

# Water Relations and Carbon Dioxide Uptake of *Agave deserti*—Special Adaptations to Desert Climates

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## Abstract

*Agave deserti* Engelm., a common agave of the Sonoran Desert, possesses Crassulacean acid metabolism. Thus, the main period for stomatal opening and net CO<sub>2</sub> uptake is at night, which leads to a high water-use efficiency. Seedling establishment occurs only when enough water-storage capacity can be generated following germination so that the young seedling can withstand the first drought. *Agave deserti* is only moderately tolerant of low tissue temperatures but extremely tolerant of high tissue temperatures, an important desert adaptation. Its rosette growth habit leads to a relatively uniform distribution of photosynthetically active radiation over the leaves, which contributes to its high productivity for a desert plant.

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## Introduction

*Agave deserti* Engelm. has become the most studied of all agaves from the ecophysiological point of view. As for other agaves, it exhibits Crassulacean acid metabolism, or CAM, which involves nocturnal stomatal opening and primarily nocturnal CO<sub>2</sub> uptake, a syndrome first clearly recognized in the Crassulaceae. The earliest reports that agaves open their stomates at night were published by Neales, Patterson, and Hartney (1968) and Ehler (1969) working on *Agave americana*. The CO<sub>2</sub> taken up at night is incorporated into 4-carbon organic acids, primarily malic acid, leading to a progressive acidification of the chlorenchyma during the night. CAM allows more CO<sub>2</sub> uptake per unit of water lost, as will be indicated shortly, and helps account for the substantial productivity of *A. deserti* and other agaves under arid conditions.

The studies reported here were conducted primarily in the northwestern Sonoran Desert at a site appropriately named "Agave Hill," which is in the University of California Philip L. Boyd Deep Canyon Desert Research Center near Palm Desert, California (site at 33°38'N, 116°24'W, 850 m elevation). *Agave deserti* (Figure 1) is the dominant plant at Agave Hill, with 0.99 plant per m<sup>2</sup>, which represents over 50% of the above-ground biomass and 29% of the ground cover (Nobel, 1976). Actually, *A. deserti* is fairly common in washes and rocky slopes below about 1700 m in southern California, western Arizona, northern Sonora, and northern Baja California (Shreve and Wiggins, 1964; Gentry, 1982). It is monocarpic, as are most agaves, with a basal rosette of up to about 70 leaves and an inflorescence about 4 m tall. The succulent leaves on a mature plant average about 35 cm in length, 500 g in wet weight when fully hydrated, and 80 g in dry weight.

## Gas Exchange and CAM

As already indicated, *A. deserti* exhibits CAM, a physiological pathway for which net CO<sub>2</sub> uptake occurs at night when there is no light and hence no photosynthesis. During the afternoon the water vapor conductance of the leaves is very low because the stomates are closed (Figure 2A). At dusk, stomatal opening begins and it is immediately accompanied by a net CO<sub>2</sub> uptake (Figure 2B). CO<sub>2</sub> uptake decreases through the night, in part due to partial stomatal closure. At dawn, the stomates reopen slightly and net CO<sub>2</sub> uptake increases for a brief period (Figure 2), which presumably reflects CO<sub>2</sub> metabolism by the conventional C<sub>3</sub> pathway (Nobel, 1976).

One might reasonably question the possible benefits of nocturnal CO<sub>2</sub> uptake. Because the CO<sub>2</sub> taken up at night must be incorporated into organic acids which are not further processed until light is available, the benefits are not metabolic. Indeed, chlorenchymatous cells of CAM plants must have large central vacuoles to store all the organic acids that accumulate during the night. To understand the benefits, one must turn to the water economy resulting from stomatal opening at night when air and tissue temperatures are lower than during the daytime. Next the consequences for water use will be considered quantitatively.

