

Effect of Nurse Plants on the Microhabitat and Growth of Cacti

Author(s): A. C. Franco and P. S. Nobel

Source: *Journal of Ecology*, Vol. 77, No. 3 (Sep., 1989), pp. 870-886

Published by: British Ecological Society

Stable URL: <https://www.jstor.org/stable/2260991>

Accessed: 15-11-2018 19:11 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Ecology*

EFFECT OF NURSE PLANTS ON THE MICROHABITAT AND GROWTH OF CACTI

A. C. FRANCO AND P. S. NOBEL*

Department of Biology and Laboratory of Biomedical and Environmental Sciences,
University of California, Los Angeles, California 90024, U.S.A.

SUMMARY

(1) Seedlings of the cactus *Carnegiea gigantea* at two sites in the Sonoran Desert were found only in sheltered microhabitats, 89% occurring under the canopy of *Ambrosia deltoidea* and *Cercidium microphyllum*. In contrast, 29% of the seedlings of *Ferocactus acanthodes*, which tolerates higher temperatures than *C. gigantea*, occurred in unsheltered microhabitats, where maximum soil surface temperatures reached 71°C. Most (70%) of the sheltered seedlings of *F. acanthodes* occurred under the canopy of the perennial bunchgrass *Hilaria rigida*.

(2) Shading by nurse plants reduced the total daily photosynthetically active radiation (PAR) available for their associated seedlings. Near an equinox, a seedling of *C. gigantea* located at the centre of an *A. deltoidea* shrub received 77% less total daily PAR, which reduces its predicted net CO₂ uptake by 90% compared with an unshaded seedling. Similarly, a seedling of *F. acanthodes* located at the centre of an *H. rigida* plant received 64% less total daily PAR and could fix 65% less CO₂ than could an unshaded seedling.

(3) *H. rigida* and *F. acanthodes* have overlapping shallow root systems (mean root depth of 0.08 m for *H. rigida* and 0.05 m for seedlings of *F. acanthodes*), which accentuates competition for water. A water uptake model, which closely predicted the soil water potential in the root zone of *H. rigida*, indicated that a seedling of *F. acanthodes* located at the centre of the bunchgrass took up 32% less water than did an exposed seedling.

(4) Assuming that the effects of temperatures, PAR, and soil water on net CO₂ uptake are multiplicative, the predicted net CO₂ uptake of a seedling of *F. acanthodes* under the canopy of *H. rigida* was only 36% of that of an exposed seedling. However, areole production by seedlings of *F. acanthodes* located under the nurse plant was 68% of that measured in exposed areas. This discrepancy probably reflects the 60% higher soil nitrogen levels under *H. rigida*.

(5) Therefore, nurse plants facilitate seedling establishment by reducing high temperatures near the soil surface and provide a microhabitat with a higher soil nitrogen level. However, shading and competition for water with the nurse plants markedly reduce seedling growth. The magnitude of the reduction depends on seedling size and location under the nurse plant.

INTRODUCTION

Seedlings of desert succulents frequently occur beneath the canopies of other perennial species, which are referred to as nurse plants (Turner *et al.* 1966; Steenbergh & Lowe 1977; Jordan & Nobel 1979). Shading by nurse plants can protect seedlings of the saguaro cactus, *Carnegiea gigantea*, from temperature extremes, thereby increasing seedling survival and extending its distributional boundaries (Turner *et al.* 1966; Steenbergh & Lowe 1977; Nobel 1980a). For a 0.05-m-tall seedling of the barrel cactus *Ferocactus acanthodes*, complete shading from direct sunlight decreases the maximum stem surface temperature by 11°C on a summer day and raises the minimum temperature by 3°C on a

* Correspondence author.

winter day (Nobel 1984a). Shading by the nurse plant also decreases the photosynthetically active radiation (PAR) available for the associated seedling, which would limit its CO₂ uptake if any of the photosynthetic surfaces are below the PAR saturation level, as is the case for several desert CAM plants (Woodhouse, Williams & Nobel 1980; Nobel 1986a).

Seedling growth for desert species can be reduced by neighbouring adult plants (Friedman 1971; Fowler 1986; Gurevitch 1986). Evidence that seedling growth is constrained by competition for water is provided by removal experiments, in which the water status and above-ground productivity of plants improve when their neighbours are removed (Fonteyn & Mahall 1981; Robberecht, Mahall & Nobel 1983; Ehleringer 1984; Nobel & Franco 1986). On the other hand, nitrogen levels can be higher around desert trees and shrubs (Garcia-Moya & McKell 1970; Charley & West 1975; Hunter, Romney & Wallace 1982), which would enhance growth of associated seedlings.

The present study investigated the effect of nurse plants on the growth of seedlings of *C. gigantea* and *F. acanthodes*, which occur in the Sonoran Desert of Mexico and southwestern United States (Shreve & Wiggins 1964) and are commonly found under the canopies of other perennials (Steenbergh & Lowe 1977; Nobel 1984a). After determining the positions of seedlings under the canopy of nurse plants, the seedling microenvironment was characterized in terms of PAR, soil surface temperatures, and soil nitrogen content. A three-dimensional simulation model of root water uptake was used to examine competition for water between a medium-sized *Hilaria rigida* and an associated seedling of *F. acanthodes* under different climatic conditions as well as various seedling sizes and locations under the nurse plant.

MATERIALS AND METHODS

Field sites

Carnegiea gigantea (Engelm.) Britt. & Rose was studied near Ajo, Arizona, at Organ Pipe Cactus National Monument (study sites at 31°58'N, 112°33'W, 500 m elevation and 32°5'N, 112°45'W, 600 m). *Ferocactus acanthodes* (Lem.) Britt. & Rose was studied near Palm Desert, California, at the University of California Philip L. Boyd Deep Canyon Desert Research Center (study site at 33°38'N, 116°24'W, 850 m). Annual precipitation averaged 227 mm year⁻¹ at the California site and 277 mm year⁻¹ at the Arizona sites (National Oceanic and Atmospheric Administration 1976–1985; Nobel 1987).

Sites totalling 4700 m² each for *C. gigantea* and 7500 m² for *F. acanthodes* were selected, subdivided into 10 m × 10 m quadrats, and searched for seedlings of *C. gigantea* up to 0.2 m tall or of *F. acanthodes* up to 0.1 m tall, heights that represent plants up to ten years of age (Jordan & Nobel 1982). A seedling was considered to be associated with a nurse plant when the seedling occurred under the canopy of another plant. The principal nurse plant for *F. acanthodes* was the bunchgrass *Hilaria rigida* (Thunb.) Benth. ex Scribn., and for *C. gigantea* it was the shrub *Ambrosia deltoidea* (Torr.) Payne, and the tree *Cercidium microphyllum* (Torr.) Rose & Johnst. In such cases, the major and the minor axes of the nurse plant canopy were measured, together with the distance and compass direction of the seedling from the centre of the nurse plant.

Soil samples for total nitrogen determinations were collected halfway along the canopy minor semiaxis (north and south) of representative, medium-sized nurse plants as well as in regions of bare soil. The average major and minor axes of the canopy were 0.87 m and 0.65 m for *A. deltoidea*, 4.5 m and 4.3 m for *C. microphyllum*, and 0.54 m and 0.40 m for

H. rigida. Soil samples were taken at depths of 0.05–0.10 m, approximately the mean root depths for seedlings of the two cactus species (Cannon 1911; Hunt & Nobel 1987a). Total soil nitrogen was determined using 1 g (dry mass) samples that were digested according to the micro-Kjeldahl method, followed by ammonia distillation and titration to pH 5 with 0.01 M HCl (Bremner 1965). Statistical significance was analysed using Student's *t*-test.

