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Effect of fruiting on leaf gas exchange in olive (*Olea europaea* L.)

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Abstract

The effect on traits of photosynthesis and water relations of assimilate demand was studied in olive tree that has strong alternate bearing. The diurnal and seasonal leaf gas exchanges, area dry mass, and saccharide and chlorophyll (Chl) contents were measured by comparing shoots with fruit of "on-trees" (heavy fruit load) with shoots without fruit on both "on-trees" and "off-trees" (light fruit load). In spite of large seasonal and diurnal differences, leaf net photosynthetic rate (P_N), stomatal conductance (g_s), sub-stomatal CO_2 concentration (C_i), transpiration rate (E), and respiration rate (R_D) were not significantly influenced by fruit load or by the presence or absence of fruit on the shoot. An only exception was at the beginning of July when the one-year-old leaves on shoots with fruit had slightly higher P_N and E than leaves on shoots without fruit. Water content, Chl and saccharide contents, and area dry mass of the leaf were not substantially influenced by the presence/absence of fruit on the shoot or fruit load. Hence the sink demand, associated with fruit growth, did not improve leaf photosynthetic efficiency in olive.

Additional key words: alternate bearing; chlorophyll; diurnal and seasonal course; photosynthesis; respiration rate; saccharides; source-sink relationships; stomatal conductance; sub-stomatal CO_2 concentration; transpiration rate.

Introduction

The olive is an evergreen plant species that has strong alternate (or biennial) bearing. A heavy yield is followed usually by an extremely low one and *vice-versa*. In general, there is a regular biennial pattern, with an "on-year" (heavy yield) followed by an "off-year" (low or no yield). Sometimes, however, two or more "on" or "off" years occur in sequence in response to genetic, climatic, cultural, or pathological conditions. Each year, most trees in a given climatic area are in the same "on" or "off" year conditions; however, it is not uncommon for individual groves or trees to alternate out of cycle with their neighbours (Monselise and Goldschmidt 1982).

The initial event that triggers alternate bearing may involve external factors (frost, lack of pollination, disease, *etc.*) which generally start the cyclic alternate behaviour by eliminating one year's crop. The perpetuation of this cycle in olive is attributed to the lack of an efficient self-thinning mechanism; the fruit overload produced during an "on-year" is the most universally recognised cause of alternate bearing (Monselise and Goldschmidt 1982). The developing olive fruit is a strong sink that requires a continuous supply of building materials (Proetti *et al.* 1999). It competes successfully with shoot growth for both newly assimilated materials and reserves previously accumulated assimilates in different tree tissues. Most assimilates for fruit developing are supplied by the leaves on the same shoot where the fruit is attached (Rallo and Suarez 1989, Proietti and Tombesi 1996). When assimilate supply is reduced, the fruit can also use substances from other nearby parts.

During an "on-year", the many growing fruits reduce the production of new shoots, which provide buds that are apt for floral induction. Therefore the number of flowers is drastically reduced. Due to an excessive consumption of assimilate reserves during a heavy yield, the differentiation potential of the buds, the viability of the flowers, and the percent of fruit set are usually lower than after an "off-year". In contrast, the strong shoot growth and abundant assimilate availability in the "off-year" favour the formation of many flowers the following year.

Alternate fruit bearing in olive occurs under both extensive and intensive growing conditions, but the degree of alternation can be reduced by establishing a very delicate balance between vegetative and reproductive activities by rational cultivation practices. While several specific interactions between fruit load and vegetative activity and characteristics of fruit and oil have already been studied in olive, further study of the effect of fruit load on tree physiology is needed in order

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to define strategies that could reduce alternate bearing (Proietti *et al.* 1995).

This study examined the diurnal and seasonal activity of olive leaves in trees with heavy or low fruit load under natural conditions, without manipulations (such as partial or complete removal of fruits) that could cause secondary effects (Daie 1985). In particular, the effects of the presence of olive fruit sink on the leaf gas exchanges, area dry mass (ADM), and saccharide and Chl contents were studied in order to test the hypothesis that high sink demand stimulates P_N as reported for several other species (Daie 1985, Dickson 1991). Considering that the possible fruiting effect on P_N could be a generalised effect rather than a localised one, shoots with fruit of "on-trees" were compared with shoots without fruit on both "on-trees" and "off-trees".

