

# Canopy transpiration of a Canary Islands pine forest

V.C. Luis<sup>a,\*</sup>, M.S. Jiménez<sup>a</sup>, D. Morales<sup>a</sup>, J. Kucera<sup>b</sup>, G. Wieser<sup>c</sup>

<sup>a</sup> Department of Plant Biology, Plant Physiology, University of La Laguna, Avda.

Astrofísico Francisco Sánchez s/n, E-38207 La Laguna, Tenerife, Spain

<sup>b</sup> Environmental Measuring Systems, Turistická 5, 62100 Brno, Czech Republic

<sup>c</sup> Federal Research and Training Centre for Forests, Natural Hazards and Landscape,

Division Alpine Timberline Ecophysiology, Remweg 1, A-6020 Innsbruck, Austria

Received 11 March 2005; received in revised form 31 October 2005; accepted 7 November 2005

## Abstract

Canopy transpiration ( $E_c$ ) of a 50-year old *Pinus canariensis* Chr. Sm. Ex DC. stand in Tenerife, Canary Islands was estimated continuously throughout 1 year from August 2000 to July 2001 by means of xylem sap flow measurements. Although there was pronounced seasonal trend in soil water availability and evaporative demand,  $E_c$  did not show any clear seasonal trend and averaged 0.80 during the cold-wet and 0.82 mm day<sup>-1</sup> during the warm-dry period. This is, because summer drought is often mitigated by a high relative humidity of the air and a high frequency of clouds due to the north-east trade winds. However, at a given solar radiation and vapour pressure deficit  $E_c$  was significantly lower during the warm and dry season than at other times during the year. The annual total of  $E_c$  was 252.3 mm, which is significantly below the values estimated for other Mediterranean forest ecosystems and thus shows a strong adaptation to low soil water availability during periods of great evaporative demand.

© 2005 Elsevier B.V. All rights reserved.

**Keywords:** Environmental factors; Evaporative demand; Soil water availability; Pine forest

## 1. Introduction

*Pinus canariensis* Chr. Sm. Ex DC. is an endemic conifer species of the western Canary Islands where it forms pure stands under widely different ecological conditions (Blanco et al., 1989). In Tenerife, the distribution limit is between 800 and 2200 m a.s.l. on north-facing slopes and from 500 up to more than 2500 m a.s.l. on south-exposed slopes (Fernández-Palacios and de Nicolás, 1995). These pine forests are essential for local forestry and contribute also to the water balance of the island by fog interception (Aboal et al., 2000). A common habitat feature of pine forests in

Tenerife is a Mediterranean climate with strong seasonal changes in water availability and evaporative demand.

In woody plants from Mediterranean regions stomatal aperture has been shown to decline significantly during the warm and dry season (Epron and Dyer, 1978; Damesin and Rambal, 1995; Borghetti et al., 1998) and thus transpiration is approaching minimum values or even ceases. In the Canary Islands however, dryness is often mitigated due to the influence of the north-east trade winds bringing moisture from the sea and thus increasing relative humidity of the air and *P. canariensis* has been shown to transpire throughout the whole year (Peters, 2001; Peters et al., 2003). Despite a few studies on gas exchange (Peters, 2001; Wieser et al., 2002; Peters et al., 2003) no studies have focused on the seasonal course of *P. canariensis* canopy transpiration based on monitoring xylem sap flow.

\* Corresponding author. Tel.: +34 922 318434;  
fax: +34 922 318447.

E-mail address: [vc Luis@ull.es](mailto:vc Luis@ull.es) (V.C. Luis).

This method provides insight into environmental limitations and yields results comparable to that of whole forest ecosystem estimates of water use (Wilson et al., 2001). Therefore, our specific goals were to investigate the seasonal variation in canopy transpiration of a *P. canariensis* stand and to analyse the impact of environmental factors on canopy transpiration.

## 2. Material and methods

The study was carried out in an open 50-year old *P. canariensis* forest at 1650 m a.s.l. growing on a northern slope of the Cordillera Dorsal (Morro de Isarda, El Gaitero, 28°35'N, 27°15'W) in the mountains of La Victoria, approximately 20 km south-west of la Laguna, Tenerife, Canary Islands. After reforestation in 1950 the canopy reached 20 m height in 2001, with a stand density of 825 trees ha<sup>-2</sup>, a basal stem area of 53.8 m<sup>2</sup> ha<sup>-1</sup>, and a leaf area index (LAI) of 3.4 m<sup>2</sup> m<sup>-2</sup>. The frequency distribution of tree diameters at breast height (DBH) at the study site is shown in Fig. 1.

