

Leaf and Stem CO₂ Uptake in the Three Subfamilies of the Cactaceae¹

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PARK S. NOBEL* AND TERRY L. HARTSOCK

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

ABSTRACT

Net CO₂ uptake over 24-hour periods was examined for the leaves and for the stems of 11 species of cacti representing all three subfamilies. For *Pereskia aculeata*, *Pereskia grandifolia*, and *Maihuenia poeppigii* (subfamily Pereskioideae), all the net shoot CO₂ uptake was by the leaves and during the daytime. In contrast, for the leafless species *Carnegiea gigantea*, *Ferocactus acanthodes*, *Coryphantha vivipara*, and *Mammillaria dioica* (subfamily Cactoideae), all the shoot net CO₂ uptake was by the stems and at night. Similarly, for leafless *Opuntia ficus-indica* (subfamily Opuntioideae), all net CO₂ uptake occurred at night. For leafy members of the Opuntioideae (*Pereskopsis porteri*, *Quiabentia chacoensis*, *Austrocylindropuntia subulata*), at least 88% of the shoot CO₂ uptake over 24 hours was by the leaves and some CO₂ uptake occurred at night. Leaves responded to the instantaneous level of photosynthetically active radiation (PAR) during the daytime, as occurs for C₃ plants, whereas nocturnal CO₂ uptake by stems of *O. ficus-indica* and *F. acanthodes* responded to the total daily PAR, as occurs for Crassulacean acid metabolism (CAM) plants. Thus, under the well-watered conditions employed, the Pereskioideae behaved as C₃ plants, the Cactoideae behaved as CAM plants, and the Opuntioideae exhibited characteristics of both pathways.

For most cacti studied, nearly all of the CO₂ is taken up at night and incorporated into organic acids such as malate by the Crassulacean acid metabolism pathway (11). Many CAM plants also fix considerable amounts of CO₂ by the C₃ pathway, e.g. during the usually wetter conditions accompanying the seedling stage (23), when adult plants are provided with extra water (9, 18), or under springtime temperature conditions (8). Also, certain plants have drought-deciduous leaves that operate with the C₃ pathway and succulent stems that use the CAM pathway, such as *Frerea indica* (12), *Euphorbia trigona* (6), and *Cissus quadrangularis* (22). Even though many cactus species have prominent leaves (2, 4, 7), nearly all the cacti studied have been devoid of leaves when gas exchange was measured (e.g. 13, 16, 17, 20, 21), except for some studies on *Pereskia* (19).

Three subfamilies of cacti are recognized: Pereskioideae, Opuntioideae, and Cactoideae (4, 7). The Pereskioideae, which is considered the most primitive subfamily, comprises 1% of the species and is divided into two genera, *Pereskia* (15-18 species) and *Maihuenia* (2-3 species). All species in the Pereskioideae have conspicuous leaves, as do the more primitive members of the Opuntioideae (2), which comprise 16% of the species of

Cactaceae and constitute seven genera. In particular, *Pereskopsis* and *Quiabentia* can have broad succulent leaves (2, 4, 7). The largest genus in the Opuntioideae is *Opuntia* (over 160 species), and its species can have small, ephemeral leaves. Just over 80% of cactus species are in subfamily Cactoideae, which has 113 genera (7). For this subfamily, leaves are vestigial and often difficult to see with the unaided eye.

In this study, net CO₂ uptake was investigated for at least three species from each of the subfamilies to determine whether differences occurred in the CO₂ fixation pathway utilized. Daytime CO₂ uptake and nighttime CO₂ uptake were separately determined, both for the leaves and for the stems. Plants were maintained and gas exchange was measured at or near optimal conditions of temperature, water status, and PAR. Because net CO₂ uptake rates of C₃ plants during the daytime respond rapidly to changes in the instantaneous PAR level while the total daily PAR is more important for net CO₂ uptake at night for CAM plants (14), PAR responses were also determined to help confirm the CO₂ fixation pathways used.

