



Resource-island soils and the survival of the giant cactus, cardon, of Baja California Sur

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Received 26 January 1999. Accepted in revised form 22 October 1999

Key words: facilitation, nurse-plant effect, *Pachycereus pringlei*, plant survival, *Prosopis articulata*, resource island, revegetation, soil temperature.

Abstract

Early survival and growth of some plants in arid environments depends on facilitation by a nurse plant. Amelioration of soil temperature extremes through shading and accumulation of mineral nutrients near nurse-plants are mechanisms of facilitation. We investigated the effects of shading (soil temperature) and soil type on survival and growth of the giant columnar cactus, cardon (*Pachycereus pringlei*). Cardon was grown either in a sandy clay-loam soil obtained from resource islands formed under mature mesquite (*Prosopis articulata*) or in the loamy-sand soil from plant-free bare areas that surround the islands. Seedlings were potted in these soils and the pots were buried to ground level in the open. We also determined plant responses to fertilization with N, P, K or NPK in the bare-area soils. Enhancement of survival and growth in the resource-island soils compared to that in the bare-area soils was highly significant. Plants survived and grew better in resource-island soils than in bare-area soil, an effect that was enhanced by shading (one-half of full sun). Greater root/shoot ratios of plants grown in bare-area soil indicated increased resource allocation to roots under limiting conditions. Significant interactions (analysis of variance) indicated that the soil and sun factors of the experiment were not independent of one another. Plant growth in bare-area soil improved considerably (>200%) in response to N fertilization (greenhouse conditions), and approximated that of plants in resource-island soil without N amendment. The growth response to P was small (<50%), while K did not affect growth significantly. Responses to NPK were similar to those to N alone. The results suggested that shading and nutritional effects interact in determining early survival and growth of cardon in different soils.

Introduction

Individual plants can significantly influence the soil in which they grow (Zinke, 1962). This is especially true for some desert legume trees (Virginia, 1986), as windborne soil deposits that collect under their canopies (Armbrust and Bilbro, 1997) change physical and chemical soil properties (Halvorson et al., 1995) and provide favorable habitats for seedlings (Belsky et al., 1989). Alleviation of nutrient (Garner and Steinberger, 1989) and temperature stress (Turner et al., 1966) are factors that

enhance seedling survival and growth in such resource-island soils (Halvorson et al., 1994).

Mesquite (*Prosopis* spp.) has been found to be particularly effective as a nurse plant in arid lands (Barth and Klemmedson, 1982; Lajtha and Schlesinger, 1986; Shearer et al., 1983; Virginia and Jarrell, 1983). There is no agreement, however, which one of this legume's contributions to the enhancement of seedling survival under its canopy is most crucial. Improved soil N content (García-Moya and McKell, 1970; Garner and Steinberger, 1989; Vinton and Burke, 1995), moderate soil-surface temperatures (Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991), and higher soil moisture levels

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(see Callaway, 1995) have been singled out as its primary contributions. We have reasoned that all of these factors, and probably others not yet fully explored (e.g. the soil microflora, Carrillo-Garcia et al., 1999; Halvorson et al., 1995) together contribute to the nurse-plant and resource-island effects (Carrillo Garcia et al., 2000).

The purpose of our study was to (1) determine the relative effects of shading (full vs. half sun) and soil type (resource-island soil vs. plant-free, bare-area soils) on the survival and growth of cardon (*Pachycereus pringlei*) cacti under modified field conditions, (2) investigate fertilization effects on cardon in bare-area soil, and (3) determine soil-type effects on the colonization of cardon roots by arbuscular mycorrhizal (AM) fungi.

Materials and methods

Study site and soils

Soils were collected near La Paz, Baja California Sur, Mexico (24° 1 N and 100° 2 W) from an alluvial coastal plain formed by sedimentation and the deposition of granitic rock fragments derived from erosion of the Sierra de la Laguna mountains (Maya and Guzmán, 1998). The climate is arid with annual mean rainfall of 180 mm, mainly in late summer. Mean monthly temperatures vary from 18 to 30 °C, but during the mid-summer drought season temperatures often exceed 40 °C. The flora is characterized as a transition between xerophilic matorral and dry tropical forest (León de la Luz et al., 1996). Ten sites were selected at random within a 1 ha plot. Of the sites, five each were centered either on a mature mesquite (*Prosopis articulata* S. Wats.) tree (resource-island soil) or contained plant-free space (bare-area soil). Five soil samples (5 to 35 cm depth) were collected from each site either at radially increasing distances from the center (tree trunk) to the edge of the canopy, or across bare areas equal in size to the mesquite areas. The replicate samples from each site were mixed, sieved (1-cm screen openings) to remove large roots and rocks and potted (1.5 L pots).

