Seasonal Reproductive and Vegetative Growth Patterns and Resource Allocation during Cactus Pear Fruit Growth

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Abstract. Flowers and stems (cladodes) of cactus pear [*Opuntia ficus-indica* (L.) Mill.] appear simultaneously in spring, and a second vegetative and reproductive flush can be obtained in early summer by completely removing flowers and cladodes of the spring flush at bloom time. The seasonal growth patterns of cactus pear fruits and cladodes were examined in terms of dry-weight accumulation and cladode extension (surface area) to determine if cladodes are competitive sinks during fruit development. Thermal time was calculated in terms of growing degree hours (GDH) accumulated from bud burst until fruit harvest. Fruits of the spring flush had a 25% lower dry weight and a shorter development period than the summer flush fruits, and, particularly, a shorter duration and a lower growth rate at the stage when most of the core development occurred. The duration of the fruit development period was better explained in terms of thermal rather than chronological time. The number of days required to reach commercial harvest maturity changed with the time of bud burst, but the thermal time (40×10^3 GDH) did not. Newly developing cladodes may become competitive sinks for resource allocation during most of fruit growth, as indicated by the cladode's higher absolute growth rate, and the fruit had the highest growth rate during the final swell of the core, corresponding to a consistent reduction in cladode growth rate. Cladode surface area extension in the first flush ceased at the time of summer fruit harvest (20 Aug.), while cladodes continued to increase in dry weight and thickness until the end of the growing season (November), and, eventually, during winter. The growth of fruit and cladodes of the summer flush occurred simultaneously over the course of the season; the cladodes had a similar surface area and a lower (25%) dry-weight accumulation and thickness than did first flush cladodes. The proportion of annual aboveground dry matter allocated to the fruits was 35% for the spring flush and 46% for the summer flush, being similar to harvest increment values reported for other fruit crops, such as peach [*Prunus persica* (L.) Batsch.]. Summer cladode pruning and fruit thinning should be accomplished early in the season to avoid resource-limited growth conditions that could reduce fruit and cladode growth potential.

Cactus pear is a crassulacean acid metabolism (CAM) species that is cultivated worldwide for fruit, forage, and vegetable (*nopalitos*) production (Barbera et al., 1995). A mature cactus pear tree annually generates fruits and flattened stem segments known as cladodes at a 4:1 ratio (Barbera and Inglese, 1993). Flowers and cladodes appear simultaneously in spring, the flowers occurring mostly at the crown edge of 1-year-old terminal cladodes, with the new cladodes usually developing on 2-year-old or even older cladodes (Inglese et al., 1994). A summer flush of both flowers and cladodes can be obtained in early summer by

completely removing the flowers and the cladodes of the spring flush at bloom time. Fruits coming from this summer flush reach commercial maturity in October to November, 2 to 3 months after the main summer fruit crop (Barbera et al., 1991).

Fruit and cladode growth have always been described and studied separately (Barbera et al., 1992; Luo and Nobel, 1993; North et al., 1995). Fruit growth follows a double sigmoid pattern in terms of fresh-weight accumulation, with three distinct stages of growth, viz.: a) a pronounced gain in dry weight for the peel and the seeds (Stage I); b) seed hardening with a lag period of growth in fresh-weight increase (Stage II); and c) the final swell of the core and the accumulation of sugars (Stage III) (Barbera et al., 1992). Cladodes are strong sinks during the sigmoidal growth period that occurs during the first 4 to 5 weeks of development. At this stage they switch to linear growth in terms of dry-weight accumulation, and change from being sinks to sources for carbohydrates (Luo and Nobel, 1993).

Limitations to fruit growth include crop load (Inglese et al., 1995), poor pollination

(Barbera et al., 1994), cladode light environment (La Mantia et al., 1997), and water deficit (Barbera, 1984). Moreover, the sink demand to support the growth of the fruit and the newly initiated daughter cladodes involves a substantial flow of stored carbohydrates from basal cladodes (Inglese et al., 1994; Luo and Nobel, 1993). In fact, when more than six fruits develop on a 1-year-old fruiting cladode, an extensive import of assimilates occurs, particularly during Stage III of fruit growth (Inglese et al., 1994). Competition for assimilates may then arise as a result of the competitive growth between newly initiated cladodes and fruit. The presence of developing cladodes may inhibit flower initiation (Inglese et al., 1994), whereas a high fruit load may reduce the initiation of new cladodes, eventually resulting in an alternate bearing behavior (Barbera et al., 1991). Moreover, high planting densities lead to an extremely high accumulation of dry matter in vegetative growth, but reduce allocation of resources to the fruit (García de Cortázar and Nobel, 1992).

