

PHOTOSYNTHETIC PATHWAYS OF HESPERALOE FUNIFERA AND *H. NOCTURNA* (AGAVACEAE): NOVEL SOURCES OF SPECIALTY FIBERS¹

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Hesperaloe funifera and *H. nocturna* are currently being studied as potential new sources of fibers for specialty papers. This study investigated canopy architecture and light interception in *H. funifera*, and gas exchange in both species. *H. funifera* is an acaulescent rosette species with stiff, upright leaves. Mean leaf angle for 3-year-old plants was 70° from horizontal, and more than 90% of the leaf surface was at angles greater than 50°. Vertical orientation of leaves reduced seasonal variation in light interception and midday light interception during summer months. High leaf angles are interpreted as an adaptation to arid habitats that could reduce this species' suitability for cultivation in more humid areas. Both *H. funifera* and *H. nocturna* had leaf-tissue water contents and mesophyll-succulence values intermediate between previously investigated Agavaceae known to be either C₃ or Crassulacean acid metabolism (CAM) plants. Both species proved to have CAM, however. Gas exchange characteristics varied with leaf age, with older leaves having higher assimilation rates, greater water-use efficiency, and a higher proportion of nighttime CO₂ uptake. Interestingly, these older leaves had mesophyll succulence values closer to those of typical C₃ species. These *Hesperaloe* species can thus be characterized as nonsucculent CAM plants. Both species showed CO₂ uptake rates of 5–8 $\mu\text{mol m}^{-2} \text{sec}^{-1}$ expressed on a total-surface-area basis and 10–18 $\mu\text{mol m}^{-2} \text{sec}^{-1}$ expressed on a projected-leaf-area basis. Expanded cultivation of species possessing CAM in marginal areas has been recommended recently; the physiological studies reported here along with previous studies of their economic botany identify these *Hesperaloe* species as good crop candidates for dry regions.

The development of new crops for arid and semiarid lands emphasizes species with high-value natural products (McLaughlin, 1985). Two species in the family Agavaceae, *Hesperaloe funifera* (Koch.) Trel. and *H. nocturna* Gentry, have very long and narrow fibers with thin cell walls (McLaughlin and Schuck, 1991, 1992). These fibers are narrower and longer than those of *Agave sisalana* Perrine (sisal), which are used both in cordage and in specialty-fiber applications. Sisal produces a paper with high porosity, tear strength, fold endurance, and absorbance; these are characteristics required in the production of specialty papers such as filters for coffee makers and vacuum, oil, and air cleaners, security papers, diapers, and tea bags (da Silva and Pereira, 1985). Sisal, however, lacks cold tolerance and is therefore not suitable for cultivation in the temperate zone. McLaughlin and Schuck (1991) reported that in Arizona, plants in small experimental plots were killed by exposure to temperatures at or below 0 C.

Additional criteria for potential new arid-land crops include good adaptation to dry environments (including low water use) and poor adaptation to more humid areas (McLaughlin, 1985). Photosynthetic metabolism greatly affects the water and carbon balance of a plant and hence is particularly important in determining a species' climatic adaptation. Plant architecture is functionally related to environmental tolerances. The purpose of this study was thus to explore light interception and gas exchange in *Hesperaloe funifera* and *H. nocturna* in order to better

assess their environmental tolerances and suitability for cultivation in arid zones.

Hesperaloe is a small genus of three species native to northern Mexico (Gentry, 1972). *H. nocturna* is known only from northeastern Sonora. It forms dense, acaulescent rosettes of long (1–2 m), narrow (1–1.5 cm), arcuately spreading leaves. *H. funifera* occurs in the Chihuahuan Desert area in northern Mexico, and has large, stiffly erect, coarse leaves, 3–6 cm wide near the base and up to 2 m long. In comparison with *H. nocturna*, *H. funifera* forms a more open rosette with fewer, straighter leaves. In both species, new leaves emerge from the central bud at an essentially vertical angle. As the leaves age they are displaced to a more horizontal position lower in the canopy. The high leaf angle of *Hesperaloe funifera* is probably an adaptation to arid environments. Vertical leaves are found in many species in hot, dry habitats; these help to reduce transpiration by reducing the interception of solar radiation from high solar angles (Ehleringer and Werk, 1986). In more humid habitats, where cloud cover is higher and total daily solar radiation is lower, such high leaf angles may limit the plant's ability to absorb sufficient radiation to support high levels of photosynthesis and growth. Plant architecture could thus place constraints on where potential crop species could be economically cultivated.

In the family Agavaceae there is variability in photosynthetic metabolism. In the extensively studied genus *Agave*, all species examined so far are capable of Crassulacean acid metabolism (CAM) (Nobel, 1976, 1988; Woodhouse, Williams, and Nobel, 1980; Martin and Kirchner, 1987). On the other hand, *Dasylirion wheeleri* S. Wats. and *Nolina microcarpa* S. Wats. show only C₃ metabolism (Kemp and Gardetto, 1982). In the genus *Yucca*, both C₃ and CAM species have been found (Szarek and Troughton, 1976; Kemp and Gardetto, 1982). Among the criteria used to define CAM are nocturnal CO₂ uptake and some degree of succulence (Ting, 1985). Kluge and

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Ting (1978) proposed the use of the mesophyll succulence value (S_m), defined as the ratio of tissue water content to chlorophyll content, as a means of quantifying succulence.