Temperature and PAR

The thermal and the PAR environments of exposed and sheltered seedlings of *C. gigantea* were determined near the autumn equinox (on 16 September 1987) for representative specimens of *A. deltoidea* and *C. microphyllum*. Soil surface temperatures were measured hourly either with copper–constantan thermocouples 0.51 mm in diameter placed 2 mm below the soil surface at the centre of the *A. deltoidea* and 0.30 m away from the centre on each cardinal direction, or with an Everest 210 infra-red thermometer at the centre of the *C. microphyllum*, 1.2 m away from the centre in each cardinal direction, and outside the canopy (measurements for an unshaded soil agreed within 1°C between techniques). To characterize the PAR environment of the seedling, a spherical replica 0.05 m tall and a cylindrical replica 0.20 m tall (shapes that resembled seedlings of *C. gigantea* at these heights) were sequentially located at the same positions as used for temperature measurements. Measurements of instantaneous PAR with a LI-COR 190S quantum flux sensor were made approximately hourly at midheight in the four cardinal directions and also at the top for the spherical replica and at one-quarter and three-quarters of the height in the four cardinal directions and at the top for the cylindrical replica.

The copper–constantan thermocouples at an exposed location and beneath the canopy of a representative plant of *H. rigida* were installed as described for *A. deltoidea*. The soil surface temperatures were recorded hourly with a Campbell Scientific CR5 digital recorder over twenty-four-hour periods on clear days approximately every two months for a two-year period at the centre, 0.15 m away from the centre in the four cardinal directions, and 0.5 m outside the canopy of the bunchgrass. To characterize the PAR environment of a seedling, a spherical replica 0.05 m tall was constructed and located at the centre or 0.11 m south of the centre (the mean seedling location) in the same specimen of *H. rigida* as used for the temperature measurements as well as outside its canopy. NEC PH201A photodiodes, calibrated in PAR units with a LI-COR 190A quantum flux sensor, were located at mid-height in the four cardinal directions and the top of the seedling replica. PAR measurements were taken approximately every half hour throughout 22 June 1987, 10 December 1987 and 15 March 1988.

Water uptake model

A three-dimensional model (Franco & Nobel 1988), developed from a two-dimensional, radially symmetric model (Hunt & Nobel 1987a), was used to predict water uptake at various soil depths and distances from the nurse plant *H. rigida* and an *F. acanthodes* located beneath it. A cylinder of soil with a radius of 0.05 m and centred on the nurse plant was surrounded by fourteen additional concentric sheaths whose radii increased in 0.05-m increments. Each concentric sheath was radially subdivided into eight wedges and vertically subdivided into two 0.02-m-thick upper layers, four 0.04-m-thick intermediate layers, and three 0.05-m-thick lower layers. To obtain root length in each subvolume at various depths and distances from the base of the nurse plant, five medium-sized plants of *H. rigida* and five 0.05-m-tall seedlings of *F. acanthodes* were excavated. During excavation two-dimensional maps (a horizontal projection and vertical projection) were

drawn showing all recovered roots of a particular plant. For larger sizes of *F. acanthodes*, the root length in the various subvolumes was adapted from Hunt & Nobel (1987a).

Evaporation from the soil surface (J_{wv}) was calculated according to Fick's law of diffusion taking into consideration the effect of the plant canopy on soil surface temperatures (Nobel & Geller 1987). No evaporation was assumed to occur from the ground area blocked by the cactus stem. Darcy's law for cylindrical symmetry was used to calculate the volume flux density of water moving in the soil toward a root surface, and root water uptake ($J_{\text{V}}^{\text{root}}$) was calculated based on the water potential drop between the root surface and the centre of the root (ψ^{root}). These two volume flux densities were equated at the root surface using iterations that varied the water potential at the root surface. ψ^{root} of *H. rigida* was calculated from field measurements of stem water potential under wet ($\psi^{\text{soil}} > -0.5$ MPa) and dry ($\psi^{\text{soil}} = -2.6$ MPa) conditions together with transpiration rates and the resistances to water flow for this species (Nobel & Jordan 1983; Hunt & Nobel 1987b; Franco & Nobel 1988). Because of the large shoot capacitance of *F. acanthodes*, its ψ^{root} was considered constant and equal to -0.5 MPa (Hunt & Nobel 1987a,c). For each time-step, J_{wv} and $J_{\text{V}}^{\text{root}}$ were determined, and then water movement among the soil subvolumes was calculated using Darcy's law in cylindrical or cartesian coordinates as appropriate (Nobel 1983a; Young & Nobel 1986).

All simulations were performed for 1.0-h intervals, routinely starting with a soil volumetric water content of $0.1 \text{ m}^3 \text{ m}^{-3}$ at the beginning of the year, a typical value for the first week of January at the field site (Nobel 1987). Unless otherwise indicated, simulations were performed for the California site using local weather data for a dry year (1973, 78 mm rainfall), an average year (1987, 169 mm rainfall), and a wet year (1983, 598 mm rainfall). Based on field observations (Nobel 1980b), leaf area for *H. rigida* was assumed to be 3% of the maximum during the first week after major rainfall, 18% during the second week, and 60% during the third week, after which the leaf area was approximately constant at the maximum value. Because *F. acanthodes* always has a functional chlorenchyma and hydration of roots occurs within a few hours after rewetting the soil (Nobel & Sanderson 1984), its transpiration was assumed to increase linearly with time, reaching the maximum values four days after rewetting of the soil (Nobel 1977).

Environmental productivity index and seedling growth

The quantitative effects of water, temperature and PAR on the net CO_2 uptake for seedlings of *F. acanthodes* were summarized using an environmental productivity index (EPI; Nobel 1984b) that accurately predicts productivity of this species (Nobel 1986b). EPI represents the product of individual indices for water status, temperature and PAR, each of which has a value of 1.00 when that variable is not limiting CO_2 uptake over a 24-h period (Nobel 1984b). The water status index was based on criteria developed for mature *F. acanthodes* (Nobel 1986b), whereby $\psi^{\text{soil}} > -0.5$ MPa at the mean root depth indicates no limitation of CO_2 uptake by soil water, but taking into consideration the higher surface area/volume ratio and the CO_2 uptake characteristics appropriate for seedlings (Jordan & Nobel 1981); ψ^{soil} at the mean root depth was predicted by the water uptake model. The temperature index was based on the average daily minimum and maximum air temperatures at the field site for each month, maximum CO_2 uptake occurring at day/night temperatures of $23^\circ\text{C}/14^\circ\text{C}$ (Nobel 1986b; Nobel & Hartsock 1986a). The PAR index, which is based on total daily PAR, took into consideration the effect of canopy shading by the nurse plant and shading by the spines of the cactus seedling (Geller & Nobel 1984).

