



Interactions Between Seedlings of *Agave Deserti* and the Nurse Plant *Hilaria Rigida*

Author(s): Augusto C. Franco and Park S. Nobel

Source: *Ecology*, Vol. 69, No. 6 (Dec., 1988), pp. 1731-1740

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/1941151>

Accessed: 01/12/2014 14:52

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

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.



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

<http://www.jstor.org>

INTERACTIONS BETWEEN SEEDLINGS OF *AGAVE DESERTI* AND THE NURSE PLANT *HILARIA RIGIDA*¹

AUGUSTO C. FRANCO AND PARK S. NOBEL

Department of Biology and Laboratory of Biomedical and Environmental Sciences,
University of California, Los Angeles, California 90024 USA

Abstract. Seedlings of the succulent crassulacean acid metabolism (CAM) plant *Agave deserti* in the northwestern Sonoran Desert were found only in sheltered microhabitats, nearly all occurring under the canopy of a desert bunchgrass, *Hilaria rigida*. Apparently because soil surface temperatures can reach 71°C in exposed areas, seedlings were generally located near the center or on the northern side of this nurse plant. Both species have shallow root systems, about half of the roots of *H. rigida* and all those for seedlings of *A. deserti* occurring above soil depths of 0.08 m.

To examine competition for water between the nurse plant and an associated seedling, a three-dimensional model for root water uptake was developed. The model divided the soil into 17 concentric sheaths each subdivided radially into eight wedges and vertically into nine layers. Predicted pre-dawn soil water potentials at the mean root depth and total shoot transpiration agreed well with field measurements. Simulated annual water uptake by a seedling of *A. deserti* was reduced $\approx 50\%$ when the seedling was moved from an exposed location to the center of the nurse plant. Shading by the nurse plant reduced total daily photosynthetically active radiation (PAR) by up to 74% compared with an exposed seedling. On the other hand, soil nitrogen under the canopy of *H. rigida* was 60% higher than in exposed locations. Assuming that the effects of nitrogen, temperature, PAR, and soil water on net CO₂ uptake are multiplicative, the predicted net CO₂ uptake by a seedling of *A. deserti* under the nurse plant was only $\approx 45\%$ of that for an exposed seedling. Thus, although the nurse plant facilitates seedling establishment by reducing maximum soil surface temperatures and provides a microhabitat with higher soil nitrogen levels, its shading and competition for water reduce seedling growth.

Key words: *Agave deserti*; CO₂ uptake; competition; desert; *Hilaria rigida*; nurse plant; photosynthetically active radiation; temperature; water relations.

INTRODUCTION

Seedlings of desert succulents often occur in sheltered microhabitats provided by the canopies of other species, referred to as "nurse plants" (Turner et al. 1966, Steenberg and Lowe 1977, Jordan and Nobel 1979). Shade from nurse plants reduces maximal soil surface temperatures, which can exceed 70°C in deserts (Hadley 1970, Körner and Cochrane 1983), temperatures that are lethal to most desert succulents (Nobel 1984a, Nobel et al. 1986). Although shading by the nurse plant reduces soil surface temperatures, it also decreases the available photosynthetically active radiation (PAR), which would limit CO₂ uptake by desert CAM plants (Woodhouse et al. 1980, Nobel 1986). On the other hand, nitrogen levels can be higher around desert trees and shrubs, which could enhance growth of associated seedlings (Garcia-Moya and McKell 1970, Charley and West 1975, Hunter et al. 1982).

Soil water availability generally controls plant establishment and growth in desert environments (Noy-Meir 1973). Competition for water can be especially critical in a seedling/nurse plant situation, because the

plants are close together and their root systems overlap. Although seedling growth is generally reduced in the presence of adult plants (Friedman 1971, Grubb 1977, Harper 1977, Gurevitch 1986), evidence of interspecific competition between nurse plants and associated seedlings is scant and based primarily on spatial analyses (Yeaton 1978, McAuliffe 1984). Evidence that seedling survival and growth is constrained by competition for water can be provided by removing neighboring plants and observing the water status and aboveground productivity of the remaining plants (Fonteyn and Mahall 1981, Robberecht et al. 1983, Ehleringer 1984, Nobel and Franco 1986). Differences in size and hence transpiring area among potentially competing individuals must also be considered (Goldberg and Werner 1983).

Agave deserti is a long-lived succulent CAM plant common on rocky slopes in the Mojave and Sonoran deserts that reproduces mainly vegetatively (Gentry 1972). Establishment from seed is rare and occurs only in sheltered microhabitats (Gentry 1972, Jordan and Nobel 1979). The desert bunchgrass *Hilaria rigida* often serves as a nurse plant for seedlings of *A. deserti* (Jordan and Nobel 1979). The roots of both species occur at approximately the same mean root depth of 0.10 m

¹ Manuscript received 4 February 1988; revised 4 May 1988; accepted 5 May 1988.

(Nobel 1976, 1981). In the present study, the positions of seedlings of *A. deserti* under the canopy of *H. rigida* were determined. Then the seedling microenvironment was characterized in terms of light, soil temperature, and soil nitrogen content. To evaluate the effect of the nurse plant on the net CO₂ exchange of seedlings of *A. deserti*, information was also needed on water uptake.

Most models for water uptake are one dimensional and assume that the water moves toward a root element from a soil cylinder surrounding the root axis (Taylor and Klepper 1978, Hanks 1981, Molz 1981, Rowse et al. 1983). These models are appropriate for uniformly spaced roots, such as in agricultural fields, where root density may change only with depth. Some two-dimensional models have been developed, incorporating changes in root density as a function of the distance from the plant base (Baldwin et al. 1972, Hunt and Nobel 1987a, b). Although more realistic than one-dimensional models, even two-dimensional models misrepresent the situation where overlap between adjacent root systems is not uniform (Caldwell and Richards 1986). Therefore, a three-dimensional simulation model of root water uptake was developed. This model was used to examine competition for water between the nurse plant and associated seedlings under different climatic conditions and various spatial arrangements.

MATERIALS AND METHODS

Field site and microclimate

The study was conducted at the Philip L. Boyd Deep Canyon Desert Research Center of the University of California (33°38' N, 116°24' W, 850 m elevation) in the northwestern Sonoran Desert. A site of 8000 m² was selected, subdivided into 10 × 10 m quadrats, and searched for seedlings of *A. deserti* that were up to 0.2 m in height. A seedling was considered to be associated with another plant when their canopies overlapped. In each such case, the major and the minor axes of the nurse plant canopy were measured, together with the distance and compass direction of the seedling with reference to the center of the nurse plant. The relationship was then scaled relative to a representative medium-sized nurse plant with 100 culms (stems).