The field site is characterised by a Mediterranean climate with a mean annual temperature of 12.6 °C (absolute minima -4.2 °C and absolute maxima 31.2 °C), a mean relative humidity of 52% and an annual sum of precipitation ranging from 460 (Aboal et al., 2000) to 930 mm (Peters et al., 2003). Opposite to the typical Mediterranean climate, summer drought is often mitigated by a high relative humidity of the air and a high frequency of clouds due to the north-east trade winds. Further details concerning stand and climatic

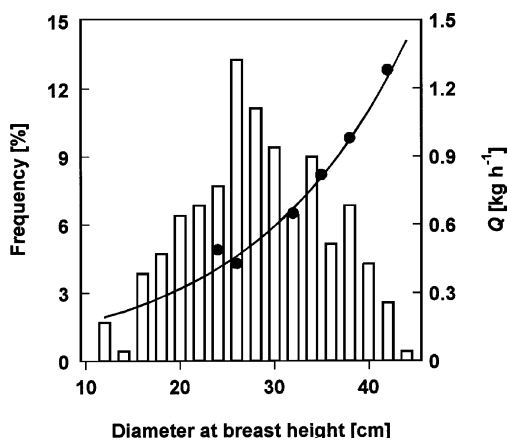


Fig. 1. Frequency distribution of tree diameters at breast height (DBH) at the study site (open bars) and the relationship between daily mean tree transpiration over the investigation period ( $Q$ ) and DBH. The DBH of the sample trees are noted by the filled circles. Points were fit by exponential regression:  $y = 0.092 \exp(0.06x)$ ;  $R^2 = 0.92$ .

conditions are given in Aboal et al. (2000) and Peters et al. (2003).

According to the World Base for Soil Resources (FAO, 1998) the soil at the study site is classified as an andosol. There was a 3–5 cm thick layer of needles on top of the mineral A (0–50 cm depth) and C (>50 cm) horizons. The A horizon was enriched with 10% of organic matter and the soil texture was dominated by the sand (64–67%) and the slit fraction (30–33%), with varying clay content (2–4%). The volumetric saturation water content in 5–50 cm soil depth averaged  $0.55 \pm 0.05 \text{ m}^3 \text{ m}^{-3}$ . The rooting depth was estimated in a 20 m deep ditch close to the study site.

Water xylem sap flow ( $Q$ ) of six *P. canariensis* trees differing in DBH (Fig. 1) was monitored continuously from 1 August 2000 to 31 July 2001 by means of the heat-balance approach (Cermák et al., 1973; Kucera et al., 1977) with a 12-channel battery-operated sap flow meter (depending on tree DBH electrode length 70 and 80 mm, covering 35 and 45 mm of sapwood depth, respectively) connected to a data logger unit (P4.1; Environmental Measuring System, EMS, Brno, Czech Republic). Data were recorded as 15-min means of measurements taken every minute. Stems were shielded with aluminium-faced foam which extended ca. 50 cm above and below the measuring points. Underestimating  $Q$  may be a potential problem because the electrode length may be shorter than the depth of the sapwood. Fifty-year old *P. canariensis* trees have average sapwood thickness of 90–120 mm. However, as there is evidence that  $Q$  in the inner sapwood is significantly lower as compared to the outer sapwood (Cermák et al., 1992; Köstner et al., 1998), we assumed that our installation sampled 100% of the water flow.

For each entire tree we estimated  $Q$  with two measuring points per tree installed at breast height on the north-south ( $Q_{\text{ns}}$ ) and east-west ( $Q_{\text{ew}}$ ) side of the stem, respectively. For each entire tree the mean sap flow rate ( $Q$ ) based on measurements on both sides was then calculated as:

$$Q = \frac{Q_{\text{ns}} + Q_{\text{ew}}}{2}$$

Whole tree transpiration was then calculated by according to the equation:

$$E_t = Q_m L_c$$

where  $E_t$  is the whole tree transpiration and  $L_c$  is the length of the circumference of the xylem at measuring height.

Canopy transpiration ( $E_c$ ) was calculated by applying a diameter class technique similar to that common in

forest inventories (Cermák et al., 1982, 2004; Cermák and Kucera, 1990). An exponential correlation between DBH and mean daily  $E_t$  was derived from the trees under study. Based on this relationship (Fig. 1) and the number of tree distribution per hectare with respect to DBH daily  $E_c$  was then calculated by integrating actual  $E_t$  for each specific day over all the DBH classes. Finally,  $E_c$  was related to ground surface area ( $\text{mm day}^{-1}$ ).

Canopy conductance related to ground surface area ( $g_c$ ) was estimated from  $E_c$  using a simplified inverted Penman–Monteith equation:

$$g_c = \gamma \lambda \frac{E_c}{\rho c_p D},$$

where  $\gamma$  is the psychrometric constant ( $\text{kPa K}^{-1}$ ),  $\lambda$  the latent heat of water vaporisation ( $\text{J kg}^{-1}$ ),  $\rho$  the density of the air ( $\text{kg m}^{-3}$ ),  $c_p$  the specific heat of air at constant pressure ( $\text{J kg}^{-1} \text{K}^{-1}$ ) and  $D$  is the vapour pressure deficit ( $\text{kPa}$ ). Because  $D$  was calculated from climatic measurements above the canopy (see below) boundary layer and aerodynamic conductance are included in the estimation of  $g_c$ . Due to the open canopy, the low LAI and hence a strong coupling to the atmosphere we assumed that  $g_c$  closely approximates stomatal conductance (Oren et al., 1999).

