

Photosynthetic behavior of Spanish Arbequina and Italian Maurino olive (*Olea europaea* L.) cultivars under super-intensive grove conditions

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Abstract

The study was carried out in a four-year-old super-high density olive grove in Central Italy to compare leaf gas exchanges of Spanish Arbequina and Italian Maurino olive cultivars. Overall, from mid July to mid November, Maurino had a slightly higher maximum light-saturated net photosynthetic rate (P_{Nmax}) than Arbequina. The lowest and the highest P_{Nmax} values were recorded at the end of July and in mid November, respectively. Current-season leaves showed similar or slightly higher P_{Nmax} values than one-year-old leaves. During the day Maurino always had slightly higher values or values similar to Arbequina, with the highest P_{Nmax} being in the morning. Maurino had similar or higher dark respiration rate (R_D) values compared to Arbequina. During the day, in both cultivars the R_D was lower at 9:00 than in the afternoon. The pattern of the photosynthetic irradiance-response curve was similar in the two genotypes, but the apparent quantum yield (Y_Q) was higher in Maurino. In both cultivars intercellular CO_2 concentration (C_i) tended to increase when P_{Nmax} decreased. The increase in C_i corresponded to a decrease in stomatal conductance (g_s). The transpiration rate (E) increased from mid July to the beginning of August, then decreased in September and increased again in November. Particularly in the morning, the current-season leaves showed similar or slightly higher E values than the one-year-old leaves. During the day, in both cultivars and at both leaf ages, E was higher in the afternoon. No effects on leaf gas exchanges due to the presence or absence of fruit on the shoot were found. Overall, there was satisfactory physiological adaptation for Arbequina to the conditions of Central Italy and for Maurino to the super-intensive grove conditions.

Additional key words: cultivar differences, dark respiration rate; intercellular CO_2 concentration; irradiance response curve; stomatal conductance; transpiration rate.

Introduction

In many countries, e.g. Italy, traditional olive growing is undergoing a period of crisis because of the high demand for manpower and the consequent high production costs, which reduce product competitiveness on the international scene. In fact, the olive oil market is becoming increasingly more globalized and the average world prices are now basically leveled at values below the production costs of some countries. Consequently, the economic sustainability of olive growing in Italy and other countries is linked to the ability to fully mechanize farming operations to reduce manpower and to lower production costs, while maintaining high production standards, in terms of quantity and quality.

In some situations, the intensive olive growing system (400–600 trees per ha) has met these requirements. However the reduction of production costs cannot go beyond certain limits, because the use of mechanized harvesting in the intensive system is discontinuous and pruning must be still performed manually or, even in the case of partial mechanization, significant manual finishing operations are required.

A new olive growing system that could potentially allow further reduction in production costs is the super-intensive olive grove (super-high-density system), with 1,600–2,000 trees per ha. In this system, trees are trained to form hedgerows, orchards can be brought into produc-

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Abbreviations: C_i – intercellular CO_2 concentration; E – transpiration rate; g_s – stomatal conductance; LAI – leaf area index; P_N – leaf net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; PPFD – photosynthetic photon flux density; R_D – dark respiration rate; Y_Q – apparent quantum yield.

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tion within only a few years after planting and over-the-row mechanical harvesters can be used (Camposeo and Godini 2010, Giametta and Bernardi 2010, Tous *et al.* 2010). The use of over-the-row mechanical harvesters allows the time and labor required for harvesting to be significantly reduced and consequently the cost; in fact, one hectare can be harvested in only 3–4 h with 2 operators. Also pruning can be largely mechanized in this kind of olive grove. It can be done with a mower and manual finishing, for a total time of about 30–40 h per ha per year.

To be cost-effective, the trees in a super-intensive olive grove must produce well (3–4 t per ha) as early as the 2nd–3rd year and reach full production (7–12 t per ha) at around the 5th year, which should continue, as much as possible, for at least 15 years. Another fundamental requirement is that the tree hedgerows must be kept at a size compatible with that of the shaking chamber of the mechanical harvesters, *i.e.* lower than 2.5–3.5 m in height and 1.5–2 m in width. These dimensions could be obtained by using low vigour cultivars, otherwise because of the heavy pruning required, an imbalance between vegetative and reproductive activity could occur. Therefore, it is essential that the cultivars used in super-intensive olive groves have a very low vigour (Tous *et al.* 2008, 2010).