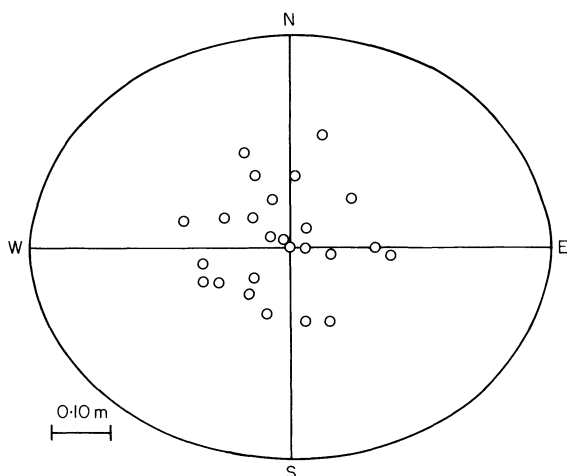


FIG. 1. Location of seedlings of *Carnegiea gigantea* under the canopy of *Ambrosia deltoidea*. The distances were scaled for a representative *A. deltoidea* with a canopy major axis of 0.88 m, the mean value for this nurse plant with associated seedlings of *C. gigantea* at Organ Pipe Cactus National Monument, Arizona.

To monitor seedling growth, the production of new areoles (axillary buds) was determined every two months during a twenty-seven-month period. Eight seedlings of *F. acanthodes* in exposed areas and eight seedlings under *H. rigida*, which have a mean location of 0.11 m south of the centre of the nurse plant, were used. For both cases the seedlings were 0.03–0.07 m tall with seven or eight ribs.

RESULTS

Characterization of microhabitats

Seedling distribution

Seedlings of *Carnegiea gigantea* up to 0.2 m tall were found only in sheltered microhabitats. The majority (twenty-five of thirty-seven) were beneath individuals of *Ambrosia deltoidea*, where the seedlings were located within 0.2 m of the canopy centre and none occurred close to the canopy edges (Fig. 1). The remaining seedlings were beneath *Cercidium microphyllum* (eight), *Oleña tesota* Gray (three), and *Larrea tridentata* (Sessé & Moc. ex DC.) Cov. (one).

Although most seedlings of *Ferocactus acanthodes* (thirty of forty-two) were found under the canopies of other plants, twelve individuals occurred in unsheltered microhabitats. Most of the shaded seedlings were beneath *Hilaria rigida* (twenty-one of thirty), where they were scattered throughout the area beneath the canopy (Fig. 2). The remaining seedlings were beneath *A. dumosa* (Gray) Payne (six) and *Ephedra aspera* Engelm. ex Wats. (three).

Temperature

Daily variations in soil surface temperatures were less under the canopy of the nurse plants than outside the canopy (Fig. 3). On a clear day in the autumn, maximum soil

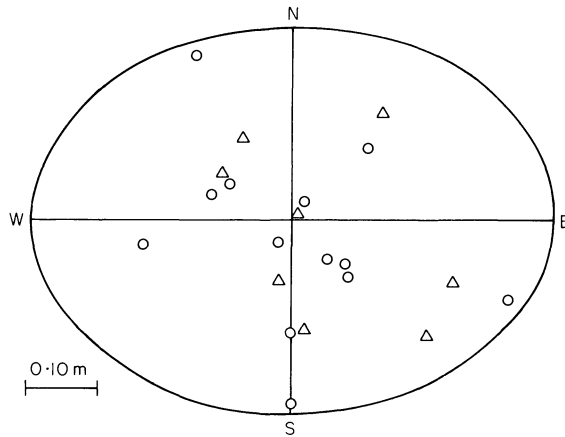


FIG. 2. Location of seedlings of *Ferocactus acanthodes* under the canopy of *Hilaria rigida*. The triangles represent the seedlings the growth of which was monitored. The distances were scaled for an *H. rigida* with a canopy major axis of 0.54 m, the mean value for this nurse plant with associated seedlings of *F. acanthodes* at Deep Canyon Desert Research Center, California.

surface temperatures reached 60.1°C outside the canopy compared with 47.4°C at the centre of *A. deltoidea* or 41.4°C at the centre of *C. microphyllum*. Minimum soil surface temperatures were 17.5°C , 18.7°C , and 20.0°C , for an exposed location, at the centre of *A. deltoidea*, and at the centre of *C. microphyllum*, respectively (Fig. 3).

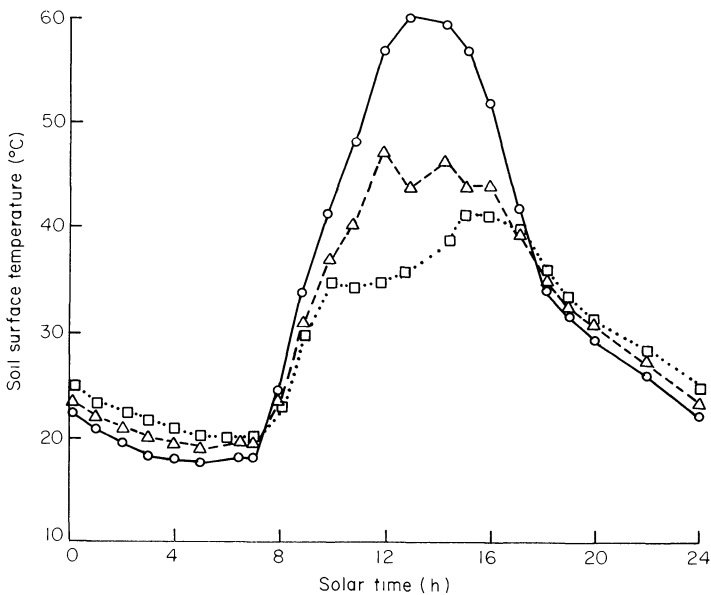


FIG. 3. Daily course of soil surface temperatures at an exposed location (○) and at the centres of a representative *Ambrosia deltoidea* (Δ) with a canopy major axis of 0.87 m and a representative *Cercidium microphyllum* (□) with a canopy major axis of 4.5 m for a clear day near the autumnal equinox (16 September 1987) near Ajo, Arizona.

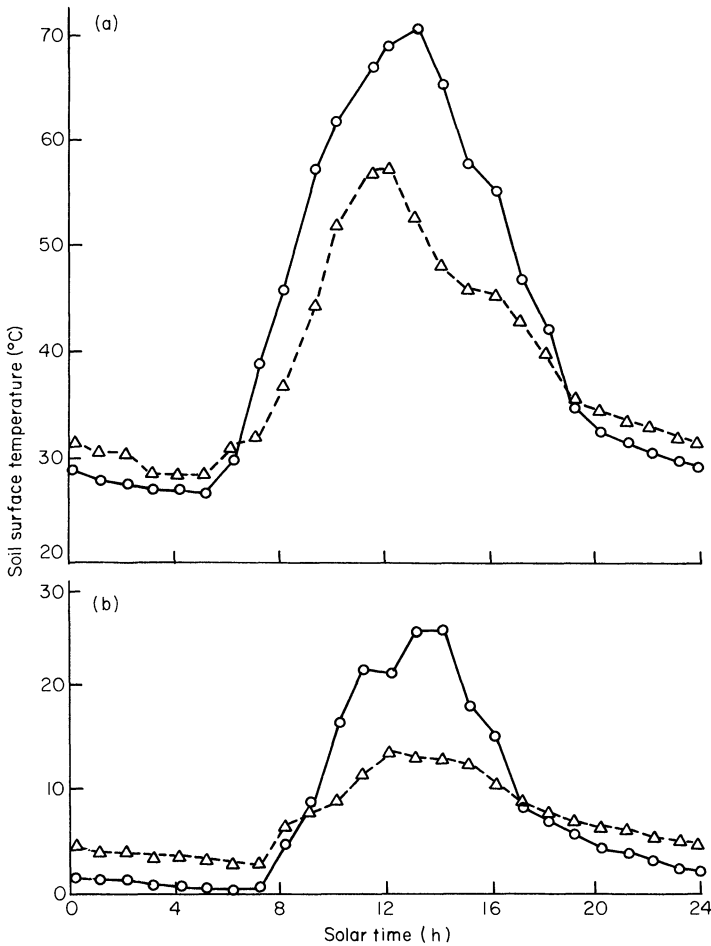


FIG. 4. Daily course of soil surface temperature at an exposed location (○) and at the centre of a representative *Hilaria rigida* (△) with a canopy major axis of 0.52 m for (a) a clear, hot day in the summer (25 June 1986) and (b) a clear, cold day in the winter (6 January 1988), near Palm Desert, California.

