

# Changes in photosynthesis and fruit characteristics in olive in response to assimilate availability

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## Abstract

The “source” level in the olive cultivar Leccino was varied by girdling at different stages of fruit growth. Afterwards, the effects on gas exchange, fruit growth, and ripening and blooming were studied. Girdling during fruit growth did not significantly influence net photosynthetic rate ( $P_N$ ) except in the last phase of fruit growth when the  $P_N$  was reduced. In the girdled branch,  $P_N$  began to decrease at the onset of starch accumulation because fruit growth ceased. In mid-November stomatal conductance ( $g_s$ ) and transpiration rate ( $E$ ) were also reduced by girdling, whereas sub-stomatal  $\text{CO}_2$  concentration ( $C_i$ ) increased in leaves from the girdled branches. The total chlorophyll content (Chl) tended to decrease in parallel with the reduced  $P_N$ . Girdling did not substantially influence the leaf and shoot water contents. The large availability of assimilates seems to cause an earlier fruit ripening. In general, girdling increased fruit dry mass. Healing before the time when the majority of pulp growth occurs reduced the effect of girdling. June girdling increased the pit dry mass. Girdling at the beginning of August and September, compared to the control, increased the pulp dry mass, but the pit dry mass did not differ with respect to the control. The percentage of oil in the fruit, on a dry mass basis, increased with August and September girdlings, but the percentage of oil in the pulp did not change. Girdling reduced shoot growth, but the internode length was unchanged. Girdling slightly stimulated differentiation of flower buds.

*Additional key words:* chlorophyll; fruit growth; girdling; gas exchange; *Olea europaea*; pulp/pit ratio; ripening; saccharides; source-sink relationships.

## Introduction

Fruit is a strong sink where assimilates are translocated and converted to fruit components. In olive, nutrients for fruit development are supplied mostly by the leaves on the same shoot where the fruit is attached (Rallo and Suarez 1989, Márquez *et al.* 1990, Proietti and Tombesi 1996). Under reduced supply of assimilates, the fruit can also attract substances from other parts, but only if they are located nearby. Olive fruit development follows a specific pathway that is influenced by assimilate availability. The mesocarp, endocarp, and seed accumulate dry matter with different intensities during the period of fruit development: the dry mass of the endocarp increases until the first days of September and then remains constant, while the mesocarp, after having a limited growth until mid-August, increases in dry mass until mid-December. The seed grows at a constant rate until the end of October and then remains constant (Proietti *et al.* 1994). The relative growth rate (RGR) of the endocarp is greater than that of the mesocarp until mid-August, then it becomes noticeably slower. The seed grows quickly during the first fruit growth stage and then follows the trend of

mesocarp growth with much less growth during the last two months. Most oil synthesis occurs in the mesocarp cells and the final fruit oil content depends on the amount of mesocarp and the percent oil content. Oil synthesis is continuous from the end of July to December.

Girdling is a system used to study the effects of accumulation of assimilates in the branch. By blocking the phloem continuum, the translocation of photosynthates produced in the leaves is blocked. In the literature there are conflicting views about whether manipulations that disturb or block the translocation of substances produced in the leaves to other organs influences the net photosynthetic rate ( $P_N$ ).

The aim of the present research was to study if variations in “source” level (great assimilate availability) in a restricted zone close to the fruit, obtained by girdling at different stages of fruit growth, influences  $P_N$ , the growth of fruit parts, and oil synthesis. This was done in order to evaluate the possibility of enhancing the assimilate reparation towards organs which are more important for production by optimising cultural practices.

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## Materials and methods

The experiment was conducted in 1999 and 2000 in central Italy under natural conditions (Foligno, 43°N latitude) in a 30-year-old non-irrigated olive grove of Leccino cultivar. The soil is clay loam and the trees are trained to the vase system with spacing of 5×5 m. The weather during the summer climate is characterised by little rainfall and high temperatures.

