Effect of water supply on leaf area development, stomatal activity, transpiration, and dry matter production and distribution in young olive trees

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Abstract.   Two-year-old olive trees cv. Cornicabra, trained in a central leader form for hedgerow planting, were grown outdoors in 45-L weighing lysimeters to evaluate the effect of water supply on growth and development. Four treatments were established and maintained for 155 days during spring–autumn. Treatment T100 was irrigated to maintain the potting medium close to water-holding capacity by progressive replenishment of consumption that was measured at weekly intervals by weighing and recording drainage. Treatments T80, T60, and T40 received 80, 60, and 40%, respectively, of the water applied to T100. For these treatments, transpiration and leaf area were measured every fortnight. Dry matter in roots, stems, and leaves was measured at the beginning and end of the experiment. Leaf conductance was measured at 09:00 and 12:00 solar time every fortnight and at *c*. 2-hourly intervals throughout one day each month. Over the experimental period, T100 produced $0.42 \pm 0.01 \, \text{m}^2$ leaf area, 319.6 ± 60.4 g dry biomass, and transpired 77.5 ± 1.1 L water. Water stress significantly reduced leaf area development and dry matter production ($P < 0.05$) in T60 and T40, but not in T80. There was no effect on dry matter partitioning to the various organs of the trees or the roots/aerial part ratio. Leaf conductance was more sensitive to water stress than vegetative growth, with significant differences ($P < 0.05$) established among treatments 3 weeks before differences were observed in transpiration. In autumn, transpiration and leaf conductance increased in all treatments independently of soil water status. Over the experiment, transpiration efficiency (TE, g/L) increased with reduced water supply, with a significant difference ($P < 0.10$) between T100 and both T60 and T40. The study has established that maximum growth of young olive plants can be achieved, without effect on the distribution of biomass between organs, at water supply less than that required to support maximum transpiration.

Additional keywords: *Olea europaea* L., water relations, stomatal response, transpiration efficiency, drought adaptation.

Introduction

Harvesting is the most expensive operation in Spanish olive cultivation due to the high cost and requirement of labour. In the mid-1990s the possibility of using mechanical harvesters was explored in areas where olive trees and grapevines were both grown. As a result, the first super-high-density olive orchards were planted with trees trained to hedgerows, generally in monocone shape pruned with a central leader, and spaced from 3 m by 1.3 m (2564 trees/ha) to 4 m by 1.5 m (1667 trees/ha).

The management of these new plantations poses a challenge for producers and researchers to adapt this typical Mediterranean crop that has been long cultivated using dry-farming methods, wide tree spacing (10 m by 10 m, 100 trees/ha), and a vase-shaped training system. In order to carry out a rational management of super-high-density olive orchards, it is necessary to identify the physiological responses of olive trees to this new system. The change in the training system incurs an increase in the leaf surface per unit of cultivated surface exposed to the sun and, therefore, an increase in water requirements that in turn demand greater water-use efficiency in the olive-growing region where water is scarce and olive trees compete with other crops for water.

Olive is a crop well adapted to drought conditions by mechanisms that have evolved to both avoid and tolerate drought (Connor and Fereres 2005). The olive tree protects internal metabolism from water stress by closing stomata (Fernández and Moreno 1999), which inevitably decreases photosynthetic rate and, therefore, growth (Moriana *et al.* 2002). Super-high-density olive orchards come into bearing after 3–4 years while the trees are trained to form a continuous hedgerow to expose maximum leaf surface to the sun. Optimum irrigation management in this phase seeks to minimise water application without reducing vegetative growth. There is a need to be both efficient in the use of water and also to avoid risks of anoxia and fungal infection associated with over-watering.

The objective of this experiment was to establish the growth response of young olive trees to water availability, the effect on dry-matter distribution as a determinant of suitability for planting, and to elucidate the response mechanism to water shortage in terms of leaf-area formation and stomatal response. For this, olive trees were grown in 45-L weighing

lysimeters under various irrigation regimes. The cultivar used was Cornicabra, the principal cultivar in central Spain, being well adapted to heat and drought in summer and to cold in autumn and winter.