For a clear hot summer day, maximum soil surface temperatures reached 71.0°C in an exposed area, compared with 57.5°C at the centre of an *H. rigida* plant (Fig. 4a). Minimum soil surface temperatures were 26.2°C outside the canopy, compared with 28.2°C at the centre of the *H. rigida*. The same pattern occurred in the winter (Fig. 4b), when maximum and minimum soil surface temperatures were 25.1°C and 0.1°C for an exposed location compared with 13.6°C and 3.0°C at the centre of *H. rigida*.

Photosynthetically active radiation

Total daily PAR incident on a seedling of *C. gigantea* was greatly reduced by the nurse plants (Fig. 5). For a seedling 0.05 m tall, total daily PAR on a clear day near the autumnal equinox decreased from 23.4 mol m⁻² for an exposed location to 5.4 mol m⁻² at the centre of *A. deltoidea* and 5.8 mol m⁻² at the centre of *C. microphyllum* (Fig. 5a). For seedlings 0.20 m tall, total daily PAR outside the canopy or beneath *C. microphyllum* was similar to

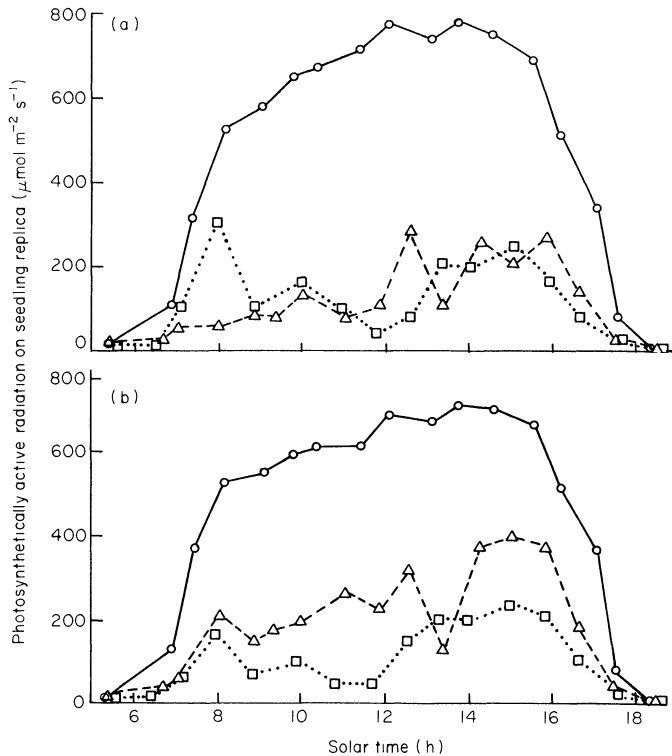


FIG. 5. Daily course of photosynthetically active radiation incident on a seedling replica of *Carnegiea gigantea* 0.05 m tall (a) and 0.20 m tall (b) located at an exposed location (○), at the centre of a representative *Ambrosia deltoidea* (△), and at the centre of a representative *Cercidium microphyllum* (□; same plants as for Fig. 3). Each datum represents the average PAR received for five locations on the 0.05-m-tall replica and nine locations for the 0.20-m-tall replica. Both sets of measurements were made near the autumn equinox (16 September 1987) near Ajo, Arizona.

the amount received by the smaller seedling at the same locations, but it was 8.7 mol m^{-2} beneath *A. deltoidea* (Fig. 5b).

In the summer (22 June 1987), total daily PAR received by a 0.05-m-tall seedling of *F. acanthodes* was 34.7 mol m^{-2} for an exposed location and 13.4 mol m^{-2} at the centre of *H. rigida*. In the winter (10 December 1987), it was 22.5 mol m^{-2} for an exposed location but only 6.2 mol m^{-2} at the centre of *H. rigida*. The distribution of PAR under the canopy of the nurse plant was not uniform; near the spring equinox, total daily PAR decreased from 28.4 mol m^{-2} for an exposed location to 19.1 mol m^{-2} on the south side to 10.3 mol m^{-2} at the centre of the nurse plant (Fig. 6).

Soil nitrogen

When compared with an exposed location, total soil nitrogen content was significantly higher ($t=6.43$ for *C. microphyllum* and $t=7.33$ for *A. deltoidea*; in both cases $P<0.001$) under the canopy of both nurse plants at Organ Pipe Cactus National Monument (Table 1). Similarly, soil nitrogen content was significantly higher ($t=3.89$, $P<0.01$)

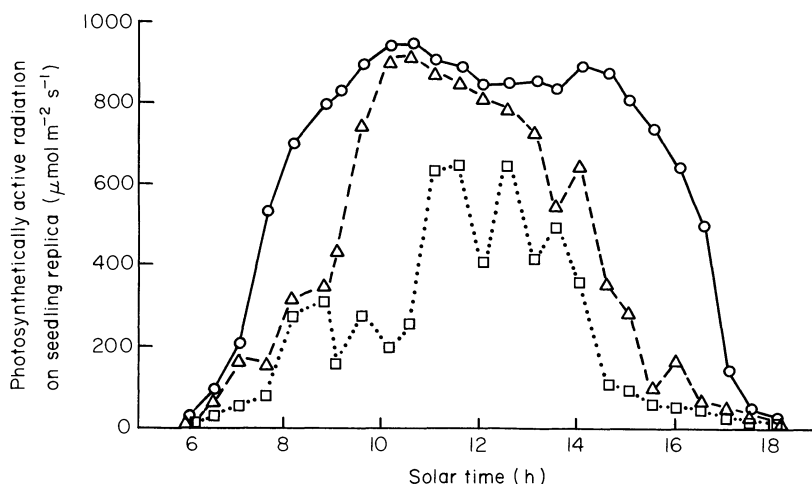


FIG. 6. Daily course of photosynthetically active radiation incident on a 0.05-m-tall seedling replica of *Ferocactus acanthodes* located in an exposed location (○), at the centre of a representative *Hilaria rigida* (□) (same plant as for Fig. 4), and 0.10 m south of the centre (Δ). Each datum represents the average PAR received for five locations on the replica taken near the spring equinox (15 March 1988) near Palm Desert, California.

under the canopy of *H. rigida* at the Deep Canyon Desert Research Center compared with outside its canopy (Table 1).

Root distribution and predictions of soil water potential

The root systems of both *H. rigida* and *F. acanthodes* were shallow, the mean root depth averaging 0.08 m for the bunchgrass and 0.05 m for 0.03–0.05-m-tall seedlings of the barrel cactus (Fig. 7). The ground area explored by the roots was 0.50 m² for *H. rigida* and 0.013 m² for seedlings of *F. acanthodes*. Averaged over the ground area explored by the roots and the upper 0.24 m of soil, total root length per soil volume for the bunchgrass was 782 m m⁻³. Roots of the barrel cactus seedlings occurred in the upper 0.16 m only, leading to a total length per soil volume of 476 m m⁻³.