Specific objectives of this study were to: 1) describe canopy architecture and light interception of *Hesperaloe funifera*; 2) determine mesophyll succulence values (S_m) of *Hesperaloe* species and compare with other Agavaceae; and 3) determine the photosynthetic pathways and assess variability in gas exchange (CO_2 uptake, A ; transpiration, E ; and water use efficiency, WUE) for both *Hesperaloe funifera* and *H. nocturna*.

MATERIALS AND METHODS

Plant material—Seedlings of both *Hesperaloe funifera* (accession A-184, McLaughlin and Schuck, 1992) and *H. nocturna* (SPM 5850) were produced in the greenhouse at the Bioresources Research Facility (BRF), University of Arizona, in Tucson. Twenty 4-mo-old plants each of *H. funifera* and *H. nocturna* were transplanted to the field on 5 February 1990 and 5 October 1990, respectively. All plants were drip-irrigated and fertilized with nitrogen, phosphorus, and potassium biweekly.

Samples of native Agavaceae species from southeastern Arizona were collected to obtain water content and mesophyll succulence values for comparison. Species collected included: *Yucca elata* Engelm., *Yucca schottii* Engelm., *Yucca thornberi* McKelvey, *Dasyllirion wheeleri*, *Nolina microcarpa*, *Agave palmeri* Engelm., and *Agave parryi* Engelm.

Plant architecture—One 10-yr-old plant (growing in a landscape in Tucson), three 3-yr-old plants, and eight 18-mo-old *Hesperaloe funifera* plants (all growing at BRF) were studied. For each leaf of each plant we determined total length, width of the outside and inside surfaces at 10-cm intervals from the base, angle of insertion with respect to horizontal, and orientation. Individual leaves were then grouped in nine leaf-angle classes. Leaf-area index for both sides was calculated based on the ground area delineated from the projection of the tips of the longest leaves.

Light interception—Observations of *Hesperaloe funifera* plants under full sunlight indicated to us that at any particular time a very small fraction of a leaf's surface was shaded by other leaves. Because of the curvature of the leaf surface, however, a large portion of the leaf is shaded by other parts of the same leaf at nearly all times. *H. funifera* leaves are crescent-shaped in cross section with the degree of curvature varying from the base to the apex. Along most of its length, the leaf curves in a 180° arc, thus partially shading itself on both upper and lower surfaces, depending on its angle and orientation and the direction of the incoming solar radiation. In order to quantify this self-shading, we constructed a model leaf out of plastic (PVC) tubing painted to match the leaf's reflectance to visible light. The purpose of using a model leaf was to scale the dimensions of the leaf to those of our photosynthetic photon flux density (PFD) sensor. The model leaf was 9 cm in width (measured directly across the curved surface), allowing us to position the sensor of a Licor LI-189 Quantum meter entirely within shaded

and unshaded sections. The model leaf was positioned at various angles and orientations to quantify the amount of PFD that a single leaf, isolated from other leaves on a plant, would receive in winter, spring, and summer. In each combination of leaf angle and orientation, PFD was measured at intervals of 10 cm from the base to the apex of the model leaf. Six measurements were taken at each 10-cm interval—in the center and toward the edges on both upper and lower surfaces. The sensor was held normal to the leaf surface.

Succulence—Chlorophyll was extracted from sections taken from the midpoint of leaves, by grinding ca. 1 g of leaf tissue in 30 ml of 80% acetone, three times. The extract was filtered, and absorption was measured at 645, 652, and 663 nm in a Beckman Spectrophotometer. Total chlorophyll per g of tissue was calculated using Arnon's (1949) formulas. Tissue dry-weight was determined by drying leaf samples at 60 C until constant weight. Mesophyll succulence (S_m) was calculated as the ratio of tissue water content to chlorophyll content.

Gas exchange—Photosynthesis (A) and transpiration (E) were measured using an LCA-3 ADC portable infrared analyzer open gas exchange system (Analytical Development Co., Hoddesdon, England). One cuvette for each of the two *Hesperaloe* species studied was constructed out of polycarbonate plastic (3 mm thick) covered with teflon film to reduce water adsorption. To achieve a seal onto the leaves, the cuvettes were supplied with foam gaskets. The cuvette for *Hesperaloe funifera* had a volume of 817 cm^3 , that for *H. nocturna* had a volume of 335 cm^3 . Testing of the cuvettes was done following Parkinson and Day's (1990) guidelines.

For each measurement an average of 5 min was required for adjustment of the chamber, equilibration, and recording the data. In order to accurately document critical phases of gas exchange (such as the dawn postillumination burst), we attempted to make successive measurements on each leaf on an hourly basis. Thus our sample size was limited to a maximum of eight to ten leaves per sampling date. Measurements were taken halfway from the base to the apex of each leaf, with leaves maintained in their natural position. All leaves were fully mature.

Different approaches were used in selecting leaves for gas-exchange measurements on each of two 2-yr-old *Hesperaloe funifera* plants. On plant 1, three similar age, sequentially produced leaves with different orientations were selected. Leaf 20 (i.e., the 20th leaf produced by the plant) was on the southwest quadrant of the plant, while leaves 21 and 22 were in the east and west quadrant, respectively. These three leaves emerged from the central bud between 12 June and 10 July 1991. On plant 2, leaves were all in the west quadrant but differed in age. Leaves 31, 38, 41, 43, and 51 emerged from the central bud 12 June, 10 July, 7 August, 4 September, and 1 October, respectively. One 2-yr-old plant of *Hesperaloe nocturna* was studied. Three different age leaves were selected based on their position within the canopy—data on exact dates of leaf emergence were not available for this plant. Gas exchange was monitored for 24 hr, on 19–20 October and 1–2 November 1991 for *Hesperaloe funifera* and on 18–19 June 1992 for *Hesperaloe nocturna*.

