Chapter VI

TRANSPIRATION
IN A SUBTROPICAL
RIDGE TOP CLOUD FOREST

VI   TRANSPIRATION IN A SUBTROPICAL RIDGE TOP CLOUD FOREST

ABSTRACT

Laurel forests survive in the Canary Islands (Spain) where humid conditions are guaranteed throughout the year. On peaks and ridges, laurel forests give way to mixed evergreen tree-heath/beech forest of low stature that has to cope with rapidly changing light, temperature and humidity conditions due to the occurrence of intermittent sunny and foggy periods during the mostly rainless summer. There is a lack of information on the interrelations between tree physiological behaviour and ambient climatic and soil water conditions in tree-heath/beech forest in the Canaries. Sap velocity was measured in two dominant species (*Myrica falla* and *Erica arborea*) in a ridge top forest in the National Park of Garajonay on the island of La Gomera. The narrow-leaved *E. arborea* exhibited higher sap velocity than the broad-leaved *M. falla*. Also, sap velocity increased with stem diameter in *E. arborea* but not in *M. falla*. Nocturnal sap flow activity was observed throughout the year and reflected ambient conditions on some occasions and stem water storage recovery on others. Strong stomatal control in response to increases in vapour pressure deficit was seen in both species. Sap velocity was reduced by 10-90% during times of fog. Average daily stand transpiration was 1.28 ± 0.22 mm (402 mm/yr). Soil water uptake during the dry summer (246 mm) was much larger than atmospheric water inputs (41 mm, rain and fog). Low moisture levels in the top 0.3 m of the soil had limited influence on transpiration rates. Hence, the vegetation must have had access to moisture in deeper layers.

VI.1   INTRODUCTION

Laurel-dominated forest, or "Laurisilva", is a subtropical evergreen vegetation type occurring predominantly on the northern slopes of the so-called Macaronesian Islands (Azores, Canaries, Cabo Verde and Madeira) between 800 and 1300 m a.s.l., where stratocumulus clouds transported by the trade winds produce a rather uniform climate with moderate temperature variation and high relative humidity throughout the year (Dorta, 1996; Marzol, 1993). The National Park of Garajonay in central La Gomera (Canary Islands, Spain) contains the largest single representative of this ecosystem within the Canaries (Pérez de Paz et al., 1990). Annual rainfall in the area is ca. 660 mm but varies strongly between years. Most of the rain falls in the autumn and winter months (see Chapter IV). The summer is mostly rainless, but humid atmospheric conditions occur frequently because of the characteristic "sea of clouds". However, these humid conditions at summit and ridge top locations are often reduced by a lowering of the position of the thermal inversion in summer (the cloud base is about 800 m) (Dorta, 1996) (see Chapter IV). Hence the vegetation has to cope with high light intensities and rapidly changing temperature and humidity conditions due to intermittent sunny and foggy periods apart from the general absence of rainfall. The laurel-dominated forests of the slopes and valley bottoms give way to a mixed tree-heath/beech forest on the ridges (so-called *fayal-brezal* vegetation) which is composed mainly of wax myrtle or beech (*Myrica faya* Ait.), tree heath (*Erica arborea* L.) and, to a lesser extent, small laurel trees (*Laurus azorica* Seub. Franco) (Golubic, 2001; Pérez de Paz et al., 1990). Whilst rainfall and fog incidence have been shown to be higher at these wind-exposed ridges compared to the more sheltered slope and valley bottom locations, net rainfall interception was lower on the ridges (see Chapter V). There is no published information on transpiration by the *fayal-brezal* forest but studies in laurel-dominated forest on nearby Tenerife suggested annual stand transpiration totals ranging between 300 and 640 mm (Morales et al., 2003).

Obtaining reliable estimates of seasonal and annual transpiration totals for ridge top forest is essential for the assessment of the National Park's overall water budget and has important implications for the Park's management. Moreover, in view of expected changes in the archipelago's climate (Hay, 2000; Sperling et al., 2004) baseline studies of the interactions between meteorological variables, soil moisture content, and vegetation water use are needed.

The present work aims to determine transpiration at the stand level in a humid (although dry in summer) mixed tree heath/beech ridge top cloud forest on a Gomera, and to identify possible traits developed by the vegetation in the face of potential drought stress during the summer. To achieve these objectives, sap velocity in two of the main tree species, *Myrica faya*

(a broad-leaved species) and *Erica arborea* (a narrow-leaved species), were studied separately, as well as their relationships with meteorological variables and soil moisture levels.

VI.2   MATERIALS AND METHODS

VI.2.1   Study area and experimental plot

The studied ridge top cloud forest is located at Laguna Grande in the headwater area of the Jelima catchment at ca. 1270 m a.s.l. (28 º 17' 41'' northern latitude and 31º 08' 06'' western longitude) in the northern central sector of the Garajonay National Park, La Gomera (Figure VI.1). The climate is humid Mediterranean with mild temperatures throughout the year (average 13.0 ºC, monthly range 8.9–19.7 ºC). Incident precipitation over 2003 was ca. 900 mm and concentrated mostly in autumn and winter, and whilst fog occurred throughout the year, the highest incidence was observed in spring (see Chapter IV). Further details on climate will be given below.

The volcanic soils on the ridges were classified as Leptosols according to the FAO (1998) scheme and have developed in trachybasaltic lava flows and dykes. The soils are shallow (0.3-0.5 m) and typically consist of an A horizon of sandy (clay) loam texture above a stony C-horizon with numerous angular basalt fragments in a grey clayey mass (Rodríguez et al., 2002). Roots were concentrated in the top 0.2 m but extended into the rocky subsoil. Soil depth increases going from the ridges to the slopes and valley bottoms underlain by Andisols (the dominant soil type within the Park). While the slopes and valley bottoms are covered by laurel-dominated forests, peaks and ridges have a mixed tree-heath/beech forest or "*fayal-brezal*" (Golubic, 2001; Pérez de Paz et al., 1990), which consists mainly of evergreen sclerophyllous tree-heath (*Erica arborea* L.), wax-myrtle or beech (*Myrica faya* Ait.), and to a lesser extent holly (*Ilex canariensis* Poivet.) and laurel (*Laurus azorica* Seub. Franco). The trees are partly covered with epiphytes and bryophytes. Beech, holly and laurel are all evergreen broad-leaved trees whereas *Erica* has tiny needle-like leaves (Figure VI.2). This type of forest covers ca. 25% of the Jelima basin (Figure VI.1, bottom right panel).

An experimental plot of 300 m^2 was delineated near Laguna Grande on the upper ridge of the Jelima catchment and had steep slopes (30-40º) of north-easterly orientation at 1270 m a.s.l. Tree density in the plot was 1266 trees/ha with a mean height of ca. 9 m (based on a survey of trees with a minimum diameter at breast height (DBH) of 0.07 m). Mean leaf area index (LAI) was 4.2 ± 1 m^2/m^2 (Golubic, 2001). Average DBH was 0.20 ± 0.17 m (cf. Figure VI.2) and stand basal area was 68 m^2/ha. *M. faya* made up the greatest proportion (57%) of stand basal area, followed by *E. arborea* (33%) and *L. azorica* (10%).

Figure VI.1 Above: General location of the Canary Islands and La Gomera. Below left: National Park of Garajonay and Leptosol distribution within the Park (after Rodríguez et al. (2002)). Below right: Mixed tree-heath/beech forest distribution within the Jelima catchment. ⌐ : Location of experimental plot.

Figure VI.2. Distribution and diameter at breast height (DBH, m) of the trees (n = 38) within the experimental plot. ▨ *E. arborea* L. sample tree with one pair of sap flow sensors; ● *M. faya* Ait. sample tree with one pair of sap flow sensors; ⊕ *M. faya* Ait. sample tree with two pairs of sap flow sensors. (xx) Location of TDR soil water probes. Right: Detail of leaves of *M. faya* (top) and *E. arboreal* (bottom).

VI.2.2   Meteorological measurements

Actual climatic conditions were monitored by an automatic weather station placed on top of a 9 m high scaffolding tower and mast of 3 m at the experimental plot. Relative humidity (*RH*, %) and air temperature (*T*, ºC) were recorded at 2 m above the canopy (Vaisala HMP45C T-RH probe), global radiation (R_g, W/m^2) was measured by a pyranometer (Campbell SP1110), and wind speed (*u*, m/s) by a switch anemometer (Vector A100R). Occurrence and density of fog were derived by recording amounts of water collected by a quarter-sized variant of the standard fog collector (0.25 m^2) of Schemenauer and Cereceda (1994) whereas rainfall was measured with a Pronomatic Professional recording gauge at 0.25 mm resolution. Rainfall amounts were corrected for topographic and wind effects (P_a*, mm) as described in detail in Chapter IV. All variables were sampled at 3 min intervals and recorded every 15 min by a Combilog datalogger and then transmitted by GSM modem (see Chapter II for details).

VI.2.3   Soil water content

Volumetric soil water content θ_v (m^3/m^3) was measured continuously in the 0-0.15 m and 0.15-0.30 m depth intervals by two time domain reflectometry (TDR) probes (TRIME-IT/EZ) inserted horizontally. The stoniness of the subsoil prevented the use of TDR sensors beyond a depth of 0.3 m. Often, Topp's function relating θ_v and the dielectric constant of the soil (K_a) (Topp et al., 1980) is applied. However, the θ_v-K_a relationship for volcanic and organic soils is known to deviate significantly from Topp's general equation because of the high porosity of such soils (Miyamoto et al., 2003; Veldkamp and O'Brien, 2000; Weitz et al., 1997), and therefore requires separate calibration. To achieve this, four TDR probes were inserted horizontally into undisturbed soil columns held in 0.14 m high PVC cylinders of 0.24 m diameter that were subjected to gradual drying after initial saturation. The K_a measurements were carried out with the same technology (TDR probes) at the laboratory (Trase Soilmoisture Equipment). Soil water content was determined gravimetrically, and TDR readings made after every 0.17 kg of weight loss. When soil weight was constant under air-dry conditions the soil columns were oven-dried in stages, from 40º up to 105º C, each time until constant weight was reached. Corresponding changes in soil volume were measured and volumetric soil water content was obtained directly by weighing at each stage.

Measured water contents during the calibration were greater than those predicted by Topp's equation (bold line in Figure VI.3) as is typically observed in soils of volcanic origin (Miyamoto et al., 2003; Tobón-Marín, 1999).
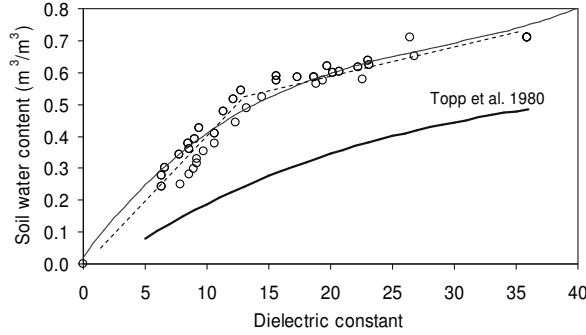
Figure VI.3 Relationship between soil dielectric constant and volumetric soil water content for ridge top soil samples of volcanic origin collected from the top 0.3 m depth (○) at Laguna Grande (La Gomera, Canary Islands) vs. the Topp et al. (1980) equation (-).

Between moisture contents of 0.5 and 0.6 m³/m³ (K_a between 12 and 15) the slope of the calibration curve changed significantly (Figure VI.3), something which was also observed by Miyamoto et al. (2003) for an Andisol in Japan around 0.4 m³/m³ moisture content. Although two different dielectric responses were observed below and above a critical soil water content value (dashed lines in Figure VI.3), it was possible to fit a single regression equation (continuous line in Figure VI.3):

$$\theta_v = 2 \cdot 10^{-5} K_a^{\ 3} - 0.0015 K_a^{\ 2} + 0.052 K_a + 0.022 \quad (r^2 = 0.90) \qquad \text{VI.1}$$

Relative extractable soil water (θ_e, m³/m³) was calculated as the ratio of actually extractable water to maximum extractable water for plants (Black, 1979):

$$\theta_e = \frac{\theta_v - \theta_r}{\theta_{fc} - \theta_r} \qquad \text{VI.2}$$

where θ_{fc} (m³/m³) is the soil water content at field capacity, and θ_r (m³/m³) the residual soil water content or wilting point which are characteristic for each soil. θ_{fc} was determined as the soil water content remaining after 48 h of drainage from an initially saturated soil ($n = 4$ undisturbed samples at 0.05 to 0.25 m depth) whereas θ_r was determined as the soil water content after equilibrating wetted disturbed soil samples ($n = 15$ at 0.05 to 0.25 m depth) exposed to a pressure of 1500 kPa.

VI.2.4   Sap velocity and the upscaling to stand level

Sap velocity was measured continuously in seven trees selected from the two most abundant tree species present in the ridge top forest (*M. faya* and *E. arborea*) using the heat

dissipation technique of Granier (1987) between February 2003 and January 2005. Three representative (in terms of DBH) individuals of *M. faya* were used plus four of *E. arborea* (Figure VI.2). The thermocouples were inserted horizontally and 0.10 m apart in the outer 20 mm of the stem of each sample tree. Data were recorded at 3 min intervals and stored every 15 min in a data logger (Combilog) and then transmitted by GSM modem. Energy was supplied by a battery (12 V, 100 Ah) recharged by a solar panel.

The temperature difference (ΔT, ºC) between the heated upper needle and unheated lower reference needle during the day combined with the temperature difference at night (usually taken as the peak nigh-time value of ΔT) allows the estimation of sap flux density (Granier, 1987) (v^1, ml/cm^2 min) also called sap velocity (Edwards et al., 1996) according to:

$$v = 0.714 \left(\frac{\Delta T_{night}}{\Delta T} - 1 \right)^{1.231}$$
VI.3[1]

Several systematic and random errors are known to affect the estimation of sap velocity: An example of the former is poor thermal contact between the thermocouples and the stem. Potential random errors include the occurrence of thermal gradients between the stem and the environment, natural gradients along the trunk, and possibly excessive stem heating during the night. The first two errors were avoided by careful installation of the probes and insulating them against rainfall and temperature variations. Furthermore, in view of the generally humid and shady conditions prevailing below the canopy, and the generally mild temperatures at the study site, the effects of natural gradients or changes in stem heat storage during the day (Grime and Sinclair, 1999) were considered negligible. Although Grime and Sinclair (1999) further suggested that nocturnal overheating may be avoided by reducing the heat input by 50% between 1h after sunset and 1h before sunrise, this was not deemed necessary in the present study because the mild temperatures during the night were not likely to produce significant changes in stem heat storage.

Tree sap flow, also called sap flow rate or sap flux (Edwards et al., 1996) (Q_t, ml/min) can be computed by multiplying sap velocity v, as measured in the outer 0.02 m, times the cross-sectional area (SA, cm^2) of the entire active xylem of the tree (with radius r, cm without bark) assuming that sap velocity is constant across the xylem:

$$Q_t = \sum_{i}^{i=r} v \cdot SA_i$$
VI.4

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[1] Empirical regression to convert temperature in wound-corrected sap velocity as obtained by UP GmbH (http://www.upgmbh.com).

However sap velocity across the xylem is often non-uniform (Cermák and Nadezhdina, 1998; Jiménez et al., 2000; Lundblad et al., 2001); therefore Q_t obtained as in Eq. VI.4, with sensors placed only in the outer parts of the sapwood is likely to be overestimated.

Jiménez et al. (2000) studied the relative sap velocity per unit cross-sectional area in *M. faya* (n=5), *E. arborea* (n=3) and *L. azorica* (n=12) trees in Tenerife using the heat field deformation method (HFD) (Nadezhdina and Cermak, 1998; Nadezhdina et al., 1998). Although that method differs to Granier's method (less amount of sensors) both are based on heat dissipation principles. The Jiménez et al. (2000) findings are the only study concerning radial profiles of sap velocity in the studied tree species. In the curved trunks of stunted *E. arborea* trees, very similar to the ones found in the presently studied plot, the outer part of the stem was shown to be conducting whereas the inner (heartwood) part was non-conducting (Figure VI.4, left-hand side). In the case of *M. faya*, in some trees the entire cross-sectional stem area was conducting (tree type 1C according to Jiménez et al., 2000; see Figure VI.4, right-hand side), but in others only part was conductive (tree type 2B; Figure VI.4, right-hand side). To obtain supplementary information on the changes in sap velocity with depth within the xylem of *M. faya*, an additional pair of thermocouples was installed in the second 20 mm (20-40 mm) of xylem in one of the bigger *M. faya* trees in the study plot (0.30 m of DBH) (Figure VI.2). The results were compared with the types of sap velocity patterns obtained by Jiménez et al. (2000) and showed an average decrease of ca. 55% in sap velocity from the outer 20 mm to the next 20 mm of xylem (two years of hourly data) (Figure VI.5a). As such, the presently measured pattern was similar to that observed by Jiménez et al. (2000) for an open-crowned type 1C *M. faya* tree of DBH 0.27 m.
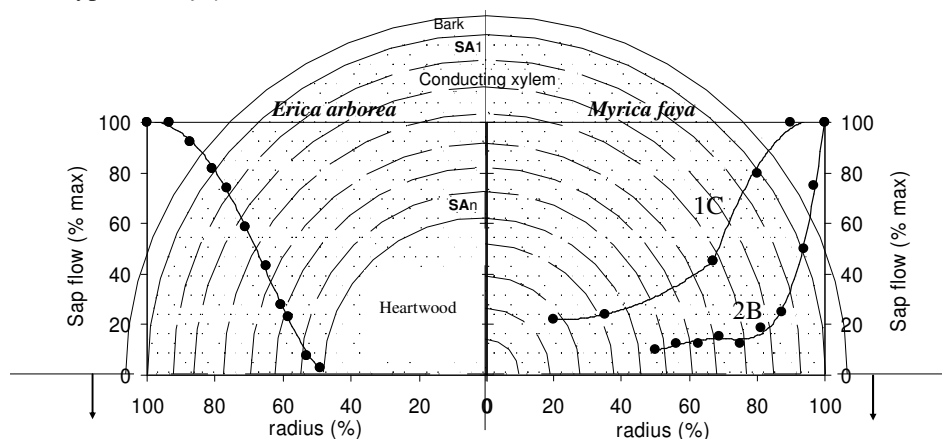

Figure VI.4 Changes in relative sap flow per unit cross-sectional stem area or sap velocity (% of maximum flow as measured in the outer 0.02 m) vs. depth of cross-sectional stem area based on Jiménez et al. (2000). Left: *Erica arborea* L. tree (0.19 m DBH). Right: *Myrica faya* Ait.

tree type 2B (0.37 m DBH) and type 1C (0.27 m DBH) in a laurel-dominated forest in Tenerife.

The combined sap velocity pattern for the entire depth of xylem is shown in Figure VI.5b, where the solid circles represent measured values (67%≤ radius ≤100%) and open circles the results of Jiménez et al. (2000) (0%< radius<67%). In order to estimate sap velocity vs. xylem depth in the three large open-crowned *M. faya* trees under study, two separate regressions were obtained (Figure VI.5b):

67%≤ radius ≤100% $c_i = -0.06r_i^2 + 11.59r_i - 466.11$ VI.5

0%< radius<67% $c_i = 0.01r_i^2 - 0.48r_i + 27.12$ VI.6

where the correction factor c_i (%) equals relative sap velocity (% of maximum) and r (%) is the radius expressed as a percentage of the total radius.
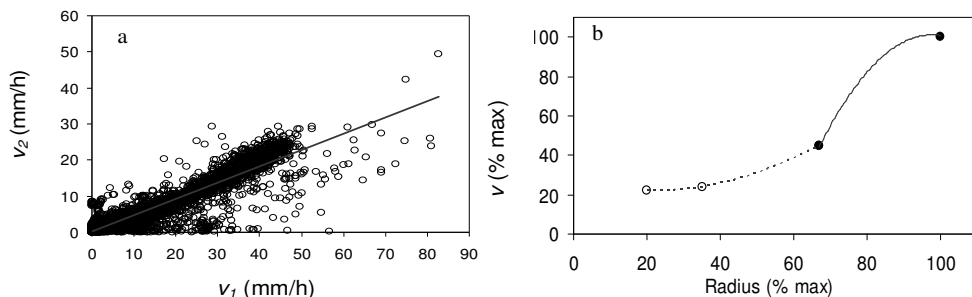

Figure VI.5 (a): Relationship between sap velocity as measured in the outer 2 cm (v_1, mm/h or l/m^2 SA h) and in the next 2 cm of xylem depth (v_2). (b) Radial pattern of relative sap flow density in *M. faya* Ait. vs. radius depth. Solid circles correspond to measured sap flow density and open circles to the results of Jiménez et al. (2000) for a large-crowned *M. faya* tree in Tenerife (type 1C).

Thus, sap flow per tree was obtained by integrating sap flow density using Eq. VI.5 and Eq. VI.6 as measured at 0.02 m radial depth intervals:

$$Q_t = \sum_i v \cdot c_i \cdot SA_i$$ VI.7

where v (ml/min) is the measured sap velocity in the outer 0.02 m, and c_i the correction factor as a function of the radius (r_i). The relationship between c_i and r_i (both as a percentage of the maximum value) for a small-crowned *E. arborea* tree (with curved trunk) was calculated from the sap flow pattern obtained by Jiménez et al. (2000) (cf. Figure VI.4, left) as:

$$c_i = -0.001r_i^3 + 0.20r_i^2 - 10.37r_i + 149.24 \qquad\qquad \text{VI.8}$$

and for a large open-crowned *M. faya* tree (Figure VI.4) as:

$$c_i = 6.1 \cdot 10^{-5}\, r_i^4 - 1.5 \cdot 10^{-2}\, r_i^3 + 1.5r_i^2 - 60r_i + 913 \qquad\qquad \text{VI.9}$$

In the absence of direct sap velocity measurements in *Laurus azorica* in the study plot, sap flows for this species were approximated using the relationship between *L. azorica* and *E. arborea* trees derived by Jiménez et al. (2000), in which the total sap flow in an individual of *L. azorica* (DBH 0.25 m) was 0.92 times the sap flow in a similarly sized *E. arborea* tree (DBH 0.19 m).