Total soil N (Bremner and Mulvaney, 1982) was determined by Kjeldahl analysis, and plant-available (NaHCO_3 -extractable) P by the molybdate blue method (Olsen and Sommers, 1982). Soil particle analysis was performed according to Gee and Bauder (1986).

Experimental design and layout

There were 2 separate experiments. The treatments of each experiment contained 6 replications, and each experimental unit (pot) had 10 cardon [*Pachycereus pringlei* (S. Wats.) Britt. & Rose] seedlings at the start. Experiment 1 (Ex 1) was designed as a 2 x 2 factorial, with shading (full sun and half sun) and soil (resource-island soil and bare-area soil) as factors. The pots were buried in soil to ground-surface level. Pots with both resource-island and bare-area soils were either covered with a screen that filtered out approximately one-half (52%) of full sunlight or were exposed to full sunlight. The screen was selected to correspond closely in its transmittance of sun light to that of mesquite canopies. The average of 50 observations made under mesquite was $980 \mu\text{mole m}^{-2} \text{s}^{-1}$, or 48% of full sunlight. The screen was arranged as a rectangular box and was 1.5 m from the plants on top and the sides. Surface and subsurface (5 cm) soil temperatures were determined in the four treatments (soil probes, Markson Model 7001 Microcomputer Thermometer. Measurements were made at 14:00 hours over a period of 4 months (May through August, 1998) and averaged.

Experiment 2 (Ex2) had a completely random design and consisted of 5 treatments: fertilization with NPK, N, P, or K and an unamended control, all in bare-area soil. Amendments approximated one-half Hoagland's solution and were applied as nutrient solutions (mM): N, 8 as $\text{Ca}(\text{NO}_3)_2$; P, 1 as NaH_2PO_4 ; and K, 2 as K_2SO_4 .

Growth conditions

Cardon seeds were pre-germinated (5 d, 30 °C) and selected for uniformity. Ten seedling were transferred from tissue paper to the soils in each pot. Plants were grown for six months: those of Ex1, March through August (season of high-temperature extremes), 1998, in the open; those of Ex2, January through June, 1998, in a screenhouse. Maximum mid-day light intensities in the screenhouse were $1000 \mu\text{mole m}^{-2} \text{s}^{-1}$, and ambient air temperatures were within the range of 20/40, night/day. Pots of Ex1 were irrigated twice weekly, those of Ex2 once a week with the nutrient solutions and were flushed with water once a week to avoid an accumulation of nutrients.

Assays and statistics

Surviving plants were counted. Shoot fresh masses were determined immediately at harvest, and dry masses after drying (70 °C, 3 d), Shoot dry matter content was calculated from the dry and fresh masses. Roots were separated into 2 parts. One part was used to measure fresh and dry masses, the other served to determine root length and root colonization by mycorrhizal fungi using the grid-line intersect method (Giovanetti and Mosse, 1980). Total root dry mass was calculated from dry/fresh mass ratio of the other root sample. Values of the individual plant parameters were summed per experimental unit (pot), and statistical evaluations were performed using replication of the experimental units ($n=6$).

Results were evaluated by analysis of variance (ANOVA). The results of Ex1 are presented in a form that facilitates a biological interpretation of significant statistical interactions. For Ex2, percent changes (%0) of plant traits in response to nutrients relative to the controls [$100 \times (\text{Nutrient-Control})/\text{Control}$] were presented in addition to the basic data set to help visualize the responses. Independent t-tests were used to assess the differences between the traits of control and the fertilized-treatment plants.