MATERIALS AND METHODS

Plant Material. Three species of subfamily Pereskioideae were used: *Pereskia aculeata* Miller and *Pereskia grandifolia* Haw. were obtained from the University of California Mildred E. Mathias Botanical Garden (West Los Angeles, CA) and *Maihuenia poeppigii* (Otto) Weber was obtained from the Cactus Ranchito (Tarzana, CA). Four species of subfamily Opuntioideae were used: *Pereskopsis porteri* (Brand.) Britt. & Rose was obtained from the Huntington Botanical Gardens (San Marino, CA), *Quiabentia chacoensis* Backeb. from the Cactus Ranchito, *Austrocylindropuntia subulata* (Mühlentpf.) Backeb. (*Opuntia subulata* (Mühlentpf.) Engelm.) from the University of California Mildred E. Mathias Botanical Garden, and *Opuntia ficus-indica* (L.) Miller from the Espinosa Cactus Farm (San Bernardino, CA). Four field-collected species of subfamily Cactoideae were used: *Carnegiea gigantea* (Engelm.) Britt. & Rose was collected near Phoenix, AZ; *Ferocactus acanthodes* (Lem.) Britt. & Rose and *Mammillaria dioica* K. Brandeg. near Palm Desert, CA; and *Coryphantha vivipara* (Nutt.) Britt. & Rose var. *deserti* (Engelm.) W. T. Marshall near Mercury, NV.

Adult plants of each species were maintained in environmental chambers with day/night air temperatures of 25/15°C. A PAR of 800 μmol m⁻² s⁻¹ on a horizontal surface and averaging 500 μmol m⁻² s⁻¹ (determined with a LiCor LI-190S quantum sensor) in the planes of the leaves or the stems considered was provided for 12 h each d (70% by Sylvania 60-W warm-white fluorescent lamps and 30% by Sylvania 300-W cool-beam tungsten lamps). The water vapor concentration was 10 g m⁻³ and the CO₂ level was 350 μl/l by volume. Plants were routinely watered twice weekly with 1/20 Hoagland solution No. 1 (10) so that the soil water potential in the root zone was always above -0.5 MPa

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(measured with Wescor PT51-05 soil thermocouple psychrometers).

Gas Exchange. Net rates of CO₂ exchange and water vapor loss were determined using a modified Siemens null-point, compensating, closed-circuit flow system (15). CO₂ was measured with an Anarad AR-500R IR gas analyzer and water vapor with an EG&G 660 dewpoint hygrometer. Air temperatures, water vapor concentration, PAR, photoperiod, and CO₂ level were routinely the same as in the environmental chambers. Preliminary experiments indicated that maximum CO₂ uptake rates by the shoot of each species occurred within $\pm 5^\circ\text{C}$ of the temperatures used here. All reported gas exchange data were replicated at least two times with similar results.

Gas exchange measurements are here expressed per unit of total surface area. This is the conventional method for stems and for terete leaves (e.g. *M. poeppigii*, *A. subulata*) but leads to half the conventional CO₂ uptake rates for flat leaves (e.g. *P. aculeata*, *P. grandifolia*), where data are usually expressed per area of one side of the leaf. For species with large leaves (*P. aculeata*, *P. grandifolia*, and *A. subulata*) sufficient leaf area for gas exchange measurement (at least 40 cm²) could be inserted into the assimilation chamber without also inserting stem; to determine stem gas exchange for these species, the leaves were removed, the cut petioles sealed with petrolatum, and the stem then inserted into the assimilation chamber (no detectable CO₂ or H₂O exchange occurred through the surfaces sealed with petrolatum, which in any case represented a very small fraction of the shoot surface). For species with small leaves (*M. poeppigii*, *P. porteri*, and *Q. chacoensis*), a portion of the shoot was inserted into the assimilation chamber so that leaf and stem gas exchanges were determined together; the leaves were then removed, the exposed surfaces sealed with petrolatum, and gas exchange by the stems determined so that leaf gas exchange could be calculated from the shoot values minus the stem contribution. The remaining five species had no leaves and hence their stem gas exchange could be directly determined.