Scaling up of tree sap flows in individual trees belonging to each of the three main species (*E. arborea*, *M. faya* and *L. azorica*) to the stand as a whole (300 m^2) was carried out in stages. First, empirical relationships were derived per species between measured Q_t (ml/min) and DBH for the respective sample trees species. Next, values of Q_t were obtained for all 38 individuals in the plot by inserting their DBH values into the respective equations. Daily stand transpiration (E_t, mm/d) was then obtained by adding up the individual daily values and dividing by plot area (A, m^2):

$$E_t = \frac{\sum\limits_{i=1}^{38} Q_t}{A} \cdot 60 \cdot 24 \cdot 10^{-3} \qquad\qquad \text{VI.10}$$

Two potential errors in the estimation of Q_t relate to the determination of sap velocity v and sapwood cross sectional area SA (Giambelluca et al., 2003). Error in sapwood cross sectional area is supposed to have a lower influence on the total sap flow than measurement of sap velocity across the xylem because sap velocity decreases with xylem depth. Assuming that v in the outer 20 mm was not subject to the systematic and random errors described above (which were either avoided or considered negligible), the error in v may be approximated by scaling v over the entire conducting area in two *E. arborea* and *M. faya* trees. *A priori* estimation of Q_t in *E. arborea* will have a higher uncertainty because of the stronger gradient in radial sap velocity (Figure VI.4, left-hand side). An error of ±5% in v throughout the conducting xylem was assumed to estimate the associated sensitivity in Q_t per species. The resulting standard deviations of Q_t were ± 6.2% for *M. faya* and ± 19.6% for *E. arborea*.

VI.3   RESULTS

VI.3.1   Soil moisture conditions

Variations in soil water content down to 0.30 m depth between February 2003 and January 2005 are shown in Figure VI.6. The soil remained wet from February to the middle of May, after which soil water content decreased throughout the next five nearly rainless months. Only after the first rains at the end of September did moisture levels begin to recover somewhat, the soil remaining wet during the subsequent autumn and spring. However, December 2003 and January 2004 were exceptionally dry and soil water content was significantly reduced until mid February. Topsoil (0-0.15 m) was generally wetter and showed larger variations in moisture content than subsoil (0.15-0.30 m), especially during wet periods (not shown). Soil moisture levels responded rapidly to precipitation throughout the year (Figure VI.6).
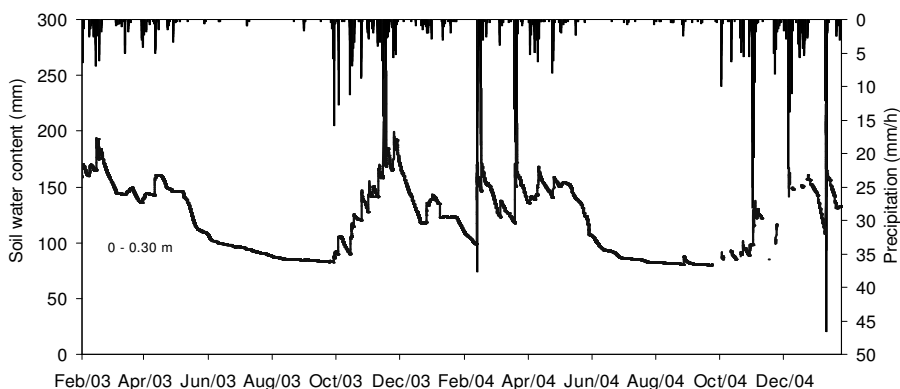

Figure VI.6 Seasonal distribution of wind-corrected rainfall inputs (mm/h) and variation in soil water content (mm) down to 0.30 m depth between February 2003 and January 2005 at the Laguna Grande ridge, Jelima catchment (La Gomera, Spain).

Tree roots in the studied horizon were considered to experience water stress when moisture content θ_v was close to residual soil moisture content (0.2 m^3/m^3 or 72 mm), i.e. when extractable water θ_e was close to zero (cf. Equation VI.2). Water stress in the top 0.3 m of the profile developed during the dry season in both years (Figure VI.7), i.e. for three months (July until the end of September) in the first year, and for almost five months (from June to October) in the second year. Significant drainage ($\theta_e > 1$) beyond 0.3 m depth occurred only after continued rainfall had wetted up the soil above field capacity ($\theta_v > 0.5$ m^3/m^3) and this was observed on a number of occasions (Figure VI.7).
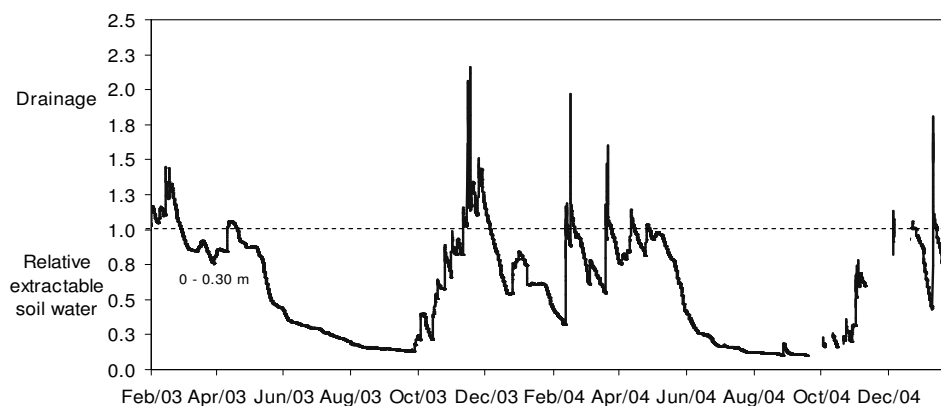
Figure VI.7 Temporal variability of relative extractable soil water content (from 0 to 1) in the top 0.3 m depth between February 2003 and January 2005 at the Laguna Grande ridge, Jelima catchment (La Gomera, Spain).

VI.3.2 Diurnal patterns of sap velocity in tree-heath and beech trees

Hourly sap velocity patterns (mm/h or l/m^2 SA·h) during two bright days (30 and 31 March 2003) in the absence of soil water limitation (θ_e >0.8) are shown for *M. faya* and *E. arborea* trees in Figure VI.8. During these two days mean temperature was 15.4 ± 3.2 ºC (10.8-21.3ºC), mean VPD was 1.26 ± 0.3 kPa (0.78-1.98 kPa), and wind speed was low (<2 m/s). Comparing trees with similar DBH for the two species (0.22-0.24 m), the higher sap flow activity in *E. arborea* compared to that in *M. faya* (four times higher) is striking. Very small differences in sap velocity were observed between *M. faya* trees with DBH of 0.24 and 0.31 m. However, in the case of *E. arborea*, sap velocity clearly increased with DBH.

In both species the start of sap flow activity was very variable in time. On some days sap flow started at sunrise, whereas on other days activity began between 1 and 3 h later. Maximum values were observed around midday in both species, after which sap flow started to decrease until 3-4 h after dusk.
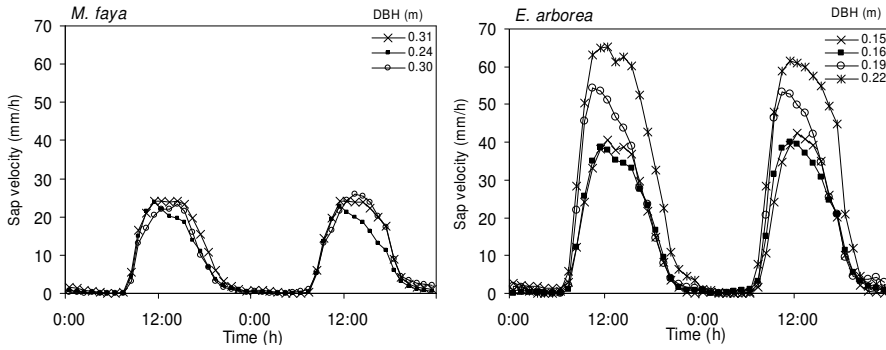
Figure VI.8 Diurnal course of mean sap flow per unit of conducting sapwood area per tree (sap velocity) and species (mm/h or l/m^2 conducting SA·h) as a function of DBH (m) on 30th and 31st March 2003 at the Laguna Grande ridge, La Gomera. Left: *Myrica faya*; Right: *Erica arborea*.

Nocturnal sap flow activity was observed throughout the year in both species (Figure VI.9). On some occasions, sap velocity after dusk was still continuing slowly until it stopped a few hours before sunrise. On other occasions, which coincided with high wind speeds, nocturnal sap velocity patterns followed the evaporative demand of the atmosphere. In such cases, maximum sap velocity at night was about 85% lower than the peak during the preceding daytime. In *E. arborea*, nocturnal sap velocity increased with tree DBH as observed for daytime conditions (cf. Figure VI.8). Total sap velocity during such nights represented 6% and 4.8% of sap velocity during the day for *M. faya* and *E. arborea*, respectively.
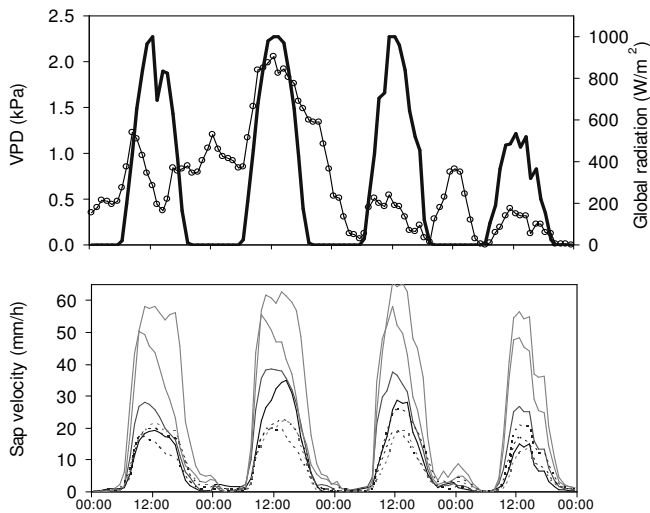

Figure VI.9 Above: Radiation (**-**R_g, W/m^2) and vapour pressure deficit (-○- *VPD*, kPa). Below: Hourly course of sap flow per unit of conducting sapwood area (mm/h or l/m^2 conducting

SA·h) for different tree species (dotted lines: *M. faya* sample trees; solid lines: *E. arborea*) between 26th and 29th April 2003 at the Laguna Grande ridge, La Gomera.

VI.3.3   Sap flow in tree-heath and beech trees

Diurnal patterns of sap flow per tree (Q_t, l/h) and species were derived using equation VI.7, an example is shown in Figure VI.10. Sap flows per tree in both *M. faya* and *E. arborea* were related to DBH. Comparing trees with similar DBH for the two species, Q_t values for *E. arborea* trees were higher than in *M. faya* despite the fact that the conducting area of *E. arborea* made up half the stem cross-sectional area (cf. Figure VI.4).
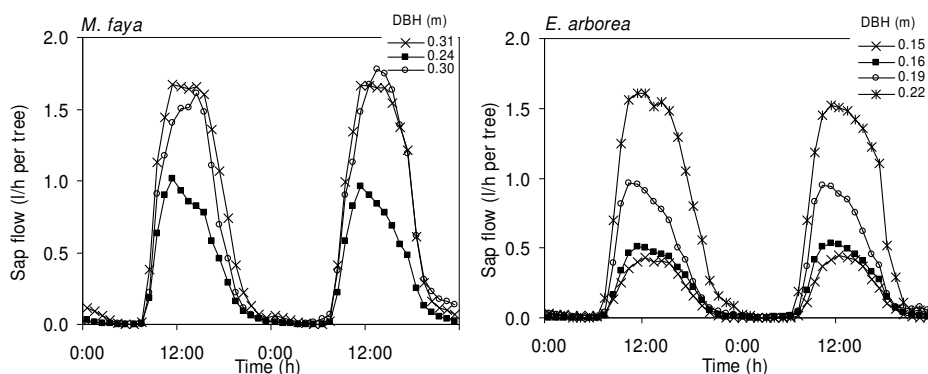

Figure VI.10 Diurnal course of total sap flow per tree (l/h) on 30th and 31st March 2003 at the Laguna Grande ridge, La Gomera. Left: *Myrica faya*; Right: *Erica arborea*.

VI.3.4   Sap flows at the stand level

Mean daily sap flows per tree and species (*M. faya* and *E. arborea*) (Q_t, l/d) for two years of data were closely related to DBH, something which was also observed by Jiménez et al. (1996) for *Laurus azorica* trees in Tenerife (see below). The following empirical regressions between measured Q_t (l/d) and DBH (m) were derived for the respective species based on the sampled trees (Figure VI.11a, solid line):

Erica arborea:

DBH ≤ 0.22 m $Q_t = 750.3 DBH^2 - 154.64 DBH + 9.77$ $r^2 = 0.99$ VI.11

Myrica faya:

DBH ≤ 0.31 m $Q_t = 202.49 DBH^2 - 13.62 DBH + 1.34$ $r^2 = 0.99$ VI.12

The same pattern as obtained by Jiménez et al. (1996) was assumed for *M. faya* trees with DBH > 0.31 m (n = 3 trees) and for *E. arborea* trees with DBH > 0.22 m (n = 2 trees) (discontinuous line in Figure VI.11a):

Erica arborea:

DBH > 0.22 m $\quad Q_t = 1\cdot10^{-4}\,DBH^5 - 0.01DBH^4 + 0.17DBH^3 - 1.29DBH^2 + 3.5DBH - 2.31$

$$r^2=0.99 \quad VI.13$$

Myrica faya:

DBH > 0.31 m $\quad Q_t = 3\cdot10^{-5}\,DBH^5 - 0.01DH^4 + 0.09DBH^3 - 1.15DBH^2 + 5.24DBH - 4.96$

$$r^2=0.99 \quad VI.14$$

Furthermore, based on the finding of Jiménez et al. (2000) that Q_t in *Laurus azorica* was 0.92 times Q_t in a similarly sized *E. arborea* tree, the following empirical expression (Eq. VI.15) was derived for *L. azorica* assuming that the shape of the sap velocity distribution vs. DBH is the same as that reported by Jiménez et al. (1996):

$$Q_t = -0.002DBH^4 + 0.09DBH^3 - 0.83DBH^2 + 2.57DBH - 1.9 \qquad r^2=0.99 \qquad VI.15$$

It is recognised that the error associated with the estimation of the sap flows for the large trees (DBH > 0.22 m for *E. arborea*, DBH > 0.31 m for *M. faya*) and *L. azorica* trees may well be considerable because of these assumptions. For this reason, the estimated errors in Q_t were arbitrarily assumed to be twice those obtained for the sampled trees (i.e. ±12.5% for *M. faya* and ±39% for *E. arborea* and *L. azorica*).

Mean daily sap flows for each DBH class (intervals of 0.02 m) and tree species were calculated using the above regressions and DBH distribution data as shown in Figure VI.11b. Mean total Q_t values per DBH class and species are shown in Figure VI.11c. Daily stand transpiration totals were obtained by summing the Q_t values per DBH class and species. Total amounts of water transpired per species were strongly controlled by the uptake of the few biggest individuals (Figure VI.11c). Overall uncertainty in average daily stand transpiration over the two years of observations was ±22%, estimated as the sum of the errors estimated per tree and species within the plot based on the estimated errors of Q_t for sampled and non-sampled *M. faya* trees (±6.2% and ±12.5% respectively), sampled and non-sampled *E. arborea* trees (±19.6% and ±39%, respectively) and non-sampled *L. azorica* trees (±39%).

VI.3.5   Contribution of the three main tree species to overall stand transpiration

Daily stand transpiration (E_t, mm) was obtained by dividing total daily stand sap flow (l) by plot surface area (m^2). Measured stand transpiration data were available for 297 and 261 days during the first and second year, respectively. Average (measured) daily E_t for the first year was 1.28 ± 0.22 mm, with absolute minimum and maximum values of 0.1 and 3.9 mm/d, respectively (Figure VI.12). The relative contributions of the three dominant tree species to total stand transpiration in the first year were 48% for *M. faya*, 40% for *E. arborea* and 12 % for *L. azorica* (Figure VI.12). Daily totals of incoming solar radiation (R_g, MJ) and E_t were

correlated ($r^2 = 0.71$, $n = 297$). Using the relationship to fill the few gaps in the E_t record gave a total transpiration of 402 mm for the first year.
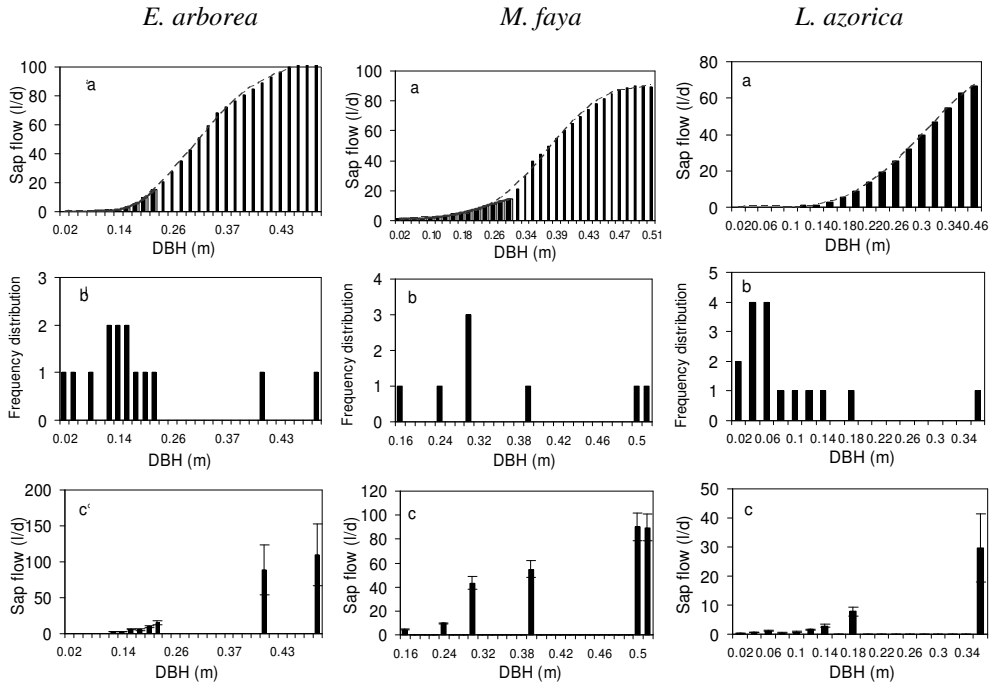
Figure VI.11 a) Mean daily sap flow per tree (l/d) vs. DBH class as calculated using empirical regressions for each species in the Laguna Grande ridge top forest, La Gomera. b) Frequency distribution of DBH classes within the plot per species. c) Scaled up total mean daily sap flow per DBH class (every 0.02 m) and species (*Erica arborea*, *Myrica faya*, *Laurus azorica*) within the studied plot.
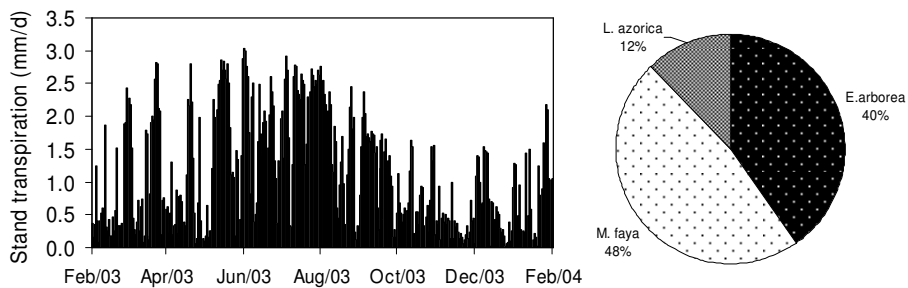
Figure VI.12 (Left) Measured and predicted (R_g vs E_t) annual course of daily stand transpiration between February 2003 and January 2004. (Right) Associated relative contributions to overall stand transpiration (402 ± 5.5 mm) by the three dominant tree species in the Laguna Grande ridge top forest.

VI.3.6   Sap velocity vs. meteorological and soil moisture conditions

Global radiation reached maximum values in the May to September period, although many short-term oscillations were observed due to cloud occurrence, and declined again in fall and winter. Fluctuations in daytime temperature were relatively modest at this elevation with a mean value of 14.9 ± 5.0 ºC. Rainfall was mainly concentrated in autumn and winter, whereas small showers often occurred during spring (Figure VI.13a). The period between May and September is typically dry in the Canaries although it is also characterized by the frequent occurrence of stratocumulus clouds at intermediate altitudes (around 800 m a.s.l.) (Marzol, 1993). At higher elevations the stratocumuli are less frequent during summer but days with fog (and therefore conditions with low or zero vapour pressure deficits) happened throughout the year at the study site (Figure VI.13a; see Chapter IV).

Sap velocity in both *M. faya* and *E. arborea* was maintained throughout the year (Figure VI.13b, c), as was also observed for that other dominant species, *L. azorica* (Jiménez et al., 1996). Pronounced short-term fluctuations in sap velocity were observed during conditions of atmospheric saturation by fog. As shown in Figure VI.13d, sap flow stopped or reached very low values when fog was registered. Reductions in sap flow activity in summer during times of fog ranged between 10% and 90% compared with preceding hours without fog or rain. On the other hand, maximum sap flow activity in both species was also observed in summer (up to 40-50 mm/h), even though extractable soil moisture in the top 0.30 m reached minimum values (Figure VI.7). Apparently, the trees were able to access moisture in deeper layers. High sap velocity values in *E. arborea* occurred also during the flowering period in spring under conditions of ample soil moisture (Figure VI.13c).

Sap velocity during the wet season (low vapour pressure deficits and no soil water limitation) was related to global radiation intensity (Figure VI.14). Under low radiation conditions sap flow activity was very low and increased with higher light intensities. The radiation level needed to reach maximum sap velocity was around 150 W/m^2 in *M. faya* (or a photon flux density of 284 μmol/m^2 s), which is in close agreement with the occurrence of maximum leaf conductance at around 300 μmol/m^2 s in laurel forest species in Tenerife as observed by Zohlen et al. (1995). Only 100 W/m^2 (189.5 μmol/m^2 s) were needed to produce maximum sap velocity in *E. arborea* (Figure VI.14). Under light-saturated conditions, sap flow activity was related asymptotically to atmospheric vapour pressure deficit for both species (Figure VI.15). However, although in both species during wet conditions (March-April 2003) sap velocity reached saturation for VPDs in excess of 0.62 kPa, and during times of soil water limitation (August 2003) at VPDs >1 kPa, sap velocity in *E. arborea* was significantly lower during the dry period. No such difference between wet and dry season was observed in *M. faya* (Figure VI.15).

