

Carbon and water balances for young fruits of platyopuntias

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Questions relating to transpired versus retained water for fruits, the xylem versus the phloem as water supplier to the fruits, and the importance of fruit photosynthesis for fruit dry mass gain were examined in the field for 6 species of platyopuntias (*Nopalea cochenillifera*, *Opuntia ficus-indica*, *O. megacantha*, *O. robusta*, *O. streptacantha* and *O. undulata*), cacti with flattened stem segments (cladodes). For plants with fruits midway between floral bud appearance and fruit maturation, transpiration was greater at night for the cladodes, as expected for Crassulacean acid metabolism (CAM) plants, but greater during the daytime for the fruits of all 6 species. Nevertheless, net CO₂ uptake by fruits of these platyopuntias occurred predominantly at night, as ex-

pected for CAM plants. The water potential of the young fruits (average of -0.41 MPa) was higher than that of the cladodes (average of -0.60 MPa), indicating that water entered the fruits via the phloem rather than via the xylem. Solution entry into the fruits via the phloem supplied the water lost by transpiration and allowed for increases in fruit fresh mass (daily transpiration averaged 3.2-fold higher than daily water content increases), while the accumulating solutes were apparently polymerized to account for the higher water potentials of the fruits compared with the cladodes. The phloem thus acts as the sole supplier of water and the main supplier of dry mass (90%) to such young fruits of platyopuntias.

Introduction

Fruits of many species are green during much of their development, suggesting that photosynthesis by the fruits can contribute to their gain in biomass (Jones 1981, Pavel and DeJong 1993). Net CO₂ uptake by young fruits ranges from 3% of that for fully expanded leaves for avocado (*Persea americana*; Whiley et al. 1992) to about 35% for orange (*Citrus sinensis*; Moreshet and Green 1980). Fruits require a supply of water, which generally enters developing organs via the xylem. For tomato (*Lycopersicon esculentum*), the proportion of water entering the fruit via the xylem decreases as the fruits mature (Ho et al. 1987). When developing organs are not photosynthetically self-sufficient, water also enters via the phloem together with solutes. For instance, substantial amounts of water enter the fruits of cotton (*Gossypium hirsutum*) via the phloem (van Iersel et al. 1994). Indeed, the water potential of young cotton fruits can be higher than that of the leaves (Trolinder et al. 1993), so water cannot enter the fruits by flowing energetically downhill in the xylem. A backflow of water can occur in the xylem from the fruits to the stem for apple (*Malus pumila*; Lang 1990) and grape (*Vitis vinifera*; Lang and Thorpe 1989).

The fruits of the prickly pear cactus *Opuntia ficus-indica* remain green until the final stages of maturation, suggesting that they are photosynthetically active. In fact, daily net CO₂ uptake occurs throughout fruit development for *O. ficus-indica* (Inglese et al. 1994). CO₂ uptake by the fruit occurs primarily at night via Crassulacean acid metabolism (CAM), just as for the cladodes (flattened photosynthetic shoot segments) of this platyopuntia (Nobel 1988). However, the phloem apparently supplies most of the dry matter and all of the water requirements for the fruits of *O. ficus-indica* throughout their development (Nobel et al. 1994). It is not known whether this is characteristic of other platyopuntias.

The water and carbon balances for fruits of *O. ficus-indica* have been investigated primarily in the laboratory. Moreover, transpiration of its fruits has not been reported, so the overall water balance is not known, as is also the case for fruits of various other species; therefore, carbon and water relations for the fruits of *O. ficus-indica* were examined in the field. To test the generality of the results, fruits of 4 other platyopuntias were studied as well as those of the closely related *Nopalea cochenillifera* [sometimes called

Opuntia cochenillifera (Britton and Rose 1963, Benson 1982, Scheinvar 1995), although its flower morphology differs from that of opuntias]. Preliminary observations of fruit growth were made in 1998 to determine size criteria for each species so that gas exchange measurements could be made on young green fruits approximately midway between floral bud appearance and fruit maturation, which occurs about 3 months later (Gutterman 1995, Nerd and Mizrahi 1995). During the development of *Opuntia* fruits, often called cactus pears, the flower receptacle that surrounds the inferior ovary becomes the peel of the fruit (Pimienta Barrios 1990, Nerd and Mizrahi 1995). Indeed, the relatively large sizes of the fruits midway through development and the apparent spatial uniformity of their peels facilitated measurements of transpiration and CO₂ uptake. Three questions were addressed: (1) what is the ratio of water transpired to water retained in the developing fruit?; (2) does the phloem or the xylem supply the water?; and (3) how much of the daily dry mass gain is contributed by net CO₂ uptake by the fruits?