Air temperature, relative humidity (RHA1, Delta-T, Cambridge, UK), solar radiation (LI190 SA, Li-Cor, Lincoln, NE, USA), wind velocity and precipitation (Skye Instruments, Landrindod, UK) were monitored at a 20 m tower; and soil water content (SWC) in 40–45 cm soil depth was monitored with a Theta Probe (Delta-T). All environmental parameters were recorded with a DL2 data logger (Delta-T) programmed to record 30-min averages of measurements taken every minute. Due to a rain gauge break down missing precipitation data for the period 1 January–12 June 2001 rainfall data for this period were obtained from the Los Rodeos Meteorological Station at 632 m a.s.l.; 20 km east of the study site (source: <http://www.tutiempo.net/clima>) which is the closest reliable station to our study site.

### 3. Results and discussion

The seasonal patterns of environmental parameters were representative for the climatic conditions at the study site, which are characterised by an alternation of a warm and dry period from May to September and a cold and wet period from October throughout April (Fig. 2). Solar radiation ( $R_s$ ) varied between  $34.2$  ( $20$  June) during the summer and  $2.2 \text{ MJ m}^{-2} \text{ day}^{-1}$  ( $20$  December) during the winter (Fig. 2). Mean average air

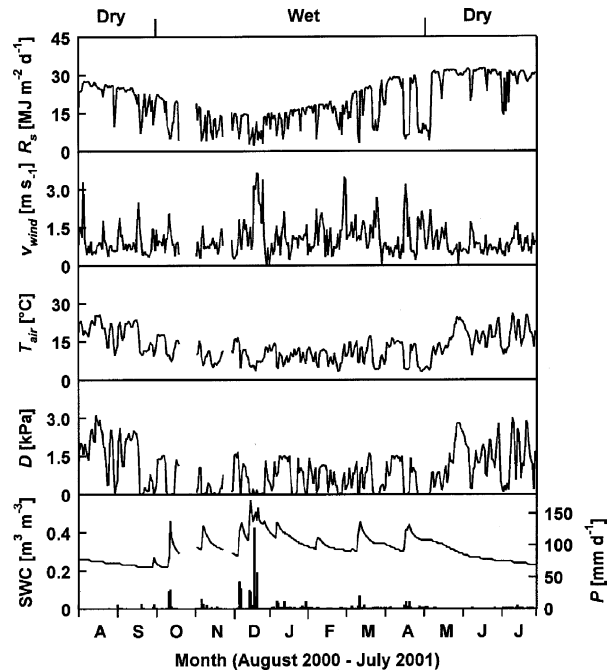


Fig. 2. Seasonal course of daily sum of solar radiation ( $R_s$ ), mean daily wind velocity ( $v_{\text{wind}}$ ), mean daily air temperature ( $T_{\text{air}}$ ), mean daily vapour pressure deficit ( $D$ ), mean daily soil water content (SWC) and daily sum of precipitation ( $P$ , solid bars) in a *Pinus canariensis* forest at 1650 m a.s.l. Tenerife, Canary Islands between 1 August 2000 and 31 July 2001.

temperature ( $T$ ) was  $13.0$  °C and varied between  $25.5$  ( $13$  July) and  $3.2$  °C ( $2$  May). Daily mean vapour pressure deficit ( $D$ ) averaged  $1.42$  and  $0.81$  kPa during the warm and dry and a cold and wet period, respectively (Fig. 2). Daily mean wind velocity ( $v$ ) averaged  $1.1 \text{ m s}^{-1}$ , and the total sum of precipitation throughout the investigation period was  $638$  mm (Fig. 2). Due to frequent precipitation during the cold and wet period ( $567$  mm), soil water content reached a maximum of  $0.57 \text{ m}^3 \text{ m}^{-3}$  on  $16$  December, and declined progressively from May throughout fall, reaching a minimum of  $0.22 \text{ m}^3 \text{ m}^{-3}$  on  $17$  September (Fig. 2). Because of the large variation in  $Q$  among individual trees (Fig. 1) values of each tree were converted to a ratio of the maximum daily mean value observed throughout the study period ( $1.98$ ,  $1.67$ ,  $1.74$ ,  $1.06$ ,  $0.89$  and  $0.76 \text{ kg h}^{-1}$ , respectively, from the largest to the smallest sample trees) and thus permitting a better comparison of  $Q$  to environmental variables. In order to avoid the problem that stem capacitance may affect the analysis of transpiration responses to variation in environmental conditions (Oren et al., 1998; Ewers et al., 1999) we averaged diurnal values of  $Q$  derived from each tree to daily means. In general,  $Q$  increased

with increasing DBH (Fig. 1) because the quantity of foliage in terms of needle biomass or surface area is positively correlated with stem diameter and hence also sapwood area (Waring et al., 1982; Margolis et al., 1995). However, the latter was not investigated. Nevertheless, the individual trees under study did not differ significantly in their responses to water availability and climatic parameters (data not shown).

In Mediterranean type evergreen forests the dominant factors controlling  $Q$  are a low soil water availability, and a high evaporative demand in terms of  $D$  (Lösch, 2000; Larcher, 2001). During the dry period, when soil water content was lower than  $0.27 \text{ m}^3 \text{ m}^{-3}$  ( $-0.3 \text{ MPa}$  soil water potential)  $Q$  decreased linearly with decreasing soil water availability (Fig. 3).