Materials and methods

This experiment was carried out in 2004 in the open air at the Universidad Politécnica de Madrid in Spain (40°26′36″N, 3°44′18″W; alt. 590 m). Two-year-old olive trees (cv. Cornicabra) were grown from 27 April to 29 September (155 days) in 45-L weighing lysimeters covered with plastic film to exclude rainfall and eliminate direct evaporation from the soil. The lysimeters were filled with a mixture of peat, organic soil, and perlite (44 : 32 : 24) over a 50-mm layer of small stones to facilitate drainage. The substrate had a porosity of 86% (v/v), easily available water was 36% (v/v), reserve water 5% (v/v), and water not easily available was 30% (v/v) obtained according to the method described by Gabriels and Verdonck (1992). The olive trees were staked to a height of 2.5 m and trained in monocones similar to those in super-high-density hedgerow plantations using 4 m by 1.5 m tree spacing.

A weather station at the study site registered wind speed and direction, rainfall, temperature, humidity, and global radiation every 30 min and calculated ETo by the Penman-Monteith method (Allen *et al*. 1998) from these climatic variables.

The experiment used a completely randomised design with 5 single tree repetitions of 4 irrigation treatments that commenced with all treatments irrigated to drained water-holding capacity. During the experiment, treatment T100 was weighed weekly and irrigated on alternate days to maintain the potting medium close to water-holding capacity while treatments T80, T60, and T40 received 80, 60, and 40%, respectively, of the water applied to T100. Transpiration was determined gravimetrically at weekly intervals with allowances for drainage in T100 and fortnightly for treatments T80, T60, and T40.

Dry matter distribution was measured in 2 olive trees, similar to those placed in the lysimeters and selected according to median trunk diameter, at the beginning of the experiment. For this, the trees were separated into roots, stems, and leaves, and dried to constant weight in an oven at 80°C. At the end of the experiment, dry matter was measured similarly in all experimental trees, also separating stems and leaves formed in the current season from those formed previously.

Leaf area of each tree was determined fortnightly as the product of total leaf number per tree and average leaf size, the latter estimated monthly for each treatment by measuring central nerve length of all leaves on one branch per tree. In this case, there was no evidence of variation in leaf size distribution between branches of individual trees. At the end of the cycle, the relationship between central nerve length and leaf area was determined. At the end of the experiment all leaves were removed, counted, and measured with an area meter (Li-3100; Li-Cor, Lincoln, NE, USA), separating the leaves formed in the current from the previous season.

Leaf conductance (g_l) was measured fortnightly at 9:00 and 12:00 UTC with a steady-state porometer (Li-1600; Li-Cor, Lincoln, NE, USA) on healthy leaves exposed to the sun. On 8 September the measurement at 9:00 could not be taken due

to cloud. On 16 June, 14 July, 11 August, and 22 September, measurements were made on 7 occasions throughout the day (7:00, 9:00, 10:30, 12:00, 14:00, 16:30, and 18:30 UTC, approx. solar time). On those days, irrigation was delayed until the measurements were completed.

Data were subjected to analysis of variance using MSTAT-C (University of Michigan, USA). Least significant differences ($P < 0.05$ and $P < 0.10$) were used to segregate differences among treatment means using Duncan's multiple range test. The biomass partitioning data were transformed before analysis of variance using the arc-sin square-root transformation method to ensure that the data were normally distributed.

Results

Environmental conditions

The measurements from the weather station are summarised as daily means in Fig. 1 and the conditions on the days of measurement of leaf conductance are presented in Table 1. During the experimental period, the highest temperature was recorded on 24 July (38°C) and the lowest on 8 May (2°C). July was the hottest month with a mean temperature of 24°C while May was the coldest (14°C). Mean solar radiation was 23.8 MJ/m^2 with June having the highest (28.7 MJ/m^2) and September the lowest (18.1 MJ/m^2). Evaporative conditions remained strong throughout the experiment, with a cumulative ETo of 813 mm. June and July presented the highest values (6.4 mm/day) and September the lowest (4.1 mm/day). The greatest ETo of 7.5 mm/day occurred on 14 June.

Table 1 shows the weather conditions on the days when diurnal measurements of leaf conductance were made. Peak values of maximum temperature and solar radiation occurred at the end of June, within the first month of the experiment. High temperatures were maintained until the end of July but solar radiation declined gradually through the remaining period of the experiment. The highest values of relative humidity (at 12:00 h) coincided with a period of rainfall in September.