On the basis of worldwide evaluations of olive cultivars, at the present time, three olive cultivars are considered to meet these requirements quite well. They are the Spanish Arbequina and Arbosana and the Greek Koroneiki. However, considering the vegetative and productive aspects, it is currently widely accepted that among these cultivars, Arbequina is the best for super-intensive olive groves (De La Rosa *et al.* 2007, Tous *et al.* 2008, 2010; Camposeo and Godini 2010). Consequently, Arbequina is progressively being introduced into new environments in all olive-growing countries.

The restriction of using only certain cultivars is one of the problems of this new planting system. There is insufficient knowledge about the adaptation of these cultivars to environments different from those of origin, and standardization of the sensory quality of the oil could occur using only the very few cultivars that have thus far been deemed suitable.

In many olive-growing countries super-intensive olive groves have been recently established, but there is still very scarce information on the response of the cultivars

introduced (Arbequina, in particular) to the specific climatic and cultural conditions, which may differ from those of origin (Allalout *et al.* 2009, 2011). Furthermore, there is little information on the suitability of using local cultivars in this new planting system. The identification of local cultivars adapted to super-intensive olive groves would allow costs to be reduced without causing a significant standardization of the sensory quality of the oil. This is important considering the growing sensitivity of consumers towards using different kinds of extra virgin olive oil in relation to individual taste and use.

In this context, it is very important to study the productive and vegetative behaviour of different cultivars grown under super-intensive olive grove conditions in different areas. Tree productivity is directly dependent on the photosynthetic capacity of the leaves (Gregoriou *et al.* 2007). The photosynthetic assimilation of the tree is affected by many factors, both internal (total leaf area, leaf orientation, leaf age, sink presence, anatomical structure, content of chlorophyll and enzymes, *etc.*) and environmental (light levels that occur in different portions of the canopy, temperature, availability of water and nutrients, CO₂ concentration, pests, *etc.*) (Ceulemans and Saugier 1991, Proietti and Famiani 2002). Therefore, to estimate the suitability of different cultivars grown under the super-intensive olive grove conditions and to improve the cultivation systems in the different areas, knowledge of leaf photosynthetic behaviour is very important.

Little is known about the daily and seasonal photosynthesis of different cultivars grown under super-intensive olive grove conditions. Also the influence of leaf age and fruiting in such conditions is not well known.

The objective of the present study was to compare the net photosynthetic rate (P_{Nmax}) of current-season and one-year-old leaves from vegetative and fruiting shoots of the Spanish cultivar Arbequina and the Italian cultivar Maurino under super-intensive olive grove conditions in Central Italy. The Arbequina cultivar was chosen to evaluate its acclimation to the specific environment of Central Italy (Allalout *et al.* 2011). Maurino, one of the most important cultivars in Central Italy, was chosen because of its low-to-medium vigour and erect growth habit, indicating it as one of the best for this kind of planting system.

Materials and methods

Plant material: The trial was carried out in 2010 in a four-year-old super-intensive olive (*Olea europaea* L.) grove at Deruta in Central Italy (12°42'E, 42°96'N, about 350 m a.s.l.). The trees of the Arbequina and Maurino cultivars were trained to the central axis system with a spacing of 4.5 × 1.5 m (1,666 trees per ha), with rows oriented north-south. The soil is medium textured and was kept under clean cultivation throughout the entire

growing season. The climate is Mediterranean with hot, dry summers and cold winters, having an annual average rainfall from 800 to 1,000 mm (Fig. 1).

The trees had never been pruned, with the exception of eliminating branches at the basal part of the trunk (up to 50 cm in height) to allow for mechanical soil management and harvesting with an over-the-row mechanical harvester. From the end of June to mid-September,