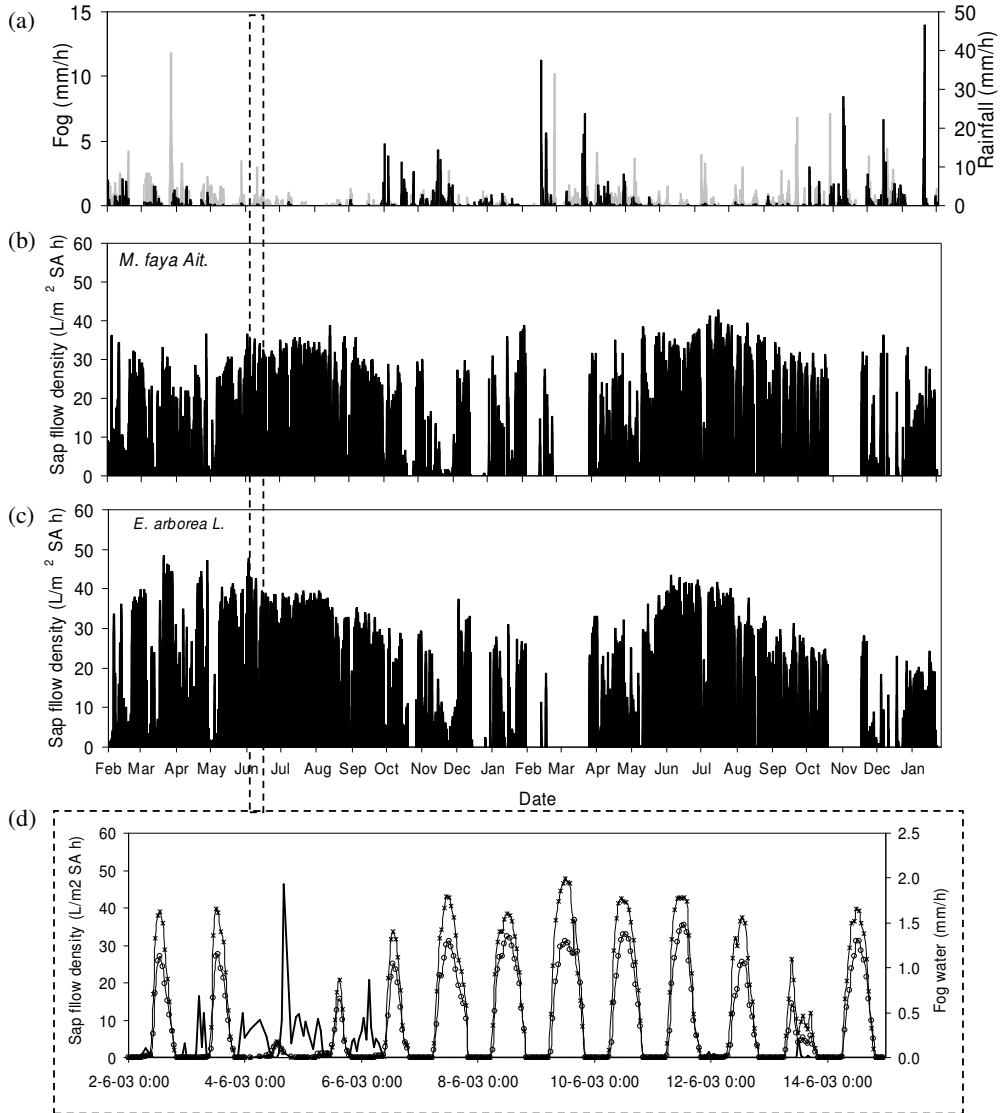Figure VI.13 . (a) Water inputs to the Laguna Grande ridge top forest: rainfall (black bars, right axis), and fog intercepted by a quarter-sized standard fog collector above the canopy (grey bars, left axis). (b) and (c) Annual course of mean sap velocity (mm/h or l/m^2 SA·h) in *Myrica faya* and *Erica arborea*. (d) Example of changes in hourly sap velocity as affected by fog occurrence between 2 and 14 June 2003.
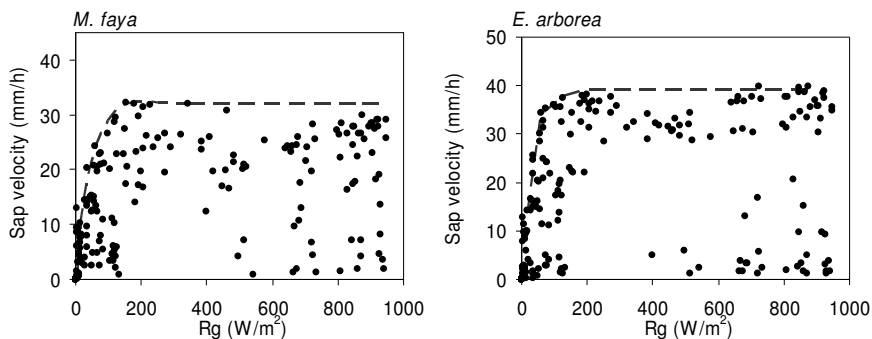
Figure VI.14 Relationship between hourly sap velocity (mm/h or l/m^2 SA·h) and global radiation (R_g, W/m^2) (left: *M. faya*; right: *E. arborea*) during a wet period (March 2003). Dashed line represents the light saturation curve.
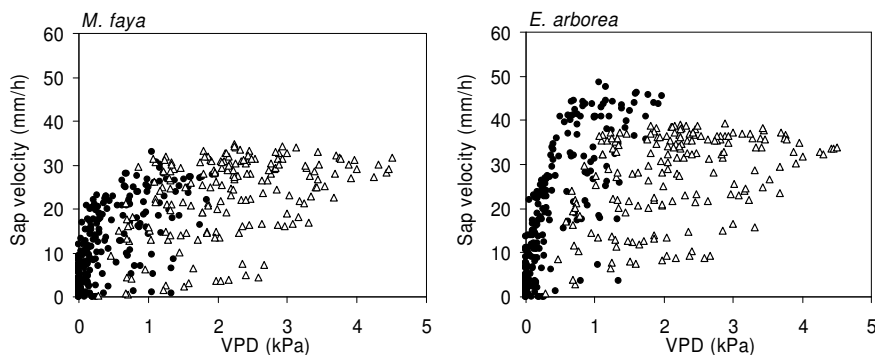
Figure VI.15 Hourly relationship between sap velocity (mm/h or l/m^2 SA·h) in *M. faya* (left) and *E. arborea* (right) and vapour pressure deficit (*VPD*, kPa) at the Laguna Grande ridge top forest site during a wet period (March 2003) (•), and during a dry period in which soil moisture was likely to be limited (August 2003) (Δ).

In the absence of limitations in soil moisture, radiation intensity or vapour pressure deficit, sap velocity was linearly related to temperature (Figure VI.16). However, under conditions of soil water limitation, sap velocity showed a clear plateau at temperatures of ca. 17-20 to 34°C for both species. Temperatures below 12 °C and above 30 °C seem to constraint sap flow activity in both species. Without limitations imposed by radiation and VPD, sap velocity was not clearly related to extractable moisture levels in the top 30 cm of soil. In addition, apparently only ca. 0.2 m^3/m^3 of extractable moisture would be needed to produce maximum sap flow activity. In view of the fact that this value of θ_e is close to the residual moisture

content for the upper layer, it is clear that the trees must have had access to moisture in deeper layers (Figure VI.17).
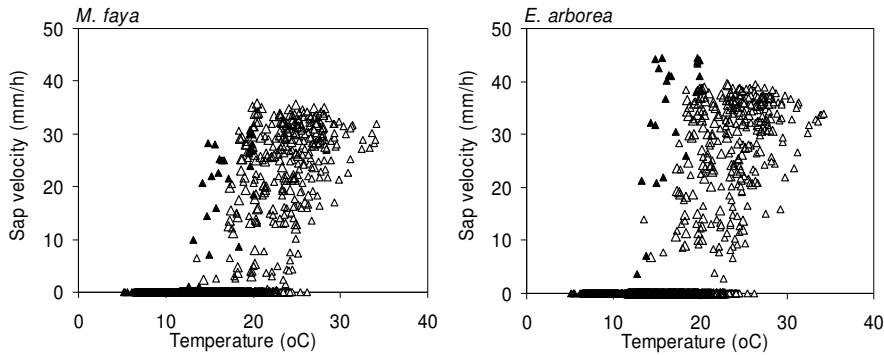
Figure VI.16 Relationship between hourly sap velocity (mm/h or l/m^2 SA·h) and air temperature (^{o}C) for *M. faya* (left) and *E. arborea* (right) at the Laguna Grande ridge top forest site in the absence of limitations imposed by radiation, vapour pressure deficit or soil moisture (▲), and during conditions of limitation by soil moisture (Δ).
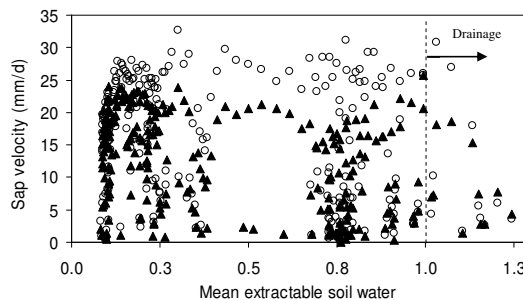
Figure VI.17 Relationship between mean daytime sap velocity (mm/d or l/m^2 SA·d) in *M. faya* (▲) and *E. arborea* (○) and mean relative extractable soil water in the upper 0.30 m between February and October 2003 at the Laguna Grande ridge top forest site.

VI.4   DISCUSSION

VI.4.1   Sap velocity and effects of meteorological and soil moisture conditions

Sap velocity in *Erica arborea* clearly increased with DBH, which may be explained by the fact that narrow crowns tend to intercept a higher portion of incident radiation in forest canopies with a pronounced vertical gradients in microclimate (Kelliher et al., 1992). However, in *M. faya* little variation in sap velocity was observed between differently sized trees (Figure

VI.8), possibly because of its broader crown. Slightly lower light intensity was needed to produce maximum sap velocity in *E. arborea* than in *M. faya* (Figure VI.14), which may explain the higher sap flow activity in *Erica*. Alternatively, in some species the relationship between foliage mass (or LAI) and stem diameter is inherently less strong than in other species (Waring et al., 1982).

Mean maximum sap velocity (55-65 mm/h) in *E. arborea* compared well with maximum rates obtained for this species in Tenerife by Jiménez et al. (1999) but no comparative information is available for *M. faya* (v_{max} 25-30 mm/h). Sap velocity in *E. arborea* trees was four times higher than in *M. faya*, which was unexpected from a water efficiency point of view. In terms of sap flow per surface area of conducting sapwood, *E. arborea* trees transpired also higher amounts of water even though sapwood area made up only half of the total cross-sectional area. The *E. arborea* trees in the ridge top forest had a lower average DBH value (0.19 m, range 0.04-0.59 m) compared with the *M. faya* trees (average DBH 0.39 m, range 0.16-0.69 m). The delay in the start of sap flow activity observed in the early morning hours in the two species are probably caused by the presence of dew or fog droplets on the leaves although in some cases it may reflect the refilling of previously depleted storage in the trunks (Waring et al., 1982).

Sap velocity followed an idealized pattern controlled largely by the prevailing evaporative conditions, with a maximum occurring around midday in both *M. fayal* and *E. arborea*. According to Zohlen et al. (1995) the stomata of some *M. faya* leaves remained closed in the absence of light. For this reason, the presently observed sap flow activity during the night (Figure VI.9) was unexpected. Nocturnal sap flow activity was observed throughout the year at the Laguna Grande site, but has also been reported for several coniferous and broad-leaved species on tropical mountains in East Africa (Fetene and Beck, 2004) and paper birch at Harvard Forest (MA, USA) (Daley and Phillips, 2006). The average water use during the night was small (4.6 and 5.7 %) compared with the daytime water use, but comparable with values published for other species, e.g. 5% in *Eucalyptus grandis* (Beyon, 1999), 6% in *Malus sylvestris* L. (Green et al., 1989), and 10% in paper birch (Daley and Phillips, 2006).

Nights with sap flow activity were more frequent during the wet season (not shown), which may be tentatively explained by the absence of any limitation in soil moisture. Two different sap velocity patterns were distinguished in the absence of light which were controlled by different factors in both species. On some days, sap velocity decreased steadily after the midday peak until stopping entirely several hours after dusk. This pattern may reflect the gradual depletion of water stored in the stem tissue, which may take several hours (Fetene and Beck, 2004). In other cases nocturnal sap flow was observed to be increased from zero or low activity to a secondary maximum that was always significantly lower than the preceding peak during the daytime. This can be explained in terms of transpiration and water storage dynamics in stem tissue under conditions of ample soil moisture. In those cases where night-time sap

flow activity was positively correlated with vapour pressure deficit and high wind speed (Figure VI.9) sap flow may be indicative of nocturnal transpiration, as also observed in eucalyptus (Beyon, 1999), poplar (Hogg and Hurdle, 1997) and paper birch (Daley and Phillips, 2006). On the other hand, nights in which the timing and magnitude of sap flow was not affected by environmental variables (not shown) may indicate stem water recharge, as also observed in red oak and red maple by Daley and Phillips (2006). Zero sap flow activity may be part of a nocturnal flow reversal. Although the direction of sap flow could not be distinguished by the presently used method, zero activity may have occurred after down ward sap flow occurred for a few hours and before normal upward flow was resumed. Hydraulic descent is still little studied but has been observed in roots of a *Fraxinus velutina* and *Juglans major* tree in the Chihuahuan desert (Hultine et al., 2003a; Hultine et al., 2003b), and an Acacia trees located in Botswana (M. Lubczynski, unpublished). The purpose of reverse sap flow may be seen as a strategy to facilitate root growth in deep soil layers and to transfer water away from shallow-rooted competitors (Hultine et al., 2003a) on the ridge top forest.

M. faya reached its maximum sap flow activity in summer (Figure VI.13b), when this species flowered, even though extractable soil moisture in the top layers was at a minimum at this time of year (Figure VI.7). Therefore, the roots must have had access to water in deeper layers. Because canopy conductance decreased under highly evaporative conditions (Figure VI.18), transpiration was maintained at a more or less constant rate despite the higher evaporative demand during the summer months. The shape of the relationship between canopy conductance in *M. faya* and VPD as well as the threshold value at which sap velocity reaches a maximum (Figure VI.15) were similar to those reported for another species (*Persea indica*) found in the Canary laurel forest (González-Rodríguez et al., 2002), as well as for Canary pine forest (Luís et al., 2005) and evergreen Mediterranean oak forest (David et al., 2004). However, these results contrast with the weak stomatal response to evaporative conditions found for *M. faya* in Tenerife by Zohlen et al. (1995) using porometry.

By contrast, *E. arborea*, exhibited its highest sap flow activity during its spring-time flowering, whereas a decrease was observed in August when extractable soil moisture in the upper 0.30 m was at a minimum (Figure VI.13c and Figure VI.8, respectively). As noted earlier for *M. faya*, canopy conductance in *E. arborea* decreased with vapour pressure deficit in summer (Figure VI.8), as also observed in *E. arborea* in Mediterranean maquis (Tognetti et al., 2000). A direct correlation between VPD and sap velocity was found, and in both species sap velocity reached a plateau for VPD values above 0.62 kPa when soil moisture was limiting, indicating stomatal limitation of transpiration (Figure VI.15). The saturation threshold of VPD increased for both species during the driest period (August 2003) to 1 kPa. Whilst in *E. arborea* sap flow activity showed a slight reduction during the dry season (indicating soil water limitation), this was not observed in *M. faya* (Figure VI.15). Reaching saturation at higher VPD values and reducing sap flow activity during low soil water conditions is a drought adaptation

mechanism that has also been observed during summer in *E. arborea* trees in Mediterranean maquis vegetation (Tognetti et al., 2000). A similar adaptation was recently reported for *Pinus canariensis* in the Canaries as well (Luís et al., 2005).

The lower sap flow activity observed during the winter months (Figure VI.13b, c) coincided with the wet season and overall lower evaporative conditions rather than that low temperatures limited sap velocity as was observed for *E. aborea* in Italy (Tognetti et al., 2000).
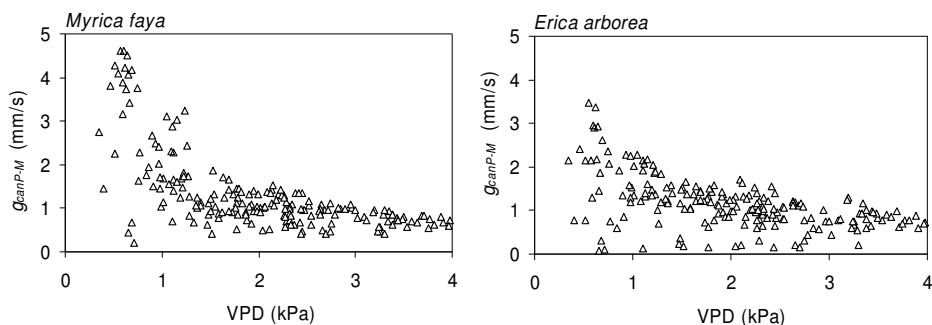
Figure VI.18 Relationship between canopy conductance (g_c) and vapour pressure deficit (VPD) in *M. faya* (left) and *E. arborea* (right) at the Laguna Grande ridge top site, La Gomera (Chapter VII).

VI.4.2   Stand transpiration

The forest at Laguna Grande transpired throughout the year, and high values (around 2.5-3 mm/d) occurred on clear days with a high vapour pressure deficit (Figure VI.12). Much higher values (up to 7 mm/d) were obtained by Jiménez *et al*. (1996) for a forest composed entirely of *L. azorica* trees in Tenerife. The presently found average E_t (1.28 ± 0.22 mm/d) resembles transpiration values obtained by micrometeorlogical techniques for equally fog-ridden (but much wetter in terms of rainfall) montane cloud forests in Puerto Rico (1.33 ± 0.95 mm/d at 800 m above sea level; Holwerda (2005)) and Costa Rica (1.0 mm/d at 1460 m; Bruijnzeel et al. (2006)), but was higher than that in a stunted ridge top cloud forest at 1010 m in Puerto Rico (0.81 ± 0.96 mm/d at 1010 m; Holwerda (2005)). Solar radiation on the ridge was about 73% of the potential value compared to a value of 50% for the Puerto Rican forest. Similarly, the canopy of the Laguna Grande forest was dry for 28% of the time vs. 20% in the Puerto Rican cloud forest (Holwerda, 2005).

Sap velocity was much reduced during times of fog incidence (Figure VI.13d), something which has also been documented for redwood forest in California (Burgess and Dawson, 2004) and windward cloud forest in Hawaii (Santiago et al., 2000). Interestingly, Burgess and Dawson (2004) demonstrated that fog water was actually absorbed by the redwood foliage, thereby reducing dehydration during times of low rainfall and occasionally even producing

reversed sap flow. Although it is not known whether the same process also occurs at Laguna Grande, the present results do illustrate the importance of fog for the reduction of tree water use, even if actual amounts of fog drip may seem limited (see Chapters IV and V).

Although the Laguna Grande ridge top forest was characterized by relatively thin trunks (DBH between 0.03 and 0.7 m), the contribution of a few dominant trees (DBH >0.3 m) to overall stand transpiration represented 90%, something which was also observed by Granier et al. (2000) for a beech forest in Germany. As for the dominant species, transpiration by *M. faya* made up nearly half of the total stand transpiration (48%) despite contributing 57% of plot basal area. Conversely, *E. arborea* (33% relative basal area) contributed 40% to overall stand transpiration whereas the contribution by *L. azorica* (11.5%) matched its relative basal area (10%).

Finally, during the five mostly dry summer months the forest´s principal loss of water was via transpiration. Total net water inputs to the forest floor between May and September 2003 were only 41 mm which was completely insufficient to satisfy vegetation water demand (ca. 246 mm). Therefore, the remaining water must have been taken up from the subsoil beyond 0.3 m depth.

VI.5   CONCLUSIONS

Stomatal control during the dry season was found to have a moderating influence on transpiration in both *Myrica faya* and *Erica arborea* in La Gomera. Estimated annual stand transpiration for the Laguna Grande ridge top forest (402 mm, average E_t 1.28 mm/day) was low compared to that obtained for typical laurel-dominated forest elsewhere in the Canaries but very similar to equally fog-ridden montane forests in Puerto Rico and Costa Rica. *M. faya* had a higher contribution to overall stand transpiration than the other two investigated species, which was mainly due to contributions by several bigger–sized individuals.

E. arborea trees were generally smaller but showed higher sap flow activity. Therefore, their relative contribution to overall stand transpiration (40%) exceeded their contribution to stand basal area (33%). The 57% basal area occupied by *M. faya* contributed 48%.

Nocturnal sap flow activity was observed throughout the year in both species but it was small compared with daytime values (4.8-6.0 %, depending on species).

In this humid ridge top forest, transpiration was limited by available energy (i.e. fog occurrence) and stomatal control (mostly on dry summer days). Although the water balance during the dry season was strongly negative and inputs by fog during this time of year were marginal, it should be emphasized that the prime importance of fog relates to diminishing evaporation. Hourly transpiration rates during times of fog were reduced by 10-90% compared to clear-sky conditions. Fog not only reduces atmospheric evaporative demand but also helps to

wet the canopy and possibly reduces dehydration of the vegetation under prolonged rainless conditions via foliar uptake of fog water (Burgess and Dawson, 2004), although the latter still needs to be demonstrated for the study site.

Chapter VII

CANOPY CONDUCTANCE
IN A SUBTROPICAL
RIDGE TOP CLOUD FOREST

VII CANOPY CONDUCTANCE IN A SUBTROPICAL RIDGE TOP CLOUD FOREST

ABSTRACT

Stand transpiration in a humid (though subject to long rainless spells in summer) ridge top cloud forest in the Garajonay National Park on La Gomera (Canary Islands) was modelled using the Penman-Monteith equation. Canopy conductance values were derived by inverting the above equation, using measured sap flow data for the two main species in the forest, *Myrica faya* (beech) and *Erica arborea* (tree-heath). Canopy conductance correlated well with global radiation and vapour pressure deficit, and the Jarvis (1976) multiplicative algorithm model reproduced the daytime and seasonal course of canopy conductance satisfactorily using only these two factors under moderate and high evaporative conditions. The artificial neural network approach performed better than the Penman-Monteith equation when filling gaps in the transpiration record. Annual transpiration losses were remarkably close for the two years of observations despite the second year having almost twice as much rainfall as the first. This reflected primarily stomatal control in response to high vapour pressure deficits during the dry summer period. There was no significant relation between moisture content in the first 0.3 m of the soil and canopy conductance, even though topsoil moisture reached very low values in summer, indicating that the roots had access to water at deeper levels.