Results and discussion

Shading and soil temperatures

All response variables of carbon in Ex1 were significantly affected by the shading regimes (Figure 1). Soil surface temperatures were lower in the shaded treatments than in those exposed to full sunlight at 14:00 hours (shade vs. sun, resource-island soil, 47.7 vs. 51.0 °C, $p=0.059$; bare-area soil, 48.1 vs. 53.4 °C, $p=0.024$). Subsurface temperatures were lower than surface temperatures and were not significantly affected by shading (shade vs. sun, resource-island soil, 37.1 vs. 41.2 °C, $p=0.207$; bare-area soil, 37.4 vs. 41.1 °C, $p=0.161$). Although the light-colored, smooth-surfaced, loamy-sand (*sensu* Gee and Bauder, 1986) bare-area soil probably reflected more incident radiation (albedo effect, Brady and Weil, 1996) than the dark, sandy-clay-loam (*sensu* Gee and Bauder, 1986) resource-island soil, temperature differences between the two soils were not significant ($p>0.5$).

Dark, rough-surfaced, and fine-textured soils tend to have higher temperatures in the sun than light-colored soils as a result of greater heat absorption. This effect

may be counteracted by the higher soil water contents of dark soils, as water requires much energy to be warmed and cools the soil as it evaporates (Brady and Weil, 1996). The similar soil temperatures in our bare-area and resource-island soils were apparently due to different factors: higher light reflectance by the former and higher soil water content of the latter. The different water contents of resource-island and of bare-area soils at field capacity (23 vs. 12%, respectively, $p=0.046$) were functions of their textures: resource-island soil had higher clay (23 vs. 8%, $p<0.001$) and silt (14 vs. 8%, $p<0.001$) contents and lower sand content (63 vs. 84%, $p<0.001$) than the bare area soil. These differences in soil characteristics probably influenced soil temperatures in addition to the shading regimes.

The intensity of incident sunlight and the concomitant soil temperatures affected all plant traits (Figure 1). All 60 plants in the shaded (half-sun) resource-island soil survived till harvest at six months (Figure 1A), while survival rates of plants in the other three treatments were lower, especially when grown in full sun and bare-area soil. The significant interaction between the factors showed that the effects of shade on survival differed between soil types: the effects diverged significantly in magnitude, indicating that the factors were not independent of one another. Our interpretation of this phenomenon is that high soil temperatures (full sun) affected survival in the sandy, low-water-content, bare-area soil more intensely than in the finer-textured resource-area soil due to the lack of soil-moisture mediated cooling effects.

The Sun and Soil main effects of ANOVA were significant for the plant-growth traits measured (Figure 113, C, F). Total plant and shoot development (Figure 2) and root length (Figure 1) were greater in resource-island than in bare-area soils, and were all enhanced by shading. The statistical interactions for growth effects were significant but differed from the pattern of the survival effects in that plant-growth responses to the two soils diverged less in full sun than in the shade. Our interpretation of this response pattern is that lower soil temperatures and higher soil quality (Doran and Parkin, 1994) had a joint, synergistic effect on growth.

This interpretation supports previous findings that ascribed plant-growth and survival responses mainly to the effects of irradiation (Franco and Nobel, 1989; Shreve, 1931; Turner et al., 1966; Valiente and Ezcurra, 1991; Valiente et al., 1991). However, it considers also the soil as a modifier of temperature effects: soils formed by different nurse