RESULTS

Pereskioideae. Net CO₂ uptake and stomatal opening, the latter manifested by a marked increase in water vapor conductance, were essentially restricted to the daytime for leaves of *Pereskia grandifolia* (Fig. 1). The highest CO₂ uptake rate occurred about 2 h into the light period, when stomatal opening was maximal, and the net CO₂ uptake rate by the leaves throughout most of the daytime was about 5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 1A). On the other hand, the stems never exhibited a net CO₂ uptake, although a small increase in water vapor conductance occurred near the beginning of the light period (Fig. 1B).

Daily patterns of net CO₂ uptake and stomatal opening similar to those of *P. grandifolia* (Fig. 1) were also found for the leaves and the stems of *Pereskia aculeata* and *Maihuea poeppigii* (data not shown). When summed over the entire daytime, net CO₂ uptake by the leaves was 156 to 209 mmol m⁻² for all three species (Table I). Also, there was a small net CO₂ release at night by the leaves and at night as well as during the daytime by the stems of all three species (Table I). All of the net shoot CO₂ uptake for these three species of Pereskioideae was thus by the leaves.

Leafy Opuntioideae. As for the species of Pereskioideae, net CO₂ uptake and stomatal opening by leaves of *Pereskia porteri* were substantial during the daytime (Fig. 2). However, some net CO₂ uptake and stomatal opening occurred for its leaves at the end of the dark period. Its stem exhibited net CO₂ uptake for a brief period during the daytime, when some stomatal opening occurred (Fig. 2). A brief period of slight stomatal opening occurred at the end of the dark period for the stems of *P. porteri*, but this opening was not accompanied by any meas-

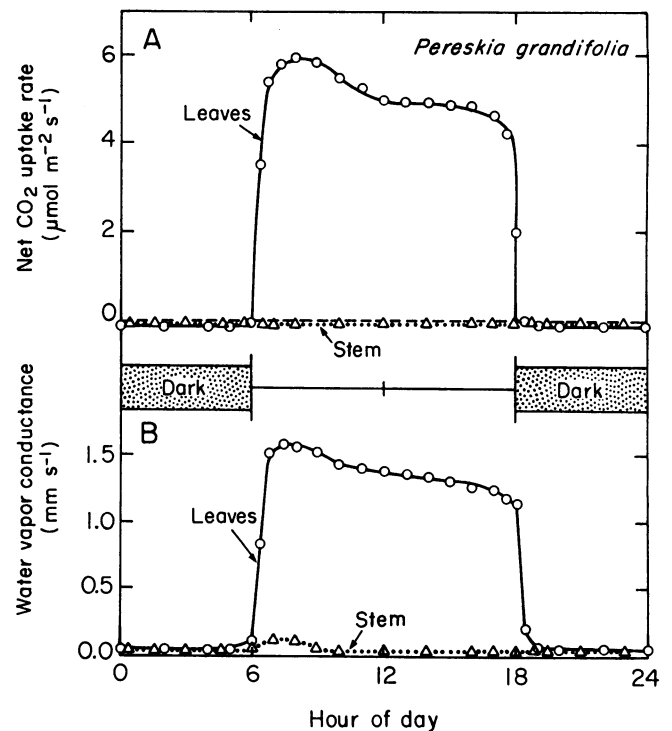


FIG. 1. Gas exchange over 24 h for leaves (O) and the stem (Δ) of *P. grandifolia*. A, Net CO₂ uptake rate; B, water vapor conductance.

urable net CO₂ uptake.