To test the accuracy of the model for predicting soil water potential under a range of soil moistures, pre-dawn ψ^{soil} under *H. rigida* was monitored for twenty-seven months in the field. Predicted ψ^{soil} at a depth of 0.10 m was in general agreement with measurements (Fig. 8). Extended drought periods interrupted by brief wet periods ($\psi^{\text{soil}} > -0.5$ MPa) up

TABLE 1. Total soil nitrogen content beneath nurse plants and in exposed regions outside the influence of their roots. Figures are means \pm 1 S.E. ($n = 6$).

Location	Nurse plant	N (% by dry mass)
Organ Pipe Cactus National Monument	None	0.014 \pm 0.001
	<i>Ambrosia deltoidea</i>	0.035 \pm 0.005
	<i>Cercidium microphyllum</i>	0.037 \pm 0.004
Deep Canyon Desert Research Center	None	0.029 \pm 0.004
	<i>Hilaria rigida</i>	0.046 \pm 0.003

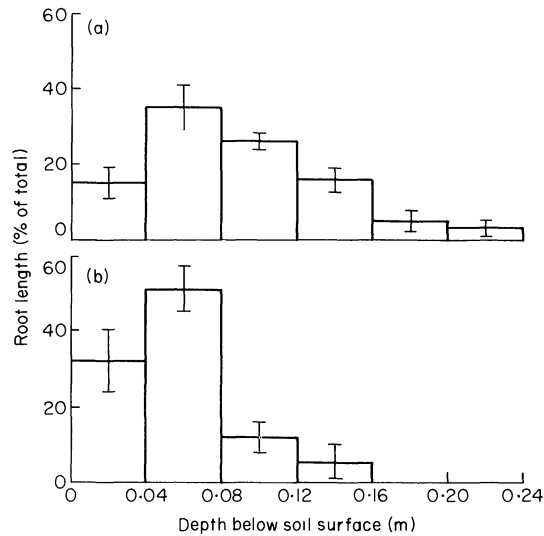


FIG. 7. Root distribution with depth for the nurse plant *Hilaria rigida* and seedlings of *Ferocactus acanthodes* for 0.04-m-thick soil layers near Palm Desert, California. Data are presented as mean ± 1 S.E. for five plants of each species.

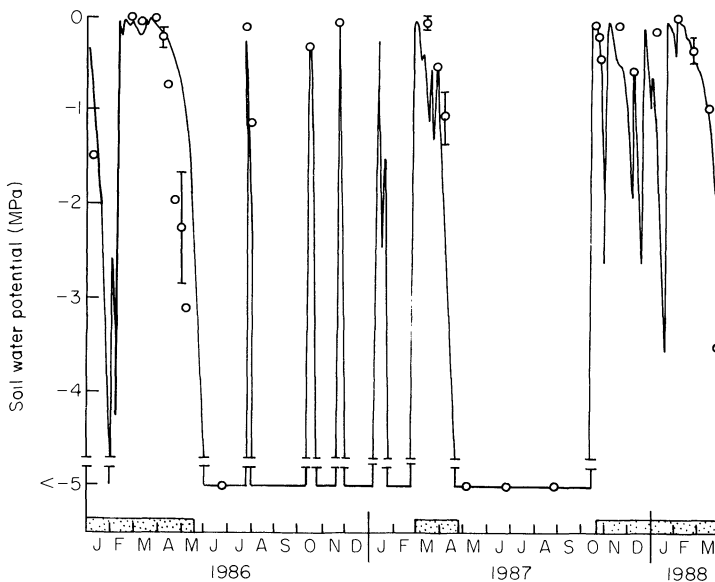


FIG. 8. Measured (O) and predicted (—) soil water potentials beneath *Hilaria rigida*, near Palm Desert, California. Data are for a depth of 0.10 m and a location 0.20 m south of the centre of a plant with 100 culms. Representative S.E.s are indicated for two soil psychrometers located under each of two plants. Stippled areas indicate periods when at least 5% of the culms on each of four plants examined had green leaves.

TABLE 2. Stimulated annual water uptake by the roots of *Ferocactus acanthodes* associated with *Hilaria rigida* for a dry, an average, and a wet year with the indicated rainfall. Cacti of three different sizes were located at the centre of the nurse plant, 0·10 m south of the centre, and in an exposed area.

Plant type	Ground area explored by the roots (m ²)	Annual rainfall (mm)	Annual water uptake by the roots of <i>F. acanthodes</i> (m ³ year ⁻¹)		
			Centre	South side	Exposed
Seedling	0·005	78	71·8 × 10 ⁻⁶	91·3 × 10 ⁻⁶	90·2 × 10 ⁻⁶
		169	176 × 10 ⁻⁶	228 × 10 ⁻⁶	317 × 10 ⁻⁶
		598	730 × 10 ⁻⁶	900 × 10 ⁻⁶	1053 × 10 ⁻⁶
Medium-sized plant	0·5	78	1·71 × 10 ⁻³	1·69 × 10 ⁻³	2·06 × 10 ⁻³
		169	5·74 × 10 ⁻³	5·77 × 10 ⁻³	8·86 × 10 ⁻³
		598	22·1 × 10 ⁻³	21·8 × 10 ⁻³	26·8 × 10 ⁻³
Large plant	1·0	78	3·43 × 10 ⁻³	3·41 × 10 ⁻³	3·85 × 10 ⁻³
		169	12·2 × 10 ⁻³	12·3 × 10 ⁻³	16·5 × 10 ⁻³
		598	44·6 × 10 ⁻³	44·5 × 10 ⁻³	52·9 × 10 ⁻³

to three days in length did not induce development of new leaves by *H. rigida*, whereas longer wet periods did (Fig. 8).

Simulations of root water uptake

Hilaria rigida reduced the simulated annual water uptake by associated *F. acanthodes* (Table 2). Averaged over the three years considered, a seedling at the centre of the nurse plant absorbed 32% less water than an exposed seedling and 21% less water than a seedling 0·10 m south of the centre. For medium-sized and large cacti, simulated annual water uptake was about the same for the two locations associated with the nurse plant, averaging 21% less than the annual water uptake by exposed *F. acanthodes* of the same sizes.

Annual water uptake by *H. rigida* was affected by the location of the cactus, although the overall effect was small (Fig. 9). The largest cactus, when located at the centre of the nurse plant, decreased the annual water uptake of *H. rigida* by about 4% for the three years considered. When the cactus was located 0·10 m south of the centre of the nurse plant, simulated annual water uptake by *H. rigida* was slightly higher than in the absence of *F. acanthodes*. For *H. rigida* associated with an *F. acanthodes* with 0·5 m² root ground area, the enhancement was 7%, and it was 5% when associated with an *F. acanthodes* with 1·0 m² root ground area (Fig. 9).