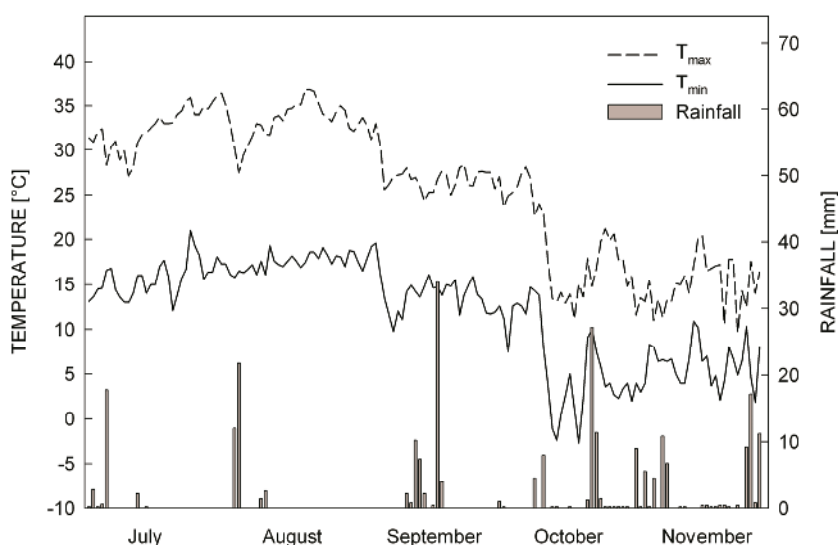


Fig. 1. Daily minimum and maximum air temperatures and rainfall of the area considered.

supplementary irrigation was applied about every four days using drip lines (about 200 m³ per ha per year). The olive grove was fertilized by spreading 200 kg per ha of urea (46% N) and 100 kg per ha of a complex fertilizer (8–24–24 N–P–K) on the soil in the first ten days of May and 100 g per tree of ammonium nitrate (34% N) in the first decade of July. Phytosanitary treatments were carried out against *Margaronia unionalis* and the *Cycloconium oleaginum*.

Leaf net photosynthetic rate (P_N), dark respiration rate (R_D), stomatal conductance (g_s), transpiration rate (E) and intercellular CO₂ concentration (C_i): Gas exchanges were determined on cloudless days on six current-season leaves (taken from the mid portion of current-season shoots) and on six one-year-old leaves (taken from the mid portion of one-year-old shoots) for each measurement. Leaves were randomly sampled from well-lit canopy portions of six trees per cultivar having vegetative and productive characteristics representative of the entire olive grove. Measurements were made in mid July, at the end of July, at the beginning of August and September and in mid November, in the morning (from 9:00 to 10:30 h) [incoming photosynthetic photon flux density (PPFD) about 1,700–1,900 and 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, in July–August–September and November]. In mid July and at the beginning of September the influence of fruit on leaf gas exchanges was determined on the current-season and one-year-old leaves on vegetative and fruiting shoots.

At the beginning of August and September, leaf R_D and the photosynthetic irradiance-response curve were determined. On these dates, diurnal gas exchanges were also determined at 9:00–10:30, 12:00–13:30, and 16:30–18:00 h. Gas exchanges were determined for both current-season and one-year-old leaves, while irradiance-response curves were determined on one-year-old leaves, only.

Gas exchanges were determined using a portable ADC

LCA-3 gas-exchange analyzer (*Analytical Development Company Ltd.*, Hoddesdon, UK) and a Parkinson-type assimilation chamber. Detached leaves were enclosed in the chamber and exposed perpendicularly to the sunrays. The flow rate of air (dried to a constant water content of about 20%) passing through the chamber was kept at 5 cm³ s⁻¹. During gas-exchange measurements, the external CO₂ concentration was about 375 cm³ m⁻³ and the air temperature inside the leaf chamber was 2–4°C higher than that in the atmosphere (varying from 28 to 32°C in July and August, 25 to 29°C in September and 14 to 17°C in November). Measurements were taken under steady-state conditions (about 30 s). R_D was measured by covering the chamber with a black cloth screen. P_N , R_D , g_s and E are expressed on a leaf-area basis.

The photosynthetic irradiance-response curves were determined in mid-morning (from 9:00 to 10:30 h) on three one-year-old leaves for each measurement, with PPFD decreasing progressively from the highest intensity to complete darkness (P_N values were taken at about 1,800; 1,300; 1,000; 800; 600; 400; 200; 100; 50; 30; 10, and 0 $\mu\text{mol PPFD m}^{-2} \text{s}^{-1}$), without changing the spectral composition, by covering the chamber with neutral shading screens (the temperature decreased about 4°C as PPFD went from 1,800 to 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

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 [$\mu\text{mol m}^{-2} \text{s}^{-1}$], e is the base of natural logarithms with a value of 2.72, and a , b , and c are coefficients.

In the linear portion of the photosynthetic irradiance-response curve, the apparent quantum yield (Y_Q) was calculated as the ratio between the increase in P_N and PPFD ($Y_Q = \Delta P_N / \Delta \text{PPFD}$).

Statistical analysis: All data were statistically analyzed by *ANOVA* and the averages were compared using the *Student-Newman-Keuls* test.

Results

The rainfall pattern in the trial year was characterized by scant rainfall in July (24.0 mm) and August (37.8 mm) (Fig. 1). The daily maximum air temperature showed peak values at the end of July (36.4°C) and in mid August (36.9°C).