For *Quiabentia chacoensis*, net CO₂ uptake and stomatal opening for the leaves was also maximal during the daytime (Fig. 3). Considerable CO₂ uptake occurred at night for the leaves of *Q. chacoensis* (Fig. 3A), but it occurred at the beginning of the night compared with uptake at the end of the night for *P. porteri* (Fig. 2A). Although net CO₂ uptake during the daytime by the stems was greater for *Q. chacoensis* than for *P. porteri*, it occurred primarily in the afternoon rather than in the morning and the maximal rate was much less than for the leaves.

The other leafy member of the Opuntioideae considered was *Austrocylindropuntia subulata*. Again, stomatal opening and net CO₂ uptake for the leaves occurred mainly during the daytime and maximal rates were much higher for the leaves compared with the stems (Fig. 4). Although some CO₂ uptake occurred at the end of the night for leaves of *A. subulata*, net CO₂ exchange was negative through most of the night. The stems exhibited a pattern different from the leaves, with net CO₂ uptake and stomatal opening being restricted to the nighttime (Fig. 4).

For the three leafy species of Opuntioideae, net CO₂ uptake occurred mainly during the daytime and CO₂ was mainly taken up by the leaves (Table I). However, in going from *P. porteri* to *Q. chacoensis* to *A. subulata*, CO₂ uptake per unit stem area increased as did the fraction of the photosynthetic surface area comprised by stems. Thus, the leaf contribution to shoot CO₂ uptake decreased from 99 to 93 to 88% in this sequence (Table I).

Leafless Cacti. For the leafless stems of *Opuntia ficus-indica* (Opuntioideae) and *Ferocactus acanthodes* (Cactoideae), net CO₂ uptake occurred essentially only at night (Fig. 5A). Stomatal opening was restricted to the nighttime (Fig. 5B), as is generally the case for stem-succulent CAM plants. The maximum net CO₂ uptake rate slightly exceeded 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *O. ficus-indica* and was nearly 6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *F. acanthodes*.

For these two species and three other species of Cactoideae, all of which had no visible leaves, CO₂ uptake by the stems was positive only at night (Table I). The amount of nocturnal CO₂

Table 1. Summary of Leaf and Stem CO₂ Uptake Characteristics of Cacti

Species	Areas		Net CO ₂ Uptake				Net Shoot CO ₂ Uptake over 24 h by Leaves ^a
	Leaf	Stem	Leaf		Stem		
			Day	Night	Day	Night	
	cm ²		mmol m ⁻²				%
Subfamily Pereskioideae							
<i>Pereskia aculeata</i>	2560	152	162	-2	-5	-3	100
<i>P. grandifolia</i>	1420	143	209	-3	-2	-2	100
<i>Maihuenia poeppigii</i>	261	46	156	-2	-9	-6	102
Subfamily Opuntioideae							
<i>Peresklopsis porteri</i>	460	225	91	5	2	-1	99
<i>Quiabentia chacoensis</i>	410	275	94	9	12	0	93
<i>Austrocylindropuntia subulata</i>	380	290	92	-1	-1	18	88
<i>Opuntia ficus-indica</i>	0	640			-6	295	0
Subfamily Cactoideae							
<i>Carnegiea gigantea</i>	0	880			-2	194	0
<i>Ferocactus acanthodes</i>	0	550			-7	171	0
<i>Coryphantha vivipara</i>	0	144			-3	104	0
<i>Mammillaria dioica</i>	0	192			-3	94	0

^a Day-plus-night leaf CO₂ uptake times leaf area divided by the sum of this quantity and day-plus-night stem CO₂ uptake times stem area, expressed as a percentage.