Transpiration ( $J_{wv}$ ) is directly proportional to the leaf-to-air water vapor concentration drop ( $\Delta c_{wv}$ ). It is also proportional to the water vapor conductance ( $g_{wv}$ ), which is primarily determined by the degree of stomatal opening:

$$J_{wv} = g_{wv} \Delta c_{wv} \quad (1)$$



**Figure 1.** *Agave deserti* at "Agave Hill", a site in the northwestern Sonoran Desert near Palm Desert, California.

For Figure 2, the leaf temperature during the daytime averaged 19°C and at night it averaged 4°C. Because air in the intercellular air spaces of leaves is essentially saturated with water vapor, such air averaged about 16.3 g water m<sup>-3</sup> during the daytime and only 6.4 g m<sup>-3</sup> at night. But the water vapor content of the ambient air was fairly constant during the 24-hour period at 3.6 g m<sup>-3</sup>. This means that for a given amount of stomatal opening (i.e., a given  $g_{wv}$ ),  $\Delta c_{wv}$  and hence the rate of water loss by transpiration would be five-fold higher during the daytime than the nighttime (see Equation 1). Such tremendous water savings is the essence of the advantage of CAM metabolism and underscores why agaves and other CAM plants can be successful in arid and semi-arid regions where water is limited.

The need for water economy justifies CAM, but what happens when water does not impose a limitation for *A. deserti*? After 12 weeks of daily watering in the laboratory, the normal nighttime stomatal opening of *A. deserti* was replaced by daytime stomatal opening and primarily daytime CO<sub>2</sub> uptake, presumably by the C<sub>3</sub> pathway (Hartsock and Nobel, 1976). Upon returning to a watering protocol more consistent with its habitat, *A. deserti* reverted back to the CAM pathway. However, such daytime stomatal opening and CO<sub>2</sub> uptake has not been observed in the field under natural conditions, although some stomatal opening can occur near

sunrise (Figure 2B). During the daytime a very high CO<sub>2</sub> level can build up behind closed stomates (30 times the external CO<sub>2</sub> concentration), which accounts for the small but detectable leakage of CO<sub>2</sub> out of *A. deserti* then (Figure 2B).

### Seedling Establishment and Growth

Seedlings of *A. deserti* are hard to find in the field and indeed only rarely become established, at least in the northwestern Sonoran Desert. Laboratory studies have indicated that approximately 90% germination of seeds occurs at 21°C to 23°C, decreasing by 50% at temperatures 10°C higher or lower (Nobel, 1977a; Jordan and Nobel, 1979). Growth of roots and cotyledons of 10-day-old seedlings is optimal near 30°C (Jordan and Nobel, 1979). As seedlings grow, their volume increases more rapidly than their surface area, leading to a greater water reservoir per unit of transpiring area. For instance, shoot volume per unit shoot area, which represents the total depth from which water can be mobilized, is 0.07 cm at 10 days of seedling age, 0.18 cm at 120 days, 0.29 cm at 445 days (Jordan and Nobel, 1979), and about 0.91 cm for adult leaves (Nobel, 1976). The increase of water storage with age is a crucial aspect of drought survival.

Because *A. deserti* can tolerate leaf water potentials down to -1.6 MPa (about -16 atmospheres) and because the plant

must have a lower water potential than the soil for water movement into the plant to occur, drought can be defined as periods when the soil water potential in the root zone is below  $-1.6$  MPa. As the seedlings become older and thus have more stored water per unit surface area, they can tolerate longer periods of such drought (Figure 3). For example, 30-day-old seedlings can tolerate only 10 days of drought while 100-day-old seedlings can tolerate 80 days of drought.