Materials and methods

The experiment was done in central Italy under natural conditions (Foligno, 43°N latitude), in a 15-year-old non-irrigated olive grove. The trees grow in clay loam soil, are trained to the vase system and spaced at 5×5 m. Climate is characterised by low rainfall and high temperatures during summer. From the beginning of July (initial stage of fruit development) to mid-December (fruit harvest) of 1997 and 1998, measurements were taken periodically on young (1-4 months) full expanded leaves and on 1-year-old leaves of Leccino cultivar, taken from well-sunlit shoots without or with fruit (about 1.5 fruit per node from 1-year-old shoot) on five trees with a high fruit load [about 160 g(yield) per cm^{-2}(trunk cross-sectional area at 20 cm from the ground)] and from shoots without fruit chosen on five trees with average-to-low fruit load [about 100 g(yield) per the same unit].

Measurements were always taken on cloudless days, in the morning from 09:00 to 10:30 and 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 a *LCA-2* portable gas exchange analyser (*Analytical Development Co.*, Hoddesdon, U.K.) 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 1200-1500 μmol m^{-2} s^{-1}). The flow rate of air passing through the chamber was kept at 5 cm^3 s^{-1} [about 10 000 cm^3 s^{-1} m^{-2} (leaf area)]. During gas exchange measurements, external concentration of CO_2 was about 370 cm^3 m^{-3} and air temperature inside the leaf chamber was 2-4 °C higher than that in the atmosphere (varying from 28 to 36 °C in July, from 25 to 34 °C in September, from 18 to 26 °C in October, and from 11 to 16 °C in December). R_D was measured by covering the chamber with a black cloth screen. Recordings were taken under steady-state conditions.

After gas exchange measurements, the leaves were immediately transferred to the laboratory in a portable refrigerator for the other determinations. Leaf area was measured using a leaf area meter (*Hayashi Denkoh Co.*, model *AAM-7*). Half of the leaves were then used to determine Chl (Bruinsma 1963) and soluble sugar and starch (Morris 1948) contents. ADM and water content of the remaining leaves were determined by drying to constant mass in a forced air oven at 90 °C.

Values obtained during the two years of sampling were averaged.

Results

Leaf P_N showed substantial seasonal and diurnal variations, but the fruit load and presence or absence of fruit on the shoot did not significantly influence it. An only exception were the measurements taken at the beginning of July when the one-year-old leaves on shoots with fruit of "on-trees" had a slightly higher P_N value than the leaves on shoots without fruit of "off-trees" (Fig. 1).

During the growing season, the highest P_N values were observed in October, while the lowest values were recorded in mid-summer and in December. The high P_N values observed in October were probably due to the temperature that was still favourable for photosynthesis, associated with good water availability. The low P_N values in mid-summer and December were due to the low water availability and to low temperature, respectively.

According to Angelopoulos *et al.* (1996), the highest P_N values were generally found in the morning (09:00-10:30), with good temperatures and humidity; subsequently, the values declined from 12:30-14:00 and more markedly from 16:00-17:30.

In summer, the P_N values in the young leaves were slightly higher than in the one-year-old ones, the differences being greater in the morning than in the afternoon. This could be attributed to the onset of senescence in the one-year-old leaves and/or to the reduced PAR availability on the leaf surface of one-year-old shoot compared with that of the young shoot.