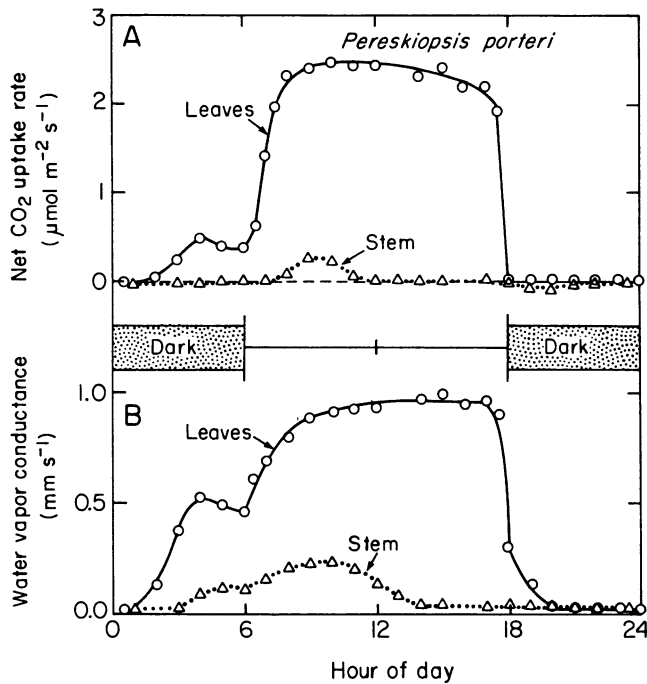


FIG. 2. Gas exchange over 24 h for leaves (O) and the stem (Δ) of *P. porteri*. A, Net CO₂ uptake rate; B, water vapor conductance.

uptake was about 100 mmol m⁻² for *Coryphantha vivipara* and *Mammillaria dioica*, nearly twice as great for *Carnegiea gigantea* and *F. acanthodes*, and about three times as great for *O. ficus-indica*.

PAR Responses. CO₂ uptake by leaves of species with substantial rates of daytime CO₂ uptake responded directly to the instantaneous PAR level (Fig. 6). Ninety percent of maximal CO₂ uptake rates occurred at a PAR of 310 μmol m⁻² s⁻¹ for *P. grandifolia*, 520 μmol m⁻² s⁻¹ for *Q. chacoensis* and *A. subulata*, and 710 μmol m⁻² s⁻¹ for *P. porteri*. Net CO₂ uptake in the dark was negative for all four species (Fig. 6), as would be expected for the C₃ pathway.

Daily net CO₂ uptake by the two stem succulents *O. ficus-*

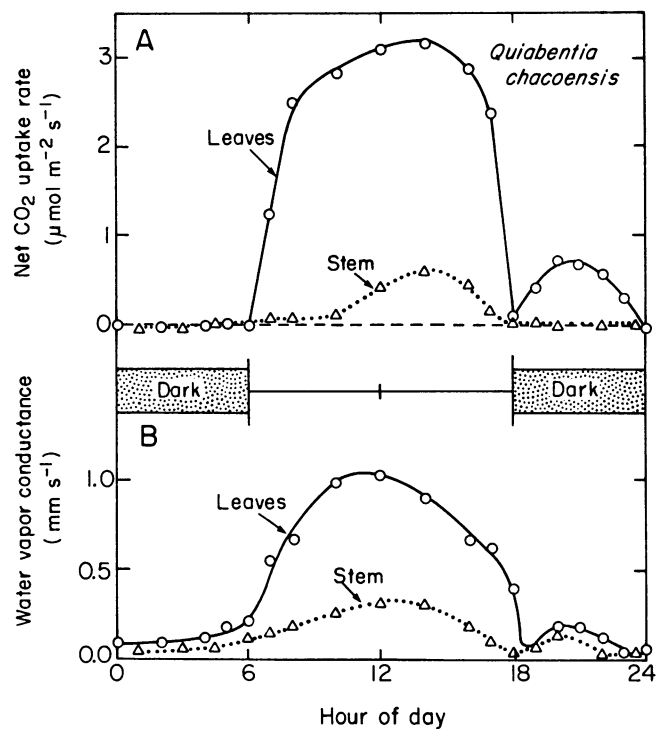


FIG. 3. Gas exchange over 24 h for leaves (O) and the stem (Δ) of *Q. chacoensis*. A, Net CO₂ uptake rate; B, water vapor conductance