Leaf area

The seasonal pattern of leaf-area development (Fig. 2) is both a determinant and a consequence of the seasonal pattern of water availability, consumption (transpiration), and water stress. At the beginning of the experiment, mean tree leaf area was 0.09 ± 0.01 m^2, increasing by the end of the period to 0.42 ± 0.01 m^2 in T100. Treatments T80, T60, and T40 developed 93, 67, and 61%, respectively, of the leaf area of T100. Significant differences from the control (T100) in leaf area were established from 21 July in T40 and from 3 August in T60. At the end of the experiment, taken in pairs, T60 and T40 had 66% of the leaf area of T80 and T100.

Table 2 reports the number, size, and specific leaf mass (SLM, g/m^2) of leaves at the end of the experiment. One-year-old leaves were those present at the outset, while current-year leaves were produced during the experimental period. More leaves were produced in T100 and T80 than in T40. At the end of the experiment, T40 had 28% fewer leaves than T100. The trees lost 15, 13, 25, and 38% of their 1-year-old leaves in T100, T80, T60, and T40, respectively (data not presented). In contrast to the response in leaf number, there was no significant
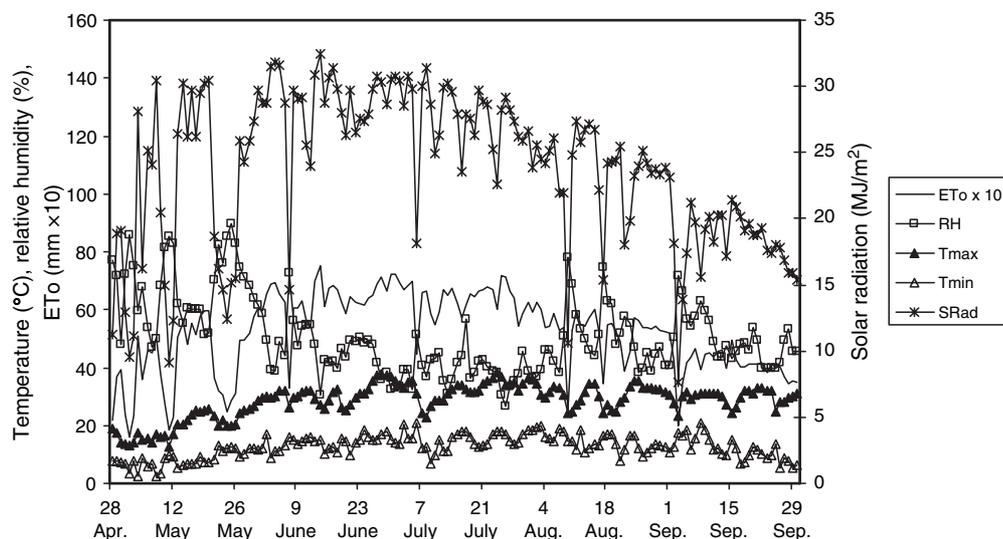
Fig. 1. Daily climatic conditions throughout the experimental period. Maximum and minimum temperature (°C), mean relative humidity (%), and accumulated solar radiation (MJ/m^2) and ETo (mm/day).

Table 1.   Daily ETo, maximum and minimum temperature, solar radiation, and temperature and relative humidity at 12:00 h solar time on the days of leaf conductance measurements

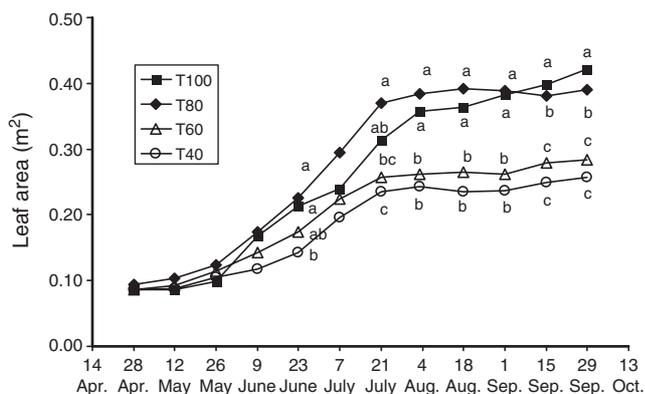|	2 June	16 June	30 June	14 July	28 July	11 Aug.	25 Aug.	08 Sept.	22 Sept.
ETo (mm/day)	6.6	6.7	7.2	6.7	6.4	5.9	5.6	3.9	4.2
Tmax (°C)	30.1	28.8	36.9	32.3	34.7	27.1	35.4	30.9	32.9
Tmin (°C)	17.1	12.3	14.9	15.9	13.5	11.6	12.1	20.9	10.1
Rsol (MJ/m^2)	28.7	30.7	30.6	29.6	27.4	27.4	24.0	15.6	19.3
Temp. 12:00 h (°C)	32.7	30.3	38.0	32.7	36.6	27.3	35.2	31.9	32.6
RH 12:00 h (%)	26.8	24.0	15.4	25.4	22.4	32.6	16.4	36.6	23.6