C_i tended to increase when P_N decreased (Fig. 2). This created condition when stomata close which is accompanied by a consequent g_s decrease (Fig. 3). This suggests that the lower P_N values observed in mid-summer or December and in the afternoon were not caused primarily by the reduced g_s, but rather by non-stomatal effects, as has been reported by Angelopoulos *et*

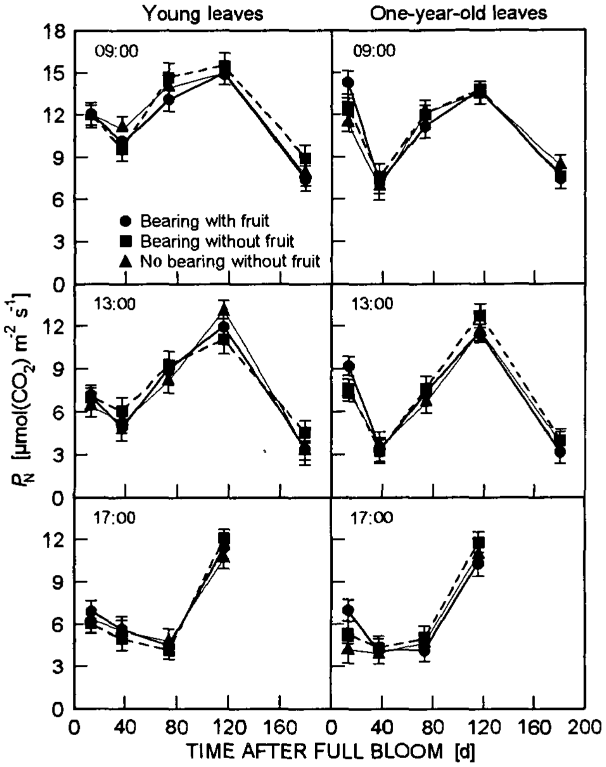

Fig. 1. Effect of fruit load on diurnal net photosynthetic rate (P_N) of young and one-year-old leaves during fruit development. Each point is the mean of 6 replicates ± standard error.

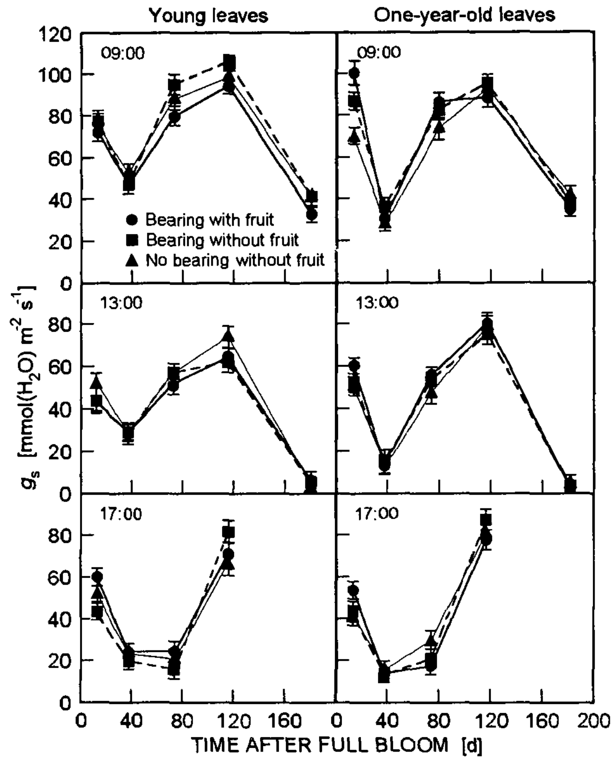

Fig. 3. Effect of fruit load on diurnal stomatal conductance (g_S) of young and one-year-old leaves during fruit development. Each point is the mean of 6 replicates ± standard error.