TABLE 1. Morphological features of *Hesperaloe funifera* of three age classes. Data are presented as mean \pm standard error. All values involving leaf area include both sides of the leaves

Character	18-mo-old plants (N = 8)	3.0-yr-old plants (N = 3)	10.0-yr-old plants (N = 1)
Number of leaves	16.4 \pm 1.0	36.0 \pm 5.5	170
Leaf length (cm)	62.3 \pm 3.7	98.2 \pm 4.1	106.9
Individual leaf area (cm ²)	163.0 \pm 17.6	515.9 \pm 53.8	493.1
Ratio lower to upper leaf surface area	1.45 \pm 0.03	1.31 \pm 0.05	1.51
Total leaf area (dm ²)	26.96 \pm 3.92	189.78 \pm 41.75	838.31
Leaf area index (LAI)	0.28 \pm 0.04	1.25 \pm 0.16	3.15
Mean angle for total leaf area	57.8 \pm 1.7	69.2 \pm 2.4	74.4

RESULTS

Plant architecture—Leaf area was evenly distributed with respect to orientation in the plants studied. Figures 1 and 2 show the leaf area distribution for 10° leaf-angle intervals for the eight 18-mo-old and three 3-yr-old *Hesperaloe funifera* plants, respectively. Younger plants had a more uniform distribution of leaf area among leaf-angle classes. In contrast, 3-yr-old plants had higher proportions of their leaf area in the higher-angle classes; i.e., they had more erect, vertical leaves. As plant age increased from 18-mo-old to 10-yr-old, the mean leaf angle for the total leaf area also increased (Table 1). Leaves of 18-mo-old plants had lower surfaces between 40% and 60% larger than the upper surface (Table 1), reflecting the crescent-shaped cross section of the leaves. This contrasts with 3-yr-old plants' leaves in which the lower surface is only about 30% larger than the upper surface. Leaves of 3-yr-old plants were longer than those of younger plants and were nearly as long as those of the 10-yr-old plant (Table 1). Individual leaf area increased greatly from 18-mo-old to 3-yr-old plants; mean leaf area in the latter plant was similar to that in the 10-year-old plant. Total leaf area increased 600% and 340% as plant age increased from 18-mo-old to 3-yr-old and from 3- to 10-yr-old, respectively, while leaf-area index (LAI) increased only 346% and 152%, consistent with the steeper leaf angles of older plants.

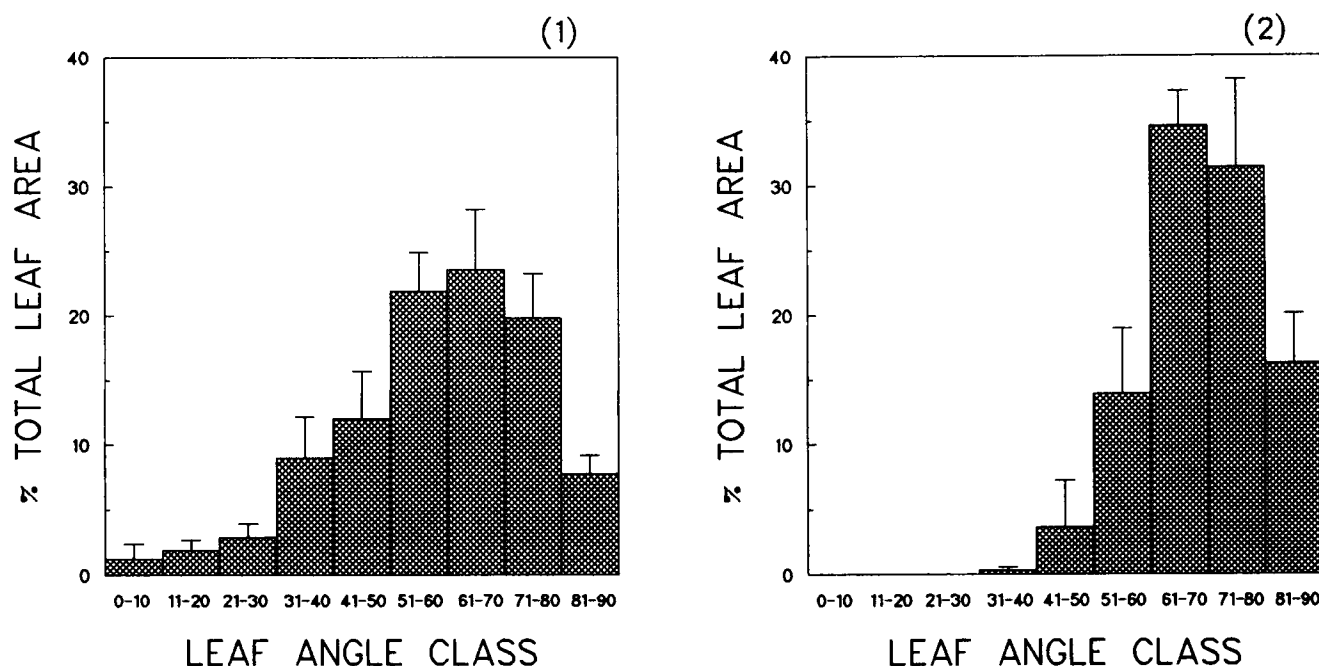
Light interception—PFD received by the model leaf positioned vertically was reduced from that of more horizontal positions at both the summer solstice and the spring equinox (Table 2). Vertical positions tended to have similar integrated daily PFD in all seasons. Seasonal variation increased with lower-angle positions. At a 0° angle (horizontal), leaves experienced almost double PFD in the summer as in winter. When separate quadrants are considered, the variation of PFD with leaf angle was less for leaves in the west and east quadrants than for those in the north and south quadrants. The model leaf positioned in the north and south quadrants at a 0° leaf angle received nearly 35 mol m⁻² per day compared to 25 mol m⁻² per day in a vertical position at the summer solstice. On the same date, east and west quadrant positions received more uniform PFD of 24–25 mol m⁻² per day for angles varying from 0 to 90°. These same differences between north-south and east-west quadrant positions were found during the equinoxes and at the winter solstice.