Each year, at the end of June after fruit-set and at the beginning of August and September, seven peripheral branches about 15 mm in diameter and homogeneous in vegetative and productive (about 1.6 and 0.5 fruits per node of 1-year-old-shoot in 1999 and 2000, respectively) appearance and exposure, were girdled at the base. For each girdled branch there was a corresponding control branch. The 10-mm wide cut was made with a two-edged girdling knife; the wound was covered with black PVC tape. At the beginning of August the healing of the June girdling was evaluated for each branch.

In mid-July for the June girdling, at the beginning of September for the June and August girdlings, and in mid-September and mid-November for the June, August, and September girdlings, the  $P_N$ , transpiration rate ( $E$ ), stomatal conductance ( $g_s$ ), and sub-stomatal  $\text{CO}_2$  concentration ( $C_i$ ) were measured on six young, fully expanded and six 1-year-old leaves that were located on well-sunlit shoots with fruit on girdled and control branches. Measurements were always taken on cloudless days, from 09:00 to 10:30 in the morning; at the beginning of September measurements were also taken in the afternoon from 12:30 to 14:00 and from 16:00 to 17:30. Leaf  $P_N$ ,  $E$ ,  $g_s$ , and  $C_i$  were measured using an *LCA-2* portable gas exchange analyser (*Analytical Development Co.*, Hoddesdon, UK) and a Parkinson leaf chamber type *PLC(n)*. The detached leaf was immediately enclosed in the chamber and exposed perpendicularly to sunrays (incoming photosynthetic photon flux density, PPFD of 1 300–1 600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). The flow rate of air passing through the chamber was kept at 5  $\text{cm}^3 \text{s}^{-1}$  [about 10 000  $\text{cm}^3 \text{s}^{-1} \text{m}^{-2}$  (leaf area)]. During gas exchange measurements, the external  $\text{CO}_2$  concentration was *ca.* 360  $\text{cm}^3 \text{m}^{-3}$  and the air temperature inside the leaf chamber was 2–4 °C higher than that

in the atmosphere (varying from 28 to 35 °C in July, 24 to 27 °C in September, and 17 to 22 °C in November). Dark respiration rate ( $R_D$ ) was measured by covering the chamber with a black cloth screen. All measurements were taken under steady-state conditions.

At the beginning of September and in mid-November, after the gas exchange measurements, the leaves were immediately taken to the laboratory in a portable refrigerator for other determinations. Leaf area was measured using a leaf area meter (model *AAM-7*, *Hayashi Denkoh Co.*, Tokyo, Japan). Half of the leaves were then used to determine the chlorophyll (Chl) content (Bruinsma 1963) as well as the reducing sugar and starch contents (Morris 1948). The leaf area dry mass (ADM) and water content of the remaining leaves were determined by drying to a constant mass in a forced air oven at 90 °C. In mid-November, these determinations were also done on the one-year-old and current season shoots.

At harvest (mid-November), the fruit detachment force was determined on about 150 fruits per thesis using a *Carpo* dynamometer. The following measurements were made on 3 olive samples per thesis: Fresh and dry mass of the whole fruit, pulp, and pit, pulp firmness using a *Effegi* penetrometer with 1-mm tip diameter. Colour (scoring as follows: 1 = epicarp completely green, 5 = beginning of mesocarp pigmentation), pulp/pit ratio, and oil content using a *Foss-let 1531* apparatus (*Foss Electric Denmark*) were determined.

Fruit-drop was estimated by taking the difference between the number of fruit on the shoot at the time of girdling and at harvest. The influence of girdling on the current season shoot growth was evaluated by measuring the shoot and internode lengths in October. In June 2000, at the time of blooming, flower bud differentiation was estimated by determining the number of inflorescences per node.

The values obtained during the two years of sampling were averaged. Data were subjected to analysis of variance and the means were compared by least significant differences at  $p \leq 0.05$ .

## Results and discussion

Most of the girdling done in June was healed by August, whereas the girdlings done in August and September were only partially healed at the time of fruit harvest.

