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ORIGINAL PAPER

Effects of the planting density on water relations and production of 'Chemlali' olive trees (*Olea europaea* L.)

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Abstract Water relations are a key factor limiting olive production. In this study, effects of plating density on physiological aspects and productivity of 'Chemlali' olive trees were analyzed under rain-fed conditions in four planting densities (156, 100, 69 and 51 trees ha^{-1}), in an experimental olive orchard located in the center of Tunisia. Seasonal changes in leaf relative water content (RWC), leaf water potential, stomatal conductance (g_s), CO_2 assimilation rate and tree production were studied. Accompanying the changes in leaf water status, all the monitored trees reduced leaf stomatal conductance (g_s) and photosynthetic rate (A) throughout the summer drought, mirroring the increase in soil moisture deficit and vapor pressure deficit. However, the decrease in gas exchange was much more pronounced in high planting densities than in low ones. Our results confirm that the increase of tree-to-tree water competition with planting density was significant in the dry climate of Tunisia. Thus, planting density is critical when planting new olive orchards in arid regions.

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Introduction

In Mediterranean regions, characterized by a long dry season in which rainfall does not meet evapotranspirative demands, olive trees (*Olea europaea* L.) are mostly grown under rain-fed conditions (Fernández and Moreno 1999), with yields limited mainly by water supply. Historically, olives were produced under dry-land conditions, where trees were spaced widely to take full advantage of the stored soil water from winter rains for spring and summer growth. More recently, orchards are irrigated by low-pressure systems and are planted at higher densities achieving greater yields and resulting in less alternate-bearing behavior (Beede and Goldhamer 1994). However, irrigation can be problematic due to limited water resources available in Mediterranean regions (Villalobos et al. 2000).

Tunisia is the largest African exporter of olive oil and fourth worldwide after Spain, Italy and Greece. The olive tree is present practically in every region of the country, up to the border of the southern dessert. In Tunisia, the 'Chemlali' cultivar occupies more than two-third of the total olive growing area and is cultivated in the center and south of the country. Several aspects concerning the capacity of the 'Chemlali' olive cultivar to resist to drought were studied, like the effect of water stress on the growth, gas exchange and the anatomy of the leaves (Boujnah 1997; Guerfel et al. 2009). However, a study on effects of planting densities on water relations and its consequences on productivity are lacking.

During the summer, olive, like other Mediterranean xerophytes, is usually subjected to high solar irradiances, high vapor pressure deficits (VPD) and limited water availability which may affect water relations of the olive tree (Nardini et al. 2006; Trifilò et al. 2007; Raimondo et al. 2009). The severity of these stresses is predicted to increase in the future as a result of global change (Fischer et al. 2001; Centritto 2002). Chartzoulakis et al. (1999) reported that numerous adaptation mechanisms are triggered in such plants to resist to severe conditions. These adjustments also led to changes in leaf water status, stomatal closure and, therefore, a reduction in photosynthetic rate. Giorio et al. (1999) have also reported that stomatal control is the major physiological factor to optimize water use under drought conditions. Moriana et al. (2002) found that gas exchange responded diurnally and seasonally to variations in tree water status and evaporative demand.

The aim of this work was to evaluate the effects of planting density on gas exchange and water relations of mature olive trees and to study the effects of planting density on olive production on a tree and stand level in arid regions of Tunisia. We hypothesized that high planting densities may affect plant water status, carbon assimilation and tree production.

Therefore, water relations and gas exchange measurements as well as productivity were compared in 'Chemlali' olive cultivar growing in four planting densities ranging from 51 to 156 tree ha^{-1}.

Materials and methods

Plant material and experimental conditions

Research work was conducted during three crop seasons (2005–2007) in a 4-ha olive orchard (cv. 'Chemlali') located in Jemmel, center of Tunisia (35°49′ N, 10°30′E). The climate of the study area is Mediterranean with an average annual rainfall of 250 mm, mostly distributed outside a 4-month summer drought period. Olives were planted in 1988 in four fields with the following tree spacing: 8 × 8 m, 10 × 10 m, 12 × 12 m and 14 × 14 m corresponding to planting densities of 156, 100, 69 and 51 trees ha^{-1}, respectively. Olive trees were subjected to identical fertilization regime and to all common olive cultivation practices. Six sample trees in the center of each field were selected for measurement, respectively.