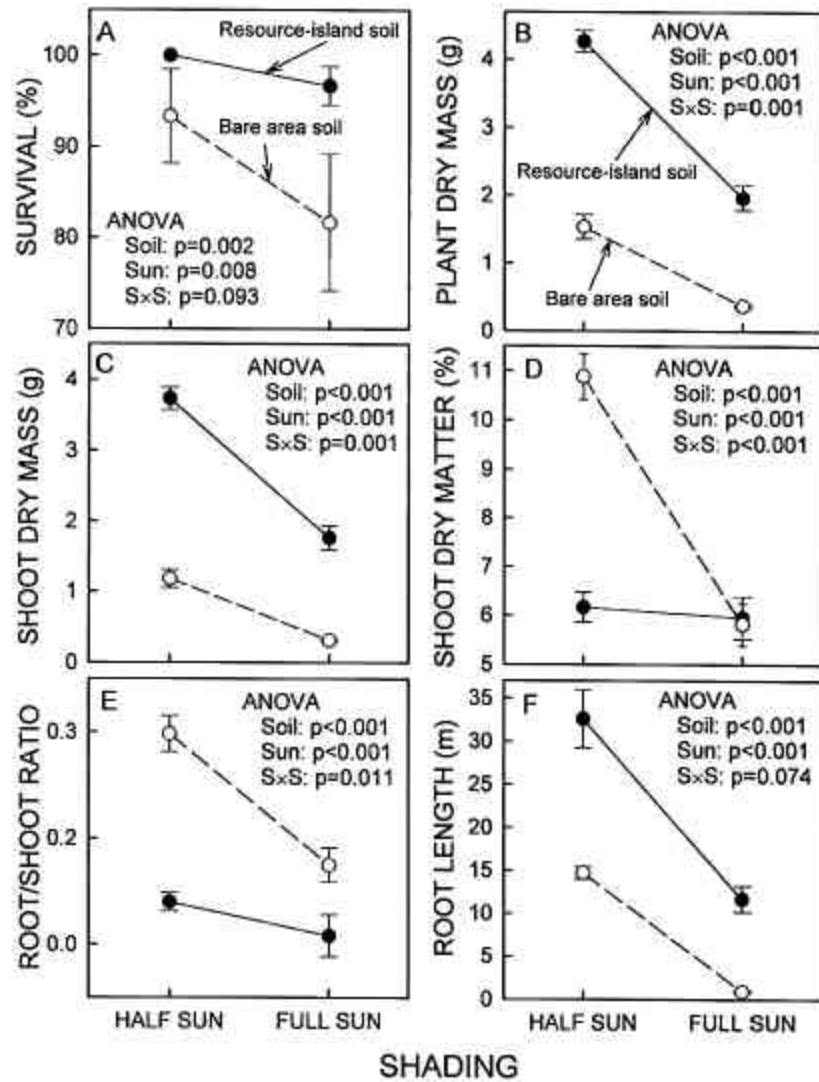


Figure 1. Shading effects on survival and growth of cardon seedlings. Plants were grown for 6 months in potted soils obtained from resource islands formed by mature mesquite trees or from surrounding bare areas free of plants. Pots were buried to ground level in the open. Plants were either shaded by screens (half sun) or exposed to full sunlight.

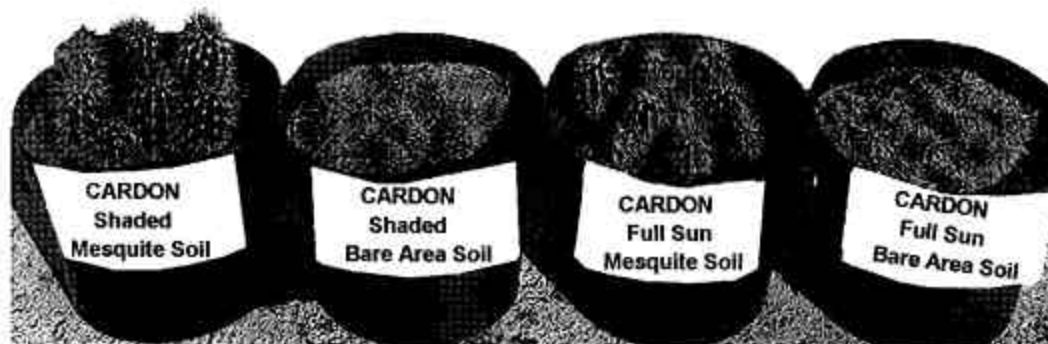


Figure 2. Cardon seedlings grown in resource-island (mesquite) or bare-area soils in one-half or full sunlight.

plants (Barth and Klemmedson, 1982; Turner, 1966) or for different lengths of time (Archer et al., 1988; Carrillo-Garcia et al., 1999) have been shown to affect seedling establishment independently of soil temperatures. Our data within this context therefore suggest that the nurseplant's role in seedling establishment is not restricted to the amelioration of temperature extremes, but includes the formation of fine-textured and structured (Joffre and Rambal, 1993) resource-island soils as part of the over-all growth effect. Improved moisture conditions in such soils (Noy-Meir, 1973) are well-known to contribute to canopy effects on seedling survival and plant growth.