Despite current horticultural practices, such as fruit thinning or summer pruning of newly developing cladodes (Barbera and Inglese, 1993), little is known about the priorities for the seasonal partitioning of assimilates among vegetative and reproductive sinks of cactus pear. In this study we examined the seasonal patterns of vegetative vs. reproductive growth in terms of stem (cladode) extension and dry-weight accumulation, and fruit dry-weight accumulation over the season. Since fruit and cladode growth of the spring flush coincide for only a limited period, whereas fruit and vegetative growth are simultaneous throughout the summer flush, this study addressed the questions: a) are vegetative and reproductive growth competitive during the cactus pear fruit development period; and b) does the seasonal pattern of this competition differ in relation to fruit ripening time?

Materials and Methods

The study site was located in a commercial orchard on sandy-loam (68% sand, 25% clay, 7% silt) soil (Mediterranean red soils) at S. Margherita Belice, Italy (lat. 37°44'N). The orchard consisted of 9-year-old 'Gialla' cactus pear trees spaced 6 × 6 m apart and trained to an open vase. Trees received routine horticultural care suitable for commercial fruit production in Italy, including fertilization, irrigation, and weed control. Trees were annually supplied with N, P, and K at 100, 60, and 120 kg·ha⁻¹, respectively, distributed in spring and during early summer, and were irrigated at bloom and again 15, 30, and 45 d after bloom, with a total of 70 mm of water through a localized irrigation system. Weeds were removed in late spring by low tillage. No rains occurred during the fruit development period. Rainfall during the previous winter (Nov. 1992–Apr. 1993) was 350 mm.

The experiment was a randomized complete-block design with 10 single-trees plots. Five trees were used to measure growth of fruits and cladodes of the spring flush. The

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spring flush of flowers and cladodes was removed from the other five trees at full bloom (6 June 1993), and, as a consequence, a summer flush of flowers and cladodes was initiated by the end of June, and summer bloom occurred during the third week of July (14–21 July).

Crop load was adjusted to six fruits per cladode as in commercial plantations (Inglese et al., 1995) to avoid the effect of inter-fruit competition, maximize fruit size (Inglese et al., 1994), and to keep the fruit to cladode ratio constant in the two fruiting cycles.

Fifty individual cladodes were selected both in the spring and the summer flush. Thickness, width, and length of these cladodes were measured weekly from bud burst until the appearance of the new cladodes the following year. Surface area of a cladode (cm^2), was calculated from $SA = 7.604 + 1.462D^2 + 0.358L^2$ ($R^2 = 0.997$), where SA is the surface area (both sides) of the cladode, D is the cladode width in centimeters, and L is cladode length in centimeters (Barbera et al., 1993). Cladode dry-weight accumulation during growth was estimated from samples removed every second week with a cork borer 1.0 cm in diameter and then dried to constant weight in a forced-air oven at 70 °C. All cladodes were detached after fruit harvest and their fresh and dry weights recorded.

Fruit width was measured weekly from flowering until harvest time on 50 fruit for the spring and 50 fruit for the summer flush. Fruit fresh weight during growth was calculated from the regression $FW = 12.0 + 0.352D + 5.07D^2$ and dry weight from the regression $DW = 11.4 - 8.29D + 1.73 D^2$, where D is the maximum diameter of the fruit in centimeters (Inglese et al., 1994).

Fruit were harvested at peel color break (Barbera et al., 1992) and fruit yield was determined in terms of fruit number and total fresh weight per tree. Fifty fruit per flush were then dried to constant weight in a forced-air oven at 65 °C to determine their individual dry weights.

The proportion of annual aboveground dry matter (fruit + newly initiated cladodes + seasonal dry-weight gain of 1-year-old mother cladodes) allocated to the fruit (Harvest Increment = HI), was calculated, at fruit harvest, from the dry weights of the fruit and the newly developed cladodes. To estimate the seasonal dry-matter accumulation into the 1-year-old cladodes, the dry weight (g) of a cladode was determined early in spring and at the end of the growing season, from the equation $0.477 \times \text{length (cm)} \times \text{width (cm)} \times \text{thickness (cm)}$ ($r^2 = 0.93$) (Luo and Nobel, 1993).

Daily maximum and minimum temperatures were measured throughout the year, and hourly temperatures were calculated from the Linvill (1990) equation. Growing degree hours (GDH) were calculated for the period from bud burst to fruit harvest, using ASYMCUR (Anderson et al., 1986). The optimum temperature was set at 25 °C and the critical temperature at 35 °C; the former allows the highest rate of nocturnal net CO_2 uptake, while the latter causes a significant reduction in

cladode assimilation rate (Nobel and Hartsock, 1984). To allow the calculation of GDH accumulated from one stage to another, the time course of spring burst, bloom, and fruit harvest was monitored. Spring bud burst refers to the time when 5% of flowers and newly initiated cladodes had appeared at the crown edge of the cladode, the beginning of flowering when 10% of the flowers were open, and the beginning of fruit harvest when 10% of the fruit had reached the peel color break stage.