Materials and methods

Six species of Cactaceae that had been planted as individual cladodes in August 1990 were examined at the Agricultural Research Station, University of California, Riverside, California. Measurements were made on 5 plants each of *Nopalea cochenillifera* (L.) Salm-Dyck (accession no. 1269 of Texas of A&M University, Kingsville, TX), *Opuntia ficus-indica* (L.) Miller (accession no. 1279), *O. megacantha* Salm-Dyck (accession no. 1292), *O. robusta* Wendland in Pfeiffer (accession no. 1240), *O. streptacantha* Lemaire (accession no. 1248) and *O. undulata* Griffiths (accession no. 1267); all plants were irrigated weekly. Data reported here were obtained in May and June 1999 approximately midway between flower bud appearance and fruit maturation, which occurred 10–14 weeks later for a particular fruit; transpiration and net CO₂ exchange were usually measured simultaneously for a particular species. Preliminary observations in 1998 indicated that at this developmental stage, which occurs 2–4 weeks after the flower petals abscise, the fruits are approximately two-thirds of their final length and one-third of their final fresh mass.

Transpiration per unit surface area was measured approximately every 2 h for fruits over 24-h periods using a LI-1600 steady-state porometer (Li-Cor, Lincoln, NE, USA); similar measurements were made on the underlying cladodes near midday and midnight. The acrylic top of the cuvette was removed to allow placement of the cuvette near the middle of a fruit or near the middle of east-facing surfaces of unshaded, terminal cladodes using a 4-mm-thick foam-rubber gasket with a hole 1.5 cm in diameter to achieve a good seal. Stomatal frequency was determined at similar locations for epidermal peels examined using a BH-2 light microscope (Olympus, Lake Success, NY, USA) with 5 fields of view totaling 8.25 mm² for each sample. The total daily transpiration per fruit was equated to the integrated daily transpiration per unit area times the fruit area, assuming that the fruits were prolate spheroids (formed by the

rotation of an ellipse about its major axis). The surface area of a prolate spheroid equals $0.5\pi d^2 + 0.5\pi d/[\sin^{-1}(1 - d^2/l^2)^{0.5}]/(1 - d^2/l^2)^{0.5}$, where d is the diameter at mid-fruit and l is the fruit length. Such an area of a smooth surface is essentially equivalent to the area basis used for expressing the gas exchange data.

The daily water gain for the same 5 fruits as used for transpiration plus 5 others of similar size was estimated from increases in their length over 8- to 10-day periods encompassing the transpiration measurements using regressions of fruit water mass (fresh mass – dry mass) against fruit length. Length was measured using a vernier caliper (readable to 0.02 mm) aligned with fine indelible ink marks on the two extreme ends of a fruit. For the regression equations, 12 fruits of various lengths were harvested from each species, weighed in the field to obtain fresh mass, sliced, and then dried at 80°C in a forced-draft oven until no further weight change occurred (generally 3 days) to obtain dry mass.

To measure organ water potential, a cork borer 14 mm in diameter was used to sample young fruits and the cladodes on which they occurred at mid-organ near midday; no significant changes in the cladode-to-fruit water potential difference were observed at other times of the day, in part reflecting the succulent nature of both organs. After slicing off the cuticle and epidermis, discs approximately 4-mm-thick were cut with a razor blade and their water potential was determined with an SC-10 thermocouple psychrometer (Decagon Devices, Pullman, WA, USA) after equilibration for 4 h. Such discs contained both outer photosynthetic tissue and inner water-storage tissue, which have experimentally indistinguishable water potentials for both cladodes and fruit (Nobel et al. 1994). For each species, data were obtained within 5 days of gas exchange measurements for fruits of similar size.

The rates of net CO₂ uptake of both fruits and the cladodes on which they occurred were measured approximately every 2 h over 24-h periods with a Li-Cor LI-6200 portable photosynthesis system. The top of the cuvette was replaced with an acrylic plate having a 2-cm cylindrical extension of 1.5 cm internal diameter, whose margin was covered with a foam-rubber gasket to facilitate sealing to organ surfaces. Measurements were made at random locations on the fruits and on the east-facing surfaces of unshaded, terminal cladodes bearing the fruits. Net CO₂ uptake per fruit was converted to a dry mass gain assuming that 1 mole of CO₂ was equivalent to 30 g of dry mass, as for a carbohydrate. The daily dry mass gains of the same fruits as used for gas exchange studies plus 5 others of similar size were estimated from increases in their length over 8- to 10-day periods encompassing the transpiration and net CO₂ uptake measurements using regressions of fruit dry mass against fruit length obtained from 12 fruits of various lengths for each species.

Data were analyzed pairwise using Student's *t*-test.

Results

The young fruits chosen for measurement of gas exchange and water potential for the 6 platyopuntias ranged in mean

Table 1. Morphology for fruits of platyopuntias approximately midway between floral bud appearance and fruit maturation. Length changes were determined for each fruit over an 8- to 10-day period; lengths and diameters are mean values over that period. Data are means \pm SE (n = 5 fruits on different plants for each species for length, diameter, and area and n = 10 fruits for length changes).

