

Laurel forests in Tenerife, Canary Islands: the annual course of sap flow in *Laurus* trees and stand

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Received 5 July 1995; accepted 20 October 1995

Abstract

Sap flow rate was continuously measured in six trees of *Laurus azorica* at the experimental site of laurel forest in Agua García mountains, Tenerife, Canary Islands, over 1 year from June 1993 to May 1994. Sample trees were of different sizes and covered the whole range of species. A sigmoid-like relationship based on basal area was applied to scale up the transpiration data from sample trees to the whole stand. Maximum transpiration for the stand was 7 mm day⁻¹. There was strong competition among the medium-sized trees in the high-density stand. The annual course of transpiration was very variable, owing to weather conditions, and was mainly controlled by the evaporative conditions. Contrasting with conditions in colder regions of the world with pronounced seasons, relatively high transpiration persisted over the mild winter. The annual total of transpiration was thus significantly higher, amounting to 636 mm year⁻¹ (about 500 mm from April to October). Nevertheless, the transpiration represented only a small portion of stand water balance (65% of potential evaporation and 80% of annual precipitation in the open).

1. Introduction

The laurel forest is an evergreen forest relict of the Tertiary Mediterranean flora which occupied southern Europe and northern Africa about 20 million years ago (Santos, 1990). There are only few regions in the world where such forests remain, and one of these regions is the volcanic Canary Islands. The evergreen laurel forest evolved in a relatively uniform climate with small temperature oscillations and high moisture throughout the year

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(González Henríquez et al., 1986). These forests have the typical appearance of a cloud forest (Hollermann, 1981) and are restricted mainly to the most humid section of the northern (windward) slope in the middle elevations where there is a cloud belt. Originally, the laurel forest occupied a great part of the central and western Canary Islands. This area decreased when the forests were exploited for fuel and building material and when they were replaced by cultivated lands. Today, only small areas of these forests remain (about 2700 ha in Tenerife).

An experimental plot was established in 1993 in the Agua García mountains, Tenerife, Canary Islands, to study in detail the structure, growth and other living processes of laurel forest species at the leaf, tree and stand levels (Morales et al., 1996a,b). Teams of researchers from a number of countries are involved in these studies (Larcher et al., 1991; Morales et al., 1992; Lösch, 1993; Aschan et al., 1994; Zohlen et al., 1995).

Forests play an important role in watershed management and form an effective erosion control, which is especially important in environments with steep slopes and high rainfall intensity. The estimation of annual values of transpiration in laurel forests will be crucial for the calculation of stand and regional water balances of Tenerife. Seasonal and diurnal dynamics of sap flow rate will explain the behaviour of species important in the stability of these forests and their survival. The sap flow method for estimating transpiration can be used continuously for long periods of time and provides an accurate method for determining the vapour flux from the dry canopy in a forest stand (e.g. Granier, 1987; Cermák and Kucera, 1987; Granier et al., 1990; Diawara et al., 1991; Cienciala et al., 1992, 1994; Kelliher et al., 1992; Cermák et al., 1993; Granier and Loustau, 1994; Pallardy et al., 1995).

The present paper is related to long-term studies of diurnal, seasonal and annual dynamics of transpiration, measured directly at the tree level and scaled up to the whole stand level. Direct measurements have been made on *Laurus azorica*, as this is the most representative species of the laurel forest in general and the most abundant in our experimental plot, and from these we have scaled up to the whole stand level.

2. Material and methods

2.1. The experimental plot

The experimental site is located in the Agua García mountains of Tenerife (28°27'32"N, 16°24'20"W, at 820–830 m altitude on a slightly sloping (12°) NNE face. It was described in detail in our previous papers (Morales et al., 1996a,b). The climate is humid Mediterranean with an average annual temperature of 13.6°C, relative humidity of 82% and precipitation of 756 mm. The bedrock of the site is a mixture of olivine basalt and volcanic ash with high permeability and drainage. Soil type is a colluvial andosol covered with a layer of litter of 2–3 cm thickness. The A-horizon (0–45 cm deep) is very colluvial reddish clay. The B-horizon (45–90 cm deep) is andic, loamy, with a poorly developed organo-mineral structure and a high content of roots. Such soils are very permeable; underground water can flow easily down to impermeable layers and there is no water table close to the soil surface. The experimental stand was about 30 years old (in 1993),

had resprouted following cutting of the original forest, and was composed of six tree species: *Laurus azorica* (Seub.) Franco, *Persea indica* (L.) Spreng., *Myrica faya* Ait., *Erica arborea* L., *Ilex platyphylla* Webb and Berth. and *I. canariensis* Poivet.). The leaf area index (LAI) of the stand was 7.8, the tallest trees reached 17.4 m in height and the canopy was 5.5 m thick. The total basal area of the experimental plot was $33.7 \text{ m}^2 \text{ ha}^{-1}$ (see Morales et al., 1996a). *Myrica* represented the greatest proportion of it (39%), followed by *Laurus* (26%), *Erica* (20%), *Persea* (14%) and *Ilex* (2%), and there were $1693 \text{ trees ha}^{-1}$ (38% *Laurus*, 27% *Erica*, 17% *Myrica*, 14% *Persea* and 4% *Ilex*). As *Laurus azorica* is the most representative laurel forest species and because it was the most abundant in our experimental plot it was selected as the first species to be studied.