Climatic conditions (average rainfall, air temperatures and global solar radiation) at the experimental site were recorded by a weather station. The soil of the four plant densities had the same textural characteristics and it was sandy with a water content of 12% at field capacity (–0.02 MPa) and 6.5% at the wilting point (–1.5 MPa). The pH was 7.6. Soil water content was determined monthly by the gravimetric method in the 0–0.8 m layer at a distance of 0.75 m from the trunk (three replicates per plant density).

Gas exchange measurements and olive production

Leaf net CO_2 assimilation rate (A) and stomatal conductance (g_s) were measured at day 15 (10:00 to 11:00 hours) each month from March to September. Measurements were on two leaves per tree with six replicates per density of plantation with a LCA-4 portable photosynthesis system (ADC BioScientific Ltd., Hoddesdon, UK) under saturating light conditions (PAR at leaf surface was up to 1,050 μmol m^{-2} s^{-1}). At the end of the growing season all the olives of sample trees were harvested manually and were weighed to obtain olive production.

Plant water status

Leaf water potential was measured using a Scholander pressure chamber model SKPM 1400 (Skye Instruments, Powys, UK). Measurements were carried out using sunlit leaves of similar age and position in the canopy (third leaf from the apex). One leaf per plant was used with six plant replicates for each density of plantation. After cutting, the leaf was immediately enclosed in a plastic bag and the determination of the leaf water potential was started in less than 1 min. These measurements were carried out from March to September on the same days as for gas exchange measurement between 10.00 and 11:00 hours. In addition, five leaves per tree were detached in similar positions, to determine relative water contents (RWC), with three replicate trees for each density of plantation. After cutting, the petiole was immersed immediately in distilled water inside a glass tube. The tubes were sealed and taken to the laboratory, where the increase in weight of the tubes was used to determine leaf fresh weight (FW). After 48 h in dim light, the leaves were weighed to obtain their turgid weight (TW). Dry weight (DW) was then measured after oven drying at 80°C for 48 h, and the relative water content was calculated as:

$$\mathrm{RWC} = 100(\mathrm{FW} - \mathrm{DW})/(\mathrm{TW} - \mathrm{DW}).$$

Statistics

Statistical analysis of data was performed by analysis of variance (ANOVA). Duncan's multiple range test was carried out for significance of differences between mean values. Regression analysis was performed to determine the relationship between leaf conductance and leaf water potential as well as photosynthesis rates.

Results

Climate

The climate was characterized by moderate temperatures during spring (25.7°C), high average temperatures from June to August (37°C) and an average temperature of 28°C during September (Fig. 1a). The maximum photosynthetically active radiation (PAR) was measured during summer coinciding with highest temperatures and lowest air humidity (Fig. 1a). Vapor pressure deficit was highest during August (Fig. 1b). Overall, the climatic conditions are typically Mediterranean characterized by scant precipitations during summer season (Fig. 1c). The largest rainfall (146 mm) was recorded in April (Fig. 1c).

Volumetric soil water content (θ_v; Fig. 1c) showed similar patterns in all fields of different planting densities. It was about 9.5% in April, decreased progressively throughout the period from June to August and increased again in September (Fig. 1c).