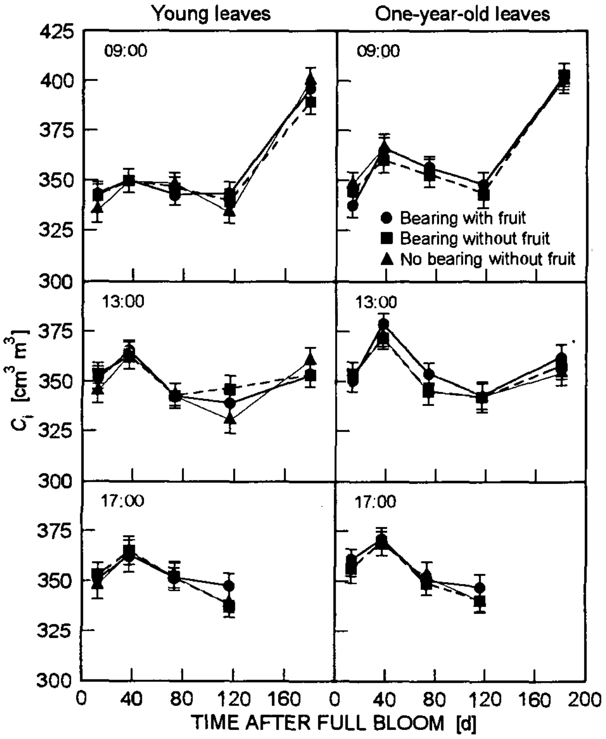

Fig. 2. Effect of fruit load on diurnal sub-stomatal CO_2 concentration (C_i) of young and one-year-old leaves during fruit development. Each point is the mean of 6 replicates ± standard error.

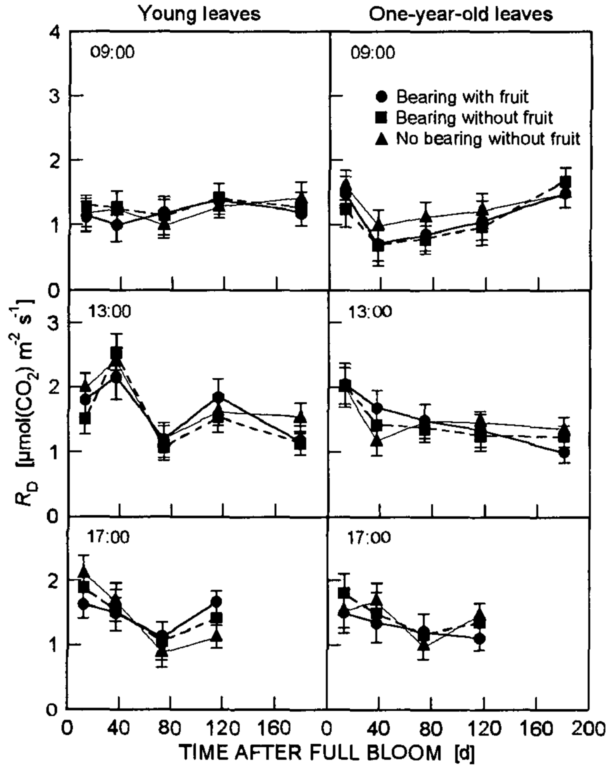

Fig. 4. Effect of fruit load on diurnal respiration rate (R_D) of young and one-year-old leaves during fruit development. Each point is the mean of 6 replicates ± standard error.

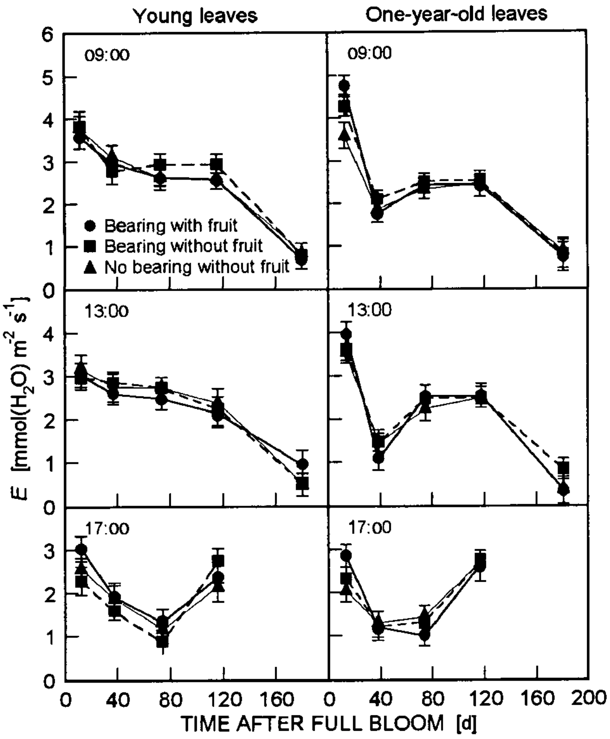

Fig. 5. Effect of fruit load on diurnal transpiration rate (*E*) of young and one-year-old leaves during fruit development. Each point is the mean of 6 replicates ± standard error.