Succulence—Mesophyll succulence value (S_m) is one potential method of differentiating C₃ and CAM plants (Kluge and Ting, 1978). In the Agavaceae, Kemp and Gardetto (1982) reported a clear separation with CAM species having S_m values above 1 and C₃ species with values below that. Water content and S_m values of both *Hesperaloe funifera* and *H. nocturna* were intermediate between those of known C₃ and CAM Agavaceae, and in *H. funifera* there was variability in S_m associated with leaf angle and, hence, leaf age (Spearman rank-order correlation between leaf angle and water content: $r = 0.71$; $P < 0.05$; Table 3). Mature leaves—those at lower leaf angles—showed lower S_m values than younger leaves (Spearman rank-order correlation between leaf angle and S_m : $r = 0.86$, $P < 0.01$). This could be due in part to a proportionally lower chlorophyll content in younger leaves.

Dasyllirion wheeleri, *Nolina microcarpa*, *Yucca elata*, *Y. thornberi*, and *Y. schottii* had mesophyll succulence values well below 1, while *Agave palmeri* and *A. parryi* values were mostly above 2. *Hesperaloe* spp. thus appear to have water contents and S_m values much lower than those of typical CAM species (*Agave*) and somewhat higher than those of known C₃ species (*Nolina*, *Dasyllirion*, and *Yucca elata*).

Gas exchange—The daily course of assimilation (A) and transpiration for leaves on plant 2 of *Hesperaloe funifera* are shown in Figs. 3 and 4, respectively; A and E for leaves of the *H. nocturna* plant are shown in Figs. 5 and 6, respectively. Both *Hesperaloe funifera* and *H. nocturna* showed nocturnal CO₂ assimilation. Daily patterns of gas exchange showed the four phases of CO₂ exchange typical of CAM plants: phase I, nocturnal CO₂ uptake; phase II, postillumination burst of CO₂ uptake; phase III, no uptake during noon hours; and phase IV, an afternoon increase in CO₂ uptake (Osmond, 1978; Ting, 1985). Both species showed a loss of CO₂ during phase III. Both *H. funifera* plants had considerably higher assimilation on 19 October than on 10 November (Table 4). Temperatures were considerably lower during the first week of November (Table 5).

Leaf age was an important factor in determining A and E. Leaves could be separated into three age groups according to their emergence from the plant's central bud. Older leaves (such as leaf 31 of plant 2) started CO₂ uptake later in the afternoon but had higher A and lower E than younger leaves that emerged in July–August (leaves 38



Figs. 1, 2. Percentage of total leaf area distributed in nine 10° leaf-angle classes from horizontal for *Hesperaloe funifera*. 1. Mean \pm SE for eight 18-mo-old plants. 2. Mean \pm SE for three 3-yr-old plants. Leaf area was calculated on a two-side basis.

and 41) and September–October (leaves 43 and 51) (Figs. 3, 4).

Integrated daily A, E, and the percentage of total A during the daytime hours differed among measurement dates (Table 5). A and E were higher in October than in November but WUE remained constant. Percentage A during daytime hours increased on the November date. Older leaves showed higher A than younger leaves with similar E, resulting in higher WUE for the older leaves. For both dates, the percentage of A during daytime hours was lower in older leaves. Older leaves thus showed greater CAM activity.

Similar-age leaves oriented in different quadrants (*H. funifera* plant 1) varied in their A and E patterns (Table 5). In October, leaf 22 (W quadrant) had the highest daytime and the lowest nighttime instantaneous A rate, while leaves 20 (SW quadrant) and 21 (E quadrant) showed higher nighttime instantaneous A and morning A similar to that of leaf 22. On 1 November, daytime and nighttime instantaneous A were reduced for all leaves. Leaf 20 had the highest morning and afternoon instantaneous A as well as the highest nighttime rates.

TABLE 2. Integrated total daily PFD (mol m^{-2}) received by a model *Hesperaloe funifera* leaf at various angles from the horizontal. Values are averages of both sides and four cardinal directions (E, S, W, and N)

Leaf angle	Summer solstice	Equinox	Winter solstice
0	29.8	25.5	15.6
45	27.5	23.3	—
55	26.6	23.6	—
65	25.2	22.6	19.8
75	24.7	21.5	20.5
85	23.6	21.7	21.6

Hesperaloe nocturna plants studied in June showed a similar pattern with regard to leaf age as that seen with *H. funifera* (Figs. 5, 6). Older leaves had higher rates of nighttime A and higher E at night as well as higher stomatal conductance (data not shown). Also, older leaves started A later in the afternoon than younger leaves. Integrated daily A increased in older leaves while E changed very little, producing higher WUE values (Table 5). The

TABLE 3. Percent water content and mesophyll succulence values (S_m) for some southeastern Arizona native Agavaceae and two *Hesperaloe* species