To contrast soil nitrogen availability, soil samples were collected under the canopy of *H. rigida* and in exposed areas. Eight medium-sized plants of *H. rigida* with ≈100 culms each were selected; samples were taken 0.10 m from the center of the clump at the mean root depth of 0.10 m (Nobel 1981). Eight samples were also taken at the same depth outside the root region. Total N determinations were performed on 10-g (dry mass) samples using an Orion ammonia electrode following Kjeldahl digestion (Bremner 1965).

To characterize the thermal and the light environment of a seedling under the canopy of *H. rigida*, a representative medium-sized nurse plant was selected (based on measurements of 26 plants with associated

seedlings). Its canopy was approximately elliptical, with the major axis pointing east-west; the major canopy axis was 0.54 m in length and the minor axis was 0.40 m. Using copper-constantan thermocouples 0.51 mm in diameter, soil surface temperatures were measured hourly over 24-h periods with a Campbell Scientific CR5 digital recorder on 12 clear days (≈ every 2 mo) during 1986 and 1987. Measurements were taken at the center of the plant, at 0.15 m away from the center in the four compass directions, and 1 m outside the canopy. To characterize the seedling light environment, seedling replicas were constructed 0.04 m in height with four leaves inclined 40° from the vertical, a typical angle for a small seedling of *A. deserti* ≈ 2 yr old (Jordan and Nobel 1979, Nobel 1985). One replica was located at the plant center, another 0.15 m away toward the north, and a third outside the canopy. Nippon Electric PH201A photodiodes, calibrated in photosynthetically active radiation (PAR) units with a LICOR 190S quantum flux sensor, were located at the abaxial and adaxial surfaces of all four leaves of the seedling replicas (at approximately the four cardinal directions). Measurements were taken every half hour through a day near the winter solstice (10 December 1986), the spring equinox (28 March 1987), and the summer solstice (22 June 1987).

Water uptake model

A three-dimensional model was developed to predict root water uptake at various depths and distances from a nurse plant and its associated seedling (Fig. 1). In the model, which is an extension of a two-dimensional model (Hunt and Nobel 1987a, b), a central cylinder of soil with a radius of 0.05 m and centered on the nurse plant was surrounded by 16 additional concentric sheaths whose radii increased in 0.05-m increments (overall diameter of 1.70 m). Each concentric sheath was radially subdivided into eight wedges and vertically into nine layers (Fig. 1). The top two layers were 0.02 m thick, the next four were 0.04 m thick, and the last three were 0.05 m thick (0.35 m total depth). For each subvolume or node of the soil, the model calculates the water that enters or leaves through the six surfaces, is absorbed by roots (if present), or changes the soil water content.

The root length in a particular node is a function of soil depth, distance from the center of the *H. rigida*, and the seedling location with respect to the nurse plant. To obtain root length at various depths and distances from the center of the nurse plant, four plants of *H. rigida* with ≈100 culms each and four associated seedlings of *A. deserti* 0.04 m tall were excavated. Each excavation required 12 h for *H. rigida* and 3 h for the much smaller *A. deserti*. Extreme care was taken to trace each root to its terminus, although some fine roots were inevitably lost. During excavation two two-dimensional maps (a horizontal projection and a vertical projection) were drawn showing all recovered roots of

a particular plant. For larger sizes of *A. deserti*, the root length in the various nodal volumes was adapted from Hunt and Nobel (1987a).

The water vapor flux density (J_{wv}^{soil} , $m^3 \cdot m^{-2} \cdot s^{-1}$ or m/s) from the upper side of each soil surface node was calculated according to Fick's law of diffusion, taking into consideration the effect of canopy shading and soil wetness on soil surface temperatures (Nobel 1983, Nobel and Geller 1987):

$$J_{wv} = D_{wv} (c_{wv}^{soil} - c_{wv}^{air}) / (\delta + l), \quad (1)$$

where D_{wv} (m^2/s) is the diffusion coefficient of water vapor in the air, c_{wv}^{soil} (m^3/m^3) is the soil water vapor concentration determined from the soil surface temperature and the water potential at the soil surface, c_{wv}^{air} is the atmospheric water vapor concentration, δ (m) is the average boundary layer thickness, and l (m) is the mean effective diffusional path length for air in the pores of the soil surface layer (Young and Nobel 1986). For an open area at the site, δ averages ≈ 0.005 m and l is 0.007 m (Young and Nobel 1986). The presence of clumps of *H. rigida* reduces the average wind speed to 30% of the value at an open site, which increases δ to ≈ 0.009 m (Nobel 1983, Nobel and Geller 1987). Soil water potential at the soil surface was allowed to vary until convergence between J_{wv} and the vertical water movement from the middle to the top of the surface layer was obtained by iteration (Hunt and Nobel 1987a).

Darcy's law for cylindrical symmetry was used to calculate the volume flux density of water moving in the soil at the root surface ($J_{\psi^{soil}}$, m/s):

$$J_{\psi^{soil}} = L_{soil}(\psi^{soil} - \psi^{rs}) / [r^{root} \ln(r/r^{root})], \quad (2)$$

where L_{soil} ($m^2 \cdot s^{-1} \cdot MPa^{-1}$) is the soil hydraulic conductivity, ψ^{soil} (MPa) is the soil water potential of the node, ψ^{rs} is the soil water potential at the root surface, r^{root} (m) is the root radius, and r is the radial distance over which water moves through the soil to a particular root. The quantity r was defined as the smaller of one-half the distance between randomly distributed roots (Taylor and Klepper 1978) or the effective distance of root influence for water uptake, which depends on L_{soil} (itself a function of ψ^{soil}), r^{root} , and the root hydraulic conductivity, L_p (Caldwell 1976, Hunt and Nobel 1987a). The distance of root influence was determined by setting L_p equal to $L_{soil} / [r^{root} \ln(r/r^{root})]$ for the driest soil where water uptake would just occur (Hunt and Nobel 1987a), which is ≈ -0.5 MPa for *A. deserti* (Nobel 1984b) and ≈ -2.8 MPa for *H. rigida* (Nobel 1981), leading to an r of 30 mm for *A. deserti* and 2.5 mm for *H. rigida*.