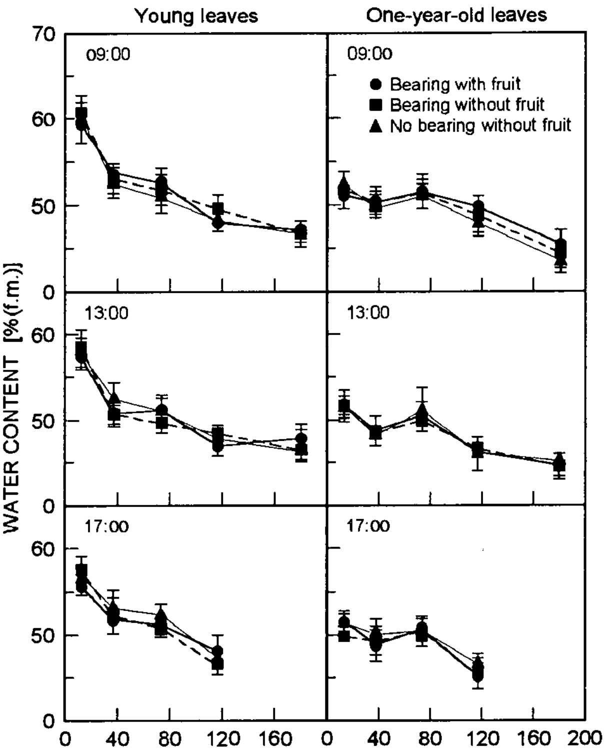

Fig. 6. Effect of fruit load on diurnal water content of young and one-year-old leaves during fruit development. Each point is the mean of 6 replicates ± standard error.

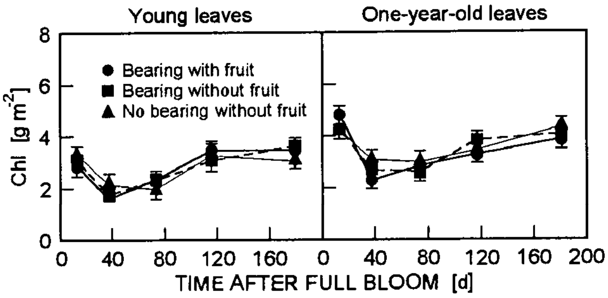

Fig. 7. Effect of fruit load on total chlorophyll (Chl) content of young and one-year-old leaves during fruit development. Each point is the mean of 6 replicates ± standard error.

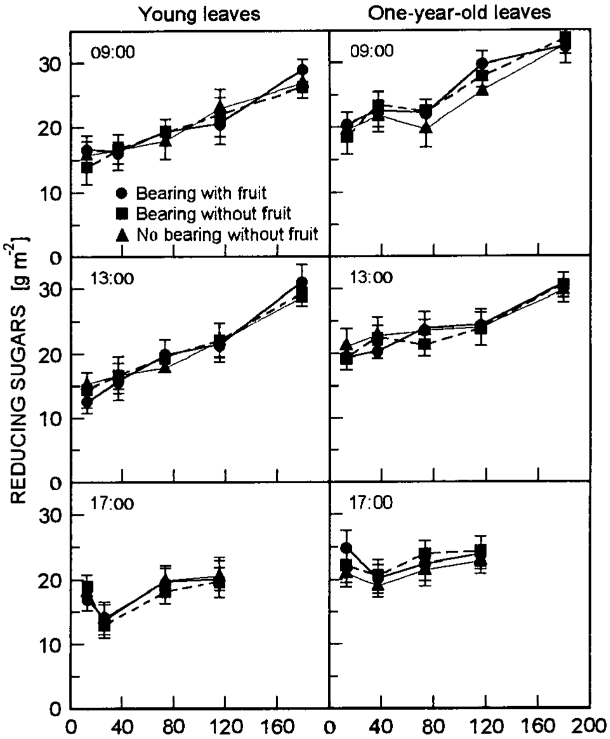

Fig. 8. Effect of fruit load on diurnal reducing sugar content of young and one-year-old leaves during fruit development. Each point is the mean of 6 replicates ± standard error.