2.2. Sample trees

Representative sizes of sample trees (*Laurus azorica*) for measurement of the sap flow rate were calculated from the forest inventory data by applying the statistical technique of quantiles of total (Cermák and Kucera, 1990). This technique defines that the sample trees are evenly distributed over the whole range of tree size and that each sample tree represents the same amount of basal area, A_{bas} , characterizing the unit of stand area. Individual trees were sorted according to their A_{bas} , in ascending manner. Total basal area of the stand, $(A_{\text{bas}})_{\text{stand}}$, was then divided into a number of equal portions corresponding to the chosen number, m , of sample trees (this number, $m = 6$, was determined practically by the number of channels of the measuring instrument available). The portions of A_{bas} (1–6) when added subsequently (1, 1+2, 1+...+ m) and compared with cumulative A_{bas} characterized border values between portions. The size of sample trees representing the portions was calculated using means of the portions, $(A_{\text{bas}})_{\text{stand}}/m$, multiplied by factors 0.5, 1.5, ..., 5.5. These values were again compared with the cumulative A_{bas} . The sizes of trees (their A_{bas}) whose corresponding cumulative A_{bas} values were closest to the products of the above portions and factors represented the optimum size of sample trees.

2.3. Sap flow rate measurement

Sap flow rate was measured with the tree trunk heat balance technique (THB), applying internal (direct electric) heating of tissues and sensing of temperature (Cermák et al., 1973, 1982b; Kucera et al., 1977). Measuring points consisted of five thin stainless steel plate electrodes inserted in parallel into the sapwood and a battery of four pairs of compensating thermocouples (Cermák and Kucera, 1981) placed in stainless steel hypodermic needles of 1 mm diameter and located at two different points within the sapwood so as to integrate temperature there. Two pairs of measuring points were installed on opposite sides (north–south and east–west) at breast height on every sample tree. One pair was used for about 6 months and then replaced with the other pair. Of every pair, one was used continuously, and the other was used periodically to check the ratio of sap flow rates on both sides of the tree. A six-channel battery-operated sap flow meter (P-602.2) with data-logger recording, made by Ecological Measuring Systems (EMS), Brno, Czech Republic, was used for the field-work. Data were stored in the data-logger as the mean values of 15 actual values

measured at 1 min intervals (four values per hour, 95 per day). The sap flow rate within the measuring points, Q_{wu} (mean of two measuring points) was expressed for radial sections of tree stems of unit length and of the circumference of the xylem ($L_{cu} = 1$ cm).

2.4. Scaling up the sap flow rate and transpiration

The above value, Q_{wu} , was multiplied by the total stem xylem circumference, L_{ct} , to obtain the total sap flow rate of the tree, Q_{wt} ; L_{ct} was calculated by subtracting the bark thickness from the total circumference of the tree. Sap flow rate data of individual sample trees were scaled up to the experimental stand (1 ha) by a technique discussed earlier (Cermák et al., 1982b; Cermák and Kucera, 1990). First, the scaling curve was calculated relating the sap flow of trees (or transpiration, as the daily values were considered) to their basal area. Then the transpiration of mean trees of individual diameter at breast height (DBH) classes was calculated from that equation. Finally, the transpiration of mean trees was multiplied by numbers of trees in classes; stand transpiration was obtained by adding values of all classes.

2.5. Environmental conditions

The meteorological data were recorded as follows. Air temperature at the level of tree crowns (using a platinum resistance thermometer), global radiation above the stand (with an SKS 1110 silicon cell pyranometer, Skye Instruments, Llandrindod, UK) and photosynthetically active radiation (PAR; with an LI 190 SA quantum sensor (Li-Cor, Lincoln, NE, USA) were measured 2 m above the canopy (on a scaffolding tower of 20 m height built on the experimental plot) and recorded by the data-logger of the sap flow meter simultaneously. Direct precipitation was also measured with a standard raingauge. Additional data of temperature, air humidity and precipitation were also available from the ordinary forest meteorological station, located at 725 m altitude and about 1 km east of the experimental plot. Daily potential evaporation (standard stand evaporation, ET , mm day^{-1}) was calculated from the simple equation of Türç (1961), positively evaluated by Federer et al (1996):

$$ET = [(R_g/41868 + 50) \times 0.013T_a]/(T_a + 15)$$

where R_g is daily total of global radiation ($\text{J m}^{-2} \text{day}^{-1}$) and T_a is mean daily air temperature

Table 1
Soil water characteristics at the beginning of the study (29 May 1993)

Depth (cm)	Dry bulk density (g cm^{-3})	Water content (% DW)	Proportion solid matter (% vol)	Proportion water (% vol)	Proportion air (% vol)
0–10	0.581	73.1	19.4	42.5	38.1
10–20	0.617	77.5	20.5	47.9	31.6
20–30	0.635	67.9	21.2	43.1	35.7
Mean	0.611	72.8	20.4	44.5	35.1

(°C). Soil water estimated gravimetrically on samples with known volume at the beginning of the study (on 29 May 1993) is shown in Table 1.