Species	Length (cm)	Diameter (cm)	Area (cm ²)	Daily length change (mm)
<i>N. cochenillifera</i>	2.76 \pm 0.13	2.01 \pm 0.05	16.0 \pm 0.9	0.23 \pm 0.02
<i>O. ficus-indica</i>	5.50 \pm 0.24	4.02 \pm 0.11	63.8 \pm 2.8	0.49 \pm 0.05
<i>O. megacantha</i>	5.20 \pm 0.19	3.79 \pm 0.13	57.3 \pm 3.7	0.51 \pm 0.08
<i>O. robusta</i>	4.39 \pm 0.11	4.04 \pm 0.16	54.8 \pm 3.6	0.58 \pm 0.06
<i>O. streptacantha</i>	4.42 \pm 0.19	3.95 \pm 0.10	53.6 \pm 3.3	0.46 \pm 0.03
<i>O. undulata</i>	7.10 \pm 0.12	3.14 \pm 0.06	59.0 \pm 1.6	0.45 \pm 0.04

length from 2.8 cm for *N. cochenillifera* to 7.1 cm for *O. undulata* (Table 1). Surface areas were calculated assuming that the fruits were prolate spheroids and using the measured lengths and diameters. The mean daily changes in fruit length, which ranged from 0.23 mm for *N. cochenillifera* to 0.58 mm for *O. robusta* (Table 1), together with regression equations of length versus fresh mass or versus dry mass were used to determine daily water and dry mass gains for the fruits.

Transpiration by the young fruits tended to increase during the afternoon, to decrease during the night, and to increase again during the morning for all 6 species (Fig. 1). Maximal transpiration rates for the fruits averaged 414 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and minimal values averaged 114 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The daily transpiration per unit fruit surface area, obtained by integrating the instantaneous values over 24 h, ranged from 16 mol $\text{m}^{-2} \text{day}^{-1}$ for *O. streptacantha* to 30 mol $\text{m}^{-2} \text{day}^{-1}$ for *O. undulata* (Table 2). The total daily transpiration per fruit, obtained by multiplying the transpi-

ration per unit area by the area per fruit (Table 1), ranged from 0.5 g day^{-1} for *N. cochenillifera* to 3.2 g day^{-1} for *O. undulata* (Table 2). Based on the changes in fruit length, the daily gain in water per fruit ranged from 0.1 g day^{-1} for *N. cochenillifera* to 0.9 g day^{-1} for *O. megacantha* and *O. robusta* (Table 2). Daily transpiration ranged from two to sixfold greater and averaged 3.2-fold greater than the daily gain in water content by the fruits.

Contrary to the case for the fruits (Fig. 1), transpiration was higher at night than during the daytime for the cladodes of all 6 species (Table 3). The water vapor (stomatal) conductance was much higher for the cladodes at midnight, averaging 140 $\text{mmol m}^{-2} \text{s}^{-1}$, than at midday, when it averaged 12 $\text{mmol m}^{-2} \text{s}^{-1}$ ($P < 0.01$; Table 3). On the other hand, the day/night difference in water vapor conductance for the fruits was not as great, averaging 37 $\text{mmol m}^{-2} \text{s}^{-1}$ at midnight and 11 $\text{mmol m}^{-2} \text{s}^{-1}$ at midday for the 6 species ($P < 0.01$; Table 3). The stomatal frequency was less for the young fruits than for the cladodes on which