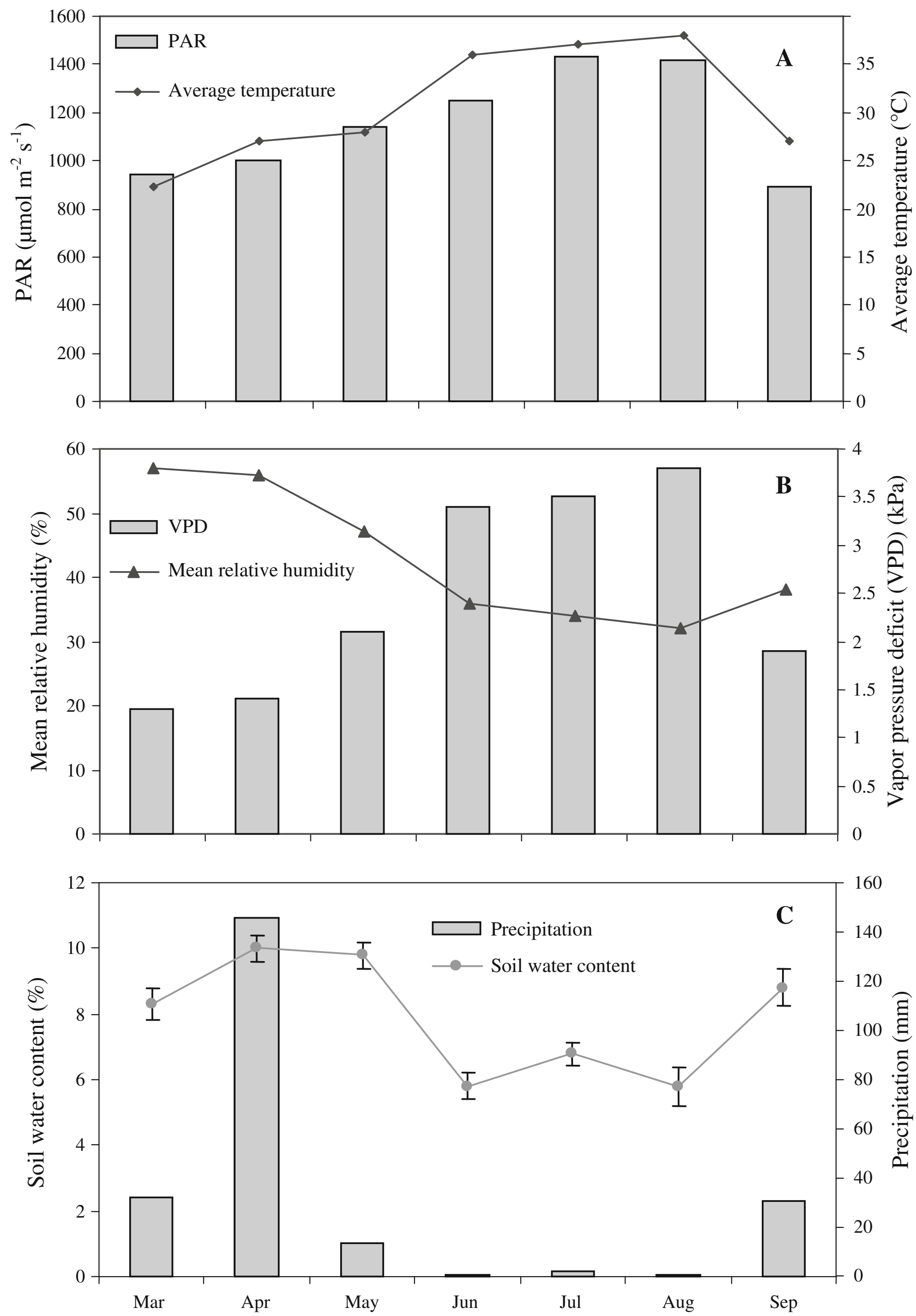

Fig. 1 Environmental parameters (**a**, **b**) and soil water content, θ_v (%) in the 0–0.8 m soil layer (**c**) during the 2007 season. There was no significant difference in the soil water content between the planting densities

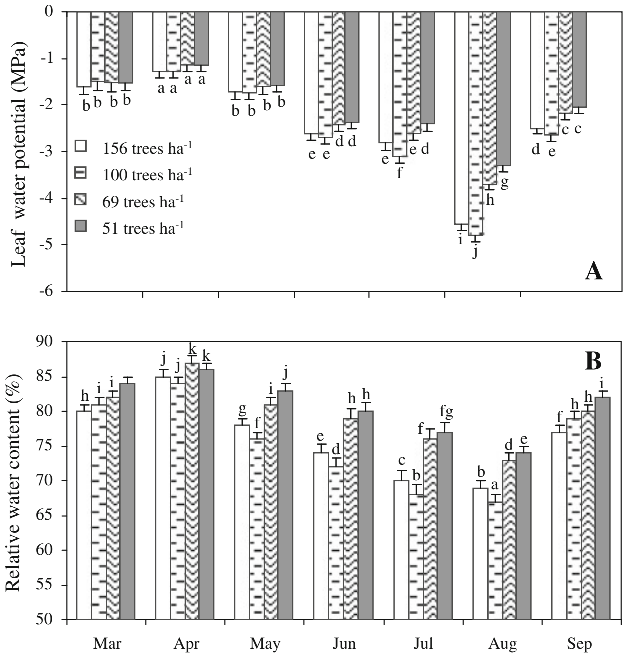

Fig. 2 Seasonal changes in leaf water potential (**a**) and leaf relative water content (**b**) of 'Chemlali' olive grown in the different planting densities during the 2007 season. Values are the means of six replicates. *Verticals bars* ±SE. Mean values with different letters (a, b, c) are significantly different at $P < 0.05$