3. Results and discussion

3.1. Sap flow rate in *Laurus* sample trees

3.1.1. Diurnal courses and maxima

Fig. 1 shows that the sap flow rate started early in the morning in all *Laurus* sample trees during fine weather. The sap flow responded sensitively to precipitation and to changes of illumination caused by passing clouds, as shown by the example of diurnal courses for a period of 16 days during which the weather changed rapidly (Fig. 2). Maximum daily transpiration of the largest sample tree was over $90 \text{ dm}^3 \text{ day}^{-1}$, and that of the (rare) largest tree of the experimental stand during cloudless days and under high evaporation demand was over $100 \text{ dm}^3 \text{ day}^{-1}$. Data of maximum sap flow rate or transpiration actually found in the field and calculated for different dimensions as the mean of 4 days with the highest sap flow are given in Table 2. Data expressed per tree were of the same order as found by Cienciala et al. (1992) in *Picea abies* growing in Sweden, and by Köstner et al. (1992) in a temperate broad-leaved forest of *Nothofagus* in New Zealand. Masarovicová (1992), using lysimeters, found the same range of water uptake in *Quercus dalechampii* and higher values in *Q. robur* (154 dm^3 per tree) in Central Europe. Much higher sap

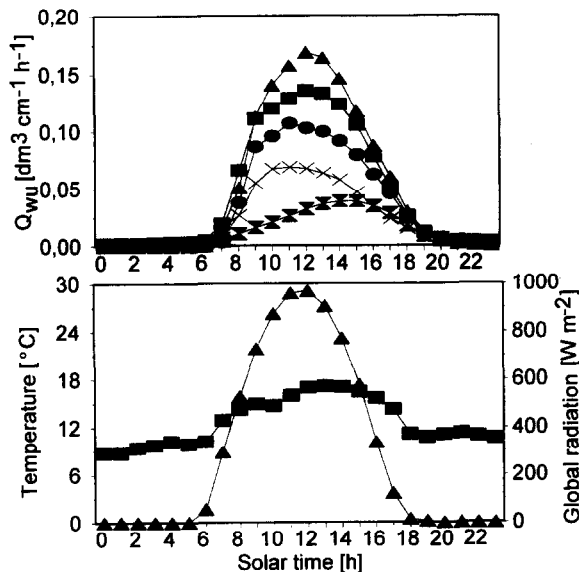


Fig. 1. Top: individual variation in sap flow rate expressed per unit segment of xylem (Q_{wu}) in five *Laurus* sample trees during 1 day record of its diurnal curves under cloudless weather. Sample tree number: 1 (●); 2 (×); 3 (▲); 4 (■); 5 (×). Bottom: variation of global radiation (▲), and air temperature (■), during the same day. All points represent mean values per hour.

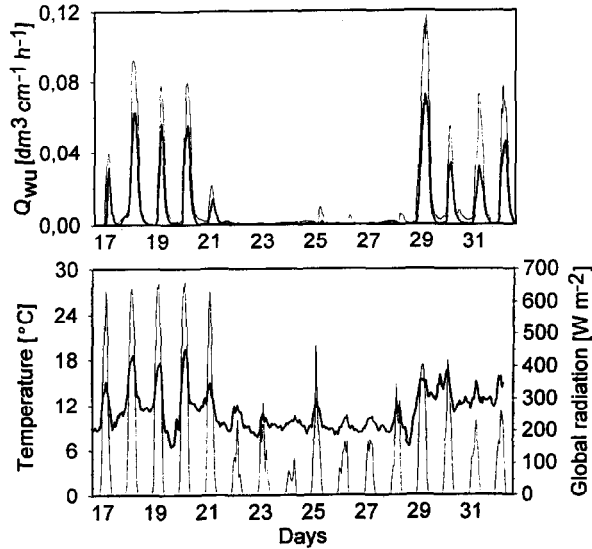


Fig. 2. Top: example of the continuous record of sap flow rate per unit segment of xylem (Q_{wu}) in two *Laurus* sample trees, during 16 days with variable weather during winter (from 17 December 1993 to 1 January 1994). Bottom: global radiation (thin line) and air temperature (thick line) during the same period. On Days 22–29 the precipitation amounted to 50 mm, so the sap flow was insignificant.

Table 2

Maximum sap flow rate (mean from 4 days with the highest annual sap flow rate) in *Laurus* sample trees of different size, calculated for various dimensions

	Sample tree no.	Sample tree (dm^3)	Unit segment ($\text{dm}^3 \text{cm}^{-1}$)	Basal area ($\text{dm}^3 \text{m}^{-2}$)	Ground plan area ($\text{dm}^3 \text{m}^{-2}$)	Leaf dry wt. ($\text{dm}^3 \text{kg}^{-1}$)	Leaf area ($\text{dm}^3 \text{m}^{-2}$)	LAI (dm^3)
Daily total	1	91.7	1.177	1784	4.95	4.43	0.61	11.4
	2	65.9	0.984	1743	4.71	4.30	0.59	8.3
	3	67.8	1.092	2080	4.89	5.11	0.71	9.8
	4	45.2	0.856	1899	4.11	4.62	0.63	7.0
	5	28.0	0.558	1296	3.18	3.16	0.43	3.8
	6	10.1	0.207	492	1.38	1.19	0.16	1.2
	Mean:	51.4	0.812	1549	3.87	3.80	0.52	6.9
Daily maximum per hour	1	8.84	0.113	172	0.48	0.43	0.059	1.1
	2	7.02	0.104	186	0.50	0.46	0.063	0.9
	3	6.06	0.097	186	0.44	0.46	0.063	0.9
	4	6.66	0.126	280	0.61	0.68	0.093	1.0
	5	3.63	0.072	168	0.41	0.41	0.056	0.5
	6	0.61	0.012	30	0.08	0.07	0.010	0.1
	Mean:	5.47	0.087	170	0.42	0.42	0.058	0.7

flow rate values (up to $400 \text{ dm}^3 \text{ day}^{-1}$) were found in floodplain forest *Q. robur* L. (Cermák et al., 1982a).