Environmental productivity index and seedling growth

For the twenty-seven-month period considered, EPI was higher for seedlings at exposed sites than under the nurse plant (Fig. 10). Maximum monthly EPI of *F. acanthodes* was 0·742 for an exposed seedling and 0·416 for a seedling under *H. rigida*. Averaged over the entire period, EPI for a seedling was 0·192 at an exposed location, 0·089 at 0·10 m south of the centre of the nurse plant, and 0·034 at the centre. Consequently areole production per plant averaged over the same period was 9·50 ± 1·02 (S.E.) areoles for eight exposed seedlings, which is significantly higher (*t* = 4·01, *P* < 0·01) than the 6·50 ± 0·57 areoles produced by eight seedlings under the nurse plant.

Averaged over the years that represent the rainfall range at the field site, EPI for a seedling at the centre of the nurse plant was 21% of the value calculated for a seedling at

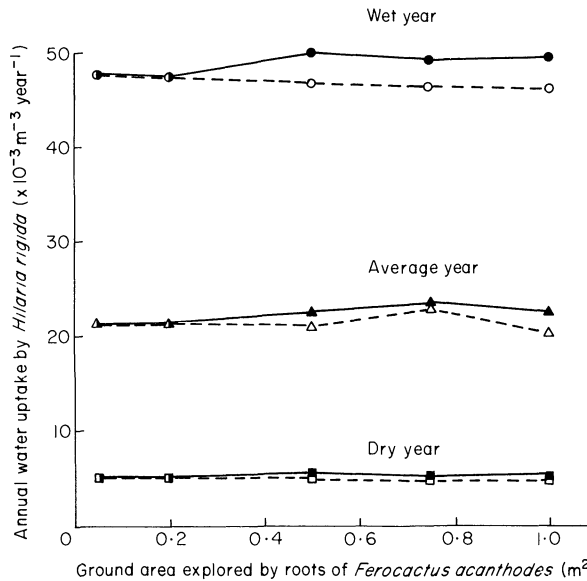


FIG. 9. Simulated annual water uptake by roots of *Hilaria rigida* associated with *Ferocactus acanthodes* of various sizes for a dry (78 mm rainfall), an average (169 mm), and a wet year (598 mm) at a site near Palm Desert, California. The cactus was located at the centre of the nurse plant (○, △, □) or 0.10 m south of the centre (●, ▲, ■).

an exposed location (Table 3). However, small variations in seedling location under the nurse plant markedly affected EPI. Averaged over the three years considered, displacing the seedling from the centre to 0.10 m south of the centre increased EPI from 0.035 to 0.089 (Table 3).

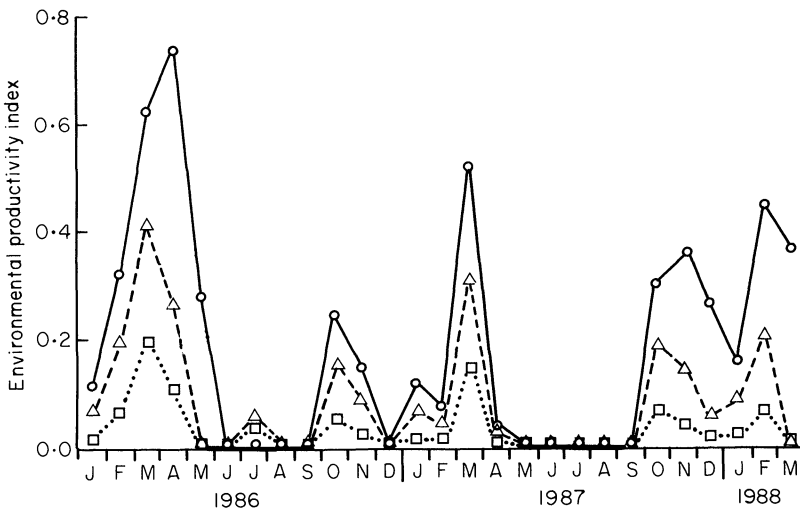


FIG. 10. Monthly values of EPI for a seedling of *Ferocactus acanthodes* located in an exposed area (○), at the centre of the nurse plant (□), and 0.10 m south of the centre (△) near Palm Desert, California.

TABLE 3. Mean monthly EPI for seedlings of *Ferocactus acanthodes* averaged over a dry, an average, and a wet year. Seedlings were located at the centre of the nurse plant, 0.10 m south of the centre, and in an exposed location.

Annual rainfall (mm)	EPI		
	Centre	South side	Exposed
78	0.020	0.044	0.064
169	0.026	0.072	0.176
598	0.058	0.152	0.343

DISCUSSION

Seedlings of *Carnegiea gigantea* were found only under the canopy of nurse plants. In contrast, 29% of the seedlings of *Ferocactus acanthodes* occurred in unsheltered microhabitats, where soil surface temperatures can reach 71°C in the summer, compared with 57°C under the nurse plant. Seedlings of *C. gigantea* can survive temperatures up to 66°C, compared with up to 71°C for *F. acanthodes* (Nobel 1984c). Because maximum shoot surface temperatures of a small cactus and maximum soil surface temperatures are approximately the same (Nobel 1984a), establishment of *C. gigantea* in unshaded habitats would not be expected. In fact, in transplant experiments utilizing seedlings, mortality among unshaded *C. gigantea* was 100% in one year, compared with 65% for shaded seedlings (Turner *et al.* 1966), in agreement with observations on the spatial distribution patterns for this species (Hutton, McAuliffe & Hogan 1986).

Shading by nurse plants also reduced the PAR available for the seedling, which would limit its CO₂ uptake. Based on the relationship between nocturnal CO₂ uptake and total daily PAR measured for cacti (Nobel 1986a), near an equinox a 0.05-m-tall seedling of *F. acanthodes* located at the centre of an *Hilaria rigida* would receive 64% less PAR and fix 65% less CO₂ than an unshaded seedling. For seedlings beneath the canopies of shrubs or perennial grasses, small changes in seedling size and location can markedly affect PAR interception. A 0.20-m-tall seedling of *C. gigantea* located at the centre of *Ambrosia deltoidea* would receive 61% more PAR per unit area near an equinox and could fix 3.4 times more CO₂ than a 0.05-m-tall seedling. Furthermore, a 0.05-m-tall seedling of *F. acanthodes* located at the south side of the nurse plant would receive 2.5 times more PAR and could fix about 2.0 times more CO₂ than a seedling located at the centre. Seedlings of *Agave deserti* located at the centre of *H. rigida* intercept 28% more PAR, which leads to a 45% higher predicted annual CO₂ uptake than for seedlings located at the north side (Franco & Nobel 1988). Thus, although deserts are characterized by a high radiation environment, light limits CO₂ uptake by seedlings of desert succulents, especially when they are shaded by nurse plants. The magnitude of the reduction depends on canopy characteristics of the nurse plant, seedling size and geometry, and its location under the nurse plant.

A water uptake model, which closely predicted the soil water potential in the root zone of *H. rigida* during a twenty-seven-month period, demonstrated that the presence of a nurse plant would reduce water uptake by an associated seedling. For instance, a seedling of *F. acanthodes* located at the centre of the nurse plant *H. rigida* took up 32% less water than an exposed seedling. In addition, small differences in location can affect the simulated water uptake by the seedling. Displacing the seedling from the centre to 0.10 m south of the nurse plant increased seedling water uptake by 27%.