Seasonal variations in daily mean  $Q$  were also correlated with  $R_s$ ,  $T$ ,  $D$  and  $v$  conditions at the study site. During the wet period with ample soil water availability  $Q$  was linearly correlated to  $R_s$  (Fig. 4),  $T$  (Fig. 5) and  $D$  above the canopy (Fig. 6) as also observed in tropical forests (Oren et al., 1996; Phillips et al., 1999), while the influence of  $v$  was negligible (Fig. 7). However, at given  $R_s$  (Fig. 4),  $T$  (Fig. 5) and  $D$  (Fig. 6);  $Q$  was significantly lower during the warm and dry season than during the wet and cold period. Moreover,  $Q$  tended to reach its maximum at mean daily  $R_s > 250 \text{ W m}^{-2}$  (Fig. 4), a mean daily  $T > 22^\circ \text{C}$  (Fig. 5) and mean daily  $D > 2 \text{ kPa}$  (Fig. 6). This

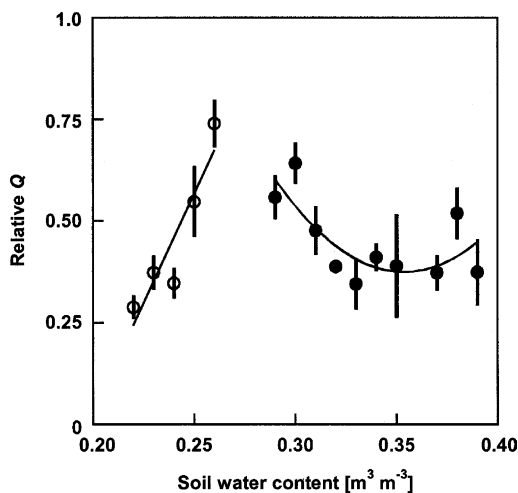


Fig. 3. Normalised mean daily sap flow ( $Q$ ) as a function of soil water content during the wet (solid circles) and the dry season (open circles) in a *Pinus canariensis* forest at 1650 m a.s.l. Tenerife, Canary Islands. Values are mean of six trees  $\pm$  S.E. Means were selected according to a stepwise increase in soil water content of  $0.01 \text{ m}^3 \text{ m}^{-3}$ . For  $\text{SWC} < 0.27 \text{ m}^3 \text{ m}^{-3}$  points were fitted by a linear regression:  $y = 10.76x - 2.12$ ;  $R^2 = 0.86$ .

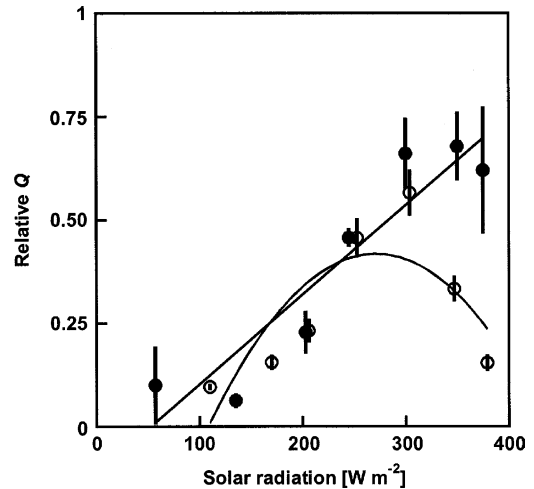


Fig. 4. Normalised mean daily sap flow ( $Q$ ) as a function of daily mean solar radiation during the wet (solid circles) and the dry season (open circles) in a *Pinus canariensis* forest at 1650 m a.s.l. Tenerife, Canary Islands. Values are mean of six trees  $\pm$  S.E. Means were selected according to a stepwise increase in daily mean solar radiation of  $50 \text{ W m}^{-2}$ . Points were fitted by regression analysis: wet season:  $y = 0.002x - 0.11$ ;  $R^2 = 0.87$ ; dry season:  $y = (-0.000015x + 0.0085)x - 0.74$ ;  $R^2 = 0.63$ .

behaviour can be attributed to a decrease in  $g_c$  with increasing  $D$  (Fig. 8) as also observed in other forest ecosystems (Lopushinsky, 1986; Meinzer et al., 1993; Granier et al., 1996, 2000; Hogg and Hurdle, 1997;