Fig. 2. Development of olive cv. Cornicabra leaf area under various irrigation treatments. T100 was irrigated to maintain the potting medium close to water-holding capacity; T80, T60, and T40 received 80, 60, and 40% of water applied to T100. Treatments with the same letter are not significantly different by Duncan's test at $P < 0.05$.

effect of treatment on leaf size (mean 205 mm^2), although leaves in T40 were 19% smaller than those in T100, and leaf rolling was observed in that treatment. These data reveal that the formation of new leaves (leaf number) was more affected by treatment than was leaf expansion.

Table 2.   Mean number, area (mm^2), and specific leaf mass (SLM, g/m^2) of leaves formed in current-year and in 1-year-old leaves in various irrigation treatments
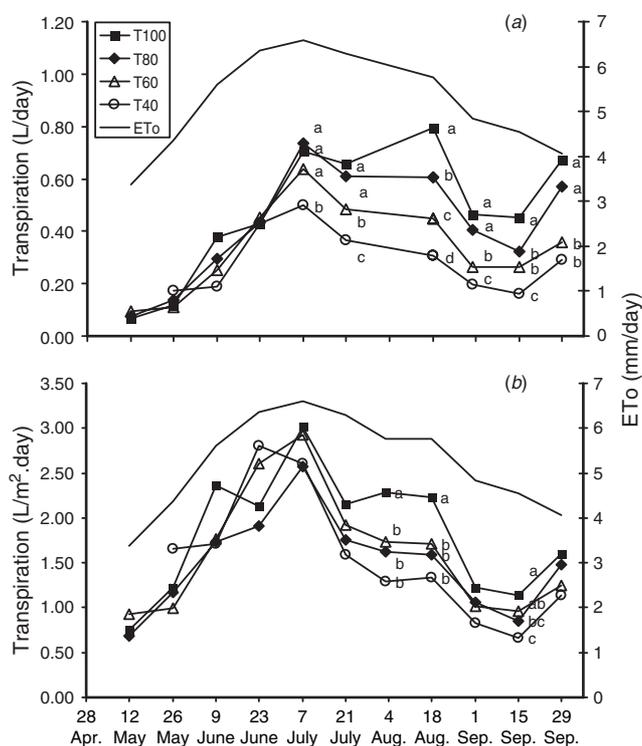
T100 was irrigated to maintain the potting medium close to water-holding capacity; T80, T60, and T40 received 80, 60, and 40% of water applied to T100. Treatments with the same letter are not significantly different by Duncan's test at $P < 0.05$

Treatment	Leaf number		Leaf size		SLM	
	Current	1-year	Current	1-year	Current	1-year
T100	1554a	272	235	254	221b	244
T80	1616a	301	196	257	231ab	252
T60	1373ab	244	181	208	243a	253
T40	1112b	204	190	213	239a	258

Specific leaf mass (SLM) of leaves increased significantly in response to restricted water availability, from 225 ± 12 g/m^2 in T100 to 243 $\pm$ 7 g/m^2 in T60 and T40 (Table 2). Leaves >1-year old (252 g/m^2) had greater SLM than leaves formed during the experiment (221–243 g/m^2).

Transpiration

The seasonal patterns of transpiration per tree and per leaf area, calculated for weekly and fortnightly periods, are presented, along with ETo, in Fig. 3. Since treatments were fully watered

Fig. 3. Daily transpiration of olive trees cv. Cornicabra in various irrigated treatments: (*a*) transpiration per tree; (*b*) transpiration per unit leaf area. T100 was irrigated to maintain the potting medium close to water-holding capacity; T80, T60, and T40 received 80, 60, and 40% of water applied to T100. Treatments with the same letter are not significantly different by Duncan's test at $P < 0.05$.

