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# *Quercus ilex* transpiration as affected by a prolonged drought period

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## Abstract

The effect of an extended drought (from 1992 to 1995) on water relations was assessed on evergreen oak (*Quercus ilex* L.) in a dehesa ecosystem (Seville, Southern Spain). Diurnal and seasonal transpiration patterns were analysed at leaf (porometry) and whole-tree level (sap flow), focusing on the relationship between tree transpiration rates ($E_t$) and potential evapotranspiration rates (PET). Daily maximum $E_t$ varied over the year, becoming higher between May and August, and lower between November and April. Annual $E_t$ (169 - 205 mm $y^{-1}$) accounted for less than 40 % of annual rainfall. The prolonged drought did not affect the water relations of the *Q. ilex*, mainly due to strong stomatal regulation avoiding the loss of water. Stomatal control was found in all seasons, although it was stronger in summer. This behaviour leads to low water consumption and low $E_t$/PET ratios throughout the year (0.05 to 0.27).

*Additional key words*: holm oak, sap flow, stomatal regulation of gas exchange, water potential, water consumption.

## Introduction

The dehesas of the South-western Iberian Peninsula are "man-made" ecosystems characterised by a savannah-like physiognomy dominated by two evergreen oak species, *Quercus ilex* L. and *Quercus suber* L. in densities ranging from 30 to 90 trees ha$^{-1}$. One of the major ecological factors acting on dehesas is water availability, due to the variable duration of the dry season and the high rainfall variability within and between years. Water relations and the ecophysiology of *Q. ilex* have been profusely studied in dense stands in Catalonia (NE Spain) (Castell *et al.* 1994, Sala and Tenhunen 1996, Peñuelas *et al.* 2000) as well as in other forests of the Mediterranean basin (Pitacco *et al.* 1992, Lo Gullo and Salleo 1993, Damesin *et al.* 1998). However, less work has been done on the water relations and ecophysiology of isolated holm oak trees in dehesas.

A key issue for sustainable management of dehesas is understanding the role of isolated trees in the ecosystem functioning. Previous work has focused on the physiological traits of the *Q. ilex* leaf, its response to low water availability and the relationships between the leaf and tree canopy level (Infante *et al.* 1997, 1999). In this study we assess the effect of an extended drought period on leaf water relations and tree transpiration analysing diurnal and seasonal transpiration patterns at leaf and whole-tree level, focusing on the relationship between transpiration and potential evapotranspiration. To determine whole-tree transpiration sap flow measurements were used, which provide a good estimate of tree transpiration both in forest and woodland stands (Granier 1987, Farrington *et al.* 1994, Hutley *et al.* 2000),

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*Abbreviations*: $\Psi_w$, - leaf water potential; $g_s$ - stomatal conductance to water vapour; $D_a$ - air water vapour pressure deficit; $E_t$ - tree transpiration rate; F - sap flow rate; $H_g$ - accumulated daily global radiation; LAI - leaf area index; PET - potential evapotranspiration; $R_g$ - global solar radiation.

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as well as in isolated trees (Čermák *et al.* 1982, Infante *et al.* 1997, Lu and Chacko 1998).

A prolonged drought affected SW Spain from 1992 to 1995, being 1994 extremely dry and hot. This study provides insights into the physiological responses of *Quercus* species under such extreme conditions, similar to the climate predicted for the Mediterranean region by global circulation models (Houghton *et al.* 1995), and may help to predict possible changes affecting the functioning of dehesa ecosystems.

## Materials and methods

**Plants:** The study site was located at Castilblanco de Los Arroyos (37° 41' N, 5° 55' W, altitude 280 m), 40 km north from Seville, in Southern Spain. Several ecological studies have been already carried out in this area (Joffre *et al.* 1987, Joffre and Rambal 1993, Fernández-Alés *et al.* 1993). Mean annual precipitation at Castilblanco for the period 1960 - 1992 was 720 mm (Regional Water Board, non-published data). Average tree density is 40 tree $ha^{-1}$, fractional vegetation cover is 0.34 with trees homogeneously distributed. Tree leaf area index (LAI) measurements have been widely described for the site by Infante *et al.* (2001).