Leaf  $P_N$  showed substantial seasonal and diurnal variations, it was not significantly influenced by girdling during the fruit growth period in either young or one-year-old leaves, except in mid-November when girdling caused a  $P_N$  reduction (Table 1). According to some authors, when the source and sink are manipulated resulting in an increased source/sink ratio, the  $P_N$  decreases. The explanation is that when the production of assimila-

tes is markedly greater than the capacity for their consumption, a sort of stress is produced by the saccharide accumulation in the leaves (Neales and Incoll 1968, Claussen and Biller 1977, Daie 1985, Foyer 1988, Proietti and Tombesi 1990, Wang *et al.* 1998, Iglesias *et al.* 2002, Zhou and Quebedeaux 2003). According to Proietti and Tombesi (1990) and Proietti *et al.* (1999), in the olive girdling on a branch with growing fruit does not result in a lower  $P_N$  because a high accumulation of assimilates in the leaves is inhibited. In fact, the olive fruit is a strong sink that can withdraw substances

Table 1. Effect of girdling at different times on net photosynthetic rate ( $P_N$ ) [ $\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$ ], transpiration rate ( $E$ ) [ $\mu\text{mol}(\text{H}_2\text{O}) \text{ m}^{-2} \text{ s}^{-1}$ ], stomatal conductance ( $g_s$ ) [ $\mu\text{mol}(\text{H}_2\text{O}) \text{ m}^{-2} \text{ s}^{-1}$ ], sub-stomatal  $\text{CO}_2$  concentration ( $C_i$ ) [ $\text{cm}^3 \text{ m}^{-3}$ ], and respiration rate ( $R_D$ ) [ $\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$ ] in young and one-year-old leaves during the vegetative season. For each time, in each column means followed by different letters are significantly different at  $p \leq 0.05$ .

Time	Girdling time	Young leaves					One-year-old leaves				
		$P_N$	$E$	$g_s$	$C_i$	$R_D$	$P_N$	$E$	$g_s$	$C_i$	$R_D$
Mid-July	End of June	7.8 a	4.0 a	116 a	333 a	-1.4 a	6.9 a	4.1 a	114 a	335 a	-1.2 a
	Control	6.7 a	4.4 a	117 a	340 a	-1.5 a	7.3 a	4.4 a	119 a	334 a	-1.1 a
Beginning of September	End of June, 09:00	13.5 c	2.5 c	86 d	331 a	-1.3 a	12.0 c	1.9 b	59 c	340 a	-1.1 a
	Beginning of August, 09:00	14.0 c	2.8 c	87 d	330 a	-1.4 ab	12.7 c	2.3 b	69 c	341 a	-1.0 a
	Control, 09:00	14.7 c	3.0 c	91 d	333 a	-1.4 ab	11.7 c	2.4 b	71 c	338 a	-1.4 a
	End of June, 13:00	5.3 ab	1.2 ab	20 b	356 b	-2.4 c	5.8 b	1.7 b	32 b	350 b	-1.5 a
	Beginning of August, 13:00	5.5 b	1.4 ab	22 bc	353 b	-2.8 c	6.5 b	2.2 b	35 b	348 b	-1.2 a
	Control, 13:00	6.1 b	1.7 b	27 c	356 b	-2.6 c	6.8 b	1.9 b	33 b	348 b	-1.1 a
	End of June, 17:00	3.9 a	0.9 a	14 a	365 b	-1.6 ab	3.3 a	1.0 a	17 a	360 c	-1.1 a
Mid-September	Beginning of August, 17:00	4.5 a	1.0 a	16 a	362 b	-1.6 ab	3.5 a	0.9 a	15 a	361 c	-1.1 a
	Control, 17:00	3.9 a	1.0 a	15 a	364 b	-1.8 b	3.2 a	1.0 a	16 a	365 c	-1.2 a
	End of June	10.0 a	4.1 a	308 a	355 a	-1.5 a	11.9 a	5.8 a	298 a	347 a	-1.8 a
	Beginning of August	11.0 a	3.8 a	309 a	365 a	-1.1 a	11.7 a	6.3 a	321 a	336 a	-2.4 a
	Beginning of September	9.9 a	4.2 a	311 a	358 a	-1.4 a	10.5 a	6.0 a	313 a	350 a	-1.8 a
Mid-November	Control	10.9 a	3.8 a	319 a	360 a	-1.3 a	11.2 a	5.9 a	300 a	347 a	-2.3 a
	End of June	10.0 a	4.1 ab	299 a	318 a	-1.3 a	11.0 a	4.2 ab	302 a	317 ab	-1.0 a
	Beginning of August	10.8 a	3.4 a	300 a	322 ab	-1.1 a	11.2 a	3.7 a	309 ab	319 ab	-1.1 a
	Beginning of September	10.7 a	4.2 ab	323 b	337 b	-1.2 a	11.0 a	4.1 a	315 b	327 b	-1.4 a
	Control	13.6 b	4.4 b	344 c	312 a	-1.2 a	13.1 b	4.7 b	333 c	312 a	-1.3 a