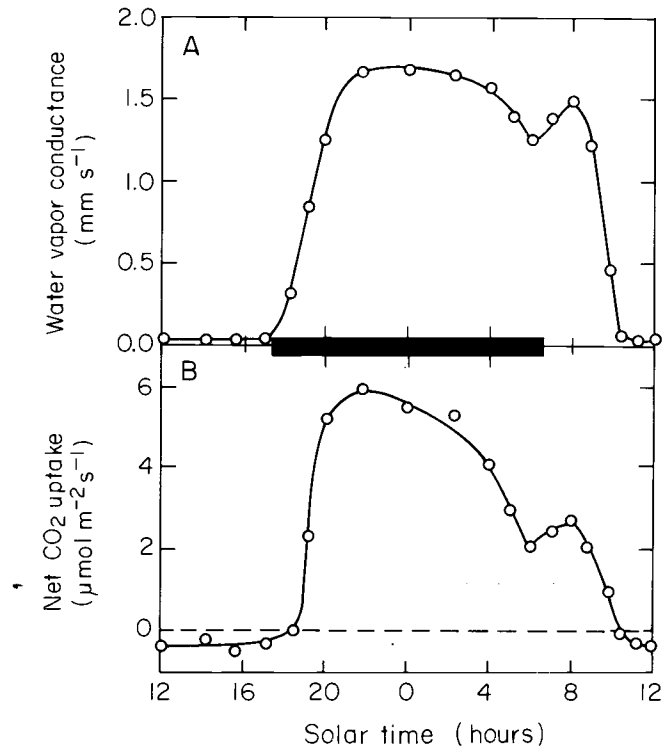
As the next step in the analysis of seedling establishment in the field, the wet periods available for initial seedling growth at Agave Hill were determined for each year beginning in 1961 and compared to the subsequent drought period that must be endured in that year (Figure 3). From 1961 to 1977, only 1967 had a long enough growing period for the seedlings to develop sufficient biomass to be able to survive the first drought. The favorable growing period began in late summer when temperatures were appropriate for seed germination as well as for root and shoot growth.

The year for successful seedling establishment was also estimated based on observations of the six smallest plants in an area containing over 1000 rosettes of *A. deserti* (Jordan and Nobel, 1979). By monitoring annual growth for a series of years in the late 1970's and extrapolating for leaf production in earlier years (dead leaves remained at the base of the plants and leaf scars were also visible), the average year for the establishment of these six plants was also found to be 1967. All six of these small plants occurred in protected habitats, an aspect that will be returned to when thermal tolerances are considered. The agreement between growth estimates in the field and microclimatic conditions serves to indicate that it is the first year which is most crucial for seedling survival (only the initial wet period and its subsequent drought are considered in Figure 3).

Since 1977, when the detailed study ended, the years 1982 and 1983 were judged to be suitable for seedling establishment (Figure 3). Indeed, three small seedlings of *A. deserti* about 3 cm tall with 3 or 4 living leaves were observed in June of 1983, a size consistent with germination near the beginning of the long wet period that commenced in July of 1982 and extended into 1983 (subsequent observations located more such seedlings). Observations in June of 1984 revealed no new seedlings from 1983, although such lack of evidence does not prove that no seedlings became established in 1983, because small seedlings are easily overlooked. However, the wet period that interrupted the first drought for such possible seedlings was short (30 days) and was followed by a long drought in 1984 (175 days), which the seedlings should not have survived. Thus, this second drought may have proved lethal to the seedlings that one might otherwise expect from 1983 (Figure 3).

### Water Relations

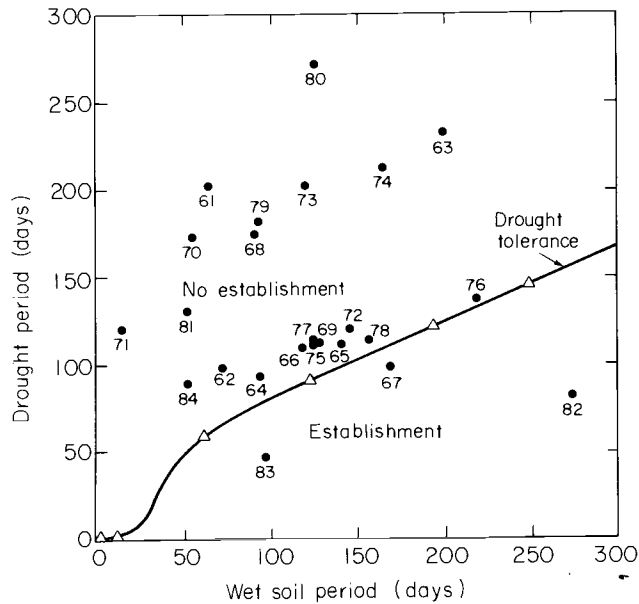
In addition to its influence on seed germination and seedling establishment, water also influences mature plants. For instance, appreciable stomatal opening with its accompanying  $\text{CO}_2$  uptake (Figure 2) only occurs when the plants are hydrated. Because of water storage in the leaves and stem, nocturnal stomatal opening can continue for up to eight days after the soil becomes drier than the plant (Nobel, 1976). Indeed, the water potential of leaves of *A.*



