Dry matter accumulation and seasonal partitioning in mature *Opuntia ficus-indica* (L.) Mill. fruiting trees

Giorgia Liguori, Paolo Inglese, Giuseppe Sortino, Guglielmo Inglese

Dipartimento di Scienze Agrarie e Forestali, Università di Palermo, Italy

Abstract

Aim of this study was to understand the allocation of biomass into different canopy and root components and to measure the stem area index and its partitioning by cladode functionality (age), for fruiting *Opuntia ficus-indica* (OFI) *Gialla* trees, spaced 6×5 m apart and trained to a globe. The net primary productivity (NPP), calculated taking into account dry weight gain for above-ground vegetative components of OFI trees was 3.6 t C ha^{-1}. Including the fruit component and 1st flush current-year cladodes, NPP of above-ground components becomes 12 t ha^{-1}, equivalent to 5.4 t C ha^{-1}. Current-year cladodes were the highest C sink (49% of total annual C fixed in the canopy), secondary growth accounted for 22% of C fixation and the fruit component for 29%. This study demonstrated that OFI trees, grown in a commercial fruit orchard, couple high productivity, in terms of fruit yield and harvest index, with relevant C fixed in the canopy.

Introduction

Opuntia ficus-indica (OFI) can have an annual dry matter productivity that exceeds that of nearly all cultivated C_3 and C_4 species. For instance, a productivity of 47 t dry weight (dw) ha^{-1} yr^{-1} of cladodes (99%) and fruit (1%) has been predicted for high density plantings (24 plants m^{-2}), while a productivity of nearly 15 t ha^{-1} was measured for lower spacing (0.24 plants m^{-2}), resulting in a lower vegetative *vs* reproductive growth, with early fruit cropping and an alternate bearing behavior (Garcia de Cortazar and Nobel, 1992). Absolute growth rate for cladode and fruits can achieve 0.12 day^{-1} and 0.16 day^{-1} respectively. The fruit component (harvest index=HI) has been not systematically studied in OFI, though Inglese *et al*. (1999) measured, in a commercial orchard HI of 34% and 46% respectively for the spring and the summer flush that results from the removal of the spring flush of flowers and cladodes. Garcia de Cortazar and Nobel (1992) showed that yearly variations in cladode *vs* fruit dry matter allocation also depend on planting densities. An increase of dry matter allocated to the fruit was accompanied by a reduction in cladode count and dry weight accumulation. Light interception, CO_2 uptake and, then, plant productivity depend on canopy architecture and stem area (both sides of the cladode) index per ground area (SAI), that is the equivalent to the leaf area index (Nobel, 1988). Despite of their importance, SAI values for OFI orchards have been poorly investigated. Maximum dry weight ha^{-1} yr^{-1} productivity has been predicted for a SAI of 4 to 5, while for a SAI<3, the total net CO_2 uptake is about linear with SAI (Nobel, 1988). These calculations include all cladodes and do not take into account that single cladode contribution to CO_2 uptake changes with cladode age (Nobel, 1988), and, also, that optimal SAI definition must include fruit quality, which also depend on PAR interception by mother cladodes (Inglese *et al*., 1999).

The study reported herein was designed to help understand the allocation of biomass into different canopy and root components, also in relation to fruit production and to measure SAI and its partitioning by cladode age, for fruiting OFI trees.

Materials and methods

The study was conducted on an experimental field near Roccapalumba (37°48'N; 13°38'E; 350 m asl), western Sicily, Italy, from May to November 2010. The semi-arid climate is characterized by a mean annual precipitation of 600 mm. A 2.5 ha cactus pear orchard with cultivars *Gialla* (90%), *Rossa* (8%), and *Bianca* (2%) was selected for the experiment. Ten-year-old trees were trained to a globe shape. Trees (maximum height of 3 m) were spaced 5 m within the row and 6 m between rows, with 333 plants ha^{-1}. Rows were oriented North-South. The annual marketable production was about 20 t ha^{-1} using the so-called practice *scozzolatura*, which means that, in June, the first flush of cladodes and flowers are removed to promote a return bloom and a later fructification (Barbera *et al*., 1991).