Root water uptake at the root surface ($J_{\psi^{root}}$, m/s) satisfies the following phenomenological equation:

$$J_{\psi^{root}} = L_p(\psi^{rs} - \psi^{root}), \quad (3)$$

where ψ^{root} is the water potential in the root and L_p ($m \cdot s^{-1} \cdot MPa^{-1}$) is the slope of the line obtained by mea-

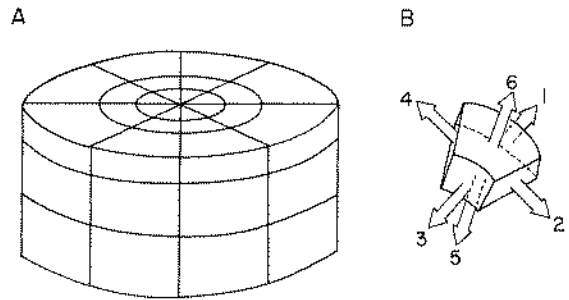


FIG. 1. (A) Schematic representation of the nodal system of the soil for the water uptake model. Only a few of the 17 concentric sheaths and the nine soil layers are indicated. (B) A nodal subvolume, with various fluxes indicated by arrows. Fluxes 1-5 represent water movement between nodes. Flux 6 represents rainfall plus the evaporation term for a surface node or the water flux between two nodes for a subsurface node. Root water uptake plus water storage in a node is algebraically equal to the net resultant of the six fluxes.

suring $J_{\psi^{root}}$ at various applied hydrostatic pressures (see Hunt and Nobel 1987a, c for values of L_p for both species). ψ^{rs} was allowed to vary in the model until convergence between $J_{\psi^{soil}}$ (Eq. 2) and $J_{\psi^{root}}$ (Eq. 3) was obtained (Hunt and Nobel 1987a).

All simulations were performed for 1.0-h intervals, starting with a soil volumetric water content of 0.1 m^3/m^3 at the beginning of the year, a typical value for the 1st wk of January at the field site (Nobel 1987). For each time step, J_{wv} and $J_{\psi^{root}}$ were determined, and then water movement among the soil nodes was calculated using Darcy's law in cylindrical or Cartesian coordinates as appropriate (Nobel 1983, Young and Nobel 1986, Hunt and Nobel 1987a). The relationships between soil volumetric water content and both ψ^{soil} and also L_{soil} have been determined for the field site (Young and Nobel 1986). As indicated above, the nurse plant was a representative medium-sized *H. rigida* with 100 culms, located at the center of the cylindrical system (Fig. 1). Agaves of various sizes were located at the center of the nurse plant or 0.15 m away on the northern side. Unless otherwise indicated, simulations were performed using local weather data for a dry year (1973, 78 mm rainfall), an average year (1984, 159 mm rainfall), and a wet year (1983, 598 mm rainfall).

Root and shoot water potential

For modeling purposes, water flow from the soil through the roots, stems, and leaves to the atmosphere in the transpiration stream is usually analyzed using a resistance-capacitance network through which water moves in response to gradients in water potential (Landsberg et al. 1976, Nobel and Jordan 1983). For nonsucculent plants with small capacitances like *H. rigida*, the time lags between water uptake by the roots and plant transpiration are small (Hunt and Nobel 1987c). The amount of water moving through each

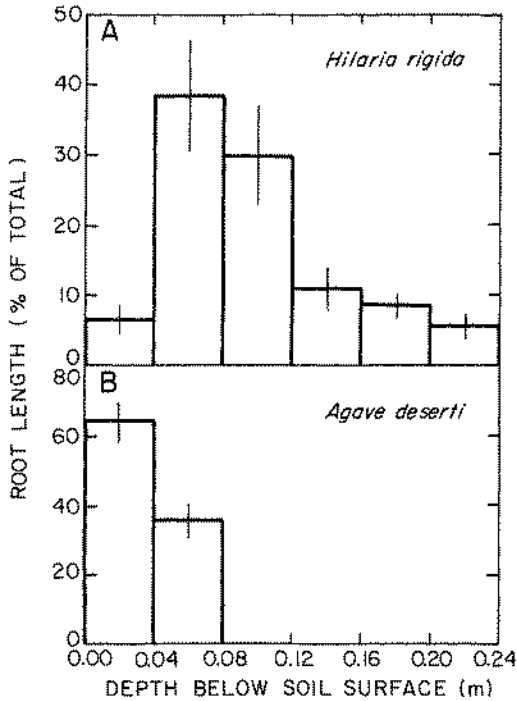


FIG. 2. Root distribution with depth for *Hilaria rigida* and *Agave deserti* for 0.04 m thick soil layers. No roots occurred below a depth of 0.24 m for either species. Data are presented as mean \pm 1 se.

portion of the water flow pathway per unit time (cubic metres per second) is then equal to that removed from the soil and lost as vapor at the shoot surface:

$$J_{\text{root}}^{\text{root}} = J_{\text{stem}}^{\text{stem}} A^{\text{stem}} + J_{\text{leaf}}^{\text{leaf}} A^{\text{leaf}}, \tag{4}$$

where A^{root} (m^2) is the total surface area of the roots, $J_{\text{stem}}^{\text{stem}}$ (m/s) is the volume flux density for water loss as stem transpiration ($1 \text{ mm/s} = 1 \text{ kg} \cdot \text{m}^{-2} \cdot \text{s}^{-1} = 56 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), A^{stem} is the total surface area of the stems, $J_{\text{leaf}}^{\text{leaf}}$ is the leaf transpiration, and A^{leaf} is total surface area of the leaves. Changes in $J_{\text{stem}}^{\text{stem}}$ or $J_{\text{leaf}}^{\text{leaf}}$ are accompanied by immediate and proportional changes in root, stem, and leaf water potentials.

Using an analog resistance-capacitance network, analysis of the water flow pathway throughout *H. rigida* has shown that a drop in water potential between the soil and the root of 0.99 MPa for wet conditions ($\psi^{\text{soil}} > -0.5 \text{ MPa}$) and 1.03 MPa for dry conditions ($\psi^{\text{soil}} = -2.6 \text{ MPa}$) is necessary to maintain the maximum simulated water uptake by the roots (Hunt and Nobel 1987c). For the root water uptake model, the minimum ψ^{root} was therefore set at 1.01 MPa below ψ^{soil} at a soil depth of 0.10 m (the mean root depth). Because field measurements indicate that between midnight and dawn ψ^{stem} of *H. rigida* is close to ψ^{soil} at 0.10 m and transpiration rates are close to zero (Hunt and Nobel 1987c), maximum ψ^{root} was equated to the pre-dawn ψ^{soil} at 0.10 m. Hourly values of ψ^{root} were then cal-

culated based on maximum and minimum ψ^{root} , and assuming that the same pattern of changes occurred as for ψ^{stem} , which was measured hourly. Because of the large shoot capacitance of *A. deserti*, ψ^{root} for this species was considered constant and equal to -0.5 MPa (Hunt and Nobel 1987a, b).