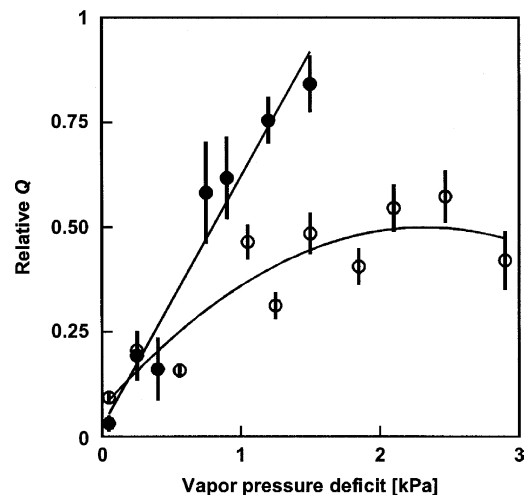


Fig. 5. Normalised mean daily sap flow ( $Q$ ) as a function of daily mean vapour pressure deficit during the wet (solid circles) and the dry season (open circles) in a *Pinus canariensis* forest at 1650 m a.s.l. Tenerife, Canary Islands. Values are mean of six trees  $\pm$  S.E. Means were selected according to a stepwise increase in daily mean vapour pressure deficit of  $0.25 \text{ kPa}$ . Points were fitted by regression analysis: wet season:  $y = 0.602x + 0.02$ ;  $R^2 = 0.95$ ; dry season:  $y = (-0.08x + 0.37)x + 0.07$ ;  $R^2 = 0.81$ .

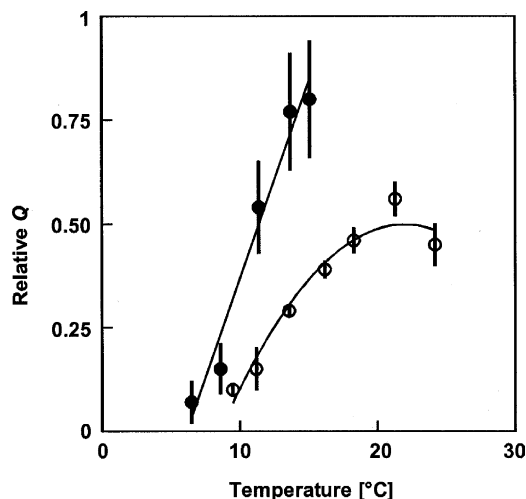


Fig. 6. Normalised mean daily sap flow ( $Q$ ) as a function of daily mean temperature during the wet (solid circles) and the dry season (open circles) in a *Pinus canariensis* forest at 1650 m a.s.l. Tenerife, Canary Islands. Values are mean of six trees  $\pm$  S.E. Means were selected according to a stepwise increase in daily mean temperature of 2.5 °C. Points were fitted by regression analysis: wet season:  $y = 0.97x - 0.58$ ;  $R^2 = 0.97$ ; dry season:  $y = (-0.0028x + 0.121)x - 0.83$ ;  $R^2 = 0.96$ .

Jiménez et al., 1996, 1999; Zimmermann et al., 2000). Stomatal closing due to increasing air and soil drought has also been found in *P. canariensis* at the leaf level (Peters, 2001; Peters et al., 2003) as well as in other Mediterranean tree species (Epron and Dryer, 1978;

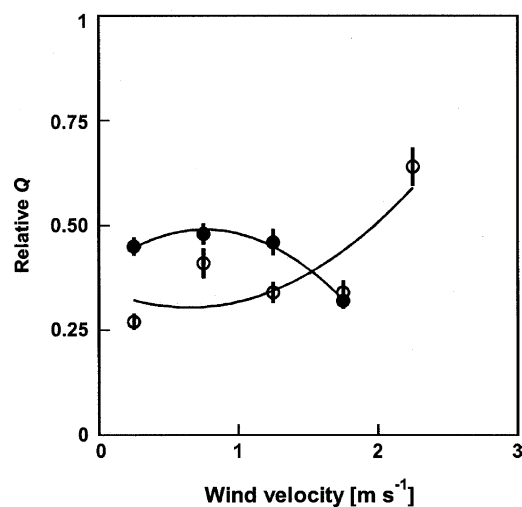


Fig. 7. Normalised mean daily sap flow ( $Q$ ) as a function of daily wind velocity during the wet (solid circles) and the dry season (open circles) in a *Pinus canariensis* forest at 1650 m a.s.l. Tenerife, Canary Islands. Values are mean of six trees  $\pm$  S.E. Means were selected according to a stepwise increase in daily mean wind velocity of 0.5 m s<sup>-1</sup>.

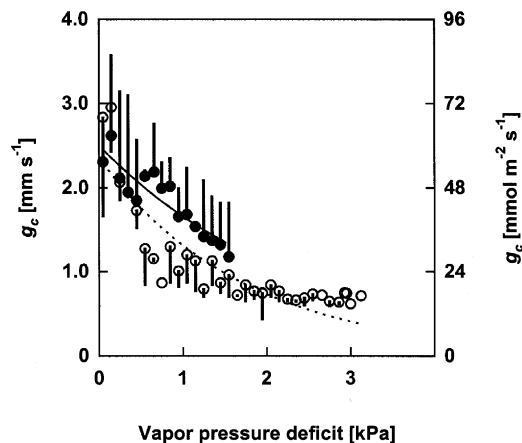


Fig. 8. Mean daily canopy conductance ( $g_c$ ) as a function of mean daily vapour pressure deficit during the wet (solid line and filled circles) and the dry season (dotted line and open circles) in a *Pinus canariensis* forest at 1650 m a.s.l. Tenerife, Canary Islands. Each data point presents the mean of two to five daily mean values  $\pm$  S.E. Points were fitted by an exponential regression: wet season:  $y = 2.5 \exp(-0.41x)$ ,  $R^2 = 0.82$ ; dry season:  $y = 2.3 \exp(-0.58x)$ ,  $R^2 = 0.75$ .