**Figure 2.** Water vapor conductance (A) and net  $\text{CO}_2$  uptake (B) for *A. deserti* on a clear day near the winter solstice. Maximum solar irradiance was  $630 \text{ W m}^{-2}$ , maximum/minimum air temperatures at 1 m above the ground were  $19^\circ\text{C}/7^\circ\text{C}$ , maximum/minimum leaf temperatures at midleaf were  $28^\circ\text{C}/2^\circ\text{C}$ , the air water vapor concentration averaged  $3.6 \text{ g m}^{-3}$ , and the soil was wet (soil water potential in the root zone above  $-0.5$  MPa). Dark bar indicates night.

*deserti* decreases only slightly (about 0.1 MPa) over a 24-h period even when they are supplying all of the transpired water, in marked contrast to thin-leaved plants (Nobel and Jordan, 1983). Taking into consideration this capacitance effect of stored water and the effect of rainfall on soil water potential (after a drought a rainfall of at least 7 mm is required to induce stomatal opening by *A. deserti*; Nobel, 1976), the times of the year favorable for growth can be determined. For the eight years from 1973 to 1980, these favorable periods averaged 4.0 months in the winter/early spring and 1.4 months in the summer, reflecting the bimodal pattern of seasonal rainfall in this part of the Sonoran Desert (Nobel, 1985).

Water relations also affect the reproductive phase of this monocarpic species. Water uptake by the roots of *A. deserti* cannot keep up with the needs of the inflorescence, part of whose 5½-month existence occurs in the generally dry late spring/early summer (Nobel, 1977a). Indeed, for mature plants at Agave Hill, a total of 18 kg of water was moved from the leaves to the inflorescence where 17% was stored in the main axis, 24% was transpired by the main axis, and 59% was lost by the lateral branches. The highest daily



**Figure 3.** Years possible for establishment of seedling of *A. deserti*. Seedlings were raised for various periods in the laboratory under conditions similar to those in the field and then subjected to various periods of drought ( $\Psi^{\text{soil}} < -1.6$  MPa) to see what drought lengths could be tolerated ( $\Delta$ ). Weather records for Agave Hill together with field measurements of soil water potential (Nobel, 1977b) as well as simulations of soil water potential (Young and Nobel, 1985) were used to determine the longest wet period ( $\Psi^{\text{soil}} > -1.6$  MPa) beginning in the indicated year and the subsequent period of continuous drought ( $\Psi^{\text{soil}} < -1.6$  MPa; the wet period and/or the drought period could extend into the next year) for all years from 1961 ("61") to 1984 ("84").

water loss [22 g/branch on inflorescences with 17 branches) occurred for the approximately eight days when flowers with their copious nectar were open (Nobel, 1977a). The fruit stage, which lasted about two months before viable seeds were developed, accounted for about half of the water lost by each lateral branch. The 18 mature fruit per lateral branch led to 66,000 seeds/plant. But because 95% of the propagation at Agave Hill is vegetative, only about 1 seed in  $1.2 \times 10^6$  leads to a mature flowering plant. We should also note that the dry weight of an inflorescence (1.3 kg) was about the same as the annual productivity of an entire mature plant (1.6 kg), and so dry weight must also be mobilized from the leaves to support reproduction (the leaves lost an average of 1.8 kg dry weight/plant from the time of inflorescence emergence to the production of viable seeds; Nobel, 1977a).