P_{Nmax} per unit leaf area changed during the growing season and during the day, and there was a cultivar effect. From mid July to mid November, in both current-season and one-year-old leaves, Maurino had a slightly higher P_{Nmax} than Arbequina (Fig. 2). In both cultivars, current-season leaves had similar or slightly higher P_{Nmax} than one-year-old leaves. The lowest P_{Nmax} values were recorded at the end of July, when the daily maximum

temperatures were very high (around 35°C) and the soil water content was very low due to the prolonged absence of rainfall, while the highest one was in November, when the daily maximum temperature was around 18°C and there was high water availability in the soil (Fig. 1).

The diurnal P_{Nmax} measurements, taken at the beginning of August and of September, showed that during the day Maurino always had values slightly higher or similar to Arbequina (Fig. 3). The highest P_{Nmax} , for both Arbequina and Maurino was in the morning (around 9:00 h); then, probably due to the increase in temperature, there was a significant decrease around 12:00 h and even more so around 16:30 h. In the morning current-season leaves

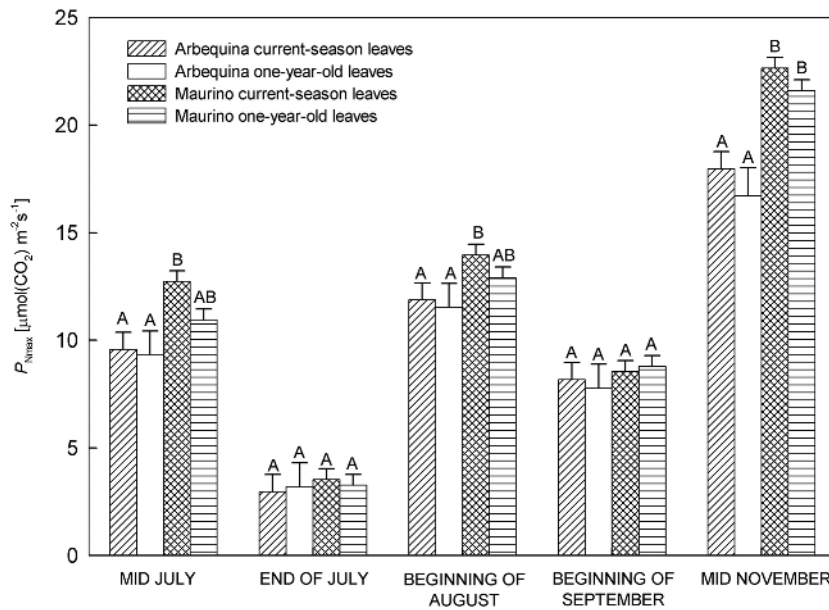


Fig. 2. Light-saturated net photosynthetic rate (P_{Nmax}) of current-season and one-year-old leaves in Arbequina and Maurino cultivars. For each time, means followed by *different letters* are significantly different at $P \leq 0.05$. Each point is the mean of 6 replicates \pm SE.

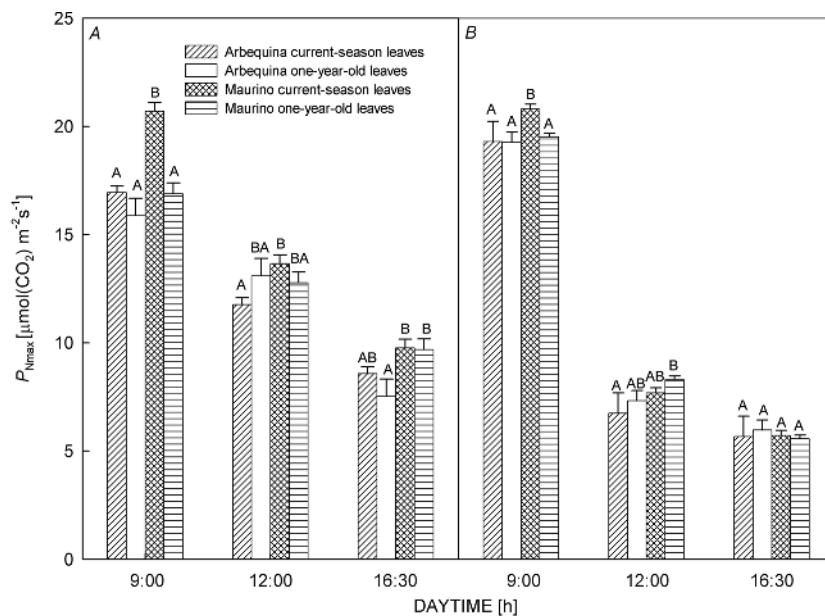


Fig. 3. Diurnal light-saturated net photosynthetic rate (P_{Nmax}) of current-season and one-year-old leaves in Arbequina and Maurino cultivars at the beginning of August (A) and September (B). For each time and day time, means followed by *different letters* are significantly different at $P \leq 0.05$. Each point is the mean of 6 replicates \pm SE.