Damesin and Rambal, 1995; Borghetti et al., 1998; Mediavilla and Escudero, 2003) and thus significantly reducing vegetation water loss.

This structural adaptation mechanism in *P. canariensis* enables to delaying desiccation through extremely conservative water use. Thus, in terms of Levitt (1980) *P. canariensis* can be classified as a water-saving and drought-avoiding species. Conservative water use behaviour has also been reported for several evergreen Mediterranean oak species (Nardini et al., 1999; Mediavilla and Escudero, 2003). Because *P. canariensis* develops up to 15 m deep roots trees can make use of ground water sources to maintain a favourable water status (Dawson, 1994; Villar-Salvador et al., 1997).

Due to the combination of a declining  $g_c$  in response to increasing evaporative demand and access to deep soil water reserves,  $E_c$  was conservative and did not show a significant reduction when the period when the soil was dry (Fig. 9).  $E_c$  averaged 0.80 and 0.82 mm day<sup>-1</sup> during the cold and wet period and during the warm and dry period, respectively, and reached maximum values up to 1.85 mm day<sup>-1</sup> during cloudless days with high evaporative demand and ample soil water availability (Fig. 9). These values are within the range obtained for evergreen coniferous forests (1–6 mm day<sup>-1</sup>) during the course of an entire growing season (Pallardy et al., 1995). Total annual  $E_c$  was 252.3 mm year<sup>-1</sup>. Thus, annual total  $E_c$  was about two to three times lower than transpiration rates reported for Mediterranean forest ecosystems (Löscher, 2000).

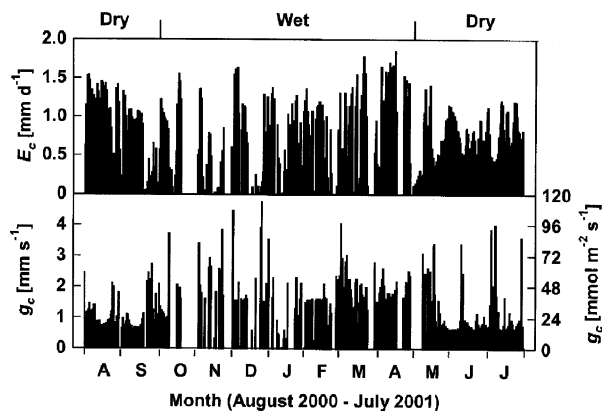


Fig. 9. Seasonal course of daily canopy transpiration ( $E_c$ ) and mean daily canopy conductance ( $g_c$ ) in a *Pinus canariensis* forest at 1650 m a.s.l. Tenerife, Canary Islands between 1 August 2000 and 31 July 2001.

The estimated annual  $E_c$  was also lower than values estimated for laurel forest ecosystems in Tenerife (Jiménez et al., 1996, 1999) but within the range given for an entire growing season in open boreal ( $320 \text{ mm year}^{-1}$ ; Grelle et al., 1997;  $265 \text{ mm year}^{-1}$ ; Kelliher et al., 1998), high elevation temperate ( $174 \text{ mm year}^{-1}$ ; Zeller and Nikolov, 2000) and European forest ecosystems ( $300 \pm 30 \text{ mm year}^{-1}$ ; Roberts, 1983).

Our last point deals with the ability of *P. canariensis* to maintain a relatively high conductance at low soil water availability (Fig. 9). At soil water contents lower than  $0.22 \text{ m}^3 \text{ m}^{-3}$  ( $-1.0 \text{ MPa}$ ), we observed daily mean  $g_c$  values around  $1.42 \text{ mm s}^{-1}$  and  $34 \text{ mmol m}^{-2} \text{ s}^{-1}$ , respectively (Fig. 9). Similar low conductance values during periods of low soil water availability and high evaporative demand were also obtained in a year round study on foliar gas exchange at the needle level (Peters, 2001) and thus allowing *P. canariensis* needles to maintain a positive carbon gain, at periods of high evaporative demand even during the dry season (Peters et al., 2003).

#### 4. Conclusions

In conclusion, our results suggest that that *P. canariensis* is well-adapted to cope with low soil water availability and high evaporative demand, as has also been shown for other Mediterranean evergreen tree species (Nardini et al., 1999; Martínez-Vilalta et al., 2003). Due to access to deep soil water reserves and due to the fact that  $g_s$  and stomatal conductance is significantly reduced during conditions of high evaporative demand (Peters et al., 2003) transpiration was

maintained at relatively high rates in spite of the low precipitation during the dry season. This is, because the  $g_s$  of *P. canariensis* trees declines very rapidly with increasing evaporative demand. These results should also be taken into consideration when forecasting the impact of increasing aridity by climate change models in Mediterranean regions (IPCC, 2001).

#### Acknowledgments

The authors want to express their gratitude to the Consejería de Educación Cultural y Deportes of the Canarian Government for supporting of the investigation project P5119118 and to the Cabildo Insular of Tenerife for logistic support.