indica and *F. acanthodes* responded to the total daily PAR (Fig. 7), the latter determined by summing the instantaneous PAR over the entire daytime. Such net CO₂ uptake, which occurred predominantly at night (Fig. 5), reached 90% of maximal at a total daily PAR of 22 mol m⁻² for *O. ficus-indica* and 25 mol m⁻² for *F. acanthodes* (total daily PARs of 22 and 25 mol m⁻² correspond to constant instantaneous values of 510 and 580 μmol m⁻² s⁻¹ for a 12-h daytime); PAR compensation for both species occurred at 3 to 4 mol m⁻² (Fig. 7).

DISCUSSION

Although most cacti never have conspicuous leaves (2, 4, 7), leaves are generally persistent in the Pereskioideae and for *Per-*

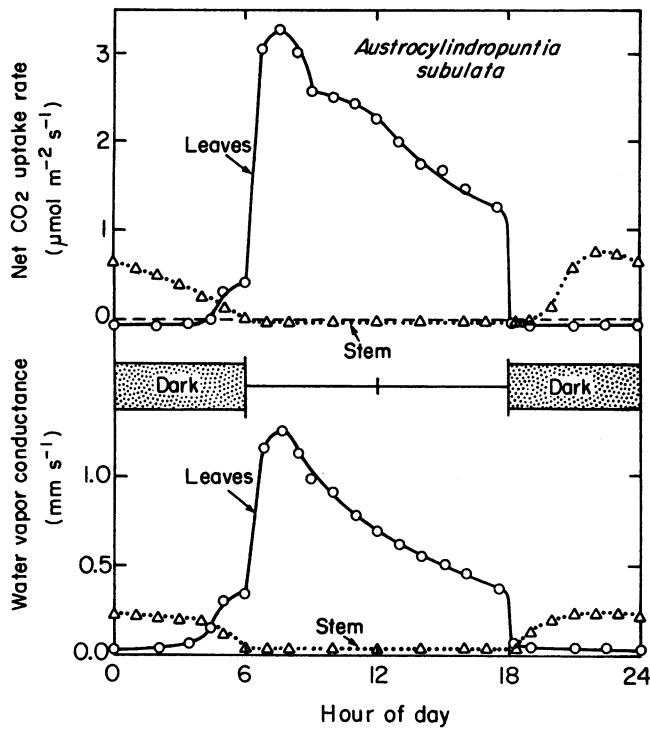


FIG. 4. Gas exchange over 24 h for leaves (O) and the stem (Δ) of *A. subulata*. A, Net CO₂ uptake rate; B, water vapor conductance.

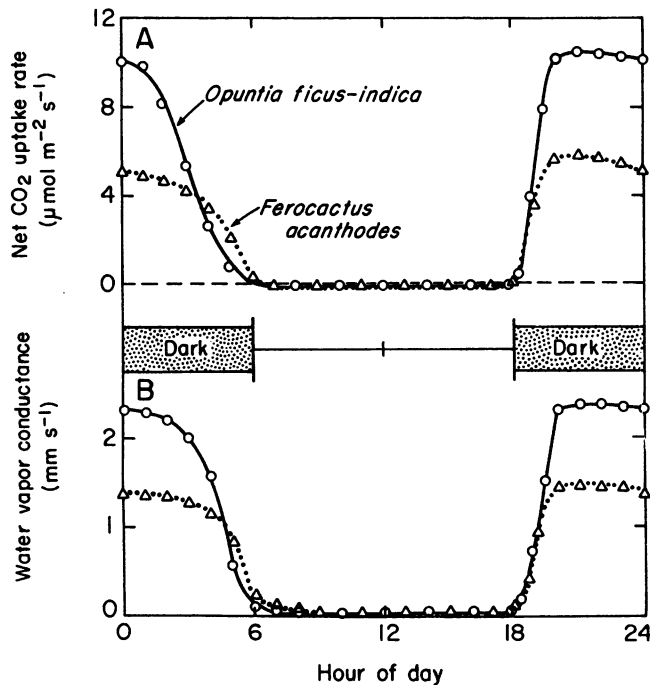


FIG. 5. Gas exchange over 24 h for stems of *O. ficus-indica* (O) and *F. acanthodes* (Δ). A, Net CO₂ uptake rate; B, water vapor conductance.