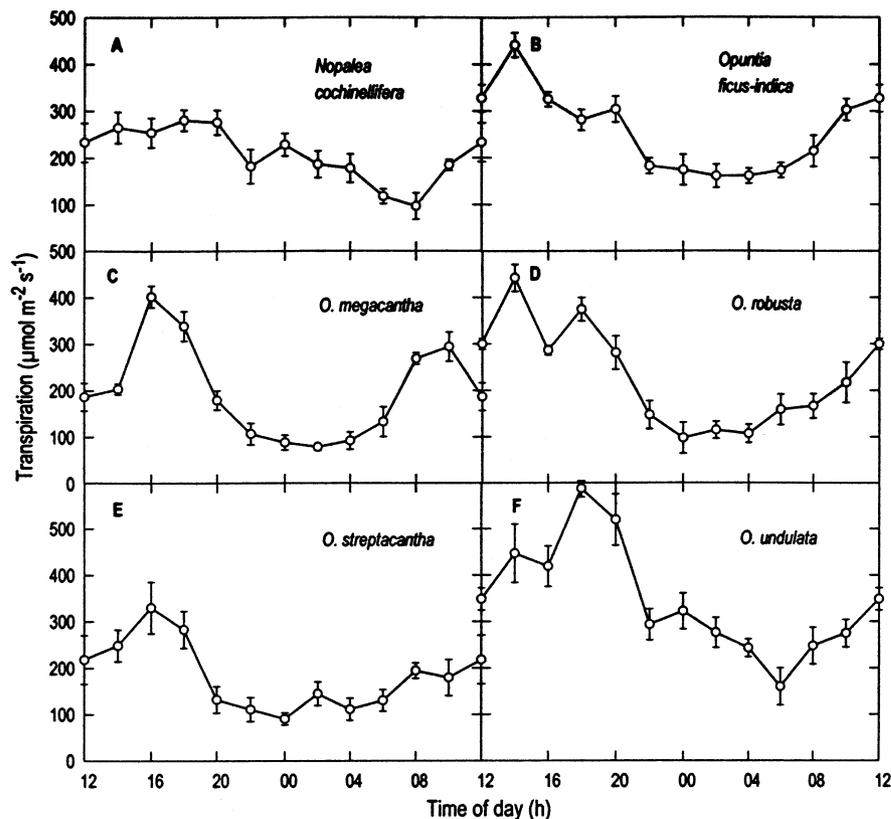


Fig. 1. Transpiration for young fruits of platyopuntias: (A) *N. cochenillifera*, (B) *O. ficus-indica*, (C) *O. megacantha*, (D) *O. robusta*, (E) *O. streptacantha* and (F) *O. undulata*. Daytime maximum air temperatures and relative humidities on clear days averaged 28.9°C and 28%, respectively, and night-time minimum ones averaged 13.2°C and 77%, respectively. Data are means \pm SE (n = 5 fruits on different plants for each species).

Table 2. Daily water balance for young fruits of platyopuntias. Data for transpiration are means \pm SE (n = 5 fruits on different plants for each species). Daily water gain was based on regressions involving changes in fruit length over 8- to 10-day periods (n = 10 fruits, Table 1).

Species	Daily transpiration per unit area (mol m ⁻² day ⁻¹)	Daily transpiration per fruit (g day ⁻¹)	Daily water gain per fruit (g day ⁻¹)
<i>N. cochenillifera</i>	17.9 \pm 1.8	0.52 \pm 0.05	0.12
<i>O. ficus-indica</i>	22.1 \pm 0.3	2.56 \pm 0.03	0.82
<i>O. megacantha</i>	17.1 \pm 1.2	1.78 \pm 0.12	0.89
<i>O. robusta</i>	19.6 \pm 1.1	1.95 \pm 0.11	0.93
<i>O. streptacantha</i>	15.6 \pm 0.4	1.53 \pm 0.04	0.72
<i>O. undulata</i>	29.8 \pm 1.2	3.20 \pm 0.13	0.56

Table 3. Transpiration and water vapor conductances for cladodes and water vapor conductances for young fruits of platyopuntias during the day and the night. Measurements were made within 1 h of midday or midnight for terminal cladodes or young fruits; data are means \pm SE (n = 5 plants). Air temperature and relative humidity averaged 28.0°C and 32% near midday and 15.2°C and 73% near midnight; cladode and fruit temperatures generally were within 1.0°C of air temperature.

Species	Cladode transpiration (μmol m ⁻² s ⁻¹)		Cladode water vapor conductance (mmol m ⁻² s ⁻¹)		Fruit water vapor conductance (mmol m ⁻² s ⁻¹)	
	12:00 h	0:00 h	12:00 h	0:00 h	12:00 h	0:00 h
<i>N. cochenillifera</i>	423 \pm 7	1022 \pm 170	16.7 \pm 0.3	224 \pm 37	9.2 \pm 1.6	50.0 \pm 5.3
<i>O. ficus-indica</i>	259 \pm 25	647 \pm 134	10.2 \pm 1.0	142 \pm 29	12.9 \pm 1.1	38.1 \pm 7.2
<i>O. megacantha</i>	253 \pm 12	446 \pm 34	10.0 \pm 0.5	78 \pm 7	7.4 \pm 1.2	19.3 \pm 3.5
<i>O. robusta</i>	234 \pm 16	428 \pm 24	9.3 \pm 0.7	79 \pm 5	11.8 \pm 0.5	21.4 \pm 7.3
<i>O. streptacantha</i>	208 \pm 15	628 \pm 155	8.3 \pm 0.6	138 \pm 34	8.6 \pm 1.5	19.9 \pm 2.3
<i>O. undulata</i>	443 \pm 36	839 \pm 65	17.5 \pm 1.4	184 \pm 14	13.7 \pm 0.9	70.6 \pm 9.6

they occurred ($P < 0.001$, except $P < 0.01$ for *O. robusta*; Table 4); the stomatal frequency averaged 51 mm⁻² for the young fruits and 105 mm⁻² for the cladodes.

The water potential of the cladodes was lower than that of the fruits produced on them for all 6 species ($P < 0.01$; Table 5). The cladode water potential, which did not differ significantly among the species, averaged -0.60 MPa. The water potential of the fruits, which also did not differ significantly among the species, averaged -0.41 MPa (Table 5).