According to the United States Department of Agriculture (USDA) classification (SCS, 1982), the soil at the experimental field has a clay-loam texture with 40% sand, 38% clay, and 22% silt. Volumetric soil water content is about 40% at field capacity. The irrigation system is made by four on-line labyrinth sprayers per plant and a discharge rate of 40 l h^{-1} per sprayer at a pressure of 150 kPa. During the irrigation period, from June throughout September 2010, a total of 150 mm of water was distributed, with an irrigation frequency ranging from 4 days to 1 week.

Correspondence: Paolo Inglese, Dipartimento di Scienze Agrarie e Forestali, Università di Palermo, viale delle Scienze 11, 90128 Palermo, Italy.
E-mail: paolo.inglese@unipa.it

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The experiment was conducted on 6 trees selected within the orchard.

The annual above-ground growth of the trees was represented by the new flush of cladodes, flowers and fruit, plus the increase of dry matter in the elder cladodes. In 2010 all removed young cladodes and flowers were weighed to obtain their fresh mass. A ventilated oven at 60 °C (M-250-VF, MPM Instruments srl, Bernareggio Monza e della Brianza, Italy) was used to dry the trees components until constant weight, for dry mass determination. Three weeks after the 2nd bloom, fruits of the fruiting trees were thinned to leave no more than 6 fruits per cladode; thinned fruit were counted and measured in terms of fresh and dry weight. At commercial maturity (November 2010), fruit were harvested to measure yield per tree (kg) and then counted; current-year cladode produced by each tree were also removed from the tree and, then counted and weighed for fresh mass determination. Samples made by 50 current-year cladodes and fruit, collected by each of the six trees, were individually weighed and dried at 60°C in a ventilated oven to constant weight, for dry mass determination. To determine fresh and dry weight accumulation during the season of 1-year, 2-year, 3-year and 4-years-old cladodes, their fresh and dry weight were measured from cork borer (1.4 cm in diameter) samples taken at the beginning (May) and the end (November) on 25 cladodes per age.

At the end of the season, to quantify the overall biomass partitioning, trees were sampled destructively and fractioned into canopy and root components. Canopy components, beside fruit and current-year cladodes, were 1-year-old cladode, two-year-old cladode, three-year-old cladodes and elder suberised cladodes; root components were fractioned into main root stem, primary and secondary roots. All cladodes were measured in terms of fresh weight, thickness, maximum length and width. All cladodes and roots subsamples were counted, weighed and then dried in a ventilated oven at 60°C to constant mass to determine their dry mass and to calculate the dry matter accumulated in the whole tree.

Moreover, to determine both photosynthetic and non-photosynthetic surface within the trees, cladode surface area (both sides) was calculated from the regression SA=0.8571 (DL* DT) + 0.3652 (R^2=0.962), where SA is the surface area of the cladode, DL and DT are respectively cladode height and width (cm). The regression was obtained from a sample of 150 cladodes whose length, width and thickness were measured and leaf area determined from paper silhouettes, with a leaf area meter (Windias, Delta-T Devices Ltd., Cambridge, UK). SAI per plant ($SAI_{orchard}$=both sides of the cladode per ground area allotted to the tree; SAI_{tree}=SAI: both sides of the cladode per ground area covered by the tree, 19.62 m^2) and dry matter production per unit cladode area were then calculated, considering cladode age. Data of canopy surface area, sorted by cladode age, were submitted to ANOVA and means were separated with Tukey's test at P≤0.05.

Results

Annual above-ground productivity, in terms of dry weight gained per tree, is reported in Table 1. In 2010 the amount of dry matter fixed in the canopy (secondary growth and current-year cladodes) was 7.9 t ha^{-1}; net primary productivity (NPP), calculated taking into account dry weight gain for above-ground vegetative components of OFI trees and a C percentage of 45% (Inglese *et al*., 2012), was 3.6 t C ha^{-1}. Including flowers and current-year cladodes of the 1st flush and thinned fruit of the 2nd flush, NPP of above ground components becomes 12 t ha^{-1}, equivalent to 5.4 t C ha^{-1}. The calculated harvest index (HI=annual dry matter allocated to the fruit component) was about 29%, considering both 1st and 2nd flush, or 26% if we only consider the reproductive and vegetative growth of the second flush.