Growth data from the spring and the summer flush were compared with Student's *t*-test, when appropriate, and means $\pm$ SE are reported for each growth sample.

Results

The spring and summer flushes were equally fruitful in terms of fruiting cladodes and fruit number. The numbers of newly developing cladodes were significantly higher in the spring than in the summer flush (Table 1).

Flower and vegetative buds began to burst by the first week of May, when 26×10^3 GDH had accumulated since 15 Feb., when 300 chilling units had accumulated. Flowers of the spring flush bloomed at the beginning of June at 38×10^3 GDH (Fig. 1), those of the summer flush on 15 July. The patterns of fresh and dry-weight accumulation for fruit were similar for the spring and the summer flushes (Fig. 2 A

and B). However, the fruits of the summer flush accumulated 25% less dry weight and 15% less fresh weight than those of the spring flush (Table 1). The duration of the fruit development period was 75 d for the spring flush and 90 d for the summer flush (Fig. 2A). No differences between flushes occurred in the duration of Stage I (37 ± 3 d), and Stage II (10 ± 0 d), or in the fresh and dry weight of the fruits at the end of the first two growth stages. The length of Stage III was significantly ($P \leq 0.01$) longer for the fruits of the summer flush, while those of the spring flush increased rapidly in fresh (Fig. 2A) and dry weight during the last 15 d of the fruit development period (Fig. 2B). Fruits needed $\approx 40 \times 10^3$ GDH to complete their development, from bud burst to harvest, regardless of the flowering period (Fig. 1).

Cladodes of the spring flush began their development at the beginning of May (12 May) while those of the summer flush started at the end of June (28 June). Despite the large difference (≈ 45 d) in the duration of the period from bud burst to the end of the growing season (Nov. 1993), cladodes of both flushes had the same surface area (Fig. 3), but those of the summer flush accumulated 25% less dry weight than did those of the spring flush (Fig. 2B and C). Surface area development and dry-weight accumulation of the cladode followed a similar pattern both in the spring and in the

Table 1. Dry weights (g) of fruits and cladodes of *O. ficus-indica* during the spring and the summer growth flushes.

Fruits			Current season cladodes			1-year-old cladodes ²		
n	Mean	Total	n	Mean	Total	n	Mean	Total
<i>Spring flush</i>								
270	11.0	2970	138	38.5	5313	45	19.4	875
<i>Summer flush</i>								
270	14.9	4023	126	30.4	3830	45	17.2	775
NS	***	***	**	***	***	NS	**	***

²Dry-weight gain from spring bud burst until the end of November.

NS, **, *** Nonsignificant or significant within columns at $P \leq 0.01$ or 0.001, respectively, by Student's *t* test.

Fig. 1. Growing degree hour (GDH) accumulation and phenological stages from spring burst to fruit harvest, at S. Margherita Belice, lat. 37°44'N.

Fig. 2. Seasonal pattern of (A) fresh and (B) dry-mass accumulation, and (C) absolute growth rate for fruits (□) and cladodes (○) of *O. ficus-indica*, of the spring flush (□, ○) and the summer flush (●, ■). The summer flush was induced by removal of the spring flush. Vertical bars indicate SE (n = 50).

summer flush. At spring fruit harvest (20 August), cladodes of the spring flush had reached 90% of their final surface area but 65% of their final dry weight (Fig. 2C). By the same date, cladodes of the summer flush had gained 65% of their final surface area and 50% of their final dry weight (Fig. 2C). Indeed, the summer flush cladodes overall had a higher absolute growth rate than spring flush cladodes and this compensated for their shorter development period (Fig. 2C). However, at the end of the growth season cladodes of the spring flush were thicker (152 ± 12 mm) than those of the summer flush (130 ± 15 mm). Cladode surface area did not change during winter, although dry weight and thickness increased 25%; dif-

ferences between spring and summer flush cladodes remained unchanged (data not shown) until the next spring (Apr. 1994).

Absolute growth rate was higher for the cladodes than for the fruits during most of the fruit development period. Absolute growth rate of the cladodes decreased when the fruits reached their highest absolute growth rate, during the final swell of the fruit core. This occurred during the last 3 to 4 weeks of the fruit development period (Fig. 2C). After harvesting the fruits of the spring flush, absolute growth rate of developing cladodes increased sharply until mid-October (Fig. 2C).

The seasonal dry-matter partitioning between fruits and newly developing cladodes

Fig. 3. Seasonal increase in calculated surface area of terminal cladodes of *O. ficus-indica*. Vertical bars indicate SE (n = 50).