The daily patterns of net CO₂ uptake per unit area for the young fruits of all 6 species were characteristic of those of leaves or stems of CAM plants, with nearly all net CO₂ uptake occurring at night (Fig. 2). The lowest maximal rate of nocturnal net CO₂ uptake was 2.9 μmol m⁻² s⁻¹ for *N. cochenillifera* and the highest rate was 6.3 μmol m⁻² s⁻¹ for *O. robusta*. For 4 cladodes of each of the 6 species, mean rates of nocturnal net CO₂ uptake per unit area obtained near midnight averaged 2.7-fold higher than that for its

fruits; in particular, the cladode rates averaged 7.7 μmol m⁻² s⁻¹ for *N. cochenillifera*, 12.3 for *O. ficus-indica*, 11.2 for *O. megacantha*, 11.9 for *O. robusta*, 15.2 for *O. streptacantha* and 14.1 μmol m⁻² s⁻¹ for *O. undulata*. The daily net CO₂ uptake per unit area of the fruits (obtained by integrating values measured every 2 h) ranged from 85 mmol m⁻² day⁻¹ for *O. megacantha* to 174 mmol m⁻² day⁻¹ for *O. undulata* (Table 6). For two cladodes of each of the 6 species, the daily net CO₂ uptake over 24 h per unit area averaged 2.6-fold higher than for the fruits. After multiplying the daily net CO₂ uptake per unit area by the surface area per fruit (Table 1) and converting the net CO₂ uptake to its dry mass equivalent, the daily dry mass gain from CO₂ uptake ranged from 5 mg day⁻¹ for *N. cochenillifera* to 31 mg day⁻¹ for *O. undulata* (Table 6). Such dry mass gains averaged only 10% of the observed daily dry mass gains for the young fruits of the 6 species, ranging from 6% for *N. cochenillifera* to 14% for *O. undulata* (Table 6).

Table 4. Stomatal frequencies for cladodes and young fruits of platyopuntias. Data are means \pm SE (n = 5 plants).

Species	Stomatal frequency (mm ⁻²)	
	Cladodes	Young fruits
<i>N. cochenillifera</i>	85 \pm 4	43 \pm 3
<i>O. ficus-indica</i>	84 \pm 3	28 \pm 3
<i>O. megacantha</i>	86 \pm 3	44 \pm 4
<i>O. robusta</i>	113 \pm 2	88 \pm 7
<i>O. streptacantha</i>	108 \pm 3	44 \pm 5
<i>O. undulata</i>	154 \pm 13	60 \pm 3

Table 5. Water potentials for cladodes and young fruits of platyopuntias. Data are means \pm SE (n = 5 fruit-cladode pairs on different plants for each species).

Species	Tissue water potential (MPa)	
	Cladodes	Young fruits
<i>N. cochenillifera</i>	-0.60 ± 0.02	-0.44 ± 0.02
<i>O. ficus-indica</i>	-0.63 ± 0.02	-0.39 ± 0.03
<i>O. megacantha</i>	-0.56 ± 0.03	-0.40 ± 0.02
<i>O. robusta</i>	-0.62 ± 0.03	-0.42 ± 0.02
<i>O. streptacantha</i>	-0.61 ± 0.03	-0.42 ± 0.02
<i>O. undulata</i>	-0.57 ± 0.02	-0.39 ± 0.04

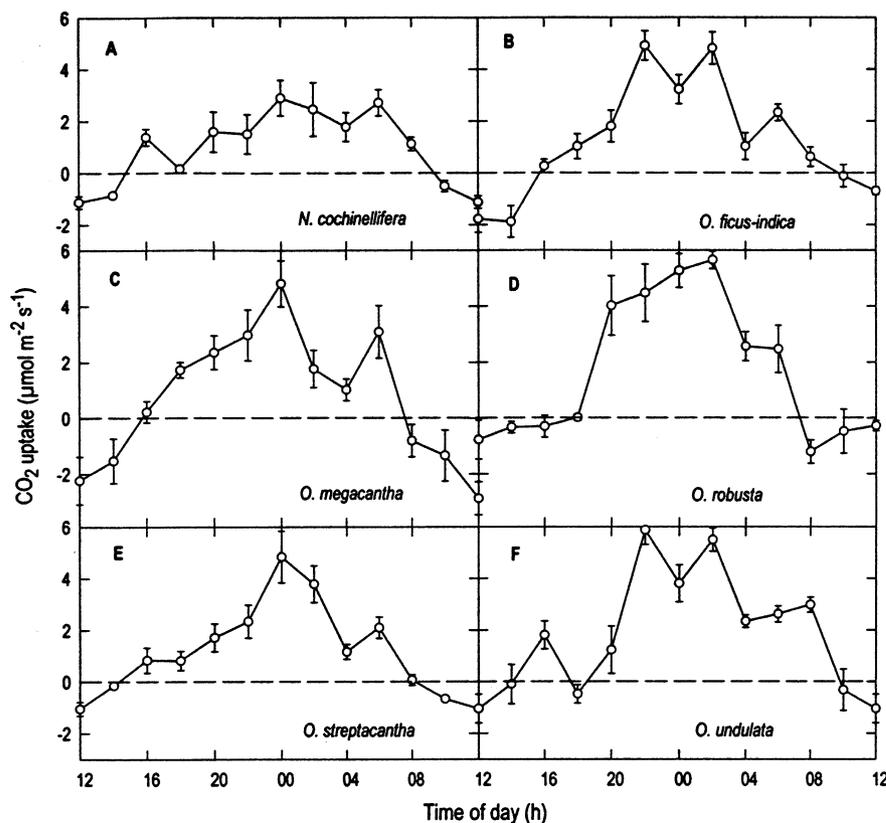


Fig. 2. Net CO₂ uptake for young fruits of platyopuntias: (A) *N. cochenillifera*, (B) *O. ficus-indica*, (C) *O. megacantha*, (D) *O. robusta*, (E) *O. streptacantha* and (F) *O. undulata*. Data were generally obtained simultaneously with those in Fig. 1 and are presented as means \pm SE (n = 5 fruits on different plants for each species).