3.1.2. Daily water storage

The diurnal curves were asymmetric in terms of their shape and position of maximum of irradiation at midday (see Fig. 1). That is why, depending on the position of the sun and of the tree crowns, the response was sometimes delayed or less pronounced. The assessed time shift of the sap flow rate behind transpiration (considered to have a similar course to radiation) was around 1 h, but Q_{wt} continued at a low and decreasing rate until late evening. These deviations between diurnal courses of sap flow and transpiration are related to changes in tissue water content, and they have been observed in other tree species (Whitehead and Jarvis, 1981; Cermák et al., 1982b, 1984a; Schulze et al., 1985; Wronski et al., 1985; Milne, 1989). Although the differences between sap flow and transpiration are important over short periods of time, they can be neglected for daily totals (Cienciala et al., 1992).

Tree water storage used during the day can be roughly assessed to be about 10% of daily transpiration for most sample trees during cloudless hot weather. This value is relatively small compared with other temperate woody species (Cermák et al., 1982b, 1984a; Schulze et al., 1985; Cienciala et al., 1994). However, as it approaches 0.4 mm day^{-1} for the forest stand it should be considered in more detailed hydrological models.

3.2. Variation of sap flow within and between trees

3.2.1. Internal variation

Table 3 shows that the internal (intra-individual) variation of the sap flow, i.e. variation in flow around stems of sample trees (mean differences between simultaneously inspected individual measuring points, south–north and east–west) reached an average value of 12%. This variation was lower in large and in small trees but higher in medium-sized trees, probably reflecting irregularities during changes in their social position when moving from the upper to the lower canopy (Cermák and Kucera, 1990).

3.2.2. Differences of internal variation between trees

Although individual values of maximum sap flow rate per hour and maximum daily totals were larger in larger trees, sap flow expressed per unit of basal area was higher in trees of medium size (see Table 2), suggesting that medium-sized trees utilize their structure more efficiently. Vigorous large trees have to allocate more carbon into the

Table 3

Internal variation of the sap flow; mean differences between individual measuring points (north–south and east–west) in the sample trees (tree number given in parentheses) characterized by their diameters at breast height (DBH)

DBH (cm)	24 (1)	21 (2)	19 (3)	17 (4)	16 (5)	14 (6)	19 (Mean)
Difference (\pm %)	2.8	3.1	14.6	30.6	11.7	9.3	12.0

supporting structures, and very small trees, which hardly survive under high competition in the canopy, have limited income of solar energy and are incapable of acquiring sufficient carbon to keep their conducting system functioning properly. However, increased efficiency is often caused by increasing limiting resources, of which light seems to be the most important in stands of high density and relatively shallow main green canopy, as in the case of the Agua García stand, which has a canopy thickness of about 5 m (Morales et al., 1996a). This is evidently responsible for the uneven development of crowns, which creates a large percentage of curved and bent stems visible all over the laurel forest stands and may be the subject of silvicultural treatment.

3.2.3. Persistence of variation

The diurnal course of sap flow rate differed slightly in individual trees according to local shading of their crowns (see Fig. 1 and Fig. 2). Irrespective of environmental and natural individual variation of sap flow, the persistence of behaviour of *Laurus* trees throughout the year was very important. The ratio of sap flow between individual trees did not change significantly during the study period, suggesting relatively stable soil water supply even during a hot summer and similar ranking of different social positions between trees. Trees were evidently not greatly dependent on variable surface soil water, but they probably absorbed most water from deeper soil layers with extensive sparse root systems, so the water uptake was more uniform, thus avoiding local depletion of soil water.

3.3. Scaling up from sample trees to forest stands

3.3.1. Relation of sap flow to biometric parameters and scaling

Daily sap flow rate in individual trees, Q_{wt} , showed the best fit to their basal area, A_{bas} , when a sigmoidal relationship was applied, particularly the Gompertz equation in the form

$$Q_{wt} = a \exp[-b \exp(-cA_{bas})]$$

where the coefficients a , b and c are 99, 5.5 and 0.0055, respectively. Basal area explained 95% of the spatial variability of the species, with a mean error of about 12% when using six sample trees, and thus could be well applied for scaling to the stand level. It is clear that the amount of foliage is theoretically better related to transpiration, but in contrast to A_{bas} it cannot be directly measured on individual trees, and estimated values might introduce much larger errors than applying A_{bas} , especially in trees with typical irregular crowns. There might be a somewhat larger error in estimating Q_{wt} values for trees outside the range of the studied species; this will be overcome by subsequent measurement of other species in further studies. The mean daily transpiration of mean trees of different DBH classes calculated from that relationship is shown in (Fig. 3(a)), and the number of trees was higher in small classes around DBH of 12–14 cm (Fig. 3(b)). The values of Q_{wt} derived from the scaling curve, multiplied by the number of trees by classes gave the daily mean transpiration of trees in individual DBH classes. These values were higher in larger classes (DBH 16–24 cm), which represent the most important functional part of the stand (Fig. 3(c)). The slope of the scaling curve was rather steep, as found in cumulative leaf