Fig. 4. Time course for the ratio between the total dry-mass accumulated in the fruit vs. total dry mass of current season's cladodes. Vertical bars indicate SE (n = 10).

indicated that the developing flowers were the major sink until bloom, then the developing cladodes became the major sink, and the fruit : cladode ratio remained fairly constant until the last stage of fruit growth. At this stage, sink demand of the fruit increased again, particularly in the summer flush (Fig. 4).

The proportion of annual dry matter accumulated by the fruit (HI) changed with the length of the fruit development period, being 34% for the spring flush and 46% for the summer flush. Indeed, the lower dry weight of the spring flush fruits was accompanied by a higher number and a greater growth of current season's cladodes and a greater secondary growth of the 1-year-old cladodes (Table 1).

Discussion

In *Opuntia ficus-indica*, a summer flush of cladodes and fruits can be obtained by removing the entire spring flush (Barbera et al., 1991). However, fruits of the summer flush attain a higher individual fresh weight than those of the spring flush (Barbera et al., 1994). The explanation for this is not clearly known but may be related to competitive sink demand or environmental constraints. In our experiment, trees received the same horticultural care and had the same crop load, but fruit of the spring flush still did not attain the size of those of the summer flush. Fruits of the spring flush have a shorter development period than the summer flush ones, and, particularly, a shorter duration of Stage III. During this stage, fruit absolute growth rates were $0.20 \pm 0.03 \text{ g} \cdot \text{d}^{-1}$ for the fruit of the spring flush and $0.24 \pm 0.02 \text{ g} \cdot \text{d}^{-1}$ for those of the summer flush. The lower fruit size of the spring flush at harvest time resulted from a shorter fruit development period and a lower growth rate during the stage (Stage III) when most of the core development occurred. Fruits of the spring flush reached Stage III in August, when the average daily temperature was 30°C day/ 24°C night, with peaks of $35/28^\circ\text{C}$, whereas fruits of the summer flush reached Stage III in October, when temperatures ($25/15^\circ\text{C}$) were the most favorable for cladode net CO_2 uptake (Nobel and Hartsock, 1984). These results indicate that high temperatures occurring during the final stage of fruit growth advance fruit ripening but apparently reduce growth, even under optimal horticultural care.

In selecting the proper environment for the cultivation of cactus pear, one should avoid areas where the highest temperature occur during fruit growth and ripening. The number of days required to reach commercial harvest maturity changes with the time of bud burst, but the thermal time (GDH from burst to harvest) does not. Thus, the duration of the fruit development period is better explained in terms of thermal rather than chronological time; different accumulation patterns of GDH apparently account for the variability in fruit ripening time that may occur from year to year and in relation to location. Consequently, GDH might be utilized to estimate the length of the fruit development period and the fruit ripening period in a new area of cactus pear cultivation.

As indicated by their high absolute growth rate, developing cladodes apparently compete with fruits for resources during most of the fruit growth period. However, they can be-

come a source of carbohydrates at an early stage of their development (Luo and Nobel, 1993), during flowering or the earliest stage of fruit development. The fruit become major sinks during the final swell of the core, and this coincides with a consistent reduction in the growth rate of the cladodes. Differences in the timing of fruit development as related to cladode growth did not significantly affect surface area of the cladodes, but affected cladode thickness and dry-weight accumulation. Indeed, cladode extension growth in the first flush ceased at the time of fruit harvest, while secondary growth lasted until the end of November. On the other hand, the growth of fruit and cladodes of the summer flush proceeded simultaneously over the course of the season, resulting in a reduced cladode dry-weight accumulation and thickness. In winter, cladodes of both flushes continued to grow in thickness and dry weight but not in terms of surface area. Similarly, increases in stem dry weight of peach is affected by fruit growth, and early ripening peach cultivars show a greater secondary growth (girth growth) than late ripening ones (Grossmann and DeJong, 1995). Summer pruning of newly initiated cladodes should then be accomplished before fruit set to avoid competition for assimilate resources.

Values of HI were similar to or even higher than those reported for deciduous fruit crops such as peach (Miller and Walsh, 1988), demonstrating the high efficiency of cactus pear as a fruit tree. On a seasonal basis, the spring flush seems less efficient than the summer one. In the spring flush, cladode vs. fruit competition was limited to 5 months, at the time from spring bud burst (April) to fruit harvest (August); this explains the greater dry weight attained by spring flush vs. summer flush cladodes. Considering that newly developing cladodes reached only 65% of their final dry weight at the time of fruit harvest, the HI of the spring was 43%, similar to that of the summer flush. A further improvement of HI may result from selected pruning, which should improve light distribution within the plant and, in turn, cladode fertility and fruit growth.

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