Measurements were carried out from May 1993 to January 1995 in three evergreen oaks (*Quercus ilex* L.) (called Tree 1, 3 and 5), which are representative (in height and size) of trees found in the area (Table 1). From 26 March 1994 to 15 January 1995, the soil under the canopy and around the trunk of Tree 3 was covered with a 170 $m^2$ sheet of plastic to exclude all precipitation and to prevent evaporation of water from the soil, in order to have trees with different soil water availability. Vegetation was removed from the covered surface. The plastic sheet extended up to ~2 m away from the canopy-projected area (75.3 $m^2$). Also, stem flow was prevented with a plastic ring installed around the trunk at 1.5 m height.

Table 1. Structural characteristics of the studied trees. Sapwood area corresponds to those used in sap flow calculations. Trunk height means the height at which the trunk is divided into its principal branches.

| | Tree 1 | Tree 3 | Tree 5 |
|---|---|---|---|
| Tree height [m] | 7 | 8 | 8 |
| Trunk height [m] | 1.65 | 1.90 | 2.55 |
| Diameter at chest height [m] | 0.37 | 0.45 | 0.54 |
| Sapwood area [$m^2$] | 0.020 | 0.025 | 0.031 |
| Projected canopy surface [$m^2$] | 66.3 | 75.3 | 119.2 |

**Sap flow measurements:** Sap flow rate (F) was estimated by the constant heating method (Granier 1985, 1987). Units consisted of two aluminium probes, 20 mm long and 2 mm in diameter, inserted in the sapwood of the trunk at breast height (about 1.5 m), one approximately 150 mm vertically above the other. The upper probe was electrically heated at a constant rate, whereas the lower (or reference) probe was at trunk temperature. Three sets of probes were installed in each tree, each set in a different orientation. The probes and the trunk were wrapped with glass wool, extending approximately 0.35 m above and below the probes (1 m wide). Measurements were made at 2 min intervals and recorded with a data logger (*Model 21X, Campbell Scientific Ltd*, Leicestershire, UK) that processed the data to give half-hourly means. The trunk radial pattern of sap flow for these trees was characterized by Infante *et al.* (2001).

The sap flow measurements were made continuously from 19 May 1993 to 21 October 1994. From 19 May to 15 August 1993 two trees were used (trees 1 and 3). From 15 August 1993 we added a third tree (tree 5). For each tree, F was averaged over the three sensors to obtain the transpiration for the tree ($E_t$). Water consumption for each sampled tree was estimated: *a)* in volume units [$dm^3$] by multiplying the averaged F by its corresponding sapwood area, and *b)* on the basis of a projected canopy area [mm] by dividing the volume measured by the projected canopy area.

**Stomatal conductance:** For leaf stomatal conductance ($g_s$) measurements, one southerly-oriented branch per tree was selected. Measurements were made hourly on the same branch of each tree, from sunrise to sunset, using a portable gas-exchange unit (*DL-2 Leaf Chamber Analyser, ADC Ltd*, Hoddesdon, UK), on 5 - 7 sunlit leaves. These measurements were carried out between June 1994 and January 1995, on June 15th to 17th, August 18th and 24th, September 5th, 21st, 28th and 30th, November 29th and 30th, and January 4th and 9th.

**Water potential:** Pre-dawn and noon leaf water potential ($\Psi_w$) were measured with a Scholander-type pressure chamber (*Model PMS 1000, PMS Instruments Co.*, Corvallis, USA) in 4 - 5 sunlit leaves per tree, also on a south-oriented branch. These measurements were made on June 22nd, August 10th and September 29th 1993. In 1994, measurements were made on March 26th, April 27th, June 15th to 17th, August 18th and 24th, September 5th, 21st, 28th and 30th and November 29th and 30th.

**Meteorological data:** Air temperature and humidity, global solar radiation ($R_g$), photosynthetically active radiation, wind speed, and rainfall volume were recorded from 15 February 1994 to 31 January 1995 by a meteorological station located in an open area 200 m from the stand. Measurements were recorded every 5 min and averaged every 30 min. Daily rainfall and potential evapotranspiration (PET) were recorded at a meteorological station of the Regional Water Board, 2 km from the experimental site. PET was estimated by the open-pan evaporation method. From May 1993 to February 1994, air temperature, air humidity and global radiation were recorded by two meteorological stations in Seville (40 km from the study site): temperature and humidity at Tablada (37° 21' N, 6° 00' W, 9 m above sea level), and global radiation at ETSII (Escuela Técnica Superior de Ingenieros Industriales; 37° 22' N, 5° 59' W, 30 m above sea level).