### Nutrient Relations

So far relatively little is known about the nutrient responses of *A. deserti*. In terms of element stresses, its seedlings are quite sensitive to salinity, with 50 mM NaCl greatly reducing root elongation in hydroponic solution and watering with 25

mM NaCl preventing growth in sand culture (Nobel and Berry, 1985). Seedlings of *A. deserti* are rather insensitive to applied calcium concentrations from 0.2 to 5.0 mM and pH from pH 5 to 8. Also, they can tolerate high levels of boron and of the heavy metals copper and zinc, such high levels often occurring in the arid southwestern United States and northwestern Mexico where *A. deserti* is found. Specific conclusions on the effects of edaphic factors on distribution must await future research.

### Temperature Responses

Seasonal changes in temperature have relatively little effect on net  $\text{CO}_2$  uptake by *A. deserti* over a 24-h period, although instantaneous nighttime values can markedly affect stomatal opening. For instance, the total nocturnal increase in acidity was reduced by only 30% for daytime leaf temperatures of 15°C or 40°C compared to the maximum uptake that occurred at daytime temperatures of 25°C to 30°C (Nobel and Hartsock, 1978). Nocturnal  $\text{CO}_2$  uptake was optimal near a night temperature of 15°C. Actually, the optimum can shift somewhat with mean nighttime temperature, from 15°C for a nighttime temperature of 10°C to 18°C for a nighttime temperature of 30°C (Nobel and Hartsock, 1981). Although  $\text{CO}_2$  uptake is maximal near 15°C, stomatal opening at night was actually greatest at the lowest temperature tested, 5°C. As the leaf chlorenchyma temperature was raised, stomatal opening decreased as shown by a progressive decrease in the water vapor conductance,  $g_{\text{wv}}$  (Equation 1), e.g.,  $g_{\text{wv}}$  decreased by 8% at 15°C, 53% at 25°C, and 92% at 35°C (Nobel, 1976; Nobel 1985; Nobel and Hartsock, 1979). Such stomatal closure at higher temperatures greatly restricts transpiration (Equation 1), which otherwise would increase substantially with temperature because the water vapor concentration in the leaves rises essentially exponentially with temperature. Additionally, calculations using a computer model showed that transpiration does not reduce leaf temperature of the succulent leaves of *A. deserti* very much, as even full stomatal opening ( $a g_{\text{wv}}$  of  $1.8 \text{ mm s}^{-1}$ ) decreased nocturnal leaf temperatures by only about 2°C compared to no transpiration at all (Woodhouse, Williams, and Nobel, 1983).

Besides effects on  $\text{CO}_2$  uptake and transpiration, temperature—in particular, extreme temperatures—affects plant establishment and distribution. To study this, one can measure the fraction of the cells that take up a vital stain such as neutral red [3-amino-7-dimethylamino-2-methylphenazine (HC1)], which is only taken up by living cells (Nobel and Smith, 1983; Jordan and Nobel, 1984). Thus, whole plants or plant parts can be subjected to a particular extreme temperature for a given period (here chosen to be 1 hour, because the temperatures of agave organs are often fairly constant at an extreme temperature for this time period in the field), and then stain uptake by the cells determined microscopically using tissue slices 2- or 3-cells thick. Moreover, stain uptake is good predictor of lethal temperatures, because when stain uptake is reduced to 0% by an extreme temperature, the tissue will die. However, because it is experimentally difficult to determine the exact limiting temperatures for stain uptake, it is more convenient to determine where the high or low temperature stress reduces the number of cells taking up the stain by 50%. Based on studies on a series of agaves including *A.*

*deserti*, death occurs 3°C to 5°C above or below the temperature leading to a 50% decrease in stain uptake for high or low temperature treatments, respectively (Nobel and Smith, 1983).