al. (1996) and Matos *et al.* (1998). According to some authors (Pearcy *et al.* 1977, Beyschlag *et al.* 1987, Angelopoulos *et al.* 1996), the lower P_N values in the summer could be the result of damage to the photosystem induced by high temperature and drought stress. High temperatures could be involved in the decreased P_N values also by influencing R_D. In summer the R_D values were lower in the morning regardless of fruit load or leaf age (Fig. 4).

The *E* values in summer were higher in the morning than in the afternoon; the maximum value was recorded at the beginning of July. The values then decreased and remained fairly stable until mid-October, after which they decreased again (Fig. 5). The E values only increased in the late afternoon in October. With the exception of the beginning of July, when the one-year-old leaves on bearing shoots had a slightly higher E value than the leaves on shoots without fruit, the presence of fruit and fruit load did not influence E values. This is in contrast to observations in other plant species (Hucklesby and Blanke 1992, Wibbe and Blanke 1997). The difference may be explained considering that in olive P_N, and consequently g_s, are not enhanced by the presence of fruit. During summer, particularly in the morning, the young leaves showed slightly higher E values than the one-year-old leaves.

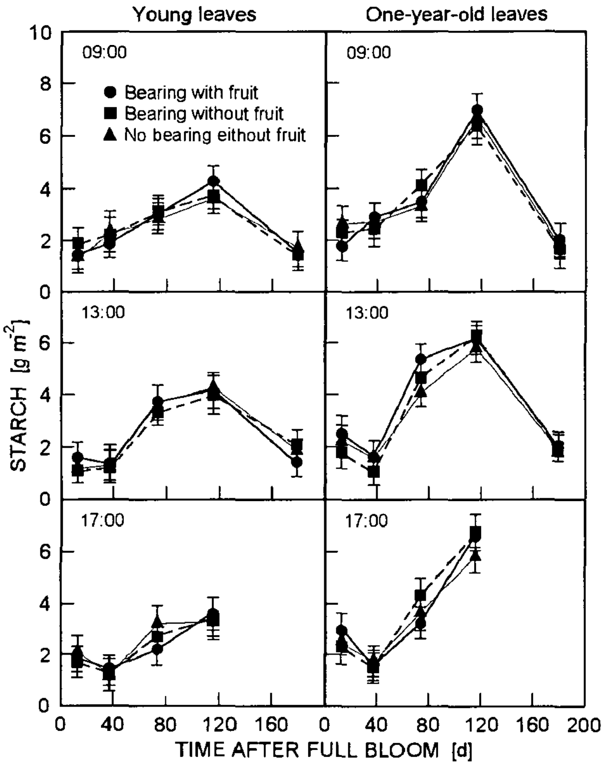

Fig. 9. Effect of fruit load on diurnal starch content of young and one-year-old leaves during fruit development. Each point is the mean of 6 replicates ± standard error.

Leaf water content decreased progressively from July to December with no differences associated with the presence or absence of fruit (Fig. 6). Water content was higher in young leaves than in the one-year-old ones, with greater differences at the beginning of July. During summer there was a slight decrease in leaf water content from the morning to the afternoon.

The presence/absence of fruit on the shoot and fruit load did not substantially influence the Chl and saccharide contents and area dry mass of the leaf (Figs. 7 to 10). The lack of differences associated with fruit presence/absence in the leaf saccharide content and dry matter and the fact that P_N did not change indicates ready translocation of assimilates within the tree.

The Chl content was lower at the end of July and at the beginning of September in comparison to the other periods. In July the one-year-old leaves had a higher Chl content than the young ones, but after that the differences decreased.