## Results

**Environmental conditions and leaf water potential:** The study period (May 1993 to October 1994), part of the drought that affected Southern Spain from 1992 to 1995, was unusually dry. During the study, the summer droughts lasted four months, from June to late September (Fig. 1*A*), being more severe in 1993. Moreover, total annual precipitation was well below the average being recorded 503 mm during the hydrological year October 1993 to September 1994. Mean daily values of air water vapour pressure deficit ($D_a$) ranged from 0 to 3.9 kPa (Fig. 1*B*). Maximum $D_a$ values were recorded in both years between early July and August. Maximum values of accumulated daily global radiation ($H_g$) were recorded in June, about 30 MJ $m^{-2}$ $d^{-1}$, and minimum values between November and December, about 10 MJ $m^{-2}$ $d^{-1}$ (Fig. 1*C*).

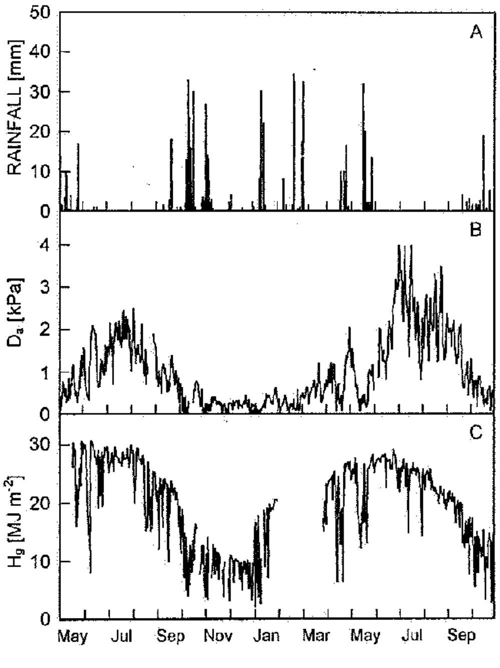

Fig. 1. Rainfall (*A*), mean daily air water vapour pressure deficit, $D_a$ (*B*) and accumulated daily global radiation, $H_g$ (*C*) during year 1993 - 1994.

Pre-dawn $\Psi_w$ reached -2.5 MPa in the summer of 1993 before the first rains. In 1994, a less dry year, pre-dawn $\Psi_w$ varied only between -0.25 and -1.9 MPa, except for tree 3, which was artificially disturbed, and for which it was not less than -1.2 MPa (Fig. 2). The relationship between daily amplitude of $\Psi_w$ and pre-dawn $\Psi_w$ showed that $\Delta\Psi$ decreases as pre-dawn $\Psi_w$ became more negative (not shown).

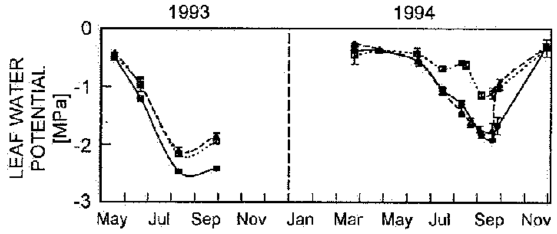

Fig. 2. Seasonal patterns of pre-dawn leaf water potential for trees 1 (*circle*), 3 (*square*), and 5 (*triangle*). *Vertical bars* indicate SE.

**Tree transpiration dynamics:** Due to the marked differences found for diurnal variations in $E_t$ between cloudy and sunny days, in order to compare diurnal dynamics among seasons, sunny days ($H_g$ > 24 MJ $m^{-2}$) were chosen. Fig. 3 shows diurnal variation in $E_t$ rates, estimated from the sap flow measurements, for tree 5 over 5 d. The days represent the four seasons, autumn (29 October 1993), winter (20 January 1994), spring (9 April 1994) and summer (19 July and 28 September 1994). The diurnal $E_t$ dynamics found for tree 5 were similar to those for trees 1 and 3 with a maximum hourly value ranging between 1.39 and 2.08 $cm^3$ $s^{-1}$ for trees 3 and 5, and between 1.11 and 1.67 $cm^3$ $s^{-1}$ for tree 1.