Species	% Water content (N)	S_m (N)
<i>Agave parryi</i>	76.5 (5)	2.96–4.47 (2)
<i>A. palmeri</i>	75.2 (5)	2.11–1.90 (2)
<i>Yucca thornberi</i>	61.0 (5)	0.48–0.67 (2)
<i>Y. schottii</i>	60.7 (5)	0.45–0.66 (2)
<i>Y. elata</i>	60.2 (5)	0.56–0.50 (2)
<i>Nolina microcarpa</i>	48.5 (5)	0.46–0.49 (2)
<i>Dasyllirion wheeleri</i>	56.6 (5)	0.42–0.43 (2)
<i>Hesperaloe funifera</i>		
47° leaf	69.1 (1)	0.62 (1)
60° leaf	67.2 (1)	0.56 (1)
60° leaf	67.9 (1)	0.58 (1)
61° leaf	66.1 (1)	0.91 (1)
65° leaf	70.2 (1)	1.26 (1)
75° leaf	73.5 (1)	1.52 (1)
80° leaf	70.2 (1)	1.01 (1)
82° leaf	71.6 (1)	1.41 (1)
90° leaf	71.4 (1)	1.88 (1)
<i>Hesperaloe nocturna</i>		
Old leaf	70.5 (2)	0.48–0.48 (2)
Intermediate leaf	71.2 (2)	0.50–0.87 (2)
New leaf	70.5 (2)	0.50–1.00 (2)

TABLE 4. Net CO_2 uptake (A), transpiration (E), water-use efficiency (WUE), and percentage of total CO_2 uptake during daytime hours, for two *Hesperaloe funifera* plants and one *H. nocturna* plant. Data were recorded on 19–20 October and 1–2 November 1992 for *H. funifera* and 19–20 June 1992 for *H. nocturna*. Leaf area was calculated on a two-side basis

	A (mmol m ⁻²)		E (mol m ⁻²)		WUE (mmol CO ₂ /mol H ₂ O)		% Daytime A	
	10/19	11/01	10/19	11/01	10/19	11/01	10/19	11/01
<i>H. funifera</i>								
Plant 1 ^a								
Lf 22	170.4	80.4	35.3	13.6	4.8	5.9	50.8	58.0
Lf 21	224.7	89.9	31.5	14.3	7.1	6.3	35.9	51.6
Lf 20	252.2	117.6	36.0	16.8	7.0	7.0	37.8	45.9
Plant 2 ^b								
Lf 31	313.9	167.7	33.8	15.9	9.3	10.5	30.0	45.0
Lf 38	205.0	102.8	28.8	14.6	7.1	7.0	44.3	59.1
Lf 41	222.5	105.4	37.8	18.4	5.9	5.7	48.3	58.6
Lf 43	167.2	91.4	34.7	17.3	4.8	5.3	59.3	75.5
Lf 51	163.3	100.7	34.3	14.6	4.8	6.9	56.0	76.1
<i>H. nocturna</i> ^c	6/19		6/19		6/19		6/19	
Lf 1	128.6		33.2		3.9		40.7	
Lf 2	101.5		39.6		2.8		46.2	
Lf 3	77.3		34.6		2.2		62.8	

^a Leaves differed in orientation (20, 21, and 22 on the southwest, east, and west quadrant, respectively).

^b Leaves differed in age (31, oldest; 51, youngest).

^c Leaves are numbered according to age: 1 oldest, 3 youngest.

percent of total A during day hours was significantly lower in older leaves.

DISCUSSION

In mature *Hesperaloe funifera* plants nearly all of the leaf area is at an angle of more than 50° from the horizontal. High leaf angles are an adaptation to arid, high solar radiation habitats (Ehleringer and Werk, 1986). Leaf morphology and orientation affect photosynthesis in two ways—light interception and temperature regulation—and these in turn affect transpiration and CO_2 diffusion (Fitter and Hay, 1981). Leaves with high insertion angles maximize light interception during morning and afternoon periods when ambient temperature is low (Smith and Ullberg, 1989). Leaf temperature is minimized during midday when solar insolation and ambient temperature are usually high (Gibbs and Patten, 1970; Smith and Ullberg, 1989). This feature would be particularly important in a CAM plant in which stomata are closed at midday, preventing transpirational cooling.

Woodhouse, Williams, and Nobel (1980) concluded that nocturnal photosynthesis in *A. deserti* is limited by daytime PFD interception. This species, with more than half its leaf area at angles less than 45° from horizontal, has lower leaf angles than *H. funifera* and would therefore

