Diurnal and seasonal changes in photosynthetic characteristics in different olive (Olea europaea L.) cultivars

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Abstract

Diurnal and seasonal changes in photosynthetic characteristics, leaf area dry mass (ADM), and reducing sugar and total chlorophyll (Chl) contents of leaves of Frantoio, Leccino, and Maurino olive cultivars were investigated in Central Italy. Leaf net photosynthetic rate ($P_N$) per unit leaf area changed during the growing season and during the day, but the cultivar did not significantly influence the changes. In both young and one-year-old leaves the highest $P_N$ values were observed in October, while the lowest values were recorded in August and December; during the day the highest $P_N$ values were generally found in the morning. The pattern of photosynthetic response to photosynthetic photon flux density (PPFD) of leaves was similar in the three genotypes. Sub-stomatal CO$_2$ concentration ($C_i$) tended to increase when $P_N$ decreased. The increase in $C_i$ was accompanied by a stomatal conductance to water vapor ($g_s$) decrease. In general, $P_N$ and dark respiration rate ($R_d$) were correlated. Transpiration rate ($E$), with no differences between the cultivars, increased from April to July, decreased greatly in August, then increased in October and finally decreased again in December. Leaf water content increased from April to June, remained high until mid July, decreased significantly in August, remaining constant until December with no differences associated with the cultivar. In both young and one-year-old leaves, the leaf water content per unit leaf area was slightly greater in Frantoio than in the other two cultivars. The one-year-old leaves had a higher Chl content than the young ones. The cultivar did not substantially influence the leaf reducing sugar content which decreased from April to August, when it reached the lowest level, then increased rapidly until October. During the day the reducing sugar content did not change significantly. The leaf ADM was slightly higher in Frantoio than in the other cultivars and one-year-old leaves had higher values than the young ones. Leaf ADM decreased from April to June and then tended to increase until December. During the day there were no substantial variations.

Additional key words: area dry mass; chlorophyll; irradiance response curve; dark respiration rate; reducing sugars; stomatal conductance; sub-stomatal CO$_2$ concentration; transpiration rate.

Introduction

Numerous factors influence fruit tree performance, but high productivity is primarily associated with the ability of the tree to produce large amounts of photosynthates over a wide range of environmental conditions. Therefore, very active photosynthesis during the growing season has always been considered a desirable characteristic. With increasing domestication and selection of cultivated tree crops, the photosynthetic capacity, that is the net rate of CO$_2$ exchange measured under optimal conditions, has been improved (Ceulemans and Saugier 1991). However, the harvestable product of a tree depends not only on photosynthetic carbon uptake by the foliage, but also on the respiration of various organs and the proportion of carbon invested into economically important organs. Consequently the relationship between photosynthesis and yield is very complex and there is only limited evidence of a positive correlation between leaf photosynthetic rate and crop yield (Evans 1975, Daie 1985, Tichá et al. 1985, Ceulemans and Saugier 1991).

$P_N$ is affected by environmental (radiation, temperature, water and nutrient availability, disease, cultural practices, etc.) as well as genetic variables (total area, orientation toward the radiation flux, anatomical structure, Chl content, ribulose-1,5-bisphosphate carboxylase/oxygenase activity of the leaves, etc.). In some species $P_N$ varies among cultivars (Evans 1975) which may be due to higher tolerance of some cultivars to environmental stress and consequently to the higher $P_N$ under poorer conditions.

$P_N$ of olive leaves and the environmental effects on it
have often been studied (Baldy et al. 1985, Bongi et al. 1987, Proietti and Tombesi 1990, Gucci et al. 1997, Proietti and Palliotti 1997, Proietti 1998, 2000, Toggetti et al. 2001), but no comparisons have been made between different cultivars. The aim of this paper was to compare \( P_n \), the relationship between PPFD and \( P_n, E, g_s, C_n, R_d \), and Chl and sugar contents of leaves of three olive cultivars under field conditions throughout the season.

**Materials and methods**

The experiment was conducted in central Italy under natural conditions (Foligno, 43°N latitude), in a 16-year-old non-irrigated olive grove. The soil is clay loam and the trees are trained to the vase system with a spacing of 5x5 m. Climate is characterised by low rainfall and high temperatures during summer. From the beginning of April (first stage of vegetative growth) to mid-December (fruit harvest) of 1998 and 1999, measurements were taken periodically on young fully expanded and one-year-old leaves of Frantoio, Leccino, and Maurino cultivars, taken from well-sunlit shoots with fruit on five trees per cultivar.