VII.1   INTRODUCTION

The wind- and fog-exposed ridges above 1200 m elevation in the central and northern parts of the National Park of Garajonay on La Gomera (Canary Islands, Spain) are covered with a mixed tree-heath/beech cloud forest ('*fayal-brezal*') which is considered to be a degraded variant of the taller laurel-dominated forests (or '*laurisilva*') found in more sheltered slope and valley-bottom locations in the wetter parts of the archipelago (Pérez de Paz et al., 1990). The relatively low *fayal brezal* forest (average canopy height ca. 9 m) is comprised mainly of tree-heath (*Erica arborea* L.) and wax-myrtle or beech (*Myrica faya* Ait.), and to a lesser extent of holly (*Ilex canariensis* Poivet.) and laurel (*Laurus azorica* Seub. Franco). The climate at these elevations is humid Mediterranean with mild temperatures throughout the year, and a seasonal precipitation regime with five nearly rainless months during the summer. Fog, although frequent during spring, winter and autumn, assumes particular hydrological importance during the dry summer period (see Chapter IV). Whilst actual inputs of water by fog deposition during this time of year are limited, transpiration during times of fog was demonstrated to be reduced by 10-90% compared to clear-sky conditions (see Chapter VI).

Recent measurements of sap flow in *fayal-brezal* vegetation on La Gomera (Chapter VI) revealed low rates of transpiration compared to laurel-dominated forest elsewhere in the Canaries (Jiménez et al., 1996). Furthermore, the ridge vegetation was shown to transpire throughout the year without marked seasonality, despite the strong seasonality in rainfall. Rather, transpiration was found to be limited by available energy and by stomatal control in response to high atmospheric vapour pressure deficits (though not soil water deficits) during summer (see Chapter VI).

Physiological studies in cloud-affected forests in areas with low or seasonal rainfall are comparatively rare (Burgess and Dawson, 2004; Cavelier and Mejia, 1990). In the Canaries, several studies have investigated canopy conductance and stomatal control in laurel-dominated forests at relatively sheltered locations in Tenerife (Tausz et al., 2004; Zohlen et al., 1995), but there is a distinct lack of information on the stomatal behaviour of *E. arborea* as well as on the seasonal course of canopy conductance of *M. faya* growing under more exposed conditions. Studies of canopy conductance in Mediterranean shrub vegetation including *E. arborea* have shown stomatal opening to decline both during the warm and dry summer (Gratani and Varone, 2004; Tognetti et al., 2000) and in the cold winter season (Tognetti et al., 2000) but these sites were likely to be essentially fog-free.

Gaps in sap flow records may be filled (e.g. for water budgeting purposes) using the Penman-Monteith equation (Monteith, 1965), provided information is available on variations in canopy conductance (g_c) as a function of environmental conditions. Jarvis (1976) derived

generalised empirical expressions relating g_c to global radiation, vapour pressure deficit, air temperature and soil water deficit. In the absence of measured values (e.g. via porometry; Roberts et al. (1990)), g_c may also be derived from known transpiration data for a given vegetation using the Penman-Monteith equation in an inverted manner (Monteith, 1965). More recently, artificial neural networks have been shown to be an effective approach in the estimation of transpiration dynamics, the success of the method being based on its high flexibility without using any *a priori* model concepts (Vrugt et al., 2002).

The initial goal of this study was to derive annual transpiration totals for a mixed ridge top cloud forest in central La Gomera as part of an assessment of the stand's overall water budget. Two methods for the estimation of transpiration on days with gaps in the sap flow record were used and their results compared:

- The Penman-Monteith equation with g_c predicted in turn from meteorological variables using either previously derived regression equations or the empirical multiplicative algorithms defined by Jarvis (1976).
- An artificial neural network approach.

VII.2   MATERIALS AND METHODS

VII.2.1   Experimental plot

An experimental plot of 300 m^2 was delineated near Laguna Grande on a ridge at the top end of the Jelima catchment, with steep slope (30-40º) of north-easterly orientation at 1270 m a.s.l. in the north-central sector of the National Park of Garajonay, La Gomera (28º 17' 41'' N, 31º 08' 06'' W). The humid Mediterranean climate (Köppen type Csb) is characterized by moderate monthly temperatures ranging from 8.9 ºC in winter to 19.7 ºC during the largely rainless summer. The mean annual gross precipitation of ca. 660 mm is mainly concentrated in autumn and winter, while fog occurs frequently, immersing the vegetation in a near-saturated atmosphere for an estimated 20-26% of the time. Fog is most frequent and dense during the period March to May but from June to August the forest is regularly exposed to clear-sky radiation when the position of the thermal inversion marking the top of the 'sea of clouds' is shifted to an elevation of 800-900 m (Dorta, 1996). During such periods relative humidity may drop to 55-60%. A screen-type fog collector installed above the canopy registered 882 mm of fog water during the period February 2003 – January 2004 (see Chapter IV). Wind speeds on the ridge typically vary between 3.5 m/s in winter and 2.8 m/s in summer. Estimated daytime global radiation inputs range from ca. 10.3 MJ/m^2 in winter to as much as 25.4 MJ/m^2 during bright summer spells.

Tree density in the plot was 1266 trees/ha with a mean height of ca. 9 m (based on a survey of trees with > 0.07 m of diameter at breast height, DBH). Mean leaf area index (LAI) was 4.2 ± 1 m^2/m^2 (Golubic, 2001). Average DBH was 0.20 ± 0.17 m and stand basal area 68 m^2/ha. *M. faya* contributed the greatest proportion (57%) to stand basal area, followed by *E. arborea* (33%) and *L. azorica* (10%). The soils on the ridges had developed in trachybasaltic intercalations (lava flows and dykes). They were shallow (<0.5 m) and classified as Leptosols (F.A.O., 1998) according to Rodríguez et al. (2002) and typically consisted of an A-horizon (sandy clay loam) overlying a subsoil containing numerous angular basalt fragments in a grey clayey mass (Rodríguez et al., 2002). Roots were concentrated in the top 0.20 m but extended into cracks in the rocky substrate (see Chapter II).

VII.2.2   Meteorological measurements, sap velocity and soil water content

The Laguna Grande forest plot was instrumented with meteorological devices above the canopy, as well as equipment for the measurement of sap velocity and soil moisture. An automatic weather station placed on top of a 12 m scaffolding tower and mast structure (3 m) provided above-canopy measurements of rainfall (corrected for wind losses and topographic effects), relative humidity, air temperature, global radiation, wind speed and wind direction. Fog water was collected by a fog screen (volumes were corrected for wind direction effects on the reduction of effective collecting surface). Details of instruments and corrections are given in Chapter IV. Stand transpiration was derived from measurements of sap velocity in seven sample trees belonging to the two main species found on the ridges (see Chapter VI for details). Volumetric soil water fraction θ_v (m^3/m^3) was measured at 0.15 m depth intervals down to 0.30 m using time domain reflectometry probes (see Chapter VI for details on probe calibration). All variables were sampled at 3 min intervals and recorded every 15 min on a Combilog datalogger and then transmitted by GSM modem. Relative extractable soil water (θ_e, m^3/m^3) was calculated as the ratio of actually to maximum extractable water (Black, 1979):

$$\theta_e = \frac{\theta_v - \theta_r}{\theta_{fc} - \theta_r} \qquad\qquad \text{VII.1}$$

where θ_{fc} (m^3/m^3) is the maximum soil water content extractable by plants (field capacity) (0.55 m^3/m^3), and θ_r (m^3/m^3) the residual soil water content (0.20 m^3/m^3) (see Chapter VI).

VII.2.3   Models of transpiration

During the two years observations of sap flow for the Laguna Grande ridge top forest, failures in the operation of the sap velocity or data logging equipment caused some gaps in the

record, especially during rainy periods (Figure VII.1). The total number of (daytime) hours with missing transpiration data amounted to 428 or ca. 5% of total daytime hours.
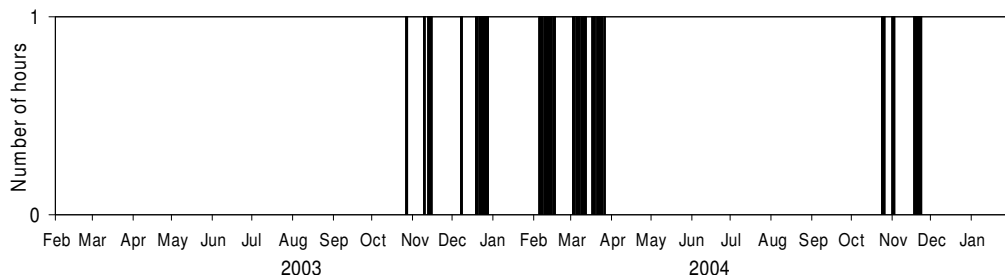
Figure VII.1 Distribution of gaps in hourly stand transpiration data for the Laguna Grande ridge top forest between February 2003 and January 2005.

Gaps in hourly records of transpiration E_T may be filled using various methodologies, such as the mean diurnal variation and other semi-empirical methods, including non-linear regressions and look-up tables (Falge et al., 2001). Here, non-linear regression approaches, such as the Penman-Monteith equation (with and without the Jarvis (1976) canopy conductance model), and artificial neural networks (ANN) are used.

VI.2.3.1   Penman-Monteith equation and Jarvis conductance model

To estimate E_T using the Penman-Monteith equation knowledge of the canopy conductance (g_c, mm/s) is required. Because no direct measurements of stomatal conductance were carried on the site, g_c was estimated in two ways. Firstly, canopy conductance ($g_{c\text{-}PM}$) values for typically wet (April 2003) and dry season conditions (August 2003) were obtained through an inverse application of the Penman-Monteith equation (VII.2) in which measured values of E_T (based on sap flow measurements) were inserted:

$$g_{c-PM} = \frac{g_a \gamma \lambda E_a}{\Delta R_n - \lambda E_a (\Delta + \gamma) + \rho_a c_p g_a (e_s - e_a)} 1000 \qquad \text{VII.2}$$

where g_a is the aerodynamic conductance (mm/s), γ the psychrometer constant (66.5 Pa/K), λ the latent heat of vaporisation ($2465 \cdot 10^3$ J/kg), E_a the measured stand transpiration (E_T) (mm/s), Δ the slope of the saturated vapour pressure vs. temperature curve, R_n the available energy (W/m^2; assumed to be equal to net radiation and ignoring the usually small changes in net soil- and canopy heat fluxes at this elevation). R_n was derived from measured global radiation using the regression obtained by Hafkenscheid et al. (2002) for a similarly structured montane forest in Jamaica. ρ_a (kg/m^3) is the density of air, c_p the specific heat of air at constant pressure (1.01 J/g K), and e_s-e_a (Pa) the saturation vapour pressure deficit. Aerodynamic

conductance (g_a, m/s) was calculated from wind speed and vegetation height according to Thom (1975):

$$g_a = \frac{u}{k^2 \left[\ln\left(\dfrac{z_m - z_d}{z_0} \right) \right]^2} \qquad\qquad \text{VII.3}$$

where k is the von Kármán constant (0.40), u (m/s) wind speed as measured at height z_m (m), z_d (m) the zero-plane displacement height ($0.75h$ where h is the average canopy height or 9 m), and z_0 (m) is the surface roughness ($0.1h$).

Next, the hourly g_c values derived with Eq. VII.2 were regressed separately against global radiation (R_g, W/m^2), vapour pressure deficit *VPD* (kPa), temperature T_a, and relative extractable soil water content (Eq. VII.1). Secondly, g_c was estimated using the empirical multiplicative algorithms defined by Stewart (1988) following Jarvis (1976):

$$g_{c-J} = g_{max} \cdot f(R_g) \cdot f(\delta q) \cdot f(T_a) \cdot f(\delta\theta) \qquad\qquad \text{VII.4}$$

where g_{c-J} is the estimated canopy conductance using the Jarvis approach, and g_{max} the maximum canopy conductance (mm/s) multiplied by the above-mentioned environmental factors that affect stomatal closing and opening and which are assigned values ranging from 0 (full closure) to 1 (maximum stomatal opening). In the Jarvis/Stewart model *VPD* is expressed as the specific humidity deficit of the air (δq, g/kg), and soil moisture status as soil water deficit relative to field capacity ($\delta\theta$, mm). The relationships between relative canopy conductance (i.e. g_c/g_{max}) and the respective environmental variables are non-linear as shown in Figure VII.2, also in Jarvis (1976) and Stewart (1988).
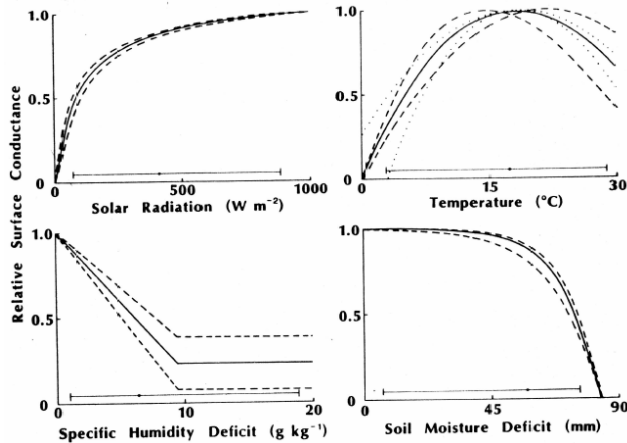

Figure VII.2 Dependence of the relative surface conductance on solar radiation, specific humidity deficit, air temperature and soil moisture deficit according to the Jarvis (1976)'s

model. The dashed lines show the change in each relationship caused by a 20% change in the respective parameter values and the dotted lines in the temperature relationship are the result of a change of 3°C in the high and low temperature limits. The horizontal lines show the range of each of the variables whereas the mean value is also indicated. After Stewart (1988).

Although it had been observed that the stomata were not always closed during the night (see Chapter VI), g_{c-J} was estimated only for daytime hours to simplify the model application and because the low rates of nocturnal transpiration did not follow a fixed pattern. In addition, only dry canopy conditions were considered (Granier et al., 2000; Harris et al., 2004; Sommer et al., 2002) and all hours with measured rainfall or fog, including a post-precipitation period of 4 h to allow the canopy to fully dry up. Values for the various constants and g_{max} in the Jarvis model were optimized for wet (April 2003) and dry (August 2003) conditions by maximizing the coefficient of determination (r^2) of the linear regression between g_{c-PM} and g_{c-J}.

VII.2.3.2   Artificial neural network

Artificial neural networks (ANN) are considered black-box models capable of reproducing highly non-linear relations between input and output variables (Schaap and Bouten, 1996). Two of the major advantages of the approach are its non-linearity, which is represented by a small number of parameters, and the fact that the model 'learns' from examples, i.e. it contains an iterative procedure known as 'training', in which the parameters (weights) of the network are adjusted. This feature makes ANN particularly suited for gap filling. The ANN consists of a number of input nodes, a hidden layer and one output node (Figure VII.3). In this study, input nodes were hourly global radiation, vapour pressure deficit, temperature, relative humidity, wind speed and soil water deficit. All variables were scaled $(X_i-meanX_n)/(maxX_n-minX_n)$ throughout the studied period (i.e. for training, testing and gap-filling data periods). Variables were combined to obtain a good fit with the simplest configuration. The output layer (Y) is calculated from the input nodes (X_i) through a complex mathematical network of connectives nodes (in the hidden layer). A sigmoid activation function was used for the hidden nodes in order to ensure maximum flexibility and to enable the network to reproduce the observed non-linear behaviour (Vrugt et al., 2002). Linear transfer functions were applied for the output layer (i.e. stand transpiration, E_{T-ANN}).

The training of the ANN was carried out using data collected immediately before and after the period that was to be modelled (i.e. data gaps). The ANN was subsequently tested against measured data for a different period (test period). The uncertainty of the predictions for the periods with data gaps was assumed to be equal to that obtained for the test period (root of mean squared error, RMS error).

The ANN was used in two ways: (i) to obtain stand transpiration during periods (both in the wet and dry season) for which sap flow measurements (E_T) were available, and (ii) to predict stand transpiration during periods for which data were missing. Results for E_{T-ANN} were compared with E_T and E_{T-PM}. The total error in predicted E_{T-ANN} was calculated as the sum of the error derived for the test period (RMS error) and the estimated error in measured E_T ($\pm 22\%$; see Chapter VI).

X₁ X₂ X₃ X₄ X₅ X₆   Y

Input layer   Hidden layer   Output layer
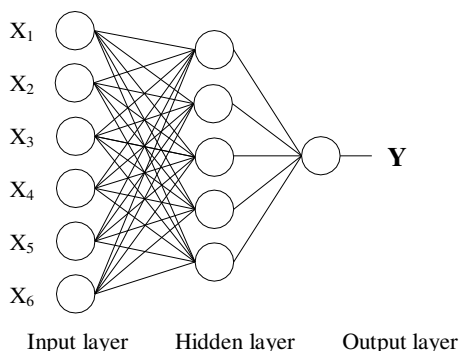
Figure VII.3 Schematic configuration of an artificial neural network with six input nodes (X_i), a hidden layer with five nodes and one output node (Y).

VII.3   RESULTS

VII.3.1   Canopy conductance of *Erica arborea* and *Myrica faya* in 2003

Diurnal patterns of global radiation (R_g, W/m^2), vapour pressure deficit (*VPD*, kPa), transpiration (E_T based on sap flow measurements, mm/hr) and canopy conductance derived from inverse application of the Penman-Monteith equation (g_{c-PM}, mm/s) for selected representative days are shown in Figure VII.4. The sample days in March represent wet season conditions (high soil moisture in top soils, moderate *VPD*) whereas the days in July and August represented the dry summer period with occasionally high *VPD* values and progressively lower soil moisture levels. The typical daytime pattern of inferred g_{c-PM} was a rapid rise in the morning to a maximum around noon which was more or less irregularly sustained during much of the afternoon, until dropping rapidly in the late afternoon and early evening hours. The pattern in g_{c-PM} closely mirrored that for *VPD* in an inverse manner, while stand transpiration increased rapidly until midday and decreased afterwards. A temporary decline in g_c of, especially *M. faya*, was observed around noon and in the early afternoon in response to increases in *VPD*. Such a response was less pronounced in *E. arborea* whereas in addition it became less evident as the summer progressed. Canopy conductance in *M. faya* was higher than in *E. arborea* during wet periods with ample soil water and slightly lower during the dry

period. Stand-level values of (maximum) $g_{c\text{-}PM}$ were highest in spring and gradually decreased during the summer (Figure VII.4).

Maximum values of $g_{c\text{-}PM}$ generally occurred around noon (Figure VII.4) and ranged between 3.5 and 54 mm/s (Figure VII.5). The highest values typically coincided with conditions of high relative humidity (>75%). Although $g_{max\text{-}PM}$ did not exhibit strong seasonality (Figure VII.5; missing data not filled in), higher values were found during the second year of observations (2004) which was significantly wetter. Indeed, the relationship between $g_{max\text{-}PM}$ and *VPD* shows a rapid decline in stomatal opening as *VPD* increases to ca. 1 kPa after which values of $g_{max\text{-}PM}$ remain rather constant (Figure VII.6). The scatter in the data for *VPD* <0.3 kPa was especially large even though the computations were restricted to hours with light levels > 100 W/m^2.
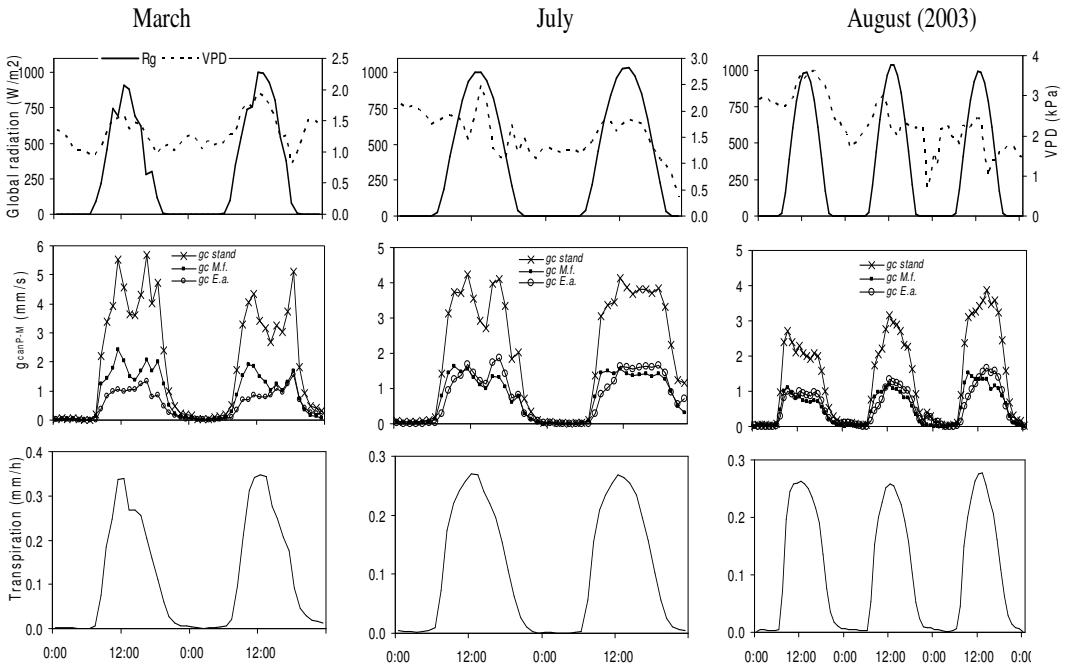
Figure VII.4. Daily course of global radiation (Rg, W/m^2), vapour pressure deficit (VPD, kPa), canopy conductance ($g_{c\text{-}PM}$, mm/s) and transpiration of the entire stand (mm/h) at Laguna grande in March, July and August 2003.
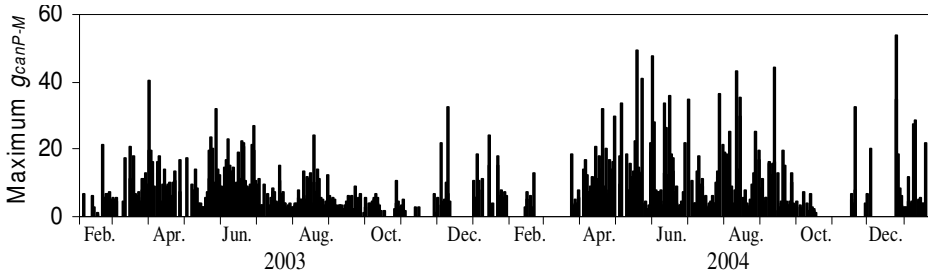
Figure VII.5 Annual course of maximum canopy conductance (g_{max-PM}, mm/s) in the Laguna Grande ridge top forest.
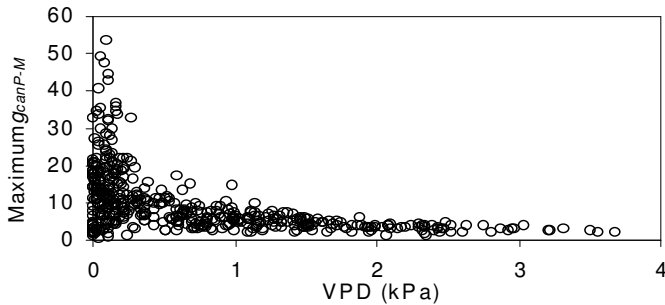
Figure VII.6 Relationship between daytime maximum stand canopy conductance (g_{max-PM}) and daytime mean vapour pressure deficit (*VPD*, kPa) for the Laguna Grande ridge top forest.