produced in the leaves from the translocation system and thus impede starch accumulation in the leaves (Proietti and Tombesi 1996, Proietti and Famiani 2002). There was a  $P_N$  reduction in girdled branches only during the last phase of fruit growth, when assimilate request by the fruit was low and climatic conditions for  $P_N$  were still good. Hence if the removal of elaborated sap is impeded,  $P_N$  may be inhibited.

In effect, the saccharide content at the beginning of September in young and one-year-old leaves on the girdled branches with respect to the control showed that there was only a slight increase in starch content in the one-year-old leaves; the values were always within the

seasonal range (Table 2). In mid-November, leaves and shoots on the girdled branches had higher starch content than the control (Tables 2 and 3). As a consequence of the saccharide content variation, in mid-November the ADM was higher in the one-year-old leaves from the girdled branches.

Girdling did not substantially influence  $E$ ,  $g_s$ ,  $C_i$ , and  $R_D$  except in mid-November when  $P_N$ ,  $g_s$ , and  $E$  were reduced by girdling (Table 1). Nevertheless, it does not seem that the increased  $g_s$  could have caused a reduction in  $P_N$ , because the  $C_i$  in leaves from the girdled branches was not less than that of the control, as was expected, but rather was greater.

Table 2. Effect of girdling at different times on water content [% f.m.], area leaf dry mass, ADM [ $\text{g m}^{-2}$ ], contents of total chlorophyll (Chl) [ $\text{g m}^{-2}$ ], reducing sugars [ $\text{g m}^{-2}$ ], and starch [ $\text{g m}^{-2}$ ] in young and one-year-old leaves at the beginning of September and in mid-November. For each time, in each column means followed by different letters are significantly different at  $p \leq 0.05$ .

Time	Girdling time	Young leaves					One-year-old leaves				
		Water content	ADM	Chl	Reducing sugars	Starch	Water content	ADM	Chl	Reducing sugars	Starch
Beginning of September	End of June	49.7 a	170 a	3.2 a	11 a	2.1 a	50.3 a	217 a	4.2 a	9 a	3.1 b
	Beginning of August	52.6 a	163 a	3.5 a	10 a	2.1 a	49.6 a	212 a	3.9 a	10 a	2.6 b
	Beginning of September	49.8 a	169 a	3.3 a	10 a	1.9 a	50.0 a	208 a	3.9 a	9 a	2.5 ab
	Control	50.3 a	163 a	3.4 a	10 a	1.9 a	49.6 a	202 a	4.2 a	11 a	2.2 a
Mid-November	End of June	47.9 a	176 b	2.3 a	22 a	3.4 ab	46.6 a	239 c	2.0 a	25 a	3.5 ab
	Beginning of August	50.6 a	163 a	2.5 a	21 a	4.1 c	49.8 b	197 b	2.2 ab	24 a	4.3 c
	Beginning of September	50.1 a	166 a	2.6 ab	22 a	3.9 bc	48.9 ab	191 b	2.1 a	26 a	3.9 bc
	Control	49.7 a	164 a	2.9 b	21 a	3.1 a	51.5 b	182.2 a	2.5 b	26 a	3.2 a

Girdling did not influence  $P_N$  in the afternoon at the beginning of September. The highest  $P_N$  values were recorded in the morning (09:00–10:00), with good temperature and humidity; the values then declined at 13:00–14:00, and declined even more markedly at 16:00–17:00.  $C_i$  tended to increase when  $P_N$  decreased. This created condition for stomata closure and  $g_s$  consequently decreased. This suggests that the lower  $P_N$  values observed in the afternoon were not caused primarily by the reduced  $g_s$ , but rather by non-stomatal effects, as reported by Angelopoulos *et al.* (1996), Matos *et al.* (1998), and Proietti (2000).