Tree transpiration presented a bell-shaped daytime variation during the autumn-winter period (Fig. 3*A*). In spring-summer, $E_t$ increased in the morning, decreased at midday and rose to a second peak in the afternoon (Fig. 3*B*). During the summer, as the drought was prolonged, the morning $E_t$ peak disappeared and lower maximums were reached at midday (*e.g.* 28 September, Fig. 3*B*).

Total daily $E_t$ was estimated by integrating the diurnal curves of the $E_t$ rates. Minimum was recorded in autumn and winter, with an average ranging between 24 ± 10 $dm^3$ $d^{-1}$ for tree 1 and 39 ± 10 $dm^3$ $d^{-1}$ for tree 5. Daily maximum ranged between 80 and 120 $dm^3$ $d^{-1}$ for trees 1 and 5, respectively and were recorded at the end of May and in early June. The lowest seasonal transpiration rates were in winter when $D_a$ was low and then increased in spring as $D_a$ and $R_g$ increased.

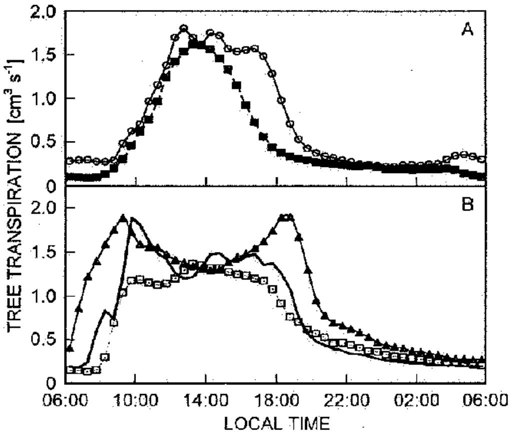

Fig. 3. Diurnal transpiration rates for tree 5 on sunny days. The symbols correspond to autumn - winter (*A*): 29 Oct. 1993 (*solid square*) and 20 Jan. 1994 (*blank circle*), and spring - summer (*B*): 9 Apr. (*solid line*), 19 Jul. (*solid triangle*) and 28 Sep. (*blank square*) of 1994.

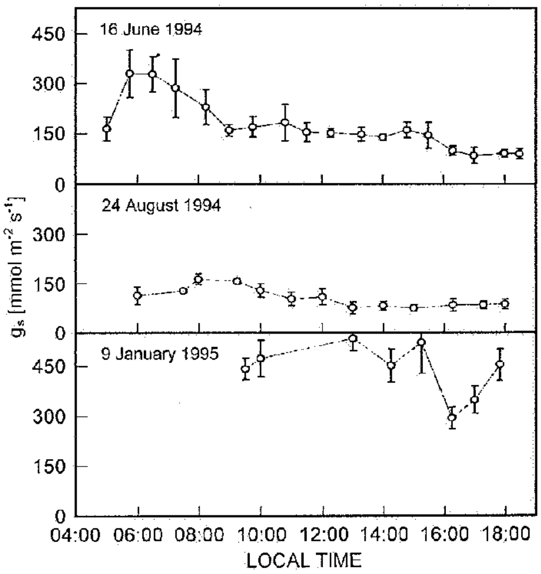

Fig. 4. Diurnal stomatal conductance ($g_s$) pattern. *Vertical bars* indicate SD.

**Leaf stomatal conductance:** Diurnal variation in $g_s$ for tree 5 is shown for three days in spring (16 June 1994), summer (24 August 1994) and autumn-winter (9 January 1995) (Fig. 4). The patterns found for trees 1 and 3 were similar. The $g_s$ ranged between 65 and 531 mmol m$^{-2}$ s$^{-1}$, with values above 400 mmol m$^{-2}$ s$^{-1}$ only in autumn - winter. Values lower than 100 mmol m$^{-2}$ s$^{-1}$ occurred mainly towards the end of the drought season. In spring, $g_s$ reached maximum values in the morning, then decreased during the day, following a negative exponential function. In summer, $g_s$ reached the daily maximum at sunrise, and decreased exponentially with time during the day. As the drought continued, the maximum daily $g_s$ decreased continuously. In autumn and winter, $g_s$ retained the daily maximum from sunrise to sunset, except when the soil under the tree canopy dried out, which coincided with a decrease in $g_s$ in the afternoon.