VII.3.2 Canopy conductance in *E. arborea* and *M. faya* vs. meteorological and soil moisture conditions

Relationships between g_{c-PM} for *M. faya* and *E. arborea* and the chief environmental factors known to affect g_c were explored for wet (April 2003) and dry (August 2003) season conditions. The results are shown in Figure VII.7. In order to avoid the extreme values of g_c that tend to be associated with early morning or evening conditions with low light, dew, or saturated atmospheric conditions (Granier et al., 2000; Harris et al., 2004; Sommer et al., 2002), only hours with $R_g > 100$ W/m^2, relative humidity <75%, and no precipitation during the four preceding hours were included in the analysis. As a result, derived g_{c-PM} values did not exceed 5 mm/s. Generally speaking, the relationships found for the two species were rather similar in shape, although values of g_{c-PM} were generally lower for *E. arborea* (a species with narrow leaves) compared to *M. faya*, especially during wet season conditions. Daytime g_{c-PM} values were positively related to radiation intensity and inversely to *VPD* and temperature. Maximum conductances were observed when radiation levels were in excess of 200-300 W/m^2 during both wet and dry conditions. Large scatter in g_{c-PM} was found for *VPD* values <1 kPa.

Maximum conductance coincided with the mean annual temperature on the ridge (ca. 13 ºC) whereas increases in temperature yielded lower g_c values. Amounts of relative extractable soil moisture in the top 0.3 m exerted comparatively little influence on g_{c-PM}, with only light decreases under very dry or very wet topsoil water conditions (Figure VII.7).
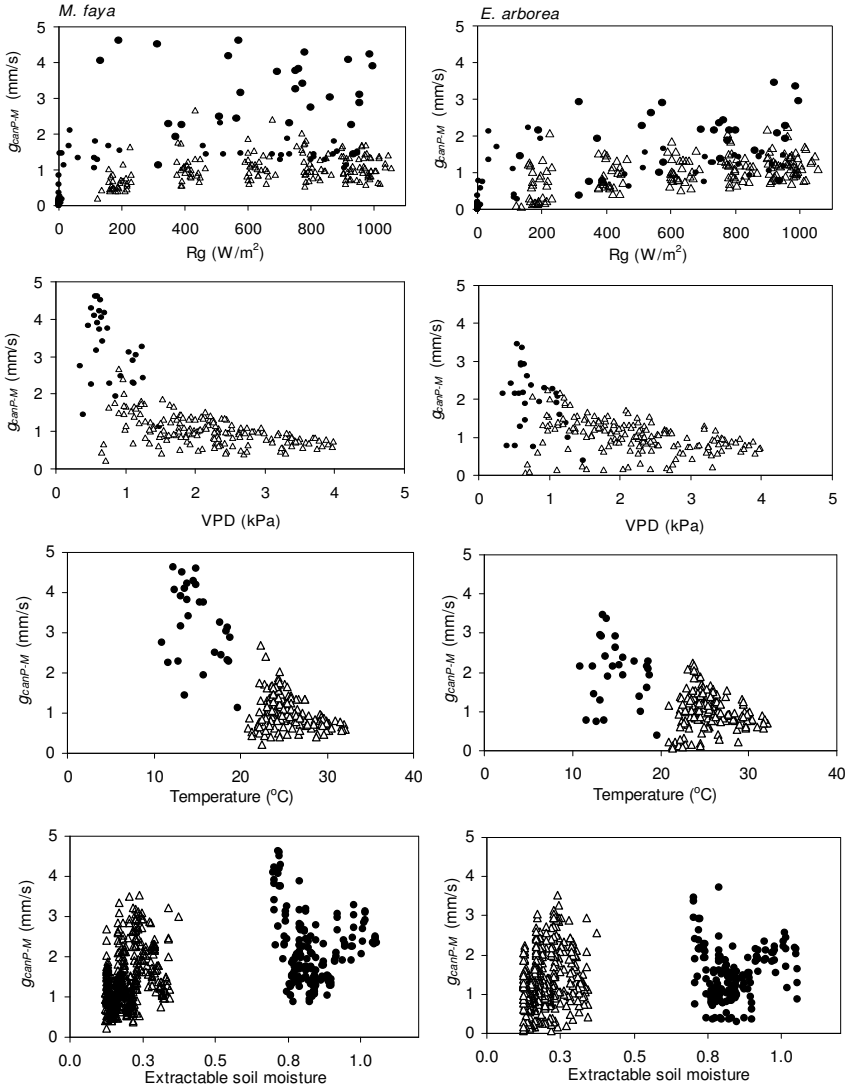
Figure VII.7. Relationships between hourly values of canopy conductance (g_{c-PM}) in *M. faya* and *E. arborea* in the Laguna Grande ridge top forest and global radiation (R_g, W/m^2), vapour pressure deficit (*VPD*, kPa), temperature (ºC) and relative extractable soil moisture content (cm^3/cm^3) during wet (●, April) and dry (Δ, August) conditions in 2003.

VII.3.3 Prediction of stand canopy conductance using Jarvis's multiplicative method

Prediction of hourly canopy conductance values using the Jarvis (1976) model (g_{c-J}, mm/s) was carried out for daytime hours with *VPD* >0.5 kPa to avoid the large scatter observed at lower *VPD* values (cf. Figure VII.6). Only global radiation (R_g, W/m^2) and specific humidity deficit (δq, g/kg) were used in the model whereas values for g_{max-J} were optimized by maximizing the coefficient of determination of the relation. The model was calibrated and validated separately for wet and dry conditions. The optimized values for g_{max-J}, a_1 in f(R_g) and a_2 in f(δq) (see Stewart, 1988 for equations) as well as the degree of variance explained by the model for wet and dry seasons are listed in Table VII.1.

Subsequently, monthly mean g_{max-J} values were related to monthly mean *VPD*:

$$\text{Monthly } g_{max-J} = -5.62 VPD + 11.90 \qquad\qquad (r^2 = 0.72, n = 7) \qquad\qquad \text{VII.5}$$

As shown in Figure VII.8, g_c values derived with the Jarvis model closely matched those obtained with the inverse application of the Penman-Monteith approach during the dry season (g_{c-J} ca. 4% higher) but g_{c-J} values were on average 24% higher than PM-based conductances during the wet season.
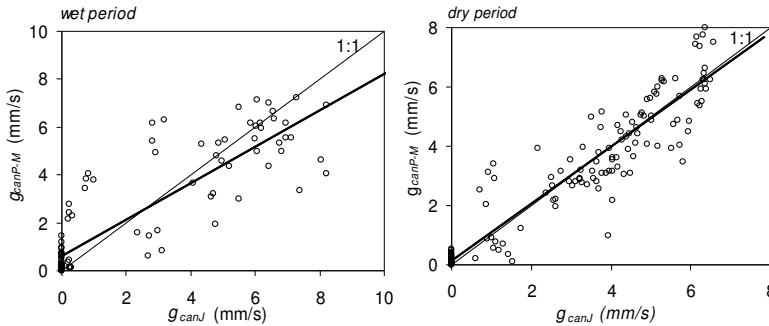
Figure VII.8. Modelled canopy conductances for the Laguna Grande ridge top forest using (i) Jarvis's multiplicative method (g_{c-J}) and (ii) an inverse application of the Penman-Monteith model during wet (February 2004) and dry (June 2003) season conditions. The thin line (−) corresponds with the 1:1 linear regression and the solid lines (—) with the linear regressions derived for the wet period ($g_{c-PM} = 0.76\ g_{c-J} + 0.63$, $r^2 = 0.76$) and the dry period ($g_{c-PM} = 0.96\ g_{c-J} + 0.13$, $r^2 = 0.86$).

Table VII.1 Optimized values of selected parameters (g_{max-J}, a_1, a_2) in Jarvis's multiplicative model and the variance explained by the model during wet and dry season conditions.

Model: $g_{c-J} = g_{max}$ f(R_g) f(δq)	n. of hours	g_{max-J}	a_1	a_2	Variance explained (%)
Wet season calibration: April 2003	77	11.8	433.1	0.084	77.7
Dry season calibration: August 2003	458	6.3	280.0	0.046	85.6

VII.3.4   Modelled stand transpiration according to different methods

Canopy conductance values as obtained with the Jarvis model were inserted into the Penman-Monteith equation to model stand transpiration (E_{T-J}) for selected days during wet and dry season conditions. Transpiration for these days was also modelled using the artificial neural network (E_{T-ANN}) approach and the results were compared with measured stand transpiration (E_T) (Figure VII.9). For wet conditions (April 2003 and February 2004) E_{T-J} was well correlated with measured E_T despite the limited number of data available to calibrate the Jarvis model (Table VII.1). Transpiration predicted by the combined model deviated by 18% from measured values whereas the model explained 60-88% of the variance. However, the ANN approach performed much better, with E_{T-ANN} essentially equalling E_T (i.e. the slope of the regression did not differ significantly from 1) and explaining 99-100% of the variance in E_T.

April 2003:
$E_T = 0.82E_{T-J} + 0.01, r^2 = 0.88$
$E_T = 1.00E_{T-ANN}, r^2 = 0.99$

June 2003:
$E_T = 0.91E_{T-J} + 0.01, r^2 = 0.91$
$E_T = 1.00E_{T-ANN}, r^2 = 0.97$

February 2004:
$E_T = 0.82E_{T-J} + 0.02, r^2 = 0.60$
$E_T = 1.00E_{T-ANN}, r^2 = 1.00$

August 2003:
$E_T = 0.94E_{T-J} + 0.02, r^2 = 0.82$
$E_T = 0.99E_{T-ANN}, r^2 = 0.93$
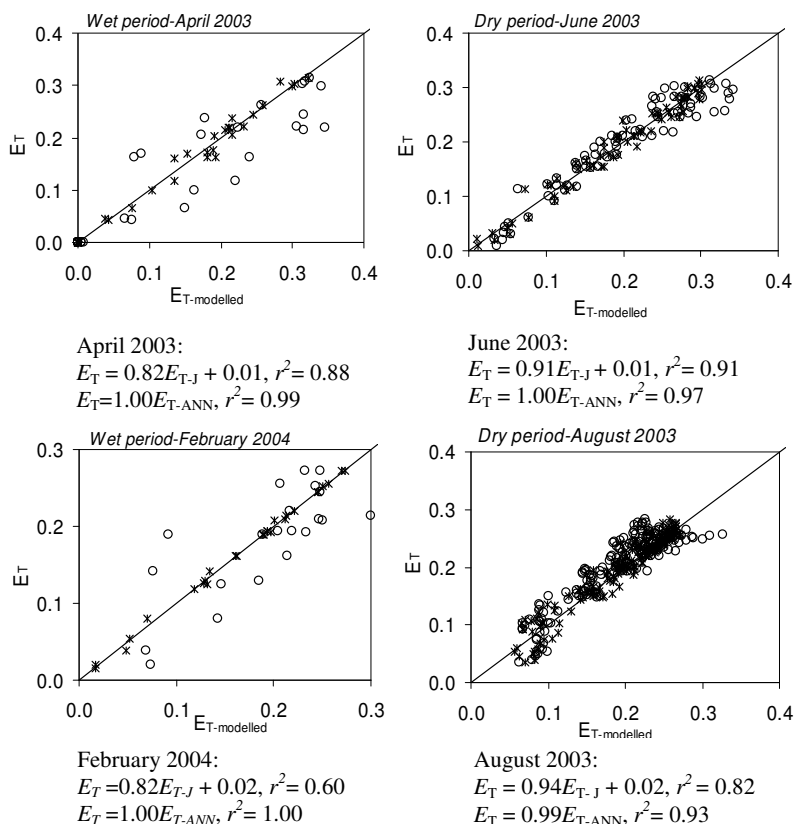
Figure VII.9 Comparison of stand transpiration as obtained by direct measurement of sap flow in a mixed tree-heath/beech forest (E_T) vs. those modelled with (i) the Penman-Monteith equation including canopy conductance values according to Jarvis´s model s (○, E_{T-J}), and (ii) an artificial neural network (ж, E_{T-ANN}).

During the dry period many more days were available to calibrate the Jarvis model (Table VII.1, Figure VII.9) and the results were correspondingly better. Modelled E_{T-J} differed only 6-9% from measured values whereas the model explained 82-91% of the variance. Again, E_{T-ANN} values essentially equalled E_T in the dry season whereas E_{T-ANN} explained 93-97% of the variance. As such, performance of the ANN was superior to the PM-Jarvis approach for both seasons although the former did slightly less well for the dry season.

VII.3.5   Annual stand transpiration

To arrive at annual transpiration totals the gaps in the wet season sap flow record (Figure VII.1) needed to be filled. The ANN approach was the preferred method to fill these gaps because of its better performance under humid conditions (Figure VII.9). The error in E_{T-ANN} was considered to equal that of the test period plus the maximum random error in measured stand transpiration (±22%, Chapter VI). Table VII.2 summarizes the data used for filling the chief gaps in the sap flow record whereas Figure VII.10 illustrates the respective configurations used for the ANN. Explained levels of variance during the training periods ranged from a low 63% in December 2003 to 97% in January-February 2004. Corresponding values during the test periods varied between 78% in December 2003 and 91% in September 2004 (Table VII.2).
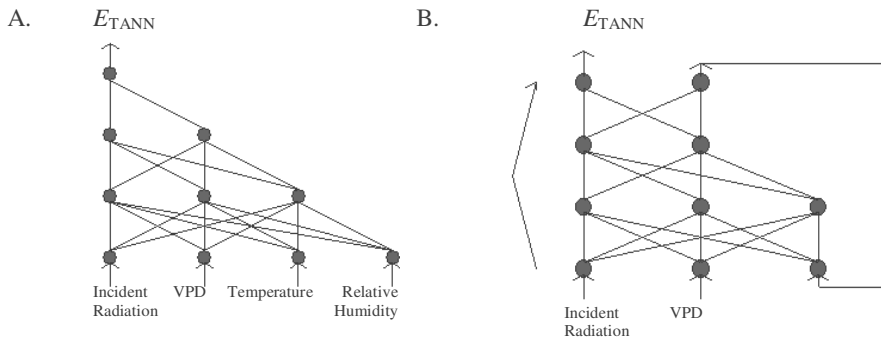
Figure VII.10 Neural network configurations used to fill up gaps in the measured transpiration data–set for the Laguna Grande ridge top forest.

After filling the gaps in the sap flow data annual stand transpiration totals were derived for the two-year period between February 2003 and January 2005 by summing the daily values shown in Figure VII.11. The two annual totals were remarkably close at 412 and 420 mm for the first and the second year, respectively, with an estimated mean maximum error of ±20% based on the estimated error in measured E_T (±22%; see Chapter VI) and the error in the predicted E_T, which was assumed to be equal to that associated with the ANN test period (example in Figure VII.12).
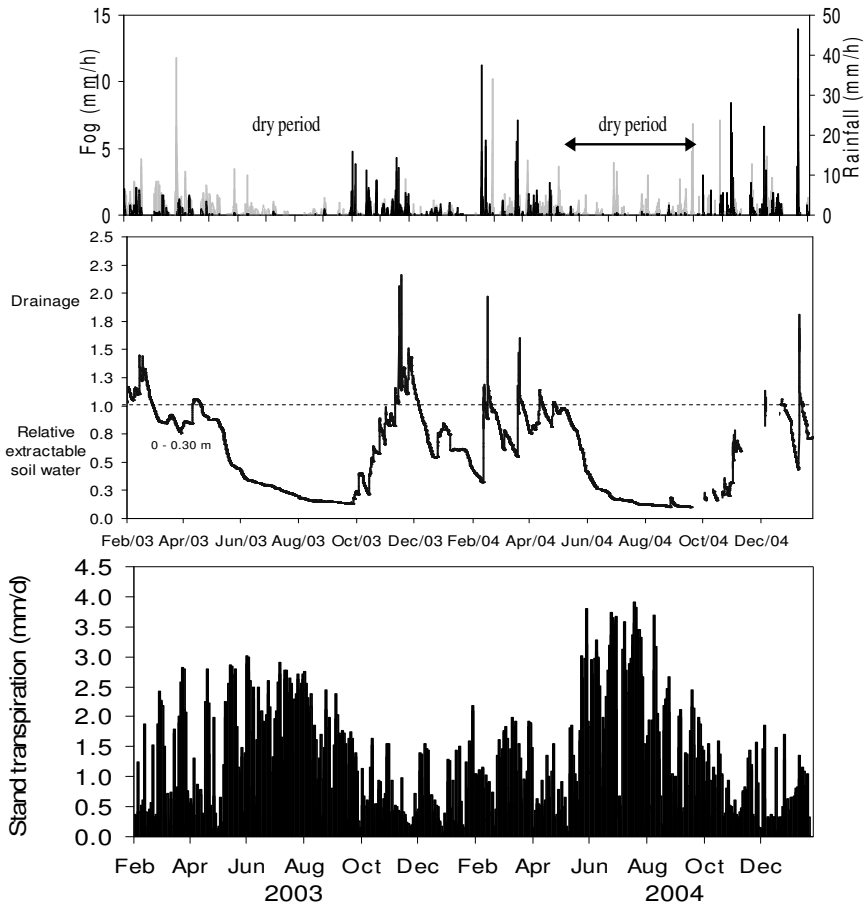
Figure VII.11 Daily rainfall and corrected fog water totals (top panel), relative available soil water in the top 0.30 m (middle panel) and (bottom panel) annual course of daily stand transpiration totals (after filling of gaps in the data) in the Laguna Grande ridge top forest.

The very similar transpiration totals for the two consecutive years are all the more remarkable because the second year was significantly wetter than the first (900 mm vs. 1695 mm of rain). As shown in Figure VII.11, the seasonal course of transpiration differed between the two years in response to differences in seasonal water inputs. Stand transpiration was low during spring in the second year as well as in May and part of November 2004 because of frequent foggy conditions. On the other hand, transpiration during the second dry season (265 mm between May and September) was higher compared with the previous summer (245 mm).

Table VII.2 Filling data gaps in the transpiration record for the Laguna Grande forest using the artificial neural network approach.

Period requiring gap filling	Input variables	ANN configuration type (Figure VII.10)	Training period	Variance explained for Training period	Test period	Variance explained for Test period
8th -27th December 2003	R_g, VPD, T and RH	A	1st -19th December 2003	63%	9th -10th January 2004	78%
5th February -26th March 2004	R_g and VPD	B	28th January- 5th February 2004	97%	3rd -7th April 2004	86%
25th October -23rd November 2004	R_g, VPD, T and RH	A	23rd October -27th November 2004	85%	10th -13th September 2004	91%
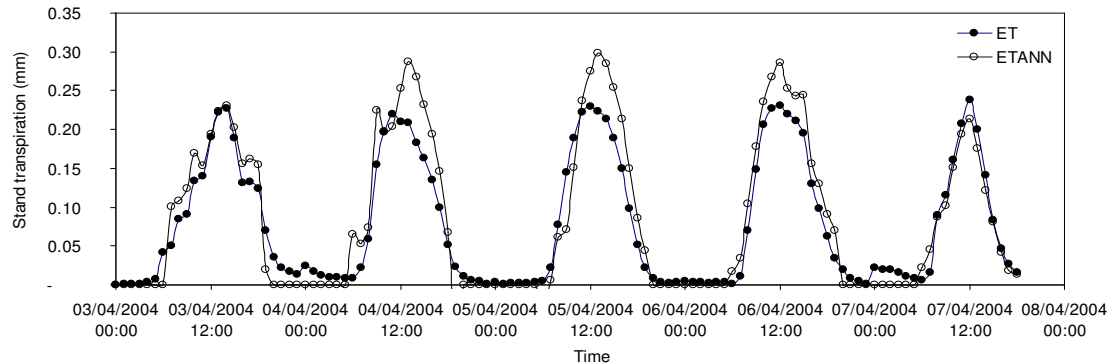
Figure VII.12 Comparison of measured stand transpiration (E_T) in the Laguna Grande ridge top forest with transpiration modelled by means of the artificial neural network method (E_{T-ANN}) for the period between 3rd and 7th April 2004.

VII.4   DISCUSSION

VII.4.1   Canopy conductance of *fayal-brezal* vegetation

Transpiration by the Laguna Grande ridge top forest increased rapidly during the morning hours and followed the equally rapid rises in global radiation R_g and atmospheric vapour pressure deficit *VPD* (Figure VII.4). Transpiration did not show any mid-day depression which is in agreement with the observed maximum in photosynthetic rates around mid-day in laurel forest species such as *M. faya* (Tausz et al., 2004). Although stomatal conductance tended to decrease during the daytime, Tausz et al. (2004) also pointed out that CO_2 fixation did not seem to be limited by this. At Laguna Grande, canopy conductance g_{c-PM} showed a marked decrease and a partial recovery during the day (Figure VII.4), while a progressive decline in measured g_c (porometer technique) at noon and later in the afternoon was found in *M. faya* by Tausz et al. (2004) as well as in *E. arborea* shrub under Mediterranean conditions by Tognetti et al. (2000). The former may be considered an artefact of the inverse application of the Penman-Monteith equation which leads to reductions in apparent g_c if *VPD* increases, and *vice versa* (Figure VII.4 and Eq. VII.2). Neglecting the very high values of g_{c-PM} that were sometimes obtained for the early morning hours because of leaf wetting by dew (Granier et al., 2000) values of g_{max-PM} ranged from 3.5 mm/s during dry periods to over 40 mm/s (often, but not always during times of ample soil water), with an absolute maximum of 54 mm/s in December 2004, a very wet period (Figure VII.5). The occurrence of g_{max} values in excess of 40 mm/s in the dry August and September 2004 period is more difficult to explain but may be related to previous contributions by several light showers. Similar ranges have been reported for Amazonian lowland forests (5-40 mm/s; Harris et al. (2004) and Sommer et al. (2002)) but comparative information for cloud-affected montane forests is rather scarce. Holwerda (2005) and Hafkenscheid et al. (2002) derived typical daytime values for g_{c-PM} of 20-40 mm/s and 15-50 mm/s for similarly sized montane cloud forests as the presently studied forest (but subject to much higher rainfall) in Puerto Rico and Jamaica, respectively. Slightly higher values (typically around 50 mm/s) were found throughout the day for tall windward cloud forest under well-watered conditions in Costa Rica (Frumau et al., 2007a).