Discussion

Although flower buds of *O. ficus-indica* take up CO₂ mainly during the daytime in the C₃ mode (Acevedo et al. 1983), fruits of various ages take up CO₂ mainly at night in the CAM mode (Inglese et al. 1994), as was observed here for young fruits midway between floral bud appearance and fruit maturation. Indeed, young fruits of the 4 other species of *Opuntia* and of *N. cochenillifera* also took up CO₂ mainly at night. The fruits considered were green and approximately two-thirds the length and one-third the mass of mature fruits. The total daily net CO₂ uptake per unit area by the fruits was about 38% of that of the cladodes on which they occurred, which is higher than for studies comparing fruits and leaves of C₃ species (Moreshet and Green 1980, Whiley et al. 1992). For the 6 species of platyopuntias considered, daily net CO₂ uptake by the young fruits accounted for an average of 10% of the daily dry mass gain of

the fruits. At a similar stage, young green fruits of peach (*Prunus persica*) take up 15% of the daily carbohydrate requirement (Pavel and DeJong 1993); averaged over the entire growing season, photosynthesis of exposed peach fruits accounts for 9% of their total growth and maintenance carbohydrate requirements.

Transpiration by the young platyopuntia fruits was higher during the daytime than at night. Such a pattern was a consequence of the higher fruit temperatures and hence greater driving forces for water loss during the daytime. In particular, the drop in water vapor mole fraction from the fruits to the air averaged 0.0253 at midday and 0.0046 at midnight. On the other hand, the water vapor conductance at midnight was about threefold higher than at midday for the young fruits compared with 12-fold higher for the cladodes. The magnitude of the water vapor conductance near midday was similar for both cladodes and young fruits,

Table 6. Daily carbon balance for young fruits of platyopuntias. Data are means \pm SE (n = 5 fruits on different plants for each species). Total daily dry mass gain was based on regressions involving changes in fruit length over 8- to 10-day periods (n = 10 fruits, Table 1).

Species	Daily net CO ₂ uptake per unit area (mmol m ⁻² day ⁻¹)	Daily dry mass gain from net CO ₂ uptake per fruit (mg day ⁻¹)	Total daily dry mass gain per fruit (mg day ⁻¹)
<i>N. cochenillifera</i>	95 \pm 19	4.5 \pm 0.9	71
<i>O. ficus-indica</i>	121 \pm 15	23.1 \pm 2.9	212
<i>O. megacantha</i>	85 \pm 28	14.4 \pm 4.8	164
<i>O. robusta</i>	155 \pm 15	25.4 \pm 2.5	260
<i>O. streptacantha</i>	114 \pm 13	18.3 \pm 2.0	221
<i>O. undulata</i>	174 \pm 14	30.8 \pm 2.5	224

Table 7. Estimated daily water and carbon supplied by the phloem for young fruits of platyopuntias. The daily water supplied by the phloem was the daily transpiration plus the daily water gain based on changes in fruit length (Table 2), ignoring water loss from the fruit to the underlying cladode by the xylem; the daily dry mass supplied by the phloem was the total daily dry mass gain based on changes in fruit length minus the dry mass gain from net CO₂ uptake (Table 4). The apparent percent dry mass in the phloem represents the dry mass supplied daily by the phloem divided by the water plus dry mass supplied daily.

Species	Daily water supplied by phloem per fruit (g day ⁻¹)	Daily dry mass supplied by phloem per fruit (mg day ⁻¹)	Apparent phloem solution dry mass (% of total)
<i>N. cochenillifera</i>	0.64	66	9.4
<i>O. ficus-indica</i>	3.38	189	5.3
<i>O. megacantha</i>	2.67	150	5.3
<i>O. robusta</i>	2.88	235	7.5
<i>O. streptacantha</i>	2.25	203	8.3
<i>O. undulata</i>	3.76	193	4.9

so the four-fold greater increase in water vapor conductance at night by the cladodes reflected their twofold greater stomatal frequency and apparently a twofold greater individual stomatal area at night than for the stomata in young fruits. In any case, the daily transpiration by the young fruits of all 6 species was greater than their daily net gain in water. Hence, 67–85% of the water imported into the fruits of the 6 species of platyopuntia was transpired compared with only 10–20% for tomato fruits (Araki et al., 1997). Nevertheless, the rates of transpiration and maximal water vapor conductances of the fruits of the platyopuntias were similar to values for avocado (Blanke and Whiley 1995), strawberry (*Fragaria* spp.) and tomato (Shirazi and Cameron 1993).