The development of current-year cladodes accounted for almost 70% of vegetative annual growth so that the other 30% was accumulated by elder cladodes. In order to perform solid scaffold throughout the years more than 23% of what is annually gained is stored in those cladodes older than 1year (Table 1).

Crop yield (fresh weight) in 2010 was 20 t ha^{-1}, and average fruit weight was 130.6±4.5 g, with a total soluble solid content of 13.1± 0.24°Brix.

The dry mass of fruit yield per unit ground area was 0.27 kg m^{-2}. If we consider flowers removed to get a second bloom and fruit thinned few weeks after fruit set, the amount of dry mass diverted to reproductive growth was 0.35 kg m^{-2} ground area. Vegetative annual growth of canopy components was 0.86 kg m^{-2} ground area.

Dry matter accumulation and partitioning per canopy component is shown in Table 2. Tree dry weight was 15% of fresh weight, excluding the fruit component. The trunk showed the highest values in terms of fresh and dry weight among the above-ground components, due to the great accumulation of lignin and the loss of the water storage activity of parenchyma by aged cladodes.

Roots accounted for 6.8% of tree fresh weight and 17.5% of tree dry matter. Destructively sampling analysis detected flashy primary roots (28% dw) spread by the main root stem, and secondary roots with almost 40% of dry matter. Moreover, main root stem and primary roots accounted for more than 90% of the whole below-ground dry mass of the trees (*data not shown*).

Specific dry weight and surface area of the trees is reported in Table 3. The seasonal dry matter (fruit, current-year cladodes, secondary growth of older canopy components) per unit of surface area of photosynthetically most active cladodes area (current-year cladodes + 1-year-

Table 1. Number, and annual fresh and dry gain (±SE) of above-ground canopy components in 10-year-old *Opuntia ficus-indica* trees (n=6) cv. *Gialla*, trained to a globe.

	Number	Fresh weight (kg)	Dry weight (kg)	Dry mass (%)
1st flush current-year cladode removed	80±14.2	9.5±0.3	2.0±0.06	5.5
Current-year cladodes	224±17.1	217.7±14.3	15.8±1.1	43.6
1st flush flowers removed	1600±93.0	32.1±0.77	2.1±0.07	5.7
2nd flush thinned fruit	180±13.1	4.5±0.4	0.4±0.02	1.1
Harvested fruit	458±35.3	59.8±1.4	7.9±0.2	21.8
Dry weight annual gain (1-year-old cladodes)	219±12.5	-	2.0±0.07	5.5
Dry weight annual gain (≥2-year-old cladodes)*	347±25.0	-	6.0±0.2	16.6
Total			36.2±1.7	100

*Include also the non-photosynthetic cladodes (scaffold).

old cladodes + 2-year-old cladodes) was 0.48 kg dw m^{-2} (0.11 kg dw m^{-2} for the fruit component). The dry weight per unit surface area of 2-years-old cladodes was twice as much than in current year ones and 30% higher than in 1-year-old ones.

A percentage of 64 of total surface area of the trees was made by current-year, 1-year-old and 2-year-old cladodes (Figure 1), which are the most active cladodes in terms of photosynthetic efficiency, with a total surface area of 77±4.0 m^2 (Table 3).

SAI_{tree} and $SAI_{orchard}$ were respectively 6.2 and 4.1. (Figure 2). SAI_{tree} was 4.0 considering just current-year, 1-year-old and 2-year-old cladodes, thus only 36% of solar radiation is intercepted by the less photosynthetically efficient cladode.