Small differences were found in stomatal conductance pattern between trees 1 and 5, and tree 3. The sheet of plastic positioned under tree 3 did not affect $g_s$. Significant differences ($P < 0.01$) in daily mean $g_s$ were only found between tree 3 and trees 1 and 5 in June. These differences were not significant for daily maximum $g_s$ for the same dates. During autumn-winter, daily maximums and diurnal variation in $g_s$ were similar for trees 1 and 5, and tree 3.

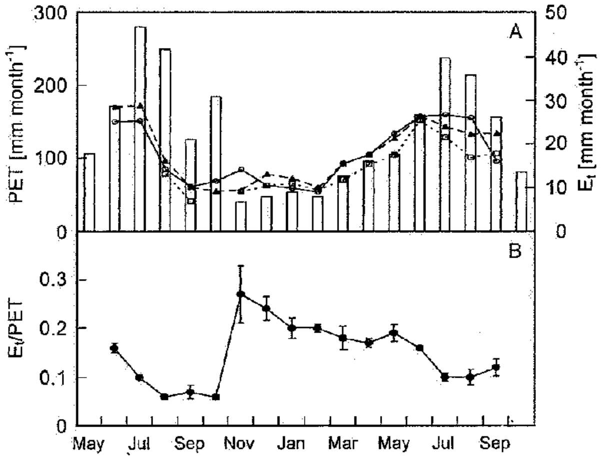

Fig. 5. Monthly potential evapotranspiration (PET, *bars*) compared to tree transpiration ($E_t$): trees 1 (*blank circle*), 3 (*solid triangle*) and 5 (*blank square*) during year 1993-1994 (*A*), and the ratio of mean tree transpiration ($E_t$; trees 1, 3 and 5) and potential evapotranspiration (PET) (*B*). *Vertical bars* indicate SE.

**Accumulated transpiration:** In the hydrological year October 1993 - September 1994, annual tree transpiration ranged from 13 000 to 20 000 dm$^3$ per tree, varying during the course of the year. About 50 % of the annual amount was transpired during the drought (June to September), about 25 % in autumn - winter (October - February) and about 25 % in the spring (March - May). These percentages were similar for the three trees measured. During the summer of 1993, the trees transpired about 20 % less than during the same period in 1994. The high water consumption during the summer of 1994 continued through October as opposed to the same period of the previous year.

Annual $E_t$ for the same hydrological year, 1993-1994, was 169, 205 and 200 mm y$^{-1}$ for trees 5, 3 and 1, respectively. This water consumption ranged between 29 mm month$^{-1}$ in June and 9 mm month$^{-1}$ in February.

Tree 5 reached 6.8 mm month$^{-1}$ in September 1993. For the same hydrological year, 1993-1994, PET was 1419 mm. Monthly $E_t$ and monthly PET patterns were similar throughout the period of study, except for the maximums (Fig. 5*A*) – $E_t$ maximums were reached in June, whereas PET maximums were reached in July. The seasonal pattern of the monthly $E_t$/PET ratios was very low, ranging between 0.05 and 0.27 (Fig. 5*B*).

Daily $E_t$ was positively correlated to daily PET ($E_t = 0.0247 \times \text{PET} + 0.0926$; $r^2 = 0.797$, $P < 0.001$). Monthly $E_t$ also showed a positive correlation with PET although with lower $r^2$ (0.404). As PET increases, $E_t$ approaches maximum values (about 27.7 mm per month) beyond which it is nearly constant because the increase in PET coincides with low water availability.

## Discussion

Southwestern Spain suffered a prolonged drought from 1992 to 1995 and our study period (May 1993 to October 1994) was unusually dry and hot. However, the minimum pre-dawn $\Psi_w$ measured in this study was not as negative as the values recorded for dense stands of *Q. ilex* (Rambal 1992, Sala and Tenhunen 1994, Damesin 1996). The pre-dawn $\Psi_w$ recorded in this work can be considered as indicative of moderate stress. In the summer of 1995, the driest year in the region in the last 70 years, the minimum pre-dawn $\Psi_w$ was about -3 MPa (Fernández Alés, unpublished data).