The water potentials of the young fruits were substantially higher than the water potentials of the underlying cladodes for all 6 species of platyopuntias. Thus water could not flow energetically downhill from the underlying cladodes to the fruits, so the xylem is not the supplier of water for the developing fruits, consistent with previous conclusions for *O. ficus-indica* under laboratory conditions (Nobel et al. 1994). For young fruits of comparable ages and sizes, the water potential difference between the fruits and the cladodes of *O. ficus-indica* was 0.17 MPa in the laboratory and somewhat greater at 0.24 MPa in the field. Besides the case for *O. ficus-indica*, the phloem must also supply water for the developing fruits of *N. cochenillifera*, *O. megacantha*, *O. robusta*, *O. streptacantha* and *O. undulata*, just as for fruits of apple (Lang 1990, Mills et al. 1997), Asian pear (*Pyrus serotina*; Behboudian et al. 1994), avocado (Blanke and Whiley 1995), cotton (Trolinder et al. 1993, van Iersel et al. 1994), grape (Lang and Thorpe 1989) and tomato (Ho et al. 1987). Perhaps the lower degree of stomatal opening for the young fruits compared with the cladodes reflects the more efficient supplying of soil water to the cladodes via the xylem compared with the supplying of shoot water to the young fruits via the phloem. For instance, the mean flow rate along the xylem generally is about sixfold greater than along the phloem (Nobel 1999).

Based on the observed water and carbon balances for the developing fruits, dry mass characteristics of the solution apparently supplied by the phloem can be calculated (Table 7). For the 6 species, the phloem apparently supplied 0.64–3.76 g of water per day and 66–235 mg of dry mass per day. This is consistent with a percentage dry

mass for the phloem solution of 4.9–9.4% for the 6 species, or an average of 6.8% (Table 7). Using severed stylets of a scale insect (*Dactylopius opuntiae*), phloem sap has been collected from terminal cladodes of *O. ficus-indica* (Wang and Nobel 1995, Wang et al. 1997). This solution has osmotic pressures of 0.90–0.98 MPa, osmolalities averaging 340 mOsm kg⁻¹, and a mean percentage dry mass content of 7.6%, which is approximately one-third as concentrated as the phloem sap of various other species (Hayashi and Chino 1990, Riens et al. 1991, Weiner et al. 1991). Thus the estimated daily requirement of dry mass and water by the young developing fruits of the 6 species of platyopuntias, about 7% (Table 7), is consistent with the solution that can be delivered by the phloem for the most studied platyopuntia, *O. ficus-indica*. Indeed, the relative diluteness of the phloem solution in *O. ficus-indica* helps supply water for fruit transpiration, whose daily value exceeded water retention in the fruits of all 6 species of platyopuntias but which is not the case for tomato fruits (Araki et al. 1997).

In conclusion, the phloem is the main supplier of dry mass and the sole supplier of water for the young fruits of 6 species of platyopuntias midway between floral bud appearance and fruit maturation. Most of the water entering the fruits at that time is lost by transpiration, suggesting a substantial build-up of solutes in the young fruits. Such solutes are presumably polymerized to form mucilage, proteins and starch so that the fruit water potential can remain higher than that of the underlying cladodes. For instance, 21% of the osmolality of the phloem solution in *O. ficus-indica* is due to amino acids and 56% is due to sucrose (Wang and Nobel 1995), both of which can be converted to polymers. The eventual degradation of certain accumulating polymers can cause an increase in sugars during the final stages of fruit ripening, leading to the observed increase in pulp sweetness (Cantwell 1995). Studies of the transpiration of the fruits together with their water potentials relative to the underlying cladode and daily dry mass gains indicate that the phloem can be the main supplier of both water and solutes to developing fruits for 6 species of platyopuntia and probably many other species.