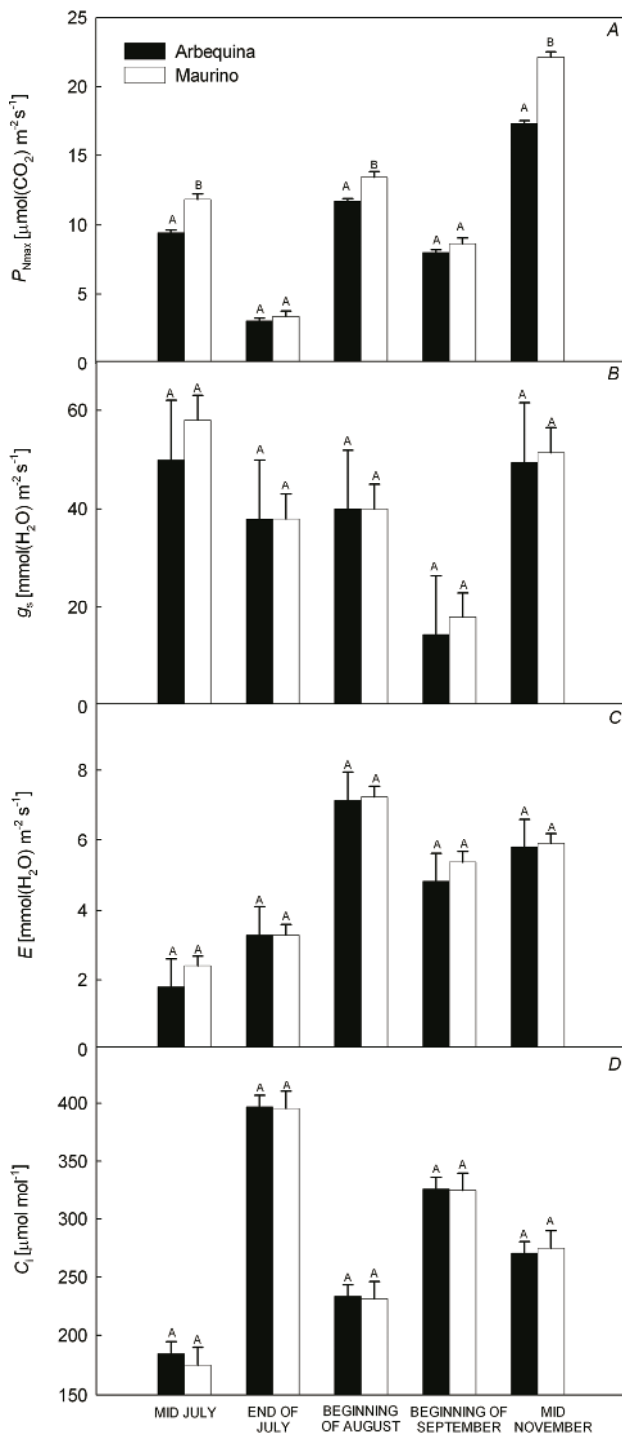


Fig. 4. Light-saturated net photosynthetic rate (P_{Nmax}), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) of current-season and one-year-old leaves in Arbequina and Maurino cultivars. Each point is the average of current-season and one-year-old leaves. For each parameter and time, means followed by *different letters* are significantly different at $P \leq 0.05$. Each point is the mean of 6 replicates \pm SE.

had a slightly higher P_{Nmax} than one-year old leaves, but at 12:00 and 16:30 h the differences disappeared.

Maurino had similar or higher R_D values compared to Arbequina (data not shown). No differences in R_D were found between current-season and one-year-old leaves. Unlike P_{Nmax} in both cultivars and at both leaf ages, R_D was higher at the beginning of September than at the beginning of August. During the day, regardless of cultivar or leaf age, R_D was lower at 9:00 than at 16:30 h and above all at 12:00 h.