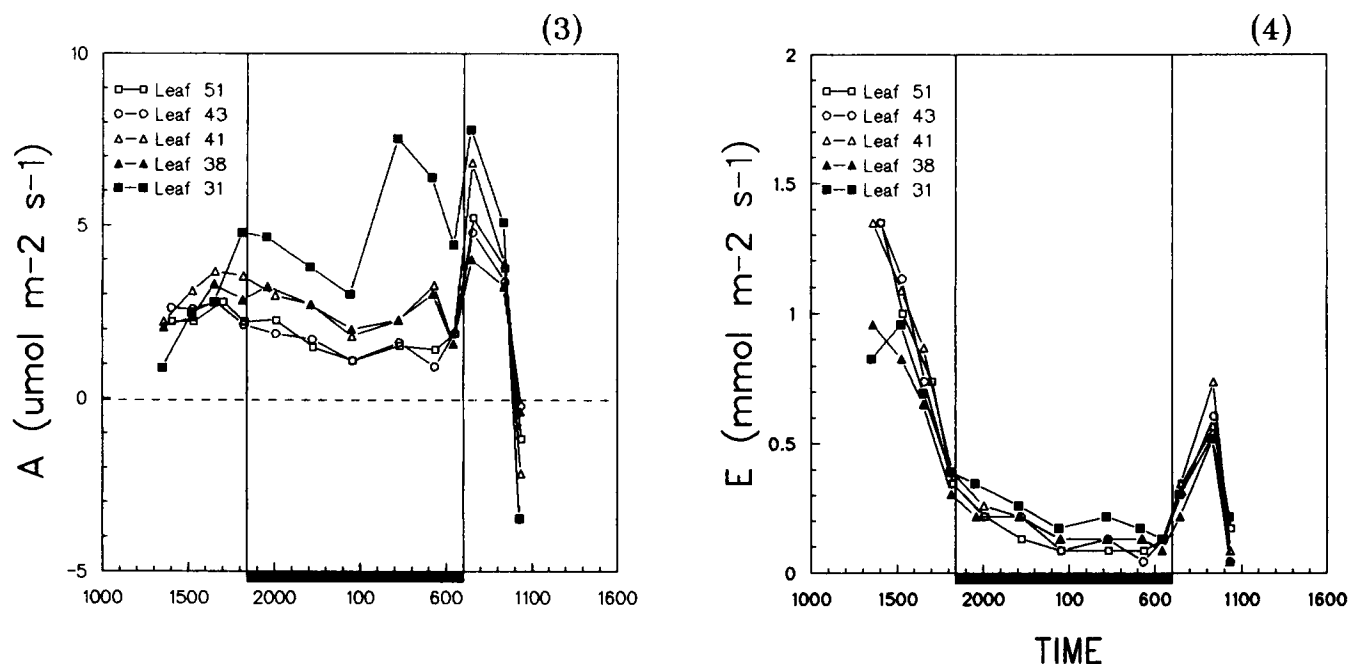
intercept relatively more light. The potential for PFD limiting photosynthesis would thus be relatively greater for *Hesperaloe* in comparison to *Agave*. Adaptations to reduce light interception in high-PFD, arid environments might prove to be disadvantageous in more humid regions with lower daily and seasonal PFD. The canopy architecture of *H. funifera* would not be conducive to high growth rates in more humid, cloudier regions.

Our measurements of light interception in *Hesperaloe funifera* do not account for inter-leaf shading. It is our impression, however, based on our observations of the plants in the field, that the amount of inter-leaf shading is minor in comparison to self-shading except at very low solar angles. Self-shading of these leaves is a consequence of their curvature. Another major effect of the curvature of the leaf surfaces, in comparison with flat leaves, appears to be to decrease variation in total daily PFD interception with respect to leaf angle and leaf orientation.

CAM is generally associated with succulence, although succulence has been defined in different ways (Kluge and Ting, 1978; Gibson, 1982; von Willert et al., 1990). The degree of CAM activity tends to be positively correlated with the thickness of photosynthetic organs and water content in diverse groups of succulents (McWilliams, 1970; Jimenez et al., 1983; Nobel and Harstock, 1990). Kluge and Ting (1978) proposed the use of mesophyll succulence, the ratio of water content to chlorophyll content, with values above 1.25 g mg⁻¹ indicative of CAM. Nobel and Harstock (1990) found values of around 1 g mg⁻¹ for cacti with a C₃-like CO_2 uptake pattern and above 1.28 g mg⁻¹ for CAM epiphytic cacti. Analyzing several species in the family Agavaceae in New Mexico, Kemp and Galletto (1982) found a clear separation of CAM species having S_m values 1.20 and above and C₃ species with values 0.65 and below. Both low leaf water content and low to intermediate S_m values for *Hesperaloe funifera* and *H. nocturna* do not clearly indicate the ability of these

TABLE 5. Maximum and minimum temperature and photon flux density (PFD) for the dates on which gas exchange was measured in *Hesperaloe funifera* and *H. nocturna*

Date	Maximum temperature (C)	Minimum temperature (C)	PFD (mol m ⁻² day ⁻¹)
19–20 October 1991	39.3	14.2	38.2
1–2 November 1991	22.7	0.8	34.5
19–20 June 1992	43.4	14.7	52.4