The two-dimensional version of the model has been validated for *A. deserti* (Hunt and Nobel 1987a, b), and the present, three-dimensional version agrees within 1% with the previous version when only a single, radially symmetric individual of this species is considered. To validate the predictions of the new model for *H. rigida*, soil water potential and transpiration for two individuals with approximately 100 culms each were determined at the field site. Wescor PCT 55-15 thermocouple psychrometers were placed 0.10 m away from shoots at root depths of 0.05, 0.10, and 0.20 m. Pre-dawn ψ^{soil} was measured using a Wescor HR 33-T microvoltmeter. $J_{\text{wv}}^{\text{leaf}}$ and $J_{\text{wv}}^{\text{stem}}$ were determined approximately hourly over three 24-h periods using a LI-COR LI-1600 porometer, and ψ^{stem} was measured hourly with a PMS 1000 pressure chamber.

Environmental productivity index

To indicate the quantitative effect of water, temperature, and PAR on the net CO_2 uptake of *A. deserti*, an environmental productivity index (EPI) was used (Nobel 1984b). EPI, which is constructed as the product of individual monthly indices for water status, temperature, and PAR, represents the relative net CO_2 uptake expected under ambient environmental conditions. It has been successfully used to predict productivity of *A. deserti* and other agaves (Nobel 1984b, Nobel and Quero 1986).

Each of the component indices of EPI is assigned a maximum value of 1.00 when that variable is not limiting net CO_2 uptake over a 24-h period. The water status index was based on the criteria developed for *A.*

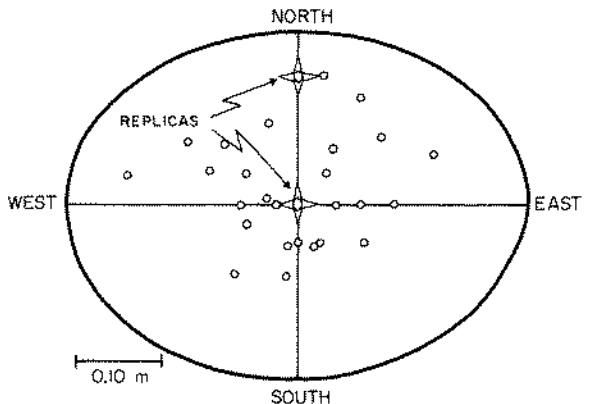


FIG. 3. Location of seedlings of *Agave deserti* under the canopy of *Hilaria rigida*. The distances were scaled for an *H. rigida* with 100 culms. The two locations for the seedling replica are also shown.

TABLE 1. Maximum (T_{max}) and minimum (T_{min}) soil surface temperatures ($^{\circ}\text{C}$) at different locations under the canopy of *Hilaria rigida* and in an exposed location for clear days in the winter (11 December 1986), the spring (8 April 1987), and the summer (26 June 1986).

Location	Winter		Spring		Summer	
	T_{max}	T_{min}	T_{max}	T_{min}	T_{max}	T_{min}
North side	23.7	4.8	32.9	15.1	48.0	29.3
Center	23.0	5.8	34.0	15.7	57.5	28.2
South side	25.6	4.6	49.8	13.7	70.2	27.0
Exposed	26.1	3.1	51.4	11.8	71.2	26.2

deserti (Nobel 1984b), where $\psi^{soil} > -0.4$ MPa at the mean root depth indicates no limitation of CO_2 uptake by soil water; ψ^{soil} at the mean root depth was predicted by the water uptake model. Because daytime temperatures have only a small influence on CO_2 uptake by *A. deserti* (Nobel and Hartsock 1978), the temperature index was based on the minimum nighttime temperature, maximum CO_2 uptake occurring at 15°C (Nobel 1984b). In the present case, the PAR index, which is based on total daily PAR, also considered the effect of canopy shading by the nurse plant. The monthly PAR index is the average of the individual PAR indices calculated for each of the eight leaf surfaces of the seedling replica.

RESULTS

Plant characteristics

The root system of *Hilaria rigida* extends radially from the plant base, and root branching is uncommon. For a plant with 100 culms, 45% of the root length occurred between soil depths of 0.00 and 0.08 m (Fig. 2A). The average root depth was 0.09 m, the average distance from the plant center to the root tips was 0.40 m, and the ground area explored by the roots was 0.50 m^2 (determined from the horizontal projection map). Averaged over the ground area explored by the roots, total root length per unit soil volume for the bunchgrass was 1029 m/m^3 for the 0.00–0.08 m layers and 779 m/m^3 for the upper 0.24 m of soil. For seedlings of *Agave deserti*, roots occurred in the uppermost 0.08 m only (Fig. 2B). Its average root depth was 0.03 m and the average distance from the plant center to the root tips was 0.05 m, leading to a ground area explored by the roots of 0.008 m^2 . Total root length per unit soil volume for *A. deserti* was 431 m/m^3 .

In a detailed examination of the 8000 m^2 plot (which would contain nearly 8000 rosettes; Nobel 1976), 33 small, individual plants of *A. deserti* were found (including one dead plant). All but the dead plant occurred in sheltered microhabitats and the majority (26) were under canopies of *H. rigida*. In the latter case, the seedlings occurred preferentially on the northern side of the nurse plant (Fig. 3; $\chi^2 = 3.85$, $P < .05$). For an *H. rigida* with 100 culms, seedlings occurred on the north-

ern side up to 0.15 m away from the east–west axis of the nurse plant compared with up to 0.08 m away on the southern side (Fig. 3).

Soil nitrogen content was also measured at 0.10 m below the soil surface. Under the canopy of *H. rigida*, the soil averaged (\pm SE) $0.046 \pm 0.003\%$ N, which is significantly higher ($t = 3.89$, $P < .01$) than the $0.029 \pm 0.004\%$ N measured for soil outside the canopy.