VII.4.2   Effects of meteorological and soil moisture conditions on canopy conductance

Light saturation for canopy conductance in both *M. faya* and *E. arborea* was reached around 200-300 W/m^2, both during wet and dry conditions (Figure VII.7). Zohlen et al. (1995) reported a light saturation level of 284 W/m^2 of PAR for *M. faya* in Tenerife in spring. Higher atmospheric evaporative demand gradually reduced canopy conductance, something also

observed in pine forests in the U.K. (Stewart, 1988), the Canaries (g_{c-PM}; Luis et al. (2005)), and in narrow-leaved shrub forest in the Mediterranean (Tognetti et al., 2000). A similar reduction was found in a range of broad-leaved forests, e.g. beech in the Canaries (Tausz et al., 2004) and France (g_{c-PM}; Granier et al. (2000)), oaks in Portugal (David et al., 2004), and rain forests in the Amazonian region (Sommer et al. (2002); g_{c-PM}; Harris et al. (2004)). No stomatal limitation with increase of *VPD* was found in *Eucalyptus* in the southern mountains of Ethiopia (Fetene and Beck, 2004).

Daytime temperatures at the Laguna Grande ridge top ranged from ca. 6 ºC to an absolute maximum of 33 ºC. The optimum temperature (in terms of maximized g_{c-PM} values) was 12-15 ºC (Figure VII.7), close to the mean annual temperature at the site (13 ºC). Similar associations between average site temperature and optimum g_c have also been reported by Harris et al. (2004) for lowland Amazonian rain forest (optimum temperature ca. 25 ºC). A decrease in g_{c-PM} with increasing temperature was found in both *M. faya* and *E. arborea* but the decline was exponential rather than parabolic as postulated by Jarvis (1976) and Stewart (1988) (cf. Figure VII.2 and Figure VII.7) and also found by Luis et al. (2005) and Harris et al. (2004). Sommer et al. (2002) also observed the same pattern in g_c with increasing temperatures beyond the optimum value for secondary growth in Eastern Amazonia. No significant differences in conductance values between species were observed during the dry season, but often higher values were found in *M. faya* during the wet season (Figure VII.4); therefore direct measurements of stomatal conductance should shed more light on the reality of these interspecific differences. Values of g_{c-PM} for *M. faya* and *E. arborea* were hardly sensitive to water availability in the first 0.3 m of soil (Figure VII.7), which reflects the lack of sensitivity to topsoil water content in measured transpiration for the site (see also Chapter VI). In the case of pines in Tenerife, daily canopy conductance decreased linearly with soil water depletion in the top 0.40-0.45 m during the dry season, although transpiration remained stable throughout the dry period (Luís et al., 2005). Apparently, the root system had continued access to water stored in deeper soil layers in the ridge forest and pine forest.

VII.4.3   Modelling stand transpiration

The shapes of the relationships between g_{c-PM} and radiation and vapour pressure deficit (Figure VII.7) were similar to those derived for a pine forest in the eastern U.K. by Stewart (1988). However, the Jarvis model did not reproduce g_c very well under wet atmospheric conditions (*VPD* <0.5 kPa and E_T <0.1 mm/h; cf. Figure VII.9). This hurdle could be taken using the ANN model (Figure VII.10).

The Penman-Monteith equation was applied for dry canopy conditions during the wet and dry seasons and compared with measured transpiration (Figure VII.9). In general, the Penman-Monteith equation with g_{canJ} performed better during the dry season than in the wet season,

which may be explained by a combination of a physical effect and the used methodology: during the dry season transpiration is controlling most of the evaporation whilst during the wet season soil and understory evaporation may also contribute; On the other hand, the better performance of g_{canJ} during the dry season may also lead to a better performance of E_{T-J}. For rates of E_T >0.1 mm/h, the Penman-Monteith equation with g_c modelled according to Jarvis performed well during both wet and dry periods and explained most of the variance in transpiration on clear and warm days. However, the ANN approach was more suitable for modelling shorter periods of transpiration (see near-perfect correlations in Figure VII.12) and therefore for filling gaps in the transpiration record. The degree of success of the method was determined mainly by the similarity in atmospheric conditions between the training and test periods. New ANN configurations will be required for applications elsewhere.

VII.5   CONCLUSIONS

This study has demonstrated the suitability of using the Penman-Monteith equation in combination with the calibrated conductance model advanced by Jarvis to estimate long-term stand transpiration in a mixed tree-heath/beech ridge top cloud forest. However, the model performed poorly under very humid atmospheric conditions (relative humidity >80%) when transpiration values were very low. Most of the variance in canopy conductance in the Jarvis model could be explained by variations in global radiation and vapour pressure deficit, partly because of the covariance with temperature. Variations in topsoil water content exerted comparatively little influence on conductance and transpiration, even during the dry summer season when water content in the top 0.3 m of soil became severely depleted. Apparently, the roots had continued access to moisture stored in deeper layers.

The artificial neural network approach performed very well when filling gaps in the transpiration record, regardless of humid or dry atmospheric conditions. The success of the predictions was very dependent on the similarity in conditions between the training and test periods, however. Therefore, the ANN method is considered particularly suitable for gap filling purposes over relatively short periods.

Stomatal control in response to high vapour pressure deficits was observed in both studied species, so that stand transpiration during summer was limited. The constancy in annual transpiration losses during the two years of observations, of which the first year received half the water input of the second, underlined the ability of this exposed ridge top vegetation to control the closure of the stomata in response to dry atmospheric conditions. Direct measurements of stomatal conductance in both *Myrica faya* and *Erica arborea* would be desirable for comparison with the indirectly derived values presented here.

Chapter VIII

SUMMARY
AND
RECOMMENDATIONS
FOR FUTURE RESEARCH

VIII SUMMARY AND RECOMMENDATIONS FOR FUTURE RESEARCH

VIII.1 BACKGROUND, SETTING AND RESEARCH OBJECTIVES

Laurisilva vegetation is a laurel-dominated subtropical forest formation of great scientific value which was widespread in the southern Mediterranean region during the Tertiary era. Today it survives in the Macaronesian Region (composed of the Cape Verde islands, the Canary islands, Madeira and the Azores between 15° and 41°N latitudes), on mountains where humid conditions are guaranteed throughout the year. The Canaries are situated close to the West African coast and experience a lack of precipitation during five months (from May to September). The survival of the *laurisilva* vegetation so close to the Sahara desert can be explained by the particular climatic setting of the Canary Islands. The combination of being located on the south-eastern edge of the Azores anticyclone, coastlines being washed by cold Atlantic currents, and the occurrence of north-easterly trade winds allows the formation of a subsidence thermal inversion that translates into a stratocumulus deck on the windward sides of several of the islands that is locally known as the 'sea of clouds'. Although the cloud belt exhibits a seasonal change in elevation (lower in summer, higher in winter), it mitigates dry atmospheric conditions where and when it occurs in two ways: not only do the trees catch moisture from the fog brought in by the trade winds but also evaporative losses are much reduced. Although all seven Canary Islands must have been covered to some extent by *laurisilva* forests, some islands such as Lanzarote lost all their forests as a direct consequence of past human activities. The most extensive contiguous area of *laurisilva* is found in central La Gomera. In 1981, the Spanish authorities declared the forests in the Garajonay area a National Park in order to better protect and conserve these unique forests and in 1986 it became a UNESCO World Heritage Site. The Park is important not only for its special biodiversity but also for the water resources of La Gomera. Underneath this relatively wet mountainous area the main water storages of the island are found in the form of volcanic aquifers. Laurel forests differ in floristic composition and structure with elevation and different forest types may occur within close proximity of each other, e.g. stunted ridge-top forests on exposed ridges and mountain summits, slope forests of intermediate stature, and tall-broad-leaved valley-bottom forests. Comparatively little is known of the ecohydrological behaviour of each of these forests but given their different degrees of exposure to the trade winds and the fog that these carry, it is expected that their respective contributions to soil- and groundwater recharge will be different.

Arguably, the hydrometeorological situation is the most complex on the exposed and windy ridges. Here, the rain can be expected to come in under variable angles (depending on wind speeds, rainfall intensity and raindrop size) whereas in addition as yet unknown amounts of wind-driven fog will be captured by the vegetation. It was hypothesized that at the more sheltered valley-bottom locations fog will be much less important in terms of frequency of occurrence and as an input of water whereas deviations in rainfall angles from the vertical would also be expected to be (much) smaller. As such, emphasis in the present work was placed on evaluating the water budget of a ridge-top forest, Here, at 1270 m in the 44 ha Jelima headwater catchment in Central La Gomera, measurements were made of rainfall and (potential) fog water inputs using passive fog screens placed above the canopy, as well as of throughfall, tree transpiration (sap flow gauges) and soil water content. In addition, rainfall, fog and throughfall were also determined at a slope forest site (1220 m) and at two valley-bottom sites (1170 and 1140 m) within the catchment.

The following sections summarize the main findings of the current research, starting with a characterization of the degree of water repellence of the volcanic soils and ways to quantify this (Chapter III). This is followed by the quantification of rainfall, fog and throughfall in the wind- and fog-exposed ridge-top forest site (Chapter IV) and at the other, more sheltered locations (Chapter V). Chapter V also discusses the results of an application of the analytical model of rainfall interception to predict canopy interception under conditions of rain-only, fog-only, and mixed precipitation events. In Chapter VI the soil water uptake of the ridge-top vegetation is examined whereas in Chapter VII the influence of key climatic variables (radiation, temperature, vapour pressure deficit) and soil water content on surface conductance behaviour in the two dominant species of this forest (*Myrica faya* and *Erica arborea*) are quantified. Apart from listing the main findings per Chapter in corresponding sections, various recommendations for further research are offered. The latter are presented in a different format within each section to facilitate distinction between results and recommendations.

VIII.2   SOIL WATER REPELLENCE

The loss of soil wettability and the temporal or permanent resistance of the soil to be wetted again are known as soil hydrophobicity or soil water repellence. In general, water repellence may be caused by drying of the soil or by coating of the soil particles with organic compounds. The latter may derive from decomposition products, fungal hyphae or sub-products of the metabolic activity of micro-organisms. The importance of detecting occurrence and degree of soil water repellence in the field relates to its effect on soil hydraulic properties and therefore on the rate of water infiltration and the behaviour of flow through the soil matrix.

Water repellence is typically observed in dry soils, particularly those of a volcanic or peaty nature.

This study investigated (i) whether the volcanic soils (Leptosols and Andosols in the FAO classification) of the Jelima catchment were potentially water repellent; and (ii) the influence of soil water content on degree of water repellence. Based on the results of two commonly used types of laboratory tests for repellence (the water drop penetration time (WDPT) test and the molarity of ethanol droplet (MED) test) and subjecting a large number of field samples of surface soils (n = 140) to a stepwise drying from saturated to oven-dry conditions, a simple model was developed to predict the persistence and degree of water repellence as a function of soil water content.

The ***presently obtained results*** showed that:

- All sampled surface soils (<0.23 m depth) exhibited water repellence upon air-drying.

- Soils developing water repellence were non-allophanic in nature (i.e. they had high Al_p/Al_o ratios), high organic matter content (8-70%), and moderately low pH (ca. 5), whereas samples with lower Al_p/Al_o ratios (<8%), and lower organic matter content were non-water-repellent.

- Organic matter content in itself did not explain the observed differences in degree and persistency of repellency.

- No clear relationships were found between water repellency occurrence and topographic position within the catchment (valley bottom, slope or ridge top) or associated vegetation type (laurel-dominated forest, transitional slope forest and mixed tree-heath/beech forest, respectively).

- The development of hydrophobicity strongly depended on soil water content.

- Soils started to become water repellent close to field capacity and maximum persistence was reached around wilting point.

- Repellence varied non-monotonically with decreasing soil water content and the patterns could be reproduced using simple equations.

- The MED method is to be preferred with strongly hydrophobic soils because it gave less variable results at maximum repellence levels.

- A better characterization of soil water repellence is obtained if the WDPT or MED test is repeated at different soil water contents, particularly at field capacity and permanent wilting point.

The following ***recommendations for further research*** are offered:

1.   Although soil organic matter content itself did not explain observed differences in degree and persistence of soil water repellence, further work characterizing the type of organic matter (humus) and compounds therein (e.g. resins, waxes) may reveal specific influences on topsoil water repellence.

2.   The behaviour of hydrophobicity strongly depended on soil water content and was reproduced by simple regression equations. However, because the water repellence tests were applied to disturbed soil samples in the laboratory further work should validate the derived equations under field conditions.

3.   Further work should assess the role of soil water repellence in the generation of overland flow on the steep slopes of the study catchment.

4.   It is important to study the temporal variability of soil water repellence throughout the year (e.g. as a function of soil water content) as this allows an assessment of soil erosion risks.

VIII.3   RAINFALL, FOG AND THROUGHFALL DYNAMICS OF A RIDGE-TOP CLOUD FOREST

The ridges of the Jelima catchment at ca. 1270 m altitude contain a good example of the kind of mixed tree heath-beech cloud forest (*fayal-brezal*) that is typically found on exposed ridge and summit locations in the Garajonay area and elsewhere in the Canaries. This section summarizes the methods and results obtained with respect to rainfall and fog water inputs and their transformation to throughfall at this wind- and fog-ridden site.

The assessment of the "true" water inputs to sites in mountainous areas subject to strong wind is surrounded with uncertainty and results are highly dependent on the methods of collection and the exact location of the site. Rainfall and fog were measured above the canopy between February 2003 and January 2005. Rainfall was measured with a conventional recording rain gauge and fog with a quarter-sized standard fog collector (0.5 x 0.5 m) with a fixed orientation facing the dominant wind direction (NE). The degree of underestimation of incoming rainfall due to wind losses around the gauge was approximated using the approach of Yang et al. (1998). Moreover, under windy conditions rainfall tends to impact against the canopy at an angle. In the case of steep topography, the combined interaction between canopy / slope angle and aspect on the one hand, and the angle and direction of the rain on the other hand, will cause the rainfall intensity as measured by a gauge to differ from that hitting the canopy. The method advanced by Sharon (1980) was used to correct for these effects. Similarly, fixed-screen fog collectors may underestimate fog incidence because for wind directions deviating from the normal (90 degrees) direction the "true" surface area of collection of the fog collector will be reduced. Therefore, the effective surface of fog collection was calculated using trigonometry as a function of wind direction, something which has not been

done in previous fog studies in the Canaries. A fog trapping efficiency of 60% was used for this type of wire mesh based on previous measurements by others. Applying the latter value to the corrected fog catch gave the potential fog incidence. Finally, it is well known that major uncertainties are also associated with the measurement of throughfall in species-rich forests. Many studies have tried to reduce the standard deviation of mean throughfall by installing a large number of small gauges that are usually checked manually. Given the remoteness of the study site and the need to have matching records of rainfall, fog occurrence and throughfall it was decided to risk a relatively large error in estimated throughfall and use two automatic throughfall gauges per site. These gauges had a collecting surface of 0.2 m^2 each, giving a total sampling area of 0.4 m^2 per plot (equivalent to 40 standard gauges of 0.01 m^2 each).

The ***presently obtained results*** showed that:

- Rainfall had a strong seasonal character: the rainiest period occurred in autumn and winter whereas rainfall was insignificant during the five-month period between May and September.

- Interannual variability was high, with (uncorrected) annual rainfall in the first year (670 mm) being close to the estimated long-term average of 660 mm but being as much as 1185 mm in the second year.

- Rainfall intensities were generally low, with 50% of the days with rain receiving ≤2 mm and 38% <1 mm. Daily totals in excess of 20 mm occurred on 13% of the rain days.

- Underestimation of measured annual rainfall due to wind losses and slope effects on these exposed ridge locations may reach up to 39% of uncorrected rainfall; 20% was due to wind losses around the gauge and 19% related to slope and rain angle effects in the respective years.

- Fog inputs after correcting for variations in wind direction (F_c) were ca. 882 and 834 mm during the first and second year, respectively. Corrections due to changes in deviation from the dominant wind direction were substantial (+63% on average).

- Relative amounts of throughfall (*Tf*) differed between precipitation type: (i) for events with rain-only, *Tf* was on average 85% of wind- and slope-corrected precipitation inputs; (ii) on days with fog-only, *Tf* constituted a very small proportion (3.0%) of potential fog incidence, suggesting that the fog trapping efficiency of the forest canopy was much smaller than that of the fog screens used; (iii) on days with mixed precipitation (rainfall and fog), average *Tf* was 108% of wind- and slope-corrected precipitation, suggesting fog to be an important contributor under these conditions although the precise mechanism involved

remains unclear. Perhaps a larger proportion of the fog may find its way to the forest floor once the canopy (including bryophytes) is first saturated by rainfall.

- Despite the small absolute amounts of fog water inputs to the ecosystem, fog was the main input of water in the dry summer and acted effectively as a supplementary input besides rainfall during spring, winter and autumn by reducing evaporation (see below), and by increasing the amount of throughfall during mixed events.

- The overall variability in *Tf* catch for rainfall between the two gauges was high (±30% SD); using eight gauges would decrease the variability to ca. 15%. In the case of events with fog-only, variability in *Tf* catch between the two gauges was even higher (±69%).

The following ***recommendations for further research*** are offered:

1.   Existing rainfall and wind records in the uplands of La Gomera and elsewhere may be used to evaluate the degree of potential underestimation in rainfall catch in the past. Future studies in windy mountain areas such as the Garajonay National Park should take into account the under-catch of rainfall due to wind losses around the gauge and slope/rainfall angle effects.

2.   To avoid underestimation of fog incidence due to variations in wind direction when using fixed screen collectors it is advisable to use cylindrical fog collectors of well-defined catch efficiency such as the louvered gauge of Juvik and Ekern (1978) or the ASRC string collector (Falconer and Falconer, 1980) unless the screens can be oriented automatically towards the prevailing wind direction.

3.   Amounts of fog deposition onto a fog screen are highly sensitive to the trapping efficiency of the wire mesh. The actual mesh efficiency of the type of collector screen used in the Canaries and any changes therein with angle of incidence of the wind-driven drops due to (extreme) variations in wind direction need to be evaluated.

4.   No data are available as yet on the liquid water content (LWC) of fog in the Canaries. Measurements of the droplet size spectrum of the fog in relation to visibility would be useful.

5.   The large contrast between the very low amounts of throughfall generated by fog-only events and the very high ratios observed during events with mixed precipitation requires further process-based research. Apart from implementing several of the previous recommendations, such work could combine a mass-balance approach for stable isotopes (e.g. 18O) to separate fog and rain water in throughfall e.g. (Dawson, 1998; van Dijk and Bruijnzeel, 2001), measurements of the biomass, water storage capacity, and wetting and drying dynamics of epiphytes and mosses (Hölscher et al., 2004; Köhler et al., 2007; Tobón-Marín et al., 2007), together with improved measurements of (the spatial variability of) throughfall by employing sufficiently replicated sampling.

VIII.4 SPATIAL VARIABILITY OF WATER INPUTS ACROSS THE CATCHMENT AND MODELLING CANOPY INTERCEPTION FOR RAINFALL, FOG, AND MIXED PRECIPITATION

Between 1090 and 1300 m elevation the Jelima catchment is covered by a representative sample of three different subgroups of forest within the subtropical laurel-dominated forest. Tall laurel-dominated forest is found in the sheltered valley bottoms, whereas transition forest of intermediate stature occurs on the slopes, and short-stature mixed tree-heath/beech forest is found on the ridges. Rainfall inputs and fog incidence above the canopy, as well as throughfall were measured using the methods described in the previous section in each of four plots representing the three forest types (two plots were in valley-bottom forest, of which only one was used in the present analysis) from February 2003 to September 2004. In addition, the analytical model of rainfall interception advanced by Gash (1979) and revised by Gash et al. (1995) was applied to predict canopy interception during times of rainfall- only (all plots) and during times of fog-only and mixed precipitation (ridge-top plot only).

The ***presently obtained results*** showed that:

- In the relatively sheltered valley-bottom and slope forests, rain was the main source of water inputs. On the ridge, days with fog or mixed precipitation were much more frequent and potentially contributed as much water as events with rain-only.

- Rainfall corrections for wind losses around the gauge were 6-9% of gross precipitation in the valley and on the slope, compared to 20% on the ridge. Underestimation of rainfall was very modest (2% of P_a^*) for slope/rain angle effects for the slope site because of its orientation towards the west but more pronounced on the windy ridge (14%) and in the valley (7%, possibly due to funnelling).

- Once rainfall was corrected for wind losses and topographic effects, spatial variability between the sites was small (±5.5%).

- Showers at the valley-bottom and slope sites were characterized by low intensities (65% of rain days had ≤2 mm/d), except during the rainiest period (October until January) when convective storms occasionally produced larger amounts (11% of rain days had >20 mm).

- Amounts of wind-corrected fog incidence (F_c) were modest in the valley (27-30 mm/yr) and on the slope (ca. 67-76 mm/yr) but increased exponentially with elevation towards the ridge (834-882 mm/yr), which is explained by the much higher fog frequency and greater wind speeds prevailing on the ridge.

- Absolute amounts of throughfall generated during conditions of fog-only were very small in the valley and on the slope, but also very modest at the ridge top, presumably

because the canopy of the mixed tree heath/beech forest was much less efficient at capturing passing fog than the screen collectors.

- Amounts of throughfall produced by rain-only events were 79% in the valley, 83% on the slope, and 85% on the ridge and exhibited an inverse trend with forest LAI. Conversely, during events with mixed precipitation, throughfall exceeded wind-corrected rainfall inputs at all three sites, suggesting that fog may contribute more to throughfall when combined with rainfall than when it occurs alone. The difference is thought to reflect the contrast in the degree of wetting of canopy and bryophytes during conditions of fog-only and mixed events.

- The analytical interception model of Gash was calibrated during days with rain-only. Derived values for canopy storage capacity for the three forests were not significantly different but increased with a greater presence of needle-leaved tree-heath.

- Storms >2 mm were estimated to produce stemflow in the valley and slope forests vs. 3.2 mm in the ridge-top forest.

- Mean rates of wet canopy evaporation $\overline{E_w}$ as derived from rainfall interception measurements at the three sites was 0.28 ± 0.02 mm/h vs. 0.04 mm/h (rainfall-only) to 0.09 mm/h (fog-only) according to the Penman-Monteith equation. This contrast is attributed to the fact that the Penman-Monteith equation does not take into account the potentially large amounts of advected energy that may be brought in from the nearby ocean. The higher $\overline{E_w}$ rate during fog events compared to rainy conditions is due to the higher radiation loads received during times of fog compared to rain.