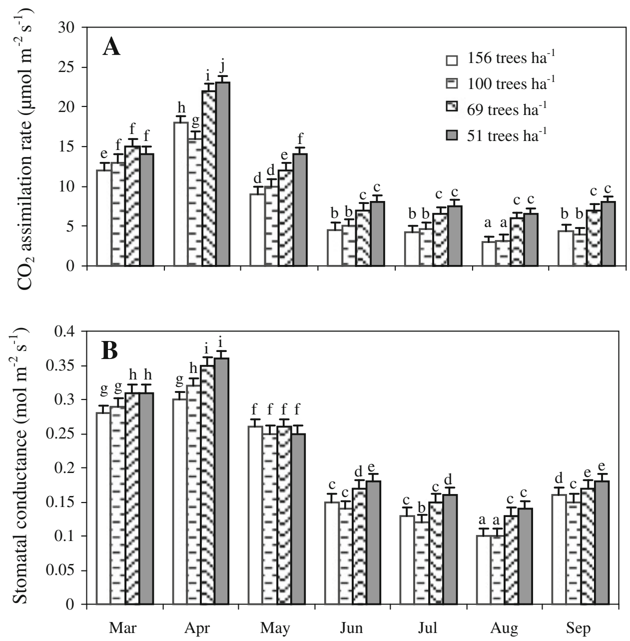

Fig. 3 Seasonal changes in CO_2 assimilation rate A (**a**) and stomatal conductance g_s (**b**), in leaves of 'Chemlali' olive trees cultivated in the different planting densities during the 2007 season. Values are the means of six replicates. *Verticals bars* ±SE. Means with different letters (a, b, c) are significantly different at $P < 0.05$

Water potential and leaf water content

Olive trees grown at the different planting densities showed maximum values of leaf water potential in spring and minimum values in summer (Fig. 2a). The summer drought response was most pronounced in the highest planting density with mean down to −4.8 MPa in August, while values for the lowest planting density (51 trees ha^{-1}) only reached −3.3 MPa. Seasonal changes as well as differences between planting densities of leaf water content (RWC) were similar to patterns in leaf water potential (Fig. 2b). In September, water potential and RWC for all planting densities increased (Fig. 2b), which was due to rainfall and lower temperatures.

Gas exchange measurements

In all planting densities, CO_2 assimilation rates were highest in spring, reached a minimum in August and increased again in September (Fig. 3a). The lowest planting density (51 trees ha^{-1}) showed highest CO_2 assimilation rates (mean maximum rate 23 µmol m^{-2} s^{-1}) throughout the season, while olive trees grown at the density of 156 and 100 trees ha^{-1} exhibited the lowest rates (mean maximum rates 16 and 18 µmol m^{-2} s^{-1}, respectively; Fig. 3a).

Stomatal conductance (g_s) followed similar trends as indicated by the high correlation between g_s and assimilation rates (data not shown). The g_s decreased from April to August and increased again in September. The mean maximum g_s value was 0.36 mol m^{-2} s^{-1} for the density of 51 trees ha^{-1} and 0.30 mol m^{-2} s^{-1} for the highest planting density (156 trees ha^{-1}; Fig. 3b). Stomatal conductance and leaf water potential were also correlated with coefficients of correlation ranging from 0.79 to 0.84 according to the planting density (data not shown).

Olive production

Higher productions were achieved with trees grown at the density of 100 trees ha^{-1} (1,200 kg ha^{-1}) and at 69 trees ha^{-1} (1,311 kg ha^{-1}). Maximum production was observed in 2006 at a density of 156 trees ha^{-1}. However, at a tree level, highest productivity was always observed at 51 trees ha^{-1} (Table 1). Furthermore, differences in alternate bearing between the densities were significant (approximately 75 and 50%, respectively, in the two highest densities and the two lowest densities) (Table 1).