eskiopsis (Opuntioideae). Other species have ephemeral leaves that are shed or shrivel after internodal elongation is completed. For instance, both cylindropuntias and platyopuntias can have small leaves, especially on new stem segments, that develop during an annual wet season and that last for 1 to 3 months (3, 4). Here, for all three species of Pereskioideae and all three leafy species of Opuntioideae, at least 88% of the net CO₂ uptake by the shoot was by the leaves for well-watered plants under approximately optimal conditions of temperature and PAR (Table

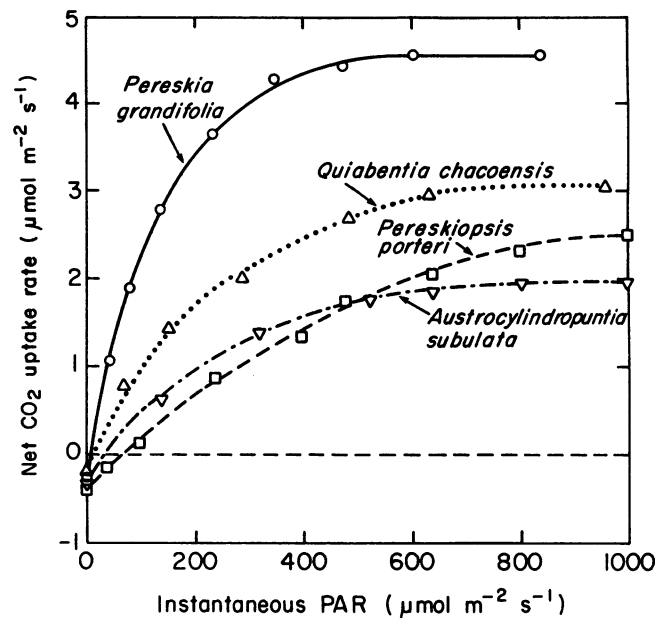


FIG. 6. Response of net CO₂ uptake rate to instantaneous PAR incident on leaves of four species. Measurements were made near midday.

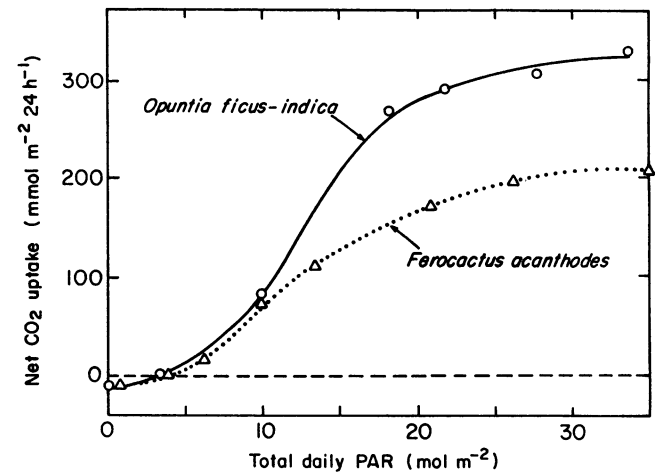


FIG. 7. Response of net CO₂ uptake integrated over 24 h to the total daily PAR incident on stems of two species. Different parts of the stem were maintained at the indicated PAR for about 1 week before measurement of net CO₂ exchange as for Figure 5.

I). On an area basis, the net CO₂ uptake rates and 24-h totals were also higher for leaves than for the stems on the same plants (Figs. 1-4). Thus, when leaves represent most of the photosynthetic surface area, they are apparently the main photosynthetic organs of cacti, at least under the conditions employed here.