Temperature and PAR

Daily variations in soil surface temperatures were less under the canopy of *H. rigida* compared with an exposed location, especially on the northern side (Table 1). Maximum soil surface temperatures were similar for an exposed location and on the south side of the nurse plant canopy. On a clear summer day, maximum temperatures were 14°C lower at the center and 23°C lower on the north side; smaller effects occurred at the

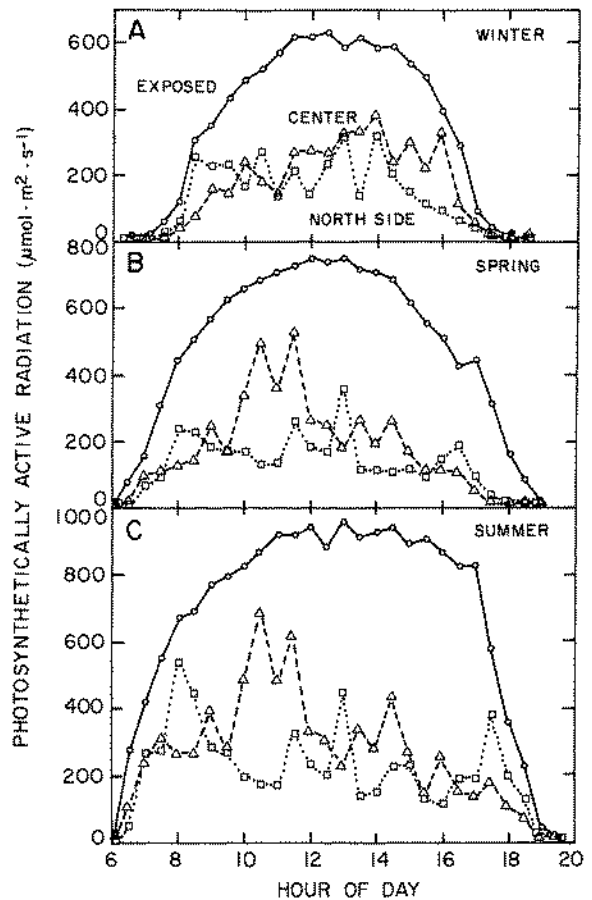


FIG. 4. Daily course of photosynthetically active radiation incident on the seedling replica located in an exposed area ($\text{O}—\text{O}$), at the center of the nurse plant ($\Delta—\Delta$), and 0.15 m north of the center ($\square \cdots \square$). Each datum represents the average for both sides of the four leaves, taken every half-hour near the winter solstice (A; 10 December 1986), the spring equinox (B; 28 March 1987), and the summer solstice (C; 22 June 1987).

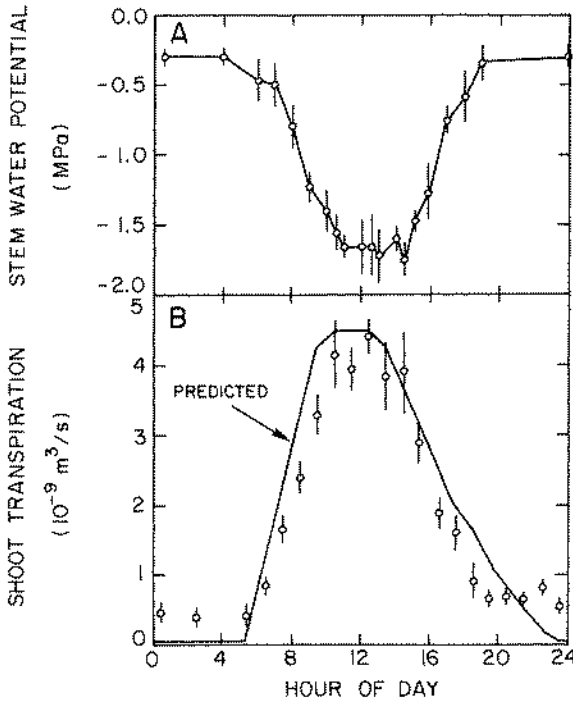


FIG. 5. Daily course of stem water potential (A) and both measured (O) and predicted (—) shoot transpiration rate (stem plus leaf) of *H. rigida* (B) for a clear day (19 October 1987). Data are presented as the average \pm SE for four or five stems and 8–10 leaves from two *H. rigida* with 100 culms each. The total stem surface area was 0.080 m² and the leaf surface area (one side) was 0.031 m².

two other times of the year (Table 1). Minimum soil surface temperatures under the canopy of *H. rigida* averaged 2° to 3° higher than for an exposed location at the three different times of the year (Table 1).

Total daily PAR incident on the seedling was greatly reduced by the nurse plant (Fig. 4). On a clear day in the winter, total daily PAR decreased from 15.9 mol/m² for an exposed location to 7.5 mol/m² for a seedling located at the center of the nurse plant to 5.8 mol/m² on the north side (Fig. 4A). In the spring, total daily PAR incident on the seedling was 23.8 mol/m² for an exposed location, 8.1 mol/m² at the center, and 6.3 mol/m² on the north side of the nurse plant (Fig. 4B). In the summer, total daily PAR was 33.2 mol/m², 13.4 mol/m², and 10.6 mol/m², for an exposed location, the center, and the north side, respectively (Fig. 4C).

Model validation

After sunrise ψ^{stem} rapidly decreased and then remained relatively constant between 1000 and 1430 (Fig. 5A). The minimum ψ^{stem} of -1.76 MPa occurred at 1430 and the maximum of -0.30 MPa at 2400. The maximum ψ^{stem} was 0.05 MPa lower than the pre-dawn ψ^{soil} at a depth of 0.10 m. Predicted shoot transpiration (stem plus leaf) was similar to the measured value (Fig. 5B). For instance, maximum transpiration of the entire

shoot was 4.4×10^{-9} m³/s compared with 4.5×10^{-9} m³/s predicted by the model. Total shoot transpiration for the 24-h period was 152×10^{-6} m³/day compared with a predicted value of 162×10^{-6} m³/day.

To test the accuracy of the model for predicting soil water potentials under a range of soil moistures, pre-dawn ψ^{soil} under *H. rigida* at a depth of 0.10 m was monitored for an extended period in the field (Fig. 6). Predicted ψ^{soil} under *H. rigida* was in close agreement with measurements as ψ^{soil} decreased from 0.0 MPa to < -6.0 MPa during a 10-wk period (Fig. 6).

Simulations of annual water uptake

The presence of the nurse plant markedly reduced the simulated annual water uptake of an agave seedling (Table 2). Although shading by *H. rigida* reduced soil water evaporation, the decrease was not enough to compensate for the amount of water taken up by the roots of the nurse plant. When the seedling was moved from an exposed location to the center of the nurse plant, simulated annual water uptake for the seedling decreased an average of 58% for the three years considered (Table 2). Displacing the seedling 0.15 m north of the center of the nurse plant increased simulated water uptake of *A. deserti* by 44% compared with water uptake at the center. The same pattern occurred for agaves of larger size (Table 2), although the fractional changes were less. For the medium-sized and large *A. deserti*, simulated annual root water uptake decreased 20 and 11%, respectively, when on the north side compared with an exposed location, and decreased an additional 10 and 14%, respectively, when the *A. deserti* was located at the center of the nurse plant. Annual water uptake by *H. rigida* was only slightly affected by