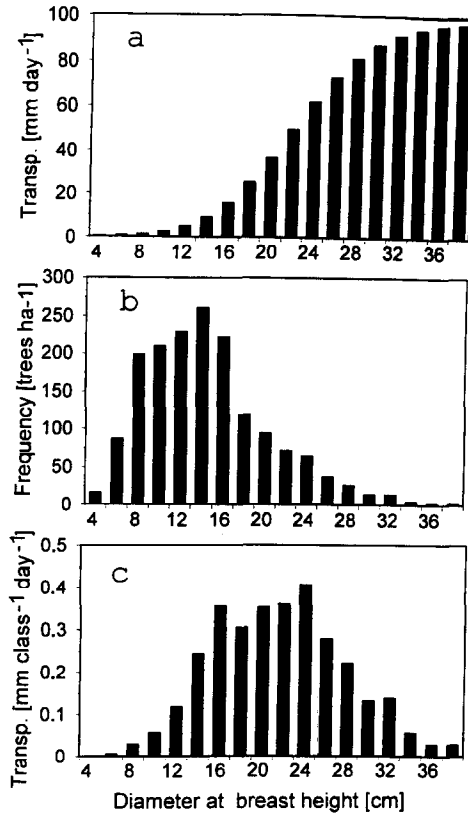


Fig. 3. Diagram applied for scaling of transpiration from individual sample trees to various DBH classes and to the experimental stand. (a) Mean daily transpiration of mean trees of DBH classes calculated from the scaling curve. (b) Number of trees in DBH classes. (c) Mean daily transpiration of all trees within every class (mean daily stand transpiration, obtained by summing values of classes, was 2.3 mm day⁻¹).

distribution of the stand (Morales et al., 1996a), which suggests that most of the competition took place between medium-sized trees.

3.4. Transpiration of laurel forest stand

3.4.1. Annual course of daily transpiration

High values of stand transpiration (mean of three subsequent days was about 5 mm day⁻¹) occurred under cloudless weather in different summer months; the seasonal maximum, observed during several days in mid-August with extremely high temperatures, reached 7 mm day⁻¹ (Fig. 4). These values were higher than those obtained by Kelliher et al. (1992) in coniferous forests (median of maximum daily evaporation rates of 4.0 mm day⁻¹) and that found by Bréda et al. (1992) in a *Quercus petraea* stand (3.8 mm day⁻¹), but lower than those found in dense plant canopies well supplied with water during summer in South East Australia (9–10 mm day⁻¹) or in the European Alps at high elevation (9 mm day⁻¹) (data of various workers given by Jones (1992)).

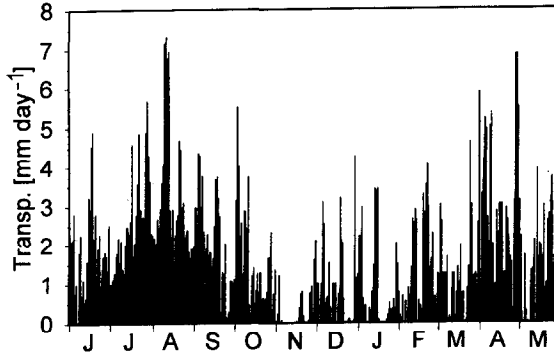


Fig. 4. Annual course of stand transpiration (daily totals) of laurel forest calculated from the continuous record of sap flow rate in the set of *Laurus* sample trees from June 1993 to May 1994 (annual stand transpiration, obtained by summing stand daily values, was 636 mm).

Transpiration was lower during autumn and winter, when there were more frequent rainy or foggy days. The annual mean of transpiration was 2.3 mm day^{-1} . Other papers (in preparation) are focused on more detailed analysis of transpiration in relation to meteorological factors. The results obtained probably represent one of the longest directly measured continuous records of sap flow rate at present, and the first in the Canarian laurel forest.

3.4.2. Monthly transpiration

Precipitation was not regularly distributed during the year: it was very scarce during summer months, and reached almost 250 mm in November (Fig. 5). Similarly, monthly potential evapotranspiration was higher during summer months (up to 130 mm). This gave a maximum climatic water deficit of about 130 mm in July and August and a surplus of about 200 mm of water in November. The cumulative climatic water deficit peaked at about 200 mm in August–September; therefore monthly transpiration increased to 100 mm in August.

Estimates of monthly transpiration for ash (*Fraxinus excelsior*) and beech (*Fagus silvatica*) stands in southern UK gave maximum values of 109 mm and 135 mm, respectively (Roberts and Rosier, 1994), values which are in the range found in laurel forest although the former stands had values of LAI significantly lower (2.7 for ash and 5.3 for beech) than in laurel forest stand.

3.4.3. Total seasonal and annual transpiration

The annual total transpiration from June 1993 to May 1994 amounted to 636 mm year^{-1} , being higher during summer months (April–October) than during winter months (November–March). Table 4 shows that the relationship of transpiration to climatic conditions varied substantially with time of year. The precipitation in the open was more than twice as high in winter than in summer. However, the potential evaporation was almost three times as high in summer compared with winter. In summer, transpiration was about two-thirds of potential evaporation and twice the precipitation. In winter, transpiration was about a half of potential evaporation and almost a third of precipitation.