Ferocactus acanthodes and *H. rigida* both have shallow root systems, which accentuates competition for water. The mean root depth for *H. rigida* was 0.08 m, similar to 0.10 m reported previously (Nobel 1981). The mean root depth for *F. acanthodes* changes from 0.05 m for a seedling to 0.10 m for adult plants (Hunt & Nobel 1987a). Within a few days of rewetting the soil, *F. acanthodes* can rehydrate old roots, produce new roots, and show nearly complete stomatal opening (Nobel 1977; Nobel & Sanderson 1984). *Hilaria rigida*, however, needs approximately three weeks to develop a full canopy and hence maximal water uptake (Nobel 1980b). Thus, for a dry year with short wet periods, a small seedling of *F. acanthodes* located 0.10 m south of the centre of an *H. rigida* would take up about the same amount of water as an exposed seedling, although if the bunchgrass developed a full canopy immediately after rainfall, it would take up 15% less water than an exposed seedling. Moreover, because *H. rigida* is capable of extracting water at soil water potentials of about -3.0 MPa (Nobel 1981) and *F. acanthodes* at only -0.5 MPa (Nobel 1977), the bunchgrass can utilize water resources not available to *F. acanthodes*.

Water uptake by a medium-sized *F. acanthodes* that occupies approximately the same total rooting area as an *H. rigida* was reduced by an average of 23% when located at the centre of the bunchgrass. In this case about 5% of the simulated water uptake of *F. acanthodes* was associated with a 1% reduction in annual water uptake by *H. rigida*. The rest came mainly from a 2% reduction in annual soil water evaporation within 1.5 m^2 ground area around the two plants. In some cases simulated water uptake by the bunchgrass can be slightly increased by the cactus. For medium-sized plants, having the *F. acanthodes* 0.10 m south of the centre of the nurse plant increased simulated water uptake by *H. rigida* by 7% compared with an *H. rigida* without an associated cactus. This enhancement reflects the elimination of evaporation from the ground area occupied by the massive cactus stem, such evaporation being the main means of water loss from the soil. Furthermore, root density for *F. acanthodes* is low, about 238 m m^{-3} for such a medium-sized individual (Hunt & Nobel 1987a). Actually, more than one cactus can be associated with a particular nurse plant. An *H. rigida* with four associated *F. acanthodes* was found, and several *C. gigantea* associated with one nurse plant are not uncommon (Turner *et al.* 1966; McAuliffe 1984).

The environmental productivity index allows quantification of the influences of the nurse plant on various physical factors affecting net CO_2 uptake by the seedling. Canopy shading by the nurse plant moderated daily variations in shoot temperature for seedlings of *F. acanthodes*, which changed the temperature index less than 5% for the range of temperatures experienced by *F. acanthodes* at the study site (Nobel 1984a, 1986b). The average PAR index and the average water index at the centre of the nurse plant were decreased about 68% and 22%, respectively, which reduced the predicted annual CO_2 uptake by 79% compared with an exposed seedling. A seedling at the centre of the nurse plant had both a lower PAR index and a lower water index than one 0.10 m south of the centre. Therefore, the predicted annual CO_2 uptake for a seedling of *F. acanthodes* for the three years considered averaged 60% lower at the centre of the nurse plant compared with 0.10 m south of the centre. In summary, small variations in seedling location under the nurse plant can markedly affect seedling growth.

The soil nitrogen levels were higher under the nurse plants than outside the region of influence of their roots, a pattern common to many desert shrubs and trees (Turner *et al.* 1966; Garcia-Moya & McKell 1970; Charley & West 1975; Hunter, Romney & Wallace 1982). Based on correlations between nocturnal acid accumulation and soil nitrogen level as well as the growth response of seedlings in hydroponics to nitrate, nitrogen appears to

be the nutrient most limiting growth of both *C. gigantea* and *F. acanthodes* (Nobel 1983b). Increasing the soil nitrogen level from 0.03% to 0.05% increases the total dry weight of seedlings of *A. deserti* by about 60% (Nobel & Hartsock 1986b). Thus, the effect of nitrogen on seedling growth may explain the apparent discrepancy between a predicted 64% reduction in growth for seedlings of *F. acanthodes* under the nurse plant compared with exposed seedlings, while measurements of areole production indicated a reduction of only 32%. In this regard, a nitrogen index has been proposed as an inclusion in a more general environmental productivity index that takes into consideration nutrient effects (Nobel 1988).

The effect of competition for water on growth of *C. gigantea* seedlings is presently difficult to evaluate. The root systems of *A. deltoidea*, *C. microphyllum*, and *C. gigantea* probably overlap to a great extent, with most of their root systems occurring in the upper 0.30 m of the soil (Cannon 1911). Although the water content of the soil at a depth of 0.15 m is usually slightly higher under *C. microphyllum* than in open areas (Shreve 1931), the significance of this difference on the water relations and growth of *C. gigantea* is not known. To examine the balance between the reduction in soil evaporation by shading and the depletion of soil water by plant transpiration, detailed information is needed on the physiology and the morphology of both the nurse plant and the seedlings of *C. gigantea*. For instance, both *A. deltoidea* and *C. microphyllum* are drought deciduous, apparently developing new leaves during wet periods only (Turner 1963; Szarek & Woodhouse 1977). On the other hand, seedlings of *C. gigantea* can quickly respond to as little as 5 mm of rainfall (Steenbergh & Lowe 1969). Light can also limit growth of *C. gigantea*. For instance, assuming that the PAR response curve of *C. gigantea* is similar to the response curves of other species of cacti (Nobel 1986a), near an equinox shading could reduce net CO₂ uptake of a seedling at the centre of the nurse plant up to 90% compared with an exposed seedling.

In conclusion, nurse plants facilitate seedling establishment by reducing maximum soil surface temperatures. However, competition for water and shading by the nurse plant greatly reduce the growth of the associated seedling compared with an exposed seedling. The magnitude of the reduction can be predicted by combining field measurements and models. The nurse plant also provides a microhabitat with higher soil nitrogen levels, which partially offsets the reduced seedling growth caused by shading and competition for soil water.

ACKNOWLEDGMENTS

Thanks are due to the personnel of the University of California, Philip L. Boyd, Deep Canyon Desert Research Center and the Organ Pipe Cactus National Monument for logistical support; to D. T. Tissue for assistance in the field; and to J. Baumer for computer facilities. Financial support was provided by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior Ministério de Educação e Cultura Brazil and by the Ecological Research Division of the Office of Health and Environmental Research, U.S. Department of Energy.

REFERENCES

- Bremner, J. M. (1965). Total nitrogen. *Methods of Soil Analysis, Part II* (Ed by C. A. Black), pp. 1149–1178. Agronomy Series, American Society of Agronomy, Madison, WI.
- Cannon, W. A. (1911). *The Root Habits of Desert Plants*. Publication 131, Carnegie Institution of Washington, Washington, DC.