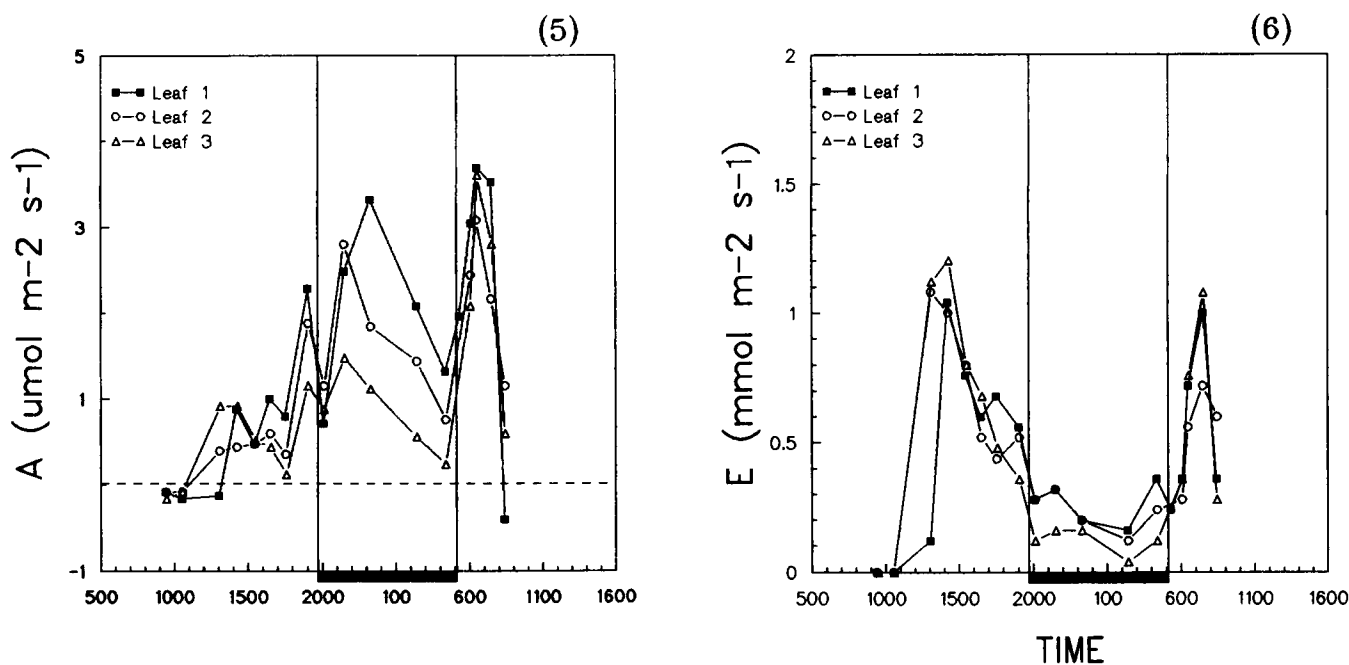


Figs. 3, 4. Net CO₂ uptake (A) and transpiration (E) for *Hesperaloe funifera* plant 2. 3. Net CO₂ uptake. 4. Transpiration. Leaves varied in age (leaf 31 the oldest, leaf 51 the youngest). Data were collected on 19–20 October 1991.

species for CAM metabolism. Older leaves show relatively greater CAM activity yet have lower S_m values.

Our mesophyll succulence values are in agreement with previous reports for *Dasyliirion wheeleri*, *Nolina microcarpa*, and *Yucca elata* (Kemp and Gardetto, 1982) and would suggest that *Y. thornberi* and *Y. schottii* are C₃ species as well, although these latter two broad-leaved species are more closely related to CAM species (*Y. bac-*

cata [Engelm.] Trel., *Y. torreyi* Schafer—all section *Sarcocarpa*) than to narrow-leaved C₃ species (*Y. elata*, *Y. campestris* McKelvey—section *Chaenocarpa*) (Webber, 1953). Both *Agave* spp. examined had very high S_m values. *A. parryi* has been previously described as CAM (Eickmeier and Bender, 1976; Nobel and Smith, 1983; Nobel and McDaniel, 1988). S_m values are in agreement with previous findings for *A. parryi* and indicate that *Agave*



Figs. 5, 6. Net CO₂ uptake (A) and transpiration (E) for *Hesperaloe nocturna*. 5. Net CO₂ uptake. 6. Transpiration. Leaves varied in age (leaf 1 the oldest, leaf 3 the youngest). Data were collected on 19–20 June 1992.

palmeri is a CAM plant as well. In comparison with other Agavaceae, it appears that *H. funifera* and *H. nocturna* are remarkably nonsucculent CAM species.

Both *Hesperaloe funifera* and *H. nocturna* showed CO₂ uptake during the night and no uptake during midday hours, typical of CAM plants. Although all selected plants performed CAM, the rates of CO₂ uptake and transpiration varied for different leaves in each plant. Variation in gas exchange between plants has been described, but variation between leaves within a single plant is not frequently considered in photosynthesis studies of CAM plants.

In this study, both *Hesperaloe funifera* and *H. nocturna* showed patterns of gas exchange related to leaf age. Older leaves started A later in phase IV, but had a higher peak by late afternoon. In phase I, older leaves had near double the A values of young leaves. This differs with findings by Woodhouse, Williams, and Nobel (1980), working with *A. deserti*, in which leaves of different age classes did not differ in nocturnal acidity increase, except for senescing leaves. Marcelle (1975) found that an older leaf of *Bryophyllum daigremontianum* had a lower instantaneous A than a younger leaf, both under short and long day conditions. He also found that the older leaf had a net CO₂ loss during midday hours. Contrary to these findings, *Hesperaloe* species showed equal or higher A for older leaves during phase II. A difference in relative age (a senescing *Bryophyllum* leaf compared to mature but active *Hesperaloe* leaves) could be responsible for the different findings in these two studies. Similar to *Hesperaloe* species, older leaves of *Senecio medley-woodii* had a higher proportion of their daily CO₂ uptake during nighttime hours than younger leaves (Eller and Ruess, 1986). Also, Holthe, Sternberg, and Ting (1987) found that young leaves of *Peperomia scandens* exhibited a typical C₃ pattern of CO₂ uptake that changed to a more characteristic CAM pattern in older leaves.

Carbon dioxide losses in phase III were greater for older than for young *Hesperaloe* leaves. CO₂ losses during phase III have been found in many CAM plants (Joshi, Boyer, and Kramer, 1965; Meinzer and Rundel, 1973; Marcelle, 1975). In the Agavaceae, CO₂ losses during phase III have also been shown (Neales, 1973; Kemp and Gardetto, 1982; Nobel, 1985; Martin and Kirchner, 1987). CO₂ losses are probably due to incomplete stomata closure when malic acid is actively decarboxylated and internally released CO₂ concentration increases (Osmond, 1978). Transpiration closely followed A, but since nighttime E rates were lower, due to a lower vapor-pressure gradient, integrated WUE was higher for older leaves.