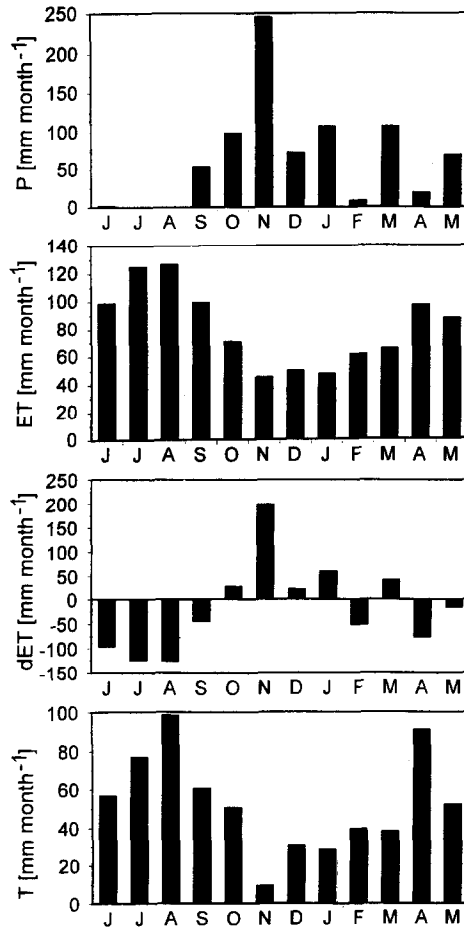


Fig. 5. Monthly and annual totals of precipitation (P), potential evaporation (ET), climatic water deficit ($dET = P - ET$) and transpiration (T) of laurel forest from June 1993 to May 1994.

In fact, total water supply to the stand could be a little different than that considered here. Contribution of fog precipitation, interception of precipitation and stem flow are being studied on the site. Fog drip may be an important additional water source in these forests, but although it is important along mountain crests and wind exposed sites, on slope sites (such as Agua García) with a nearly stagnant cloud layer it may be insignificant, (Kämmer, 1974; Hollermann, 1981).

3.5. Evaluation of transpiration of the laurel forest

3.5.1. Transpiration of laurel forest compared with other forests

Transpiration of 636 mm year^{-1} in laurel forest is in the range of forests and stand of trees (from $200\text{--}400 \text{ mm year}^{-1}$ in forested steppe of Russia to $2300\text{--}3000 \text{ mm year}^{-1}$ in tree plantations of Java; data from various workers given by Larcher (1983)).

Table 4

Annual and seasonal totals of laurel forest stand transpiration, precipitation (*P*) and potential evaporation (*ET*) from June 1993 to May 1994

	Potential evaporation (mm)	Precipitation (mm)	Transpiration laurel forest		
			mm	% <i>ET</i>	% <i>P</i>
Annual total	977	797	636	65.2	80.0
Summer (Apr.–Oct.)	707	249	488	69.2	195.9
Winter (Nov.–March)	270	548	148	54.9	27.1
Proportion of annual	100	100	100	–	–
Summer (Apr.–Oct.)	72.3	31.3	76.7	–	–
Winter (Nov.–March)	27.7	68.7	23.3	–	–

Considering the size of *Laurus* sample trees, their seasonal, daily and maximum actual transpiration were high, approaching the upper limit of values observed in many other broad-leaved species (Cermák, 1991; Pallardy et al., 1995), e.g. annual stand transpiration of laurel forest was significantly higher when compared with forest stands in other geographical regions. For example, in southern UK the annual transpiration in *Fraxinus excelsior* and *Fagus silvatica* stands was 407 mm and 393 mm, respectively (Roberts and Rosier, 1994), and in conditions of Central Europe seasonal total (over the leafy period from May to October) of stand transpiration in *Quercus petraea* in highlands was found to be 200–350 mm, i.e. 40–70% of potential evaporation, and in *Quercus robur* in lowland floodplain forest 260–470 mm, i.e. 60–80% of potential evaporation (higher numbers represent the highest observed values of seasonal transpiration under good water supply and predominantly fine weather and lower numbers transpiration under predominantly cloudy weather or drought) (Cermák et al., 1982a,b, 1984b, 1991; Pallardy et al., 1995). The last percentages of potential evaporation were rather close to those observed in laurel forest during the summer period (see Table 4), which correspond to the growing period of the above-mentioned species. The percentage of precipitation (80%) in laurel forest was the same as that found in evergreen rainforests of Kenya (data from various workers given by Larcher (1983)). The observed annual variation of transpiration (see Fig. 4) suggests that transpiration of laurel forest in 1993–1994 did not reach its potential, owing to frequent cloudy weather.

3.5.2. Importance of daylength and length of growing season

The high value of annual transpiration was not surprising in a sub-tropical region. However, there were contradictory causes for this. It is clear from the records that during the diurnal period the sap flow took place in a rather short time, owing to relatively short days in the region. The longest days were about 14 h day⁻¹, when the sunrise was at 05:00 h and the sunset at 19:00 h (solar time). Naturally, this was less than in sub-boreal regions; e.g. daylength was about 16 h day⁻¹ in Sweden (Cienciala et al., 1992). In contrast, the annual course of transpiration was much longer in this sub-tropical region owing to the uninterrupted growing season throughout the year. This impact prevailed on the total annual value of stand transpiration.