In general, the  $E$  and  $g_s$  values were higher in the morning than in the afternoon, whereas  $C_i$  was higher in

the afternoon. Chl content was lower in mid-November than at the beginning of September. In September, the one-year-old leaves contained more Chl than the young ones, but in November these differences disappeared. At the beginning of September, girdling did not significantly influence leaf Chl content; it was lower in the girdled branches in mid-November (Table 2). The decrease in Chl content, parallel to the reduction in  $P_N$ , was probably due to the elevated starch content in the leaves.

The leaf and shoot water contents were not substantially influenced by girdling, with the exception of a slight reduction in one-year-old leaves and shoots in November; this result seems to indicate that water stress was not associated with girdling (Tables 2 and 3).

Table 3. Effect of girdling at different times on water [% f.m.], reducing sugars [% f.m.], and starch [% f.m.] contents in young and one-year-old shoots in mid-November. In each column, means followed by different letters are significantly different at  $p \leq 0.05$ .

Girdling time	Current season shoots			One-year-old shoots		
	Water content	Reducing sugars	Starch	Water content	Reducing sugars	Starch
End of June	49.0 a	5.4 b	4.0 b	45.5 a	4.8 b	5.1 ab
Beginning of August	52.4 a	5.0 b	4.0 b	47.5 a	4.3 ab	5.5 b
Beginning of September	51.0 a	4.9 b	3.9 b	48.7 ab	4.1 a	5.5 b
Control	52.6 a	4.1 a	3.0 a	51.1 b	3.8 a	4.9 a

With respect to the control, a June girdling tended to increase fruit-drop, while August and September girdlings tended to reduce fruit-drop (Table 4).

At harvest (mid-November) on the girdled branches, the olives were darker and fruit detachment force and

pulp firmness were slightly lower than in the control (Table 5). Therefore, the abundant availability of assimilates probably caused an earlier ripening as has been observed in other species (Allan *et al.* 1993, Augusti *et al.* 1998).

Table 4. Effect of girdling at different times on fruit-drop [%] from girdling to harvest in mid-November. Means followed by different letters are significantly different at  $p \leq 0.05$ .

Girdling time	Fruit-drop on girdled branches	Fruit-drop on the control branches
End of June girdling - not healed in August	16.9 c	15.8 bc
Beginning of August girdling	14.1 b	15.6 bc
Beginning of September girdling	9.7 a	11.2 a

In general, girdling increased fruit dry mass (Table 6). Compared to the control, the pulp dry mass was higher in olives from the shoots that had been girdled at the end of June. In these branches the girdling was not yet healed in August, whereas the pulp dry mass of olives from the shoots, in which the June girdling was healed in August, did not increase. Evidently, healing before the major period of pulp growth reduced the effect of girdling. In every case, a June girdling increased dry mass of the pit.

Compared to the control, girdling done at the beginning of August and September increased the pulp dry mass, whereas the pit dry mass was similar to that of the control. Consequently, the pulp/pit ratio, on a dry mass basis, compared to the control, increased notably with the August and September girdlings, whereas it decreased for the June girdling in the shoots where the girdling was

healed in August.

The percentage of oil in the fruit, on a dry mass basis, increased due to the August and September girdlings, while the percent of oil in the pulp did not change.

In accord with the results obtained in other species (Piller *et al.* 1998, Wilton 2000), girdling reduced the current season shoot growth without modifying the internode length (Table 7).

Girdling slightly stimulated flower bud differentiation, confirming that the abundant availability of assimilates influences flower induction (Sarmiento *et al.* 1976). However, the limited effect of girdling on this parameter can be attributed to the great competition caused by the high fruit load in 1999 and the consequent low level of food reserves in the tree (Proietti and Tombesi 1996).