No clear pattern was observed for *H. funifera* plant 1 between equal-age leaves with varying orientation. Woodhouse, Williams, and Nobel (1980) did not find significant effects of compass direction on nocturnal acidity increase in *Agave deserti*. Light interception does not vary strongly with orientation in *H. funifera*, however, particularly for leaves at high angles. Although leaves in the east and west quadrant of the plant receive the same amount of total daily PFD, east-quadrant leaves receive higher instantaneous PFD during morning hours, and west-quadrant leaves receive greater instantaneous PFD in the afternoon (data not shown). Such differences could be responsible for differences in the integrated daily A. Alternatively,

random leaf-to-leaf variation in interleaf shading might have accounted for the differences observed in our small sample.

Given the measurement constraints on sample size— instrumentation and the time required to make measurements—it is not possible to examine differences in leaf orientation or the combination of leaf orientation and angle in a statistically rigorous manner. At this point we can state that there is considerable within-plant (leaf-to-leaf) variation in the daily course of photosynthesis, and that conclusions based on measurements taken from a single leaf are unlikely to provide an adequate description of gas exchange in such leaf-rosette succulents.

In *Hesperaloe funifera*, the low nighttime temperature in November greatly reduced photosynthesis. According to Kluge and Ting (1978), temperatures below 5 C inhibit nocturnal malic acid synthesis. It has been reported that *Agave vilmoriniana* Berger had a greater reliance on A at night during high day/night temperatures, leading to a decrease in water loss during the daytime (Nobel and McDaniel, 1988). In contrast to *H. funifera*, *A. vilmoriniana* nighttime A was reduced to almost zero when temperatures decreased from 40/30 to 20/10 (day/night), increasing the ratio day A/night A. This ratio is known to vary with environmental conditions, including water availability (Harstock and Nobel, 1976) and day and night temperatures (Neales, 1973). Although the morning and afternoon peaks were similar for both October and November dates in *Hesperaloe funifera*, reduced nighttime A resulted in lower integrated 24-hr A for the November date. Integrated daily E was also highly reduced in November, so WUE remained constant.

WUE values found in *Hesperaloe* are similar to those reported in other CAM Agavaceae species (Kluge and Ting, 1978; Nobel, 1988). WUE, however, is known to vary with temperature, radiation, and soil water availability. To assess the effects of climatic factors on A, E, and WUE, long-term seasonal measurements are needed.

Plant species possessing CAM have low water requirements and high tolerance to water stress. Nevertheless there are few examples of crop species possessing CAM metabolism, with pineapple (*Ananas comosus* (L.) Merr., Bromeliaceae) the only intensively cultivated CAM crop (Bartholomew, 1982). Other minor CAM crops are sisal (*Agave sisalana*) and henequen (*A. fourcroydes* Lem.), both used for fibers; *A. tequilana* Weber and *A. salmiana* Otto, used in the preparation of alcoholic beverages; and *Opuntia ficus-indica* (L.) Mill. (Cactaceae), cultivated for its fruits and young cladodes (Gentry, 1982; Nobel, 1988). Furthermore, there are no reports of recent domestication of CAM plants. Part of the reason for this paucity of CAM crops is that many CAM plants are reported to have very low growth rates (Szarek and Ting, 1975; Osmond, 1978). Some CAM plants are capable of high productivity, however (Osmond, Nott, and Firth, 1979; Nobel, 1991). Recently, average annual productivities of 40 Mg ha⁻¹ yr⁻¹ for *Agave mapisaga* Trel. and *A. salmiana* have been reported (Nobel, Garcia-Moya, and Quero, 1992). For many CAM species, the environmental factors associated with high productivity are: nighttime temperatures near 15 C (Hanscom and Ting, 1978), high ambient solar radiation achievable in mid-latitude regions lacking extensive cloudiness, and absence of prolonged freezing tem-

peratures (Nobel, 1991). Also, these same environmental requirements would prevent some CAM species from achieving high productivities in more mesic areas, avoiding competition for crop land with other crops.

When expressed per unit projected area (as for C_3 and C_4 species), total daily A for *Hesperaloe funifera* showed maximum values for individual leaves above 720 mmol $m^{-2} day^{-1}$, with an average of 493 mmol $m^{-2} day^{-1}$ measured under field conditions. Nobel (1985, 1991) found values between 700 and 1,170 mmol $m^{-2} day^{-1}$ for *Agave tequilana* and *A. mapisaga* growing under optimal conditions. Nobel concluded that CAM plants can, under optimal conditions, have a net CO_2 uptake similar to that found in C_3 and C_4 plants when computed on a 24-hr basis.

Nobel (1991; Nobel, Garcia-Moya, and Quero, 1992) advocates increased cultivation of CAM species in areas where water is a major limiting factor. However, the markets for most existing CAM crops are relatively small and unlikely to grow substantially. Expanded cultivation of CAM species will require the identification of plants with potentially valuable natural products. *Hesperaloe funifera* or *H. nocturna*, with their excellent fiber properties, high leaf angles in a rosette plant structure, and CAM photosynthetic pathway with attendant high WUE, would appear to fulfill the criteria for candidate plant species for development as new crops for arid lands.

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