4. Conclusions

Laurus trees and forest transpired a large amount of water under prevailing fine weather conditions. The high annual transpiration of the Agua García laurel forest was the result of both the high level of individual tree transpiration and especially the length of growing season, which persisted throughout the year in the sub-tropical islands. The high daily transpiration was caused by high daily maxima around noon, as transpiration took place for only relatively short diurnal periods. The transpiration was maintained throughout the year, as indicated by the behaviour of trees, which suggests more uniform conditions of water supply, probably from deeper soil layers.

The hydrological role of laurel forests, which transpired significantly lower amounts of water than that coming to the site by precipitation and less than that reached by potential evaporation, was positive. For more precise evaluation of this role and the living strategy of the species, quantification of all parts of the stand water balance and evaluation of tree and stand transpiration in relation with other physiological processes scaled for the same level of biological organization is required. This is the task of further research at the site.

Acknowledgements

Thanks are due to Viceconsejería de Educación and Viceconsejería de Medio Ambiente (Canary Islands Government) for financial help, and to Excmo. Ayuntamiento de Tacoronte for all facilities in the forest. Participation of J. Cermák was supported in part as Visiting Professor by the Viceconsejería de Educación. We also thank Professor Dr. W. Larcher, whom suggested this research. In part this work has been carried out thanks to DGICYT Project PB94-0580.

References

- Aschan, D., Jiménez, M.S., Morales, D. and Lösch, R., 1994. Aspectos microclimáticos de un bosque de laurisilva en Tenerife. *Vieraea*, 23: 125–141.
- Bréda, N., Cochard, H., Dreyer, E. and Granier, A., 1992. Water transfer in a mature oak stand (*Quercus petraea*): seasonal evolution and effects of a severe drought. *Can. J. For. Res.*, 23: 1136–1143.
- Cermák, J., 1991. Transpiration of trees and its significance in forest ecology (in Czech). *Assoc. Prof. Habilitation Work (a review of author's papers)*, Agric. Univ., Brno, 95 pp.
- Cermák, J. and Kucera, J., 1981. The compensation of natural temperature gradient in the measuring point during the sap flow rate determination in trees. *Biol. Plant.*, 23: 469–471.
- Cermák, J. and Kucera, J., 1987. Transpiration of mature stands of spruce (*Picea abies* (L.) Karst.) as estimated by the tree-trunk heat balance method. *IAHS Publ.*, 167: 311–317.
- Cermák, J. and Kucera, J., 1990. Scaling up transpiration data between trees, stands and watersheds. *Silva Carel.*, 15: 101–120.
- Cermák, J., Deml, M. and Penka, M., 1973. A new method of sap flow rate determination in trees. *Biol. Plant.*, 15: 171–178.
- Cermák, J., Kucera, J., Stepankova, M. and Bednarova, E., 1982a. Measurement and evaluation of transpiration of trees at the water balance site in Nedamov (in Czech). *Res. Rep. Inst. of Forest Ecology, Agric. Univ., Brno (for the Construction Geology Enterprise, Prague)*, 44 pp.

- Cermák, J., Ulehla, J., Kucera, J. and Penka, M., 1982b. 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., Jenik, J., Kucera, J. and Zidek, V., 1984a. Xylem water flow in a crack willow tree (*Salix fragilis* L.) in relation to diurnal changes of environment. *Oecologia*, 64: 145–151.
- Cermák, J., Kucera, J., Bednarova, E. and Stepankova, M., 1984b. Measurement and evaluation of transpiration of trees at the water balance site in Nedamov (in Czech). *Res. Rep. Inst. of Forest Ecology, Brno* (for the Construction Geology Enterprise, Prague), 50 pp.
- Cermák, J., Kucera, J. and Stepankova, M., 1991. Water consumption of full-grown oak (*Quercus robur* L.) in a floodplain forest after the cessation of flooding. In: M. Penka, M. Vyskot, E. Klimo and F. Vasicedk (Editors), *Floodplain Forest Ecosystem. Developments in Agricultural and Managed Forest Ecology 15B*. Elsevier, Amsterdam, pp. 397–417.
- Cermák, J., Matussek, R. and Kucera, J., 1993. Rapid response of large, drought stressed beech trees to irrigation. *Tree Physiol.*, 12: 281–290.
- Cienciala, E., Lindroth, A., Cermák, J., Hallgren, J-E. and Kucera, J., 1992. Assessment of transpiration estimates for *Picea abies* trees during a growing season. *Trees*, 6: 121–127.
- Cienciala, E., Eckersten, H., Lindroth, A. and Hällgren, J-E., 1994. Simulated and measured water uptake by *Picea abies* under non-limiting soil water conditions. *Agric. For. Meteorol.*, 71: 147–164.
- Diawara, A., Loustau, D. and Berbigier, P., 1991. Comparison of two methods for estimating the evaporation of a *Pinus pinaster* stand: sap flow and energy balance with sensible heat flux measurements by an eddy covariance method. *Agric. For. Meteorol.*, 54: 49–66.
- Federer, C.A., Vorosmarty, C. and Fekete, B., 1996. Intercomparison of methods for potential evaporation in regional or global water balance models. *Water Resour. Res.*, in press.
- González Henríquez, M.N., Rodrigo Pérez, J.D. and Suárez Rodríguez, C., 1986. *Flora y Vegetación del Archipiélago Canario*. Edirca, Las Palmas de Gran Canaria, 335 pp.
- Granier, A., 1987. Evaluation of transpiration in a Douglas fir stand by means of sap flow measurements. *Tree Physiol.*, 3: 309–320.
- Granier, A. and Loustau, D., 1994. Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data. *Agric. For. Meteorol.*, 71: 61–81.
- Granier, A., Bobay, V., Gash, J.H.C., Gelpe, J., Saugier, B. and Shuttleworth, W.J., 1990. Vapour flux density and transpiration rate comparisons in a stand of Maritime Pine (*Pinus pinaster* Ait.) in Les Landes Forest. *Agric. For. Meteorol.*, 51: 309–319.
- Holler mann, P., 1981. Microenvironmental studies in the laurel forest of the Canary Islands. *Mt. Res. Dev.*, 1: 193–207.
- Jones, H.G., 1992. *Plants and Microclimate. A Quantitative Approach to Environmental Plant Physiology*, 2nd edn. Cambridge University Press, Cambridge, 428 pp.
- Kämmer, F., 1974. *Klima und Vegetation auf Tenerife, besonders im Hinblick auf den Nebelniederschlag*. Scripta Geobotanica. Erich Goltze KG, Göttingen, 78 pp.
- Kelliher, F.M., Köstner, B.M.M., Hollinger, D.Y., Byers, J.N., Hunt, J.E., McSeveny, T.M., Meserth, R., Weir, P.L. and Schulze, E.D., 1992. Evaporation, xylem sap flow, and tree transpiration in a New Zealand broad leaved forest. *Agric. For. Meteorol.*, 62: 53–73.
- Köstner, B.M.M., Schulze, E.-D., Kelliher, F.M., Hollinger, D.Y., Byers, J.N., Hunt, J.E., McSeveny, T.M., Meserth, R. and Weir, P.L., 1992. Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia*, 91: 350–359.
- Kucera, J., Cermák, J. and Penka, M., 1977. Improved thermal method of continual recording of the transpiration flow rate dynamics. *Biol. Plant.*, 19: 413–420.
- Larcher, W., 1983. *Physiological Plant Ecology*, 2nd edn. Springer, Berlin, 303 pp.
- Larcher, W., Wagner, J., Neuner, G., Méndez, M., Jiménez, M.S. and Morales, D., 1991. Thermal limits of photosynthetic function and viability of leaves of *Persea indica* and *Persea americana*. *Acta Oecol.*, 12: 529–541.
- Lösch, R., 1993. Water relations of Canarian laurel forest trees. In: M. Borghetti, J. Grace and A. Raschi (Editors), *Water Transport in Plants under Climatic Stress*. Cambridge University Press, Cambridge, pp. 243–245.