Table 3. Effect of water supply on transpiration per tree (L) over the experimental period, the mean transpiration per unit leaf area (L/m^2.day) calculated from progressive measurements of transpiration and tree leaf area, and transpiration efficiency (g biomass/L) in production of biomass

T100 was irrigated to maintain the potting medium close to water-holding capacity; T80, T60, and T40 received 80, 60, and 40% of water applied to T100. Treatments with the same letter are not significantly different by Duncan's test at $P < 0.05$

Treatment	Tree transpiration	Mean transp./ leaf area	Transpiration efficiency
T100	77.5a	1.958a	3.868b
T80	67.0b	1.704ab	4.248ab
T60	53.4c	1.715ab	4.347a
T40	40.7d	1.467b	4.466a

Treatment T100 consumed 77.5 ± 1.1 L, while T80, T60, and T40 consumed 87%, 69%, and 53% of T100, respectively. On the basis of leaf area, a significant difference was established only between extreme treatments, T100 and T40, this reflecting the variation in leaf area within treatments. Mean daily transpiration for T100 was 2.0 ± 0.3 L/m^2.day, falling to 1.5 ± 0.2 L/m^2.day in T40.

Biomass and partitioning

At commencement of the experiment in April the trees had 50 ± 6 g dry biomass that by September had increased to 369.6 ± 60.4 g in T100 (Table 4). In April, 20 ± 4 g, 9 ± 1 g, and 21 ± 3 g was in roots, leaves, and stems, repectively. By the end of the experiment, tree biomass was significantly reduced from the control (T100) in T60 and T40 but not in T80. Biomass in T60 and T40 was 75 and 63%, respectively, of T100.

Significant differences in the distribution of biomass in component organs of roots, stems, and leaves were observed among treatments (Table 4). The greatest proportion of biomass both at the beginning (43% in April) and at the end of the season (50% in September) was in stems. In September, 66% of aerial dry matter was found in stems of which 74% was in stems formed before the start of the experiment. Dry matter content in these stems increased from 21.4 g in April to 115.7 g in September, while dry matter content of new stems was 40.3 g in September. Dry matter content in stems was significantly different among irrigation treatments. Leaf mass was significantly greater in T100 and T80 than in T60 and T40, while root mass was significantly greater in T100 and T80 than in T40. In all treatments, leaves were the organs that showed the greatest increase in biomass. Over all treatments, biomass in leaves, stems, and roots increased 9, 7, and 3 times, respectively. Root/aerial dry matter ratio (Table 4) and biomass partitioning among organs (data not presented) were not significantly affected by irrigation treatments.
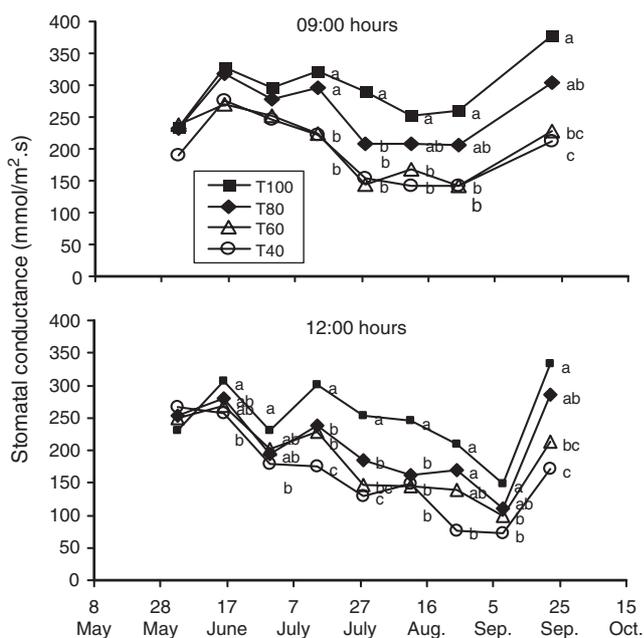
Leaf conductance

Two sets of measurements are available to evaluate the seasonal and diurnal responses of stomata, respectively. The first set, presented in Fig. 4, records the leaf conductance (g_l) at 09:00 and 12:00 h at fortnightly intervals during the experiment. These data reveal a common trend of decline during the summer months

at the beginning of the experiment, no significant differences in transpiration were observed in the stress treatments until the easily available water (16.2 L) had been consumed. Thus, treatment effects on tree transpiration (Fig. 3*a*) appeared successively: first in T40 on 7 July, followed by T60 on 21 July, and finally by T80 on 18 August. Transpiration then decreased until 29 September when a sharp increase was observed in all treatments. Maximum transpiration per tree (0.7–0.8 L/day) was observed in July and August responding to increasing leaf area (Fig. 2) rather than coinciding with maximum values of ETo (6.0–6.5 mm/day).