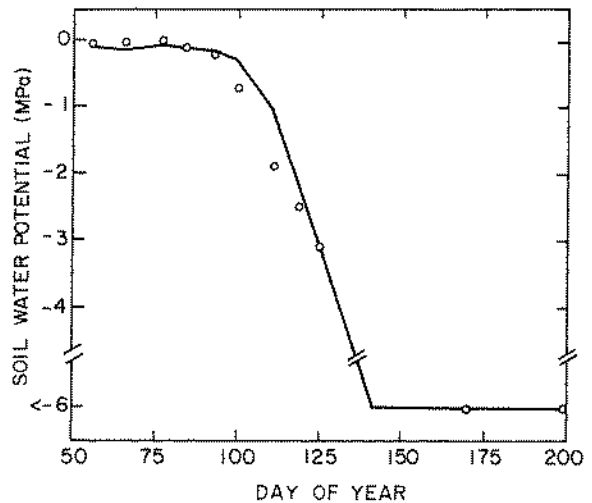


FIG. 6. Measured (O) and predicted (—) values of soil water potential at a depth of 0.10 m and 0.10 m north of the center of two *H. rigida* with 100 culms each. Measurements were taken from 25 February 1986 to 19 July 1986 at the field site.

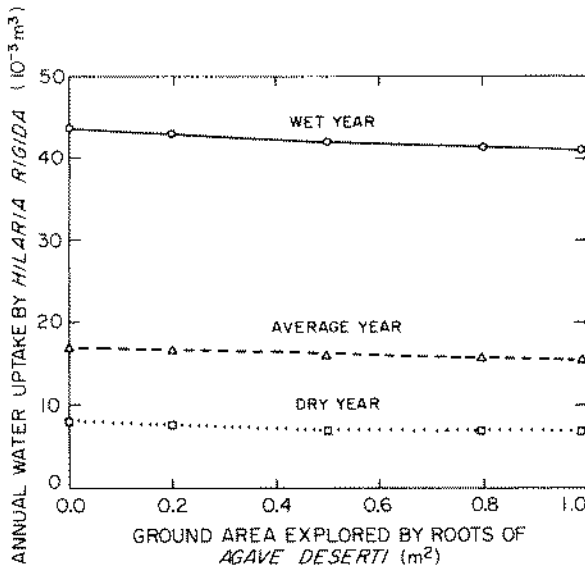


FIG. 7. Simulated annual water uptake by roots of the *H. rigida* associated with *A. deserti* of various sizes for a dry, an average, and a wet year. The agave was located at the center of the nurse plant.

even a large agave located at its center (Fig. 7), which led to a maximum decrease of only 13% for the dry year. Similar results occurred when the agave was located 0.15 m north of the center of the nurse plant (data not shown).

In all cases, annual water uptake by both plants increased markedly from a dry to a wet year (Table 2, Fig. 7). For the medium-sized plant, the eightfold increase in rainfall from the dry to the wet year led to a twelvefold increase in annual water uptake by *A. deserti* and a fivefold increase for *H. rigida*, whose lower water potential allows a greater duration of soil water extraction under dry conditions.

Predictions of net CO₂ uptake for seedlings of A. deserti

For an average year (159 mm rainfall), the maximum monthly EPI for an exposed seedling was 0.453, but

only 0.151 for a seedling under a nurse plant (Fig. 8). Averaged over the entire year, EPI for a seedling was 0.110 at an exposed location, 0.030 at the center of the nurse plant, and 0.021 at a point 0.15 m north of the center. Compared with seedlings protected by nurse plants, the higher EPI for an exposed seedling reflected its more favorable PAR and water status indices. A seedling at the center of the nurse plant had a higher average PAR index than a seedling 0.15 m north of the center; the higher PAR index led to a higher average EPI even though the average water status index was lower at the center of the nurse plant. In a wet and a dry year, EPI averaged 0.308 and 0.063, respectively, for an exposed seedling, 0.109 and 0.018 for a seedling in the center of the nurse plant, and 0.067 and 0.014 for a seedling 0.15 m north of the center.

DISCUSSION

Seedlings of *Agave deserti* were found only in sheltered microhabitats, 81% occurring under the canopy of *Hilaria rigida*. Apparently because of limitations caused by high temperature, most of the seedlings were located near the center or on the northern side of the nurse plant. In particular, soil surface temperatures in the summer reached 71°C at an exposed location and nearly as high on the southern side of a medium-sized *H. rigida* compared with 48° at 0.15 m north of its center. Maximum shoot temperatures of a small agave and maximum soil surface temperatures are approximately the same (Nobel 1984a). Because seedlings of *A. deserti* survive temperatures only up to ≈65°, they are therefore unable to survive at the field site without nurse plants or other means of shading (Nobel 1984a). In fact, the only small agave seedling found in an unsheltered microhabitat had died.

Roots were shallow for both species. Mean root depth for *H. rigida* was 0.09 m, similar to the 0.10 m reported previously (Nobel 1981). However, mean root depth was only 0.03 m for a small seedling of *A. deserti* compared with 0.11 m for adult plants (Hunt and Nobel 1987a). The soil water potential in the root zone of *H. rigida* predicted by the three-dimensional water uptake

TABLE 2. Simulated annual water uptake by the roots of an *Agave deserti* of three different sizes for a dry, an average, and a wet year. The agave had three different locations: an exposed area, a point 0.15 m north of the center of the nurse plant, and at the center.

Plant type	Ground area explored by the roots (m ²)	Annual rainfall (mm)	Annual water uptake by the roots of <i>A. deserti</i> (m ³)		
			Exposed	North side	Center
Seedling	0.005	78	149 × 10 ⁻⁶	62.7 × 10 ⁻⁶	37.3 × 10 ⁻⁶
		159	364 × 10 ⁻⁶	168 × 10 ⁻⁶	114 × 10 ⁻⁶
		598	947 × 10 ⁻⁶	754 × 10 ⁻⁶	652 × 10 ⁻⁶
Medium-sized plant	0.5	78	9.19 × 10 ⁻³	7.41 × 10 ⁻³	6.61 × 10 ⁻³
		159	26.4 × 10 ⁻³	18.2 × 10 ⁻³	14.8 × 10 ⁻³
		598	110 × 10 ⁻³	101 × 10 ⁻³	91.5 × 10 ⁻³
Large, mature plant	1.0	78	16.6 × 10 ⁻³	14.3 × 10 ⁻³	11.9 × 10 ⁻³
		159	45.6 × 10 ⁻³	37.4 × 10 ⁻³	29.7 × 10 ⁻³
		598	196 × 10 ⁻³	194 × 10 ⁻³	172 × 10 ⁻³