The pattern of the photosynthetic irradiance-response curve was similar in the two genotypes. P_N per unit leaf area was saturated by PPFD at 1,100–1,200 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$; at 400–450 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$, the P_N was half that at photon saturation. The compensation irradiance was 50–60 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$ and R_D was about $-1.5 \mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$. The Y_Q , calculated from the linear part of the photosynthetic irradiance-response curve, was higher in Maurino [$0.015 \text{ mol}(\text{CO}_2) \text{ mol}^{-1}(\text{photon})$] than in Arbequina [$0.010 \text{ mol}(\text{CO}_2) \text{ mol}^{-1}(\text{photon})$].

In both cultivars and in both current-season and one-year-old leaves, C_i tended to increase when P_{Nmax} decreased (Fig. 4). The increase in C_i was accompanied by a decrease in g_s , although with different intensity at the different dates.

In both cultivars, probably due to the increase in the daily maximum temperatures from around 28 to 35°C, E increased from mid July, when the lowest values were observed, to the beginning of August when the maximum values were reached; then, it decreased in September, following the reduction in g_s , and increased in November (Fig. 4). From mid July to the end of July, despite the increase in E , g_s decreased, even if it remained relatively high, following the trend of P_{Nmax} . It seems that high levels of E are compatible with a not very high g_s .

The current-season leaves, particularly in the morning, had similar or slightly higher E values than the one-year-old leaves (Table 1). During the day, in both cultivars and at both leaf ages, E was higher at 12:00 h at the beginning of August and at 16:30 h at the beginning of September.

Comparing current-season and one-year-old leaves of vegetative and fruiting shoots (in mid July and at the beginning of September), no effect on leaf gas exchanges due to the presence or absence of fruit on the shoots was found. The only exception was in Maurino in mid July when the one-year-old leaves on shoots with fruit had a higher P_{Nmax} value than the leaves on shoots without fruit (Table 2).

Discussion

The results obtained in this trial in the four-year-old super-high density olive grove in Central Italy indicate that Maurino had a slightly higher P_{Nmax} per unit leaf area at saturating light conditions and a higher Y_Q compared to Arbequina. This could be one of the reasons for the higher production efficiency (calculated by expressing production over both the trunk cross sectional area and the leaf area per tree) of Maurino (3.52 kg of olives per tree, 0.76 kg of olives per m² leaf area, and 0.33 kg of olives per cm² trunk sectional area) than Arbequina (2.31 kg of olives per tree, 0.43 kg of olives per m² leaf area, and 0.24 kg of olives per cm² trunk sectional area), which was observed in the same olive grove by Proietti *et al.* (2011).

Overall, Arbequina showed satisfactory levels of P_{Nmax} , which indicate a good adaptation to the environment considered.

In Maurino, not only P_{Nmax} but also R_D values were similar or higher than in Arbequina. These results would indicate a higher metabolism of Maurino compared to Arbequina in the environment studied.

The lowest values of P_{Nmax} were recorded at the end of July in both cultivars. This could be due to very high

daily maximum temperatures (around 35°C) and a persistent drought that was not fully compensated by supplementary irrigation; the highest P_{Nmax} values, found in November, were presumably due to the greater water availability and the still mild daily maximum temperatures (around 18°C). This trend confirms that obtained by Proietti and Famiani (2002) for Leccino, Frantoio, and Maurino cultivars in environmental conditions similar to those of this trial. As suggested by Ben Ahemed *et al.* (2007), the large decrease in P_{Nmax} , which occurred at the end of July and at the beginning of September, could be linked not only to insufficient water availability but also to a resting phase that the olive goes into when temperatures are very high in order to avoid damaging its survival mechanism.

The higher P_{Nmax} in both cultivars of current-season leaves compared to one-year-old leaves during the period considered (mid-July to beginning of November), as observed by Proietti (2000) for the Leccino cultivar and Hagidimitriou and Pontikis (2005) for the most important Greek olive cultivars, could be attributed to the onset of senescence in the one-year-old leaves and/or to the reduced PPFD availability on the leaf surface of

Table 1. Diurnal transpiration rate (E) of current-season and one-year-old leaves in Arbequina and Maurino cultivars at the beginning of August and September. For each column, means followed by *different letters* are significantly different at $P \leq 0.05$. Each value is the mean of 6 replicates \pm SE.