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References

- Acevedo E, Badilla I, Nobel PS (1983) Water relations, diurnal acidity changes, and productivity of a cultivated cactus, *Opuntia ficus-indica*. *Plant Physiol* 72: 775–780
- Araki T, Kitano M, Eguchi H (1997) Respiration, sap flux, water balance and expansive growth in tomato fruit. *Biotronics* 26: 95–102
- Behboudian MH, Lawes GS, Griffiths KM (1994) The influence of water deficit on water relations, photosynthesis and fruit growth in Asian pear (*Pyrus serotina* Rehd.). *Sci Hortic* 60: 89–99
- Benson L (1982) The Cacti of the United States and Canada. Stanford University Press, Palo Alto, CA, pp 377–383. ISBN 0-8047-0863-0
- Blanke MM, Whaley AW (1995) Bioenergetics, respiration cost and water relations of developing avocado fruit. *J Plant Physiol* 145: 87–92
- Britton NL, Rose JN (1963) The Cactaceae: Descriptions and Illustrations of Plants of the Cactus Family, Vol. I. Dover, New York, NY, pp 33–39. ISBN 0-486-21191-6
- Cantwell M (1995) Post-harvest management of fruits and vegetable stems. In: Barbera G, Inglese P, Pimienta-Barrios E (eds) *Agro-Ecology, Cultivation and Uses of Cactus Pear*. FAO, Rome, pp 120–136. ISBN 92-5-103735-3
- Gutterman Y (1995) Flower and fruit developmental stages of the xerophyte *Opuntia ficus-indica*. *Isr J Plant Sci* 43: 271–280
- Hayashi H, Chino M (1990) Chemical composition of phloem sap from the uppermost internode of the rice plant. *Plant Cell Physiol* 31: 247–251
- Ho LC, Grange RI, Picken AJ (1987) An analysis of the accumulation of water and dry matter in tomato fruit. *Plant Cell Environ* 10: 157–162
- Inglese P, Israel AA, Nobel PS (1994) Growth and CO₂ uptake for cladodes and fruit of the Crassulacean acid metabolism species *Opuntia ficus-indica* during fruit development. *Physiol Plant* 91: 708–714
- Jones HG (1981) Carbon dioxide exchange of developing apple (*Malus pumila* Mill.) fruits. *J Exp Bot* 131: 1203–1210
- Lang A, Thorpe MR (1989) Xylem, phloem and transpiration flows in a grape: Application of a technique for measuring the volume of attached fruits to high resolution using Archimedes' principle. *J Exp Bot* 40: 1069–1078
- Lang A (1990) Xylem, phloem and transpiration flows in developing apple fruits. *J Exp Bot* 41: 645–651
- Mills TM, Behboudian MH, Clothier BE (1997) The diurnal and seasonal water relations, and composition, of 'Braeburn' apple fruit under reduced plant water status. *Plant Sci* 126: 145–154
- Moreshet S, Green GC (1980) Photosynthesis and diffusion conductance of the Valencia orange fruit under field conditions. *J Exp Bot* 120: 15–27
- Nerd A, Mizrahi Y (1995) Reproductive biology. In: Barbera G, Inglese P, Pimienta-Barrios E (eds) *Agro-Ecology, Cultivation and Uses of Cactus Pear*. FAO, Rome, pp 49–57. ISBN 92-5-103735-3
- Nobel PS (1988) *Environmental Biology of Agaves and Cacti*. Cambridge University Press, New York, NY, pp 12–15. ISBN 0-521-34322-4
- Nobel PS (1999) *Physicochemical and Environmental Plant Physiology*, 2nd Ed. Academic Press, San Diego, CA, pp 373–384. ISBN 0-12-520025-0
- Nobel PS, Andrade JL, Wang N, North GB (1994) Water potentials for developing cladodes and fruits of a succulent plant, including xylem-versus-phloem implications for water movement. *J Exp Bot* 45: 1801–1807
- Pavel EW, DeJong TM (1993) Estimating the photosynthetic contribution of developing peach (*Prunus persica*) fruits to their growth and maintenance carbohydrate requirements. *Physiol Plant* 88: 331–338
- Pimienta Barrios E (1990) El Nopal Tunero. Universidad de Guadalajara, Guadalajara, Jalisco, pp 55–66. ISBN 968-895-140-4
- Riens B, Lohaus G, Heineke D, Heldt HW (1991) Amino acid and sucrose content determined in the cytosolic, chloroplastic, and vacuolar compartments and in the phloem sap of spinach leaves. *Plant Physiol* 97: 227–233
- Scheinvar L (1995) Taxonomy of utilized opuntias. In: Barbera G, Inglese P, Pimienta-Barrios E (eds) *Agro-Ecology, Cultivation and Uses of Cactus Pear*. FAO, Rome, pp 20–27. ISBN 92-5-103735-3
- Shirazi A, Cameron AC (1993) Measuring transpiration rates of tomato and other detached fruit. *HortScience* 28: 1035–1038
- Trolinder NL, McMichael BL, Upchurch DR (1993) Water relations of cotton flower petals and fruit. *Plant Cell Environ* 16: 755–760
- van Iersel MW, Oosterhuis DM, Harris WM (1994) Apoplastic water flow to cotton leaves and fruits during development. *J Exp Bot* 45: 163–167
- Wang N, Nobel PS (1995) Phloem exudate collected via scale insect stylets for the CAM species *Opuntia ficus-indica* under current and doubled CO₂ concentrations. *Ann Bot* 75: 525–532
- Wang N, Zhang H, Nobel PS (1997) Phloem-xylem water flow in developing cladodes of *Opuntia ficus-indica* during sink-to-source transition. *J Exp Bot* 48: 675–682
- Weiner H, Blechschmidt-Schneider S, Mohme H, Eschrich W, Heldt HW (1991) Phloem transport of amino acids. Comparison of amino acid contents of maize leaves and of the sieve tube exudate. *Plant Physiol Biochem* 29: 19–23
- Whaley AW, Schaffer B, Lara SP (1992) Carbon dioxide exchange of developing avocado (*Persea americana* Mill.) fruit. *Tree Physiol* 11: 85–94