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 \( C_l \) were measured using an 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 PPFD 1200-1600 \( \mu \)mol m\(^{-2}\) s\(^{-1}\)). The flow rate of air passing through the chamber was kept at 5 cm\(^{-2}\) s\(^{-1}\) (about 10000 cm\(^{3}\) s\(^{-1}\) m\(^{-2}\) (leaf area)). During gas exchange measurements, the external concentration of \( \text{CO}_2 \) was about 370 cm\(^{-3}\) m\(^{-1}\). The air temperature inside the leaf chamber was 2-4 °C higher than that in the atmosphere (varying from 17 to 25 °C in April, from 25 to 37 °C in June, July, and August, from 16 to 26 °C in October, and from 12 to 16 °C in December). \( R_d \) was measured by covering the chamber with a black cloth screen. The photosynthetic irradiance response curves were determined in mid June at 10:00 by covering the chamber with neutral shading nets to progressive decrease of PPFD until darkness (temperature decreased by about 4 °C as PPFD went from 1300 to 0 \( \mu \)mol m\(^{-2}\) s\(^{-1}\)). An exponential rise to maximum function \[ y = a (1 - e^{bx}) + c \] provided the best fit for the relationship between PPFD and \( P_n \), where \( x \) is PPFD [\( \mu \)mol m\(^{-2}\) s\(^{-1}\)], \( e \) is the base of natural logarithms with values of 2.718, and \( a, b, \) and \( c \) are coefficients. Recordings were taken under steady-state conditions.

After gas exchange measurements, the leaves were immediately taken to the laboratory in a portable refrigerator for the other determinations. Leaf area was measured using a leaf area meter (Hayashi Denkoh, model AAM-7, Tokyo, Japan). Half of the leaves were then used to determine the contents of Chl (Bruinsma 1963) and reducing sugars (Morris 1948). Leaf ADN 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 and discussion**

Leaf size was larger in Leccino and Frantoio (5.5±0.5 and 5.7±0.6 cm\(^2\), respectively) than in Maurino (4.1±0.4 cm\(^2\)).

\( P_n \) per unit leaf area changed with the growing season and during the day, but there was no cultivar effect. The only exception was in the morning at the beginning of April and in mid June when both the young and one-year-old leaves of Frantoio had a higher \( P_n \) value than the leaves of the other cultivars (Fig. 1).

With no differences between the cultivars during the growing season, considering the entire day, the highest \( P_n \) values occurred in October, while the lowest ones were found in August and December. These trends confirm those obtained by Proietti (2000). The high \( P_n \) values in October were probably due to the temperature, which was still favourable for photosynthesis, associated with good water availability. This is important because during autumn, particularly in heavy cropping years, the olive tree can replace some of the saccharide reserves lost during shoot and fruit growth. The low \( P_n \) values were due to high temperatures and/or low water availability in mid-summer and to low temperatures in December. The effect of high temperature on the reduction of photosynthetic capacity could be due to chloroplast damage (Matos et al. 1998).

Angeloopoulos et al. (1996) found that the highest \( P_n \) values were generally found in the morning, due to optimum temperatures and humidity; subsequently, with higher temperatures and lower humidity, the values declined. The only exception occurred in October when the \( P_n \) was similar during the entire day, probably because of optimum temperatures and water availability also in the afternoon.

In each cultivar, there were no substantial differences between the \( P_n \) values of young and one-year-old leaves.

The pattern of photosynthetic response of leaves to PPFD was similar in the three genotypes, without substantial differences between young and one-year-old leaves (Fig. 2). \( P_n \) per unit leaf area was saturated by
DIURNAL AND SEASONAL CHANGES IN PHOTOSYNTHETIC CHARACTERISTICS

Fig. 1. Diurnal net photosynthetic rate ($P_N$) of young and one-year-old leaves of Leccino, Frantoio, and Maurino cultivars during the growing season. Each point is the mean of 5 replicates ± standard error.

Fig. 2. Photosynthetic irradiance response curves of young and one-year-old leaves of Leccino, Frantoio, and Maurino cultivars.

PPFD at 1000-1200 μmol(photon) m⁻² s⁻¹; at around 400 μmol m⁻² s⁻¹ the $P_N$ was half that at photon saturation. The compensation irradiance was 60-70 μmol m⁻² s⁻¹ and $R_0$ was about −2 μmol(CO₂) m⁻² s⁻¹. The apparent quantum yield [μmol(CO₂) μmol⁻¹( photon)], calculated from the linear part of the photosynthetic irradiance response curve, was 0.030, 0.027, and 0.029 in young leaves and 0.027, 0.023, and 0.032 in 1-year-old leaves for Leccino, Frantoio, and Maurino, respectively.

$C_t$ tended to increase when $P_N$ decreased (Fig. 3);

Fig. 3. Diurnal sub-stomatal CO₂ concentration ($C_t$) of young and one-year-old leaves of Leccino, Frantoio, and Maurino cultivars during the growing season. Each point is the mean of 5 replicates ± standard error.

Fig. 4. Diurnal stomatal conductance to water vapour ($g_s$) of young and one-year-old leaves of Leccino, Frantoio, and Maurino cultivars during the growing season. Each point is the mean of 5 replicates ± standard error.

173
only in mid July, when $C_1$ had the lowest values of the entire period, there were low $P_N$ values. The increase in $C_1$ was accompanied by a decrease in $g_s$ (Fig. 4). The high $C_1$ values at low $g_s$ values suggest that the lower $P_N$ values in August or December and in the afternoon were not caused primarily by the lower $g_s$, but rather by nons stomatal effects, as reported by Angelopoulos et 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 $P_N$ in the summer could be the result of damage to the photosystem induced by high temperature and drought stress.