Table 5. Effect of girdling at different times on colour, water content [% f.m.], detachment force [N], and pulp firmness [kg] of the fruit at harvest (mid-November). In each column, means followed by different letters are significantly different at  $p \leq 0.05$ .

Girdling time	Colour (1÷5)	Water content	Detachment force	Pulp firmness
End of June – not healed in August	3.74 b	65.5 a	347 a	1.90 a
Beginning of August	3.67 b	64.8 a	346 a	1.87 a
Beginning of September	3.61 b	65.3 a	365 b	1.79 a
Control	2.64 a	64.3 a	368 b	2.19 b

Table 6. Effect of girdling at different times on fruit, pulp and pit dry masses [g], pulp/pit ratio [d.m./d.m.], and fruit and pulp oil content [% d.m.] at harvest (mid-November). In each column, means followed by different letters are significantly different at  $p \leq 0.05$ .

Girdling time	Dry mass			Oil content		
	Fruit	Pulp	Pit	Pulp/pit	Fruit	Pulp
End of June – not healed in August	1.19 c	0.69 b	0.50 b	1.38 b	44.2 a	76.2 a
End of June – healed in August	1.08 b	0.57 a	0.51 b	1.12 a	43.8 a	75.4 a
Beginning of August	1.07 b	0.67 b	0.40 a	1.68 c	47.3 b	75.6 a
Beginning of September	1.06 ab	0.65 ab	0.41 a	1.58 c	46.9 b	76.5 a
Control	0.99 a	0.58 a	0.41 a	1.41 b	44.6 a	76.3 a

Table 7. Effect of girdling at different times on current season shoot and internode length [cm] in October and blooming [inflorescences per node] in June. In each column, means followed by different letters are significantly different at  $p \leq 0.05$ .

Girdling time	Length		Blooming
	Shoot	Internode	
End of June	22.8 a	1.7 a	0.6 b
Beginning of August	26.0 b	1.9 a	0.5 ab
Beginning of September	32.1 c	1.8 a	0.5 ab
Control	31.9 c	1.7 a	0.4 a

In conclusion, in olive the accumulation of assimilates caused a reduction in  $P_N$ . In particular, in a girdled branch,  $P_N$  began to decrease at the onset of starch accumulation that occurred at the end of fruit growth. This confirms that saccharide accumulation in the leaf is a sort of stress that occurs when the production of photosynthates significantly exceeds the capacity to use them. During fruit growth, the availability of a large part of assimilates benefits fruit growth and oil content, whereas there is only a slight improvement in bud induction, and

shoot growth is reduced.

The changes in assimilate availability at different phases of fruiting result in a variation in their distribution between different components of the fruit. The availability of many assimilates in July primarily affects endocarp growth, whereas from August until November it affects mesocarp growth and oil synthesis. An abundant availability of assimilates seems to cause an earlier fruit ripening.

The healing of early girdling (June) during the time of most intense pulp growth (from mid-August onwards) reduces the effectiveness of the treatment. Early girdling increased pit growth in all cases. Consequently, the effect on pulp growth, pulp/pit ratio, and fruit oil content was more evident when girdling was done in August, that is, when the mesocarp undergoes the most intense growth. This suggests that the modulation of certain cultural practices that influence the availability of assimilates, such as irrigation, fertilisation, and pruning, during various stages of fruit development could enhance the re-partitioning of assimilates into components of commercial value.

## References

Allan, P., George, A.P., Nissen, R.J., Rasmussen, T.S.: Effects of girdling time on growth, yield, and fruit maturity of the low chill peach cultivar Flordaprince. – *Aust. J. exp. Agr.* **33**: 781-785, 1993.

Angelopoulos, K., Dichio, B., Xiloyannis, C.: Inhibition of photosynthesis in olive trees (*Olea europaea* L.) during water stress and rewatering. – *J. exp. Bot.* **47**: 1093-1100, 1996.

Augusti, M., Andrei, I., Juan, M., Almela, V., Zacarias, L.: Effects of ringing branches on fruit size and maturity of peach and nectarine cultivars. – *J. hort. Sci. Biotechnol.* **73**: 537-540, 1998.