Cultivar	Leaves	E [mmol(H ₂ O) m ⁻² s ⁻¹]					
		Beginning of August			Beginning of September		
		9:30	12:30	16:30	9:30	12:30	16:30
Arbequina	Current-season	8.16 \pm 0.7 ^B	8.33 \pm 0.9 ^A	6.12 \pm 0.7 ^A	3.93 \pm 0.5 ^A	5.37 \pm 0.7 ^A	7.06 \pm 0.2 ^B
	One-year-old	7.00 \pm 0.3 ^A	7.41 \pm 0.8 ^A	6.13 \pm 0.8 ^A	3.68 \pm 0.4 ^A	4.88 \pm 0.8 ^A	5.66 \pm 0.8 ^A
Maurino	Current-season	7.60 \pm 0.2 ^B	8.22 \pm 0.8 ^A	6.08 \pm 0.9 ^A	5.05 \pm 0.6 ^B	6.37 \pm 0.2 ^B	5.77 \pm 0.8 ^A
	One-year-old	6.45 \pm 0.4 ^A	8.36 \pm 0.9 ^A	6.66 \pm 0.9 ^A	4.96 \pm 0.5 ^B	5.17 \pm 0.9 ^A	6.51 \pm 0.3 ^A

Table 2. Light-saturated net photosynthetic rate (P_{Nmax}), transpiration rate (E), stomatal conductance (g_s), and intercellular CO₂ concentration (C_i) of current-season and one-year-old leaves on vegetative and fruiting shoots in Arbequina and Maurino cultivars, in mid July and at the beginning of September. For each column and time, means followed by *different letters* are significantly different at $P \leq 0.05$. Each value is the mean of 6 replicates \pm SE.

Cultivar	Leaves	P_{Nmax} [μ mol(CO ₂) m ⁻² s ⁻¹]		E [mmol(H ₂ O) m ⁻² s ⁻¹]		g_s [mmol(H ₂ O) m ⁻² s ⁻¹]		C_i [μ mol mol ⁻¹]	
		No fruit	With fruit	No fruit	With fruit	No fruit	With fruit	No fruit	With fruit
Mid July									
Arbequina	Current-season	9.26 \pm 0.9 ^A	9.57 \pm 0.9 ^A	1.39 \pm 0.6 ^A	1.24 \pm 0.09 ^A	52.97 \pm 5.5 ^B	45.94 \pm 5.8 ^B	171 \pm 8.4 ^A	179 \pm 8.4 ^A
	One-year-old	9.30 \pm 0.9 ^A	9.33 \pm 0.9 ^A	1.48 \pm 0.4 ^A	1.44 \pm 0.10 ^A	55.76 \pm 6.5 ^B	54.11 \pm 5.5 ^B	185 \pm 7.4 ^A	189 \pm 10.8 ^A
Maurino	Current-season	12.64 \pm 1.1 ^B	12.73 \pm 1.2 ^B	2.25 \pm 0.9 ^A	2.04 \pm 0.80 ^A	94.37 \pm 7.1 ^C	86.01 \pm 8.5 ^C	174 \pm 9.4 ^A	165 \pm 14 ^A
	One-year-old	10.04 \pm 1.2 ^A	12.99 \pm 1.3 ^B	0.83 \pm 0.55 ^A	0.83 \pm 0.42 ^A	31.51 \pm 4.9 ^A	30.49 \pm 5.0 ^A	184 \pm 8.2 ^A	183 \pm 9.2 ^A
Beginning of September									
Arbequina	Current-season	8.29 \pm 0.5 ^A	8.35 \pm 0.8 ^A	3.90 \pm 0.4 ^A	3.93 \pm 0.9 ^A	14.83 \pm 1.9 ^A	14.79 \pm 1.6 ^A	199 \pm 9.9 ^A	198 \pm 8.8 ^A
	One-year-old	8.25 \pm 0.9 ^A	8.33 \pm 0.8 ^A	3.27 \pm 0.8 ^A	3.68 \pm 0.8 ^A	12.24 \pm 3.0 ^A	13.85 \pm 2.5 ^A	200 \pm 11.8 ^A	209 \pm 8.2 ^A
Maurino	Current-season	9.78 \pm 0.9 ^A	9.31 \pm 0.9 ^A	4.77 \pm 1.0 ^A	5.05 \pm 0.9 ^A	18.61 \pm 3.6 ^A	19.50 \pm 3.2 ^A	219 \pm 10.9 ^B	206 \pm 8.2 ^A
	One-year-old	9.18 \pm 0.8 ^A	9.49 \pm 0.8 ^A	4.34 \pm 0.9 ^A	4.96 \pm 0.5 ^A	16.89 \pm 1.6 ^A	18.66 \pm 0.9 ^A	218 \pm 9.3 ^B	217 \pm 11.4 ^A

one-year-old shoots compared with that of the current-season shoots: PFD availability, determined in July in the morning, on average was about 25% higher in current-season leaves (PPFD about $830 \mu\text{mol m}^{-2} \text{s}^{-1}$) than in one-year-old leaves, without substantial differences between the cultivars.