![Fig. 5. Diurnal dark respiration rate ($R_D$) of young and one-year-old leaves of Leccino, Frantoio, and Maurino cultivars during the growing season. Each point is the mean of 5 replicates ± standard error.](image1)

In general, but not always, $P_N$ and $R_D$ were correlated (Fig. 5). From April to August the young leaves had an $R_D$ slightly higher than the one-year-old leaves.

$E$ increased from April to July when it reached the maximum. It decreased sharply in August, then increased in October, and finally decreased again in December (Fig. 6). There were no substantial differences between cultivars.

![Fig. 6. Diurnal transpiration rate ($E$) of young and one-year-old leaves of Leccino, Frantoio, and Maurino cultivars during the growing season. Each point is the mean of 5 replicates ± standard error.](image2)

Leaf water content increased from April to June, remained high until mid-July, and then greatly decreased in August, being constant until December, with no differences associated with the cultivar (Fig. 7). In June and July, the water content was slightly higher in young leaves than in the one-year-old leaves. No substantial differences were found during the day with the exception of slightly higher water content in the afternoon from April to July.

![Fig. 7. Diurnal water content of young and one-year-old leaves of Leccino, Frantoio, and Maurino cultivars during the growing season. Each point is the mean of 5 replicates ± standard error.](image3)

The Chl content per unit leaf area, both in young and in one-year-old leaves, was slightly higher in Frantoio than in the other two cultivars (Fig. 8). In one-year-old leaves the Chl content of Maurino tended to be slightly higher than in Leccino, whereas the opposite was observed in the young leaves. In general the one-year-old leaves had a higher Chl content than the young ones.

The cultivar did not substantially influence the leaf reducing sugar content (Fig. 9). The reducing sugar
DIURNAL AND SEASONAL CHANGES IN PHOTOSYNTHETIC CHARACTERISTICS

Fig. 8. Total chlorophyll (Chl) content of young and one-year-old leaves of Leccino, Frantoio, and Maurino cultivars during the growing season. Each point is the mean of 5 replicates ± standard error.

Fig. 9. Diurnal content of reducing sugars of young and one-year-old leaves of Leccino, Frantoio, and Maurino cultivars during the growing season. Each point is the mean of 5 replicates ± standard error.

content, above all in October and December, was slightly higher in one-year-old leaves than in the young ones. In general, the content of reducing sugars decreased from April to August, when it reached the minimum, then increased rapidly until October. The decrease from April to August was due to consumption for vegetative growth and reproductive processes. In particular, the lower values in August were due to the consumption for fruit growth associated with the low $P_N$ in this period. The increase in reducing sugars observed until October was due to the high $P_N$ and probably to a cold acclimation mechanism. During the day, in spite of the large diurnal differences in $P_N$, the reducing sugar content did not change significantly in either young or one-year-old leaves. Evidently, photosynthates are very efficiently transferred from leaves to other tree organs.

The leaf ADM tended to be slightly higher in Frantoio than in the other cultivars. This suggests that $P_N$ per unit leaf mass in Frantoio is slightly lower than in Leccino and Maurino. One-year-old leaves had higher values than the young ones. In general, leaf ADM decreased from April to June and then tended to increase until December (Fig. 10). During the day there were no substantial variations.

Fig. 10. Diurnal leaf area dry mass (ADM) of young and one-year-old leaves of Leccino, Frantoio, and Maurino cultivars during the growing season. Each point is the mean of 5 replicates ± standard error.

In conclusion, in contrast to what has been observed in other plant species (Evans 1976), our results indicate that the Leccino, Frantoio, and Maurino olive cultivars, under the conditions considered, did not have a different leaf $P_N$ per unit leaf area. In general, all parameters studied showed only few significant differences between the three cultivars. The exception was the larger leaf size in Leccino and Frantoio compared to Maurino and the greater leaf ADM and Chl content in Frantoio per unit leaf area compared to the other cultivars. The negative correlation between leaf size and $P_N$, reported by some authors in herbaceous species (Evans 1976), was not found. Absence of correlation between Chl content and $P_N$ was observed by Martin et al. (1997) in pear species.

Obviously, before excluding differences in photo-
synthetic capacity between the tested cultivars, it is necessary to carry out other trials in different locations and years in order to study the behaviour under a range of conditions. Furthermore, it is important to consider that $P_N$ of a canopy is basically the combination of $P_N$ of all leaves that form the canopy (Ceulemans and Saugier 1991). Therefore, in order to define the $P_N$ of the tree, it is necessary to consider not only the photosynthetic response of the single leaf but also the canopy structure (leaf area index, total leaf area, leaf orientation toward radiation flux), which varies considerably between cultivars. The canopy structure influences the profile of radiation and $P_N$ within the crown (Evans 1975). This and further studies on the carbon balance in relation to cultivar variation may contribute to yield improvements.

References