Bruinsma, J.: The quantitative analysis of chlorophylls *a* and *b* in plant extracts. – *Photochem. Photobiol.* **2**: 241-249, 1963.

Claussen, W., Biller, E.: Die Bedeutung der Saccharose- und Stärkegehalte der Blätter für die Regulierung der Netto-Potosyntheseraten. – *Z. Pflanzenphysiol.* **81**: 189-198, 1977.

Daie, J.: Carbohydrate partitioning and metabolism in crops. – *Horticult. Rev.* **7**: 69-108, 1985.

Foyer, C.H.: Feedback inhibition of photosynthesis through source-sink regulation in leaves. – *Plant Physiol. Biochem.*

26: 483-492, 1988.

Iglesias, D.J., Lliso, I., Tadeo, F.R., Talon, M.: Regulation of photosynthesis through source:sink imbalance in citrus is mediated by carbohydrate content in leaves. – *Physiol. Plant.* **116**: 563-574, 2002.

Márquez, J.A., Benloch, M., Rallo, L.: Seasonal changes of glucose, potassium and rubidium in "Gordal Sevillana" olive in relation to fruitfulness. – *Acta Horticult.* **286**: 191-194, 1990.

Matos, M.C., Matos, A.A., Mantas, A., Cordeiro, V., Vieira Da Silva, J.B.: Diurnal and seasonal changes in *Prunus amygdalus* gas exchanges. – *Photosynthetica* **35**: 517-524, 1998.

Morris, D.L.: Quantitative determination of carbohydrates with Dreywood's anthrone reagent. – *Science* **107**: 254-255, 1948.

Neales, T.F., Incoll, L.D.: The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: A review of the hypothesis. – *Bot. Rev.* **34**: 107-125, 1968.

Piller, G.J., Greaves, A.J., Meekings, J.S.: Sensitivity of floral shoot growth, fruit set and early fruit size in *Actinidia deliciosa* to local carbon supply. – *Ann. Bot.* **81**: 723-728, 1998.

Proietti, P.: Effect of fruiting on leaf gas exchange in olive (*Olea europaea* L.). – *Photosynthetica* **38**: 397-402, 2000.

Proietti, P., Famiani, F.: Diurnal and seasonal changes in photosynthetic characteristics in different olive (*Olea europaea* L.) cultivars. – *Photosynthetica* **40**: 171-176, 2002.

Proietti, P., Palliotti, A., Nottiani, G.: Availability of assimilates and development of olive fruit. – *Acta Horticult.* **474**: 297-300, 1999.

Proietti, P., Tombesi, A.: Effect of girdling on photosynthetic activity in olive leaves. – *Acta Horticult.* **286**: 215-218, 1990.

Proietti, P., Tombesi, A.: Translocation of assimilates and source-sink influences on productive characteristics of the olive tree. – *Adv. hort. Sci.* **10**: 11-14, 1996.

Proietti, P., Tombesi, A., Boco, M.: Influence of leaf shading and defoliation on oil synthesis and growth of olive fruit. – *Acta Horticult.* **356**: 272-277, 1994.

Rallo, L., Suarez, M.P.: Seasonal distribution of dry matter within the olive fruit-bearing limb. – *Adv. hort. Sci.* **3**: 55-59, 1989.

Sarmiento, R., Val Puesta, V., Catalina, I., Gonzalez Garcia, F.: [Variation in contents of starch and soluble carbohydrates in leaves and buds in trees of *Olea europaea* var. Manzanillo in relation to vegetative and productive processes.] – *Anal. Edafol. Agrobiol.* **35**: 687-695, 1976. [In Span.]

Wang, Z., Yin, Y., He, M., Cao, H.: Source-sink manipulation effects on postanthesis photosynthesis and grain setting on spike in winter wheat. – *Photosynthetica* **35**: 453-459, 1998.

Wilton, J.: Girdling studies. – *Orchardist* **73**: 14-17, 2000.

Zhou, R., Quebedeaux, B.: Changes in photosynthesis and carbohydrate metabolism in mature apple leaves in response to whole plant source-sink manipulation. – *J. amer. Soc. hortic. Sci.* **128**: 113-119, 2003.