The developing olive fruit is a strong sink that requires a continuous supply of building materials (Proietti *et al.* 1999), but, in contrast to what has been observed in other species (Daie 1985) and according to Proietti (2000) and Hagidimitriou and Pontikis (2005), the results of this study indicate that the sink demand associated with fruit growth in olive does not improve the leaf photosynthetic efficiency of leaves near the fruit. Fruit load can influence leaf saccharide content that could be a regulatory factor which matches P_N to sink demand (Daie 1985, Foyer 1988). Evidently, in olive, even in the absence of fruit, photosynthates are very efficiently transferred from leaves to other tree organs, avoiding the excessive formation of leaf starch that is temporarily stored in the chloroplasts, as observed in leaves on nonfruiting shoots of other species, which in turn decreases further synthesis, due to a feedback process. Actually, in olive, nutrients for fruit development are supplied mostly by the leaves on the same shoot where the fruit is attached, but the fruit can also attract substances, if available, from other nearby parts (Rallo and Suarez 1989, Proietti and Tombesi 1996).

The high C_i values at low g_s values suggest that the lower $P_{N_{\max}}$ values at the end of July or at the beginning of September were not caused primarily by the lower g_s but rather by nonstomatal effects, as reported by Angelopoulos *et al.* (1996), Matos *et al.* (1998), and Proietti (2000). According to some authors (Pearcy *et al.* 1977, Beyschlag *et al.* 1987, Angelopoulos *et al.* 1996), the lower $P_{N_{\max}}$ 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 decreasing $P_{N_{\max}}$ during the season and during the day, also by influencing R_D values. It is possible to suppose that the increase in C_i due to reduction in $P_{N_{\max}}$ caused stomatal closure, with a consequent decrease in g_s .

In contrast to observations in other plant species (Wibbe and Blanke 1997), the presence of fruit did not influence E values. This difference may be explained considering that $P_{N_{\max}}$ in olive, and consequently g_s , was not enhanced by the presence of fruit.

In conclusion, unlike what was observed by Proietti

and Famiani (2002), who did not find different $P_{N_{\max}}$ per unit leaf area comparing the three cultivars Leccino, Frantoio, and Maurino, largely diffused in Central Italy, and according to Hagidimitriou and Pontikis (2005), who found differences in the leaf CO_2 assimilation rate among the most important Greek olive cultivars, in this trial a cultivar effect was found comparing Maurino with Arbequina, a Spanish cultivar that has been recently introduced in some regions of Italy to establish super-intensive olive groves. The satisfactory $P_{N_{\max}}$ response of Maurino to this kind of planting system is of great interest in an effort to improve productive competitiveness, maintaining, at the same time, the sensorial differentiation of the olive oils. Overall, the gas-exchange results indicate that Arbequina also had a satisfactory physiological adaptation to the environment considered and hence there are no counter indications to the introduction of this cultivar in Central Italy.

The results of this study contribute to understanding the gas-exchange behaviour and to evaluating the potential production of different cultivars in super-high density olive groves in new environments using a local or the Spanish Arbequina cultivar. However, since the total net photosynthesis of a canopy is the result of combining the P_N of all the leaves that form the canopy (Ceulemans and Saugier 1991), to evaluate the total net photosynthesis of the tree, not only the P_N response of a single leaf to light has to be considered, but also the structure of the canopy in terms of volume, leaf area index (LAI), total leaf area, the proportion between current and one-year-old leaves, and the distribution of light in the canopy, which vary considerably between cultivars. In an experiment in the same olive grove it was found that the total leaf area per tree of Maurino was lower than Arbequina, whereas the LAI was similar (about 2.5), but Maurino showed the best light interception of the canopy due to the more uniform distribution of the leaves (fewer empty spaces in the foliage) and to the orientation of the leaves in the space that tends more towards the vertical, reducing shading of the leaves in the middle and basal portions of the canopy by those located in the apical part (Proietti, unpublished results).

In addition to scaling photosynthesis from the leaf to the canopy level, in future studies it should be useful to study the gas-exchange behaviour of the other cultivars in super-intensive olive groves under a range of environmental conditions.

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