- Masarovicová, E., 1992. Morphological, physiological, biochemical and production characteristics of three oak species. *Acta Physiol. Plant.*, 14: 99–106.
- Milne, R., 1989. Diurnal water storage in stems of *Picea sitchensis* (Bong.) Carr. *Plant Cell Environ.*, 12: 63–72.
- Morales, D., Jiménez, M.S., Wagner, J. and Larcher, W., 1992. Caracterización morfológica e histológica de las hojas de sol y sombra de *Persea indica* (L.) Spreng. y *Persea americana* Mill. *Vieraea*, 21: 61–76.
- Morales, D., Jiménez, M.S., González-Rodríguez, A.M. and Cermák, J., 1996a. Laurel forests in Tenerife, Canary Islands: I. The site, stand structure and stand leaf area distribution. *Trees*, in press.
- Morales, D., Jiménez, M.S., González-Rodríguez, A.M. and Cermák, J., 1996b. Laurel forests in Tenerife, Canary Islands: II. Leaf distribution patterns in individual trees. *Trees*, in press.
- Pallardy, S.G., Cermák, J., Ewers, F.W., Kaufmann, M.R., Parker, W.C. and Sperry, J.S., 1995. Water transport dynamics in trees and stands. In: W.K. Smith and T.M. Hinckley (Editors), *Ecophysiology of Conifers*. Academic Press, New York, pp. 299–387.
- Roberts, J. and Rosier, P.T.W., 1994. Comparative estimates of transpiration of ash and beech forest at a chalk site in southern Britain. *J. Hydrol.*, 162: 229–245.
- Santos, A., 1990. Evergreen Forests in the Macaronesian region. Council of Europe, Strasbourg, 79 pp.
- Schulze, E.-D., Cermák, J., Matyssek, R., Penka, M., Zimmerman, R., Vasicek, F., Cries, W. and Kucera, J., 1985. Canopy transpiration and water fluxes in the xylem of the trunk of *Larix* and *Picea* trees—a comparison of xylem flow, porometer and cuvette measurements. *Oecologia*, 66: 475–483.
- Türc, L., 1961. Evaluation des besoins en eau d'irrigation évapotranspiration potentielle. *Ann. Agron.*, 12: 13–49.
- Whitehead, D. and Jarvis, P.G., 1981. Coniferous forests and plantations. In: T.T. Kozłowski (Editor), *Water Deficits and Plant Growth*. Academic Press, New York, pp. 49–152.
- Wronski, E.B., Holmes, J.W. and Turner, N.C., 1985. Phase and amplitude relations between transpiration, water potential and stem shrinkage. *Plant Cell Environ.*, 8: 613–622.
- Zohlen, A., González-Rodríguez, A.M., Jiménez, M.S., Lösch, R. and Morales, D., 1995. Transpiración y regulación estomática en árboles de la laurisilva canaria medidos en primavera. *Vieraea*, 24: 93–106.