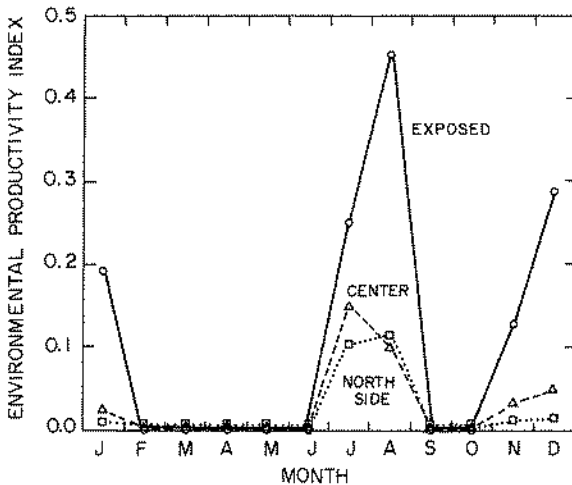


FIG. 8. Monthly values of the environmental productivity index (EPI) for a seedling located in an exposed area, at the center of the nurse plant, and 0.15 m north of the center. EPI was calculated for a year with an average rainfall at the field site (1984; 159 mm rainfall).

model agreed with pre-dawn ψ^{soil} , especially between 0.0 and -3.0 MPa, a range that encompasses the ψ^{soil} for which water uptake by *H. rigida* occurs (Nobel 1981). The predicted maximum transpiration rate and the predicted total daily shoot transpiration were within 6% of measured values.

Although temperature limits seedling establishment, water was the main factor limiting growth of exposed seedlings of *A. deserti*, in agreement with results for adult plants of this species and for other agave species (Nobel 1984b, Nobel and Quero 1986). For an exposed seedling, an eightfold increase in rainfall led to a fivefold increase in the predicted net CO_2 uptake. Because leaf self-shading was minimal for an exposed seedling of the size used, its total available PAR per unit leaf area was $\approx 60\%$ higher than that measured for an adult plant at the same time of year (Woodhouse et al. 1980).

Use of specific environmental indices allows evaluation of the effects of nurse plants on selected physical factors affecting net CO_2 uptake over 24-h periods. For instance, canopy shading by the nurse plant moderated daily variations in shoot temperature for seedlings of *A. deserti*, which affected the temperature index less than 5% at the study site (Nobel 1984a, b). The PAR index and the water index at the center of the nurse plant were decreased ≈ 50 and 35%, respectively, which reduced the predicted annual CO_2 uptake by 70% compared with an exposed seedling. A seedling at the center of the nurse plant has a much higher PAR index and a slightly lower water index than one 0.15 m north of the center. Therefore, the predicted annual CO_2 uptake for a seedling of *A. deserti* for the three years considered averaged 45% higher at the center of the nurse plant compared with 0.15 m north of the center.

Hilaria rigida and *A. deserti* that occupy approxi-

mately the same total rooting area compete for soil water, which reduces annual water uptake of an agave located at the center of the bunchgrass by an average of 30%. For such medium-sized plants, 9% of the simulated annual water uptake of *A. deserti* was associated with a 5% reduction in simulated annual water uptake by *H. rigida*. The rest came mainly from a 3% reduction in annual soil water evaporation within a 2.0-m² ground area around the two plants (reduction in annual soil water storage accounted for only 2% of the annual water uptake by *A. deserti*). *Hilaria rigida* is more effective than *A. deserti* in extracting water from the soil during dry periods, because *H. rigida* is capable of extracting water down to soil water potentials of ≈ -3.0 MPa (Nobel 1981), whereas *A. deserti* operates down to only -0.5 MPa (Nobel and Jordan 1983). Indeed, *H. rigida* could take up water for twice as many days as a similar-sized *A. deserti* located at its center in a year with 78 mm of rainfall. Simulated annual water uptake of both plants increased markedly from a dry to a wet year. Because of induction of new lateral roots following soil rewetting and high root conductances for *A. deserti* (Nobel and Sanderson 1984, Hunt and Nobel 1987c), an eightfold increase in annual rainfall led to a twelvefold increase in water uptake for *A. deserti*.

Soil nitrogen content was 60% higher under the nurse plant than outside the region of influence of its roots, a pattern common to many desert shrubs (Garcia-Moya and McKell 1970, Charley and West 1975, Hunter et al. 1982). Nitrogen appears to be the nutrient most limiting CO_2 uptake and nocturnal acid accumulation for agaves (Nobel and Berry 1985). Increasing the soil nitrogen level 60% over that for bare ground would increase the total dry mass of seedlings of *A. deserti* by $\approx 60\%$ (Nobel and Hartsock 1986).

In summary, the presence of the nurse plant reduced the PAR index of the associated *A. deserti* seedling by an average of 61% and reduced the water index by 28%, compared with an exposed seedling, for the two seedling locations modeled under the canopy of *H. rigida*. The temperature index was not significantly affected, but the soil nitrogen level was raised $\approx 60\%$. Assuming that the effect of soil nitrogen level on net CO_2 uptake is multiplicative, as are the other factors in EPI, the nurse plant would decrease seedling growth $\approx 55\%$ compared with an exposed seedling. Therefore, even though the nurse plant leads to a higher soil nitrogen level and ameliorates soil surface temperatures, the latter allowing seedling establishment, competition for water and shading by the nurse plant greatly reduces the growth of the associated seedling compared with an exposed seedling.

ACKNOWLEDGMENTS

We thank Gary N. Geller for assistance with the computer model. Financial support was provided by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior Ministério de Educação e Cultura Brazil to A. C. Franco and U.S. Depart-

ment of Energy Ecological Research Division contract DE-AC03-76-SF00012 to P. S. Nobel.