Responses by the derived traits, shoot dry matter (Figure 1 D) and root/shoot ratio (Figure 1 E), indicated that the Sun Factor affected developmental aspects (the extent of shoot-tissue hydration and differential resource allocation to plant parts, respectively) more in plants grown in bare-area than in resource-island soil. While in resource-island soil shoot dry matter did not respond to shading ($p=0.340$), there was a large response in the bare-area soil, accounting for the highly significant interaction and suggesting soil-related differences in physiological responses to shading. For plants grown in the moister resource-island soil, dry matter accumulation and tissue hydration were apparently little affected by differences in stresses imposed by the shading regimes between waterings. The high shoot dry matter content of bare-area plants grown in the shade indicates a significantly more efficient assimilatory processes than in the sun. The pattern for root/shoot ratios was similar; root development relative to total plant mass was greater in the bare-area soil, reflecting the enhancement of root development commonly observed under nutrient limitation. Better root development in the shade (Figure 1E, F) reflects directly more benign subsurface soil temperatures.

None of the roots in either experiment were colonized by mycorrhizal fungi. Since mycorrhiza (fungusroot) formation does depend on soil conditions, such as temperature and nutrient levels (Sieverding, 1991), the absence of mycorrhization under any of the conditions of our treatments indicated that carbon is either not mycotrophic, or that the onset of root colonization is delayed or incidental (Carrillo-Garcia et al., 2000).

Nutrients

In a previous study, Carrillo-Garcia et al. (2000) showed significant growth enhancement of cardon when grown in resource-island soil compared to bare-area soil under conditions identical to those of Ex2. We therefore tested the

capability of nutrient amendments to produce plant growth in bare area soil similar to that found earlier in resource-island soil. Fertilization of the bare-area soil with N or P had a significant effect on plant growth (Figure 3, Table 1) and survival (Table 1). Of the 60 seedlings per treatment, only 48% of the controls survived till harvest, compared to 72% of the plants fertilized with NPK or with P alone. The difference between survival in the NPK and N regimes was not significant ($p=0.613$) nor was that between the K and control regimes ($p=0.284$). Both N and P therefore enhanced survival individually, but their effects were not synergistic (Figure 4A).

Nitrogen amendment (Table 1) increased the dry mass of plants grown in the greenhouse in the bare area soil to the same level ($p=0.465$) observed in the shaded resource-island soil in the open (Figure 1B), and the dry masses of these NPK- or N-amended plants (4.7 and 4.2 g, respectively) did not differ from those grown earlier in the greenhouse without fertilization in resource-island soil (4.6 g, $p > 0.5$). This growth response to N reflected the significant differences in soil N contents (resource-island vs. bare-area soils, 0.34 vs. 0.24 g/kg, $p=0.006$). The dry masses of the nutrient-free controls grown in the greenhouse or in shade in the open were also the same statistically ($p=0.506$). Since the light intensities to which plants were exposed in the greenhouse and under shade in the open were comparable, growth enhancement by resource-island soil in the shade was equivalent to N fertilization at the levels applied. In full sunlight, however, this 'N-equivalent' resource-island-soil effect was attenuated (Figure 113, C). Nitrogen also increased shoot dry mass (Figure 413) and root length (Figure 4F). The percentage of shoot dry matter, however, was smaller in N-fertilized plants indicating increased shoot-tissue hydration (Figure 4D), while the smaller root/shoot ratios of these plants suggested relatively smaller resource allocation to the roots (Figure 4C).

Plant-available P concentration, like that of N, was considerably lower (0.0028 vs. 0.0045 g/kg, $p=0.007$) in bare-area soil than in the mesquite soil, yet plant response to P was much smaller than to N (Figure 4B, E, Table 1). Although P fertilization decreased relative root growth (Figure 4C), it did not affect root length (Figure 4F) or shoot dry matter concentration (Figure 4D). The effects of K (soil concentration was not determined) were generally small and not significant (Figure 4, Table 1).

Table 1. Response of cardon plants grown in bare-area soil to fertilization. Numbers are the means and (SE) of six replications

Nutrients	Plant traits					
	Survival (%)	Shoot dry mass (g)	Root/shoot ratio	Shoot dry matter content (%)	Plant dry mass (g)	Root length (m)
Control	48 (7)	1.0 (0.2)	0.31 (0.06)	7.3 (0.5)	1.3 (0.2)	13.3 (3.0)
NPK	72 (5)	4.1 (0.8)	0.15 (0.02)	3.9 (0.3)	4.7 (0.9)	33.6 (6.6)
N	67 (5)	3.5 (0.6)	0.20 (0.01)	4.3 (0.2)	4.2 (0.7)	36.0 (5.8)
P	72 (9)	1.5 (0.1)	0.18 (0.02)	6.6 (0.5)	1.7 (0.2)	12.1 (1.4)
K	55 (10)	0.8 (0.1)	0.23 (0.04)	6.9 (0.3)	1.0 (0.1)	7.9 (0.8)
ANOVA (<i>p</i> -values)	0.084	<0.001	0.021	<0.001	<0.001	<0.001