Discussion

Climatic conditions during the experiment were typically Mediterranean, and resulted in a high evaporative demand as well as a large decrease in soil moisture and therefore in

Table 1 Average olive production of 'Chemlali' olive trees cultivated in the different planting densities during three crops seasons (2005–2007)

Crop season	156 trees ha^{-1}		100 trees ha^{-1}		69 trees ha^{-1}		51 trees ha^{-1}	
	kg $tree^{-1}$	kg ha^{-1}	kg $tree^{-1}$	kg ha^{-1}	kg $tree^{-1}$	kg ha^{-1}	kg $tree^{-1}$	kg ha^{-1}
2005	6 ± 2 a	936 ± 10 f	5 ± 1 a	500 ± 10 c	13 ± 2 b	897 ± 12 e	15 ± 3 b	765 ± 10 d
2006	24 ± 3 a	3,744 ± 15 g	26 ± 3 a	2,600 ± 23 f	30 ± 4 b	2,070 ± 18 e	36 ± 2 c	1,836 ± 16 d
2007	5 ± 1 a	780 ± 12 e	6 ± 2 a	600 ± 15 d	14 ± 2 b	966 ± 12 g	17 ± 2 c	867 ± 15 f
Mean	11 a	1,716 g	12 a	1,200 e	19 b	1,311 f	22 c	1,122 d

Results represent the mean production of 6 trees and were statically tested each crop season and within each planting density. Mean values with different letters (a, b, c) are significantly different at $P < 0.05$

leaf water content particularly in August. Leaf water content decreased markedly in the two highest planting densities (Fig. 2). Accordingly, seasonal changes in leaf water potential showed that drought stress had smaller effects on the water status of trees grown in low densities compared to those cultivated in high ones (Fig. 2). In the present study, the minimum leaf water potential was −4.8 MPa. Olive leaves tolerate an extremely low water potential (−10 MPa) and lose up to 40% of tissue water with an unimpaired capacity for rehydration (Rhizopoulou et al. 1991). According to Tognetti et al. (2004), whole olive tree hydraulic resistance increases during summer, which might be explained by the reduction of soil water content in the upper horizons inducing a decrease in hydraulic conductance of the soil compartment. Moreover, olive xylem has an intrinsically low hydraulic conductivity (Lo Gullo and Salleo 1988) and can tolerate water potential values below the turgor loss point without relevant seasonal xylem embolism (Salleo and Lo Gullo 1993). Clement climatic conditions in September caused an increase in leaf water status as shown by Angelopoulos et al. (1996), Chartzoulakis et al. (1999) and Giorio et al. (1999).

Accompanying these changes in water status, all the monitored trees reduced leaf stomatal conductance (g_s) and photosynthetic rate (A) throughout the summer drought, mirroring the increase in soil moisture deficit. However, the decrease was much more acute in high planting densities than in low ones, probably because roots of trees explored different volumes of soils. Thus, the soil water availability in low planting densities was higher although volumetric soil water contents shown in Fig. 1 was similar to high planting densities. Different authors have reported threshold soil moisture values to affect water relations, with levels of 20–40% of the relative extractable soil water content (Fernandez et al. 1997; Tognetti et al. 2006).

The extremely low values of A and g_s in higher planting density were even lower than those reported by Boujnah (1997). The response of olive trees to VPD conditions, which was also observed in the present study, has been widely described and is part of their strategy for resisting severe drought conditions (Connor and Fereres 2005). The control of leaf conductance during photosynthesis (Angelopoulos et al. 1996; Moriana et al. 2002) reduces the latter in conditions of high evaporative demand. Other internal effects in addition to VPD may also be involved (Moriana et al. 2002). According to Buckley and Mott (2002), stomata regulation during dry periods enables maintenance of the integrity of the conducting system by preventing water potentials from falling below cavitation thresholds.

Differences in drought stress intensities and, in consequence, g_s and A led to differences in production between planting densities. While low planting densities were optimal for productivity on a tree level, production based on orchard area was highest at highest density (Table 1). Olive is an alternate fruit-bearing species, and it is characterized by its ability to alternate season of high yields 'on year' with others of low yields 'off year'. The yield in the 'off year' can be reduced by as much as 90% in comparison to those of the 'on year' (Serrano 1998). Table 1 shows that 2005 was a typical 'on year'. Due to high drought stress, the reduction in olive production between the 'on year' (2006) and the 'off years' (2005 and 2007) was more pronounced in higher planting densities. More productive olive plantations and more efficient water use could be achieved on soils with increased hydraulic conductivity and through appropriate orchard management (pruning, planting density, as well as other factors influencing plant microclimate and canopy properties; Tognetti et al. 2004). Besides, it is well known that water stress affects not only fruit yield, but also fruit quality Fereres et al. (2003). Water availability increases shoot growth, flowering, fruit set and reduces fruit drop and alternate bearing (Michelakis 1990).

Conclusion

Lower planting densities can lead to an improved hydraulic situation of trees within orchards. However, the resulting higher productivity of trees might not cause increased yields at a stand level. Future studies should also focus on possible effects of planting density on olive oil quality.

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