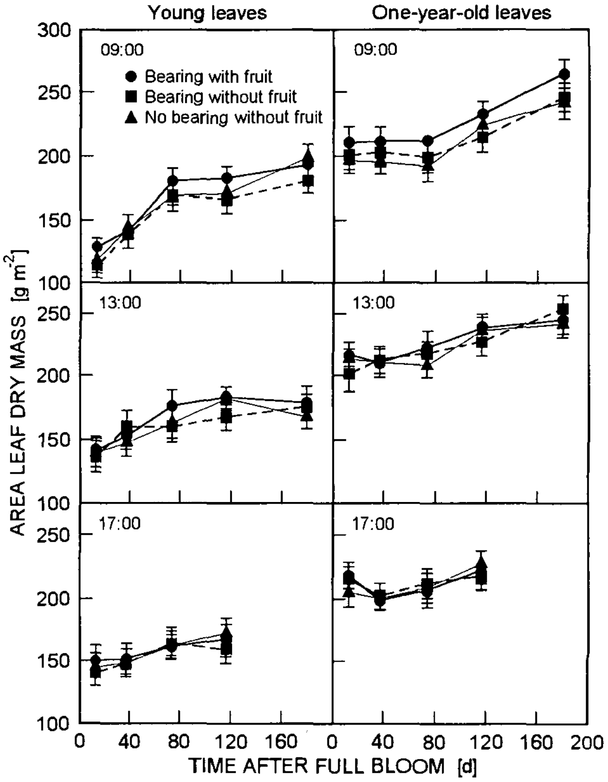

Fig. 10. Effect of fruit load on diurnal leaf area dry mass of young and one-year-old leaves during fruit development. Each point is the mean of 6 replicates ± standard error.

The reducing sugar and starch contents were always slightly higher in one-year-old leaves than in the young ones. In general, content of reducing sugars increased slowly from July to mid-October and then increased rapidly. In July, the starch level was low due to its consumption for vegetative growth and reproductive processes. It increased significantly until mid October and then decreased drastically. A drop in temperature favours the hydrolysis of polysaccharides into soluble saccharides which reduces cold sensitivity. During the day, there was no correlation between the concentration of leaf saccharides and P_N. In spite of the large diurnal differences in P_N, the saccharide content did not change significantly in either young or one-year-old leaves.

The ADM increased with leaf age, whereas during the day there were no substantial variations (Fig. 10).

In contrast to what has been observed in other species (Daie 1985, Tichá *et al.* 1985), the results of this study indicate that the sink demand, associated with fruit growth, in olive does not improve the leaf photosynthetic efficiency. Fruit load did not influence leaf saccharide content, that could be a regulatory factor which matches P_N to sink demand (Daie 1985, Flore and Gucci 1988, Foyer 1988, Stitt *et al.* 1995). Even in the absence of fruit, photosynthates are very efficiently transferred from leaves to other tree organs. As consequence, there is no excessive formation of leaf starch that is temporarily stored in the chloroplasts, as observed in leaves on non-fruiting shoots of other species, which in turn decreases further synthesis, due to a feedback process. In olive, a reduction in P_N due to the accumulation of starch was only found when the translocation of assimilates from the leaves to other tree organs was blocked by obstructing the phloem continuum in non-fruiting shoots by girdling (Proietti and Tombesi 1990). According to Monselise and Goldschmidt (1982), lack of the increase of leaf photosynthetic efficiency in the presence of a fruit sink could also be due to a certain stress caused by the overload of fruit. Considering the leaf water content, no leaf water stress was associated with presence of fruit in olive.

In conclusion, in olive there is no clear correlation between sink demand, associated with a heavy fruit load and the presence of fruit near the leaves, and P_N. The large assimilate consumption and reduction of new leaf area (due to the heavy crop) are not compensated by a higher leaf photosynthetic efficiency. This depletion of saccharide reserves during an "on-year" can negatively influence the flower bud formation leading to a subsequent "off-year". In order to reduce alternation, it is important to increase photosynthetic tree efficiency by ensuring optimal conditions through irrigation, fertilisation, pruning, and pest control. This is especially important when the demand for assimilates is high and during the autumn following a heavy cropping year, while temperatures are still favourable for photosynthesis, because in this way the olive tree, after fruit ripening and harvest, can replace some of the saccharide reserves lost.

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