In contrast, when evaluated against leaf area (Fig. 3*b*), maximum transpiration was reached between mid-June and mid-July, earlier than for tree transpiration (Fig. 3*a*), and coinciding with maximum ETo. There were no differences among treatments to that time. T100 achieved the greatest transpiration, nearly 3.0 ± 0.4 L/m^2.day, at the beginning of July and maintained a higher rate than the other treatments almost to the end of the experiment when transpiration increased suddenly in all treatments. Significant differences in transpiration were recorded among treatments on 3 August, 18 August, and 15 September, when transpiration was significantly greater in T100 than in T60 and T40.

Cumulative tree transpiration over the experimental period was significantly different among treatments (Table 3).

Table 4. Dry matter contents (g) in trees at the end of the experiment and its distribution in roots, stems, and leaves, together with the relationship between root/aerial dry matter content (g/g) in various irrigation treatments

T100 was irrigated to maintain the potting medium close to water-holding capacity; T80, T60, and T40 received 80, 60, and 40% of water applied to T100. Treatments with the same letter are not significantly different by Duncan's test at $P < 0.05$

	Roots	Stems	Leaves	Total biomass	Root/aerial dry matter
T100	80.8a	190.7a	98.1a	369.6a	0.272
T80	76.0ab	169.2b	89.8a	334.9a	0.293
T60	63.2bc	146.5c	72.1b	281.8b	0.288
T40	53.4c	117.5d	61.1b	232.0c	0.293

Fig. 4. Leaf conductance at 09:00 and 12:00 h in olive trees cv. Cornicabra in various irrigation treatments. T100 was irrigated to maintain the potting medium close to water-holding capacity; T80, T60, and T40 received 80, 60, and 40% of water applied to T100. Treatments with the same letter are not significantly different by Duncan's test at $P < 0.05$.

that is more marked at 12:00 than at 09:00 h. They also show that treatment differences were established 3 weeks earlier than were differences in leaf area (Fig. 2). Significant differences were observed among treatments after 14 July at 9:00 and after 19 June at 12:00 h. After these dates, g_l was significantly greater in T100 than in T40. Significant differences in g_l were only found between T60 and T40 on 14 July at 12:00 h and between T80 and T60 on 14 July at 09:00 h. Maximum values of g_l were around 379 mmol/m^2.s, falling to 70 mmol/m^2.s in T40 towards the end of the summer. Mean g_l at 09:00 h throughout the season was 295 ± 42, 256 ± 18, 208 ± 15, and 198 ± 35 mmol/m^2.s in T100, T80, T60, and T40, respectively, while at 12:00 h the corresponding values were 251 ± 34, 209 ± 14, 188 ± 9, and 164 ± 23 mmol/m^2.s. Combining both times of measurement,

mean g_l was 85, 73, and 66% of T100 in T80, T60, and T40, respectively.

A significant feature of these data is the recuperation of g_l in all treatments at the end of the season. Leaf conductance rose then to 400 mmol/m^2.s in T100, its highest value recorded in this experiment. Temperature and evaporative demand (ETo) were less than during the previous measurements so the data suggest some internal plant response controlling this aspect of behaviour.