Rayder and Ting (19) examined the two species of *Pereskia* considered here and also observed a C₃-like pattern for the leaves when the plants were well-watered. The maximum water vapor conductance they observed was only 0.4 mm s⁻¹ for *P. aculeata* and 0.2 mm s⁻¹ for *P. grandifolia*, compared with approximately 2 mm s⁻¹ for *P. aculeata* (7) and *P. grandifolia* (Fig. 1) (all data are expressed here on the basis of the area of both leaf surfaces). Reported maximal net CO₂ uptake rates for these two species have varied from about 3 μmol m⁻² s⁻¹ (19) to 6 μmol m⁻² s⁻¹ (Fig. 1). The responses of leaves of *P. aculeata* (7) and *P. grandifolia* (Fig. 6) to PAR are quite similar, exhibiting 90% of saturation near a PAR of 300 μmol m⁻² s⁻¹. Both of these species are native to tropical woodland or tropical scrub, where consid-

erable shading would be expected, consistent with their saturation at relatively low PAR levels.

The six species of Cactaceae with leaves had essentially all their net shoot CO₂ uptake take place by the leaves and during the daytime, presumably by the C₃ pathway. In contrast, the five species without leaves had all of their net shoot CO₂ uptake at night by the stems using the CAM pathway (Table I). Stems of the leafy species did not make a major contribution to shoot CO₂ uptake by employing the CAM pathway. Indeed, the only leafy cactus that had essentially C₃ leaves on CAM stems, a phenomenon found in certain other plants (6, 12, 22), was *A. subulata* (Fig. 4).

Although no CO₂ uptake occurred at night for the leaves or stems of the three Pereskioideae, leaves of all the Opuntioideae showed some CO₂ uptake during part of the night and stems showed some nocturnal stomatal opening (Figs. 2–5). Thus, although the contribution of this CAM-like behavior to net CO₂ uptake by the leafy cacti was not appreciable, it suggests a wider range of biochemical expression in the Opuntioideae. In this regard, 2-week-old cladodes of *O. ficus-indica* exhibit a daytime stomatal opening pattern consistent with the C₃ pathway, but for mature cladodes both the stomatal opening and the CO₂ uptake patterns are those of the CAM pathway (1). Thus, age and perhaps environmental factors can elicit CAM behavior in Opuntioideae. Indeed, even the two species of *Pereskia* considered here can exhibit CAM-like changes in tissue acidity when subjected to drought, although a net uptake of CO₂ was not observed at night (19). Also, the small daily oscillations of acidity in *Pereskia guamacho* observed under natural conditions in Venezuela are greater in the dry season (5).

The CAM pathway leads to a much higher water-use efficiency (CO₂ fixed/water transpired) than the C₃ pathway (7, 11). In particular, for a given degree of stomatal opening the lower temperatures at night can lead to as much as 10-fold less water loss compared with daytime water loss. Maximal CO₂ uptake rates and the integrals for the appropriate 12 h periods were here similar for the cases of C₃ and CAM behavior; net CO₂ uptake averaged 176 mmol m⁻² during the daytime for the leaves of the three species of Pereskioideae and 141 mmol m⁻² during the night for the four species of Cactoideae (Table I). Thus, the evolutionary shift from leaves using the C₃ pathway in Pereskioideae to stems using the CAM pathway in the more advanced Cactoideae was most likely for water conservation reasons. The Opuntioideae show much greater diversity in CO₂ uptake patterns. In particular, the leaves of all three leafy species showed some CO₂ uptake at night and the stems always made a positive contribution to shoot CO₂ uptake (Figs. 2–5; Table I). Future research should be directed toward understanding the biochemical diversity within the Opuntioideae and to determining the influence of environmental factors on the relative contributions of the C₃ and the CAM pathways to net shoot CO₂ uptake in this subfamily.

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