Discussion

Above-ground NPP values of 5.1, 4.7, and 5.5 t C ha^{-1} have been recently measured for peach, apple, and citrus orchards, respectively (Tagliavini *et al*., 2008). Seasonal C fixation by single tree canopy, vegetative, components was 10.8 kg C tree^{-1}, which is very similar to 10.7 kg C tree^{-1} reported for 14-year-old *Tarocco* orange trees spaced 4.5×4.5 m apart, and twice as much as annual C fixed in 12-year-old *New Hall* orange trees spaced 4.0×2.5 m apart (Liguori *et al*., 2009). Current-year cladodes were the highest C sink (49% of total annual C fixed in the canopy), while secondary growth accounted for 22% of C fixation and the fruit for 29%. In other words, even in a year of particularly high production, the orchard was able to divert most of its C to the new vegetation and the secondary growth of vegetative components. Acevedo *et al*. (1983) measured a cladode dry mass production of 1 kg m^{-2} ground area and 0.3 kg fruit m^{-2} year^{-1}. Recently Pinos-Rodríguez *et al*. (2010) reported a dry mass production of 1.39 kg m^{-2}, for OFI grown to produce fresh biomass for cattle use. Nobel (1988) reports maximum values of 2 kg dry mass m^{-2} ground area year^{-1}. Working in a commercial orchard for fruit production we found similar values (1.2 kg m^{-2} ground area considering the first and the second flush of fruits and cladodes). At the end of the first season of growth, current-year cladodes reach almost entirely the surface area of 1-year-old cladodes, but only 65% of their dry weight. During the second year of growth they show a marginal increase in terms of surface area, but a significant accumulation of dry weight (+30%). From then onwards, cladodes marginally develop in term of surface area, but continue to accumulate dry weight. Scaffold cladodes have a twice as high specific dry weight than 1-year-old cladodes. Maximum productivity (>30 t of total biomass dry weight ha^{-1} year^{-1}) has been predicted (Nobel, 1988) for a SAI of 4 to 6, with 20,000 and 6000 plants ha^{-1}. Though our commercial plantations for fruit production had a much lower plant density (333 trees ha^{-1}), we measured very similar values than Nobel (1988), but for a much lower total biomass (dry weight) and a commercial fruit weight. However, the photosynthetically active canopy components (Liguori *et al*., 2013) account for 60% of canopy surface, with $SAI_{orchard}$ (2.6) and SAI_{tree} (4.0), values that are much lower than those reported by Nobel (1988). LAI values of

Table 2. Number, fresh weight and dry weight (±SE) of canopy and root components in 10-year-old *Opuntia ficus-indica* trees (n=6) cv. *Gialla,* trained to a globe.

	Number	Fresh weight (kg)	Dry weight (kg)	Dry mass (%)
Current-year cladodes	224±17.1	217.7±14.3	15.8±1.1	5.0
1-year-old cladodes	219±12.7	301.9±9.3	28.5±1.6	9.0
≥2-year-old cladodes	259±9.0	550.3±14.8	60.9±1.6	19.3
Scaffold	88±8.5	288.9±8.6	31.7±1.6	10.1
Trunk	-	723.8±15.3	123.1±6.6	39.1
Roots	-	152.3±8.6	55.0±1.8	17.5
Total	-	2234.9±70.9	315±14.3	100

Table 3. Number, specific dry weight, surface area, stem area index of photosynthetic active cladodes and scaffolds in trees (n=6) of *Opuntia ficus-indica* cv. *Gialla*, trained to a globe.

	Cladodes (n)	Specific dry weight (mg dw cm^{-2})	Cladode mean surface area (cm^2)	Canopy surface area (m^2)	SAI tree	SAI orchard
Current-year-cladodes	231±13.7	61.4±0.17	1242.9±3.19	28.7±1.77	1.5±0.10	1.0±0.06
1-year-old-cladodes	219±12.7	91.6±0.50	1425.5±3.33	31.2±1.85	1.6±0.10	1.0±0.06
2-year-old-cladodes	109±9.0	121.6±2.71	1584.3±9.97	17.2±1.44	0.9±0.08	0.6±0.03
3-4 year-old-cladodes	150±7.0	150.5±3.51	1893.9±9.97	28.3±1.32	1.4±1.32	0.9±0.05
Scaffold	88±8.5	190.3±1.74	1894.6±7.13	16.7±1.21	0.8±1.32	0.6±0.02
Total	797±24.4	-	-	122.1±3.09	6.2±0.17	4.1±0.10

SAI, stem area index.