The diurnal measurements of g_l presented in Fig. 5 confirm aspects of the fortnightly data. The diurnal trends show the same pattern of early development of stress in T40, followed by gradually increasing stress in the other treatments as the season progressed. Differences in g_l became greater between treatments as the season progressed. On 16 June, g_l in T100 was significantly greater than in T40 at 12:00, 16:30, and 18:30 h. On 14 July, significant differences were observed among treatments throughout the day except at 09:00 h. Significantly greater g_l was observed in T100 than in T40. After 10:30 h, g_l in T80 was not significantly different from that in T60, while after 12:00 h, g_l in T40 was significantly smaller than in the rest of the treatments, except at the end of the day. On 11 August, g_l in T100 was significantly greater than in T40 from 09:00 h and significantly greater than in T60 from 12:00 h onwards. After 12:00 h, no significant differences were found among T80, T60, and T40. On 22 September, the greatest g_l was registered and the greatest differences were found among treatments. Leaf conductance was significantly greater in T100 than in T60 and T40 at all times of measurement.
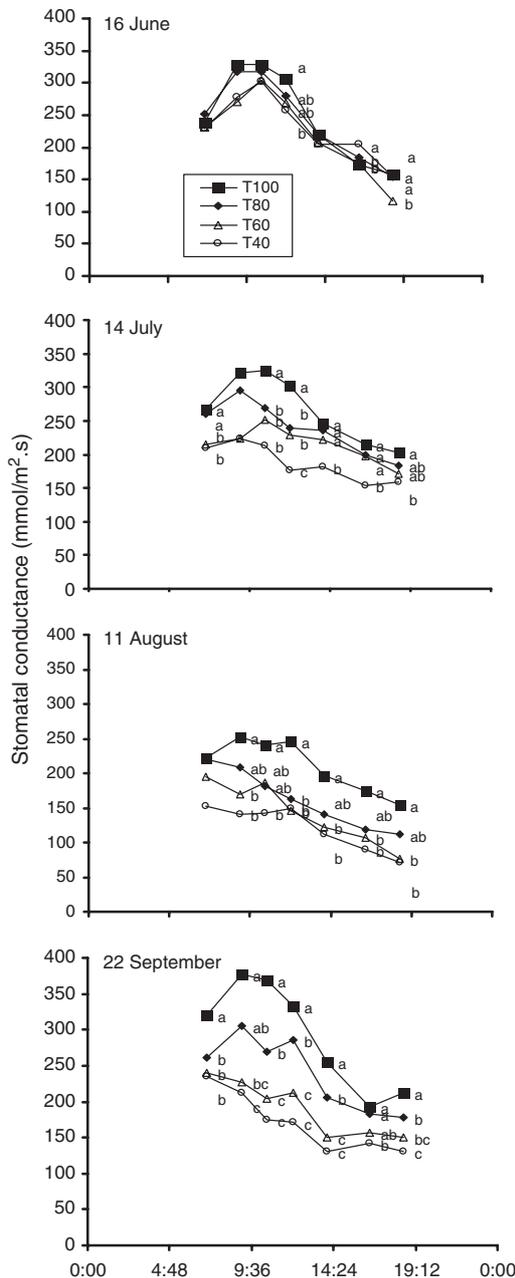
The data also showed another aspect of stomatal response of olive to water stress and environment in the form of a common diurnal trend that persisted throughout the season in all treatments. Even when water was readily available and transpiration demand was low due to small leaf area (e.g. 18 June), g_l attained maximum values in the morning with declining values in the afternoon. As the stress developed, the pattern was maintained but the time of peak g_l occurred earlier in stressed treatments. Thus all treatments attained maximum g_l at 10:00–11:00 h at the start of the season, but by August, maximum g_l for T60 and T40 was recorded on the first occasion of measurement (07:00 h).

Transpiration efficiency (TE)

The relationship between biomass production and total transpiration defines TE over the experimental period (Table 3). The value of this relationship reveals a gradual increase in TE with restricted water supply, with significant differences established ($P < 0.10$) between T100 and extreme treatments T60 and T40.

Discussion

The observations of growth and transpiration reveal that maximum growth of olive cv. Cornicabra can be achieved at a water supply less than required to support maximum transpiration. The transpiration of trees grown without water stress (T100) during 155'days from spring to summer amounted to 77.5 ± 1.1 L, which is low compared with ETo and the area (6 m^2) allocated to each tree. Irrigation at T80 that sustained a total seasonal transpiration of 67.0 L/tree maintained the same

Fig. 5. Leaf conductance throughout the day on 19 June, 14 July, 11 August, and 22 September in olive trees cv. Cornicabra in various irrigation treatments. T100 was irrigated to maintain the potting medium close to water-holding capacity; T80, T60, and T40 received 80, 60, and 40% of water applied to T100. Treatments with the same letter are not significantly different by Duncan's test at $P < 0.05$.

maintain maximum growth in young actively growing trees with a dominance of new leaves well exposed to the sun. Management can use this information to avoid over-watering during this formation phase because that introduces risks of poor growth under anaerobic conditions and of establishing diseases such as *Verticillium* in planting stock. The data also define the cost in terms of growth at suboptimal water supply. Irrigation at T60 reduced transpiration to 69% but growth to 75%. At T40, the corresponding values were 53% and 63%, respectively.