#### References

- Aboal, J.R., Jiménez, M.S., Morales, D., Gil, P., 2000. Effects of thinning on throughfall in Canary Islands pine forest—the role of fog. *J. Hydrol.* 238, 218–230.
- Blanco, A., Castroviejo, M., Fraile, J.L., Gandullo, J.M., Muñoz, L.A., Sánchez Palomeras, O., 1989. Ecological studies on *Pinus canariensis*. In: Ministerio de Agricultura, Pesca y Alimentación, Serie Técnica, Número 6, ICONA, Madrid.
- Borghetti, M., Cinnirella, S., Magani, S., Sarracín, A., 1998. Impact of long-term drought on xylem embolism and growth in *Pinus halepensis*. *Trees* 12, 187–195.
- Cermák, J., Kucera, J., 1990. Scaling up transpiration data between trees, stand and watersheds. *Silva Carrel.* 15, 171–178.
- Cermák, J., Deml, M., Penka, M., 1973. A new method of sap flow determination in trees. *Biol. Plant.* 15, 171–178.
- Cermák, J., Uleha, J., Kucera, J., Penka, M., 1982. Sap flow rate and transpiration dynamics in the full grown oak (*Quercus robur* L.) in floodplain forest exposed to seasonal floods as related to potential evapotranspiration and tree dimensions. *Biol. Plant.* 24, 446–460.
- Cermák, J., Cienciala, E., Kucera, J., Hällgren, J.-E., 1992. Radial velocity profiles of water flow in trunks of Norway spruce and oak and the response of oak to severing. *Tree Physiol.* 10, 367–380.
- Cermák, J., Kucera, J., Nadezhdina, N., 2004. Sap flow measurements with some thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forests. *Trees* 18, 529–546.
- Damesin, C., Rambal, S., 1995. Field studies on leaf photosynthetic performance by a Mediterranean deciduous oak (*Quercus pubescens*) during severe summer drought. *New Phytol.* 131, 159–167.
- Dawson, D.E., 1994. Determining water use by trees and forests from isotopic, energy balance, and transpirational analyses: the role of tree site and hydraulic lift. *Tree Physiol.* 18, 177–184.
- Epron, D., Dryer, E., 1978. Long term effects of drought on photosynthesis of adult oak trees [*Quercus petraea* (Mat.) Liebl. and *Quercus robur* L.] in a natural stand. *New Phytol.* 125, 381–389.
- Ewers, B.E., Oren, R., Albaugh, T.J., Dougherty, P.M., 1999. Carry-over effects of water and nutrient supply on water use of *Pinus taeda*. *Ecol. Appl.* 9, 513–525.
- FAO, ISRIC, ISSS, 1998. World Reference Base for Soil Resources. FAO, Rome, 109 pp.