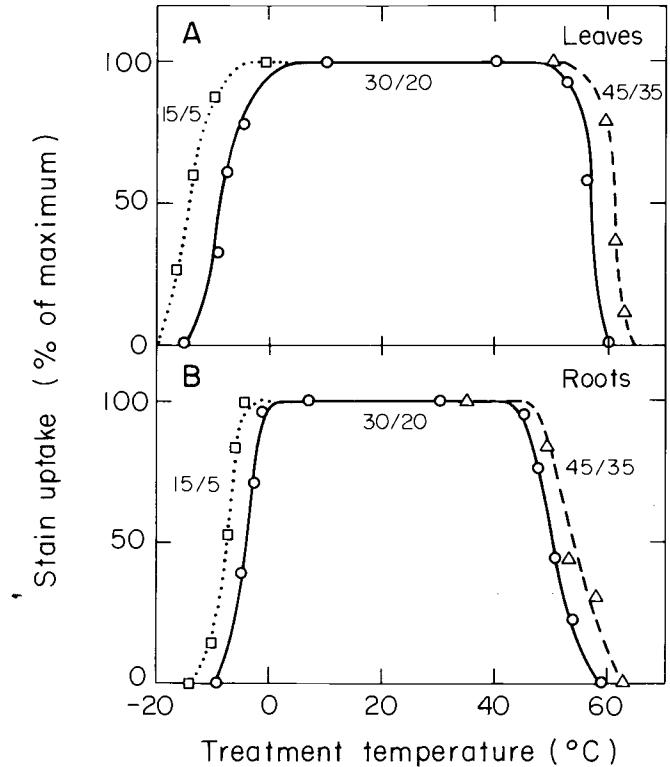
Figure 4 shows the thermal tolerances of leaves and roots of *A. deserti* as well as acclimation to high and low growth temperatures. For plants maintained in environmental growth chambers with day/night air temperatures of 30°C/20°C, stain uptake is reduced 50% at -9°C and 57°C for leaf chlorenchyma cells and -4°C and 50°C for root cortical cells. If the growth temperatures are lowered 15°C to 15°C/5°C, the 50% inhibition temperature was reduced 5°C for leaves and 3°C for roots (Figure 4). As growth temperatures were raised 15°C to 45°C/35°C, the high temperature for 50% inhibition of stain uptake increased by 4°C for both leaves and roots (Figure 4). Such acclimation can help *A. deserti* adjust to seasonal changes in temperature.

Seedlings of *A. deserti* were slightly more sensitive to temperature extremes than mature plants. Specifically, 1-, 4-, and 12-month-old seedlings grown at 30°C/20°C had 50% inhibition of stain uptake by the leaves at -7°C and 56°C (Nobel, 1984a). Even after taking acclimation into consideration, the seedlings could not tolerate the 70°C that can occur at the exposed soil surface, and indeed all seedlings observed in the field occurred in protected microhabitats. Roots were 5°C to 7°C more sensitive than leaves to temperature extremes (Figure 4). This helps account for the absence of roots of *A. deserti* in the upper 3 cm of the soil, where soil temperatures can be extreme, except directly under a plant where temperature extremes are moderated (Jordan and Nobel, 1984). Even though roots were absent from the upper part of the soil, the mean root depth of *A. deserti* was only 8 cm (Nobel, 1976), which facilitates responses to the often light desert rainfalls.

### PAR Responses

Despite the high radiation environment of deserts, net CO<sub>2</sub> uptake by unshaded plants of *A. deserti* is on the verge of being limited by the total daily photosynthetically active radiation (PAR) on clear days, i.e., more PAR would generally lead to greater growth. Also, because the leaves are opaque, the orientation of each surface must be considered in order to predict productivity. Actually, when totaled over a day near an equinox, average PAR on the leaves of an unshaded plant of *A. deserti* with 56 leaves is extremely similar for leaves radiating toward the upper, middle, or lower part of the canopy, about 15 mol photons m<sup>-2</sup> (Figure 5). Variation is also slight (±7%) with compass direction. Again at an equinox, the abaxial (lower) surface receives 38% less PAR than the upper surface (Nobel, 1984b).