Olive has a range of avoidance and tolerance mechanisms to assist productivity and survival in low-water environments (Connor and Fereres 2005). Although the classic partitioning response of greater root/shoot ratio that improves water balance (Kozlowski and Pallardy 1997) was not observed in this experiment, important responses in rate of leaf formation, leaf morphology, and leaf conductance led to shifts in the relationship between transpiration and growth. Leaf size and SLM recorded in this study with mean values of 205 ± 37 mm^2 and 237 ± 12 g/m^2 are consistent with many other observations in the olive literature, bearing in mind that both parameters exhibit variation among cultivars and responses to growing conditions (Bosabalidis and Kofidis 2002; Hagidimitriou and Pontikis 2005). Under extreme stress, leaf size is known to decline, SLM to increase (Abdel-Razik 1989; Fernández and Moreno 1999), and finally leaves to curl and fall. In this experiment, with its controlled development of stress, leaf size did not vary among treatments, SLM was greater in T60 and T40 than in the control (Table 2), and while leaf fall of 1-year-old leaves did increase with water shortage, the effect was small so the development of leaf area was dominated by the production and expansion of new leaves during the experiment.

The regular measurements of stomatal conductance (g_l) that were made throughout the experiment reveal important aspects of the drought resistance of olive (Figs 4 and 5). First, the usual levels of g_l (range 234–378 mmol/m^2.s) in well watered olive are low by comparison with other horticultural tree species (Connor and Fereres 2005) but also with the high values at 9:00 UTC (300–444 mmol/m^2.s) that were observed in autumn (see below). Second, stomatal closure was the first response to water shortage observed in this experiment. Reduction in g_l was observed 3 weeks before effects on leaf area development were recorded. Leaf conductance at noon fell gradually from 250 to 72 mmol/m^2.s in T60 and T40, as the stress deepened. Third, the daily behaviour of stomata, more open in the morning than in the afternoon, is consistent with the optimisation theory of stomatal control that maximises TE (Cowan 1982) during the diurnal cycle. Olive, with low internal conductance to CO_2 due to leaf anatomy, is a good candidate for greater TE with stomatal closure. The effect is seen in these data as TE increased gradually with water restriction and was significantly different ($P < 0.10$) between extreme treatments (Table 3). The consequence is the potential for water saving without growth penalty in commercial practice.

The fortnightly observations also detected an unexpected marked increase in g_l in autumn (August–September) (Fig. 4). That response, inferred from a greater transpiration rate at the leaf level, was also evident in the plant transpiration data shown in Fig. 3. Hagidimitriou and Pontikis (2005) have recently reported a similar response in g_l in all 5 Greek cultivars of

leaf area (Fig. 2) and accumulated the same final biomass (Table 4) as T100. Final leaf area (0.42 ± 0.01 m^2) (Fig. 2) and final dry matter in T100 (369.6 ± 60.4 g) (Table 4) are comparable with those of similar aged trees of other cultivars observed in the field by Nuzzo *et al*. (1997) and Mariscal *et al*. (2000). It is an important finding of this work that water supply limited to 80% of potential transpiration can also

olive they studied, also grown outdoors in pots. In that case, all plants were well watered, whereas in the present experiment, the response was also evident, without re-watering, in the low-water-supply treatments. There is no obvious explanation for this response, which takes g_l in olive, in both studies, to the highest values (*c*. 450 mmol/m^2.s in the Greek study) reported in the literature. The response cannot be readily associated with changes in temperature or humidity but rather seems to be due to a modification in tree physiology, perhaps to increased water uptake due to root activity or greater xylem conductivity within the plant. This stomatal response is apparently distinct from that reported by Moriana *et al*. (2003) in a field orchard in autumn. There, a marked increase in g_l could be explained as a response to sudden resumption of soil water supply when substantial rainfall terminated an extended dry summer–autumn period. The response observed here and in the Hagidimitriou and Pontikis (2005) study warrants further investigation.

Acknowledgments

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