- The analytical model predicted measured amounts of throughfall associated with rainfall-only events quite well. Furthermore, the calibrated model for days with fog-only indicated that actual amounts of fog stripped by the canopy of the ridge-top forest were 13% (on average) of the potential fog deposition as measured above the canopy (D_{Fc}) whereas for mixed precipitation events optimized actual amounts of captured fog was 20% of D_{Fc}.

The following ***recommendations for further research*** are offered:

1. To complement the current preliminary study of spatial variability of fog inputs in the Jelima catchment additional fog collectors (preferably of the cylindrical type) should be installed to cover slopes of different orientation. The results may be usefully compared with predictions made by the spatially explicit FIESTA_fog delivery model of Mulligan and Burke (2006).

2. Throughfall measurements need to be improved by using a sufficiently replicated number of gauges. The improved data set may be used to re-calibrate the Gash model to better predict net water inputs to the soils of the valley and slope forests where fog incidence was not important (see also the final recommendation of the previous section).

VIII.5   STAND TRANSPIRATION AND CANOPY CONDUCTANCE OF MIXED TREE-HEATH / BEECH FOREST ON THE RIDGE

Next to rainfall and fog water inputs and their conversion to throughfall, measurements were made of transpiration (soil water uptake) and soil water content in the ridge-top forest at 1270 m. Sap flow was measured continuously in seven trees selected from the two most abundant tree species present in the forest, *Myrica faya* and *Erica arborea*, using the heat dissipation technique. Sap flow rates in individual trees were scaled to the stand level using empirical relationships between sap flux and tree diameter at breast height (DBH) per species and information on DBH distribution per species in the plot. Soil water content was measured using Time Domain Reflectometry (TDR) probes down to a depth of 0.3 m. This section summarizes the main results obtained with respect to transpiration and derived estimates of canopy conductance, and the effects of changes in climatic parameters and soil water content on transpiration and conductance.

The ***presently obtained results*** may be summarized as follows:

- Sap flow activity in similarly sized trees of *Erica arborea* (narrow-leaved) and *Myrica faya* (broad-leaved) trees were roughly four times higher in *E. arborea*. In addition, fluxes increased markedly with stem diameter in *Erica* but not in *Myrica*.
- Estimated contributions to overall stand transpiration by *E. arborea, M. faya* and *Laurus azorica* were 40%, 48%, and 12%, respectively, compared to relative contributions to stand basal area of 33%, 57% and 10%, respectively.
- Night-time transpiration was observed in both *Erica* and *Myrica*; rates were ca. 5% of daytime transpiration rates.
- In this humid (although rainless in summer) ridge-top forest, transpiration was limited by available radiant energy (governed in turn by fog occurrence) and by stomatal control (mostly during the dry summer months).
- During times of fog, transpiration was reduced by 10-90%.
- Because of reduced transpiration during times of fog, and because of stomatal control during dry periods, annual transpiration losses during the two years of observation were very similar (412 and 420 mm), despite rainfall inputs being almost twice those of the first year.
- Canopy conductance was inversely related to vapour pressure deficit of the atmosphere and increased with radiation at low intensities. However, there was no significant relationship with soil moisture content in the first 0.3 m depth, even though soil moisture reached very low values in summer. It was inferred that roots had access to water present in deeper layers, e.g. through cracks in the rocks below 0.3 m depth.

- Similarly, during the five dry months of the year (May - September), atmospheric water inputs hardly contributed to soil water reserves. Because the reserves in the top 0.3 m were insufficient to satisfy vegetation water demand, the water must have been supplied from the subsoil.

- Gaps in the stand transpiration record may be filled using the Penman-Monteith equation combined with the calibrated Jarvis model for the estimation of canopy conductance. However, the model performed less satisfactorily under very humid atmospheric conditions (>80% of relative humidity) when transpiration values were low and variations in conductance high.

- To fill short gaps in the transpiration record, the performance of the artificial neural network (ANN) approach was superior to the Penman-Monteith/Jarvis approach. Results obtained with the ANN improved as the conditions between the 'training' and 'test' periods were more similar, regardless whether atmospheric conditions were humid or dry.

The following *recommendations for further research* are offered:

1. Sap-flow measurements need to include the largest trees within the experimental plot because these dominated overall stand water use. In addition, sensors need to be installed at different depths within the trunks to adequately characterize changes in sap-flow patterns with depth.

2. In order to validate the various assumptions that were made to scale sap-flow measurements made at a single-point to the whole tree, further work should address the exact area of conducting sapwood in the studied trees (particularly for Myrica faya) as well as variations therein between individual trees.

3. Direct measurements of stomatal conductance (and leaf area) are needed for comparison with the indirect estimations of canopy conductance derived in the present study.

4. Transpiration and canopy conductance were not affected by moisture content in the top 0.3 m of the soil. Measurements are needed of the moisture content in deeper layers as well to establish whether transpiration is influenced by soil moisture at all.

VIII.6   WATER BALANCE OF THE RIDGE TOP FOREST OF THE JELIMA CATCHMENT

Regional water budget studies are necessary for the assessment of available water resources and for adjusting La Gomera's water policies in the light of expected climate change (Hay, 2000; Sperling et al., 2004). In this section the results obtained in the respective chapters are combined to solve the simplified water budget equation for the ridge-top forest site in terms

of the residual input to soil and groundwater recharge. The simplified annual site water balance, in which soil and understory evaporation were considered negligible, can be stated as:

$$Tf + Sf = OF + E_T + \Delta S + D \qquad\qquad\qquad VIII.1$$

where *Tf* is throughfall, *Sf* stemflow, *OF* overland flow, E_T transpiration (soil water uptake), *ΔS* the change in soil moisture storage, and *D* drainage to deeper layers and the groundwater table, with all values expressed in mm/year. The *OF* term was assumed to be negligible because no overland flow was ever observed in the plot, not even during high rainfall. Furthermore, Höllermann (1981) found minimal surface runoff and erosion during rainstorms of very high intensity (>100 mm/d) under laurel and tree-heath forests. Throughfall, transpiration and change in soil water storage down to 0.30 m depth were measured directly whereas stemflow was estimated using regressions against uncorrected rainfall derived by previous investigators (see Chapter V for details). Because *Tf* data were not available after September 2004, *Tf* totals for the remainder of the second year were estimated using regressions that were derived separately for days with rain-only, fog-only, or mixed precipitation during the first year. The simplified water budgets for the ridge-top forest during the two years are summarized in Table VIII.1 (values of inferred drainage rounded off to the nearest 5 mm).

Table VIII.1 Site water balance (mm/yr) for the mixed tree-heath/beech forest at 1270 m in the Jelima catchment, La Gomera, between February 2003 and January 2005.

	Tf + Sf (rain-only)	*Tf* (fog-only)	*Tf + Sf* (Mixed)	*Tf + Sf* (Total)	E_T	*ΔS*	*D*
February 2003-January 2004							
Amount of water (mm)	546	22	297	865	412	-50	505
Maximum random absolute error (mm)				±253[1]	±91[2]	±5[3]	190[4]
February 2004- January 2005							
Amount of water (mm)	1242	28	305	1575	420	20	1135
Maximum absolute random error (mm)				±472[1]	±92[2]	±2[3]	±430[4]

([1]) based on ±30% standard deviation in total throughfall (see Chapter IV); [2] based on ±22% standard deviation in total transpiration (see Chapter VI); [3] ±10% (see Chapter VI); [4] Square root of the quadratic error.

Annual net precipitation inputs to the forest floor between February 2003 and January 2004 amounted to 865 ± 178 (S.E.) mm including 19 mm of stemflow (the error of which is unknown but considered small in absolute terms). For a stand-level transpiration value of 412

mm and a change in soil water storage of -50 mm, a residual net recharge to deeper layers (below 0.30 m) of 505 mm was obtained.

The second year (February 2004 - January 2005) was much wetter (wind-corrected rainfall P_a* 1695 mm vs. 900 mm in the first year). Throughfall was 1542 ± 323 (S.E.) and stemflow 33 mm. Taking into account the transpiration of 420 mm and the change in soil water storage (20 mm) implied an estimated net recharge of 1135 mm/yr, i.e. more than double the value derived for the first year. This large inter-annual variability illustrates the importance of long-term monitoring of atmospheric water inputs. Furthermore, cloud-affected ridge-top forest occupied ca. 25% of the catchment area and as such its positive water budget is important for the overall water budget of the catchment. Additional sap-flow work would be needed in the slope and valley-bottom forests to derive the water budget for the catchment as a whole.

The uncertainty associated with the two estimates for recharge is quite large because the residual estimate of a water budget calculation contains the sum of the errors of the respective components. The standard deviation of the mean *Tf* was ±30%; the overall maximum error in stand transpiration was estimated at ±22%, whereas that in soil water storage was taken to be equal to the error in the fitted calibration curve for the TDR probes (10%). The overall error in the estimated drainage was calculated as the square root of the sum of the squared errors of each water balance component: ±38% mm (Table VIII.1).

Finally, Sperling et al. (2004) predicted for the period until the end of 21st century a strengthening of the subsidence of dry, warm air in the Canaries and a lowering of the trade wind inversion, which is expected to constrain the limit of the cloud tops. This, in turn, will increase the diurnal temperature range, vapour pressure deficits and the occurrence of intense radiation, and decrease the frequency of clouds during the dry season. If true, these forecasts imply that the currently experienced humid atmospheric conditions provided by the clouds in the study area during the dry season would be replaced by enhanced evaporative demand of the atmosphere and increased soil water depletion. According to the findings of the present study, stand transpiration of the mixed forest on the ridges during prolonged rainless conditions is controlled by stomatal closure. Nevertheless, a rise in tree water use may be expected due to this expected drying of the atmosphere, with correspondingly negative results for the recharging of soil- and groundwater reserves (on top of the expected 10% reduction in annual rainfall; Sperling et al. (2004)).

Chapter IX

NEDERLANDSE SAMENVATTING

IX   NEDERLANDSE SAMENVATTING (SUMMARY IN DUTCH)

IX.1   DOELSTELLING EN ONDERZOEKSVRAGEN

Het *Laurisilva* bos, een subtropische bosformatie die door lauriersoorten wordt gedomineerd, was gedurende het Tertiair wijdverspreid in het zuid Mediterrane gebied. Tegenwoordig komt de *Laurisilva* vegetatie nog voor in de zogenaamde Macaronesische regio (het gebied bestaande uit de Kaapverdische- en Canarische Eilanden, Madeira en de Azoren, tussen 15 en 41 graden noorderbreedte), op berghellingen die het gehele jaar door vochtig blijven. De Canarische eilanden, voor de West-Afrikaanse kust gelegen, hebben een droge periode van mei tot en met september. De overleving van de *Laurisilva* vegetatie zo dicht bij de Sahara kan worden toegeschreven aan locale klimaatsomstandigheden. De combinatie van de eilanden hun ligging aan de zuidoostelijke kant van het lage drukgebied rond de Azoren, de koude Atlantische Golfstroom, en de noordoostelijke passaatwinden veroorzaakt een thermale inversie met daaronder een stratocumulus wolkendek aan de loefzijde van de eilanden, lokaal aangeduid als de "wolkenzee". De seizoensgebonden verandering in hoogte van deze wolkenband ('s zomers is ze lager en 's winters hoger) werkt op twee manieren verzachtend op de droge atmosferische condities: niet alleen wordt het wolkenvocht (mist) aangevoerd door de passaatwinden door de bomen opgevangen, maar ook wordt vochtverlies door verdamping gereduceerd door de hoge luchtvochtigheid. Waarschijnlijk hebben alle zeven Canarische eilanden, ooit een *Laurisilva* vegetatie gekend, maar sommige eilanden, zoals Lanzarote, zijn alle bossen kwijtgeraakt als direct gevolg van menselijk ingrijpen. Het grootste aaneengesloten *Laurisilva* bos bevindt zich momenteel in het centrale gedeelte van La Gomera. Om dit bos beter te kunnen beschermen en conserveren hebben de Spaanse autoriteiten in 1981 besloten om van de unieke bossen van het Garajonay gebied een nationaal park maken, wat in 1986 resulteerde in plaatsing van het park op de werelderfgoedlijst van UNESCO. Niet alleen is het park belangrijk wegens haar speciale biodiversiteit, maar ook voor de waterreserves van La Gomera. Onder dit relatief natte berggebied bevinden zich de belangrijkste watervoorraden in vulkanische aquifers. Laurierbossen variëren in floristische samenstelling en structuur met de hoogte boven zeeniveau en verschillende bostypes kunnen dicht naast elkaar voorkomen; bijvoorbeeld dwergbossen op bergruggen en toppen, iets hogere bossen op de hellingen, en bossen met de grootste bomen in de bergdalen. Er is betrekkelijk weinig bekend over de hydrologische eigenschappen van deze bossen, maar door de verschillende gradaties in

blootstelling aan de passaatwinden en de mist die zij meevoeren, is het aannemelijk dat de aanvulling van bodem- en grondwater onder de verschillende bostypes zal verschillen.

Zoals bekend doet de meest gecompliceerde hydrometeorologische situatie zich voor op aan de wind blootgestelde bergruggen. De invalshoek van de regen op deze kammen is afhankelijk van de windsterkte, de regenintensiteit en de grootte van de regendruppels, waarbij onbekende hoeveelheden mist door de vegetatie worden ingevangen. Verondersteld wordt dat het voorkomen van mist in de meer afgeschermde dalen minder frequent is en minder belangrijk als extra bron van water voor het ecosysteem, en tevens dat de regen daar meer verticaal is. In dit proefschrift ligt de nadruk daarom op de evaluatie van de waterbalans van het bos op de bergkammen.

Op een hoogte van 1270 m in het 44 ha tellende Jelima stroomgebied in Centraal La Gomera, zijn metingen verricht aan regenval, (potentiële) mistwateraanvoer (verricht met behulp van boven de boomtoppen geplaatste passieve mistopvangschermen), aan doorval van regen- en mistwater, aan verdamping door de vegetatie (m.b.v. sapstroomsensors), en aan de hoeveelheden vocht in de bodem. Daarnaast zijn regenval, mist en doorval van regenwater gemeten in een hellingbos op 1220 m hoogte en op twee plekken onder in het dal van het stroomgebied (respectievelijk op 1170 en 1140 m hoogte).

De belangrijkste bevindingen van het onderzoek (in de vorm van samenvattingen van de hoofdstukken), worden in de hieronder volgende secties weergegeven, beginnend met de karakterisering van de mate van waterafstoting van de vulkanische bodems en de manieren om dit te kwantificeren (hoofdstuk III). Vervolgens wordt de regen, mist en doorval op het aan de wind en mist blootgestelde bergkambos (hoofdstuk IV) en op de meer beschermde helling- en dallocaties (hoofdstuk V) gekwantificeerd. Hoofdstuk V behandelt tevens de resultaten van een toepassing van het zogenaamde analytische interceptie model om de onderschepping door het bladerdek te voorspellen onder omstandigheden met alleen regen, alleen mist, of een mengsel van beiden. Daarna is de bodemwateropname (verdamping) van de bergkamvegetatie bestudeerd (hoofdstuk VI) en is de invloed van de belangrijkste weersvariabelen (straling, temperatuur, luchtvochtigheid) en de hoeveelheid bodemwater op de hoogte van de fysiologische weerstand tegen verdamping (uitgedrukt als geleidingvermogen) van het bladerdek gekwantificeerd voor de twee dominante soorten in dit bostype (*Myrica faya* en *Erica arborea*) (hoofdstuk VII).

IX.2   MATE VAN WATERAFSTOTING DOOR DE BODEM

De tijdelijke of permanente weerstand van de bodem tegen bevochtiging wordt wel hydrofobie of hydrofobiciteit (afstoting van water) genoemd. Dit kan worden veroorzaakt door uitdroging van de bodem of door verkitting van fijnverdeelde organische materie in de vorm

van decompositieproducten, schimmels, of bijproducten van microbiële activiteit. Het is belangrijk om het voorkomen en de mate van hydrofobiciteit van een bodem vast te stellen, omdat deze een effect hebben op de hydraulische eigenschappen van de bodem en daardoor op de hoeveelheid water die kan infiltreren of door de bodemmatrix stroomt. Waterafstoting komt voornamelijk voor in droge bodems, in het bijzonder in vulkanische of venige bodems.

In dit onderzoek is (i) de potentiële waterafstoting van de vulkanische bodems (Leptosols en Andosols, FAO classificatie) in het Jelima stroomgebied, en (ii) de invloed van het bodemwatergehalte op de mate en duur van waterafstoting bestudeerd. Gebaseerd op de resultaten van twee veelgebruikte laboratoriumproeven voor waterafstoting (de waterdruppelpenetratietijdtest (WDPT) en de ethanoldruppelmolariteitstest (MED)) en het onderwerpen van 140 bodemmonsters aan stapsgewijze uitdroging tot ovendroge condities, is een simpel model ontwikkeld om de persistentie en gradatie van waterafstotendheid als functie van het bodemvochtgehalte te voorspellen.

De hier verkregen resultaten lieten het volgende zien:

- Alle oppervlakte bodemmonsters (< 0,23 m diepte) vertoonden waterafstoting na droging aan de lucht.

- Bodems die waterafstoting ontwikkelden waren *non-allophanisch* (d.w.z. ze hadden een hoge Al_p/Al_o ratio), hadden een hoog organisch gehalte (8-70%) and een pH van minstens 5. Monsters met een lagere Al_p/Al_o ratio (<8%) en een lager gehalte aan organische stof werden niet waterafstotend.

- Het organische gehalte van een monster op zich kon de geobserveerde verschillen in gradatie en persistentie van waterafstoting niet verklaren.

- Relaties tussen het voorkomen van waterafstoting enerzijds en topografische positie in het stroomgebied (dalbodem, helling of bergrug) of het daaraan gerelateerde vegetatietype (respectievelijk laurierbos, overgangsbos en gemengd boomheide-beukenbos), zijn niet gevonden .

- De ontwikkeling van hydrofobiciteit is sterk afhankelijk van het bodemwatergehalte.

- Bodems met een vochtgehalte rond veldcapaciteit werden waterafstotend terwijl maximale persistentie werd bereikt bij het verwelkingpunt.

- Waterafstoting varieerde niet-monotoon met afnemende bodemwaterhoeveelheid en de patronen konden worden gereproduceerd met behulp van eenvoudige wiskundige vergelijkingen.

- Bij metingen aan sterk waterafstotende bodems is de MED-methode te prefereren omdat deze minder gevarieerde resultaten opleverde bij een maximale mate van waterafstoting.

- Een betere karakterisering van waterafstoting wordt verkregen wanneer de WDPT of de MED test wordt herhaald bij verschillende bodemwaterhoeveelheden, in het bijzonder bij veldcapaciteit en het permanente verwelkingpunt.

IX.3 DE DYNAMIEK VAN REGENVAL, MIST EN DOORVAL IN EEN BOS OP DE BERGKAM

Op de bergruggen van het Jelima stroomgebied op 1270 m hoogte bevindt zich een goed voorbeeld van het type gemengde boomheide-beukenbos (*fayal-brezal*) dat op aan harde wind en regen blootgestelde kammen en toppen in het Garajonay gebied en elders op de Canarische eilanden wordt aangetroffen. Deze sectie vat de methoden en resultaten samen die zijn verkregen met betrekking tot de regenval, mistaanvoer en hun transformatie tot doorval op deze door wind, regen en mist geteisterde plekken.

chattingen van de "werkelijke" groote van de wateraanvoer op aan de wind blootgestelde plekken in bergachtig terrein zijn onzeker en de resultaten worden sterk bepaald door de toegepaste meetmethoden en de exacte locatie van de plek. Tussen februari 2003 en januari 2005 werden regenval en mist boven het bladerdak gemeten. De regen werd gemeten met conventionele regenmeters; mist werd gemeten met behulp van een opvangscherm van 0,5 m bij 0,5 m dat loodrecht op de dominante (noordoostelijke) windrichting was geplaatst. De onderschatting van de hoeveelheid inkomend regenwater ten gevolge van luchtwervelingen rond de regenmeters werd benaderd door gebruikmaking van de correctiemethode van Yang et al. (1998). Tijdens winderige omstandigheden valt het regenwater onder een bepaalde hoek op het bladerdak (in plaats van vertikaal). In het geval van een steile topografie verschilt de regenintensiteit zoals gemeten door een regenmeter (met een horizontale meetopening) van de intensiteit waarmee de regen het bladerdak op de helling treft. Het exacte verschil wordt bepaald door complexe interacties tussen het bladerdak, de hoek en de oriëntatie van de helling enerzijds, en de invalshoek en richting van de regen anderzijds, De door Sharon (1980) ontwikkelde methode is gebruikt om voor deze effecten te corrigeren. Zo is er ook een mogelijke onderschatting van de hoeveelheden mist die worden ingevangen door de gebruikte schermen doordat wind komend vanuit andere richtingen dan de hoofdrichting een kleiner vangoppervlak treft. Daarom zijn met behulp van goniometrie de effectieve oppervlaktes van de mistinvangschermen berekend als functie van de windrichting, iets wat niet eerder is gedaan in voorgaande miststudies op de Canarische eilanden. Gebaseerd op eerdere metingen is een invangefficiëntie van 60% toegepast voor de gebruikte schermen. Samen met de eerdere correctie voor windrichtingseffecten gaf dit de potentiële mistinvang (D_{Fc}). Het is welbekend dat er grote onzekerheden zijn rond de meting van doorval in soortenrijke bossen. Vele studies hebben getracht de standaardafwijking van de gemiddelde doorval te verkleinen door een groot

aantal (kleine) doorvalmeters te installeren die gewoonlijk met de hand worden geleegd. Gegeven het afgelegen karakter van het studiegebied en de behoefte aan gelijktijdige metingen van regenval, mistvoorkomen en doorval werd besloten om een relatief grote fout in de geschatte hoeveelheden doorval te riskeren en twee automatische doorvalmeters per onderzoeksplot te gebruiken. Deze collectoren hadden elk een vangoppervlak van 0,2 m^2, daarmee een totaal vangoppervlak genererend van 0,4 m^2 per plot (equivalent aan 40 standaard regenmeters van elk 100 cm^2).

De resultaten van het onderzoek lieten het volgende zien:

- Regenval had een sterk seizoensgebonden karakter: de meest regenachtige periode was in de herfst en winter, terwijl in de periode tussen mei en september de regenintensiteit laag was.

