area ratio may have contributed to greater initial shoot growth at sandy sites, higher root efficiency at rocky sites may allow *A. deserti* to take advantage of the longer availability of water associated with rocks. The unexpected success of *A. deserti* at sandy sites in terms of leaf production and root growth suggests that its absence from the sandiest sites may be due less to properties of mature plants than to seedling characteristics. Specifically, seedling root growth may not be sufficient to keep pace with the rate of soil drying at sandy sites, and water films associated with rocks near the soil surface may be essential to sustain young plants of *A. deserti*.

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