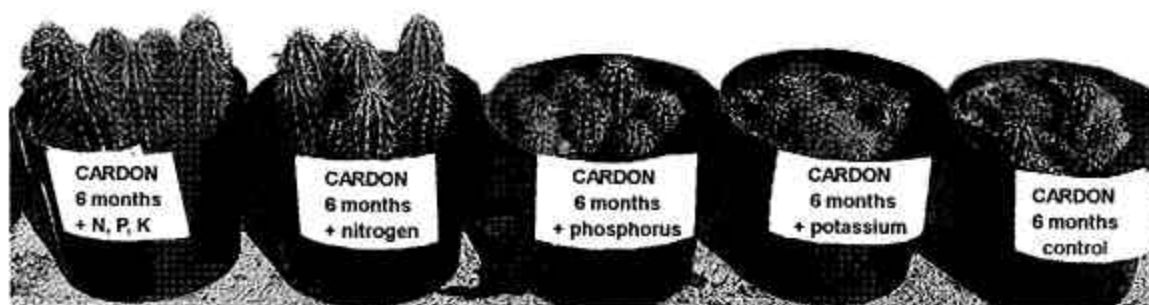


Figure 3. Cardon seedlings grown in bare-area soil (control) or amended with N, P, K, or NPK.

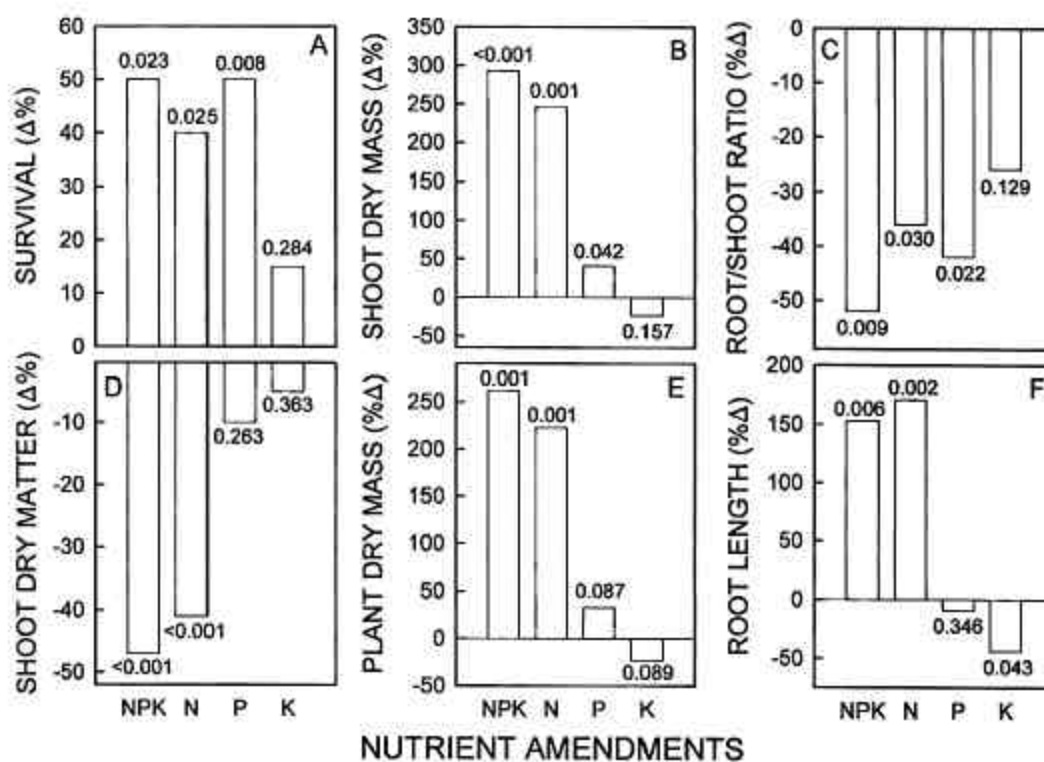


Figure 4. Plant responses to nutrient amendments N, P, K, or NPK expressed as percent change [%Δ, 100×(nutrient-control)/control]. Numbers are probability values and represent the significance of differences between controls and nutrient treatments by independent *t*-test.