3.5, 5.4, 4.1 have been reported, respectively for orange (Liguori *et al*., 2009), peach (Caruso *et al*., 1999), apple (Forshey *et al*., 1983) optimal productions. Orchard yield (20 t ha^{-1}) was very high (Inglese *et al*., 2002); however, we measured only 6.0 fruit m^{-2} of photosynthetic active surface area, and 14 fruit m^{-2} of 1-year-old cladodes that means no more than 2 fruit $cladode^{-1}$. Indeed, only 114 out of 219 1-year-old cladodes bore fruit though a fertile cladode may support 6-7 fruit (Inglese *et al*., 1994) with no apparent reduction of their final size and weight. This suggests the need for a deeper knowledge on plant fertility and the development on new strategy to optimize orchard design and canopy architecture, *i.e*. 1-year-old cladode distribution within the canopy, with the ultimate goal of increasing SAI photosynthetically active components, and cladode fertility.

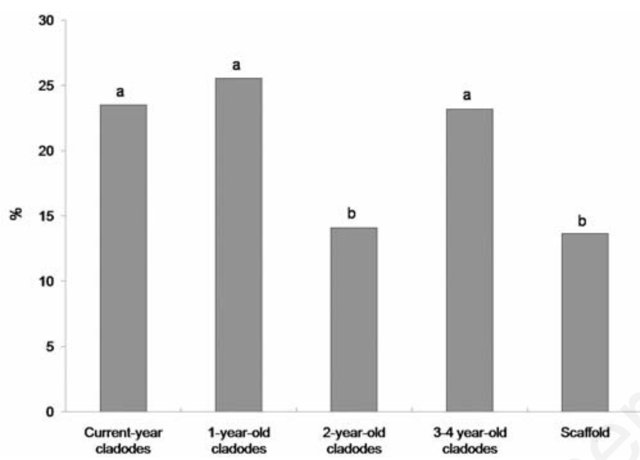

Figure 1. Percent of total surface area of cladodes partitioned by age in 10-year-old *Opuntia ficus-indica* trees (n=6) cv. *Gialla*. Different letters denote significant difference at P≤0.05 with Tukey's test.

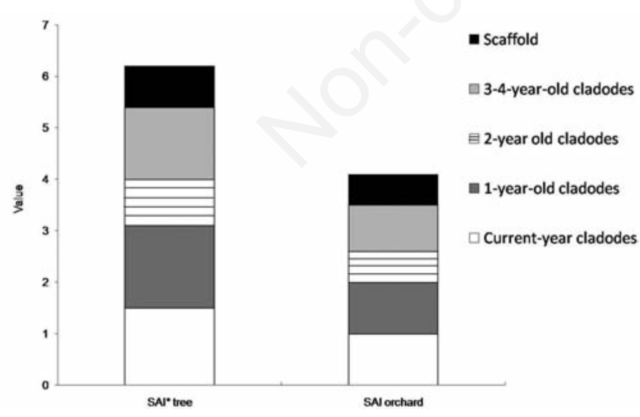

Figure 2. Relative contribution on stem area index (SAI) calculated on tree and orchard basis of current-year, 1-year-old, 2-year-old, 3-4-year-old cladodes and scaffold (non photosyntetically active) in 10-year-old *Opuntia ficus-indica* trees cv. *Gialla*.

Conclusions

Opuntia ficus-indica fruiting trees showed high productivity, both in terms of fruit crop yield and C fixed in the canopy. However, the fruit density in the canopy was relatively low and the harvest index was lower than 30%, suggesting a possible further increase in yield with no reduction of fruit size. One of the major issues to be addressed is the reduction of large (35%) portions of the canopy that show no photosynthesis and shade the active cladodes as well. This claims for new strategy in orchard design, plant architecture and pruning.

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