As the total daily PAR on the leaves increases, nocturnal CO<sub>2</sub> uptake and the accompanying acidity both increase. Ninety percent PAR saturation for *A. deserti* occurs at 19 to 23 mol m<sup>-2</sup> (Nobel, 1984b; Nobel and Hartsock, 1978). The PAR level for the unshaded plant with 56 leaves on a clear day at the equinox leads to about 70% of the maximal CO<sub>2</sub> uptake. Near the summer solstice the higher PAR causes nearly 90% PAR saturation of net CO<sub>2</sub> uptake, while the lower trajectory of the sun near the winter solstice leads to less than 50% of the maximum net CO<sub>2</sub> uptake on clear days (Woodhouse et al., 1980; Nobel, 1984b, 1984c, 1985).

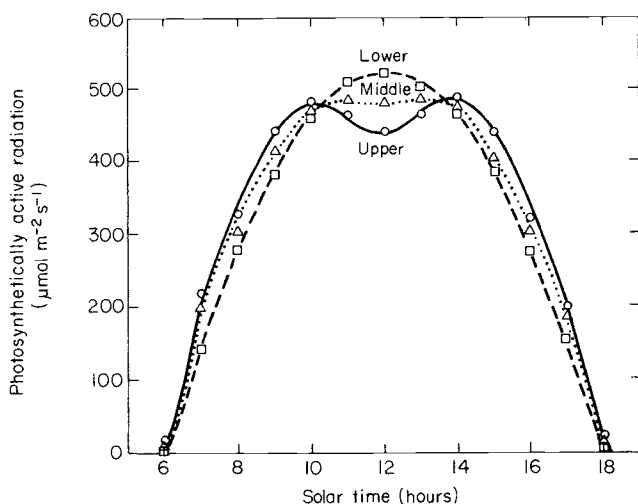


**Figure 4.** Temperature tolerance of leaves (A) and roots (B) of *A. deserti* as measured by cellular stain uptake. Data are from Nobel and Smith (1983), Jordan and Nobel (1984b), and unpublished observations. Day/night growth temperatures are indicated adjacent to the curves.

### Productivity

All of the physical factors discussed above have an impact on productivity. However, the key factor for a desert plant like *A. deserti* is water, without which there is no stomatal opening or net CO<sub>2</sub> uptake. Indeed, a water status index has been developed (Figure 6A) that indicates month-by-month the fraction of maximal CO<sub>2</sub> uptake expected based on the soil water potential plus tissue water storage (Nobel, 1984c). This index ranged from 1.00 for a month with wet soil (soil water potential above -0.5 MPa) or when stomatal opening can be supplied by water stored in the succulent leaves and stem to 0.00 for a drought month in which water storage in the tissue has already been exhausted.

Indices for temperature and PAR have also been developed for *A. deserti*, which show the fraction of maximal CO<sub>2</sub> uptake expected for various values of these physical factors. The seasonal range for the PAR index on clear days has already been discussed. Clouds decreased the available PAR about 4% for a relatively clear June to 17% for a cloudy August during the period of interest (March 1983-October 1984), leading to corresponding reductions in the PAR index. Because of thermal acclimation of net CO<sub>2</sub> uptake and the moderate temperatures at Agave Hill, the temperature index ranged only from 0.67 to 0.97 over the period of interest, being lowest from July through September when even the nights were too warm for optimal CO<sub>2</sub> uptake.