The importance of N to plant growth in arid soils, as compared to that of other nutrients, has been observed by others (Franco and Nobel, 1989; Virginia, 1986; Virginia and Jarrell, 1983). Our results confirm these findings and relate them to light and temperature effects (Valiente-Banuet et al., 1991; Valiente and Ezcurra, 1991) that together with drought (Jordan and Nobel, 1981) and land-use practices (Niering and Lowe, 1985) determine the types and dynamics of populations in arid environments (Niering et al., 1963; Noy-Meir, 1973). The determination of the levels of critical factors that limit plant communities within their particular environments has long been a goal of research in physiological plant ecology (Niering et al., 1963). As growing human populations impose ever-increasing pressure on natural communities, however, an understanding of interrelations between limiting factors, such as nutrients and soil temperatures, becomes even more important in the context of restoration ecology (Hobbs and Norton, 1996) and the reversal of land degradation (Agnew and Warren, 1996).

Acknowledgement

This work was supported partially by a grant (#2626213) of the Consejo Nacional de Ciencia y Tecnología (CONACyT) of Mexico. The corresponding author (GJB) is indebted for the award of a Catedra Patrimonial de Excelencia fellowship by CONACyT that made his participation in this work possible, and thanks Robert G. Linderman and Jan van Schilfgaarde of USDA-ARS for their enthusiastic personal support.

References

- Agnew C and Warren A 1996 A framework for tackling drought and land degradation. *J. Arid Environ.* 33, 309-320.
- Archer S, Sciffres C, Bassham C R and Maggio R 1988 Autogenic succession in a subtropical savanna: Conversion of grassland to woodland. *Ecol. Monogr.* 58, 111-127.
- Armbrust D V and Bilbro J D 1997 Relating plant canopy characteristics to soil transport capacity by wind. *Agron. J.* 89, 157-162.
- Barth R C and Klemmedson J O 1982 Amount and distribution of dry matter, nitrogen, and organic carbon in soil-plant systems of mesquite and palo verde. *J. Range Manage.* 35, 412-418.
- Belsky A J, Amudson R G, Duxbury D M, Riha S J, Ali A R and Mwonga S M 1989 The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *J. Appl. Ecol.* 26, 1005-1024.
- Brady N C and Weil R R 1996 *The Nature and Properties of Soils*, 12th ed. Prentice Hall, Upper Saddle River, NJ.
- Bremner J M and Mulvaney C S 1982 Nitrogen-total. *In Methods of Soil Analysis, Part 2, Chemical and Biological Methods*, 2nd edition. Ed. A L Page. pp 5-624. American Society of Agronomy and Soil Science Society of America, Madison, WI.
- Callaway R M 1995 Positive interactions between plants. *Bot. Rev.* 61, 306-349.
- Carrillo-García A, Bashan Y, Diaz Rivera E and Bethlenfalvay G J 2000 Effects of resource-island soils, competition, and inoculation with *Azospirillum* on survival and growth of *Pachycereus pringlei*, the giant cactus of the Sonoran Desert. *Restor. Ecol.* (*In press*).
- Carrillo-García A, Leon de la Luz, J L, Bashan Y and Bethlenfalvay G J 1999 Nurse plants, mycorrhizae and plant establishment in a disturbed area of the Sonoran Desert. *Restor. Ecol.* (*In press*).
- Doran J W and Parkin T B 1994 Defining and assessing soil quality. *In Defining Soil Quality for a Sustainable Environment*. Eds Doran J W, Coleman D C, Bezdicek D F and Stewart B A. pp. 3-21. Special Publication Number 35, Soil Science Society of America, Madison, WI.
- Franco A C and Nobel P S 1989 Effect of nurse plants on the microhabitat and growth of cacti. *J. Ecol.* 77, 870-886.
- García-Moya E and McKell C M 1970 Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51, 81-88.
- Garner W and Steinberger Y 1989 A proposed mechanism for the formation of 'Fertile Islands' in the desert ecosystem. *J. Arid Environ.* 16, 257-262.
- Gee G W and Bauder J W 1986 Particle-size analysis. *In Methods of Soil Analysis, Part 1, Physical and Mineralogical Methods*, 2nd edition. Ed. A Klute. pp 383-411. American Society of Agronomy and Soil Science Society of America, Madison, WI.
- Giovanetti M and Mosse B 1980 An evaluation of techniques for measuring vesicular-arbuscular mycorrhizal infections in roots. *New Phytol.* 84, 489-500.
- Halvorson J J, Bolton H Jr, Smith J L and Rossi R E 1994 Geostatistical analysis of resource islands under *Artemisia tridentata* in the shrub-steppe. *Great Basin Naturalist*, 54, 313-328.
- Halvorson J J, Smith J L, Bolton H Jr and Rossi R E 1995 Evaluating shrub-associated spatial patterns of soil properties in a shrub-steppe ecosystem using multiple-variable geostatistics. *Soil Sci. Soc. Am. J.* 59, 1476-1487.
- Hobbs R J and Norton D A 1996 Towards a conceptual framework of restoration ecology. *Restor. Ecol.* 4, 93-110.
- Joffre R and Rambal S 1993 How tree cover influences the water balance of Mediterranean rangelands. *Ecology* 74, 570-582.
- Jordan P W and Nobel P S 1981 Seedling establishment of *Ferocactus acanthodes* in relation to drought. *Ecology* 62, 901-906.
- Lajtha K and Schlesinger W S 1986 Plant response to variations in nitrogen availability in a desert shrubland community. *Biogeochemistry* 2, 29-37.
- León de la Luz J L, Coria Benet R and Cruz Estrada M 1996 Fenología floral de una comunidad arido-tropical de Baja California Sur, Mexico (Floral phenology of an arid-tropical community of Baja California Sur, Mexico). *Acta Botánica Mexicana* 35, 45-64.
- Maya Y and Guzman J 1998 Recursos terrestres y suelo (Terrestrial resources and soil). *In Ed. Sociedad de la Historia Natural Niparaja*. pp 165-242. Diagnóstico Ambiental de Baja California Sur. Fundación Mexicana para la Educación Ambiental. Mexico City, Mexico.
- Niering W A and Lowe C H 1985 Vegetation of the Santa Catalina Mountains: community types and dynamics. *In Plant Community Ecology*. Ed. R K Peet. pp 159-184. W. Junk Publishers, Amsterdam.