- Charley, J. L. & West, N. E. (1975). Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *Journal of Ecology*, **63**, 945–963.
- Ehleringer, J. R. (1984). Intraspecific competitive effects on water relations, growth and reproduction in *Encelia farinosa*. *Oecologia*, **63**, 153–158.
- Fonteyn, P. J. & Mahall, B. E. (1981). An experimental analysis of structure in a desert plant community. *Journal of Ecology*, **63**, 883–896.
- Fowler, N. (1986). The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, **17**, 89–110.
- Franco, A. C. & Nobel, P. S. (1988). Interactions between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida*. *Ecology*, **69**, 1731–1740.
- Friedman, J. (1971). The effect of competition by adult *Zygophyllum dumosum* Boiss. on seedlings of *Artemisia herba-alba* Asso in the Negev Desert of Israel. *Journal of Ecology*, **59**, 775–782.
- Garcia-Moya, E. & McKell, C. M. (1970). Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology*, **51**, 81–88.
- Geller, G. N. & Nobel, P. S. (1984). Cactus ribs: influence on PAR interception and CO₂ uptake. *Photosynthetica*, **18**, 482–494.
- Gurevitch, J. (1986). Competition and local distribution of the grass *Stipa neomexicana*. *Ecology*, **67**, 46–57.
- Hunt, E. R., Jr. & Nobel, P. S. (1987a). A two-dimensional model for water uptake by desert succulents: implications of root distribution. *Annals of Botany*, **59**, 559–569.
- Hunt, E. R., Jr. & Nobel, P. S. (1987b). Non-steady-state flow for three desert perennials with different capacitances. *Australian Journal of Plant Physiology*, **14**, 363–375.
- Hunt, E. R., Jr. & Nobel, P. S. (1987c). Allometric root/shoot relationships and predicted water uptake for desert succulents. *Annals of Botany*, **59**, 571–577.
- Hunter, R. B., Romney, E. M. & Wallace, A. (1982). Nitrate distribution in Mojave Desert soils. *Soil Science*, **134**, 22–30.
- Hutto, R. L., McAuliffe, J. R. & Hogan, L. (1986). Distributional associates of the saguaro (*Carnegiea gigantea*). *Southwestern Naturalist*, **31**, 469–476.
- Jordan, P. W. & Nobel, P. S. (1979). Infrequent establishment of seedlings of *Agave deserti* (Agavaceae) in the northwestern Sonoran Desert. *American Journal of Botany*, **66**, 1079–1084.
- Jordan, P. W. & Nobel, P. S. (1981). Seedling establishment of *Ferocactus acanthodes* in relation to drought. *Ecology*, **62**, 901–906.
- Jordan, P. W. & Nobel, P. S. (1982). Height distributions of two species of cacti in relation to rainfall, seedling establishment and growth. *Botanical Gazette*, **143**, 511–517.
- McAuliffe, J. R. (1984). Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. *Oecologia*, **64**, 319–321.
- National Oceanic and Atmospheric Administration. (1976–1985). *Climatological Data. Annual Summary, Arizona. Volumes 80–89*. U.S. Department of Commerce, Washington, D.C.
- Nobel, P. S. (1977). Water relations and photosynthesis of a barrel cactus, *Ferocactus acanthodes*, in the Colorado Desert. *Oecologia*, **27**, 117–133.
- Nobel, P. S. (1980a). Morphology, nurse plants, and minimum apical temperatures for young *Carnegiea gigantea*. *Botanical Gazette*, **141**, 188–191.
- Nobel, P. S. (1980b). Water vapor conductance and CO₂ uptake for leaves of a C₄ desert grass, *Hilaria rigida*. *Ecology*, **61**, 252–258.
- Nobel, P. S. (1981). Spacing and transpiration of various sized clumps of a desert grass, *Hilaria rigida*. *Journal of Ecology*, **69**, 735–742.
- Nobel, P. S. (1983a). *Biophysical Plant Physiology and Ecology*. W. H. Freeman, San Francisco.
- Nobel, P. S. (1983b). Nutrient levels in cacti—relation to nocturnal acid accumulation and growth. *American Journal of Botany*, **70**, 1244–1253.
- Nobel, P. S. (1984a). Extreme temperatures and thermal tolerances for seedlings of desert succulents. *Oecologia*, **62**, 310–317.
- Nobel, P. S. (1984b). Productivity of *Agave deserti*: measurements by dry weight and monthly prediction using physiological responses to environmental parameters. *Oecologia*, **64**, 1–7.
- Nobel, P. S. (1984c). High temperature responses of North American cacti. *Ecology*, **65**, 643–651.
- Nobel, P. S. (1986a). Form and orientation in relation to PAR interception by cacti and agaves. *On the Economy of Plant Form and Function* (Ed by T. J. Givnish), pp. 83–103. Cambridge University Press, Cambridge.
- Nobel, P. S. (1986b). Relation between growth of *Ferocactus acanthodes* and an environmental productivity index. *American Journal of Botany*, **73**, 541–547.
- Nobel, P. S. (1987). Water relations and plant size aspects of flowering for *Agave deserti*. *Botanical Gazette*, **148**, 79–84.
- Nobel, P. S. (1988). *Environmental Biology of Agaves and Cacti*. Cambridge University Press, New York.
- Nobel, P. S. & Franco, A. C. (1986). Annual root growth and intraspecific competition for a desert bunchgrass. *Journal of Ecology*, **74**, 1119–1126.
- Nobel, P. S. & Geller, G. N. (1987). Temperature modelling of wet and dry desert soils. *Journal of Ecology*, **75**, 247–258.

- Nobel, P. S. & Hartsock, T. L. (1986a). Environmental influences on the productivity of three desert succulents in the southwestern United States. *Plant, Cell and Environment*, **9**, 741–749.
- Nobel, P. S. & Hartsock, T. L. (1986b). Influence of nitrogen and other nutrients on the growth of *Agave deserti*. *Journal of Plant Nutrition*, **9**, 1273–1288.
- Nobel, P. S. & Jordan, P. W. (1983). Transpiration stream of desert species: resistances and capacitances for a C₃, a C₄, and a CAM plant. *Journal of Experimental Botany*, **34**, 1379–1391.
- Nobel, P. S. & Sanderson, J. (1984). Rectifier-like activities of roots of two desert succulents. *Journal of Experimental Botany*, **35**, 727–737.
- Robberecht, R., Mahall, B. E. & Nobel, P. S. (1983). Experimental removal of intraspecific competitors—effects on water relations and productivity of a desert bunchgrass, *Hilaria rigida*. *Oecologia*, **60**, 21–24.
- Shreve, F. (1931). Physical conditions in sun and shade. *Ecology*, **12**, 96–104.
- Shreve, F. & Wiggins, I. L. (1964). *Vegetation and Flora of the Sonoran Desert, Volumes I and II*. Stanford University Press, Stanford.
- Steenbergh, W. F. & Lowe, C. H. (1969). Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. *Ecology*, **50**, 825–834.
- Steenbergh, W. F. & Lowe, C. H. (1977). *Ecology of the Saguaro: II. Reproduction, Germination, Establishment, Growth and Survival of the Young Plant*. National Park Service Scientific Monograph Series 8, Washington, DC.
- Szarek, S. R. & Woodhouse, R. M. (1977). Ecophysiological studies of Sonoran Desert plants. II. Seasonal photosynthesis patterns and primary production of *Ambrosia deltoidea* and *Olneya tesota*. *Oecologia*, **28**, 365–375.
- Turner, R. M. (1963). Growth in four species of Sonoran Desert trees. *Ecology*, **44**, 760–765.
- Turner, R. M., Alcorn, S. M., Olin, G. & Booth, J. A. (1966). The influence of shade, soil and water on saguaro seedling establishment. *Botanical Gazette*, **127**, 95–102.
- Woodhouse, R. M., Williams, J. G. & Nobel, P. S. (1980). Leaf orientation, radiation interception, and nocturnal acidity increases by the CAM plant *Agave deserti* (Agavaceae). *American Journal of Botany*, **67**, 1179–1185.
- Young, D. R. & Nobel, P. S. (1986). Predictions of soil-water potentials in the north-western Sonoran Desert. *Journal of Ecology*, **74**, 143–154.

(Received 1 July 1988; revision received 19 December 1988)