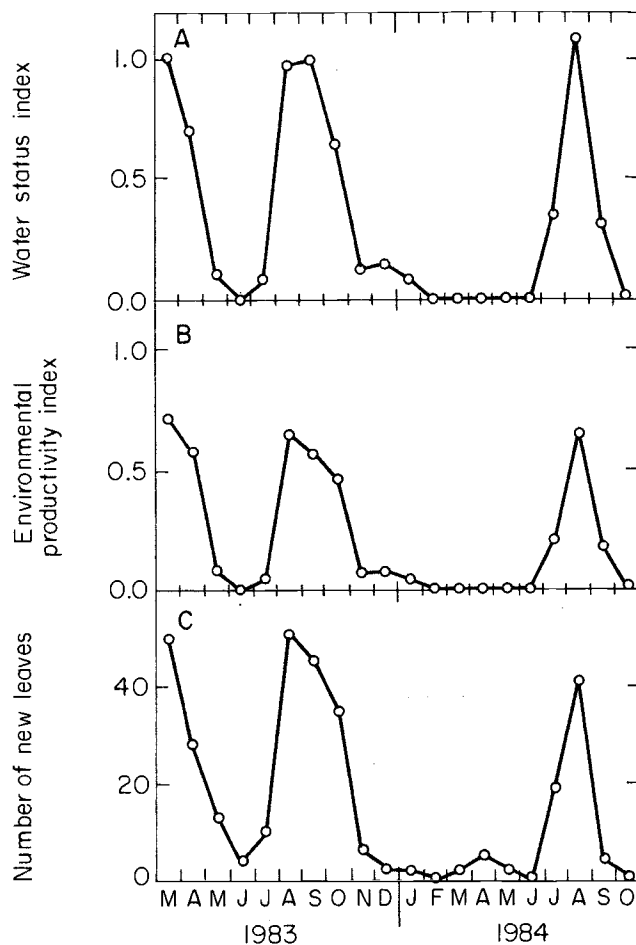
**Figure 5.** Diurnal course of PAR incident on various positions within the rosette. Data represent the averages for the entire adaxial and abaxial surfaces for 18 to 20 leaves radiating toward the upper, middle, or lower part of the canopy. Simulations were performed for 34°N on a clear day at the equinox using the computer model of Woodhouse et al. (1980).

The indices for water, PAR, and temperature can be multiplied together to obtain an overall "environmental productivity index" (Figure 6B). This latter index indicates month-by-month the fraction of maximal CO<sub>2</sub> uptake expected. Moreover, because CO<sub>2</sub> uptake is expressed on a leaf area basis (cf. Figure 2) and the leaf area per plant is known, the environmental productivity index can be used to calculate CO<sub>2</sub> uptake per plant. Assuming that CO<sub>2</sub> is incorporated into carbohydrate, correcting for root and stem respiration, and expressing the data on the basis of the ground area explored by the roots, productivity can be expressed per unit ground area. In this way, the annual productivity of *A. deserti* was predicted to be 0.60 kg m<sup>-2</sup> y<sup>-1</sup>, in excellent agreement with a measured productivity of 0.57 kg m<sup>-2</sup> y<sup>-1</sup> (Nobel, 1984c). Such a productivity is about six-fold higher than the average values for deserts (Noy-Meir, 1973; Leith and Whittaker, 1975).

Another interesting feature of the productivity studies with *A. deserti* relates to the unfolding of its leaves from the central spike of the rosette. In particular, the monthly unfolding of new leaves (Figure 6C) was highly correlated ( $r^2 \geq 0.93$ ) with the environmental productivity index (Figure 6B) and the water status index (Figure 6A). Because monitoring such leaf unfolding is nondestructive and easily done in the field, the opportunity is available for new types of studies on the productivity of *A. deserti* and other agaves under a wide range of field conditions.

### Future Research

Now that it has been shown to be a reliable estimate of productivity, the environmental productivity index should be used to assess the growth and productivity of *A. deserti* at other sites. It can also be applied to the study of nutrient relations, about which little is presently known. Moreover, this approach developed for *A. deserti* is being applied to productivity studies for other agaves, such as *A. fourcroydes*



**Figure 6.** Monthly values of the water status index (A), the environmental productivity index (B), and the total number of newly unfolding leaves on 50 plants (C).

Lem. (Henequen) in the Yucatan and *A. lechuguilla* Torr. in the Chihuahuan Desert. Another area ripe for ecophysiological research is a comprehensive study of root properties of *A. deserti* and other agaves, embracing root growth, distribution in the soil, and consequences for competition with other plants. Such studies may well uncover other interesting adaptations to desert climates for this remarkable group of plants.

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