Progressive stomatal closure with decrease in $\Psi_w$ indicates conservative water use, and explains the decrease in $\Delta\Psi$ during the drought. Hickman (1970) noted that the pattern of increasing $\Delta\Psi$ with water stress is common to species characterised as "conformers". The decrease in $\Delta\Psi$ with water stress characterises "regulator" species like *Q. ilex* (Rambal 1992). In order to control gas exchange under the more severe drought, stomatal closure occurred earlier in the morning and remained at the minimum throughout the day (Fig. 4). This allows the plant to reconcile moderate rates of net $CO_2$ assimilation (early in the morning) (Infante *et al.* 1999) with moderate rates of water loss (during the day).

Variation in transpiration among trees was higher during the dry period than during the wet period, as noted by Čermák *et al.* (1995) and Becker (1996). Differences between periods were due to differences in diurnal dynamics and length of day. Thus, hourly maximums (6 - 7.5 dm$^3$ h$^{-1}$) were reached at any time of the year, except at the end of the dry period when low water availability strongly limited tree transpiration.

Daily $E_t$ maximums (between 1.2 and 1.4 mm d$^{-1}$) were lower than in conifers (Granier *et al.* 1990, Arneth *et al.* 1996, Saugier *et al.* 1997), European oaks (Nizinski and Saugier 1989, Breda *et al.* 1993, 1995) or *Laurus* species (Jiménez *et al.* 1996), and similar to values obtained by Moreno *et al.* (1996) in irrigated olive trees (about 1.6 mm d$^{-1}$).

$E_t$ values obtained (169 - 205 mm y$^{-1}$) were comparable to those previously estimated in the same ecosystem from water balance studies by Joffre and Rambal (1993) in two hydrological years, wet year 1984 - 1985 and dry year 1985 - 1986. Annual transpiration by trees estimated in this work accounted for less than 40 % of annual rainfall. Such low transpiration can be explained by both the strong stomatal control found even under moderate water stress as noted in previous works (Infante *et al.* 1997, 1999), and the low tree density of the stand (Joffre and Rambal 1993).

Seasonal water use patterns observed in the monitored trees of this study were similar to those found for *Q. ilex* of a dense stand in NE Spain (Sala and Tenhunen 1996). Annual water consumption can be calculated on the basis of leaf area by dividing average annual $E_t$ (191.3 mm y$^{-1}$) by the tree leaf area index (LAI) (mean annual tree LAI = 1.9 m$^2$ m$^{-2}$; Fernández Alés, unpublished data). The figure obtained, 100.7 mm y$^{-1}$, is comparable to the estimates obtained by Sala and Tenhunen (1996) for *Q. ilex* in a dense stand (between 87.5 and 98.5 mm y$^{-1}$) but lower than that reported by Rambal (1993) for *Q. coccifera* (193 mm y$^{-1}$) and Poole and Miller (1981) in a Californian chaparral (200 mm y$^{-1}$). Therefore, leaf area appears to strongly affect annual water consumption, as previously noted by Rambal (1993). This control seems particularly strong for LAI values of less than 2.

In the dense stand of *Q. ilex*, Sala (1992) and Piñol (1990, cited by Sala and Tenhunen 1994) noted annual $E_t$/PET ratios between 0.95 and 1, which is higher than the 0.13 ratio found in our study. Nizinski and Saugier (1989) recorded daily values ranging from 0.44 to 0.83 for a dense stand of *Q. petraea*. We have to take into account that the ratio found in our study corresponds exclusively to the tree transpiration not including the evapotranspiration from the grass under the canopy. Considering the ecosystem (tree-grass component) the $E_t$/PET ratio is more realistic during the summer period when the tree transpiration is the exclusive component of the stand evapotranspiration.

In conclusion, the long-term physiological measurements carried out in this study reveal that the prolonged drought seems not to have affected the water relations of the *Q. ilex* individuals studied, mainly due to the strong stomatal regulation, and secondarily due to low tree density of the stand. The long-term measurements of stomatal conductance and sap flow indicate stomatal control in all seasons, although it is stronger in summer, presenting progressive stomata closure earlier in the morning as the season progresses, avoiding the loss of water. This behaviour leads to low water consumption per individual (169 - 205 mm y$^{-1}$) estimated on a projected canopy-area basis and also to permanently low $E_t$/PET ratios throughout the year.

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