- Niering W A, Whittaker R H and Lowe C H 1963 The saguaro: a population in relation to environment. *Science* 142, 15-23.
- Noy-Meir I 1973 Desert ecosystems: environment and producers. *Annu. Rev. Ecol. System.* 4, 25-51.
- Olsen S R and Sommers L E 1982 Phosphorus. *In* *Methods of Soil Analysis, Part 2, Chemical and Biological Methods*, 2nd edition. Eds A L Page and R H Miller. pp. 403-430. American Society of Agronomy and Soil Science Society of America, Madison, WI.
- Shreve F 1931 Physical conditions in sun and shade. *Ecology* 12, 96-105.
- Shearer G, Kohl D H, Virginia, R A, Bryan B A, Skeeters J L, Nilsen E T, Sharifi M R and Rundel P W 1983 Estimates of N₂-fixation from variation in the natural abundance of ¹⁵N in Sonoran Desert ecosystems. *Oecologia* (Berlin) 56, 356-373.
- Sieverding E 1991 Vesicular-arbuscular mycorrhiza management in tropical agrosystems. Bremer Verlag, Berlin.
- Turner R M, Alcorn S M, Olin G and Booth J A 1966 The influence of shade, soil, and water on saguaro seedling establishment. *Bot. Gaz.* 95, 95-102.
- Valiente-Banuet A, Bolongaro-Crevenna A, Briones O, Excurra E, Rosas M, Nuñez H, Barnard G and Vazquez E 1991 Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. *J. Veget. Sci.* 2, 15-20.
- Valiente-Banuet A and Ezcurra E 1991 Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *J. Ecol.* 79, 961-971.
- Virginia R A 1986 Soil development under legume tree canopies. *Forest Ecol. Manage.* 16, 69-79.
- Virginia R A and Jarrell W M 1983 Soil properties in a mesquitedominated Sonoran Desert ecosystem. *Soil Sci. Soc. Am. J.* 47, 138-144.
- Zinke P J 1962 The pattern of influence of forest trees on soil properties. *Ecology* 43, 130-133.

Section editor: E Garnier