- De variatie in jaarlijkse neerslag was hoog met een niet voor wind en topografie gecorrigeerde jaarlijkse neerslag van 670 mm in het eerste jaar (dat dicht tegen het geschatte meerjarig gemiddelde van 660 mm ligt) en 1185 mm in het tweede jaar.

- De gemiddelde regenintensiteiten zijn laag; 50% van de dagen ontvangt ≤ 2 mm neerslag en 38% van de dagen < 1 mm neerslag. Dagelijkse hoeveelheden van meer dan 20 mm neerslag kwamen op 13% van de regendagen voor.

- Onderschatting van de gemeten jaarlijkse neerslag door wind- en topografische effecten op deze winderige bergkammen kan oplopen tot 39% van de ongecorrigeerde regenval; ca. 20% hiervan is toe te schrijven aan turbulentie rond de regenmeters terwijl ca. 19% het gevolg is van effecten gerelateerd aan de hellings- en invalshoek van de neerslag.

- De vochtinbreng door mist na correctie voor variaties in windrichting (F_c) was ca. 882 mm gedurende het eerste jaar en 834 mm gedurende het tweede jaar. Correctie voor afwijkingen van de dominante windrichting waren substantieel (gemiddeld 63%).

- Relatieve hoeveelheden doorval (*Tf*) verschilden per neerslagtype. Voor buien met alleen regen was *Tf* gemiddeld gelijk aan 85% van de inkomende regenval na correctie voor wind- en hellingeffecten. Op dagen met alleen mist maakte *Tf* slechts 3% van de potentiële mistaanvoer uit, daarmee een mistinvang efficiency van het bladerdek suggererend die veel lager is dan die van de gebruikte mistschermen. Op dagen met zowel regenval als mist was de gemiddelde *Tf* 108% van de gecorrigeerde neerslag. Dit suggereert dat de bijdrage van mist onder deze omstandigheden een belangrijke factor is, hoewel het precieze mechanisme erachter onduidelijk blijft. Wellicht vindt een groter deel van de ingevangen mist

zijn weg naar de bosvloer nadat het bladerdak (inclusief de daarin aanwezige mossen) verzadigd is geraakt door regenval.

- Ondanks de in absolute zin kleine hoeveelheden ingevangen mist was mist toch de belangrijkste vorm van wateraanvoer gedurende de droge zomerperiode en vertegenwoordigde mist een effectieve aanvulling op de regenval gedurende de lente, herfst en winter doordat zij enerzijds de verdamping sterk reduceerde (zie onder) en anderzijds de hoeveelheid doorval tijdens perioden van gelijktijdige regen en mist leek te verhogen.

- De ruimtelijke variabiliteit van de gemeten doorval was hoog (±30% standaardafwijking); het gebruik van 8 doorvalmeters zou de variabiliteit reduceren tot ongeveer 15%. In het geval van alleen door mist veroorzaakte doorval was de variabiliteit tussen de twee collectoren het hoogst (±69%).

IX.4 RUIMTELIJKE VARIABILITEIT VAN BRUTO- EN NETTO NEERSLAG EN MODELLERING VAN NEERSLAGONDERSCHEPPING

Tussen 1090 en 1300 m hoogte boven zeeniveau is het Jelima stroomgebied bedekt met representatieve voorbeelden van drie verschillende soorten *laurisilva*. In de beschutte dalen vindt men bos dat door verschillende soorten laurier wordt gedomineerd (en met de grootste bomen), terwijl overgangsbos van intermediaire boomhoogte op de hellingen voorkomt, met gemengd dwergbos van boomheide en lokale beuken op de bergkammen. Van februari 2003 tot en met januari 2005 werden de regenval en het voorkomen van mist boven het bladerdek alsmede de doorval gemeten, met gebruikmaking van de methoden zoals beschreven in de voorgaande sectie. Dit is gedaan op elk van vier plekken die representatief geacht werden voor de drie voornoemde bostypen (twee locaties ware in het dal gelegen, waarvan er slechts één is gebruikt in deze analyse). Bovendien is het door Gash et al. (1995) gereviseerde analytische model gebruikt om de onderschepping van neerslag door het bladerdek te voorspellen. Hierbij werd onderscheid gemaakt tussen gevallen met alleen regen (uitgevoerd op alle drie de meetlocaties), gevallen met alleen mist, en gevallen met zowel regen als mist (de beide laatste alleen in het dwergbos op de bergkam).

De resultaten lieten het volgende zien:

- In de relatief beschutte dalbodem- en hellingbossen was regen de voornaamste bron van water. Dagen met mist of gemengde neerslag waren op de bergkam veel frequenter en droegen potentieel evenveel bij aan de totale wateraanvoer als buien met alleen regen.

- Correcties voor turbulentie (*wind loss*) rond de regenmeters bedroegen 6 tot 9% van de totale neerslag op de dalbodem- en hellinglocaties, tegen 20% op de

bergkam. Onderschatting van regenval op de helling ten gevolge van interacties tussen de invalshoek van de regen en de steilte en oriëntatie van de helling was gering (2%) vanwege de westelijke oriëntatie van de meetplek, maar was groter op de winderige kam (14%) en zelfs in de vallei (7%, waarschijnlijk ten gevolge van topografisch veroorzaakte versnelling van de wind).

- Na correctie voor turbulentie-, regenhoek-, en topografische effecten was de ruimtelijke variabiliteit tussen de verschillende meetplekken klein (±5.5%).

- Buien in het dal en op hellingstations werden gekarakteriseerd door lage intensiteiten (op 65% van de regendagen viel minder dan 2 mm), behalve tijdens de meest regenachtige periode (oktober - januari) waarin convectieve buien soms grote hoeveelheden water produceerden (tijdens 11% van de regendagen viel meer dan 20 mm).

- De voor windrichting gecorrigeerde hoeveelheden door de schermen ingevangen mist (F_c) in het dal en op de helling waren bescheiden (27-30 mm in het eerste jaar en 67-76 mm in het tweede jaar) maar namen exponentieel toe met de hoogte tot aan de kam (834-882 mm/jaar), wat kan worden toegeschreven aan de veel hogere mistfrequentie en hogere windsnelheden die daar heersen.

- De absolute hoeveelheden doorval die tijdens mistcondities zonder regen gegenereerd worden waren zeer gering in het dal en op de helling, maar ook bescheiden op de kam. Waarschijnlijk komt dit doordat het bladerdak van het gemengde boomheide- en beukenbos veel minder efficiënt de passerende mist uitfilterde dan de kunstmatige invangschermen.

- De hoeveelheden doorval die tijdens buien met alleen regen werden geproduceerd bedroegen 79% (dalbodem), 83% (helling) en 85% (bergkam), en vertoonden derhalve een omgekeerde trend met het geprojecteerde bladoppervlak van het bos (*leaf area index*). Dit in tegenstelling tot gemengde neerslag: op alle drie de meetplaatsen overschreed doorval de voor wind gecorrigeerde regeninvoer. Dit suggereert dat mist gecombineerd met regen een hoger aandeel levert aan de hoeveelheid doorval dan tijdens mistvoorkomen zonder regen. Dit contrast wordt eventueel verklaard door de verschillende mate van bevochtiging van het bladerdek en de daarin aanwezige mossen tijdens situaties met alleen mist of gemengde neerslag.

- Het analytische interceptiemodel van Gash werd in eerste instantie gecalibreerd voor dagen met alleen regen. De verkregen waarden voor de bergingscapaciteit van het bladerdak van de drie bostypes waren niet significant verschillend maar namen wel toe met het aandeel bomen met naaldvormige bladeren (met name boomheide).

- In het bos in de vallei en op de helling werd tijdens buien van meer dan 2 mm regen stamafvoer geproduceerd. In het bos op de kam gebeurde dit voor regenval boven de 3,2 mm.

- De gemiddelde verdampingssnelheid vanaf een nat bladerdek ($\overline{E_w}$) zoals afgeleid van de interceptiemetingen op de drie locaties bedroeg 0.28± 0.02 mm/uur. Daarentegen werden waarden van 0.04 mm/uur (alleen regen) tot 0.09 mm/uur (alleen mist) berekend met de Penman-Monteith vergelijking. Dit contrast kan worden toegeschreven aan het feit dat deze vergelijking geen rekening houdt met de potentiële grote hoeveelheden advectieve energie die aangevoerd kunnen worden vanaf de nabijgelegen oceaan. De hogere mate van $\overline{E_w}$ tijdens mist, in vergelijking met regen, kan worden teruggevoerd op de grotere hoeveelheden inkomende straling tijdens mist.

- De hoeveelheden doorval tijdens buien met alleen regen werden redelijk goed voorspeld door het analytische model. Het gekalibreerde model voor dagen met alleen mist liet zien dat de actuele hoeveelheid mist die ingevangen werd door het bos op de kam gemiddeld 13% bedroeg van de potentiële mistdepositie zoals gemeten boven de vegetatie (D_{Fc}). In het geval van gemengde neerslag was dit 20% van D_{Fc}.

IX.5 TRANSPIRATIE EN STOMATAAL GELEIDINGSVERMOGEN IN GEMENGD BOOMHEIDE- EN BEUKENBOS

Naast metingen aan regenval en mistwateraanvoer en de omzetting daarvan tot doorval, zijn metingen gedaan aan transpiratie (bodemwateropname) en bodemvochtgehalte in het kambos op 1270 m hoogte boven zeeniveau. De snelheid van de sapstroom in zeven geselecteerde individuen van de twee meest voorkomende boomsoorten in het bos, *Myrica faya* en *Erica arborea*, werd continu gemeten met behulp van de zogenaamde *heat dissipation* techniek. De sapstroomsnelheden in de individuele bomen werden opgeschaald tot gemiddelden voor het bos als geheel met behulp van empirische verhoudingen tussen de sapstroomsnelheid en boomdiameter op borsthoogte (DBH) per soort, en informatie over de ruimtelijke verdeling van DBH's per soort op de locatie. Bodemwatergehaltes werden gemeten met behulp van zogenaamde *Time Domain Reflectometry* (TDR) sensoren tot een diepte van 0,3 m. Hieronder worden de belangrijkste resultaten voor wat betreft de transpiratie en afgeleide schattingen van het stomatale geleidingsvermogen in de bladeren samengevat:

- Sapstroomsnelheden in bestudeerde *Erica arborea* (smalle naaldvormige bladeren) en *Myrica faya* (brede bladeren) individuen van gelijke diameter (0,22

m) waren ruwweg vier keer hoger in eerstgenoemde. De sapstroomsnelheid was gecorreleerd met de stamdikte voor *Erica*, maar niet voor *Myrica.*

- De geschatte bijdragen aan de totale transpiratie op plotniveau door *E. arborea*, *M. faya* en *Laurus azorica* waren respectievelijk 40%, 48% en 12%, tegen respectievelijke bijdragen aan het totale geprojecteerde basale stamoppervlak (*basal area*) van 33%, 57% en 10%.

- De geobserveerde nachtelijke wateropname door zowel *Erica* als *Myrica* bedroeg 5% van die van overdag.

- De transpiratie werd beperkt door de hoeveelheid beschikbare stralingsenergie (tengevolge van frequent voorkomen van mist) en door controle door de huidmondjes (stomata), met name gedurende de droge zomermaanden.

- Tijdens mist werd de transpiratie met 10-90% gereduceerd.

- Vanwege de gereduceerde transpiratie tijdens mist en door stomatale controle tijdens droge periodes verschilden de transpiratietotalen voor de twee jaren van de meetcampagne erg weinig (412 en 420 mm), hoewel de regenval in het tweede jaar twee keer zo hoog was als in het eerste.

- Het fysiologisch geleidingsvermogen van het bladerdek als geheel was omgekeerd evenredig met het atmosferisch dampdruktekort en nam toe met de stralingshoeveelheid bij lage intensiteiten. Dit niettegenstaande het feit dat er geen significante relatie was met het vochtgehalte in de bovenste 0,3 m van de bodem, alhoewel bodemvocht erg lage waarden bereikte in de zomer. Hieruit werd opgemaakt dat de bomen toegang hadden tot water in diepere lagen, bijvoorbeeld via spleten in de rotsen beneden 0,3 m.

- Tijdens de vijf droge maanden (mei - september) werden de bodemwaterreserves nauwelijks gevoed door atmosferische wateraanvoer. Omdat de waterreserves in de bovenste 0,3 m van de bodem onvoldoende waren om de vegetatie blijvend van water te voorzien, moet er water vanuit de onderliggende bodem zijn onttrokken.

- Gaten in de transpiratiegegevens kunnen worden opgevuld met behulp van de Penman-Monteith vergelijking gecombineerd met het gekalibreerde Jarvis model voor de schatting van het stomatale geleidingsvermogen. Echter, voor zeer vochtige atmosferische condities (>80% relatieve luchtvochtigheid) was de prestatie van het model minder bevredigend: de transpiratiewaarden waren laag en voorspelde variaties in het geleidingsvermogen hoog.

- De resultaten die verkregen werden met behulp van de kunstmatige neurale netwerkbenadering (*artificial neural network*, ANN) om korte onderbrekingen in de transpiratiegegevens op te vullen waren veel beter dan die met de Penman-

Monteith/Jarvis benadering. De resultaten verkregen met ANN waren beter omdat de condities tussen de "training" en "test" perioden zowel onder droge als vochtige atmosferische omstandigheden beter vergelijkbaar waren.

IX.6   WATERBALANS VAN HET GEMENGDE BERGKAMBOS

Studies naar het regionale waterbudget zijn nodig om de aanwezige watervoorraden te kunnen beoordelen en om La Gomera's waterbeleid aan te passen in het licht van de verwachten klimaatsverandering (Hay, 2000; Sperling et al., 2004). Hieronder worden de resultaten van de respectievelijke hoofdstukken gecombineerd om de vereenvoudigde waterbalansvergelijking op te lossen voor het gemengde bos op de bergkam en zo de bodem- en grondwateraanvulling te schatten. De gesimplificeerde vergelijking voor de jaarlijkse waterbalans kan als volgt worden geschreven:

$$Tf + Sf = OF + ET + \Delta S + D \qquad\qquad\qquad \text{VIII.1}$$

waarbij *Tf* staat voor doorval, *Sf* voor stamafvoer, *OF* voor oppervlakkige afstroming, E_T voor transpiratie (bodemwateropname), *ΔS* voor de verandering in bodemvochtberging, en *D* voor drainage naar diepere lagen en het grondwater. Alle waarden zijn uitgedrukt in mm/jaar. Aangenomen was dat de OF verwaarloosbaar was omdat er nooit oppervlakkige afstroming was waargenomen in het studiegebied, zelfs niet tijdens hevige regenval. Ook Höllermann (1981) nam slechts minimale oppervlakkige afvoer en erosie waar tijdens zeer intensieve regen (>100 mm/dag) onder laurier- en boomheidebossen. Doorval, transpiratie en verandering van bodemwaterberging tot 0,30 m diepte werden direct gemeten, stamafvoer daarentegen is geschat met behulp van regressies met de regenval afkomstig van voorgaande onderzoekers (details in Hoofdstuk V). Omdat er geen *Tf* gegevens na september 2004 beschikbaar waren, werden de totalen voor de rest van het tweede meetjaar geschat met gebruikmaking van regressies die apart werden afgeleid voor dagen met alleen regen-, alleen mist-, en gemengde neerslag tijdens het eerste meetjaar. De vereenvoudigde waterbalansen voor het kambos tijdens de twee jaren zijn in Tabel VIII.1 samengevat (de waarden voor de afgeleide drainage zijn afgerond op 5 mm).

Tabel IX.1 De waterbalans (in mm/jaar) voor het gemengde boomheide/beukenbos op 1270 m hoogte in het Jelima stroomgebied, La Gomera, tussen februari 2003 en januari 2005.

	$Tf + Sf$ (regen)	Tf (mist)	$Tf + Sf$ (regen en mist)	$Tf + Sf$ (totaal)	E_T	ΔS	D
Februari 2003-januari 2004							
Hoeveelheid water (mm)	546	22	297	865	412	-50	505
Maximale toevallige fout (mm)				±253[1]	±91[2]	±5[3]	190[4]
Februari 2004- januari 2005							
Hoeveelheid water (mm)	1242	28	305	1575	420	20	1135
Maximale toevallige fout (mm)				±472[1]	±92[2]	±2[3]	±430[4]

[1] gebaseerd op ±30% standaardafwijking in totale doorval (zie Hoofdstuk IV); [2] gebaseerd op ±22% standaardafwijking in totale transpiratie (zie Hoofdstuk VI); [3] ±10% (zie Hoofdstuk VI); [4] Wortel van de kwadratische fout.

De jaarlijkse netto-neerslag op de bosbodem tussen februari 2003 en januari 2004 bedroeg 865 ± 178 (standaardfout) mm inclusief 19 mm waterafvoer langs de stam (met onbekende maar naar aangenomen kleine fouten marge in absolute termen). Met een transpiratietotaal van 412 mm en een verandering in bodemwaterberging van -50 mm, werd een netto-aanvulling van 505 mm naar diepere lagen (onder de 0,3 m) berekend.

Het tweede meetjaar (februari 2004 tot en met januari 2005) was veel natter (de voor wind gecorrigeerde regenval P_a* was 1695 mm vergeleken met 900 mm in het eerste jaar). Doorval was 1542 ± 323 en stamafvoer was 33 mm. Voor een transpiratie van 420 mm en een verandering in bodemvochtopslag van 20 mm kwam de geschatte netto aanvulling van het bodem- en grondwater dit jaar uit op 1135 mm, meer dan het dubbele van de waarde voor het voorafgaande jaar. Dit resultaat illustreert hoe belangrijk het is om meerjarige observaties uit te voeren. Door wolken beïnvloede bossen besloegen ca. 25% van het stroomgebied en als zodanig is hun positieve bijdrage aan het totale waterbudget belangrijk. Verder onderzoek is nodig aan de sapstroomsnelheden in de helling- en dalbossen om de waterbalans van het gehele stroomgebied te kunnen berekenen.

De onzekerheid rond de twee schattingen voor de jaarlijkse grondwateraanvulling (*recharge*) is vrij groot doordat deze de som van de fouten in de respectievelijke componenten van de waterbalans bevat. De standaardafwijking van de gemiddelde *Tf* was ±30%; de maximale fout in de transpiratie werd geschat op ±22% terwijl die voor de bodemwateropslag gelijk werd gesteld met de fout in de calibratiecurve voor de TDR sensors (10%). De totale fout in de geschatte drainage werd berekend als de wortel van de som van het kwadraat van de fouten van elke component van de waterbalans: ±38% (Tabel VIII.1).

Sperling en anderen (2004) hebben een toekomstige versterking van de neerwaartse beweging van droge, warme lucht boven de Canarische Eilanden en een daarmee gepaard

gaande verlaging van de temperatuurinversie voorspeld. Als gevolg hiervan zal naar verwachting de ligging van de wolkentoppen veranderen en een afname optreden in de frequentie van mist en lage bewolking gedurende de droge perioden. Dit, op zijn beurt, zal een toename in de dagelijkse gang van de luchttemperatuur, het dampdruktekort, en het vaker optreden van intense straling tot gevolg hebben. Als dit juist blijkt, dan zullen de vochtige atmosferische condities die de wolken momenteel nog in het studiegebied handhaven tijdens het droge seizoen worden vervangen door een situatie met een toenemende verdampingsvraag vanuit de atmosfeer en een toenemende uitputting van het bodemvocht. Volgens de bevindingen van de huidige studie wordt de transpiratie van het gemengte bos op de bergkammen tijdens langdurige regenloze condities beperkt door gedeeltelijke sluiting van de huidmondjes. Niettemin kan een toename in waterverbruik door de vegetatie worden verwacht vanwege de verwachte verdroging van de atmosfeer met negatieve gevolgen voor de aanvulling van bodem- en grondwaterreserves (bovenop de verwachte 10% afname in jaarlijkse regenval; Sperling en anderen, 2004).

Annex

Protocol of Water droplet time penetration (WDTP) method

Natural air-drying

Moisture ← ← Natural air-drying of soil constant weight

Sieve (2 mm)

Leaves, stones, roots... ← ← Sieve, 2 mm

Sieve (<2mm)

Aggregates ← ← Sieve, <2mm

Homogenization

Moisture ← ← Spoon

Soil moisture (%) determination ← Air-drying (24 h)

Soil sample

← Scales

Field-moist weight, P_0

Oven-drying 105ºC

← Scales

Oven-dry weight, P_d

Transfer 25 cc of soil to petri dishes (3 replications) ← Transparent plastic petri dishes

Soil moisture (%)
$w = (P_0 - P_d) \times 100 / P_d$

To level the soil samples

To clean instrumentation

waste ← ← Distalled water

Lay three water droplets on the soil surface

← Distalled water; syringe; bottle

← Droplets (4-5 mm diameter or 250-500 μL volume)

Measure time required by the three droplets to infiltrate into the soil

Consider average infiltration time and classify soil water repellency

Classification	Water droplet penetration time (s)	Description
0	0-5	Not repellent
1	5-60	Slightly repellent
2	60-600	Strongly repellent
3	600-3600	Severely repellent
4	> 3600	Extremely repellent

Protocol of Molarity of Ethanol Droplet (MED) Test

Natural air-drying

Moisture ←   ← Natural air-drying of soil constant weight

Sieve (2 mm)

Leaves, stones, roots... ←   ← Sieve, 2 mm

Sieve (<2mm)

Aggregates ←   ← Sieve, <2mm

Homogenization

Moisture ←   ← Spoon

Air-drying (24 h)

Transfer 25 cc of soil to petri dishes (3 replications) ← Transparent plastic petri dishes

Solution preparation

Clean instruments

waste ←   ← Distilled water

To level the soil samples

Lay three water droplets on the soil surface   Ethanol x M

← Droplets (4-5 mm diameter or 250-500 µL volume)

0.2M   0.3M   0.4M   ...6M

Distilled water + Ethanol
Syringes
Bottles

To measure 10 s

-Molarity
-Surface tension
-Contact angle

← Droplets infiltrate before the first 10 s   Droplets infiltrate after the first 10 s

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Chapter III is a reworked version of the paper "Caracterización de la zona no saturada de un bosque maduro de laurisilva en el Parque Nacional de Garajonay: Hidrofobicidad e implicaciones hidrológicas" (in Spanish) by Regalado, C.M., García-Santos, G., Hernández Moreno, J.M., Pérez Buenafuente, A., and Socorro A.R., (2003). In "*Estudios de la Zona no saturada del Suelo*" (J. Álvarez-Benedi, P. Marinero, ed.), I.T.A. Monograph, Vol. 6, pp. 193-199. ITA, Valladolid (Spain).

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