LITERATURE CITED

- Baldwin, J. P., P. B. Tinker, and P. H. Nye. 1972. Uptake of solutes by multiple root systems from soil. II. The theoretical effect of rooting density and pattern on uptake of nutrients from soil. *Plant and Soil* 36:693-708.
- Bremner, J. M. 1965. Total nitrogen. Pages 1149-1178 in C. A. Black, editor. *Methods of soil analysis*, part 2. American Society of Agronomy, Madison, Wisconsin, USA.
- Caldwell, M. M. 1976. Root extension and water absorption. Pages 63-85 in O. L. Lange, L. Kappen, and E.-D. Schulze, editors. *Water and plant life, problems and modern approaches*. Ecological studies. Volume 19. Springer-Verlag, Berlin, Germany.
- Caldwell, M. M., and J. H. Richards. 1986. Competing root systems: morphology and models of absorption. Pages 251-273 in T. J. Givnish, editor. *On the economy of plant form and function*. Cambridge University Press, Cambridge, England.
- Charley, J. L., and N. E. West. 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 (Berlin)* 63:153-158.
- Fonteyn, P. J., and B. E. Mahall. 1981. An experimental analysis of structure in a desert plant community. *Journal of Ecology* 69:883-896.
- 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., and C. M. McKell. 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51:81-88.
- Gentry, H. S. 1972. The Agave family in Sonora. United States Department of Agriculture, Agriculture Handbook Number 399.
- Goldberg, D. E., and P. A. Werner. 1983. Equivalence of competitors in plant communities: a null hypothesis and field experimental approach. *American Journal of Botany* 70:1098-1104.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* 52:107-145.
- Gurevitch, J. 1986. Competition and local distribution of the grass *Stipa neomexicana*. *Ecology* 67:46-57.
- Hadley, N. F. 1970. Micrometeorology and energy exchange in two desert arthropods. *Ecology* 51:434-444.
- Hanks, R. J. 1981. Modeling desert soil water systems. Pages 235-243 in D. D. Evans and J. L. Thames, editors. *Water in desert ecosystems*. Hutchinson and Ross, Stroudsburg, Pennsylvania, USA.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, New York, New York, USA.
- Hunt, E. R., Jr., and P. S. Nobel. 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., and P. S. Nobel. 1987b. Allometric root/shoot relationships and predicted water uptake for desert succulents. *Annals of Botany* 59:571-577.
- Hunt, E. R., Jr., and P. S. Nobel. 1987c. Non-steady-state flow for three desert perennials with different capacitances. *Australian Journal of Plant Physiology* 14:363-375.
- Hunter, R. B., E. M. Romney, and A. Wallace. 1982. Nitrate distribution in Mojave Desert soils. *Soil Science* 134:22-30.
- Jordan, P. W., and P. S. Nobel. 1979. Infrequent establishment of seedlings of *Agave deserti* (Agavaceae) in the north-western Sonoran Desert. *American Journal of Botany* 66:1079-1084.
- Körner, Ch., and P. Cochrane. 1983. Influence of plant physiognomy on leaf temperature on clear days in the Snowy Mountains, south-eastern Australia. *Acta Oecologia/Oecologia Plantarum* 4:117-124.
- Landsberg, J. J., T. W. Blanchard, and B. Warritt. 1976. Studies on the movement of water through apple trees. *Journal of Experimental Botany* 27:579-596.
- McAuliffe, J. R. 1984. Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. *Oecologia (Berlin)* 64:319-321.
- Molz, F. J. 1981. Models of water transport in the soil-plant system: a review. *Water Resources Research* 17:1245-1260.
- Nobel, P. S. 1976. Water relations and photosynthesis of a desert CAM plant, *Agave deserti*. *Plant Physiology* 58:576-582.
- . 1981. Spacing and transpiration of various sized clumps of a desert grass, *Hilaria rigida*. *Journal of Ecology* 69:735-742.
- . 1983. *Biophysical plant physiology and ecology*. W. H. Freeman, San Francisco, California, USA.
- . 1984a. Extreme temperatures and thermal tolerances for seedlings of desert succulents. *Oecologia (Berlin)* 62:310-317.
- . 1984b. Productivity of *Agave deserti*: measurement by dry weight and monthly production using physiological responses to environmental parameters. *Oecologia (Berlin)* 64:1-7.
- . 1985. Water relations and carbon dioxide uptake of *Agave deserti*—special adaptations to desert climates. *Desert Plants* 7:51-56, 70.
- . 1986. Form and orientation in relation to PAR interception by cacti and agaves. Pages 83-103 in T. J. Givnish, editor. *On the economy of plant form and function*. Cambridge University Press, Cambridge, England.
- . 1987. Water relations and plant size aspects of flowering for *Agave deserti*. *Botanical Gazette* 148:79-84.
- Nobel, P. S., and W. L. Berry. 1985. Element responses of agaves. *American Journal of Botany* 72:686-694.
- Nobel, P. S., and A. C. Franco. 1986. Annual root growth and intraspecific competition for a desert bunchgrass. *Journal of Ecology* 74:1119-1126.
- Nobel, P. S., and G. N. Geller. 1987. Temperature modelling of wet and dry desert soils. *Journal of Ecology* 75:247-258.
- Nobel, P. S., G. N. Geller, S. C. Kee, and A. D. Zimmerman. 1986. Temperatures and thermal tolerances for cacti exposed to high temperatures near the soil surface. *Plant, Cell and Environment* 9:279-287.
- Nobel, P. S., and T. L. Hartssock. 1978. Resistance analysis of nocturnal carbon dioxide uptake by a crassulacean acid metabolism succulent, *Agave deserti*. *Plant Physiology* 61:510-514.
- Nobel, P. S., and T. L. Hartssock. 1986. Influence of nitrogen and other nutrients on the growth of *Agave deserti*. *Journal of Plant Nutrition* 9:1273-1288.
- Nobel, P. S., and P. W. Jordan. 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., and E. Quero. 1986. Environmental productivity indices for a Chihuahuan Desert CAM plant, *Agave lechuguilla*. *Ecology* 67:1-11.
- Nobel, P. S., and J. Sanderson. 1984. Rectifier-like activities of roots of two desert succulents. *Journal of Experimental Botany* 35:727-737.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25-51.

- Robberecht, R., B. E. Mahall, and P. S. Nobel. 1983. Experimental removal of intraspecific competitors—effects on water relations and productivity of a desert bunchgrass, *Hilaria rigida*. *Oecologia* (Berlin) **60**:21–24.
- Rowse, H. R., W. K. Mason, and H. M. Taylor. 1983. A microcomputer simulation model of soil water extraction by soybeans. *Soil Science* **136**:218–225.
- Steenbergh, W. F., and C. H. Lowe. 1977. Ecology of the saguaro: II. Reproduction, germination, establishment, growth and survival of the young plant. National Park Service Scientific Monograph Series **8**.
- Taylor, H. M., and B. Klepper. 1978. The role of rooting characteristics in the supply of water to plants. *Advances in Agronomy* **30**:99–128.
- Turner, R. M., S. M. Alcorn, G. Olin, and J. A. Booth. 1966. The influence of shade, soil and water on saguaro seedling establishment. *Botanical Gazette* **127**:95–102.
- Woodhouse, R. M., J. G. Williams, and P. S. Nobel. 1980. Leaf orientation, radiation interception, and nocturnal acidity increases by the CAM plant *Agave deserti* (Agavaceae). *American Journal of Botany* **67**:1179–1185.
- Yeaton, R. I. 1978. A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan Desert. *Journal of Ecology* **66**:651–656.
- Young, D. R., and P. S. Nobel. 1986. Predictions of soil-water potentials in the north-western Sonoran Desert. *Journal of Ecology* **74**:143–154.