- Fernández-Palacios, J.M., de Nicolás, J.P., 1995. Altitudinal pattern of vegetation variation on Tenerife. *J. Veg. Sci.* 6, 183–190.
- Granier, A., Huc, R., Barigah, S.T., 1996. Transpiration of natural rain forests and its dependence on climatic factors. *Agric. Forest Meteorol.* 78, 19–29.
- Granier, A., Loustau, D., Bréda, N., 2000. A generic model for forest canopy conductance dependent on climate, soil water availability and leaf area index. *Ann. Forest Sci.* 57, 755–765.
- Grelle, A., Lundberg, A., Lindroth, A., Moren, A.-S., Cienciala, E., 1997. Evaporation components in a boreal forest: variations during the growing season. *J. Hydrol.* 197, 70–87.
- Hogg, E.H., Hurdle, P.A., 1997. Sap flow in trembling aspen: implications for stomatal responses to vapour pressure deficit. *Tree Physiol.* 17, 501–509.
- IPCC, 2001. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., Van der Linden, P.J., Day, X., Maskell, K., Johnson, C.A. (Eds.), *Climate Change 2001: The Scientific Basis*. Cambridge University Press, Cambridge, 881 pp.
- Jiménez, M.S., Cermák, J., Kucera, J., Morales, D., 1996. Laurel forests in Tenerife, Canary Islands: the annual course of sap flow in *Laurus* trees and stands. *J. Hydrol.* 183, 307–321.
- Jiménez, M.S., Morales, D., Kucera, J., Cermák, J., 1999. The annual time course of transpiration in a Laurel forest of Tenerife. Estimation with *Myrica faya*. *Phyton* 39, 85–90.
- Kelliher, F.M., Lloyd, J., Arneth, A., Byers, J.N., McSeveny, T.M., Milukova, I., Grigoriev, S., Panfourov, M., Sogatchev, A., Varlargin, A., Ziegler, W., Bauer, G., Schulze, E.-D., 1998. Evaporation from a central Siberian pine forest. *J. Hydrol.* 205, 279–296.
- Köstner, B., Granier, A., Cermák, J., 1998. Sap flow methods in forest stands: methods and uncertainties. *Ann. Forest Sci.* 55, 13–27.
- Kucera, J., Cermák, J., Penka, M., 1977. Improved thermal method of continual recording the transpiration rate dynamics. *Biol. Plant.* 19, 413–420.
- Larcher, W., 2001. *Ökophysiologie der Pflanzen: Leben, Leistung und Stressbewältigung der Pflanzen in ihrer Umwelt (Physiological Plant Ecology)*. UTB für Wissenschaft, Ulmer, Stuttgart, 408 pp.
- Levitt, J., 1980. *Responses of Plants to Environmental Stresses*. Academic Press, New York, 697 pp.
- Lopushinsky, W., 1986. Seasonal and diurnal trends of heat pulse velocity in Douglas-fir and ponderosa pine. *Can. J. Forest Res.* 16, 814–821.
- Lösch, R., 2000. *Wasserhaushalt der Pflanzen (Plant Water Retention Relationships)*. UTB für Wissenschaft, Quelle und Meyer, Wiebelsheim, 595 pp.
- Margolis, H., Oren, R., Whitehead, D., Kaufmann, M.R., 1995. Leaf area dynamics of coniferous forests. In: Smith, W.K., Hinckley, T.M. (Eds.), *Ecophysiology of Coniferous Forests*. Academic Press, San Diego, pp. 181–223.
- Martínez-Vilalta, J., Magirión, M., Ogaya, R., Sauret, M., Serrano, L., Peñuelas, J., Piñol, J., 2003. Sap flow of three co-occurring Mediterranean woody species under varying atmospheric and soil water conditions. *Tree Physiol.* 23, 747–758.
- Mediavilla, S., Escudero, A., 2003. Stomatal responses to drought at a Mediterranean site: a comparative study of co-occurring woody species differing in leaf longevity. *Tree Physiol.* 23, 987–996.
- Meinzer, F.C., Goldstein, G., Holbrook, N.M., Jackson, P., Cavelier, J., 1993. Stomatal and environmental control of transpiration in a lowland tropical forest tree. *Plant Cell Environ.* 16, 429–436.
- Nardini, A., Lo Gullo, M.A., Salleo, S., 1999. Competitive strategies for water availability in two Mediterranean *Quercus* species. *Plant Cell Environ.* 22, 109–116.
- Oren, R., Zimmermann, R., Terborgh, J., 1996. Transpiration in upper Amazonia floodplain and upland forests in response to drought breaking rains. *Ecology* 77, 968–973.
- Oren, R., Phillips, N., Katul, G., Ewers, B.E., Pataki, D.E., 1998. Scaling xylem sap flux and soil water balance and calculating variance. A method for partitioning water flux in forests. *Ann. Forest Sci.* 55, 191–216.
- Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N., Schäfer, K.V.R., 1999. Intra- and interspecific responses of canopy stomatal conductance to water vapour pressure deficit. *Plant Cell Environ.* 22, 1515–1526.
- Pallardy, S.G., Cermák, J., Ewers, F.W., Kaufmann, M.R., Parker, W.C., Sperry, J.S., 1995. Water transport dynamics in trees and stands. In: Smith, W.K., Hinckley, T.M. (Eds.), *Resource Physiology on Conifers: Acquisition, Allocation and Utilization*. Academic Press, San Diego, pp. 301–389.
- Peters, J., 2001. *Ecophysiology del Pino canario (Ecophysiology of Pinus canariensis)*. Ph.D. Thesis University, La Laguna, Spain, 257 pp.
- Peters, J., Morales, D., Jiménez, M.S., 2003. Gas exchange characteristics of *Pinus canariensis* needles in a forest stand on Tenerife, Canary Islands. *Trees* 17, 492–500.
- Phillips, N., Oren, R., Zimmermann, R., 1999. Temporal patterns of water flux in trees and lianas in a Panamanian moist forest. *Trees* 14, 116–123.
- Roberts, J.M., 1983. Forest transpiration: a conservative hydrological process? *J. Hydrol.* 66, 133–141.
- Villar-Salvador, P., Castro-Díez, P., Pérez-Rontomé, C., Montserrat-Marté, G., 1997. Stem xylem features in three *Quercus* (fagaceae) species along a climatic gradient in NE Spain. *Trees* 12, 90–96.
- Waring, R.G., Schroeder, P.E., Oren, R., 1982. Application of the pipe model theory to predict canopy leaf area. *Can. J. Forest Res.* 3, 556–560.
- Wieser, G., Peters, J., Luis, V.C., Morales, D., Jiménez, M.S., 2002. Ecophysiological studies on the water relations in a *Pinus canariensis* stand, Tenerife, Canary Islands. *Phyton* 42, 291–304.
- Wilson, K.B., Hanson, P.J., Mulholland, P.J., Baldocchi, D.D., Wullschlegel, S.D., 2001. A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance. *Agric. Forest Meteorol.* 106, 153–168.
- Zeller, K.F., Nikolov, N.T., 2000. Quantifying simultaneous fluxes of ozone, carbon dioxide and water vapor above a subalpine forest ecosystem. *Environ. Pollut.* 107, 1–20.
- Zimmermann, R., Schulze, E.-D., Wirth, C., Schulze, E.-E., McDonald, K.C., Vygodskaya, N.N., Ziegler, W., 2000. Canopy transpiration in a chronosequence of Central Siberian pine forests. *Global Change Biol.* 6, 25–37.